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CONSIDERATIONS ON MIDDLE AND UPPER DEVONIAN THAMNOPHYLLIDAE SOSHKINA IN POLAND

PART II*

Abstract. — Corals with horse-shoe dissepiments and resting on them trabecular fans, formerly included 'by the writer in the subfamily Pachyphyllinae Stumm, are now referred to the family Thamnophyllidae Soshkina. The systematic division of this family is given. An analysis of correlation between the number of septa and the diameter of calice or of tabularium (n/d or n/t) in genera *Thamnophyllum* Penecke, *Macgeea* Webster, *Pexiphyllum* Walther and *Pachyphyllum* Edward & Haime has made possible the determination of the range of individual variability and the elucidation of evolutionary tendencies within the quoted genera. The coefficient of correlation for particular species is of diagnostic value and may constitute their stratigraphical index. It has been established that species previously described and referred (Różkowska, 1953, 1956) to the genera *Pseudoacervularia* Schlüter and *Pachyphyllum* Edwards & Haime should be assigned to genus *Pachyphyllum*. Within this genus four groups of species, with peculiar, similar coefficients of correlation, should be differentiated. Conclusions concerning speciation have been deduced from biometrical treatment and from ontogenic and morphological studies. A description is given of the phyletic and chronological evolution of Thamnophyllidae. In addition to material from the Holy Cross Mts. specimens collected at Dębnik and in the Sudeten were used by the writer for the present work.

INTRODUCTION

The taxonomy of Paleozoic corals has not, thus far, been adequately established. Different systematics are adapted by various authors, based on their own taxonomic criteria. The morphology of corals, however, ought not to be regarded as the only adequate taxonomic criterion, since forms belonging to distant phyletic lines may, in consequence of convergence, produce similarities of structure. Microstructure should be made the main basis here as it is closely connected with the mechanism

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of excretion by the polyp of exoskeletal parts (A. Schouppé, 1956). Coral_
lites commonly known under the name of Pachyphyllinae have a most
peculiar microstructure, by E. D. Soshkina (1949) called hexacoralloid,
since in these forms, as in Hexacoralla, the trabeculae have a fan-like
arrangement. Horse shoe dissepiments being the base of their line of
divergence, the distal edge of septa is arched, with strongest convexity
above the horse-shoe line. The arrangement of trabecular granules on
septa resembles that in Hexacoralla as the granules are parallel to the
distal edge of septum. Septa protrude beyond the pseudotheca as „costae".
From the outside they are masked by a thin epitheca, which, however,
does not reach to the edge of calyx, but terminates somewhat lower.
The body of the polyp must have, therefore, been overhanging the calyx
on the outside. Simple and colonial forms are always provided with
a talon for attachment. This is a feature common in the Tetracorals. In
Protomacgeea dobruchnensis Różk. which is a small and primitive form,
the writer has nevertheless observed the presence of a pedicil so common
in Hexacoralla. And yet Thamnophyllidae are typical Tetracorals whose
ontogeny is characterised by numerical increase of septa and by bilateral
symmetry peculiar to this group. This is markedly strong in some
genera, particularly so in youthful stages when the cardinal septum is
remarkably long or short, while the fossula has a prominent outline.

The hexacoralloid structure authorises the establishment for this
tetracoral group of a separate systematic unit distinguished by
exceptional progressiveness. Most likely it is not an accidental
occurrence, but may possibly suggest a latent evolutionary potentiality
in this group of Tetracorals. The writer believes this fact to support the
hypothesis that Hexacorals have a direct genetic connection with
Tetracorals.

This morphology, quite unusual for Tetracorals, has attracted the
attention of a number of students who have stressed its peculiar features
without, however, bringing them into the systematics of this group. It
is only during the last few years that some authors have expressed the
opinion that this group ought to be placed in a separate systematic unit.
Soshkina (1941) united forms having a hexacoralloid structure and
horse-shoe dissepiments into the family of Thamnophyllidae which
included the genera *Thamnophyllum* Penecke, *Macgeea* Webster,
Synaptophyllum Simpson and *Pachyphyllum* E. & H. In 1954 this writer
took a step further in establishing a "group" of Thamnophyllida Soshkina
with one family, Thamnophyllidae Soshkina, only. The exceptional
position occupied by this group of species is also stressed by Schouppé [1]

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[1] Prof. Dr A. v. Schouppé of Münster wrote to the author in 1956 that his studies
on the genotype of *Phillipsastraea hennahi* Lonsdale enabled him to ascertain the

(1956) who strongly advises its separation as a distinct systematic unit in opposition to other Tetracoral groups.

Two groups may be differentiated among forms having more or less symmetrical trabecular fans:

1) forms without horse-shoe dissepiments, e.g. *Ceratophyllum* Gürich, *Haplothecia* Frech, and

2) forms with horse-shoe dissepiments, e.g. *Thamnophyllum* Penecke, *Synaptophyllum* Simpson, *Macgeea* Webster, *Pachyphyllum* Edwards & Haime, *Pexiphyllum* Walther. In this group are, thus, assembled the genera which the present writer has so far included into the subfamily Pachyphyllinae Stumm, while Soshkina and Schouppé have referred them to the family Thamnophyllidae Soshkina. The name of the subfamily Pachyphyllinae Stumm, 1949, used by the present writer in her papers published in 1953 and 1956, thus becomes obsolete. The family Thamnophyllidae Soshkina into which the writer now includes all genera with symmetrically arranged trabecular fans and rows of horse-shoe dissepiments, is here divided into two subfamilies, viz. Thamnophyllinae mihi and Macgeeinae mihi. The subfamily Thamnophyllinae essentially includes colonial forms displaying the pattern of phacelloid or massive colonies with indistinct bilateral symmetry. The subfamily Macgeeinae represents simple forms. Budding is here extremely rare and there is no ,,massive colony" stage, while bilateral symmetry is distinct throughout the ontogeny. Each of these subfamilies links several mutually related species. The classification of the family Thamnophyllidae is therefore as follows:

Family **Thamnophyllidae** Soshkina, 1941

Subfamily **Thamnophyllinae mihi**
Genus *Thamnophyllum* Penecke, 1894
   ,,   *Synaptophyllum* Simpson, 1900, emend. Różkowska, 1953
   ,,   *Pachyphyllum* Edwards & Haime, 1850.

Subfamily **Macgeeinae mihi**
Genus *Protomacgeea* Różkowska, 1956
   ,,   *Macgeea* Webster, 1889
   ,,   *Pexiphyllum* Walther, 1928, emend. mihi.

Out of the above quoted genera, *Trapezophyllum* Etheridge, 1899, is the only one thus far never recorded in Poland. It has been described

from the Lower Devonian and Eifelian of Australia and recently from the Eifelian of the Rhine Province (A. Glinski, 1955).

In the text and explanations of tables and figures the following symbols are used: c — class, n — number of septa, d — diameter of calyx, Mn — arithmetic mean of septa in classes, Md — arithmetic mean of diameters in classes, Mc — correlation coefficient of classes, Ms — correlation coefficient of species.

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VARIATIONS OF SPECIFIC CHARACTERS WITHIN GENUS
THAMNOPHYLLUM PENECKE

The variability of corals belonging to the Thamnophyllidae is strong but fits into the structural scheme characteristic of the particular
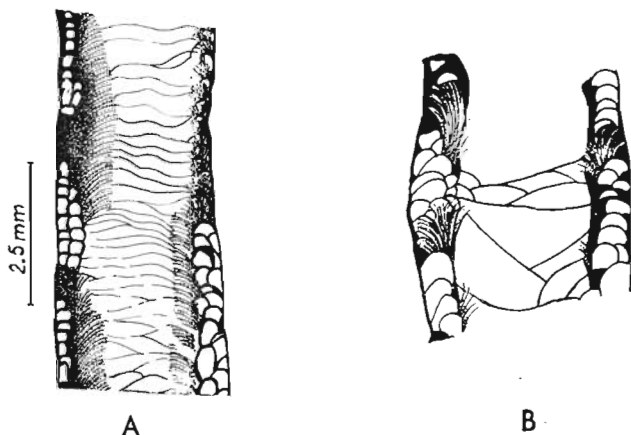

Fig. 1. — *Thamnophyllum kunthi* (Dames), topotype. Mokrzeszów, Upper Frasnian. Longitudinal section: *A* of specimen with closely spaced complete tabulae, *B* of specimen with widely spaced and incomplete tabulae.

systematic unit. Strongest variability is observed in the pattern of tabulae as is clearly shown in two specimens of *Thamnophyllum kunthi* (Dames) from the Upper Frasnian in Mokrzeszów, figured in fig. 1 *A, B*. Closely

aligned, parallel, complete tabulae occur here along with distant, irregular and incomplete ones. Dissepiments and septa are less variable, while microstructure is the most constant feature. Number of septa in relation to the corresponding diameter of calyx (n/d ratio) is a diagnostic specific and subspecific feature. Every correlation, however, is subject to fluctuation and changes with the age of the individual. This can be distinctly seen in variation curves plotted on measurements of individuals belonging to one population. It is difficult to ascertain correlation changes dependent on ontogenic stages by studying them on a single fossil corallite only. Hence the n/d correlation data must be based on individuals of whole populations in different ontogenic stages. The mean values here will approach those of increase correlation of one individual. The term *"increase correlation"* was introduced by H. Klähn (1920, p. 25-26), whose methods were given the preference by the present writer in her statistical treatment. The variability of fossil corals by means of biometrical analysis has so far been studied by R. Richter (1916) in the case of *Calceola sandalina* L. and by K. G. Voynovskiy-Kriger (1956). The latter author, when inquiring into the ontogeny of Paleozoic corals, has also taken account of both the n/d and a/d correlations, viz. the relation of the distance between septa to the diameter of calyx.

Variations of quantitative characters
in Thamnophyllum kozłowskii Różk.

In corals the soundest basis for biometrical analysis of variability is provided by the correlation between number of septa and diameter of calyx (n/d) since these values are most susceptible to numerical representation. For this purpose auxiliary tables (table 1) have been drawn up, subdividing the diameters of calices into classes of 1 mm distance each, measured with accuracy of 0.1 mm. Such a table enables the Mc correlation coefficient of classes to be calculated on the relation of the arithmetical mean of the number of septa and the diameter of calyx with respect to every class. The mean class coefficient of Mc1-Mcx correlation constitutes a constant and diagnostic value. It is the correlation coefficient of species, viz. Ms.

The first correlation studied by the present writer was that of mentioned features in *Thamnophyllum kozłowskii*. The correlation for the population from Sitkówka and that for the Wietrznia specimens — both from the Lower Frasnian — were calculated independently.

Table 1 specified measurements for 97 Wietrznia specimens. The range of diameters varies from 5 to 15 mm. There are from 16 to 29 major septa. The greatest number of variants is found in class Md6. The mean number

of septa (Mn6) is 23. The mean values of septa are in extrabold. The line which joins these mean Mn1-10 is oblique and nearly rectilinear thus resembling the line which represents correlation of ontogenic increase (Klähn, 1920).

Table 1

Correlation between number of septa and diameter of calyx in *Thamnophyllum kozłowskii* Różk. from the Lower Frasnian in Wietrznia

Diameter of calyx (Mdl-10) in mm / Number of major septa	Md1 5.5	Md2 6.5	Md3 7.5	Md4 8.5	Md5 9.5	Md6 10.5	Md7 11.5	Md8 12.5	Md9 13.5	Md10 14.5
16	**2**	3								
17	1	**2**								
18	1	2	1	2						
19			**2**	4	1					
20			2	**2**	1	1				
21			1	6	4	3				
22					**5**	6				
23					3	**3**	3			
24				1	1	5	**4**	1		
25						4	3	**3**	2	
26						2	1	3	1	
27									1	1
28									2	
29										1
Total:	4	7	6	15	15	24	11	7	6	2

97 specimens

Numerical data resulting from table 1 are as follows (table 3): row 1 — specifies data for classes c1-c10; row 2 — those of the relation between the mean number of septa and the mean diameter of calyx for every class; row 3 — results of calculated correlation constituting the class coefficient of correlation Mc1-Mc10. Finally the correlation coefficient of species Ms for the Wietrznia *Thamnophyllum kozłowskii* is given.

In the case of *Th. kozłowskii* from Sitkówka, represented by 148 specimens, correlation table 2 shows similar values. Range of diameters is from 5 to 16, while that of the number of septa is slightly higher being 14 to 32. The maximum number of frequents is noted in class 6, where the mean number of septa is 24. This figure exceeds by one the mean number

Table 2

Correlation between number of septa and diameter of calyx in *Thamnophyllum kozłowskii* Różk. from the Lower Frasnian in Sitkówka

Number of major septa / Diameter of calyx (Mdl—11) in mm	Md1 5.5	Md2 6.5	Md3 7.5	Md4 8.5	Md5 9.5	Md6 10.5	Md7 11.5	Md8 12.5	Md9 13.5	Md10 14.5	Md11 15.5
14	1	2									
15	1										
16											
17	1	1	1								
18			1								
19		2	4	1							
20		1	5	3	1						
21				5		1					
22			1	5	7	5	1				
23			1	3	3	7	1				
24				4	4	9	7				
25					1	3	4	2			
26					5	7	6	4	1		
27						2		1	3	1	
28						3	3	1	1	2	
29								1		1	1
30								1		1	1
31											1
32											1
Total:	3	7	13	21	21	37	22	10	5	5	4

148 specimens

Table 3

Numerical data of class correlation coefficients for *Thamnophyllum kozłowskii* Różk. from the Lower Frasnian in Wietrznia

Classes	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10
Mn/Md	$\frac{16}{5.5}$	$\frac{17}{6.5}$	$\frac{19}{7,5}$	$\frac{20}{8.5}$	$\frac{22}{9,5}$	$\frac{23}{10.5}$	$\frac{24}{11.5}$	$\frac{25}{12.5}$	$\frac{26}{13.5}$	$\frac{27}{14.5}$
Mcl-Mcl0	2.9	2.6	2.5	2.4	2.3	2.2	2	2	1.9	1.8

Ms *kozłowskii*, Wietrznia $=$ 2.28

of major septa in Wietrznia specimens. Correlation coefficients calculated for the different classes on table 2 are as follows:

Table 4

Numerical data of class correlation coefficients for *Thamnophyllum kozłowskii* Różk. from the Lower Frasnian in Sitkówka

Classes	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10	c11
Mn/Md	$\frac{15}{5.5}$	$\frac{17}{6.5}$	$\frac{20}{7.5}$	$\frac{22}{8.5}$	$\frac{23}{9.5}$	$\frac{24}{10.5}$	$\frac{25}{11.5}$	$\frac{26}{12.5}$	$\frac{27}{13.5}$	$\frac{28}{14.5}$	$\frac{30}{15.5}$
Mc1-Mc11	2.7	2.6	2.6	2.6	2.4	2.3	2.2	2.1	2	1.9	1.9

Ms *kozłowskii*, Sitkówka = 2.30

These data show the correlation coefficient of species for specimens of *Th. kozłowskii* from the localities of Wietrznia and Sitkówka to be virtually identical though the specimens belong to somewhat different facies, namely:

Ms
Th. kozłowskii (Wietrznia) from a near-reef facies = 2.23
Th. kozłowskii (Sitkówka) from a reef built by Tabulata and Tetracoralla = 2.30

Graphs of correlation coefficients for specimens of *Thamnophyllum kozłowskii* collected from these two localities are plotted in fig. 2. The curves run very close, are of similar character and intersect in young stages. The difference in distance of both lines, equivalent to approx. one major septum, suggests that the Wietrznia specimens may be of a slightly younger geological age as will be seen from fig. 3. The variants converge in the proximity of the line of correlation, but their variations range is different. The course of graphs and the arrangement of variants indicate that both assemblages are conspecific, but that most likely they are referable to somewhat different stratigraphical zones.

Variations of quantitative characters in other species of genus Thamnophyllum Penecke

The following seven species and subspecies of genus *Thamnophyllum* have been recorded (1953, 1956) by the writer from Devonian beds of Poland:
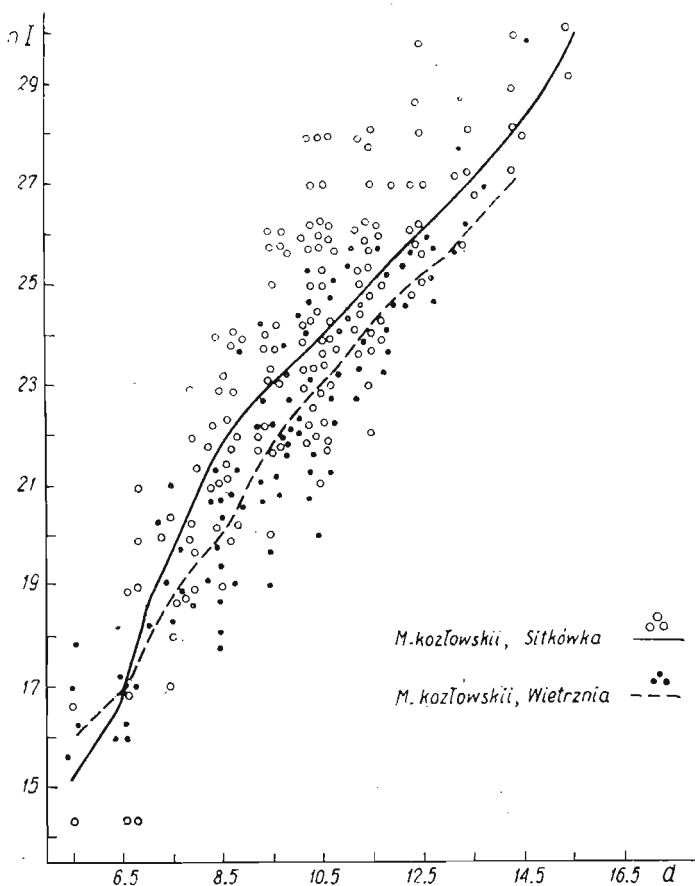
Fig. 2. — *Thamnophyllum kozłowskii* Różk. Graph of correlation curves n/d (relation of number of major septa (I) to diameter of calices, in mm). Continuous line — for Lower Frasnian specimens from Sitkówka; variants marked by empty circles. Interrupted line — for Wietrznia specimens; variants marked by dots. Numerical data given in tables 3 and 4.

Upper Frasnian:	*Th. kunthi* (Dames)	
Middle ,,	*Th. kozłowskii superius* Różk.[2]	
Lower ,,	*Th. kozłowskii* Różk.	
Givetian:	*Th. caespitosum* (Goldfuss)	
	Th. trigemme pajchelae Różk.	
	Th. trigemme (Quenstedt)	
	Th. skalense Różk.	

[2] The Middle Frasnian form from the Holy Cross Mts., in 1953 referred by this writer to *Th. monozonatum* Soshkina, is not identical with the Ural species, since it does not display lateral budding; its variation curve is practically the same as that of the ancestral form *Th. kozłowskii*. The present writer regards it, therefore, as a mutation of the latter species.

