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MORPHOGENESIS AND SYSTEMATICS OF THE
DEVONIAN STROMATOPOROIDEA FROM THE
HOLY CROSS MOUNTAINS, POLAND

(MORFOGENEZA I SYSTEMATYKA DEWONSKICH
STROMATOPOROIDEA Z GÓR ŚWIĘTOKRZYSKICH)

BY

JÓZEF KAŻMIERCZAK

(WITH 20 TEXT-FIGURES, 3 TABLES AND 41 PLATES)



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INTRODUCTION

The present paper contains the results of morphological and taxonomic studies on the Devonian (Givetian-Frasnian I γ) Stromatoporoidea from the Holy Cross Mountains, Poland. The work has been done on the basis of a rich collection of excellently preserved stromatoporoids accumulated by the writer in 1966—1968 and of which more than 1500 thin sections were prepared. Despite their abundant occurrence, the stromatoporoids were among the least known faunal groups from the Devonian of the Holy Cross Mts. Among older palaeontological works, noteworthy is GÜRICH'S (1896) paper, superficially describing several species only some of which being illustrated by drawings. Newer works (GOGOLCZYK 1956, 1959) are devoted to some of the representatives of the dendroid stromatoporoids (*Amphipora* and *Stachyodes*).

In 1969, as a Polish Academy of Sciences scholarship holder, the writer stayed for six months in the Soviet Union having ample opportunity to study vast collections of the stromatoporoids ranging from the Ordovician to the Carboniferous, from the following areas of the U. S. S. R.: Russian Platform (Podolia, Estonia, Main Devonian Field, Petchora Basin, Timan), Ural Mts., Soviet Arctic (Novaya Zemlya), Siberia (Kuznetsk Basin, Tunguska Basin, Altai Mts., Salair Mts., Saian Mts.).

By the courtesy of the management of the U. S. National Museum in Washington, D. C., the writer was also able to conduct comparative studies on a collection of the holotypes of the stromatoporoids from the Middle Devonian of the U. S. A. (Indiana, Kentucky, Ohio), described by GALLOWAY & ST. JEAN (1957).

Getting familiar with so extensive materials allowed the writer to devote himself to the studies on a so far little-investigated problem of the morphogenesis of the Stromatoporoidea, to seek to explain the origin and evolutionary changes in their microstructure and to attempt to elucidate the main evolutionary trends marked in the Palaeozoic stage of the history of this group.

The work was done between 1965 and 1970 at the Polish Academy of Sciences' Palaeozoological Institute at which the collection described is housed.

The following abbreviations are used in the present paper:

- Z. Pal. — Palaeozoological Institute of the Polish Academy of Sciences, Warsaw, Poland.
- CNIGR — Central Scientific-Research Geological Exploration Museum, Leningrad, U. S. S. R.
- VNIGRI — All-Union Petroleum Institute, Leningrad, U. S. S. R.
- EAS — Geological Institute of the Estonian Academy of Sciences, Tallinn, U. S. S. R.
- USNM — United States National Museum, Washington, D. C., U. S. A.

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Professor R. KOZŁOWSKI and Professor A. URBANEK (Department of Geology, Warsaw University) the manuscript was improved on many important points.

Owing to the Polish Academy of Sciences' scholarship, part of the present study was completed in the Soviet Union. The writer's heartfelt thanks are extended to Professor R. F. HECKER (Palaeontological Institute, Moscow) for his care of and aid given to the writer during his entire stay in the Soviet Union as well as for valuable advice, discussions and a palaeoecological excursion to the Main Devonian Field.

Thanks are also expressed to the following Soviet paleontologists and Institutions: Professor M. M. MOSKVIN (Department of Geology, Moscow University), Dr. H. NESTOR (Geological Institute, Tallinn), Dr. O. V. BOGOYAVLENSKAYA (Uralian Geological Institute, Sverdlovsk), Dr. L. N. BOLSHAKOVA (Palaeontological Institute, Moscow), Dr. V. K. KHALFINA and Dr. V. G. KHROMYCH (Institute for Geology and Geophysics, Novosibirsk), Dr. P. N. VARFOLOMEEV (Chernyshev CNIGR Museum, Leningrad), Dr. P. K. IVANCHUK (All-Union Petroleum Institute, Leningrad). All of them helped in a most friendly manner, making their collections available for comparative studies and supplying all possible information.

Separate thanks are also due to Dr. R. S. BOARDMAN, Curator of Invertebrate Paleontology, Smithsonian Institution, Washington, D. C. and to the management of the U. S. National Museum, Washington, D. C. for lending the collections of holotypes of the Devonian stromatoporoids, described by GALLOWAY & ST. JEAN (1957).

The writer feels indebted to Professor M. RÓŹKOWSKA and Docent A. STASIŃSKA (Polish Academy of Sciences' Palaeozoological Institute) for the identification of some of the tetracorals and tabulates accompanying the stromatoporoids described.

The writer's gratitude is also due to Dr. M. SZULCZEWSKI (Department of Geology, the University of Warsaw) for information on conodonts that occur in the uppermost part of the Kadzielnia Beds.

Thanks are extended to the following persons who helped the writer to obtain older literature on the stromatoporoids: Dr. N. A. FLEROVA (Chernyshev CNIGR Museum, Leningrad), Professor. E. FLÜGEL (Technische Hochschule, Darmstadt), Professor T. KOBAYASHI (Geological Institute, University of Tokyo), Dr. K. MORI (Geologiska Institutionen, Stockholm), Dr. J. ST. JEAN Jr. (Department of Geology, University of North Carolina).

The writer is also indebted to Mrs. K. BUDZYŃSKA for drawing text figures and to Miss D. KOŚCIELSKA for preparing thin sections.

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GENERAL PART

OUTLINE OF THE STRATIGRAPHY, LITHOLOGY AND SEDIMENTATION OF THE STROMATOPOROID LIMESTONES

The stromatoporoids described come mostly from a thick (about 550 to 600 m) series of carbonate deposits of the Middle and Upper Devonian (Givetian through Frasnian) of the western part of the Palaeozoic massive of the Holy Cross Mountains, exposed in many quarries and natural outcrops (Text-fig. 1). These deposits were formed in an area designated by CZARNOCKI (1927) as the Kielce sedimentary region which, during the Givetian-Frasnian period, was marked by a clear carbonate shallow-water sedimentation, in contradistinction to the Łysogóry sedimentary region situated more to the north and whose carbonate sedimentation was more deep-water one in character and had, in some places, a considerable admixture of a terrigenous material (MICHALSKI, 1883; SOBOLEV, 1909, 1912; CZARNOCKI, 1919, 1938, 1950, 1957; PAJCHŁOWA, 1959, 1962, 1967). The stromatoporoid limestones, from which the specimens here described were collected, belong to the western part of the Chęciny-Klimontów anticlinorium (PAJCHŁOWA, 1968) and their best outcrops are situated in the region of Miedzianka, Chęciny, Bolechowice, Kowala and Sitkówka (Text-fig. 1). In the eastern part of the Chęciny—Klimontów anticlinorium, the stromatoporoid limestones of Givetian age are outcropped in a few localities in the environs of Jurkowie-Budy (for location see PAJCHŁOWA, 1968, Text-fig. 64). In the northern part of the Kielce sedimentary region, the Givetian-Frasnian stromatoporoid limestones are components of the western part of the Kielce-Łagów synclinorium, exposed in several large quarries in the environs of Kielce (Text-fig. 1).

The stratigraphic position of the stromatoporoid limestone from the western part of the Kielce sedimentary region has only superficially been recognized. On the whole, well-stratified limestones with many stromatoporoids and corals, underlaid by dolomites, were assigned to the Givetian (GÜRICH, 1896; SOBOLEV, 1904, 1909, 1912; CZARNOCKI, 1938, 1948; PAJCHŁOWA, 1959, 1962, 1967) and massive, poorly stratified limestones with stromatoporoids and corals usually termed reefoid ones (SOBOLEV, 1909, 1912; CZARNOCKI, 1948; PAJCHŁOWA & STASIŃSKA, 1965, 1967) — to the Frasnian. According to the authors named above, the Givetian age of stromatoporoid-coral limestones and dolomites is emphasized primarily by *Amphipora ramosa* (PHILLIPS) and *Stringocephalus burtini* DEFR. and the Frasnian age of reef limestones by the occurrence of brachiopods *Hypothyridina cuboides* (SOW.), *H. coronula* DREVERM. and an assemblage of tetracorals and tabulates characteristic for Frasnian (see RÓŹKOWSKA, 1953, 1957; STASIŃSKA, 1953, 1958). These limestones are directly overlaid by cephalopod limestones, containing, among other fossils, *Manticoceras intumescens* BEYR. (GÜRICH, 1896).

A division of stromatoporoid limestones (see Table 1) of the western part of the Holy Cross Mts. into two lithostratigraphic units, that is, Sitkówka Beds and Kadzielnia Beds,

Table 1

STRATIGRAPHIC POSITION OF THE DEVONIAN STROMATOPOROID LIMESTONES IN THE WESTERN HOLY CROSS MOUNTAINS (KIELCE SEDIMENTARY REGION)

UPPER DEVONIAN	FRASNIAN	CEPHALOPOD LIMESTONES	
		* KADZIELNIA BEDS	
MIDDLE DEVONIAN	GIVETIAN	stromatoporoid limestones	?
			Upper
		Lower	SITKÓWKA BEDS
	Lower	DOLOMITES	

* Conodonts of *Ancyrognathus triangularis* zone (Frasnian I γ) (personal communication of dr. M. Szulczewski, Dept. of Geology, Warsaw University).

suggested by the present writer, makes up an attempt to specify terminologically and stratigraphically general lithofaunal determinations in use so far. Each of thus separated units is characterized by an assemblage of stromatoporoid fauna and accompanying corals. Stromatoporoid assemblages characteristic of separated lithostratigraphic units, have been correlated with analogous assemblages, described from thoroughly studied Middle and Upper Devonian section of Belgium, Canada, the U. S. A. and some of the U. S. S. R.'s areas (Timan, Main Devonian Field, Kuznetsk Basin). This enabled a biostratigraphic determination of stromatoporoid limestones from the Holy Cross Mts. more accurate than the previous ones. A more accurate study on stratigraphic ranges of particular species of the Devonian stromatoporoids will enable a future, more extensive than before use of the stromatoporoids for the purposes of biostratigraphy, which is justified by their abundant occurrence and a very extensive geographical distribution. The fact should be emphasized that the stromatoporoids have already been used successfully for biostratigraphic studies on the Silurian of Estonia (NESTOR, 1964, 1966; NESTOR & KALA, 1968) and the Island of Gotland (MORI, 1968).

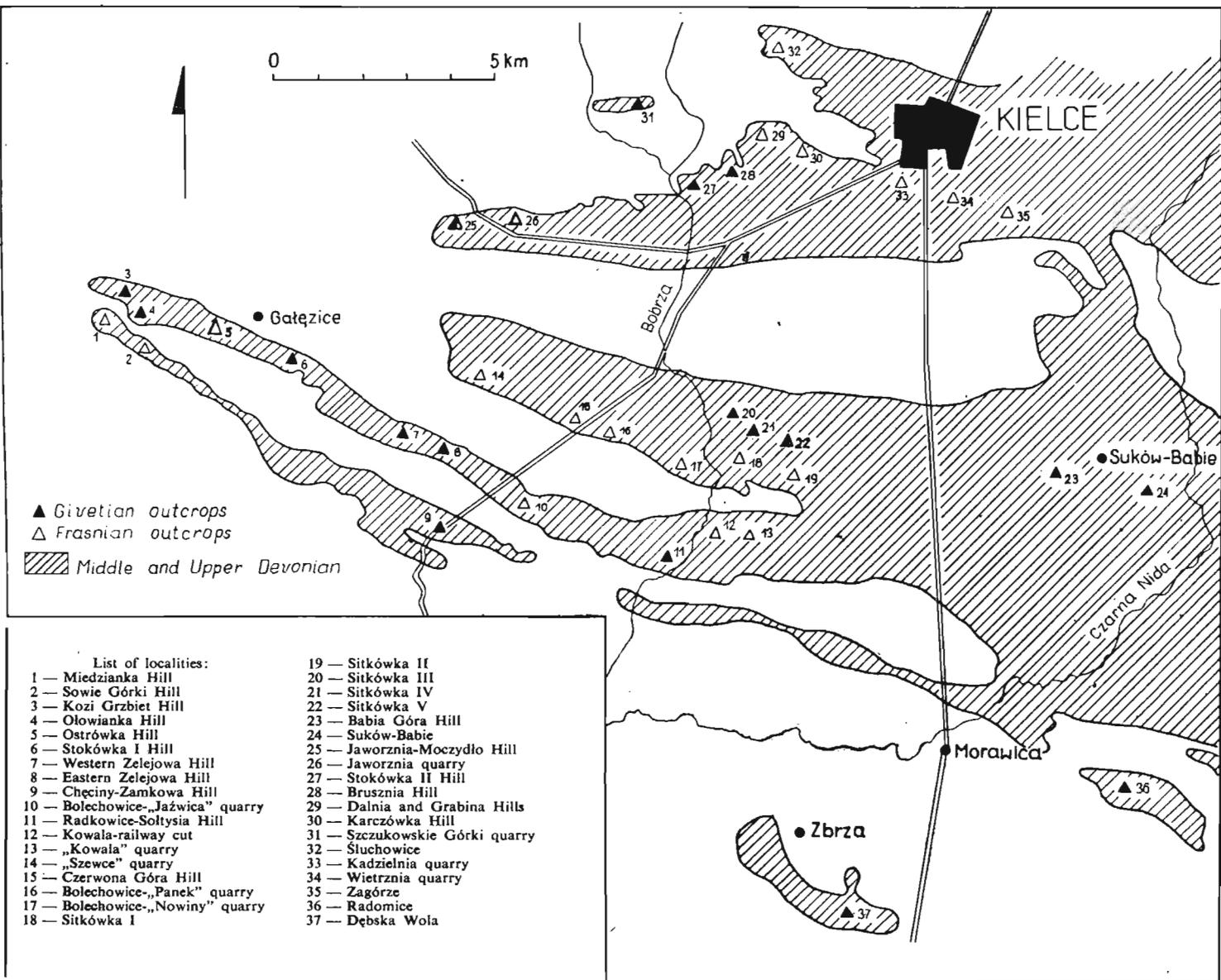


Fig. 1
 Index map of stromatoporoid localities in the Western Holy Cross Mountains (geological boundaries after CZARNOCKI, 1938).

Brief lithologic-faunal characteristics of the lithostratigraphic units, separated within the stromatoporoid limestones are given below. An extensive palaeoecological and sedimentological analysis of the stromatoporoid limestones from the Holy Cross Mts. will be given in a separate paper.

1. *Stringocephalus burtini* Beds

The above term has been used by the writer to designate a 30 m thick complex of gray and black, stratified limestones and marls with numerous specimens of *Stringocephalus burtini* DEFR., outcropped at Jurkowice Budy in the eastern part of the Holy Cross Mts. (eastern part of the Chęciny-Klimontów anticlinorium). Brief characteristics of the stromatoporoid-coral limestones from Jurkowice-Budy were given by SAMSONOWICZ (1930) and more detailed studies were conducted by PAJCHŁOWA & STASIŃSKA (1965) who give in their paper a lithologic-faunal section of the outcrop. In the present paper, the term „*Stringocephalus burtini* Beds“ is used tentatively to distinguished the beds under study from the lowermost limestones of the Sitkówka Beds in the western part of the Chęciny-Klimontów anticlinorium which in all likelihood are younger and in which no *S. burtini* has so far been found.

Stringocephalus burtini Beds are marked by beds of dark-gray biopelmicritic calcarenites whose average thickness ranges between 0.25 and 0.40 m and which sometimes have very numerous stromatoporoids with spherical, irregularly bulbous or, less frequently, columnar coenostea. The beds with stromatoporoids are intercalated by black, platy calcilutites or gray nodular marls which vary in thickness and are except of trilobites devoid of macrofauna. The stromatoporoids are usually associated with a very rich assemblage of colonial and solitary tetracorals, massive and ramose tabulates many brachiopods and gastropods. Stromatoporoids and corals are mostly preserved in a growth position. The degree of mechanical destruction of all other forms is also very low. Platy dolomites sometimes with many *Amphipora* sp. usually very strongly recrystallized occur, below the *Stringocephalus burtini* Beds.

In addition to a taxonomically differentiated assemblage of stromatoporoids, consisting of 14 species (see Table 2), the following fossils have been identified within the *Stringocephalus burtini* Beds:

Tabulata:

Caliapora battersbyi (M. EDWARDS & HAIME)
Alveolites sp.
Thamnopora sp.

Tetracoralla:

Hexagonaria laxa GÜRICH
Hexagonaria jurkovicensis RÓZKOWSKA
Thamnophyllum sp.
Acanthophyllum sp.

Palaeoenvironmental remarks — The development of stromatoporoid assemblages within *S. burtini* Beds took place in an environment marked by a low degree of hydrodynamic activity and undoubtedly situated below the wave-base. It was only sporadically that waving reached, for brief periods, the surface of the bottom and, overthrowing some of the colonies resting on a soft substratum, destroyed part of the population. During the periods of accumulation of larger amounts of a clayey sediment and an organic detritus, a deterioration took place in the aeration of the bottom part of the basin, resulting in a partial or complete stoppage of the development of benthonic assemblages. At that time, marls and strongly bituminous limestones were formed which were either very poor in or even devoid of fauna. The sedimentary environment, on the whole calm in character and the way of distributing the representatives of a stromatoporoid assemblage in the deposit do not confirm a reef origin of these forms, suggested by PAJCHŁOWA & STASIŃSKA (1965). In regard to ecology, the stromatoporoid-coral

Table 2

DISTRIBUTION OF DEVONIAN STROMATOPOROIDEA IN THE HOLY CROSS MOUNTAINS

Geographic regions		Eastern Holy Cross Mts.	Western Holy Cross Mts.		
Standard stages		Upper Givetian		Frasnian	
Species	Local divisions	<i>S. burtini</i> Beds	Sitkówka Beds		Kadzielnia Beds
			Lower	Upper	
<i>Stromatopora colliculata</i> NICHOLSON					
<i>Stromatopora divergens</i> GALLOWAY & ST. JEAN					
<i>Stromatopora mononensis</i> GALLOWAY & ST. JEAN					
<i>Trupetostroma laceratum</i> LECOMPTE					
<i>Syringostroma densum</i> NICHOLSON					
<i>Neosyringostroma logansportense</i> (GALLOWAY & ST. JEAN)					
<i>Hermatostroma porosum</i> (LECOMPTE)					
<i>Hermatostroma perseptatum</i> LECOMPTE					
<i>Actinostroma compactum</i> RIPPER					
<i>Stictostroma lensiforme</i> (LECOMPTE)					
<i>Ferestromatopora parksi</i> STEARN					
<i>Hermatostroma schlüteri</i> NICHOLSON					
<i>Hermatostroma crassum</i> (LECOMPTE)					
<i>Actinostroma expansum</i> (HALL & WHITFIELD)					
<i>Tienodictyon zonatum</i> YABE & SUGIYAMA					
<i>Pseudostromatoporella moosensis</i> (PARKS)					
<i>Ferestromatopora cellulosa</i> (LECOMPTE)					
<i>Trupetostroma pingue</i> LECOMPTE					
<i>Actinostroma</i> aff. <i>geminatum</i> LECOMPTE					
<i>Stromatopora stricta</i> LECOMPTE					
<i>Stromatopora minutitexta</i> (LECOMPTE)					
<i>Ferestromatopora talovenskyi</i> YAVORSKY					
<i>Ferestromatopora krupemikovi</i> YAVORSKY					
? <i>Pseudoactinodictyon dartingtonense</i> (CARTER)					
<i>Pseudoactinodictyon actinostromiforme</i> (RIABININ)					
<i>Trupetostroma gebum</i> (YAVORSKY)					
<i>Hermatostroma episcopale</i> NICHOLSON					
<i>Atelodictyon pseudocolumnare</i> (RIABININ)					
<i>Actinostroma stellulatum</i> NICHOLSON					
<i>Actinostroma papillosum</i> (BARGATZKY)					
<i>Actinostroma bifarium</i> NICHOLSON					
<i>Stromatopora cooperi</i> LECOMPTE					
<i>Tienodictyon albertense</i> (STEARNS)					
<i>Stromatopora spissa</i> (LECOMPTE)					
<i>Ferestromatopora uchtensis</i> (RIABININ)					
<i>Ferestromatopora percanaliculata</i> (LECOMPTE)					
<i>Ferestromatopora dubia</i> (LECOMPTE)					
<i>Talestroma confertum</i> STEARN					
<i>Pseudoactinodictyon juxi</i> E. FLÜGEL					
<i>Parallelopora kudebensis</i> (RIABININ)					
<i>Parallelopora longitubulata</i> (RIABININ)					
<i>Atelodictyon trautscholdi</i> (RIABININ)					
<i>Anostylostroma ponderosum</i> (NICHOLSON)					
<i>Stictostroma kolymense</i> (YAVORSKY)					
<i>Stromatopora undata</i> RIABININ					
<i>Actinostroma crassepilatum</i> LECOMPTE					
<i>Pseudostromatoporella huronensis</i> (PARKS)					
<i>Pseudostromatoporella dammoniensis</i> (NICHOLSON)					
<i>Stictostroma sociale</i> (NICHOLSON)					
<i>Stromatoporella mudlakensis</i> GALLOWAY					

assemblages of *S. burtini* Beds did not display the capability of forming rigid frameworks resistant to a strong water agitation and, consequently, they did not satisfy a fundamental condition required by reef structures (*sensu* LOWENSTAM, 1950). According to the genetic classification of skeletal limestones of NELSON et al. (1962), the stromatoporoid limestones from *S. burtini* Beds may be termed *biostromal banks*.

Biostratigraphy and correlation. — The presence of *Stringocephalus burtini* might be indicative of Givetian age of the unit under study (LECOMPTE, 1951; DVORÁK & HAVLIČEK, 1963; CHLUPÁČ, 1967). In regard to *S. burtini* it is not, however, unlikely that it may also occur exceptionally in the basal Frasnian (ERBEN & ZAGORA, 1967) and, consequently lose its significance as an index fossil of the Givetian. Givetian age of *S. burtini* Beds is also indicated by the presence of corals *Caliopora battersbyi*, *Hexagonaria laxa* and *H. jurkovicensis* whose occurrence is limited to this stage only (LECOMPTE, 1939; ROŻKOWSKA, 1957). On the basis of the stromatoporoids, the age of the beds under study may be determined most likely as a lower part of the Upper Givetian. Such a conclusion is based primarily on the presence of *Stromatopora mononensis* GALLOWAY & ST. JEAN, *S. divergens* GALLOWAY & ST. JEAN and *Neosyringostroma logansportense* GALLOWAY & ST. JEAN which occur only within Logansport Limestone of the North Central Region, U. S. A. (GALLOWAY & ST. JEAN, 1957), corresponding mostly to the Lower Givetian (COLLINSON, 1967; BIRKHEAD, 1967). The presence of *Actinostroma compactum* RIPPER, described from Buchan Caves Limestone, Australia, might be indicative of the presence of the Early Middle Devonian (TALENT, 1967) stromatoporoid species within *S. burtini* Beds of the Holy Cross Mts. In addition, the assemblage of the stromatoporoids from *S. burtini* Beds differs radically from that occurring in the Lowermost Sitkówka Beds in the western part of Chęciny-Klimontów anticlinorium. In the last-named assemblage except for few species, most of them are new and contain in addition to the Givetian species, many forms characteristic for the lowermost Frasnian. Thus, in the western part of the Holy Cross Mts. dolomites, occurring at the base of Sitkówka Beds (see Table 1), might be an equivalent of *S. burtini* Beds. Such a stratigraphic interpretation might confirm the suggestions of SAMSONOWICZ (1917) and CZERMIŃSKI (1960) on a diachronous conversion of the dolomitic into calcareous sedimentation in the area of the Kielce sedimentary region. However, it seems to follow from the biostratigraphic relations of *S. burtini* and Sitkówka beds that, in contrast to the views of the authors mentioned above the conditions of the dolomitic sedimentation persisted for a longer time in the western and not in the eastern area.

2. Sitkówka Beds

The term Sitkówka Beds is suggested by the present writer to determine a lithostratigraphic unit represented by a thick (about 550 to 600 m) series of stromatoporoid limestones outcropped in several quarries in the region of Sitkówka, Kowala, Bolechowice and Chęciny (Text-fig. 1). In the literature known so far, the deposits distinguished in the present paper as Sitkówka Beds, have generally been termed as either coral limestones („Korallenkalke von Chęciny“, GÜRICH, 1896), or coral-stromatoporoid limestones (SOBOLEV, 1904, 1909, 1911; CZARNOCKI, 1919, 1948, 1950; PAJCHŁOWA, 1959, 1962, 1967, 1968). Part of limestones from the environs of Sitkówka has been interpreted by PAJCHŁOWA & STASIŃSKA (1965) as reef deposits of the biostromal type. The lower boundary of Sitkówka Beds is made up by plate dolomites whose contact with stromatoporoid limestones is visible, in among other places, sections of the Sołtysia Hill, near Radkowice (Text-fig. 4E) and Zamkowa Hill at Chęciny (loc. 9, see Text-fig. 1). The boundary between Sitkówka Beds and overlaying Kadzielnia Beds is not outcropped and consequently the mutual relation of both units is not quite clear.

In regard to lithology, the limestones of Sitkówka Beds display in addition to a strong vertical, a considerable lateral variability and, therefore, a horizontal correlation of section, even from the outcrops situated very near each other, is extremely difficult.

Stratified coarse-grained limestones, which may be determined structurally as biosparitic and biomicritic stromatoporoid calcirudites and calcarenites (Pl. IV, Figs. 1—6) are predominant deposits within Sitkówka Beds. These limestones form beds varying in thickness within an interval of a dozen or so cm to 1.5 m, averaging 0.40 to 0.50 m (Pl. I, Figs. 1—2). These deposits are usually marked by a considerable concentration of massive stromatoporoids, sometimes accompanied by few dendroid forms (*Amphipora*, *Stachyodes*, *Dendrostroma*). Stromatoporoids are very rarely preserved in growth position (Pl. II, Fig. 1), the majority of colonies being most frequently either overthrown (Pl. II, Fig. 2; Pl. III, Figs. 4—5), or more or less crushed and forming breccia (Pl. III, Fig. 1). The stromatoporoid limestones of the nature of biolithites (FOLK, 1959), which are among the rarities, have been found, e. g., in the section of Sitkówka III quarry (loc. 20, see Text-figs. 1 and 2A). In the cases of considerable concentrations stromatoporoids occur exclusively, but most stromatoporoid assemblage are accompanied by other benthonic organisms, of which very frequent are massive and ramose tabulates and less so solitary and colonial tetracorals. Relatively frequent are also gastropods which usually occur in a nest-like manner (Text-figs. 2—5). Thick-valved pelecypods (*Megalodon* sp., see Pl. III, Fig. 6) are sometimes frequent within the stromatoporoid calcirudites in the upper part of Sitkówka Beds. Considerable amounts of problematic microfossils, assigned to *Calcisphaera* WILLIAMSON, are often observed in thin sections of stromatoporoid calcirudites and calcarenites. Much rarer are calcareous algae which occur, in the form of a detritus, in some of the thin sections (Solenoporaceae, see Pl. IV, Fig. 2). In some of the stromatoporoids banks, abundant blue-green algae appear in the form of irregular aggregates of chambers composed of a dark, microcrystalline calcite (Pl. V, Figs. 4—6). These algae belong to the genus *Renalcis* VOLOGDIN. Irregular, thinner or thicker, dark cryptocrystalline coatings occurring on many skeletal fragments (Pl. IV, Fig. 3; Pl. V, Fig. 3) are a presumable effect of the activity of blue-green algae. Stromatoporoid calcirudites and calcarenites are interbedded with deposits within which one can distinguish non-fossiliferous, fine-grained calcarenites and calcilutites, *Amphipora*-calcilutites, solitary tetracoral-brachiopod-gastropod calcilutites, laminated, non-fossiliferous calcarenites and calcilutites of the nature of algal mats (Pl. V, Figs. 1—2). Sometimes, intercalations of echinoderm-pelmicrites occur within and above stromatoporoid calcirudites and calcarenites (Pl. IV; Fig. 5; Text-figs. 3D and 5F).

The limestones assigned to Sitkówka Beds has been divided into the Lower and Upper Sitkówka Beds (see Table 1), whose boundary runs at the base of a 35 to 40 m thick complex of light colored, platy calcilutites and fine-grained *Amphipora* calcilutites and calcarenites (Text-figs. 3C, unit 18), forming a conspicuous index lithological horizon in the area under study. A complex of limestones separating the Lower the Upper Sitkówka Beds is exposed in the section of Sitkówka V quarry (Text-figs. 1 and 3C), as well as in the quarries at Jaworznia (loc. 26) and on the Ostrówka Hill (loc. 5). Despite a generally similar lithological development, the Lower Sitkówka Beds differ from the Upper Sitkówka Beds in a smaller part of coarse-grained deposits and skeletal limestones. The composition of the stromatoporoid-coral fauna is, despite the presence of many species in common, also different on the whole.

Lower Sitkówka Beds (about 300 to 370 m thick). — Localities (Text-fig. 1): Kozi Grzbiet Hill (loc. 3), Ołowianka Hill (loc. 4), Stokówka I Hill (loc. 6), Zelejowa Hill (loc. 7 and 8), Chęciny—Zamkowa Hill (loc. 9), Radkowice—Sołtysia Hill (loc. 11), Sitkówka III and IV (loc. 20 and 21), (partly) Sitkówka V (loc. 22), Babia Góra Hill (loc. 23), Suków—Babie (loc. 24),

ORGANIC COMPONENTS

stromatoporoids:

biostratigraphy:

 in growth position

 overturned

 fragmented

shape of cerostea

 tabular

 disc-like

 globular

 columnar

 dendroidal (mainly *Amphipora*)

other organisms:

 colonial tetracorals

 solitary tetracorals

 massive tabulates

 ramose tabulates

 brachiopods

 gastropods

 *Megalodon*

 crinoids

 „*Stromatactis*” burrows

algae and algal structures:

 Solenoporaceae

 phylloid calcareous algae (*Keega*)

 blue-green algae (*Renalcis*)

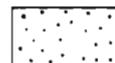
 algal coatings

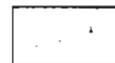
 algal mats

LITHOLOGY:

 biosparitic calcitrites

 biomicritic calcitrites

 biosparitic calcarenites

 biomicritic calcarenites

 calcitrites

 biolithite (bank)

 flat pebbles

Fig. 2a

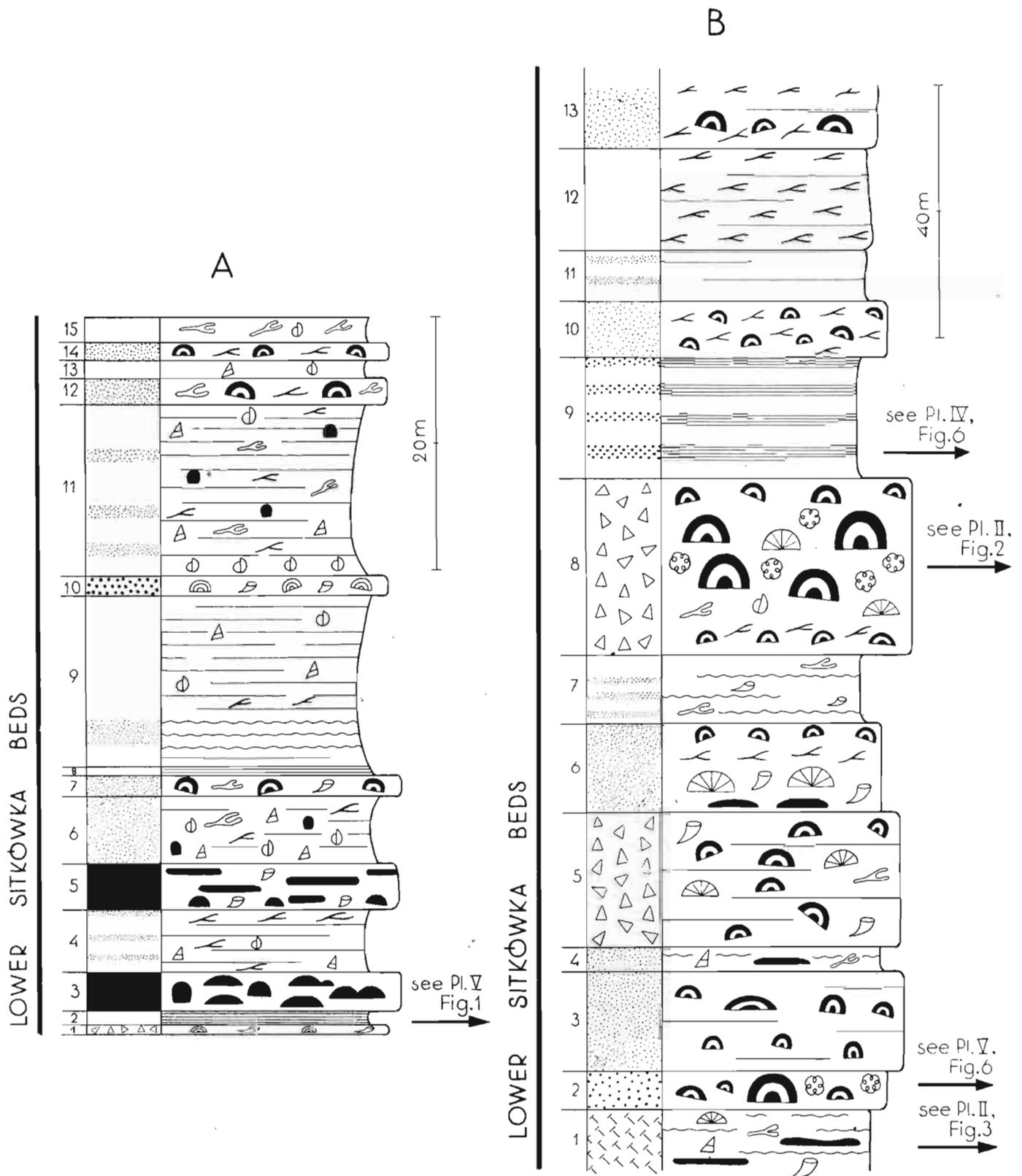


Fig. 2b

Lithological and palaeoecological sections of the stromatoporoid limestones: A — Sitkówka III (loc. 20), B — Sitkówka IV (loc. 21)

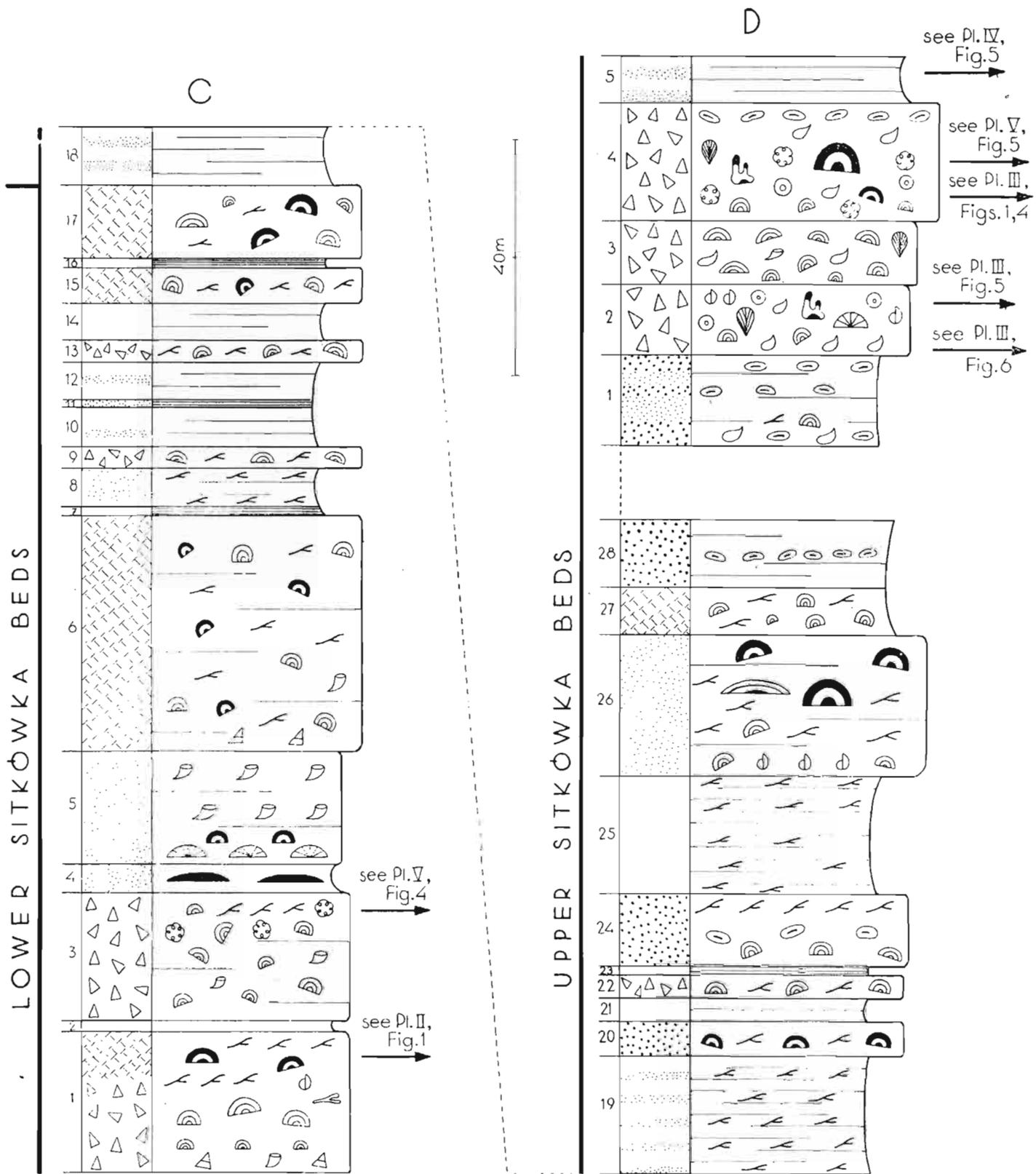


Fig. 3

Lithological and palaeoecological sections of the stromatoporoid limestones: C — Sitkówka V (loc. 22), D — Sitkówka I (loc. 18). For explanations see Fig. 2, p. 14

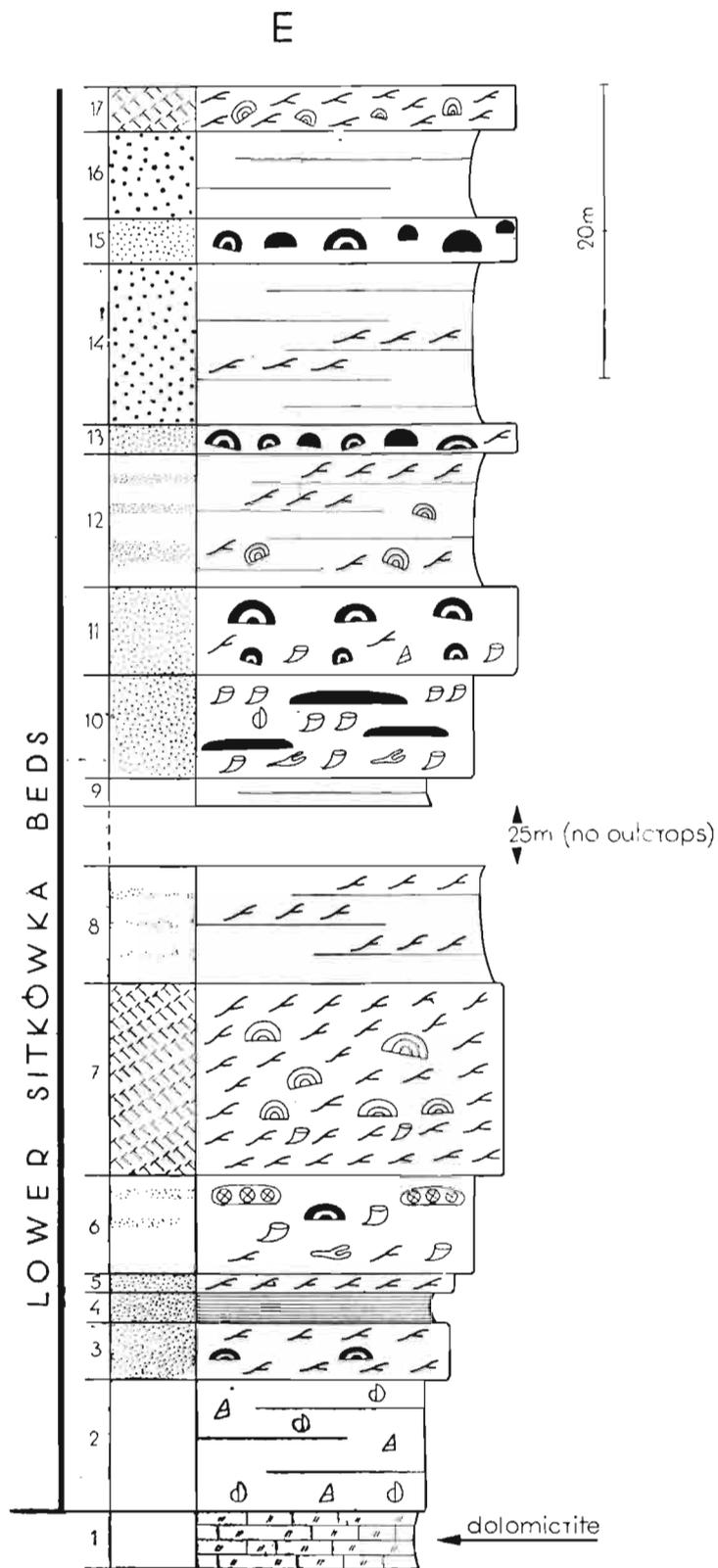


Fig. 4

Lithological and palaeoecological section of the stromatoporoid limestones: E — Radkowiec-Soltysia Hill (loc. 11).
For explanations see Fig. 2a, p. 14

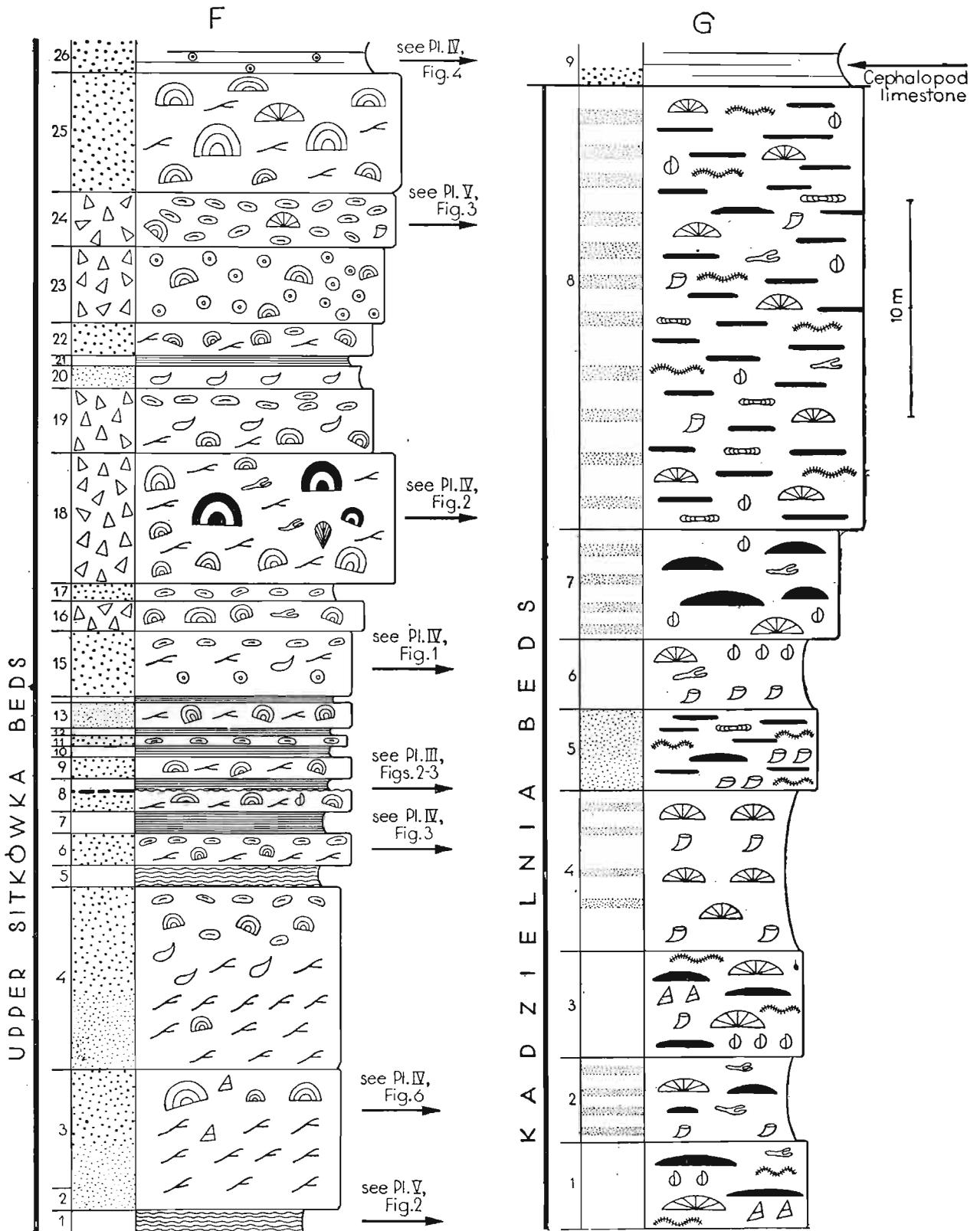


Fig. 5

Lithological and palaeocological sections of the stromatoporoid limestones: *F* — Bolechowice-„Panek“ quarry (loc. 16)
G — Kadzielnia quarry (loc. 33). For explanations see Fig. 2a, p. 14

(partly) Jaworznia—Moczydło Hill (loc. 25), ?Stokówka II Hill (loc. 27), ?Brusznia Hill (loc. 28), ?Szcukowskie Górki quarry (loc. 31), Radomice (loc. 36), Dębska Wola (loc. 37).

Fossils. — Within the Lower Sitkówka Beds, twenty-two species of stromatoporoids (Table 2) have been identified, along with the following species of corals:

Tabulata:

Crassialveolites crassus (LECOMPTE)
Alveolites mailleuxi LECOMPTE
Alveolites obtortus LECOMPTE
Scoliopora denticulata (M. EDWARDS & HEIME)
Thamnopora dubia BLAINVILLE
Coenites subramosus LECOMPTE

Tetracoralla:

Thamnophyllum germanicum SCRUTTON
Disphyllum geinitzi LANG & SMITH
Hexagonaria hexagona (GOLDFUSS)

Upper Sitkówka Beds (about 220 to 260 m thick). — Localities (Text-fig. 1): Miedzianka Hill (loc. 1), Sowie Górki Hill (loc. 2), Ostrówka Hill (loc. 5), Bolechowice — „Jaźwica“ quarry (loc. 10), Kowala — railway cut (loc. 12), „Kowala“ quarry (loc. 13), „Szewce“ quarry (loc. 14), Czerwona Góra Hill (loc. 15), Bolechowice — „Panek“ quarry (loc. 16), Sitkówka I and II (loc. 18 and 19), (partly) Sitkówka V (loc. 22), (partly) Jaworznia—Moczydło Hill (loc. 26), Jaworznia quarry (loc. 26).

Fossils. — Within the Upper Sitkówka Beds, thirty-one species of stromatoporoids (Table 2) have been identified, along with the following species of corals.

Tabulata:

Syringopora vocensis TŠHERNYSHEV
Syringopora fragilis SOKOLOV

Tetracoralla:

Phillipsastrea smithi RÓZKOWSKA
Macgea berdensis SOSHKINA
Marisastrum sedgwicki (M. EDWARDS & HAIME)
Disphyllum caespitosum (GOLDFUSS)
Thamnophyllum germanicum SCRUTTON
Neostromatophyllum sp.

Palaeoenvironmental remarks. — The Sitkówka Beds represent a cycle of carbonate sedimentation which was started after the deposition of dolomitic sediments had been completed. The dolomites were formed in restricted shelf lagoons with an abnormal, most likely raised salinity. The clear carbonate character of the deposits in Sitkówka Beds is indicative of an off-shore position of this part of the sedimentary basin. A mosaic facies arrangement of limestones in Sitkówka Beds, expressed in rapid lateral changes in deposits and organic assemblages, gives evidence for a variable morphology of the bottom. On the whole, the sedimentary environment of Sitkówka Beds was divided into the areas of shoals which oscillated near a mean sea-level and, somewhat deeper areas of inter-shoals in which fine-grained carbonate mud was deposited, sometimes with a considerable number of *Amphipora* and, less frequent, solitary tetracorals, gastropods and brachiopods. A considerable thickness of Sitkówka Beds might indicate a sedimentation on an unstable shelf with a relatively high rate of subsidence. Slight bathymetric oscillations expressed in frequent changes in vertical lithologic sequences, were connected with the unstable character of the bottom. Bathymetric changes in environment also clearly express vertical successions of faunal assemblages (Text-figs. 2—5) in which stromatoporoids predominate. The stromatoporoid assemblages observed in particular sections display strong differences in thickness, concentration and degree of abrasion. Except relatively rare *biostromal banks* (NELSON *et al.*, 1962), a decided majority of stromatoporoids bears traces of abrasion, expressed in their overthrowing or crumbling of their coenostea. The variable degree of destruction, observed in particular assemblages, of stromatoporoids, is a clear index

of an environmental turbulence, as well as the resistibility of the colony to a strong water agitation. As follows from the studies, optimum conditions for the development of massive stromatoporoids existed in the shallow zone of the basin with slight or moderate turbulence below the permanent wave-base. Only such assemblages had a possibility of preservation in life position. The observations of the stromatoporoid limestones of Sitkówka Beds have revealed that during the periods of a raised hydrodynamic activity of the environment, probably connected with repeated storms, lunar tides and tsunamis, when the wave-base reached much deeper considerable part of colonies was usually overthrown and redeposited frequently together with fragments of an autochthonous sediment. After normal conditions have been restored in the environment, the development of the assemblage was started anew up to the next stage of destruction. When the stromatoporoid community was exposed to a permanent strong waving connected with the shallowing of the basin, they were rapidly destroyed and transformed in a bioclastic sediment. Fragments of crushed colonies were frequently overgrown by algal coatings. The phenomenon of a disappearance and reappearance of the stromatoporoid communities as a rule strongly destroyed and overgrown by algal coatings, repeatedly occurring in the sections of Sitkówka Beds, might indicate rapid, fluctuating changes in mean sea-level. The consistently repeated shallowing of the basin, emphasized by the encroachment of the bottom, settled by stromatoporoids, in the zone of permanent waving, is underlined in many cases by the appearance, above the destroyed stromatoporoid banks, of a sediment with many algal coatings, laminated limestones of the nature of algal mats, as well as erosion surfaces covered with flat pebbles. Such sediments are generally interpreted as symptoms of an extreme shallow-water character of a marine environment (shallow subtidal, intertidal and supratidal zones (e.g., GINSBURG, 1957, 1960; MONTY, 1967; LAPORTE, 1967). Since no ecologic potential to erect rigid, wave-resistant structures which should be characteristic of reef organisms (LOWENSTAM, 1950), is displayed by the stromatoporoid communities observed in Sitkówka Beds, determining them as biostromal reefs (PAJCHŁOWA & STASIŃSKA, 1965) is, in the present writer's opinion, groundless.

In examining the whole of the sedimentary environment of Sitkówka Beds, it should be emphasized that the Lower Sitkówka Beds were generally marked by calmer and relatively deeper sedimentation whereas during the deposition of the Upper Sitkówka Beds a considerable shallowing of the basin took place which was expressed in an increased part of biocalcirudites, algal coatings and algal mats. A thick complex of calcirudites and fine-grained *Amphipora*-calcarenites separating the Lower from Upper Sitkówka Beds, is indicative of a longer period of calm conditions of sedimentation over the entire area under study.

Biostratigraphy and correlation. — The age of the stromatoporoid limestones, assigned by the writer to Sitkówka Beds, has hitherto been determined, on the basis of a superficial faunal analysis, as Givetian, most likely the Upper one (GÜRICH, 1896; SOBOLEV, 1909, 1911; CZARNOCKI, 1938, 1948; PAJCHŁOWA, 1959, 1962, 1968). It has however, been shown by the analysis of the stromatoporoid assemblage of Sitkówka Beds (Table 2) that, in addition to the Givetian species, many forms characteristic of the Frasnian are represented in these beds. The mixed composition of the stromatoporoid fauna might indicate that, in regard to age, the Sitkówka Beds comprise deposits which correspond to the uppermost Givetian — lowermost Frasnian marked by a uniform facies development. The most typical and, at the same time, most numerous stromatoporoid species of the entire Sitkówka Beds are *Actinostroma papillosum* (BARGATZKY), *A. stellulatum* NICHOLSON and ?*Pseudoactinodictyon dartingtonense* (CARTER) which make up about 40 per cent of all specimens collected from these deposits. In addition to many species common to the entire Sitkówka Beds (Table 2), many species occur only in the

Lower Sitkówka Beds. *Tienodictyon zonatum* YABE & SUGIYAMA, occurring only in the Givetian (YABE & SUGIYAMA, 1941; BOGOYAVLENSKAYA, 1965; STEARN, 1969) being the most characteristic of them. Now, in turn, the Upper Sitkówka Beds contain several species lacking in the Lower Sitkówka Beds and of which the most characteristic ones are, *Tienodictyon albertense* (STEARNS), *Atelodictyon trautscholdi* (RIABININ), *Stromatopora undata* RIABININ and *Taleastroma confertum* STEARN are known only from the Frasnian (STEARNS, 1961, 1962, 1969; RIABININ, 1941, 1955).

Judging by distinct differences in the stromatoporoid communities, the Lower Sitkówka Beds would correspond to the Upper Givetian and the Upper Sitkówka Beds to the lowermost members of the Frasnian. Such an interpretation of the stratigraphic position of both parts of the Sitkówka Beds is also confirmed by tabulates and tetracorals which in the Lower Sitkówka Beds are clearly Givetian and in the Upper—Frasnian in character. In the present state of studies, an accurate determination of the boundary between the Givetian and the Frasnian is not possible in this section. On the whole, it may be supposed to run in the middle part of the Sitkówka Beds. Since the boundary between the Sitkówka Beds and the unquestionably Frasnian Kadzielnia Beds is not exposed, the mutual relation of the two stratigraphic units is not quite clear. Under such circumstances, it is unlikely that the stromatoporoid limestones, now assigned to the uppermost part of the Sitkówka Beds from the sections in the Kowala-railway cut (loc. 12), „Kowala“ quarry (loc. 13) and „Nowiny“ quarry (loc. 17), may — as a result of future studies — turn out to be an equivalent of the Kadzielnia Beds.

3. Kadzielnia Beds

The term „Kadzielnia Beds“ is being introduced by the writer to designate a 50 m — thick complex of poorly stratified and massive stromatoporoid — coral limestones which have so far been called Kadzielnia limestones (GÜRICH, 1896; SOBOLEV, 1909, 1911, 1912; CZARNOCKI, 1948; PAJCHŁOWA, 1959, 1962, 1967, 1969) and usually interpreted as reef formations (SOBOLEV, 1909, 1911; CZARNOCKI, 1948; PAJCHŁOWA & STASIŃSKA, 1965, 1967). The Kadzielnia Beds, outcropped in a few localities in a direct neighborhood of Kielce, form the Dalnia, Karczówka, Psie Górki, Góra Cmentarna and Wietrznia (locs. 29 to 34; Text-fig. 1) hills, all of them assigned to the Kadzielnia chain which makes up part of the southern zone of the Kielce—Łagów synclinorium. The most complete section of the Kadzielnia Beds occurs in the Kadzielnia quarry (Pl. I, Fig. 4), situated within the city of Kielce.

The lower boundary between the Kadzielnia and the underlying Sitkówka Beds is not exposed, while platy cephalopod limestones, with which the development of the stromatoporoid facies terminated in the Devonian of the western Holy Cross Mts. (Table 1), form their upper boundary.

The Kadzielnia Beds are developed mostly in the form of light-colored calcilutites with irregular intercalations of fine-grained biomicritic calcarenites. These deposits turn laterally into larger complexes of biosparitic, coarse-grained calcarenites or calcirudites. Stromatoporoids which in calcilutites and fine-grained calcarenites are always preserved in growth position are the main faunal elements of the Kadzielnia Beds. Forms with lenticular coenostea, usually reaching considerable dimensions (to 1.5 m in diameter), predominate in the lower part of the Kadzielnia Beds in the section of the Kadzielnia quarry (Text-fig. 5G), while very thin, sheetlike colonies, a dozen or so cm in diameter and not exceeding 2 cm in height, are a predominant element in the upper part. Many flat colonies encrust brachiopod nests or phylloid algae (*Keega* WRAY), which are particularly abundant in the upper part of the section (Text-fig. 5G). Stromatoporoids are widely spaced in the deposit and the degree of their concentration in the sediment as a rule does not exceed 25 to 30 per cent of the volume of the rock. Sometimes,

they are accompanied by numerous, massive and ramose tabulates and less frequent solitary or colonial tetracorals, which in some parts of the profile form independent assemblages. Brachiopods and large gastropods, which, particularly in the lower part of the section, occur in larger accumulations, are also common within the Kadzielnia Beds. The presence of bioherdimentary structures of the type of „*Stromatactis*“ especially numerous in the lower and uppermost part of the section, is a characteristic feature of the Kadzielnia Beds. Most likely, the „*Stromatactis*“ are traces of burrowing organisms (SHINN, 1968), making up systems of irregular canals or cavities which penetrate the deposit mostly in the horizontal plane and are filled with a sparry calcite.

The stromatoporoid assemblage in the Kadzielnia Beds is represented by nine species (Table 2). The following corals were identified:

Tabulata:

Alveolites parvus LECOMPTE
Alveolites suborbicularis LAMARCK

Tetracoralla:

Macgea supradevonica (PENECKE)
Macgea berdensis SOSHKINA
Thamnophyllum kozlovskii RÓZKOWSKA
Thamnophyllum monozonatum (SOSHKINA)
Phillipsastrea ananas (GOLDFUSS).

Paleoenvironmental remarks. — In regard to paleogeography the Kadzielnia Beds represent deposits of the marginal zone of a carbonate platform which separates the shelf of the Kielce sedimentary region from the basinal Łysogóry sedimentary region. It follows from the lithologic and faunal analyses of the sections of particular outcrops of the Kadzielnia Beds that this area was probably strongly differentiated morphologically and consequently, also in regard to the hydrodynamic activity of the environment.

Fine- and crypto-grained sediments, predominant in the sections of the Kadzielnia quarry or Dalnia Hill, indicate a generally low energy index of this part of the sedimentary basin. Only rare and irregular intercalations of echinoderm or calcisphaera biopelsparites would be symptoms of brief periods of raised turbulence which, however, did not cause any major destruction in the bottom zone. A quiet character of this part of the sedimentary environment of the Kadzielnia Beds is also emphasized by the *in situ* position of most of the organisms. This concerns both stromatoporoids and corals and both brachiopods and gastropods which as a rule do not display redeposition or abrasion. Characteristically lenticular and tabular shapes of coenostea of stromatoporoids are adaptation to the life on a soft substratum. According to the interpretation of MURRAY (1966) and STEARN (1967), the tabular form of stromatoporoids coenosteum might be connected with their development on a more steeply sloping bottom on which it assured a better stability of a colony. The marginal shelf position of the sedimentary area of the Kadzielnia Beds allows one to presume that the bottom was considerably, sloping northwards or north-eastwards. The unquestionable softness of the substratum on which tabular stromatoporoids developed within the Kadzielnia Beds is emphasized by many colonies shaped like an inverted, flattened hat (Text-fig. 6) whose central part plunged with its growth in the calcareous ooze as an effect of its own weight. In search for a harder substratum, stromatoporoids readily used for settlement thin layers of brachiopods or encrustations of phylloid calcareous algae, which made up a firmer substratum than the quaggy sediment.

In some places the facies of fine- and crypto-grained limestones with tabular stromatoporoids turns laterally into coarse-grained deposits of the nature of biosparitic calcarenites and calcirudites, whose best outcrops are observed on the Psie Górki and Cmentarna Góra hills and in the Wietrznia quarry. These deposits represent products of abrasion of the stromatoporoid-coral assemblages, developing in the areas which directly adjoin the zones referred to

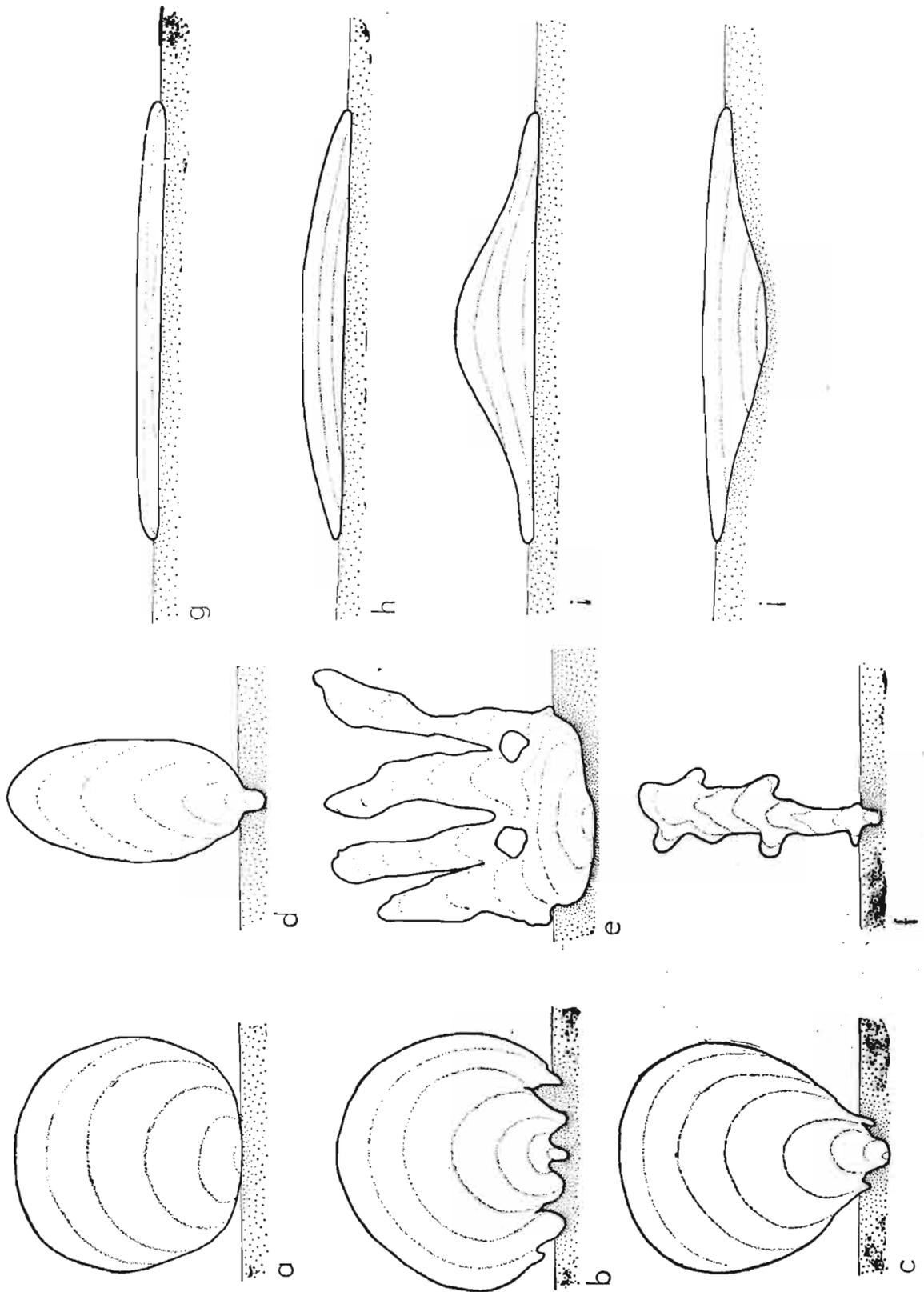


Fig. 6

Main types of the morphology of coenosteum in massive stromatoporoids from the Devonian of the Holy Cross Mts. and their life-position on substratum: *a-d* spherical, hemispherical and bulbous forms, *e-f* columnar and cylindrical forms, *g-j* tabular and lenticular forms. Not to scale

above. These areas were either permanently, or periodically included by a strong water agitation. Part of the bioclastic material, occurring in these deposits, was probably redeposited from the area of carbonate platform situated somewhat to the south of the marginal zone of shelf and subsequently accumulated on its slope. Together with a local material, these deposits were frequently subject to a mass displacement deep into the basin. Such displacements in the form of turbidities are known from several outcrops of Frasnian basinal deposits (SZULCZEWSKI, 1968).

The lack of terrigenous particles in the stromatoporoid limestones of the Kadzielnia Beds is indicative of an off-shore position of the sedimentary environment.

Many suggestions concerning the reef character of these deposits (SOBOLEV, 1909; CZARNOCKI, 1948; PAJCHLOWA & STASIŃSKA, 1965, 1967) have not been confirmed by the writer's observations of the sedimentary environment of the Kadzielnia Beds. In addition to the lithological and sedimentary characters of these deposits cited above, the non-reefoid origin of these beds is also indicated by the presence of burrows of the „*Stromatactis*“ type, particularly abundant in the section of the Kadzielnia quarry (Text-fig. 5G) which was considered as the most representative part of reef deposits in the Holy Cross Mts. The presence of the traces of an intensive activity of the burrowers unequivocally indicates an environment quite different than a reef environment (GOLDRING, 1964; SEILACHER, 1957; SHINN, 1968; LAPORTE, 1968). The poor stratification of the Kadzielnia Beds, frequently serving as an argument for the followers of the reef origin of these deposits, is, in this case, only an evidence for uniform conditions of sedimentation which persisted for a longer time. Poorly or non-stratified deposits are known from many non-reefoid platform carbonate sequences (SANDERS & FRIEDMAN, 1967; JENKYN, 1970). In regard to ecology, the stromatoporoid assemblages preserved *in situ* within the Kadzielnia Beds, may be determined, in conformity with the classification of skeletal limestones of NELSON et al. (1962), as biostromal banks with a relatively low concentration of organisms.

Biostratigraphy and correlation. — Frasnian age of the Kadzielnia Beds follows from studies of the fauna, published thus far. On the basis of *Hypothyridina cuboides* (SOWERBY), which occurs in massive Kadzielnia limestones, the age of the Kadzielnia Beds was determined by GÜRICH (1896) as the Middle part of the Early Upper Devonian. SOBOLEV (1912) considered the Kadzielnia limestone as a time and facies equivalent of the Frasnian Iberg limestone of the Harz Mts. According to CZARNOCKI (1948), massive stromatoporoid-coral limestones might correspond to the Lower and Middle Frasnian and overlaying cephalopod limestones with *Manticoceras* might represent the Upper Frasnian. CZARNOCKI's tripartite division of the Frasnian in the Kielce sedimentary region, supplement by descriptions of coral fauna (STASIŃSKA, 1953; RÓŻKOWSKA, 1953, 1956, 1957) has been used until now. This division differs radically from standard cephalopod-zones and correlated conodont-zones now in general use for the Upper Devonian biostratigraphy. In the course of recent biostratigraphic studies on the Upper Devonian of the Holy Cross Mts., conodonts of *Ancyrognathus triangularis* (Frasnian I γ) have been found by Dr. M. SZULCZEWSKI (personal communication) in the uppermost part of the Kadzielnia Beds exposed in the Kadzielnia quarry. Since the underlying Upper Sitkówka Beds have been determined by the present writer on the basis of stromatoporoids as the lowermost Frasnian, the stromatoporoid limestones of the Kadzielnia Beds would probably correspond to a brief period between the Lowermost Frasnian and Frasnian I γ , which is not likely to exceed one conodont zone. Furthermore since the boundary between the Upper Sitkówka and the Kadzielnia Beds is not exposed, the correlation of the two units is difficult to determine precisely. The fact that several new species, which are not represented in the Upper Sitkówka Beds, appear

in the assemblage of stromatoporoids of the Kadzielnia Beds, seems to indicate a higher stratigraphic position of the last-named unit. Unfortunately, stratigraphic ranges of stromatoporoid species characteristic of the Kadzielnia Beds are insufficiently studied and such species are recorded from both the Upper Givetian and the Frasnian of Europe and North America (NICHOLSON, 1886*b*, 1892; PARKS, 1936; KLOVAN, 1966).

STRUCTURE OF THE STROMATOPOROIDEA

FORMATION OF THE SKELETON IN THE STROMATOPOROIDEA

General. — Despite collecting a considerable factual material and a rapid increase in the number of the species described (cf. Fossilium Catalogus — FLÜGEL & FLÜGEL-KAHLER, 1968), several authors of new papers, devoted to general morphological and taxonomic problems of the Stromatoporoidea (KÜHN, 1939; YAVORSKY, 1955; LECOMPTE, 1951, 1956; GALLOWAY, 1957; STEARN, 1966*b*), avoided the subjects related to the biological interpretation of some regularities involved in the process of skeleton formation in the stromatoporoids and a presumably position of the soft parts in the course of growth. The undertaking of an attempt at an explanation of the mechanism of forming skeletal elements in the stromatoporoids is particularly important in determining their suitability for the purposes of taxonomy which, within the range of this group of fossils, passes through a profound crisis clearly visible in various diagnostic criteria used in recently published works (SLEUMER, 1968, 1969; MORI, 1968; KHALFINA, 1968*a, b*; BOGOYAVLENSKAYA, 1969*b*).

After more than 140 years of studies on the stromatoporoids, the view has been accepted, first expressed by LINDSTRÖM (1876) who believed in the relationship of this group of fossil organism to some of the Recent Hydrozoa. LINDSTRÖM's view was initially accepted and developed by CARTER (1877, 1878*a, b*) and NICHOLSON (1886*b*). The latter author divided the order Stromatoporoidea, he erected, into „Hydractinoid“ and „Milleporoid“ groups which were supposed to emphasize a morphological similarity of the stromatoporoids to the Recent Hydrozoa: *Hydractinia* VAN BENEDEN and *Millepora* LAMARCK. Following HEINRICH's (1914) studies and yet more the studies on the Recent gymnoblastic hydroids, conducted by TRIPP (1929), the stromatoporoids turned out, however, contrary to NICHOLSON's (1886*b*) suppositions not to have zooidal tubes in coenosteum, which would be comparable with systems of zooidal pores (cyclo systems) of the Recent *Millepora*. Thus, the gymnoblastic hydroids secreting their skeleton only at the base of a colony, are the only Recent forms with which the stromatoporoids are compared.

Unfortunately, except for more accurate studies on a few representatives of the Recent Gymnoblastina with chitinous skeletons, conducted by TRIPP (1929), the mechanism of skeleton formation in this group of the Hydrozoa is recognized very poorly. Particularly important studies might be conducted from this viewpoint on such forms as, *Hydrocorella africana* STECHOW and *Janaria mirabilis* STECHOW (STECHOW, 1921) having calcareous coenostea devoid of zooidal tubes. It is clear from GOETTE's (1916), TRIPP's (1929), BRAVERMAN's & SCHRANDT's (1966) and VERVOORT's (1966) studies that in the Recent gymnoblastic hydroids secreting a basal skeleton, there occur three fundamental types of the organization of coenosarc, a different structural type of skeleton being connected with each of them. Skeletons are, in all cases, of the

ectodermal origin. The two statements given above are of a great importance to the understanding of skeleton formation processes in the Stromatoporoidea.

Type 1 — is represented by encrusting colonies of *Hydractinia echinata* (FLEMMING) whose coenosarc occurs in the form of a compact, thin ectoderm layer, with gastrodermal canals, shaped like a dense, irregular network (TRIPP, 1929; HYMAN, 1940), running within it. Epithelial ectoderm is naked, without an external peridermal sheath. A chitinous skeleton is deposited by a slightly folded internal layer of ectoderm (Text-fig. 7A₁), from which irregular coenosarcular strands, penetrating inside the skeleton, may detach themselves locally. This type of the basally deposited skeleton was termed by TRIPP (*l. c.*) as an „open“ one. With the growth of a colony, the layer of coenosarc gradually shifts upwards on thick pillars connected with each other at irregular intervals by horizontal trabeculae. Skeletal elements have a lamellar structure and the entire skeleton displays, in vertical section, a system of an irregular lattice (Text-fig. 7A₂).

Type 2 — is represented by rhizocaulomic colonies of *Solanderia secunda* (INABA), *Rosalinda williamsi* TOTTON (see VERVOORT, 1966), as well as by encrusting colonies of *Rosalinda incrustans* (KRAMP) and *Hydractinia sodalis* STIMPSON (see STECHOW, 1909; TRIPP, 1929). The coenosarc consists here of a considerably thicker, compact mass of ectoderm, with thin tubes of entodermal (gastrodermal) canals running within it (Text-fig. 7B). A chitinous skeleton is composed of twisted fibers connected with each other to form an irregular spatial lattice completely embedded in ectoderm. Epithelial ectoderm occurs in the form of a naked layer devoid of a peridermal sheath. Skeletal elements are secreted in the course of growth by a strongly folded ectoderm directly below a layer of epithelium. With growth coenosarc increases only its volume and does not leave the previously formed skeleton.

Type 3 — is represented by encrusting colonies of *Podocoryne carnea* M. SARS, whose coenosarc, in contradistinction to Types 1 and 2, does not form a compact layer, but consists of a relatively loose meshwork of stolons, connecting particular individuals of the colony, externally covered with a thin layer of periderm (Text-fig. 7C₁). A chitinous skeleton is deposited in the basal zone of stolons (horizontal skeletal elements) and interstonlonally (vertical skeletal elements). In the course of their growth, stolons penetrate through the peridermal cover and form on it another layer of stolons, also depositing the skeletal substance. Such a manner of forming skeleton was termed by TRIPP (1929) „closed“. Stolons of the upper and lower layer connect with each other with passages not overgrown by the skeleton. Skeletal elements, formed as a result of a repeated deposition of stolonial layers, are tubular (Text-fig. 7C₂).

Summing up the characteristics of the main coenosarc-skeleton systems in gymnoblastic hydroids, attention should be attracted to a clearly higher degree of folding the coenosarc in type 2 as compared with type 1 and, in this connection, a larger complexity of the skeletal system. In all the cases under study, zooids budding in a mosaic-like manner do not participate in forming skeletal elements.

The coenosarc-skeleton relation in the Recent gymnoblastic hydroids results in a conclusion important to the considerations on the distribution of soft parts in the coenosteum of the stromatoporooids. This conclusion is as follows: two elements: a) a general organization of the coenosarc and b) a position of the skeletogenic layer of ectoderm in relation to the skeleton in the course of its growth, may be reconstructed on the basis of the morphology of skeleton. The coenosteum in the stromatoporooids may, therefore, be determined as a result of the calcicoblastic activity of the basal zone of ectoderm changing its configuration (degree of folding) in various stages of the growth of a colony.

It follows from the morphological observations of so far described Paleozoic stromatoporoids that their skeletons were formed, without any exceptions, analogously to those of the Recent *Hydractinia echinata* (Type 1 or TRIPP's (1929) „opcn“ type) whose compact coenosarc

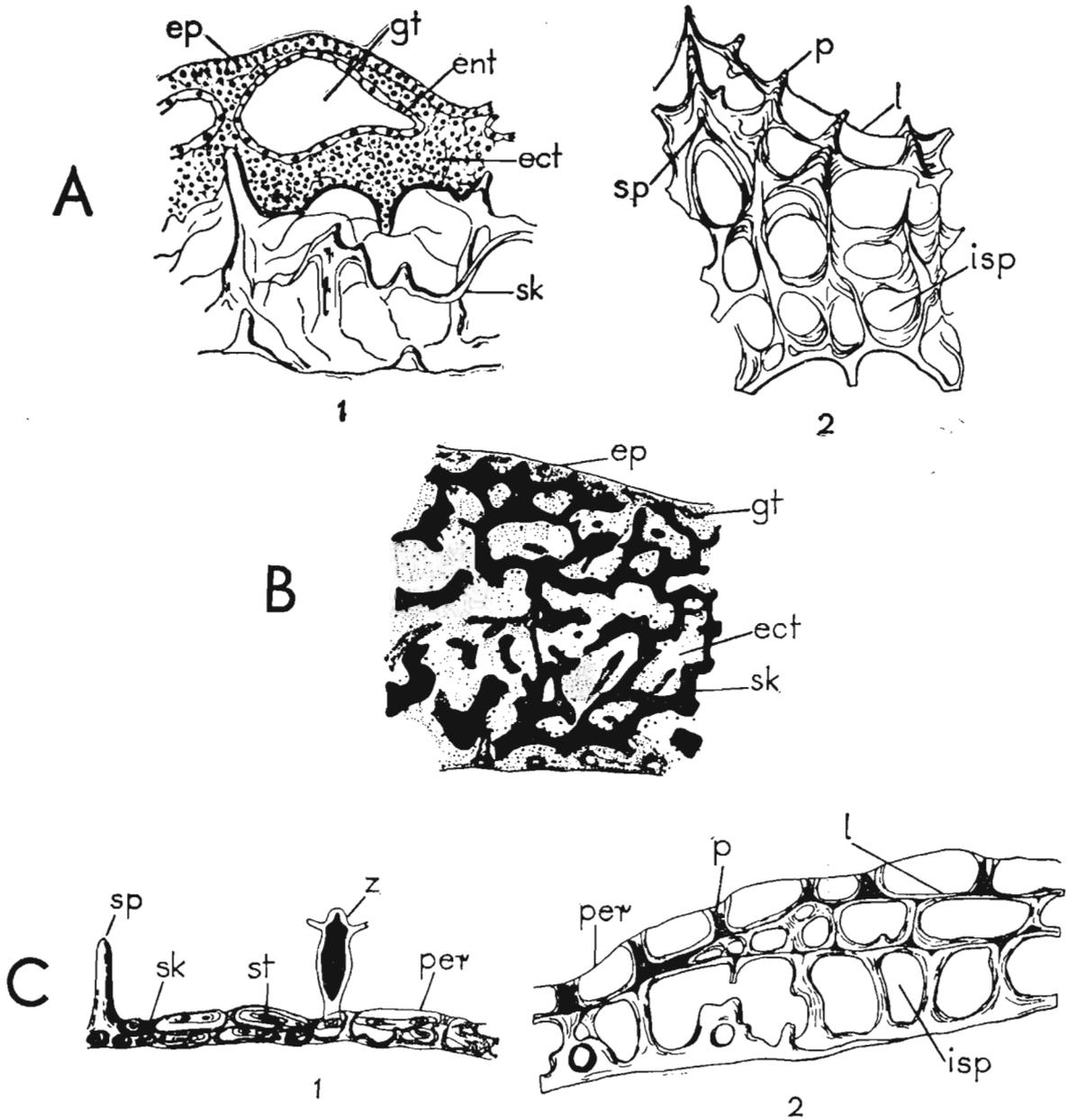


Fig. 7

Main types of the organization of coenosarc and of the structure of skeleton in the Recent gymnoblastic hydroids. A — *Hydractinia echinata* (FLEMMING): 1 distribution of coenosarc in relation to skeleton, 2 a fragment of basal skeleton; B — *Hydractinia sodalis* STIMPSON; C — *Podocoryne carnea* M. SARS: 1 distribution of stolons of hydrorhiza in relation to skeleton, 2 a fragment of interstolonal skeleton. (All after TRIPP, 1928); *ect* ectoderm, *ent* entoderm, *ep* epithelium, *gt* gastrodermal tubes, *per* periderm, *st* stolons, *z* zooid, *sk* skeleton, *p* pillar, *l* lamina, *sp* spine, *isp* interskeletal space

displayed a clearly progressive tendency to increase its folding and to form, in some lineages, coenosarc strands penetrating deeper into the skeleton. Despite the fact that judging from the complex system of skeletal elements in the interlaminar space, the degree of folding in some of the Middle and Upper Devonian stromatoporoids (e.g., *Tienodictyon* YABE & SUGIYAMA) had to be already very high, the skeleton does not seem to have been formed within the ectoderm as is the case in the Recent *Hydractinia sodalis* (Type 2). Likewise, contrary to TRIPP'S (1929) supposition, no skeletons may be found among Paleozoic stromatoporoids which would correspond to the tubular interstolonal skeletons of the Recent *Podocoryne carnea* (Type 3 or TRIPP'S „closed“ type).

GRÓWTH PATTERN OF THE STROMATOPOROIDEA

To understand the manner of growth of the skeleton in the stromatoporoids, it is necessary to determine the zone occupied by coenosarc in succeeding stages of growth of coenosteum, as well as the manner in which skeleton contacted coenosarc. Various morphological elements of skeletons of the stromatoporoids whose observation allows one to conclude on skeleton-coenosarc growth relations in various morphological groups of the Stromatoporoidea are discussed below.

Growth discontinuities

Only few stromatoporoids have skeletons formed as a result of a continuous growth process, usually manifested by the occurrence of long, uninterrupted vertical elements of the skeleton (e. g., *Labechia* EDWARDS & HAIM). Most of the Stromatoporoidea display a growth periodicity, resulting in the occurrence in the coenosteum of various kinds of planes which may be commonly termed as growth discontinuity surfaces. The presence of a growth discontinuity surface indicates that now and then the growth of skeleton was inhibited or stopped and after some longer or shorter period was continued once again.

Growth inhibition surfaces are the most common type of the growth discontinuity. They are visible in the skeleton in the form of thin dark-coloured layers distinctly discernible in the microscopic picture (in vertical section against the background of the rest of the skeletal substance, regardless of its microstructural character (Pl. X, Fig. 2; Pl. XI, Figs. 1 and 3a; Pl. XVII, Fig. 1d). Growth inhibition surfaces, which occur in coenostea with laminar structure run always in the plane of laminae, usually in their upper and, less frequently, middle part (Pl. XX, Fig. 2a-b; Pl. XXXI, Figs. 1a and 2c). The segments of skeleton, contained between successive growth inhibition surfaces may be called growth increments of a colony. Particular increments may be of equal size, but usually they vary within a considerable interval (Pl. XX, Fig. 2a-b). Discordances in the trace of vertical elements of skeleton on the boundary of dark-coloured layers give evidence that these layers were actually formed during the periods of growth inhibition, sometimes equivalent to its complete stoppage. This shows that a normal secretion of the skeletal substance was resumed, after the completion of each growth increment, regardless of a skeleton deposited earlier (Pl. X, Fig. 2). Thus, the growth inhibition surfaces determine the boundary of the range of coenosarc in a given stage of growth of a colony and simultaneously allow one to find that in the skeletons displaying periodicity of growth inhibition the layer of coenosarc could not exceed the part of skeleton contained between two successive discontinuity surfaces. The dark coloration of the skeleton in the plane of growth inhibition may be explained by a considerable decrease, during that period of the

calcification activity of the ectoderm or, *vice-versa*, by an increase in the secretion of organic matter. This phenomenon was probably evoked by brief changes in the metabolism of a colony, periodically repeated in the process of growth. Despite the darker coloration, the growth inhibition surfaces do not differ microstructurally from the skeleton within which they run.

The growth inhibition surfaces of the nature of darker layers occur mainly in the group of microreticulate stromatoporoids (group „B“, see p. 49). In older representatives of this group (e.g., *Densastroma* E. FLÜGEL, *Actinostromella* BOEHNKE, *Parallelostroma* NESTOR), they are still relatively rare and irregular; afterwards, their number gradually, increases. This might be evidence for a progressive increase in growth rhythmicity in stromatoporoids younger geologically. A similar phenomenon is observed in the development of growth rhythmicity in several other groups of marine invertebrates (PANNELLA & MACCLINTOCK, 1968).

