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BLASTOGENY AND INDIVIDUAL VARIATIONS IN TETRACORAL COLONIES FROM THE DEVONIAN OF POLAND

Abstract. — In order to investigate the process of blastogeny and individual variations in tetracoral colonies, comparative studies have been made of the following forms from the Middle and Upper Devonian strata of Poland: *Disphyllum geinitzi* L. & S., *Hexagonaria laxa* Gürich, *Hexagonaria laxa jurkowicensis* n. subsp., *Peneckiella minor kunthi* (Dames) and *Sudetia lateseptata* n. gen., n. sp.

INTRODUCTION

A stimulus to the study of individual variation in colonies of a given coral species has been provided to the writer by Professor R. Kozłowski, Head of the Palaeozoological Institute of the Polish Academy of Sciences. The most sincere words of gratitude are here conveyed to him for this suggestion as well as for his constructive criticism and revision of the manuscript.

Thanks are due to Mrs M. Pajchel and Dr J. Czermiński for important information on Devonian deposits of the eastern part of the Holy Cross Mountains (Góry Świętokrzyskie) and for the courtesy of discussing with the writer the associated stratigraphic problems.

Acknowledgement is similarly made to Mrs J. Gruszczyńska for the execution of graphs and drawings from photographs of thin sections, and to Mrs J. Humnicka for the English translation of the Polish text.

The writer's one month visit at the Palaeontological Institute of the Academy of Sciences of the U.S.S.R. in Moscow was sponsored by the Polish Academy of Sciences. The deepest thanks are expressed to Professor J. A. Orlov, Director of the Institute, for the untiring courtesy and the free access to the greatly valuable Devonian tetracoral collections which have been worked out by Dr E. D. Soshkina, a leader of the study of this group.

T. A. Dobroljubova, an authority on Carboniferous corals in the Soviet Union, has given the writer access to her collections and held some most interesting discussions on Carboniferous colonial tetracorals and their

variability. Sincere thanks are here conveyed for the friendly assistance tendered by her during the writer's visit in Moscow.

Similar acknowledgements are made to: N. V. Kabakovitsh of the Academy of Sciences in Moscow, V. A. Sytova of the Lomonosov Moscow University, and Dr V. A. Ivania of the Tomsk University.

Professor A. v. Schouppé of the Münster University in Westphalia, has been kind enough to exchange critical remarks on Devonian corals. The writer is obligated to him for sending some greatly useful microscopic sections of the topotypes of *Peneckiella minor* (Roemer) from Grund.

Sincere thanks are likewise due to Professor H. Flügel of the Graz University, for his letters containing most interesting remarks and for sending tetracoral specimens from the Devonian of Austria.

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In the text and explanations of tables and figures the following abbreviations are used: *c1-c9* — successive classes, *Mn* — arithmetic mean of septa in classes, *Mn I* — arithmetic mean of major septa, *Mn II* — arithmetic mean of minor septa, *Md* — arithmetic mean of calyx diameters, *Mc* — correlation coefficient of classes, *Ms* — correlation coefficient for species, *Mt* — mean diameter of tabularium.

PALAEOECOLOGICAL CHARACTERISTICS OF LOCALITIES

Disphyllum geinitzi Lang & Smith occurs at Sitkówka (S of Kielce) in large phaceloid colonies. A part of a colony, approx. 0.5 m long, has been recovered there, probably from its natural biotope. The rock embedding the colony is a grey zoogenetic limestone of Upper Givetian age. The Givetian here is embraced by the Gałęzice syncline (fig. 1). It crops out in a big quarry near to the local railway station. According to Gogolczyk (1956, 1959), the occurrence is here noted of banks with *Amphipora ramosa* (Phillips) and *Stachyodes caespitosa* Lecompte, and — according to Stasińska (1958) — that of *Thamnopora cervicornis* (de Blainville). Fragmentary isolated tetracorals, e.g. *Thamnophyllum trigeminum* Pen. and some thick-walled *Disphyllum geinitzi* are sporadically encountered. The exposed surface of the above mentioned *D. geinitzi* colony has been strongly weathered so that the corallite walls are mostly strongly damaged. Hence, thin sections have been cut mainly in the deeper portion of the colony. On one side the surface of the colony is covered by numerous shells of *Atrypa* sp. from the *aspera* group. The rock cementing the corallites consists of fragmentary specimens of *D. geinitzi*, remains of *Atrypa* sp. and fragments of other organisms occurring in the vicinity. Thus it is probable that the colony was formed in situ.

The fragility of the colonial skeleton, its fasciculate pattern, the parallel upwards growth of corallites, showing no conspicuous divergence, also the

Fig. 1. — Sketch map showing distribution of localities

frail skeletons of the surrounding fauna, all suggest that the biotope of this coral bank was a calm sea or quiet lagoon (Kühn, 1926, p. 130).

Hexagonaria laxa Gürich was found in a stromatoporoid-tabulate reef in Dziewki, 4 km north of the township of Siewierz. Gürich (1896, p. 73), when describing the coral limestones of Dziewki, mentions *H. laxa* among the long list of fossils there.

Śliwiński (1956) ascertained that Givetian limestones at Dziewki stretch out in a belt 2250 m long and 250 m wide. Reef limestones occur at its western end, dipping NE at an angle of 25°. The predominance of *Amphipora* banks is noted in the western portion, that of globose stromatoporoids in the east and south. Intercalations packed with colonial *Hexagonaria laxa* occur in the north-eastern walls near to the pond. Next to them are noted layers with *Plagiopora dziwkiensis* Gürich, *Striatopora cristata* Blum. and beds of *Stachyodes verticillata* (M'Coy). In Mr Śliwiński's opinion, the presence of *Stringocephalus* suggests the Givetian. The presence of corallites from the tetracoral family of Stringophyllidae, including the genera *Stringophyllum* sp. and *Neospongophyllum* sp. (the latter approaching *Sinospongophyllum planotabulatum* Yoh; Yoh, 1937, p. 56, 57), is suggestive of the upper Middle Givetian (after Wedekind's stratigraphic chart of 1924).

Since *Hexagonaria* colonies recovered from the bed are usually small and strongly weathered, that selected by the writer as topotype for the study of variations was 30 cm long and embedded in a huge limestone boulder. The same rock contains an abundant fauna of above mentioned fossils. It is a reef limestone, probably formed at the lagoon side, as is indicated by the frail skeletal structure of the colony and the predominance of ramose forms in the associated fauna. *H. laxa* populations have persisted in their natural biotope within the stromatoporoid-tabulate reef.

Hexagonaria laxa jurkowicensis n. subsp. — A stromatoporoid-tabulate reef, locally crowded with globose stromatoporoids of the genera *Actinostroma* and *Stromatopora*, is under exploitation in a quarry adjacent to the Jurkowice wood, about 4 km west of Opatów (Samsonowicz, 1917, p. 39). A mass occurrence is likewise noted there of circular colonies of *Alveolites suborbicularis, H. laxa jurkowicensis,* individual tetracorals, also *Amphipora* beds and large brachiopods. The complete reef population here occurs in situ. Large circular colonies of Stromatoporoidea, Tabulata, also the globose *Hexagonaria* with thick skeletal structure, suggest a reef exposed to the strong action of waves (Kühn, 1926, p. 130). According to Samsonowicz (1917), reef limestones are encountered in the Żerniki-Karwów syncline, stretching from the Pokrzywianka (Żerniki) to the Łagówka (Karwów). They share in the composition of Givetian and Frasnian rocks of this syncline.

Peneckiella minor (Roemer) *kunthi* (Dames) and *Sudetia lateseptata* n. gen., n. sp. — These two species are reef-builders at Mokrzeszów[1] in the Sudeten Mountains. The Mokrzeszów rocks participate in the composition of the Świebodzice basin lying in the north-western corner of the gneiss Sowie Mountains block. This is a deep Hercynian synclinorium filled in by non-metamorphic Upper Devonian and lowermost Culm rocks (Reg. Geol. Polski, 1957, p. 93-100). Marine transgression here began during the *Manticoceras* period. The sea was on the whole a shallow one and flooded basins cut off by barriers. The Świebodzice Devonian displays diversity of character with rapidly altering facies: conglomerates, greywackes, shales, limestones and marls. Limestone intercalations are usually rather small, the only larger one being that of Mokrzeszów; it is 200 m in length, exploited to its very limits and now under Nature Protection. It crops out

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[1] Oberkunzendorf — of the German authors.

around an overflooded abandoned quarry, being part of the coral reef running NW from Witoszów across Mokrzeszów. The occurrence of land south of this reef seems very probable.

Mokrzeszów has been made known by descriptions of the fossils recovered there. In 1873, Dybowski (p. 402) described two coral species from that reef: *Spongophyllum pseudovermiculare* M'Coy (= *Tabulophyllum priscum* (Münster)) and *Fascicularia kunthi* (Dames) (= *Peneckiella minor kunthi*). In 1939, Pawlik worked out the stratigraphy of the Upper Devonian of Świebodzice, Mokrzeszów included. The following beds have been here differentiated by that author: 1) top conglomerates; 2) Famennian clay shales with *Cheiloceras sacculum* Sandb. etc.; 3) marly brachiopod limestones and shales with numerous globose algae *Sphaerocodium zimmermanni* Rothpl., including *Productella sericea* Dames, *Spirifer archiaci* Murch. and *Productus hallanus* Walcott; 4) limestones crowded with coral fossils. They comprise a reef built up by *Peneckiella minor kunthi* and *Sudetia lateseptata*. There are also banks with *Tabulophyllum priscum* and Tabulata of the genera *Thamnopora, Coenites* and *Alveolites.*

Tetracorals are the main builders of the Mokrzeszów reef. Stromatoporoids are completely lacking. According to Lecompte (1954), Palaeozoic reef corals were considerably less susceptible to the presence of clay suspensions than their contemporaneous Stromatoporoidea and the living Hexacoralla. Therefore, they were able to exist in somewhat deeper waters, while stromatoporoids lived within the surf zone (*l. c.*, p. 171). It may thus be inferred that the Mokrzeszów reef either developed in somewhat deeper waters than did the reef-building stromatoporoids, or that the pelitic suspensions driven from the nearby land were not harmful to the coral reefs with *Peneckiella minor kunthi* and *Sudetia lateseptata* though they were unfavourable to the development of massive stromatoporoids.

DESCRIPTIONS

Disphyllum geinitzi Lang & Smith, 1935

(fig. 2-8)

1935. *Disphyllum geinitzi* L. & S.; W. D. Lang & S. Smith, Cyathophyllum..., p. 570, 571, fig. 26; pl. 36, fig. 1-3.

Material. — A large phaceloid colony 17×12×30 cm, recovered from zoogenetic limestones in the southern wall of the Kostrzewa quarry at Sitkówka (fig. 1). 34 thin slides with transverse and longitudinal sections.

Diagnosis. — Subcylindrical corallites forming phaceloid colonies, locally with coalescing walls, or calicinal expansions. Corallites circular in

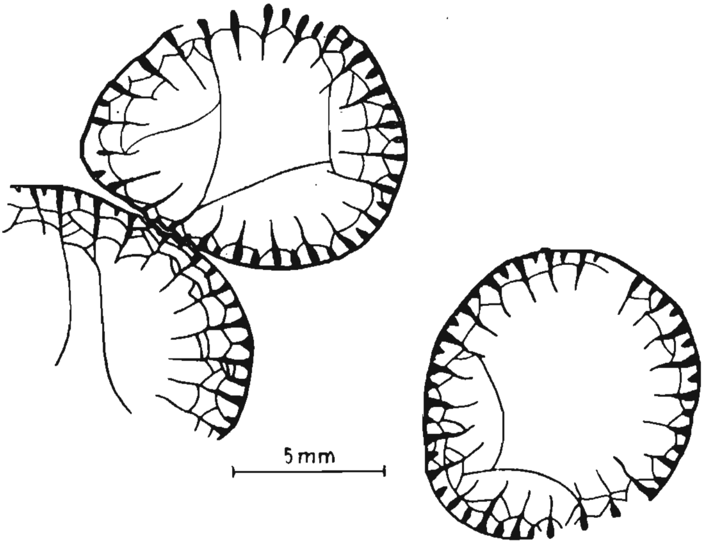

Fig. 2. — *Disphyllum geinitzi* Lang & Smith; Sitkówka, Givetian. Cross section of corrallites (slide no 2).