Results of calculations and measurements are specified in table 5, separately for every one of these forms, as above for *Th. kozłowskii.*

The following conclusions may be drawn on these numerical data (fig. 3):
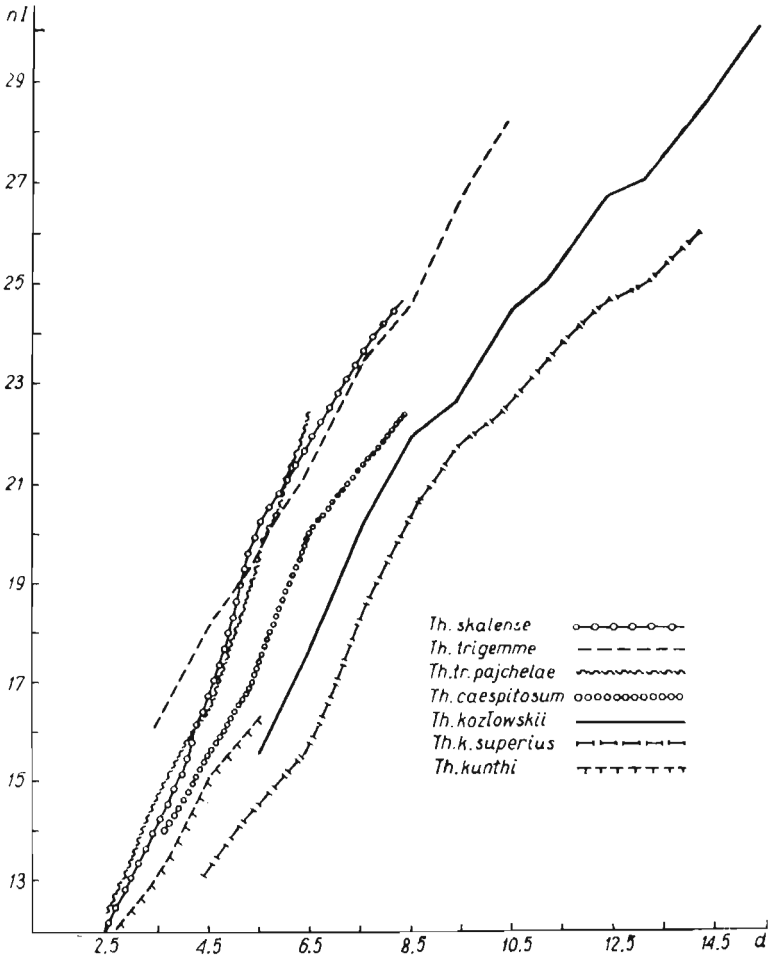

Fig. 3. — Graph of correlation curves n/d of some *Thamnophyllum* species from the Middle and Upper Devonian of Poland. Numbers of major septa — on ordinate, diameters of calices — on abscissa, in mm. Numerical data given in table 5.

a) The range of variation in number of septa is limited, there being 12 to 30 major septa. Species with greatest range of variation are most plastic, namely the Givetian *Th. trigemme* and the Frasnian *Th. kozłowskii.* In dwarfed species this range is very small *(Th. trigemme pajchelae, Th. kunthi);*

b) Class coefficients of correlation are higher in Givetian forms, being markedly lower in the Frasnian specimens as shown here below:

Frasnian: *Th. kozłowskii* = 2.8 - 1.9
Givetian: *Th. trigemme* = 5.0 - 2.7
Th. skalense = 4.8 - 3.0

Upon comparing the various n/d correlations it is to be noted that during ontogenic evolution and phylogeny of *Thamnophyllum* the number of septa increases at a smaller rate than the diameter of calices (negative allometry). In consequence, the proportions in classes are reduced. Negative growth allometry in relation to number of septa is thus an evolutionary trend in genus *Thamnophyllum* and a characteristic generic feature;

c) The above conclusion is also confirmed by data of correlation coefficients for the different species according to their stratigraphical age. Specimens of these species have namely been collected from a sequence of layers:

		Ms
Frasnian:	*Th. kozłowskii superius* =	2.20
	Th. kozłowskii (from Sitkówka) =	2.30
Givetian:	*Th. caespitosum* =	3.17
	Th. trigemme =	3.42
	Th. skalense =	3.64

The above quoted values may, therefore, be a useful stratigraphical index since the correlation coefficient of Givetian species has a value exceeding three, while that of the Frasnian species is only slightly higher than two. It is easy to note that the correlation value decreases in species of *Thamnophyllum* occurring in successive Givetian and Frasnian layers. Hence the inference that the value of correlation n/d is foremost a function of time;

d) The dwarfed forms *Th. trigemme pajchelae* and *Th. kunthi* have not been included among those specified above in paragraph c). The subspecies *Th. trigemme pajchelae*, although one of the youngest Givetian representatives of genus *Thamnophyllum* and pene-contemporaneous with *Th. trigemme*, shows a high correlation coefficient (3.60) nearest to that of *Th. skalense*, the oldest Middle Givetian form (Ms = 3.64). Similarly, *Th. kunthi*, the youngest species from the Upper Frasnian of Mokrzeszów, also displays a high correlation coefficient (Ms = 3.70). Both these dwarfed forms which have probably lived under unfavourable environmental conditions thus show a certain regression in relation to *Th. skalense*, a more primitive form;

Table 5

Constant biometrical data in respect to various species of *Thamnophyllum*

a. *Thamnophyllum skalense* — 67 measured specimens

Classes	c1	c2	c3	c4	c5	c6	c7
Mn/Md	$\dfrac{12}{2.5}$	$\dfrac{14}{3.5}$	$\dfrac{16.7}{4.5}$	$\dfrac{20}{5.5}$	$\dfrac{21.6}{6.5}$	$\dfrac{23.4}{7.5}$	$\dfrac{24.6}{8.5}$
Mcl—Mc7	4.8	4	3.7	3.6	3.3	3.1	3
Number of specimens in per cent figures	2	8	18	34	16	10	12

Ms *skalense* = 3.64

b. *Thamnophyllum trigemme* — 109 measured specimens

Classes	c1	c2	c3	c4	c5	c6	c7	c8
Mn/Md	$\dfrac{16}{3.5}$	$\dfrac{18}{4.5}$	$\dfrac{19.6}{5.5}$	$\dfrac{31.4}{6.5}$	$\dfrac{23.2}{7.5}$	$\dfrac{24.3}{8.5}$	$\dfrac{26\,5}{9.5}$	$\dfrac{28}{10.5}$
Mcl—Mc8	5	4	3.6	3.3	3	3	2.8	2.7
Number of specimens in per cent figures	1	3	6	16	36	21	9	7

Ms *trigemme* = 3.42

c. *Thamnophyllum caespitosum* = 15 measured specimens

Classes	c1	c2	c3	c4	c5	c6
Mn/Md	$\dfrac{14}{3.5}$	—	$\dfrac{17.3}{5.5}$	$\dfrac{20}{6.5}$	—	$\dfrac{22.5}{8.5}$
Mcl—Mc6	4	(3.5)	3.1	3	(2.8)	2.6

Ms *caespitosum* = 3.17

Classes	c1	c2	c3	c4	c5	c6	c7
Mn/Md	$\dfrac{12}{2.5}$	$\dfrac{14.5}{3.5}$	$\dfrac{16.4}{4.5}$	$\dfrac{19.4}{5.5}$	$\dfrac{22.2}{6.5}$	$\dfrac{22.7}{7.5}$	$\dfrac{24}{8.5}$
Mc1—Mc7	4.8	4.1	3.6	3.5	3.4	3.0	2.8
Number of specimens in per cent figures	3	30	40	14	7	5	1

Ms *pajchelae* = 3.60

e. *Thamnophyllum kozłowskii*, Sitkówka — 148 measured specimens

Classes	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10	c11
Mn/Md	$\dfrac{15.5}{5.5}$	$\dfrac{17.5}{6.5}$	$\dfrac{20}{7.5}$	$\dfrac{22}{8.5}$	$\dfrac{22.5}{9.5}$	$\dfrac{24.4}{10.5}$	$\dfrac{25}{11.5}$	$\dfrac{26.8}{12.5}$	$\dfrac{27}{13.5}$	$\dfrac{28.4}{14.5}$	$\dfrac{30}{15.5}$
Mc1—Mc11	2.8	2.8	2.7	2.6	2.4	2.3	2.2	2.1	2.0	1.9	1.9
Number of specimens in per cent figures	2	4.7	9	14	15	25	16	7	3.2	3.3	1.3

Ms *kozłowskii* = 2.30

f. *Thamnophyllum kozłowskii superius* — 85 measured specimens

Classes	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10	c11
Mn/Md	$\dfrac{13}{4.5}$	$\dfrac{14.5}{5.5}$	$\dfrac{15.4}{6.5}$	$\dfrac{18.1}{7.5}$	$\dfrac{20}{8.5}$	$\dfrac{21.7}{9.5}$	$\dfrac{22.3}{10.5}$	$\dfrac{23.6}{11.5}$	$\dfrac{24.5}{12.5}$	$\dfrac{25}{13.5}$	$\dfrac{26}{14.5}$
Mc1—Mc11	2.7	2.6	2.4	2.4	2.3	2.3	2.1	2	1.9	.1.8	1.8
Number of specimens in per cent figures	1	2.1	11	13	18	19	20	6	7	2.4	1.2

Ms *superius* = 2.20

g. *Thamnophyllum kunthi* — 40 measured specimens

Classes	c1	c2	c3	c4
Mn/Md	$\dfrac{12}{2.5}$	$\dfrac{13}{3.5}$	$\dfrac{15}{4.5}$	$\dfrac{16.2}{5.5}$
Mc1—Mc4	4.8	3.7	3.3	3

Ms *kunthi* = 3.70

e) It has been ascertained that correlation coefficient in species of *Thamnophyllum* decreases in forms belonging to a younger geological period. This phenomenon is clearly illustrated by table 6, where *Thamnophyllum* species are arranged in chronological order. Every species has a different number of septa with a 6 mm diameter of calyx. Middle Givetian species are multiseptal (22 and 21 major septa), *Th. caespitosum* being somewhat younger, hence with a smaller number of septa (20). Here a stratigraphical gap follows. If Upper Givetian specimens had been available, species with 19 and 18 septa would most likely have been found. Frasnian species occurring above this gap are mesoseptal (Voynovskiy-Kriger, 1956). At a 6 mm diameter of calyx the Lower Frasnian forms have 17 septa, while the Middle Frasnian have 15. Data specified in the below given table confirm the supposition that in representatives of genus *Thamnophyllum* the number of septa decreases along with their geological age for a given diameter of calyx. This phenomenon is due to negative allometry in relation to septa prevailing in *Thamnophyllum·*

Table 6

Number of septa in *Thamnophyllum* with 6 mm diameter of calyx

Species	Number of major septa								Age
	15	16	17	18	19	20	21	22	
Th. kozłowskii superius	+								Middle Frasnian
Th. kozłowskii (Sitkówka)			+						Lower „ Upper Givetian
Th. caespitosum						+			Middle „ (top)
Th. trigemme							+		„ „
Th. skalense								+	„ „ (bottom)

Graphs have been plotted in respect to *Thamnophyllum* species (fig. 3), based on the correlation table. Every curve passes through mean septal values Mn and the corresponding diameters of calices Md. The following conclusions may be deducted from the pattern of these curves:

1. Young corallites display similar correlation curves, converging with but few exceptions into a class with diameter at 2.5 mm. The young ontogenic stages of Givetian and Frasnian species show resemblances of numerical data which suggests their monophyletic descent. Their successive occurrence characterises them as historical species;

2. During later evolution distinct, fan-like deviation of correlation curves is noted. Givetian species in which septa are most numerous, are

placed furthermost to the left and in the proximity of the Y axis. In the phylogeny of species the diameter of calices augments conspicuously while the increase of the number of septa is disproportionately less Frasnian forms occupy the right sector of the graph;

3. Correlation curves are almost rectilinear, hence they represent the natural growth line. Occasional deviations may, perhaps, be due to the inadequacy of material since individual variations do not compensate;

4. Curves for *Th. skalense* and *Th. trigemme* are markedly similar and intersecting, they thus indicate the close relationship and short geological gap separating these two species. *Th. trigemme pajchelae* comes nearest to *Th. skalense* as is also suggested by its correlation coefficient. Additional graphs in respect of geologically younger species are more widely spaced. The Middle Frasnian mutation *Th. kozłowskii superius* n. mut. is separated from the ancestral form by a distance of approx. two major septa. The correlation line for *Th. kozłowskii* from Wietrznia would run at mid-distance between these two.

Graphs of biometrical data are thus seen to illustrate the gradual evolution of historical species.

Objectiveness of species in genus
Thamnophyllum Penecke

Should the type of budding be accepted as the sole specific criterion, two species only could be differentiated within genus *Thamnophyllum:* type 1 would include forms with parricidal budding, such as *Th. trigemme, Th. trigemme pajchelae, Th. skalense, Th. kozłowskii, Th. kozłowskii superius*, and type 2 — forms with the less frequent lateral budding, such as *Th. caespitosum, Th. kunthi.* In addition to the type of budding, other features are accepted by authors as diagnostic for *Thamnophyllum,* viz. morphological characters and coefficient of correlation. Several species and subspecies may on these grounds be differentiated from the available Polish material. Variation curves plotted for these forms confirm the sound separation of these systematic units (fig. 4). Correlations n/d are arranged along axis X, the per cent number of variants along the Y axis. One-top curves are obtained for all species and subspecies; *Th. skalense* and *Th. trigemme* are distinctly separated. Bases of curves for Givetian forms partly fit into one another, while the Frasnian *Th. kozłowskii* is almost entirely separated from them. Its descendant, *Th. kozłowskii superius,* shares nearly the same area with the ancestral species, the summits, however, of these two forms are separated. The following conclusions may be deducted from the pattern of curves:

1) Specific evolution was gradual and linked with the geological range;

2) All variation curves have the same character and partly fit into one another indicating near relationship of species displaying the same evolutionary trends;
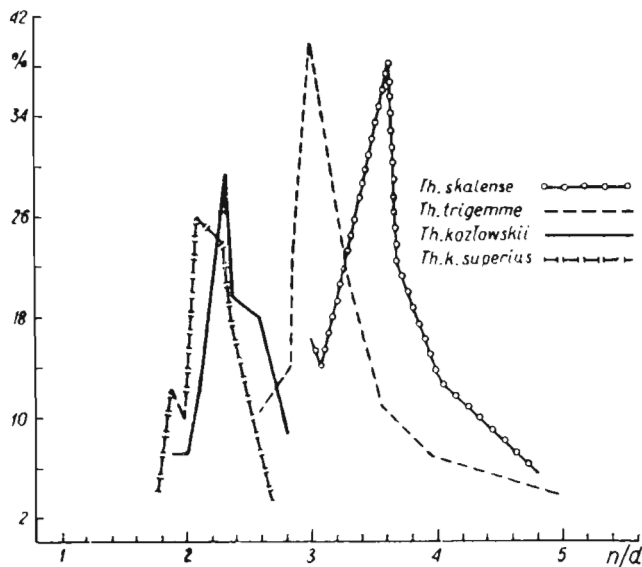

Fig. 4. — Curve of correlation n/d for several *Thamnophyllum species*. Percentage number of corallites — on ordinate, n/d correlation — on abscissa, in mm.

3) There is a distinct gap in connection with the lack of *Thamnophyllum* from Upper Givetian beds, since the Middle Givetian *Th. trigemme* is clearly separated from the Lower Frasnian *Th. kozłowskii*;

4) Curves for the particular species are aligned in historical succession and indicate the successive evolution of species.

Th. caespitosum has been disregarded in graphs owing to scarcity of material.

On the other hand, the regressive forms *Th. trigemme pajchelae* and *Th. kunthi* have almost identical correlation coefficients as *Th. skalense*. The summits of their curves are in the same class with *Th. skalense* which is the most primitive form in our collection (fig. 5).

Problem of removal of septa

K. Voynovskiy-Kriger (1956) has recently stressed the fact that during the juvenile stage the septa of corallites are very close. They
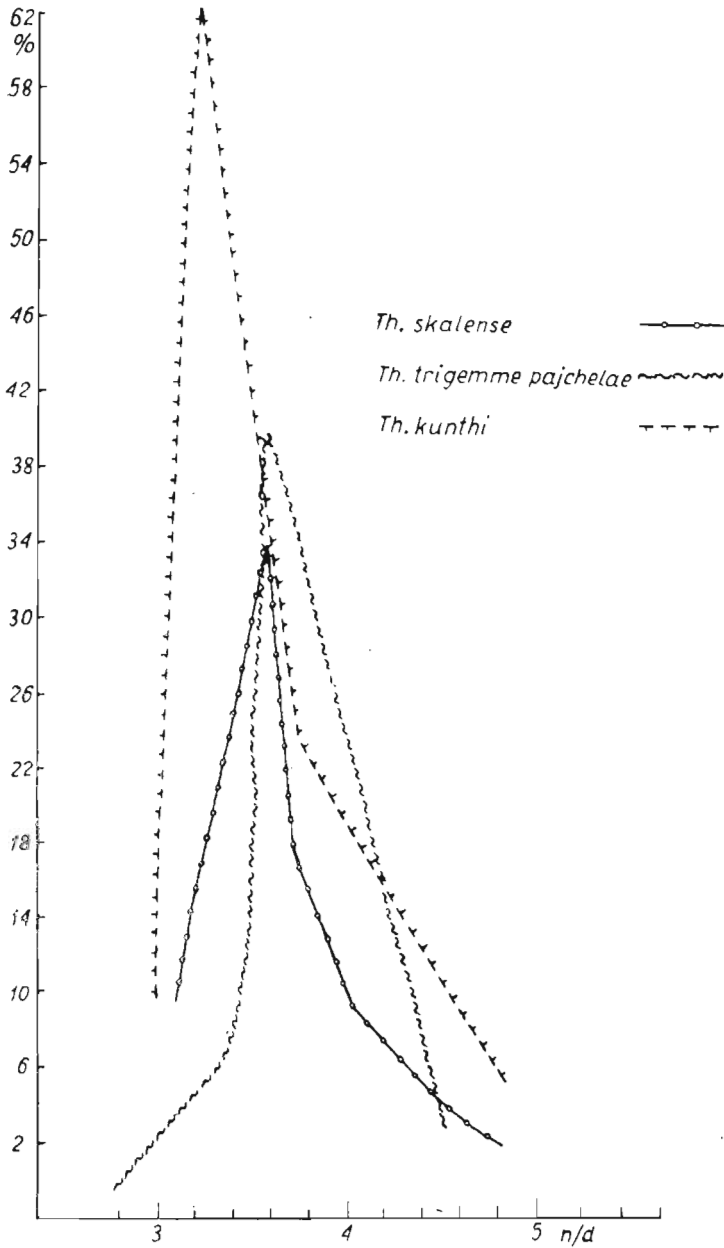
Fig. 5. — Variation curve for *Thamnophyllum skalense* Różk. from the Middle Givetian of Skały, and for regressive species *Th. trigemme pajchelae* and *Th. kunthi* frcm the Upper Frasnian of Mokrzeszów.

remove along with the ontogenic age of the individual since the gradient of septal growth changes too. The gradient here means the rate of the increase or decrease of the number of septa in relation to the diameter of calyx. The distance between two major septa was measured by taking the intersection of the trabecular line with the outer wall of the horse-
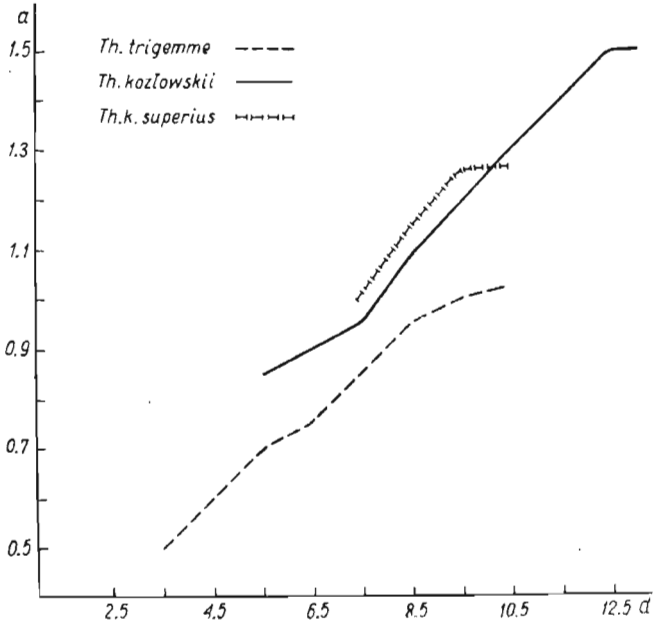
Fig. 6. — Graph of correlation a/d (relation of the distance of major septa to calicular diameter) in several *Thamnophyllum* species. Interseptal distance — on ordinate, diameters of calices — on abscissa, in mm.

shoe dissepiment (fig. 6) as the stable point. The correlation between the distance of septa and the diameter of calyx (a/d) is not constant, but changes too during phylogeny, as is illustrated by fig. 6. The graphs here show a pattern reversed to that of the corresponding graphs in fig. 3, which represents lines of correlation n/d. In graphs showing the a/d correlation, *Th. trigemme* — the oldest species, is nearest to the X axis, while the youngest — *Th. kozłowskii superius*, is the one most distant from this axis. The slight septal distance in immature stages, gradually increasing together with individual age, is also conspicuous. When the same diameter is taken, for instance that of 8.5 mm, the septal distance is as follows:

$$
\begin{array}{lll}
Th.\ trigemme & = & 0.95\ \text{mm} \\
Th.\ kozłowskii & = & 1.10\ \text{,,} \\
Th.\ kozłowskii\ superius & = & 1.15\ \text{,,}
\end{array}
$$

Hence, the a/d correlation is the ontogenic index for individuals, while it will also be a useful stratigraphical index, when the same diameter is being considered, since the a/d value also constitutes the function of geological age.

Morphological changes in ontogeny

Ontogenic changes in representatives of genus *Thamnophyllum* have not been satisfactorily investigated since the proximal end in phacelloid colonies is very rarely preserved. In the youngest stage polyps produce a talon as a means of attachment, preferably to a tabulate corallite. The talon is placed along the cardinal septum, less frequently laterally. The „talon stage" has been ascertained by the writer (1956) in several species, that in *Th. skalense* being the earliest and the most conspicuous (fig. 7), those in *Th. trigemme* and *Th. trigemme pajchelae* later. In the youngest „*skalense*" stage the corallite is with a diameter of 1.5 to 2 mm (without the talon) and has 12 major septa. The symmetry of the interior of calyx is then radial, that within the talon being bilateral. The free cardinal septum rests as if in a groove produced by the pinnately arranged neighbouring septa. With diameter of 2.5 mm the talon is already lacking, while septa are arranged with distinct radial symmetry.

Fig. 7.— *Thamnophyllum skalense* Różk. Skały, Middle Givetian. Early ontogeny, „talon stage"; *1* cardinal septum, × 10 after Różkowska, 1956. fig. 29).

The above leads to the inference that ontogenic development in thus far described species is uniform and fixed. Prominent conservatism prevails here contrary to the ontogeny of thus far studied numerous representatives of *Macgeea*.

All species of genus *Thamnophyllum* produce dendritic or fasciculate colonies. The buds proceed either from the interior of the calyx, between the septa („*intraseptal*", Wells, 1955), or on the periphery of the calyx („*extraseptal*", Wells, 1955). The former of these modes of budding prevails in *Thamnophyllum* and is called parricidal budding. The latter is an apparently recessive feature and occurs more rarely (fig. 8). In both cases the buds are in their youth connected by the dissepimental tissue external to the horse-shoe dissepiments. In parricidal budding certain progress in development may be noted in geologically younger forms. The number of buds increases: *Th. skalense* has one or two parricidal buds, *Th. trigemme* has three — as is suggested by its very name. It is

not known whether the budding process is repeated more than once within a *Th. trigemme* colony. In the subspecies *Th. trigemme pajchelae* three or four buds are simultaneously produced, occasionally five. The most ramifying form is that of *Th. kozłowskii,* in which five buds are the rule. This budding process is repeated several times
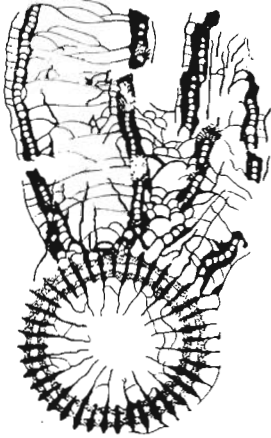

Fig. 8.— *Thamnophyllum caespitosum* (Goldf.), Skały, Middle Givetian. Dissepimental "caenogenetic" tissue between lateral buds, × 4 (after Różkowska, 1956, fig. 30).