The dark surfaces of growth inhibition were termed „dark lines“ (NICHOLSON, 1886*b*, LECOMPTE, 1956), „primary laminae“ (PARKS, 1936) or „microlaminae“ (GALLOWAY, 1957, ST. JEAN, 1960), but their formation was not interpreted by any of the authors mentioned, except for, TRIPP (1929, 1932), who considered the dark lines, occurring in the plane of laminae, as a suture formed as a result of a simultaneous bilateral deposition of the skeletal substance, identical with that in the Recent *Podocoryne carnea* (Text-fig. 7*C*₂). TRIPP'S interpretation is, however, contradicted by the fact of a general occurrence of dark layers in the skeletons which do not display laminar structure (e.g. most of *Stromatopora* GOLDFUSS, *Densastroma* E. FLÜGEL, *Syringostromella* NESTOR), as well as by the position of the alleged „suture“, which usually occurs in the upper and not central part of laminae. Primarily, however, no tubular skeletal elements, characteristic of interstolonally secreted skeletons of *Podocoryne carnea* (Text-fig. 7*C*₁), have ever been observed in the stromatoporoids with dark-coloured layers of growth inhibition.

Another type of growth periodicity in the stromatoporoids are *growth interruption surfaces*, in which secretive activity of ectoderm had to be completely interrupted for a certain period. As a result, the occurrence, of a discontinuity in the character of fissures (Pl. VII, Fig. 6; Pl. XVI, Figs. 2 and 3*a*) is observed in vertical sections of some of the skeletons. In the skeletons with laminar structure, fissures always occur in the plane of laminae and in the skeletons, in which vertical elements predominate, fissures intersect, at more or less regular intervals, pillars or vertical walls. The presence of fissures is an evidence that the secretion of skeletal substance took place, after a growth interruption, independently of a previously deposited skeleton. In a new growth cycle, it served only as a substratum for a newly formed skeletal layer. Depending on the degree of the adjustment of the basal zone of the new growth cycle to the substratum, fissures may be narrow or wide, even or irregular with sudden extensions and contractions. Over some parts of the skeleton, fissures disappear (Text-fig. 8*a*) and in this connection it may be presumed that an interval in the secretive activity of ectoderm did not include simultaneously the entire colony. This is indicated, in addition, by frequent lateral transitions of the fissures of growth interruptions into dark-coloured layers of growth inhibition. If, however, in the planes of growth inhibition coenosarc continued to occur on the surface of skeleton, in the case of growth interruptions there is every reason for the statement that it might periodically disappear from some parts of the skeleton. Since the deposition of a thin layer of sediment and even the development of the bundles of blue-green algae (Text-fig. 8*b*) could come about on some growth interruption surfaces, the period of the absence of coenosarc from some places of the colony had to be fairly long. Such a considerable lateral lability of the coenosarc in the stromatoporoids is not unusual if we consider the well-known fact of a high degree of plasticity of coenosarc in the Recent *Gymnoblastina* during the growth of which frequently large masses of cells become

resorbed in certain parts of the colony and shifted to other parts in which a more intensive growth is just taking place.

The surfaces of skeleton, periodically devoid of coenosarc, were frequently encrusted by larvae of some Tabulata (*Aulopora*, *Syringopora*, *Syringoporinus*) and less so by solitary Rugosa and sedentary polychaetes (e.g., *Spirorbis*), whose development required a hard substratum. After the resumption of the growth of skeleton, these organisms grow together with the stromatoporoid colony, adjusting to it the rate of their growth. The biotic associations of this type were called by most authors commensal ones (CLARKE, 1908, 1921; GALLOWAY, 1957; FLÜGEL, 1959 and others). In the present writer's opinion, the fact of the adjustment of the earliest growth stages of the organisms associated with the stromatoporoids, having growth interruption surfaces, indicates that these associations were rather loose and may be assigned to an epibiotic category. It is not unlikely, however, that some of the epibionts might pass to a closer cooperation with the stromatoporoids. In all the cases of a common growth of the Tabulata and stromatoporoids, observed by the writer, the development of the tabulates was always started from the growth discontinuity surface which mostly was of the nature of a distinct interruption. This fact allows one to consider the presence of the tabulates in the skeletons of stromatoporoids as a general index of the occurrence of growth discontinuity in the process of the growth of coenosteum.

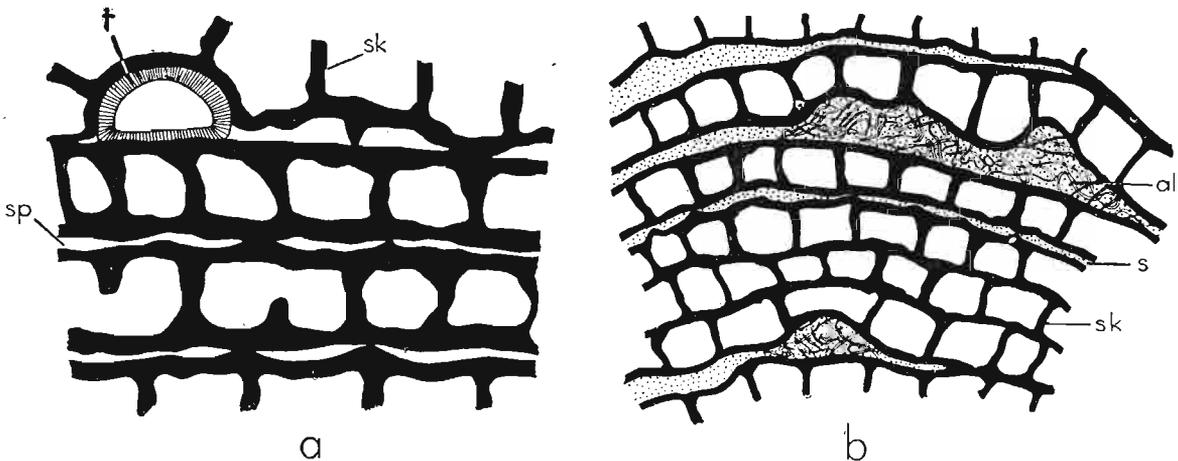


Fig. 8

Growth interruptions in vertical sections of the coenosteum of „*Diplostroma*“ NESTOR: a „*Diplostroma*“ *yavorskyi* NESTOR (based on holotype EAS — Co 3140); b „*Diplostroma*“ *validum* NESTOR (based on holotype EAS — Co 3138); $\times 10$ approx. *al* bundles of blue-green algae covering the surface of a growth interruption, *sk* skeleton, *sp* irregular splits of growth interruption, *ta* tabulate coral *Aulopora* sp. encrusting the growth interruption surface

Closely spaced distributed and rhythmically repeated growth interruption surfaces, visible in vertical sections of some of the stromatoporoids as thinner or thicker white strands (e.g., *Stromatopora mononensis* GALLOWAY & ST. JEAN; Pl. XII, Fig. 1) have so far been described as „light microlaminae“ (GALLOWAY, 1957; GALLOWAY & ST. JEAN, 1957; ST. JEAN, 1960) and erroneously considered as a skeletal element of coenosteum. The fissures of growth interruptions in the planes of laminae (Pl. VII, Fig. 6; Pl. XVI, Figs. 2a and 3a) have descriptively been termed as a „light axial zone“ (STEARNS, 1966b), whereas the laminae themselves with fissures as „bipartite laminae“ (LECOMPTE, 1951) or „tripartite laminae“ (LE MAÎTRE, 1949; STEARNS, 1966b). A separate term „tubulate microstructure“ (LE MAÎTRE, 1949; LECOMPTE, 1951; STEARNS,

1966b) have been introduced to designate laminae with irregular fissures of growth interruptions, frequently bifurcating in the plane of laminae.

Growth interruption much the same as growth inhibition surfaces indicate that the position of coenosarc in relation to skeleton was, in the process of the growth of a colony, limited to its most superficial zone, of skeleton now contained between two successive growth interruption surfaces (one growth cycle).

It follows from the variable character and different frequency of occurrence of two types of growth discontinuity discussed above that, despite their formation being connected, in both cases with periodical changes in metabolism of the colony, the process under study was variously reflected in the skeleton, even within one, and the same coenosteum. In this connection, in some phases of the growth of the colony, the secretive periodicity of coenosarc was very poorly or not at all expressed in the skeleton (Text-fig. 8b). The above statement considerably minimizes the taxonomic value of a growth discontinuity surfaces. The genus *Diplostroma* NESTOR, (NESTOR, 1966), separated only on the basis of irregular fissures of growth interruptions, separating some of the laminae and sometimes filled with sediment, may here serve as an example. In many parts of the skeleton of *Diplostroma*, these fissures do not occur and in such cases this genus does not differ at all from *Simplexodictyon* BOGOYAVLENSKAYA (Text-fig. 19b), of which it is probably a junior synonym. Very variable in character are also growth discontinuities (= „axial microlaminae“ or „axial light or dark zones“, STEARN, 1966b), usually occurring in the plane of laminae in the representatives of such genera as, *Stromatoporella* NICHOLSON, *Stictostroma* PARKS (Pl. XVI, Figs. 1a, 2 and 3a; Pl. XVII, Figs. 1a and 1d-e), *Trupetostroma* PARKS (Pl. XXIX, Fig. 1a; Pl. XXX, Fig. 2a; Pl. XXXI, Figs. 2a and 2c), *Hermatostroma* NICHOLSON (Pl. XXXIV, Fig. 1a; Pl. XXXV, Figs. 1a, 2a and 3a) and *Clathrocoilona* YAVORSKY. In many species of these genera, growth discontinuities are very rare or do not occur at all.

Laminae and latilaminae as symptoms of growth periodicity

In addition to growth discontinuity surfaces, the growth periodicity of skeletons of the stromatoporoids is expressed in the presence of laminae, that is, horizontal calcareous sheets deposited at more or less regular intervals by octoderm, which in this growth stage was flat. Part of skeleton, contained between two successive laminae and usually called an interlaminar space (GALLOWAY, 1957), corresponds to a single growth increment of the colony. Depending on the height of interlaminar spaces, the growth increments of colonies may be called either large or small. Large growth increments are characteristic features of the skeletons the representatives of, for instance, *Tienodictyon* YABE & SUGIYAMA (Pl. XII, Figs. 1—3), while some of the species of *Clathrodictyon* NICHOLSON & MURIE, *Simplexodictyon* BOGOYAVLENSKAYA (Pl. VII, Fig. 8) and *Stictostroma* PARKS (Pl. XI, Fig. 4a) have considerably smaller growth increments. Skeletons with uniform growth increments are rare. Usually, larger and smaller growth increments occur within one and the same coenosteum, irregularly interlacing each other.

The presence or absence of laminae is a permanent specific feature, whereas a variable height of interlaminar spaces is connected with the influence of environmental conditions, disturbing the internal growth rhythmicity of colonies (environmental control). The occurrence of epibiontic tabulates (Pl. XV, Fig. 1a-b; Pl. XVI, Fig. 1a) on the surfaces of laminae in some of the skeletons enables the supposition that at least part of them might correspond to the surfaces of very brief growth interruptions.

When alternate series of large and small growth increments repeatedly occur wider zones, termed latilaminae (NICHOLSON, 1886b), frequently visible with the naked eye, are marked

in the skeleton. They have most often been interpreted as a colony's response to seasonal climatic changes (LECOMPTE, 1951, 1956; GALLOWAY, 1957; NESTOR, 1964 and others), or as changes in its growth rate evoked by a varying rate of sedimentation (JUX, 1957; BROADHURST, 1966). A concurrence of species with and without latilaminae in one and the same assemblage may be explained by their different degree of susceptibility to the changes in environmental conditions.

GROWTH RELATIONSHIP BETWEEN HORIZONTAL AND VERTICAL SKELETAL ELEMENTS

Growth of horizontal elements

Straight or gently twisted laminae, probably deposited periodically by a flat basal ectoderm, are most common horizontal skeletal elements in the stromatoporoids. In the cases in which laminae are of the nature of compact plates (e. g., *Simplexodictyon* BOGOYAVLENSKAYA, *Plexodictyon* NESTOR, *Tienodictyon* YABE & SUGIYAMA), they were undoubtedly formed as a result of the secretion of skeletal substance by the entire surface of ectoderm. In addition, compact laminae indicate, that, after their secretion, coenosarc lost contact with the skeleton situated below, that is, that the zone of its occurrence was limited to the most superficial layer of skeleton (no more than one interlaminar space). Frequently, however large circular pores, often called foramina (GALLOWAY, 1957), connecting adjoining interlaminar spaces (Pl. XIII, Figs. 1a, 1c-d; Pl. XIV; Fig. 1c; Pl. XV, Fig. 2a) occur in laminae. The frequency of their occurrence in laminae is more or less constant for definite species.

Foramina may be interpreted as traces of coenosarc strands which penetrated deeper parts of the skeleton. In the process of the deposition of a lamina, when the basal ectoderm became flattened these strands were situated on a lower „tier“ of the skeleton and only later they were shifted upwards (Text-fig. 9B₂). Openings left by strands in the plane of laminae were usually covered with thin, convex plates of the nature of tabulae deposited by the distal zone of strands.

What is known as „ring-pillars“ (GALLOWAY, 1957), tubular structures formed as a result of a sudden upward bend of laminae around foramina and characteristic of species of *Stromatoporella* NICHOLSON and *Pseudostromatoporella* n. gen. (Pl. XIII, Fig. 1a-b; Pl. XVIII, Fig. 1a-d) make up a modification of foramina. In some of the species, ring-pillars are very low, hardly projecting over the surface of a lamina, in some others they reach halfway the height of an interlaminar space (Pl. XVIII, Fig. 1c). Species are also known in which ring-pillars intersect the interlaminar space and connect two neighboring laminae. In the last-named case, ring-pillars may be limited to only one interlaminar space (e. g., *Pseudostromatoporella eriensis* (PARKS), cf. GALLOWAY & ST. JEAN, 1957, Pl. 10, Fig. 2a) or continue, in the form of long, vertical tubes, through several laminae (e. g., *Pseudostromatoporella columbusensis* (GALLOWAY & ST. JEAN) cf. GALLOWAY & ST. JEAN, 1957, Pl. 10, Fig. 3a; *Stromatoporella tubulipilata* (KHALFINA), cf. KHALFINA, 1968b, Pl. 2 Fig. 1a). Ring-pillars, much the same as foramina, may be, in the upper part, open or closed by tabulae. Frequently, they gradually narrow upwards so that in some of the species they may ultimately turn into cones closed on the top (e. g., *Stromatoporella selwyni* NICHOLSON, cf. GALLOWAY & ST. JEAN, 1957, Pl. 8, Fig. 1a). In the present writers opinion, ring-pillars, like foramina, are also traces of the coenosarc strands, departing from a principal mass of the superficially situated coenosarc and making up the same function as typical foramina. Ring-pillars were probably formed when the coenosarc strands still remained in foramina and when the principal mass of coenosarc started to separate from laminae, to fold and to form vertical

elements on which it rose upwards (Text-fig. 9 B₃). In fact, ring-pillars are, therefore, vertical elements of the skeleton, whose functionality terminated at the moment when they were covered with tabulae or overgrown.

The above interpretation of the function of foramina and ring-pillars is based on TRIPP'S (1929) observations of the distribution of coenosarc in the Recent *Hydractinia echinata* (FLEMMING), in which strands, composed of a non-differentiated mass of cells, remaining for a certain time in contact with coenosarc and subsequently resorbed or degenerated, detach themselves in many places from the superficial layer of coenosarc and run inside the skeleton. Since foramina, followed by ring-pillars appear gradually in the development of some of the groups of the Stromatoporoidea and express fundamental evolutionary changes in the organization of coenosarc, they should be included among more important taxonomic characters of the Stromatoporoidea (cf. also GALLOWAY & ST. JEAN, 1957; GALLOWAY, 1957; STEARN, 1966b; ST. JEAN, 1967).

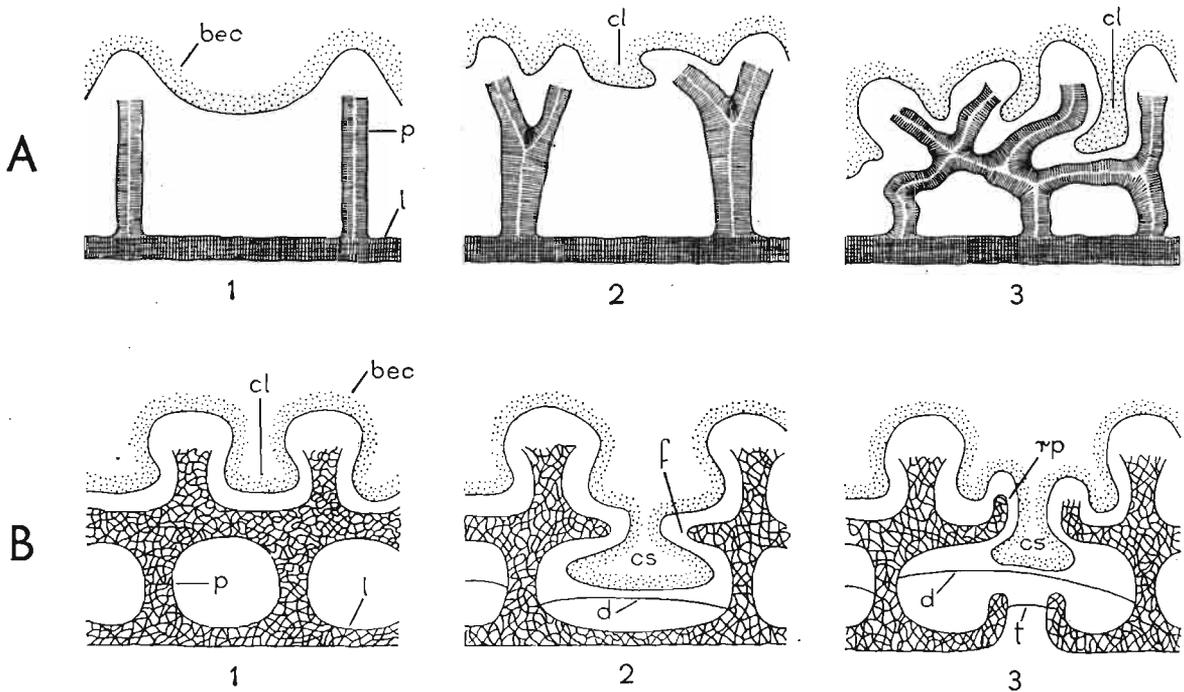


Fig. 9

A schematic reconstructions of the situation of basal ectoderm in some stromatoporoid genera: A — morphological group „A“: 1 *Simplexodictyon* BOGOYAVLENSKAYA, 2 *Anostylostroma* PARKS, 3 *Tienodictyon* YABE & SUGIYAMA; B — morphological group „B“: 1-2 *Stictostroma* PARKS, 3 *Stromatoporella* NICHOLSON; all in vertical section; not to scale. *bec* basal ectoderm, *cl* coenosarcal lobes, *cs* coenosarcal strands, *d* dissepiments, *f* foramina, *l* laminae, *p* pillars, *rp* ring-pillars, *t* tabulae

Some of the stromatoporoids of the microreticulate group (group „B“, cf. Table 3) have laminae in the form of a fairly loose reticulum, formed by reduction and thickening of the fibers of an primary microreticulum (e.g., species of *Actinostroma* NICHOLSON and *Atelodictyon* LÉCOMPTE). Angular outlines of the meshes in laminae of these forms preclude the possibility of comparing them with foramina. Reticular laminae were probably deposited by an almost completely flat ectoderm, however not by its entire surface, as was the case of compact

laminae, but in the form of certain strands, which resulted in the formation of lists which connected at one level vertical elements of the skeleton.

Dissepiments, frequently termed also cyst plates (GALLOWAY, 1957; GALLOWAY & ST. JEAN, 1957), are commonly occurring horizontal elements of the skeleton in many stromatoporoids. Like laminae, they were deposited by flat parts of the basal ectoderm. Dissepiments began to occur earlier than laminae and they were one of the first structural elements of the skeleton to appear in the history of the Stromatoporoidea. Many of the Ordovician to Lower Silurian stromatoporoids have skeletons, composed almost exclusively of more or less convex dissepiments (e.g., *Cystostroma* GALLOWAY & ST. JEAN, *Pseudostylodictyon* OZAKI, *Stratodictyon* WEBBY). In others, which developed vertical elements (pillars, vertical tubes, vertical walls), dissepiments with a varying degree of curve occur as an only horizontal element of the skeleton (e.g., *Labechia* M. EDWARDS & HAIM, *Stromatocerium* HALL, *Cystistroma* ETHERIDGE, *Actinodictyon* PARKS). In many younger stromatoporoids, having well-developed laminae, dissepiments occur in varying numbers within the interlaminar space (e.g., *Pseudoactinodictyon* E. FLÜGEL, Pl. XXIX, Fig. 2a; *Tienodictyon* YABE & SUGIYAMA, Pl. XII, Figs. 1—3; *Ferestromatopora* YAVORSKY, Pl. XXV, Fig. 1a). It follows from the examples cited above that with the development of laminae, dissepiments turn from the main into the supplementary skeletal elements destined to support the coenosarc uplifted on pillars or vertical walls. In many lineages, laminae are gradually replaced by flat dissepiments. This process leads sometimes to an almost complete removal of laminae (e.g. *Trupetostroma laceratum* LECOMPTE, Pl. XXX, Figs. 1a and 1d; *Hermatostroma perseptatum* LECOMPTE, Pl. XXXIV, Fig. 2). Tabules, covering foramina and ring pillars and intersecting closed interskeletal spaces, which are of the nature of vertical tubes or what is known as autotubes (HUDSON, 1957; NESTOR, 1966), are structures similar in character to dissepiments.

The formation of dissepiments in the stromatoporoids, probably took place identically, as in the Recent Zoantharia (WELLS, 1969; OEKENTORP & SORAUF, 1970), that is, as a result of an centrifugal and centripetal secretion of skeletal substance by the basal ectoderm vesicularly bent upwards probably by the hydraulic action of a special fluid. Following such a secretion, irregularly circular or angular pores, which only in the last growth stage are covered by skeletal substance (WELLS, 1969, Pl. 1, Figs. 2—6), may occur in the central part of not fully developed dissepiments. In the writer's opinion, some of the dissepiments in the representatives of the genus *Forolinia* NESTOR (NESTOR, 1964, Pl. 10, Figs. 1—5) or *Labechia* M. EDWARDS & HAIM (GALLOWAY & ST. JEAN, 1961, Pl. 7, Figs. 1—2), which have, in their central part, irregular pores, are underdeveloped dissepiments from which coenosarc withdrew prior to the completion of secretion.

The fact of a general occurrence of dissepiments in the stromatoporoids is one of essential features for assigning these fossils to the coelenterates.

Growth of vertical elements

The morphology and distribution of vertical elements depended on the degree of folding of the basal ectoderm and distribution of calcification centers in the process of lifting the coenosarc of a colony. In the case of a punctual secretion of skeletal substance pillars were formed, whereas calcification centers distributed in ectoderm in the form of strands produced vertical walls. Since in vertical sections of the skeleton, pillars, and vertical walls look identically, most authors erroneously called both types of vertical structures by the term „pillars“, despite the fact that in tangential sections it is very easy to distinguish irregularly meandering vertical walls from isolated spots corresponding to transverse sections of pillars. A clear terminological,

distinction of pillars from vertical walls is necessary on account of a considerable taxonomic significance of the two types of structures whose formation depended after all on different types of the organization of coenosarc.

In individual genera, pillars and vertical walls display a considerable morphological variability. Thus, for instance, straight cylindrical pillars occur in *Simplexodictyon* BOGOYAVLENSKAYA or, *Stictostroma* PARKS, more complex being the pillars of *Anostylostroma* PARKS which branch in the upper part, while the most complex, tangled systems of pillars are recorded in some *Tienodictyon* YABE & SUGIYAMA. An increase in the morphological complexity of pillars in the last-named case was undoubtedly connected with an increasing degree of folding the ectoderm (Text-fig. 9A₁₋₃). In transverse sections, pillars are only rarely perfectly circular, the most frequent ones being irregularly oval or even subangular (Pl. XI, Figs. 3—4; Pl. XII, Fig. 1b). A similar morphological variability is displayed by vertical walls (Pl. XXIII, Fig. 3b; Pl. XXIV, Fig. 1b-c; Pl. XXVIII, Figs. 1c and 3; Pl. XXIX, Fig. 1a-b). Vertical walls form long meanders, usually connected with each other (Pl. IX, Figs. 1—2) but frequently they are interrupted and form short, vermicularly twisted segments (Pl. XXIV, Fig. 1b) which sometimes are so small that they almost equal pillars (Pl. IX, Fig. 5). Pillars and vertical walls concur in many species (e.g., *Trupetostroma gebum* (YAVORSKY), Pl. XXXI, Fig. 2b).

What is known as denticles and villi (GALLOWAY, 1957), occurring on the upper surface of dissepiments in *Rosenella* NICHOLSON, *Stratodictyon* WEBBY and some of *Cystostroma* GALLOWAY & ST. JEAN are primitive pillars. Extremely thick pillars occur in some representatives of *Labechia* EDWARDS & HAIM, *Actinostroma* NICHOLSON and *Syringostroma* NICHOLSON and similarly thick vertical walls are recorded in some of *Hermatostroma* NICHOLSON, *Trupetostroma* PARKS and *Parallelopora* BARGATZKY.

In the case of skeletons very irregular in structure (e.g., *Stromatopora*, s.s.), parts of skeleton displaying vertical orientation, that is, corresponding to vertical walls, are termed for the sake of distinction — coenostelae and corresponding horizontal segments — to distinguish from laminae — coenostromae (BOGOYAVLENSKAYA, 1968; NESTOR, 1966a).

Vertical elements may be limited to one interlamina space (Pl. VII, Fig. 8) or to a space delimited by two successive growth discontinuity surfaces (Pl. VII, Fig. 6). In many cases, pillars and vertical walls also display a continuous growth over long stretches of coenosteum (Pl. VIII, Fig. 3). A vertical superposition of pillars or vertical walls which occur regardless of the presence of distinct laminae or growth discontinuities (e.g., *Hermatostroma porosum* (LECOMPTE), Pl. VIII, Fig. 5; *Trupetostroma pingue* LECOMPTE, Pl. XXIX, Fig. 1a) is a frequent phenomenon. The superposition of skeletal elements of this type may be explained by a considerable stability of calcification centers, which do not change their position in ectoderm in particular growth cycles.

The ring pillars discussed above, which appear in some forms in addition to pillars and vertical walls, should also be included among vertical skeletal elements. The ring-pillars display the tendency to a vertical superposition in particular growth stages of the colony, forming thus systems of long tubes irregularly intersected by tabules and cyst plates. Such tubes, improperly called pillars, appear very early in the history of the stromatoporoids (e.g., the Ordovician *Cliefdenella etheridgei* WEBBY; WEBBY, 1969, Pl. 125, Figs. 1—5) providing evidence for a relatively rapid rate of the differentiation of coenosarc in some representatives of the Stromatoporoidea.

On the other hand, quite different is, in the present writer's opinion, the origin of short, vertical tubes occurring in some of *Cystostroma* GALLOWAY & ST. JEAN (e.g., *C. estoniense* NESTOR; NESTOR, 1964, Text-fig. 1) and *Aulacera* PLUMMER (e.g., *A. radiata* GALLOWAY & ST.

JEAN; GALLOWAY & ST. JEAN, 1961, Pl. 4, Fig. 1a). Similar, but considerably longer vertical tubes occur in *Stromatocerium* HALL (e.g., *S. rugosum* HALL; GALLOWAY & ST. JEAN, 1961, Pl. 8, Fig. 2a) and *Cystistroma* ETHERIDGE; (e.g., *C. donelli* ETHERIDGE; WEBBY, 1969, Pl. 123, Figs. 1—5). In transverse section, these tubes are usually irregularly polygonal, meandering or even bilaterally and unequally flattened in outline and only rarely circular. The skeletons of stromatoporoids with vertical tubes of this type are composed exclusively of thin dissepiments with a varying degree of convexity. In contrast to the systems of tubes composed of superposed ring-pillars, vertical tubes are always empty and without tabulae. Vertical tubes cannot be (as ring-pillars are) traces left by coenosarc strands, because of the lack of tabulae and of the irregularly polygonal, outline of the tubes in transverse section. Attention is attracted by the fact that in stromatoporoids, composed of strongly convex dissepiments, tubes are rarer and short, while in those, consisting of flat dissepiments, they elongate and become more frequent. Such an interdependence might be evidence that vertical tubes were modified dissepiments which served as the main supports for the coenosarc shifting upwards, that is, they played the role of pillars.

THE ORIGIN AND CHARACTER OF INTERSKELETAL SPACES

The interskeletal spaces were formed as a result of shifting the coenosarc by stages in the process of growth, and consequently a colony might more rapidly rise over the substratum with a simultaneously decreased secretion of skeletal substance. Despite reaching a considerable degree of porosity skeletal structures were bound to maintain an appropriate mechanical resistance.

The only stromatoporoids described so far whose coenosteum lacks interskeletal spaces are some species of *Lophiostroma* NICHOLSON. Their thin, platy skeletons consist of a great number of delicate lamellae undulated in more or less regular cones (e.g., *L. schmidti* NICHOLSON, Pl. VI, Fig. 6). The type of skeletal structure, recorded in *Lophiostroma*, is among the most primitive ones within the range of the Stromatoporoidea.

Chambers, galleries, coenotubes, autotubes and astrorhizal canals may be distinguished within interskeletal spaces.

The term „chamber“ was used by GALLOWAY & ST. JEAN (1957) to designate closed spaces, completely separated from each other which occur in skeletons of the forms composed almost entirely of dissepiments (= cyst plates in GALLOWAY & ST. JEAN, *l.c.*).

This structure can be observed in species of the genera *Cystostroma* GALLOWAY & ST. JEAN, *Labechia* EDWARDS & HAIM, *Aulacera* PLUMMER, *Pseudostylodictyon* OZAKI, *Cystistroma* ETHERIDGE and others. The formation of chambers was connected in these forms with blistering of the basal ectoderm prior to the secretion of skeletal substance, much the same as during the formation of dissepiments in the Recent Zoantharia (WELLS, 1969). Obviously, then, with such a manner of forming skeletal elements, soft parts of the colony never occurred in chambers. Identically, that is, by the blistering of basal ectoderm may, in the present writer's opinion, be explained the formation of spherical spaces which occur in the skeletons of some species of *Clathrodictyon* NICHOLSON & MURIE (e.g., *C. vesiculosum* NICHOLSON & MURIE), *Ferestromatopora* YAVORSKY (e.g. *F. dubia* (LECOMPTE) as well as in all species of *Parallelostroma* NESTOR (Pl. X, Figs. 1—2). Irregularly lenticular interskeletal spaces, sometimes intersected by thick, continuous pillars, characteristic of the representatives of *Pachystylostroma* NESTOR (Pl. VI, Figs. 1—3) and some of *Forolinia* NESTOR (e.g., *F. pachyphylla* (NICHOLSON), Pl. VI, Fig. 5), contained between skeletal elements and having the nature of flattened, thick dissepiments,

should be also considered as chambers. Likewise, the some category of interskeletal spaces includes irregular spaces closed by zig-zagging skeletal plates characteristic of the genera *Ecclimadictyon* NESTOR and *Plexodictyon* NESTOR (Pl. VII, Figs. 1, 2 and 5). In all these cases, the basal ectoderm formed a compact sheet resting on the surface of skeleton and devoid of folds or lobes.

The formation of interskeletal spaces of the nature of galleries, coeno- and autotubes is a symptom of the reorganization of coenosarc consisting in a change in the system of shifting soft parts of the colony in the process of growth. It is also a symptom of an increase in the degree of penetration of coenosarc in the skeleton.

The term „galleries“ was suggested by GALLOWAY & ST. JEAN (1957) for designating interlaminar spaces intersected by pillars. The present writer suggests to extend this term also over interlaminar spaces in which, meandering, shorter or longer vertical walls are developed instead of pillars. Coenotubes (NESTOR, 1966) is a name given to vermicular canals varying in thickness which penetrate the skeleton of some of the stromatoporoids, not displaying a definite spatial orientation and usually intersected by dissepiments (cf. *Stromatopora cooperi* LECOMPTE, Pl. XIX, Figs. 1 and 2). Autotubes are vertical canals in the form of tubes intersected by tabulae (cf. *Stromatopora divergens* GALLOWAY & ST. JEAN, Pl. XXI, Fig. 1 a-b). The coeno- and autotubes were described by some authors under a common name of „pseudozooidal“ or „zooidal tubes“ (NICHOLSON, 1886b; LECOMPTE, 1951, 1956; YAVORSKY, 1955; GALLOWAY, 1957).

In the present writer's opinion, galleries, which in vertical section, are rectangular (Pl. XXXVI, Figs. 2a and 3), subrectangular (Pl. XI, Fig. 4a) and irregular (Pl. X, Fig. 6) in outline indicate that the position of the coenosarc was limited, in all stages of growth to the most superficial zone of skeleton on which it rested in the form of a slightly folded, compact layer which only to a very small extent contacted galleries (Text-fig. 9A₁). A slight increase in the degree of folding the coenosarc, which led to the formation of a more complex system of vertical elements (branching of pillars and vertical walls), also increased slightly the extend to which the coenosarc was sunk in the skeleton and, consequently, galleries became more rounded (Text-fig. 9A₂₋₃). A considerable percentage of stromatoporoids have galleries which in vertical section are almost perfectly circular in outline (Pl. XIII, Figs. 1a, c and d; Pl. XIV, Figs. 1c and 3; Pl. XXIX, Fig. 1a). The formation of such galleries may be explained by the development of deep folds in the principal layer of coenosarc. These folds filled the forming galleries, took active part in the precipitation of the skeletal substance (Text-fig. 9B₁) and were resorbed at the moment when the formation of an overlaying lamina was started. The formation of coenosarc folds was a transitional stage leading to an increase in the degree of penetration of coenosarc deep into the skeleton, which resulted in the formation of coenosarc strands whose traces are now observed in the form of foramina and ring-pillars occurring in laminae (Text-fig. 9B₂₋₃).

Coeno- and autotubes are developed in many stromatoporoids of the reticular group (group „B“, Table 3), that is in the representatives of such genera as, *Stromatopora* GOLDFUSS *sensu* NESTOR, 1966a, *Actinostromella* NESTOR, *Syringostromella* NESTOR and *Parallelopore* BARGATZKY. The skeletons of these stromatoporoids usually have very poorly developed laminae or even are devoid of them.

Most likely, the formation of coenotubes was connected with a gradual modification of an initially flat coenosarc which consisted in the formation, in the basal zone, of a system of irregular folds or short lobes which were sunk in the skeleton deeper than the rest of coenosarc. In the process of growth of a colony, folds and lobes were shifted upwards and their basal ectoderm periodically secreted thin plates of the nature of dissepiments or tabulae. Coeno-

tubes formed in the case of the occurrence in coenosarc of irregular folds, which changed their configuration in particular growth stages. Consequently, vermicularly twisted canals, intersected by dissepiments (e. g. in *Stromatopora discoidea* (LONSDALE), cf. MORI, 1968, Pl. 19, Figs. 5 and 6) are observed in vertical sections. In tangential section through the colony, canals are also vermicular or, less frequently circular in outline.

Autotubes were probably formed in the case of the occurrence in coenosarc of folds and lobes which, in the process of growth of the colony, did not for a long time change their shape and position and, therefore, their traces observed in skeleton, are shaped like long, vertical tubes intersected by tabulae (e. g., *Actinostromella vaiverensis* NESTOR, cf. NESTOR, 1966, Pl. 15, Figs. 5 and 6).

In many species, coeno- and autotubes occur together within one coenosteum and interlace each other (e. g., *Syringostromella borealis* (NICHOLSON); cf. NESTOR, 1966, Pl. 17, Figs. 3 and 4). In younger stromatoporoids, the tendency is clearly visible to turn coeno- in autotubes (e. g., *Parallelopora* BARGATZKY, *Salairella* KHALFINA). This tendency expresses a morphological stabilization of the coenosarc.

In the stromatoporoids in which laminae become reduced and replaced by dissepiments (e. g., *Hermatostroma porosum* (LECOMPTE), Pl. XXXIV, Fig. 1 a-b), superposed galleries may be considered as interskeletal spaces of the nature of coeno- and autotubes.

The concurrence of coeno- and autotubes and their frequent turning into each other preclude the possibility of interpreting autotubes as zooidal tubes, as suggested by some of the authors (NESTOR, 1966, p. 43).

Astrorhizal canals, more or less densely occurring in many stromatoporoids, should be also considered as interskeletal spaces. The morphology and the way of distribution of astrorhizae in coenostea allow one to presume that they make up traces of foreign organisms associated at their life time with stromatoporoids. Such an interpretation of astrorhizae has been presented elsewhere (KAŻMIERCZAK, 1969) and confirmed by almost identical conclusions of JORDAN (1969) who, on the basis of a morphological similarity of astrorhizae to boring trace-fossil *Clionolithes radicans* CLARK, considered the astrorhizal structures as an effect of the activity of parasites. Despite the fact that the two authors' interpretations do not explain in detail the biological character of possible symbionts of stromatoporoids, they allow one, however, to exclude astrorhizae from diagnostic characters in taxonomic studies on this group. KAŻMIERCZAK (*l.c.*) and JORDAN (*l.c.*) also attracted attention to the fact that frequent changes in skeleton in the region of superposed astrorhizae, occurring in the form of vertical, thickened zones most frequently called „astrorhizal columns“ (GALLOWAY & ST. JEAN, 1957; GALLOWAY, 1957) were probably a result of a stromatoporoid's response to the infestation by a foreign organism. Astrorhizal columns are frequently visible on the surface of coenosteum as more or less prominent mamelons. Under such circumstances, the genera *Styloporella* and *Flexiostroma*, separated by KHALFINA (1956, 1960) mostly on the basis of astrorhizal columns, are thus rather problematic.

A manner of connecting astrorhizal canals with skeletal tissue allows one for certain conclusions concerning the position of coenosarc in relation to skeleton during the growth of the colony. Astrorhizal canals may either be freely connected with interskeletal spaces, or separated from them by the skeletal substance (*intergrated* and *separated* types of astrorhizae, KAŻMIERCZAK, 1969). Canals of the *intergrated* type are usually considerable thinner than those of the *separated* type. If we assume that the astrorhizal symbionts of stromatoporoids were connected with coenosarc of the host, the thickness of astrorhizal canals is an index of the thickness of coenosarc and the manner of connecting astrorhizae with skeleton determines

an extent to which coenosarc was sunk in skeleton. Thus, the presence of small astrorhizae of the *integrated* type might be an evidence of a thin layer coenosarc and its limited contact with skeleton. On the other hand, the presence of bigger astrorhizae of *separated* type might be indicative for a thicker layer of coenosarc to a considerable extent sunk in skeleton (KAŹMIER-CZAK, 1969). Dissepiments and tabulae, occurring in astrorhizal canals, were probably deposited by the basal zone of coenosarc which, during growth, of the colony, shifted upwards together with symbionts.

THE MICROSTRUCTURE OF THE STROMATOPOROIDEA

General remarks. — The microstructure of the Stromatoporoidea denotes a microscopic appearance of the skeletal tissue, which forms structural elements of coenosteum such as, laminae, pillars, vertical walls, dissepiments, cysts and tabulae. It follows from comparative studies on the stromatoporoids, ranging from the Middle Ordovician to the Upper Devonian, conducted by the present writer, that tracing an accurate boundary between their microstructural and structural elements is in many cases impossible, because of frequently observed turning into each other, depending on a stage in the morphological development. NICHOLSON (1886*b*), HEINRICH (1914), GALLOWAY (1957), ST. JEAN (1960, 1967), STEARN (1966*b*) and others found that, of all morphological elements of stromatoporoids, microstructure was to the smallest extent, subject to changes caused by environmental factors. Consequently they emphasized its fundamental importance to taxonomic studies, frequently neglected by many authors. The observation of microstructural changes, which occur in the process of evolution of the stromatoporoids, allows one to conclude on the morphogenesis and phylogeny of this group. The interest in microstructures of stromatoporoids dates from the time when the method of thin sections (ROSEN, 1867; NICHOLSON, 1886—1892) was introduced to the studies on these fossils. Up to now, a considerable amount of factual materials has been collected (PARKS, 1936; LECOMTE, 1951—1952; GALLOWAY, 1957; ST. JEAN, 1960, 1962, 1967; STEARN, 1966*b*; SLEUMER, 1969 and others). The interpretation of these materials is, however, controversial.

In contradistinction to descriptive classifications of the microstructures of the Stromatoporoidea, used so far, a genetic classification, here suggested by the writer, is based on the comparison with microstructures which occur in other, Recent and fossil, coelenterates, particularly the Anthozoa. This classification also takes into account changes undergone by some of the microstructures during the evolution of the Stromatoporoidea.

TYPES OF MICROSTRUCTURES

Three types of microstructure: 1. fibro-normal, 2. trabecular and 3. reticular occur in the Palaeozoic stromatoporoids. Each of the type of microstructure mentioned above may, in the case of a poor state of preservation of coenosteum, occur in a more or less changed, most frequently amorphous, form. Fibro-normal and trabecular microstructures are well known and described in both Recent and fossil Anthozoa, whereas the reticular type occurs in stromatoporoids only.

1. Fibro-normal microstructure

The term „fibro-normal“ is here adopted after KATO (1963, 1968) who used it for determining the microstructure of skeletal elements in the Anthozoa, formed as a result of a uni- or bilateral deposition of microcrystallites of CaCO₃ by a flat or slightly convex layer of a ske-

letotrophic ectoderm. The fibro-normal structure is primarily observed in horizontal skeletal elements of corals such as, dissepiments and tabulae (unilateral deposition) and sometimes in vertical ones such as, septa and columellae (bilateral deposition). A fibro-normal microstructure is marked by a „normal“, that is, perpendicular orientation of long axes of microcrystallites in relation to the secretive surface of ectoderm (BRYAN & HILL 1941; KATO, 1963; WAINWRIGHT, 1963). The last-named character, enables — in the case of fossil forms — a reconstruction of the situation of ectoderm in relation to skeleton (Text-fig. 17). A fibro-lamellar microstructure makes up a modification of a fibro-normal one (KATO, 1963, 1968). It is formed as a result of a multiple superposition of single layers composed of microcrystallites (multiple deposition) and hence parallel growth lines are observed in a microscopic image. KATO pointed out that a lamellar type of microstructure, distinguished by ALLOITEAU (1957) in Scleractinia was only a modification of the fibro-normal microstructure. Within the range of the Stromatoporoidea, the formation of the fibro-normal microstructure depends on the now observed character of the morphology of coenosteum resulting from a uni-, bi- and also multilateral deposition. In several genera the entire skeletal tissue is composed of the fibro-normal microstructure only.

Fibro-normal microstructure of skeleton is characteristic of the oldest known stromatoporoids, among them, the Middle and Upper Ordovician *Cystostroma* GALLOWAY & ST. JEAN, *Aulacera* PLUMMER, *Stromatocerium* HALL and *Pseudostylodictyon* OZAKI. The representatives of these genera have coenosteum composed of very thin calcareous plates more or less of the nature of convex cysts which display the tendency to form equally thin-walled vertical elements (*Pseudostylodictyon*), these plates are result of a local steep bend of cysts and are sometimes connected with each other to form long vertical tubes (*Stromatocerium*). A small thickness of the cysts (0.025 to 0.05 mm) might indicate that they were formed as an effect of a single deposition, after which the coenosarc was shifted to a higher level. A darker line, sometimes preserved at the base of cysts, is indicative of a unilateral deposition of skeletal substance, probably analogous to the formation of dissepiments in the Recent corals (WELLS, 1969). The microstructure of the genera mentioned above has so far been determined as „compact“ (GALLOWAY, 1957; GALLOWAY & ST. JEAN, 1961) or as a „dark line of specks“ (STEARNS, 1966b). In addition, some of the authors (e.g., NICHOLSON, 1886b; GALLOWAY & ST. JEAN, 1961; NESTOR, 1964) considered accumulations of mineral substance occurring on the bottom side of cysts and darker than calcite which filled skeleton, as original elements reinforcing delicate cysts. The writer agrees with STEARNS (1966b) who expressed the supposition that this substance was concentrated in the skeleton secondarily and resulted from the process of preservation.

The fibro-normal character of the skeletal tissue is considerably more distinct in the representatives of the genera which are undoubtedly related to those mentioned above and in which a conspicuous thickening of skeletal elements took place, along with a strong development of pillars. *Rosenella* NICHOLSON, *Pachystylstroma* NESTOR, *Labechia* M. EDWARDS & HAIM, as well as some of the species of *Forolinia* NESTOR (Pl. VI, Figs. 1—6; Text-fig. 12) may serve as examples in this respect. In the horizontal elements of these genera, there took place a superposition of several growth layers, much the same as in vertical ones, in which, following an upward bend of a fold of ectoderm, particular layers are, however, of the nature of cones superposed on each other (Pl. VI, Fig. 4). In the representatives of the genera mentioned above, as well as in *Lophiostroma* NICHOLSON (Pl. VI, Fig. 6), successive growth strands of the skeleton are much better visible than microcrystallites and the skeletal tissue is most frequently of the fibro-lamellar type.

A skeletal tissue with the fibro-normal microstructure forms coenostea of the representatives of a lineage which includes the following genera: *Clathrodictyon* NICHOLSON & MURIE, *Simplexodictyon* BOGOYAVLENSKAYA, *Anostylostroma* PARKS, *Tienodictyon* YABE & SUGIYAMA and *Pseudostromatoporella* n. gen. These forms are probably direct descendants of the Ordovician *Cystostroma* (cf. also GALLOWAY, 1957; NESTOR, 1966). Their relatively thick laminae were probably formed by a unilateral deposition of a flatly spread ectoderm, whereas pillars were formed punctually and multilaterally by a strongly conically bent folds of ectoderm (Text-fig. 9A₁₋₃) which caused microcrystallites to be oriented vertically and radially to the axis of pillars. Describing the microstructure of the genera *Clathrodictyon*, *Anostylostroma* and *Tienodictyon*, most authors determine it as „compact“ or „transversely fibrous, the latter type being considered by them as most likely to be secondary and developed in the process of recrystallization (STEARNS, 1966b; SLEUMER, 1969). In the writer's opinion, such a standpoint is erroneous, since the fibrosity of the skeletal tissue of the representatives of, for instance, *Anostylostroma* (ST. JEAN, 1960) or *Tienodictyon* (YABE & SUGIYAMA, 1941; STEARNS, 1966b, 1969) is a constant character independent of the type of deposit in which the specimens described, frequently coming from areas very distant geographically from each other were found.

The fibro-normal microstructure is observed in dissepiments and tabulae, commonly occurring in greater or smaller amounts in almost all genera of stromatoporoids regardless of the microstructural character of all other skeletal elements.

2. Trabecular microstructure

The trabecula is a name generally used to determine (BRYAN & HILL, 1941; WELLS, 1956; KATO, 1963) a cylindrical skeletal element which displays in transverse section radially arranged fibers (microcrystallites). In longitudinal, axial section, the arrangement of fibers is pinnate and they run from the middle of trabecula (calcification center) outwards, as well as upwards. The mechanism of forming trabeculae is in principle the same as in the case of skeletal elements with fibro-normal microstructure, with the only difference that, in trabeculae, the basal ectoderm, which deposits them, was folded differently, probably forming additional invaginations within the principal fold (KATO, 1963, Text-fig. 1₄, 13). In the Anthozoa, trabeculae are connected with each other, forming sets with different spatial arrangements and are components which form vertical elements of corallum, mostly septa.

In stromatoporoids, the trabecular microstructure appears later than the fibro-normal one and probably makes up, in all known cases of its occurrence, a final stage in a gradual transformation of the initial microreticular tissue. Much the same as in corals, the trabecular structure in stromatoporoids is displayed only by the vertical elements of skeleton, that is, pillars and vertical walls.

Pillars, composed of single trabeculae, occur in *Neosyringostroma logansportense* (GALLOWAY & ST. JEAN) (Pl. XXXII, Figs. 1a and 1c), in which laminae have preserved a conspicuously reticular microstructure. Pillars in some of the species of *Actinostroma* NICHOLSON in which darker spots of calcification centers are usually visible in tangential and, less frequently, vertical sections, are single trabeculae, usually poorly preserved. Pillars and vertical walls in *Pseudoactinodictyon juxi* E. FLÜGEL (Pl. XXIX, Figs. 2a and 2c), as well as less visible vertical walls in *?Pseudoactinodictyon dartingtonense* (CARTER) (Pl. XXVIII, Fig. 1a, b) are also composed of distinct trabeculae.

„Incomplete“ trabeculae are, in the writer's opinion, pinnate pillars in some of the species of *Vikingia* BOGOYAVLENSKAYA such as, *V. vikingi* (NESTOR), *V. tenue* (NESTOR), and *V. podolica*

BOGOYAVLENSKAYA (NESTOR, 1966; BOGOYAVLENSKAYA, 1969*a*). In pillars of these species, particular fibers are arranged more loosely than in typical trabeculae. Such a microstructure might represent a transitional stage in the process of „trabecularization“ of vertical elements of the *Pseudolabechia* YABE & SUGIYAMA — *Vikingia* lineage (Text-fig. 15*b-c*). Fibers, arranged in a similarly spray-like manner, but even more loosely than, in *Vikingia*, occur within the reticular skeletal tissue in the pillars of some of *Syringostroma* NICHOLSON (e.g., *S. densum* NICHOLSON). It is also in this case that trabeculae were formed by a further condensation of the microreticulum (Text-fig. 19*b-c*).

Among trabeculae which occur in the stromatoporoids, the same as in corals, there occur simple trabeculae with a single centrally situated calcification center (e.g., *Neosyringostroma* n. gen.), as well as compound trabeculae with several calcification centers (e.g., *Pseudoactinodictyon* and some of the species of *Actinostroma*). In the cases in which trabeculae form vertical walls, their arrangement may be similar to that of septa in corals (WELLS, 1956, KATO, 1963), that is in a uni- or multiserial manner.

Most authors call trabecular microstructure in stromatoporoids „feather structure“ or „water jet microstructure“ (STEARNS, 1966*b*) interpreting them as secondary ones, formed in the process of preservation. The „water jet microstructure“ have been described by STEARNS (1961, 1962) in *Taleastroma confertum* STEARNS, *Syringostroma bifurcum* STEARNS and *Trupestostroma pycnostylosum* STEARNS. In the present writer's opinion, the microstructure of pillars in these species is fit for assigning it to the trabecular group.

Hard problems in the identification of trabeculae are posed not only in the case of a poor state of preservation. In identifying trabeculae in thin sections, a considerable importance should be attached to the thickness of section and a proper orientation of a section through the trabecula. In longitudinal section of trabeculae which do not run exactly along the axis of trabecula, the pinnate arrangement of fibers is indistinct and usually even invisible at all (KATO, 1963, Text-fig. 2). The trabecular microstructure must not be confused with recrystallizing cleavage patterns, which, arranging linearly the calcite mosaic into interskeletal spaces, also intersect skeletal elements and form pinnate systems with straight strands intersecting each other, but in all cases considerably thicker than trabecular fibers.

The trabecular microstructure in the Anthozoa displays an evolutionary tendency to pass into a fibro-normal microstructure (KATO, 1963). No such tendency is recorded in the Paleozoic Stromatoporoidea. It is not unlikely, however, that the lack of trabeculae and a common occurrence of fibro-normal microstructure (STEINER, 1932, HUDSON, 1958), in the Mesozoic Sphaeractinoidea, related to the stromatoporoids, was connected with such an evolutionary process.

3. Reticular microstructure and its derivatives

Among the coelenterates, the reticular microstructure occurs only in the Paleozoic Stromatoporoidea. In contrast to the fibro-normal and trabecular microstructures, this type is not exactly a microstructure as understood literally but should be rather assigned to a mesostructural category. As shown below, the reticular microstructure originated from primary structural elements of skeleton. In the development of some of the stromatoporoidal lineages, a secondary transformation is observed of the reticular microstructure in structural elements of coenosteum. On the basis of the material studied which comes from the Ordovician, Silurian and Devonian of the U. S. S. R. and Devonian of the U. S. A. and Poland, as well as from the literature, the present writer attempts to reconstruct the history of the reticular microstructure and to discuss changes it underwent in various stromatoporoid lineages.

The appearance, in the Ordovician, of a group of stromatoporoids with coenostea composed of a very dense, uniform reticulum, that is, forms with a reticular structure, was a starting moment of the formation of reticular microstructure. Particular representatives of this group display a considerable differentiation in density and manner of a spatial arrangement of fibers of the reticulum. Such representatives of the genus *Plumatalinia* NESTOR: as *P. ferax* NESTOR 1964 from the Upper Ordovician (Pirgu horizon) of Estonia and *P. densa* MORI, 1968 from the Wenlockian (Visby Beds) of the Island of Gotland, whose skeletons are formed by an almost homogenous, randomly arranged reticulum, may here be named as examples. A similar structure of skeleton, but with the tendency to a horizontal arrangement of the fibers, is displayed by specimens of „*Clathrodictyon*“ *delicatulum* NESTOR, known from the Upper Ordovician through Middle Silurian of Estonia and the Island of Gotland (NESTOR, 1964, Pl. 18, Fig. 4; Pl. 21, Fig. 6; MORI, 1968, Pl. 5, Figs. 1 and 2). The fine-reticular structure of skeleton, tending arrange reticular fibers into distinct vertical and horizontal elements, is also recorded in the forms jointly assigned to the genus *Densastroma* E. FLÜGEL and abounding in the Lower and Middle Silurian of Estonia, Podolia and the Island of Gotland (YAVORSKY, 1929; RIABININ, 1951, 1953; NESTOR, 1966; MORI, 1968). It should be emphasized that the oldest of the forms assigned to *Densastroma* (e.g., „*Densastroma*“ cf. *pexisum* (YAVORSKY), cf. RIABININ, 1953, Pl. 1, Fig. 1) and have a decidedly denser and more irregular skeletal reticulum than that in later forms. Stromatoporoids with fine-reticular skeletons probably appeared considerably earlier than the form described so far. A considerable similarity to the fine-reticular coenostea of the stromatoporoids mentioned above which, however, have still finer and more densely distributed fibers, is displayed by the Ordovician problematic fossils, mostly described as algal structures (e.g., *Cryptozoon* HALL, cf. JOHNSON & HØEG, 1961, Pl. 31, Fig. 1; BIRKHEAD, 1967, Pl. 5, Figs. 1—4) and frequently occurring along with the stromatoporoids of the group Labechiidae.

Skeletons with the fine-reticular structure were probably secreted, the same as in the group of stromatoporoids with lamellar skeletal elements (e.g. *Cystostroma* GALLOWAY & ST. JEAN, *Lophiostroma* NICHOLSON), by a layer of basal ectoderm. The only difference was that these skeletons were deposited not in the form of compact aggregates of microcrystallites, but as punctually secreted fibers with a fairly irregular spatial orientation.

The reticular structures became microstructural elements of skeleton at the moment of either the beginning of a zonal differentiation of an initially uniform reticulum, or of the formation of interskeletal spaces (e.g., galleries), that is, division of the reticulum into systems of laminae and pillars. This process was undoubtedly connected with the reorganization of coenosarc, which led to an increase in the degree of its folding and, at the same time, with appropriate modifications in the calicoblastic zone of ectoderm. The formation of galleries, in the dense reticular skeletal tissue, simultaneously included forms which displayed a considerable differentiation in the density and degree of arrangement of the reticulum. This is confirmed by a variable character of the reticular microstructure observed in skeletal elements, which surround galleries in the oldest representatives of this microstructural group. In the oldest representatives of the genus *Stromatopora* GOLDFUSS (e.g., *S. impexa* NESTOR, *S. discoidea* (LONSDALE), the microreticulum occurring in skeletal elements is very dense and irregular, while in the concurrent *Parallelostroma* NESTOR (e.g., *P. typicum* (ROSEN), *P. tuberculatum* (YAVORSKY), *P. malinovzyensis* (RIABININ), it is considerably looser and arranged in a fairly, regular lattice (Pl. X, Figs. 1 and 2). The skeletons of the representatives of *Actinostromella* BOEHNKE (e.g. *A. vaiverensis* NESTOR, cf. Pl. VIII, Fig. 1) and of the closely

related genus *Syringostromella* NESTOR (e.g., *S. borealis* (NICHOLSON), Pl. VIII, Fig. 2) are composed of a loose and irregular microreticulum.

PARKS (1936) found that the reticular microstructure is similar to the reticular structure occurring in *Actinostroma* NICHOLSON but expressed on a considerably smaller scale. His finding is confirmed by the fact that *Actinostroma* was evolved from fine-reticular *Densastroma* as a result of the reduction and thickening of the fibers of primary dense reticulum (Pl. XLI, Figs. 1—6).

The reticular microstructure also becomes gradually modified with the progressing development of the structural elements of coenosteum. These modifications vary in character depending on the evolutionary trends in the morphology of structural elements of skeletons which mostly tend to develop pillars and vertical walls and reduce laminae (Table 3, group „B“).

The following two processes may be distinguished in the course of changes undergone by the microreticulum:

a) a condensation of fibers leading to a partial or complete homogenization and atrophy of microreticulum and b) a reduction of fibers resulting in a strong loosening of microreticulum with a simultaneous, considerable swelling of the rest of fibers.

a) Examples of the condensation and homogenization of microreticulum

The progressive condensation of microreticulum in skeletal elements is clearly observable in a lineage which leads from the Silurian representatives of *Actinostromella* BOEHNKE and *Syringostromella* NESTOR, through the Lower and Middle Devonian *Parallelopora* BARGATZKY and some of the *Stromatopora* GOLDFUSS, up to the Middle and Upper Devonian *Syringostroma* NICHOLSON and *Neosyringostroma* n. gen. (Text-fig. 18; Pl. VIII, Figs. 1—3). The representatives of these genera are marked by a strong development of vertical elements of the skeleton with poorly developed, or frequently even reduced laminae. Of particular interest is the transformation of a very strongly condensed microreticulum in the pillars of some of the *Syringostroma* (e.g., *S. densum* NICHOLSON) into trabeculae which occur in *Neosyringostroma* (e.g., *N. logansportense* GALLOWAY & ST. JEAN). The process of „trabecularization“ of the condensed microreticulum was usually preceded by the appearance, within microreticulum, of thicker, fibers arranged in a spraylike manner which should be interpreted as incipiences of a pinnate system of later microcrystallites in trabeculae (Text-fig. 12e). Usually, after microreticula having been transformed, in pillars, trabeculae, laminae continued to preserve their reticular microstructure (Text-fig. 19c).

A conspicuously progressing condensation of microreticulum, leading to its strong homogenization, also occurs in the development of *Stromatopora* (Text-fig. 10B₁₋₃). The Silurian species of this genus differ from the Middle and Upper Devonian ones in more loosely distributed fibres of microreticulum which, in the last-named, is usually so strongly condensed that its meshes in the form of small, round or subangular light-colored spots only (= „maculae with clear centers“ in GALLOWAY, 1957; ST. JEAN, 1967; „cellules“ in LECOMPTE, 1951—1952, 1956; STEARN, 1966b) are visible within a slightly darker skeletal substance (Pl. IX, Fig. 1; Pl. XX, Fig. 1d). In other species of *Stromatopora*, microreticular fibers fuse together to form a compact mass of skeletal substance, in which only darker dots of calcification centers of particular fibers (= „dark dots“ in NICHOLSON, 1886; „maculae without clear centers“ in GALLOWAY, 1957; ST. JEAN, 1967; „melanospheres“ in STEARN, 1965b), giving a granular consistence to the skeletal tissue, occur as a remains of an original reticulum.

An advanced stage of homogenization of the microreticular tissue is recorded in the representatives of the genus *Taleastroma* GALLOWAY, which is probably a direct descendent

of *Stromatopora*. As a result of a continued homogenization of the skeleton and reduction in the number of calcification centers, progressing from the central part of skeletal elements, the traces of microreticulum are preserved in *Taleastroma* only in the peripheral zone of laminae and pillars, as well as, sometimes, in the form of small vacuoles irregularly scattered within the homogenous skeletal substance (Text-fig. 10B₃).

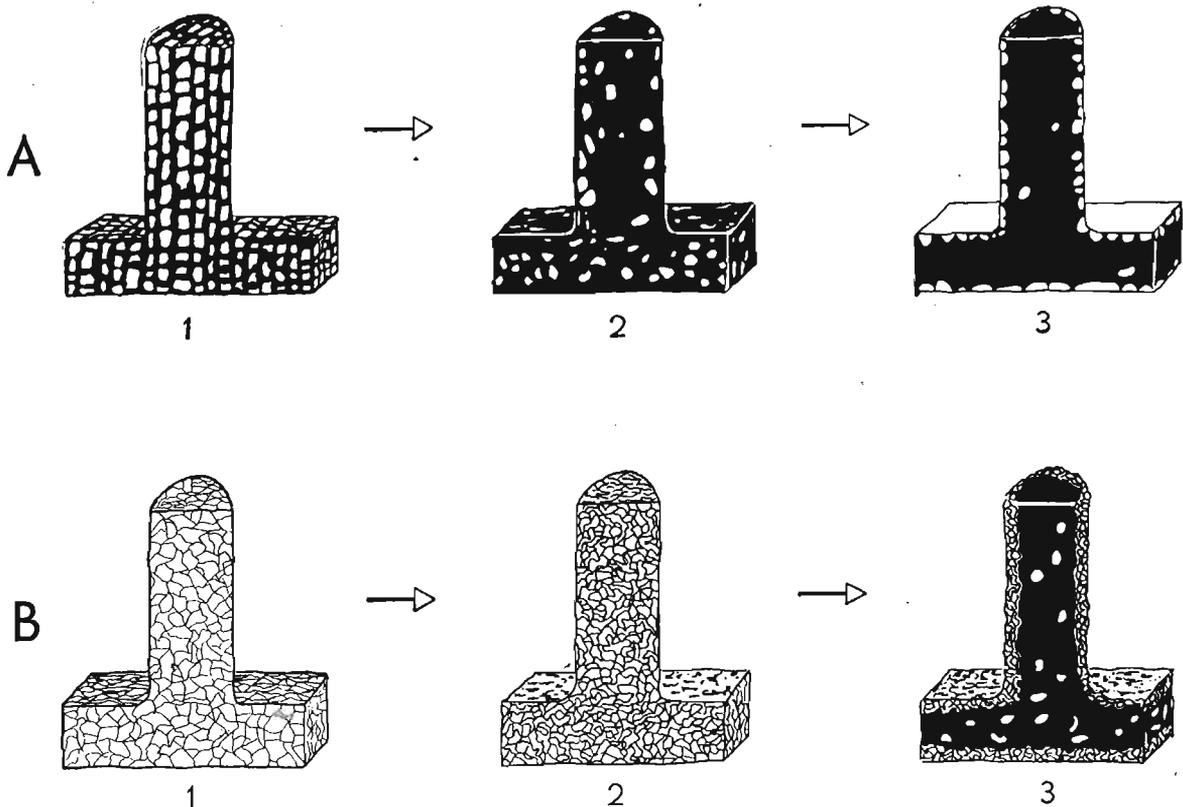


Fig. 10

Exemplary condensation and homogenization of microreticular tissue in structural elements of the stromatoporoids of morphological group „B“: A — a lineage (see Lineage VI, p. 65) represented by the genera: 1 *Parallelopora* BARGATZKY, 2 *Trupetostroma* PARKS, 3 *Hermatostroma* NICHOLSON; B — a lineage (see Lineage VII, p. 67) represented by the genera: 1-2 *Stromatopora* GOLDFUSS, 3 *Taleastroma* GALLOWAY

The thickening and condensation of microreticular fibers in forms, having their skeletal tissue of the type of *Parallelostroma* BARGATZKY, probably resulted in the formation of the genus *Trupetostroma* PARKS with an almost completely homogenous microstructure and with the remains of microreticulum in the form of vacuoles, mostly concentrated in the peripheral zone of skeletal elements (Pl. VIII, Fig. 5; Text-fig. 10A₂). As a result of further homogenization, *Trupetostroma* probably evolved into *Hermatostroma* NICHOLSON having vestigially preserved peripheral vacuoles or vesicles covered with thin membranes (Pl. VIII, Fig. 6; Text-fig. 10A₃).

A considerably condensed microreticular tissue occurs in the representatives of *Gerrostroma* YAVORSKY, *Stictostroma* PARKS and *Stromatoporella* NICHOLSON (Pl. XI, Figs. 2—4; Pl. XVI, Figs. 1—3; Pl. XVIII, Fig. 1). Since skeletal elements, in particular laminae are in these forms relatively thin, the reticular character of the microstructure is frequently invisible in the case of a strong recrystallization. Likewise, these forms may be so strongly homogenized

that only dark spots of calcification centers, more numerous in laminae and less in pillars and vertical walls (Pl. XVII, Figs. 1c-e), are visible within a homogenous skeletal substance. In thin laminae of some of the species of *Stictostroma* (e.g., *S. mamilliferum* GALLOWAY & ST. JEAN, cf. STEARN, 1966b, Pl. 16, Fig. 4) or *Gerronostroma* (e.g., *G. elegans* YAVORSKY, cf. STEARN, 1966b, Pl. 16, Fig. 6), an only single row of microreticular meshes is visible in vertical section. The microstructure of this type has mostly been termed as „ordinicellular tissue“ (STEARNS, 1966b; SLEUMER, 1969). On the other hand, in some of the *Stromatoporella* (e.g., *S. tyrganensis* YAVORSKY, cf. Pl. XI, Fig. 2; *S. granulata* NICHOLSON, cf. STEARN 1966b, Pl. 15, Figs. 6 and 8; SLEUMER, 1968, Fig. 15), the condensed microstructure is multi-lamellar with meshes arranged in horizontal rows („microlaminate tissue“ in SLEUMER, 1969). In some of the *Stictostroma* and *Stromatoporella*, having laminae composed of a single layer of a condensed microreticulum with thickened and vertically arranged fibers, laminae in vertical section give an impression of being transversely porous (GALLOWAY, 1957; ST. JEAN, 1960; STEARN, 1966b). These „pores“ have also been termed „transverse microtubules“ (ST. JEAN, 1960, 1962).

The condensation and subsequently homogenization of the microreticular tissue was undoubtedly connected with a change in the mechanism of calcification, i.e., reorganization of the calcicoblastic zone of basal ectoderm. This process resulted in a gradual decrease in the number of calcification centers with a simultaneous considerable increase in the amount of mineral substance deposited around each of the centers. This might supply evidence that the secretive yield of ectoderm did not decreased at all, but, on the contrary, was increased. Consequently, many of the Middle and Upper Devonian stromatoporoids, whose ancestors had microreticular, frequently very irregular, skeletal elements, display pillars with a single calcification center, which, in the process of the growth of coenosteum, may continue over very long stretches. Thus, skeletons regular structurally (long, continuous and or superposed pillars and vertical walls) are formed in this way.

STEARNS (1966b) believed that a condensed microreticular tissue (named by him partially „cellular“ and partially „melanospheric“) was formed as a result of secondary recrystallization processes, which led to the obliteration on the boundaries between cellules and to the formation of dark-coloured melanospheres. These melanospheres, in his opinion, were formed in the process of translocating the skeletal substance rather unclearly presented by him. A standpoint much closer to the present writer's views, is taken by ST. JEAN (1967, p. 442), who, despite being inclined to consider the condensed microreticulate tissue (named by him „maculate“) as syn- or postdiagenetic one, does not preclude the possibility that a reticulate and maculate tissue are closely related biologically and, consequently, that the maculate tissue is evolutionally derived from the reticulate one.

b) Examples of the reduction of microreticulum

In some of the lineages of the Stromatoporoidea, a distinct tendency is observed to a gradual reduction of fibers of the primary microreticulum up to the formation of loose but thickened skeletal elements. The same as in the case of condensation and homogenization, the aim of reduction of a microreticulum was, in the present writer's opinion, a decrease in the number of calcification centers with a simultaneous thickening of fibers which remained in the skeleton.

The reduction primarily included the microreticulum which formed vertical elements of skeleton, that is, pillars, vertical walls and, to a smaller extent, laminae. Some of the species of *Actinostroma* NICHOLSON such as, *A. verrucosum* (GOLDFUSS), *A. mamontovi* YAVORSKY (Pl. IX, Fig. 6; Pl. XI, Fig. 5) or *A. stellulatum* NICHOLSON (Pl. XXXVII, Fig. 3a-b), which in the present writer's opinion evolved from forms related to the Silurian *Parallelostroma* NESTOR

by a progressing reduction in the amount of fibers, at first including only pillars and subsequently also laminae, may serve as examples of such a selective reduction in the microreticular tissue. This lineage terminates in *A. stellulatum* in which pillars are already composed of a single, strongly thickened fiber with one or few calcification centers and in which laminae, intersecting pillars, are formed by a very thin layer of a loose reticular tissue (Text-fig. 16 B_{1-3}).

The tendency to loosening the microreticulum is also marked in some of the species of the genus *Ferestromatopora* YAVORSKY in which, in addition to species with thick skeletal elements formed of a relatively dense microreticulum (e. g., *F. dubia* (LECOMPTE), cf. Pl. XXVII, Fig. 1 *a-c*), there also occur species with coenostea consisting of thinner elements with a very loose microreticulum (e. g., *F. cellulosa* (LECOMPTE), cf. Pl. XXV, Fig. 1 *a-b*; *F. parksi* STEARN, cf. Pl. XXIII, Fig. 3 *a*; *F. uchtensis* (RIABININ), cf. Pl. XXIV, Fig. 1 *a-c*). The last-named species might, through a continued reduction of microreticular fibers, probably evolve into forms with vertical walls composed of single fibers and very thin laminae in the form of a loosened reticulum. These forms are assigned to the genus *Atelodictyon* LECOMPTE (e. g., *A. trautscholdi* (RIABININ), *A. pseudocolumnare* (RIABININ), *A. fallax* LECOMPTE, cf. Pl. X, Fig. 6; Pl. XXXVI, Figs. 1 and 2).

A partly reduced microreticular tissue is also observed in many species whose generic assignment has not so far been settled to any degree of certainty. These are, for instance, „*Trupetostroma*“ *spatiosum* YAVORSKY (Pl. IX, Fig. 5; Pl. X, Fig. 4) and „*Stromatopora*“ *pellucida* YAVORSKY (Pl. XI, Fig. 1).

The reduction of microreticular tissue was now and then started with the formation, in the axis of vertical element of the skeleton, of conspicuously thicker single fibers which subsequently became thicker and a fine reticulum, surrounding them, gradually disappeared (e. g., „*Hermatostroma episcopale*“ var. *talovens* YAVORSKY, cf. Pl. X, Fig. 3).

INTERPRETATION OF THE MORPHOGENESIS OF THE STROMATOPOROIDEA

General remarks. — The development of skeleton in the stromatoporoids was primarily related with obtaining a strong adherence of the colony to the substratum which assured protection against strong currents and waving. At the same time, the formation of skeleton enabled uplift of the colony above the bottom and, consequently, assured better respiration and feeding conditions, as well as a protection against covering by deposit under the conditions of a rapid sedimentation. On the other hand, the morphology of skeletons does not reveal the possibility that individuals of the colony might find shelter in them. Hence the conclusion that the protective function of stromatoporoid skeletons was, in contradistinction to the skeletons of other invertebrates, rather insignificant. The development of their own substrata by the growing colonies of the stromatoporoids made them independent to a considerable extent of the character of the bottom and, at the same time, gave the possibility of a conspicuous increase in the size of colonies and of settling the zones of basin marked by stronger hydrodynamic activity.

Determining the character of the oldest, ancestral skeletal structure and first trends in their morphological differentiation is a fundamental problem in the interpretation of the morphogenesis of stromatoporoids. The development of the first skeletons in stromatoporoids was bound to be preceded by obtaining the capability of an extracellular secretion of a calcifiable organic matrix whose presence was an indispensable condition of the initiation of all biomineralization processes (GLIMCHER 1960; MOSS, 1968; NEEDHAM, 1964). The organic matrix

consists of an organized phase, mostly in the form of a system of fibers and an unorganized phase, which usually makes up a viscous, highly hydrated, polyanionic colloid (Moss, 1964). A final form of the calcified tissue is always determined by the character of the organic matrix, in which the ratio of the two phases mentioned above is usually variable. It follows from histochemical studies, conducted on Recent Scleractinia (WAINWRIGHT, 1963), that the spatial orientation of chitinous fibers, making up a fundamental component of the organic matrix in *Pocillopora damicornis* (L.), exerts a decisive influence on the spatial orientation, size and density of arrangement of the aragonite microcrystallites precipitated.

As results from the observations of the oldest stromatoporoids, the first stages of the process of skeletogenesis were not uniform in character, most likely due to a different organization of the calcifiable matrix. In connection with a variable composition of the organic matrix, secreted by the basal ectoderm of primitive, naked colonies, there were formed the first skeletal tissues in the stromatoporoids which were marked by the following two, radically different, ancestral structures:

A) A primary, compact, calcareous basal plate composed of microcrystallites arranged perpendicularly to the skeletotrophic surface of ectoderm;

B) A primary spongy plate, composed of a very dense reticulum (microreticulum) of calcareous fibers, usually without definite spatial orientation.

Each of the structural types of primary basal plates may be considered as an ancestor of two separate morphological groups of the Stromatoporoidea, provisionally termed by the writer as „A“ and „B“ (Table 3) and whose morphological differentiation took place independently of each other. The presence of the two distinct morphological groups in the stromatoporoidea is, at the same time, evidence of the diphyletic character of these organisms. However, as a result of generally identical evolutionary trends observed in the development of both groups, the phenomena of both hetero- and isochronous, morphological parallelisms are relatively frequent.

The interpretation of the main evolutionary trends in both morphological groups (Table 3), has been based on the observation of structural and microstructural changes in the skeletons of stromatoporoids ranging Middle Ordovician — Lower Carboniferous and examined from the viewpoint of the functionality of the coenosarc-skeleton system. The following elementary processes are more or less strongly marked in the evolution of the stromatoporoids.

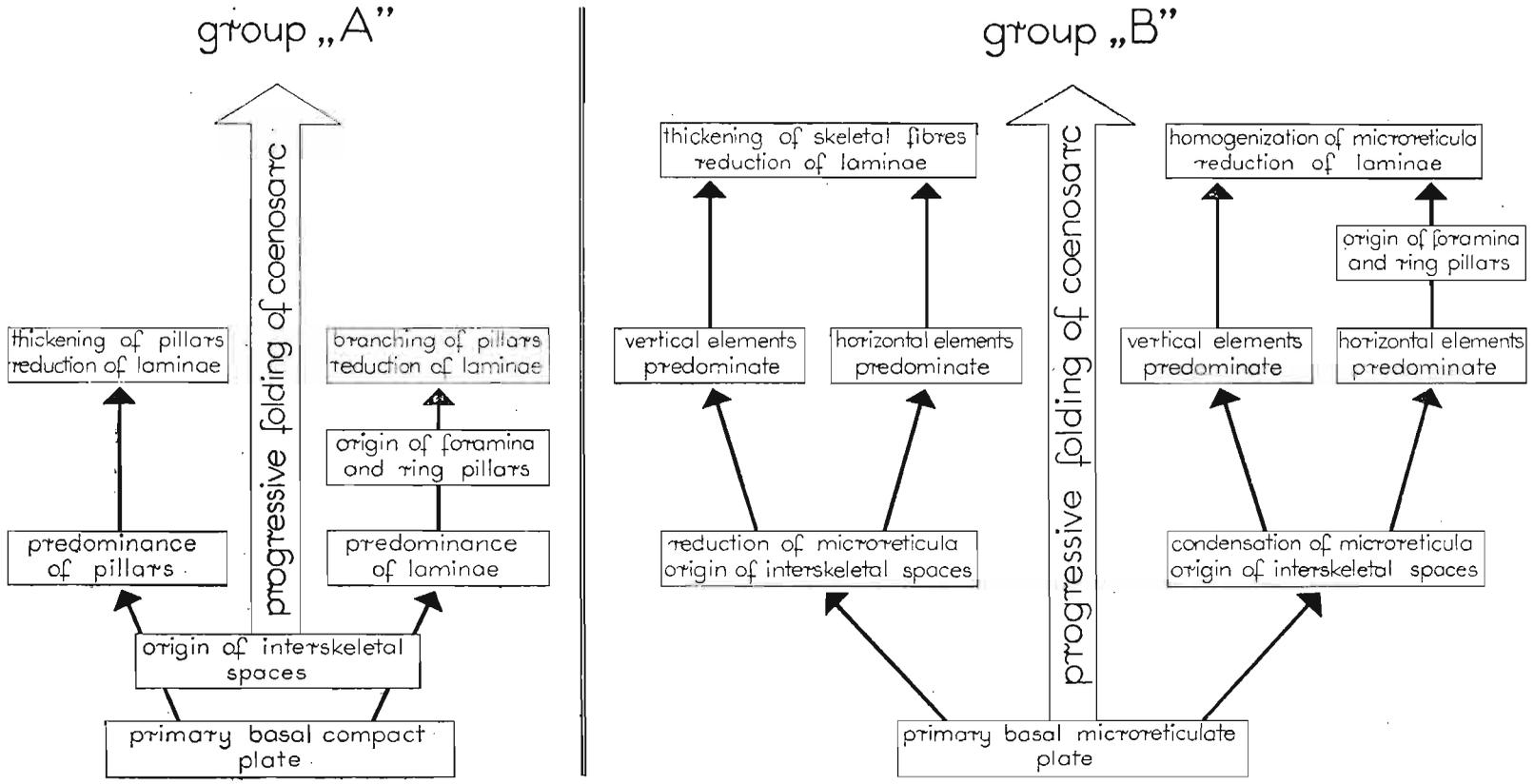
1) A progressive differentiation of coenosarc, taking place through an increase in the degree of its folding and leading to an increase in its volume and extent of its penetration in the skeleton. As a result of this process, a permanent tendency is observed in skeletons to develop vertical elements and reduce laminae, as well as to increase the interskeletal spaces occupied by coenosarc.

2) An oligomerization of calcification centers with a simultaneous increase in their secretive efficiency. The thickening of vertical elements in many skeletons and transformation of microreticular skeletons (reduction, condensation and homogenization) were the effect of this process.

3) A growth stabilization of the skeletotrophic zone of coenosarc, which resulted in the formation of permanent calcification centers or zones. As an effect of this process, a distinct tendency is observed in many stromatoporoids younger geologically to a regular geometric spatial orientation of vertical skeletal elements.

4) An increase in growth periodicity, expressed in a gradual development of regular growth cycles marked in skeletons by the presence of laminae and growth discontinuity surfaces (growth inhibitions and interruptions).

Table 3
 INTERPRETATION OF THE MAIN MORPHOGENETIC TRENDS IN STROMATOPOROIDEA



MORPHOLOGICAL GROUP „A“

Examples of lineages

Lineage I. — A lineage represented by the genera *Lophiostroma* NICHOLSON, *Dermatostroma* PARKS (in part) and *Pachystylostroma* NESTOR. A gradual development of pillars and increase in interskeletal spaces in originally compact, platelike basal skeletons (Text-fig. 11a-c) are characteristic features of the representatives of this lineage.

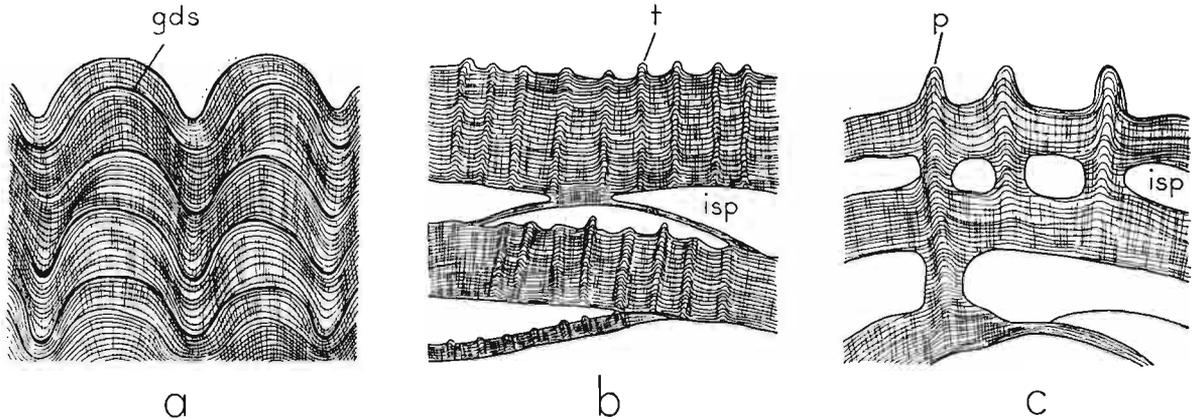


Fig. 11

Morphological group „A“. Forms representing lineage I: *a* *Lophiostroma* NICHOLSON, *b* *Pachystylostroma* NESTOR (forms of *P. rosensteinae* NESTOR type), *c* *Pachystylostroma* NESTOR (forms of *P. opiparum* NESTOR type); all in vertical section; not to scale. *gds* growth discontinuity surfaces, *isp* interskeletal spaces (chambers), *p* pillars, *t* tubercles

The representatives of *Lophiostroma*, known since the Middle Ordovician and being among the oldest stromatoporoids described thus far have the most primitive skeletons. Their coenosteum is composed of a thin plate, consisting of many fibro-normal lamellae twisted into fairly regular tubercles and superposed very densely without any interskeletal spaces (Pl. VI, Fig. 6; Text-fig. 11a). Dark-coloured growth inhibition surfaces are conspicuously marked in vertical sections. With a very primitive structure of its coenosteum, *Lophiostroma* is, at the same time, a conservative genus whose species, almost not differing from each other, appear sporadically as late as the Upper Devonian (YAVORSKY, 1957).

A primitive, thin, platelike skeleton, similar to that of *Lophiostroma*, is a characteristic feature of the Upper Ordovician stromatoporoids, assigned with a reservation by GALLOWAY & ST. JEAN (1961) to the genus *Dermatostroma* PARKS. These are: ?*D. corrugatum* (FOERSTE), ?*D. glyptum* (FOERSTE) and ?*D. escanabense* GALLOWAY & EHLERS. In contrast to *Lophiostroma*, skeletons of these species are, however, composed not of laminae, but of closely distributed, thick, vertical, trabeculae whose terminations are visible on the surface of coenosteum in the form of papillae. The thickness of skeletons in these species is small and does not exceed 1 cm.

Compact skeletons of *Lophiostroma* and *Dermatostroma* were undoubtedly formed as a result of the secretion of CaCO₃ by the entire surface of a slightly differentiated basal layer of coenosarc, which, despite its considerable secretive activity, was incapable of forming high skeletons. A slightly folded basal ectoderm, shifting upwards in the process of growth on the basis of successively deposited fine layers of skeleton, formed a calcification system which was not very effective for a rapid rate of the colony's growth. The first tendency to the modi-

fication of the manner of growth through passing from a continuous to a intermittent shifting of the coenosarc is observed in ?*Dermatostroma glyptum* whose skeleton is composed from two layer with irregular interskeletal spaces occurring between them (GALLOWAY & ST. JEAN, 1961, Pl. 10, Fig. 4a).