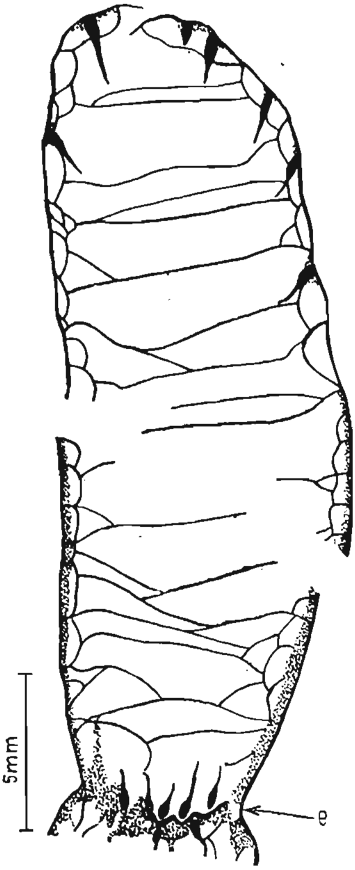

Fig. 3. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. Longitudinal section of mature individual separated from bud by partly formed new epitheca — *e* (slide no 1).

section (fig. 2), mature individuals 9.5 to 11.5 mm in diameter, 22—24 major septa with length one-fourth that of the calyx diameter, minor septa extremely short: one-fourth to one-fifth the length of major septa. Beneath the epitheca[2] is the outer pseudotheca, and near it — the inner pseudotheca. One row of minute dissepiments; tabularium broad, consisting of generally complete tabulae either flat or slightly arched. Budding[3] lateral, trabecular microstructure of the disphylloidal type.

Footnotes 2 and 3 — see opposite page.

A. *Blastogeny*

1. *Development of bud* (fig. 4-8). Buds are produced in the periphery of the calyx. Within the studied colony budding is not frequent. Even young corallites are rare too. The following stages may be distinguished in the budding process.

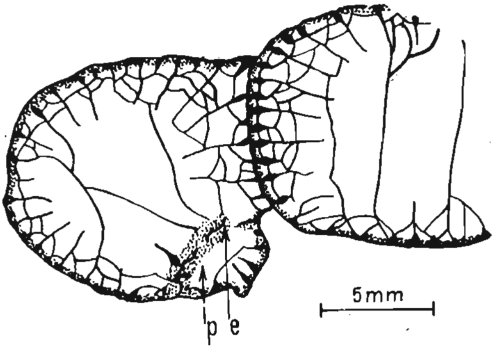

Fig. 4. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. Cross section of a bud in nepionic stage; rudimentary new epitheca (*e*) and pseudotheca (*p*), (slide no 6).

a) Stage I (fig. 4) — the budding corallite doming outwards. The wall separating the bud from the parent corallite begins to be laid down and, on either side of it, new irregular zigzag septa are produced, on one side belonging to the bud, on the other — to the budding corallite. Septa present

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[2] In view of the confused meaning of the term "wall" the writer thinks it necessary to state that in her present paper she distinguishes the epitheca (which is the outer mantle of the corallite) from the adjacent wall. The wall is the pseudotheca since it consists either of thickened distal ends of septa (septotheca) connected by laminate stereozone, or of thick-walled dissepiments (paratheca). The epitheca is a thin layer of stereozone deposited on the wall (on the outer pseudotheca). In the here considered representatives of Disphyllidae and Thamnophyllidae the occurrence is noted of epitheca exclusively and of septotheca and paratheca. In cerioid colonies of Disphyllidae, each corallite is surrounded by the outer pseudotheca and the epitheca. In cerioid Thamnophyllidae the outer pseudotheca only is present, while in the aphroidal (e. g. *Phillipsastraea ibergensis progressa* Rozk.) the individual polyps are not isolated from each other by a wall. Hence Alloiteau (1955, p. 424) is not correct in postulating the presence of at least a thin wall in colonial tetracorals. An inner wall often occurs next to the outer. It is the pseudotheca made up of septa and dissepiments which are here locally thickened by the deposition of stereozone.

[3] Every one of the examined blastogenies is originally intracalicinal, subsequently the bud becomes lateral if it bends outwards at a certain angle from the parent corallite: the bud is intermural if it develops between the walls in the cerioid corallum, parricidal — if it occupies the whole inside, while the parent corallite dies.

before the beginning of budding occur along the outer bud wall. The wall separating the bud from the parent corallite is not yet completed; it consists of three layers: the epitheca which is in common, and two pseudothecae. These belong on one side to the bud, on the other — to the budding corallite. Such a triple wall is always formed during the blastogeny in *Disphyllum,* hence this type of budding may be called "disphylloidal".

b) Stage II (fig. 5) — the bud has nearly completely separated from the parent corallite, it is 4.5 to 4.7 mm in diameter, the number of septa is 18, some of the septa are shorter. One bud only is generally produced; if there are two — they may or may not be of the same age (fig. 6), separated from the parent corallite and from each other by the characteristic triple wall. Fig. 7 represents a budding corallite in longitudinal section. The lateral bud bends outwards at an angle of 75°, growing out from the dissepimental area of the mature corallite. During the nepionic stage the wall separating the bud has not yet been completed, the periaxial part of the budding corallite tabula is the first tabula of the bud. The bud is still in close depen-

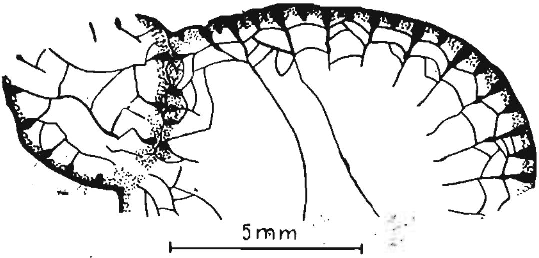

Fig. 5. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. Cross section of a bud in late nepionic stage; partly formed epitheca and new septa (slide no. 3).

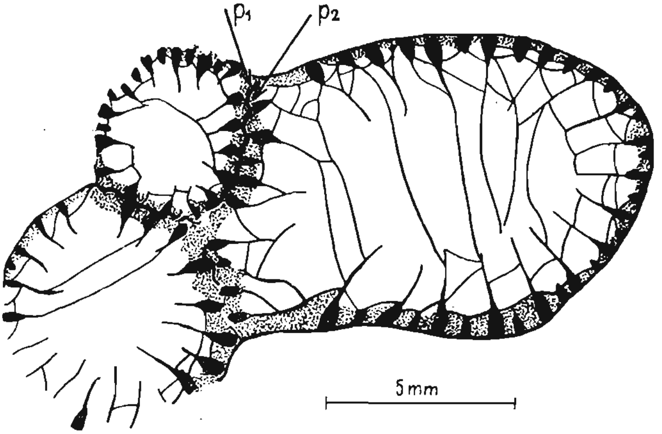

Fig. 6. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. Cross section of a bud in early neanic stage; new epitheca nearly complete between two pseudothecae (p_1, p_2) in three corallites intimately fused by budding (slide no. 5).

dence on the parent corallite. The neanic stage begins slightly higher up; it is indicated by the appearance of the "triple" wall. Along this wall the bud as well as the parent corallite display diaphragmatophoric structure.

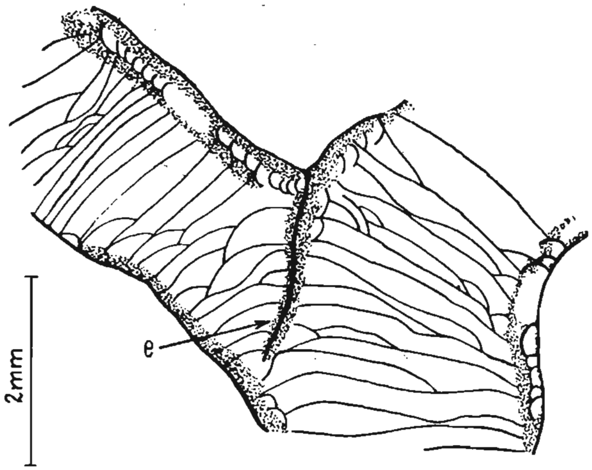

Fig. 7. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. Longitudinal section of a bud with epitheca (e) separating it from parent corallite in the neanic stage (slide no. 7).

Dissepiments appear directly before the bud has bent outwards from the budding individual. The structure becomes pleonophoric. The juvenile corallite is at that time 5 mm in diameter.

2. *The n/d ratio variations during ontogeny.* There is close correlation between the number of septa (n) and the diameter of calyx (d). In the ephebic stage corallites produce buds even when only 7.2—8.5 mm in diameter and with 20—22 major septa. Table 1 shows the mean number of septa at mean diameter of calyx in each of the mentioned classes.

Table 1

Mean number of septa (Mn) at mean diameter of calyx (Md) ratio with respective coefficients (Mc, Ms)

Classes	c1	c2	c3	c4	c5	c6	c7	c8	c9
$\frac{\text{Mn I}}{\text{Md}}$	$\frac{12}{3.5}$	$\frac{14}{4.5}$	$\frac{17.5}{5.5}$	$\frac{19}{6.5}$	$\frac{20.3}{7.5}$	$\frac{22.5}{8.5}$	$\frac{23}{9.5}$	$\frac{24}{10.5}$	$\frac{24}{11.5}$
Mc1-Mc9	3.4	3.1	3.1	2.9	2.7	2.6	2.4	2.3	2.1

Ms n/d = 2.75

The above data indicate less rapid increase in the number of septa than in the diameter of calyx. This is negative allometry in relation to septa. The value of the n/d ratio decreases slowly in the progressively higher classes. The number of septa (24) in the two highest classes becomes static.

The n/d ratio curve (fig. 8) rises considerably in the juvenile stage, deviating nearly uniformly from either axis. In individuals with 22 or more septa this curve is subparallel to the X axis, since increase of diameter distinctly dominates over increase in number of septa. In character the n/d ratio curve approaches that of the n/t ratio in *Hexagonaria laxa* (fig. 15), since they display similar dynamics during ontogeny.

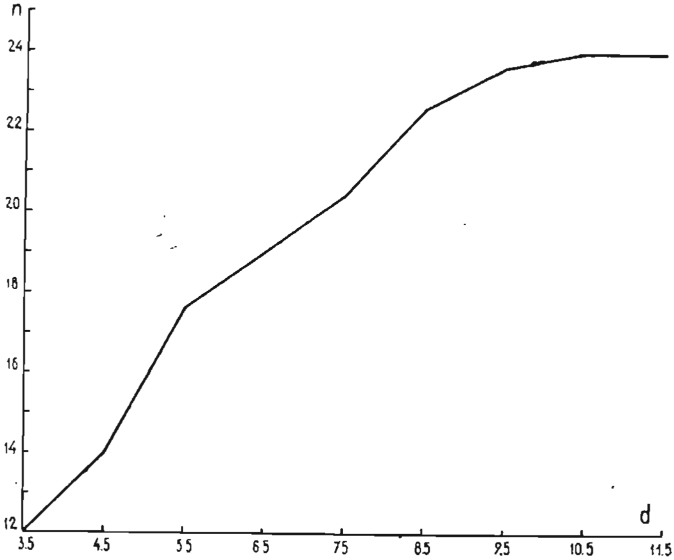

Fig. 8. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. The n/d ratio curve; corallite diameters (*d*) — on abscissa, number of major septa (*n*) — on ordinate.

B. *Individual variations*

Individual variation within the colony is not strong. Corallites are in obvious harmony with environmental conditions. They have attained their optimum development and this is emphasized by their complete adaptation. The corallite structure is not complex. The skeletal elements are fully developed and do not bear signs of regression. When any slight variations do occur, they are phenotypic, seemingly expressing direct reaction to the position occupied in the colony and to the danger of being covered up with sediments, which threatens the corallites.

1. *Colonial variability pattern.* Practically throughout its length the colony is phaceloid, some less crowded places occur, however, where buds bend out at a slightly greater angle. There the appearance of the colony becomes dendroid.

2. *Tabularium(t)/dissepimentarium(diss) ratio.* At diameter of 5 mm the t/diss ratio is 3.7 : 1.3. Thereafter the tabularium width increases reluctantly, while the dissepimentarium augments but little. In somewhat larger corallites the t/diss ratio is as follows (in mm):

9.0 : 1.9 = 5.0
9.0 : 1.2 = 7.5
9.5 : 1.8 = 5.0
9.5 : 1.5 = 6.3
10.0 : 1.2 = 8.3

These data show lack of uniformity in dissepimentarium width variations. There is no correlation between the tabularium and the dissepimentarium. Another row of vesicles or a larger dissepimentum makes its appearance in reaction to incidental stimulus, and thus the t/diss ratio is diminished.

3. *Number of tabulae in 2 mm.* The arrangement of tabulae varies strongly even within one individual. Their spacing is controlled by outside factors only and it is not coordinated with any structural characters. E. g. at diameter of 8.5 mm the number of tabulae over 2 mm ranges from 2 to 8.