Fig. 9. — *Thamnophyllum kozłowskii* Różk. Sitkówka, Lower Frasnian. Fasciculate colony with repeated parricidal budding, × 0.6.

producing a fasciculate colony (fig. 9). In mature corallites variability is moderately strong, but does not transgress the characteristic plan of structure. The change does not involve one feature only, but a whole complex of them and distinct interrelations of the skeletal elements are readily observable, e. g. in *Thamnophyllum trigemme* septa are thin, horse- shoe dissepiments thin-walled, tabulae rather far spaced. Similar structure characterises *Th. caespitosum,* while *Th. skalense* and *Th. kozłowskii* display a different morphology. Their various skeletal elements such as septa and

Fig. 10. — *Thamnophyllum kunthi* (Dames). Mokrzeszów, Upper Frasnian. Transverse section of topotype.

horse-shoe dissepiments — hence the pseudotheca too — are strongly thickened by a stereome deposit. In spite of similarity in structural features, the quoted species are distinctly differentiated, either by another
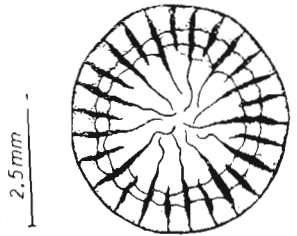
type of budding *(Th. caespitosum* is with lateral budding, *Th. trigemme* with parricidal), or by greater number of buds *(Th. skalense* with one or two buds, *Th. kozłowskii* not unfrequently with as many as five buds). In regressive species such as *Th. trigemme pajchelae* and *Th. kunthi*, calices are similar, minute, tabulae mostly complete but septa short in *Th. trigemme pajchelae*, while in *Th. kunthi* long and nearly contiguous in the axial part of the corallite (fig. 10). The mode of budding differs too, being parricidal in the former species and lateral in *Th. kunthi*.

Diagnostic features in genus Thamnophyllum Penecke

Representatives of this genus occur in Devonian beds of Poland from the Middle Eifelian through Upper Frasnian. Thus far they have not been recorded by the writer from the Famennian. Penecke's diagnosis (1897) of *Thamnophyllum* was based on a most primitive species, such as the genotype of *Th. stachei* Pen. Hence the generic definition was not quite complete. The writer's observations have enabled her to make this diagnosis more complete, viz.: Corals always colonial, either fasciculate or dendritic, producing mostly parricidal buds, less often peripheral, in principle coated by an epitheca which, however, does not extend to the margin of calyx; talon present in immature ontogeny too; symmetry bilateral; septa spindle-shaped, amplexoid, only occasionally attaining to the axis, always lamellar, made up of trabecular fans resting on horse-shoe dissepiments; they protrude beyond the pseudotheca as „costae". One row of flat dissepiments adjacent to the epitheca, along with a row of horse-shoe dissepiments often thick walled which, together with septa thickened into a spindle-like shape, form the pseudotheca. Tabulae vary, being complete, incomplete, concave, convex, or horizontal. Normal dissepiments are sometimes discernible next to their periaxial parts. Dissepimental tissue developed, in early immature stages only, outside of horse-shoe dissepiments, between buds and within the talon. During the talon stage, symmetry bilateral.

A. Schouppé (1949) in a critical review of species and genera, aiming at the simplification of synonymics, made *Thamnophyllum* a subgenus of *Macgeea*. The present writer does not believe this to be correct. Subgenus is not a frequently used taxonomic category since, in E. Mayr's opinion (1949), it leads to quadrinomial nomenclature. In addition, the writer regards the genera *Macgeea* and *Thamnophyllum* as objective, independent units. *Thamnophyllum* displays a number of features, not observed in *Macgeea*, which are illustrated in table 7.

Table 7

Differences in the morphology and evolutionary trend of the genera
Thamnophyllum Penecke and *Macgeea* Webster

Features	Genus *Thamnophyllum* Penecke	Genus *Macgeea* Webster
Habitus	Colonies phacelloid or fasciculate	Simple corals
Budding	Is a rule	Exceptionally
Individuals	Cylindrical	Conical
Carinae	Lacking	Distinct
Interior morphology	Simple, tabulae complete or not, normal dissepiments usually lacking	Complicated, tabulae in bundles. Normal dissepiments a rule
Symmetry	Usually radial, in talon stage bilateral	Bilateral symmetry during the whole ontogeny
Evolutionary tendency	Negative allometry in relation to septal growth	Positive allometry in relation to septal growth

VARIATIONS OF SPECIFIC CHARACTERS WITHIN GENUS *MACGEEA* WEBSTER

Quantitative variations

Representatives of this genus are less numerous than and not so well differentiated as those of *Thamnophyllum,* but their ontogeny and chronology are more complicated. All Givetian forms are referable to one species, that of *Macgeea bathycalyx* (Frech) showing markedly intraspecific variability. Three species have been recorded by the writer from the Frasnian: *M. berdensis* Soshkina, *M. czarnockii* Różk. and *M. multizonata* Reed, all·less abundant than Givetian species. Frasnian specimens are always damaged which makes this material less useful for biometrical analyses.

Quantitative analyses have been carried out in respect to species and subspecies of genus *Macgeea* in the same way as in respect to representatives of *Thamnophyllum.* Correlation n/d and its ontogenic and phylogenic changes were the first to be studied. Graphs have been plotted (fig. 11) on biometrical data.

These numerical data suggest the following inferences:

1. Range of diameter of calices in species of *Macgeea* is subject to strong oscillations. *M. bathycalyx kasimiri* and *M. bathycalyx josephi* show a similar variation range (3.5 to 14,5 mm), but in *M. bathycalyx*
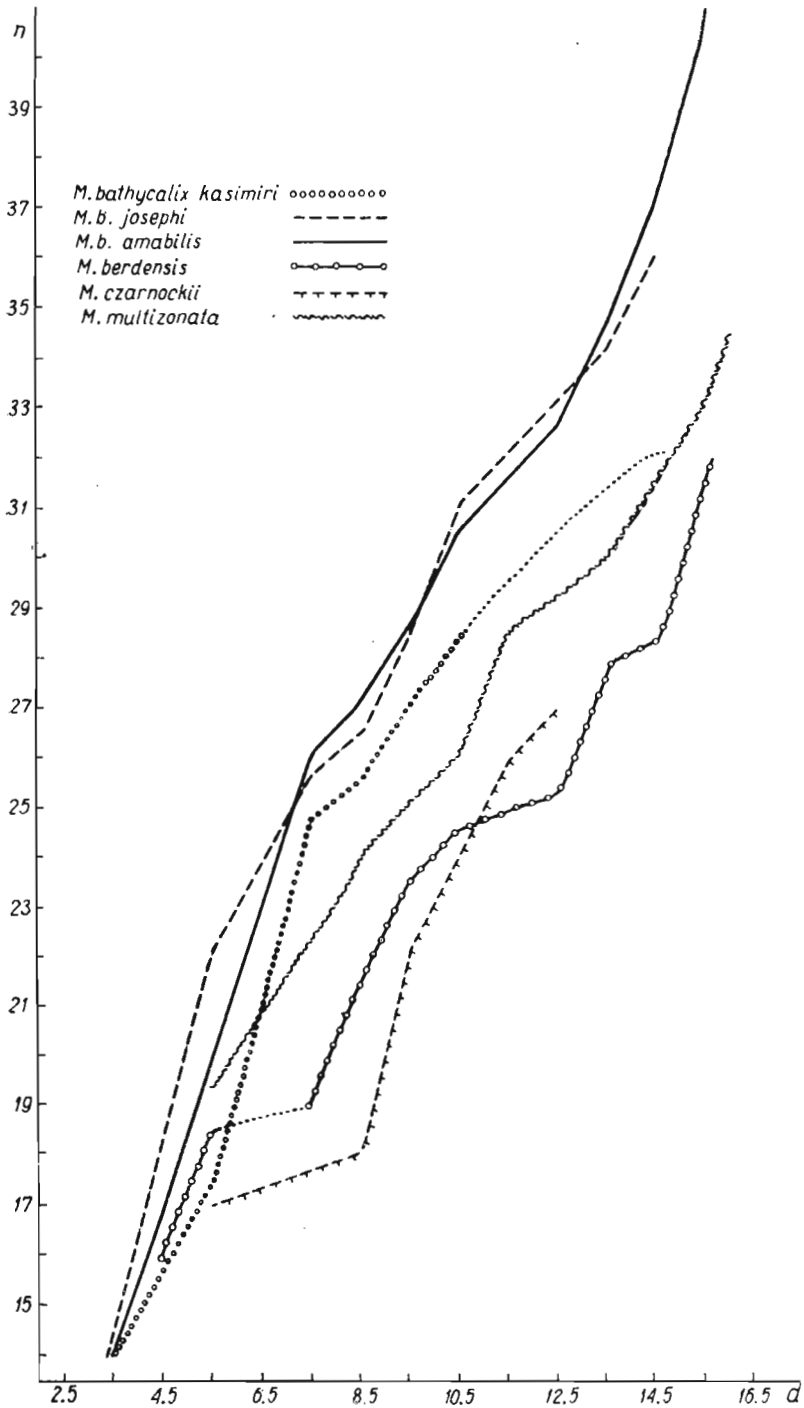
Fig. 11. — Graph of correlation n/d for *Macgeea* species from Middle
and Upper Devonian deposits in Poland.

josephi the number of septa is greater — being 36 with diameter at 14.5 mm — than in *M. bathycalyx kasimiri* in which there are only 32 septa with the same diameter. *M. bathycalyx amabilis*, the youngest subspecies, has as many as 37 septa with a diameter of 14.5 mm. Hence the conclusion that in the Givetian geologically younger forms are provided with a progressively greater number of septa for the same diameter of calyx.

Two large multiseptal forms occur in the Frasnian, to say *M. berdensis* with diameter ranging from 4 to 24 mm and major septa up to 38, and *M. multizonata* with diameter ranging from 5 to 22 mm and number of septa up to 37. In Frasnian forms we also ascertain that the number of septa increases, with diameter unchanged, in beds younger geologically speaking. *M. czarnockii* is an exception, it is a minute form with diameter not exceeding 13 mm and only 27 septa.

2. The correlation coefficient of classes decreases gradually and very slowly. For Givetian forms these coefficients are relatively large — 4 to 2.2 mm, and smaller for the Frasnian forms — 3.5 to 1.5 mm. Since Md augments equally, the growth gradient for number of septa decreases progressively. Therefore in *Macgeea*, as in *Thamnophyllum*, negative allometry in relation to the number of septa prevails during ontogeny.

3. Upon comparison of the various ontogenies it will be ascertained that in geologically younger forms the value of class coefficient Mc is greater in the corresponding classes, e. g. *Macgeea berdensis* shows in class c17 a proportion of 31.5 : 20.5 and class coefficient Mc = 1.5, while in the same class for *M. multizonata* the proportion is 35.6 : 20.5, the coefficient being 1.7. The number of septa is thus seen to increase and with the same diameter it is greater in geologically younger forms· The n/d proportion differs, since in geologically younger forms, the gradient for the number of septa augments resulting in positive allometry.

The conclusion common for 2 and 3 is as follows: in Frasnian and Givetian species of *Macgeea* there is, in ontogeny, negative allometry in relation to septa, while perspectively to geological age, i. e. in phylogeny the allometry becomes positive.

4. The specific correlation coefficient in genus *Macgeea* is as follows:

		Ms
M. bathycalyx kasimiri	=	2.93
M. bathycalyx josephi	=	3.20
M. bathycalyx amabilis	=	3.16
M. berdensis	=	2.14
M. multizonata	=	2.38
M. czarnockii	=	2.44

Reducing all specific coefficients to one greatest diameter (12.5 mm) we find that the Ms values change as follows:

		Ms
M. bathycalyx kasimiri	=	3.06
M. bathycalyx josephi	=	3.20
M. bathycalyx amabilis	=	3.20
M. berdensis	=	2.64
M. multizonata	=	2.82
M. czarnockii	=	2.44

In Givetian geologically younger forms of species M. bathycalyx, Ms augments, since — as is known — the number of septa increases progressively with same diameter. The same tendency predominates among Frasnian representatives of Macgeea. In Frasnian forms, however, the coefficients do not constitute a direct prolongation of the Ms values of Givetian forms since they begin with much lower Ms values which increase progressively in geologically younger forms.

The exceptionally low correlation coefficient in M. czarnockii for diameters from 5.5 to 12.5 mm may be explained solely by regression.

5. Changes occurring in septal growth in the history of Macgeea have been tabulated in table 8.

Table 8

Changes occurring in septal growth in the history of Macgeea

Species	Number of major septa*																	Age
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
M. multizonata					a		b		c			d	e					Frasnian
M. czarnockii	+a							+c		+d								,,
M. berdensis		a		b			c	d			e							,,
M. bathycalyx amabilis										ab				c	d		e	Givetian
M. bathycalyx josephi									a	b				c	d	e		,,
M. bathycalyx kasimiri								a	b		c		d					,,

* Number of septa in species of Macgeea with diameters of 7.5, 8.5, 10.5, 12.5 and 13.5 mm.
Diameters have been lettered as follows: 7.5=a, 8.5=b, 10.5=c, 12.5=d, 13.5=e. The plus sign indicates the position of M. czarnockii.

Table 8 shows that the number of septa is greater in geologically younger forms, with the same diameter. In Givetian forms, with

diameter of 7.5 mm we have 25, 26, 27 septa. In Frasnian forms the number of septa is smaller, but augments progressively from 19 to 22. Similarly conspicuous regression is observed in Frasnian forms with different diameters. Table 8 thus supports the inference mentioned earlier that the number of septa increases with geological age. The same tendency prevails in Givetian and Frasnian forms but contrary to *Thamnophyllum* there is no continuous progression in *Macgeea* which, in the Lower Frasnian, experiences a reversion to a small number of septa. Givetian forms are multiseptate only, those from the Frasnian are mesoseptate and multiseptate.

The evolutionary trends predominating in *Macgeea* are fairly well illustrated by the pattern of graphs in fig. 11. Curves for species represented by numerous specimens are nearly rectilinear *(M. bathycalyx josephi* and *M. bathycalyx amabilis).* Others, particularly so in respect to Frasnian species, are strongly bent. Owing to the strongly irregular pattern of curves, especially in the ephebic stage, correlation for diameters up to 15.5 mm only have been taken into account by the writer.

1. The two-phase evolution in the history of *Macgeea* species is clearly seen in fig. 11. Multiseptate Givetian forms occupy the upper field of the graph. Frasnian species begin with mesoseptate forms. Their lines of correlation, therefore, occupy the lower portion of the graph.

2. The tendency is uniform in both phases. Septal growth predominates over the increase of diameter. Correlation curves ascend strongly and approach the Y axis. Givetian species attain a greater number of septa (41 septa with diameter of 15.5 mm), while Frasnian forms whose evolution commenced with mesoseptate forms, do not exceed the number of 33 septa with the same diameter.

3. Evolutionary trends in *Thamnophyllum* and *Macgeea* are different (comp. fig. 3 and 11). In *Thamnophyllum* growth of diameter predominates and curves run to the X axis; in *Macgeea,* on the other hand, curves are directed to the Y axis since septal growth predominates here.

4. *Macgeea czarnockii* is a regressive form, as has been shown above.

The objectiveness of species and subspecies is confirmed by curves plotted for Givetian subspecies and one of the Frasnian species. Mn/Md correlations are so poorly differentiated that whole binomial curves could not be plotted.

Curves for species and several subspecies of *Macgeea* are not complete, the summit parts only have been shown. Mc class coefficients change very slowly. Differences between them in neighbouring Mc either do not exist at all, or are extremely slight and not revealed by
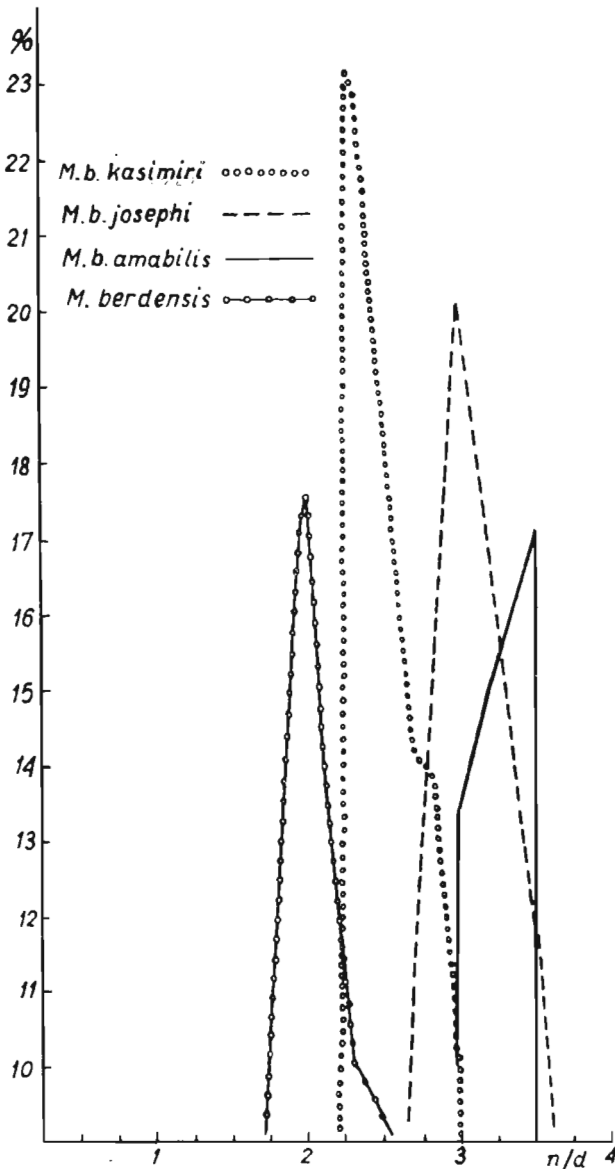
Fig. 12. — Variation curves for several species and subspecies of *Macgeea* from the Middle and Upper Devonian of Poland. Percentage number of specimens — on ordinate, correlation n/d — on abscissa, in mm.

the graph. Mean class correlation values Mc have been placed on the X axis. The per cent of individuals is marked on the Y axis.

Conclusions to be drawn from graph fig. 12 are the following:

1) The separation from *M. bathycalyx* of the three above subspecies is done on a sound basis, since each of them has its own summit;

2) The above subspecies are closely interallied since their graphs fit into one another at the base, with only the summits protruding. Subspecies *M. bathycalyx kasimiri* is more isolated, while *M. bathycalyx josephi* and *M. bathycalyx amabilis* are very close;

3) Apexes of binomial curves show a different value than that of the specific correlation coefficient in *Macgeea* species, namely:

Macgeea bathycalyx kasimiri — maximum class frequency at Mc10.5 = 2.3; Ms 2.93
M. bathycalyx josephi —   ,,   ,,   ,,   Mc7.5 = 3.0; Ms 3.20
M. bathycalyx amabilis —   ,,   ,,   ,,   Mc4.5 = 3.5; Ms 3.16
M. berdensis —   ,,   ,,   ,,   Mc12.5 = 2.0; Ms 2.14

Hence the conclusion that in the case of *M. bathycalyx kasimiri* the sample contains mostly large individuals, while in the case of *M. bathycalyx amabilis* smaller specimens predominate. This confirms the fact that corallites *M. bathycalyx kasimiri* do not belong to one population, while those of *M. bathycalyx amabilis* do.

Morphological changes in ontogeny of Macgeea Webster

The problem of ontogeny is closely linked with that of phylogeny and is of foremost importance for research work on specific and supraspecific evolution. Conspecific representatives may display differences of ontogeny in the case of progressive or more conservative individuals. These are plastic forms particularly distinct in the Givetian *M. bathycalyx*. Genus *Thamnophyllum*, however, inasfar as the writer has been able to ascertain, displays identical ontogeny throughout all its species, thus being in this respect a static form.

In representatives of *Macgeea* ontogenic changes are prominent and are subject to further modifications together with phylogeny. The studied material contains a number of specimens with satisfactorily preserved proximal end, which made possible the cutting of serial thin sections. The result of these studies are given below.

Protomacgeea dobruchnensis, which is most likely the ancestral form of *Macgeea*, has also been placed into the evolutionary ranks of *Macgeea*. Its development was described in detail by the present author in 1956 (Różkowska, 1956, p. 284). Three stages are of importance in the ontogeny of this species:

1) Early neanic stage (fig. 13*A*), with a diameter of 1.7 mm. Cardinal septum still indiscernible being masked by the stereoplasme. Counter septum very long and broad;

2) Late neanic stage (fig. 13 *B*), with a diameter of 6 mm. Cardinal septum short, resting in an open, parallel-walled groove. Counter septum longer than the neighbouring. All septa joint by stereome;

3) Ephebic stage (fig. 13 C), with a diameter of 7 mm. Cardinal septum almost completely reduced. Counter septum nearly equalised with the neighbouring septa·
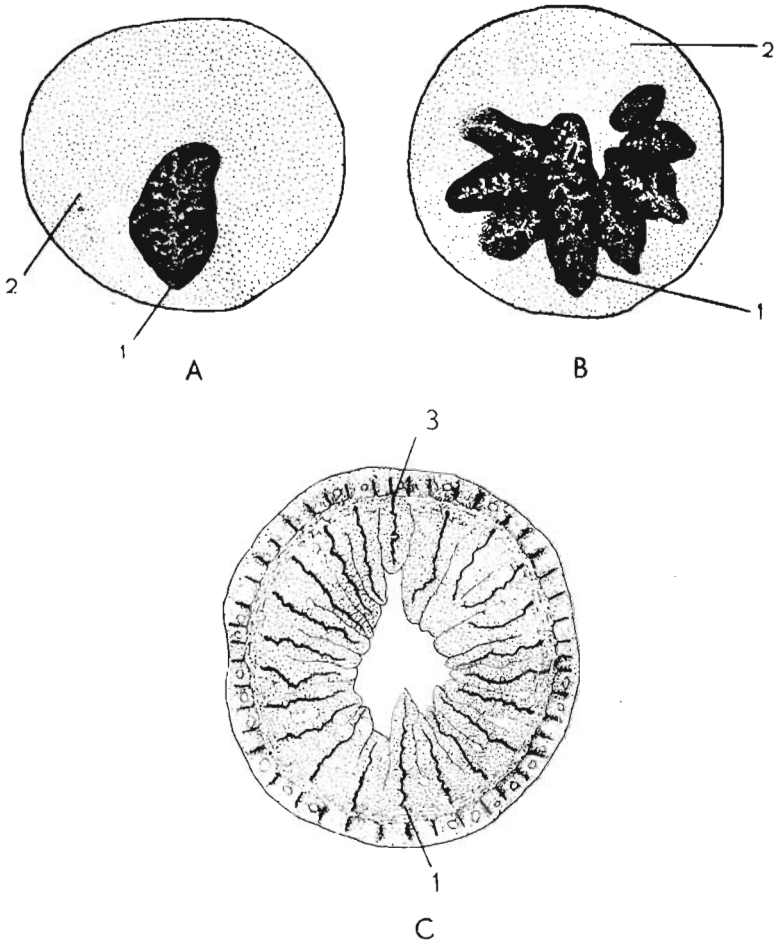

Fig. 13. — *Protomacgeea dobruchnensis* Różk. Grzegorzowice. Middle Eifelian. Three ontogenetic stages: *A* neanic, × 40; *B* late neanic, × 23; *C* ephebic, × 7.5; *1* counter septum, *2* stereome, *3* reduced cardinal septum (after Różkowska. 1956, fig. 6 B-C, and 7).