At the turn of the Ordovician to the Silurian, forms, assigned to the genus *Pachystylostroma*, were separated, from compact, platelike skeletons by a gradual formation of pillars. Since the upward shifting of coenosarc was much more effective with the use of pillars as a base for it, *Pachystylostroma* developed relatively large interskeletal spaces in the form of lenticular chambers. The development of pillars, was initiated in *Pachystylostroma* by the formation of fine denticles on the surface of basal plates. These denticles correspond to the first stages of the folding of a flat coenosarc (e.g., the lowermost Silurian *P. rosensteinae* NESTOR, cf. Pl. VI, Fig. 2), and gave the possibility of a much more rapid growth of skeleton and hence the coenostea of *Pachystylostroma* reach much larger dimensions. The denticles became subsequently longer and thicker with a simultaneous reduction in the thickness of horizontal plates (e.g., *P. opiparum* NESTOR, cf. Pl. VI, Fig. 3). In some of the younger species of *Pachystylostroma*, pillars are continuous over relatively long stretches of skeleton and slightly convex basal plates turn into regular laminae. In some others forms basal plates are to a considerable extent replaced by dissepiments and very strongly developed vertical elements take the form of irregular, thick columns (e.g., *P. exile* NESTOR, cf. Pl. VI, Fig. 1). Since in the Wenlockian, in addition to species with very strongly developed pillars or columns, there also occur ones with only small denticles on the surface of slightly convex, thick basal plates (e.g., *P. visbyense* MORI, cf. MORI, 1968, Pl. 1, Fig. 4), the rate of the development of pillars was not uniform in all *Pachystylostroma*.

Lineage II. — This lineage includes genera having massive skeletons as, *Cystostroma* GALLOWAY & ST. JEAN, *Rosenella* NICHOLSON, *Rosenellinella* YAVORSKY, *Stratodictyon* WEBBY, *Labechia* M. EDWARDS & HAIM, *Labechiella* YABE & SUGIYAMA and *Stylostroma* GORSKY (= *Pennatostroma* DONG), as well as genera with cylindrical skeletons as, *Sinodictyon* YABE & SUGIYAMA and *Cryptophragmus* RAYMOND. The representatives of these genera, occurring from the Middle Ordovician to the Early Carboniferous make up a continuous lineage marked primarily by progressively developing vertical elements of skeleton (Text-fig. 12A₁₋₃).

Cystostroma, numerously represented in the Middle and Upper Ordovician of North America (GALLOWAY & ST. JEAN, 1961), Estonia (NESTOR, 1964) and Australia (WEBBY, 1969) were undoubtedly starting forms for the lineage under study. Skeletons of *Cystostroma* are composed of more or less convex dissepiments which served as a base of coenosarc on which it was shifted upwards in the process of growth and which, may consequently be considered as serially superposed basal plates. The tendency to increase and flatten the strongly convex dissepiments and to form on their surface short processes known as villae, which may be treated as incipient pillars, relatively early appeared in some of *Cystostroma* (e.g., *C. simplex* GALLOWAY & ST. JEAN, cf. GALLOWAY & ST. JEAN, 1961, Pl. 1, Fig. 3a). Shifting coenosarc during its growth was probably easier with villae used as bases. The process of the formation of pillars, started by the appearance of villae, is already much more strongly emphasized in species of the Middle Ordovician *Sinodictyon*, Upper Ordovician and Lower Silurian *Rosenella* and Lower Silurian *Rosenellinella*, in which conspicuous denticles (e.g., *R. woyuensis* OZAKI, cf. WEBBY, 1969, Pl. 120, Fig. 5) or pillars (e.g., *R. tuberculata* (RIABININ), cf. NESTOR, 1964, Pl. 11, Fig. 3; Text-fig. 12) occur on the surface of strongly flattened and sometimes thickened dissepiments. A similarly strong development of pillars, but with delicate dissepiments preserved, is displayed by the representatives of the genus *Stratodictyon*, described from the Ordovician (?Caradoc)

of Australia (*S. ozakii* WEBBY and *S. columnare* WEBBY, cf. WEBBY, 1969, Pl. 119, Figs. 4—6). Representatives of *Labechia*, having massive coenostea and related *Cryptophragmus* with a cylindrical coenosteum, having a large axial canal intersected by dissepiments (cf. YABE & SUGIYAMA, 1930; GALLOWAY & ST. JEAN, 1961; WEBBY, 1969 and others) are a derivative of the forms similar in structure to *Stratodictyon* and evolved as a result of a very strong development of long, thick pillars with the dissepiments preserved. The type of skeleton structure, reached by *Labechia*, is indicative of a considerable degree of conservatism, as they occur

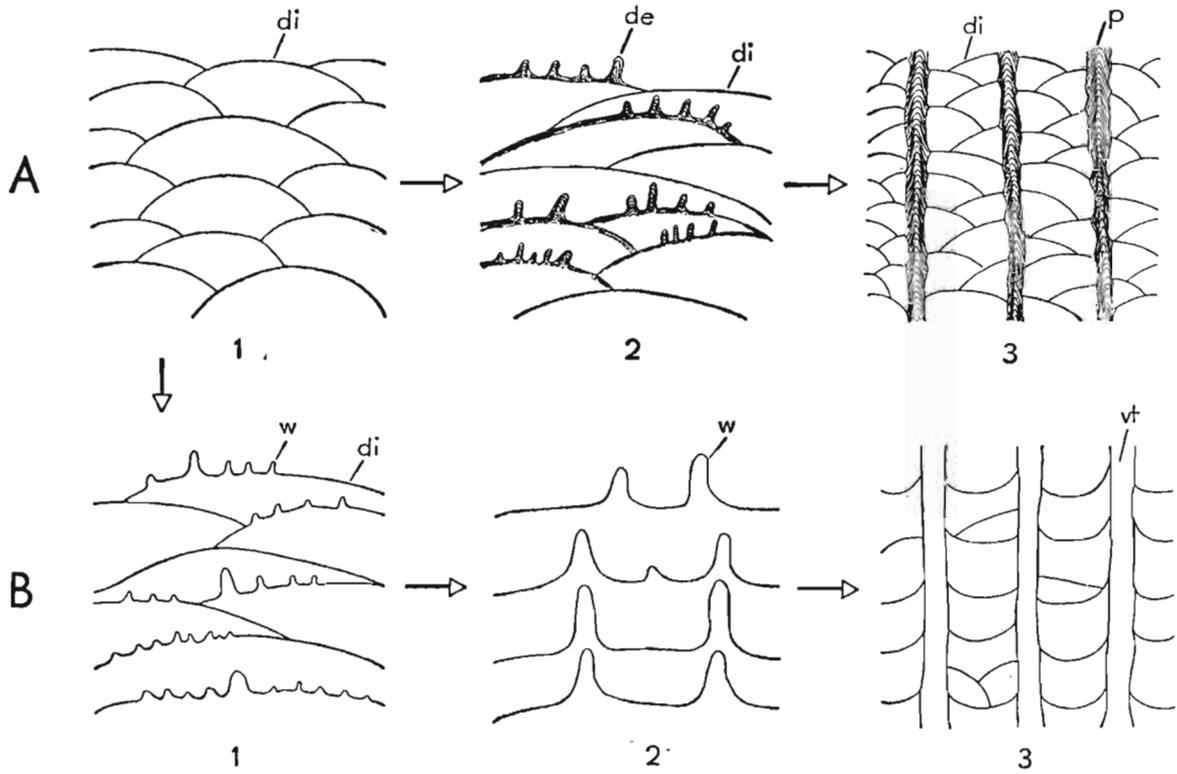


Fig. 12

Morphological group „A“. A — forms representing Lineage II (see p. 51): 1 *Cystostroma* GALLOWAY & ST. JEAN, 2 *Rosenella* NICHOLSON, 3 *Labechia* M. EDWARDS & HAIME; B — forms representing Lineage III (see p. 53): 1 *Pseudostylodictyon* OZAKI, 2 *Stromatocerium* HALL (forms of *S. canadense* NICHOLSON & MURIE type), *Stromatocerium* HALL (forms of *S. australe* PARKS type); all in vertical section; not to scale. *de* denticles, *di* dissepiments, *p* pillars, *vt* vertical tubes, *w* wrinkles

almost without any changes over the Silurian and Devonian (RIABININ, 1932; YAVORSKY, 1957; NESTOR, 1966; MORI, 1968 and others). It was only at the turn of the Devonian to Carboniferous that, as a result of the transformation of simple, isolated pillars of *Labechia*, forms were evolved assigned to *Stylostroma* (= *Pennatostroma*) in which vertical elements may have the form of thick, vertical columns or megapillars, ramified in herring-bone pattern (e. g., *S. yangi* (DONG) — cf. DONG, 1964, Pl. 4, Figs. 3, 5).

In some of *Labechia*, thin laminae were developed as a result of flattening dissepiments and their deposition at even levels. Such forms are assigned to the genus *Labechiella*. They have already been known in the Ordovician, as well as, less frequently, in the Silurian and

Devonian (NICHOLSON, 1886*b*; YABE & SUGIYAMA, 1930). As a result of the progressing development of pillars in *Labechia* and *Labechiella*, forms with pillars connected with each other in systems of longer or shorter, meandering vertical walls were evolved in the Early Carboniferous. Such forms were described by DONG (1964) from the lowermost Carboniferous of China and erroneously assigned by him to the genus *Stromatocerium* HALL. In the present writer's opinion, they should have been separated to form another genus. Some of the species of „*Stromatocerium*“, described by DONG, such as, „*S.*“ *sinense* DONG, „*S.*“ *kwangsiense* DONG and „*S.*“ *kueichowense* DONG, having thin laminae formed by flattening dissepiments, may probably be derived directly from *Labechiella*, while „*S.*“ *hybridium* DONG, with strongly convex dissepiments, from *Labechia*.

The process of the modification of skeleton, described above that is a strong development of vertical elements, undoubtedly reflects a selective adoption of the manner of displacement of coenosarc connected with a more economical secretion of the colony, with the preservation of an existing or usually increased mechanical resistance of the coenosteum.

Morphological changes, almost identical with those occurring in the lineage under study, are observed in the development of coenenchyme in the order Proporida (Heliolitoidea). In the Ordovician — Lower Silurian species of *Propora* M. EDWARDS & HAIM and *Laminoplasma* BONDARENKO, short denticles or pillars appear on the surface of strongly convex dissepiments. In the Wenlockian *Plasmopora* M. EDWARDS & HAIM they become elongated to transform, in the Upper Silurian *Squameolites* BONDARENKO and in *Eolaminoplasma* BONDARENKO, into long, vertical pillars and vertical walls connected with each other by tabulae formed of modified, flattened dissepiments (cf. SOKOLOV, 1955; BONDARENKO, 1963).

Lineage III. — This lineage is represented by species of the genera *Pseudostylodictyon* OZAKI, *Cystistroma* ETHERIDGE and *Stromatocerium* HALL, having massive coenosteae, as well as *Aulacera* PLUMMER whose coenosteae are cylindrical. The same as in lineage II, the progressive development of vertical elements in originally dissepimental skeletons (Text-figs. 12A₁, and B₁₋₃) is a characteristic feature of the development of the forms referred to above, but in this lineage it is reached in a quite different way of shifting coenosarc in the process of the colony's, growth (for further explanations see p. 35).

As in lineage II, skeletons with the structure of the type of *Cystistroma* GALLOWAY & ST. JEAN, undoubtedly direct ancestors of *Pseudostylodictyon* with strongly flattened dissepiments displaying the presence of fine wrinkles (e. g., *P. kayi* GALLOWAY & ST. JEAN, cf. GALLOWAY & ST. JEAN, 1961, Pl. 6, Fig. 1*a*), were initial forms of the lineage under study. A similar, although steeper and higher, local bend of flattened dissepiments, resembling tubes whose narrowing upper ends are closed at the top, is displayed by the representatives of older *Stromatocerium* (e. g., the Middle Ordovician *S. canadense* NICHOLSON & MURIE, cf. GALLOWAY & ST. JEAN, 1961, Pl. 9, Figs. 1 and 2) and *Aulacera* (e. g., the Upper Ordovician *A. radiata* GALLOWAY & ST. JEAN, cf. GALLOWAY & ST. JEAN, 1961, Pl. 4, Fig. 1*a*). Long, angular, continuous vertical tubes sometimes fused together and forming systems of twisted vertical walls are already observed in later species of *Stromatocerium* (e. g. *S. australe* PARKS, cf. GALLOWAY & ST. JEAN, 1961, Pl. 9, Fig. 3*a-b*) and in the representatives of *Cystistroma* (e. g., *C. donneli* ETHERIDGE, cf. WEBBY, 1969, Pl. 122, Figs. 3—8). In all these cases, the development of tubular vertical elements is usually accompanied by the flattening and arrangement in equal level of dissepiments which are transforming into laminae.

Lineage IV. — A lineage represented by species of *Forolinia* NESTOR and probably *Cliefdenella* WEBBY, the initial forms for which were, the same as in lineages III and II, the Ord-

vician *Cystostroma* GALLOWAY & ST. JEAN. As a result of the flattening of strongly convex dissepiments in *Cystostroma* and of the formation of circular pores called foramina (NESTOR, 1964), developed in them forms were evolved which are assigned to the genus *Forolinia*. In the oldest, Ordovician (Lower Catheys Formation, Tennessee), *Forolinia* such as, for instance, *F. pustulosa* (SAFFORD), erroneously assigned by GALLOWAY & ST. JEAN (1961) to *Labechia*, dissepiments are yet fairly strongly convex and have many foramina tending to a vertical superposition over longer stretches of the coenosteum (cf. GALLOWAY & ST. JEAN, *l.c.*, Pl. 7, Fig. 2a). Similar in structure are specimens of *F. implana* NESTOR, described from the Upper Llandoveryan of Estonia (cf. NESTOR, 1964, Pl. 10, Figs. 1—4). They already concur with *Forolinia* having very flat dissepiments intersected by numerous foramina as, for instance, *F. paka* NESTOR, from which, as a result of a very strong thickening of dissepiments, *F. pachyphylla* (NICHOLSON) (cf. Pl. VI, Fig. 5) were subsequently evolved in the Uppermost Llandoveryan (Adavere stage). The *Forolinia* lineage is among the few lineages in the development of the Stromatoporoidea, in which no development of vertical skeletal elements is observed. In this lineage, the differentiation of coenosarc mostly consisted in the formation of coenosarc strands detaching themselves from the principal layer of coenosarc which was distributed superficially and which penetrated deep into the skeleton. Foramina might be traces left in the skeleton by these coenosarc strands. Similarly interpreted foramina occur in several other genera (e.g., *Pseudostromatoporella* n. gen., *Stromatoporella* NICHOLSON, *Stictostroma* PARKS, *Tienodictyon* YABE & SUGIYAMA). The tendency to the superposition of foramina testifies to the stabilization of the position of coenosarc strands in the course of successive growth stages of the colony.

The precipitation of the skeletal substance around coenosarc strands was probably the cause of the formation of short, tubular bends in the axial part of some of the dissepiments observed in, for instance, the Upper Ordovician *Cystostroma estoniense* NESTOR (NESTOR, 1964, Text-fig. 1). In the present writer's opinion, a similar genesis should be ascribed to long, vertical tubes, intersected by tabulae, which are observed in *Cliefdenella*, described from the Upper Ordovician (Lower Eastonian) of Australia (*C. etheridgei* WEBBY, cf. WEBBY, 1969, Pl. 125, Figs. 1—4). In *Cliefdenella*, dissepiments were transformed into even laminae. With such an interpretation, vertical tubes in *Cliefdenella* were a modified equivalent of foramina, comparable functionally with systems of superposed ring-pillars, occurring in some of the species of *Stromatoporella* of morphological group „B“ (microreticular).

Lineage V. — A lineage represented by the genera *Clathrodiction* NICHOLSON & MURIE, *Simplexodiction* BOGOYAVLENSKAYA (= ?*Diplostroma* NESTOR), *Anostylostroma* PARKS, *Tienodiction* YABE & SUGIYAMA and *Pseudostromatoporella* n. gen. *Amphipora* SCHULZ is most likely to be related to this lineage. Reaching a regularly laminar structure of coenosteum, gradual increase in the complexity of vertical elements and a reduction of laminae through a strong development of foramina and ring-pillars (Text-fig. 13a-e) in some forms are characters of the representatives of the lineage under study. These changes were connected with a progressive folding of coenosarc and increase in the degree of its contact with the skeleton.

The representatives of *Clathrodiction* are undoubtedly derived from forms with a dissepimental structure of the type of *Cystostroma* GALLOWAY & ST. JEAN (cf. also PARKS, 1936; GALLOWAY & ST. JEAN, 1961; NESTOR, 1966b). A close relationship between the two genera is indicated by the character of skeletons of the oldest representatives of *Clathrodiction*, composed of slightly convex dissepiments, usually arranged in layers (e.g., the Upper Ordovician *C. vormsiense* RIABININ, cf. NESTOR, 1964, Pl. 12, Fig. 6; Text-fig. 13). Such a character of morphological changes is a symptom of replacing a not very effective manner of shifting coenosarc with dis-

sepiments serving as a base by that in which coenosarc shift is supported by pillars precipitated in particular spots. This process was connected with the replacement of dissepiments by rhythmically deposited laminae. According to the views of GALLOWAY & ST. JEAN (1957), species, so far described as those of the genus *Clathrodictyon* and in which the dissepimental structural pattern was obliterated and replaced by the laminae-pillars system, should be excluded from

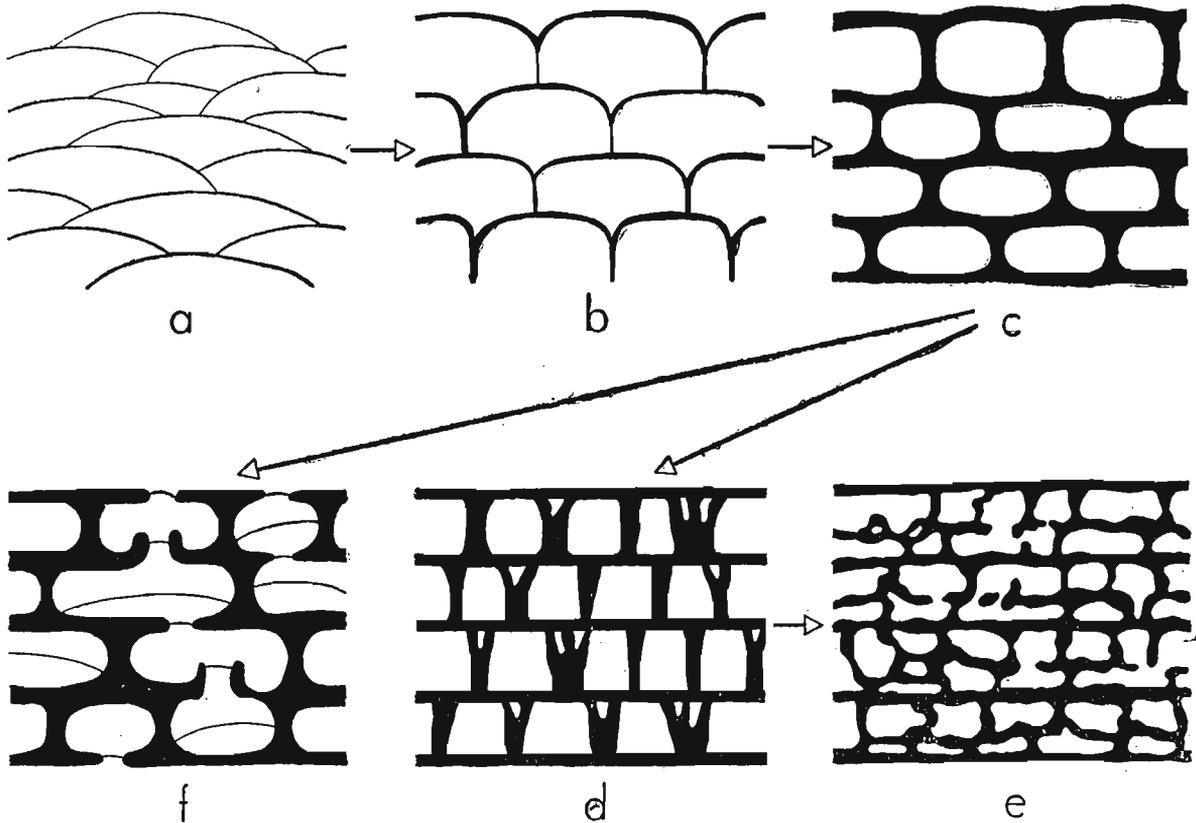


Fig. 13

Morphological group „A“. Forms representing Lineage V (see p. 54): *a* *Cystostroma* GALLOWAY & ST. JEAN, *b* *Clathrodictyon* NICHOLSON & MURIE, *c* *Simplexodictyon* BOGOYAVLENSKAYA, *d* *Anostylostroma* PARKS, *e* *Tienodictyon* YABE & SUGIYAMA, *f* *Pseudostromatoporella* n. gen.; all in vertical section; not to scale

this genus (e.g., *C. ostiolatum* NICHOLSON, *C. linnarsoni* NICHOLSON) and assigned to *Simplexodictyon*. The occurrence of several stromatoporoids whose skeletal tissue displays alternate zones with their structure of the type of *Clathrodictyon* and *Simplexodictyon* (e.g., *C. lenticulare* PETRYK, cf. MORI, 1968, Pl. 3, Fig. 3), indicates a close relationship between these two genera. Galleries in *Simplexodictyon*, at first rectangular and subrectangular and having straight, thin pillars (e.g., *S. gotlandense* (MORI), cf. MORI, 1968, Pl. 3, Fig. 5), gradually become rounded and, consequently, pillars acquire a spool-shaped outline (e.g., *S. uralicum* (YAVORSKY), *S. lazutkini* (YAVORSKY), Pl. VII, Figs. 6 and 8). In the present writer's opinion, the phenomenon of rounding the galleries may be explained by the penetration of the folds of coenosarc into galleries as the coenosarc shifts in the process of growth over the stretches, contained between two successive laminae. A further folding of coenosarc led to the formation of coenosarc strands, whose traces are observed in the form of foramina or ring-pillars in the representatives

of the Devonian *Pseudostromatoporella*, direct descendants of *Simplexodictyon*. The Middle Devonian *Anostylostroma*, in which, as a result of additional invaginations of the basal ectoderm, pillars ramify in the upper part of the interlaminal space (Text-figs. 9A₂ and 13d), were probably also evolved from *Simplexodictyon*. Species of *Tienodictyon* which, in particular in the Upper Devonian (e.g., *T. albertense* (STEARNS), Pl. XII, Fig. 3a) reached a maximum degree of the ramification of pillars (cf. also Text-figs. 9A₃ and 13e), were developed from *Anostylostroma* through a yet more intensive folding of ectoderm.

The lineage under study is marked by the highest degree of morphological differentiation of all other lineages of morphological group „A“, continuing from the Middle Ordovician to the Uppermost Devonian, while most genera of the remaining lineages become extinct considerably earlier or are only vestigially represented in the Upper Devonian (e.g., *Labechia*, *Stylostroma* and *Rosenella*).

Lineage VI. — A lineage including the representatives of the genera *Ecclimadictyon* NESTOR, *Plexodictyon* NESTOR, *Yabeodictyon* MORI, *Actinodictyon* PARKS (in part) and *Intexodictyon* YAVORSKY (in part). A progressive development of vertical elements in some of the forms (Text-fig. 14a-c) and, in others, a gradual increase in growth rhythms, expressed in a gradual development of laminae, are characters of this lineage.

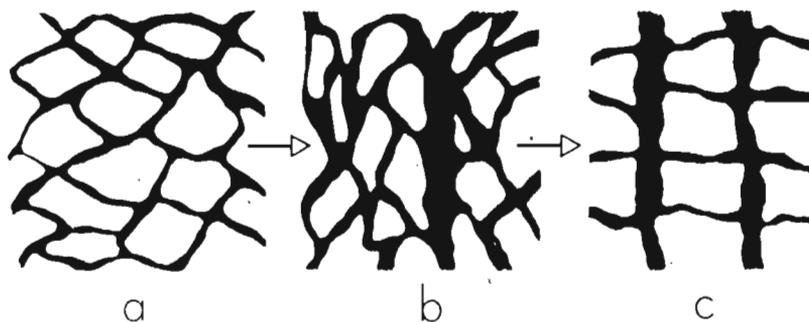


Fig. 14

Morphological group „A“. Some of the representatives of Lineage VI: a *Ecclimadictyon* NESTOR (forms of *E. fastigiatum* (NICHOLSON) type), b *Ecclimadictyon* NESTOR (forms of *E. robustum* NESTOR type), c *Actinodictyon* PARKS (forms of *A. suevicum* (NICHOLSON) type); all in vertical section; not to scale

The Upper Ordovician *Ecclimadictyon* with skeletons composed of irregular, obliquely connected plates displaying in vertical section of coenosteum a characteristic chevron-like outline were ancestral forms of this lineage. It was as very early as the Late Ordovician, that a tendency was marked in some of the species of *Ecclimadictyon* to form, in the skeleton, vertical elements shaped like twisted pillars (e.g., *E. amzassensis* (KHALFINA), cf. WEBBY, 1969, Pl. 128, Figs. 3 and 5). Much more definitely developed pillars and thickened skeletal elements occur in the Silurian *Ecclimadictyon* (e.g., the Llandoveryian *E. laminaeungulatum* (RIABININ), cf. NESTOR, 1964, Pl. 24, Fig. 1 or the Wenlockian *E. robustum* NESTOR, Pl. VII, Fig. 5). A further, strong development of pillars in *Ecclimadictyon* resulted in the formation, in the Wenlockian, of forms assigned to the genus *Yabeodictyon* and in which, in addition to thick, long pillars, skeletal plates had yet a conspicuously chevron-like arrangement typical of *Ecclimadictyon* (e.g., *Y. balticum* MORI, cf. MORI, 1968, Pl. 18, Fig. 1). As a result of a change from the oblique into horizontal arrangement of skeletal plates, forms were evolved, included in *Actinodictyon* (e.g., *A. suevicum* (NICHOLSON), cf. NESTOR, 1964, Pl. 30, Figs. 3—6).

The development of *Ecclimadictyon* was conspicuously divergent in character since in addition to changes tending to form pillars, some of the forms of this genus took an opposite trend, that is, towards developing compact laminae. The first laminae, observed in *Ecclimadictyon* are thin, uneven and, irregularly occurring in skeletons (e.g., the Upper Ordovician *E. gregale* (NESTOR), Pl. VII, Fig. 1). Strongly developed and regularly repeated laminae are recorded only in the Middle and Upper Silurian *Plexodictyon* (e.g., *P. savaliense* (RIABININ), Pl. VII, Fig. 2). Together with the development of laminae and primarily with a gradual decrease in the height of interlaminae spaces (growth increments), there occurs in *Plexodictyon* a gradual reduction in the number of densely distributed and at first oblique plates in interlaminae spaces which results in the evolution of forms, most frequently assigned to the genus *Intexodictyon* (e.g., *I. copulatum* YAVORSKY, cf. YAVORSKY, 1963, Pl. 7, Figs. 6 and 7). Not taking into account the microstructural character of the type species, the diagnosis of *Intexodictyon*, given by YAVORSKY (1963) and supplemented by NESTOR (1964) is unclear. In the present writer's opinion, some of the species, assigned at present to *Intexodictyon* and which, despite their similarity in a general arrangement and morphology of skeletal elements, display a reticular microstructure (e.g., *I. perplexum* YAVORSKY, cf. YAVORSKY, 1963, Pl. 8, Figs. 1—4), belong to morphological group „B“ and should, therefore, be excluded from *Intexodictyon*. These species must be assigned to the recently erected genus *Intexodictyonella* YAVORSKY (cf. YAVORSKY, 1969).

MORPHOLOGICAL GROUP „B“

Examples of lineages

Lineage I. — A lineage including representatives of the genera *Densastroma* E. FLÜGEL (in part), *Desmostroma* BOLSHAKOVA, *Pseudolabechia* YABE & SUGIYAMA and *Vikingia* BOGOYAVLENSKAYA.

A vertical zonal condensation of a uniformly microreticular tissue, first marked by the appearance of thick, columnar, elements which subsequently become transformed into systems of trabecular pillars, is the main trend in the development of successive morphological links. Between condensed vertical elements, the microreticulum becomes strongly reduced with progressive thickening of the remaining loose fibers (Text-fig. 15a-c).

The Lower Silurian *Densastroma* with skeletons composed of a very dense, homogenous reticulum (e.g., *D. pexisum* (YAVORSKY), cf. NESTOR, 1964, Pl. 13, Fig. 1; Pl. 14, Figs. 1 and 2) were initial forms of the lineage under study. At the turn of the Lower to Upper Silurian, some of the species of *Densastroma* evolved, into forms assigned to *Desmostroma*. In this genus the process was started of a differentiation of the structurally uniform skeleton into thick, irregular columns with a considerably looser reticulum occurring between them (e.g., the Wenlockian *D. columnatum* BOLSHAKOVA, cf. BOLSHAKOVA, 1969, Pl. 5, Fig. 1a-b). In other *Desmostroma*, columns are already much thinner, composed of thick vertical fibers, connected with each other by an irregular reticulum of finer fibers; the reticulum occurring between columns, is subject to further reduction (e.g., *D. yakovlevi* (RIABININ), cf. RIABININ, 1953, Pl. 2, Figs. 1—3).

Desmostroma are direct ancestors of the Wenlockian, and Ludlovian *Pseudolabechia*. In *Pseudolabechia* columns are composed, like in *Desmostroma*, of fibers thicker than the rest of skeleton, but arranged fanwise and connected with each other by thin fibers much rarer than those in *Desmostroma* (Text-fig. 15b). The fibers of its reticulum between columns become yet more reduced and thickened (e.g., *P. granulata* YABE & SUGIYAMA, cf. YABE & SUGIYAMA,

1930, Pl. 22, Figs. 11 and 12 (vertical section in an inverted position!). The fanwise arrangement of fibers in columns of *Pseudolabechia* was probably connected with an invagination of the basal ectoderm, which, at the same time, started the process of trabecularization of skeletal tissue in columns. This process was fully developed in the representatives of the next evolutionary link of the lineage under study, that is, in the Ludlovian *Vikingia* (e.g., *V. podolica* BOGOYAVLENSKAYA, cf. BOGOYAVLENSKAYA, 1969a, Pl. 4, Fig. 1a-b). The Wenlockian representatives of *Vikingia* (e.g., *V. vikingi* (NESTOR) and *V. tenue* (NESTOR), cf. NESTOR, 1966, Pl. 24, Figs. 1—6) are marked by distinct transitional characters between *Pseudolabechia* and *Vikingia*. They are expressed in a strong concentration of pinnately arranged fibers in columns, which, however, are connected with each other by thinner and rarer fibers. A primary reticulum between columns in *Vikingia* is reduced to a maximum extent, forming rare, thick and almost horizontally arranged fibers. (Text-fig. 15c).

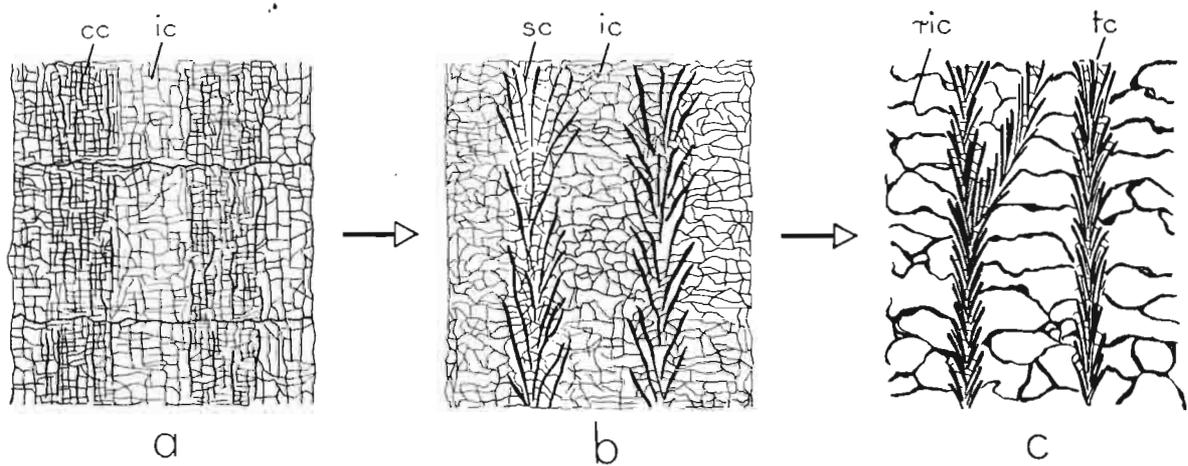


Fig. 15

Morphological group „B“. Genera representing Lineage I (see p. 57): a *Desmostroma* BOLSHAKOVA, b *Pseudolabechia* YABE & SUGIYAMA, c *Vikingia* BOGOYAVLENSKAYA; all in vertical section; not to scale. cc condensed microreticular tissue in columns, sc spray-like microreticular columns, ic intercolumnar microreticular tissue, ric reduced intercolumnar microreticular tissue

Lineage II. — A lineage represented by forms assigned to the genera *Densastroma* E. FLÜGEL (partly), *Plectostroma* NESTOR and *Actinostroma* NICHOLSON (partly). A uniform reduction in the initial microreticular tissue with a simultaneous gradual thickening of all remaining fibers of reticulum (Text-fig. 16A₁₋₃) is a main trend in the morphological development of particular links of the lineage under study. The reduction takes place primarily in the fibers of reticulum which take a vertical orientation and gave origine to pillars, excellently developed in further stages. The reduction in microreticular fibers is accompanied by an oligomerization of calcification centers and by obtaining growth rhythmicity expressed in the formation of even periodically deposited laminae in the forms younger geologically. The degree of folding coenosarc, at first low, in younger forms is marked by the presence of foramina in laminae, by the rounding of galleries and by a gradual replacement of reticular laminae by dissepiments.

The initial stages of this lineage, were marked by the appearance in Lower Silurian of stromatoporoids with skeletons composed of a dense, homogenous reticulum, assigned generally to the genus *Densastroma*. These forms were marked by a pronounced tendency to a uniform loosening of reticulum and a stronger development of fibers with a vertical orientation (e.g., the

Lower Wenlockian *D. incrustans* (RIABININ), cf. Pl. XLI, Fig. 1). In some of younger species of *Densastroma* (e.g., the Lower Ludlovian *D. sociale* (RIABININ), cf. Pl. XLI, Fig. 2), pillars are already expressed considerably more conspicuously. As a result of a further, rapidly progressing reduction of reticulum and thickening of its fibers, *Densastroma* evolved, into *Plectostroma*. The last genus has long, strongly expressed pillars connected with each other by fibers formed like horizontal processes (arms), detaching themselves at various levels and left over after the reduction in reticulum (e.g., the Ludlovian *P. mirificum* NESTOR, cf. Pl. XLI, Fig. 3).

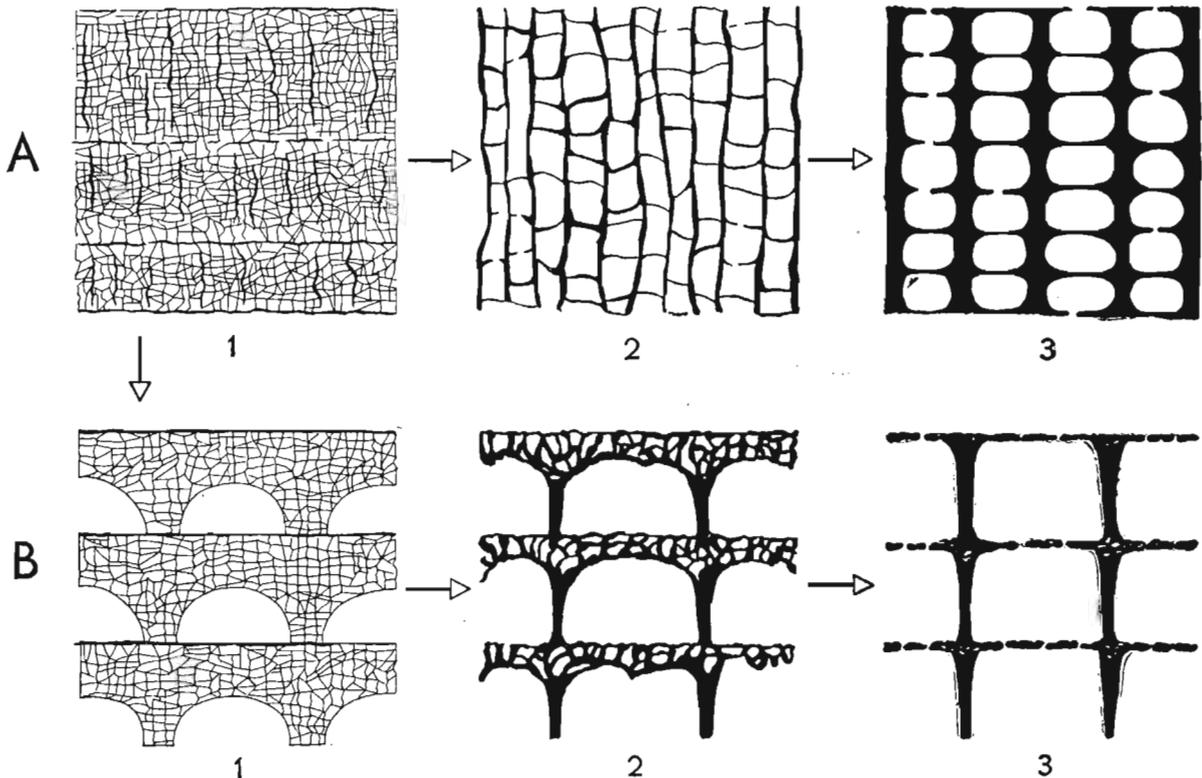


Fig. 16

Morphological group „B“. A — genera representing Lineage II (see p. 58): 1 *Densastroma* E. FLÜGEL (forms of *D. incrustans* (RIABININ) type), 2 *Plectostroma* NESTOR, 3 *Actinostroma* NICHOLSON (forms of *A. papillosum* (BARGATZKY) type); B — genera representing Lineage III (see p. 60): 1 *Parallelostroma* NESTOR, 2 *Actinostroma* NICHOLSON (forms of *A. mamontovi* YAVORSKY type), 3 *Actinostroma* NICHOLSON (forms of *A. stellulatum* NICHOLSON type); all in vertical section; not to scale

At the turn of the Silurian to the Devonian, *Plectostroma* evolved into *Actinostroma* in which the tendency is observed to arranging horizontal arms in even laminae. This process is connected with a further, strong thickening of pillars and a gradual rounding of galleries, indicating an intensive folding of coenosarc (e.g., *A. compactum* RIPPER, cf. Pl. XXXVII, Fig. 1a-b; *A. papillosum* (BARGATZKY), cf. Pl. XL, Fig. 1a-b). The thickening of pillars, progressing in the Devonian and accompanied by the reduction in laminae and their replacement by dissepiments, has in the Upper Devonian led to the formation of species of *Actinostroma*, having extremely thick pillars and slightly expressed interpillar skeleton (e.g., *A. crassepilatam* LECOMPTE, cf. Pl. XL, Fig. 3a; Pl. XLI, Fig. 6).

It follows from the successive stages of the *Densastroma* — *Actinostroma* lineage described above that considerable part of the species, so far assigned to *Actinostroma*, probably belong to another phylogenetic lineage whose terminal links display only a structural parallelism with *Actinostroma* proper, resulting from evolutionary tendencies on the whole similar in both lineages. Species assigned to the groups *A. verrucosum* (GOLDFUSS), *A. stellulatum* NICHOLSON and *A. sertiforme* LECOMPTE (cf. LECOMPTE, 1951) belong to non-typical *Actinostroma*. In addition, *A. bifarium* NICHOLSON is probably also a non-typical *Actinostroma*. Differences between the two lineages of *Actinostroma* are discussed in detail below.

Lineage III. — A lineage including forms belonging to *Densastroma* E. FLÜGEL (partly), *Parallelostroma* NESTOR and *Actinostroma* NICHOLSON (partly). The formation of and gradual increase in interskeletal spaces, which, at first of the nature of chambers, and later on — after a stronger reduction in microreticulum and formation of monofibril pillars — of galleries make up characteristic features of this lineage. Microreticular laminae, at first thick, are subsequently subject to gradual reduction, connected in many cases with loosening of the fibers of reticulum and with their thickening. In extreme cases, laminae occur in the form of a monolaminar reticulum. Pillars display the tendency to superposition, probably connected with growth stabilization of calcification centers in the basal ectoderm (Text-figs. 16A and B₁₋₃).

Older Silurian *Densastroma* with skeletons, consisting of a dense microreticulum whose fibers are rather disorderly arranged spatially which is indicated by the character of the skeletal tissue in most species of *Parallelostroma* (e. g., the Ludlovian *P. typica* (ROSEN), cf. Pl. X, Fig. 2), were ancestral forms of the Upper Silurian *Parallelostroma*. The formation of *Parallelostroma* was connected with the development, in uniform reticular skeletons of the *Densastroma* type, of interskeletal spaces shaped like hemispherical chambers arranged in even levels and emphasizing growth rhythmicity of skeletons. The formation of the hemispherical chambers was, in the present writer's opinion, connected with vesicular bends of the basal ectoderm at the beginning of each successive growth cycle. The growth periodicity in *Parallelostroma* is additionally underscored by usually dark-coloured growth inhibition surfaces (Pl. X, Fig. 3).

The writer believes that the mechanism of the formation of hemispherical chambers was homologous to the process of the formation of spaces between dissepiments in the Recent Zoantharia (cf. chapter „The origin and character of interskeletal spaces, p. 36). The chambers in *Parallelostroma* are at first small and low (e. g., *P. malinovzyensis* (RIABININ), cf. Pl. X, Fig. 1) and, consequently, laminae are very thick and pillars only slightly separated. The chambers subsequently gradually increase and lose their original hemispherical outlines. This process is connected with a considerable reduction in the thickness of laminae and development of higher pillars which in their lower part are thin, frequently reduced to a single fiber and extend upwards, uniting their microreticular tissue with the reticulum of a lamina. Such a structure of skeleton is characteristic of many forms assigned thus far to the genus *Actinostroma* (e. g., the Middle Devonian *A. mamontovi* YAVORSKY, Pl. X, Fig. 6; *A. verrucosum* (GOLDFUSS), cf. LECOMPTE, 1951, Pl. 10, Figs. 1 and 2; *A. geminatum* LECOMPTE, cf. LECOMPTE, 1951, Pl. 8, Fig. 5). In some of them, the original microreticulum in laminae is strongly loosened (*A. mamontovi*, *A. verrucosum*) and pillars are limited by the planes of laminae. In some others, the reticulum in laminae is dense and some of the pillars continue through several laminae (*A. geminatum*). As a result of a further reduction in thickness, laminae take the form of a very thin, unilayered reticulum. At the same time, monofibril pillars are well superposed in particular growth cycles (e. g., *A. stellulatum* NICHOLSON, Pl. XXXVII, Fig. 3a-b). Such forms become deceptively similar to *Actinostroma* proper (e. g., *A. papillosum* (BARGATZKY), from which they, however, conspi-

cuously differ in having no distinct horizontal arms turning from pillars typical of *Actinostroma* proper and in pillars being intersected by laminae. A further evolutionary stage of this group is probably *Actinostroma bifarium* NICHOLSON (Pl. XXXIX, Figs. 1 and 2), in which, in addition to many pillars limited by one interlaminar space, there occur considerably thicker, continuous pillars intersecting several laminae. In *A. bifarium*, laminae are observed which are composed of either a thick, irregular (Pl. XXXIX, Fig. 2), or strongly reduced reticulum which occurs in the form of horizontal arms connecting pillars (Pl. XXXIX, Fig. 1b). This fact might indicate that these forms, united in one species, might be of different origin. A clearly diphyletic origin of the forms, now assigned together to *Actinostroma*, makes up, in the writer's opinion, a basis for excluding from this genus the species related to this lineage and separating them in a new genus.

Lineage IV — A lineage represented by the species belonging to the genera *Densastroma* E. FLÜGEL (partly), *Intexodictyon* YAVORSKY (partly), *Intexodictyonella* YAVORSKY and *Atelodictyon* LECOMPTE. A gradual and uniform reduction in a dense primary reticulum, connected with the oligomerization of calcification centers, is a main tendency in the evolution of the representatives of this lineage. The reduction in reticulum resulted in the thickening of some of the fibers and mostly in taking vertical position by the remaining fibers. It was in early stages of the development of skeleton in the species discussed that a growth periodicity was expressed in even, thin, reticular laminae in which the process of reduction in fibers was marked to a considerably smaller extent than in an interlaminar skeleton (Text-fig. 17a-d).

Some of *Densastroma*, in which, in addition to the tendency to reduce microreticular fibers, thin, even laminae were formed of a denser reticulum than that in the rest of skeleton (e.g., the Middle and Upper Wenlockian *D. dniestrense* (RIABININ) and *D. ustiense* (RIABININ), cf. RIABININ, 1953, Pl. 3, Fig. 4; Pl. 4, Fig. 3) were initial forms of the lineage under study. The formation of laminae may be explained by a change from a continuous to a periodical deposition of skeleton. A considerably larger condensation of microreticulum in laminae than in the interlaminar skeleton might be evidence for inhibition periods repeatedly occurring in the growth of coenosteum. The formation of laminae took place in some of *Densastroma* during the period when the original microreticulum was already to a certain extent loosened and when considerable part of its fibers displayed a vertical orientation. A further development of *Densastroma* was connected with a strong reduction and thickening of reticular fibers in interlaminar spaces. At the same time, the remaining fibers in some of the forms had a conspicuously vertical orientation (e.g., the Middle Devonian *D. subpodolicum* (KHALFINA), cf. KHALFINA, 1960a, Pl. D-1, Fig. 2a-b) — or more frequently — were distributed very irregularly. The morphology of the last-named forms corresponds to the definition of the genus *Intexodictyonella*, recently separated by YAVORSKY (1969) with *Stromatoporella undata* (YAVORSKY) from the Givetian of the Kuznetsk Basin as the type species (cf. YAVORSKY, 1969, Pl. 16, Figs. 1—4). Species, assigned by KHALFINA (1960a) with a reservation, to the genus *Stromatoporella* NICHOLSON and which were described from the Lower and Middle Devonian of Salair Mts. (Siberia), such as, ?*S. rara* KHALFINA and ?*S. alternata* KHALFINA, should also be assigned to *Intexodictyonella*. This genus also includes some species of *Intexodictyon* having microreticular laminae (e.g., *I. perplexum* YAVORSKY, cf. YAVORSKY, 1963, Pl. 8, Figs. 1—4).

Forms with a very strongly reduced reticulum, of which straight or slightly ramified fibers, sometimes connected with each other and forming a loose reticulum, were left in interlaminar spaces, are mostly assigned to the genus *Atelodictyon*. The oldest of such forms are recorded as early as the Lower Devonian (e.g., *A. krekovi* (KHALFINA) and *A. verrucosum*

(KHALFINA) from Krekov Beds in Salair Mts., cf. KHALFINA, 1960a, Pl. D-2, Fig. 1; Pl. D-13, Fig. 3a-b) and are evidence for an uneven rate of reduction in reticulum of various species of *Atelodictyon*. In many progressive species of the Middle and Upper Devonian *Atelodictyon*, a loose reticulum in interlaminar spaces was finally transformed into systems of monofibril vertical walls, frequently interrupted and having meandering outline in tangential sections

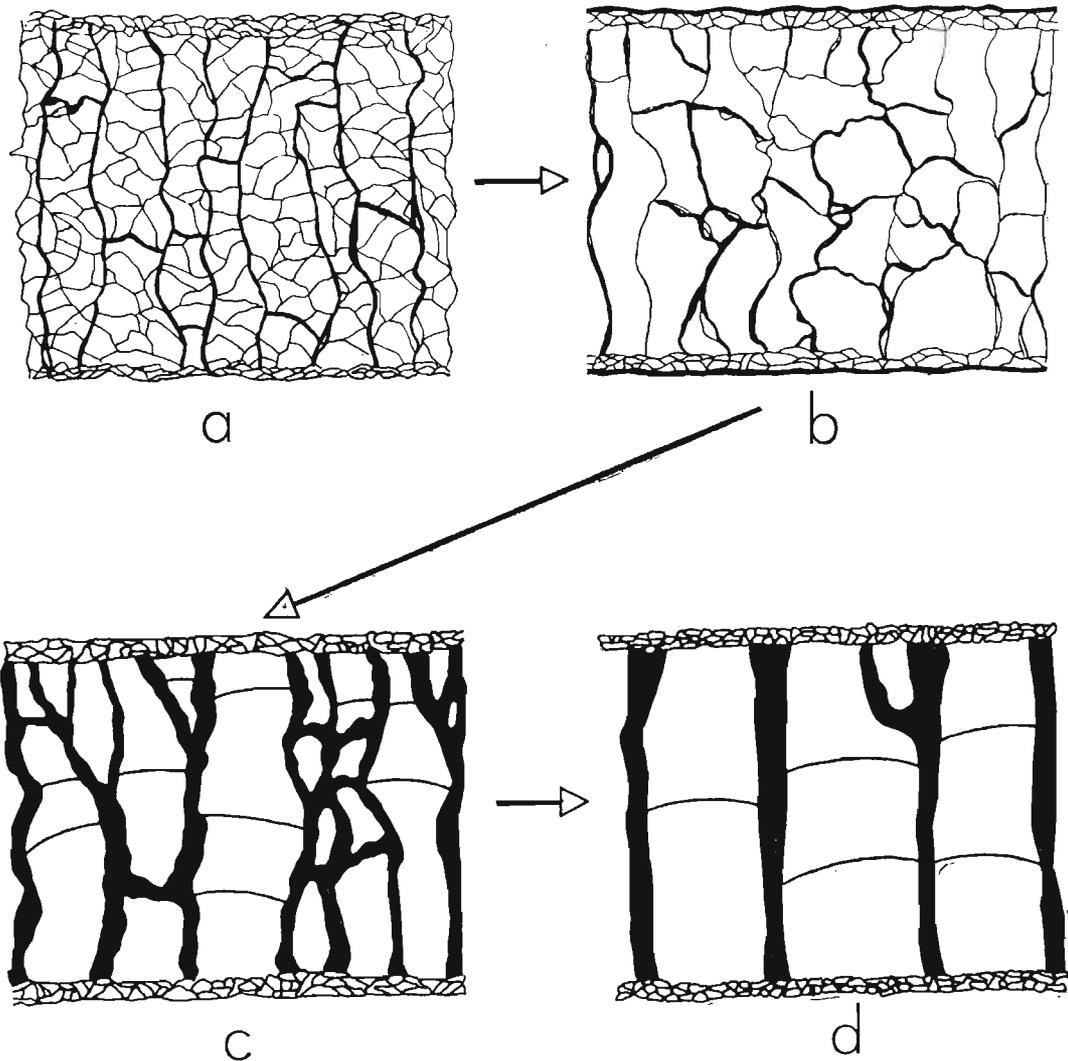


Fig. 17

Morphological group „B“. Some of the representatives of Lineage IV (see p. 61): *Densastroma* E. FLÜGEL (forms of *D. dniestrense* (RIABININ) type), *b Intexodictyonella* YAVORSKY, *c Atelodictyon* LECOMPTE (forms of *A. kreкови* (KHALFINA) type), *d Atelodictyon* LECOMPTE (forms of *A. fallax* LECOMPTE type); all in vertical section; not to scale

(e.g., the Couvinian *A. fallax* LECOMPTE, cf. LECOMPTE, 1951, Pl. 15, Figs. 1 and 2; the Upper Devonian *A. trautscholdi* (RIABININ), Pl. XXXVI, Figs. 2 and 3). To such *Atelodictyon* also belong the Middle Devonian formes from Kuznetsk Basin and Salair Mts., assigned by KHALFINA (1960a, b) to the genus *Flexiostroma* she separated on the basis of only the occurrence of astrorhizal columns which, however, abundantly occur in many other genera. These are

F. flexuosum KHALFINA, *F. pestereviense* KHALFINA and *F. crispum* KHALFINA. The genus *Aculatostroma*, separated by KHALFINA (1968a) with the type species *Syringostroma verrucosum* KHALFINA (cf. KHALFINA, 1960a, Pl. D-13, Figs. a-v) is also a junior synonym of *Atelodictyon*. In addition to *Atelodictyon*, having a strongly reduced interlaminar skeleton, in the Middle and Upper Devonian, there also occur species of this genus in which the process of reduction in reticulum is considerably less advanced (e.g., *A. ordinatum* STEARN, cf. STEARN, 1961, Pl. 35, Fig. 1; *A. pseudocolumnare* (RIABININ), Pl. X, Fig. 6; Pl. XXXVI, Figs. 1a-c). The appearance, in some of the species, of dissepiments in interlaminar spaces and rare foramina in laminae (Pl. XXXVI, Fig. 3) is a characteristic feature of the Upper Devonian *Atelodictyon*. This phenomena may be evidence of the beginning of a gradual penetration of coenosarc into skeleton in these forms.

Lineage V. — A lineage represented by forms belonging to the following genera: *Actinostromella* BOEHNKE, *Syringostromella* NESTOR, *Parallelopora* BAGRGATZKY (partly), *Syringostroma* NICHOLSON and *Neosyringostroma* n. gen. (partly). A gradual development of interskeletal spaces in the form of coeno- and autotubes, probably evoked by an increase in coenosarc folds and strands penetrating the skeleton is a characteristic feature of this lineage. A considerable extent of taking vertical position by skeletal elements and poorly developed or even absent laminae result from this process. A gradual growth stabilization of calcification centers leads to an increase in the degree of the spatial arrangement of skeletons. The primary microreticular tissue, which forms skeletal elements, gradually becomes condensed and subsequently homogenized primarily in vertical elements (Text-fig. 18a-f). In some cases, the transformation in microreticular tissue in pillars leads to the formation of trabeculae.

The Wenlockian *Actinostromella* with skeleton composed of a very dense reticulum, within which there run relatively long, thin vertical tubes circular in transverse section and intersected by tabulae, are the oldest representatives of the lineage under study. Such tubes are mostly called autotubes (e.g., *A. slitensis* MORI, cf. MORI, 1968, Pl. 13, Figs. 5 and 6). It is beyond any doubt that *Actinostromella* originate from uniformly reticular stromatoporoids having a structure of the type of *Densastroma* E. FLÜGEL. In those forms the process of the differentiation of coenosarc was connected with the formation of coenosarc strands in its basal zone. These strands penetrated the skeleton and shifted upwards, together with coenosarc, periodically depositing tabulae in the process of growth. In younger *Actinostromella*, autotubes are considerable larger and, consequently, the thickness of skeleton which surrounds them is strongly reduced (e.g., the Ludlovian *A. vaiverensis* NESTOR, — Pl. VIII, Fig. 1). As a result of a further development of the system of coenosarc strands, autotubes lose their individuality and meandering, vertical canals vermicular in outline in transverse section and intersected by tabulae or dissepiments are formed. An increasing degree of the skeleton being penetrated by coenosarc led to a further reduction in skeletal elements. Such a structure of skeleton is characteristic of the forms assigned to the genus *Syringostromella* (e.g., the Ludlovian *S. borealis* (NICHOLSON), cf. Pl. VIII, Fig. 2 and NESTOR, 1966, Pl. 17, Figs. 3 and 4). The microreticular tissue in skeletal elements of *Syringostromella* is in some of the species loose (e.g., *S. borealis*) and fairly strongly condensed in some others (e.g., *S. tenerrima* MORI, cf. MORI, 1968, Pl. 20, Figs. 5 and 6).

At the turn of the Silurian to the Devonian, *Syringostromella* probably evolved forms, assigned to *Parallelopora*, having regularly superposed skeletal elements surrounding wide, meandering, vertical canals, intersected by tabulae and dissepiments. Horizontal elements in the skeletons of *Parallelopora* are developed in the form of relatively irregular laminae dis-

playing — in younger species — a tendency to disappear and be replaced by dissepiments. Much the same as in *Syringostromella*, within *Parallelopora* there occur species with a skeleton composed of a loose microreticular tissue (e.g., the Middle Devonian *P. ostiolata* BARGATZKY, cf. GALLOWAY & ST. JEAN, 1957, Pl. 19, Fig. 2a-b), as well as with a very strongly condensed microreticulum (e.g., the Middle Devonian *P. pulchra* GALLOWAY & ST. JEAN, Pl. VIII, Fig. 3).

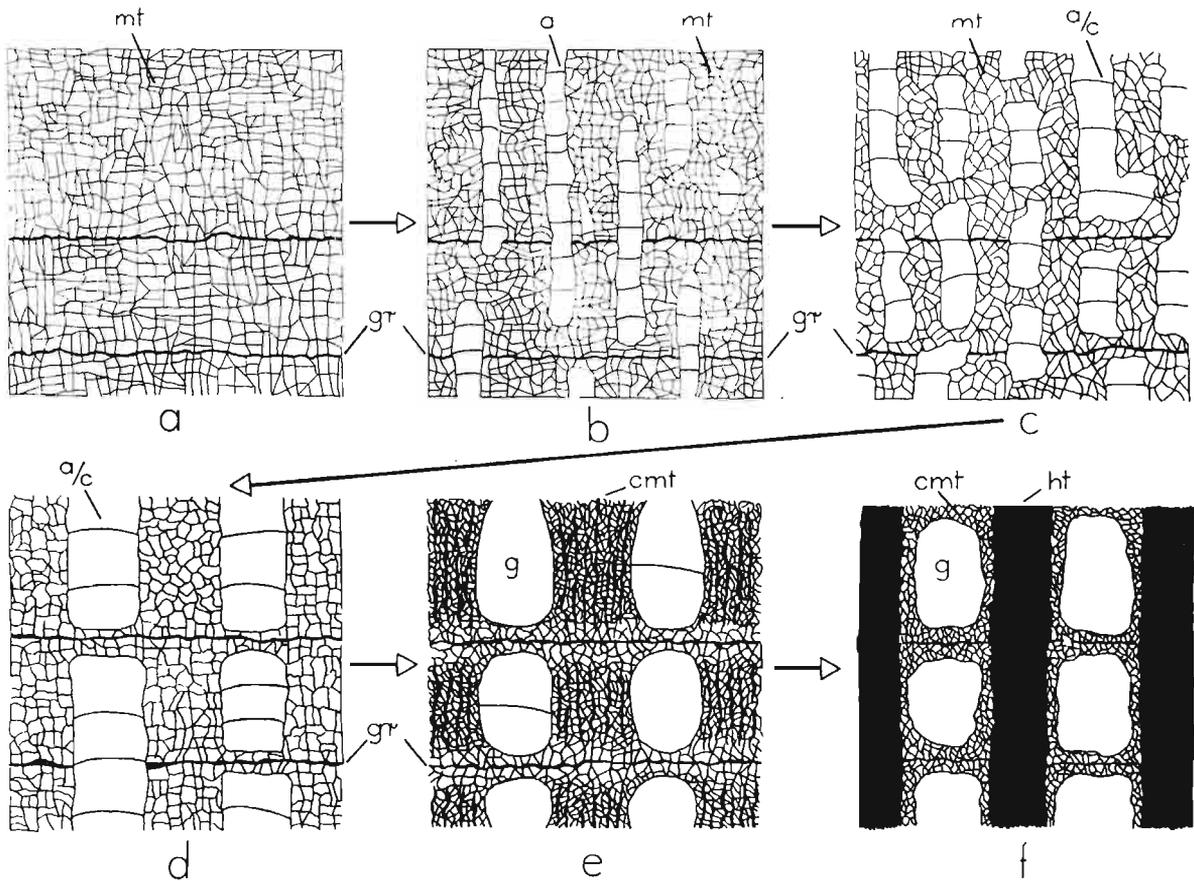


Fig. 18

Morphological group „B“. Genera representing Lineage V (see p. 63): a *Densastroma* E. FLÜGEL, b *Actinostromella* BOEHNKE, c *Syringostromella* NESTOR, d *Parallelopora* BARGATZKY, e *Syringostroma* NICHOLSON (forms of *S. densum* NICHOLSON type), f *Neosyringostroma* n. gen. (forms of *N. aurorum* (PARKS) type); all in vertical section; not to scale. a autotubes, a/c auto- or coenotubes, g galleries, gr growth inhibition surfaces, cmt condensed microreticular tissue, ht homogenized tissue, mt loose microreticular tissue

Parallelopora, having a loose microreticular tissue, evolved into a group of forms, making up a separate morphological lineage, leading through *Trupetostroma* PARKS to *Hermatostroma* NICHOLSON, which is discussed below. On the other hand *Parallelopora*, displaying a tendency to the condensation of microreticulum in vertical skeletal elements, evolved, at the turn of the Lower to Upper Devonian, into forms assigned to *Syringostroma*. In this genus the condensation of microreticulum was first marked in columnar pillars formed within normal vertical walls of skeleton. In some latterly *Syringostroma* (e.g., the Middle Devonian *S. densum* NICHOLSON, cf. GALLOWAY & ST. JEAN, 1957, Pl. 16, Fig. 3a-b), reticular fibers in pillars are considerably more condensed than in the rest of the skeleton and some of them, conspicuously thickened, are gathered to form bundles arranged in a slightly fanwise manner (Text-fig. 18e).

In the present writer's opinion, the following species, described by GALLOWAY & ST. JEAN (1957) from the Middle Devonian of the U. S. A. should be excluded from the genus *Syringostroma*: *S. perdensum* GALLOWAY & ST. JEAN, *S. superdensum* GALLOWAY & ST. JEAN, *S. papillatum* GALLOWAY & ST. JEAN, *S. tuberosum* GALLOWAY & ST. JEAN and *S. radicosum* GALLOWAY & ST. JEAN. Thick, mostly homogenous mamelon columns, occurring in these species at the bends of densely arranged microreticular laminae, make them suitable to be assigned rather to the genus *Stylodictyon* NICHOLSON & MURIE, erroneously considered by STEARN (1966b) as a junior synonym of *Syringostroma* (for the discussion of *Stylodictyon* — see lineage VIII).

Syringostroma are a direct ancestor of *Neosyringostroma* in which the microreticulum in pillars becomes homogenized. In the initial stages of this process, traces of the original microreticulum are preserved in the form of dark spots of calcification centers (or what is known as „maculae“) visible in transverse sections against the background of a lighter-coloured skeletal substance (e.g., the Middle Devonian *N. propinquicolumnae* (FRITZ & WAINES), cf. FRITZ & WAINES, 1956, Pl. 3, Figs. 8 and 11). The number of calcification centers is subsequently decreased (e.g., the Middle Devonian *N. aurorum* (PARKS), cf. GALLOWAY & EHLERS, 1960, Pl. 10, Fig. 1 a-b). In the interpillar skeleton, the microreticular tissue, at first preserved vestigially in the peripheral zone of pillars and in horizontal elements, is almost completely removed in younger *Neosyringostroma* as a result of a strong thickening and approximation of vertical skeletal elements (e.g., the Upper Devonian *Syringostroma* sp., cf. KLOVAN, 1966, Pl. 9, Figs. 1—3). *Neosyringostroma* also include species displaying the presence of thick, continuous pillars having a homogenous or trabecular microstructure of skeletal tissue and distributed within the microreticular interpillar skeleton. These forms differ, however, from the *Neosyringostroma* described above in irregular, frequently oblique horizontal elements (e.g., the Middle Devonian *N. logansportense* (GALLOWAY & ST. JEAN), Pl. XXXII, Figs. 1 and 2). We cannot preclude that such *Neosyringostroma* might be formed, independently of those described above, as a result of the development of continuous thick pillars within irregularly — obliquely arranged microreticular plates of skeletons of the type of *Ferestromatopora* YAVORSKY (= *Angulatostroma* KHALFINA). If such was the case, they would be only isochronously parallel to *Neosyringostroma* evolved from *Syringostroma*. If, as a result of more accurate studies, it will turn out that each of the types of *Neosyringostroma* referred to above belongs to a different lineage of microreticular Stromatoporoidea, the necessity will arise to separate some of the species into a distinct genus (cf. also lineage VIII).

Lineage VI. — A lineage including the representatives of the genera *Parallelopora* BARGATZKY (partly), *Trupetostroma* PARKS, *Hermatostroma* NICHOLSON and *Pseudoactinodictyon* E. FLÜGEL. This lineage is most probably related to cylindrical stromatoporoids assigned to the genus *Stachyodes* BARGATZKY (partly) and most of the species of the genus *Idiostroma* WINCHELL. A progressive oligomerization of calcification centers, manifested by an irregular homogenization of microreticular tissue, which first included the vertical elements of skeleton and, in later stages, also laminae (Text-fig. 10A₁₋₃), is a main evolutionary trend in the development of the lineage under study. Frequently, as a result of the transformation in microreticular tissue, trabeculae were formed in vertical elements. The process of homogenization was connected with a gradual reduction of laminae, in which foramina were formed or laminae were replaced by dissepiments. It is likely that the reduction of laminae was caused by an increased penetration of skeleton by coenosarc. Vertical skeletal elements are developed mostly in the form of vertical walls and less frequently of pillars. They are perfectly superposed

which might be evidence of growth stabilization in calcification zones of the basal ectoderm.

As mentioned in connection with the previous lineage, some of the species of *Parallelopora* were characterized by skeletal elements composed of a loose microreticular tissue. In these forms, the tendency was marked on the one hand to thicken microreticular fibers, in particular of vertical ones (e.g., the Middle Devonian *P. ostiolata* BARGATZKY, cf. LECOMPTE, 1952, Pl. 51, Fig. 3a) and, on the other, to reduction in microreticular fibers. As a result of the former process, in some species of *Parallelopora* the thickened fibers gradually fused with each other and formed irregular concentrations of a homogenous substance within microreticulum (e.g., the Upper Devonian *P. planulata* (HALL & WHITFIELD), cf. LECOMPTE, 1951, Pl. 50, Fig. 1a; *P. longitubulata* (RIABININ), Pl. XXXIII, Fig. 2c). A continued homogenization of the microreticulum led to the development of forms assigned to the genus *Trupetostroma* with almost completely homogenous skeletal elements, in which a loose, original microreticulum is preserved vestigially forming irregular vacuoles frequently concentrated in the peripheral zone of skeletal elements (e.g., the Middle-Upper Devonian *T. laceratum* LECOMPTE and *T. pingue* LECOMPTE, Pl. XXX, Figs. 1 and 2). In many *Trupetostroma*, homogenization took place more uniformly and consequently no or very few vacuoles occur in them (e.g., *T. gebum* (YAVORSKY), Pl. XXXI, Fig. 2a-c).

From *Trupetostroma* evolved forms assigned to *Hermatostroma* (cf. also LECOMPTE, 1952), having a very strongly homogenized skeletal substance and a vestigial microreticulum occurring in the form of irregular vacuoles in the peripheral zone of vertical walls and laminae which are additionally covered with thin, marginal plates called membranes (e.g., *H. porosum* [LECOMPTE], Pl. VIII, Fig. 5). In *Hermatostroma*, which are more advanced evolutionary, vacuoles disappear and the peripheral zone of skeletal elements is covered by membranes only (e.g., *H. perseptatum* LECOMPTE, Pl. XXXIV, Fig. 2a-b). Membranes were probably deposited by the ectoderm of the folds of coenosarc which penetrated deep into galleries or coenotubes during the last phases of each, successive growth cycle of the skeleton. The appearance of membranes in *Hermatostroma* is not closely correlated with the process of the homogenization of microreticulum and it only gives evidence for an increasing degree of folding the coenosarc. For this reason, membranes are also recorded in species of *Hermatostroma* which have an only slightly changed microreticulum (e.g., *H. episcopale* NICHOLSON, Pl. XXXV, Fig. 1a-b).

From *Parallelopora* tending to reduce microreticular fibers with a simultaneous consolidation of the remaining vertical fibers were probably evolved Middle and Upper Devonian *Pseudoactinodictyon*. In this genus vertical elements occur in the form of continuous, thin pillars and of vertical walls composed of a homogenous substance in which rare, darker spots of calcification centers are visible in transverse sections (e.g., *P. actinostromiforme* (RIABININ), Pl. XXVII, Fig. 2a-c).

In some of *Pseudoactinodictyon*, vertical elements display a trabecular microstructure (compound trabeculae) (e.g., *P. juxi* E. FLÜGEL, Pl. XIX, Fig. 2c-d; ?*P. dartingtonense* (CARTER), Pl. XXVIII, Fig. 1b).

To the *Parallelopora-Hermatostroma* lineage are directly related the forms with cylindrical coenostea (cf. also STEARN, 1966a) such as some of *Stachyodes* with their skeletons either similar in structure to those of *Parallelopora* with a condensed microreticular tissue and superposed vertical elements (e.g., *S. paralleloporoides* LECOMPTE), or of the vacuolar type corresponding to those of *Trupetostroma* (e.g., *S. radiata* LECOMPTE). Likewise many species of the genus *Idiostroma* represent the type of structure either of *Trupetostroma* (e.g., *I. fililaminatum* LECOMPTE), or of *Hermatostroma* (e.g., *I. roemeri* NICHOLSON).

Lineage VII. — A lineage which includes the representatives of the genera *Stromatopora* GOLDFUSS (sensu NESTOR, 1966a), ?*Salirella* KHALFINA and *Taleastroma* GALLOWAY. The main developmental tendencies, manifested within this lineage are as follows: a gradual condensation of the microreticular tissue of skeletal elements, leading to its almost complete homogenization and the development, in initially irregular skeletons, of clearly defined vertical elements (Text-fig. 10B₁₋₃).

The oldest Wenlockian *Stromatopora* were evolved from uniform very fine reticular skeletons in which, as a result of a differentiation in a superficially distributed coenosarc, there were formed irregularly twisted canals termed as coenotubes, frequently joining each other and intersected by thin plates of the nature of tabulae or dissepiments. Coenotubes are probably traces left by the folds of coenosarc. A vermicular arrangement of coenotubes may be explained by the lability of the folds referred to above, changing their position and configuration during growth of colony. The coenotubes at first very short (e.g., the Wenlockian *S. impexa* NESTOR, cf. NESTOR, 1966, Pl. 16, Fig. 1), become rapidly elongated and arranged vertically (e.g., the Ludlovian *S. bekkeri* NESTOR, cf. NESTOR, 1966, Pl. 17, Fig. 1). In many Devonian species of *Stromatopora*, coenotubes are subject to further elongation and take a more vertical position which might give evidence for an increased growth stabilization of the folds of coenosarc (e.g., the Middle Devonian *S. divergens* GALLOWAY & ST. JEAN, Pl. XXI, Fig. 1a-b). Consequently, forms might be evolved assigned to the genus *Salirella* in which coenotubes were replaced by autotubes, that is, long, vertical canals round in transverse outline and having many tabulae (e.g., the Middle Devonian *S. multicea* KHALFINA, cf. KHALFINA, 1960a, Pl. D-5, Fig. 3a). It is not unlikely however, that the forms with a structure of the type of *Salirella* may be related to the *Syringostromella-Parallelopora* lineage (cf. also NESTOR, 1966, p. 48).

In addition to species of *Stromatopora* tending to develop vertical elements of skeleton, there are numerous Devonian species, marked by a disorderly, vermicular trace of coenotubes and very rare autotubes which give evidence of a considerable structural conservatism of *Stromatopora* (e.g., the Middle-Upper Devonian *S. stricta* LECOMPTE and *S. undata* (RIABININ), Pl. XXII, Figs. 2 and 3).

Regardless of the structural character of their skeleton, a gradual condensation of primary microreticular tissue is displayed by almost all Devonian species of *Stromatopora*. Owing to this fact, it is relatively easy to distinguish the Silurian-Lower Devonian *Stromatopora* from the younger ones, frequently identical structurally. Forms, in which, a strongly condensed microreticulum begins its homogenization, are already assigned to the genus *Taleastroma*, but a strict determination of a boundary between *Stromatopora* and *Taleastroma* is frequently impossible in taxonomic practice. This may be seen in, e.g., *Stromatopora cooperi* LECOMPTE, in which, with a partial homogenization of skeletal tissue, most of the skeleton is still reticular (Pl. XIX, Fig. 1c-d). The process of homogenization of the condensed microreticulum is usually marked in central parts of vertical skeletal elements (e.g., *T. conicomamillatum* (GALLOWAY & ST. JEAN), cf. GALLOWAY, 1960, Pl. 75, Fig. 3a-b), but it is only in younger *Taleastroma* that an almost entire skeletal substance is homogenized and the traces of primary microreticulum are preserved only in the marginal zone of skeletal elements (e.g., *T. confertum* STEARN, Pl. XXV, Fig. 2a-c). In the development of *Stromatopora*, noteworthy is a gradually increasing growth rhythmicity, which — in the older, silurian species — is only marked in the form of irregular growth inhibition surfaces. On the other hand, many Devonian species display horizontal, skeletal elements, deposited periodically and resembling laminae, in which dark layers of growth inhibition occur frequently (e.g., *S. colliculata* NICHOLSON, Pl. XX, Fig. 2a-b) or in which fissures on the boundary

of growth interruption surfaces are distributed very densely and at regular intervals (e.g., *S. mononensis* GALLOWAY & ST. JEAN, Pl. XXII, Fig. 1a-b).

Lineage VIII. — A lineage including forms assigned to the genera *Ferestromatopora* YAVORSKY (= *Angulatostroma* KHALFINA), *Neosyringostroma* n. gen. (partly) and *Stylodictyon* NICHOLSON. Cylindrical and dendroidal stromatoporoids assigned to the genera *Paramphipora* YAVORSKY, *Clavodictyon* SUGIYAMA and *Dendrostroma* LECOMPTE also are probably related to this lineage. The tendency to increase growth rhythmicity through the formation of laminae and periodical growth discontinuities is observed in the development of the representatives of this lineage. In some of those forms, vertical elements are strongly developed in the form of continuous columnar pillars (Text-fig. 19b-c) or mamelon columns. As a result of a gradual oligomerization of calcification centers, the primary microreticular tissue displays, in some of the forms, the tendency to condensation and homogenization and, in some others, to reduction through an elimination of some of the fibers and thickening the rest of them.

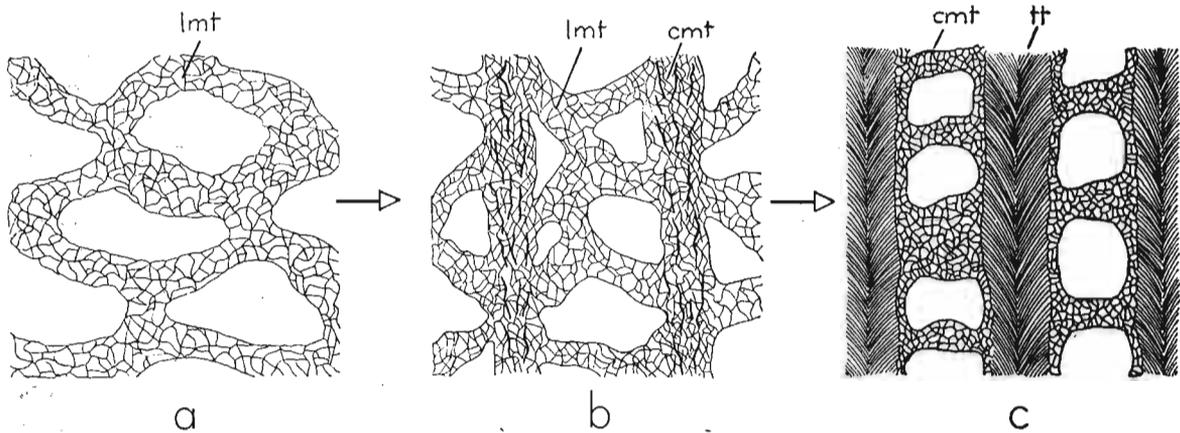


Fig. 19

Morphological group „B“. Some of the representatives of Lineage VIII: a *Ferestromatopora* YAVORSKY (forms of *F. angulata* (YAVORSKY) type), b *Syringostroma* NICHOLSON (forms of *S. sherzeri* (GRABAU) type), c *Neosyringostroma* n. gen. (forms of *N. logansportense* (GALLOWAY & ST. JEAN) type); all in vertical section; not to scale. lmt loose microreticular tissue, cmt condensed microreticular tissue, tt trabecular tissue

The oldest forms of the lineage under study, assigned to *Ferestromatopora*, were evolved, as other microreticular stromatoporoids, as a result of the formation — in homogenous, primitive, reticular skeletons — of spaces which were of the nature of irregular chambers. The presence of these chambers differs *Ferestromatopora* from *Stromatopora* s.s., in which interskeletal spaces are developed in the form of coeno- or autotubes. In younger *Ferestromatopora*, chambers were replaced by irregular galleries. In some of *Ferestromatopora*, skeletal elements have the form of laminae, obliquely connected with each other and displaying, in vertical sections of coenosteum, a chevron-like arrangement similar to that in the genus *Ecclimadictyon* NESTOR (e.g., *Ferestromatopora inornata* (KHALFINA), cf. KHALFINA, 1960a, Pl. D-4, Fig. 2a; *F. angulata* (YAVORSKY), cf. YAVORSKY, 1947, Pl. 4, Fig. 11). In some of *Ferestromatopora*, laminae began to occur relatively early (e.g., the Wenlockian *F. insularis* MORI, cf. MORI, 1968, Pl. 22, Figs. 1 and 3). As soon as laminae were formed, the interlaminar skeleton started to decrease gradually (e.g., the Ludlovian *F. nikiforovae* (RIABININ), cf. RIABININ, 1953, Pl. 22, Fig. 4). In younger, Devonian *Ferestromatopora*, a further increase is observed in growth rhythmicity

of the skeleton which is expressed in more and more densely arranged laminae or growth discontinuity surfaces (e.g., the Upper Devonian *F. uchtensis* (RIABININ) or *F. percanaliculata* (LECOMPTE), Pl. XXIV, Figs. 1 and 2). At the same time, the microreticular tissue is subject to strong reduction and consequently laminae become thinner and thinner, while interlaminal elements are frequently reduced to irregular vertical walls composed of a loose reticulum (e.g., *F. cellulosa* (LECOMPTE), Pl. XXVI, Fig. 1). Species of *Ferestromatopora*, having very strongly reduced microreticular fibers, are similar in skeletal morphology to some of *Atelodictyon* LECOMPTE and it is not unlikely that some of the species of this genus with vertical walls, composed of irregular reticulum, descend from *Ferestromatopora*.

Species assigned by the present writer to the group *Ferestromatopora dubia* (cf. Systematic Part, p. 97) are similar in thick laminae and small galleries, circular or semicircular in outline, to *Parallelostroma* NESTOR. They differ only in a considerably condensed microstructural reticulum (Pl. XXVII, Fig. 1*b-c*).

In other *Ferestromatopora*, there were formed thick, long columnar pillars, which at first were composed, like other skeletal elements, of microreticular tissue and represented pillars of the type recorded in *Syringostroma* NICHOLSON (Text-fig. 19*b*). The systematic position of such forms is rather problematic and they may be provisionally assigned with a reservation to *Syringostroma* (e.g., ?*S. pseudotyrganica* (KHALFINA), cf. KHALFINA, 1960*a*, Pl. D-5, Figs. 1 and 2). The microreticular tissue in columnar pillars is subject to subsequent gradual condensation (e.g., *S. sherzeri* (GRABAU), cf. GALLOWAY & EHLERS, 1960, Pl. 10, Fig. 4) and, finally — in some of the forms — to homogenization or trabecularization, observed in forms assigned by the writer to the new genus *Neosyringostroma* (e.g., *N. logansportense* (GALLOWAY & ST. JEAN), Pl. XXXII, Figs. 1 and 2). *Neosyringostroma*, evolved from *Ferestromatopora*, are frequently indistinguishable in practice from the *Neosyringostroma* which descend from the *Actinostromella-Syringostroma* lineage (cf. lineage V), in particular in the case in which their interpillar skeletal elements are strongly reduced or have a laminar structure. Due to the fact that both lineages are closely related to one another and probably descend from those same ancestors, which are uniformly microreticular, it is difficult to separate them generically.

In some of *Ferestromatopora*, which developed laminae, very specific skeletal structures were formed as thick, vertical columns composed of a strongly condensed or homogenized microreticular tissue. These columns form mamelons on the surface of coenosteum. Such forms, abundant in the Middle Devonian, were assigned by NICHOLSON (1886*a*) to the genus *Stylodictyon*. In the representatives of *Stylodictyon*, columns may be either rare and very thick (e.g., *S. radicosum* (GALLOWAY & ST. JEAN), cf. GALLOWAY & ST. JEAN, 1957, Pl. 18, Fig. 1), or numerous, occupying considerable part of the volume of skeleton and much thinner (e.g., *S. subfuscum* (GALLOWAY & ST. JEAN), cf. GALLOWAY & ST. JEAN, 1957, Pl. 18, Fig. 3). The fact of a general formation of vertical elements of the type of columnar pillars and mamelon columns in the representatives of the lineage under study may be explained as a compensation for a poor development of normal pillars which, in nearly all groups of the stromatoporoids, is manifested as a general tendency to the development and growth stabilization of vertical skeletal elements that is, the main supports for coenosarc as it shifts upwards.

Lineage IX. — A lineage including the representatives of the genera *Hermatostromella* KHALFINA (= ?*Gerronodictyon* BOGOYAVLENSKAYA) and *Gerronostroma* YAVORSKY. An early development of very regular skeletons composed of laminae and pillars, which gradually reduce their thickness, is a progressive character of this lineage. This process is accompanied by a strong condensation of microreticular tissue. The progressive folding of coenosarc led to the de-

velopment, in some forms of this lineage, of rounded galleries and foramina, indicating an increase in the penetration of skeleton by coenosarc (Text-fig. 20 A₁₋₂).