4. *Basal thickness of septa.* During the juvenile stage septa may be thick and hence laterally coalescent, so as locally to form a continuous stereozone. In some corallites the walls are thickened even during the ephebic stage. In our colony the septa are mostly slender and widely spaced even during early ontogeny. Both the major and minor septa are with the same basal thickness. About 80 septa have been measured in corallite sections from one colony, providing the following data:

Thickness (in mm)	Per cent of septa
0.1	3
0.2	20
0.3	40
0.4	30
0.5	7

5. *Length ratio of major and minor septa.* Both types of septa are short, but the length of major septa is several times that of minor, as is shown here below:

Per cent of major septa	X-times as long as minor septa
10	three
40	four
30	five
20	seven to nine

The length of major septa and their length ratio to minor septa depends mainly on the site of the section. In one cut in between the tabulae the major septa are short, while in another cut across the tabula they are longer, so much so as to be nine times the length of minor septa.

Hexagonaria laxa Gürich, 1896
(fig. 9-16)

1896. *Hexagonaria laxa* Gürich; G. Gürich, Das Palaeozoicum..., p. 172-173, pl. 4, fig. 5.

Material. — One large colony from the zoogenetic limestone of Góra Kadzina, north of the Dziewki village. Also 30 detached colonies from the eastern quarry wall. 25 thin slides prepared from the large colony, including cross and longitudinal sections.

Diagnosis. — Colonies tabular, cerioid (fig. 9). Calices separated by thin epitheca, deep, with steep flanks and flat bottom. Maximum diameter 12 × 12 mm, tabularium 5.5 mm, greatest number of major and minor septa 38. Septa amplexoid, with tendency to split up into radial rows of spines, provided with carinae. Dissepimentarium broad; distinct inner pseudotheca between tabularium and dissepimentarium; tabulae horizontal or slightly arched, complete or incomplete, with supplementary plates (fig. 10). Budding intermural. Microstructure trabecular of the disphylloid type.

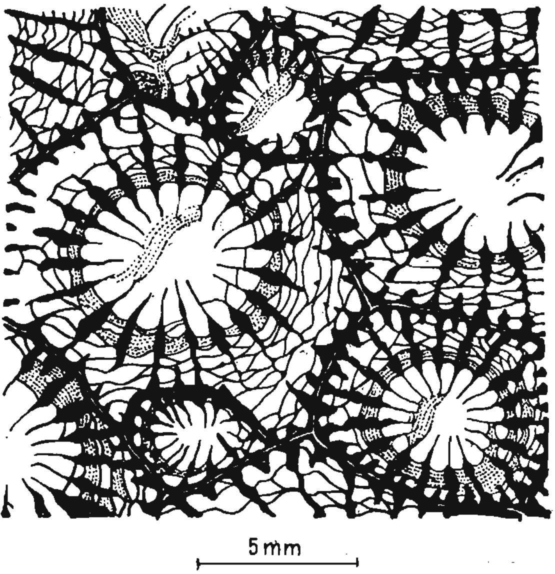

Fig. 9. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Cross section of a cerioid colony (slide no. 8).

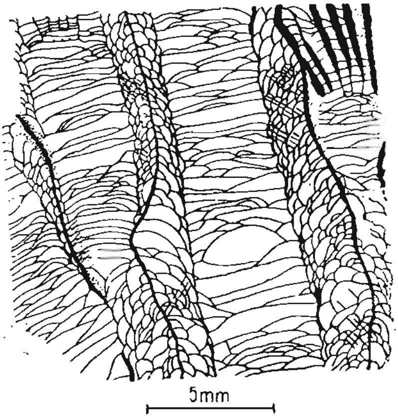

Fig. 10. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Longitudinal section of a cerioid colony (slide no. 10).

A. *Blastogeny*

1. *Development of bud.* The corallite attains maturity with greater diameter (8—10 mm) and 36—38 septa present. Buds are produced in place of the maximum width of the dissepimentarium, dissepiments notably large. In this part of dissepimentarium major septa have been reduced to short conical bases in the periphery, a row of spines on dissepiments and a larger spine on the inner pseudotheca. Several ontogenetic stages are observable in cross section of the bud.

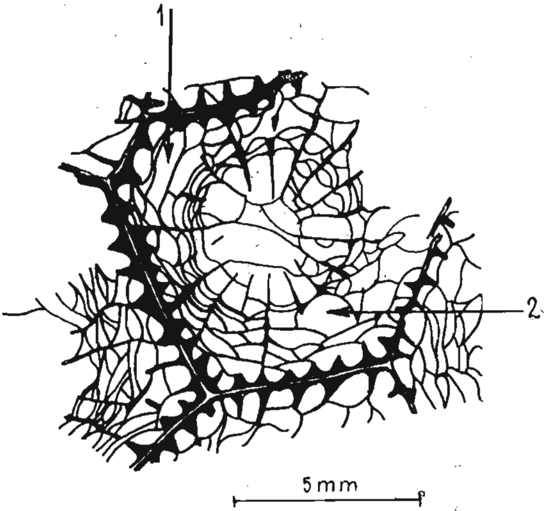

Fig. 11. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Cross section of a corallite making place for two buds — 1, 2 (slide no. 11).

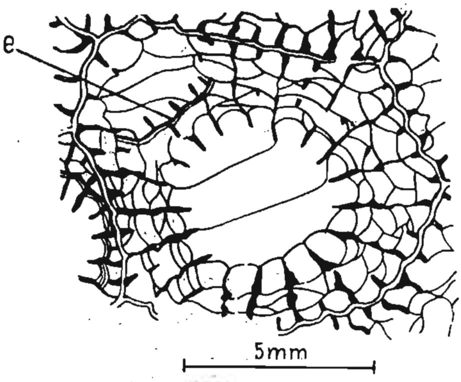

Fig. 12. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Cross section of a bud in nepionic stage; *e* new epitheca of bud (slide no. 8).

a) In stage I — space is prepared for the new bud (fig. 11). Bases of 5 septa only are discernible in the periphery. Septa of dual length here grow even. Nearer to the axis dissepiments only are seen. Among them, two or three vesicles slightly larger than others have the walls united into an arch concave towards the corner, and forming the initial wall of the new bud. This is the new epitheca separating the budding corallite from the parent.

b) In stage II (fig. 12) — the new wall of the bud has thickened since new septa have been produced. Their dilated ends are attached to the epitheca. Major septa of the parent corallite are attached to the other surface of the epitheca, with minor septa soon arising between them. A new outer pseudotheca is thus formed on this side of the epitheca too. The wall separating the bud from the parent corallite is "triple", similarly as in *D. geinitzi*. The new bud wall is very close to the inner pseudotheca of the parent corallite. Hence it is clearly seen by which of the adjacent corallites the bud has been produced.

c) In stage III (fig. 13) — the new bud wall is not yet complete. One of its ends leans against the outer wall of the parent corallite, the other against a major septum. Eight short septa have arisen on the new wall.

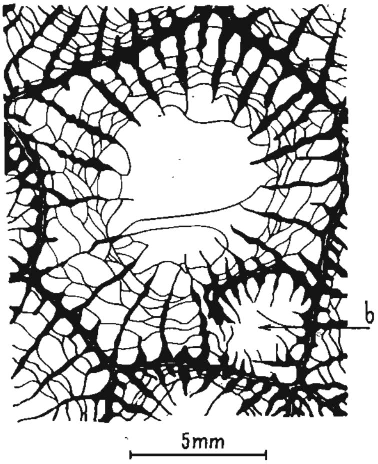

Fig. 13. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Cross section of a bud *(b)* in late nepionic stage; epitheca still incomplete (slide no. 12).

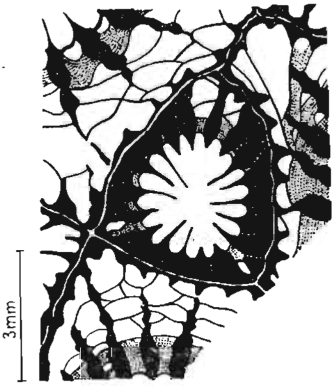

Fig. 14. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Cross section of a bud in neanic stage (slide no. 13).

d) In stage IV, neanic (fig. 14) — the bud is wholly surrounded by the epitheca. Septa have united into one thick wall. From it protrude the axial ends of major septa (18), nearly reaching to the axis, also minor septa have appeared not protruding beyond the wall. Major and minor septa of the parent corallite, as well as its dissepiments, are still discernible in one corner.

e) In stage V (ephebic) — the number of septa does not increase, but the calyx is widened; septa grow longer, slender and more widely spaced;

major septa differ distinctly from the minor in their length. Septa are spanned by vesicles, and carinae appear on the septa. There may be as many as 38 septa. Buds are produced in corners when space for them is available.

Fig. 10 shows the ontogeny of the bud in longitudinal section. The vesicles form a base for the bud, while the next dissepiment is the first tabula. One wall is made of the thick-walled, periaxial dissepiments of the parent corallite, the other of the outer corallite wall. In early youth this is the diaphragmatophoric stage. Somewhere higher up, with diameter of 3 mm, commences the pleonophoric structure, when dissepiments appear on one side.

The budding process in *Hexagonaria laxa* resembles that in the phaceloid form *Disphyllum geinitzi.*

2. *The n/t ratio variations during ontogeny.* Observations and graphs show close correlation of these two characters. The value of the n/t ratio decreases progressively during ontogeny, as is shown in table 2.

Table 2

Mean number of septa (Mn) and mean diameter of tabularium (Mt) ratio with respective coefficients (Mc, Ms)

Classes	c1	c2	c3	c4	c5	c6	c7
Mn I, II / Mt	$\frac{24}{2.8}$	$\frac{31}{3.3}$	$\frac{32}{3.8}$	$\frac{35}{4.3}$	$\frac{36}{4.8}$	$\frac{37}{5.3}$	$\frac{38}{5.8}$
Mc1-Mc7	8.6	9.4	8.4	8.1	7.5	7.0	6.5
Ms n/t = 7.9							

During youth the number of septa increases rapidly from 24 to 35. The class correlation coefficient augments slightly in class 2. Later its value diminishes since the number of septa has slightly augmented, while the tabularium diameter continues uniformly to increase.

These developmentary dynamics are excellently illustrated by the n/t ratio graph in fig. 15. In the nepionic stage the number of septa increases rapidly. In the next, neanic stage the rate of increase is cut down. In mature corallites, with 35—38 septa, the increase is extremely slow.

Budding is not frequent in the studied colony. Among the 17 thin slides prepared from 99 corallites in transverse section, three only budding specimens have been discovered by the writer. Most probably budding on a mass scale occurs at the beginning of colonial growth, while later corallite bundles grow straight up.

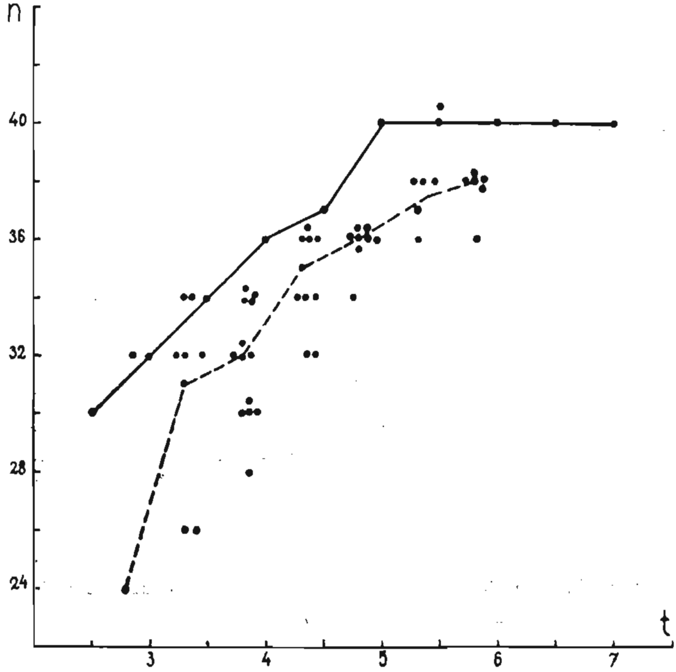

Fig. 15. — The n/t ratio curves; tabularium diameters (*t*) — on abscissa, number of major and minor septa (*n*) — on ordinate. Broken line and dots refer to *Hexagonaria laxa* Gürich (Dziewki, Givetian); continuous line — to *H. laxa jurkowicensis* Rozk. (Jurkowice, Givetian).

B. *Individual variations*

Strong polymorphism, expressed in all the structural elements, is observable in the studied colony.

1. *Shape of corallites.* In cross section the shape of mature corallites varies considerably. Upon examining 14 calices the writer ascertained the following diameters (in mm): 6 × 8, 7 × 8, 7 × 11, 7 × 12, 8 × 9, 8 × 10, 9 × 10, 10 × 10, 12 × 12. Tabularium width ranges from 4 to 6.5 mm. The calicinal outline is usually roughly hexagonal, in a few cases heptagonal or trigonal.