A very distinctly expressed tendency prevails in the ontogeny of *P. dobruchnensis,* i. e. the cardinal septum, shortened from the very beginning, is almost completely reduced; while the counter septum, which is long and strongly developed, becomes equal with its neighbours.

Macgeea bathycalyx kasimiri inherits from its ancestors the following features: a) stereome mass filling in nearly the whole inside- of the

young corallite; b) shortened cardinal septum; c) extremely long counter
septum. During the early neanic stage the inside is as a rule so compactly
filled by stereome that the septa are not readily discernible. Occasionally,
however, the corallites are not so closely packed and it is then possible
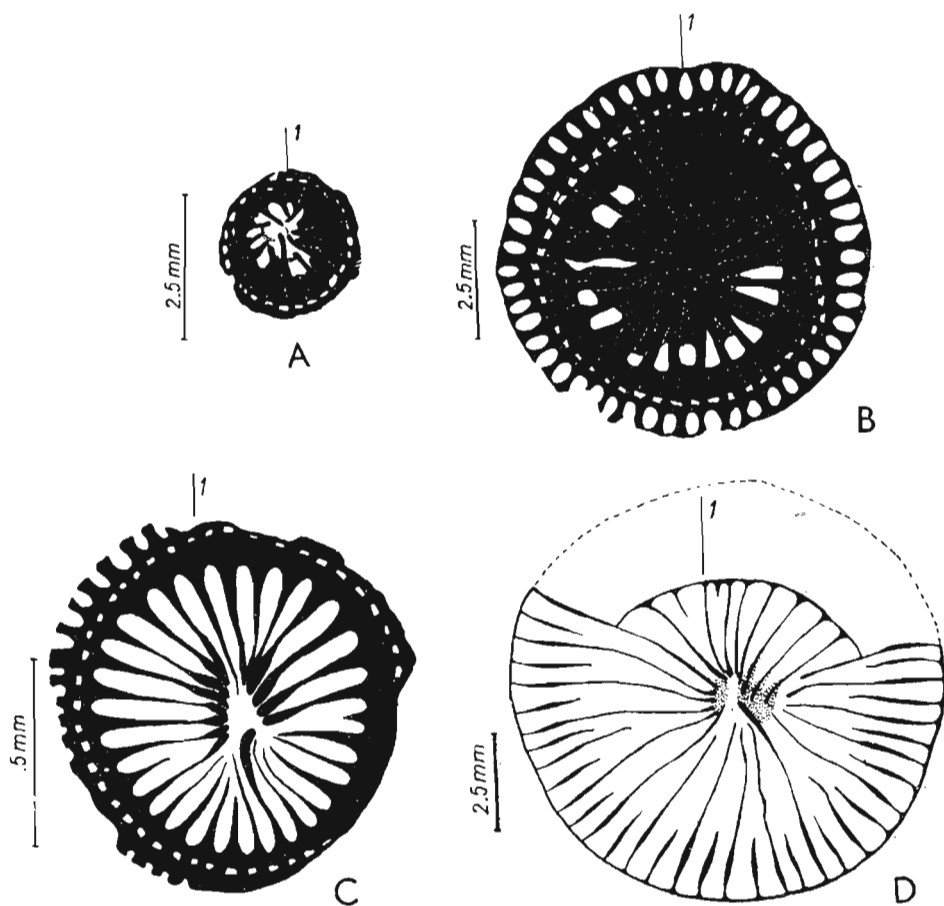
Fig. 14. — *Macgeea bathycalyx kasimiri* Różk. Skały, Middle Givetian. Three
ontogenetic stages: *A* early neanic, with triangular fossula; *B* late neanic, with
groove-like fossula; *C* ephebic, fossula open, long cardinal septum (*1*); *D* ephebic,
triangular fossula, short cardinal. septum.

to distinguish (fig. 14 *A*) that the cardinal septum is somewhat shorter
than or of the same length with the neighbouring metasepta, and that
it rests in a triangular fossula produced by divergent neighbouring septa.
The „triangular fossula" stage occurs during early ontogeny in all
Givetian representatives of *Macgeea*. The late neanic stage (fig. 14 *B*),
observed with diameter of 8 mm, displays gradual reduction of stereome

on the side of the counter septum. The cardinal septum is of equal length with the neighbouring ones, sometimes even somewhat longer since the fossula is open and with parallel walls. This is an „open fossula" stage. The counter septum continues to be long, but occasionally grows even with the adjacent septa. In the ephebic stage, with a diameter of 10 mm (fig. 14 C-D), the arrangement followed by septa at the bottom of a broad and flat calyx can be of two patterns:

a) Cardinal septum lying in an open grooved fossula, of the same length as or sometimes even longer than the neighbouring septa. All septa within the cardinal septum quadrants shorter than those within the counter septum quadrants since they do not reach far down to the bottom of the calyx. On the other hand, the counter septum and the neighbouring septa are very long (fig. 14 C);

b) In other, more conservative corallites, with a diameter of 10 mm, the cardinal septum rests at the bottom of the calyx in a closed triangular fossula (fig. 14 D).

In the *Macgeea* ontogeny strong dependence may thus be noted of the cardinal septum on structure of the fossula. Bilateral symmetry still persists in the ephebic stage, since on the calyx wall the cardinal septum is seen to be narrower than the neighbouring septa which bend laterally producing a distinct fossula.

In the ontogeny of *M. bathycalyx kasimiri* the tendency is to replace the triangular fossula by one groove-like and to prolong the cardinal septum which, however, as a rule, does not exceed the length of the neighbouring septa. The counter septum, at first extremely long, becomes of equal length with the neighbouring septa.

In *Macgeea bathycalyx josephi*, with a diameter of 3 mm, the early neanic stage (fig. 15 A) is as in *M. bathycalyx kasimiri*. Septa thickened by stereome compactly fill up the interior. Some reduction of stereome is sometimes observable. Counter septum long. Fossula triangular, with the enclosed cardinal septum of the same length as the neighbouring septa. In a somewhat later stage the corallite with diameters 6×7 mm (fig. 15 B) has the fossula prolonged into a slit open to the axis. Cardinal septum somewhat elongated, but without exceeding the length of neighbouring septa. Counter septum also enclosed in a narrow groove, often very long. In the ephebic stage, with diameters of 12×14 mm, fossula of the cardinal septum is still groove-like and open, but the cardinal septum and the neighbouring ones are shorter than the neighbouring second and third pair of metasepta. Counter septum continues to be extremely long. During the open fossula stage, the cardinal septum is not longer and does not extend beyond its interior outlet. A section of the upper part of calyx shows the cardinal septum

to be less stoutly developed, shorter than the neighbouring septa. There is still a fossula since the neighbouring septa bend out to the sides.

The evolutionary tendency is as in *M. bathycalyx kasimiri*, to say, for the triangular fossula to be replaced by one that is groove-like and
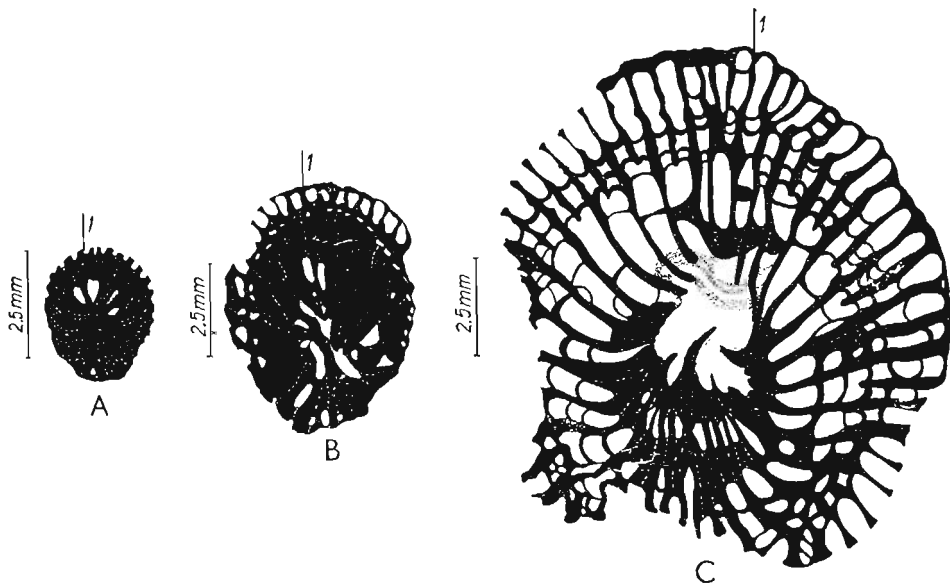

Fig. 15. — *Macgeea bathycalyx josephi* Różk. Skały, Middle Givetian. Three ontogenetic stages: *A* early neanic, with triangular fossula and short cardinal septum (*1*); *B* late neanic, with open groove-like fossula; *C* ephebic, with open fossula.

for the elongation of the cardinal septum, which grows shorter again at the end of ontogeny. During the ontogeny of *M. bathycalyx josephi* the cardinal septum is never longer than the fossula, as is sometimes also the case in *M. bathycalyx kasimiri*.

Macgeea bathycalyx amabilis, when compared with forms described above, is seen to be distinctly progressive. In the neanic stage the corallite having a diameter of 8 mm (fig. 16 *A*) continues to be in the triangular fossula stage, with the cardinal septum inclosed by it. The counter septum in longer than the neighbouring. In late neanic stage, with the diameter of 11 mm, the fossula is shorter (fig. 16 *B*), broadly open facing the interior of the corallite, while the cardinal septum extends beyond it since it is considerably longer than neighbouring septa. Counter septum very long. In the ephebic stage, with a diameter of 16 mm, the cardinal septum is not longer than the neighbouring septa, occasionally even shorter. The counter septum grows equal with the adjacent septa.

Ontogenic changes are still more striking in the geologically younger representatives of *M. bathycalyx amabilis* from zone 11 (Różkowska, 1956,
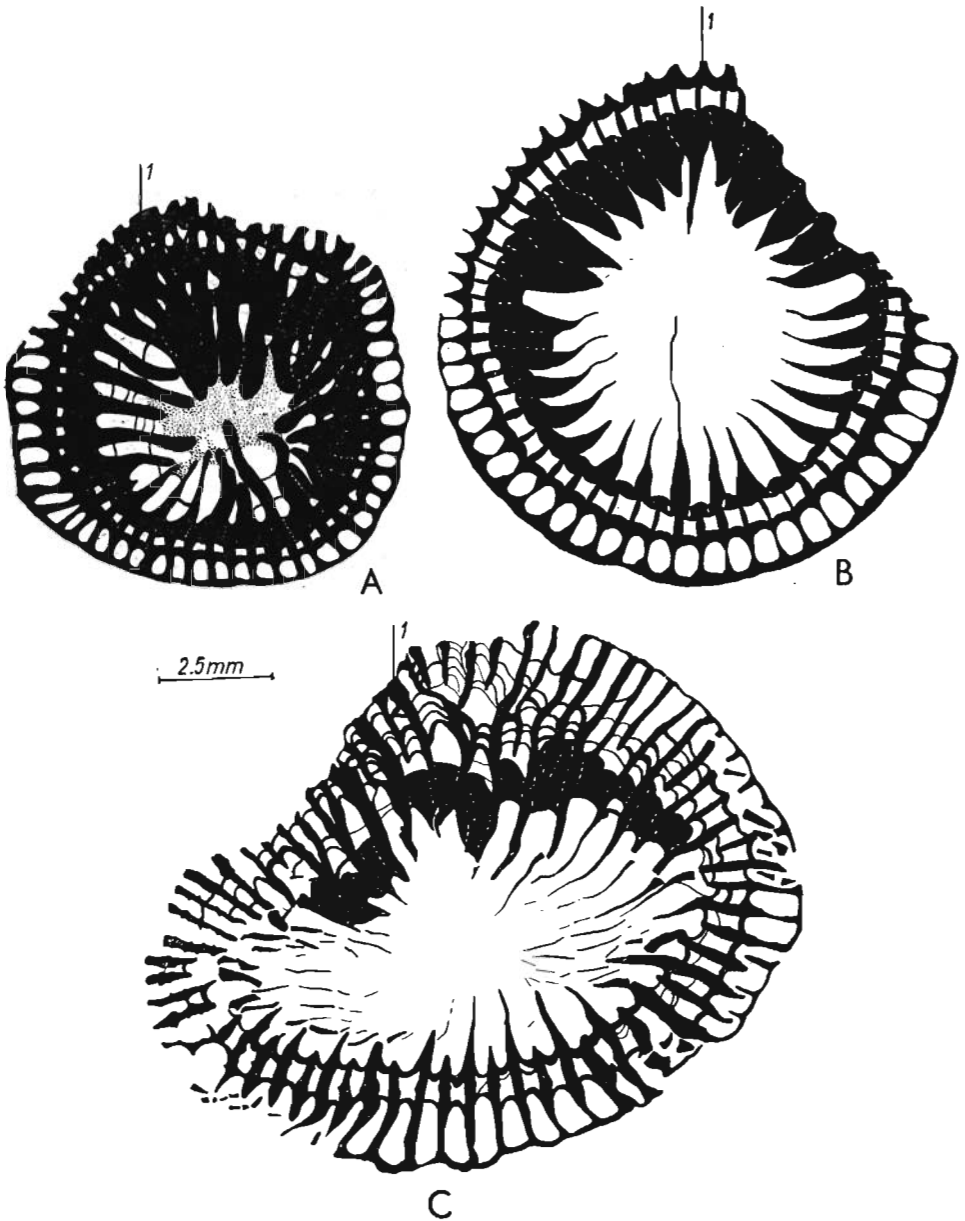
Fig. 16. —. *Macgeea bathycalyx amabilis* Różk. Skały, Middle Givetian. Three ontogenetic stages: *A* neanic, with triangular fossula; *B* late neanic, with open fossula and long cardinal septum (*1*); *C* ephebic, with shortened cardinal septum.

p. 278). *M. bathycalyx amabilis* (fig. 17 *A-B)* has a very elongated cardinal septum, longer than three pairs of the neighbouring metasepta. With a somewhat larger diameter (10 mm) it is still slightly longer than the
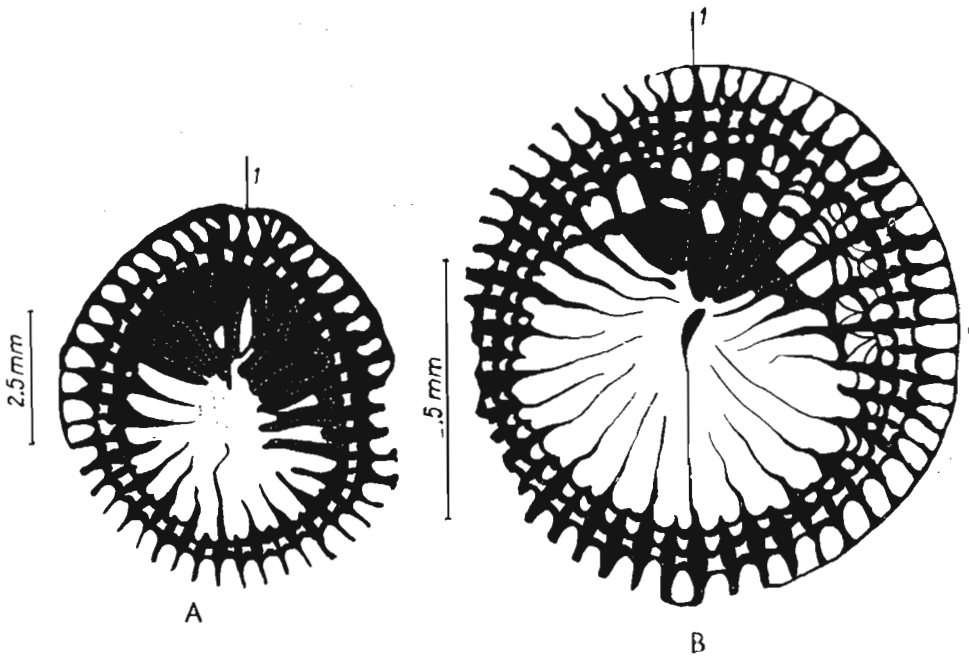

Fig. 17. — *Macgeea bathycalyx amabilis* Różk. Skały, Middle Givetian, a geologically younger form. Two ontogenetic stages: *A* neanic, with very long cardinal septum (*1*); *B* late neanic, with cardinal septum still long.
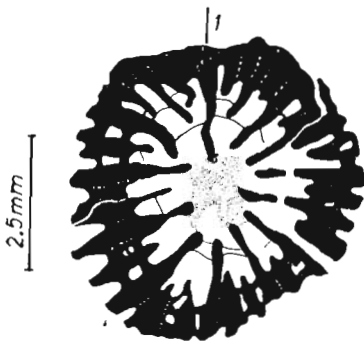
Fig. 18. — *Macgeea berdensis* Soshkina. Wietrznia, Lower Frasnian. Neanic stage; *1* cardinal septum.

neighbouring septa, stouter, more rhopaloid and united with those adjacent by the stereome. Counter septum very long and thin, with a rhopaloid axial end.

The evolutionary trend of this subspecies is expressed in the elongation of the cardinal septum beyond the interior outlet of the open fossula. In the ephebic stage the cardinal septum again retreats into the interior of the groove.

In the Frasnian the ontogeny of *Macgeea* representatives is different. Regretfully, the proximal end of studied specimens is usually damaged. Observations on some thin sections have yielded the following results:

Macgeea berdensis Soshkina (fig. 18). — With a diameter of 6 mm, several metasepta reach nearly to the axis of calyx, the cardinal septum is longer than any of them, the fossula open forming an obtuse angle. Counter septum equal with other metasepta. In later stages the cardinal septum is also equal with adjacent septa.

Macgeea czarnockii Różk. (fig. 19). — In the nepionic stage, with a diameter of 2 mm, the cardinal septum is considerably longer than
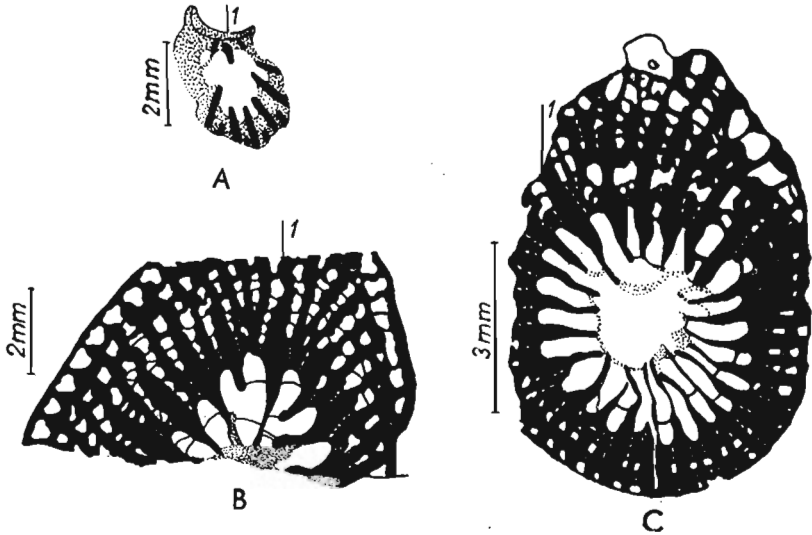

Fig. 19. — *Macgeea czarnockii* Różk. Wietrznia, Middle Frasnian. Three ontogenetic stages: *A* nepionic, with open fossula and long cardinal septum; *B* neanic, with open fossula and long cardinal septum (*1*); *C* ephebic.

the neighbouring which produce an open fossula. Counter septum of equal length with adjacent metasepta. In the next stage, with a diameter of 5 mm, the cardinal septum predominates distinctly by its length and is contained in the open, groove-like fossula (fig. 19 *B*). In the ephebic stage the cardinal septum is longer than all the remaining septa (fig. 19 *C*).

Macgeea multizonata (Reed) (fig. 20). — With a diameter of 5 mm, the fossula is seen to be open and containing the cardinal septum, which is nearly equal with the adjacent metasepta. The counter septum does not predominate by its length. In the ephebic stage it is the cardinal septum that displays a distinctly predominant length in all individuals. The counter septum is not different from its neighbours (fig. 20 *B*).

From here mentioned data it seems probable that *Macgeea* evolved from *Protomacgeea dobruchnensis* and that it inherited from that form some of its evolutionary tendencies, though developing some new trends as well, such as follows:

1) In immature stage the Givetian *Macgeea* is with the interior of the corallite closely filled up by stereome deposits, present on all elements but progressively reduced in later ontogeny, as in *Protomacgeea,* and persisting longest in the side of the cardinal septum. In phylogeny the same tendency continues through the Middle Givetian. Complete reduction of stereome takes place in the Frasnian;
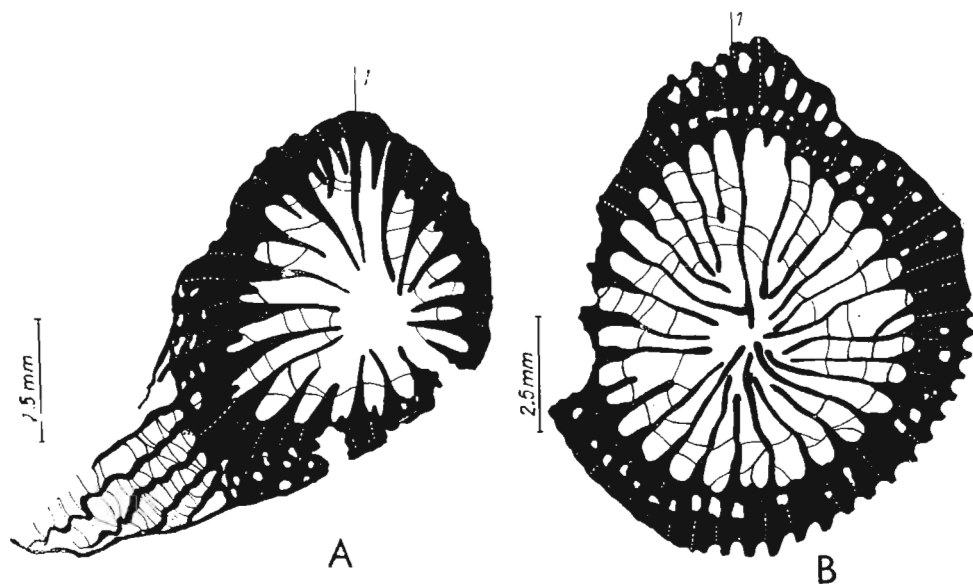

Fig. 20. — *Macgeea multizonata* (Reed). Wietrznia, Middle Frasnian. Two ontogenetic stages: *A* neanic, cardinal septum (*I*) of the same length with the adjacent; *B* ephebic, cardinal septum very long.