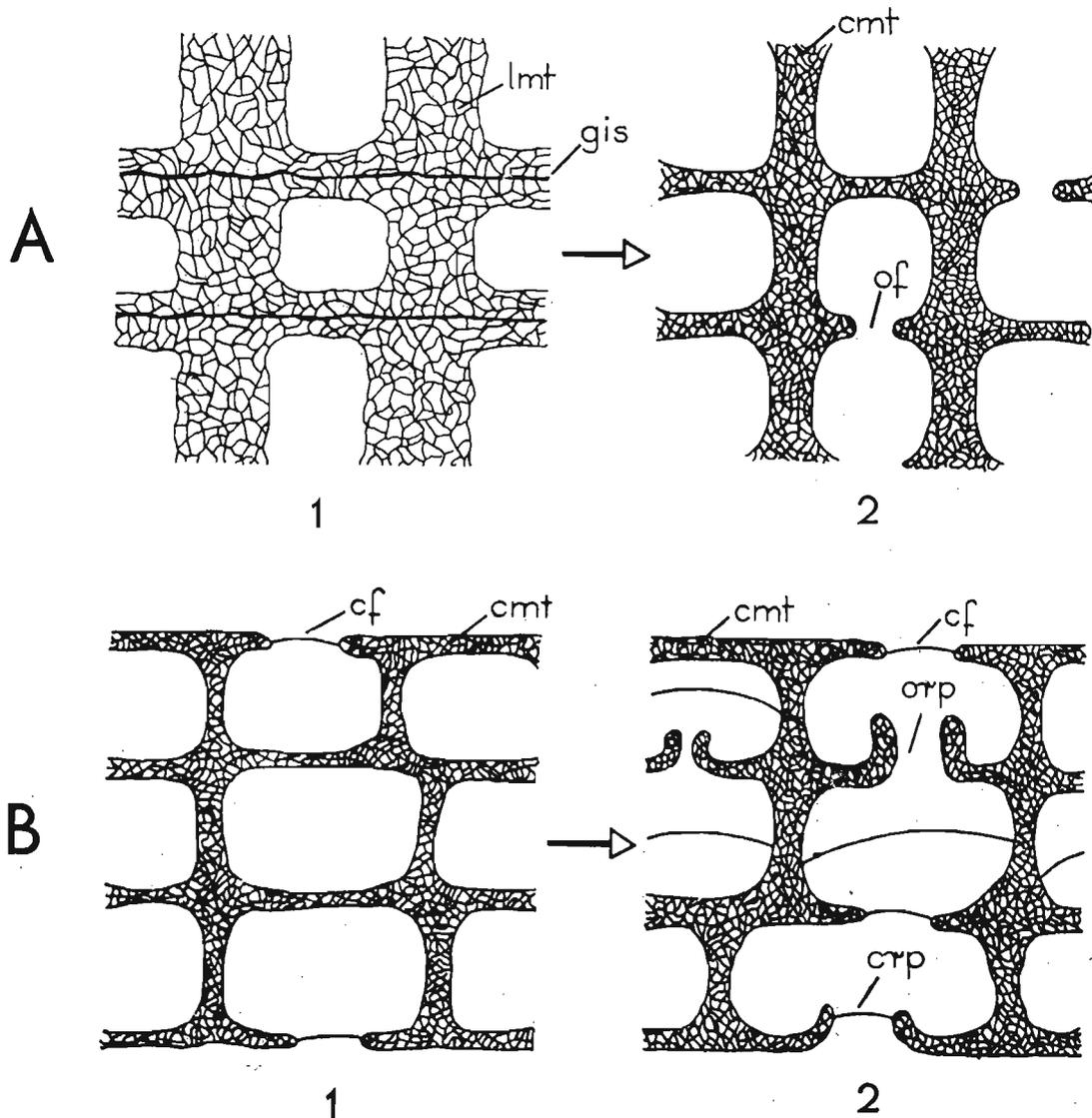


Fig. 20

Morphological group „B”. A — genera representing Lineage IX (see p. 69): 1 *Hermatostromella* KHALFINA, 2 *Gerrostroma* YAVORSKY; B — genera representing Lineage X (see p. 71): 1 *Stictostroma* PARKS, 2 *Stomatoporella* NICHOLSON; all in vertical section; not to scale. *lmt* loose microreticular tissue, *cmt* condensed microreticular tissue, *of* open foramina, *cf* closed foramina, *orp* open ring-pillars, *crp* closed ring-pillars, *gis* growth inhibition surfaces

The Upper Silurian-Lower Devonian *Hermatostromella* were probably evolved from homogenous, very fine-reticular stromatoporoids in which — as a result of the formation of interskeletal spaces of the nature of galleries — skeleton was disintegrated into thick laminae and pillars and less frequently into vertical walls superposed on each other to a considerable extent (e.g., the Upper Silurian, *H. sibirica* (YAVORSKY), Pl. XI, Fig. 5; the Lower Devonian *H. parasitica* KHALFINA, cf. KHALFINA, 1960a, Pl. S-5, Fig. 1 a-b). Thick and regularly deposited laminae in *Hermatostromella*, as well as rounded galleries, give evidence of rhythmical growth

and folding of coenosarc which penetrated into the galleries of skeleton. It was relatively as early as the Upper Silurian that in the laminae of some of *Hermatostromella* there appeared foramina which indicated an increase in the degree of penetration of skeleton by coenosarc (e.g., the Ludlovian *H. incisa* (BOGOYAVLENSKAYA), cf. BOGOYAVLENSKAYA, 1969b Pl. 3, Fig. 2a-b).

Hermatostromella are directly related to forms assigned to *Gerronostroma* with a very regular, lattice-like arrangement of laminae and pillars (Text-fig. 20A₁₋₂). As compared with *Hermatostromella* the pillars of *Gerronostroma* are much more superposed and their laminae, having foramina, very strongly reduced (e.g., the Middle Devonian *G. elegans* YAVORSKY, cf. YAVORSKY, 1931, Pl. 2, Figs. 3-6).

Lineage X. — A lineage including forms assigned to the genera *Stictostroma* PARKS, *Stromatoporella* NICHOLSON (= ?*Tubuliporella* KHALFINA and ?*Styloporella* KHALFINA) and *Clathrocoilona* YAVORSKY (= *Synthetostroma* LECOMPTE).

A gradual reduction of well developed laminae, at first expressed in a gradual decrease in the thickness of laminae and afterwards in the formation of numerous foramina and ring-pillars (Text-fig. 20B₁₋₂) is observed in the development of this lineage. Vertical elements in the form of pillars and vertical walls, at first irregular, gradually take a spool-shaped outline and, at the same time, skeletal galleries became round. The microreticular tissue is subject to strong condensation and, in some of the younger forms, homogenization.

Some of the Silurian stromatoporoids, somewhat similar in structure to the genus *Parallelostroma* NESTOR, but with a finer microreticulum and more irregular, twisted laminae and pillars or vertical walls, were probably ancestral forms of the lineage under study. The features named above are characteristic for *Stromatopora dniestrensis* RIABININ, *Stromatopora lamellosa* YAVORSKY and *Stromatopora pseudokaugatomica* RIABININ described by RIABININ (1953) from the Silurian of Podolia. As a result of a strong reduction in laminae and development of straight pillars, such forms might evolve into the Devonian *Stictostroma*, in which microreticulum in skeletal elements was strongly condensed and growth inhibition surfaces (e.g., *S. ivdeliense* (YAVORSKY), Pl. XI, Fig. 3a-b) or irregular fissures of growth interruption (e.g., *S. kolymsense* (YAVORSKY), Pl. XI, Fig. 6) occurred in laminae. In most of *Stictostroma* galleries are already round in outline and more or less numerous foramina appear in laminae (Pl. XVI, Figs. 1-3).

Stromatoporella, in which ring-pillars are formed around foramina, are a direct evolutionary continuation of *Stictostroma*. The number and manner of distributing ring-pillars in the skeletons of *Stromatoporella* are variable. They range from rare and irregular (e.g., *S. mudlakensis* GALLOWAY, Pl. XVIII, Fig. 1), through very numerous but limited to one interlamina space (e.g., *S. perannulata* GALLOWAY & ST. JEAN, cf. GALLOWAY & ST. JEAN, 1957, Pl. 9, Fig. 3a-b), up to superposed and forming longer or shorter vertical tubes, penetrating through several laminae and intersected by tabulae (e.g., *S. altaica* (KHALFINA), cf. KHALFINA, 1968b, Pl. 2, Fig. 3a).

The structural type of *Stictostroma* is also represented by forms assigned to the genus *Clathrocoilona*. But these forms, despite their fairly well defined straight or spool-shaped pillars, have, however, laminae which are considerably thicker, more irregular than those in *Stictostroma* and frequently with growth interruption fissures (e.g., *C. abeona* YAVORSKY, cf. GALLOWAY & ST. JEAN, 1957, Pl. 21, Fig. 3a-b). In part of the species of *Clathrocoilona*, the thickness of laminae was also subject to gradual reduction, but they always had a very irregular and frayed appearance. Closely spaced dissepiments usually occur in increasing interlamina spaces

which are frequently outlined like angular galleries (e.g., *C. sokolovi* (KHALFINA), cf. KHALFINA, 1960, Pl. D-12, Fig. 2a-b).

Forms with irregular laminae, few foramina, pillars limited to one interlaminar space and composed of a loose microreticular tissue, displaying a tendency to reduce fibers, probably make up a side-branch of *Clathrocoilona*. It is until now that such forms having had no clear taxonomic position, are most frequently assigned to *Stromatopora* GOLDFUSS or *Trupetostroma* PARKS (e.g., „*Stromatopora*“ *pellucida* YAVORSKY, Pl. XI, Fig. 1; „*Trupetostroma*“ *spatiosum* YAVORSKY, Pl. IX, Fig. 5; Pl. X, Fig. 4).

SYSTEMATIC PART

MORPHOLOGICAL GROUP „A”

Genus **TIENODICTYON** YABE & SYGIYAMA, 1941

Type species: Tienodictyon zonatum YABE & SYGIYAMA, 1941; Middle Devonian, China (Eastern Yunnan).

- 1941. *Tienodictyon*; YABE & SUGIYAMA, p. 139.
- 1957. *Tienodictyon*; GALLOWAY, p. 456.
- 1956. *Tienodictyon*; LECOMPTE, p. F 137.
- 1965. *Tienodictyon*; BOGOYAVLENSKAYA, p. 37.
- 1966a. *Hammatostroma*; STEARN, p. 92.
- 1966b. *Hammatostroma*; STEARN, p. 44.
- 1968. *Tienodictyon*; FLÜGEL & FLÜGEL-KAHLER, p. 579.
- 1968. *Hammatostroma*; FLÜGEL & FLÜGEL-KAHLER, p. 546.
- 1969. *Tienodictyon*; STEARN, p. 755.
- 1969. *Hammatostroma*; STEARN, p. 757.

Diagnosis. — Laminae compact, with rare foramina; pillars, restricted to one interlaminar space, are of two types: straight and more or less irregularly bent, sometimes forming secondary laminae; dissepiments common; microstructure fibro-normal.

Discussion. — *Tienodictyon* differs from the genera *Simplexodictyon* BOGOYAVLENSKAYA and *Anostylostroma* PARKS, related to it by their microstructure, in a characteristic folding of its skeletal elements within the interlaminar space and, from *Pseudostromatoporella* n. gen., in a lack or very rare foramina.

The type species was described from the deposits whose age was determined on the basis of *Amphipora ramosa*, occurring in them, as the Devonian, probably the Middle Devonian. On the basis of only the type of microstructure of *Tienodictyon zonatum*, called, in the original description, trabecular, Devonian age of this species was, however, questioned by GALLOWAY (1957) who referred it to the Mesozoic order Sphaeractinoidea. The Devonian age of the representatives of *Tienodictyon* was, on the other hand, confirmed by many specimens of this genus found and described by BOGOYAVLENSKAYA (1965) from the Devonian of Northern Ural Mts. At the same time, BOGOYAVLENSKAYA conducted an analysis of the species assigned to *Tienodictyon*, including in it some species of *Clathrodactyon*, described by YAVORSKY (*C. tschusovense* YAVORSKY, 1930; *C. katavense* YAVORSKY, 1930) and acknowledging the genus *Hammatostroma* STEARN, 1961 to be a younger synonym of the genus *Tienodictyon*. The latter view of BOGOYAVLENSKAYA, along with similar suggestions of NESTOR (1966a) and FLÜGEL & FLÜGEL-KAHLER (1968) were called in question by STEARN (1969) who continued to consider *Hammatostroma* as a separate genus. In the present writer's opinion, the characters which, according to STEARN'S diagnosis (1969) are supposed to differ *Hammatostroma* from *Tieno-*

dictyon, that is, a greater extent of bending skeletal elements in the interlaminar space and, consequently, less strongly expressed pillars, are not sufficient to accept *Hammatostroma* and *Tienodictyon* as separate genera.

Tienodictyon represents a link in the morphological lineage of stromatoporoids with the fibro-normal microstructure which leads from the Silurian *Clathrodiction*, through the Silurian-Lower Devonian *Simplexodiction*, to *Tienodictyon* and, subsequently, through an increase in the number of foramina and formation of ring-pillars, to *Pseudostromatoporella* n. gen. The genus *Anostylostroma* seems to be a side-branch of this lineage.

Within the genus *Tienodictyon*, the following three groups may be separate on the basis of a progressively increasing degree of folding of skeletal elements in the interlaminar space:

1) A group of *Tienodictyon carnicum*, in which most pillars still straightly intersect the interlaminar space and only rare ones are slightly bent and may form indistinct secondary laminae.

Species: *T. carnicum* (CHARLESWORTH, 1915),
T. undatum (YAVORSKY, 1950).

2) A group of *Tienodictyon zonatum*, in which skeletal elements in the interlaminar space already form distinct zones of tangled pillars joining each other to form secondary laminae from which straight pillars proper detach themselves subsequently.

Species: *T. zonatum* YABE & SUGIYAMA, 1941,
T. tschusovense (YAVORSKY, 1930),
T. katavense (YAVORSKY, 1930),
T. rarum BOGOYAVLENSKAYA, 1965.

3) A group of *Tienodictyon albertense*, in which skeletal elements in the interlaminar space are folded to the highest degree and in which tangled pillars only now and then form vestigial secondary laminae. The pillars proper are very short or do not occur at all.

Species: *T. albertense* (STEARNS, 1961),
T. delicatulum (KLOVAN, 1966),
T. nodosum (KLOVAN, 1966),
T. rectum (YAVORSKY, 1967).

Stratigraphic and geographical range. — Middle Devonian: China; Middle and Upper Devonian: Canada (Alberta, Canadian Rocky Mts.), USSR (Ural, Timan), Poland (Western Holy Cross Mts.).

***Tienodictyon zonatum* YABE & SUGIYAMA, 1941**

(Pl. XII, Figs. 1a, b and 2a, b)

1941. *Tienodictyon zonatum* YABE & SUGIYAMA; H. YABE & T. SUGIYAMA, *Tienodictyon...* pp. 139—141, Figs. 1-6.
non 1965. *Tienodictyon zonatum* YABE & SUGIYAMA; O. V. BOGOYAVLENSKAYA, *Rod...*, p. 38, Pl. 4, Figs. 1-3.
1968. *Tienodictyon zonatum* YABE & SUGIYAMA; E. FLÜGEL & E. FLÜGEL-KÄHLER, *Foss. Cat.*, Pt. 116, p. 492.
1969. *Tienodictyon zonatum* YABE & SUGIYAMA; C. W. STEARNS, *The stromatoporoid...* pp. 755-757, Pl. 99, Figs. 1-2; Pl. 100, Fig. 1.

Localities. — Radkowice, Sołtysia Hill (loc. 11); Chęciny, Zamkowa (Castle) Hill (loc. 9).

Material. — Two fragmentary (Z. Pal. St. I/5—6) and three complete (Z. Pal. St. I/9—11) colonies.

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/6 mm	min/6 mm	thickness	max/6 mm	min/6 mm	thickness
St. I/5	5	4	0.07—0.24	6	10	0.12—0.22
St. I/11	5	4	0.10—0.22	7	9	0.11—0.22

Description. — Coenosteum massive, irregularly hemispherical, on the average a dozen or so cm in diameter; its surface gently folded, smooth.

Laminae conspicuous, compact, slightly vary, frequently gently overlapping each other tangentially. In some places steeply bent laminae form mamelons which do not exceed in height one interlaminar space. Rare foramina and still rarer ring-pillars formed by upturned laminae (Pl. XII, Fig. 1*b*) occur in laminae. Both are covered by flat or convex tabulae. Foramina may also occur superposing each other by a few successively overlaying laminae. A zone of short pillars, vermicularly connected with each other and which, together with dissepiments which additionally bind them to each other, form a sort of a secondary lamina, occurs in the lower part of the interlaminar spaces approximately at one third of their height. Straight, cylindrical pillars, joining an overlaying lamina, detach themselves from this zone and run upwards sub-vertically. In addition to the two types of pillars referred to above, there also occur straight, cylindrical pillars which run perpendicular or obliquely to the surface of laminae.

Microstructure of laminae fibro-normal, with a dark zone sometimes visible at the base and of pillars — fibro-normal with a dark line in the axial part.

Discussion. — The specimens described are conspecific with the holotype, recently revised by STEARN (1969). Insignificant differences in an average thickness of laminae and number of pillars that occur over a length of 6 mm are contained within an interval limits of specific variability. Similarly small deviations from the holotype of *T. zonatum* are displayed by two species assigned by the writer to the group *Tienodictyon zonatum*, that is, *T. tschusovense* YAV. and *T. rarum* BOG. As a result of the revision, it may turn out that they should be assigned to *T. zonatum*, the more so as they occur almost synchronously with it. *Tienodictyon zonatum* differs from *Tienodictyon katavense* YAVORSKY in a more strongly expressed zone of tangled pillars and a greater number of foramina in laminae.

Stratigraphic and geographical range. — Middle Devonian, China (Eastern Yunnan), USSR (Northern Ural), Poland (Western Holy Cross Mts.).

***Tienodictyon albertense* (STEARNS, 1961)**(Pl. XII, Figs. 3*a, b*)

1961. *Hammatostroma albertense* STEARN; C. W. STEARN, Devonian..., pp. 940-941, Pl. 106, Figs. 2-4.
 ?1965. *Tienodictyon zonatum* YABE & SYGIYAMA; O. V. BOGOYAVLENSKAYA, Rod..., p. 38, Pl. 4, Figs. 1-3.
 1966*b*. *Hammatostroma albertense* STEARN; C. W. STEARN, Upper..., p. 45, Pl. 13, Fig. 3; Pl. 26; Fig. 3.
 1966. *Hammatostroma albertense* STEARN; J. E. KLOVAN, Upper..., p. 13, Pl. 3, Fig. 1*a-b*.
 1966. *Hammatostroma cf. albertense* STEARN; J. E. KLOVAN, Upper..., p. 11, Pl. 2, Fig. 5*a-b*.
 ?1966. *Hammatostroma nodosum* KLOVAN; J. E. KLOVAN, Upper..., p. 13, Pl. 3, Fig. 3.

1968. *Hammatostroma albertense* STEARN; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat. pt. 115, p. 20.

1969. *Hammatostroma albertense* STEARN; C. W. STEARN, The stromatoporoid..., pp. 757-758, Pl. 99, Figs. 7-8.

Localities. — Jaworznia-Moczydło Hill (loc. 25), Bolechowice — „Panek“ quarry (loc. 16).

Material. — Four large fragments of colonies (Z. Pal. St. I/7 and 12 to 14).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/6 mm	min/6 mm	thickness	max/6 mm	min/6 mm	thickness
St. I/7	6	3	0.10—0.12	—	—	0.07—0.17
St. I/12	5	3	0.08—0.12	—	—	0.07—0.15
St. I/14	7	4	0.07—0.12	—	—	0.07—0.17

Description. — Coenosteum massive, hemispherical, 15 cm in diameter at the base and 7 to 10 cm high. Surface slightly folded, smooth.

Laminae conspicuous, solid, strongly folded, rarely interrupted by foramina which are mostly closed by convex cyst plates. Small mamelons whose height does not exceed the size of one interlaminar space are formed sometimes as a result of the bend of laminae. Laminae are irregularly spaced, but no regular latilaminae are observed. Microstructure of laminae fibro-normal, with a dark line preserved sometimes at the base of a lamina. Pillars, confined to one interlaminar space, are irregularly bent and sometimes form secondary laminae. Cylindrical pillars, visible in tangential sections in the form of isolated dots (Pl. XII, Fig. 3b) run vertically or obliquely from a secondary lamina situated halfway or at two thirds of the height of an interlaminar space. Microstructure of pillars fibro-normal, with a dark axial line visible in the well-preserved specimens.

Discussion. — The specimens described are identical with the illustrations of the holotype (STEARNS, 1961, 1969). Insignificant differences in the dimensions of skeletal elements are caused by frequent growth disorders and are contained within the interval of specific variability. As mentioned in the discussion of the genus, *Tienodictyon albertense* is a representative of the group of *Tienodictyon* species with most strongly folded pillars. In addition to the species mentioned in the synonymy, such species as, *T. rectum* (YAV.) and *T. delicatulum* (KLOVAN) whose separation is based on only small differences in dimensions, should be probably included in this species. *T. albertense* differs from the species of the group of *T. zonatum* and *T. carnicum* in a higher degree of entanglement of pillars and in secondary laminae which are situated less conspicuously and higher up in the interlaminar space.

Stratigraphic and geographical range. — Middle (?) and Upper Devonian of Canada (Alberta, Northwest Territories); Middle Devonian of the USSR (Northern Ural); Middle (Upper Givetian) and Upper (Frasnian) Devonian of Poland (Western Holy Cross Mts.).

Genus PSEUDOSTROMATOPORELLA n. gen.

Type species: *Stictostroma huronense* PARKS, 1936; Middle Devonian (Hamilton Formation) of the U. S. A. (Alpena, Michigan).

Derivation of the name: *pseudo* = Lat. alleged, supposed, *Stromatoporella* = a genus of the Stromatoporoidea erected by Nicholson (1886).

Diagnosis. — Laminae conspicuous, compact, with many foramina. Pillars restricted to one interlaminar space, straight (spool-shaped or cylindrical) or irregularly bent. Common ring-pillars formed by the upturns of laminae. Many cyst plates and dissepiments. Microstructure fibro-normal.

Discussion. — The genus *Pseudostromatoporella* has been separated on the basis of some species which until now were included in the genus *Stromatoporella* NICHOLSON. The latter was hitherto understood by different authors not identically. Some of them (e.g. NICHOLSON, 1886; LÉCOMPTE, 1951) believed that regularly developed, spool-shaped pillars restricted to one interlaminar space only and straight laminae are the main diagnostic character of *Stromatoporella*. In their opinion, skeletal elements of *Stromatoporella* have microstructure similar to that of the forms of the genus *Stromatopora* s.l., that is, reticular or cellular. Some other authors (e.g. PARKS, 1936; GALLOWAY & ST. JEAN, 1957; ST. JEAN, 1967) emphasized an all-important diagnostic significance of ring-pillars. Under such circumstances, forms with a similar arrangement of skeletal elements but with radically different microstructures were placed within the genus *Stromatoporella*. On the basis of comparisons with the holotype of *S. granulata* (type species) attention was attracted by STEARN (1966*b*) to an improper assignment to *Stromatoporella* of the species which had not ring-pillars and laminae with a cellular microstructure.

Fundamental differences in the microstructure of *Stromatoporella* and *Pseudostromatoporella* are indicative of, on the one hand, a different (diphyletic) origin of both genera and, on the other, of a parallel and synchronous development of an almost identical system of skeletal elements, connected with one and the same trend in the modifications of the coenosarc (see General Part). The appearance of foramina in laminae, which subsequently transform into ring-pillars, is observed in various stages of complication of vertical elements of coenosteum as recorded in, for instance, a group of forms related to *Pseudostromatoporella* such as, *Simplexodictyon* BOGOYAVLENSKAYA, *Anostylostroma* PARKS or *Tienodictyon* YABE & SUGIYAMA. In the present writer's opinion, the species of the genera referred to above which display the presence of ring-pillars should also be transferred to *Pseudostromatoporella* n. gen.

The following two groups stand apart within the range of species referred to *Pseudostromatoporella* n. gen.:

1) A group of *Pseudostromatoporella huronensis* which contains species with many foramina and ring-pillars. The pillars proper are in this group straight or straight and bifurcated in the upper part and cylindrical or spool-shaped in outline.

- Species: *P. huronensis* (PARKS, 1936),
 ?*P. cellulosa* (NICHOLSON & MURIE, 1878),
P. eriensis (PARKS, 1936),
P. moosensis (PARKS, 1904),
P. insularis (PARKS, 1936),
 ?*P. solitaria* (NICHOLSON, 1886),
 ?*P. tuberculata* (NICHOLSON, 1873),
P. sniatkovi (YAVORSKY, 1931),
P. duplex (KHALFINA, 1953),
P. perelegans (KHALFINA, 1956*b*),
P. columbusensis (GALLOWAY & ST. JEAN, 1957).

2) A group of *Pseudostromatoporella insolita* which contains species with many foramina and ring-pillars, but with more or less irregularly bent pillars which may form secondary laminae in the interlaminar space.

Species: *P. insolita* (YAVORSKY, 1950),
P. loutougini (YAVORSKY, 1931),
P. voltschensis (YAVORSKY, 1950),
P. gapeevi (YAVORSKY, 1950),
P. abensis (YAVORSKY, 1950),
 ?*P. convicta* (YAVORSKY, 1950),
 ?*P. tyrganensis* (YAVORSKY, 1950).

Stratigraphic and geographical range. — Lower Devonian (rare): USSR (Salair); Middle Devonian: USA (Michigan, Ohio, Indiana), USSR (Kuznetsk Basin); Poland (Western Holy Cross Mts.); Upper Devonian: USSR (Salair), Poland (Western Holy Cross Mts.).

***Pseudostromatoporella huronensis* (PARKS, 1936)**

(Pl. XIII, Fig. 1*a-d*)

1936. *Stictostroma huronense* PARKS; W. A. PARKS, Devonian..., p. 83, Pl. 7, Figs. 1-3.
 (part) 1951. *Stromatoporella saginata* LECOMPTE; M. LECOMPTE, Les Stromatoporoides..., p. 171, Pl. 23, Figs. 1-3.
 1957. *Stromatoporella huronensis* (PARKS); J. J. GALLOWAY, Structure..., Pl. 36, Fig. 6.
 1957. *Stromatoporella huronensis* (PARKS); J. J. GALLOWAY & J. ST. JEAN, Middle..., p. 139, Pl. 9, Fig. 1*a-d*.
 1968. *Stictostroma huronense* PARKS; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss Cat. pt. 115, p. 192.

Locality. — Wietrznia quarry (loc. 34).

Material. — One large colony (Z. Pal. St. I/237).

Dimensions (in mm):

Z. Pal Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/237 A	10	6	0.04—0.10	8	5	0.07—0.10
St. I/237 B	10	7	0.03—0.11	8	6	0.05—0.10

Description. — Coenosteum solid, shaped like a flattened bell 52 cm in diameter at the base and 35 cm high. Conspicuous mamelons 3 to 5 cm high, mostly with an astrorhiza in the central part, occur on the surface.

Laminae well developed, with fibro-normal or compact (in poorly preserved parts) microstructure and with very numerous foramina. Spaces between laminae strongly varying within one and the same colony. In the zone of mamelons (astrorhizae), laminae are more densely arranged and thicker, while further from them laminae are more widely spaced and thinner (Pl. XIII, Fig. 1*a, c*). Similarly arranged are the spool-shaped pillars restricted to one interlaminar space. Very numerous ring-pillars are formed as a result of an upturn of laminae near foramina. Ring-pillars are 0.25 to 0.35 mm in outer diameter and their height on the average equals a half of an interlaminar space, only rarely reaching an overlaying lamina. Some of them are incompletely developed and in tangential section C-shaped in outline. Microstructure of ring-pillars and cylindrical pillars is fibro-normal or, in worse preserved parts of the colony, compact. Dissepiments not very numerous. Foramina and ring-pillars are covered with cyst plates.

Discussion. — *Pseudostromatoporella huronensis* displays a considerable similarity to *Pseudostromatoporella eriensis* (PARKS) and ?*Pseudostromatoporella solitaria* (NICHOLSON). According to GALLOWAY & ST. JEAN (1957), these species differ from one another in characters insignificant diagnostically such as, the size of mamelons, frequency of the occurrence of astrorhizae and a variable number of pillars. As a result of the revision, it may turn out that *P. huronensis* and *P. eriensis* should be considered as younger synonyms of *P. solitaria*. *Pseudostromatoporella huronensis* differs from the species of the group *Pseudostromatoporella insolita* in straight pillars which are not connected with each other in the interlaminae space.

Stratigraphic and geographical range. — Middle Devonian: the USA (Michigan, Ohio, Indiana); Upper Devonian (Frasnian): Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

Pseudostromatoporella moosensis (PARKS, 1904)

(Pl. XIV, Fig. 1a-c)

1904. *Actinostroma moosensis* PARKS; W. A. PARKS, Devonian..., p. 183, Pl. 2, Fig. 3; Pl. 3, Figs. 3-4.

1936. *Clathrodictyon moosense* (PARKS); W. A. PARKS, Devonian..., p. 34, Pl. 8, Figs. 3-4.

?1951. *Clathrodictyon amygdaloides* var. *subvesiculosum* LÉCOMPTE; M. LÉCOMPTE, Les Stromatoporoïdes..., p. 143, Pl. 18, Figs. 3, 3a, b.

1968. *Actinostroma moosense* PARKS; E. FLÜGEL & E. FLÜGEL-KÄHLER, Foss. Cat., pt. 15, p. 276.

Locality. — Radkowiec—Sołtysia Hill (loc. 11).

Material. — Two large fragments of colonies (Z. Pal. St. I/242 and 243).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/242	9	8	0.05—0.08	8	7	0.07—0.09
St. I/243	8	6	0.05—0.08	7	6	0.5—0.14

Description. — Coenosteum solid, the fragments available are 8 × 5 × 5 cm in size. The character of surface indiscernible. Indistinct latilaminae occur on broken lateral surfaces. Laminae clearly visible, conspicuous, mostly gently undulated, with widely spaced mamelons which are 2 to 5 mm high. Numerous foramina, sometimes turning into low ring-pillars, occur in laminae. In the region of mamelons, skeletal elements are clearly thicker and condensed. Astrorhizae of the type of integrata (KAZMIERCZAK, 1969) are situated centrally along the axis of mamelons. Thickness and spacing of laminae irregular. Pillars, restricted to one interlaminae space, are straight, cylindrical or spool-shaped, isolated or connected with each other to form, short, C-shaped in tangential section vertical walls. There also occur slightly bent pillars which sometimes branched in the upper part. Pillars are oriented vertically or, less frequently, slightly obliquely to the surface of laminae. Galleries suboval or subrectangular. Thickness of pillars rather considerably differentiated (cf. dimensions): between closely spaced laminae pillars are thicker and spool-shaped and in the case of wider spaced laminae they are thin and cylindrical. Microstructure of skeletal elements fibro-normal or compact.

Discussion. — *Pseudostromatoporella moosensis* differs from *P. huronensis* in less numerous and less strongly developed ring-pillars and sometimes branched cylindrical pillars. The latter character relates *P. moosensis* to the representatives of the genus *Anostylostroma* PARKS. Transferring the species *Actinostroma moosensis*, originally described by him, to the genus *Clathrodictyon* NICHOLSON & MURIE, PARKS emphasized however that it was to a considerable extent related to the representatives of *Stromatoporella* NICHOLSON, to which this species was subsequently assigned by GALLOWAY & ST. JEAN (1957). In the parts of its coenosteum with more strongly bent pillars, *P. moosensis* resembles some species of *Tienodictyon* YABE & SUGIYAMA, but secondary laminae characteristic of the latter have never been observed in *P. moosensis*.

Stratigraphic and geographical range. — Middle Devonian: Canada (Ontario), ?Belgium (Dinant), Poland (Givetian, Western Holy Cross Mts.).

***Pseudostromatoporella dammoniensis* (NICHOLSON, 1886)**

(Pl. XV, Fig. 2a-c)

1886a. *Stromatoporella dammoniensis* NICHOLSON; H. A. NICHOLSON, On some..., p. 237, Pl. 8, Figs. 3-4.

1968. *Stromatoporella dammoniensis* NICHOLSON; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 123 (with synonymy).

Localities. — Karczówka Hill (loc. 30), Dalnia and Grabina Hills (loc. 29).

Material. — Two specimens: a complete colony (Z. Pal. St. I/213) and a fragment (Z. Pal. St. I/232).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/213	10	7	0.05—0.10	9	8	0.08—0.13
St. I/232	7	6	0.07—0.12	7	6	0.07—0.15

Description. — Coenosteum solid, bulbous or cylindrical. Dimensions of the bulbous colony are 15 × 8 × 10 cm. Surface smooth or with mamelons.

Laminae not very clearly outlined, frequently irregular, thick, with many foramina and rarer ring-pillars, sometimes conically closed at the top. Ring-pillars large, 0.3 to 0.4 mm in outer diameter, with walls as thick as laminae. Pillars thick, limited by one interlaminae space, straight, cylindrical in longitudinal section, frequently connected with each other to form short, vermicularly curved, vertical walls. Some pillars superposed. Tabulae and dissepiments very rare or lacking. Microstructure fibro-normal. No astrorhizae observed.

Discussion. — Very thick laminae and pillars, the latter displaying a distinct tendency to superposition, are characteristic features of the species under study. A mean number of ring-pillars may, within the species, considerably fluctuate in relation to the holotype. For instance, *P. dammoniensis*, described by KLOVAN (1966) from the Upper Devonian (Upper Leduc Formation) of Canada has no ring-pillars. In the parts of coenosteum with a lesser number of foramina, *P. dammoniensis* is similar to some species of *Anostylostroma* PARKS

(for instance, *A. dupontense* GALLOWAY & ST. JEAN), from which it differs, however, in a lack of branched pillars.

Stratigraphic and geographical range. — Middle Devonian: England, Germany, Canada; Upper Devonian (Frasnian): Canada (Northwest Territories), Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

Genus *ANOSTYLOSTROMA* PARKS, 1936

Type species: Anostylostroma hamiltonense PARKS, 1936; Middle Devonian (Hamilton Formation), the USA (Michigan).

Diagnosis. — Laminae conspicuous, with very rare foramina. Pillars limited to one inter-laminar space, isolated, straight, mostly branched at the top, sometimes superposed. Columns formed by thickened pillars or bent and superposed segments of laminae may also occur. Tabulae and dissepiments not very numerous. Microstructure fibro-normal.

Discussion. — *Anostylostroma* belongs to the best studied and defined genera of the Stromatoporoidea. Most of its species were described from the area of North America. PARKS' typical material was revised by GALLOWAY (1967) and STEARN (1966*b*). According to these authors, the microstructure of *Anostylostroma* is transversely fibrous, but they did not determine whether it is original or secondary since they observed its transition into compact or into what is known as melanospherical microstructure. In the present writer's opinion, the transversely fibrous microstructure is an original one, much the same as observed in the genera *Simplexodictyon* BOGOYAVLENSKAYA, *Tienodictyon* YABE & SUGIYAMA and *Pseudostomatoporella* n. gen. genera closely related to *Anostylostroma*, from which the latter differs however, in characteristically branched pillars, much less numerous foramina and a lack of ring-pillars.

Stratigraphic and geographical range. — Middle Devonian: cosmopolite and abundant in North America, less so in Eurasia; Upper Devonian (less frequent): Canada, Belgium, the USSR, Poland.

Anostylostroma ponderosum (NICHOLSON, 1875)

(Pl. XIV, Figs. 2*a*, *b* and 3)

1875. *Stromatopora ponderosa* NICHOLSON; H. A. NICHOLSON, Descriptions..., p. 246, Pl. 24, Figs. 4, 4*a-b*.

1936. *Clathrodictyon ponderosum* (NICHOLSON); W. A. PARKS, Devonian..., p. 42, Pl. 5, Figs. 5—6.

1956. *Clathrodictyon ponderosum* (NICHOLSON); E. FLÜGEL, Revision..., p. 49.

1957. *Anostylostroma ponderosum* (NICHOLSON): J. J. GALLOWAY & J. ST. JEAN, Middle..., p. 111, Pl. 4, Figs. 2*a-b*.

?1962. *Anostylostroma ponderosum* (NICHOLSON); J. A. FAGERSTROM, Middle..., p. 245, Pl. 65, Figs. 1-8.

1968. *Stromatopora ponderosa* NICHOLSON; E. FLÜGEL and E. FLÜGEL-KAHLER, Foss. Cat. pt. 115, p. 326.

Localities. — Kadzielnia quarry (loc. 33) and Bolechowice — „Panek“ quarry (loc. 16).

Material. — Two colonies (Z. Pal. St. I/214 and 215).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/214	10	8	0.07—0.11	8	7	0.05—0.15
St. I/215	10	9	0.05—0.09	10	10	0.07—0.11

Description. — Coenosteum large, massive, irregularly hemispherical, 30 cm in diameter at the base and 20 cm high. Surface with conspicuous astrorhizal mamelons. Indistinct latilaminae on the broken lateral surfaces.

Laminae solid, thick, with very rare foramina, strongly bent in the zone of astrorhizal mamelons. Pillars restricted by one interlaminar space, straight, cylindrical in longitudinal section and sometimes slightly branched at the top. Pillars usually somewhat darker in tint than laminae. Some of the pillars superposed through several laminae. Dissepiments rare. Skeletal elements in the zone of mamelons condensed. Astrorhizae of the „separate“ type, (KAŻMIERCZAK, 1969) occurring in the central part of mamelons. Microstructure compact, fibro-normal microstructure preserved here and there.

Discussion. — The specimens under study are almost identical with NICHOLSON's original, whose description was supplemented by GALLOWAY & ST. JEAN (1957). Specimens, described by FAGERSTROM (1962) as *A. ponderosum* have reticular laminae and probably belong to the genus *Atelodictyon* LEC. *A. ponderosum* conspicuously differs from other species of *Anostylostroma* in a small number of bifurcated pillars and their frequent vertical superposition.

Stratigraphic and geographical range. — Middle Devonian: USA (Indiana, Ohio); Upper Devonian (Frasnian): Poland (Western Holy Cross Mts.).

Morphological group „B“

Genus *STICTOSTROMA* PARKS, 1936

Type species: Stictostroma mamilliferum GALLOWAY & ST. JEAN, 1957; Middle Devonian (Onondaga limestone), Canada (Ontario).

Diagnosis. — Laminae well developed, sometimes with rare foramina. Pillars limited to one interlaminar space, straight, cylindrical or spool-shaped, sometimes connected with each other to form longer or shorter vermicularly curved vertical walls. Pillars perpendicular or, less frequently, oblique to the laminae. Dissepiments and tabulae not very numerous. Microstructure reticular, condensed.

Discussion. — PARKS' separation of the genus *Stictostroma* became the subject of many discussion, in which some of the authors were of the opinion that it is a synonym of *Stromatoporella* NICHOLSON (cf. LECOMPTE, 1951). The present writer agrees, however, with the view of GALLOWAY (1957) and ST. JEAN (1962) that despite a considerable similarity in the arrangement

of laminae and pillars and in the microstructure, the lack of ring-pillars is a sufficient argument for distinguishing *Stictostroma* as a separate genus. As a result of the transformation of foramina into ring-pillars, a process which was most likely to be related with a change in the type of skeletal secretion around coenosarcular strands penetrating deeper into coenosteum, *Stictostroma* was transformed into *Stromatoporella* (see General Part). There are several species marked by transitional characters, that is, foramina developed to an equal extent and incipient ring-pillars which are sometimes difficult to be unequivocally classified in one of the genera referred to above. *Stictostroma* differs from *Pseudostromatoporella* n. gen., in a small number of ring-pillars, and a reticular microstructure. The reticular microstructure of *Stictostroma* is mostly considerably better visible in pillars (in a tangential section) than in laminae in which it is subject to obliteration and may give the impression of a compact or even transversely porous one (ST. JEAN, 1962). The reticular structure of laminae is emphasized, in the case of well-preserved specimens, by dark — or light-coloured zones related with a growth periodicity (for explanation see p. 28).

Stratigraphic and geographical range. — Middle Devonian (abundant): North America (mostly), Eurasia; Upper Devonian (less frequent): Canada, Belgium, Poland.

***Stictostroma sociale* (NICHOLSON, 1892).**

(Pl. XV, Fig. 1a-c)

1892. *Stromatoporella socialis* NICHOLSON; H. A. NICHOLSON, A monograph..., p. 206, Pl. 26, Figs. 5-7.

1951. *Stromatoporella socialis* NICHOLSON; M. LECOMPTE, Les Stromatoporoïdes..., p. 163, Pl. 21, Figs. 2, 2a, 3.

1968. *Stromatoporella socialis* NICHOLSON; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 393.

Locality. — Kadzielnia quarry (loc. 33).

Material. — Three, almost complete colonies (Z. Pal. St. I/239—241).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/239	8	6	0.05—0.14	7	6	0.05—0.12
St. I/240	10	7	0.06—0.12	7	6	0.05—0.12
St. I/241	9	6	0.05—0.12	7	6	0.05—0.11

Description. — Coenosteum solid, irregularly bulbous or sheet-like. Diameter of the largest colony about 40 cm at the base, height about 32 cm. Surface smooth, gently folded, with slightly projecting numerous corallites of *Syringopora* sp. Latilaminae obscure.

Laminae well defined, compact, gently undulated and frequently wedging out. Thickness and spacing of laminae considerably differentiated within one and the same colony (Pl. XV, Fig. 1b). Foramina very rare. Pillars limited by one interlaminar space, straight, cylindrical or spool-shaped, running perpendicularly or, less frequently, obliquely to the surface of laminae. Pillars irregularly spaced, which causes a considerable differentiation in the width of galleries. The latter are from perfectly circular to subrectangular in outline. Most pillars isolated, only some of them join each other to form short, vertical walls. Dissepiments rare. The reticular

microstructure very strongly condensed, with centers of calcification clearly visible in tangential sections. Light-coloured growth discontinuity surfaces are sometimes marked in laminae.

Discussion. — *Stictostroma sociale* (NICHOLSON) was described in detail by LECOMPTE (1951) as *Stromatoporella socialis*. Emphasizing the lack, in this species, of ring-pillars characteristic of *Stromatoporella*, STEARN (1966*b*) assigned it, however, to the genus *Stictostroma*. *S. sociale* probably includes a considerable number of species, described by YAVORSKY either as *Stromatoporella* or *Clathrodictyon* (e.g.: *S. strelnensis*, *S. tschernensis*, *S. aff. gapeevi*, *C. uralicum*, *C. tyzhnovi*) from Ural Mts. and Kuznetsk Basin. A complete comparison will be possible only when information is obtained on the microstructure of these species. *S. sociale* differs from *Stictostroma lensiforme* (LECOMPTE) in a looser reticulum of microstructure with a greater number of the centers of calcification and a more closely spaced skeletal elements and from *Stictostroma maclareni* STEARN and *S. kolymense* (YAVORSKY) — in finer and more delicate laminae and pillars and rare ring-pillars.

Stratigraphic and geographical range. — Middle Devonian: England, Belgium, Germany, ?USSR (Ural Mts., Kuznetsk Basin); Upper Devonian: USSR (Ural Mts., Kuznetsk Basin), Poland (Western Holy Cross Mts.).

Stictostroma kolymense (YAVORSKY, 1961)

(Pl. XVI, Figs. 1*a-b*; 2, 3*a-b*)

1961. *Parallelopora kolymensis* YAVORSKY; V. I. YAVORSKY, *Stromatoporoidea...*, pp. 48-49, Pl. 29, Figs. 4-7.

?1961. *Parallelopora ulatuaensis* YAVORSKY; V. I. YAVORSKY, *Stromatoporoidea...*, pp. 46-47, Pl. 27, Figs. 6-8.

1968. *Parallelopora kolymensis* YAVORSKY; E. FLÜGEL & E. FLÜGEL-KAHLER, *Foss. Cat.*, pt. 115, s. 224.

Localities. — Sitkówka (locs. 19 and 20), „Kowala“ quarry (loc. 13), Dalnia Hill (loc. 29).

Material. — Four colonies, including two preserved completely (Z. Pal. St. I/182 and St. I/234 to 236).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/182	6	4	0.12–0.24	7	4	0.12–0.19
St. I/235	5	4	0.10–0.22	6	5	0.14–0.20
St. I/236	5	4	0.12–0.24	7	5	0.14–0.20

Description. — Coenosteum massive, bulbous or tabular. The largest colony is 17×17×10 cm in size. Surface smooth with frequent and numerous outlets of the corallites *Syringopora* sp.

Laminae conspicuous, irregular in thickness, disappearing in some parts and replaced by horizontal dissepiments. Many foramina 0.10 to 0.70 mm in diameter, open freely towards an overlaying interlaminar space or covered by slightly convex cyst plates, occur in laminae. Pillars limited to one interlaminar space, straight, cylindrical or spool-shaped, in tangential sections of coenosteum round or oval in outline. A considerable number of pillars superposed over long stretches. Galleries high, subrectangular or round in outline. Dissepiments rare or

lacking. Microstructure of laminae and pillars reticular, condensed, here and there with traces of a looser reticulum. Closely spaced, dark calcification centers are clearly visible in tangential sections through laminae and pillars. In some parts of laminae, white, irregular growth interruption streaks are marked in vertical sections.

Discussion. — The specimens under study are identical with a type specimen, erroneously assigned by YAVORSKY (1961) — to the genus *Parallelopora* BARG. Attention was attracted to YAVORSKY'S mistake by FLÜGEL & FLÜGEL-KAHLER (1968) who suggested the possibility that this species may belong to the genus *Trupetostroma* PARKS. The latter possibility is precluded, in the present writer's opinion, by a clearly reticular microstructure of the species described which is well visible in the type specimen refigured in the present paper (Pl. XI, Fig. 6), as well as by the lack of large vacuoles in pillars characteristic of *Trupetostroma*. *Stictostroma kolymense* is most closely related to *Stictostroma maclareni* STEARN, from which it differs radically in thicker and more widely spaced laminae and pillars and in a greater number of foramina.

Stratigraphic and geographical range. — Middle Devonian: USSR (Kolyma River), Poland (Givetian of the Western Holy Cross Mts.); Upper Devonian (Frasnian): Poland (Western Holy Cross Mts.).

Stictostroma lensiforme (LECOMPTE, 1951)

(Pl. XVII, Fig. 1a-e)

1951. *Syringostroma lensiforme* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 211-212, Pl. 34, Figs. 5, 5a-b; Pl. 35, Fig. 1.
 (part) 1951. *Syringostroma percanaliculatum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 204-206, Pl. 32, Fig. 1.
 1957. *Stromatoporella tomiensis* YAVORSKY; V. I. YAVORSKY, Stromatoporoïde..., pp. 52-53, Pl. 27, Figs. 1-3.
 1957. *Stromatoporella* aff. *tomiensis* YAVORSKY; V. I. YAVORSKY, Stromatoporoïde..., p. 53, Pl. 27, Figs. 4-6.
 1957. *Stromatoporella izylensis* YAVORSKY; V. I. YAVORSKY, Stromatoporoïde..., p. 54, Pl. 27, Figs. 7-8; Pl. 28, Figs. 1-2.
 1961. *Clathrodictyon copulatum* YAVORSKY; V. I. YAVORSKY, Stromatoporoïde..., pp. 24-25, Pl. 11, Fig. 3; Pl. 12, Fig. 1.
 1968. *Syringostroma lensiforme* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 242.

Localities. — Sitkówka (locs. 21 and 22), Jurkowiec-Budy (Eastern Holy Cross Mts.).

Material. — Fifteen colonies, including five complete (Z. Pal. St. I/145 to 152 and St. I/199 to 205).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars and/or vertical walls		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/146	12	9	0.04—0.07	11	9	0.06—0.12
St. I/149	14	11	0.04—0.07	10	8	0.06—0.10
St. I/199	10	9	0.04—0.08	10	8	0.06—0.13
St. I/202	12	8	0.04—0.07	11	9	0.06—0.11

Description. — Coenosteum massive, spherical, hemispherical or irregularly bulbous, with or without mamelons. Surface smooth, even or slightly undulated. Many outlets of coral-lites of *Syringopora* sp. are visible on the surface of some colonies. Latilaminae distinct.

Laminae conspicuous, thin, even or irregularly bent and frequently overlapping each other tangentially. Numerous foramina, usually freely open towards an overlaying interlaminar space, less frequently covered by a tabula in the plane of a lamina, occur in laminae. Laminae irregularly spaced; more or less regular latilaminae repeatedly appear in vertical sections through coenosteum. Vertical elements of skeleton limited by one interlaminar space varying in thickness and frequently superposed. Meandering vertical walls, sometimes connected by dissepiments, primarily make up vertical elements. More widely spaced, cylindrical or spool-shaped pillars are visible in tangential sections in the form of isolated, round or oval dots. Vertical walls and pillars run perpendicularly to the laminae and may be slightly bent in vertical plane. Galleries round or oval in outline.

Microstructure of skeleton, except for tabulae and dissepiments, reticular, condensed, with clearly visible (particularly in polarized light) — both in tangential and vertical sections — dark calcification centers. Reticular microstructure much more clearly expressed in laminae in which very many, dark dots of calcification centers are visible in tangential sections (Pl. XVII, Fig. 1 b-c). Their number in pillars and vertical walls is considerably decreased. They display the tendency to form monocenters, surrounded by a thick mass of a homogenous, light-coloured calcite (Pl. XVII, Fig. 1 c-e).

Dark growth inhibition surfaces are clearly visible in planes of laminae.

Discussion. — *Stictostroma lensiforme* is one of the species, mistakenly assigned by LECOMPTE (1951) to the genus *Syringostroma* NICH. This species was transferred by GALLOWAY & ST. JEAN (1957) to *Stictostroma*. *S. lensiforme* differs from *Stictostroma kolymense* (YAVORSKY) in a much more condensed reticular microstructure and more finer structure of skeleton and from *Stictostroma mamilliferum* GALLOWAY & ST. JEAN and *Stictostroma jeffersonvillense* GALLOWAY & ST. JEAN in a small number of pillars which occur with well-developed vertical walls and a considerable degree of their vertical superposition. Noteworthy is a considerable variability which is marked in the structure of coenosteum, both within one and the same colony and between colonies coming from one and the same time assemblage (from one and the same bed). This variability primarily concerns the number of skeletal elements per measured unit of coenosteum (cf. table of dimensions), these values being indiscriminately considered by many authors as an only basis for separating new species.

Stratigraphic and geographical range. — Middle Devonian (Givetian): Belgium (Dinant), Poland (Western and Eastern Holy Cross Mts.); Upper Devonian (Frasnian): Belgium (Dinant), USSR (Ural Mts., Kuznetsk Basin), Poland (Givetian-Frasnian transitional beds in Western Holy Cross Mts.).

Genus **STROMATOPORELLA** NICHOLSON, 1886

Type species: Stromatopora granulata NICHOLSON, 1873; Devonian (Corniferous Limestone), Canada (Lake Erie).

Diagnosis. — Laminae well-developed, with or without foramina. Vertical elements of coenosteum limited by one interlaminar space formed as ring-pillars by laminae upturned around foramina and as simple, cylindrical pillars straight or spool-shaped. Pillars and ring-pillars may be partly superposed. Dissepiments and tabulae common. Microstructure reticular, variously condensed.

Discussion. — The diagnosis given above is based on NICHOLSON's (1873, 1886b) original description and on a revision of the type material conducted by STEARN (1966b). In the diagnosis

of *Stromatoporella*, STEARN's attention was focused on a reticular (called by STEARN „ordinicellular“ or „cellular“) nature of the microstructure and on the presence of ring-pillars. These facts allow one to eliminate from the genus *Stromatoporella*, several species which have not the characters mentioned above. The reticular nature of the microstructure of *Stromatoporella* makes it similar to *Stromatopora* GOLDFUSS, which has already been noticed by, among other authors, PARKS (1936) and LECOMPTE (1951), despite the fact that the genera differ from each other radically in the arrangement of their skeletal elements. SLEUMER (1969, and also personal communication) expressed the view that the forms, which have ring-pillars but their laminae are composed of microlaminae should not be included in *Stromatoporella*. He separates these forms from those with the cellular (ordinicellular) microstructure. Considering SLEUMER's view as a sound one, the writer has suggested in the present paper a separation of forms with their structure identical with that of *Stromatoporella*, but with a microlaminar (here called fibro-normal) microstructure of laminae, to erect a new genus, namely *Pseudostromatoporella*.

In the present writer's opinion, the microstructure of *Stromatoporella* s.s. is a derivative of the reticular microstructure of such genera as *Parallelostroma*, *Stromatopora*, *Syringostromella*, etc. preserved vestigially. Much the same as in other lineages of the group of microreticulate stromatoporoids, the original reticulum was, in this genus, subject to a gradual condensation up to the appearance of seemingly compact skeletal elements, the original nature of which reveals, however, the presence of many calcification centers within the homogenous calcite. In many species of *Stromatoporella* these calcification centers are visible only in tangential sections of laminae and pillars. The process of condensation of reticulum was combined in *Stromatoporella* with acquiring a considerable regularity in the geometry of skeleton (an excellently expressed laminarity and growth periodicity) and a progressively increasing number of ring-pillars. The last-named provide a convenient index allowing one to separate *Stromatoporella* from undoubtedly more primitive representatives of *Stictostroma* which sometimes have only foramina.

Assuming the number of ring-pillars and the degree of their development for a fundamental diagnostic criterion of the species of *Stromatoporella* s.s., we may divide them into the following two groups;

- 1) species with very numerous ring-pillars, usually connecting two neighbouring laminae; pillars relatively few (e.g., *Stromatoporella selwyni* NICH.);
- 2) species with only few low and frequently C-shaped ring-pillars, many foramina and pillars, on the whole, these forms are similar to some *Stictostroma* (e.g., *Stromatoporella mudlakensis* (GALL.).

In view of a considerable variability within the range of a colony or of an intraspecific (intrapopulation) variability characteristic of most stromatoporoids, it is very likely that the revision will result in the necessity of a considerable reduction in the number of the species of *Stromatoporella*, most of which were separated on the basis of insignificant differences in the number of laminae or pillars on a definite section of coenosteum.

A new genus *Tubuliporella*, separated by KHALFINA (1968) is probably a synonym of *Stromatoporella* and represents only a special case of the species of this genus in which ring-pillars superpose each other on longer sections of coenosteum.

A more extensive discussion of *Stromatoporella* as a link in the lineage of forms having a reticular microstructure is presented in the General Part (see p. 71).

Stratigraphic and geographical distribution. — Middle Devonian (abundant and cosmopolitan): North America, Eurasia, Australia; Upper Devonian (Frasnian): Canada (Alberta), Belgium (Dinant), Poland (Western Holy Cross Mts.).

***Stromatoporella mudlakensis* GALLOWAY, 1960**

(Pl. XVIII, Fig. 1a-d)

1960. *Stromatoporella mudlakensis* GALLOWAY; J. J. GALLOWAY & G. M. EHLERS, Some..., pp. 77-78, Pl. 7, Figs. 2a-b, 3, 4a-b, 5a-b.

1968. *Stromatoporella mudlakensis* GALLOWAY; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat. pt. 115, p. 277.

Localities. — Wietrznia quarry (loc. 34), Kadzielnia quarry (loc. 33).

Material. — One complete (Z. Pal. St. I/238) and three fragmentary colonies (St. I/453, 454, 451).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/238	5	4	0.05—0.24	5	4	0.05—0.20
St. I/451	8	5	0.07—0.18	7	5	0.07—0.18

Description. — Coenosteum irregularly cylindrical with nodelike lateral branches. Surface smooth. Height of the preserved colony 8 cm, width about 5 cm.

Laminae well developed, folded, thin in the axial zone of coenosteum and even and thicker in the peripheral zone. Numerous foramina 0.14 to 0.16 mm in diameter, most frequently covered with horizontal or slightly convex tabulae, occur in laminae. Vertical elements, limited by one interlaminar space, are mostly composed of straight, cylindrical pillars, perpendicular to laminae and rare ring-pillars. The last-named are low and rarely reach halfway the length of an interlaminar space. Distances between laminae and pillars are uneven and, consequently, the height of galleries is strongly variable. The outline of galleries in vertical section round to subrectangular. Dissepiments rare. Microstructure of laminae and pillars irregularly reticular, condensed.

Discussion. — The species described is an instance of a representative of *Stromatoporella* similar in a small number of ring-pillars to species of the genus *Stictostroma* PARKS. The presence of many ring-pillars in this species, mentioned in the original description (GALLOWAY & EHLERS, 1960, p. 77), is a misunderstanding which results from applying this term to many foramina excellently visible in the plane of laminae in tangential sections illustrated by GALLOWAY (*l.c.*, Pl. 7, Figs. 2b and 4b), whereas ring-pillars proper, occurring in the interlaminar space, are few and not fully developed (C-shaped). Other characters, of the species described are identical with those of the holotype, including a subcylindrical shape of coenosteum and the lack of axial canal.

Stratigraphic and geographical distribution. — Middle Devonian (Petoskey Formation) USA (Michigan); Upper Devonian (Frasnian) Poland (Western Holy Cross Mts.).

Genus **STROMATOPORA** GOLDFUSS, 1826

Type species: Stromatopora concentrica GOLDFUSS, 1826; Middle Devonian, Germany (Eifel).

Diagnosis. — Coenosteum composed of irregularly twisted, frequently anastomosing, thick skeletal elements of which neither laminae nor pillae are individualized. Vermiculary

twisted canals (coenotubes) which may pass in vertical tubes (autotubes) are surrounded by the skeletal tissue. Many dissepiments occur in coenotubes and tabulae in autotubes. Skeletal microstructure irregularly reticular, loose or condensed.

Discussion. — The genus *Stromatopora*, very broadly understood by previous authors, has recently been restricted. The diagnosis presented above characterizes *Stromatopora s.s.* after two new genera, *Parallestroma* and *Syringostromella*, were separated from it by NESTOR (1966). The necessity of dividing *Stromatopora s.s.* was also justified by STEARN (1966*b*) who, after analyzing the microstructure of various species of *Stromatopora*, took the standpoint that the forms with a regularly reticulate microstructure (e.g., in *S. typica* ROSEN), as well as the species which are marked by the presence of microlaminae in their skeletons (e.g., *S. laminosa* LECOMPTE), should be excluded from this genus. In the present writer's opinion, emphasizing a distinct separateness of the two types of microstructure in *Stromatopora*, called by STEARN (*l.c.*) „cellular“ and „microreticular“, is not sufficiently justified. Both these microstructures are only various combinations of one, reticular microstructure which may be expressed either in a regular or irregular form. Both forms of the reticular microstructure may occur simultaneously in various places of the skeleton of one and the same colony (cf. Pl. X, Fig. 2). More or less closely spaced, dark or light colored bands, called by STEARN „microlaminae“, are in the writer's interpretation a symptom of growth rhythmicity not having a major diagnostic importance.

Stromatopora differs from *Syringostroma* NICHOLSON in the lack of columnar pillars, from *Salirella* KHALFINA and *Parallelopore* BARGATZKY in an only slight superposition of skeletal elements forming systems of vertical walls and from *Talaestroma* GALLOWAY in a reticulate microstructure of the skeleton. *Stromatopora* is one of the most conservative genera of the Stromatoporoidea continuously occurring from the Middle Silurian up to the end of the Devonian. Particular species of this genus may, however, be relatively easily separated on the basis of a progressive tendency, displayed by many of them, to 1) setting in order initially irregular coenostelae and forming of them systems of superposed vertical walls, 2) arranging of coenostromae in more or less regular laminae, 3) decreasing the thickness of skeletal elements and primarily, 4) on the one hand, condensation and, on the other, reduction of the microstructural reticulum. Hence, despite its conservative nature, *Stromatopora* probably gave origin to new genera such as *Syringostroma* NICH., *Talaestroma* GALL., or *Ferestromatopora* YAV. The range of the variability in the morphology of *Stromatopora*, presented above, may become a basis for revision and certainly also for a considerable decrease in the number of species of this genus, which are frequently separated on the basis of characters devoid of a diagnostic importance such as, differences in dimensions and number of skeletal elements, shape of coenosteum, presence or absence of astrorhizae, etc.

Stratigraphic and geographical distribution. — Silurian (Wenlockian) — Devonian (Frasnian) cosmopolitan: North America, Eurasia, Australia.

Stromatopora cooperi LECOMPTE, 1952

(Pl. XIX, Figs. 1*a-d*, 2)

1952. *Stromatopora cooperi* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 285-288, Pl. 59, Fig. 2; Pl. 60, Fig. 1-4.
 1960. *Stromatopora planulata* (HALL & WHITEFIELD)?; J. J. GALLOWAY, Devonian..., pp. 629-630, Pl. 75, Fig. 1*a-b*.
 1963. *Stromatopora cooperi* LECOMPTE; C. W. STEARN, Some..., pp. 664-665, Pl. 87, Figs. 6-7; Pl. 88, Fig. 2.
 1968. *Stromatopora cooperi* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KÄHLER, Foss. Cat., pt. 115, pp. 103-104 (with synonymy).

Localities. — Kowala-railway cut (loc. 12), Sitkówka III (loc. 21), Sitkówka IV (loc. 22), Kadzielnia-quarry (loc. 33).

Material. — Six colonies, including three preserved completely (Z. Pal. St. I/15—20).

Description. — Coenosteum massive, irregularly bulbous, reaching $20 \times 20 \times 16$ cm in size. Surface smooth, slightly folded, with a variable number of small (8—14 mm) astrorhizae. Distinct latilaminae on lateral surfaces.

In coenosteum are marked alternate zones, composed of vermicularly twisted coenostelae which surround coenotubes with a predominantly horizontal arrangement, as well as zones in which meandering coenostelae are oriented mostly vertically and surround coenotubes sinusoidal in tangential section. The last-named coenotubes are sometimes turned into autotubes as a result of being closed by vertical walls. The skeletal tissue occupies 60 to 70 per cent of the volume of coenosteum. The walls of coenostelae are 0.09 to 0.12 mm thick, a mean diameter of coenotubes and autotubes being 0.12 mm. Coeno- and autotubes are intersected by many, on the whole regularly distributed, dissepiments and tabulae. In some specimens (Z. Pal. St. I/20), wide zones are observed in which coenotubes disappear as a result of the formation of laminae. The laminarity is frequently emphasized by dark lines of growth inhibition in the planes of laminae. Skeletal microstructure irregularly reticulate, condensed. Degree of condensation is higher in vertical segments of coenostelae.

Discussion. — *S. cooperi* is characterized by a considerable intracolony variability, which is manifested by zonal changes in the system of elements of coenosteum. A similar variability is also observed in the type material (LECOMPTE, 1952). The tendency to setting in order the system of skeletal elements is displayed by *S. cooperi* as two simultaneous trends: on the one hand, the coenostelae become more and more vertical and, on the other, regular laminae are formed. Under such circumstances, it is difficult to decide which of the two systems represents a „normal“ skeletal tissue. *S. cooperi* is one of the few species of *Stromatopora* which survived up to the Upper Devonian and, at the same time, preserved the irregular structure of their coenosteum very similar to that of the Silurian species. *S. cooperi* differs, however, from the older species of *Stromatopora* in a high degree of condensation of microreticulate tissue. The last-named character brings them very close to some of the species of *Taleastroma* GALLOWAY, in particular to those, in which the homogenization process of microstructure is still not very far advanced (e.g., *T. cumingsi* (GALLOWAY & ST. JEAN). A still clearly reticular character of microstructure in *S. cooperi* (cf. Pl. XIX, Fig. 1d) seems to contradict GALLOWAY'S (1957) suggestion on a possible assignment of this species to *Taleastroma*. *S. cooperi* differs from *S. planulata* (HALL & WHITFIELD) *sensu* LECOMPTE (1952) in a considerably more condensed microstructure and less vertical position of coenostelae and from *S. hüpschi* BARGATZKY in finer and more condensed skeletal structural elements, as well as more condensed microstructure.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian) — Upper Devonian (Frasnian): Canada (Alberta, Mackenzie Valley), Belgium (Dinant Basin), Czechoslovakia (Moravia), Poland (Western Holy Cross Mts.).

Stromatopora colliculata NICHOLSON, 1886

(Pl. XX, Figs. 1a-c, 2a-b)

- 1886b. *Stromatopora concentrica* var. *colliculata* NICHOLSON; H. A. NICHOLSON, A monograph..., Pl. 3, Fig. 5; Pl. 5, Fig. 16-17.
 1891b. *Stromatopora concentrica* var. *colliculata* NICHOLSON; H. A. NICHOLSON, A monograph..., p. 165.
 1968. *Stromatopora concentrica colliculata* NICHOLSON; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 90 (with synonymy).

Locality. — Jurkowice-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.).

Material. — Five completely preserved coenostea (Z. Pal. St. I/168—170, 219, 220).

Description. — Coenosteum massive, irregularly bulbous or cylindrical with surface smooth or covered with variously sized mamelons. Part of the colonies overgrown on colonies of Tabulata (*Caliapora* sp.).

Skeletal elements thick, occupying about 50 per cent of the volume of coenosteum. Distinct coenostromae, interrupted by vermicular coenotubes round in transverse section and 0.24 to 0.65 mm in diameter are visible in the skeleton. Autotubes rare, short. Coenostelae in a nearly vertical position and usually superposed on each other over considerable lengths of coenosteum, meandering in tangential section. Coenostelae are 0.12 to 0.36 mm thick. In some places, coeno- and autotubes disappear while coenostromae acquire the character of laminae with coenostelae perpendicular to them. Galleries thus formed are usually round in outline (Pl. XVI, Fig. 2*a-b*). Distinct dark-coloured lines of growth inhibition are visible in the plane of coenostromae. Growth increments very uneven, but no regular latilaminae are observed. Coeno- and autotubes are intersected by dissepiments and tabulae which as a rule are regularly distributed. Microstructure irregularly reticular, condensed, particularly clearly visible in tangential sections (Pl. XX, Fig. 1*c*).

Discussion. — The separation of the variety *colliculata* from *Stromatopora concentrica* GOLDF. was justified by NICHOLSON (1891*b*, pp. 165—166) by the presence, in *colliculata*, of mamelons, astrorhizae different than those in *S. concentrica* and a differently shaped coenosteum. According to most authors, these characters in Stromatoporoidea are insignificant diagnostically. In the present writer's opinion, the specific separateness of *Stromatopora colliculata* is, however, expressed sufficiently clearly. *S. colliculata* differs from *S. concentrica* GOLDFUSS (*sensu* NICHOLSON, 1886*b*) in more strongly developed coenostromae, more vertically arranged coenostelae and a more condensed reticulum of microstructure.

Stratigraphic and geographical distribution. — Middle Devonian (mainly Givetian): Australia (Victoria), USSR (Kuznetsk Basin), Germany (Eifel). Czechoslovakia (Moravia), Poland (Eastern Holy Cross Mts.).

***Stromatopora divergens* GALLOWAY & ST. JEAN, 1957**

(Pl. XXI, Fig. 1*a-b*)

1957. *Stromatopora divergens* GALLOWAY & ST. JEAN; J. J. GALLOWAY & J. ST. JEAN, Middle..., pp. 173-174, Pl. 13, Fig. 4*a-b*.

1957. *Stromatopora divergens* GALLOWAY & ST. JEAN; J. J. GALLOWAY, Structure..., Pl. 36, Fig. 5.

1967. *Trupetostroma adriani* BIRKHEAD; P. K. BIRKHEAD, Stromatoporoides..., pp. 63-64, Pl. 11, Fig. 3*a-d*.

1968. *Stromatopora divergens* GALLOWAY & ST. JEAN; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 138.

Locality. — Jurkowice-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.).

Material. — One complete coenosteum (Z. Pal. St. I/194).

Description. — Coenosteum massive, irregularly bulbous, with prominent but gently rounded mamelons mostly with an astrorhiza in the central part. Diameter at the base 8 cm, height 4 cm. Latilaminae indistinct.

Skeletal tissue solid, occupying about 75 per cent of the volume of coenosteum. Very thick (on the average 0.5 mm) coenostelae surround long and thin (0.12 to 0.15 mm in dia-

meter) autotubes, sometimes twisted vermicularly, occurring in a number of four over a 2 mm stretch. Tabulae are regularly distributed in autotubes. Many lines of growth inhibition, darker than skeletal substance, give the skeleton its laminated character. Growth increments, marked by the growth discontinuity lines, uneven, frequently considerable condensed and forming latilaminae. Skeletal microstructure homogenous, compact, with dark points which represent not very closely distributed calcification centers visible in tangential sections.

Discussion. — The specimen described differs from the holotype in slightly thicker and longer autotubes, as well as a more solid skeleton, the remaining characters being identical. The most characteristic of *S. divergens* are strongly developed and numerous autotubes and a high degree of homogenization of the microstructural reticulum with calcification centers more widely spaced than those in *Stromatopora spissa* LEC. *S. divergens* differs from the related *S. obscura* GALL. & ST. JEAN, *S. marpleae* GALL. & ST. JEAN and *S. laminosa* LEC. in the lack of a distinctly reticular microstructure. The presence of autotubes brings *S. divergens* close to the representatives of *Salirella* KHALFINA, from which it differs in a less regular system of coenostelae and in microstructure. GALLOWAY and ST. JEAN (1957) erroneously used the term laminae to designate zones cut off by successive surfaces of growth discontinuities which are only growth increments varying in size. Likewise, the term „galleries“, used by them, does not correspond to the galleries proper which occur only in the case of the presence of clear laminae. The „galleries“ in *S. divergens* are more sections of autotubes contained between successive growth discontinuity surfaces. A striking similarity should be emphasized in the system of skeletal elements and microstructure of the species described to those of two representatives of dendroid stromatopoids, that is, *Stachyodes verticillata* (MCCOY) and *Stachyodes radiata* LEC. (see LECOMPTE, 1952; Pl. 61, Figs. 2—3; Pl. 62, Figs. 1—3). This example seems to be one more proof for the artificiality of the group Idiostromatidae, many representatives of which have their equivalents among massive forms (see also General Part).

Stratigraphic and geographical distribution. — Middle Devonian: USA (Missouri, Indiana), Poland (Eastern Holy Cross Mts.).

Stromatopora spissa (LECOMPTE, 1951)

(Pl. XXI, Fig. 2a-b)

1951. *Stromatoporella spissa* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 187-189, Pl. 27, Figs. 1, 1a-c, 2, 2a, 3-4.

1951. *Stromatoporella spissa* LECOMPTE mut. *latitexta* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 189-191, Pl. 28, Figs. 1-2.

1968. *Stromatoporella spissa* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 399.

Locality. — Sitkówka V (loc. 22).

Material. — Two fragmentary colonies (Z. Pal. St. /216—217).

Description. — Coenosteum lamellar or irregularly bulbous. Height of the fragmentary colonies: lamellar — 3 cm, bulbous — 5 cm. The lamellar colony is alternately interlaced with *Actinostroma stellulatum* NICH.

Thick, condensed skeletal elements make up about 80 to 85 per cent of the volume of coenosteum. Vermicular, anastomosing coenotubes run through a compact mass of skeletal tissue. Coenotube varying in diameter from 0.12 to 0.45 mm, usually averaging about 0.20 mm. In addition to coenotubes, transverse sections of much thicker (0.8 mm) astrorhizal canals are

visible in the skeleton. Coenotubes are distributed in the skeleton zonally, that is, at some levels of coenosteum they occur abundantly and at some others less so. Autotubes rare and short. Coenotubes, autotubes and astrorhizal canals are intersected by irregularly distributed dissepiments or tabulae. Usually poorly visible, dark bands of growth inhibitions, emphasizing fairly high (0.5 to 0.7 mm) growth increments, are the only horizontal elements in coenosteum. Microstructure homogenous, with many, dark points of calcification centers clearly visible in tangential sections.

Discussion. — The species under study was assigned by LECOMPTE (1951) to the genus *Stromatoporella* with which it has almost none characters in common. LECOMPTE's mistake was pointed out by STEARN (1961, 1966a), who suggested assigning it to the genus *Clathrocoilona* YAV. The last-named genus is, however, marked by regular pilars, laminae and an open-work skeleton, but it primarily is devoid of coeno- or autotubes, typical of *Stromatopora* and strongly developed in both the specimens here described and in LECOMPTE's material (1951, Pl. 27, Figs. 2, 2a). *Stromatopora spissa* is, therefore, marked by typical characters of this genus, which is in conformity with NESTOR's (1966) diagnosis of *Stromatopora*, adopted by the present writer. The most important characters of the species described which enable its easy distinction from other species of *Stromatopora* are primarily an exceptionally massive skeleton and a considerable degree of homogenization of the reticulate microstructure, whose traces are preserved only in the form of calcification centers. In addition, to *Stromatopora maculata* (LECOMPTE), *Stromatopora undata* RIABININ and *Stromatopora stricta* LECOMPTE, *S. spissa* belongs to the group of Late Devonian representatives of *Stromatopora*, in whose development the skeletal elements did not, as was the case in others, take a conspicuously vertical orientation and whose progressive nature was emphasized only by profound changes in microstructure.

Stratigraphic and geographical distribution. — Upper Devonian (Frasnian): Belgium (Dinant); Givetian-Frasnian transitional beds: Poland (Western Holy Cross Mts.).

Stromatopora mononensis GALLOWAY & ST. JEAN, 1957

(Pl. XXII, Fig. 1a-b)

1957. *Stromatopora mononensis* GALLOWAY & ST. JEAN; J. J. GALLOWAY & J. ST. JEAN, Middle..., pp. 178-179, Pl. 15, Fig. 1a-b.

1960. *Stromatopora mononensis* GALLOWAY & ST. JEAN; N. R. FISCHBUCH, Stromatoporoids..., p. 121, Pl. 2, Figs. 3-4.

1968. *Stromatopora mononensis* GALLOWAY & ST. JEAN; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 273.

Locality. — Jurkowice-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.).

Material. — One uncomplete colony (Z. Pal. St. I/193).

Description. — Coenosteum massive, spherical, 7 cm in diameter, with irregular mamelons on the surface. Small (10 to 12 mm) astrorhizae occur in the central parts of some of the mamelons.

Skeletal elements strongly condensed, occupying about 85 per cent of the volume of coenosteum. Skeleton composed of very thick cenostelae within which run very thick, vermicularly twisted and anastomosing coenotubes and less numerous, short autotubes about 10 mm in transverse section. Rare dissepiments and tabulae occur in coeno- and autotubes. Very closely spaced growth interruption surfaces (according to GALLOWAY & ST. JEAN, 1957 „microlaminae“), cutting off more or less even growth increments, numbering 12 to 15 in 2 mm. Microstructure irregularly reticular, loose, in the region of astrorhizal mamelons more condensed.

Discussion. — The specimen described is conspecific with the holotype of *Stromatopora mononensis*, described by GALLOWAY & ST. JEAN (1957). *S. mononensis* is most similar to *S. laminosa* LECOMPTE from which it differs in a more compact skeleton, less regular coenotubes and lack of coenostromae which, in the latter, are well developed. *S. mononensis* together with other species of *Stromatopora*, described by GALLOWAY & ST. JEAN (1957), such as, *S. marpleae*, *S. obscura*, and *S. larocquei*, belong to the representatives of *Stromatopora* which are marked by a distinctly reticular microstructure, thick, condensed skeleton and rare and thin autotubes. The stratigraphic range of these species is limited to the Lower and Middle Givetian. *S. laminosa* LECOMPTE has so far been the only species of this group described from the area of Europe.

Stratigraphic and geographical distribution. — Middle Devonian: USA (Indiana), Canada (Alberta), Poland (Eastern Holy Cross Mts.).

Stromatopora stricta LECOMPTE, 1952

(Pl. XXII, Fig. 2a-b)

1952. *Stromatopora stricta* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 277-278, Pl. 56, Figs. 3, 3a-b.

1968. *Stromatopora stricta* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 410.

Localities. — Sitkówka IV (loc. 21), Sitkówka V (loc. 22).

Material. — Two complete (Z. Pal. St. I/222 and St. I/230) and one fragmentary colony (St. I/175).

Description. — Coenosteum massive, lenticular (20 × 8 cm) or irregularly cylindrical (13 × 8 cm). Surface smooth, gently folded, with rare astrorhizae.

Skeleton solid, occupying about 70 per cent of the volume of coenosteum. Vermicularly twisted coenostelae are the main elements of skeleton, although here and there indistinct coenostromae are visible which, however, do not form continuous levels. Coenotubes numerous, strongly varying in diameter (0.05 to 0.25 mm), vermicularly penetrating the skeletal tissue. Autotubes very rare, short. Dissepiments and tabulae not very numerous. Growth discontinuity surfaces slightly marked, growth increments varying in size, averaging 0.20 mm. Transverse sections of astrorhizal canals, much thicker than coenotubes, are observed. Microstructure irregularly reticular, strongly condensed and passing here and there in a homogenous one but with many traces of calcification centers.

Discussion. — *S. stricta* together with *S. baccata* LECOMPTE, *S. minutitexta* (LECOMPTE), *S. maculata* LECOMPTE and *S. undata* RIABININ, make up a group of species characteristic of the uppermost Middle Devonian and Upper Devonian. In this group one can observe a progressive tendency to the homogenization of the reticular microstructure. At the same time these forms preserve such characters of the older representatives of *Stromatopora* as a poorly realized verticality of the system of coenostelae and a low degree of development of autotubes. Of all the species referred to above, *S. stricta* has the most irregular system of skeletal elements.

Stratigraphic and geographical distribution. — Middle-Upper Devonian transitional beds: Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): Belgium (Dinant Basin).

***Stromatopora undata* RIABININ, 1932**

(Pl. XXII, Fig. 3a-b)

1932. *Stromatopora undata* RIABININ; V. N. RIABININ, Devonskye..., pp. 861—862, Pl. 2, Figs. 9-10.
 1939. *Stromatopora undata* RIABININ; V. N. RIABININ, Paleozoyskye..., pp. 38-39, Pl. 11, Figs. 2-3.
 ?1951. *Syringostroma baccatum* LECOMPTE; M. LECOMPTE, Les Stromatoporoides..., pp. 212-214, Pl. 35, Figs. 2, 2a-d.
 1955. *Stromatopora undata* RIABININ; V. N. RIABININ, Verkhnedevonskye..., pp. 23-24, Pl. 15, Figs. 1-4.
 1955. *Stromatopora pseudoundata* RIABININ; V. N. RIABININ, Verkhnedevonskye..., pp. 22-23, Pl. 14, Figs. 1-5.
 1955. *Stromatopora laschenkoi* RIABININ; V. N. RIABININ, Verkhnedevonskye..., pp. 25-26, Pl. 16, Figs. 3-4.
 ?1960. *Stromatopora undata* RIABININ; K. A. ERMAKOVA, Nekotorye..., p. 76, Pl. 3, Fig. 1.
 1968. *Stromatopora undata* RIABININ; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 116, p. 448.

Localities. — Bolechowice — „Panek“ quarry (loc. 16). Śluchowice (loc. 32), Kadzielnia-quarry (loc. 33).

Material. — Four fragmentary colonies (Z. Pal. St. I/163 to 165 and St. I/231).

Description. — Coenosteam massive, irregularly bulbous or lamellar, interlaced with alternate bands, 1—2 mm high, of *Stromatopora spissa* (LECOMPTE). Surface smooth, with irregular mamelons.

Skeletal elements relatively thick and considerably condensed, making up 60 to 70 per cent of the volume of coenosteam. Coenostelae, on the average 0.15 mm thick, visible in tangential sections in the form of irregular meanders. Coenotubes vermicularly twisted, 0.12 to 0.14 mm in diameter. Short, irregularly distributed autotubes occur at some levels of coenosteam. Coeno- and autotubes intersected by dissepiments and tabulae. Fairly numerous are astrorhizal canals with diameters much larger than those of coeno- and autotubes (0.40 to 0.50 mm). Coenostromae well developed, passing, in some parts of coenosteam, in irregular laminae 0.05 to 0.10 mm thick. Growth discontinuity surfaces very slightly marked. Growth increments strongly varying in height (0.15 to 1.55 mm). Microstructure reticular, strongly condensed, with very numerous, dark-coloured calcification centers visible in tangential sections. The degree of condensation of microreticulum in the skeletal tissue is not uniform. In the places in which the growth of skeleton was disturbed (according to GALLOWAY 1957, a „repair tissue“), the microstructure reticulum is considerably looser.

Discussion. — The species described, together with *S. spissa* (LECOMPTE), *S. maculata* LECOMPTE and *S. stricta* LECOMPTE, belong to the representatives of *Stromatopora* characteristic of the turn of the Middle to the Upper Devonian and mostly of the Upper Devonian (Frasnian). In contradistinction to the species referred to above, *S. undata* displays, however, a much larger regularity of the system of skeletal elements expressed in the presence of both fairly numerous autotubes and strongly developed coenostromae which are frequently of the nature of true laminae. A considerable intracolony variability, observed in the specimens studied by the writer, allowed him to include in the synonymy of *S. undata* such species as, *Syringostroma baccatum* LECOMPTE, *Stromatopora pseudoundata* RIABININ and *S. laschenkoi* RIABININ. These species differ from *S. undata* only in the character and dimensions of astrorhizae, as well as in slightly different dimensions and number of skeletal elements.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Belgium (Dinant Basin); Upper Devonian (Frasnian): Belgium (Dinant Basin), USSR (Timan, Western Ural Mts., Russian Platform), Poland (Western Holy Cross Mts.).

Stromatopora minutitexta (LECOMPTE, 1951)

(Pl. XXIII, Figs. 1a-b, 2a-b)

1951. *Syringostroma minutitextum* LECOMPTE; M. LECOMPTE, Les Stromatoporoides..., pp. 209-210, Pl. 34, Figs. 1-4.
 1968. *Syringostroma minutitextum* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 269.

Localities. — Sowie Górki Hill (loc. 2), Bolechowice — „Panek“ quarry (loc. 16), Sitkówka III (loc. 20), Sitkówka V (loc. 22).

Material. — Five colonies, including three preserved completely (Z. Pal. St. I/184, St. I/224 to 227).

Description. — Coenosteum massive, irregularly bulbous. The largest colony is 30 × 30 × 20 cm. in size. Surface smooth, gently undulating.

Skeleton occupying about 50 per cent of the volume of coenosteum. Horizontal elements of the skeleton partly expressed by coenostromae and partly by the laminae which are on the average 0.12 mm thick and interrupted by irregularly twisted coenotubes which are mostly arranged horizontally. Vertical elements of the skeleton are partly expressed by meandering coenostelae and partly by isolated, straight pillars sometimes vertically superposed. Zones with better developed vertical elements predominate in the skeleton of some of the colonies studied and with better developed horizontal elements in some others. Autotubes do not occur. Dissepiments rarely and irregularly distributed. Growth discontinuity surfaces slightly marked. Growth increments very uneven. Microstructure, at first vestigially reticular, is in principle almost completely homogenous with very rare dark-coloured points of calcification centers visible in tangential sections of the skeleton.

Discussion. — In LECOMPTE'S (1951) original description, the species under study was assigned to the genus *Syringostroma*. GALLOWAY & ST. JEAN (1957) pointed out that such a systematic position of this species is improper and suggested that it should be transferred to the genus *Stictostroma* PARKS. Acknowledging this species to be a representative of the genus *Stromatopora*, STEARN (1966b, p. 98) did not agree with the standpoint of GALLOWAY & ST. JEAN. The assignment of the species described to *Stromatopora* is primarily supported by the presence of coenotubes and coenostelae and therefore, the present writer agrees with STEARN'S suggestion. It should be, however, emphasized that *S. minutitexta* considerably deviates from typical species of *Stromatopora* in relatively strongly developed horizontal elements of the skeleton, presence of pillars and lack of autotubes. These characters relate this species to some of the species of *Stictostroma* PARKS and *Ferestromatopora* YAVORSKY. In its system of skeletal elements, *S. minutitexta* is similar to *S. maculata* LECOMPTE and *S. stricta* LECOMPTE from which it differs in the lack of autotubes, considerably better developed coenostromae and a very strongly changed microstructural reticulum.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Belgium (Dinant Basin), Poland (Western Holy Cross Mts.): Upper Devonian (Frasnian): Poland (Western Holy Cross Mts.).

Genus **FERESTROMATOPORA** YAVORSKY, 1955

Type species: Ferestromatopora krupennikovi YAVORSKY, 1955; Middle Devonian (Givetian — *Indospirifer* horizon USSR (Kuznetsk Basin).

Diagnosis. — Coenosteum consisting of either twisted skeletal structure which do not display a distinct vertical or horizontal orientation, or more or less regular reticular laminae,

connected with each other by meandering, vertical walls or, less frequently, pillars. Coenotubes rare, autotubes lacking. Dissepiments common. Microstructure irregularly reticular, loose to condensed.

Discussion. — The genus *Ferestromatopora* is, as correctly emphasized by YAVORSKY (1955), most similar to *Stromatopora* GOLDFUSS, from which it differs primarily in the lack of autotubes (according to other authors, „pseudozooidal tubes“), very rare coenotubes and laminarity of coenosteum, distinctly expressed in most of the species. *Ferestromatopora* differs from the genus *Parallelostroma* NESTOR, separated from *Stromatopora*, in a more reduced skeleton, larger chambers and irregular, frequently strongly condensed, reticulum of microstructure.

In the present writer's opinion such species of *Stromatopora* as, *S. marplea* GALLOWAY & ST. JEAN, *S. larocquei* GALLOWAY & ST. JEAN and *S. obscura* GALLOWAY & ST. JEAN have incorrectly been transferred by GALLOWAY (1957) to *Ferestromatopora*. Despite the fact that these species have not very strongly developed autotubes, their assignment to *Stromatopora* is, due to a strongly developed system of coenotubes and thick coenostelae with a reticular microstructure, fully justified. Suggesting their assignment to the genus *Clathrocoilona* YAVORSKY (= *Synthetostroma* LECOMPTE) rather, STEARN (1966*b*) also declared himself against placing the species referred to above within the genus *Ferestromatopora*. STEARN does not, however, give any grounds for his standpoint, which, in the present writer's opinion, is a misunderstanding, since none of the species mentioned above has, either laminae or pillars, very well developed in the representatives of *Clathrocoilona*.

A new genus *Angulatostroma* with a type species *Stromatopora angulata* YAVORSKY, 1947, recently separated by KHALFINA (1968) is probably a synonym of *Ferestromatopora*. The main diagnostic characters, ascribed by KHALFINA to *Angulatostroma*, that is a „chevron-like“ system of skeletal elements and a reticular microstructure are precisely characteristic of *Ferestromatopora krupennikovi*, type species of *Ferestromatopora*.