2. *Tabularium/dissepimentarium ratio.* 120 mature corallites have been measured in order to correlate in longitudinal sections the tabularium width and its relation to the dissepimentarium. These correlation data are plotted in the graph of fig. 16, in which the t/diss correlation value is placed on the abscissa, the per cent number of individuals — on the ordinate. The

curve is distinctly asymmetrical, since the most frequent individuals are those with the ratio value at 1. This means equal width of the tabularium and dissepimentarium on either side of it. The per cent number of individuals,

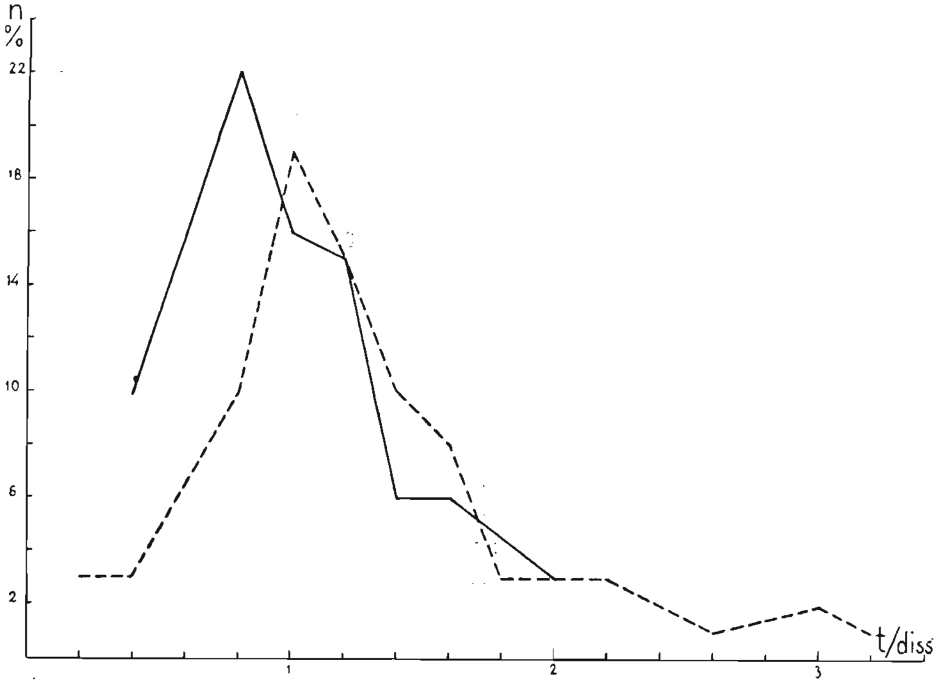

Fig. 16. — The t/diss ratio curves; tabularium (*t*) to dissepimentarium (*diss*) diameter ratio — on abscissa, per cent of specimens — on ordinate. Broken line refers to *Hexagonaria laxa* Gürich (Dziewki, Givetian); continuous line — to *H. laxa jurkowicensis* Rozk. (Jurkowice, Givetian).

in which width of dissepimentarium exceeds that of the tabularium, is small (0.2—0.8). On the other side of the apex, however, the curve has a gentler slope, thereby raising this value to 3.2.

3. *Number of vesicular rows.* The number of the rows of vesicles varies conspicuously even within one corallite. Mature corallites only, not producing buds, have been taken into account by the writer. It is well known that new buds completely reduce the dissepimentarium and substitute it. In mature corallites with morphology not disturbed by budding processes, dissepimentarium variability is as shown in table 3.

These measurements have been taken with the use of a micrometer, under 50-fold microscopic magnification. Data tabulated here above indicate that dissepimentarium displays strong variations, there not being two identical places within one corallite. Dissepimentarium width varies on either side and, independently thereof, the number of dissepimental rows

Table 3

Dissepimentarium variability and number of vesicular rows

Corallite no.	Left dissepimentarium width (mm)	Number of rows	Width of dissepiments (mm)	Right dissepimentarium width (mm)	Number of rows	Width of dissepiments (mm)
1	1.0	2	0.5 0.3	1.3	3	1.5 1.0 0.5
	2.5	4	1.0 0.5 0.5 0.3	3.0	4	1.4 0.8 0.6 0.4
2	2.5	6	1.5 1.0 0.8 0.8 0.5 0.4	2.0	4	0.7 0.6 0.5 0.5
	2.5	3	3.5 2.5 1.5	3.5	8	1.5 1.3 0.8 0.7 0.7 0.6 0.6 0.3
3	3.8	4	3.5 2.5 1.5 1.5	2.0	2	2.0 1.5

varies too. Variations of vesicle width occurs too, since large ones are present together with tiny ones.

4. *Number of tabulae in 2 mm.* Dissepimentarium width is controlled by the amount of space available for the growth of individual corallites within the corallum; the size and hence the number of dissepiments is affected by environmental conditions, while tabularia display some constancy. On the other hand, the position and arrangement of the tabulae varies strongly. Tabulae, similarly as dissepiments, are more plastic and probably depend mainly on exogenetic factors.

In order better to clear up this problem, the writer has measured about 30 mature corallites, thus ascertaining the following data: a) tabulae are mostly convex or nearly flat, the presence of concave tabulae has been ascertained in four cases only; b) number of tabulae in 2 mm varies strongly: two tabulae over that distance is a rare occurrence, most frequently there are 5 or 6, this being the case in 50 per cent of the examined corallites; c) tabulae may be complete or incomplete. Those consisting of axial and periaxial parts and provided with supplementary plates predominate. Their occurrence is most irregular, since they have been encountered in very young corallites as well as in large tabularia. Moreover, wide-spaced, complete tabulae may occur side by side with vesicular ones.

5. *Numerical ratio of complete septa to septa subject to reduction.* The characteristic feature of *Hexagonaria laxa* is the splitting up of some septa in mature calices into radial segments. A short conical base of the reduced septum always persists on the peripheral wall. This rudiment is of the same length as minor septa. The farther septal segments are placed on dissepiments. Occasionally only the peripheral base of the major septum and its axial end on the inner pseudotheca are present. These two extreme ends never disappear. Minor septa, if somewhat longer, are likewise reduced to a short row of radiate spines which, however, never protrude beyond the inner wall. In order to ascertain the number of septa, it has been found most convenient to count the axial ends of major septa, since the number of minor septa is always the same as that of the major.

The number of septa subject to reduction varies strongly. This depends on the presence of large dissepimental vesicles in a wide dissepimentarium, since it is there that the buds arise. The septal spines constitute the initial stage preparing space for budding, hence they are a caenogenetic character. The number of septa subject to reduction has been counted by the writer in 55 calices. The obtained data are given in table 4.

Table 4

Variability in number of reducing septa

Total number of major septa	Number of septa subject to reduction in calices										
	0	1	2	3	4	5	6	7	8	9	10
19	3	1	—	1	2	—	—	1	1	1	—
18	2	1	2	3	3	1	1	1	1	1	1
17	1	1	1	—	—	—	1	2	2	1	1
16	2	—	1	—	2	2	1	—	—	—	—
15	5	—	—	—	—	—	—	—	—	—	—

Exclusively complete septa occur only in 25 per cent of the examined calices, provided with 15—19 major septa. Calices with 18 major septa contain the highest per cent (33) of reduced septa.

6. *Septal thickness*. Septa are a structural element exhibiting notably strong variability. Thickness is one of the variable features. In the neanic stage septa are broad in section, gradually narrowing towards the axis. In mature corallites we note great diversity in this respect, each septum of any one part of the corallite being different. About 200 septa have been measured by the writer in sections of corallites from one colony, with the use of the micrometer under a 50-fold magnification. The obtained data show that on the whole peripheral bases of septa are as follows:

Thickness (in mm)	Per cent of septa
0.10 - 0.12	6
0.14 - 0.16	40
0.18 - 0.24	37
0.26 - 0.40	17

Similarly dilated septa occur in the inner pseudotheca, being those which, together with the inner whorl of dissepiments, form this wall. The following data have been ascertained by the writer:

Thickness (in mm)	Per cent of septa
0.10 - 0.12	3
0.14 - 0.16	22
0.18 - 0.24	39
0.26 - 0.40	34
0.40 - 0.60	2

Data tabulated above show that septa attain on the average greater thickness within the inner wall than on the peripheries. Thus, septa with thickness of 0.18—0.40 mm predominate in the wall (73 per cent), while those of 0.14—0.24 mm are most frequent at the base (77 per cent).

Besides the two most conspicuous dilations septa may show several constrictions or even gaps. In 5 per cent of septa the most constricted places are 0.02 mm thick, in 75 per cent 0.03—0.08 mm, while in 20 per cent the most constricted places do not much differ from the unconstricted parts and are 0.1—0.19 mm thick.

7. *Number of carinae on septa*. The examination of this character presents some difficulties since the carinae are very fragile. On some septa where they lie opposite, they are distinct, on others where alternating, they may be hardly discernible, so that septal sinuosity or dilations only indicate their presence. Dissepiments are attached to carinae, these are most conspicuous along thin septa and when the thin walls of vesicles are added to the bead-like dilations. 170 septa have been minutely examined by the writer, showing that 13 per cent are without carinae, 20 per cent have one

or two pairs of carinae, 50 per cent have 3—4 pairs, while 17 per cent are provided with as many as 5—8 pairs. The Dziewki form differs from the Jurkowice variety in lack of conspicuous carinae.

8. *Septal length.* 140 septa have been measured; the obtained data show that major septa vary strongly in length, the longest being 3.2 mm, the shortest 0.6 mm. As usual, mature calices only have been measured. Minor septa are considerably shorter, ranging from 0.06 to 0.64 mm. The length ratio of the major to minor septa is shown here below:

Per cent of examined septa	Major/minor septal length
25	3 - 4
60	5 - 8
15	9 - 11

The following are the most frequent figures of length (in mm):

Major septa	Minor septa
2.72	0.54
2.48	0.48
1.76	0.32

Notably long major septa, 9 or 10 times as long as the minor, are very rare. E. g.

Major septa	Minor septa
3.00	0.35
2.56	0.24
2.07	0.19

The Dziewki form is characteristic foremost by extremely short minor septa. This suggests an obvious tendency to reduction.

Hexagonaria laxa jurkowicensis n. subsp.

(fig. 15-19)

Material. — Two subcircular colonies, 9 cm in diameter, from a stromatoporoid-tabulate reef in Jurkowice near Opatów.

Diagnosis of holotype (fig. 17-19, microscopic sections 14 and 16). — This variety of the species *H. laxa* differs from the type form in larger calices (largest one 16 × 18 mm), slightly broader tabularium (up to 7 mm in diameter), and greater number of septa. In mature calices there may occur as many as 20 major septa, tending to break up into short irregular segments. All septa are conspicuously carinate. Trabeculae thick (0.16 mm), budding intermural.

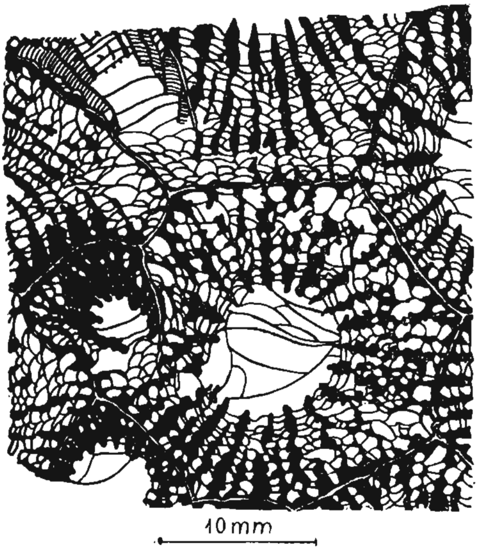

Fig. 17. — *Hexagonaria laxa jurkowicensis* Rozk.; Jurkowice, Givetian. Cross section of a cerioid colony (slide no. 14).

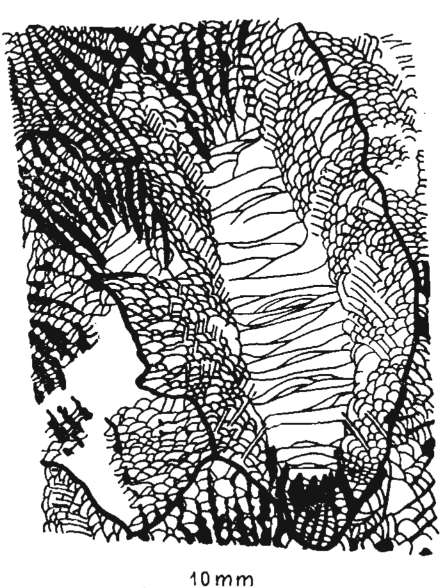

Fig. 18. — *Hexagonaria laxa jurkowicensis* Rozk.; Jurkowice, Givetian. Longitudinal section of a cerioid colony (slide no. 15).