2) The counter septum predominates during early ontogeny of *Protomacgeea* and the Middle Givetian *Macgeea,* while in later ontogenic stages its length suffers reduction. In the Frasnian this feature is stabilised since the counter septum does not differ in length in any of its stages;

3) In *Protomacgeea* the cardinal septum displays a tendency to complete reduction, while in *Macgeea* the tendency is inverted. During early ontogeny all forms from the Givetian of Poland have the cardinal septum short, though lengthened in later ontogeny and shortened again during the ephebic stage. The tendency to the supremacy of the cardinal septum persists throughout the Middle Givetian. It is in the youngest form of *M. bathycalyx amabilis* only that the cardinal septum is lengthened beyond other septa during a certain ontogenic stage, to retreat again in the ephebic stage. Similar features may also be encountered in some progressive individuals of *M. bathycalyx kasimiri.* In the Frasnian,

however, the supremacy of the cardinal septum has already been established. Beginning with the earliest ontogeny it is longer and persists as the longest septum during the ephebic stage in geologically youngest species, for instance in *M. multizonata* and *M. czarnockii;*

4) The problem concerning the fossula is an interesting one too. Throughout its ontogeny *Protomacgeea* is with the fossula open. In the Middle Givetian *Macgeea,* on the other hand, the construction of the fossula is variable. During early ontogeny it is triangular and closed. This is a new feature with which are linked the evolutionary dynamics of the cardinal septum. This septum is short as long as the fossula is closed, but grows longer as the fossula opens up. During later ontogeny, in all Givetian representatives of *Macgeea,* the fossula lengthens, its walls open out providing free space for the lengthened cardinal septum. In the Frasnian forms the fossula is always open, so that this is another feature established during the Frasnian.

It may be thus assumed that in the early ontogeny of *Macgeea,* the Givetian is a period of settling of the different morphological elements, while the Frasnian is a period of stability.

The morphological features of adult individuals also undergo various shifts.

Macgeea is a simple form. In our collection there is no budding Middle Givetian form. Among Frasnian forms *M. multizonata* alone produced buds. No dendritic colonies have been observed by the writer among macgeean forms. In her paper published in 1953 *Thamnophyllum kozłowskii,* living in fasciculate colonies, was incorrectly referred to *Macgeea.* Subsequently, however, during work on the whole collection of Thamnophyllidae from the Devonian in Poland, the writer gained a knowledge in respect to the essential diagnostic features of these two genera and has now included the mentioned species into the genus *Thamnophyllum.*

The habitus of the corallite in *Macgeea* is always conical; low, broad cones occur along with long, slender corallites. They are all covered by an epitheca.

The inner structure is complicated, consisting of numerous skeletal elements, which are all subject to changes. The shifts here are great, and concern one feature only or a whole complex of linked structures. In subspecies of *M. bathycalyx* two fundamental types of construction occur within the Middle Givetian, they are: a) low, broad corallites with a markedly deep calyx, thick stereome cover on the skeletal elements and stout, vesiculate tabulae; b) elongate, conical corallites with the calyx somewhat less deep, with tabulae arranged into bundles and thin skeletal elements.

The Frasnian forms also display two extreme structural types, namely: a) the *M. berdensis* type showing stout, straight and short septa, thick pseudotheca and a fasciculate arrangement of tabulae; b) *M. multizonata* type of delicate structure, with long, wavy, fine septa and thin vesiculate tabulae.

Diagnostic features in genus Macgeea Webster

Observations made on Givetian, and Lower and Middle Frasnian forms of *Macgeea,* involving studies of morphology and evolution, indicate that *Macgeea* is an independent genus with distinct diagnostic features, to say:

1) The corallites are conical, either short or elongate, straight or bent, provided with a talon for attachment to the bottom. Their surface is covered by an epitheca terminating below the calicular edge;

2) Budding is an extremely rare phenomenon. The buds are of the parricidal type only. From a collection consisting of 22 specimens of *M. bathycalyx kasimiri,* 75 specimens of *M. bathycalyx josephi,* 47 specimens of *M. bathycalyx amabilis,* 40 specimens of *M. berdensis,* 15 specimens of *M. czarnockii* and 35 specimens of *M. multizonata,* — four budding specimens only, belonging to the last named species, were discovered;

3) Septa with prominent, opposite carinae (fig. 21);

Fig. 21. — *Macgeea bathycalyx kasimiri* Różk. Skały, Middle Givetian. Photograph of corallite; distinct carinae on distal edges of septa not masked by epitheca; × 6

4) Bilateral symmetry persisting throughout the ontogeny, due to the presence of the fossula. The cardinal septum inclosed in fossula is either longer or shorter as compared with the metasepta;

5) A peculiar evolutionary tendency is noted: negative allometry in relation to septa persists during ontogeny, while during phylogeny positive allometry is displayed;

6) Internal morphology complicated: normal dissepiments occur on the inside of horse-shoe dissepiments, tabulae always incomplete, axial parts often arranged into bundles (2-5 tabulae) or split up into vesicules;

7) Minor septa always somewhat longer and protruding beyond the inner ring of pseudotheca since they extend as far as the dissepiments.

The following should be mentioned as important specific features: habitus of corallite, number of septa as well as their length and thickness. Compactness of pseudotheca and lumen of horse-shoe dissepiments connected therewith are also of importance. Structure of tabularium and width of dissepimentarium should also be taken into account. Other specific features are the value of the correlation coefficient and the structure of fossula.

VARIATIONS OF QUANTITATIVE CHARACTERS IN GENUS PEXIPHYLLUM WALTHER EMEND. MIHI

In 1928 the family Pexiphyllidae was erected by Walther to include the genera *Temnophyllum* Walther and *Pexiphyllum* Walther. Since neither genotypes nor topotypes are available to the writer she can only make some suggestions in respect to this family.

Temnophyllum. — Microstructure was not taken into account in the diagnosis of this genus· The macrostructure mentioned by that author is that characteristic of Disphyllidae. This was confirmed by H. Wang (1950), when he placed *Temnophyllum* among Disphyllidae, and by the present writer (1953), who referred some corallites from the Upper Devonian in Poland to genus *Temnophyllum*. The microstructure of specimens from the Holy Cross Mts. displays a type of structure characteristic of Disphyllidae; parallel and obliquely upward pattern of trabeculae.

Pexiphyllum. — In the writer's conception, this is a representative of the family Thamnophyllidae, as has been previously stressed by E. C. Stumm (1949). According to Walther (1928) this genus displays the following diagnostic features, typical of the Thamnophyllidae: epitheca with an underlying row of flat dissepiments and spherical ones alongside of these normal dissepiments together with convex vesiculate tabulae near the axis. Microstructure and ontogeny of this genus have not been described by Walther.

That author has included five species within *Pexiphyllum*, separated into two groups. Group 1 includes: *P. primum* Walther, *P. rectum* Walther and *P. altum* Walther. Group 2 contains: *P. arcuatum* Walther and *P. ultimum* Walther.

Forms of group 1 are with a large stereozone and septa not reaching to the axis. In the opinion of the present writer they are most likely representatives of *Macgeea*. Of the Polish specimens *M. czarnockii* Różk. closely resembles *P. rectum*.

Species included in group 2 have a large stereozone too and septa
fused into a columella. These two species are thus distinct from forms
of group 1 and, in the present author's opinion, ought to be included into
genus *Pexiphyllum* s. str. According to Walther's definition, *Pexiphyllum*
must be considered as a heterogenic genus — as has already been remarked
by H. Flügel in 1956 — since it embraces the genera *Macgeea* and
Pexiphyllum s. str.

The present writer in 1953 accepted *Pexiphyllum* Walther on the
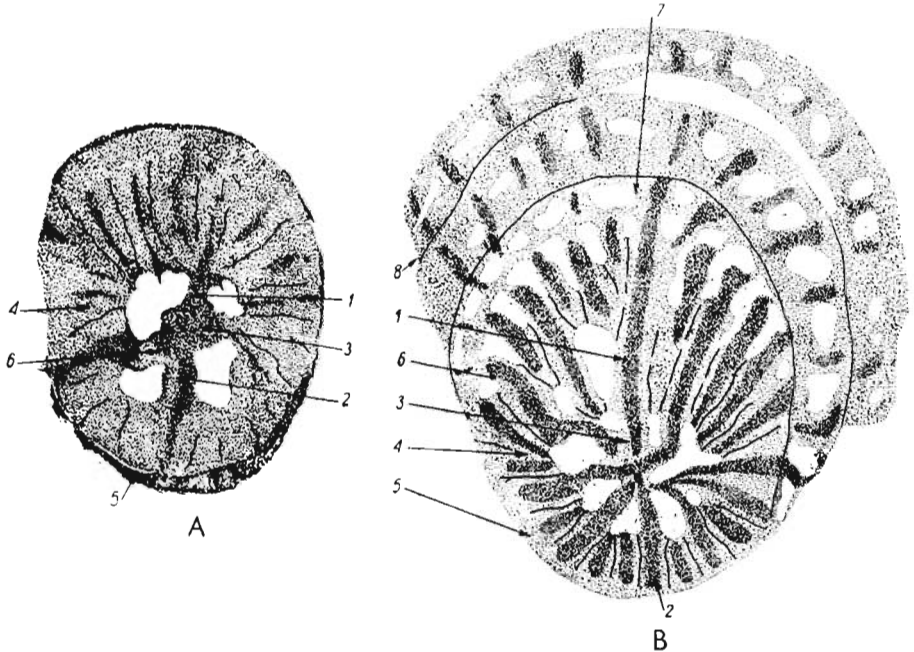ground that it is provided with a columella which constitutes a new

Fig. 22. — *Pexiphyllum ultimum* Walther. Wietrznia. Middle Frasnian. Two
stages of ontogeny: *A* nepionic, septa fused into a columella, × 33; *B* neanic,
with open fossula and long cardinal septum, columella still present, × 20;
1 cardinal septum, *2* counter septum, *3* pseudo-columella, *4* pseudo-theca,
5 epitheca, *6* first pair of lateral septa, *7* talon, *8* epitheca of talon (after
Różkowska, 1953, fig. 17, 19).

feature not occurring in *Macgeea*. The generic diagnosis of *Pexiphyllum*
Walther, with the genolectotype *P. ultimum* Walther, may be therefore
as follows: corallites simple, conical, circular in section, with rare
peripheral budding and epitheca, and talon. One row of flat dissepiments.
One or two rows of horse-shoe dissepiments usually masked by flat
symmetrical trabecular fans having lines of divergence on the horse-shoe
dissepiments; normal dissepiments along with convex incomplete tabulae;
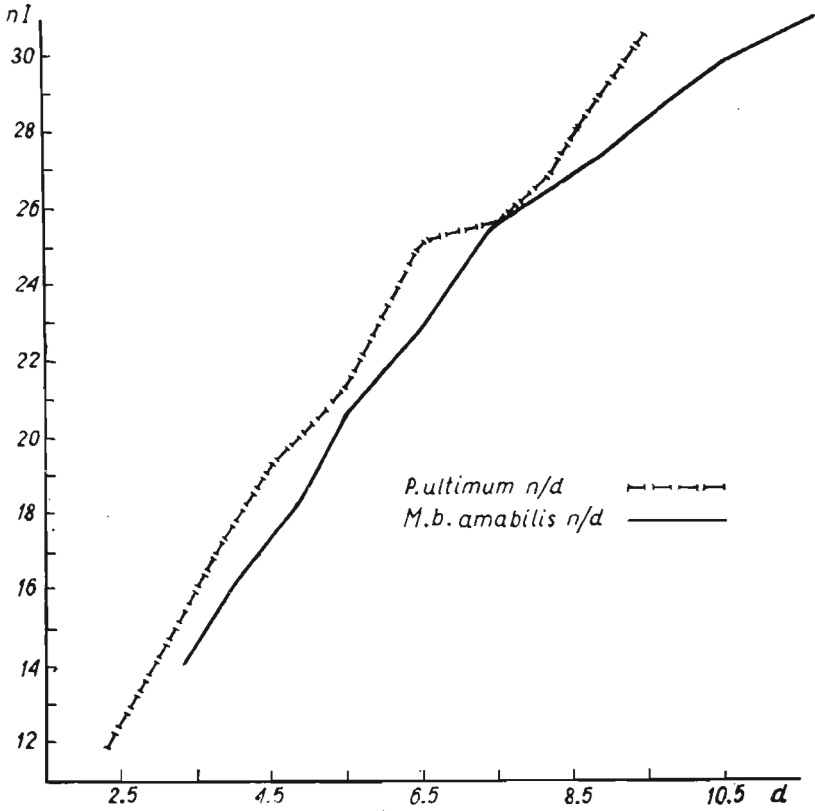septa thickened within the pseudotheca, closely contiguous, with axial ends

Fig. 23. — Correlation curves n/d for *Pexiphyllum ultimum* and *Macgeea bathycalyx amabilis*. Number of major septa — on ordinate, diameter of calices — on abscissa, in mm.
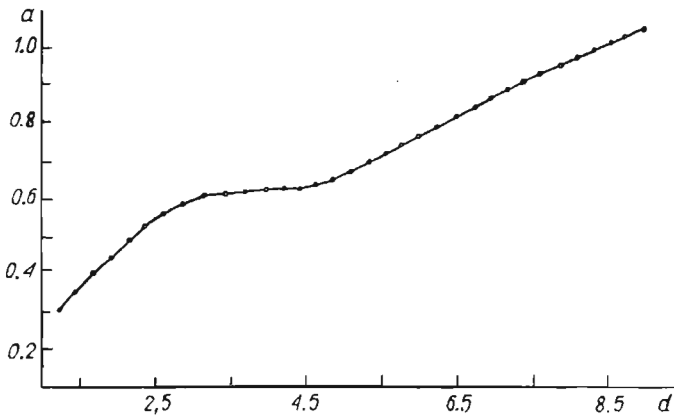

Fig. 24. — Correlation curves a/d for *Pexiphyllum ultimum*. Interseptal distances — on ordinate, diameters of calices — on abscissa, in mm.

fused into a columella and peripheral ends protruding beyond the pseudotheca as „costae". Bilateral symmetry occurs throughout the ontogeny owing to the presence of a distinct fossula and the long cardinal septum inclosed in it (fig. 22 A-B).

The above quoted genus occurs in Poland from the Middle through the Upper Frasnian and is represented by two species showing similar structure, namely P: *ultimum* Walther and P. *siemiradzkii* Rożk. On the analysis of 61 thin transverse sections, the writer has calculated the n/d and a/d correlation in respect to species P. *ultimum*. Results of these calculations are plotted in graphs (fig. 23-24). Correlation coefficients of classes are high, whence the coefficient for this species is also high. Numerical data come nearest to those of M. *bathycalyx amabilis*, as is illustrated by the following tabulated data:

Macgeea bathycalyx amabilis			Pexiphyllum ultimum		
diameter (in mm)	major septa	Mc	diameter (in mm)	major septa	Mc
5.5	21	3.8	5.5	21	3.8
7.5	26	3.5	7.5	26	3.5
8.5	27	3.2	8.5	28	3.3
9.5	29	3.0	9.5	31	3.2

The n/d correlation line for M. *bathycalyx amabilis* has been placed in fig. 23 near to that for species P. *ultimum*. Up to diameter of 8.5 mm these curves show a similar pattern since they touch and even intersect in stages of smaller diameters.

The a/d correlation line for P. *ultimum* is plotted in the graph fig. 24. It indicates that the growth of septal distance is gradual and progressive with individual ontogeny of the corallite. This increase of distance between septa is more rapid during youth when the diameters range from 1.5 to 3.5 mm, growing slower in later stages.

VARIATIONS OF QUANTITATIVE CHARACTERS IN SPECIES OF GENUS PACHYPHYLLUM EDWARDS & HAIME

Within the family of Thamnophyllidae, *Pachyphyllum* represents the massive colony type. In the Devonian of Poland it is recorded from the top beds of the Middle Givetian and from the Upper Frasnian. Its numerous species may be subdivided into four groups:

1) Group of *Pachyphyllum sobolewi* Różk· from the Middle Givetian, thus far monotypic;

2) Group of *Pachyphyllum lacunosum* Gürich from the Upper Frasnian contains *P. smithi* Różk. and *P. friedbergi* Różk., both with primitive structure, complete tabulae and septa mostly amplexoid;

3) Group of *Pachyphyllum ananas* (Goldfuss) assembles more complicated forms. Tabulae are here arranged in bundles extending anteriorly and upwards. Normal dissepiments occur typically on the inner side of horse-shoe dissepiments, septa are long during earliest ontogeny and may touch in the axial part of the corallite;

4) Group of *Pachyphyllum ibergense* (F. A. Roemer), intermediate between group 2 and 3, is characterised by a large tabularium, tabulae often incomplete along with complete ones, and by short septa.
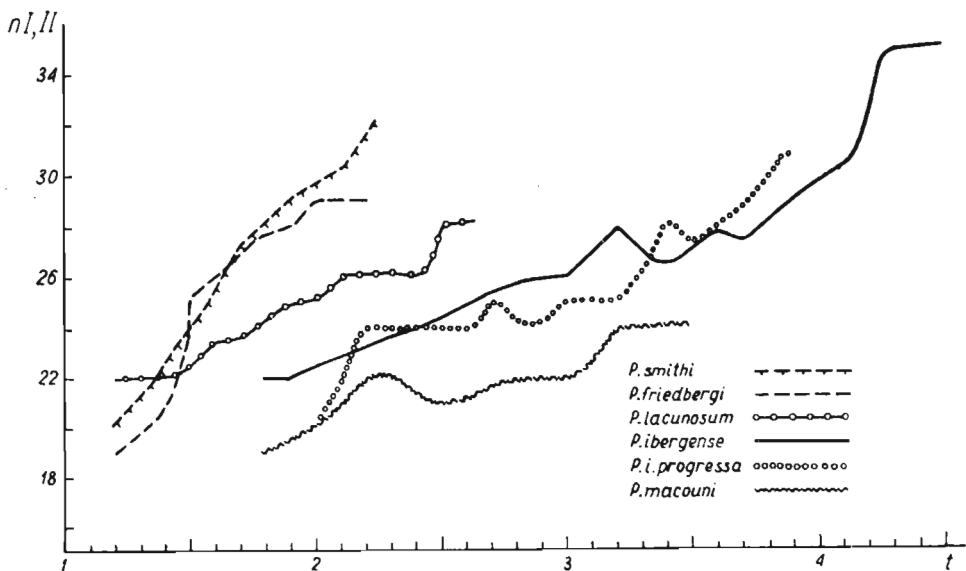

Fig. 25. — Correlation curves n/t for species of group *Pachyphyllum lacunosum* Gürich and *P. ibergense* (F. A. Roemer) from the Upper Frasnian of the Kielce region. Major and minor septa — on ordinate, diameter of tabularium (t) — on abscissa, in mm.

A statistical inquiry has also been made for this genus. Two correlated features have been taken into account, namely diameter of tabularium(t), encircled by a very distinct inner pseudotheca, and the number of major and minor septa. The diameter of tabularium was measured in places where minor septa after passing the circle of horse-shoe dissepiments suddenly grow narrow. This proportion is lettered n/t. Graph of fig. 25 has been plotted on statistical data as is also that of fig. 26 representing the schematical graph of the n/t line of correlation for species of 3 groups. Statistical data result in the following conclusions:

Certain irregularities noted in the progressively decreasing class coefficients may be due to the scarcity of material available to the writer. Only very few measurements could be taken on transparent thin sections, whence individual deviations were not equalized. Even some proper sizes of tabularia are lacking in numerous classes, but in spite of this features
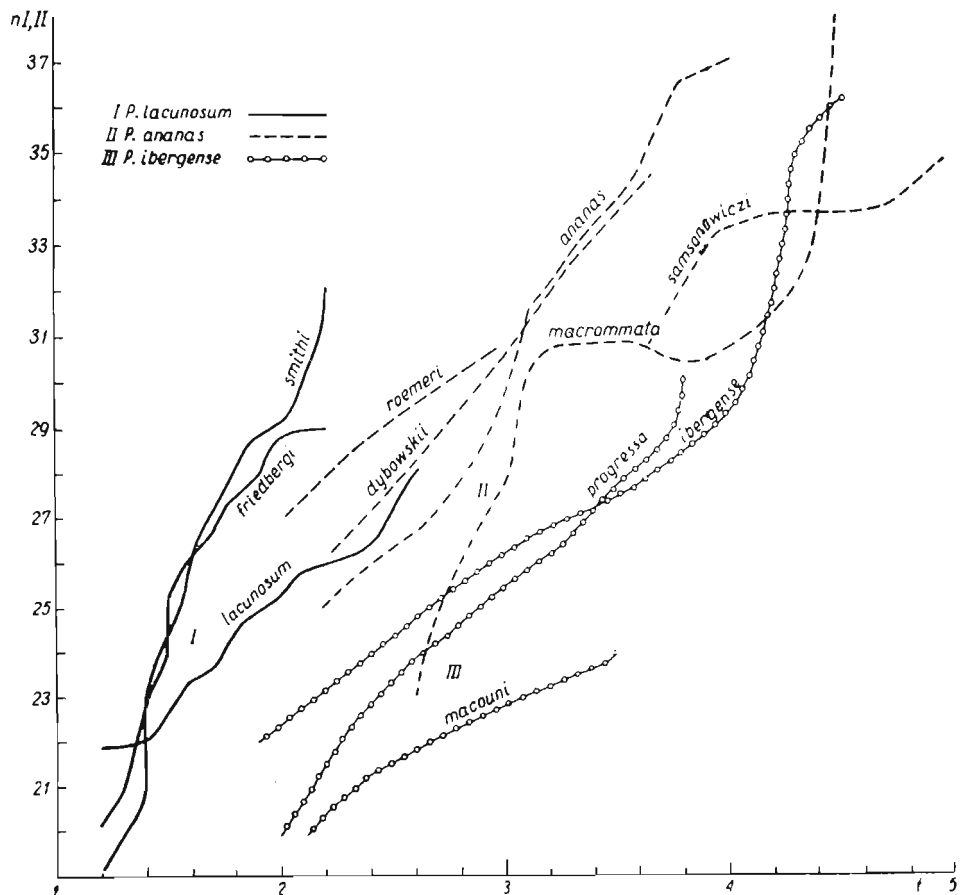

Fig. 26. — Schematic diagram of correlation curves n/t for species of three species-groups: *Pachyphyllum lacunosum, P. ibergense, P. ananas.*

characteristic of a given species as well as differences of various groups are quite distinct.