The following three distinct groups of species distinguish themselves among *Ferestromatopora*:

1) a group of *F. dubia* which is marked by very thick laminae and massive, short vertical walls, surrounding small mostly hemispherical chambers; microstructure irregularly reticular, condensed;

species: *F. dubia* (LECOMPTE, 1952),
F. tenuitextilis (YAVORSKY, 1955),
F. tcherskii (YAVORSKY, 1955);

2) a group of *F. krupennikovi* with considerably thinner, chevron-like or irregularly tangled skeletal elements, in which no distinct laminae or pillars are separated; chambers considerably larger than in the previous group and irregular in outline; microstructure irregularly reticular, loose or condensed;

species: *F. krupennikovi* YAVORSKY, 1955,
F. angulata (YAVORSKY, 1947),
F. tyrganensis YAVORSKY, 1955,
F. padalkoi (YAVORSKY, 1955),
F. fortuita (YAVORSKY, 1955),
F. jacquensis GALLOWAY, 1960,
F. kennisoni (BIRKHEAD, 1967),
F. turbinata BIRKHEAD, 1967,
F. contexta STEARN, 1966;

3) a group of *F. cellulosa* with a yet more delicate skeleton, with a well expressed laminae having a reticular structure and irregular, meandering vertical walls and pillars; galleries irregular, small or large; microstructure reticular, usually loose;

species: *F. cellulosa* (LECOMPTE, 1952),
F. maculosa (PARKS, 1936),
F. talovensis YAVORSKY, 1955,
F. czekanowskii (YAVORSKY, 1955),
F. percanaliculata (LECOMPTE, 1951),
F. bifida (LECOMPTE, 1951),
F. uchtensis (RIABININ, 1955),
F. vesiculosa (STEARN, 1963),
F. parksi STEARN, 1966.

The first two groups of species still display a considerable similarity to *Parallelostroma* NESTOR and *Stromatopora* GOLDFUSS from which they probably derive. The species of the third group, with a very strongly reduced skeleton are similar to some of the species of *Atelodictyon* LECOMPTE (e.g., *A. stelliferum* STEARN, *A. mirabilis* YAV.) from which they differ only in reticular vertical elements which in *Atelodictyon* are reduced to thin (usually monofibril) pillars or meandering vertical walls. The species belonging to the group of *Ferestromatopora cellulosa*, as well as to *Atelodictyon* have an identical type of reticular laminae, except for the fact that in *Atelodictyon* they are reduced to a single, very thin network.

Stratigraphic and geographical distribution. — Middle Devonian: Canada (Alberta), USSR (Kuznetsk Basin, Western Ural Mts., Salair Mts.), Belgium (Dinant Basin), Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): Canada (Alberta, Canadian Rocky Mts.), USSR (Timan), Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

Ferestromatopora parksi STEARN, 1966

(Pl. XXIII, Fig. 3a-b)

- 1966a. *Ferestromatopora parksi* STEARN; C. W. STEARN, Upper..., pp. 58-59, Pl. 23, Figs. 1-6; Pl. 24, Fig. 1; Pl. 26, Fig. 7.
 1961. *Ferestromatopora jacquensis* GALLOWAY; C. W. STEARN, Devonian..., pp. 943-944, Pl. 107, Figs. 4-5.
 1963. *Ferestromatopora* sp.; C. W. STEARN, Some..., pp. 666-667, Pl. 88, Fig. 6.
 1968. *Ferestromatopora parksi* STEARN; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 307.

Localities. — Sitkówka III (loc. 20), Radkowice-Sołtysia Hill (loc. 11), Bolechowice-„Panek“ quarry (loc. 16), Jurkowice-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.).

Material. — Four incomplete colonies (Z. Pal. St. I/56, St. I/180—181, St. I/185).

Description. — Coenosteum massive, hemispherical, 12 cm in diameter and 8 cm high. Surface smooth, irregularly and gently undulated.

Skeleton composed of alternate zones varying in structure. Conspicuously thicker (3 to 4 mm) zones consist of irregularly twisted walls on the average 0.12 mm thick and not displaying a horizontal or vertical orientation. Irregularly oval spaces of the nature of galleries are closed between these walls. In addition to the irregular, thick zones, the skeleton has bands, consisting of regular, fine-reticular laminae 0.05 to 0.12 mm thick and here and there interrupted by small foramina. Laminae are connected with each other mostly by thin (0.05 to 0.08 mm), meandering, vertical walls and rare pillars. The vertical walls and pillars are limited to one inter-

laminar space and may, here and there, superpose each other but on stretches not longer than two interlaminar spaces. Pillars are usually twisted, irregularly ramified, less frequently, straight and 0.05 to 0.10 mm thick. The meandering vertical walls, form here and there closed loops which, in tangential sections, are visible in the form of rings. Skeletal tissue is fairly densely intersected by astrorhizal canals with diameters considerably larger than those of galleries (0.55 to 0.75 mm). Growth discontinuity surfaces are considerably better marked in skeletal zones having a regular structure. Microstructure irregularly reticular, looser in regularly formed zones. Growth increments variable in irregular, and more or less stable (0.25 mm in size) in regular zones.

Discussion. — *F. parksi* is marked by the concurrence of the two types of skeletal tissue mentioned above. It should be emphasized that each of these types of skeletal tissue, treated separately, might be a basis for separating two species of *Ferestromatopora* of which one would be contained within the group of *F. krupennikovi* and the other *F. cellulosa*. The structure of *F. parksi* displays characters which are transitional from thick irregular representatives of *Ferestromatopora* to regular forms similar to *Atelodictyon* LECOMPTE. At the same time, it is a good example illustrating the tendency towards the reduction in the thickness of skeleton with a simultaneous increase in growth rhythmicity.

Very similar in structure to *F. parksi* is *Atelodictyon trautscholdi* (RIABININ), in which the process of the reduction of skeleton is, however, considerably more advanced and in which the zones of a thick, irregular skeletal tissue occur in the vestigial form.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Poland (Holy Cross Mts.); Middle — Upper Devonian transitional beds: Canada (Alberta, Canadian Rocky Mts.); Upper Devonian (Frasnian): Canada (Alberta, Canadian Rocky Mts.), Poland (Western Holy Cross Mts.).

Ferestromatopora uchtensis (RIABININ, 1955)

(Pl. XXIV, Fig. 1a-c)

1955. *Stromatoporella uchtensis* RIABININ; V. N. RIABININ, Verkhnedevonskye..., p. 27, Pl. 17, Figs. 4-7; Pl. 18, Fig. 1.
 1955. *Stromatoporella uchtensis* RIABININ var. *ravituberculata* RIABININ; V. N. RIABININ, Verkhnedevonskye..., p. 28, Pl. 18, Figs. 2-5; Pl. 19, Figs. 1-4.
 1968. *Stromatoporella uchtensis* RIABININ; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 116, p. 447.

Localities. — Sitkówka V (loc. 22), Jaworznia-Moczydło Hill (loc. 25), Jaworznia-quarry (loc. 26).

Material. — Four large fragmentary colonies (Z. Pal. St. I/186 to 189).

Description. — Coenosteum massive, irregularly bulbous. The largest fragment is 25 × 30 × 15 cm in size. Surface smooth, with irregularly distributed mamelons 2 to 3 cm high.

Skeletal tissue fine, occupying about 40 per cent of the volume of coenosteum. System of skeletal elements zonal, in the form of alternate bands more or less equal in height. Some of them have a regular and some others irregular structure. In some of the specimens, the proportions of the regular and irregular tissue are uneven, in favour of the former.

The irregularly formed skeletal zones are composed of strongly twisted walls, sometimes displaying, in vertical sections, a chevron-like system. The twisted walls surround small chambers, irregularly subcircular in outline and intersected by slightly convex dissepiments. An average thickness of walls amounts to 0.07 mm.

Regularly formed skeletal zones are marked by more delicate elements. They are composed of very thin, even, reticular laminae 0.02 to 0.03 mm thick, spaced closely but at variable intervals. Laminae are connected with each other by vertical elements limited to a single interlaminar space. Vertical elements are developed mostly in the form of thin (0.05—0.09 mm), reticular, vertical walls, twisted meandrically in a vertical plane and frequently interrupted. Also frequent are single, reticular pillars with irregular transverse sections and 0.07 to 0.12 mm thick (Pl. XXIV, Fig. 1c). Vertical walls and pillars usually ramify irregularly in the upper part, in which they are connected with a lamina to form a reticular layer. Galleries small, oval or semicircular in outline, sometimes intersected by convex dissepiments. Skeletal tissue is penetrated by irregularly thick (0.35 to 0.40 mm) astrorhizal canals. Growth rhythms well expressed in regularly formed parts of coenosteum, usually variable with the predominance of small increments. In the zones of coenosteum with an irregular structure, growth increments are marked by dark-coloured growth inhibition surfaces. Microstructure irregularly reticular, loose.

Discussion. — A very delicate structure of skeleton and a loose reticulum of microstructure make up characteristic features of the species described, which differs in them radically from a related species *F. parksi* STEARN. *F. uchtensis* differs from otherwise very similar *F. percanaliculata* (LECOMPTE) in the presence of wide zones with an irregular system of skeletal elements and a looser reticulum of microstructure.

In his original description, RIABININ (1955) placed the species under study within the range of the genus *Stromatoporella* NICHOLSON and, in addition to *S. uchtensis*, separated its variety, that is, *S. uchtensis* var. *raritytuberculata* which, in his opinion, is marked by rarer mamelons and larger astrorhizae than those in *S. uchtensis*. In the present writer's opinion these characters are not of a diagnostic importance and do not give basis for separating the two taxa.

Stratigraphic and geographical distribution. — Middle Upper Devonian transitional beds: Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian, Ukhta Beds): USSR (Timan).

***Ferestromatopora percanaliculata* (LECOMPTE, 1951)**

(Pl. XXIV, Fig. 2a-c)

1951. *Syringostroma percanaliculatum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 204-206, Pl. 31, Fig. 3; Pl. 32, Figs. 1-2.

1968. *Syringostroma percanaliculatum* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 310.

Locality. — Kowala-railway cut (loc. 12).

Material. — One fragmentary colony (Z. Pal. St./I/190).

Description. — Coenosteum massive, irregularly spherical, 8 cm in diameter. Surface corroded. Skeletal tissue delicate, occupying about 50 per cent of the volume of coenosteum. Skeleton consisting of thin, reticular laminae 0.02 to 0.04 mm thick, frequently interrupted by foramina. Laminae closely spaced, on the average 20 to 25 per 2 mm. Vertical elements of skeleton limited by a one interlaminar space, mostly composed of irregularly twisted, reticular vertical walls and rarer, also reticular, pillars. In transverse section, pillars are irregularly circular in outline. Thickness of vertical walls and pillars strongly differentiated and varying within limits of 0.04 and 0.15 mm, mostly averaging 0.10 mm. Galleries very small, irregularly circular in outline. Skeletal tissue is penetrated by fairly closely spaced astrorhizal canals whose diameters are considerably larger than those of galleries (0.25 to 0.40 mm). Thin

zones consisting of thicker and irregularly twisted skeletal elements and devoid of a laminar and irregularly twisted skeletal elements and devoid of a laminar system, sporadically occur within a normal skeleton. Growth increments varying in size from 0.05 to 0.17 mm and averaging 0.12 mm. Growth discontinuity surfaces not marked. Microstructure irregularly reticular.

Discussion. — In LECOMPTE'S original description, *Ferestromatopora percanaliculata* was erroneously placed within the range of the genus *Syringostroma* NICHOLSON. LECOMPTE'S error was pointed out by GALLOWAY & ST. JEAN (1957, p. 258) who transferred the species under study to the genus *Stictostroma* PARKS. The present writer shares, however, the opinion of STEARN (1966*b*, p. 98) who, after revising the diagnosis of *Stictostroma*, found it necessary to transfer the species described to *Ferestromatopora*.

F. percanaliculata is most closely related to *F. uchtensis* (RIABININ), from which it differs in a more regular system of skeletal elements and more condensed reticulum of microstructure. Both differ from all remaining species of *Ferestromatopora* in very delicate skeletal elements and very closely spaced, low growth increments.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Belgium (Dinant Basin); Upper Devonian (Frasnian): Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

Ferestromatopora cellulosa (LECOMPTE, 1952)

(Pl. XXV, Fig. 1*a-b*; Pl. XXVI, Fig. 1*a-c*)

1952. *Trupetostroma cellulosum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 233-234, Pl. 41, Figs. 1, 1*a-b*, 2.
1968. *Trupetostroma cellulosum* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 65.

Localities. — Radkowice-Sołtysia Hill (loc. 11), Sitkówka III (loc. 22).

Material. — Twenty colonies, including six preserved completely (Z. Pal. St. I/42 and 43, St. I/46, St. I/50 to 55, St. I/57 to 62, St. I/43 and St. I/144).

Description. — Coenosteum massive, spherical, cylindrical or irregularly bulbous. The largest colony is 30×40×28 cm in size. Surface smooth, with or without mamelons.

Skeletons occupying about 40 per cent of the volume of coenosteum. Laminae well expressed, even or gently twisted, reticular in structure. Thickness of laminae, strongly varying (0.05 to 0.25 mm). Rare foramina occurring in laminae. Vertical elements of coenosteum, limited by one interlaminar space and consisting mostly of reticular vertical walls irregularly twisted in vertical plane. Much less numerous are straight, thin pillars, frequently ramified in the upper part. Thickness of vertical walls strongly varying (0.07 to 0.25 mm). Galleries large, circular, subcircular and subrectangular in outline, usually intersected by dissepiments. Growth increments more or less equal in size, averaging 0.22 mm, sometimes emphasized by darker growth discontinuity surfaces. Indistinct latilaminae are formed in the zones of stronger condensation. Microstructure irregularly reticular, loose, with a reduced number of calcification centers. Large, parallel meshes of the microstructural reticulum, which are termed (STEARNS, 1966*b*) as „ordinicellular“, microstructure, are frequently visible in vertical sections of coenosteum.

Discussion. — *F. cellulosa* was assigned by LECOMPTE (1952) to the genus *Trupetostroma* PARKS. In the present writer's opinion, such an interpretation of the systematic position of the species described is, however, contradicted by a coarse-reticular nature of the microstructure of

F. cellulosa and by the lack of thick, spool-shaped and usually superposed pillars, characteristic of *Trupetostroma*. In addition, the species of *Trupetostroma* have strongly reduced laminae which, in *F. cellulosa*, are mostly thick. Lecompte (*l.c.*) erroneously interpreted large meshes of the loose microstructural reticulum in the species under study as vacuoles sometimes occurring within the range of a homogenous skeleton of some of the *Trupetostroma* (e.g., *T. warreni* PARKS, *T. iowense* PARKS).

A regularly laminar structure of skeleton and a considerably degree of its reduction caused by loosening the reticulum of microstructure, which in turn takes place by the decrease in the number of calcification centers (crystallization axes) are characteristic features, differing *Ferestromatopora cellulosa* from the related species *F. uchtensis* (RIABININ), *F. percanaliculata* (LECOMPTE) and *F. talovensis* YAVORSKY. Due to this fact, *F. cellulosa* becomes similar to *Atelodictyon* LECOMPTE whose species were probably formed as a result of a still more advanced reduction of skeleton up to the formation of open-work skeletons, composed of single vertical walls and thin, monofibril pillars connecting monolamellar, reticulate laminae. In regard to the reduction of skeleton, *F. cellulosa* is similar to *F. maculosa* (PARKS), which, due to its still more advanced reduction of skeleton, is yet more similar to *Atelodictyon* than the species described.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Belgium (Dinant Basin), Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): Belgium (Dinant Basin).

Ferestromatopora talovensis YAVORSKY, 1955

(Pl. XXV, Fig. 2a-b)

1955. *Ferestromatopora krupennikovi* YAVORSKY var. *talovensis* YAVORSKY; V. I. YAVORSKY, *Stromatoporoidea...*, pp. 110-111, Pl. 58, Figs. 6-8; Pl. 40, Fig. 1.
 (part) 1952. *Trupetostroma ruedemani* LECOMPTE; M. LECOMPTE, *Les Stromatoporoïdes...*, Pl. 40, Figs. 2, 2a.
 1961. *Parallelopora vojvensis* YAVORSKY; V. I. YAVORSKY, *Stromatoporoidea...*, pp. 46-47, Pl. 28, Fig. 1-6.
 1968. *Ferestromatopora krupennikovi* YAVORSKY, var. *talovensis* YAVORSKY; E. FLÜGEL & E. FLÜGEL-KAHLER, *Foss. Cat.*, pt. 115, p. 226-227.

Localities. — Radkowice-Sołtysia Hill (loc. 11), Jaworznia-Moczydło Hill (loc. 25).

Material. — Four, large fragmentary colonies (Z. Pal. St. I/44 and 45, St. I/48, and 49).

Description. — Coenosteum massive, irregularly bulbous or lenticular. The largest fragment 15 cm high. Surface smooth, with low mamelons (1—2 mm in height), usually having astrorhiza in the central part.

Skeleton consisting of straight or gently undulated reticular laminae, rarely interrupted by foramina. Thickness of laminae very variable within limits of 0.02 and 0.24 mm, most of them being, however, more than 0.08 mm thick. Vertical elements of coenosteum, limited by a single interlamellar space, are mostly composed of irregularly meandering, reticular vertical walls. These walls are usually considerably thinner in the lower part, gradually extending towards the top where they join a lamina. In addition to vertical walls, rare, reticular pillars, irregularly branched upwards occurs in the interlamellar space. Galleries (?chambers) relatively large, irregularly oval in outline, here and there horizontally elongated. Numerous, flat or slightly convex dissepiments occur in galleries. Growth increments emphasized by growth discontinuity surfaces in laminae varying in size from 0.12 to 0.48 mm and averaging about 0.25 mm. Zones of growth disturbances of the coenosteum (called by other authors a „repair tissue“) are

composed of an irregular, loose reticulum, which, viewed in the passing light, is darker than the normal skeletal tissue. Microstructure irregularly reticular, loose, with a reduced number of calcification centers.

Discussion. — *F. talovensis* was considered by YAVORSKY as a variety of *F. krupennikovi* YAVORSKY. In the present writer's opinion, *F. talovensis* should be raised to the rank of a separate species because of its well developed vertical walls and laminae which, in *F. krupennikovi*, occur only sporadically, as well as of its considerably more regular growth periodicity which, in *F. krupennikovi*, is strongly variable and marked in the form of rare growth discontinuity surfaces, occurring within anastomosing walls of skeleton.

F. talovensis is most closely related to *F. cellulosa* (LECOMPTE) and *F. maculosa* (PARKS) from which it differs in thicker skeletal elements and a lower degree of reduction in the reticulum microstructure. YAVORSKY'S (see FLÜGEL & FLÜGEL-KAHLER, 1968, p. 227) unpublished remark that *F. talovensis* should be placed within the genus *Trupetostroma* is groundless. The characters of the holotype of the species described, which the present writer had an opportunity to see at the CNIGR Museum in Leningrad, as well as YAVORSKY'S (1955) original description and illustrations preclude such a possibility.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): USSR (Kuznetsk Basin, Petchora Basin), Poland (Western Holy Cross Mts.); Middle-Upper Devonian transitional beds: Poland (Western Holy Cross Mts.).

Ferestromatopora krupennikovi YAVORSKY, 1955

(Pl. XXV, Fig. 3a-b)

1955. *Ferestromatopora krupennikovi* YAVORSKY; V. I. YAVORSKY, *Stromatoporoidea...*, pp. 109-110, Pl. 58, Figs. 1-5.

(part) 1952. *Trupetostroma ruedemani* LECOMPTE; M. LECOMPTE, *Les Stromatoporoïdes...*, Pl. 40, Fig. 3a.

1962. *Ferestromatopora krupennikovi* YAVORSKY; V. I. YAVORSKY, *Osnovy...*, Pl. 5, Figs. 6-7.

1968. *Ferestromatopora krupennikovi* YAVORSKY; E. FLÜGEL & E. FLÜGEL-KAHLER, *Foss. Cat.*, pt. 115, p. 226.

Localities. — Radkowiec-Sołtysia Hill (loc. 11), Sitkówka III (loc. 20), Jaworznia-Moczydło Hill (loc. 25).

Material. — Three slightly broken-off colonies (Z. Pal. St. I/47, St. I/141 and 142).

Description. — Coenosteum massive, irregularly bulbous 15 cm in diameter and 9 cm high. Surface smooth, with irregular, gentle elevations.

A delicate skeleton occupies about 45 to 50 per cent of the volume of coenosteum. Skeletal tissue differentiated in zones with an irregular and regular structure. Zones with an irregular structure are wider and composed of anastomosing walls, frequently displaying a zigzag system. These walls surrounded uneven galleries, irregularly oval in outline. The anastomosing walls are intersected at irregular intervals by even growth discontinuity surfaces which mark high growth increments and are darker than the normal skeletal tissue. The zones of coenosteum, whose structure is irregular, are composed of even, reticular laminae 0.05 to 0.22 and mostly 0.08 to 0.10 mm in thickness, connected with each other by meandering vertical walls averaging 0.12 mm in thickness and pillars. Vertical walls and pillars are frequently wider in the upper part. Galleries, irregularly circular in outline, are intersected by strongly convex dissepiments. In this zone of skeleton, growth increments are less variable and considerably smaller (on the average 0.25 mm) than in the irregular zone. Microstructure irregularly reticular.

Discussion. — Irregular or chevron-like, anastomosing skeletal elements, still including some vestigially preserved coenotubes, divided by growth discontinuity surfaces into zones varying in height and, at the same time, bands with a regularly laminar structure, are characteristic features of *F. krupennikovi*. The chevron-like system, occurring in part of the skeleton, makes the species described similar to *F. tyrganensis* (YAVORSKY) and *F. angulata* (YAVORSKY), from which it differs in a more delicate and partly laminar skeleton.

F. krupennikovi differs from *F. talovensis* YAVORSKY and *F. cellulosa* (LECOMPTE), otherwise very similar to it in the structure of the coenosteum, in the presence of high zones with a chevron-like or irregular arrangement of skeletal elements.

The presence of two alternately recurring types of skeletal structure in *F. krupennikovi* may be interpreted as a symptom of periodically changing abiotic factors of the environment. On the other hand, the two types of structure indicate that, much the same as in other groups of the Stromatoporoidea, the genus *Ferestromatopora* tends to acquire a regular structure of skeleton by forming even laminae and vertical walls and pillars which connect laminae. In *F. krupennikovi* and *F. parksi* STEARN, this process is yet expressed in a not very high degree as compared with a completely laminar structure of *F. talovensis* and *F. cellulosa*.

YAVORSKY's unpublished note, coming from his correspondence (see — FLÜGEL & FLÜGEL-KAHLER, 1968, pp. 226 and 544), that *F. krupennikovi* should be transferred to the genus *Intexodictyon* YAVORSKY is, in present writer's opinion, groundless. *F. krupennikovi* is characterized by a pronouncedly reticular microstructure, which in the representatives of *Intexodictyon*, the type species included, is compact, which has also been pointed out by FLÜGEL & FLÜGEL-KAHLER (*l.c.*). In the present writer's opinion, despite a certain structural similarity, *Ferestromatopora* and *Intexodictyon* belong to quite different lineages of the Stromatoporoidea, that is, *Ferestromatopora* to reticular and *Intexodictyon* to fibro-normal ones of the *Clathrodiction-Ecclimadiction-Plexodiction* group (cf. also STEARN, 1969).

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): USSR (Kuznetsk Basin), Poland (Western Holy Cross Mts.); Middle — Upper Devonian transitional beds: Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): Belgium (Dinant Basin).

***Ferestromatopora dubia* (LECOMPTE, 1952)**

(Pl. XXVII, Fig. 1a-c)

1952. *Stromatopora dubia* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., p. 279, Pl. 57, Figs. 1, 1a-b, 2.

1957. *Stromatopora dubia* LECOMPTE; J. J. GALLOWAY & J. ST. JEAN, Middle..., pp. 170-177, Pl. 14, Fig. 3a-c.

non 1966. *Ferestromatopora dubia* (LECOMPTE) (= ?*Pseudoactinodictyon dartingtonense* (CARTER); J. E. KLOVAN, Upper..., p. 25, Pl. 8, Fig. 1a-b.

1968. *Stromatopora dubia* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 141.

Localities. — „Kowala“ quarry (loc. 13), Sitkówka V (loc. 22).

Material. — Two fragmentary colonies (Z. Pal. St. I/198 and 229).

Description. — Coenosteum massive, hemispherical, 28 cm in diameter at the base and 15 cm high. Surface smooth, with irregular elevations.

Skeletal tissue compact, occupying about 60 per cent of the volume of coenosteum, Laminae reticular with even upper and not very distinct lower surface. The thickness of laminae varying within limits of 0.12 and 0.24 mm, mostly 0.15 mm. On the average, 8 to 10 laminae occur per 2 mm. Vertical elements in the form of low, thick, irregularly meandering vertical

walls and pillars which are irregular in transverse section. Vertical walls and pillars, thinner at the bottom, gradually extend upwards, passing in laminae without any distinct boundary. Some of the vertical walls and pillars are superposed. Galleries, circular or semicircular in outline, have strongly varying (0.05—0.25 mm) — diameters and sometimes are intersected by dissepiments. Some of the spaces between vertical walls and pillars are of the nature of short coenotubes or, less frequently, autotubes. Growth increments, emphasized by dark growth inhibition surfaces, are variable in size (0.10 to 0.25 mm). Microstructure irregularly reticular, partly condensed, with very numerous dark calcification centers.

Discussion. — The specimens described have, as compared with the holotype, slightly thicker laminae and, on the average, a lesser number of laminae per 2 mm of coenosteum. *F. dubia* has originally been assigned to the genus *Stromatopora* GOLDFUSS. Its few poorly expressed coenotubes have, however been correctly pointed out by GALLOWAY (1957) who transferred this species to *Ferestromatopora*. Transferring *F. dubia* to the genus *Clathrocoilona* YAVOR-SKY, suggested by STEARN (1966b, p. 111), is precluded by the lack, in the species described, of numerous, cylindrical pillars characteristic of *Clathrocoilona*.

F. dubia differs from the remaining species of this genus in a very thick skeletal structures and in the presence of few coeno- or autotubes. The latter character relates this species to the representatives of *Stromatopora*. In its short vertical walls extending upwards and small semi-circular galleries, *F. dubia* resembles some of the species of *Parallelostroma* NESTOR from which it differs, however, in markedly thinner laminae, more clearly expressed growth increments and irregular, condensed reticulum of microstructure.

Stratigraphic and geographical distribution. — Middle Devonian (Logansport limestone), USA (Indiana); Middle-Upper Devonian transitional beds, Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

Genus TALEASTROMA GALLOWAY, 1957

Type species: Stromatopora cumingsi GALLOWAY and ST. JEAN, 1957; Middle Devonian (Logansport limestone), USA (Indiana).

Diagnosis. — Coenosteum composed of irregular, frequently strongly reduced, laminae and strongly developed pillars or meandering vertical walls (coenostelae). Spaces, contained between the last-named, are of the nature of coenotubes or irregular, sometimes considerably reduced, galleries. Microstructure of laminae reticular, condensed or homogenous and that of vertical elements — homogenous, with traces of reticular one occurring mostly in the peripheral zone.

Discussion. — *Stromatopora cumingsi*, a type species of *Taleastroma*, has been selected by GALLOWAY (1957) rather inappropriately since, as compared with other species of *Taleastroma*, the process of homogenization of the original microstructural reticulum, characteristic of this genus, is only slightly marked in this species. Most of the skeletal tissue in the holotype, which the present writer had an opportunity to see by the courtesy of the management of the U. S. National Museum in Washington, has a strongly condensed reticulate microstructure, as well as well developed coeno- and autotubes. This tissue strongly resembles some of the species of *Stromatopora* (e.g., *S. cooperi* LECOMPTE).

In the present writer's opinion, *Taleastroma* undoubtedly derives from *Stromatopora* in which skeletal elements took a vertical position with a simultaneous reduction of laminae

and homogenization of the original microreticulum which took place beginning from the middle of pillars and vertical walls. STEARN (1966*b*, p. 113) also expressed his opinion concerning the possibility of the derivation of *Taleastroma* compact microstructure from the reticulate (cellular) one; but he ascribed the homogenous character of the central part of vertical elements in *Taleastroma* to secondary processes of destruction caused by recrystallization.

In the species of *Taleastroma*, which have a extremely homogenous microstructure, including an almost entire skeleton (e.g., *T. confertum* STEARN), an almost complete disappearance of the primary microstructural reticulum is observed together with an almost complete reduction of laminae. The process of a progressing homogenization of skeleton in the stromatoporoids which have a reticular microstructure is observed in all lineages of this group without any exception and regardless, of any differences in the arrangement of skeletal elements. Hence, with a poor state of preservation, one should be careful so as not to confuse the species of *Taleastroma* with some, structurally related species of such genera as, *Syringostromella* NESTOR, *Syringostroma* NICHOLSON, *Neosyringostroma* n. gen. and *Hermatostroma* NICHOLSON. Usually, *Taleastroma* may be easily distinguished from *Syringostromella* and *Syringostroma* by a compact skeletal microtissue of the central parts of pillars and by the lack of reticulate columnar pillars, from *Neosyringostroma* n. gen., by the lack of columnar pillars with a trabecular or homogenous microstructure and from *Hermatostroma* — by the lack of a peripheral, loose reticulum covered outwardly with a membrane.

Stratigraphic and geographical distribution. — Middle Devonian: USA (Indiana), Canada (Alberta, Mackenzie Valley) ?USSR (Altai Mts., Salair Mts.), Belgium (Dinant Basin); Upper Devonian: Canada (Alberta), Poland (Western Holy Cross Mts.).

Taleastroma confertum STEARN, 1962

(Pl. XXVI, Fig. 2*a-c*)

1962. *Taleastroma? confertum* STEARN; C. W. STEARN, *Stromatoporoid...*, pp. 10-11, Pl. 5, Figs. 1-3.
 ?1963. *Taleastroma confertum* STEARN; C. W. STEARN, *Some...*, p. 667, Pl. 88, Figs. 7-8.
 1966*a*. *Syringostroma? confertum* (STEARNS); C. W. STEARN, *Upper...*, pp. 62-63, Pl. 25, Figs. 1-2.
 1968. *Taleastroma confertum* STEARN; E. FLÜGEL and E. FLÜGEL-KÄHLER, *Foss. Cat.*, pt. 115, p. 95.

Locality. — Sowie Górki Hill (loc. 2).

Material. — One completely preserved colony (Z. Pal. St. I/221).

Description. — Coenosteum irregularly bulbous with a smooth surface, 18 × 16 × 14 cm in size.

Skeletal elements strongly compact, occupying about 80 per cent of the volume of coenosteum. Straight, vertically continuing pillars, irregularly circular in transverse section, varying in thickness within limits of 0.09 and 0.28 mm and mostly being about 0.13 mm thick. Pillars, usually very near each other, 7 to 8 of them per 2 mm, frequently contact each other forming irregular groups of vertical walls varying in thickness. Pillars are composed of a homogenous substance, light coloured in thin-sections and with a thin rim of a condensed, reticular microstructure occurring in peripheral parts. Horizontal elements are expressed slightly in the form of reduced laminae 0.09 mm thick, 7 to 8 of them being distributed at more or less equal intervals over a stretch of 2 mm. The laminae disappear in the parts of coenosteum in which pillars are situated near or contact each other. Galleries high, very narrow and subrectangular in outline. Microstructure of laminae, like that of pillars, almost completely homogenous, with

traces of reticulum in the peripheral zone. Irregular growth rhythmicity is marked by very rare growth discontinuity surfaces.

Discussion. — The specimen described displays a somewhat less compact system of skeletal elements than that in the holotype, particularly so considering pillars of the holotype which are frequently fused together and form a homogenous mass of calcite. *T. confertum* has only with a reservation been assigned by STEARN (1962) to the genus *Talestroma*. He emphasized that it also may be a representative of the genus *Syringostroma* NICHOLSON and later (STEARNS, 1966a) transferred it to this genus also with a reservation. The present writer believes that the assignment of the species described to *Syringostroma* should be precluded by a conspicuously homogenous microstructure of *T. confertum* which is not recorded in the species of *Syringostroma*. *T. confertum* differs from the remaining species of its genus in a most advanced homogenization of microstructure and almost complete absence of laminae. At the same time, these characters allow one to assign the species under study to one of the phylogenetically most progressive representatives of the Devonian Stromatoporoidea. A feather-like character of calcite in pillars, observed by STEARN (1962, 1963, 1966b) in some of the Canadian specimens of *Talestroma confertum*, is also marked in some places of the specimen under study and, in the present writer's opinion, it represents a secondary phenomenon most likely to be caused by the processes of recrystallization and tectonic deformation (cleavage).

Stratigraphic and geographical distribution. — Upper Devonian: Canada (Alberta, Athabasca River, Northwest Territories), Poland (Western Holy Cross Mts.).

Genus PSEUDOACTINODICTYON E. FLÜGEL, 1958

Type species: Pseudoactinodictyon juxi E. FLÜGEL, 1958; Middle Devonian (Upper Givetian), Germany (Sauerland).

Diagnosis. — Coenosteum composed of thin, irregular laminae, sometimes reduced and replaced by dissepiments as well as meandering vertical walls and cylindrical pillars which are usually superposed and may continue through several laminae or be limited by a single inter-laminar space. Galleries with many dissepiments. Microstructure of laminae reticular, condensed, of pillars — homogenous with numerous calcification centers or trabecular.

Discussion. — *Pseudoactinodictyon* E. FLÜGEL differs from *Trupestostroma* PARKS in the lack of vacuoles in skeletal tissue, strongly reduced laminae and a considerable number of dissepiments and from *Gerronostroma* YAVORSKY — in thin laminae, frequently replaced by dissepiments and vertical elements of skeleton developed mostly in the form of vertical walls.

The diagnosis of *Pseudoactinodictyon* given above supplements characteristics of this genus, presented by E. FLÜGEL (1958) and repeated by STEARN (1962, 1966b) and BIRKHEAD (1967). The new data primarily concerns the character of microstructure in *Pseudoactinodictyon* which, in the type species, has originally been described as what is known as maculate („gefleckt“) and which more or less is an equivalent of the term „condensed reticular“, used in the present work. On the basis of the typical material he looked through, STEARN (1966b) considered, however, the microstructure of *Pseudoactinodictyon* as flocculent or compact, that is — in the present writer's terminology — homogenous. Since a reticular character of laminae and a more condensed one of pillars and vertical walls are distinctly visible in the photographs of the holotype published in FLÜGEL'S (1958, Pl. 1, c-d) work, the present writer believes STEARN'S statement to be erroneous. Other species of *Pseudoactinodictyon* have the microstructure of

their vertical elements within the range from a condensed reticular to trabeculoid one, with a marked tendency to a decrease in the number of calcification centers. At the same time, the microstructure of laminae in all places in which they are developed always preserves its reticular, frequently even loose character.

The microstructure of *Pseudoactinodictyon* clearly indicates that this genus is a derivative of the group of the stromatoporoids which have a reticular microstructure. The same has also been emphasized by GALLOWAY & ST. JEAN (1957). In the present writer's opinion this genus probably evolved from *Parallelopora* BARGATZKY as a result of a further reduction of laminae, replaced by dissepiments and by a simultaneous condensation of a formerly loose microstructural reticulum in vertical elements of the skeleton. The last-named process led first to the homogenization of the skeletal substance with the preservation of numerous crystallization centers and subsequently, through a further decrease in the number of these centers, to the formation of a trabecular microstructure with single secretion axes.

Stratigraphic and geographical distribution. — Middle Devonian: USA, Germany, Poland; Upper Devonian (Frasnian): Canada, USSR (Main Devonian Field), Belgium, Poland.

Pseudoactinodictyon actinostromiforme (RIABININ, 1941)

(Pl. XXVII, Fig. 2a-c)

1941. *Clathrodiction actinostromiforme* RIABININ; V. N. RIABININ, *Stromatoporoidei...*, pp. 89-90, Pl. 1, Figs. 6-7.
 1951. *Syringostroma vesiculosum* LECOMPTE; M. LECOMPTE, *Les Stromatoporoïdes...*, pp. 206-208, Pl. 32, Figs. 3, 3a-b.
 ?1966a. *Pseudoactinodictyon bullulosum* STEARN; C. W. STEARN, *Upper...*, pp. 53-54, Pl. 21, Figs. 1-3; Pl. 22, Fig. 4; Pl. 26, Fig. 1.
 1968. *Clathrodiction actinostromiforme* RIABININ; E. FLÜGEL & E. FLÜGEL-KAHLER, *Foss. Cat.*, pt. 115, p. 18.

Localities. — Sitkówka IV and V (loc. 21 and 22), Jaworznia-Moczydło Hill (loc. 25).

Material. — Five fragmentary coenostea (Z. Pal. St. 1/88 to 90 and St. 1/119 to 120).

Description. — Coenosteum massive, hemispherical, 10 cm in diameter at the base and 6 cm high. Surface smooth, with rare mamelons being 3—4 mm high and frequently with astrorhizae in the middle.

Skeleton composed of very thin, irregular laminae, 7 to 8 of them per 2 mm, here and there interrupted by foramina. Laminae frequently disappearing and replaced by flat dissepiments fused together horizontally to form continuous lamellae. Vertical elements in the form of twisted vertical walls on the average 0.12 mm thick, and of rare pillars. Some of the vertical walls and pillars are limited by interlaminar spaces, but most of them are superposed through several laminae. Also some of them are irregularly branched on contacting a lamina. Galleries, large, oval or subrectangular in outline, filled to a varying degree with dissepiments. Growth increments variable in height, emphasized by growth inhibition surfaces darker than the skeleton. Microstructure of laminae irregularly reticular, of pillars condensed.

Discussion. — *P. actinostromiforme* was placed by RIABININ (1941) within the genus *Clathrodiction* NICHOLSON & MURIE. On the basis of the presence of short and long pillars and many dissepiments FLÜGEL & FLÜGEL-KAHLER (1968) transferred this species to the genus *Pseudoactinodictyon*.

P. actinostromiforme differs from the nearest species *P. juxi* E. FLÜGEL in considerably less distinct laminae and a condensed microreticulum of vertical elements; from *?P. dartington-*

nense (CARTER) — in much thinner, regularly superposed vertical elements of the skeleton and the presence of laminae and from *P. vagans* (PARKS) and *P. norrisi* STEARN — in considerably thicker and more regularly distributed skeletal elements.

Stratigraphic and geographical distribution. — Middle-Upper Devonian transitional beds: Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): USSR (Main Devonian Field), Canada (Alberta), Belgium (Dinant Basin).

?*Pseudoactinodictyon dartingtonense* (CARTER, 1880)

(Pl. VIII, Fig. 4; Pl. XXVIII, Figs 1a-c, 2, 3)

1880. *Stromatopora dartingtoniensis* CARTER; H. J. CARTER, On Stromatopora..., p. 346, Pl. 18, Figs. 1-5.
 1891b. *Parallelopora dartingtonensis* (CARTER) var. *filitexta* NICHOLSON; H. A. NICHOLSON, A monograph..., p. 210, Pl. 25, Figs. 2-3.
 ?1896. *Parallelopora polonica* GÜRICH; G. GÜRICH, Das Palaeozoicum..., pp. 122-123, Pl. 1, Fig. 3a-b.
 1941. *Stromatopora schelonensis* RIABININ; V. I. RIABININ, Stromatoporoidei..., p. 97, Pl. 4, Figs. 5-6.
 1952. *Parallelopora dartingtonensis* (CARTER) var. *filitextum* NICHOLSON; M. LECOMPTE, Les Stromatoporoïdes..., pp. 296-297, Pl. 49, Fig. 4.
 1963. *Synthetostroma timanicum* YAVORSKY; V. I. YAVORSKY, Stromatoporoidea..., pp. 72-73, Pl. 22, Figs. 1-4.
 1966. *Ferestromatopora dubia* (LECOMPTE); J. E. KLOVAN, Upper..., p. 25, Pl. 8, Fig. 1a-b.
 ?1966a. *Stromatopora mikkwaensis* STEARN; C. W. STEARN, Upper..., pp. 55-56, Pl. 19, Fig. 5; Pl. 20, Figs. 1-4.
 1968. *Parallelopora dartingtonensis* var. *filitexta* NICHOLSON; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 124.
 1968. *Stromatopora dartingtoniensis* CARTER; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., Pl. 115, p. 124-125.

Localities. — Sowie Górki Hill (loc. 2), Zelejowa Hill (loc. 7 and 8), Bolechowice-„Jazwica“ quarry (loc. 10), Radkowice-Sołtysia Hill (loc. 11), „Szewce“ quarry (loc. 14), Sitkówka II, III and V (locs. 19, 21 and 22).

Material. — Twenty-seven fragmentary and complete colonies (Z. Pal. St. I/63 to 87, St. I/464).

Description. — Coenosteum massive, spherical, hemispherical or irregularly bulbous. The largest specimens are to 32 cm in diameter and 28 cm high. Surface smooth, slightly folded or with mamelons mostly astrorhizal. A few coenostea have *Syringopora* sp. embedded in them.

Skeleton occupies 40 to 60 per cent of the volume of coenosteum. Skeletal tissue is composed almost completely of shorter or longer vertical walls, irregularly twisted in many planes and usually superposed over fairly long stretches of coenosteum. Vertical walls vary in thickness within limits of 0.07 and 0.25 mm, averaging 0.12 mm. Frequently, they extend fanwise and join each other at various levels. Short processes, directed obliquely and upwards, detach themselves from vertical walls and give them a pinnate appearance. Walls surround vertical or vermiculate spaces of the nature of coeno- and autotubes and intersected by numerous but irregularly distributed dissepiments. Laminae lacking. Growth increments great, irregular, marked by growth discontinuity surfaces. Microstructure of vertical walls reticular, very strongly condensed. Calcification axes marked in tangential sections in the form of dark points, are usually clearly visible in vertical sections.

Discussion. — The taxonomic position of the species under study is not quite clear. Most authors assigned it to the genus *Parallelopora* BARGATZKY. STEARN (1966b, p. 104) found its compact microstructure not to correspond to a loose, reticular microstructure characteristic of *Parallelopora* and suggested transferring *Parallelopora dartingtonensis* to *Pseudoactinodictyon*.

He based his suggestion on the type specimen of *P. dartingtonensis* var. *filitexta* from NICHOLSON's collection and found it to be much better preserved than topotypes of *Parallelopora dartingtonensis* included in that collection. According to NICHOLSON (1891b, p. 201), both taxa only slightly differ from each other in the thickness of skeletal elements. In the present writer's opinion, a considerable variability in the thickness of vertical walls, observed in the specimens from the Holy Cross Mts., allows one to join *P. dartingtonensis* and *P. dartingtonensis filitexta* into one taxon.

?*Pseudoactinodictyon dartingtonense* differs from the remaining species of this genus in the lack of laminae and pillar proper, as well as in dark lines of crystallization axes, arranged in a characteristically parallel or pinnate manner in vertical walls. This character was the reason why this species has been assigned to *Parallelopora*. ?*P. dartingtonense* was probably evolved from *Parallelopora* as a result of the condensation of a loose microstructural reticulum of the latter. There are several species of *Parallelopora* in which particular stages of the condensation of a reticulum may be observed: from a very loose (e.g. in *P. ostiolata* BARGARZTKY) through transitional forms (e.g. *P. typicalis* GALLOWAY & ST. JEAN) to strongly condensed (e.g. *P. pomarevi* YAVORSKY or *P. bücheliensis* BARGATZKY).

In the parts of coenosteum, having more strongly twisted and sometimes anastomosing walls, ?*P. dartingtonense* resembles skeletal structures of *Stromatopora* GOLDFUSS or *Ferestromatopora* YAVORSKY with the representatives of which it may be easily confused in slightly oblique sections.

The species described is among the most numerous representatives of the Stromatoporidea in the area under study and it well characterizes the deposits of the stromatoporoid-coral facies of transitional beds of the Middle and Upper Devonian and Frasnian. The Frasnian specimens usually have a somewhat more delicate structure of the skeleton and calcification axes arranged in a plumose (trabecular) manner in vertical walls (see Pl. XXIV, Fig. 1a-b).

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): USA (Missouri), England, Germany, Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): USSR (Timan, Kuznetsk Basin, Western Ural Mts.), Canada (Alberta), Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

***Pseudoactinodictyon juxi* E. FLÜGEL, 1958**

(Pl. XXIX, Fig. 2a-d)

1958. *Pseudoactinodictyon juxi* E. FLÜGEL; E. FLÜGEL, *Pseudoactinodictyon*..., pp. 137—139, Pl. 1, Fig. 1a-d.

1968. *Pseudoactinodictyon juxi* E. FLÜGEL; E. FLÜGEL & E. FLÜGEL-KAHLER, *Foss. Cat.*, pt. 115, p. 216.

Localities. — Bolechowice-„Jaźwica“ quarry (loc. 10), Jaworznia-Moczydło Hill (loc. 25).

Material. — Two large fragments of coenosteum (Z. Pal. St. I/96 and St. I/118).

Dimensions (in mm):

Z. Pal. Cat. No.	L a m i n a e			Pillars and/or vertical walls		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/96	8	6	0.05—0.16	6	5	0.08—0.20
St. I/118	10	8	0.05—0.14	7	5	0.08—0.15

Description. — Coenosteum massive, irregularly bulbous or lenticular. The larger fragment is $8 \times 8 \times 4$ cm in size. The character of surface invisible.

The skeleton, marked by a delicate structure, occupies about 40 per cent of the volume of coenosteum. Skeletal tissue composed of even laminae, varying in thickness and sometimes replaced by flat dissepiments. Rare foramina occur in laminae. Vertical elements consisting of walls perpendicular to laminae and pillars usually regularly superposed. Vertical walls vermicularly twisted, here and there forming closed spaces appearing in tangential sections as round loops. Vertical walls and pillars usually intersect a considerable number of laminae but sometimes are limited to one interlaminar space. In the lower part of the interlaminar space, they are always somewhat thinner extending upwards and, consequently, in vertical section they may occur in the form of superposed, inverted cones. Galleries are intersected by closely spaced, convex dissepiments, 3 to 4 of them being frequently superposed on each other. Growth increments strongly marked, more or less equal in size, sometimes more condensed but not forming distinct latilaminae. Microstructure of laminae reticular, condensed, with very numerous calcification centers and of pillars and vertical walls — trabecular, with a considerably reduced number of calcification centers. Some of the pillars are monocentric (simple trabecula).

Discussion. — One of the specimens under study (Z. Pal. St. I/96) is identical with the type specimen while the other (Z. Pal. St. I/118) has more closely distributed skeletal elements. Particular attention is attracted by the trabecular microstructure clearly visible in the two specimens. Microstructure of *P. juxi* was a subject of discussion. FLÜGEL (1958) termed it as „maculate“ and STEARN (1966*b*) as „compact“. Both authors are right, since the trabecular microstructure, characteristic of *P. juxi*, in vertical sections gives an impression of being homogenous (= compact, according to other authors), while dark spots of calcification centers (= maculate microstructure of GALLOWAY & ST. JEAN, 1957) are visible in tangential sections.

P. juxi differs from the remaining species of this genus in strongly developed laminae and regularly superposed vertical walls and pillars.

Stratigraphic and geographical distribution. — Middle Devonian (Upper Givetian): Germany (Sauerland); Middle-Upper Devonian transitional beds: Poland (Western Holy Cross Mts.).

Genus TRUPETOSTROMA PARKS, 1936

Type species: Trupetostroma warreni PARKS, 1936; Middle Devonian (Presquile dolomite) Canada (Great Slave Lake).

Diagnosis. — Coenosteum consisting of reticular laminae variable in thickness, sometimes replaced by dissepiments and interrupted by numerous foramina. Vertical elements in the form of thick, meandering vertical walls and usually superposed pillars. Dissepiments frequent. Microstructure of laminae reticular, condensed and with very numerous calcification centers, of vertical walls and pillars — reticular, condensed or homogenous with characteristic vacuoles, irregularly scattered or grouped in the peripheral zone of vertical elements.

Discussion. — The concept and scope of the genus *Trupetostroma* has for a long time been a subject of discussion, which was summed up by STEARN (1966*b*). After having looked through PARKS' typical collection, STEARN arrived at the conclusion that out of the seven species described by PARKS (1936), only the type species, that is, *T. warreni* corresponds to the definition of *Tru-*

petostroma, the remaining ones either being very poorly preserved or belonging to other genera. The presence of three-layered laminae, also emphasized by PARKS (1936, p. 53), has been given by STEARN (1966*b*) as one of the main diagnostic characters of *Trupetostroma*. In the present writer's opinion, this character is devoid of any essential diagnostic significance since the light- or dark-coloured zones („primary laminae“ according to PARKS, 1936), which occur inside laminae, are a symptom of more or less rhythmically repeated interruption or inhibitions in the growth of a colony and are commonly met with in many other genera of the Stromatoporoidea. The laminae themselves are also frequently reduced and replaced by dissepiments.

A very irregularly condensed microstructure of the vertical skeletal elements, which is expressed in the presence of vacuoles, irregularly scattered within a usually homogenous skeletal substance, is a character which differs *Trupetostroma* from other genera. Vacuoles, as found by PARKS (*l. c.*, p. 53), are angular or round in outline, occur in varying numbers and are variously distributed. In the present writer's opinion, vacuoles in *Trupetostroma* are vestigially preserved fragments of an original reticular microstructure which was subject to condensation and homogenization. The view that the vacuolar microstructure of *Trupetostroma* may derive from the cellular (= reticular in the present paper) one has also been expressed by LECOMPTE (1951) and ST. JEAN (1967). It is likely that *Trupetostroma* was evolved from the stromatoporoids having a coarse-reticular microstructure, such as the structure of *Parallelopora* BARGATZKY in which the process of reduction and coarsening of reticular fibers took place irregularly. Such a view is justified by the existence of the species of *Parallelopora* (e. g., *P. ostiolata* BARGATZKY) with irregularly scattered spots of a homogenous skeletal substance within a loose microreticulum. On the other hand, one can hardly agree with PARKS (1936, p. 55) who considered *Trupetostroma* as a starting form of *Parallelopora*. The formation of a reticular microstructure from a compact, homogenous one is not recorded in any of the lineages of the Stromatoporoidea, while the opposite process is generally observed (cf. General Part). The present writer agrees with LECOMPTE (1951) who expressed the supposition that a cystose microstructure of the marginal, membrane-covered zones of vertical walls and laminae of the genus *Hermatostroma* NICHOLSON was formed as a result of the homogenization of central zones of vertical walls and pillars yet more advanced than in *Trupetostroma*. Judging by PARKS' (1936, Pl. 10, Fig. 2) description and illustrations, in the type species, that is, *T. warreni*, vacuoles are mostly grouped in the marginal zone of pillars, which here and there are covered outside with lamellae of the nature of membranes occurring in *Hermatostroma*. This is an additional argument in favour of a close relationship between the two genera. *Hermatostroma porosum* (LECOMPTE), having a marginal zone of vertical elements, consisting of vacuoles covered outside with a strongly developed membrane, is a transitional form between these genera.

The present writer attracts attention to the fact that vertical elements in the species of *Trupetostroma* are only partly composed of pillars and mostly of vertical walls, which, on the basis of a picture observed in vertical sections, are most frequently described erroneously as pillars. Vertical walls are clearly visible in tangential sections through interlaminar spaces, as, for instance, in *T. iowense* PARKS, *T. laceratum* LECOMPTE and *T. raricystosum* GALLOWAY & ST. JEAN, as well as, to a smaller extent, in *T. warreni* PARKS.

Trupetostroma differs from *Taleastroma* in the presence of laminae and vertical walls, from *Neosyringostroma* n. gen. — in the lack of columns and vacuolar structure and from *Gerronostroma* YAVORSKY — in reticular laminae and vacuolar microstructure.

Stratigraphic and geographical distribution. — Middle and Upper Devonian (abundant and cosmopolitan): North America, Eurasia, ?Australia.

Trupetostroma pingue LECOMPTE, 1952

(Pl. XXIX, Fig. 1a-b; Pl. XXX, Fig. 2a-b)

1952. *Trupetostroma pingue* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 230-231, Pl. 38, Figs. 2, 2a-b; Pl. 39, Figs. 1-3.

1963. *Trupetostroma pseudopingue* STEARN; C. W. STEARN, Some..., pp. 658-659, Pl. 85, Figs. 5-7; Text-fig. 3 D.

1968. *Trupetostroma pingue* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 317.

Locality. — Radkowiec-Sołtysia Hill (loc. 11).

Material. — One completely preserved colony (Z. Pal. St. I/94).

Description. — Coenosteum massive, hemispherical, 20 cm in diameter and 12 cm high. Surface strongly weathered.

Skeleton occupying about 55 per cent of the volume of coenosteum. Skeletal tissue composed of strongly developed laminae and vertical walls. Laminae, 9—10 of them per 2 mm, are usually even, 0.05 to 0.09 mm thick and interrupted by numerous foramina which give them a reticular character. Meandering, twisted vertical walls, limited by one interlaminar space, are mostly superposed over long stretches and thicker than laminae (0.10—0.25 mm). Pillars lacking. Galleries variable in size, round in outline, intersected by rare dissepiments. Growth increments, marked by dark-coloured growth inhibition surfaces, varying in height between 0.06 and 0.65 mm. Microstructure of laminae condensed, reticular near vertical walls passing in a homogenous one. Microstructure of vertical walls homogenous with vacuoles and rare calcification centers.

Discussion. — *T. pingue* differs from *T. warreni* PARKS and *T. iovense* PARKS in considerably thicker vertical elements developed only in the form of vertical walls. LECOMPTE (1952) expressed the supposition that *T. pingue* might possibly be a subspecies of *Trupetostroma bassleri* LECOMPTE (= ?*Trupetostroma laceratum* LECOMPTE). In the present writer's opinion, laminae of *T. pingue* much thicker as compared with thin and here and there reduced laminae of *T. bassleri*, as well as an excellent degree of the superposition of vertical walls and the presence of pillars in the last-named species, are sufficient arguments for acknowledging the separateness of the two species.

Stratigraphic and geographical distribution. — Middle Devonian (?Upper Givetian): Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): Canada (Alberta), Belgium (Dinant Basin).

Trupetostroma laceratum LECOMPTE, 1952

(Pl. XXX, Fig. 1a-d)

1952. *Trupetostroma laceratum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 228-230, Pl. 38, Figs. 1, 1a-b.

1952. *Trupetostroma tenuilamellatum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 223-225, Pl. 36, Figs. 1-5, Pl. 37, Fig. 1.

?1952. *Trupetostroma bassleri* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 227-228, Pl. 37, Figs. 3, 3a-b.

1957. *Gerronostroma porkhovense* YAVORSKY; V. I. YAVORSKY, Stromatoporoïdes..., p. 15, Pl. 15, Figs. 1-2.

?1962. *Trupetostroma papulosum* STEARN; C. W. STEARN, Stromatoporoïdes..., pp. 4-5, Pl. 1, Figs. 1-5.

1963. *Trupetostroma laceratum* LECOMPTE; K. YANG & D. DONG, Stromatoporoïdes..., pp. 156-157, Pl. 7, Figs. 6-7.

1968. *Trupetostroma laceratum* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 232.

Locality. — Jurkowiec-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.).

Material. — Two fragmentary coenostea (Z. Pal. St./132 and St. I/136).

Description. — Coenosteum massive, hemispherical, 9 cm in diameter and 5 cm high. Surface smooth, slightly folded, with very large (3—4 cm) astrorhizae.

Skeleton occupying about 40 to 50 per cent of the volume of coenosteum. Laminae thin, on the average 0.07 cm in thickness, 10 to 12 of them per 2 mm, uneven, frequently replaced by flat dissepiments. Numerous foramina give the laminae the form of network with large meshes. Vertical elements, limited to one interlaminar space, are composed mostly of vermicularly twisted vertical walls and rare, straight pillars. Both of them are usually regularly superposed. Vertical walls, considerably thicker than laminae, averaging 0.12 to 0.25 mm. They surround subcircularly or subrectangularly the galleries whose sections are more or less equal to the thickness of vertical walls. Galleries are intersected by closely spaced dissepiments. The regularity of the system of skeletal elements is here and there disturbed. In such places, vertical walls are bent and irregularly branched within a single interlaminar space. Growth increments equal in size, averaging 0.25 mm. Microstructure homogenous with more or less numerous vacuoles irregularly scattered over the skeletal tissue. Peripheral zone of vertical walls here and there covered with membranes.

Discussion. — A sporadic occurrence of membranes in vertical walls of *Trupetostroma laceratum* shows that this species displays characters transitional between *Trupetostroma* PARKS and *Hermatostroma* NICHOLSON. It is only an incomplete development of membranes that differs the species described from *Hermatostroma porosum* (LECOMPTE) identical with it structurally. On the other hand, the presence of fragmentary membranes and very numerous vacuoles differs *T. laceratum* from *T. warreni* PARKS, *T. iowense* PARKS and *T. pingue* LECOMPTE.

A considerable intracolony variability, observed by the writer in the specimens described and concerning primarily the thickness of laminae and vertical walls, as well as the number of vacuoles, became a basis for including in *T. laceratum* several other species which differed from the species under study only in the dimensions of skeletal elements (cf. synonymy).

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Belgium (Dinant Basin), China (Gueizhou), Poland (Eastern Holy Cross Mts.); Upper Devonian (Frasnian): Canada (Alberta), USSR (Main Devonian Field), Belgium (Dinant Basin).

Trupetostroma gebum (YAVORSKY, 1931)

(Pl. XXXI, Fig. 2a-c)

1931. *Syringostroma geba* YAVORSKY; V. I. YAVORSKY, Nekotorye..., pp. 1401-1402, Pl. 4, Fig. 6-9.
 1931. *Syringostroma strahlenbergi* YAVORSKY; V. I. YAVORSKY, Nekotorye..., p. 1402, Pl. 4, Figs. 10-11.
 1957. *Gerronostroma gromotuchense* YAVORSKY; V. I. YAVORSKY, Stromatoporoidea..., p. 12, Pl. 4, Fig. 7; Pl. 5, Figs. 1-2.
 ?1957. *Gerronostroma solomenense* YAVORSKY; V. I. YAVORSKY, Stromatoporoidea..., pp. 13-14, Pl. 5, Figs. 3-5.
 ?1960a. *Trupetostroma virgatulum* KHALFINA; V. K. KHALFINA, Otryad Stromatoporoidea..., p. 344, Pl. D-14, Fig. 3a-b.
 ?1960a. *Trupetostroma abieculum* KHALFINA; V. K. KHALFINA, Otryad Stromatoporoidea..., p. 345, Pl. D-14, Fig. 4a-b.
 1966. *Trupetostroma* sp.; J. E. KLOVAN, Upper..., p. 24, Pl. 7, Figs. 3a-b, 4a-b.
 1968. *Syringostroma geba* YAVORSKY; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 171.

Localities. — Kozi Grzbiet Hill (loc. 3), Radkowice-Sołtysia Hill (loc. 11), „Nowiny“ quarry (loc. 17), Sitkówka IV and V (locs. 21 and 22).

Material. — Fifteen complete and fragmentary coenostea (Z. Pal. St. I/155 to 157, St. I/159 to 161, St. I/174, St. I/206 to 212).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars and/or vertical walls		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/155	10	8	0.05—0.07	8	6	0.08—0.25
St. I/157	12	10	0.04—0.07	8	7	0.10—0.26
St. I/161	8	7	0.05—0.08	8	7	0.07—0.22
St. I/206	9	8	0.06—0.08	7	6	0.11—0.25
St. I/210	8	7	0.07—0.09	7	6	0.10—0.21

Description. — Coenosteam spherical hemispherical or irregularly bulbous. The largest specimens is 24 cm in diameter and 18 cm high. Surface smooth, even or with irregularly distributed mamelons a few mm to 2 cm high. Large (1.5 to 2.5 cm) astrorhizae occurring on the surface of some of the specimens.

Skeletons occupying about 50 per cent of the volume of coenosteam. Laminae strongly developed, very thin, interrupted by foramina which are covered with flat dissepiments. Vertical elements composed mostly of meandering vertical walls considerably thicker than laminae and, to a smaller extent, of pillars. Both of them are limited to one interlamina space and usually regularly superposed. In vertical section, walls and pillars are spool-shaped in outline. Galleries small, slightly smaller in width than the thickness of vertical walls and pillars, round or irregularly oval in outline and only rarely intersected by dissepiments. Growth increments well-expressed equalling in height interlamina spaces, with dark-coloured growth inhibition surfaces occurring in the planes of laminae. Microstructure condensed, in the case of vertical walls and pillars — homogenous with dark coloured spots of calcification centers in tangential sections through the skeleton, which are considerably less frequent than in laminae. Very small, irregularly scattered vacuoles occur sporadically within the skeletal substance.

Discussion. — Specimens of *T. gebum* are very common in the Middle-Upper Devonian transitional beds of the investigated area. Since *T. gebum* has not clear reticular microstructure characteristic of *Syringostroma*, YAVORSKY'S (1931) erroneous assignment of this species to *Syringostroma* NICHOLSON was pointed out by GALLOWAY & ST. JEAN (1957, p. 258) and FLÜGEL & FLÜGEL-KAHLER (1968, p. 171). *T. gebum* does not, however, display such a high degree of homogenization of the original microreticulum and the presence of numerous vacuoles as those recorded in other species of *Trupetostroma* (e.g., *T. warreni* PARKS, *T. iowense* PARKS, *T. pingue* LECOMPTE). In addition, many calcification centers are observed in vertical elements of *T. gebum*. The vacuolary of the skeletal substance is also considerable less strongly expressed in *T. gebum* than in the species referred to above. *T. gebum* is most similar to *T. raricystosum* GALLOWAY & ST. JEAN from the Middle Devonian of the U. S. A., from which it differs in considerably more superposed vertical walls and pillars and in a more delicate skeleton.

Stratigraphic and geographical distribution. — Middle Devonian: USSR (Kuznetsk Basin, ?Salair Mts.), Poland (Western Holy Cross Mts.); Upper Devonian: Canada (Alberta), USSR (Kuznetsk Basin), Poland (Western Holy Cross Mts.).

Genus *SYRINGOSTROMA* NICHOLSON, 1875

Type species: Syringostroma densum NICHOLSON, 1875; Middle Devonian (Corniferous limestone), USA (Kelley's Island, Ohio).

Diagnosis. — Coenosteum composed of more or less regular laminae, here and there replaced by dissepiments. Vertical elements, limited by a single interlaminar space, consist of meandering vertical walls and long columnar pillars whose thickness equals or, usually, exceeds that of vertical walls. Microstructure of laminae and vertical walls reticular, of columnar pillars—also reticular, but usually more strongly condensed than in the rest of the skeleton.

Discussion. — The diagnosis of *Syringostroma* was revised by GALLOWAY & ST. JEAN (1957), on the basis of a topotypical material of the type species, that is, *Syringostroma densum* NICH. These authors found that out of the three species, assigned by NICHOLSON (1875, 1886*b*, 1891*a*) to *Syringostroma*, that is, *S. densum*, *S. nodulatum* and *S. ?ristigouchense*, only the first corresponded to the characteristics of *Syringostroma*. They also pointed out that NICHOLSON's original assignment of the species varying structurally to *Syringostroma* caused an erroneous assignment of many new species to this genus by several later authors (e.g., LECOMPTE, 1951, YAVORSKY, 1931, 1955, 1957). According to GALLOWAY & ST. JEAN (1957), numerous microlaminae (= growth discontinuity surfaces in the present paper), as well as long columnar pillars and columns are the most characteristic features of *Syringostroma*. Since, as found by STEARN (1966*b*), microlaminae occur commonly in other genera of the Stromatoporoidea, the presence of columnar pillars and columns is the main diagnostic feature of *Syringostroma*. In the present writer's opinion, GALLOWAY & ST. JEAN (1957) groundlessly included in *Syringostroma* the species which, instead of columnar pillars, developed thick columns composed of a strongly condensed microreticulum or a homogenous skeletal substance. These species are: *Syringostroma perdensum* GALLOWAY & ST. JEAN, *S. superdensum* GALLOWAY & ST. JEAN, *S. tuberosum* GALLOWAY & ST. JEAN and *S. radicosum* GALLOWAY & ST. JEAN. A fine-laminar structure, reticular microstructure and the presence of columns qualify these species as representatives of the genus *Stylodictyon* NICHOLSON & MURIE, which was incorrectly recognized by GALLOWAY (1957) and STEARN (1966*b*) as a junior synonym of *Syringostroma*. Columns, characteristic of *Stylodictyon* should not be related with astrorhizal columns which occur in many other genera of the Stromatoporoidea and are probably devoid of any diagnostic importance (KAŻMIERCZAK, 1969).

Syringostroma has been most likely derived from *Stromatopora* Goldfuss and represents a next stage in the process of taking vertical position by the coenostelae and condensation of the microstructural reticulum of skeletal elements, which in turn leads to the formation of *Neosyringostroma* n. gen. in which columnar pillars have changed the microstructure from reticular to trabecular or homogenous.

Stratigraphic and geographical distribution. Devonian (mainly Middle): North America, Eurasia, Australia.

Syringostroma densum NICHOLSON, 1875

(Pl. XXXI, Fig. 1*a-b*)

1875. *Syringostroma densa* NICHOLSON; H. A. NICHOLSON, *Amorphozoa*..., p. 251, Pl. 24, Figs. 2, 2*a-b*.

1968. *Syringostroma densum* NICHOLSON; E. FLÜGEL & E. FLÜGEL-KAHLER, *Foss. Cat.*, pt. 115, p. 130-131 (with synonymy).

Locality. — Jurkowiec-Budy (*Stringocephalus burtini* Beds-Eastern Holy Cross Mts.).

Material. — Two fragmentary coenostea (Z. Pal. St. I/166 and St. I/220).

Description. — Coenosteum massive, irregularly spherical, about 10 cm in diameter. Surface smooth.

Skeleton occupying about 60 per cent of the volume of coenosteum. Tightly arranged, meanderingly twisted vertical walls, 0.18 to 0.26 mm thick, usually strongly superposed are predominant elements of the skeleton. Long columnar pillars, equalling in thickness or slightly smaller than vertical walls, runs within the range of vertical walls. Columnar pillars have a more condensed microstructural reticulum than that of vertical walls and consequently are visible in tangential sections in the form of areas darker than the rest of the skeleton. Vertical walls and columnar pillars are intersected by even laminae, averaging 0.10 mm in thickness, numbering 5–6 per 2 mm and interrupted by rare foramina. Dark growth inhibition surfaces are clearly visible in the planes of laminae. Microstructure of laminae reticular, slightly condensed. Galleries varying in size, which on the average amounts to 0.15 mm, round or suboval in outline, with rare dissepiments. Growth increments high, within limits of 0.25 and 0.50 mm.

Discussion. — The specimens described are almost identical with illustrations of the holotype (NICHOLSON, 1886*b*, Pl. 11, Figs. 13 and 14, 1891*a*, Pl. 10, Figs. 8 and 9; STEARN, 1966*b*, Pl. 18, Fig. 6) from which they differ, however, in somewhat thinner columnar pillars which, in the holotype, exceed the thickness of vertical walls. A topotype of *Syringostroma densum*, illustrated by GALLOWAY & ST. JEAN (1957, Pl. 16, Fig. 3*a-b*), has yet thicker columnar pillars and more irregular structure of skeleton between them.

S. densum is similar to *S. sanduskyense* GALLOWAY, but differs from it in regularly superposed vertical walls and considerably better developed columnar pillars. *S. densum* differs from the remaining species of *Syringostroma* in thinner columnar pillars with a low degree of condensation of the microstructural reticulum. Specimens of *S. densum* with a poorly preserved microstructure are very similar to *Stromatopora colliculata* NICHOLSON, from which they differ in more strongly superposed vertical walls and in a lack of coenotubes.

Stratigraphic and geographical distribution. — Middle Devonian: USA (Ohio, Indiana, Michigan), Canada (Ontario), ?Australia (Victoria), Poland (Eastern Holy Cross Mts.).

Genus NEOSYRINGOSTROMA n. gen.

Type species: *Hermatostroma logansportense* GALLOWAY & ST. JEAN, 1957, Middle Devonian (Logansport limestone), Indiana, U. S. A.

Derivation of the name: Lat. neo=new; an evolutionary advanced form of *Syringostroma* NICHOLSON.

Diagnosis. — Coenosteum consisting of even or irregularly undulated laminae with a reticular microstructure, which are intersected by long columnar pillars having a homogenous or trabecular microstructure. Dissepiments rare or lacking.

Discussion. — *Neosyringostroma* n. gen. differs from *Syringostroma* NICHOLSON in a homogenous-trabecular microstructure of columnar pillars, from *Stylodictyon* NICHOLSON & MURIE — in the lack of columns and a microlaminar structure of skeleton between pillars and from *Taleastroma* GALLOWAY — in the presence of columnar pillars and a reticular microstructure of skeleton between pillars. In contradistinction to *Hermatostroma* NICHOLSON, *Neosyringostroma* is devoid of membranes on vertical and horizontal elements characteristic of the former genus. The type species of *Neosyringostroma* has originally been assigned to *Hermatostroma* (GALLOWAY & ST. JEAN, 1957), but later, STEARN (1966*b*) pointed out that *Herma-*

tostroma logansportense, having a cellular (here called reticular) microstructure of twisted laminae, did not correspond to the diagnosis of *Hermatostroma*.

Species in which columnar pillars display a change from a reticular and reticular condensed into a homogenous and trabecular microstructure are grouped within *Neosyringostroma*. This genus makes up a direct continuation of the process of condensation of the microstructural reticulum in columnar pillars which has been started in *Syringostroma*. An originally reticular character of the microstructure in *Neosyringostroma* is visible in the form of condensed bundles of secretion axes which occur within the homogenous substance of columnar pillars in some species (e.g., *N. logansportense*, *N. urazovense*). Similar secretion axes, distributed in a fanwise manner, are marked within the reticular skeletal substance of columnar pillars even in some species of *Syringostroma* (e.g., *S. densum* NICHOLSON, *S. sherzeri* GRABAU). In most species of *Neosyringostroma*, the skeletal substance of columnar pillars is already completely homogenous.

The following species are assigned to *Neosyringostroma*:

- N. logansportense* (GALLOWAY & ST. JEAN, 1957),
- N. aurorum* (PARKS, 1904),
- N. bifurcum* (STEARNS, 1962),
- N. pseudotyrganicum* (KHALFINA, 1960),
- N. urazovense* (YAVORSKY, 1963),
- N. propinquicolumnae* (FRITZ & WAINES 1956),
- ?*N. aurorella* (FRITZ & WAINES, 1956),
- ?*N. distincticolumnae* (FRITZ & WAINES, 1956),
- ?*N. boiarschinovi* (YAVORSKY, 1961).

Stratigraphic and geographical distribution. — Middle Devonian: USA (Indiana), Canada (Alberta, Ontario), USSR (Salair Mts., Ural Mts.), Poland (Eastern Holy Cross Mts.).

Neosyringostroma logansportense (GALLOWAY & ST. JEAN, 1957)

(Pl. IX, Fig. 3; Pl. XXXII, Figs. 1a-d, 2)

- 1957. *Hermatostroma logansportense* GALLOWAY & ST. JEAN; J. J. GALLOWAY & J. ST. JEAN, Middle..., pp. 219-221, Pl. 21, Fig. 2a-b.
- 1957. *Hermatostroma logansportense* GALLOWAY & ST. JEAN; J. J. GALLOWAY, Structure..., Pl. 31, Fig. 17.
- 1967. *Hermatostroma logansportense* GALLOWAY & ST. JEAN; J. ST. JEAN, Maculate..., pp. 424-425, Pl. 2, Figs. 4-5.
- (part) 1886b. *Stromatopora beuthi* BARGATZKY; H. A. NICHOLSON, A monograph..., Pl. 5, Figs. 12-13.
- (part) 1891b. *Stromatopora beuthi* BARGATZKY; H. A. NICHOLSON, A monograph..., Pl. 23, Fig. 12.
- 1951. *Stromatopora beuthi* BARGATZKY; V. I. YAVORSKY, Nekotorye..., p. 10, Pl. 2, Figs. 4-5.
- 1955. *Stromatopora beuthi* BARGATZKY; V. I. YAVORSKY, Stromatoporoidea..., p. 106, Pl. 56, Figs. 1-2.
- 1968. *Hermatostroma logansportense* GALLOWAY & ST. JEAN; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 245.

Locality. — Jurkowice-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.).

Material. — Two almost complete colonies (Z. Pal. St. I/139 and 140).

Description. — Coenosteum massive, shaped like a strongly flattened lens 30 cm in diameter and 8 cm high. Surface smooth.

Skeleton occupying about 55 per cent of the volume of coenosteum. Irregularly twisted laminae are here and there arranged in a chevron-like manner. Laminae, averaging 0-12 mm

in thickness, are intersected by irregularly distributed, long, straight columnar pillars 0.25 to 0.35 mm thick, numbering 4 per 2 mm. Galleries small, irregularly oval, without dissepiments. Microstructure of laminae reticular, of columnar pillars — homogenous with traces of a trabecular one. A thin cover of a loose reticular skeletal tissue, 0.05 mm thick and being an extension of laminae occurs around columnar pillars. Growth rhythmic lacking.

Discussion. — The specimens described are identical with the holotype of *Neosyringostroma logansportense* which the present writer examined due to the courtesy of the U. S. National Museum in Washington. Polish specimens are considerably better preserved than the holotype which allows one to observe the trabecular microstructure of columnar pillars (Pl. XXXII, Fig. 1c) almost completely obliterated in the holotype (cf. ST. JEAN, 1967, Pl. 2, Fig. 4). The species under study has previously been assigned to the genus *Hermatostroma* NICHOLSON. The type specimen was described and illustrated in an opposite position (GALLOWAY & ST. JEAN, 1957, Pl. 21, 2a) and, for this reason, the trabecular microstructure was erroneously interpreted as conically superposed growth lines in the middle of columnar pillars. GALLOWAY & ST. JEAN (*l.c.*) attracted attention to a considerable similarity of *H. logansportense* to the specimen illustrated (also in an opposite position!) in NICHOLSON'S (1886b, Pl. 5, Fig. 13) work and erroneously referred by the last-named author to *Stromatopora beuthi* BARGATZKY (cf. also LECOMPTE, 1952; STEARN, 1966b). In the present writer's opinion, the specimen presented by NICHOLSON as *Stromatopora beuthi* is conspecific with *Neosyringostroma logansportense*, much the same as the specimens of *Stromatopora beuthi*, described and illustrated by YAVORSKY (1951, 1955) and which the author saw in the CNIGR Museum in Leningrad.

The absence of membranes in the peripheral zone of pillars, characteristic of *Hermatostroma* and a coarse-reticular microstructure of the skeleton between pillars are arguments against assigning the species described to this genus. In *N. logansportense*, vertical elements of the skeleton are developed only in the form of continuous columnar pillars, while in *Hermatostroma* twisted vertical walls are predominant elements.

N. logansportense differs from *Neosyringostroma pseudotyrganicum* (KHALFINA) in a considerably more homogenous microstructure of columnar pillars and from *Neosyringostroma aurorum* (PARKS) and *N. bifurcum* (STEARNS) in an irregularly suturelike arrangement of laminae and thinner columnar pillars.

Stratigraphic and geographical distribution. — Middle Devonian: USA (Indiana), England (Devonshire), Germany (Paffrath District), USSR (Ural Mts., Kuznetsk Basin), Poland (Eastern Holy Cross Mts.).

Genus PARALLELOPORA BARGATZKY, 1881

Type species: Parallelopora ostiolata BARGATZKY, 1881; Middle Devonian, Germany (Paffrath District).

Diagnosis. — Meandering and usually superposed vertical walls with a loose, reticular microstructure are the main skeletal element. The microstructural reticulum sometimes displays a regular orientation of the meshes, arranged in vertical rows. Laminae thin, with reticular microstructure. Frequently, they are completely replaced by dissepiments. Spaces surrounded by vertical walls are of the nature of irregular galleries or coeno- and autotubes, intersected by numerous dissepiments and tabulae.

Discussion. — *Parallelopora* differs from *Stromatopora* GOLDFUSS (*sensu* NESTOR, 1966) in regularly superposed vertical walls and a coarse-reticular microstructure, from *Syringostroma*

NICHOLSON — in a lack of columnar pillars and from *Syringostromella* NESTOR — in reduced and thickened fibres of the microstructural reticulum and regularly superposed vertical elements of the skeleton.

As follows from the discussion of *Parallelopora*, conducted by LECOMPTE (1951—1952), YAVORSKY (1963), STEARN (1966*b*) and ST. JEAN (1967), this genus is not understood unequivocally which is a result of different interpretations of the microstructure of the type species *P. ostiolata* BARGATZKY, given by BARGATZKY (1881) and NICHOLSON (1886*b*). Meshes of the microstructural reticulum, arranged in regular, vertical rows within vertical walls, are visible in NICHOLSON'S drawings. However, this geometrical picture, of the microstructure of vertical walls, in the type species is much less visible in photographs of the holotype (LECOMPTE, 1952, Pl. 51, Fig. 3*a*). LECOMPTE found that the reticular microstructure, clearly visible in *Parallelopora ostiolata* related this genus to *Stromatopora* GOLDFUSS and expressed a doubt about a generic separateness of *Parallelopora*, since, in his opinion, the vertical skeletal elements more strongly developed in *Parallelopora* than in *Stromatopora* represented the only character in which the two genera differed from each other.

In the present writer's opinion, a distinct, orderly arrangement of the skeletal structure in *Parallelopora*, expressed in the tendency of skeletal elements to take a vertical position, with a simultaneous considerable reduction of laminae give ample evidence for a more advanced development of the representatives of *Parallelopora* as compared with species of *Stromatopora* irregular structurally. In addition, *Parallelopora* differs from *Stromatopora* in a considerably looser microstructural reticulum which, in some species (e.g., *P. longitubulata* (RIABININ), *P. ostiolata* BARGATZKY) becomes reduced, with a simultaneous thickening of the remaining fibres of reticulum. At the same time the genus *Parallelopora* includes species which, with a skeletal structure typical of this genus, display the tendency to form columnar pillars, having their microstructural reticulum more condensed than the rest of the skeleton and being identical with those of *Syringostroma* NICHOLSON (e.g., *Parallelopora pulchra* GALL. & ST. JEAN).

In the present writer's opinion, the first of the morphological groups of *Parallelopora* mentioned above would indicate an evolutionary trend towards the formation of skeletal structure of the type of *Trupetostroma* PARKS and further, of *Hermatostroma* NICHOLSON and the second — towards *Syringostroma* NICHOLSON and, further, *Neosyringostroma* n. gen. (for further discussion see General Part). The genus *Parallelopora* was probably evolved from the Upper Silurian *Syringostromella* NESTOR by an increase in the regularity of distribution of the vertical skeletal elements and reduction of the horizontal parts of coenosteum which in *Syringostromella* are still thick.

Stratigraphic and geographical distribution. — Middle and Upper Devonian (cosmopolitan): North America, Eurasia, Australia.

Parallelopora kudebensis (RIABININ, 1941)

(Pl. XXXIII, Fig. 1*a-c*)

1941. *Stromatopora kudebensis* RIABININ; V. N. RIABININ, *Stromatoporoidei...*, pp. 95-96, Pl. 4, Fig. 1.

1968. *Stromatopora kudebensis* RIABININ; E. FLÜGEL & E. FLÜGEL-KAHLER, *Foss. Cat.*, pt. 115, p. 227.

Locality. — Kowala-railway cut (loc. 12).

Material. — One almost complete colony (Z. Pal. St. I/228).

Description. — Coenosteum dislike, 10 cm in diameter and 3 cm high. Surface smooth.

Skeleton compact, occupying about 70 per cent of the volume of coenosteum. Meandering vertical walls, varying in thickness and composed of an irregular reticulum, here and there more strongly condensed, are the main skeletal elements. Their thickness, between 0.08 and 0.24 mm, averages 0.15–0.20 mm. Most vertical walls are superposed. Slightly developed laminae are frequently replaced by flat dissepiments. Laminar structures are also formed of extended parts of vertical walls connected with each other in horizontal plane. Skeletal tissue surrounds spaces of the nature of galleries subcircular in outline or irregular coeno- and autotubes intersected by dissepiments and tabulae. Growth rhythmic slightly marked emphasized by irregularly distributed, dark-coloured growth inhibition surfaces.

Discussion. — The species described is marked by characters of both genera, that is, *Parallelopora* and *Stromatopora* GOLDFUSS and which are expressed by, on the one hand, superposition of vertical walls, reduction of laminae and a loose microstructural reticulum typical of *Parallelopora* and, on the other, meandering and here and there anastomosing vertical walls and coenotubes which make it similar to *Stromatopora*. The specimen described by the writer is identical with the holotype of *Parallelopora kudebensis* and with the paratypes housed at the Palaeontological Museum in Moscow.

Parallelopora kudebensis is strongly similar to the topotype of *P. planulata* (HALL & WHITFIELD), illustrated by LECOMPTE (1952, Pl. 50, Figs. 1–2), from which it differs, however, in somewhat thinner vertical walls and a more delicate microstructural reticulum. *P. kudebensis* differs from *P. longitubulata* (RIABININ) in a considerably finer microstructural reticulum.

Stratigraphic and geographical distribution. — Upper Devonian (Frasnian): USSR (Main Devonian Field), Poland (Western Holy Cross Mts.).

Parallelopora longitubulata (RIABININ, 1941)

(Pl. XXXIII, Fig. 2a-c)

1941. *Stromatopora longitubulata* RIABININ; V. N. RIABININ, *Stromatoporoidei...*, p. 95, Pl. 3, Figs. 7-8.

non 1957. *Stromatopora longitubulata* RIABININ; V. I. YAVORSKY, *Stromatoporoidea...*, p. 50, Pl. 25, Figs. 6-8.

1966a. *Stromatopora* cf. *S. mononensis* GALLOWAY & ST. JEAN; C. W. STEARN, *Upper...*, pp. 56-57, Pl. 22, Figs. 1-3.

Locality. — Sitkówka V (loc. 22).

Material. — One large fragment of coenosteum (Z. Pal. St. I/95).

Description. — Coenosteum massive, irregularly bulbous. The fragment described is 15 × 13 × 8 cm in size. Surface, smooth, gently undulated.

Skeleton occupying about 60 per cent of the volume of coenosteum. Skeletal tissue composed of usually accurately superposed, meandering vertical walls, varying in thickness from 0.07 to 0.25 mm and limited by interlaminar spaces. Vertical walls consisting of an irregular, large-meshed but thick-fibrillar reticulum which in some places turns into compact concentrations of a homogenous calcite. Laminae, with a reticular microstructure, very poorly developed, not exceeding 0.05 mm in thickness, frequently replaced by dissepiments. Galleries small, round in outline. Numerous, long, vertical coenotubes are intersected by slightly convex dissepiments. Growth increments varying in size, on the whole small (0.15 to 0.25 mm), emphasized by growth discontinuity surfaces.

Discussion. — The specimen described has — as compared with the holotype, the writer examined at the Palaeontological Museum in Moscow — slightly thinner vertical walls and

better expressed growth rhythmicity. *P. longitubulata* differs from all other species of *Parallelopora* in strongly thickened fibers of the microstructural reticulum and in partly, homogenous skeletal substance in vertical walls. These characters bring the species described close to some of the representatives of *Trupetostroma* PARKS (e.g., *T. laceratum* LECOMPTE), except for the fact that *P. longitubulata* has not yet vacuoles, closed within a homogenous skeletal substance, characteristic of *Trupetostroma*. *P. longitubulata* displays a considerable similarity to the specimen described by YAVORSKY (1951) as *Idiostroma elegans* and which reveals characters common to *Parallelopora*, *Trupetostroma* and *Hermatostroma*. In „*Idiostroma*“ *elegans*, the process of the homogenization of the reticulum, is, however, considerably more advanced than in *Parallelopora longitubulata* and its vacuoles, accumulated in the marginal zone of vertical walls covered in some places with membranes as in *Hermatostroma*, are fairly clearly visible (cf. Pl. IX, Fig. 2).