A. *Blastogeny*

1. *Development of bud.* Longitudinal section shows that budding is more frequent here than in the Dziewki form. Many buds are produced growing subradially from some central corallite at an angle of 70-80°. Their further development is similar to that in *H. laxa* (fig. 17).

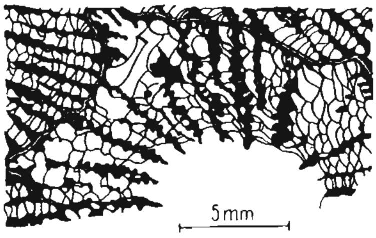

Fig. 19. — *Hexagonaria laxa jurkowicensis* Rozk.; Jurkowice, Givetian. Cross section of a part of corallite with bud in the nepionic stage; new epitheca still lacking (slide no. 16).

2. *The n/t ratio variations during ontogeny* (fig. 15). Correlation of the number of septa with the tabularium width and its ontogenetic variations are shown in table 5.

Ms coefficients of the two forms, from Dziewki and Jurkowice, are very similar, being 7.9 and 8.3 respectively. The slightly higher figure in the Jurkowice variety is due to the greater number of septa there. 40 septa continue to be present throughout 5 classes, beginning with the tabularium diameter at 5-7 mm. This indicates distinct tendency for the diameter growth to dominate over the numerical increase of septa. The correlation curve placed near the n/t ratio line of the Dziewki form (fig. 15)

Table 5

Mean number of septa (Mn) and mean diameter of tabularium (Mt) ratio with respective coefficients (Mc, Ms)

Classes	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10
Mn I, II	30	32	34	36	37	40	40	40	40	40
Mt	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0
Mc1-Mc10	12.0	10.7	9.7	9.0	8.2	8.0	7.1	6.7	6.1	5.7
Ms n/t = 8.3										

suggests similarities in character. The only deviation consists in the numerical increase of septa during the ephebic stage of the Dziewki form, while in the Jurkowice form there is no varation in this respect.

B. *Individual variations*

Differences are very strong in mature forms. The contour of the corallite is roughly polygonal. The maximum corallite diameter in an exactly cross section is 18 mm.

1. *The tabularium/dissepimentarium ratio* (fig. 16) comes close to that of the Dziewki form, as is shown by the correlation curve running parallel to the t/diss curve of the Dziewki form (fig. 16). Their course is analogous, but the summits are placed in different classes. The majority of the Dziewki specimens are with the t/diss ratio = 1, while in the Jurkowice colony that value is slightly lower (0.8). It has been ascertained that 46 per cent of the specimens have the tabularium narrower than the dissepimentarium. The evolutionary trend is to enlarge the colony by dissepimental growth.

Table 6

Dissepimentarium variability and number of vesicular rows

Corallite no.	Left dissepimentarium width (in mm)	Number of rows	Right dissepimentarium width (in mm)	Number of rows
1	6.5	8	5.0	9
	3.5	5	2.0	3
	2.1	4	1.0	2
	1.0	2	0.5	2
2	3.5	6	5.3	8
	3.2	5	2.5	5
	2.5	3	2.0	3
	1.0	2	0.6	1

2. *Number of vesicular rows* (fig. 18). This character varies strongly. It does not correlate with dissepimentarium width, but is strictly connected with the size of vesicles and, most likely, it is merely a function of outer environmental conditions (see table 6).

3. *Number of tabulae in 2 mm.* This is a strongly variable feature, as in the Dziewki topotype. Number of tabulae ranges from 2 to 6 in 2 mm. Tabularia with only 2 tabulae in 2 mm are unusual. Closely spaced tabulae are the most frequent, the majority being complete.

4. *Complete and reducing septa.* In mature calices, with a well developed dissepimentarium (fig. 17), septa begin to break up into segments. A short base invariably persists on the periphery, farther segments have yard-arm carinae united by thin stereozone strips. Upon further reduction, trabecules loose their junctions so that shapeless septal segments only persist comprising several conspicuous carinae covered by stereoplasm. In *H. laxa* they break up according to another pattern. There the septum separates into thin, slender septal spines fixed on the arched dissepimental wall. The peripheral bases of septa in the Jurkowice variety are then short, hardly discernible, but the axial ends are complete and strong, as in the topotype.

Similarly as in *H. laxa*, the number of regressive septa in the several calices varies. The number of reducing major septa ranges from 0 to 19. The same septum may disintegrate once or as many as six times (see table 7). The disintegration of septa into elongated parallel segments is rather frequent. Moreover, it has been ascertained that minor septa, though still slightly longer than in the topotype, are reduced more rapidly than the major septa. Analogously accelerated reduction is observable in the Dziewki form also.

Table 7

Numerical data showing interrelation of calyx diameter and septal disintegration

Calyx no.	Calyx diameter (mm)	Tabularium diameter (mm)	Number of major septa	Separation			Number of complete septa	Disintegration into elongated segments
				one-fold	two-fold	three-fold		
1	17.0	7.0	20	12	6	—	2	10
2	13.0	7.0	20	5	2	2	11	1
3	10.0	5.5	20	1	—	—	19	—

As is shown in the above table, which illustrates three haphazardly picked out mature calices, progressive septal regression is associated with size of calyx.

5. *Septal thickness* (fig. 17). Septa here show notably stronger structure than those in the type form, as well as greater diversity of thickness: distinctly spindle-like ones occur together with slender ones, which have rounded carinae and the appearance of a string of beads.

For the sake of comparison the writer has measured, with the use of a micrometer under 50-fold magnification, the septal thickness at the peripheral base, in the inner pseudotheca and in places of greatest constriction. On these measurements it has been established that:

a) minimal basal thickness = 0.3-0.4 mm in 15 per cent of septa, most frequent thickness = 0.5-0.8 mm in 62 per cent, and maximum thickness = = 0.9-1.3 mm in 23 per cent of septa;

b) as regards thickness within the pseudotheca, measurements show that the peripheral base of septa and the periaxial dilations have similar value, i.e. that in these two points the septa are analogously dilated. In the Jurkowice form these dilations are stronger, but the two above mentioned, equally strong thickenings, occur in the topotype too:

	Hexagonaria laxa	*H. laxa jurkowicensis*
Dilation at base	0.1 - 0.4	0.3 - 1.3
Dilation within inner pseudotheca	0.1 - 0.6	0.5 - 1.3

Thread-like connections of the lumpy trabecules are as fine as those in the type form where the sharp-pointed end of septal spines makes its appearance. The narrowest constrictions range from 0.03 to 0.08 mm and are not rare.

6. *Number of carinae on septa* (fig. 19). The Jurkowice variety is provided with markedly conspicuous carinae, readily observable in transverse and longitudinal sections. The opposite arrangement predominates, the alternating pattern is less common. Dissepiments, strongly dilated in the periaxial part of the corallite, are attached to the processes of carinae.

Upon measuring 50 septa, it is possible to describe the numerical occurrence of carinae on septa. Some septa are without distinguishable carinae. If so, the trabecules are mutually closely connected throughout their length by stereoplasm. On other septa carinae are conspicuous. Their number varies. Septa, provided with 5—6 pairs of carinae each, are frequent, the majority have 9 pairs, but occasionally 13, 15 or even 17 pairs may occur. In the Dziewki form 3—4 pairs of carinae are the most frequent, while 5—9 pairs on one septum is the maximum recorded number.

7. *Septal length*. Length correlation of major and minor septa in the Dziewki form differs completely from that in the Jurkowice form. Minor septa are considerably longer in the Jurkowice colony, nearly reaching to

the inner wall. Figures relating to length of both septal types are as follows: in 70 per cent of septa the sI/sII ratio = 1.1-2. This means that major septa are either only slightly longer than, or twice the length of minor septa. In *H. laxa* from Dziewki, however, the sI/sII ratio = 5-7-9, with the predominance of calices having septa as many as nine times the length of minor septa.

C. *Comparison with the type form*

Morphology, microstructure, ontogeny and individual variability of two closely allied forms have been investigated: i.e. the Dziewki topotype *H. laxa* and the variety *H. laxa jurkowicensis* from Jurkowice. The two forms come from similar environments in a tabulate-stromatoporoid reef.

1. Characters in common have been ascertained providing evidence for assignment of both forms to the *H. laxa* group. They are with similar structural pattern and similar ontogeny. The latter is indicated by arrangement and development of buds, and correlation curves of the same type. Individual variability displays analogous tendencies.

2. Differences, however, occur reasonably suggesting separation into a variety. They are as follows: shape of colony is tabular in the type form, but subcircular in the Jurkowice form. In the type form buds grow vertically upward, in the latter — latero-radially. In the variety budding is frequent. Calices attain the size of 16 × 18 mm in the Jurkowice variety, as compared against 12 × 12 mm in the Dziewki form. The tabularium has a greater mean diameter, attaining the maximum figure of 7 mm against 6 mm in the Dziewki corallites. Septa more numerous and rapidly stabilized. All skeletal elements more massive. Septal regression is expressed in the Jurkowice form in more robust and more closely spaced numerous carinae and in the separation of septa into numerous thick lumps. The inner wall is less compact in the Jurkowice variety.

3. Greater diameter of calyx, greater number of septa, and more advanced reduction of the septal system indicate more advanced phylogeny, as compared with the type species. Hence the writer regards the Jurkowice form as a mutation.

4. Another morphological difference confirms the supposition that the Jurkowice variety cannot be a straight line descendant of the type form, but merely belongs to the *H. laxa* group. It consists in the considerable constant length of the minor septa in the Jurkowice colony throughout all the ontogenetic stages, while in the type form the septa are mostly short. Although the tendency for septal reduction mainly involves minor septa, nevertheless in the Jurkowice variety they nearly always remain long

through the later ontogenetic stages. The original structural pattern here is, therefore, somewhat different and the evolutionary trend in this respect has a different degree of intensity.

Peneckiella minor (Roemer) *kunthi* (Dames)

(fig. 20-29)

1869. *Cyathophyllum kunthi* Dames; W. Dames, Herr Dames an..., p. 699.
1873. *Fascicularia kunthi* Dames; W. N. Dybowski, Beschreibung zweier aus Oberkunzendorf..., p. 406 - 408, pl. 13, fig. 3, 4.
1881. *Fascicularia kunthi* Dames; C. Schlüter, Über einige Anthozoen..., p. 104.
1885. *Cyathophyllum kunthi* Dames; F. Frech, Die Korallenfauna..., p. 35 - 36, pl. 1, fig. 4 a - b.
1935. *Disphyllum (Phacellophyllum) caespitosum* (Goldf.), partim; W. D. Lang & S. Smith, Cyathophyllum..., p. 573.
1949. *Macgeea (Thamnophyllum) caespitosum* (Goldf.) var. *minus* (Roemer), partim; A. v. Schouppé, Die „Thamnophyllen"..., p. 154 - 155, pl. 11, fig. 38 - 39.
1956. *Macgeea (Thamnophyllum) kunthi* (Dames); H. Flügel, Kritische Bemerkungen..., p. 360 - 361.
1957. *Thamnophyllum kunthi* (Dames); M. Różkowska, Considerations..., p. 84, fig. 1 A; p. 100, fig. 10; p. 140.

Material. — Reef built up of phaceloid colonies of this species and of dendroid colonies of *Sudetia lateseptata*, all cemented by dark bituminous zoogenic limestone. South shore of Daisy Pond near Mokrzeszów, Upper Frasnian. 34 thin slides have been cut with transverse and longitudinal sections.

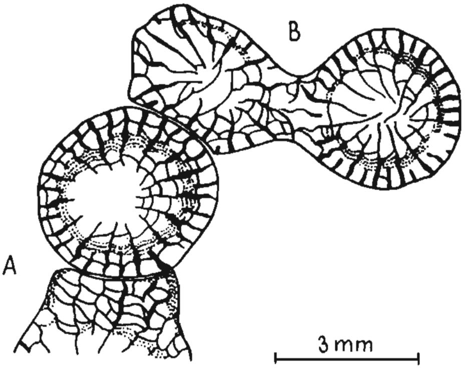

Fig. 20. — *Peneckiella minor kunthi* (Dames); Mokrzeszów, Upper Frasnian. Cross sections of mature corallites: *A* corallite coalesces with neighbour by its elongated part, *B* bud in contact with parent corallite (slide no 35).

Diagnosis. — Phaceloid colony; corallites straight, covered by thick epitheca, locally touching. Diameter 2.5 to 4.8 mm. Number of septa ranging from 12 × 2 to 16 × 2, only exceptionally 18 × 2. Major septa long with bent axial ends, thick and zigzagged, within the dissepimentarium frequently carinate. Minor septa short. Double row of diversely shaped dissepiments (horizontal, horse-shoe, sigmoidal, peneckielloid). Tabulae usually complete, horizontal or concave. Trabecular fans, trabeculae thick (0.08—0.16 mm). Budding latero-thamnophylloid.