The range of diameters of tabularia varies, since there are groups with markedly small tabularia and others with large ones.

The group of *Pachyphyllum lacunosum* is the most „microtabular". The means of tabularia oscillate here from 1.1 to 2.6 mm. The number of septa is relatively great, being up to 32, whence Ms coefficient of 15.8— 15.0—13.5 is proportionally high in this group.

In a macrotabular group *P. ananas* et *P. ibergense* the Ms coefficient is somewhat lower than in the preceding group, being 11.7—7.7, since the increase in number of septa is proportionally less.

The Givetian species *P. sobolewi* shows an isolated character. Here the tabularia are large (up to 5.2 mm), septa numerous (up to 44), the Ms coefficient being thus correspondingly different (9.6).

Hence, the distinction within genus *Pachyphyllum* of four specific groups is attested by biometrical data.

The value of class coefficients decreases progressively. We are thus dealing here with an allometric phenomenon. Proportions in classes decrease very slowly in all groups. Differences in value of Ms in neighbouring classes are extremely small indicating that the growth of septal number and of tabularium diameter is proportionally similar, though somewhat smaller in the case of septa. Owing to the great number of septa (as both major and minor septa were taken into account) and the markedly small diameters of tabularia — measured with the accuracy of 0.1 mm — class coefficients are great when compared with those in *Thamnophyllum* and *Macgeea*.

The correlation coefficient of species is also very high. On comparing the Ms value in various species we find related values concentrated within the limits of several groups:

Group I.

Pachyphyllum lacunosum includes:

	Ms
P. smithi	= 15.8
P. friedbergi	= 15.0
P. lacunosum	= 13.5

Group II.

Pachyphyllum ananas:

	Ms
P. roemeri	= 11.7
P. dybowskii	= 11.5
P.ananas	= 10.2

Group III.

Pachyphyllum ibergense:

	Ms
P. ibergense	= 8.9
P. ibergense progressa	= 8.9
P. macouni	= 8.8

Constitute separate items in

Group II.

	Ms
P. macrommatum	= 8.9
P. samsonowiczi	= 7.7

These statistical data also confirm the objectiveness of specific groups differentiated on basis of similar morphological features.

FACTORS OF SPECIATION IN THE FAMILY THAMNOPHYLLIDAE
SOSHKINA

Speciation may be studied most conveniently on genera rich in species and occurring within beds immediately succeeding one another. The genera *Thamnophyllum* and *Macgeea* will prove particularly useful for an inquiry into this phenomenon.

Variations of quantitative characters
in genus Thamnophyllum Penecke

Quantitative features dealt with in the present paper are those most susceptible to numerical representation, namely diameter of calyx and number of septa. Biometrical measurements indicate the existence of rigorous inter-relation of these features. The n/d correlations, however, are not constant, since allometry changes with individual age and in phylogeny of species within genus *Thamnophyllum*. The allometric shift follows some tendencies characteristic of certain genera. Within *Thamnophyllum* negative allometry prevails in relation to septal growth. It is expressed by the gradually decreasing Ms correlation coefficient of species. The decrease is an orthogenic progress which advances in one and the same direction in the course of geological time, independent of facies changes. It is only within unusually unadvantageous environment (in terrigenic deposits) that a check or even regression to primitive forms takes place. Quantitative changes are, therefore, gradual. Changes in the Ms value, however, most likely constitute an advantageous feature for the genus *Thamnophyllum*. Selection may have favoured advantageous mutations following the once taken course. If we were to distinguish species of *Thamnophyllum* solely on the basis of quantitative features, three species could be differentiated within our material: one lasting from the bottom of the Middle Givetian to the top of the Middle Frasnian, whose lower Ms correlation coefficient would suggest the geologically younger age of the given specimen; the second and the third including regressive forms with very high correlation coefficient. Hence the deduction that in Corals species may not be established exclusively on quantitative features.

Variations of qualitative characters
in genus Thamnophyllum Penecke

Six species and two subspecies may be distinguished from representatives of genus *Thamnophyllum* recorded in Poland. They all differ in varying qualitative features. These are adaptive features as they appear along with changes in the character of sediments and re-occur in similar lithological facies. If the lithology of successive strata does not change the same morphological features last, as for instance in *Th. kozłowskii* and its mutation *Th. kozłowskii superius*. Under sedimentary changes the morphology of the corallite changes too. Marly sediments, laid down within a quiet, rather deep sea where fine particles had been precipitated, yield *Thamnophyllum* with thin skeletal elements, distant tabulae and spherical horse-shoe dissepiments. Detrital and reef

limestones, deposited in a shallow stormy sea, yield *Thamnophyllum* with thick septa, compact pseudotheca and small lumen in horse-shoe dissepiments. It may be supposed that changes re-occurring within strata of similar character are a reaction against environmental conditions and are due to accidental mutation. We are not, therefore, dealing here with lasting orthogenic evolutionary changes of qualitative features. Similar structural features are not, however, an expression of phenotypic changes, since they are always accompanied by characteristic second rate qualitative features, e. g. lateral or parricidal type of budding in *Th. caespitosum* or *Th. trigemme,* and different number of buds, e. g. two in *Th. skalense,* five in *Th. kozłowskii.* Qualitative features occurring as a reaction against environmental changes constitute the basis on which six species and two subspecies may be distinguished within Devonian beds in Poland. Their objectiveness has been confirmed by uniapical allometric curves. They are probably ecogenotypes, but it is difficult to establish this with certainty since fossil species may be differentiated on morphology only.

Phenomena of speciation in genus *Thamnophyllum* Penecke

In Middle Devonian strata *Thamnophyllum* shows strong specific differentiation. This points out distinctly that differentiation of species was connected with lithological changes of facies. New species appear suddenly with sedimentary changes. They do not, however, appear by saltation; it may rather be inferred that they immigrated from environmental conditions similar to those under which the given bed had formed. Within the Holy Cross Mts. area the Middle Devonian sea offered particularly advantageous conditions for speciation. The sea bottom there was subject to frequent positive and negative oscillations, while the neritic zone abounded in bays where ecological conditions changed rapidly, and isolation enabled differentiation of new species. Populations of different species display strong polymorphism, due to which new species could arise. Similarly as numerous geographic races arise among the Recent fauna so used also races and historical species to arise within genus *Thamnophyllum.* The early stages in all species being identical, it is probable that new forms differentiated in the course of ontogeny.

To sum up we note that there were two cardinal factors responsible for the differentiation of new species within genus *Thamnophyllum:* those of time and environment. Quantitative features change gradually with time, but environmental changes favoured the development of new structures. Selection supported by isolation cooperated in the given environment.

Orthogenic variations of quantitative and qualitative characters in genus Macgeea Webster

Within genus *Macgeea* variability is more complicated than that in *Thamnophyllum,* the problem of speciation being also more intricate. Representatives of *Macgeea* display strong polymorphism in structure of morphological elements. This great variability accounts for the origin of numerous species and subspecies. Changes leading up to speciation were sometimes progressive and sometimes accidental. Orthogenic changes affected not only quantitative features, as in genus *Thamnophyllum,* but qualitative as well.

In the history of *Macgeea* different feature complexes change progressively, namely:

1) The stereome cover is reduced gradually. In oldest forms such as *M. bathycalyx kasimiri* it is strongly developed and almost completely fills up the proximal part of corallites. It does not undergo a complete reduction before the appearance of geologically youngest forms such as *M. multizonata;*

2) The whole complex of features correlated with the structure of fossula is subject to ontogenic changes. The triangular closed fossula changes into an open groove, the cardinal septum lengthens out at the same time while the counter septum shortens up and becomes equalized with the adjacent septa. In spite of fluctuations this ontogenic change progresses and is not stabilised before the Frasnian;

3) Diameter of calices and number of septa increase gradually. In spite of the check noted at the beginning of the Frasnian this evolution progresses in one and the same direction in the course of the geological time;

4) The two-phase evolution of septa is also reflected in the coefficient of species. The Ms value of various *Macgeea* forms increases with geological time.

It may be supposed that, as in *Thamnophyllum,* orthogenic changes existed unquestionably, but we may hardly imagine that they took place without the eliminating participation of selection. The lasting morphological changes must, therefore, have been of orthoselectional character.

Considering that the changes were gradual one might suppose that two species only are to be distinguished within genus *Macgeea:* one for the Middle Givetian, the other for the Frasnian. These two species would be clearly cut by a sedimental gap and by a certain hiatus in the gradually increasing correlation coefficient of species; whereas the presence of a long cardinal septum, in Frasnian forms occurring from the earliest

ontogeny, may be an argument for the differentiation of two genera. One would include Givetian representatives displaying a short cardinal septum during early ontogeny, the other those of the Frasnian with a long cardinal septum. An inquiry into the ontogeny of numerous Givetian and Frasnian forms has, however, revealed evolutionary continuity of this process. Thus the length of the cardinal septum may not be a generic or even a specific criterion.

Phenomena of speciation in genus Macgeea Webster

Gradual and orthoselective evolution of both quantitative and qualitative features do not distinctly separate the various species. If no sedimentary changes had taken place within Givetian and Frasnian deposits, which contributed to the development of adaptation features, it would hardly be possible to separate from this uninterrupted stream of forms the existing subspecies and species of *Macgeea*.

Several species and varieties have been distinguished in our collection. In the Middle Givetian there is but one species: *M. bathycalyx*. In spite of frequent lithological changes this species persists all the time, evolving only subspecies adaptive to various facies. Their objectiveness is confirmed by one-summit allometric curves. The lack of specific differentiation may perhaps be explained by the young phyletic age of *Macgeea* which did not arise before the Givetian thus not being able to evolve specific morphological adaptations. There is, however, another possibility, that of recognising as independent those species which are concentrated round *M. bathycalyx* and together with it form a group of species. Taking into account both these possibilities the writer is inclined to believe, as she also was in 1956, that there was but one Middle Givetian species with three ecological subspecies. Continuity noted in ontogenetic evolution confirms the integrity of this species.

If morphological features in the Frasnian forms of *Macgeea* will be accepted as specific criteria, three distinct species may be distinguished, namely: the short-septate *M. berdensis* common within zoogenic Lower Frasnian and phytogenic Middle Frasnian limestones; the long-septate *M. czarnockii*, most abundant within detrital limestones of the Middle Frasnian, and finally *M. multizonata* with long thin septa, delicate structure, peculiar to marly shales of Middle Frasnian beds. It may be supposed that species with thick skeletal elements were adapted to the environment of a shallow agitated sea and existed there in their biotope. Delicately built forms, mostly damaged, sometimes occurring along with strongly built species, had most likely been brought here by waves, while their original biotope was that in a quiet, somewhat deeper sea where fine

pelitic sediments were deposited. Complete specimens in a satisfactory state of preservation are recorded from marly shales only.

Homogenic mutations produced, due to selection, an orthoselective evolution of the septal apparatus and of the quantitative features. This evolution is evidenced by the progressive shift of the specific correlation coefficient (Ms). On the other hand, lithological changes establish in this evolutionary plexus certain limits for forms adapted to various environments. It results that species and subspecies of *Macgeea* as well as those of *Thamnophyllum* are historical forms and that time and environment were their evolutionary factors.

EVOLUTION OF THE FAMILY THAMNOPHYLLIDAE SOSHKINA

Phylogeny

The origin of family Thamnophyllidae is not yet known. *Protomacgeea dobruchnensis* from the Middle Couvinian of Grzegorzowice is its earliest representative in Poland. Earlier representatives of this group have been, however, recorded in literature. Penecke (1894) and Soshkina (1952) described *Thamnophyllum* species from the Lower Devonian. Soshkina (1951) believes *Thamnophyllum* to be probably related most closely with *Pseudoamplexus* Weissermel or with *Zelophyllum* Wedekind (the family Kodonophyllidae Wedekind). Parricidal budding and ring of stereozone on the calicular circumference are common characters to all these three species.

Thamnophyllum is the ancestral genus for the whole family. As suggested by its general structure, it is a uniform genus. Its ontogeny is stabilised and evolutionary tendencies orthogenic. The main stem of *Thamnophyllum* was long-lived, while less important offshoots, some of them but short-lived, appeared repeatedly. Hypothetical relationships, the time of the existence of various genera and their relative frequency have been figured in a schematic graph (fig. 27). The first offshoot, most important in results, was genus *Protomacgeea*, which gave rise to that great plexus of forms comprising the subfamily Macgeeinae mihi. *Thamnophyllum*, on the other hand, together with its small offshoots, constitutes the subfamily Thamnophyllinae mihi. Thus, Thamnophyllinae and Macgeeinae were running parallel, as two phyletic lineages.

Evolutionary trends within the subfamily

Thamnophyllinae mihi

This subfamily comprises the genera *Pachyphyllum, Synaptophyllum* and *Thamnophyllum.*
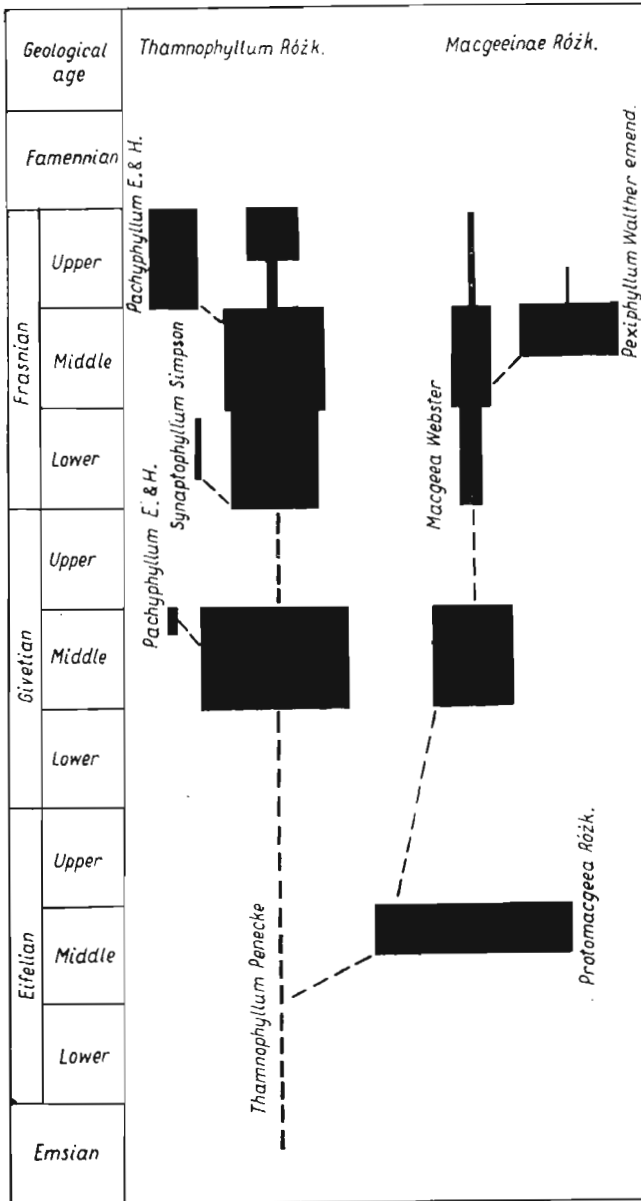
Fig. 27. — Occurrence of Thamnophyllidae genera during various Devonian periods of the Holy Cross Mts. showing relative specific frequency.

(Replace at top: *Thamnophyllum* Różk. for Thamnophyllinae Różk.)

Table 9

Numerical specification of collected specimens belonging to species of the Thamno-phyllidae family, according to geological formations

Species	Frasnian			Middle Givetian	Middle Eifelian
	Upper	Middle	Lower		
Protomacgeea dobruchnensis Różk.					212
Thamnophyllum skalense Różk.				155	
Th. trigemme (Quenst.)				129	
Th. caespitosum (Goldf.)				15	
Th. kozlowskii Różk.			174*		
Th. kozlowskii superius Różk.		193			
Th. kunthi (Dames)	100**				
Macgeea bathycalyx (Frech)				164***	
M. berdensis Soshkina	2	47	27		
M. czarnockii Różk.	1	12	4		
M. multizonata (Reed)	5	16	3		
M. supradevonica (Penecke)		1			
Pexiphyllum ultimum Walther	2	92			
P. siemiradzkii Różk.		1			
Synaptophyllum soshkinae Różk.			3		
Pachyphyllum sobolewi Różk.				13	
P. smithi Różk.	4				
P. macouni (Smith)	2				
P. friedbergi Różk.	3				
P. lacunosum Gürich	21				
P. ibergense (F. A. Roemer)	9				
P. ananas (Goldf.)	15				
P. macrommatum (F. A. Roemer)	36				
P. roemeri (Vern. & H.)	10				
P. samsonowiczi Różk.	2				
P. dybowskii Różk.	2				

*) This figure comprises specimens recovered from samples collected at Wietrznia and Sitkówka. 50 specimens were recovered at Sitkówka in one day of field work.

**) The number of specimens collected from the reef has been approximately estimated as one hundred.

***) All subspecies have been here included.

Thamnophyllum is a genus structurally uniform, but specifically well differentiated. Table 9 specifies the numerical occurrence of specimens belonging to different species within various stratigraphical horizons. Numerically predominant are the Middle Givetian species of *Thamnophyllum* (approx. 300 specimens). Within the Frasnian they are markedly less abundant since 180 specimens have been recorded from the Lower Frasnian and about the same number from the Middle Frasnian. In the Kielce region these corals are recorded only sporadically from

Upper Frasnian beds. At the locality of Mokrzeszów (Lower Silesia) there is a reef built up by *Th. kunthi.*

During its phylogeny *Thamnophyllum* produces fasciculate colonies in which the Middle Givetian *Th. skalense* has minute slender corallites producing one˙ or two buds; the Frasnian *Th. kozłowskii* occurs in fasciculate colonies with several ramifications and numerous buds. In the Middle Givetian, within a reef built up by the Tabulata, specimens belonging to this genus occur but sporadically. In the Frasnian *Th. kozłowskii* participates importantly in the formation of mixed reefs, while in the Upper Frasnian of Mokrzeszów *Th. kunthi* constitutes the dominant element of the reef.

The tendency for adaptation to the reef facies is already observable within genus *Thamnophyllum* whose participation in the formation of the reef facies increases gradually. Under favourable conditions new genera arise from *Thamnophyllum,* more adapted to life in a true reef.

Pachyphyllum. — The formation of the tabulata-stromatoporoid reef in Kamieniec favoured the appearance of genus *Pachyphyllum.* The occurrence of this genus in the Givetian is surprising. In literature *Pachyphyllum* is mentioned to appear in the Upper Frasnian, and as being then strongly differentiated. It would, therefore, seem that the morphological type corresponding to genus *Pachyphyllum* has been twice separated from the *Thamnophyllum* stem: once during the Middle Givetian and again in the Upper Frasnian. During both these periods its colonies are massive, while internal morphology displays in both cases features characteristic of *Pachyphyllum:* horse-shoe dissepiments and trabecular fans resting on them. Structural differences are specific only: the Givetian form is with thin septa and horse-shoe dissepiments, the pseudotheca being formed of scarcely discernible septal thickenings and closely spaced dissepimental rings; in Frasnian forms these elements are coarser.

The following observations might give some suggestions about the differentiation of *Pachyphyllum* and *Thamnophyllum.* During parricidal budding young buds within the calyx are connected by dissepimental tissue („*caenogenetic*" after Soshkina, 1956), as if constituting an incipient massive colony. It is not as yet known in what way massive *Pachyphyllum* colonies, with peripheral budding, have twice originated, as intermediate forms have not been recorded. Perhaps, *Pachyphyllum* originated in another part of the Givetian sea and thence immigrated into the area of Holy Cross Mountains. For the time being it is a cryptogenic form, but its origin was in any case connected with caenogenesis; in later stages of *Thamnophyllum* ontogeny the dissepimental tissue between the buds

disappears, while in *Pachyphyllum* it persists throughout the whole existence and constitutes a platform surrounding the tabularium.

Pachyphyllum thus makes its first appearance in the Middle Givetian, the second in the Upper Frasnian. Between the two periods there is a long gap of time when this genus is not recorded. Its species in the two phases are not, therefore, genetically connected. This phenomenon is to be interpreted as an iterative evolution. The same genus branched off twice from the conservative stem of *Thamnophyllum*.