Stratigraphic and geographical distribution. — Middle-Upper Devonian transitional beds: Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): USSR (Main Devonian Field) ?Canada (Alberta).

Genus **HERMATOSTROMA** NICHOLSON, 1886

Type species: Hermatostroma schlüteri NICHOLSON, 1886; Middle Devonian, Germany (Paffrath District).

Diagnosis. — Coenosteum composed of even laminae, variable in thickness, sometimes replaced by dissepiments. Vertical elements composed of pillars and meandering vertical walls, usually well superposed and limited by interlaminal spaces. Microstructure of the central parts of laminae, pillars and vertical walls — homogenous or reticular-condensed, turning in the marginal zone into a coarse-reticular or vacuolar one. Peripheral zone of skeletal elements covered with a thin membrane.

Discussion. — *Hermatostroma* differs from *Trupetostroma* PARKS and *Taleastroma* GALLOWAY in the presence of membranes in the peripheral zone of skeletal elements. As found by STEARN (1966*b*), the degree of homogenization of skeletal elements varies in different species of *Hermatostroma* and, in this connection, within the range of this genus, there occur species with almost completely homogenous laminae and pillars, covered outwardly with membranes (e.g., *H. schlüteri* NICHOLSON, *H. perseptatum* LECOMPTE), as well as species in which the marginal zone of skeletal elements, reticular-vacuolar in structure, is wide and in which single vacuoles may also occur in the central parts of pillars and vertical walls (e.g., *H. porosum* (LECOMPTE), *H. episcopale* NICHOLSON). STEARN (1966*b*) tried to explain this considerable microstructural variability of *Hermatostroma* by its diphyletic origin and, at the same time, suggested a separation from it of a new genus which would include species with a reticular (called by STEARN „cellular“) microstructure and strongly developed peripheral membranes. The present writer believes that, in the case under study, suspecting diphyletism in *Hermatostroma* is not justified. First of all, the microstructure of all, so far described, species of *Hermatostroma* has never been recorded to be clear reticular but it is always more or less condensed or homogenized with closely spaced calcification centers (e.g., *H. porosum* (LECOMPTE)), or, in some other cases, the fibers of microstructure are reduced, strongly thickened and, in some places, fused to form irregular accumulations of a homogenous substance (e.g., *H. episcopale* NICHOLSON). In other words, the process of a homogenization of the primary microreticular skeletal substance, advanced to a varying degree, is observed in particular species of *Hermatostroma*, the presence of peripheral membranes being a common character which relates all these species. *Herma-*

tostroma is very closely related to *Trupetostroma* PARKS. In some of the species of the latter genus, a concentrations of vacuoles is visible in the marginal zone of pillars and vertical walls, as well as a formation may be observed of incipient membranes (e.g., *T. warreni* PARKS). In the writer's opinion, both *Trupetostroma* and *Hermatostroma* were probably evolved from *Parallelopora* BARGATZKY by a uniform or non-uniform condensation of microstructural reticulum.

Stratigraphic and geographical distribution. — Devonian: Canada, USSR, China, France, Belgium, Germany, England, Poland.

Hermatostroma porosum (LECOMPTE, 1952)

(Pl. VIII, Fig. 5; Pl. XXXIV, Fig. 1a-b)

1952. *Trupetostroma porosum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 236-237, Pl. 42, Figs. 3a; Pl. 43, Fig. 1.
 1952. *Trupetostroma mailleuxi* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 237-239, Pl. 43, Figs. 2, 2a, 3, 3a.
 non 1960. *Trupetostroma porosum* LECOMPTE; J. J. GALLOWAY, Devonian..., p. 626, Pl. 73, Fig. 2a-b. (= *Trupetostroma laceratum* LECOMPTE).
 1960. *Trupetostroma mailleuxi* LECOMPTE; J. J. GALLOWAY, Devonian..., p. 626, Pl. 73, Fig. 3a-b.
 1968. *Trupetostroma porosum* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, pp. 327-328.
 1968. *Trupetostroma mailleuxi* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, pp. 252-253.

Locality. — Jurkowice-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.).

Material. — Six, well preserved colonies (Z. Pal. St. I/111, 112, 114, 128, 129 and 137).

Description. — Coenosteum massive, spherical or irregularly bulbous, 20 cm in diameter and 12 cm high. Surface smooth, even or with large mamelons, 2 to 3 mm high, usually with a large astrorhiza in the central part.

Skeleton occupying about 50 per cent of the volume of coenosteum. Thick, vermiculate vertical walls, usually perfectly superposed, are the main skeletal elements. Walls are sometimes irregularly branched and surround vertical, meandering canals, intersected by convex dissepiments. Walls are on the average 0.25 mm and canals 0.20 to 0.25 mm thick. Laminae vestigial, marked only in some places as horizontal extensions of vertical walls. Mostly, laminae are replaced by dissepiments. Vertical walls are composed of a homogenous substance with traces of calcification centers and many subspheroid vacuoles about 0.025 mm in diameter, concentrated mostly in the marginal zone of walls. Outwardly, vertical walls are covered with membranes. Growth increments more or less equal in size, marked by growth discontinuity surfaces intersecting vertical walls.

Discussion. — *Hermatostroma porosum*, much the same as its synonym *H. mailleuxi*, was originally assigned to the genus *Trupetostroma* PARKS because of its vacuoles occurring within the range of vertical walls. However, attention was attracted by STEARN (1966b) to the fact that this species has already strongly developed membranes on skeletal elements and is more similar to *Hermatostroma*. The transitional character of *H. porosum* between *Trupetostroma* and *Hermatostroma* is yet more strongly emphasized by its vacuoles concentrated however, in contradistinction to *Trupetostroma*, mostly in the marginal zone of vertical walls. The presence of vacuoles differs, at the same time, *H. porosum* from all other species of *Hermatostroma* and primarily from the most related *H. episcopale* NICHOLSON, in which well de-

veloped laminae occur in addition. *H. porosum* is related to *Trupetostroma laceratum* LECOMPTE in an equally vacuolar microstructure and poorly developed laminae. It differs from the last-named species in the presence of membranes.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian); Canada (Mackenzie Valley). Poland (Eastern Holy Cross Mts.); Upper Devonian (Frasnian): Belgium (Dinant Basin).

Hermatostroma perseptatum LECOMPTE, 1952

(Pl. VIII, Fig. 6; Pl. XXXIV, Fig. 2a-b)

1952. *Hermatostroma perseptatum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., p. 251, Pl. 45, Figs. 2, 2a-b.

1968. *Hermatostroma perseptatum* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 314.

Locality. — Jurkowiec-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.).

Material. — Two complete colonies (Z. Pal. St. I/131 and 138).

Description. — Coenosteum massive, spherical or hemispherical, 12 cm in diameter. Surface with conspicuous mamelons (1.5 to 2 cm high), having, very large astrorhizae with a span of their lateral canals exceeding 5 cm.

Skeleton occupying about 55 per cent of the volume of coenosteum. Very thick, well superposed and meandering vertical walls which are limited by interlaminar spaces are the main elements of the skeleton. Their thickness averages 0.30—0.45 mm. Laminae straight, considerably thinner than vertical walls (0.07 to 0.12 mm), numbering 5 to 6 per 2 mm, frequently interrupted by foramina and replaced by dissepiments. Galleries round in outline, here and there turning into vertical coenotubes averaging 0.30 mm in width and intersected by dissepiments. Microstructure of laminae and vertical walls homogenous with a coarse-reticular rim 0.07 mm thick in marginal zone. All skeletal elements are covered outwardly with membranes. Growth increments irregular, marked by indistinct growth discontinuity surfaces visible mostly in vertical sections of vertical walls.

Discussion. — The specimens under study differ from the holotype of *H. perseptatum* in thicker vertical walls and a lower stratigraphic position. *H. perseptatum* differs from *H. crassum* (LECOMPTE), *H. pustulosum* LECOMPTE and *H. schlüteri* NICHOLSON in thicker vertical elements and poorly developed laminae, and from *H. porosum* (LECOMPTE) and *H. episcopale* NICHOLSON in a homogenous microstructure of central zones of vertical walls in which no traces are observed of vacuoles and microreticula.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Poland (Eastern Holy Cross Mts.); Upper Devonian (Lower Frasnian): Belgium (Dinant Basin).

Hermatostroma episcopale NICHOLSON, 1892

(Pl. XXXV, Fig. 1a-b)

1892. *Hermatostroma episcopale* NICHOLSON; H. A. NICHOLSON, A monograph..., pp. 219-221, Pl. 28, Figs. 4-11.

1955. *Syringostroma kielzeense* YAVORSKY; V. I. YAVORSKY, Stromatoporoidea..., pp. 135-136, Pl. 71, Figs. 7-8; Pl. 72, Figs. 1-2.

1968. *Hermatostroma episcopale* NICHOLSON; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. cat., pt. 115, p. 150 (with synonymy).

Localities. — Stokówka I (loc. 6), Bolechowice — „Panek“ quarry (loc. 16), „Nowiny“ quarry (loc. 17), Jaworzna quarry (loc. 26).

Material. — Twelve fragmentary colonies (Z. Pal. St. I/124—127 and 105—110).

Description. — Coenosteam masive, irregularly bulbous. The largest fragment is $18 \times 12 \times 10$ cm in size. Surface smooth, with conspicuous mamelons 1 to 2 cm high.

Skeleton composed of regularly distributed vertical elements and horizontal ones which in vertical section form an almost isometric lattice pattern. Laminae straight, 0.07 to 0.15 mm thick, 6 to 7 of them occurring in 2 mm, sporadically interrupted by foramina. Vertical elements, limited by one interlaminar space, consist of spool-shaped pillars round or oval in transverse section or longer or shorter, irregularly twisted vertical walls. An average thickness of pillars and vertical walls amounts to about 0.15 mm. Both are usually perfectly superposed. Galleries high, subrectangular or, less frequently, oval in outline, intersected by dissepiments. Coenotubes continuing through a few interlaminar spaces occur here and there. Microstructure of laminae homogenous with many calcification centers. A thin coating of a coarse-reticular substance covered outwardly with a membrane occurs on both sides of laminae. Microstructure of pillars and vertical walls condensed-reticular, in some places vacuolar, with calcification centers visible in tangential section. Much the same as in the peripheral zone of laminae, here occurs a sheath composed of a thick reticulum covered outwardly with a membrane (Pl. XXXV, Fig. 1b). Growth rhythmic distinct due to dark growth inhibition surfaces in laminae.

Discussion. — The specimens described are identical with the holotype presented in NICHOLSON's illustrations (1892, Pl. 28, Figs. 4—11) and refigured by LECOMPTE (1952, Pl. 48, Fig. 4). *Hermatostroma episcopale* differs from *H. schlüteri* NICHOLSON, *H. perseptatum* LECOMPTE and *H. crassum* (LECOMPTE) in a less homogenized microstructure of vertical elements of the skeleton with preserved fragments of a thick reticulum and vacuoles concentrated mostly in the marginal zone. A markedly homogenous central part of pillars and vertical walls does not allow one to acknowledge the microstructure of the species under study as a „cellular“ (= reticular in the present paper) one, as suggested by STEARN (1966b, p. 109).

H. episcopale represents a transitional link between the species of *Trupetostroma* PARKS, having a strongly vacuolar microstructure (e.g., *T. laceratum* LECOMPTE) and typical *Hermatostroma* with a completely homogenous structure of the central zone of laminae and vertical elements.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): England (South Devonshire), Germany (Eifel), France (Ancienies District), China (Gueizhou), Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): ?Canada (Northwest Territories), Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

***Hermatostroma schlüteri* NICHOLSON, 1886**

(Pl. XXXV, Fig. 2a-b)

- 1886b. *Hermatostroma schlüteri* NICHOLSON; H. A. NICHOLSON, A monograph..., Text-fig. 16 A-B, Pl. 3, Figs. 1-2.
 1892. *Hermatostroma schlüteri* NICHOLSON; H. A. NICHOLSON, A monograph..., pp. 215-219, Text-fig. 29-31. Pl. 28, Figs. 12-13.
 (part) 1952. *Hermatostroma polymorphum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 258-259, Pl. 47, Figs. 3, 3a; Pl. 48, Figs. 1, 1a.
 1955. *Hermatostroma verchovense* RIABININ; V. N. RIABININ, Verkhnedevonskye..., pp. 30-31, Pl. 21, Figs. 1-2.

1955. *Hermatostroma dzejimense* RIABININ; V. N. RIABININ, Verkhnedevonskye..., p. 31, Pl. 21, Figs. 3-5.
 1968. *Hermatostroma schlüteri* NICHOLSON; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 380-381 (with synonymy).

Localities. — Jurkowice-Budy (*Stringocephalus burtini* beds — Eastern Holy Cross Mts.), Sowie Górki Hill (loc. 2), Western Zelejowa Hill (loc. 7), Bolechowice-„Jaźwica“ quarry (loc. 16), Sitkówka IV (loc. 20), Wietrznia quarry (loc. 34).

Material. — Two complete and nine fragmentary colonies (Z. Pal. St. I/100 to 104, 121 to 123 and 133 to 135).

Description. — Coenosteum massive, irregularly bulbous. The largest specimen is 28 × 25 × 18 cm in size. Surface smooth with conspicuous mamelons 1 to 3 cm high.

Skeleton occupying 40 to 60 per cent of the volume of coenosteum. In the region of mamelons, laminae are strongly bent upwards, their thickness varying within limits of 0.09 and 0.16 mm. On the average 5 to 6 laminae occur in 2 mm. Vertical elements, limited by one interlaminar space, consist mostly of longer or shorter, twisted vertical walls and rare pillars. Both are usually well superposed and their thickness amounts to 0.13 to 0.25 mm. Galleries round or vertically extended oval in outline, varying in size between 0.12 and 0.27 mm and usually intersected by dissepiments. Microstructure of skeletal elements homogenous, but with a characteristic sheath, composed of thick, large-meshed reticulum covered with membrane. Traces of trabecular structure are sometimes preserved in pillars and vertical walls in which single, dark-coloured calcification axes are also visible (Pl. XXXV, Fig. 2b). Growth rhythmic regular, with growth discontinuity surfaces occurring in planes of laminae.

Discussion. — The specimens described are identical with the holotype, illustrated by NICHOLSON (1886b, 1892) and refigured by LECOMPTE (1952) and STEARN (1966b). *Hermatostroma schlüteri* differs from *H. perseptatum* LECOMPTE in a considerably more regular structure of the skeleton and presence of laminae, from *H. crassum* (LECOMPTE) in a sheath of a coarse-reticular substance occurring in the marginal zone of skeletal elements and from *H. episcopale* NICHOLSON and *H. porosum* (LECOMPTE) in a considerably higher degree of homogenization of the axial parts of skeletal elements. In the writer's opinion, *H. verchovense* and *H. dzejimense*, described by RIABININ (1955) and separated by him only on the basis of the presence of astro-rhizae and small differences in the dimensions of particular skeletal elements, are junior synonyms of *H. schlüteri*.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Germany (Rhenish Mts.), Poland (Holy Cross Mts.); Upper Devonian (Frasnian): USSR (Timan), Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

***Hermatostroma crassum* (LECOMPTE, 1952)**

(Pl. XXXV, Fig. 3a-b)

1952. *Trupetostroma crassum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 239-240, Pl. 43, Fig. 4; Pl. 44, Figs. 1, 1a.
 1968. *Trupetostroma crassum* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 112.

Localities. — Jurkowice-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.), Bolechowice — „Nowiny“ quarry (loc. 17), Sitkówka V (loc. 22).

Material. — One complete and three fragmentary colonies (Z. Pal. St. I/115 to 117 and 130).

Description. — Coenosteum massive, hemispherical or irregularly bulbous, 16 cm in diameter and 10 cm high. Surface smooth, gently folded, with 0.5 to 1.5 cm high mamelons.

Skeleton occupying about 70 per cent of the volume of coenosteum. Very massive, twisted vertical walls and pillars 0.25 to 0.42 mm thick, limited by one interlaminar space and usually well superposed are the main elements of the skeleton. Laminae poorly developed, composed mostly of horizontal swellings of pillars and vertical walls connected with each other or interrupted by foramina. Galleries high and narrow, oval in outline, in some places turning into 0.12 to 0.26 mm thick coenotubes intersected by many dissepiments. Microstructure of skeleton homogenous with a very thin, irregular sheath of a loose, reticular substance covered outwardly with a membrane. Rare spots of calcification centers are visible in transverse sections of vertical elements. Growth rhythmic emphasized by the presence of darker growth discontinuity surfaces in planes of laminae.

Discussion. — The species described, was originally assigned to the genus *Trupetostroma* PARKS (LECOMPTE, 1952) but, later, STEARN (1966*b*) attracting attention to the presence of membranes in the type specimen, suggested transferring this species to *Hermatostroma*. *H. crassum* differs from *H. schlüteri* NICHOLSON in considerably thicker vertical walls and pillars having a much thinner cover of a coarse-reticular substance and less strongly developed laminae and from *H. perseptatum* LECOMPTE in better expressed laminae, which are to smaller extent replaced by dissepiments and in a less solid skeleton.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Belgium (Dinant Basin), Poland (Eastern and Western Holy Cross Mts.); Upper Devonian (Frasnian): Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

Genus ATELODICTYON LECOMPTE, 1951

Type species: Atelodictyon fallax LECOMPTE, 1951; Middle Devonian (Couvin-*Calceola sandalina* beds), Belgium (Dinant Basin).

Diagnosis. — Coenosteum consisting of straight, reticular laminae, here and there interrupted by foramina and twisted, longer or shorter, thin vertical walls, straight or irregularly branching and limited by one interlaminar space. Galleries subrectangular or irregular, usually intersected by dissepiments. Microstructure of laminae reticular, frequently condensed or reduced, loose, of vertical walls reticular, usually reduced to single, homogenous or fibro-normal fibers.

Discussion. — *Atelodictyon* differs from *Actinostroma* NICHOLSON in the presence of vertical elements, expressed not by pillars but by vertical walls limited by one interlaminar space and from *Anostylostroma* PARKS, *Simplexodictyon* BOGOYAVLENSKAYA and *Tienodictyon* YABE & SUGIYAMA in reticular laminae.

In the characteristics of *Atelodictyon* published so far (cf. LECOMPTE, 1951; GALLOWAY, 1957; GALLOWAY & ST. JEAN, 1957; STEARN, 1966*a* and others), vertical elements of this genus were erroneously determined as pillars, whereas they are expressed mostly in the form of vertical walls which in fact are visible in tangential sections of the type specimen (LECOMPTE, 1951, Pl. 15, Figs. 1 and 1*d*).

The reticular character of laminae and frequently also of the interlaminar skeleton, indicates, in the present writer's opinion, a relationship of *Atelodictyon* to the stromatoporoids with a typically reticular microstructure. *Atelodictyon* was most likely originated as a result of

a gradual reduction in the original microreticulum which in extreme cases became limited in vertical elements to single, thickened, straight or twisted fibers (for further explanation see General Part).

Stratigraphic and geographical distribution. — Devonian (cosmopolitan): North America, Eurasia, Australia.

***Atelodictyon pseudocolumnare* (RIABININ, 1941)**

(Pl. X, Fig. 6; Pl. XXXVI, Fig. 1a-c)

1941. *Clathrodiction pseudocolumnare* RIABININ; V. N. RIABININ, *Stromatoporoidei...*, pp. 90-91, Pl. 1, Fig. 8; Pl. 2, Figs. 1-5.

1957. *Clathrodiction compositum* YAVORSKY; V. I. YAVORSKY, *Stromatoporoidea...*, p. 18, Pl. 7, Figs. 4-7.

1968. *Clathrodiction pseudocolumnare* RIABININ; E. FLÜGEL and E. FLÜGEL-KAHLER, *Foss. Cat.*, pt. 115, p. 332.

Localities. — Radkowiec-Sołtysia Hill (loc. 11), Bolechowice-„Panek“ quarry (loc. 16), Sitkówka III and IV (loc. 20 and 21).

Material. — Twelve fragmentary colonies (Z. Pal. St. I/22 to 24, 28 to 32, 34, 36, 37, 39).

Description. — Coenosteum massive, irregularly bulbous. Dimensions of the largest fragments amount to 34 × 24 × 18 cm. Surface smooth with irregular mamelons 0.3 to 1.2 mm high.

Skeleton very delicate, occupying about 35 per cent of the volume of coenosteum. Laminae reticular, straight, frequently wedged out, very thin (0.05 to 0.09 mm), 5 to 7 of them occurring in 2 mm. Rare, small foramina occur in laminae. Vertical elements, limited by one interlaminar space, occur in the form of very thin (0.03 to 0.06 mm), interrupted vertical walls vermicularly twisted, frequently irregularly branched and forming a loose, tangled mass within an interlaminar space. Galleries variable in height, usually high, irregular or subrectangular in outline, intersected by slightly convex dissepiments. Growth increments uneven the smallest 0.15 mm, the largest 0.95 mm high. Growth inhibition surfaces, darker than the skeleton, are distributed in upper parts of laminae. Microstructure of laminae coarse-reticular, of vertical walls homogenous with traces of a fibro-normal one.

Discussion. — The species described was assigned by RIABININ (1941) to the genus *Clathrodiction* NICHOLSON & MURIE and, later, transferred by GALLOWAY & ST. JEAN to *Anostylostroma* PARKS. The type specimen of *Atelodiction pseudocolumnare* which the present writer had an opportunity to examine at the Palaeontological Museum in Moscow (Cat. No. 101—5) had, however, markedly reticular laminae which allows one to assign it unequivocally to *Atelodiction*.

A. pseudocolumnare differs from the related *A. trautscholdi* (RIABININ) and *A. fallax* LECOMPTE in thinner and more tangled vertical walls and a looser reticulum in laminae, from *A. intercalare* GALLOWAY & ST. JEAN in strongly developed laminae and from *A. stelliferum* STEARN and *A. ordinatum* STEARN in considerably more reduced vertical walls, which, in the last-named species, form a dense reticulum within the interlaminar space.

Stratigraphic and geographical distribution. — Middle Devonian: USSR (Kuznetsk Basin), Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): USSR (Main Devonian Field), Poland (Western Holy Cross Mts.).

Atelodictyon trautscholdi (RIABININ, 1941)

(Pl. XXXVI, Figs. 2a-b, 3)

1941. *Actinostroma trautscholdi* RIABININ; V. N. RIABININ, *Stromatoporoidei...*, pp. 87-88, Pl. 1, Figs. 1-2.
 1951. *Stromatoporella bifida* LECOMPTE; M. LECOMPTE, *Les Stromatoporoides...*, pp. 192-193, Pl. 29, Figs. 1, 1a, 2, 2a, 3-4.
 1955. *Stromatoporella mirabilis* YAVORSKY; V. I. YAVORSKY, *Stromatoporoidea...*, pp. 120-121, Pl. 64, Figs. 2-5.
 1957. *Actinostroma mirum* YAVORSKY; V. I. YAVORSKY, *Stromatoporoidea...*, pp. 8-9, Pl. 2, Figs. 1-2.
 1957. *Actinostroma trautscholdi* RIABININ; V. I. YAVORSKY, *Stromatoporoidea...*, pp. 9-10, Pl. 2, Figs. 3-4.
 1957. *Hermatostroma porkhovense* YAVORSKY; V. I. YAVORSKY, *Stromatoporoidea...*, p. 58, Pl. 30, Figs. 2-4.
 1966. *Stromatoporella* cf. *mirabilis* YAVORSKY; J. E. KLOVAN, *Upper...*, p. 10-11, Pl. 2, Figs. 3, 4a-b.
 1968. *Actinostroma trautscholdi* RIABININ; E. FLÜGEL & E. FLÜGEL-KAHLER, *Foss. Cat.*, pt. 116, p. 429-430.

Locality. — Bolechowice, „Panek“ quarry (loc. 16).

Material. — Seven large fragmentary colonies (Z. Pal. St. I/21, 25 to 27, 38, 40, 41).

Description. — Coenosteum massive, hemispherical or irregularly bulbous. Dimensions of the largest fragment amount to 22 × 21 × 15 cm. Character of surface invisible.

Skeleton delicate, occupying about 35 per cent of the volume of coenosteum. Laminae straight, intersected by rare foramina, 6 to 8 of them occurring in 2 mm, their thickness varying from 0.05 to 0.10 mm. Vertical elements in the form of short, twisted vertical walls and rare pillars 0.07 mm thick and limited by a single interlaminae space. Walls and pillars are perpendicular to the surface of laminae but sometimes they bend and branch. Microstructure of laminae reticular-condensed, of vertical elements homogenous, here and there fibro-normal. Growth increments variable (0.10—0.75 mm), their size corresponding to the height of interlaminae spaces.

Discussion. — The species described was assigned by RIABININ (1941) to the genus *Actinostroma* NICHOLSON and subsequently transferred by GALLOWAY & ST. JEAN (1957, p. 241) to *Anostylostroma* PARKS. YAVORSKY (cf. FLÜGEL-KAHLER, 1968, p. 430) expressed the view that it should be transferred to *Trupetostroma* PARKS. The characters of the type specimen of *Atelodictyon trautscholdi*, which the present writer had an opportunity to study at the Palaeontological Museum in Moscow (Cat. No. 101—18), indicated that it belonged to *Atelodictyon*. *A. trautscholdi* has not superposed vertical elements of skeleton characteristic of *Actinostroma* and *Trupetostroma* and vacuoles typical of the latter genus and it differs from *Anostylostroma* in microreticular laminae, the presence of vertical walls and very few pillars.

A. trautscholdi differs from *A. pseudocolumnare* (RIABININ) in straight vertical elements of skeleton and more condensed microreticulum which forms laminae and from *A. stelliferum* STEARN and *A. ordinatum* STEARN in vertical walls and pillars reduced to single fibers and branching to a very small extent only.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): USSR (Kuznetsk Basin); Upper Devonian (Frasnian): USSR (Main Devonian Field), Canada (Alberta), Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

Genus **ACTINOSTROMA** NICHOLSON, 1886

Type species: *Actinostroma clathratum* NICHOLSON, 1886 (= ?*Actinostroma papillosum* (BARGATZKY, 1881)); Middle Devonian (?Givetian), Germany (Rhenish Mts.).

1968a. *Bifariostroma*; KHALFINA, p. 58.

Diagnosis. — Coenosteum consisting of coarse reticular laminae sometimes replaced by dissepiments. In laminae, rare foramina are hidden by dissepiments. Vertical elements

consisting only of pillars which continue through several laminae, or, less frequently, limited by one interlaminar space. Microstructure of skeleton homogenous with traces of a trabecular one in pillars.

Discussion. — *Actinostroma* differs from *Plectostroma* NESTOR in the presence of straight, regular laminae, from *Atelodictyon* LECOMPTE in the lack of vertical walls and from *Gerronostroma* YAVORSKY in reticular laminae.

Actinostroma clathratum, determined by NICHOLSON (1886*b*) as a type species of *Actinostroma* is a subject of controversy. As follows from studies on the typical material (cf. LECOMPTE, 1951) NICHOLSON very broadly understood the range of *A. clathratum*, whereas in the opinion of some other authors (SLEUMER, 1969), at least part of the typical collection of specimens belongs to the previously described *Actinostroma papillosum* (BARGATZKY). Until a penetrating revision is made of typical materials of the two species mentioned above, the present writer acknowledges with a reservation *A. clathratum* to be a type species.

Actinostroma is among the most numerous and most cosmopolitan Devonian representatives of the Stromatoporoidea. On account of its very simple structure of skeleton, most authors separated species on the basis of quantitative characters or differences in the outer morphology of coenosteum devoid of a diagnostic significance, which led to the division of this genus into a vast number of species. This number, amounting to 141, was reduced by E. FLÜGEL (1959) to 36. This author conducted the revision of *Actinostroma*, basing it mostly on a statistical analysis of the number and dimensions of skeletal elements and not explaining in detail its origin and evolutionary trends in the morphology of skeleton. Most structural differences between the species of *Actinostroma* which remained after FLÜGEL's (*l.c.*) revision were considered by SLEUMER (1969) as symptoms of an intraspecific variability, caused mostly by environmental factors. According to the last named author, *Actinostroma* is represented merely by a few species, *Gerronostroma* YAVORSKY and *Atelodictyon*, LECOMPTE, as well as probably *Clathrostroma* YAVORSKY and *Plectostroma* NESTOR being junior synonyms of this genus. SLEUMER, much the same as FLÜGEL, does not try to explain the origin of *Actinostroma* and indicate its possible relationships to other genera of the Stromatoporoidea. In contradistinction to all other authors, SLEUMER was of the opinion that laminae in *Actinostroma* were not composed of horizontal processes connecting pillars („arms“) but of cystlike plates which only in tangential sections gave an impression of processes. SLEUMER's interpretation of laminae is, in the present writer's opinion, a misunderstanding, resulting from the material SLEUMER had at his disposal and which mostly belonged to non-typical group of *Actinostroma verrucosum* (GOLDFUSS) with thickened microreticular laminae and with interlaminar spaces containing, in addition to a loose, irregular mesh, also numerous dissepiments. In all other species of *Actinostroma*, laminae consist of a single-layer network with thick fibers, termed by NICHOLSON (1886*b*) as a „hexactinelloid“ structure and which has never been observed in stromatoporoids having pillars connected with each other by dissepiments arranged in laminae (e.g., *Labechia* M. EDWARDS & HAIM). Dissepiments, if they occur at all in species of *Actinostroma*, always make up only supplementary elements of laminae composed of horizontal processes. Compact, thick microreticular laminae of *Gerronostroma* YAV. are indicative of the separateness of this genus from *Actinostroma*.

The identity of *Atelodictyon* and *Actinostroma*, suggested by SLEUMER (1969), is, in the present writer's opinion, only seeming, since vertical walls, occurring in the former, give evidence for the fact that *Atelodictyon* belongs to another evolutionary lineage of the Stromatoporoidea (cf. General Part).

The coarse reticular character of laminae in *Actinostroma*, in the writer's opinion, serves to show a relationship of the representatives of this genus to a group of the stromatoporoids with a microreticular structure. *Actinostroma* makes up a continuation of a lineage started in the Early Silurian by *Densastroma* FLÜGEL having a very fine, irregular skeletal reticulum. As a result of a gradual reduction of skeletal fibers, with a simultaneous thickening of pillars, *Densastroma* evolved into the Silurian-Lower Devonian *Plectostroma* NESTOR, in which horizontal elements formed a reticulum not yet arranged in regular laminae. Through the formation of straight laminae and a continued thickening of pillars, *Plectostroma* evolved into the Middle and Late Devonian *Actinostroma* (cf. Pl. XLI, Figs. 1—6). The process of the thickening of pillars reaches its peak stage in several species of the Late Devonian *Actinostroma* (e.g., *A. crassepilatum* LECOMPTE, *A. crassum* LECOMPTE, *A. petrovi* RIABININ).

Another lineage of *Actinostroma* is probably represented by species of *Actinostroma verrucosum* (GOLDFUSS) group in which thick laminae still have a fine-reticular character and pillars are limited to one interlamina space and by species of *Actinostroma stellulatum* NICHOLSON group, in which, with the reduction of laminae to a single-layer, large-meshed reticulum, pillars are not superposed and are also limited by one interlamina space. This group is likely to be also related to *Actinostroma bifarium* NICHOLSON in which, in addition to long, continuous pillars, there occur numerous, thinner ones which are limited by one interlamina space.

Stratigraphic and geographical distribution. — Devonian (mainly Middle and Upper): North America, Eurasia, Australia.

Actinostroma compactum RIPPER, 1933

(Pl. XXXVII, Fig. 1a-b)

1933. *Actinostroma compactum* RIPPER; E. A. RIPPER, The Stromatoporoids..., pp. 153-154, Fig. 5A-B.

1937. *Actinostroma compactum* RIPPER; E. A. RIPPER, On the stromatoporoids..., pp. 15-16, Pl. 2, Figs. 7-8.

1959. *Actinostroma compactum* RIPPER; E. FLÜGEL, Die Gattung..., pp. 134-135 (revision).

1968. *Actinostroma compactum* RIPPER; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 81 (with synonymy).

Locality. — Jurkowice-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.).

Material. — Three complete colonies (Z. Pal. St. I/271, 275, 356).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/271	11	8	0.05—0.09	11	9	0.08—0.12
St. I/275	10	8	0.05—0.08	12	10	0.07—0.11
St. I/356	10	9	0.06—0.09	12	10	0.08—0.11

Description. — Coenosteum massive, spherical or hemispherical, 11 cm in diameter. Surface smooth, with irregular, 0.5 to 1.5 cm high mamelons. Laminae poorly developed, consisting of horizontal processes, which irregularly detach themselves from pillars and, in tangential sections, form a thick, singlelayer network. Horizontal processes deviate from pillars at various levels and, consequently, laminae are irregular and frequently interrupted. Pillars

long, sometimes slightly twisted, intersecting several interlaminar spaces, round in transverse sections. Galleries irregularly oval or subrectangular in outline. Dissepiments absent. Microstructure of skeleton homogenous. Traces of a calcification axis, darker- or brighter-coloured than the skeletal substance, occur in the central part of pillars.

Discussion. — Horizontal processes in *Actinostroma compactum*, not yet arranged in a laminar system, indicate that this species makes up a form transitional from the representatives of *Plectostroma* NESTOR devoid of laminae to typical *Actinostroma* with clearly defined laminae (e.g., *Actinostroma papillosum* (BARGATZKY)). The writer does not agree with FLÜGEL's (1959, p. 135) suggestions that *A. compactum* is a transitional form between the group of species of *A. clathratum* and that of *A. stellulatum*, as this species has continuous pillars, radically differing from short pillars of *A. stellulatum*, limited by one interlaminar space.

A. compactum differs from species, related in the structure of coenosteum to *A. verrucosum*. (GOLDFUSS) in single-layer, coarse reticular laminae and continuous pillars and from *A. crassepilatum* LECOMPTE in irregular, interrupted laminae and considerably thinner pillars.

Stratigraphic and geographical distribution. — Lower Devonian (Upper Siegenian): Australia (Victoria); Middle Devonian: Australia (Victoria), Austria (Carnic Alps), Poland (Eastern Holy Cross Mts.).

***Actinostroma* aff. *geminatum* LECOMPTE, 1951**

(Pl. XXXVII, Fig. 2a-b)

1951. *Actinostroma geminatum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 106-107, Pl. 8, Figs. 5, 5a.

1959. *Actinostroma geminatum* LECOMPTE; E. FLÜGEL, Die Gattung..., p. 120.

1968. *Actinostroma geminatum* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 172.

Locality. — Sitkówka IV (loc. 21).

Material. — Two fragmentary colonies (Z. Pal. St. I/383 and 410).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/383	11	8	0.10—0.25	8	7	0.08—0.18
St. I/410	10	6	0.09—0.25	8	6	0.09—0.16

Description. — Coenosteum massive, irregularly bulbous. The larger of the two specimens is 24 × 14 × 12 cm in size. Character of surface invisible.

Laminae thick, strongly expressed, with upper surface even and lower irregularly frayed, strongly varying in thickness, in extreme cases replaced by dissepiments and composed of a denser or looser, irregular microreticular tissue. Pillars two of types: thicker, intersecting several laminae and thinner, more numerous and limited by one interlaminar space. Both are straight and round in transverse section. Galleries wide, subrectangular in outline, intersected by rare, large, flat dissepiments. Microstructure of pillars homogenous with dark axes of calcification centers preserved in central part of some of the pillars.

Discussion. — The specimens described are identical with the holotype illustrated in LECOMPTE'S work, but for the lack of photographs of a tangential section of the holotype, cannot be fully compared with it. Photographs of the holotype's vertical sections are in LECOMPTE'S work reproduced in a reverse position which is clearly indicated by the situation of astrorhizae.

Thick, fine-reticular laminae of *A. aff. geminatum* are indicative of this species relationship to *Actinostroma verrucosum* (GOLDFUSS), from which it differs in the presence of thick, continuous pillars. *Actinostroma geminatum* is also related to *A. conglomeratum* LECOMPTE and *A. mamontovi* YAVORSKY, from which it differs in considerably thicker laminae and the presence of two types of pillars.

The occurrence of long and short pillars makes the species described similar to *A. bifarium* NICHOLSON, from which it differs in thick laminae having a dense, microreticular structure (cf. Pl. XXXVII, Fig. 2b).

Stratigraphic and geographical distribution. — Middle Devonian: Belgium (*Calceola sandalina* beds — Dinant Basin), Poland (Givetian — Western Holy Cross Mts.).

Actinostroma stellulatum NICHOLSON, 1886

(Pl. XXXVII Fig. 3a-b)

1886a. *Actinostroma stellulatum* NICHOLSON; H. A. NICHOLSON, On some..., pp. 231-233, Pl. 6, Figs. 8-9.

?1951. *Actinostroma sertiforme* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 123-125, Pl. 15, Figs. 1-2.

1959. *Actinostroma stellulatum* NICHOLSON; E. FLÜGEL, Die Gattung..., pp. 179-185, Pl. 6, Fig. 5; Pl. 7, Fig. 4 (revision).

1968. *Actinostroma stellulatum* NICHOLSON; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, pp. 401-403 (with synonymy).

Localities. — Bolechowice — „Jaźwica“ quarry (loc. 10), Radkowice — Sołtysia Hill (loc. 11), Kowala — railway cut (loc. 12), „Kowala“ quarry (loc. 13), Sitkówka V (loc. 22).

Material. — Thirty seven fragmentary and complete colonies (Z. Pal. Cat. No. St.I/308 to 318, St. I/320 to 340, St. I/342 to 343), St. I/269, St. I/274, St. I/277).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/269	14	11	0.03—0.09	13	11	0.05—0.09
St. I/277	13	9	0.04—0.11	13	10	0.05—0.11
St. I/323	14	10	0.03—0.10	12	10	0.05—0.09
St. I/335	14	9	0.04—0.12	13	9	0.04—0.10

Description. — Coenosteum massive, spherical, hemispherical or irregularly bulbous. The largest, complete colonies reach 32 cm in diameter. Surface smooth, with or without mamelons.

Laminae clearly defined thin, composed mostly of a one-layer network sometimes thickened. Most laminae are even, but there also frequently happen irregularly folded or wedging-out ones. In the zones of growth disturbance (latilaminae), the laminar system of the structure of coenosteum is obliterated and horizontal elements of the skeleton are deve-

loped in the form of twisted lamellae or flat dissepiments. In addition to thin horizontal processes deviating from pillars, a very fine, dense reticulum forms another component of laminae. Spaces between laminae varying within limits of 0.05 and 0.25 mm and averaging 0.12 mm.

Pillars, limited by one interlaminar space, are perpendicular to the surface of laminae and usually conspicuously extended in the upper part. A considerable number of pillars is superposed over longer stretches of coenosteum. In transverse section, pillars are irregular in outline and display the presence of usually dark spots of calcification centers (traces of compound trabeculae?). Galleries wide, semicircular or subrectangular in outline, intersected by rare, flat dissepiments.

Discussion. — *A. stellulatum* differs from all other species of *Actinostroma* in very fine skeletal elements, laminae with only slightly developed horizontal processes and pillars limited by one interlaminar space. In the writer's opinion, the presence of numerous astrorhizae, emphasized by NICHOLSON (1886a) and which are very few or, in many specimens, lacking at all, is insignificant diagnostically for this species. The structure of coenosteum makes *A. stellulatum* similar to some of the representatives of *Atelodictyon* LECOMPTE (e.g. *A. fallax* LECOMPTE). *Actinostroma sertiforme* LECOMPTE, which, in the writer's opinion, was erroneously transferred by FLÜGEL (1959) to the genus *Clathrodiction* NICHOLSON & MURIE, is probably a junior synonym of *A. stellulatum*. This species is identical in structure and dimensions of skeletal elements with *A. stellulatum* and differs only, in some places, in a somewhat greater number of twisted laminae and dissepiments which does not seem to be a sufficient reason for acknowledging the specific separateness of this form.

Stratigraphic and geographical distribution. — Middle Devonian (cosmopolitan): USSR (Ural Mts., Kazakhstan, Kuznetsk Basin), Australia (Victoria), Germany (Eifel, Sauerland), England (Devonshire), Belgium (Dinant Basin), Austria (Carnic Alps), Italy (Carnic Alps), Marocco (Tizi Merakib), Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian); Belgium (Dinant Basin) Poland (Western Holy Cross Mts.).

Actinostroma papillosum (BARGATZKY, 1881)

(Pl. XXXVIII, Fig. 1a-b; Pl. XL, Fig. 1a-b)

1881. *Stromatopora papillosa* BARGATZKY; A. BARGATZKY, Die Stromatoporen..., p. 282.
 1951. *Actinostroma papillosum* (BARGATZKY); M. LECOMPTE, Les Stromatoporoïdes..., p. 85, Pl. 1, Fig. 11 (illustration of holotype).
 1959. *Actinostroma papillosum* (BARGATZKY); E. FLÜGEL, Die Gattung..., pp. 167-172 (revision).
 1968. *Actinostroma papillosum* (BARGATZKY); E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, pp. 303-304 (with synonymy).
 (part) 1969. *Actinostroma papillosum* (BARGATZKY); B. H. G. SLEUMER, Devonian.; pp. 30-32, Pl. 15, Fig. 1, Pl. 18, Fig. 2.
 ?1886a. *Actinostroma clathratum* NICHOLSON; H. A. NICHOLSON, On some..., pp. 226-228, Pl. 6, Figs. 1-3. For a complete synonymy see FLÜGEL, 1959, p. 129 and FLÜGEL & FLÜGEL-KAHLER, 1968, p. 69.
 ?1886a. *Actinostroma hebbornense* NICHOLSON; H. A. NICHOLSON, On some..., pp. 228-229, Pl. 7, Figs. 7-8. For a complete synonymy see FLÜGEL, 1959, p. 146, and FLÜGEL & FLÜGEL-KAHLER, 1968, p. 186.

Localities. — Radkowice-Sołtysia Hill (loc. 11), „Kowala“ quarry (loc. 13), Sitkówka III, IV and V (locs. 20, 21 and 22).

Material. — Sixty complete and fragmentary colonies (Z. Pal. St. I/245, St. I/261, St. I/265, St. I/270, St. I/272, St. I/276, St. I/297, St. I/299 to 301, St. I/357, St. I/391 to 409, St. I/411 to 415, St. I/418, to 433, St. I/434 to 438, St. I/445 to 449).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/261	9	8	0.05—0.12	7	6	0.08—0.15
St. I/270	9	8	0.05—0.10	7	6	0.06—0.13
St. I/276	10	8	0.05—0.11	8	6	0.06—0.12
St. I/357	9	7	0.06—0.11	8	7	0.08—0.13

Description. — Coenosteum massive, spherical, hemispherical, bell-like or irregularly ball-shaped. The largest colony is 70 cm wide at the base and 40 cm high. Surface smooth, irregularly folded, sometimes with mamelons.

Laminae clearly defined, straight or gently undulating, composed of thin horizontal processes of pillars forming a loose network clearly visible in tangential sections. In some of the specimens, the laminar network is here and there covered with thin, flat lamellae of the nature of dissepiments. Pillars continuous, intersecting several interlaminar spaces, usually straight but in some of the specimens bent or bifurcated. In transverse sections, pillars are angular or irregularly circular in outline. Galleries variable in height, wide, mostly rectangular and less frequently subrectangular or oval in outline. Dissepiments occur sporadically in galleries. Microstructure homogenous. Traces of calcification axes in the form of one or a few darker spots against the back-ground of a lighter-coloured skeletal substance (?traces of simple and compound trabeculae) are visible in transverse sections through pillars.

Discussion. — *A. papillosum* is the most numerous representative of the Stromatoporoidea occurring in the section of the uppermost Middle Devonian and transitional beds between the Middle and Upper Devonian of the area under study. If LECOMPTE'S (1951), SCHOUPEPÉ'S (1954) and SLEUMER'S (1969) suggestions, concerning the identity of *A. papillosum* and *A. clathratum* NICHOLSON would prove true the species described will turn out to be one of the most widely distributed species of all the stromatoporoids described thus far.

A. papillosum differs from *A. crassepilatum* LECOMPTE and *A. expansum* (HALL & WHITFIELD) in considerably thinner pillars and in laminae having more delicate horizontal processes. Uni-lamellar coarse-reticular laminae and continuous pillars differ *A. papillosum* from *A. verrucosum* (GOLDFUSS) and *A. geminatum* LECOMPTE. In contradistinction to *A. bifarium* NICHOLSON, *A. papillosum* has pillars of one type only and which are more or less uniform in thickness and continuing over long stretches of coenosteum.

Stratigraphic and geographical distribution. — Middle Devonian (mainly Givetian) — Upper Devonian (Lower Frasnian): Canada (Alberta), Australia (Victoria), Germany, England, Austria, Italy, Czechoslovakia, USSR (Ural Mts., Turkestan), Poland (Western Holy Cross Mts.).

Actinostroma bifarium NICHOLSON, 1886

(Pl. XXXVIII, Figs. 2a-b and 3; Pl. XXXIX, Figs. 1a-b and 2a-b)

1886a. *Actinostroma bifarium* NICHOLSON; H. A. NICHOLSON, On some..., p. 231, Pl. 6, Figs. 4-5.

1951. *Actinostroma bifarium* NICHOLSON; M. LECOMPTE, Les Stromatoporoïdes..., pp. 104-105, Pl. 8, Figs. 1-3.

1959. *Actinostroma bifarium* NICHOLSON; E. FLÜGEL, Die Gattung..., pp. 127-129, Pl. 7, Fig. 2 (revision).

1968. *Actinostroma bifarium* NICHOLSON; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, p. 46 (with synonymy).

Localities. — Western Zelejowa Hill (loc. 7), Bolechowice-„Jaźwica“ quarry (loc. 10), Radkowiec-Sołtysia Hill (loc. 11), Kowala — railway cut (loc. 12), „Kowala“ quarry (loc. 13), Bolechowice-„Panek“ quarry (loc. 16), Sitkówka III, IV and V (locs. 20, 21 and 22), Kadzielnia quarry (loc. 33).

Material. — Forty complete and fragmentary colonies (Z. Pal. St. I/248, St. I/251 to 259, St. I/266 to 267, St. I/273, St. I/363 to 382, St. I/384 to 387, St. I/389 to 390, St. I/467).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars			
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness short long	
St. I/254	13	11	0.03—0.05	9	7	0.05—0.08	0.13—0.25
St. I/259	12	9	0.03—0.04	9	8	0.05—0.07	0.17—0.26
St. I/266	11	10	0.03—0.05	8	7	0.07—0.09	0.12—0.20
St. I/273	11	9	0.04—0.05	8	7	0.05—0.08	0.12—0.22

Description. — Coenosteum massive, irregularly bulbous disclike or lamellar. The largest colony is $42 \times 34 \times 28$ cm in size. Surface smooth, irregularly folded, with or without mamelons.

Laminae clearly defined, usually straight, arcuate between pillars, frequently interrupted and replaced by dissepiments, consisting of horizontal processes deviating from pillars and forming a uni-lamellar, loose network with meshes polygonal in outline. In some parts of coenosteum, horizontal processes deviate from pillars at various levels and the laminar system of structure is obliterated in such places (cf. Pl. XXXV, Fig. 1a). Pillars are of two types: short and thin ones, limited by one interlaminar space, usually extended in upper parts and longer ones, considerably thicker and intersecting several interlaminar spaces. Shorter pillars are usually much more numerous, but in some of the specimens longer pillars may predominate. Galleries wide, variable in height, subrectangular in outline, rarely intersected by dissepiments. Microstructure of skeleton homogenous. Dark, centrally situated spots of calcification centers are visible in transverse sections of pillars.

Discussion. — The presence of the two types of pillars referred to above differs the species described from the species of *Actinostroma*. Two types of pillars are also a character of *Actinostroma geminatum* LECOMPTE but *A. bifarium* differs from it in thin, uni-lamellar laminae composed of horizontal processes. The species described was probably evolved from forms, having the structure of *A. geminatum*, as a result of a far-advanced reduction of microreticulum in laminae.

Stratigraphic and geographical distribution. — Middle Devonian (Givetian): Germany (Rhenish Mts.), Belgium (Dinant Basin), Austria (Graz, Carnic Alps), Italy (Carnic Alps), Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): Belgium (Dinant Basin), Poland (Western Holy Cross Mts.).

Actinostroma expansum (HALL & WHITFIELD, 1873)

(Pl. XL, Fig. 2a-b; Pl. XLI, Fig. 5)

1873. *Stromatopora expansa* HALL & WHITFIELD; J. HALL & R. WHITFIELD, Descriptions..., p. 226, Pl. 9, Fig. 1.
 1891a. *Actinostroma expansum* (HALL & WHITFIELD); H. A. NICHOLSON, On some..., pp. 316-317, Pl. 10, Figs. 1-2.
 1936. *Actinostroma expansum* (HALL & WHITFIELD); W. A. PARKS, Devonian..., pp. 118-121, Pl. 19, Figs. 3-6 (rediscription of topotypes).

1957. *Actinostroma expansum* (HALL & WHITFIELD); J. J. GALLOWAY, Structure..., Pl. 1, Fig. 9 (refigured topotype).
 1959. *Actinostroma expansum* (HALL & WHITFIELD); E. FLÜGEL, Die Gattung..., pp. 143-145 (revision).
 1968. *Actinostroma expansum* (HALL & WHITFIELD); E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, pp. 154-155 (with synonymy).

Localities. — Jurkowiec-Budy (*Stringocephalus burtini* Beds — Eastern Holy Cross Mts.), Sitkówka III and IV (locs. 20 and 21), Jaworznia-Moczydło Hill (loc. 25), Jaworznia quarry (loc. 26).

Material. — Five complete and four fragmentary colonies (Z. Pal. St. I/260, St. I/262 to 264, St. I/296, St. I/442 to 444, St. I/468).

Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/260	11	10	0.05—0.07	6	5	0.12—0.22
St. I/262	11	9	0.04—0.06	6	5	0.16—0.25
St. I/296	10	9	0.06—0.08	7	6	0.12—0.20
St. I/468	10	9	0.06—0.09	7	5	0.15—0.22

Description. — Coenosteum massive, spherical or hemispherical, 18 cm in diameter in the largest specimen. Surface smooth, gently undulating.

Laminae clearly defined, straight or slightly twisted, frequently interrupted and, in some parts, replaced by dissepiments. Laminae composed of thick horizontal processes deviating from pillars and forming a wide- and polygonal-meshed reticulum, here and there supplemented by dissepiments. Pillars continuous, straight, considerably thicker than laminae, in transverse section circular or subangular in outline. Galleries variable in height, wide, mostly subrectangular and less frequently circular in outline. Dissepiments lacking in galleries. Microstructure homogenous with single calcification centers occurring in pillars.

Discussion. — The specimens under study are identical with the topotypes described and figured by PARKS (1936). In its structure and dimensions of skeletal elements, *A. expansum* makes up a transitional link between *A. papillosum* (BARGATZKY), having thinner pillars and horizontal processes, and species of *Actinostroma* with extremely thick pillars which occur mostly in the Upper Devonian (e.g., *A. crassepilatum* LECOMPTE, *A. petrovi* RIABININ).

Stratigraphic and geographical distribution. — Middle Devonian (Upper Givetian): USA (Missouri), Canada (Dawson Bay), Poland (Holy Cross Mts.); Upper Devonian (Frasnian): USA (Iowa), Poland (Holy Cross Mts.).

Actinostroma crassepilatum LECOMPTE, 1951

(Pl. XL, Fig. 3a-b; Pl. XLI, Fig. 6)

1951. *Actinostroma crassepilatum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 122-123, Pl. 13, Figs. 3, 3a.
 1951. *Actinostroma tabulatum* LECOMPTE var. *crassum* LECOMPTE; M. LECOMPTE, Les Stromatoporoïdes..., pp. 103-104, Pl. 7, Fig. 3.
 1958. *Actinostroma crassepilatum* LECOMPTE; V. ZUKALOVÁ, Stromatoporoïdes..., p. 317, Pl. 1, Fig. 1.
 1959. *Actinostroma crassepilatum* LECOMPTE; E. FLÜGEL, Die Gattung ..., pp. 137-139 (revision).

1966. *A. cf. crassepilatum* LECOMPTE; J. E. KLOVAN, Upper..., pp. 20-21, Pl. 6, Fig. 2a-b.
 ?1966. *Actinostroma redwaterense* KLOVAN; J. E. KLOVAN, Upper..., pp. 19-20, Pl. 6, Fig. 1a-b.
 1968. *Actinostroma crassepilatum* LECOMPTE; E. FLÜGEL & E. FLÜGEL-KAHLER, Foss. Cat., pt. 115, pp. 109-110 (with complete synonymy).

Localities. — Bolechowice-„Jaźwica“ quarry (loc. 10), Kowala — railway cut (loc. 12), „Szewce“ quarry (loc. 14), Czerwona Góra Hill (loc. 15), Bolechowice — „Panek“ quarry (loc. 16), Bolechowice — „Nowiny“ quarry (loc. 17), Sitkówka I, II and V (locs. 18, 19 and 22), Babia Góra Hill (loc. 23), Suków-Babie (loc. 24), Kadzielnia quarry (loc. 33), Wietrznia quarry (loc. 34), Zagórze (loc. 35).

Material. — Thirty-four complete and fragmentary colonies (Z. Pal. St. I/246, St. I/250, St. I/279 to 298, St. I/302 to 307, St. I/416 to 417, St. I/439 to 441, St. I/465 to 466).
 Dimensions (in mm):

Z. Pal. Cat. No.	Laminae			Pillars		
	max/2 mm	min/2 mm	thickness	max/2 mm	min/2 mm	thickness
St. I/250	10	9	0.05—0.12	6	5	0.18—0.28
St. I/282	8	7	0.07—0.15	7	6	0.15—0.25
St. I/441	8	7	0.06—0.12	6	5	0.20—0.33
St. I/465	7	6	0.07—0.12	6	5	0.17—0.31

Description. — Coenosteam massive, irregularly bulbous, bell-shaped or tabular. Colonies usually very large, the largest of them being 130 cm in diameter at the base and 75 cm high. Surface smooth with irregular mamelons.

Laminae clearly defined straight or twisted, variable in thickness, frequently interrupted and replaced by dissepiments, composed of thick horizontal processes giving them the character of a network with angularly outlined meshes. Pillars continuous, straight or slightly bent, very thick, circular or subangular in transverse section. Galleries wide rectangular in outline, devoid of dissepiments. Microstructure homogenous with single calcification centers occurring axially in pillars.

Discussion. — *A. crassepilatum* is marked by extremely thick pillars, clearly differing it from all other species of *Actinostroma*. The species under study differs from *A. uchtense* RIABININ in straight, single pillars which in the last-named species are partly twisted and frequently irregularly branched.

The specimens described display a considerable intracolony variability in thickness of laminae and spaces between pillars. In the present writer's opinion, several Upper Devonian species of *Actinostroma* with very thick pillars are likely to be junior synonyms of *A. crassepilatum*. In addition to those mentioned in the synonymy, here probably belong: *A. piriformis* KHALFINA, *A. petrovi* RIABININ and *A. scheraiolense* RIABININ.

A process of thickening of pillars advanced to a maximum extent and started as early as the Upper Silurian in the genus *Plectostroma* NESTOR, is observed in *A. crassepilatum*.

Stratigraphic and geographical distribution. — Middle Devonian (Upper Givetian): Belgium (Dinant Basin), Poland (Western Holy Cross Mts.); Upper Devonian (Frasnian): ?Canada (Alberta), ?USSR (Timan, Salair Mts.), Belgium (Dinant Basin), Czechoslovakia (Moravia), Poland (Western Holy Cross Mts.).

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PLATES

(All photographs made by the author)

J. KAŹMIERCZAK: MORPHOGENESIS AND SYSTEMATICS OF THE DEVONIAN STROMATOPOROIDEA

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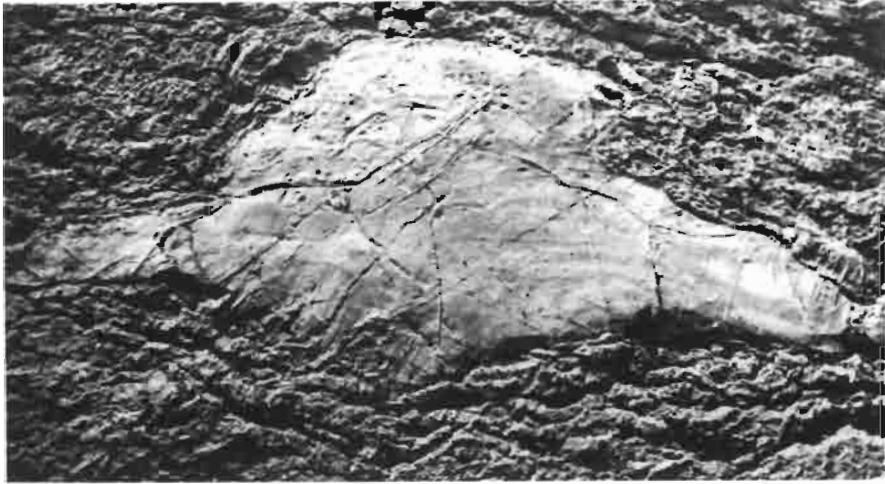
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PLATE II

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- Fig. 2. Vertical section of an overturned hemispherical coenosteum of *Trupetostroma gebum* (YAVORSKY) in stromatoporoid calcirudite. Sitkówka IV (see also section in Text-fig. 2 B, unit 8); Upper Givetian, Lower Sitkówka Beds (Z. Pal. St. I/174); $\times 0.25$.
- Fig. 3. Vertical section of a tabular coenosteum of *Trupetostroma gebum* (YAVORSKY) in coarse-grained mieritic calcarenites. Sitkówka IV (see also section in Text-fig. 2 B, unit 1); Upper Givetian, Lower Sitkówka Beds (Z. Pal. St. I/153); $\times 0.25$.
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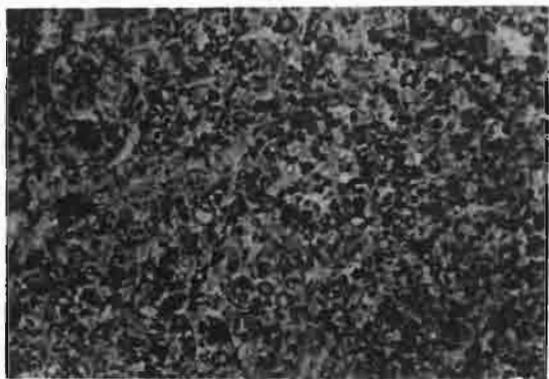
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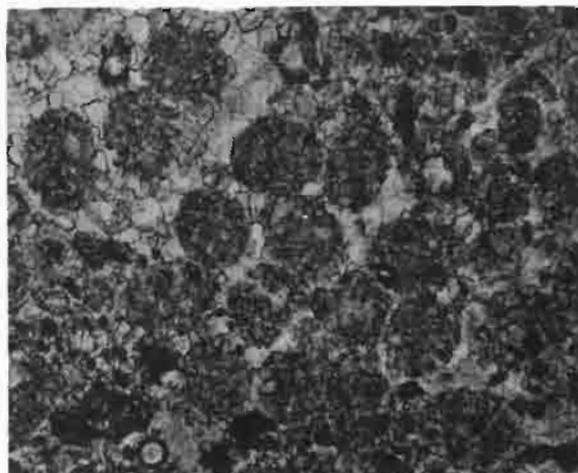
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PLATE IV

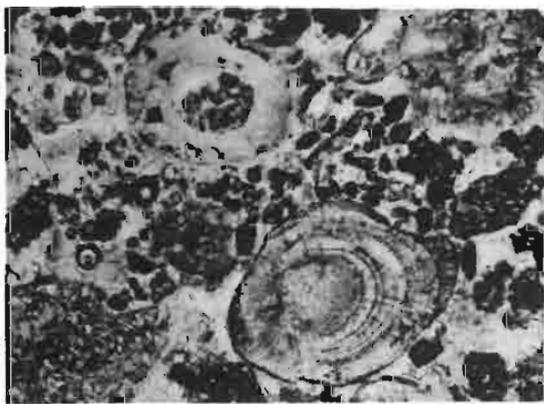
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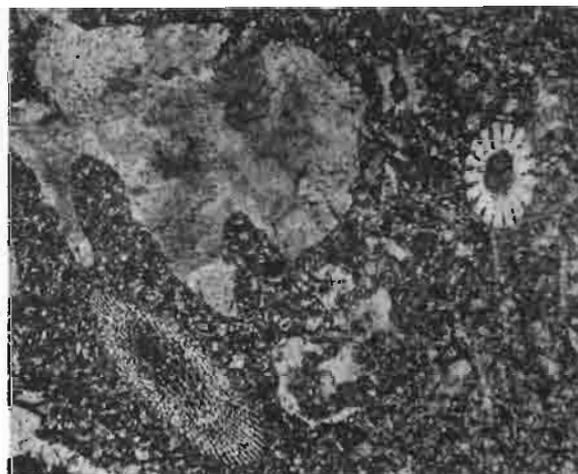
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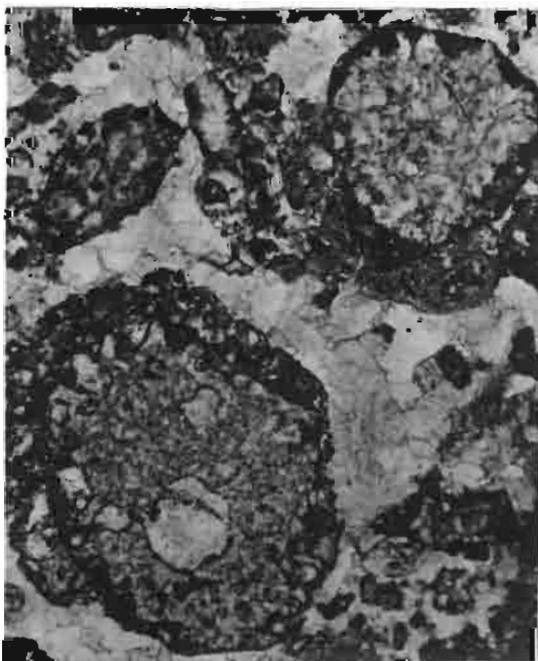
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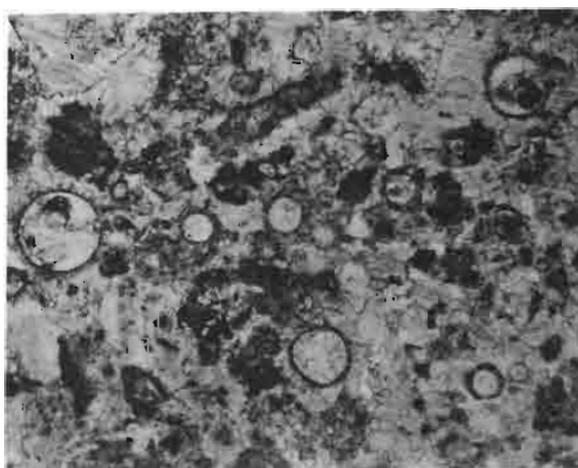
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PLATE V

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Algae and algal structures associated with stromatoporoid limestones . . 13, 21

- Fig. 1. Polished vertical section of irregularly laminated algal mats (biocalcilitite) with bird's-eye structures. Sitkówka III (see also section in Text-fig. 2A, unit 2); Upper Givetian, Lower Sitkówka Beds; $\times 1$.
- Fig. 2. Thin-section of an algal mat with birds's-eye structures. Bolechowice — „Panek“ quarry (see also section in Text-fig. 5F, unit 1); lowermost Frasnian, Upper Sitkówka Beds; $\times 15$.
- Fig. 3. Thick, irregular algal coatings around fragments of stromatoporoids and solitary tetracorals. Bolechowice — „Panek“ quarry (see also section in Text-fig. 5F, unit 24); lowermost Frasnian, Upper Sitkówka Beds; $\times 1$.
- Fig. 4. Blue-green algae *Renalcis turbitus* WRAY in a sparry-micritic stromatoporoid calcirudite. Sitkówka V (see also section in Text-fig. 3C, unit 3); Upper Givetian, Lower Sitkówka Beds; $\times 15$.
- Fig. 5. Blue-green algae *Renalcis devonicus* JOHNSON in a sparry-micritic stromatoporoid calcirudite. Sitkówka I (see also section in Text-fig. 3D, unit 4); lowermost Frasnian, Upper Sitkówka Beds; $\times 15$.
- Fig. 6. Blue-green algae *Renalcis devonicus* JOHNSON in a sparry-micritic stromatoporoid calcirudite. Sitkówka IV (see also section in Text-fig. 2B, unit 2); Upper Givetian, Lower Sitkówka Beds; $\times 30$.
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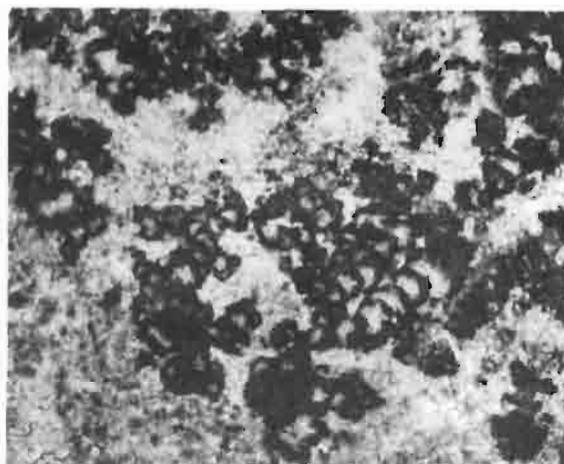
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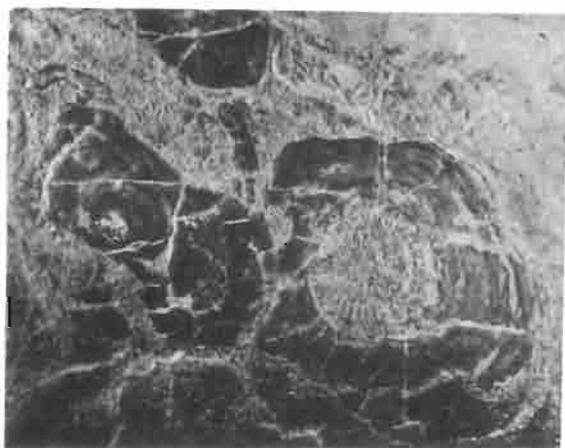
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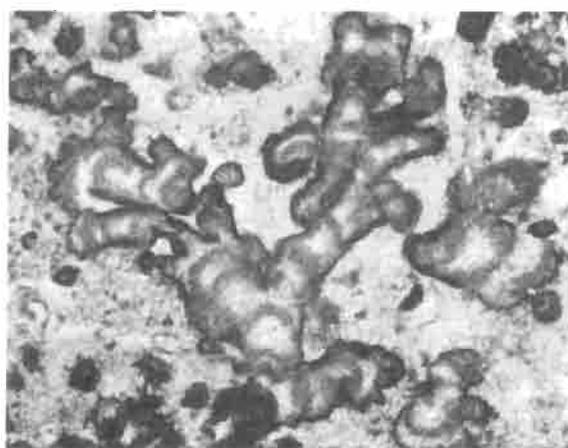
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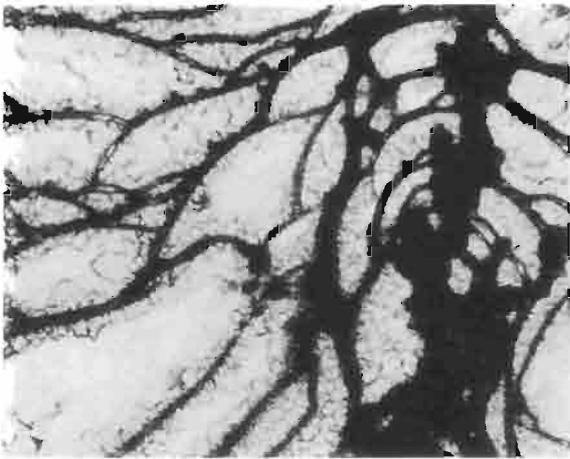


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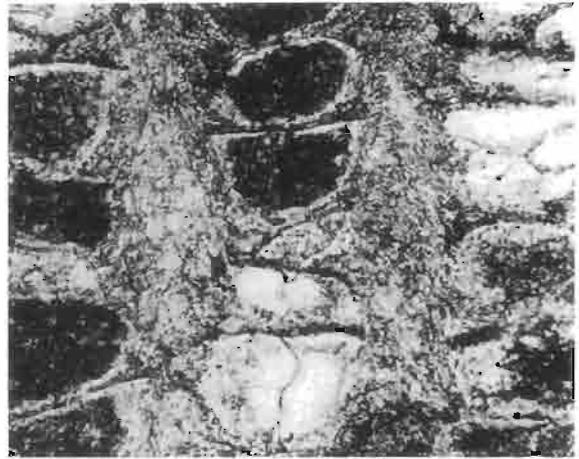
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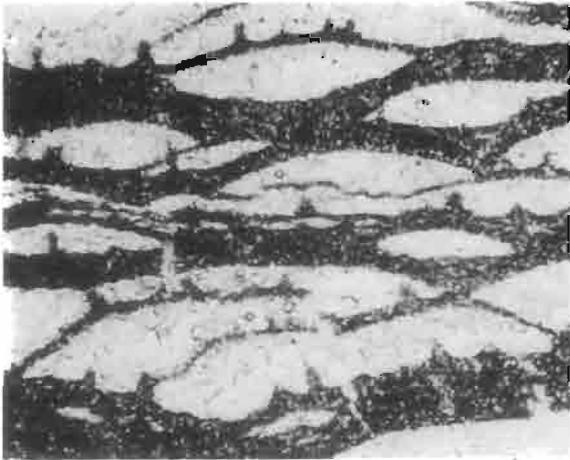
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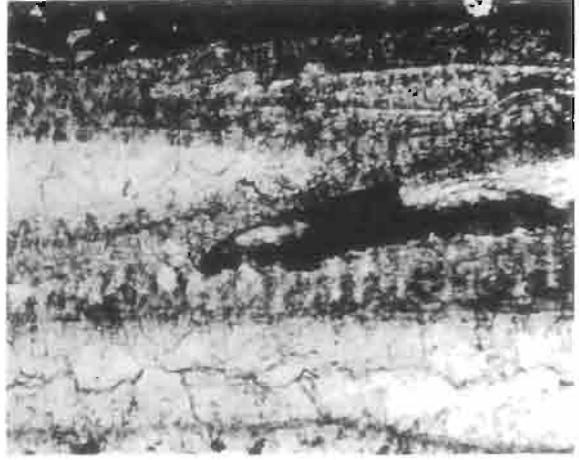
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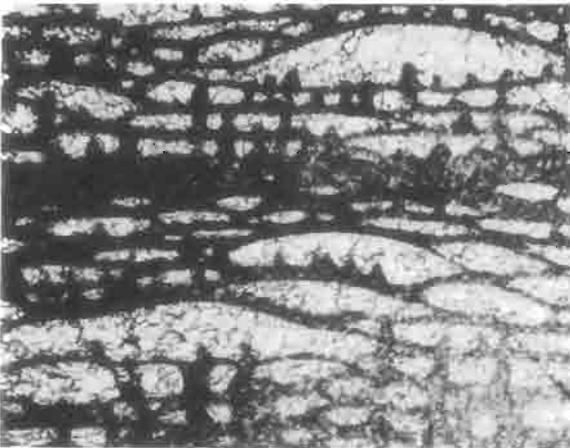
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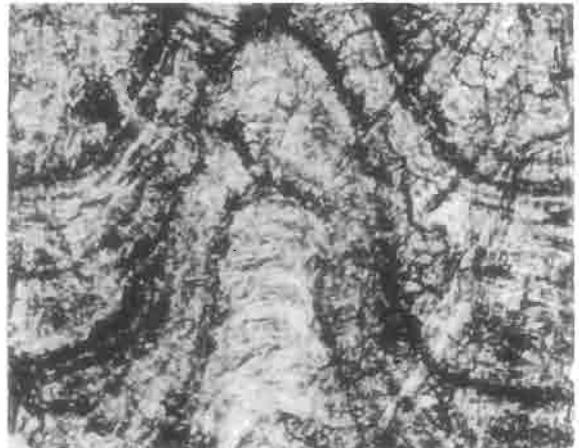
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PLATE VII

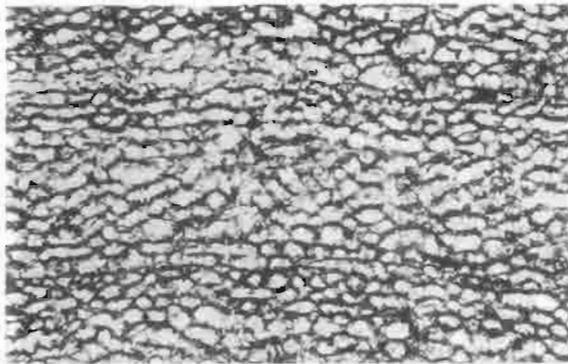
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Examples of skeletal structure in morphological group „A“ 50

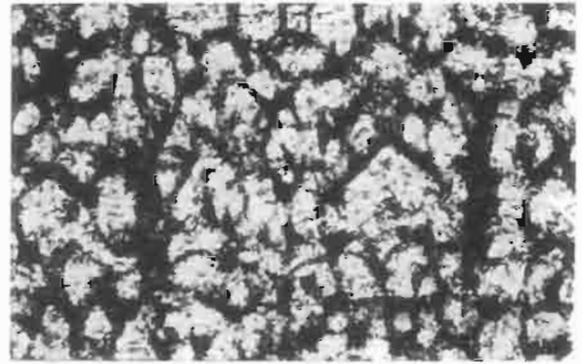
- Fig. 1. *Clathrodictyon gregale* NESTOR. Narrow zones of the *Clathrodictyon* structure type and wide ones of the *Ecclimadictyon* structure type are visible. Porkuni, Estonia, U. S. S. R.; Uppermost Ordovician, Porkuni stage (EAS Co 3048 — paratype); $\times 15$.
- Fig. 2. *Plexodictyon savaliense* (RIABININ). Note growth periodicity expressed by even laminae and an interlaminar skeleton of the *Ecclimadictyon* structure type. Zbruch River, Podolia, U. S. S. R.; Ludlovian, Middle Skalsk horizon (VNIGRI 390/171 — holotype); $\times 15$.
- Fig. 3. *Tienodictyon katavense* (YAVORSKY). Note rare foramina in laminae and tangled vertical elements forming irregular secondary laminae. Ukhta River, Timan, U. S. S. R.; Frasnian, Ukhta Beds (VNIGRI 474/45); $\times 15$.
- Fig. 4. *Pseudostromatoporella insolita* (YAVORSKY). Note strongly tangled vertical elements, numerous ring-pillars and foramina. Kara-Chumysh River, Kuznetsk Basin, U. S. S. R.; Eifelian (CNIGR 6337/13 — holotype); $\times 35$.
- Fig. 5. *Ecclimadictyon robustum* NESTOR. The tendency to form thick pillars within irregularly chevron-like skeleton is clearly visible. Saaremaa Island, Estonia, U. S. S. R.; Upper Wenlockian, Jaagarahu stage (EAS Co 3129 — paratype); $\times 35$.
- Fig. 6. *Simplexodictyon uralicum* (RIABININ). Irregular splits of growth interruption are clearly visible in planes of laminae. Kysynga River, Ural Mts., U. S. S. R.; Middle Devonian (CNIGR 4487/60 — holotype); $\times 35$.
- Fig. 7. „*Stromatoporella*“ *sniatkovi* YAVORSKY. Fibro-lamellar character of skeletal tissue is visible. Chumysh River, Kuznetsk Basin, U. S. S. R.; Middle Devonian (CNIGR 3338/25 — holotype); $\times 35$.
- Fig. 8. „*Clathrodictyon*“ *lazutkini* YAVORSKY. Fibro-normal microstructure, rare foramina and irregularly laminar structure of skeleton indicating that this form is marked by characters transitional from *Simplexodictyon* to *Pseudostromatoporella*. Chernaya Bachat River, Kuznetsk Basin, U. S. S. R.; Gedinnian (CNIGR 7351/64 — holotype); $\times 35$.

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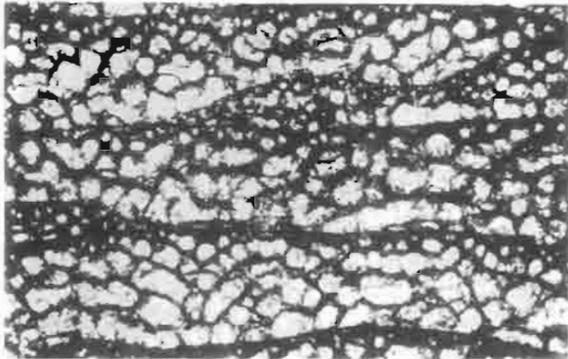




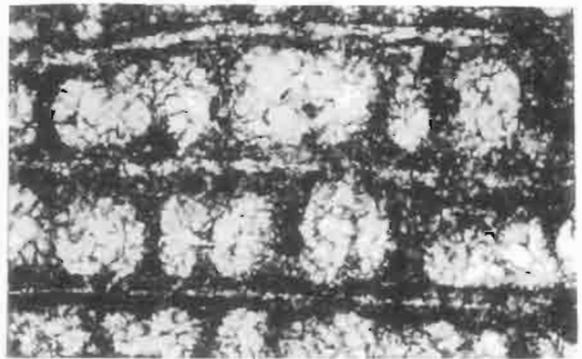
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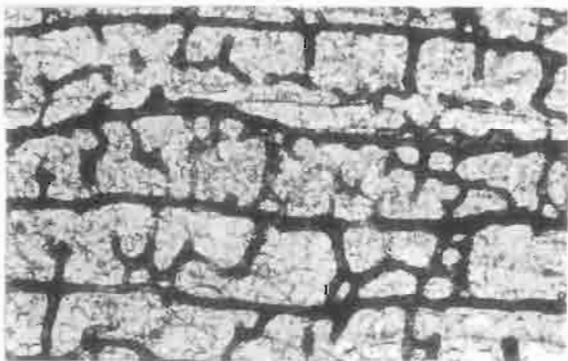
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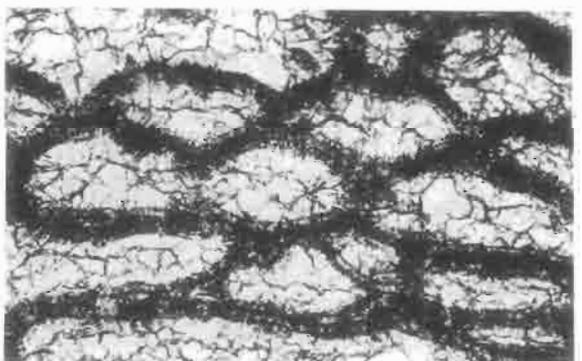
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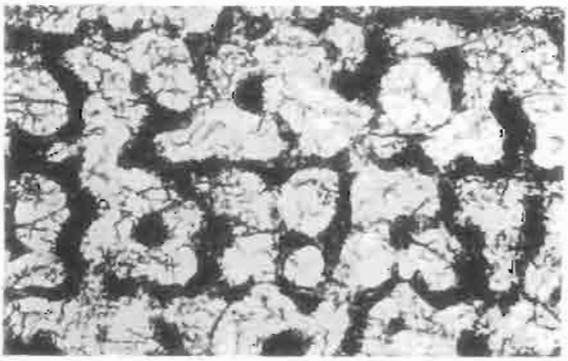
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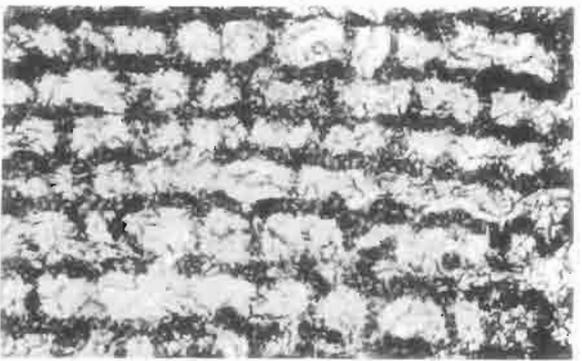
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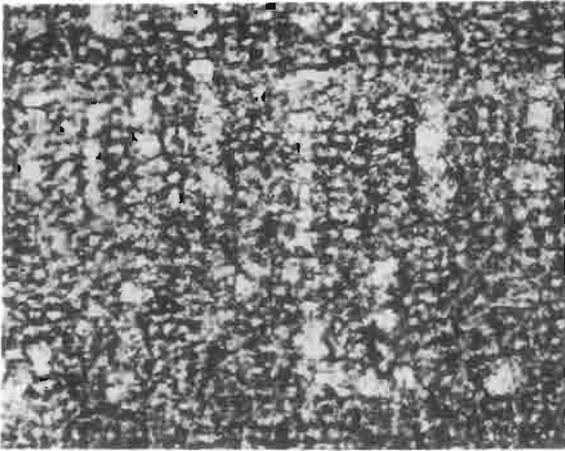


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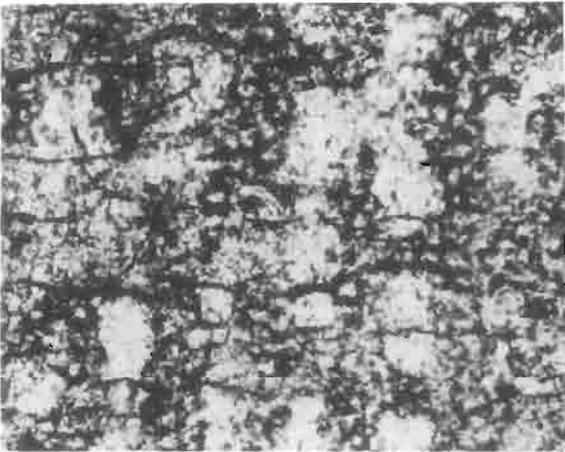
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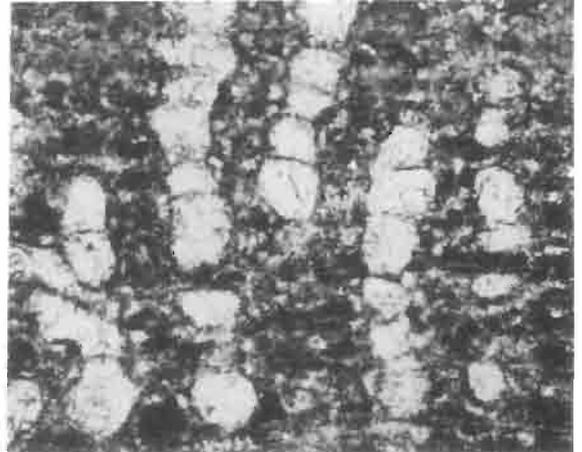
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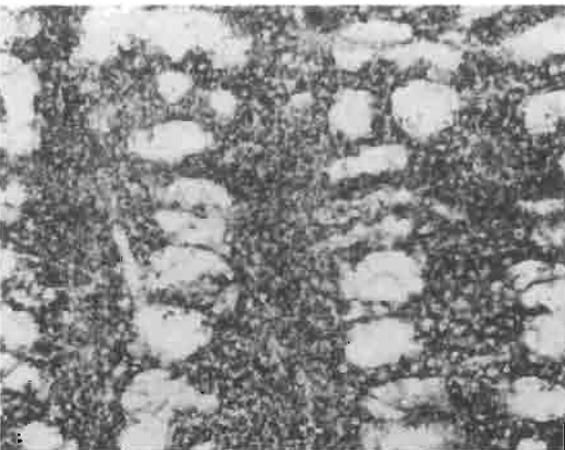
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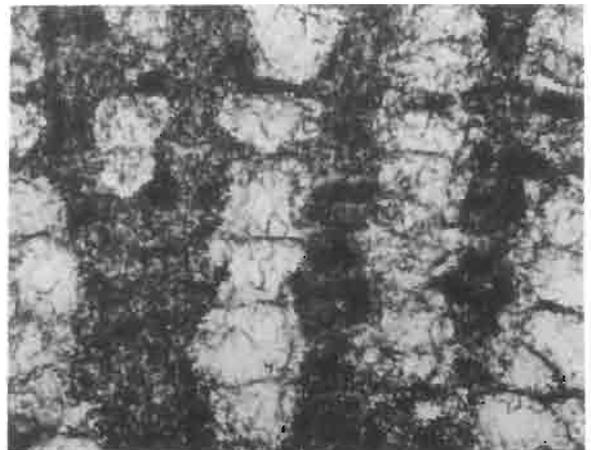
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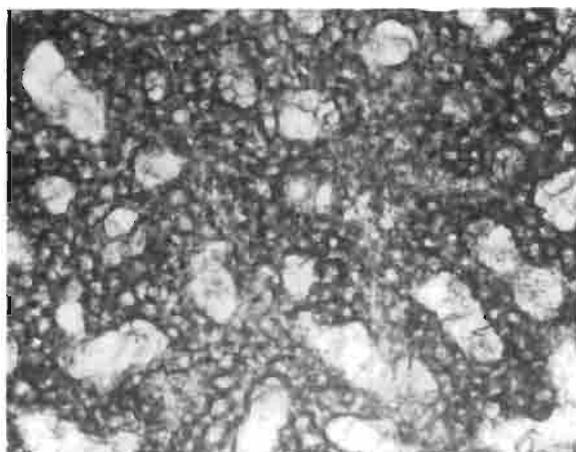
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J. KAŹMIERCZAK: MORPHOGENESIS AND SYSTEMATICS OF THE DEVONIAN STROMATOPOROIDEA

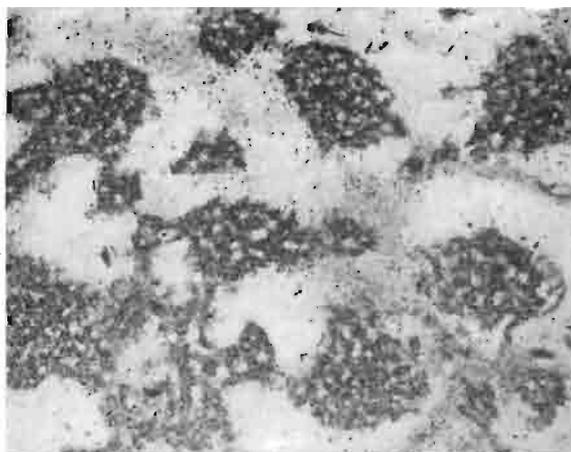
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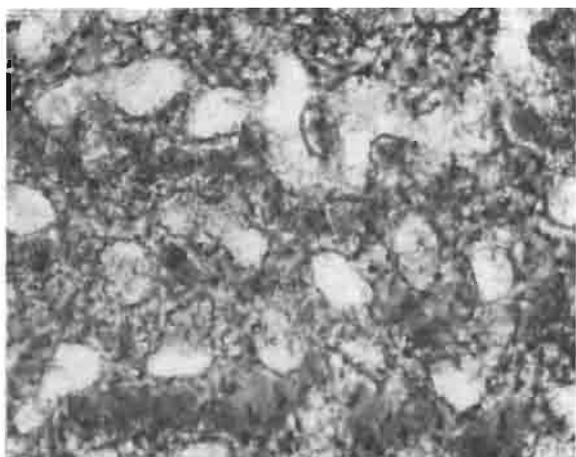
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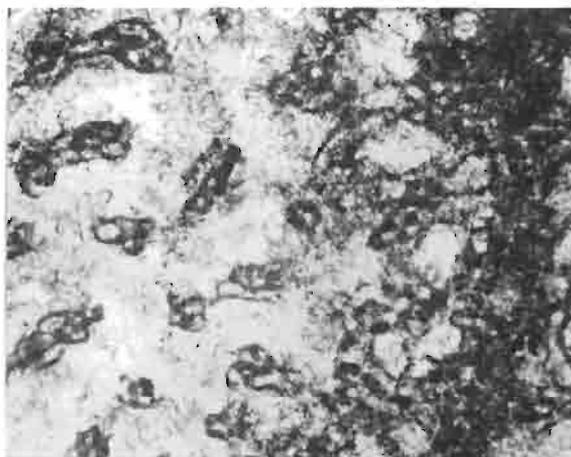
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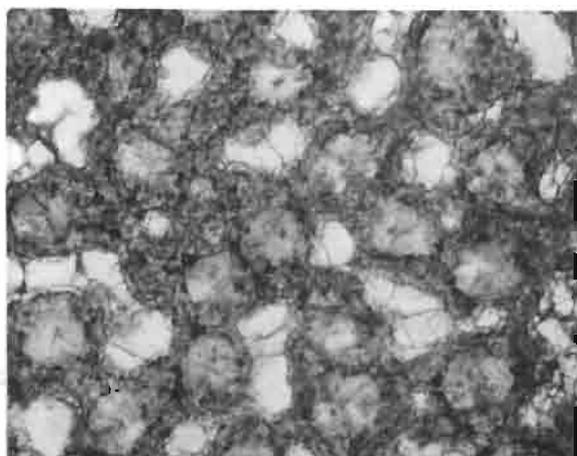
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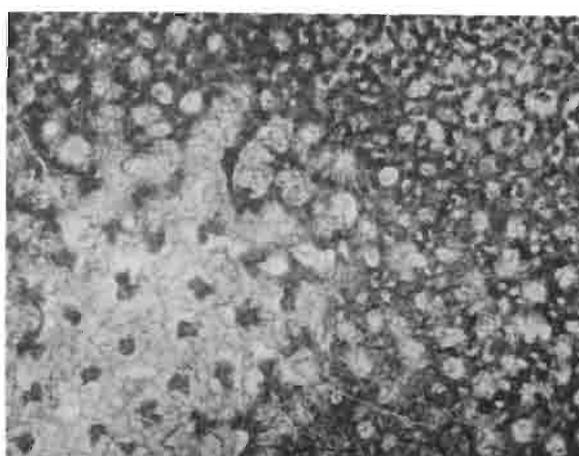
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PLATE X

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Examples of progressive reduction of microreticular tissue in morphological group „B“ 46

Fig. 1. *Parallelostroma malinovzyense* (RIABININ). Very thick laminae separated by low hemispherical interskeletal spaces (chambers) are visible. Muksha River, Podolia, U. S. S. R.; Lower Ludlovian, Malinovetsk horizon (VNIGRI 390/111 — holotype); $\times 15$.