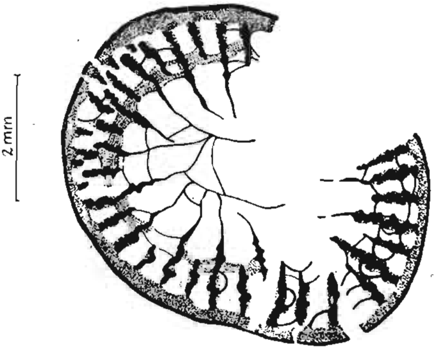

Fig. 21. — *Peneckiella minor kunthi* (Dames); Mokrzeszów, Upper Frasnian. Cross section of a corallite with distinctly carinate septa, frequently not surrounded by stereoplasm (slide no. 41).

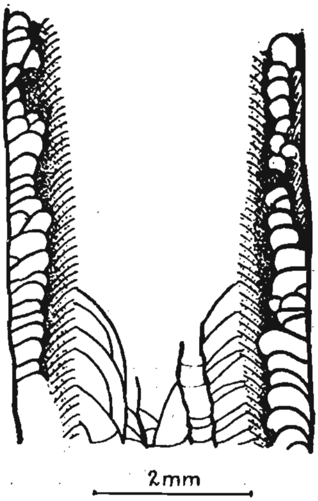

Fig. 22. — *Peneckiella minor kunthi* (Dames); Mokrzeszów, Upper Frasnian, Longitudinal section of a corallite (slide no. 22).

A. *Blastogeny*

1. *Development of bud* (fig. 23—25). The above named species produces lateral buds, arising from the dissepimental tissue of the budding corallite. Similar mode of budding occurs in *Thamnophyllum caespitosum* (Goldf.). In the latter form the bud bends at a right angle, in the Mokrzeszów form — at 45°. During the early stage (fig. 23) some of the major and minor septa of the parent corallite grow longer and become part of the bud's septal

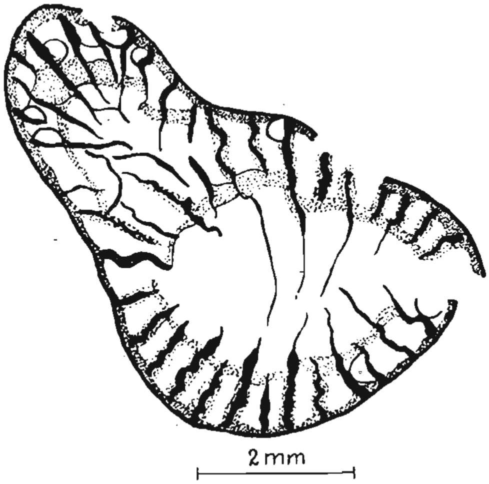

Fig. 23. — *Peneckiella minor kunthi* (Dames); Mokrzeszów, Upper Frasnian. Cross section of corallite with bud: elongated septa of parent corallite enter the bud (slide no. 35).

apparatus resting on the outer and the periaxial side in relation to the budding polyp. This is thamnophylloid lateral budding not common in the *Thamnophyllum* lineage. It is distinguishable from lateral buds of the disphylloid type where septa of the parent corallite persist on the outer side of the bud (fig. 4, 5).

During the following stage (fig. 24), with diameter of 2.5 mm, the bud is provided with a completely developed interior pseudotheca, but the epitheca never separates the bud from the parent corallite.

In longitudinal section (fig. 25) the bud is seen to arise from the dissepimental tissues consisting of normal vesicles and horse-shoes. During the primary stage the structure is diaphragmatophoric. On the outer side of the bud is the epitheca, absent from the inner side, hence the bud there is directly united with the parent corallite.

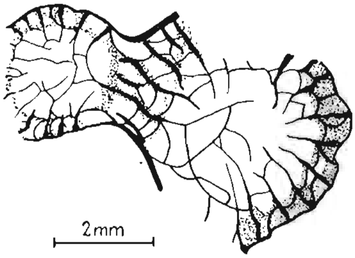

Fig. 24. — *Peneckiella minor kunthi* (Dames); Mokrzeszów, Upper Frasnian. Section of a bud with complete pseudotheca (slide no. 10).

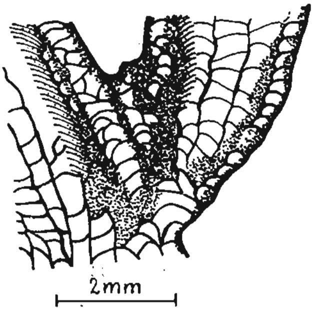

Fig. 25. — *Peneckiella minor kunthi* (Dames); Mokrzeszów, Upper Frasnian. Longitudinal section of a bud; lack of epitheca between two corallites (slide no. 16).

2. *The n/d ratio variations during ontogeny* (fig. 26). In the neanic and nepionic stages septa increase rapidly, the diagram curve rises almost steeply. During the ephebic stage, with diameter of 3.4 to 4.4 mm, the number of septa is already constant and the morphogeny complete. A slight increase in the calicinal diameter occurs only.

3. *Septal length* (fig. 26) varies distinctly. In young individuals septa are long, in the axis of the corallite nearly mutually coalescent. During further growth of bud septa diminish conspicuously. The c/d correlation curve shows changes during ontogeny within the axial portion without septa. This area expands nearly uniformly with the increase of the corallite diameter. With diameter of 2.4 to 3.9 mm the corallite centre, not provided with septa, is minute (0.3—0.5 mm), later widening up to an average of 1 mm in the largest specimens.

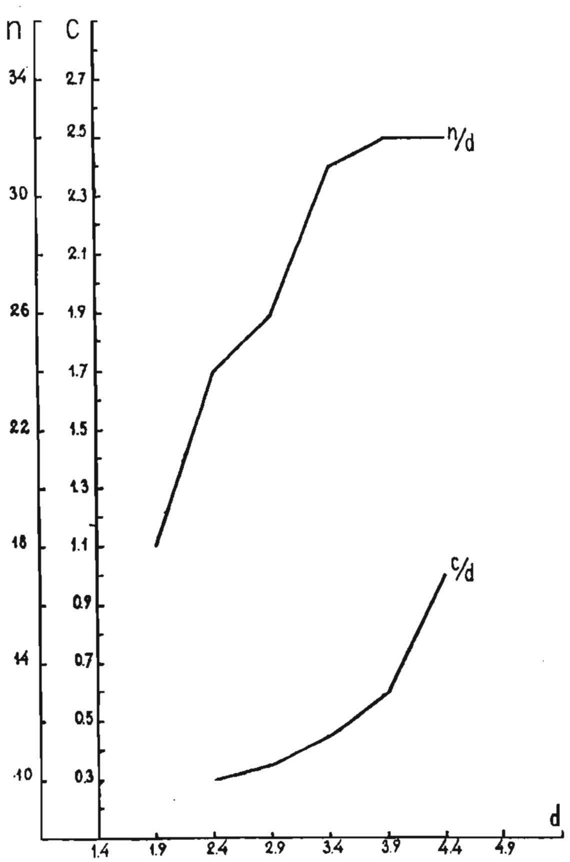

Fig. 26. — *Peneckiella minor kunthi* (Dames); Mokrzeszów, Upper Frasnian. Ratio curve of total septal number (*n*) and corallite diameter (*d*), also with ratio curve of axial area (c) free of septa and corallite diameter (*d*); c, *d* — in mm.

B. *Individual variability*

Individual variability is strong. It is most conspicuously expressed in regressive elements, such as dissepiments and septa. Tabulae vary considerably too.

1. *Dissepimental structure* (fig. 27-28). Dissepimentarium extremely narrow, involving one, never more than two vesicular rows. Dissepiments vary notably in shape and dimensions, the following types being distinguished: a) small horse-shoe dissepiments with both arms resting on the underlying vesicle; the symmetry line of the trabecular fan occurs at the uppermost part of the vesicle; b) „horizontal" dissepiments, in this species slightly arched upward, occur outside the horse-shoe dissepiments; in some places they are missing near the horse-shoe, in others may be underlain over the entire width; c) normal, „peneckielloid" dissepiments, distally flattened, are

the most common and the largest; their inner arm rests on the underlying vesicle, the outer one enters the thick wall; it does not, however, participate in its formation, but seemingly leans against it; d) another, rather rare dissepimental type is that apparently due to the fusion of two distinct vesicles: the horse-shoe and the horizontal; in shape it is sigmoidal (fig. 27).

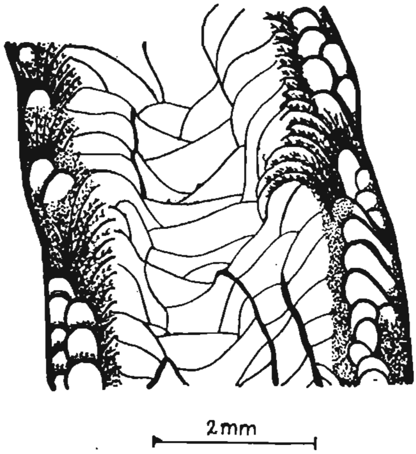

Fig. 27. — *Peneckiella minor kunthi* (Dames), Mokrzeszów, Upper Frasnian. Longitudinal section showing horse-shoe dissepiments, peneckielloid, horizontal and sigmoidal vesicles; trabecular fans resting on horse shoe dissepiments or on normal (peneckielloid) vesicles (slide no. 40).

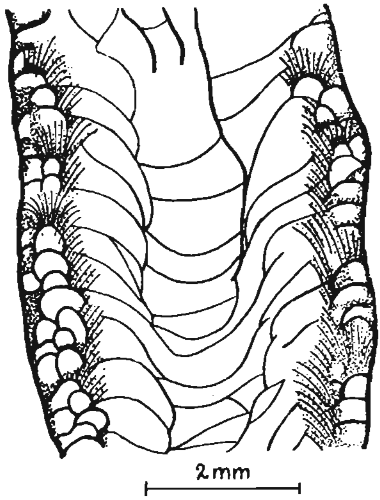

Fig. 28. — *Peneckiella minor kunthi* (Dames); Mokrzeszów, Upper Frasnian. Longitudinal section showing various dissepiments (slide no. 25).

The disappearance of horse-shoe dissepiments calls for closer attention, since — together with the symmetric trabecular fans — they constitute the most characteristic features of the Thamnophyllidae. The symmetry line of the trabecular fans is shifted towards the epitheca together with the extinction of horizontal dissepiments. Although both the horse-shoe and the horizontal dissepiments become obsolete, trabecular fans persist and continue to occur in the descendant form *Sudetia lateseptata* n.sp.

2. *Peneckielloid and horse-shoe dissepiments.* Peneckielloid vesicles dominate over horse-shoe dissepiments. Through the investigation of their numerical ocurrence in 40 corallites, involving 20 dissepiments, the following data have been obtained by the writer: in one third of the examined corallites the number of peneckielloid dissepiments slightly exceeds that of the horse-shoe type, the ratio being 2 : 1; in another third of the corallites the peneckielloid type is three or four times as numerous, while in the remaining 37 per cent its number is five to seven times that of the horse-shoes. This indicates rapid extinction of thamnophylloid characters. More-

over, observations confirm that the part played by horse-shoe dissepiments in the formation of dissepimentarium is not at all connected with ontogenetic age.

3. *Septal thickness* is a feature not controlled by age, and strongly variable throughout ontogeny. Thin septa may occur together with the spindle-like type even in the youngest corallites. Their maximum thickness ranges from 0.08 to 0.32 mm. In the same mature calyx we may encounter thin, wide spaced septa, together with those inflated to such an extent by the superimposition of stereoplasm that their width is two or three times greater. Septa have been measured at their maximum width, within the inner wall. The fracture lines there distinctly separate the septum from the inflated vesicular wall touching them. This observation is illustrated by the following numerical data (in mm):

Diameter of calyx	Thickness of major septa
2.5 - 2.7	0.09 - 0.32
3.0 - 3.9	0.09 - 0.32
4.0 - 4.5	0.08 - 0.32

4. *Septal carinae*. The presence of carinae in this species has been ascertained without doubt. Outside they are not always discernible, being masked by the stereoplasm. Septa are then broad, spindle-like; carinae most conspicuous (fig. 21) when reduction of stereoplasm has occurred. Schouppé (1958, p. 230), when stating the generic diagnosis of *Peneckiella* (based on the genotype *Diphyphyllum minus* Roemer), writes that „septa are not distinctly carinate". In her diagnosis of the newly established genus *Peneckiella,* with genotype as mentioned above, Soshkina (1939, p. 23) postulates that „septa are zigzagged and occasionally provided with few septal carinae". Three possibilities are suggested on the Mokrzeszów specimens with macro- and microstructure elements occasionally excellently preserved: a) thin non carinate septa, b) septa thickened, carinae indistinct, c) strongly carinate septa. In microscopic sections of the Grund genotype microstructure is not readily discernible. Thin as well as thicker, spindle-like septa occur; carinae are indistinct, like in some Mokrzeszów specimens. The presence of carinae in the Mokrzeszów specimens indicates the maturity of the corallite; in corallites with diameter of up to 2.8 mm septa and the trabecular line are straight. Beginning with a 3 mm diameter septa may be zigzagged, but without distinct carinae. With diameter from 3.7 mm upwards carinate septa make their appearance. Their number varies: carinae are either completely lacking or occur on 1-3 septa, occasionally on as many as seven septa.