Pachyphyllum sobolewi is the only Givetian species, while there is strong specific differentiation within the Frasnian. These forms have been referred by the writer to three groups of species: 1) group of *Pachyphyllum lacunosum* with allied species *P. smithi* and *P. friedbergi;* 2) group of *Pachyphyllum ananas* with species *P. roemeri, P. macrommata, P. samsonowiczi* and *P. dybowskii;* 3) group of *Pachyphyllum ibergense* with subspecies *P. ibergense progressa* and species *P. macouni.*

In 1953, the numerous Upper Frasnian forms with massive colonies were by the writer referred to two genera: *Pachyphyllum* Edwards — Haime, 1850, and *Pseudoacervularia* Schlüter, 1881. *Pachyphyllum* (genotype *P. bouchardi* E. & H., 1850) often quoted in literature, contained microtabular species with short septa and complete tabulae. For specimens with large tabularia, long septa and complicated incomplete tabulae, the name of *Pseudoacervularia* Schlüter (genolectotype *Acervularia macrommata* F. A. Roemer, 1855) has been accepted by the writer (1953). In the present paper the name of *Pseudoacervularia* has been eliminated and all of its species referred to *Pachyphyllum*. This change was done with a view of simplifying systematics by the elimination of genera without objective evidence. Genera *Pachyphyllum* and *Pseudoacervularia* were not distinctly separated since there exists a group of species belonging to *Pachyphyllum ibergense* F. A. Roemer that displays features of micro- and macrotabular groups. The correctness of referring all the species thus far known to the present writer to genus *Pachyphyllum* is supported by statistical graph (fig. 26).

The strong differentiation of forms towards the close of phyletic evolution of the subfamily Pachyphyllinae is most surprising. As is seen from table 9, ten different species of *Pachyphyllum* occur together in the Upper Frasnian almost simultaneously. Perfectly new structures arise but without producing new evolutionary lineages since they disappear together with the neritic facies.

Another problem must be considered in connection with the repeated appearance of genus *Pachyphyllum*. A great interval of time occurred between the Middle Givetian and the Upper Frasnian. The presence of

Pachyphyllum is not noted within this interval though the prevailing conditons were favourable, as for instance in Wietrznia where reef facies of the coral-stromatoporoid type predominated. These conditions are illustrated by the statement here below:

Age	Massive colonies [3]
Upper Frasnian	*Pachyphyllum, Phillipsastraea*
Middle Frasnian	*Phillipsastraea, Hexagonaria*
Lower Frasnian	„ „
Middle Givetian (top)	*Pachyphyllum*
„ „ (central part)	*Hexagonaria*

Hexagonaria predominate as a rule within the reef facies of the Middle Givetian. It is in Kamieniec only, that large *Pachyphyllum* colonies occur to the top of Middle Givetian beds, among stromatoporoids and Tabulata, where *Hexagonaria* are wholly missing. It is to be inferred that conditions must have prevailed there unfavourable to the latter genus. Within the Lower and Middle Frasnian all the free niches within the reefs are occupied by differentiated colonies of *Phillipsastraea* of unrivalled strength, which do not allow the development of other forms of massive colonies. In the Upper Frasnian, *Phillipsastraea* partly retreats to be replaced by the new plastic genus *Pachyphyllum*.

To the subfamily Thamnophyllinae also belongs genus *Synaptophyllum* Simpson, 1900, which makes its appearance in the Devonian of Poland during the Lower Frasnian. It forms phacelloid colonies resembling those of *Thamnophyllum* in parricidal budding. New features also appear: septa are carinate and the individual corallites of a colony are, throughout ontogeny, interconnected by dissepimental tissue which produces side processes. The origin of genus *Synaptophyllum* is thus again connected with caenogenesis. It constitutes as if an intermediate stage between *Thamnophyllum* and *Pachyphyllum.* The ontogeny of the representatives of *Synaptophyllum* is not known to the present writer, making it impossible to ascertain whether the "talon stage" and bilateral symmetry are equally conspicuous as in *Thamnophyllum.* In *Synaptophyllum soshkinae* Różk. distinct convergence is noted with the species *Pachyphyllum samsonowiczi* since both these forms display a similar subphacelloid habitat and their syringoporoidal processes contain dissepimental tissue. Reversibility of the evolutionary process is here apparently possible, but this is not the case. In the history of the

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[3] D. Hill (1935) distinguished simple and compound corals. Among the latter she mentions fasciculate and massive forms.

family Thamnophyllidae both these forms represent quite different evolutionary stages. *Synaptophyllum soshkinae* is, so to say, at the beginning of the starting point of the massive colonies, while *Pachyphyllum samsonowiczi* is at their end when they again become phacelloid.

The subfamily Thamnophyllinae is thus characterised by the power to produce fasciculate and massive forms, which enables it to participate in the formation of reefs.

Evolutionary trends within the subfamily
Macgeeinae mihi

This subfamily unite the genera *Protomacgeea, Macgeea* and *Pexiphyllum*. It has most likely developed from *Protomacgeea* since its representatives display similar characters: dominating conical shape, all species, but a few, simple, with extremely rare parricidal *(Macgeea)* or peripheral *(Pexiphyllum)* budding. The massive colony stage is never attained by any representatives of this subfamily. Ontogenic development is most complicated. Bilateral symmetry is followed throughout the ontogeny.

Protomacgeea appears in the top of Middle Eifelian beds, it is not recorded from younger strata. We do not know the origin of this genus as it is a distinctly cryptogenic form. It probably descended from *Thamnophyllum,* since, according to present information, it is the only genus that existed in the Lower Devonian and the Lower Eifelian (besides the cerioidal *Trapezophyllum*). The origin of *Protomacgeea* was connected with the phenomenon of rejuvenescence and with strong morphological changes. All the specimens are of markedly small dimensions and simple structure, the structural scheme being as in other representatives of Thamnophyllidae, except for a few generic characters. The origin and evolution of this form must have taken place in a different sea and subsequently it found favourable environmental conditons within the Eifelian sea of the Holy Cross Mts. region. *Protomacgeea* occurs, as we now know, only in the Middle Eifelian and is characteristic by almost complete reduction of the cardinal septum· It represents the first stage of phylogenetic evolution of *Macgeea*.

The second phylogenetic stage was produced by *Macgeea* s. str. The shortened cardinal septum has been inherited from *Protomacgeea,* its probable ancestor. During the life history of *Macgeea*, the cardinal septum is lengthened and after fluctuating during the Givetian, it becomes during the Frasnian the dominating septum in the calyx. The

beginning of genus *Macgeea* in the Holy Cross Mts. region is unknown as Upper Eifelian and Lower Givetian beds are dolomitic and do not yield corals. The oldest representatives of *Macgeea* in Poland occur from the base of the Middle Givetian to the top of the ·Upper Frasnian. Its evolutionary top is attained in the Middle Frasnian. By that time *Macgeea* has become a strongly differentiated and specialised form. During the Middle Givetian maximum frequency is noted (table 9). It is quite sporadical in the top of the Upper Frasnian and does not pass into the Famennian.

The third and last evolutionary stage of Macgeeinae is represented by *Pexiphyllum* Walther. This genus possibly arose from *Macgeea czarnockii* (Ms = 2.44). The origin of *Pexiphyllum,* as is often observable in Corals, was connected with regression expressed by a decrease in growth of the corallite and in markedly high value of the correlation coefficient (Ms = 4.3). In spite of these regressions the length of the cardinal septum progresses continuously during the Frasnian. In *Macgeea czarnockii* the cardinal septum is the longest one even in its youngest stage, while during later stages it reaches, together with some other metasepta, near to the axis of the corallite (fig. 19 *A-B*)·

In *Pexiphyllum* (fig. 22 *A-B*), beginning with the earliest youth, the cardinal septum and some metasepta reach to the axis and are fused into a columella, which persists throughout the corallite's life-time. Such changes are known as acceleration but this pattern of structure must have proved disadvantageous as it did not persist long. Fragmentary specimens of large individuals of this genus are occasionally encountered in the base of the Upper Frasnian, but they are its last representatives.

An inspection of the Macgeeinae shows clearly that its evolutionary trends in the first place involve the lengthening of the cardinal septum until it touches with other metasepta the axis of the corallite. Macgeeinae did not alter their habitus since they produced neither fasciculate nor massive colonies. During the Givetian they occurred mostly in a somewhat deeper sea with marly sediments, during the Frasnian they passed to a more shallow sea but were not able to adapt to the reef facies.

STRATIGRAPHICAL DISTRIBUTION OF THE FAMILY THAMNOPHYLLIDAE SOSHKINA

In the course of its existence from the Middle Eifelian through the Upper Frasnian five genera of Thamnophyllidae evolved, thus far recorded in Poland, as shown by the table 10.

Table 10

Occurrence of genera of Thamnophyllidae
(those underlined appeared during that particular period)

Upper	Middle	Lower	Middle Givetian	Middle Eifelian
	F r a s n i a n			
Thamnophylum *Macgeea* *Pexiphyllum* *Pachyphyllum*	*Thamnophyllum* *Macgeea* *Pexiphyllum*	*Thamnophyllum* *Macgeea* *Synaptophyllum*	*Thamnophyllum* *Macgeea* *Pachyphyllum*	*Thamnophyllum* *Protomacgeea*

Some of these genera were but short-lived, such as *Protomacgeea* and *Synaptophyllum*, others, such as *Thamnophyllum* and *Macgeea* lived long. The short duration of some forms was probably due to their less favourable construction, which eliminated them by selection. New genera appear with new biotopes: *Protomacgeea* is linked with the appearance of a facies rich in limestone; *Macgeea* with a somewhat deeper facies of mudstones and marls; *Pachyphyllum* with the shallowing of the sea and reef formation, as is also *Synaptophyllum*; *Pexiphyllum* with the detrital facies. In the neritic zone of Devonian sea, abounding in bays, where epirogenetic action caused environmental changes, conditions prevailed distinctly favourable for the persistance of new genera, particularly so where probable barriers made isolation easy.

What geological period had witnessed the maximum development of the Thamnophyllidae? As is shown in table 10, genus *Thamnophyllum* was most likely already in existence during the Middle Eifelian while *Protomacgeea* then made its appearance. Two new genera: *Macgeea* and *Pachyphyllum* appeared during the Givetian, *Synaptophyllum* — during the Lower Frasnian, *Pexiphyllum* — during the Middle Frasnian, while *Pachyphyllum* re-appeared during the Upper Frasnian. The Middle Givetian is thus shown to have been the time of the most intense differentiation, all morphological types had appeared by that time, i. e. the simple *Macgeea*, the fasciculate or phacelloid *Thamnophyllum* and the massive colonies of genus *Pachyphyllum·* Thus, the stage of intensified morphological differentiation co-incides with the middle part of the existence of Thamnophyllidae (if we take account of the fact that *Thamnophyllum* was recorded beginning with the Emsian). After that time the power to produce new forms continues but it is weaker. Newly produced types must have been less fit since they were short-lived, e. g. *Synaptophyllum* and *Pexiphyllum*. *Pachyphyllum* re-appears during the Upper Frasnian displaying great specific differentiation.

While simple forms and poorly ramified colonies persist through the Eifelian, the Givetian, and the Lower and Middle Frasnian, the Upper Frasnian shows a predominance of forms with massive colonies, and simple forms grow very scarce though conditions profitable to them continued also in the shallowed sea. The time of their blossom, connected with a facies of marls and mudstones, had, however, already past.

Two phases may thus be distinguished in the life history of Thamnophyllidae, one characterised by the domination of simple and fasciculate forms with sporadical massive colonies, and the second, an end-phase, of Upper Frasnian age, where forms with massive colonies predominate. While during the first phase Thamnophyllidae had to struggle against strong competition of an abundant and markedly differentiated tetracoral fauna, conditions are reversed during the second phase as other families retreat and Thamnophyllidae predominate. In the Givetian Thamnophyllidae were plastic, but they did not continue during the Famennian though coral fauna from Famennian beds in Wietrznia and Gałęzice is fairly differentiated and abounds in other assemblages.

We do not know the cause of the extinction of Thamnophyllidae. Neither do we know whether they have given rise to a new group. Forms nearing the end of their existence do not, as a rule, pass into a changed facies.

During the Upper Frasnian, Pachyphyllidae display every symptom of specialisation, though hypertrophy hardly occurs at all. There is no distinct peripheral reduction of septa nor stout and closely spaced carinae. Nevertheless simple forms die out already at the beginning of the Frasnian. Genera *Macgeea* and *Thamnophyllum* perish. The regressive reef-building species of *Thamnophyllum kunthi,* recorded from Mokrzeszów, is an exception. The strongly differentiated *Pachyphyllum* occupies the reef facies of the shallow sea of the Kielce anticline, with water pure at some distance from the continent. But *Pachyphyllum* disappears in Poland too, together with deep sea transgression during the Famennian·

PALEOGEOGRAPHICAL DISTRIBUTION OF THE FAMILY THAMNOPHYLLIDAE SOSHKINA

In papers published in 1953 and 1956 the present writer has described Thamnophyllidae recorded from the Holy Cross Mts. only, namely from the Kielce region and from the Grzegorzowice-Skały section. This area is perfectly suitable for research work since the Devonian beds here display a mostly limestone facies, continuity of sedimentation is long-

lasting and the coral fauna copious and strongly differentiated. Besides the here mentioned areas, Devonian corals have been collected also in the vicinity of Siewierz, near Dębnik, and in the Sudeten where Upper Devonian beds have long ago been ascertained at the locality of Mokrzeszów (Oberkunzendorf, Iberg beds, of German authors).

Mokrzeszów

Cyathophyllum kunthi Dames was in 1868 described from this locality by W. Dames. An exhaustive description of this species, under the name of *Fascicularia kunthi* (Dames) was in 1873 given by W. N. Dybowski. The specific and generic appurtenance of this form was manifoldly interpreted. A. Schouppé (1949) gave a detailed account of its history regarding it then as synonymous with *Macgeea (Thamnophyllum) caespitosum* (Goldfuss) var. *minus* (Roemer). H. Flügel (1956), on the other hand, made it an independent species and described it under the name of *Macgeea (Thamnophyllum) kunthi* (Dames).

Having at her disposal a rich collection of corals from Mokrzeszów, especially samples of *Thamnophyllum kunthi*, of which 17 microscopic sections have been cut, the writer wishes to make some comments on this problem.

The Mokrzeszów specimens belonging to species *kunthi* Dames are undoubtedly referable to genus *Thamnophyllum*, since they are provided with horse-shoe dissepiments and symmetrical trabecular fans resting thereon. In some corallites the horse-shoe dissepiments are thick-walled and regularly oval. If the epitheca is preserved a row of horizontal dissepiments appears along with those of the horse-shoe type (as shown by Dybowski, 1873, p. 13, fig. 3). Such specimens are rare since the epitheca falls off in most cases and the horse-shoe dissepiments are then a marginal structural element. There is another eventuality: the horse-shoe dissepiments are thin-walled (fig. 1) and dissepiments, if preserved, are convex towards the top and occur without distinct separation from the horse-shoe dissepiments. The decisive structural element here are the symmetrical trabecular fans always resting on the horse-shoe dissepiments. It is in this detail that individuals of species *kunthi* Dames differ from convergent representatives of genus *Peneckiella*. After Soshkina (1951) the latter are with trabeculae disposed in a parallel pattern, characteristic for the majority of Tetracorals. The following are noteworthy morphological details: *Thamnophyllum kunthi* is sometimes provided with syringoporoidal processes and increases by peripheral and not parricidal budding, whence the irregular structure in transverse sections.

T. kunthi is accompanied by numerous simple forms of *Tabulophyllum priscum* Münster. This is the only element in common with the coral Upper Frasnian assemblages from the Holy Cross Mts., but massive colonies of *Phillipsastraea* and *Pachyphyllum* are altogether lacking.

Special local conditions probably prevailed in the Mokrzeszów bay favouring the occurrence of *T. kunthi* which has not, thus far, been recorded from the Holy Cross Mts.

Another representative of Thamnophyllidae, viz. *Macgeea berdensis* has been collected by the writer from the Sudeten area. A pebble of grey marly limestone, probably derived from Lower or Middle Frasnian deposits, thus far not recorded in situ from the Sudeten area, was found in Devonian or Culm conglomerates in Witoszów near Świebodzice. This pebble has yielded *Macgeea berdensis* Soshkina showing a structural characteristic of this species [4].

Siewierz — Góra Dziewki

Colonies of *Hexagonaria laxa* Gürich were collected and described by G. Gürich (1896) from Givetian beds in coral reef limestones of this locality, made up mostly of banks with *Amphipora* and Stromatoporoids. This species is occasionally reef building, other Tetracorals are rare here [5]. No specimens of Thamnophyllidae have thus far been recorded by the writer within the Devonian beds of Siewierz.

Dębnik

Within limestones of the Givetian, banks with amphipors and stromatoporoids occur here containing few simple corallites of *Amplexus,* but representatives of the Thamnophyllidae have not been here encountered.

The Upper Frasnian Dębnik beds, however, yield a fauna of corals from the family Thamnophyllidae abounding in species identical with those from the Kielce region. At the locality of Zarówczany Dół, specimens have been collected whose morphology agrees with that displayed by representatives of the same species from the Holy Cross Mts. The specific coefficient is very close in both. The presence of following forms has been here recorded by the writer:

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[4] All corals quoted in the present paper have been described by the present author in 1953 and 1956.

[5] Data on the Devonian of Siewierz have been kindly supplied to the writer by Mr. St. Śliwiński for which her sincere thanks are due to him.

Pachyphyllum macrommatum (F. A. Roemer). — One large colony. Measurements were taken of 23 calices in order to establish the n/t correlation. The Ms value for *macrommatum* from Dębnik is 7.87, for the same form from the Holy Cross Mts. it is 7.70. These values are very near. Account must be taken of the measurements having been taken within one colony only where proportions of practically all calices closely approach;

Pachyphyllum friedbergi Różkowska. — Correlation coefficient of species calculated on measurements of six calices is rather high as compared with that of specimens from the Holy Cross Mts., to say: the Ms value for *friedbergi* from Dębnik is 15.6, for the same form from Kielce it is 15.0. Juvenile corallites predominate in this colony, their correlations are with higher values. When the Mn/Mt relation of small diameters (1.1 to 1.6 mm) is taken into account, Ms value of *friedbergi* from the Holy Cross Mts. is nearer (15.9) to that of the Dębnik species;

Pachyphyllum ibergense (F. A. Roemer) — preserved as two small fragments of an astreoidal colony. Their morphology and the n/t relation fully agree with the Kielce specimens;

Pachyphyllum roemeri (Vern. & H.). — Minute fragments of a colony preserved in concretionary limestone. Correlation coefficient of species calculated on relation within several calices is Ms = 11.4, thus being near to that of the Kielce forms (Ms = 11.7).

Macgeea aff. *supradevonica* (Penecke). — One damaged specimen with diameter of 3 cm and 80 major + minor septa. It is larger than the only one specimen thus far recorded from Wietrznia (near Kielce). Differences of growth may be explained by its geologically younger age, since the Wietrznia specimen has been recorded from the Middle Frasnian, that from Dębnik being from the Upper Frasnian, as is indicated by the presence of *Phillipsastraea goldfussi* E. & H..;

Macgeea multizonata Reed. — Four fragments have been found with parricidal budding discernible on one of them;

Pexiphyllum ultimum Walther. — One specimen only in a longitudinal section. *Pexiphyllum ultimum* is abundant in Middle Frasnian deposits of Wietrznia, but it also passes into the Upper Frasnian;

Thamnophyllum kunthi (Dames) — After polishing a specimen set in a concretionary limestone, with diameter of 4 mm, 28 major + minor septa were noted, the longest reaching to the axis.

A revision of the Thamnophyllidae family, in respect to localities mentioned above, indicated that they developed in various facies and basins without changing their fundamental family features (Soshkina, 1951), but nevertheless producing numerous species. Their presence has

been ascertained in Poland within Middle Devonian deposits of Grzegorzowice, Skały and Śniadka[6]. They are absent, however, from vicinity of banks with *Amphipora* in Sitkówka, Dębnik, Siewierz and Chęciny. The predominant form here is *Disphyllum*. Other ecological niches favouring *Disphyllum* but unsuitable for Thamnophyllidae must have prevailed then within the quoted areas.

Pachyphyllum was predominant within Upper Frasnian deposits of the Holy Cross Mts. and in the Kraków region. No representatives of the Thamnophyllidae with massive colonies have, however, been found by the writer at Mokrzeszów which is not far distant. A different, isolated environment is thus represented in that locality.

Identical coral assemblages occur within Upper Devonian deposits of Kielce and Dębnik. Hence the deduction that the same ecological conditions prevailed within basins of these two regions. The correlation coefficient of species is mostly somewhat lower in forms recorded from the Kielce region. This may be probably interpreted by a slight stratigraphical difference of these two Upper Frasnian assemblages.

Thamnophyllidae, as stated by the writer in 1953, are known throughout the globe. Some species have a wide geographical range, while others are regarded as local forms, but after better inquiries, some of the latter may also prove to be more widespread.

FINAL CONCLUSIONS

I. Biometrical analyses done on material belonging to the Thamnophyllidae have resulted in the following inferences:

a) the objectiveness of species and genera, previously established on morphological criteria, has been confirmed;

b) intraspecific and intra-subspecific relationships have been elucidated;

c) the role played by such phyletic phenomena as regression and rejuvenescence has been stressed;

d) speciation is shown to have been a gradual process, while species are historical entities;

e) correlation coefficient of species is stated to be subjected to gradual and directional evolution whence it may also be a stratigraphical index;

f) correlation coefficient of species can be a diagnostic feature for synchronical forms;

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[6] Mrs. M. Pajchel and Miss W. Gogolczyk have kindly presented this writer with a collection of Tetracorals containing a Givetian specimen of *Thamnophyllum caespitosum*.

g) variation of coefficients indicates certain evolutionary trends characteristic of congeneric species;

h) evolutionary tendencies are linked by the phenomenon of allometry, which changes during ontogeny as well as phylogeny. Negative or positive allometry is displayed by various skeletal elements in different genera.

II. The study of early ontogenetic stages of species inter-related during historical development indicates that:

a) there may exist species of a given genus, whose ontogeny was stabilized, while new species were evolving from it by deviation;

b) species of some genus gradually shorten their ontogeny, accelerating the evolution of a certain feature;

c) variability of ontogeny after a certain time passes into stability.

III. Ontogenic studies of different genera indicate that:

a) new genera appear as rejuvenated minute forms, new structural features being displayed from the earliest stages of ontogeny (tachygenesis);

b) during the differentiation of genera an important part is played by the phenomenon of caenogenesis.