Fig. 2. *Parallelostroma typicum* (ROSEN). A loose microreticular tissue with dark lines of growth inhibition and hemispherical interskeletal spaces here and there superposed are visible. Saaremaa Island, Estonia, U. S. S. R.; Ludlovian, Paadla stage (EAS Co 3009 — holotype); $\times 35$.

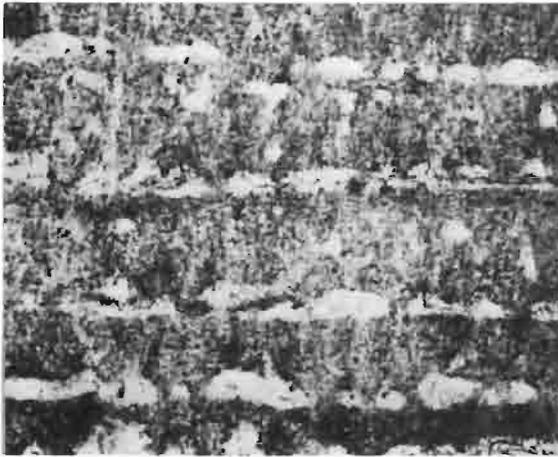
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Fig. 4. „*Trupetostroma*“ *spatiosum* YAVORSKY (see also Pl. IX, Fig. 5). Microreticular tissue reduced to a system of rare thickened fibers. Korail River, Magadan, U. S. S. R.; Eifelian (CNIGR 7351/507); $\times 35$.

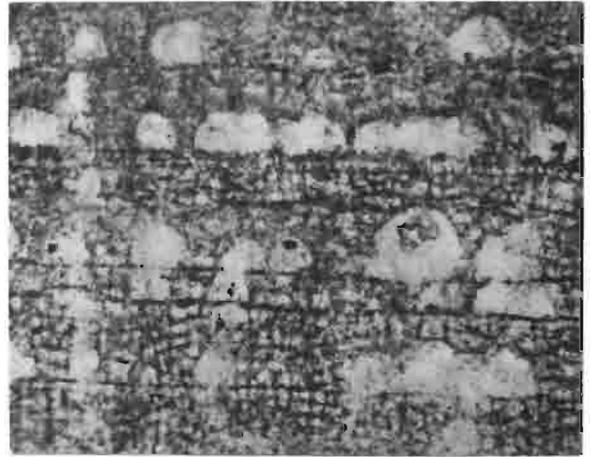
Fig. 5. *Actinostroma mamontovi* YAVORSKY (see also Pl. IX, Fig. 6). A microreticular tissue reduced in pillars to single, thick fibers, in laminae — to a single-layer network. Kara-Chumysh River, Kuznetsk Basin, U. S. S. R.; Middle Devonian, *Pentamerus pseudobaschkiricus* beds (CNIGR 7351/22); $\times 35$.

Fig. 6. *Atelodictyon pseudocolumnare* (RIABININ) (see also Pl. XXXVI, Fig. 1). Microreticular tissue reduced in vertical elements of skeleton to rare, thick fibers, in laminae — to a single-layer network. Bolechowice-„PANEK“ quarry, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/22); $\times 35$.

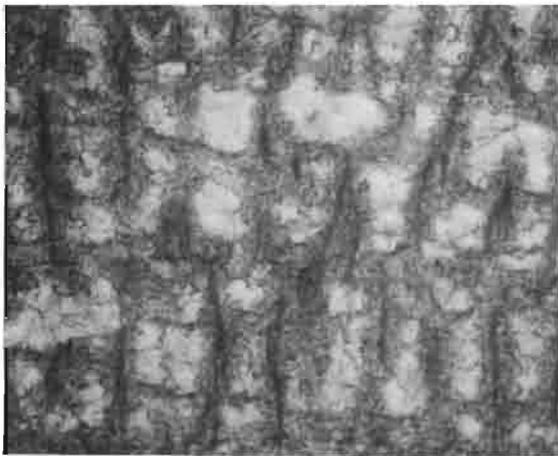
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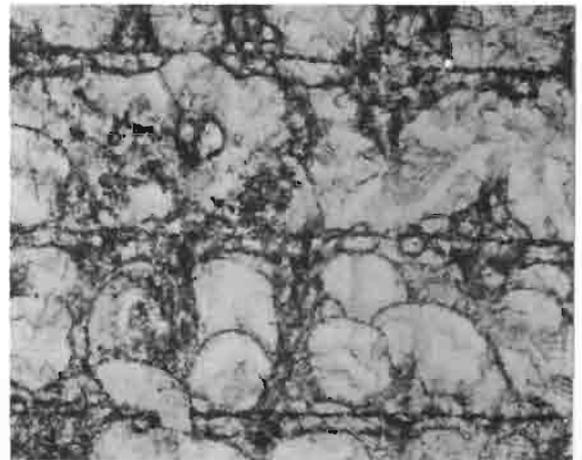
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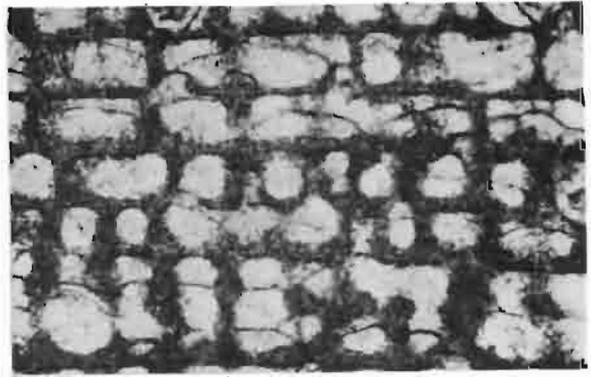
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PLATE XI

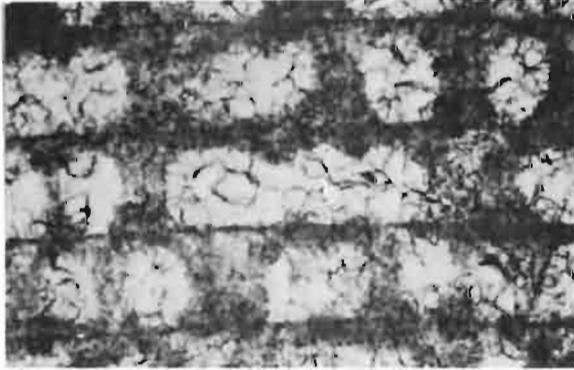
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Fig. 1. „ <i>Stromatopora</i> “ <i>pellucida</i> YAVORSKY. Vertical section. Note loose microreticular tissue in skeletal elements and dark growth inhibition lines in the planes of laminae. Chernevaya Bachat River, Kuznetsk Basin, U. S. S. R.; Lower Devonian, Krekov horizon (CNIGR 7351/132 — holotype); × 15.	
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Fig. 6. <i>Stictostroma kolymense</i> (YAVORSKY) (see also Pl. XVI, Figs. 1-3). Vertical section. A condensed character of microreticular tissue and irregular growth interruption splits in laminae are visible. Kolyma River, U. S. S. R.; Middle Devonian (CNIGR 7351/437 — holotype); × 15.	



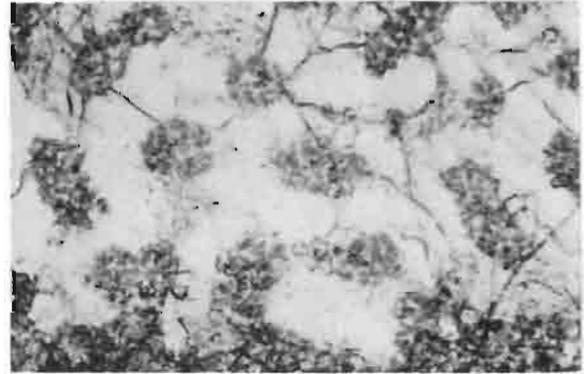
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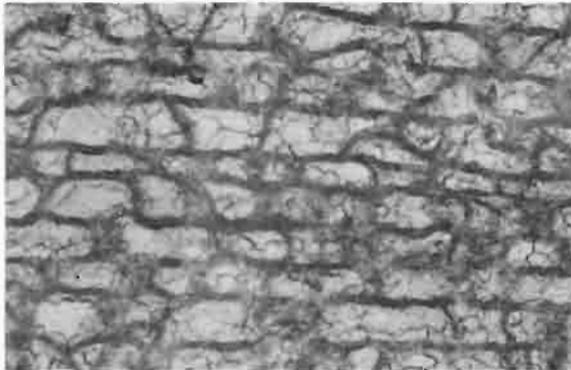
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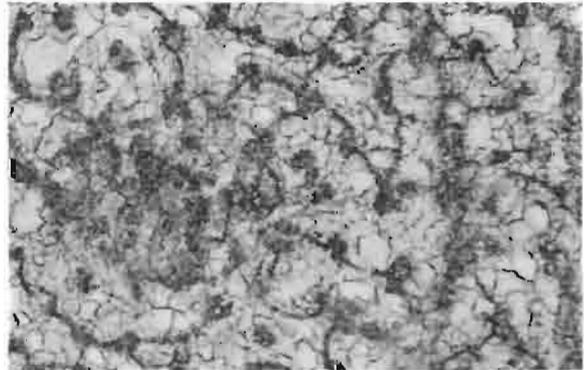
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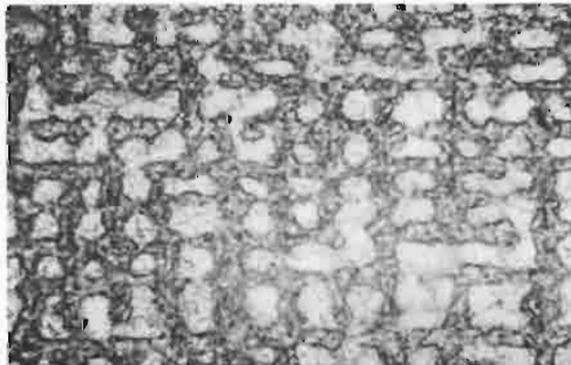
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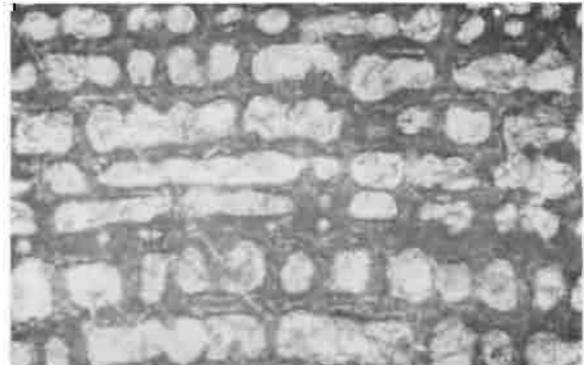
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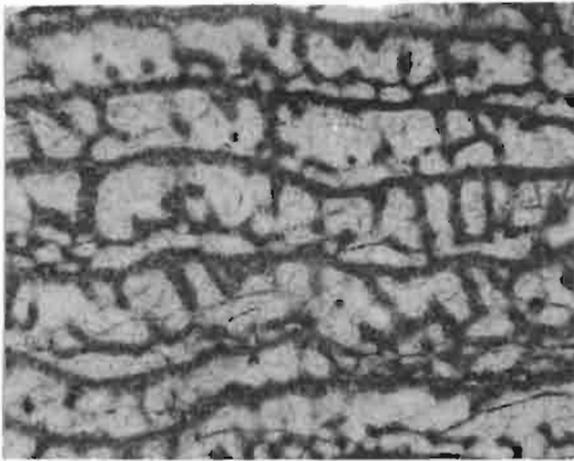


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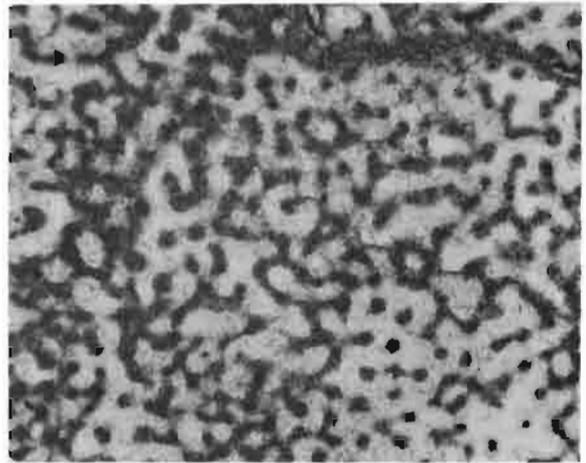
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Fig. 3. <i>a</i> vertical section; <i>b</i> tangential section. Jaworznia-Moczydło Hill, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/14); × 15.	



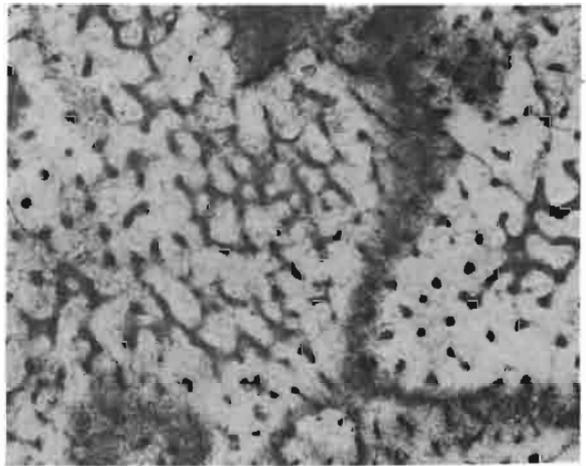
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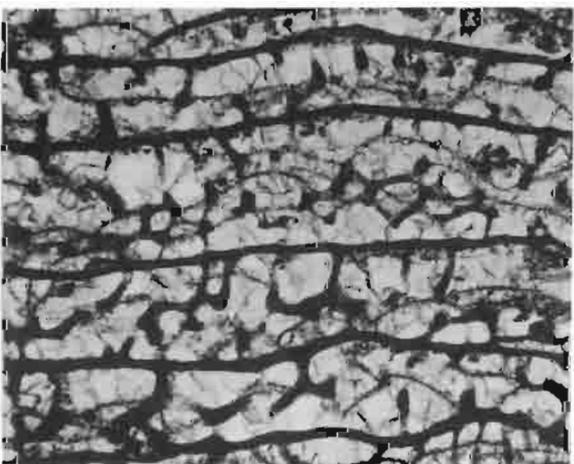
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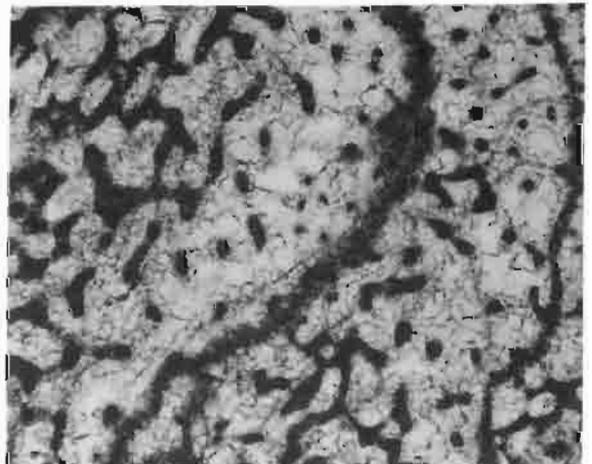
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2b



3a



3b

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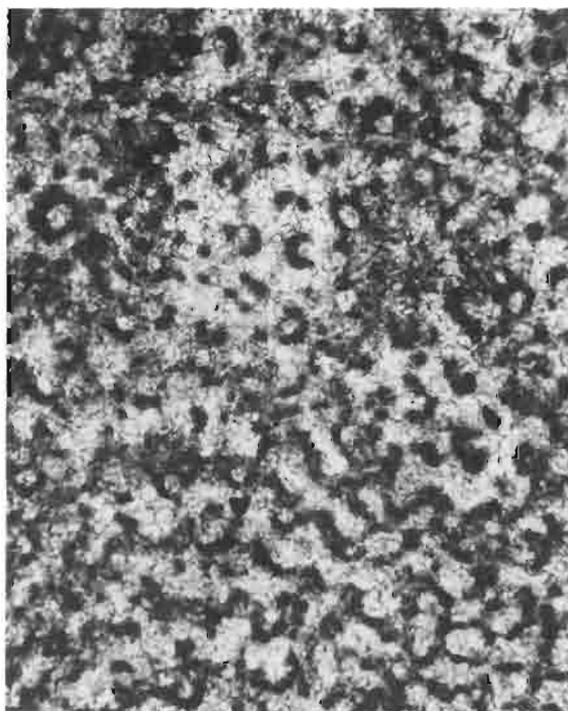
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Fig. 1. *a* vertical section; *b* tangential section; × 15; *c-d* vertical section; × 35. Wietrznia quarry, Poland; ?Frasnian I_γ, Kadzielnia Beds (Z. Pal. St. 1/237).



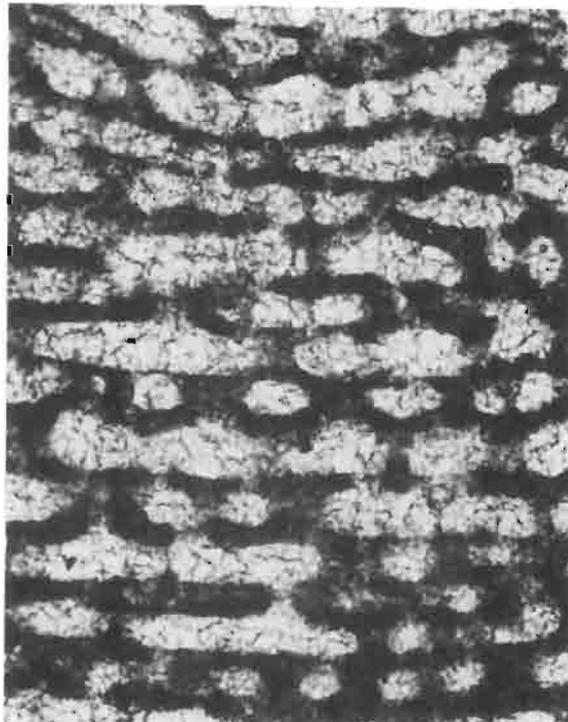
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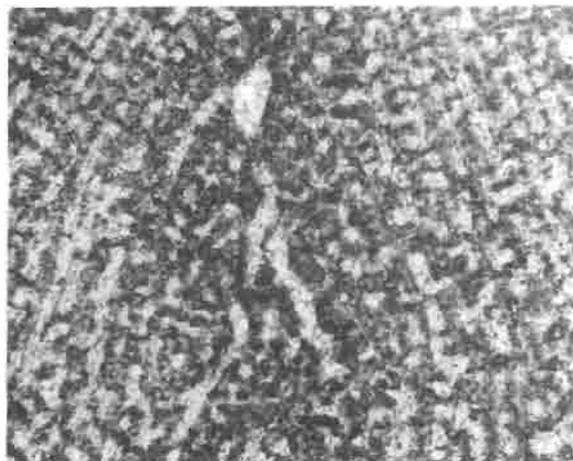
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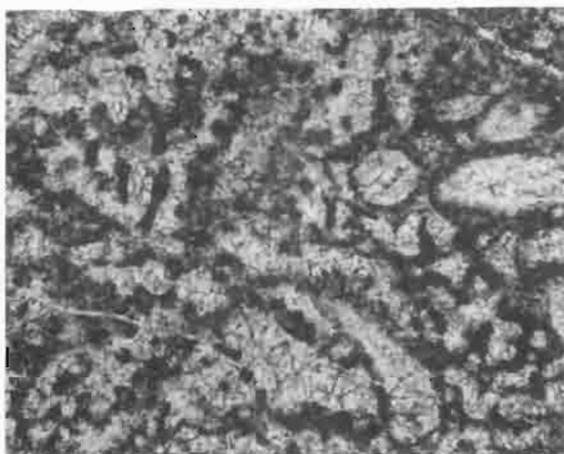
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<i>Pseudostromatoporella moosensis</i> (PARKS)	79
Fig. 1. <i>a</i> vertical section; <i>b</i> tangential section; × 15; <i>c</i> vertical section; × 35. Radkowiec-Soltysia Hill, Poland; Upper Givetian, Lower Sitkówka Beds (Z. Pal. St. I/242).	
<i>Anostylostroma ponderosum</i> (NICHOLSON)	81
Fig. 2. <i>a</i> vertical section; <i>b</i> tangential section. Bolechowice-„Panek“ quarry, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/215); × 15.	
Fig. 3. Vertical section. Kadzielnia quarry, Poland; ?Frasnian I _γ , Kadzielnia Beds (Z. Pal. St. I/214); × 35.	



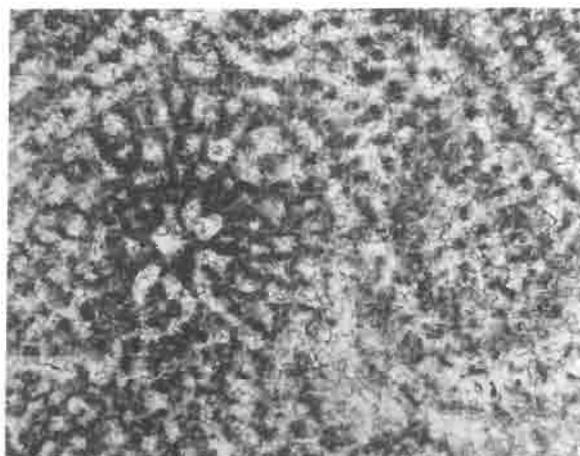
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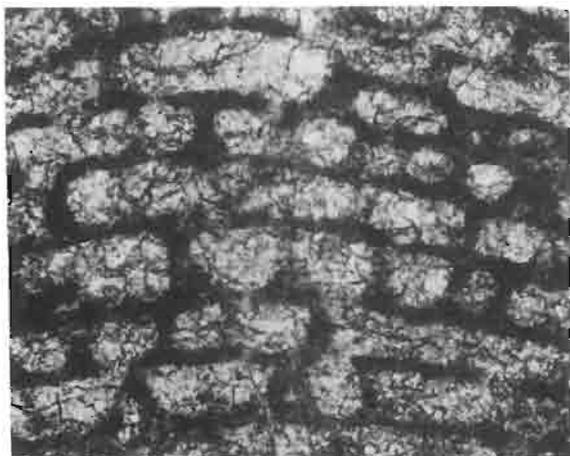
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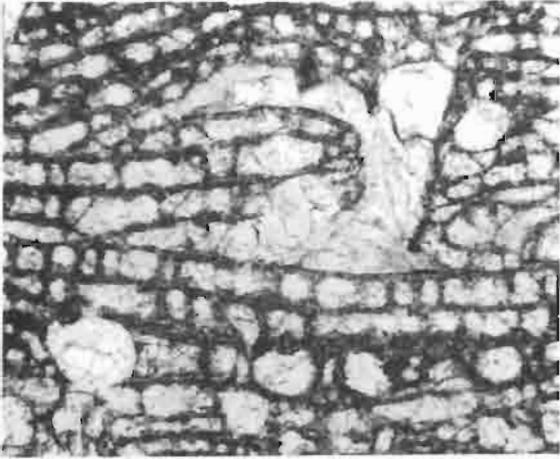


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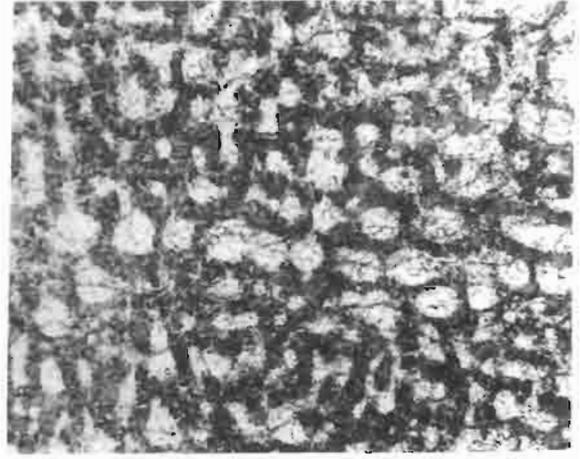
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Fig. 1. <i>a-b</i> vertical section; <i>c</i> tangential section. Kadzielnia quarry, Poland; ?Frasnian I γ , Kadzielnia Beds (Z. Pal. St. I/239); \times 15.	
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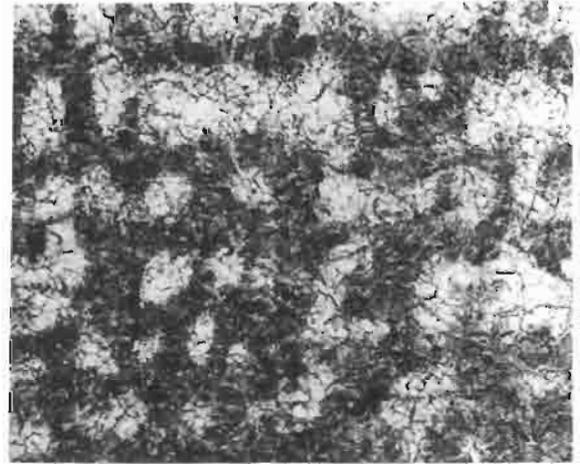
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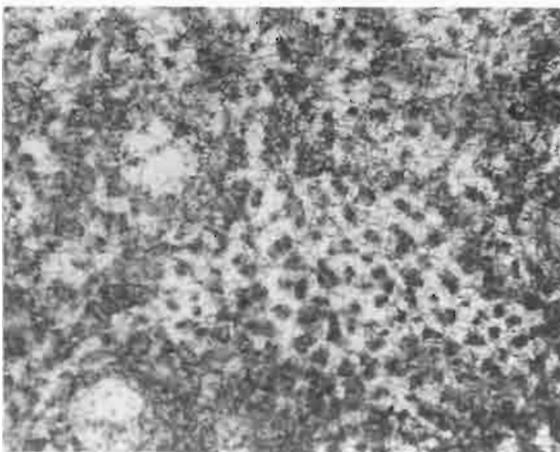
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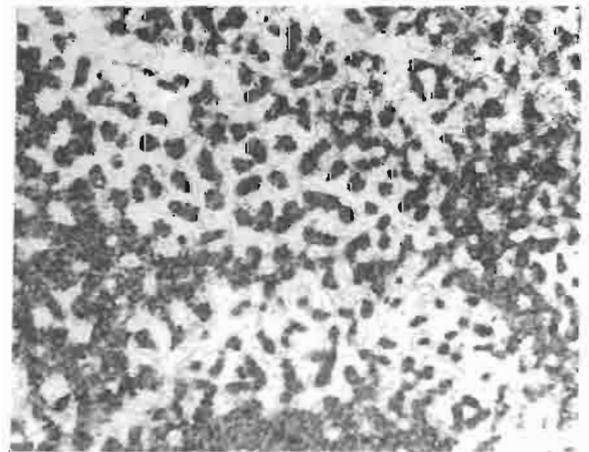
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2b



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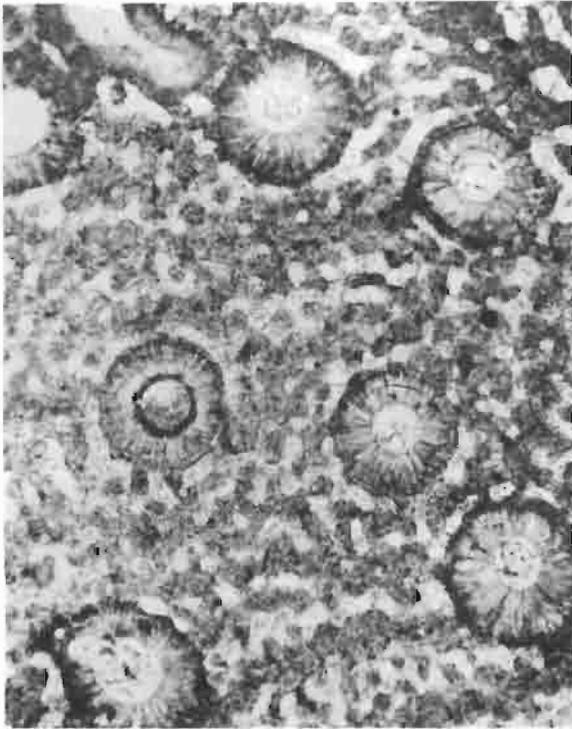


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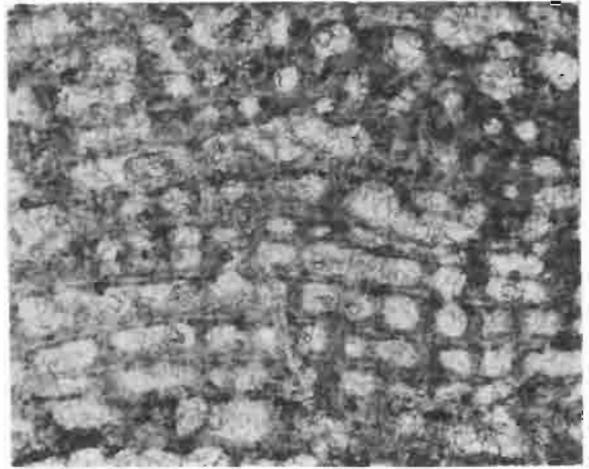
J. KAŻMIERCZAK: MORPHOGENESIS AND SYSTEMATICS OF THE DEVONIAN STROMATOPOROIDEA

PLATE XVI

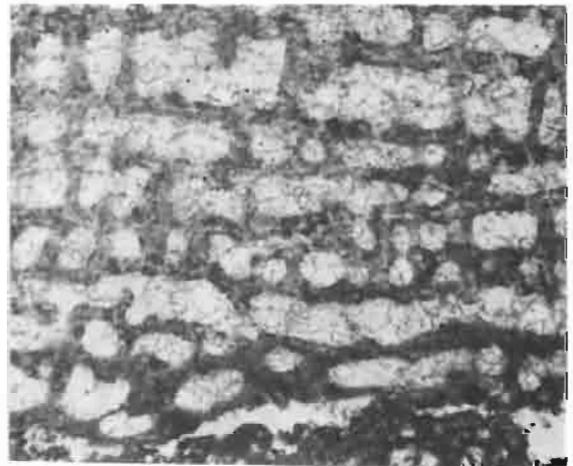
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Fig. 1. <i>a</i> vertical section; <i>b</i> tangential section. „Kowala“ quarry, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/236); × 15.	
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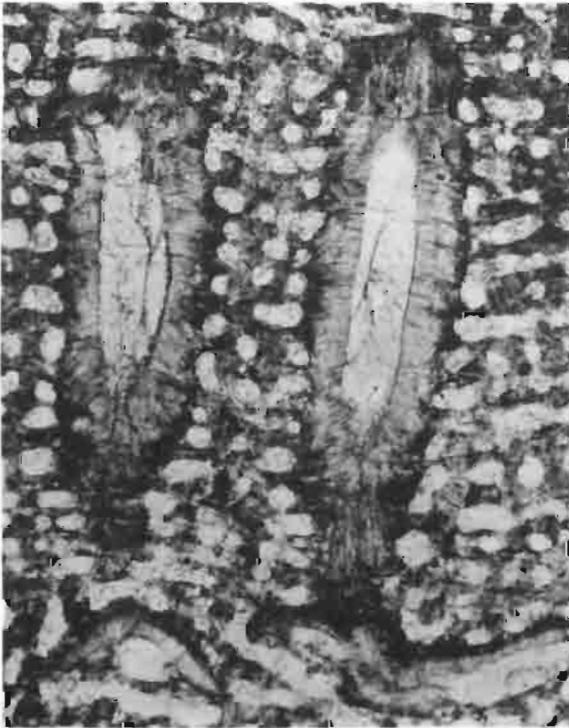
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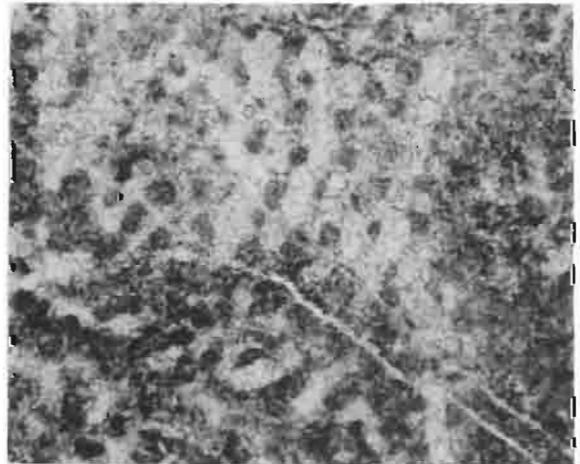
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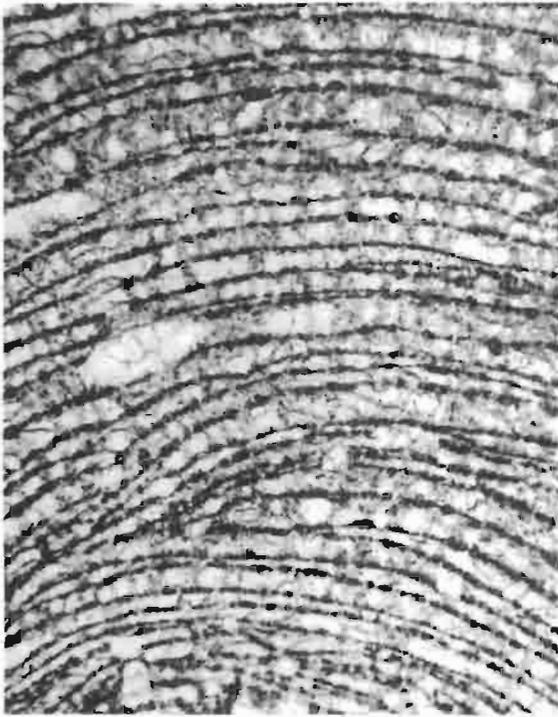


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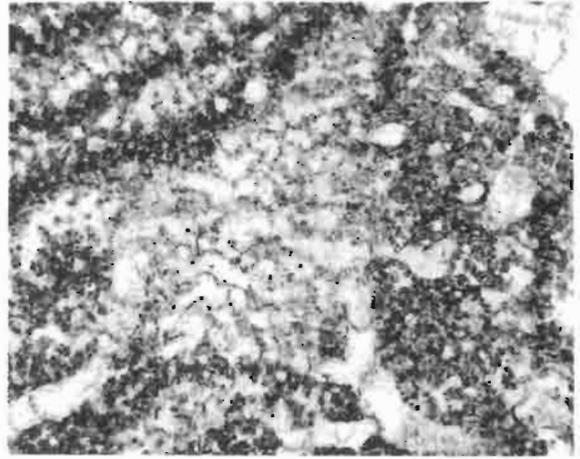
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<i>Stictostroma lensiforme</i> (LECOMPTE)	Page 85
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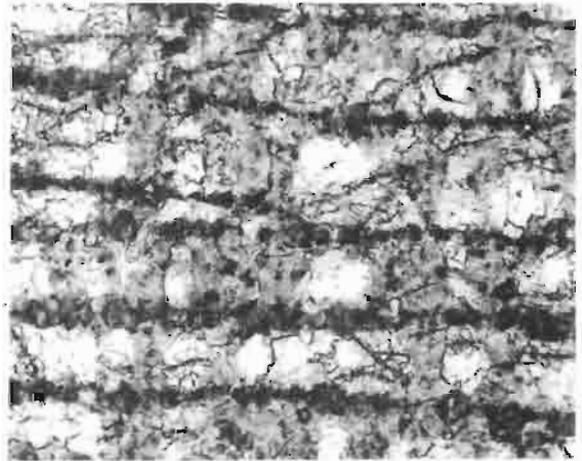
Fig. 1. *a* vertical section; *b* tangential section; × 15; *c* tangential section; × 35. Note dark dots of calcification centers in a light-gray skeletal tissue; *d* vertical section; × 35. Dark growth inhibition lines are clearly visible; *e* same as *d* in polarized light; × 35. Calcification centers are visible in vertical skeletal elements. Jurkowiec-Budy, Poland; Lower Upper Givetian, *Stringocephalus burtini* Beds (Z. Pal. St. I/199).



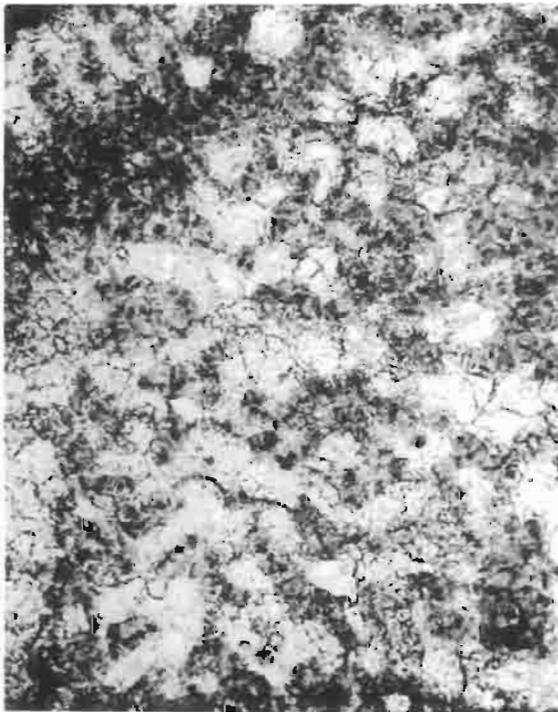
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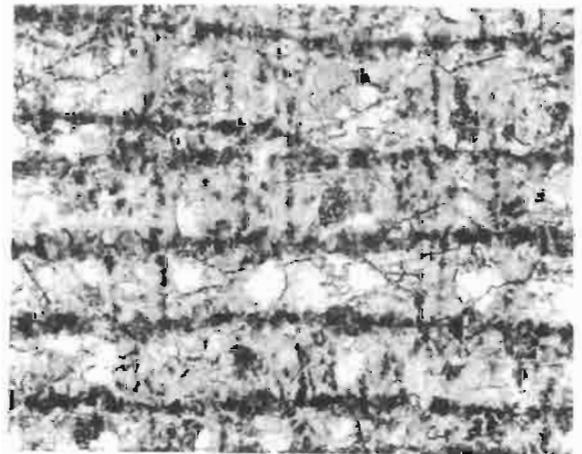
1b



1d



1c



1e

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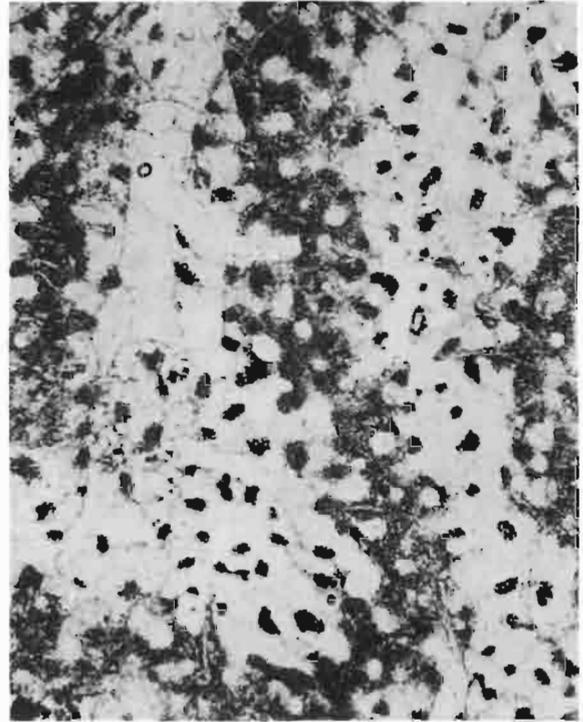
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Fig. 1. *a* vertical section; *b* tangential section; × 15; *c* vertical section; × 35; *d* tangential section; × 35. Wietrznia quarry, Poland; ?Frasnian Iγ, Kadzielnia Beds (Z. Pal. St. I/238).

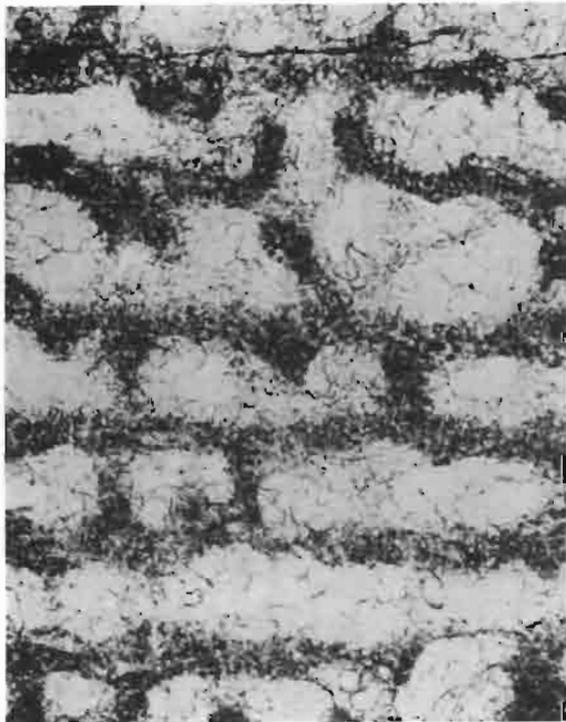




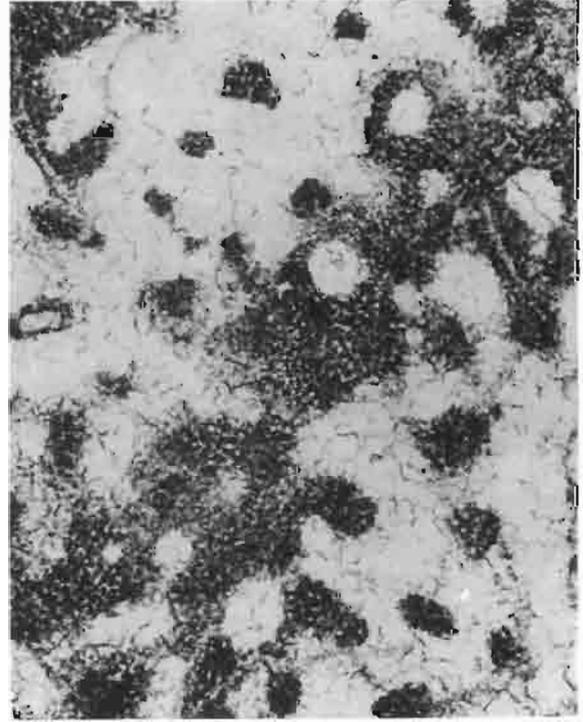
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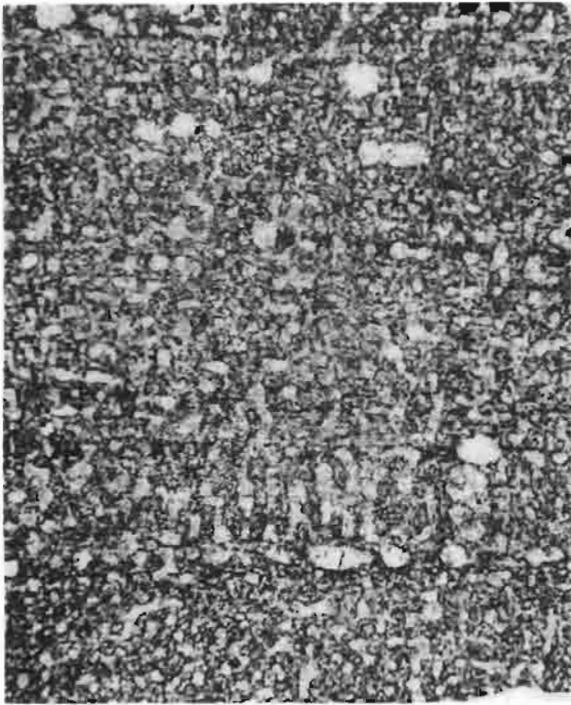


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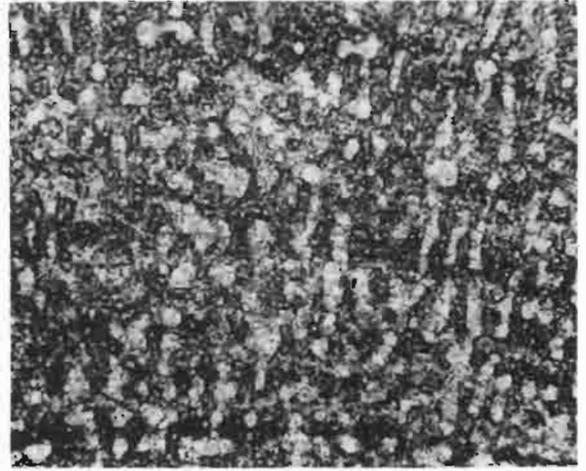
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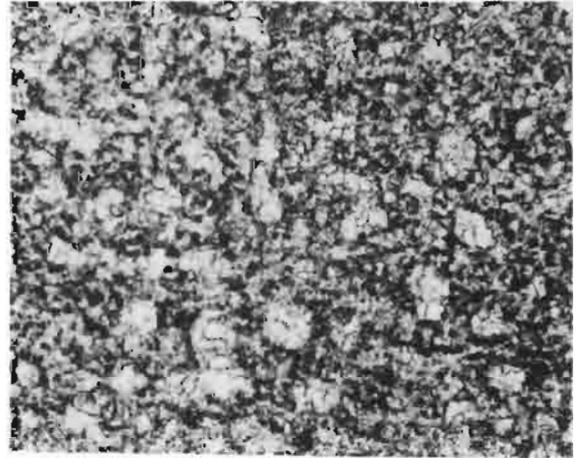
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<i>Stromatopora cooperi</i> LECOMPTE	89
Fig. 1. <i>a</i> vertical section; × 15; <i>b</i> tangential section; × 15; <i>c</i> vertical section; × 35; <i>d</i> tangential section; × 35. Kowala-railway cut, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/19).	
Fig. 2. Vertical section. Sitkówka V, Poland; Upper Givetian, Lower Sitkówka Beds (Z. Pal. St. I/18); × 15.	



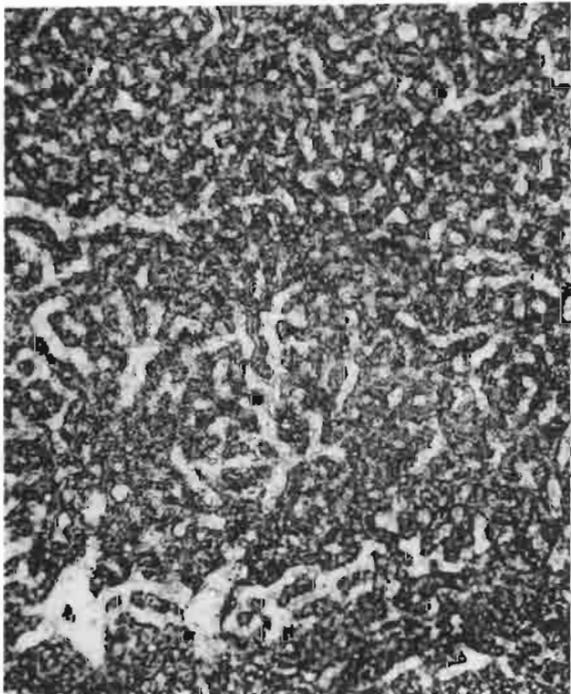
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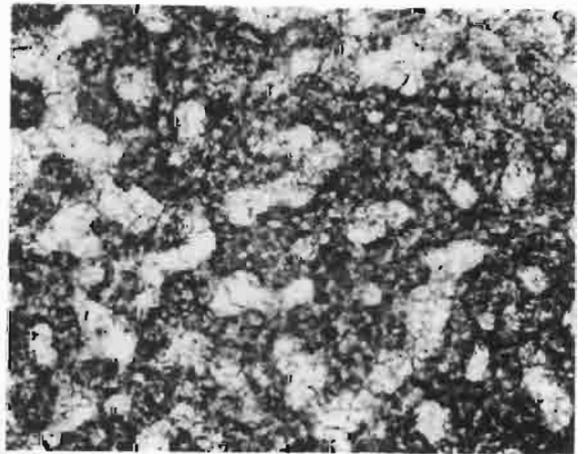
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1c



1b



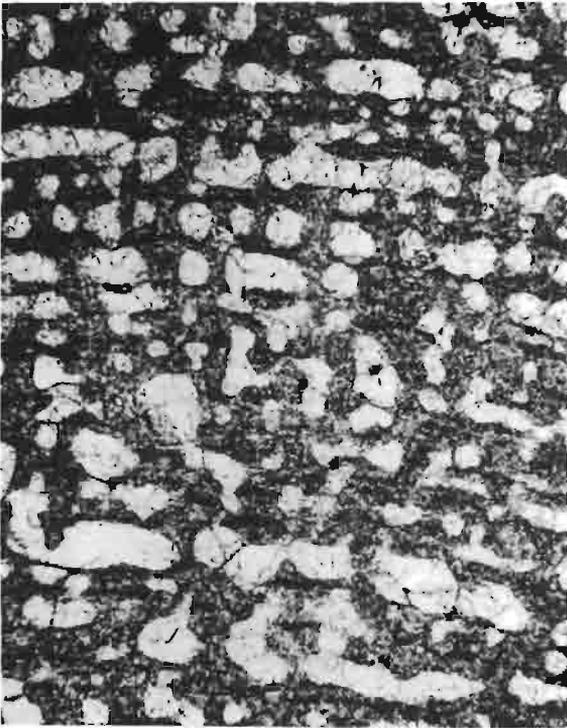
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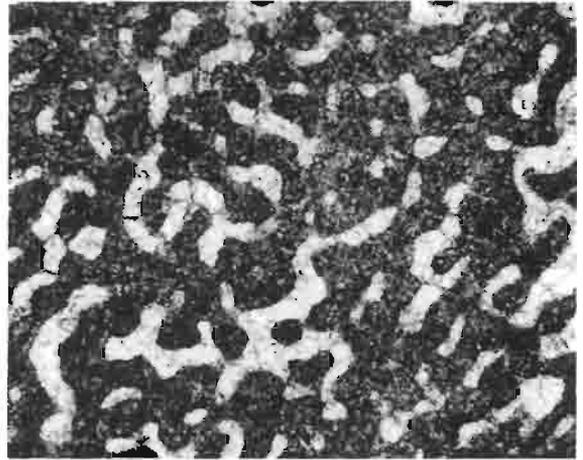
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<i>Stromatopora colliculata</i> (NICHOLSON)	90
(Jurkowice-Budy, Poland; Lower Upper Givetian, <i>Stringocephalus burtini</i> Beds)	
Fig. 1. <i>a</i> vertical section; × 15; <i>b</i> tangential section; × 15; <i>c</i> tangential section; × 35. Note a strongly condensed microreticular tissue (Z. Pal. St. I/219).	
Fig. 2. <i>a</i> vertical section; × 35; <i>b</i> vertical section; × 15. Irregularly distributed dark growth inhibition lines are clearly visible (Z. Pal. St. I/167).	

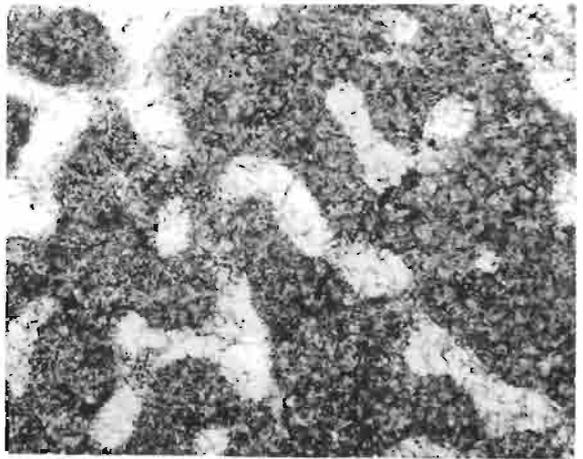




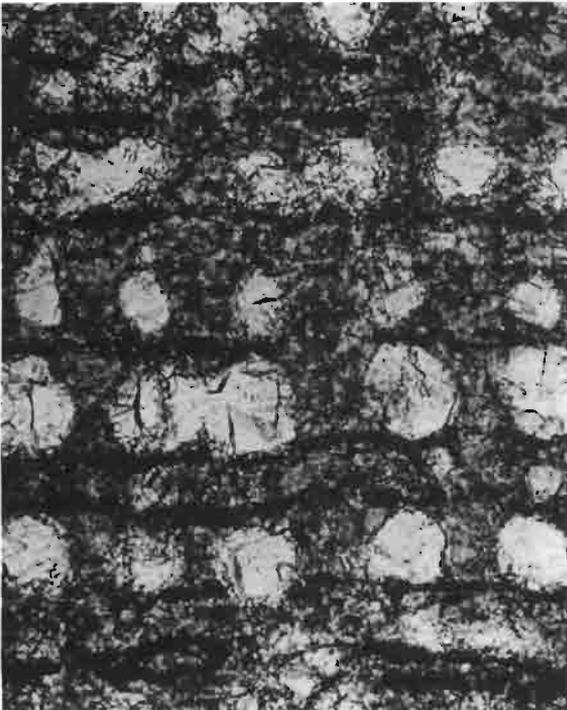
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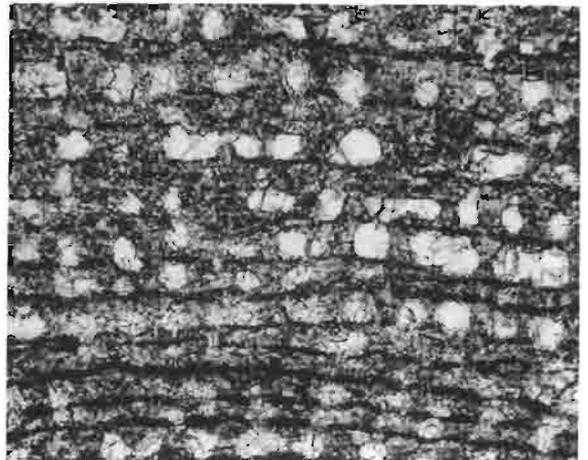
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1c



2a



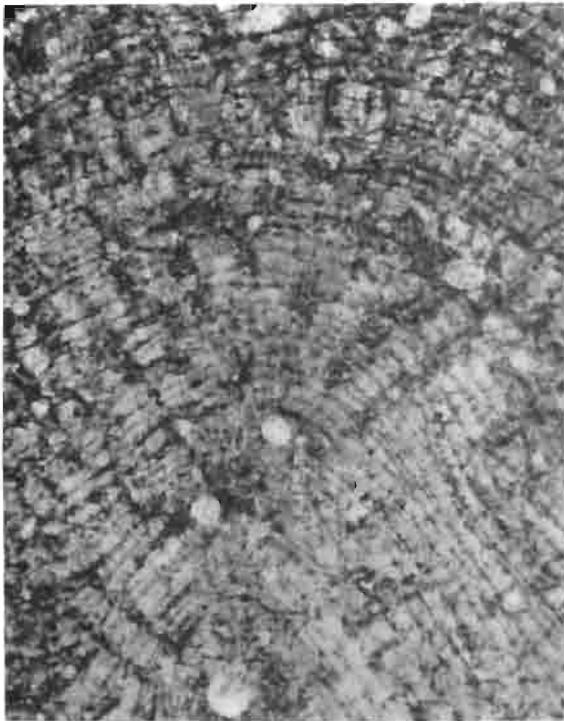
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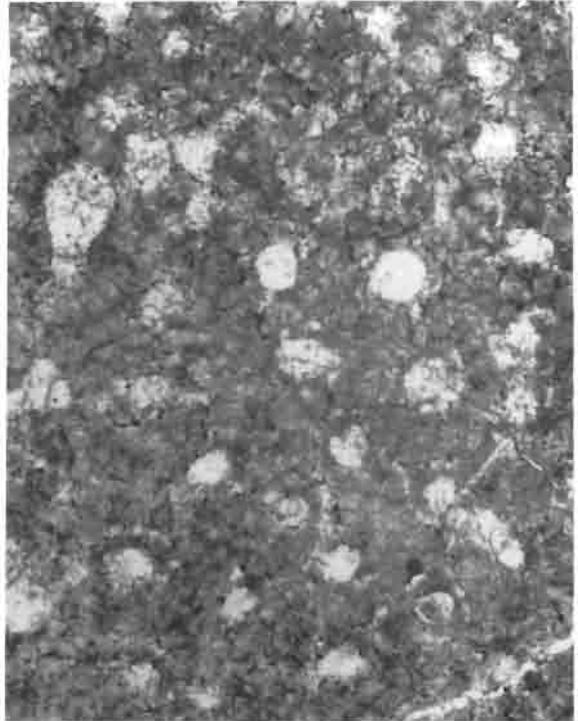
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Fig. 1. <i>a</i> vertical section; <i>b</i> tangential section. Jurkowice-Budy, Poland; Lower Upper Givetian, <i>Stringocephalus burtini</i> Beds (Z. Pal. St. I/194); × 15.	
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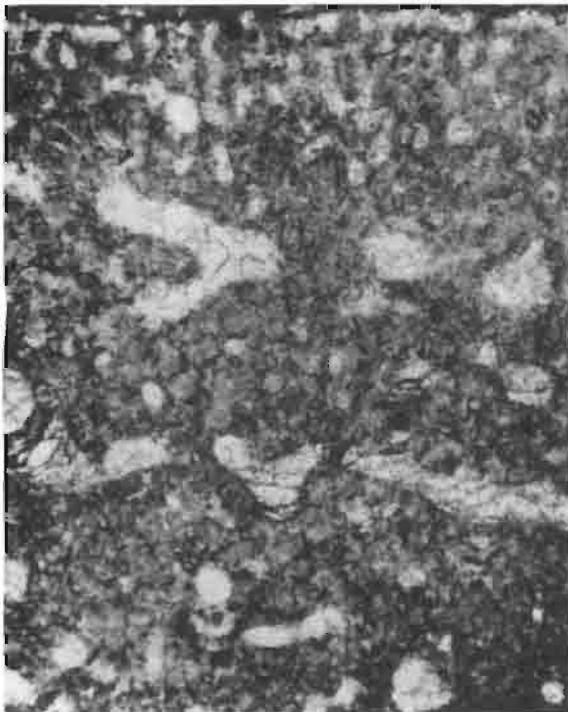




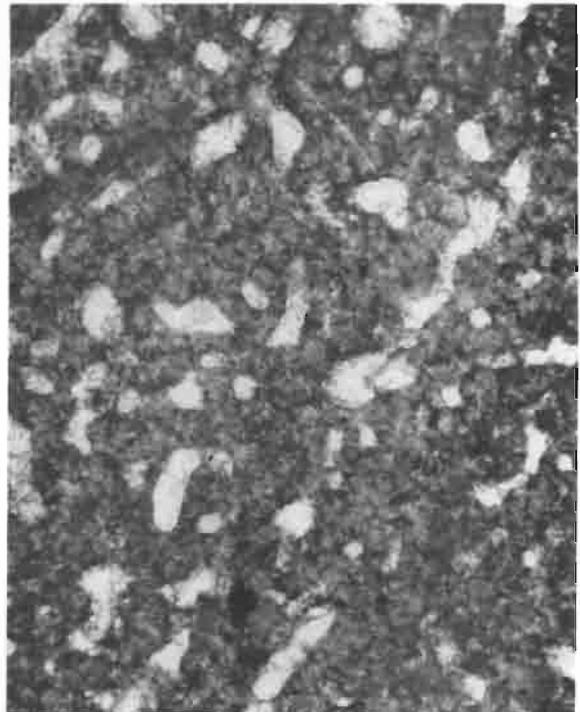
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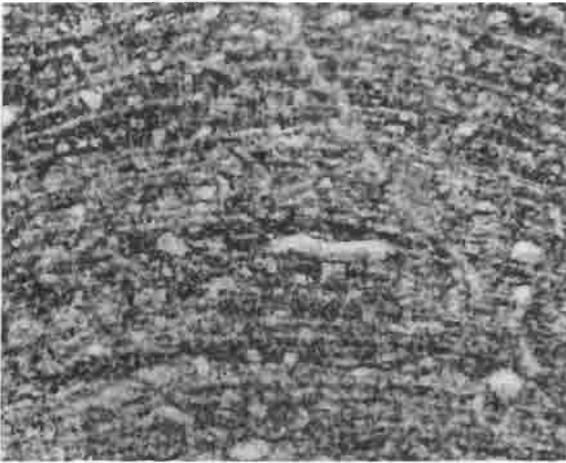


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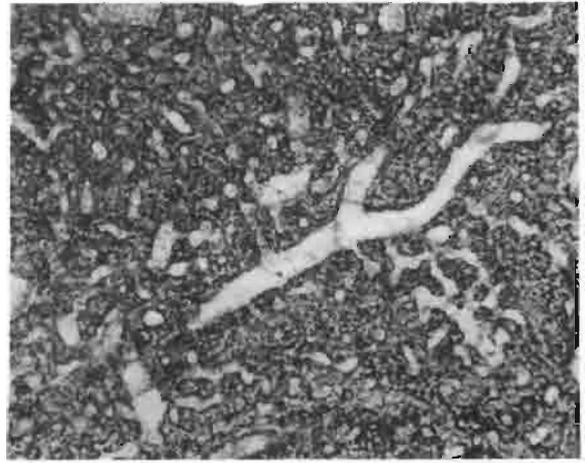
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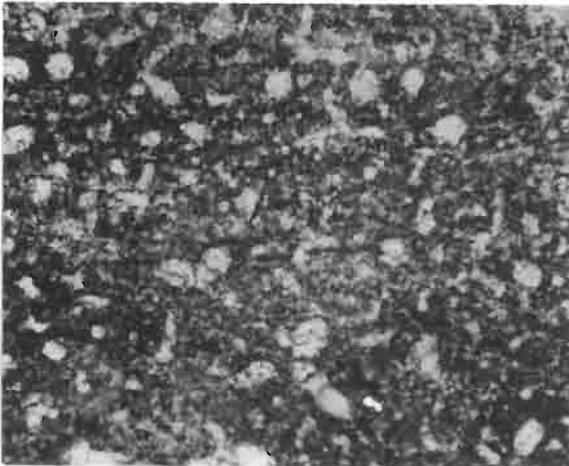
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<i>Stromatopora mononensis</i> GALLOWAY & ST. JEAN	93
Fig. 1. <i>a</i> vertical section; <i>b</i> tangential section. Jurkowice-Budy, Poland; Lower Upper Givetian, <i>Stringocephalus burtini</i> Beds (Z. Pal. St. I/193); × 15.	
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<i>Stromatopora undata</i> RIABININ	95
Fig. 3. <i>a</i> vertical section; <i>b</i> tangential section. Bolechowice-„Panek“ quarry, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/321); × 15.	



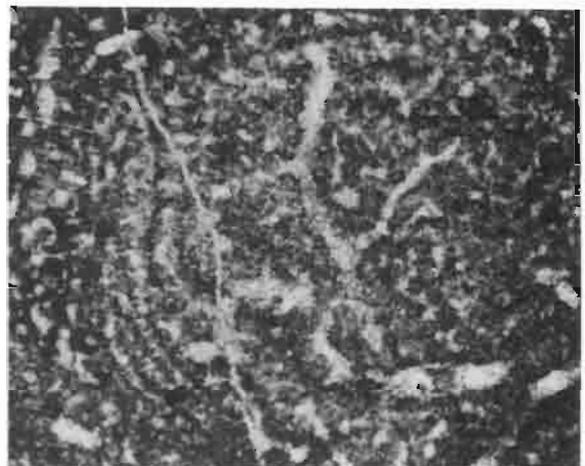
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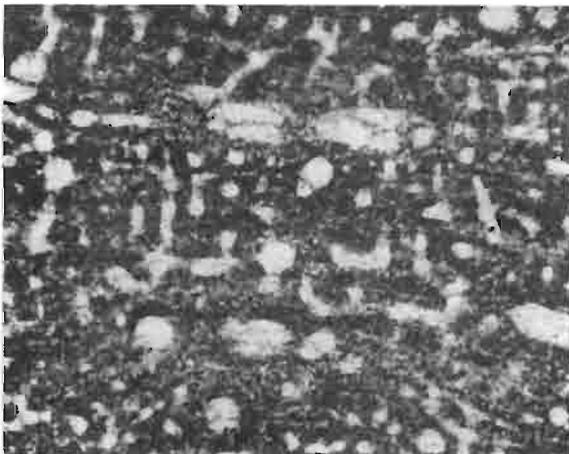
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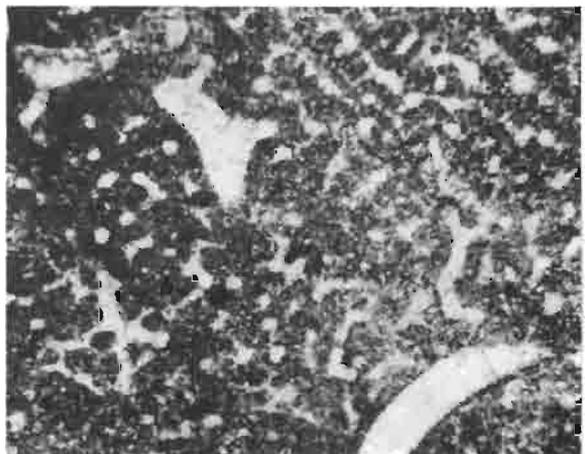
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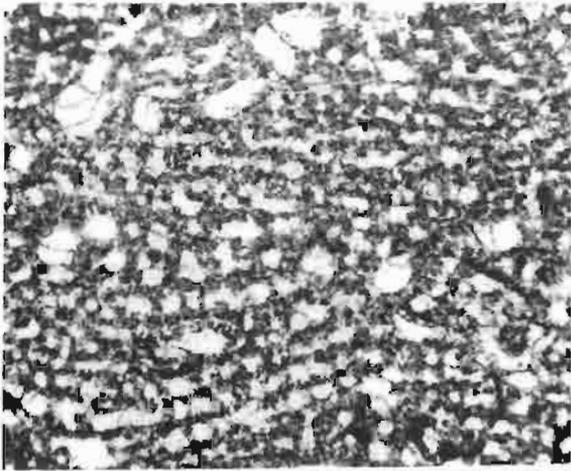
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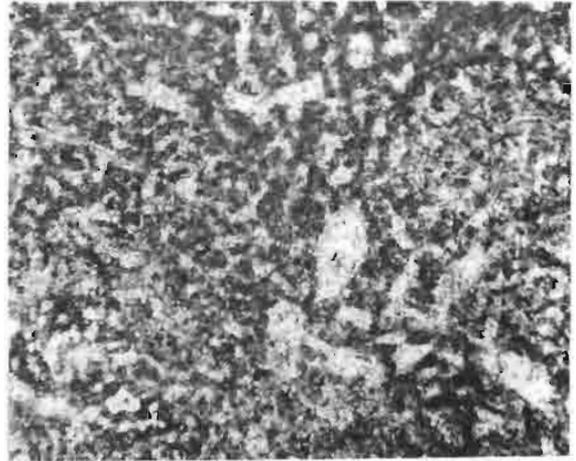
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Fig. 1. <i>a</i> vertical section; <i>b</i> tangential section. Sitkówka III, Poland; Upper Givetian, Lower Sitkówka Beds (Z. Pal. St. I/184); × 15.	
Fig. 2. <i>a</i> vertical section; <i>b</i> tangential section. Sowie Górki Hill, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/226); × 15.	
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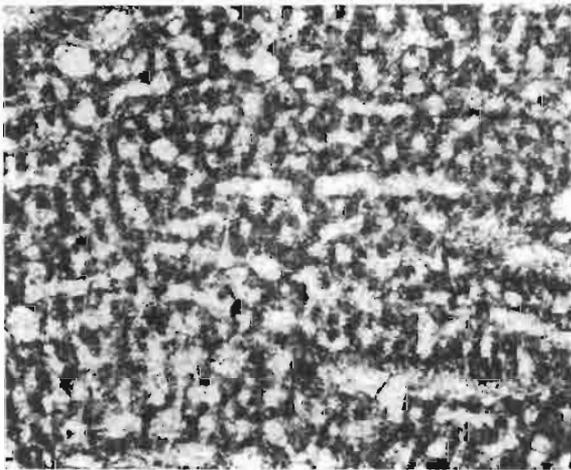




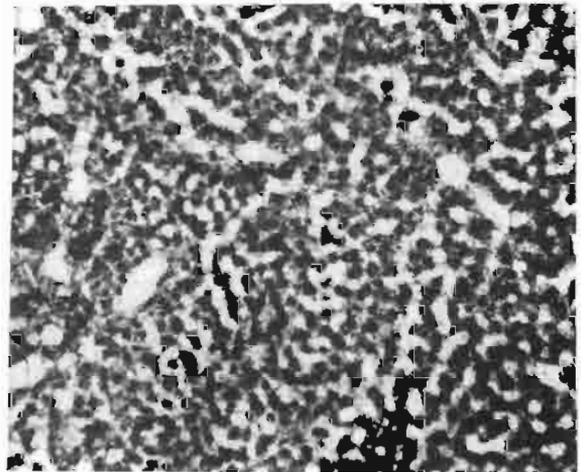
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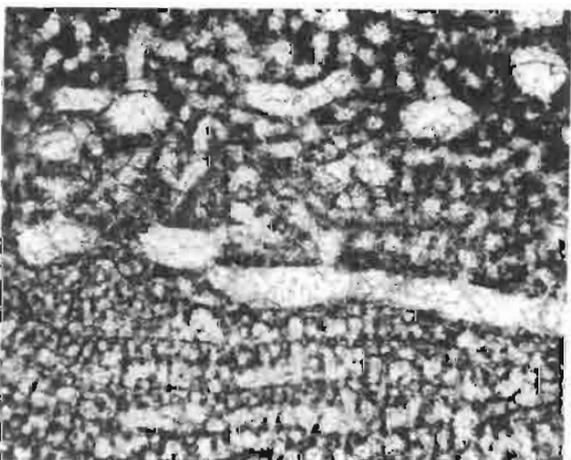
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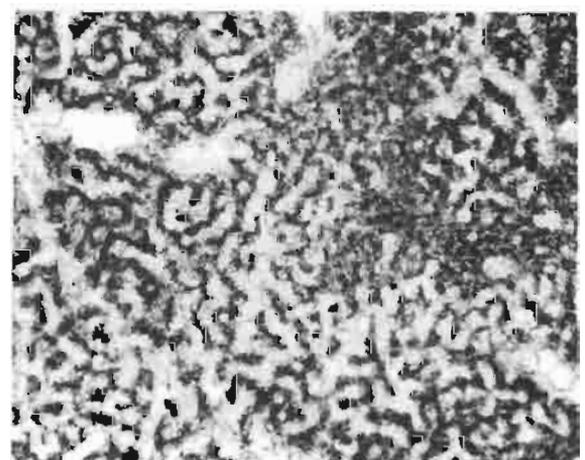
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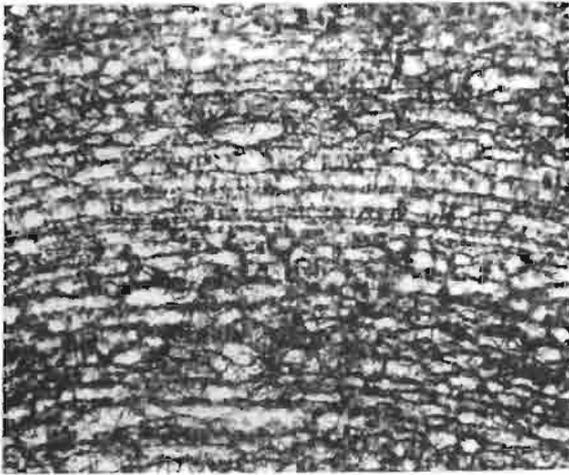
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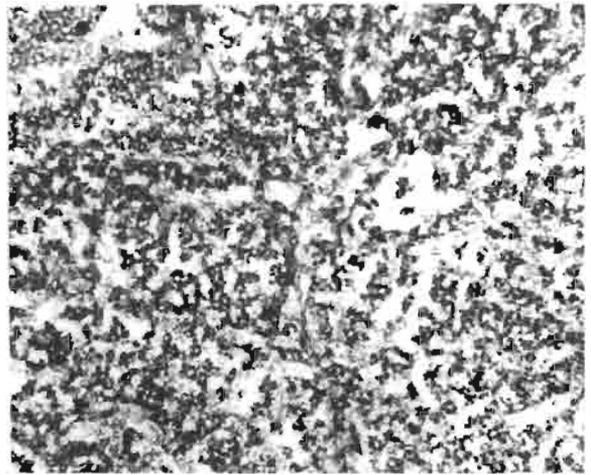
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<i>Ferestromatopora uchtensis</i> (RIABININ)	99
Fig. 1. <i>a</i> vertical section; × 15; <i>b</i> tangential section; × 15; <i>c</i> tangential section; × 15. Jaworznia-Moczydło Hill, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/188).	
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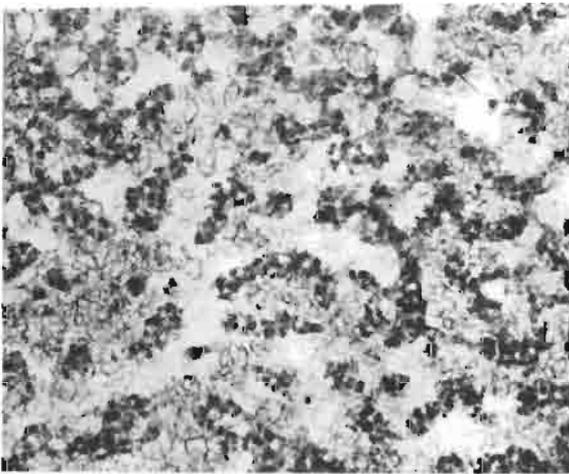




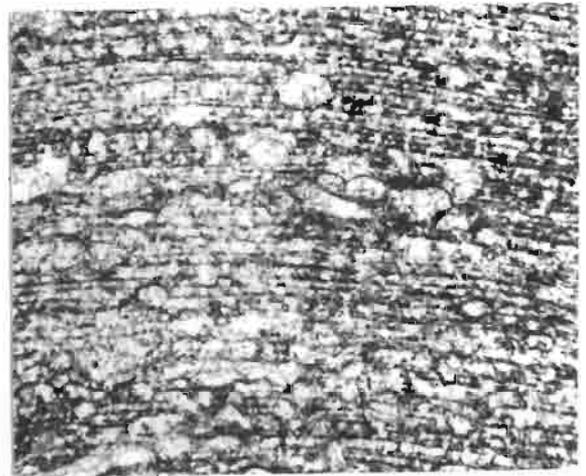
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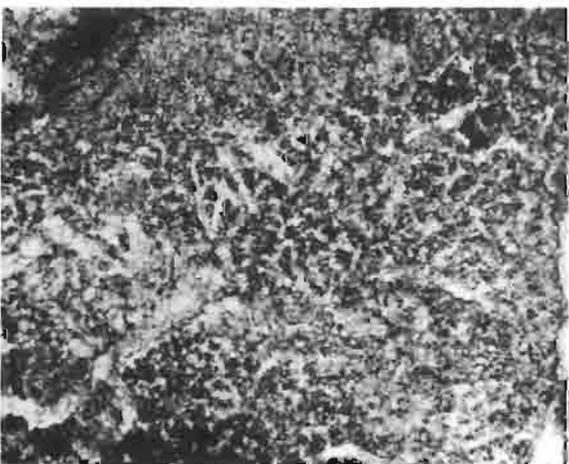
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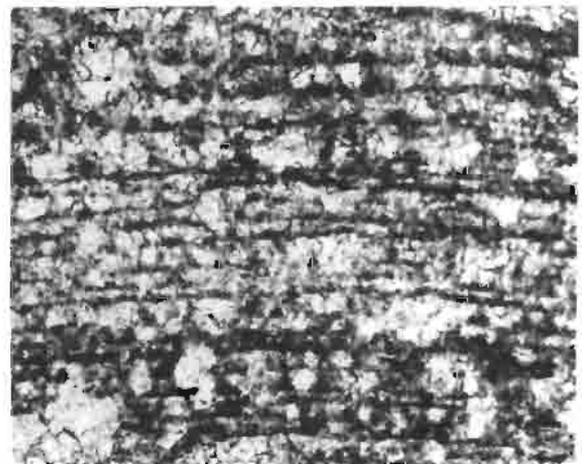
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2a



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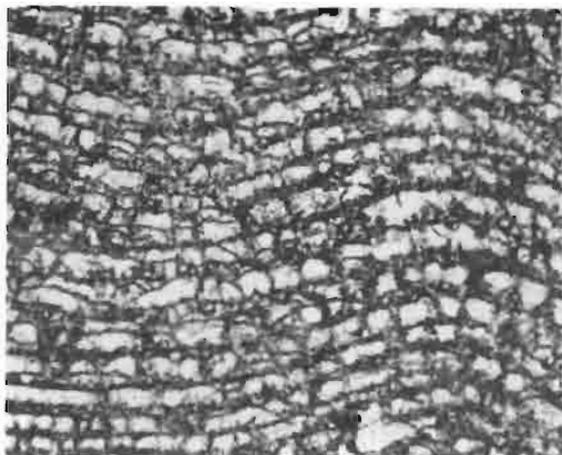