5. *Spacing of tabulae*. The arrangement of tabulae is not affected by ontogenetic age, being rather a function of environmental conditions. Two

cardinal types of tabulae occur: a) closely spaced, horizontal, with a slight groove-like depression in the axial area, usually complete (fig. 29) and b) incomplete, deeply concave, widely spaced (fig. 27-28). In type a) 9-12 tabulae fit into 2 mm, in type b) there may be from 4 to 7 tabulae in 2 mm.

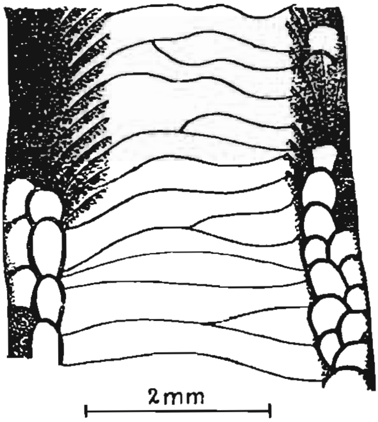

Fig. 29. — *Peneckiella minor kunthi* (Dames); Mokrzeszów, Upper Frasnian. Longitudinal section showing various dissepiments and closely spaced, horizontal tabulae (slide no. 21).

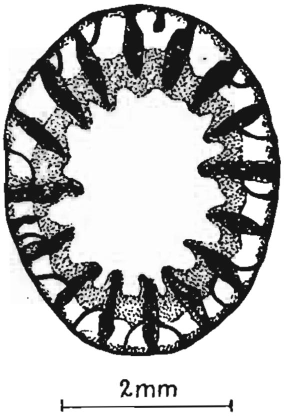

Fig. 30. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Cross section of a corallite; minor septa nearly completely reduced (slide no. 12).

Remarks. A comparison of the Mokrzeszów form with sections of the Grund genotype shows very close similarities; it is in fact hardly possible to distinguish forms from these two localities. Since the author is not familiar with the variation range of the species *P. minor*, she postulates that the Mokrzeszów form is a geographical variety. It is characterized by fewer septa with corresponding calicinal diameter (16 × 2 septa in the Mokrzeszów form against 18 × 2 septa in *P. minor*, with diameter of 3.6 mm).

Genus *Sudetia* n. gen.

Sudetia lateseptata n. sp.

(fig. 30 - 43)

Material. — Large irregularly dendroid colony (9 × 15 × 6 cm), also numerous small fragments cemented in dark bituminous Upper Frasnian limestone of Mokrzeszów, accompanied by *Peneckiella minor kunthi*. 15 thin slides have been prepared with transverse and longitudinal sections.

Diagnosis (holotype, fig. 30-33, microscopic sections nos. 12, 15). — Dendroid colony with zigzag corallites provided with 32-36 major and minor septa, at diameter of 3.0 to 4.6 mm. Thick epitheca, conspicuous inner pseudotheca occurring on the boundary line between the tabularium and the dissepimentarium. Calyx deep, with flat bottom and steep walls, completely surrounded by the epitheca as far as the distal end of septa. Major septa short, spindle-like, mostly touching laterally, with wide carinae usually covered by stereoplasm; minor septa of varying length, often completely reduced. One row of flattened peneckielloid dissepiments. Tabulae mostly complete, concave or horizontal. Trabecular fans asymmetrical, with the divergence line near to the wall, resting on the distal end of a peneckielloid vesicle. Trabeculae thick (0.06-0.18 mm). Two modes of budding: either lateral, thamnophylloid, rather rare, or syringoporoid, with aseptal and breviseptal stages, most common. Numerous connecting processes.

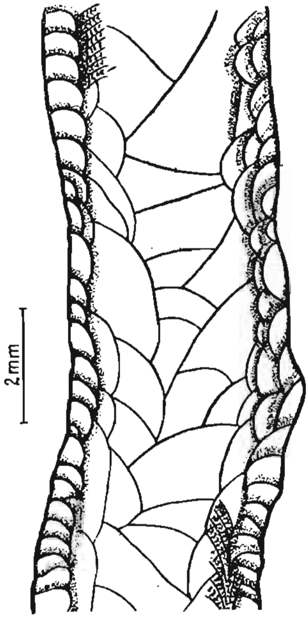

Fig. 31. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Longitudinal section (slide no. 23).

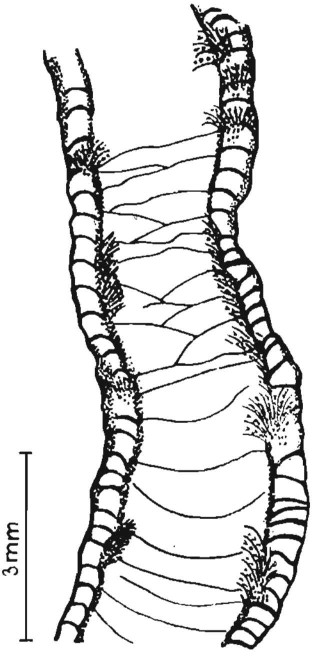

Fig. 32. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Longitudinal section (slide no. 12).

A. *Blastogeny*

1. *Development of bud* (fig. 34-42). The corallite frequently produces processes. Some (left side, fig. 33), involving dissepiments as well as tabulae, are connecting processes, others inclining from the mature corallite at an angle of 45°, are buds filled by large vesicles responsible for their cystiphylloid appearance.

The following stages are distinguishable during syringoporoid blastogeny:

a) Stage I (fig. 34, 35) — in cross sections septa lacking in the bud which, together with the parent corallite, is enclosed in a common epitheca. Septa of a mature individual are not introduced into the bud, which contains only widely spaced dissepiments and tabulae. This aseptal stage continues until the bud attains a diameter of 2.2 mm. In fig. 35 one side of the bud touches the adjacent corallite.

b) Stage II, breviseptal (fig. 36, 37) — septa present in buds with diameter from 1.8 to 2. 8 mm. In this stage, common in our thin slides, beginning major septa are discernible. In fig. 36 the young bud coalesces with *Peneckiella minor kunthi,* being on this side provided with 3 short septa. The bud is provided with the epitheca and tabulae. The same thin slide shows a breviseptal bud, slightly older, already with 16 short thin major septa, some of which probably belong to the minor group. The inner pseudotheca and the dissepimentarium have been formed. The bud is attached with a process to *P. minor kunthi* (fig. 37).

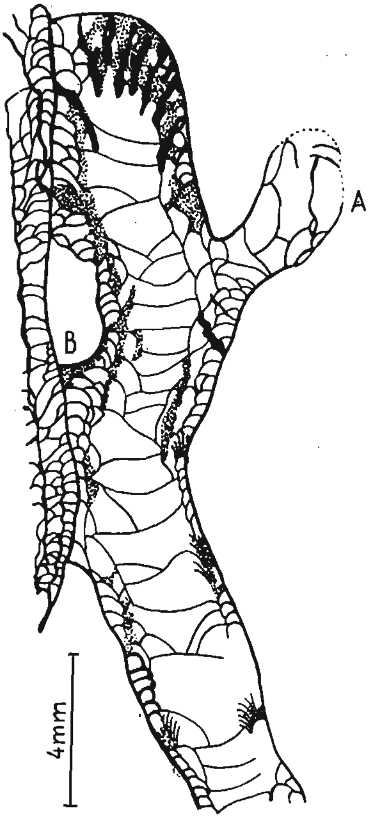

Fig. 33. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Longitudinal section showing shape of corallite with syringoporoid bud (*A*) and connecting process (*B*) (slide no. 15).

c) Stage III — with 14-16 major septa which are thick, zigzag (fig. 38), with short minor septa locally intervening. Bud 2.5 mm in diameter, coalescing with *P. minor kunthi.* Fig. 39 shows distinctly syringoporoid budding. The bud arises from the transversely cut parent corallite with short, thick major septa and partly reduced minor septa. It is thick-walled, and provided with large vertical vesicles. Septa of the budding corallite are not introduced into the bud. Normal peneckielloid dissepiments make their appearance at diameter of 2.4 mm. Eight zigzag major septa, with thickness uniform throughout the length, are seen on the distal end of bud. Their axial ends hardly protrude beyond the inner wall. Several minor septa occur too. Complete and incomplete tabulae present. A short and broad trabecular fan (fig. 39) observable on the convex wall of the vesicle.

Lateral, thamnophylloid budding (fig. 40), as in *P. minor kunthi*, less common, may occur together with syringoporoid budding. In the thamnophylloid type septa of the parent corallite elongate to attain the interior of the bud, and form short septa on the outer and inner bud wall. The epitheca

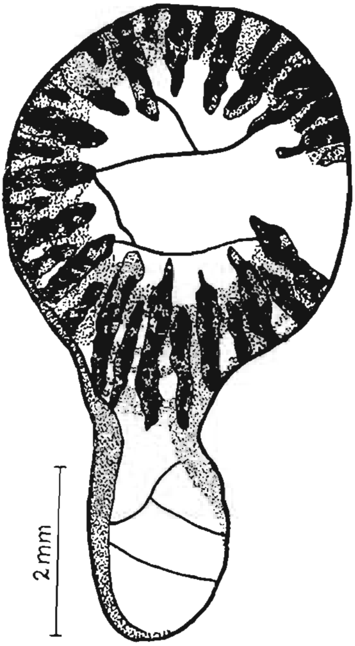

Fig. 34. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Cross section of a corallite with aseptal bud (slide no. 12).

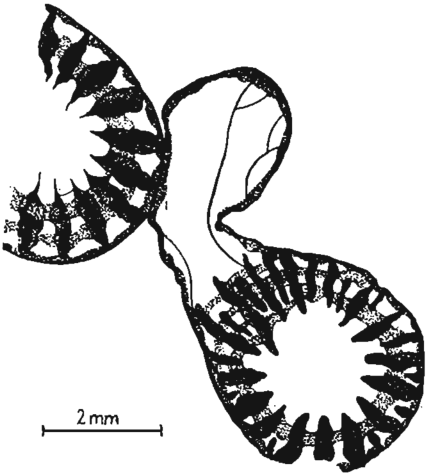

Fig. 35. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Cross section of a budding corallite with aseptal bud, slightly obliquely cut (slide no. 47).

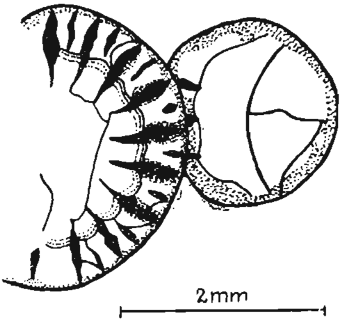

Fig. 36. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Bud with three septa, touching the adjacent corallite; both in cross section (slide no. 51).

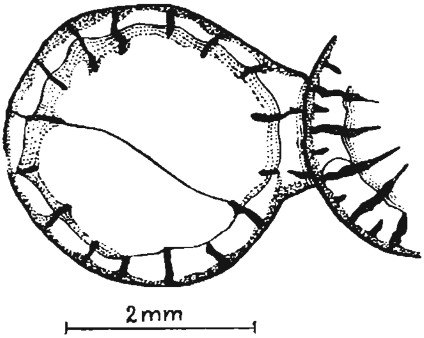

Fig. 37. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Bud slightly more developed, breviseptal stage with connecting process (slide no. 51).

does not, however, separate the bud from the parent corallite, the two individuals are intimately connected in both types of budding.

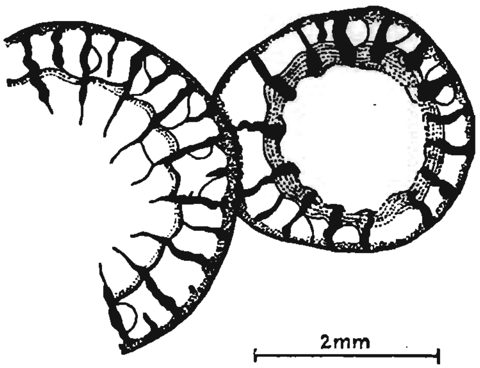

Fig. 38. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Young individual in neanic stage, touching the adjacent corallite (slide no. 51).