IV. A comparison of morphological features has shown that:

a) there is a distinct relation between corallite morphology and the lithological character of sediment;

b) time and environment are chief factors in the formation of species;

c) in a rapidly shifting environment there is a succession of dissembling species; these are probably allopatric species;

d) repeated complexes of specific morphological features indicate random mutation and eliminating selection;

e) phenomenon of iteration may take place under re-occurring similar conditions of environment;

f) extinction of phyletic lineages is connected with strong environmental changes to which forms of limited plasticity could not adapt.

V. A comparison of paleogeographic environments shows that the Thamnophyllidae are known throughout the globe, but particular species have a limited geographical range owing either to their distinct facial requirements, or to the existence of isolated marine basins into which they were not always able to penetrate.

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MARIA RÓŻKOWSKA

ROZWAŻANIA OGÓLNE DOTYCZĄCE RODZINY THAMNOPHYLLIDAE SOSHKINA W ŚRODKOWYM I GÓRNYM DEWONIE POLSKI

Część II *

Streszczenie

Praca niniejsza jest uzupełnieniem badań, których rezultaty ogłosiłam w latach 1953 i 1956. Podano wówczas opisy cech jakościowych gatunków rodziny Thamnophyllidae. Badania nad tą grupą Tetracoralla trwały 10 lat; w toku pracy wyłoniły się różne ciekawe problemy, które przedstawiam obecnie. Nie są one jeszcze wyczerpujące, lecz będą może pomocne innym pracownikom w tej dziedzinie.

W poprzednich pracach umieściłam wszystkie korality, mające dissepimenta w kształcie podkówek i na nich oparte wachlarze trabekularne, w podrodzinie Pachyphyllinae Stumm (rodzina Dysphyllidae Hill). Obecnie, podobnie jak Soshkina (1941) i Schouppé (1956), wyodrębniłam je w samodzielną rodzinę Thamnophyllidae Soshkina. Podział systematyczny tej rodziny podałam w zestawieniu (str. 83).

Korale są bardzo plastyczne, co wyraża się w wielkiej zmienności osobniczej i gatunkowej. Poza pracami Richtera (1916) i Voynovskiego-Krigera (1956), zmienność cech ilościowych nie doczekała się jeszcze szerszego opracowania. W niniejszej pracy przeprowadziłam analizę biometryczną cech ilościowych, łatwo dostępnych do po-

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* Część I, pt. Pachyphyllinae ze środkowego dewonu Gór Świętokrzyskich, ukazała się w „Acta Palaeont. Pol.", vol. I/4, 1956.

miarów, a mianowicie średnicy kielicha i liczby septów. Najpierw obliczyłam dla różnych stadiów ontogenetycznych zmiany korelacji n/d, tj. stosunku między liczbą septów a średnicą kielicha. Porównałam dane biometryczne dolno-frańskiego gatunku Th. kozłowskii Różk. z Sitkówki i okazami tegoż gatunku z Wietrzni (tab. 1—4 i fig. 2). Współczynnik gatunkowy (Ms) dla osobników z dwóch różnych środowisk jest prawie równy. Mała różnica świadczy o nieco młodszym wieku geologicznym okazów z Wietrzni.

Opracowanie statystyczne wszystkich gatunków Thamnophyllum (tab. 5 i fig. 3) dało następujące ważne wyniki.

Wraz z wiekiem geologicznym warstw zmniejsza się współczynnik gatunkowy, lecz jest on stały dla tego samego gatunku, pochodzącego z równowiekowych warstw. Dla gatunków środkowo-żyweckich jest on nieco wyższy niż 3, dla frańskich zaś nieco wyższy niż 2; służyć więc może prawdopodobnie jako wskaźnik wieku geologicznego.

Obiektywność gatunków została potwierdzona przez jednowierzchołkowe krzywe zmienności (fig. 4 i 5). Gatunki Thamnophyllum mają jednolitą, ustabilizowaną ontogenezę i wykazują dość dużą, lecz niezbyt urozmaiconą zmienność struktury. Na podstawie obserwacji ontogenezy, morfologii oraz tendencji rozwojowej gatunków stwierdziłam zasadnicze różnice taksonomiczne między rodzajami Thamnophyllum i Macgeea (tab. 7). Wskazują one wyraźnie na samodzielność obu rodzajów. Połączenie Thamnophyllum i Macgeea w jeden rodzaj Macgeea, jak to czyni Schouppé, nie jest wobec tego uzasadnione.

Takie same badania przeprowadziłam dla gatunków rodzaju Macgeea (tab. 8 i fig. 11). Współczynnik gatunkowy (Ms) powiększa się u form geologicznie coraz młodszych. Wypływa stąd wniosek, że w korelacji n/d w odniesieniu do liczby septów panuje allometria dodatnia. U Thamnophyllum, odwrotnie, panuje allometria ujemna. U Macgeea liczba septów wzrasta progresywnie podczas żywetu i franu, mimo że na początku franu występuje regresja. W ten sposób obserwuje się dwuetapowość w filogenezie tego rodzaju; u Thamnophyllum natomiast rozwój posuwa się ortogenetycznie naprzód, bez zahamowania.

Mając do dyspozycji liczne i dobrze zachowane okazy z rodzaju Macgeea można było przeprowadzić obserwacje w odniesieniu do ontogenezy. Wyniki są następujące: długość septum głównego zwiększa się progresywnie podczas żywetu i franu. Formy żyweckie wykazują pod tym względem podczas ontogenezy pewne wahania. We franie septum główne stabilizuje się jako septum dominujące (fig. 14-20).

Rodzaje Thamnophyllum i Macgeea są gatunkowo urozmaicone i długotrwałe, dlatego badania biometryczne można było przeprowadzić kolejno u gatunków historycznie coraz młodszych. Rodzaj Pexiphyllum jest krótkotrwały i jeden tylko gatunek mógł dostarczyć okazów do analizy statystycznej. Jego współczynnik gatunkowy (Ms) jest względnie duży, zbliżony do wartości u Macgeea bathycalyx amabilis, co świadczy, być może, o regresji i pochodzeniu jego od rodzaju Macgeea (fig. 23 i 24).

Zbadana została również zmienność cech ilościowych u przedstawicieli rodzaju *Pachyphyllum*. W 1953 r. zaliczyłam Thamnophyllinae o koloniach masywnych do dwóch rodzajów: *Pachyphyllum* i *Pseudoacervularia* Schlüter. Badania biometryczne wykazały jednak, że gatunki te należą do jednego rodzaju *Pachyphyllum*, wśród którego wyróżnić można 4 grupy gatunków (fig. 25 i 26).

Wśród dalszych, rozpatrzonych w niniejszej pracy zagadnień, wymienić należy problem specjacji. Uwydatnia się on najwyraźniej u gatunków rodzajów *Thamnophyllum* i *Macgeea*, ponieważ pojawiają się one w litologicznie różnych warstwach, leżących bezpośrednio jedne nad drugimi. U *Thamnophyllum* cechy ilościowe rozwijają się stopniowo i ortoselekcyjnie, są wobec tego funkcją czasu i selekcji. Cechy jakościowe zmieniają się bezkierunkowo, gdyż pojawiają się wraz ze zmianą środowiska, wykazują więc wyraźną adaptację. Zróżnicowanie gatunkowe jest dość duże. gdyż w środkowym żywecie dno morza ulegało ruchom pozytywnym i negatywnym; w związku z tym zmieniały się facje i osady, a równocześnie imigrowały gatunki przystosowane do danego środowiska. Gatunki *Thamnophyllum* rozwijają się stopniowo, czynnikami zaś specjacji są tu czas i środowisko wraz z selekcją i izolacją.

Podobne wyniki uzyskałam w odniesieniu do rodzaju *Macgeea*. Tutaj jednak występuje, obok kierunkowej zmienności cech ilościowych, również stopniowa zmienność niektórych cech jakościowych. Taka płynność ewolucyjna utrudnia wyodrębnienie gatunków, zwłaszcza w żywecie. We franie cechy jakościowe są ustabilizowane i na podstawie pokroju koralitów i ich wewnętrznej morfologii gatunki można łatwiej odgraniczyć.

Rozważania nad filogenezą rodziny Thamnophyllidae dały następujące wyniki.

Niektóre rodzaje, jak *Pachyphyllum* i *Protomacgeea*, są typami kryptogenicznymi. U innych rodzajów nowe cechy jakościowe pojawiają się od najwcześniejszej ontogenezy i przyśpieszają jej przebieg *(Pexiphyllum)*. Powstanie niektórych rodzajów łączy się ze zjawiskiem cenogenezy *(Pachyphyllum* i *Synaptophyllum)*. *Pachyphyllum* oddziela się dwukrotnie od konserwatywnego pnia *Thamnophyllum:* raz w środkowym żywecie, drugi raz we franie górnym (ewolucja iteratywna?).

W obrębie podrodzin Thamnophyllinae i Macgeeinae tendencje rozwojowe są różne, a mianowicie: Thamnophyllinae rozbudowują kolonie krzaczaste w masywne, wchodzą w fację rafową i w końcu biorą czynny udział w budowie raf; Macgeeinae natomiast rozbudowują aparat septalny, kolonii nie tworzą (poza kilku słabo rozgałęzionymi formami) i nie występują w facji rafowej jako czynnik twórczy.

W historycznym przeglądzie (tab. 10) tej rodziny stwierdza się, że okresem najbardziej intensywnego jej rozwoju był środkowy żywet; występują wtedy już wszystkie 3 typy budowy: osobniczy, krzaczasty i kolonii masywnej. W czasie od środkowego eiflu do śr. franu dominują formy osobnicze i krzaczaste, które w górnym franie ustępują, a nisze płytkiego morza górno-frańskiego zajmowane są przez formy o koloniach masywnych. W Polsce Thamnophyllidae nie przechodzą do famenu, wygasając

z końcem górnego franu. Po okresach silnego zróżnicowania nie miały już one zdolności przystosowania się do głębokich zmian, występujących w morzu fameńskim.

Zbadano również Thamnophyllidae z innych obszarów dewonu Polski. Stwierdzono przy tym, że fauna Mokrzeszowa (Sudety) ma w górnym franie odmienny skład zespołowy, co wytłumaczyć można przystosowaniem się do innej facji, panującej w odciętej zatoce. Fauna Gór Świętokrzyskich i Dębnika natomiast we franie górnym jest identyczna, musiały więc tutaj istnieć podobne warunki facjalne.

Z obserwacji paleogeografii wynika, że Thamnophyllidae występują prawie na całym świecie, mają jednak swoiste wymagania ekologiczne. Nie występują bowiem w każdej facji płytkomorskiej dewonu Polski, gdzie natrafiamy na Tetracoralla. Thamnophyllidae w dewonie Polski znane są dotychczas tylko z obszaru kieleckiego, profilu Grzegorzowice-Skały, ze Śniadki, Dębnika i z Sudetów.

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 84)

Thamnophyllum kunthi (Dames), topotyp. Mokrzeszów, górny fran. Przekrój podłużny: *A* okazu z gęstymi, kompletnymi tabulami, *B* okazu o rzadkich, niekompletnych tabulach.

Fig. 2 (p. 89)

Thamnophyllum kozłowskii Różk. Linie korelacji n/d (stosunek liczby septów I rzędu do średnicy kielichów, w mm). Linia ciągła — dla okazów z dolnego franu Sitkówki; poszczególne warianty oznaczone kółkiem. Linia przerywana — dla okazów z Wietrzni; poszczególne warianty oznaczone kropkami. Odnośne dane pomiarowe — na tab. 3 i 4.

Fig. 3 (p. 90)

Linie korelacji n/d u gatunków rodzaju *Thamnophyllum* ze środkowego i górnego dewonu Polski. Na osi rzędnych umieszczono liczby septów I rzędu, na osi odciętych — średnice kielichów, w mm. Odnośne dane pomiarowe — na tab. 5.

(Fig. 4 (p. 96)

Krzywe zmienności korelacji n/d dla kilku gatunków rodzaju *Thamnophyllum*. Na osi rzędnych — liczba koralitów, w %%; na osi odciętych — korelacje n/d, w mm.

Fig. 5 (p. 97)

Krzywe zmienności dla *Thamnophyllum skalense* Różk. ze środkowego żywetu Skał i dla form regresywnych *Th. trigemme pajchelae* i *Th. kunthi* z górnego franu Mokrzeszowa.

Fig. 6 (p. 98)

Linie korelacji a/d (stosunek oddalenia septów I rzędu do średnicy kielichów) u kilku gatunków rodzaju *Thamnophyllum*. Na osi rzędnych podane odległości międzyseptalne, na osi odciętych — średnice kielichów, w mm.

Fig. 7 (p. 99)

Thamnophyllum skalense Różk. Skały, środkowy żywet. Wczesna ontogeneza stadium „talonu"; *1* septum główne, × 10 (wg Różkowskiej, 1956, fig. 29).

Fig. 8 (p. 100)

Thamnophyllum caespitosum (Goldf.). Skały, środkowy żywet. Między pączkami lateralnymi tkanka dissepimentalna „cenogenetyczna", $\times$ 4 (wg Różkowskiej, 1956. fig. 30).

Fig. 9 (p 100)

Thamnophyllum kozłowskii Różk. Sitkówka, dolny fran. Kolonia krzaczasta z kilkakrotnie powtarzającym się pączkowaniem parycydalnym, $\times$ 0,6.

Fig. 10 (p. 100)

Thamnophyllum kunthi (Dames). Mokrzeszów, górny fran. Przekrój poprzeczny topotypu.

Fig. 11 (p. 103)

Linie korelacji n/d dla gatunków rodzaju *Macgeea* ze środkowego i górnego dewonu Polski.

Fig. 12 (p. 107)

Krzywe zmienności dla kilku gatunków i podgatunków rodzaju *Macgeea* ze środkowego i górnego dewonu Polski. Na osi rzędnych — liczba osobników, w $^0/o^0/o$; na osi odciętych — korelacje n/d, w mm.

Fig. 13 (p. 109)

Protomacgeea dobruchnensis Różk. Grzegorzowice, środkowy eifel. Trzy stadia ontogenezy: *A* neaniczne, $\times$ 40, *B* późnoneaniczne, $\times$ 23; *C* efebiczne, $\times$ 7.5. *1* septum przeciwległe, *2* stereoma, *3* zredukowane septum główne (wg Różkowskiej, 1956, fig. 6 B-C i 7).

Fig. 14 (p. 110)

Macgeea bathycalyx kasimiri Różk. Skały, środkowy żywet. Trzy stadia ontogenezy: *A* wczesnoneaniczne, z trójkątną fossulą; *B* późnoneaniczne, z rynienkowatą fossulą; *C* efebiczne, fossula otwarta, septum główne (*1*) długie; *D* efebiczne, fossula trójkątna. septum główne krótkie.

Fig. 15 (p. 112)

Macgeea bathycalyx josephi Różk. Skały, środkowy żywet. Trzy stadia ontogenezy: *A* wczesnoneaniczne, z fossulą trójkątną i krótkim septum głównym (*1*); *B* późnoneaniczne, z fossulą otwartą, rynienkowatą; *C* efebiczne, z fossulą otwartą.

Fig. 16 (p 113)

Macgeea bathycalyx amabilis Różk. Skały, środkowy żywet. Trzy stadia ontogenezy: *A* neaniczne, z fossulą trójkątną; *B* późnoneaniczne, z fossulą otwartą i długim septum głównym (*1*); *C* efebiczne, septum główne skrócone.

Fig. 17 (p. 114)

Macgeea bathycalyx amabilis Różk. Skały, środkowy żywet, forma geologicznie młodsza. Dwa stadia ontogenezy: *A* neaniczne, septum główne (*1*) bardzo długie; *B* późno-neaniczne, septum główne nadal długie.

Fig. 18 (p. 114)

Macgeea berdensis Soshkina. Wietrznia, dolny fran. Stadium neaniczne; *1* septum główne.

Fig. 19 (p. 115)

Macgeea czarnockii Różk. Wietrznia, środkowy fran. Trzy stadia ontogenezy: *A* nepioniczne, fossula otwarta, septum główne (*1*) długie; *B* neaniczne, fossula otwarta, septum główne długie; *C* efebiczne.

Fig. 20 (p. 116)

Macgeea multizonata (Reed). Wietrznia, środkowy fran. Dwa stadia ontogenezy: *A* neaniczne, septum główne (*1*) tej samej długości co septum sąsiednie; *B* efebiczne, septum główne bardzo długie.

Fig. 21 (p. 118)

Macgeea bathycalyx kasimiri Różk. Skały, środkowy żywet. Fotografia koralita; na dystalnych brzegach septów, nie zasłoniętych epiteką, wydatne listewki; × 6.

Fig. 22 (p. 120)

Pexiphyllum ultimum Walther. Wietrznia, środkowy fran. Dwa stadia ontogenezy: *A* nepioniczne, septa połączone w kolumellę, × 33; *B* neaniczne, z fossulą otwartą i długim septum głównym, kolumella nadal istnieje, × 20; *1* septum główne, *2* septum przeciwległe, *3* pseudokolumella, *4* pseudoteka, *5* epiteka, *6* pierwsza para septów bocznych, *7* talon, *8* epiteka talonu (wg Różkowskiej, 1953, fig. 17, 19).

Fig. 23 (p. 121)

Linie korelacji n/d dla *Pexiphyllum ultimum* i *Macgeea bathycalyx amabilis*. Na osi rzędnych — liczba septów I rzędu, na osi odciętych — średnice kielichów, w mm.

Fig. 24 (p. 121)

Linie korelacji a/d dla *Pexiphyllum ultimum*. Na osi rzędnych — odległości międzyseptalne, na osi odciętych — średnice kielichów, w mm.

Fig. 25 (p. 123)

Linie korelacji n/t dla gatunków kręgu *Pachyphyllum lacunosum* Gürich i *P. ibergense* (F. A. Roemer) z górnego franu obszaru kieleckiego. Na osi rzędnych — septa I i II rzędu, na osi odciętych — średnica tabularium (*t*), w mm.

Fig. 26 (p. 124)

Schematyczny wykres linii korelacji n/t dla trzech kręgów gatunków: *Pachyphyllum lacunosum, P. ibergense, P. ananas.*

Fig. 27 (p. 131)

Występowanie rodzajów Thamnophyllidae w poszczególnych okresach dewonu Gór Świętokrzyskich, z uwzględnieniem liczebności względnej ich gatunków.

(Na rysunku, u góry, zamiast: *Thamnophyllum* Różk., winno być: Thamnophyllinae Różk.).

МАРИЯ РУЖКОВСКА

ОБЩИЕ РАССУЖДЕНИЯ КАСАЮЩИЕСЯ СЕМЕЙСТВА THAMNOPHYLLI-DAE SOSHKINA В СРЕДНЕМ И ВЕРХНЕМ ДЕВОНЕ ПОЛЬШИ

Часть II*

Резюме

Статья является дополнением исследований, опубликованных в 1953 и 1956 годах, и касается некоторых проблем семейства Thamnophyllidae. В предыдущих статьях автор причисляла кораллы, характеризующиеся подковами и симметрическими трабекулярными веерами, к подсемейству Pachyphyllinae и семейству Disphyllidae. Теперь автор признала эту группу самостоятельной и выделила в семейство Thamnophyllidae — подобно тому, как это сделали Е. Д. Сошкина (1941) и А. Шуппе (Schouppé, 1956).

В пределах отдельных популяций и видов была изучена изменчивость количественных и качественных признаков. Был произведен биометрический анализ корреляции n/d, т.е. соотношение количества септ к диаметру чашечки. В пределах родов были сравнены кривые корреляции n/d и видовые коэффициенты Ms. Установлено притом, что у видов рода Thamnophyllum коэффициент Ms уменьшается прогрессивно с геологическим возрастом, так как аллометрический рост по отношению к септам отрицательный. У видов рода Macgeea — напротив — видовый коэффициент Ms возрастает у более молодых геологических форм, хотя в начале франского яруса проявляет некоторую регрессию. Эволюционная тенденция этого рода проявляется в постепенном увеличении количества септ; таким образом, по отношению к септам, господствует здесь положительная аллометрия.

Исследования онтогенезиса представителей Macgeea показывают постепенное удлинение главной септы, которое — помимо колебаний в онтогенезисе — продолжается в течение живетского яруса. Во франском ярусе эта черта стабилизируется, и уже доминирует главная септа.

Биометрические исследования в пределах представителей массивных колоний доказали, что все описанные до сих пор автором виды следует включить в род Pachyphyllum, который содержит четыре группы видов.

Образованию вида способствуют два фактора: время и среда. Время делает возможной прогрессивную изменчивость количественных и некоторых качественных признаков. Среда же способствует изменению качественных признаков, так как виды приспособляются к изменной фации. В бассейнах девонского моря взаимодействовали, как обычно, селекция и изоляция.

Сравнение стадий онтогенеза у отдельных родов показало, что существуют роды о неизвестном происхождении, т.е. криптогенические (Protomacgeea и Pachyphyllum), другие же (Pexiphyllum) проявляют явную акцелерацию. Сущест-

вуют также роды, у которых можно заметить явление ценогенеза (*Pachyphyllum* и *Synaptophyllum*).

Эволюционная тенденция в пределах подсемейства Thamnophyllinae проявляется в увеличении колоний и овладении ними рифовой фации, а в подсемействе Macgeeinae — в реконструкции септального аппарата. Последние не образуют массивных колоний и не проникают в рифовые комплексы.

Хронологические данные показывают, что в середине живетского яруса имели место наиболее интенсивные морфологические изменения конструкции скелета. В истории семейства Thamnophyllidae можно выделить два этапа: одиночные и разветвленные формы господствуют от эйфеля до верхнего франа, тогда как формы, создающие массивные колонии, преобладают в верхнем фране. В Польше Thamnophyllidae не переходят в фаменский ярус, исчезая с концом верхнего франа.

Автор исследовала также Thamnophyllidae из других районов девона Польши. Она констатировала притом, что верхне-франская фауна из Мокржешова в Судетах имеет иной состав, который объясняется приспособлением фауны к фации господствующей в отрезанном заливе. Верхне-франская фауна Свентокржиских Гор и Дембника тождественны. Отсюда заключение, что Thamnophyllidae имели специальные экологические требования.