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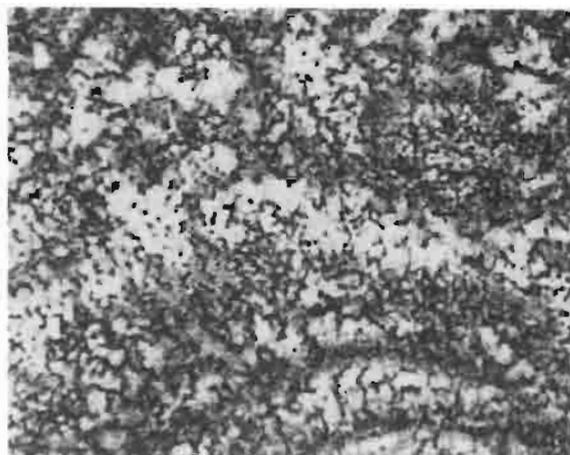
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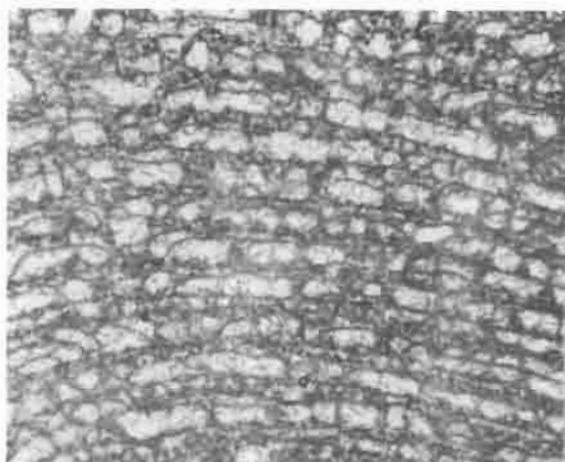
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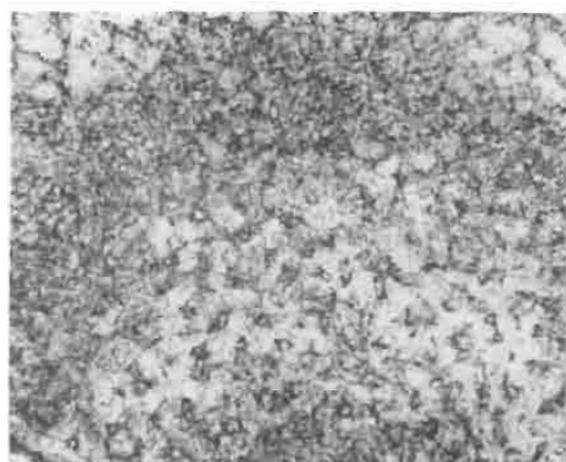
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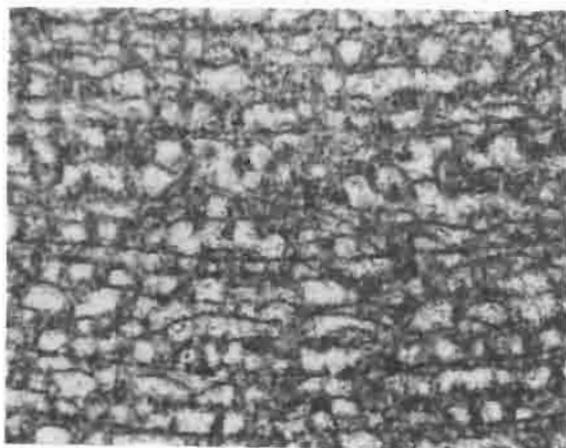
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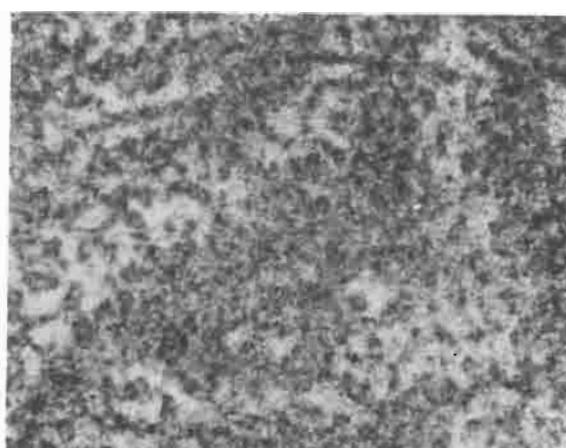
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3a



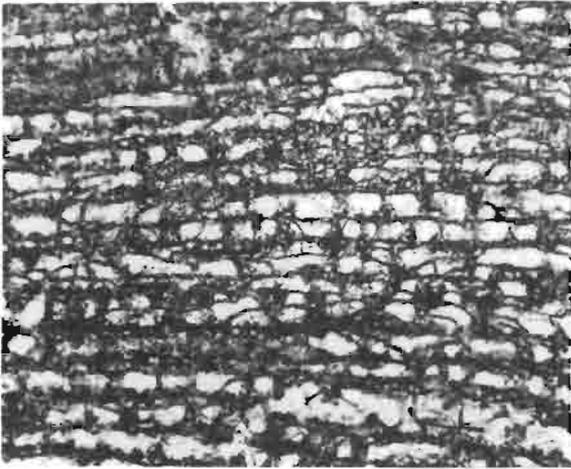
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J. KAŻMIERCZAK: MORPHOGENESIS AND SYSTEMATICS OF THE DEVONIAN STROMATOPOROIDEA

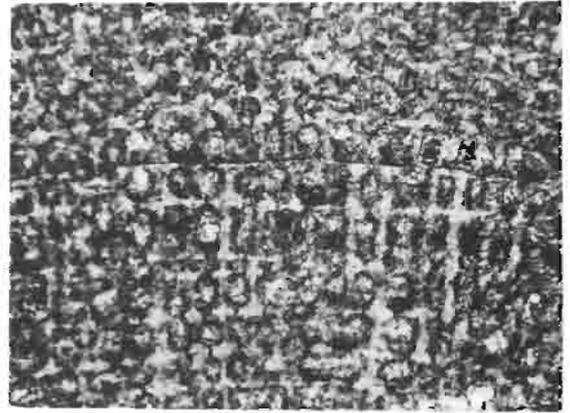
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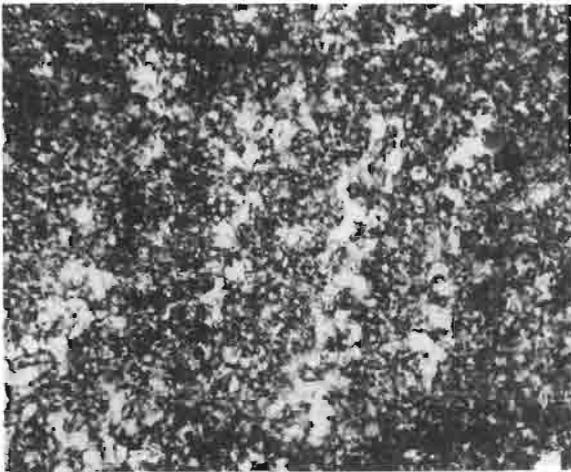




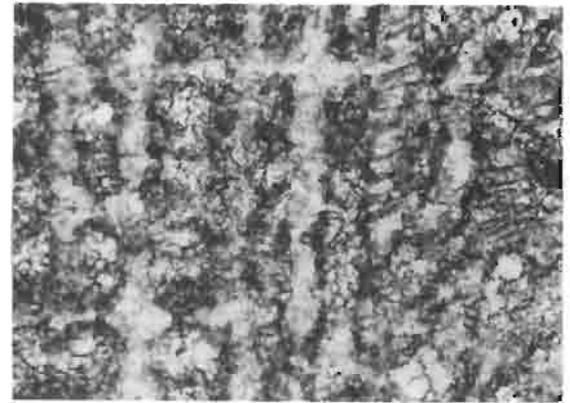
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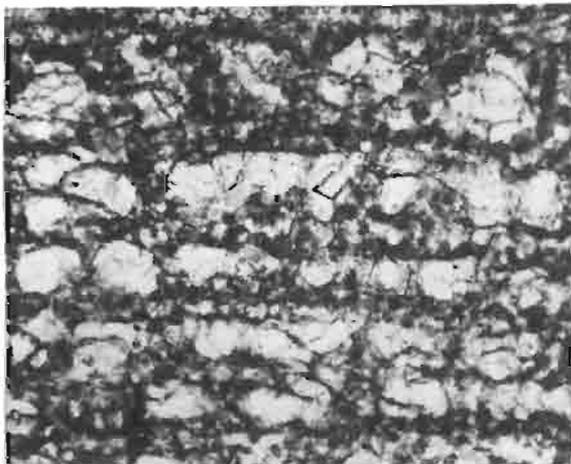
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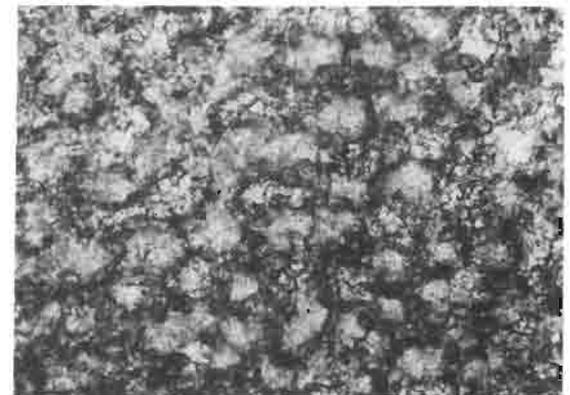
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2b



1c

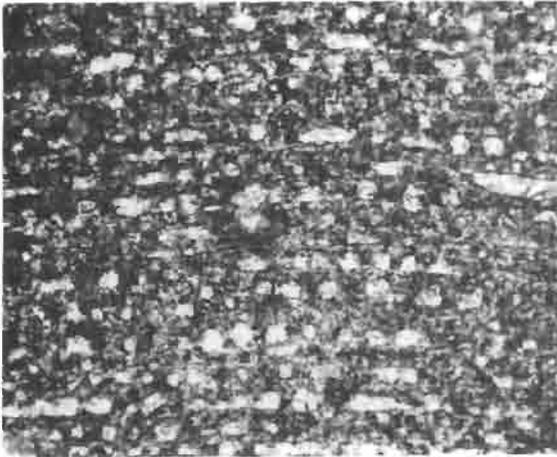


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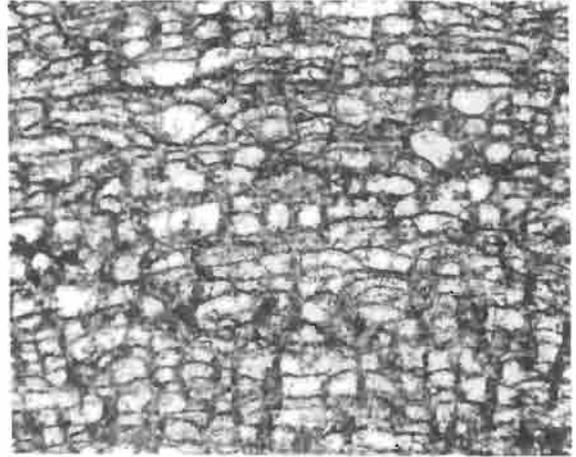
J. KAŻMIERCZAK: MORPHOGENESIS AND SYSTEMATICS OF THE DEVONIAN STROMATOPOROIDEA

PLATE XXVII

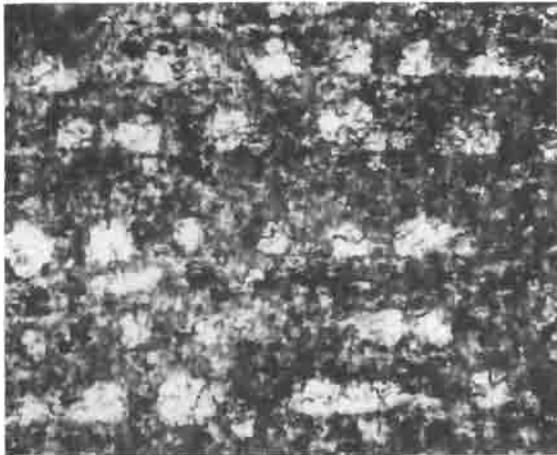
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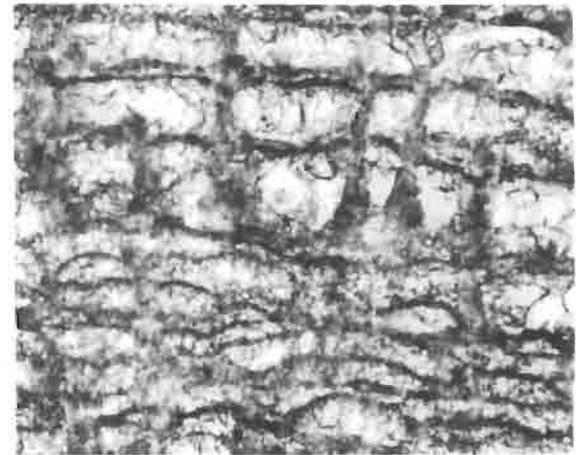
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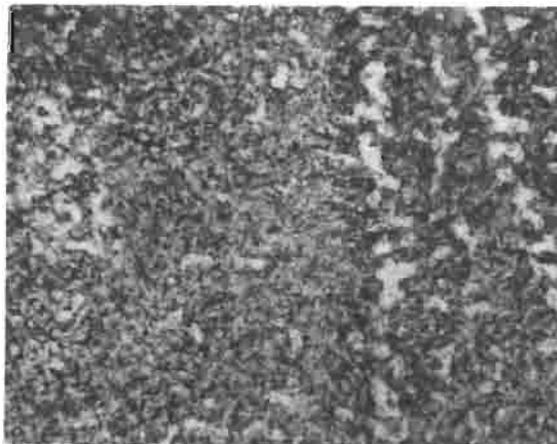
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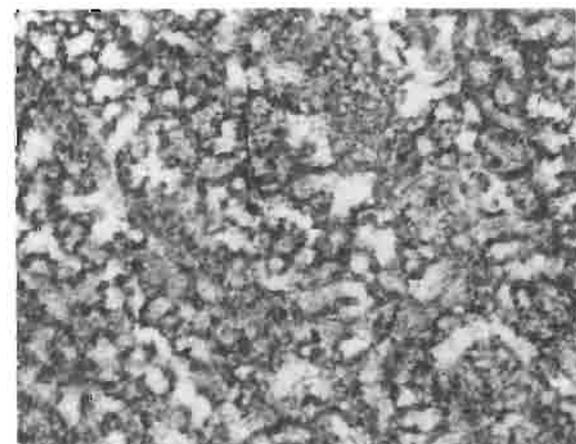
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2b



1c



2c

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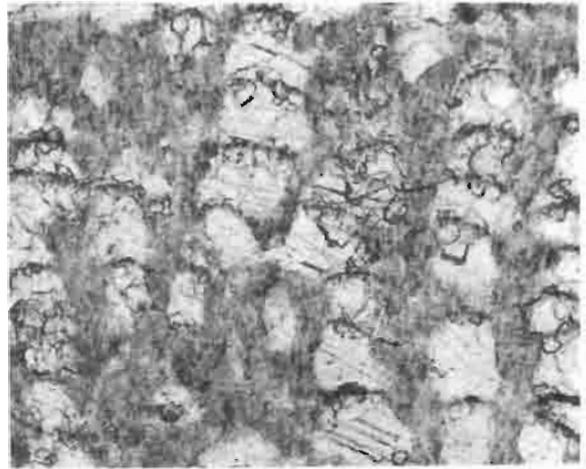
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Fig. 1. <i>a</i> vertical section; × 15; <i>b</i> vertical section; × 35; <i>c</i> tangential section; × 15. Bolechowice-„Panek“ quarry, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/464).	
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Fig. 3. Tangential section. Bolechowice-„Panek“ quarry, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/64); × 15.	

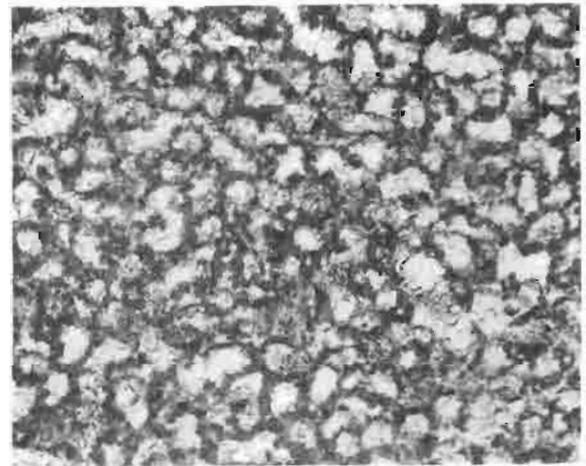




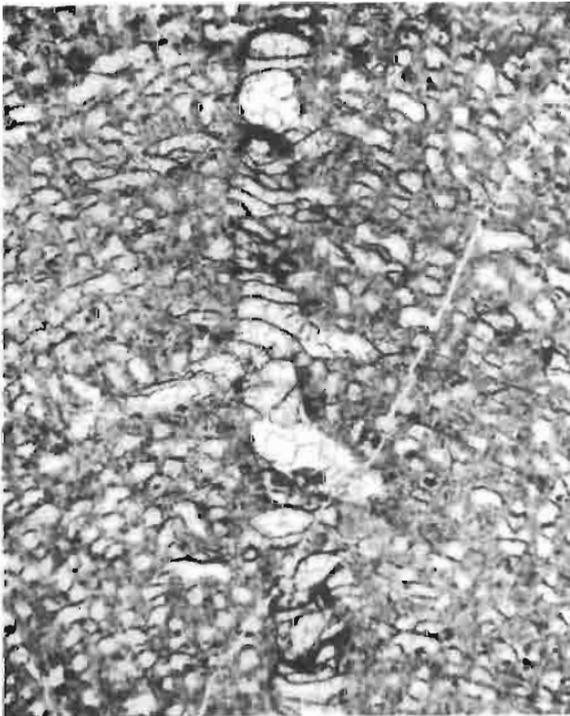
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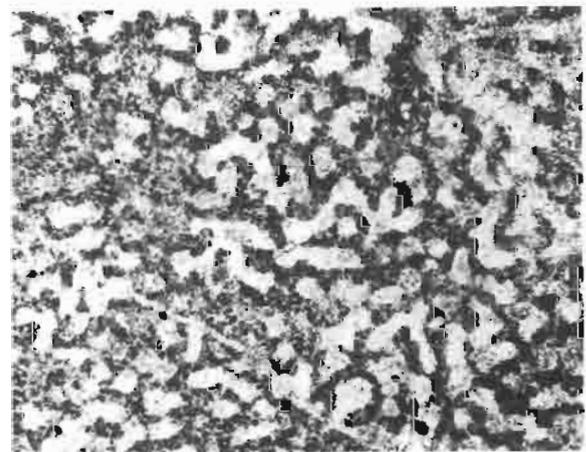
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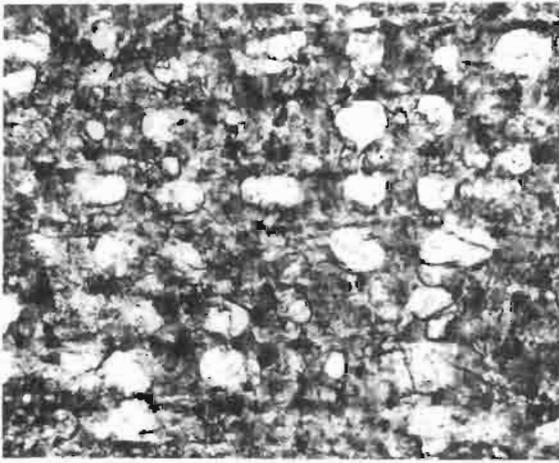
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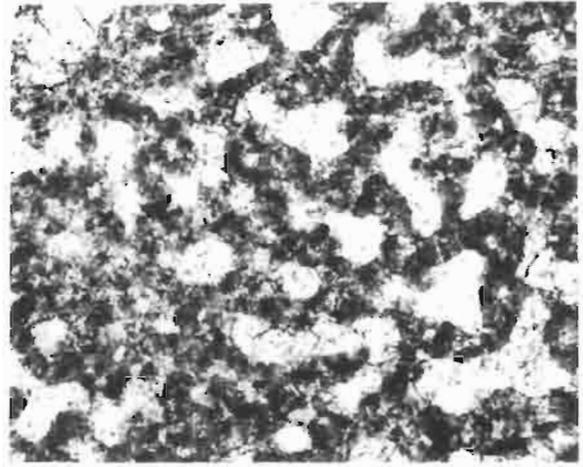
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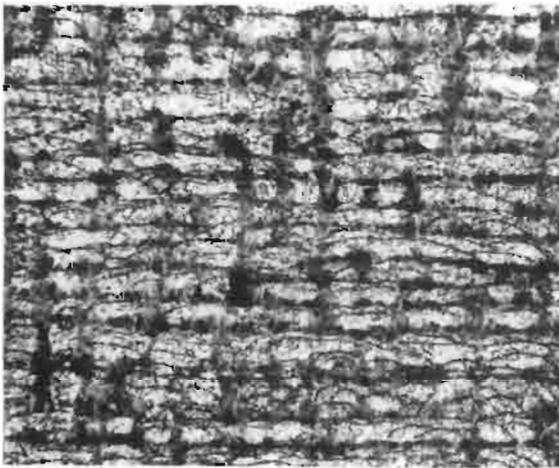




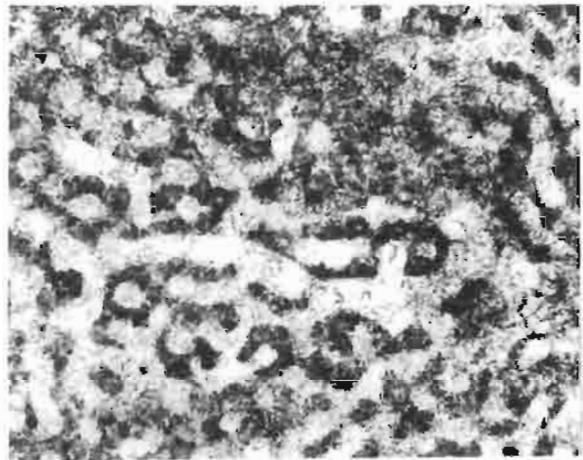
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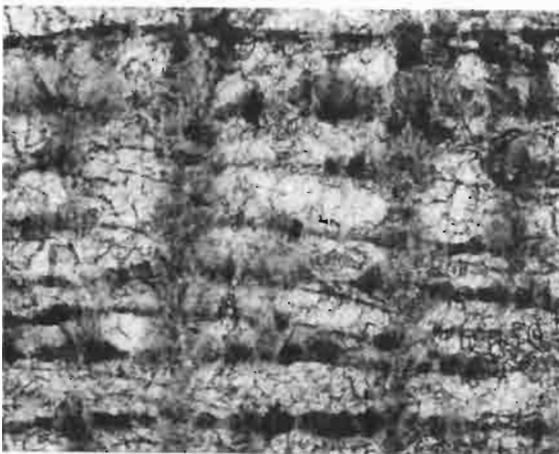
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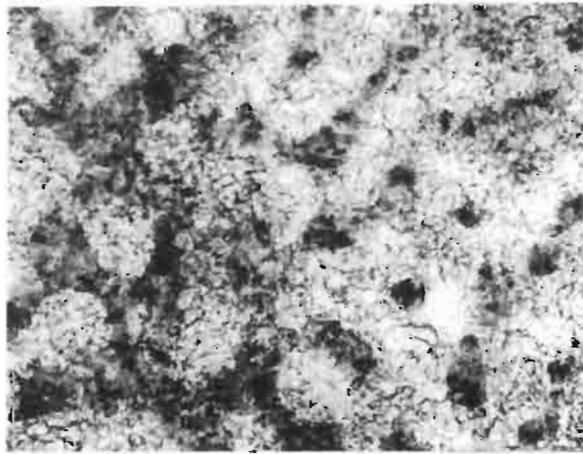
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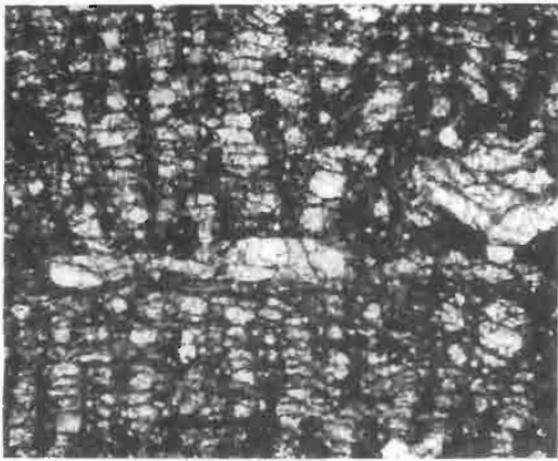
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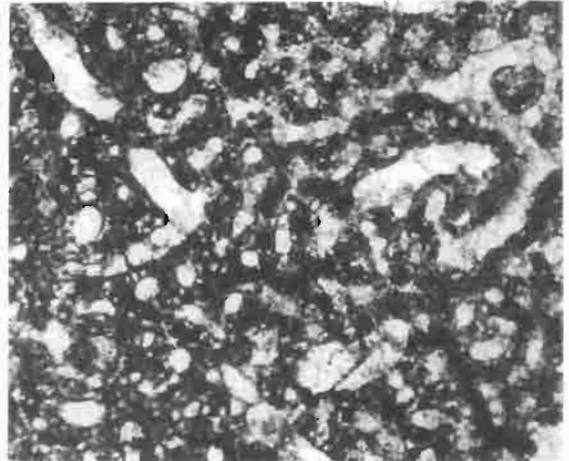
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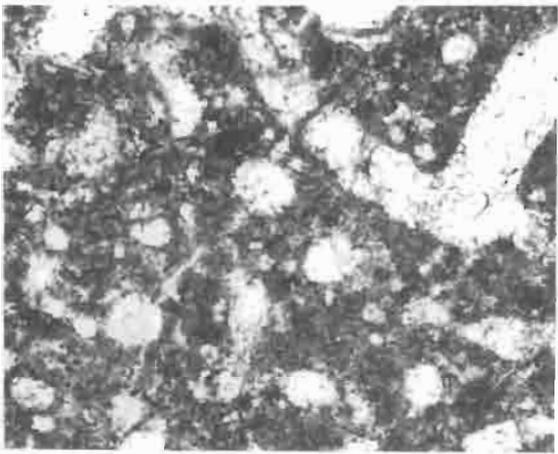




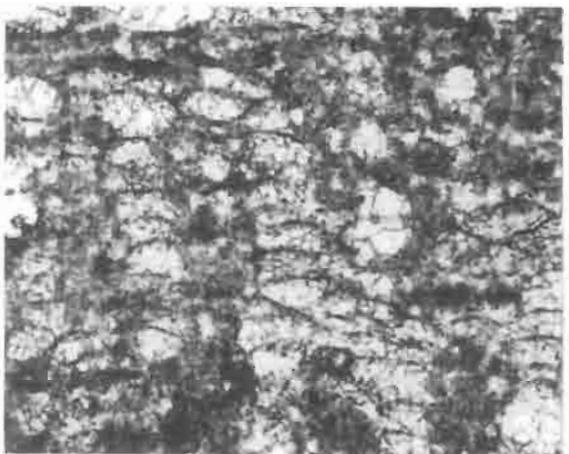
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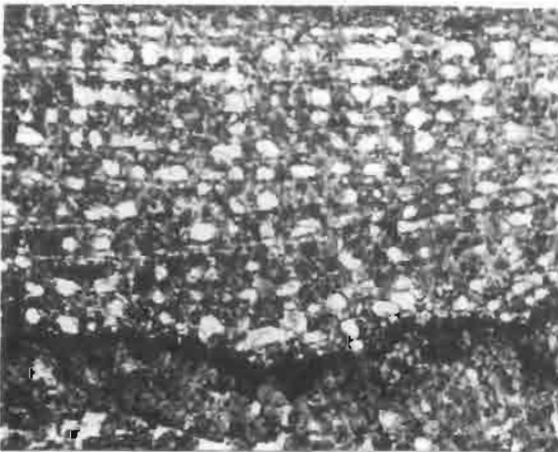
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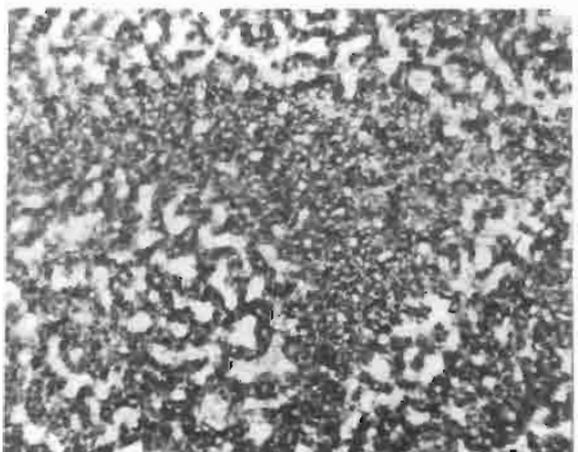
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2a



2b

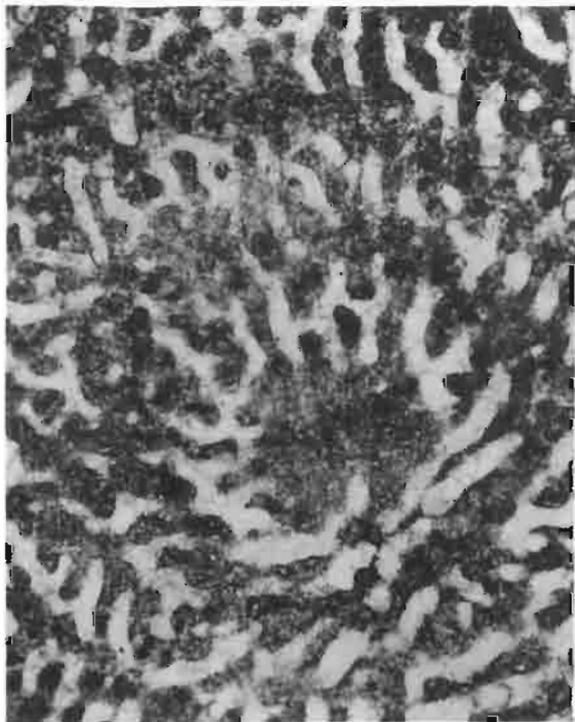
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PLATE XXXI

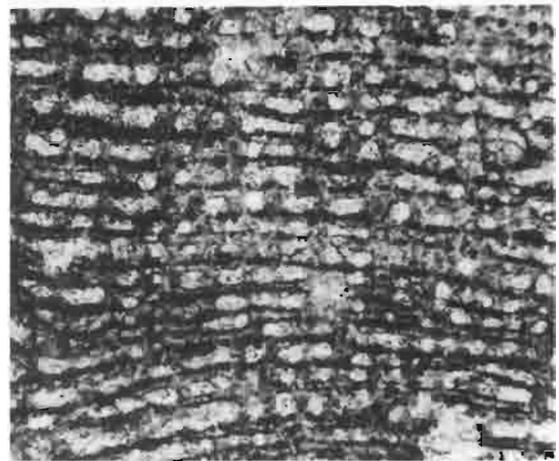
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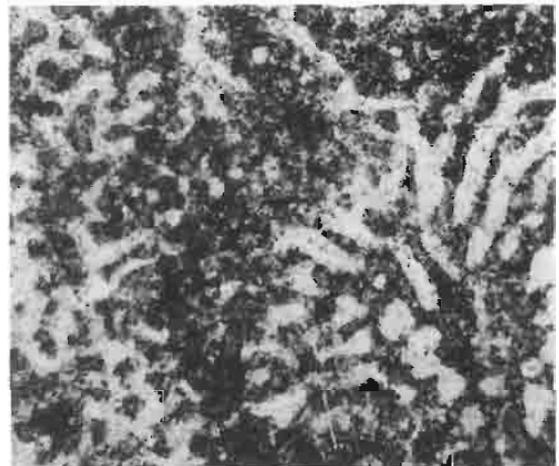
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1b



2a



2b



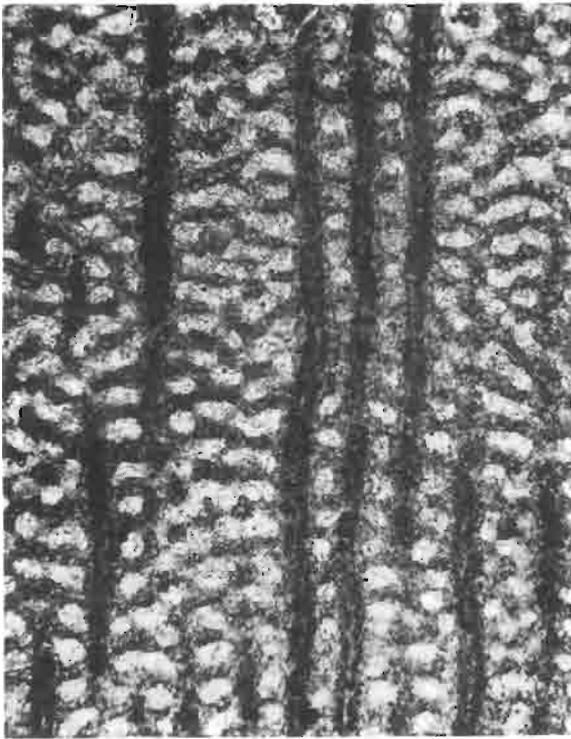
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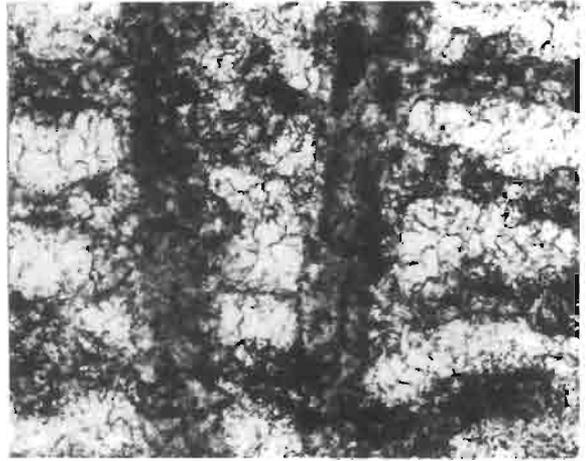
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Fig. 1. <i>a</i> vertical section; × 15; <i>b</i> tangential section; × 15; <i>c</i> vertical section; × 35; <i>d</i> tangential section; × 35. Jurkowice-Budy, Poland; Lower Upper Givetian, <i>Stringocephalus burtini</i> Beds (Z. Pal. St. I/139).	
Fig. 2. Vertical section. Saehyl-Tau, Southern Ural Mts., U. S. S. R.; Middle Devonian, ?Eifelian (CNIGR 5640/6); × 35.	

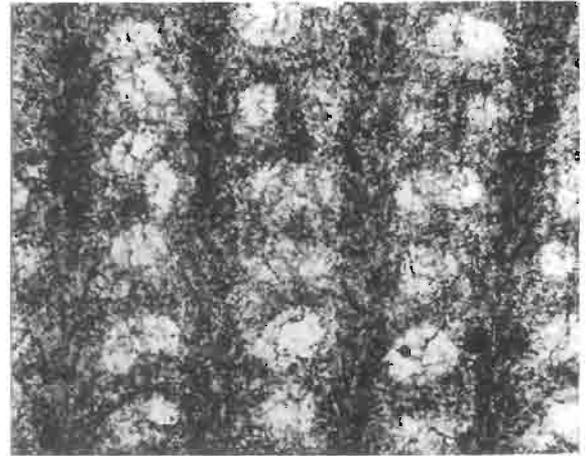




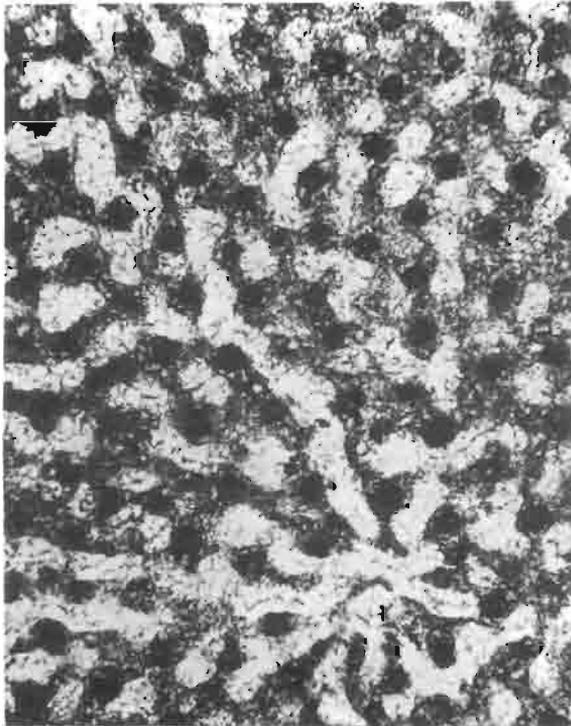
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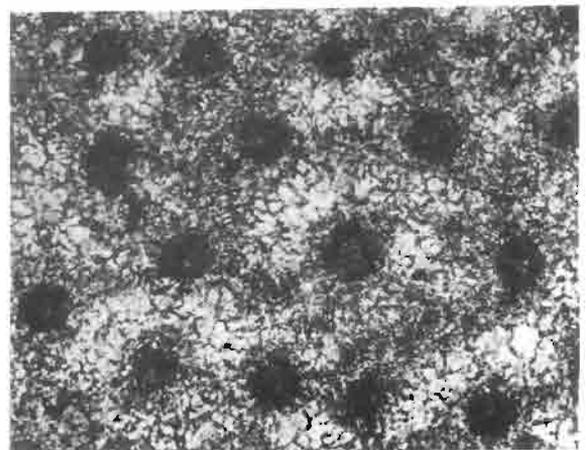
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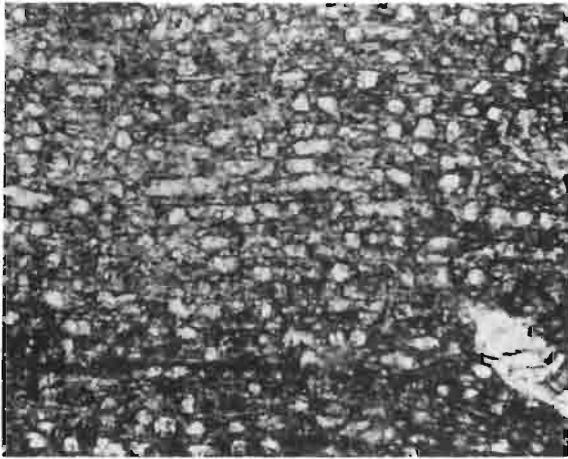
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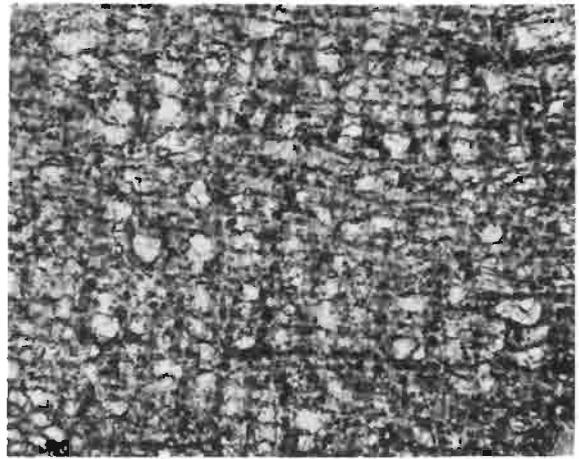
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PLATE XXXIII

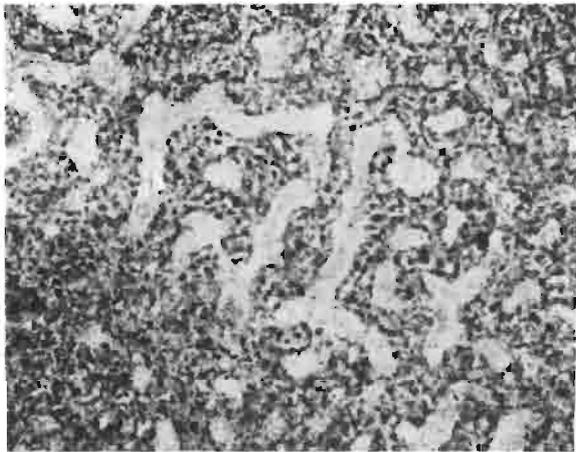
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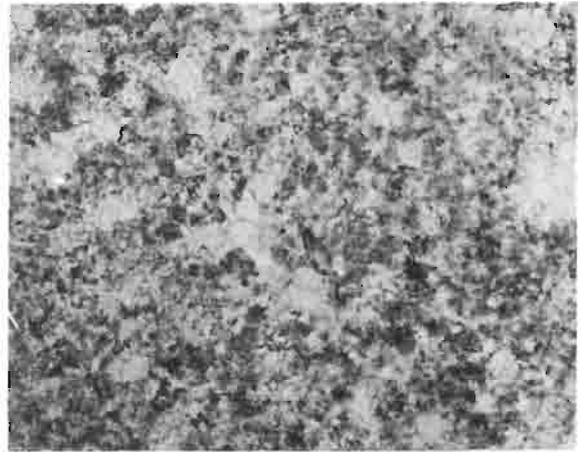
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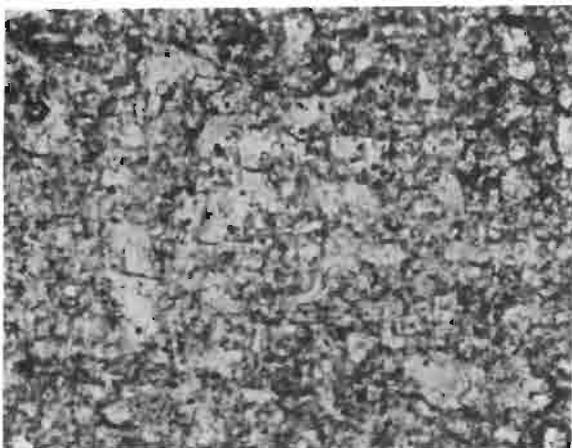
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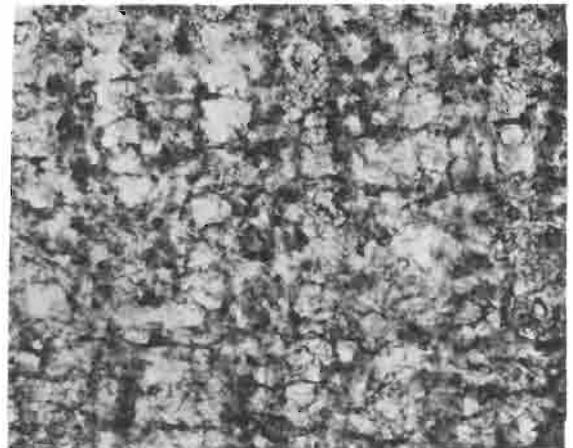
1b



2b



1c



2c

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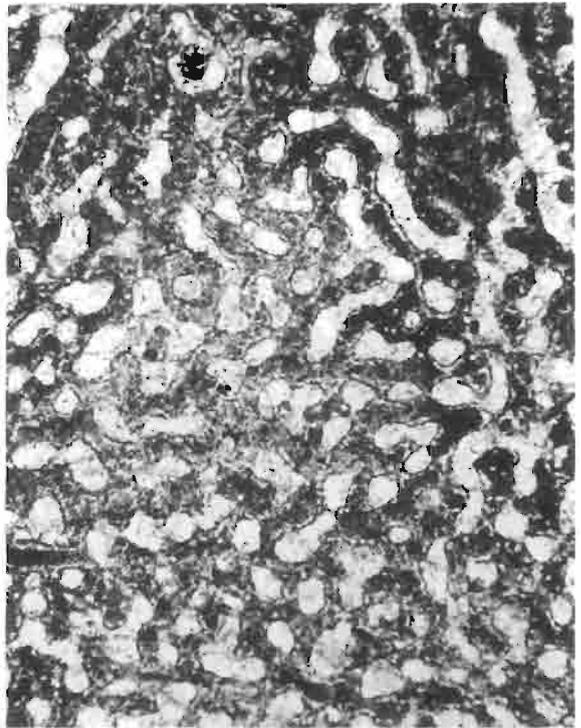
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Fig. 2. <i>a</i> vertical section; <i>b</i> tangential section. Jurkowiec-Budy, Poland; Lower Upper Givetian, <i>Stringocephalus burtini</i> Beds (Z. Pal. St. I/131); × 15.	

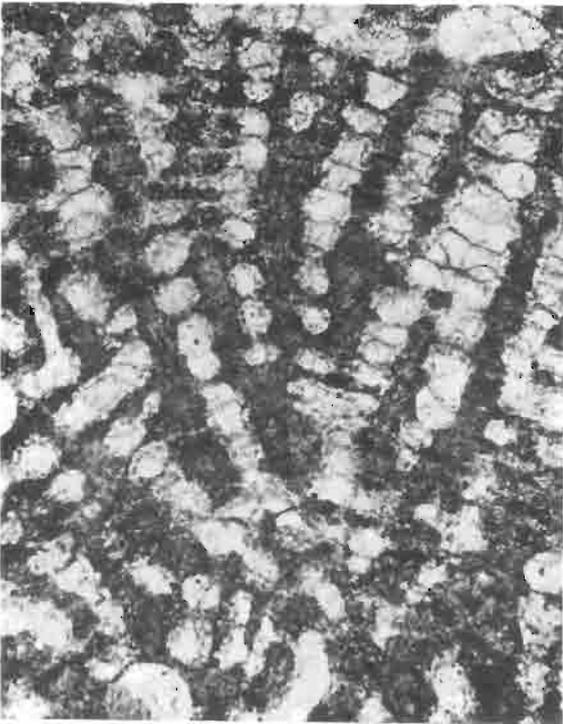




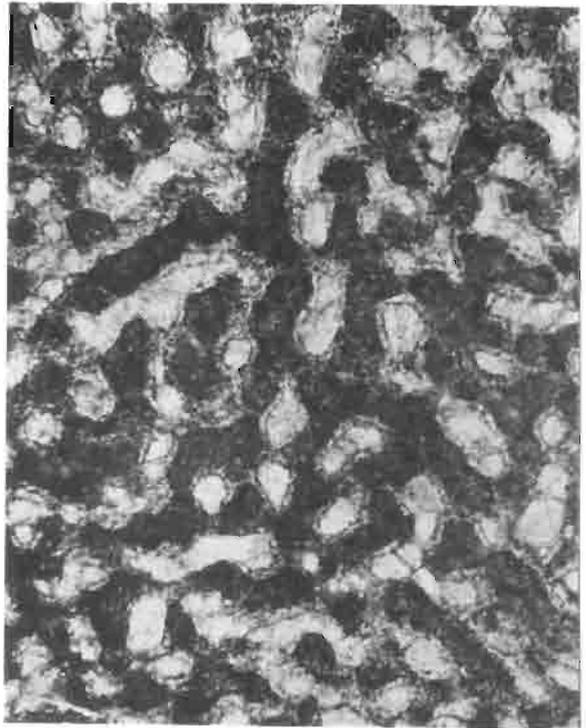
1a



1b



2a

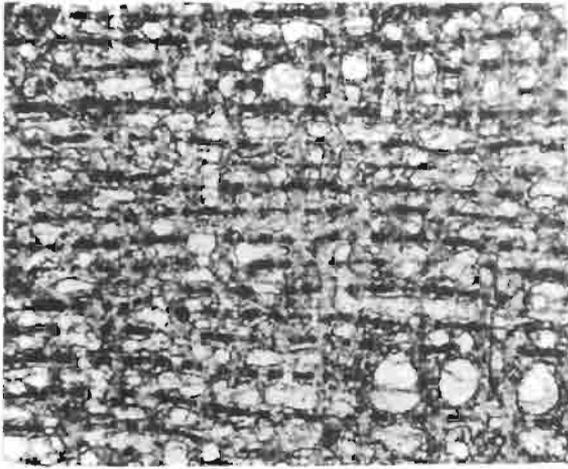


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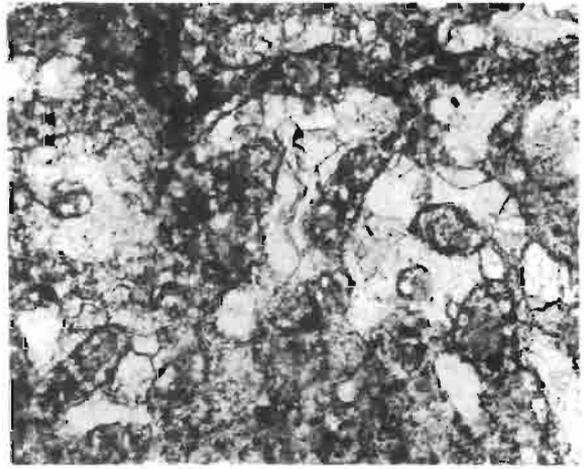
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PLATE XXXV

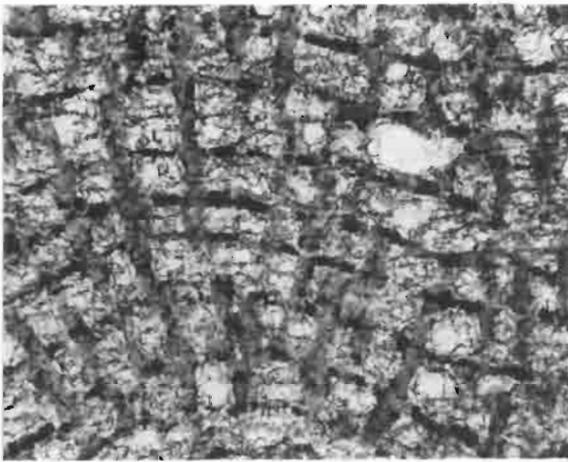
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Fig. 1. <i>a</i> vertical section; × 15; <i>b</i> tangential section; × 35. Jaworznia quarry, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/127).	
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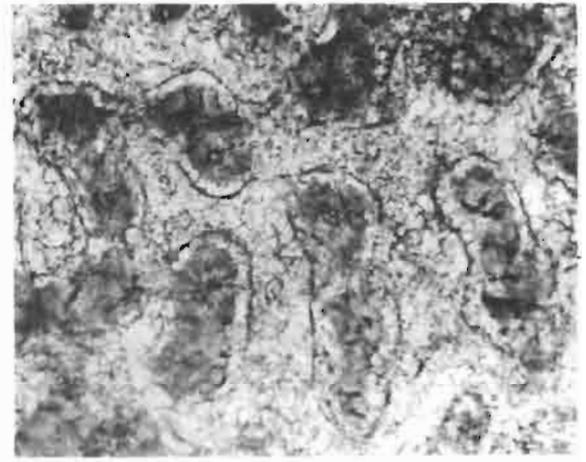
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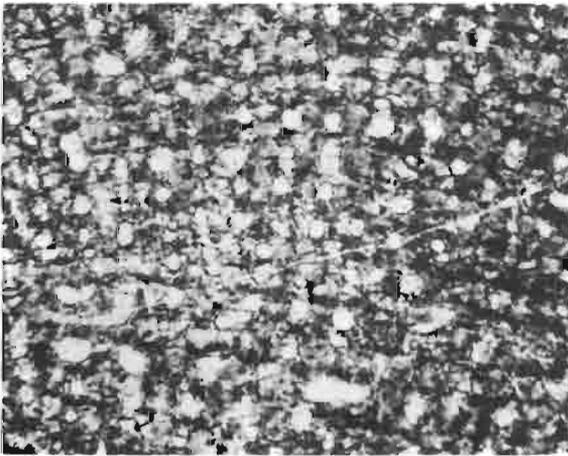
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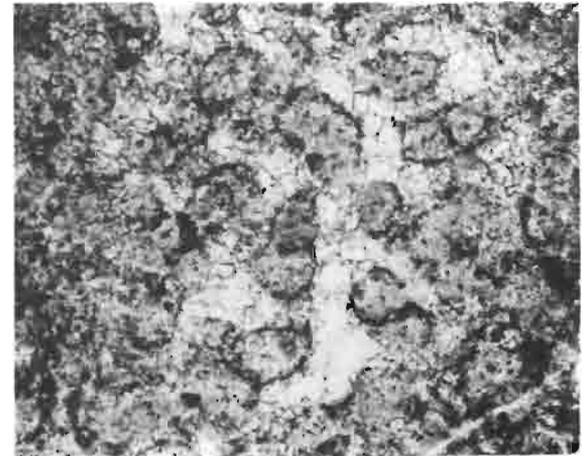
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2b



3a



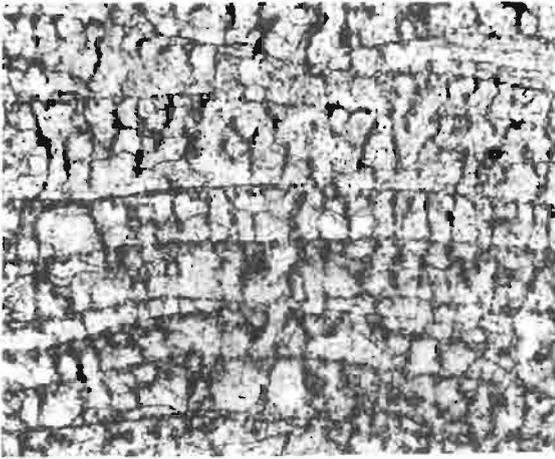
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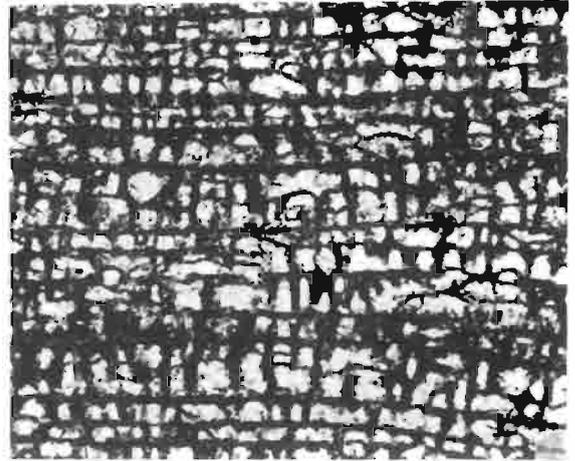
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<i>Atelodictyon pseudocolumnare</i> (RIABININ)	128
(see also Pl. X)	
Fig. 1. <i>a</i> vertical section; × 15; <i>b</i> tangential section; × 15; <i>c</i> tangential section; × 35. Bolechowice-„Panek“ quarry, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/22).	
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Fig. 2. <i>a</i> vertical section; × 15; <i>b</i> tangential section; × 15; <i>c</i> vertical section; × 35. Bolechowice-„Panek“ quarry, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/25).	

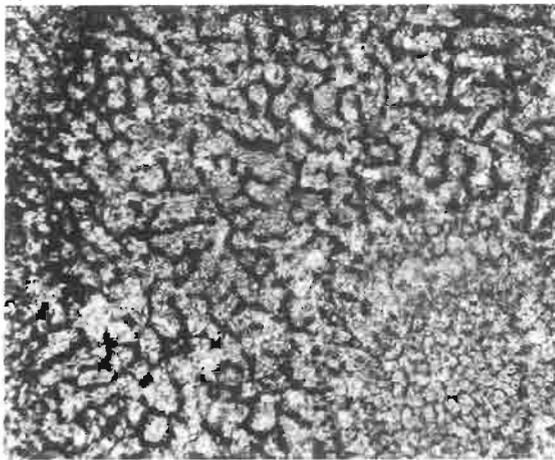




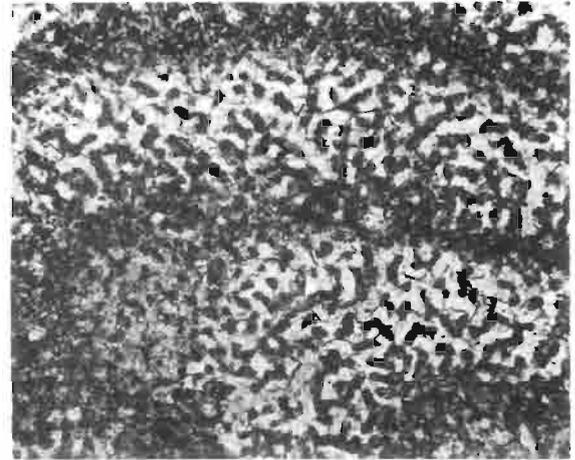
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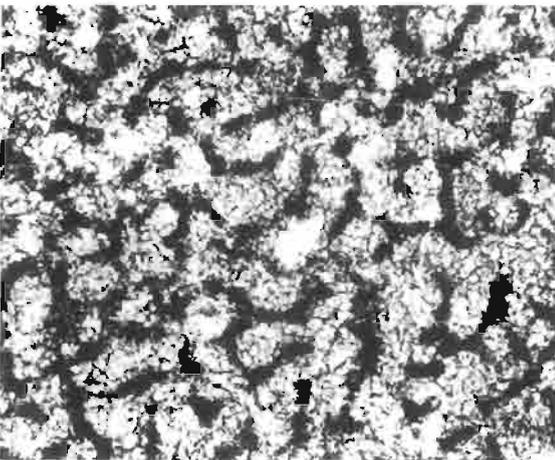
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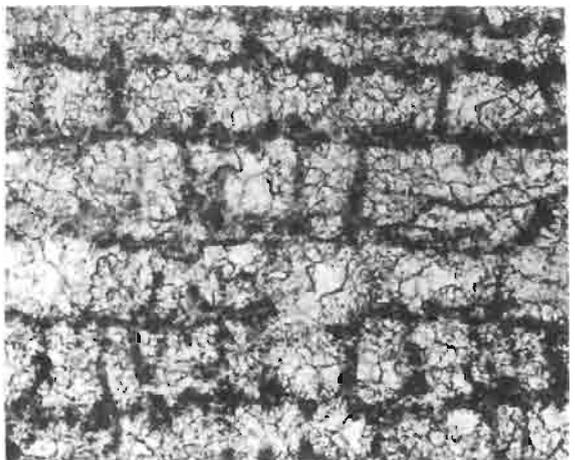
1b



2b



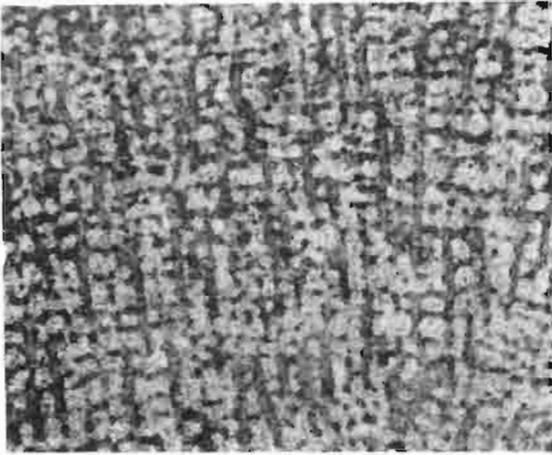
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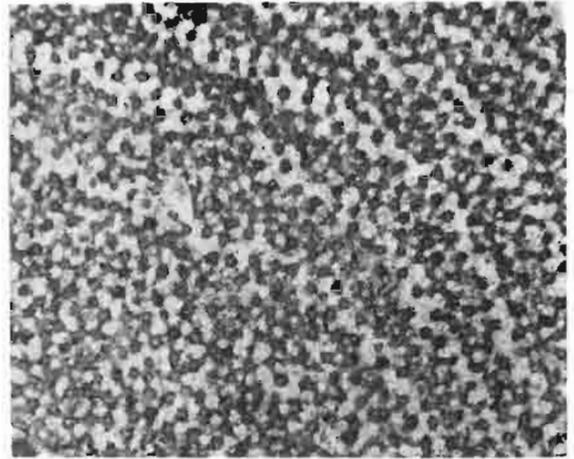
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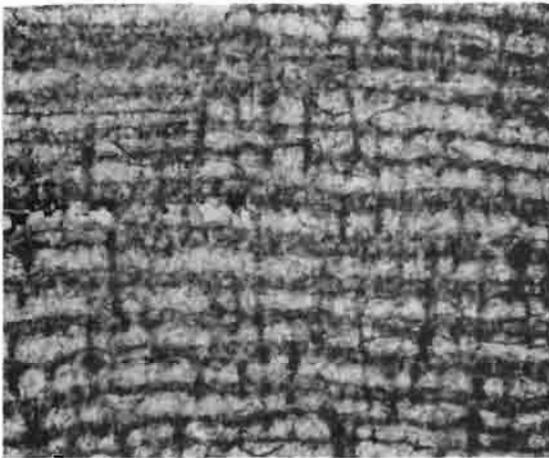
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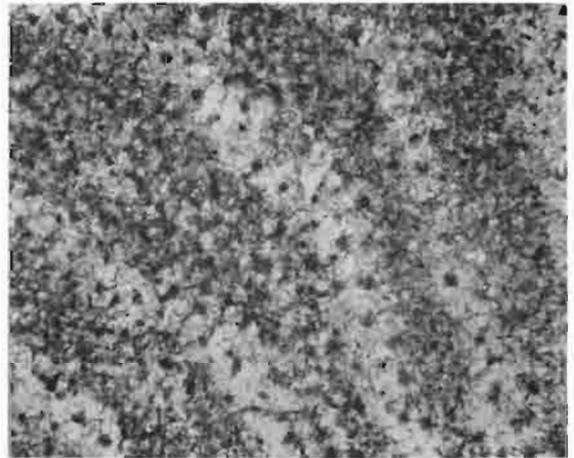
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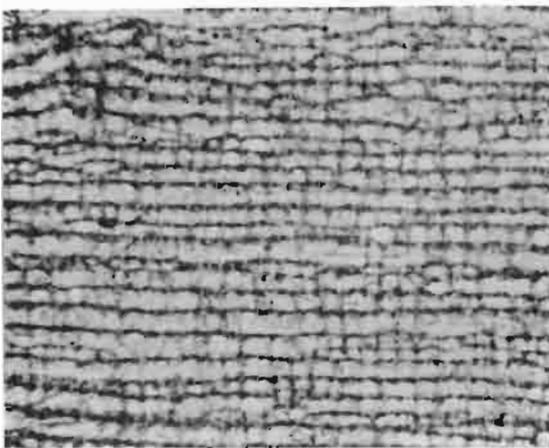
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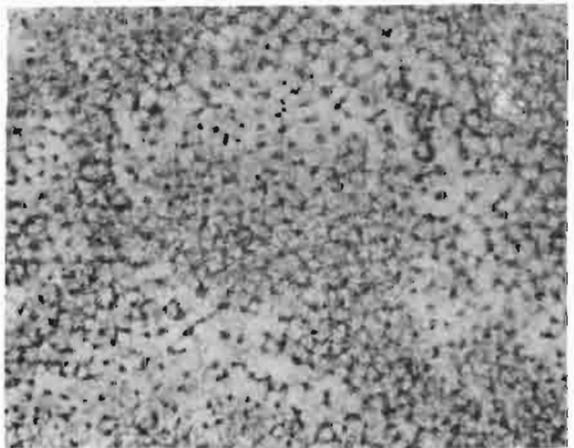
2a



2b



3a

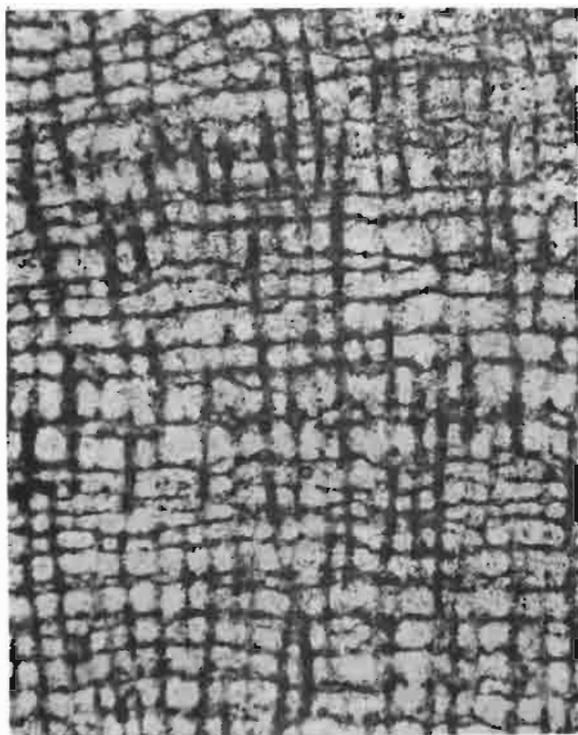


3b

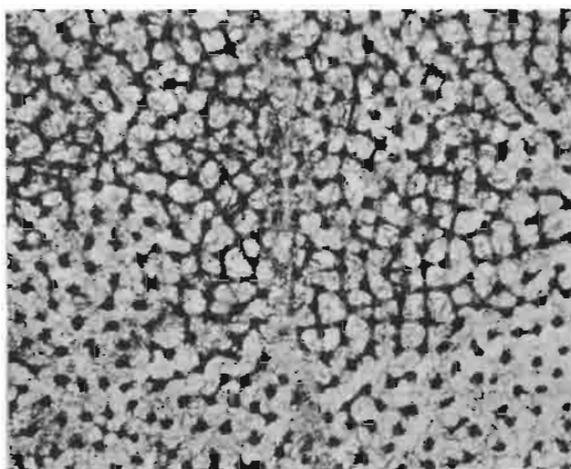
J. KAŻMIERCZAK: MORPHOGENESIS AND SYSTEMATICS OF THE DEVONIAN STROMATOPOROIDEA

PLATE XXXVIII

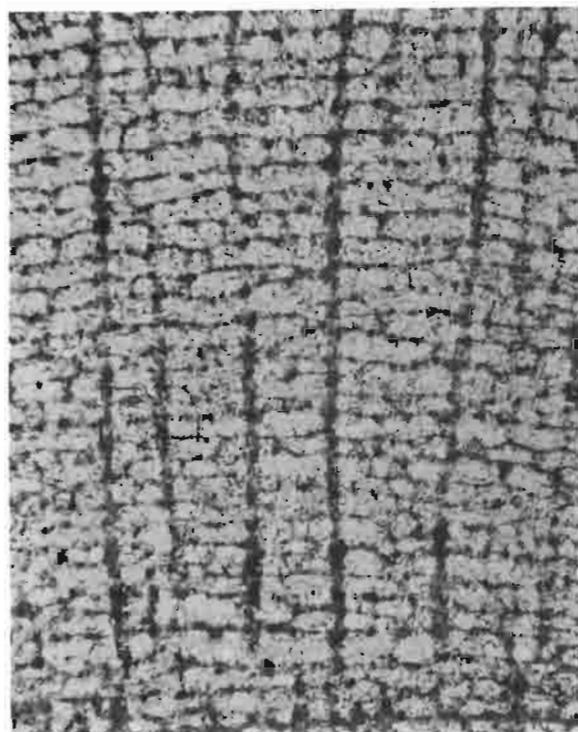
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<i>Actinostroma papillosum</i> (BARGATZKY)	134
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Fig. 1. <i>a</i> vertical section; <i>b</i> tangential section. Sitkówka V, Poland; lowermost Frasnian, Upper Sitkówka Beds (Z. Pal. St. I/276); × 15.	
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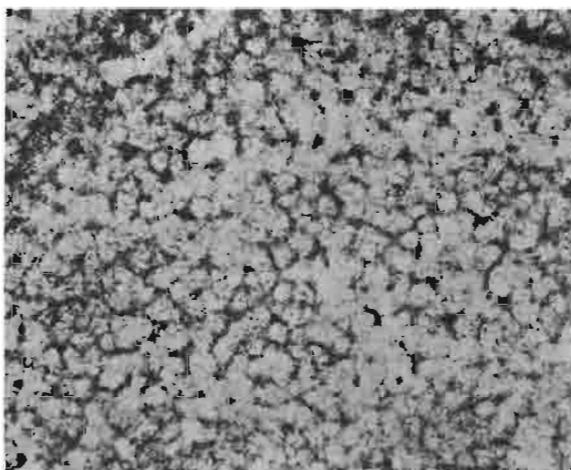
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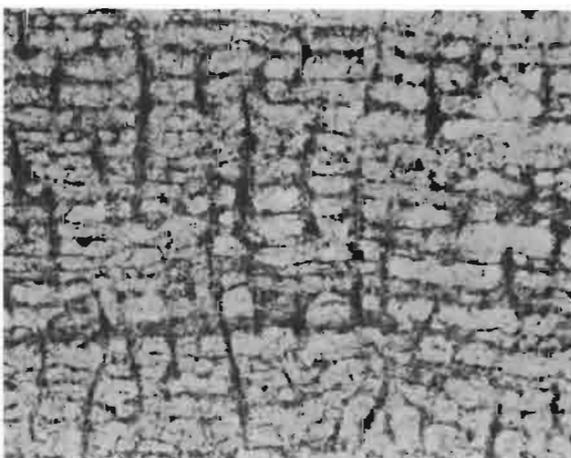
1b



2a



2b



3

J. KAŻMIERCZAK: MORPHOGENESIS AND SYSTEMATICS OF THE DEVONIAN STROMATOPOROIDEA

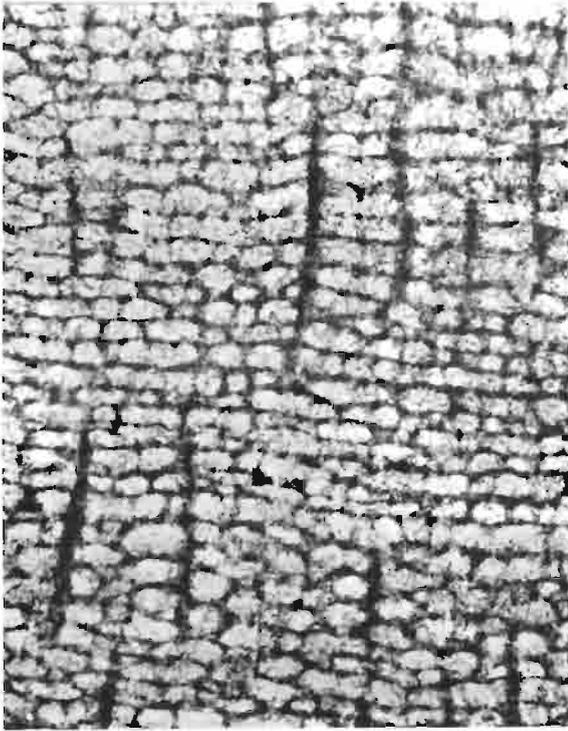
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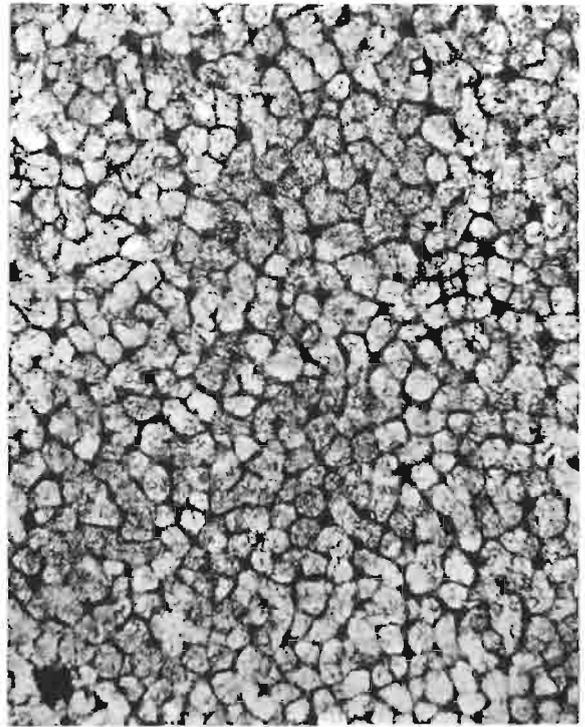
Fig. 1. *a* vertical section; *b* tangential section. Radkowiec-Sołtysia Hill, Poland; Upper Givetian, Lower Sitkówka Beds (Z. Pal. St. I/259); × 15.

Fig. 2. Vertical section. Sitkówka V, Poland; Upper Givetian, Lower Sitkówka Beds (Z. Pal. St. I/254); × 15.





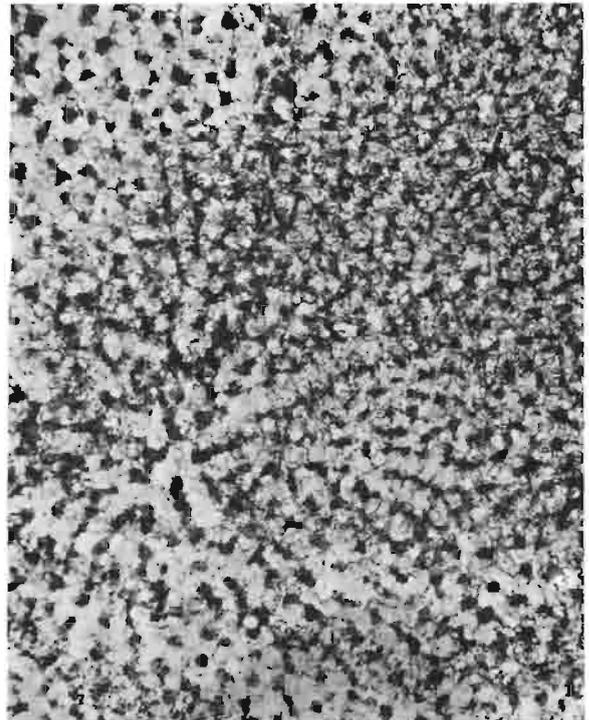
1a



1b



2a

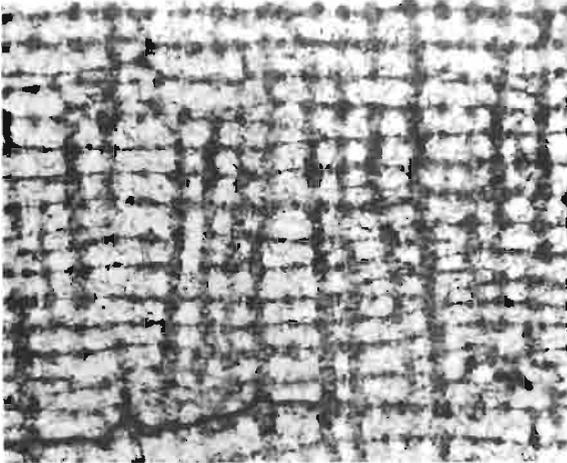


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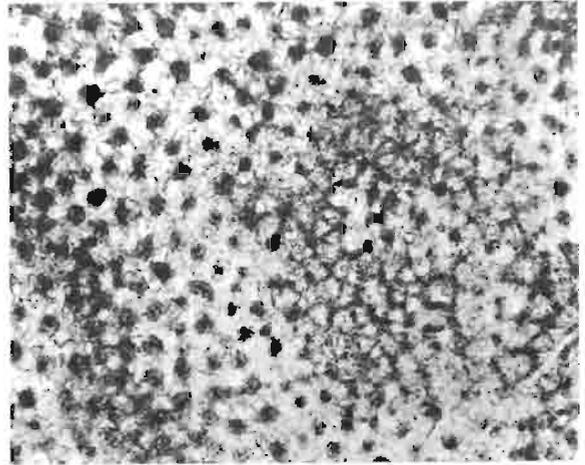
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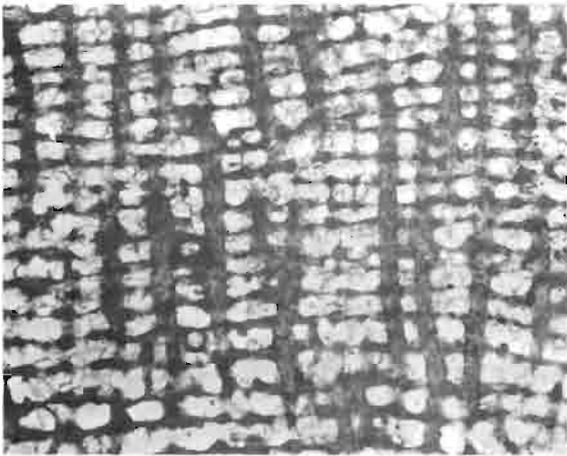




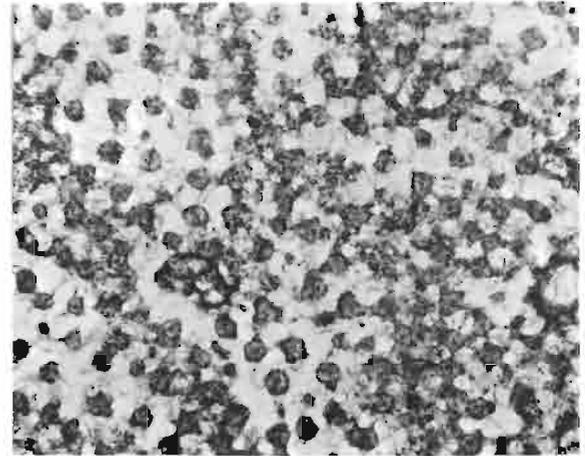
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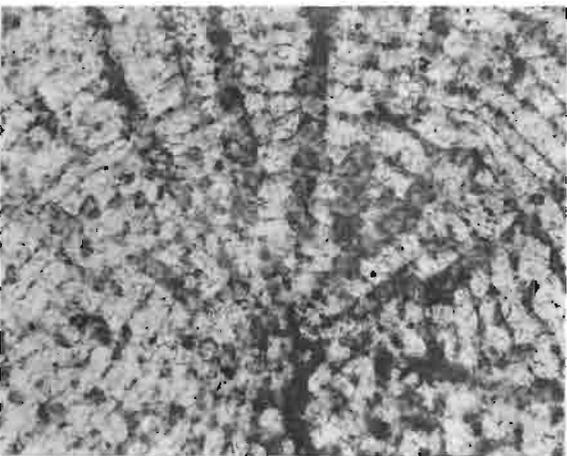
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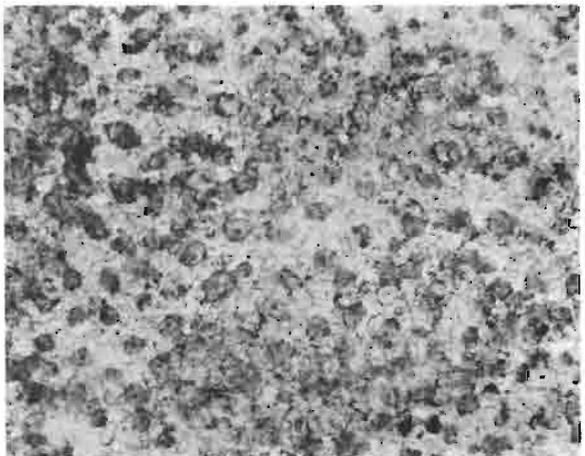
2a



2b



3a

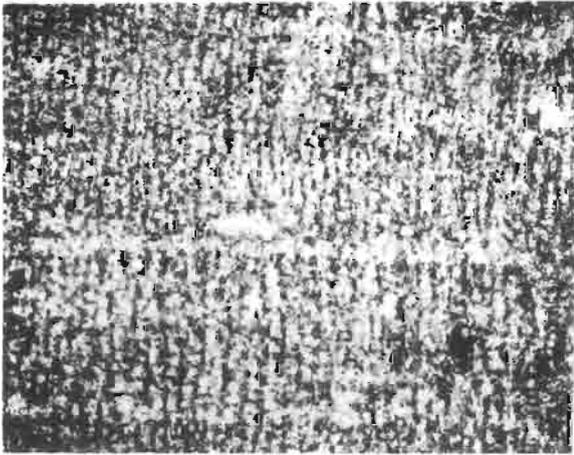


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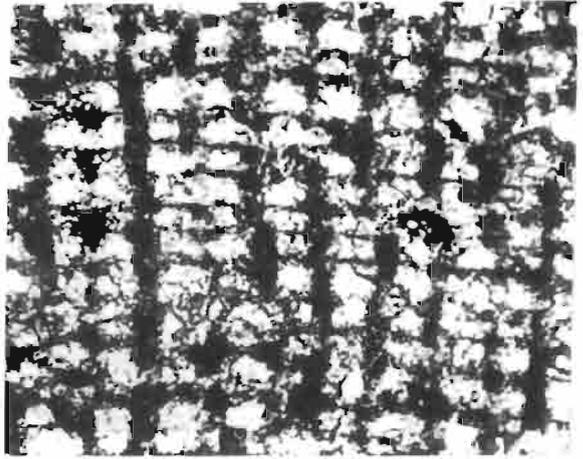
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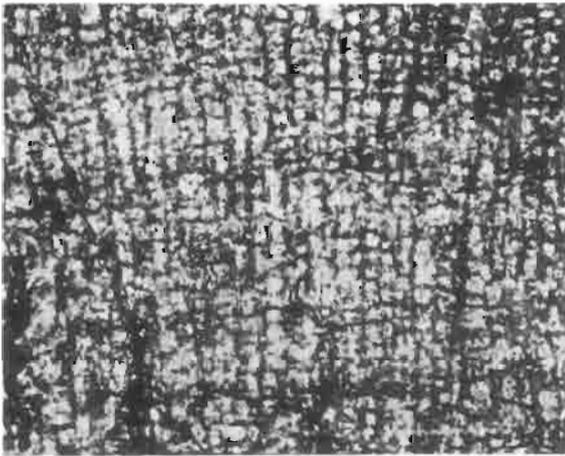
All in vertical sections; $\times 35$



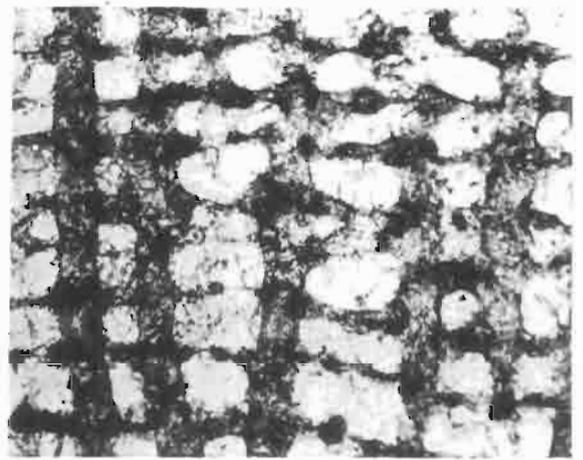
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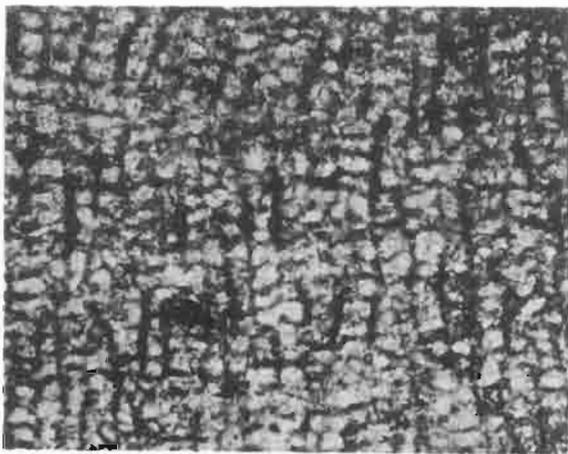
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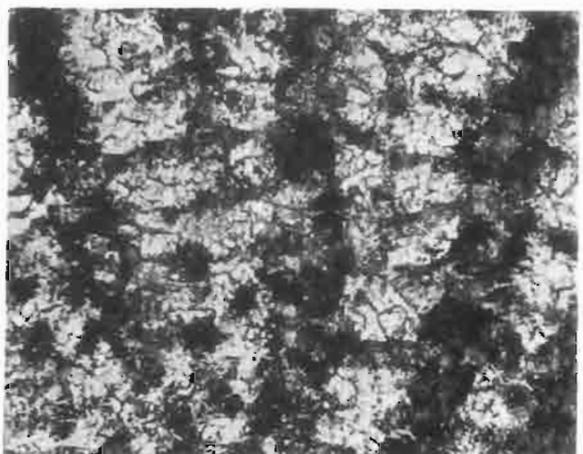
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5



3



6

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