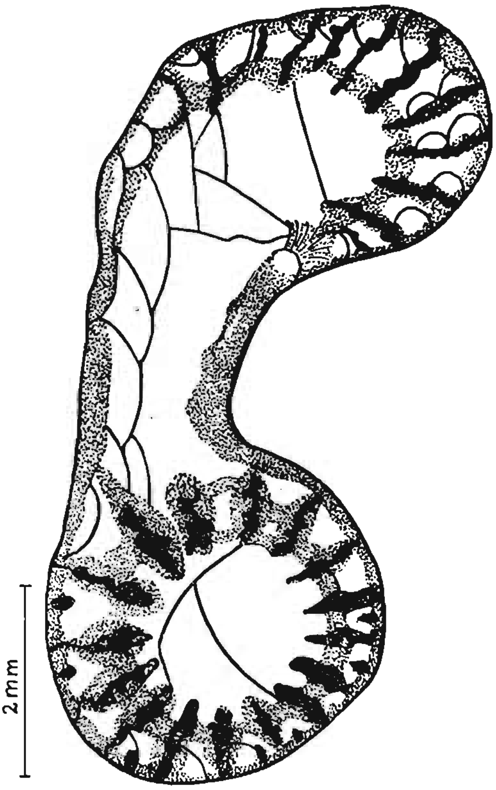

Fig. 39. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Budding corallite with a bud, in longitudinal, slightly oblique section (slide no. 52).

Fig. 40. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Thamnophylloid budding, elongated septa of budding corallite enter the bud (slide no. 50).

In the same thin slide we can also see young individual corallites, possibly the equivalents of oozoids. From the very beginning (fig. 41), with diameter of 1 mm, they are provided with major septa as well as with large vesicles and complete tabulae. Several major and minor septa, divided into radiating segments, occur on the distal, somewhat obliquely cut end.

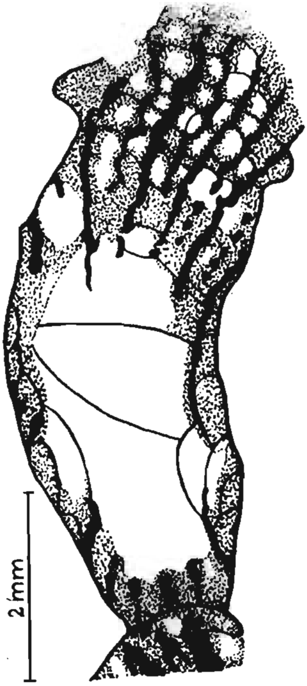

Fig. 41. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Juvenile corallite, probably an oozoid, provided with septa in the earliest stage, at the very base (slide no. 52).

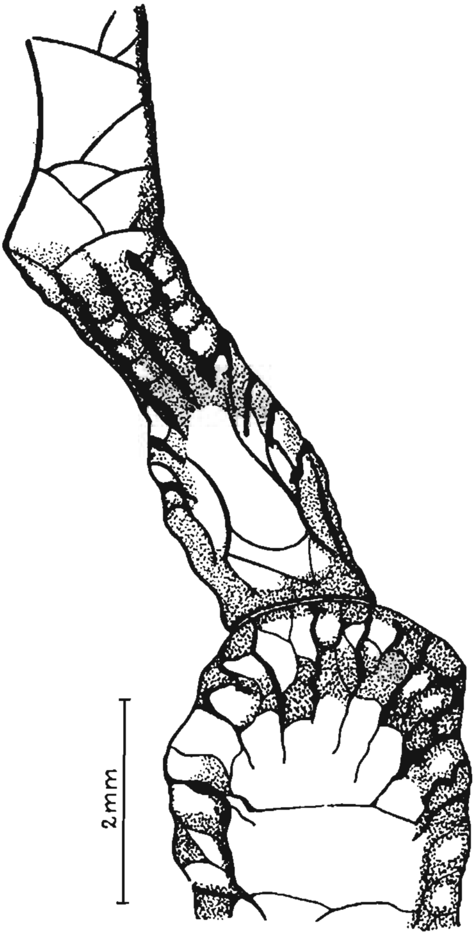

Fig. 42. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Juvenile corallite, probably oozoid, in longitudinal, slightly oblique section, with cystiphylloid bud at the distal end (slide no. 54).

An interpretation of the young corallite in fig. 42 presents some difficulty. It is probable that a larva, secreting a calyx with septa, 1.5 mm in diameter, has been attached to a mature corallite of *Sudetia lateseptata*.

A cystiphylloid aseptal bud arises from the young corallite even with diameter of only 2 mm.

Remarks. Soshkina (1954, p. 36, pl. 5, fig. 2), when describing *Peneckiella jevlanensis* Bulvanker from Livonian strata of the Russian Platform, mentions buds occurring in the form of cystiphylloid vesicles. At a diameter of 1.5 mm these buds are without septa, their beginnings only being discernible as short spines on the wall. Similar buds have been ascertained by Soshkina (1954) in *Donia rossiensis* Soshkina, in Upper Frasnian beds.

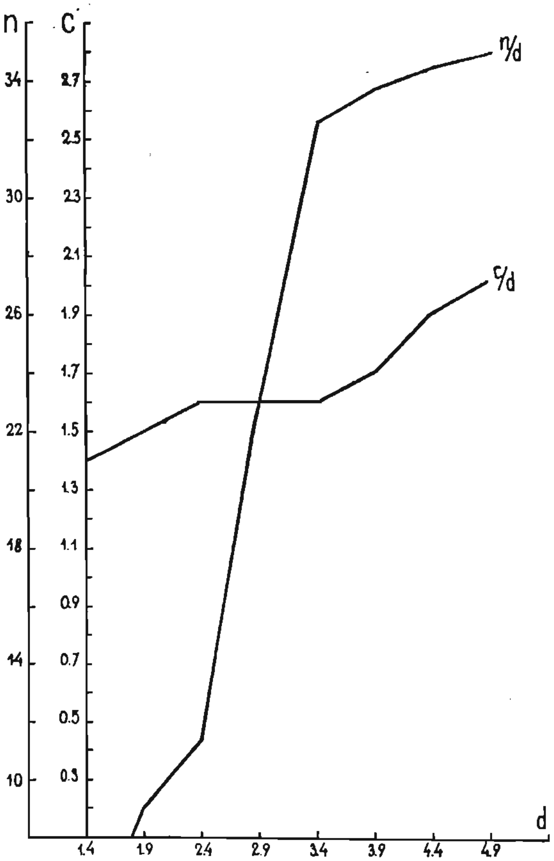

Fig. 43. — *Sudetia lateseptata* Rozk.; Mokrzeszów, Upper Frasnian. Ratio curve of total septal number (*n*) and corallite diameter (*d*), also width ratio curve of axial area (*c*) free of septa and corallite diameter (*d*); *c*, *d* — in mm.

The above mentioned species of that author may possibly be referable to the same group as *Sudetia*, insomuch that they display similarities of structural pattern and of microstructure.

2. *Ontogenetic variations in the number of septa* (fig. 43). 62 corallites in various ontogenetic stages have been examined for the n/d ratio. The number of septa is shown to increase rapidly during the neanic stage, with

diameter of up to 3.4 mm. Major and minor septa may be as many as 32. From that point on, during the ephebic stage, major and minor septa together attain slowly the number of 34. The frequent loss of minor septa in mature corallites has not been here taken into account.

3. *Width variations of axial aseptal area.* The c/d ratio, i.e. diameter of axial aseptal area (c) and diameter of corallite (d), similarly as the n/d ratio, is strictly governed by the stage of ontogeny. During the aseptal stage the whole interior is free of septa. Later, short septa appear and elongate rapidly. The axial area free of septa hardly augments at all at diameters ranging from 1.4 to 3,4 mm. During the ephebic stage septa still continue to grow, but slowly, as is shown by the following numerical data (in mm):

Diameter	Septal length
1.4	—
2.4	0.4
3.4	0.9
4.4	1.3
4.5	1.3

4. *Development of septal carinae dependent on ontogeny.* In young individuals (with diameter of up to 3.4 mm), the septa are thin, zigzag, and the whole interior is filled by a dark bituminous substance; carinae are not discernible although uncovered by superimposed stereoplasm. In mature specimens, however, 6 to 9 conspicuous, distinctly separated trabeculae are discernible in practically every septum, usually masked by stereoplasm. When the stereoplasm disappears, trabeculae grow more distinct in the form of carinae on septal edges.

B. *Individual variations*

In mature individuals skeletal elements vary strongly. The variation here involves shape of corallite, size and arrangement of dissepiments, spacing and structure of tabulae, thickness of septa and reduction of minor septa.

1. *Shape of corallites* varies largely, as is shown in cross and longitudinal sections. They are only exceptionally circular, being mainly elliptic, irregularly elongated into one or two directions. The epitheca becomes convex, while septa and dissepiments are introduced into the connecting processes (fig. 33). Moreover, lateral and syringoporoid buds arise, into which the prolongation of septa does not penetrate.

2. *Septal thickness variations.* Septa are the most plastic skeletal element of the studied species. Thin straight ones may occur in the same calyx with others elliptically inflated. Mature corallites have been measured with a micrometer, under 50 fold magnification, for thickness of septa, supplying the following numerical data:

Thickness of septa (in mm)	Number of septa (per cent)
0.1	16
0.2	23
0.3	28
0.4	20
0.5	18
0.6	4

The above figures show that septa 0.3 mm thick are the most common.

3. *Reduction of minor septa.* A tendency to the reduction of minor septa is a characteristic feature of this genus. The length of septa varies considerably, even within one corallite. Their rudimentary traces may be encountered with length one sixth to one eight that of major septa. Others, however, are long, attaining three fourths of the length of major septa. Minor septa are often completely reduced. There may be one or two; in some calices, however, as many as 16.

4. *Dissepimental variation* is not markedly strong. Peneckielloid vesicles only occur, arranged into one, exceptionally two rows. The size only of dissepiments varies, as is illustrated by numerical data representing the number of dissepiments in 2 mm:

Number of dissepiments	Number of corallites
3	1
4	8
5	11
6	9
7	5
8	1
9	1

Thus, extremely minute vesicles occur along with large ones. The predominant corallites, however, are those with large vesicles (5 dissepiments in 2 mm). The arrangement pattern of dissepiments varies too, usually vesicles rest horizontally, their vertical position is less common (fig. 31, 32).

5. *Spacing and structure of tabulae.* The arrangement of tabulae is not constant. Most frequently they are complete, flat, sometimes so regularly arranged as to give in longitudinal section the semblance of ladder steps, widely or closely spaced. In the same corallites, together with complete tabulae, the occurrence is noted of incomplete concave tabulae, consisting of strongly concave axial areas and of periaxial parts steeply inclined to the axial (fig. 31, 32).

GENERAL CONSIDERATIONS

1. *Problems of colonial development*

In 1934 D. Hill pointed out the existence of several evolutionary trends in the phylogeny of some tetracoral lineages. One of them involves evolution from individual to colonial forms and, among the colonial group, from phaceloid and dendroid to massive forms. This concept finds its confirmation in the Thamnophyllidae where we can trace the evolution of the genus *Thamnophyllum*. In that lineage able of producing buds, which — after Alloiteau (1955, p. 396) — is the essential condition, the occurrence is noted of the three above mentioned colonial types: phaceloid in *Peneckiella minor kunthi*, dendroid in *Sudetia lateseptata* and *Th. trigeminum kozłowskii*, and massive in the genus *Phillipsastraea*[4]. On the other hand, the genus *Macgeea* — throughout its phylogeny from the Lower Givetian to the Upper Frasnian — persists as an individual form. Very exceptionally only it produces 2-3 parricidal buds, although it occurs in the same facies with the dendroid *Thamnophyllum*. In the genus *Phillipsastraea*, the massive colonial stages have twice been attained by the *Thamnophyllum* lineage, i.e. in the Middle Givetian and the Upper Frasnian. Hence, we may assume that colonial development is not connected with facies or phylogeny, but with the adaptability of the given lineage.

A coral colony is an assemblage of corallites, more or less intimately united and produced by agamic multiplication (blastogeny) from one zooid. Hence it is a truly homogeneous population, consisting of genetically interrelated individuals. All the corallites of one colony are expected to display analogous reaction to outside stimulus, phenotypic variations of a continuous nature, and the occurrence of different mutations due to spontaneous changes in the genetic system.

Colonial corals have been recorded as early as from the Middle Ordovician (*Favistella*), up to recent times. A colony of Palaeozoic tetracorals, however, differs from a hexacoral one. In a tetracoral colony each corallite is separated from its neighbour by an epitheca. The epitheca is compact and stretches to the edge of the calyx, completely surrounding the polyp living there. It is formed during earliest ontogeny, as has been ascertained by the writer in representatives of Disphyllidae. Inspite of this isolation of polyps in the colony, they must have been somehow connected by the soft tissues. This is indicated by the presence of a common holotheca covering the whole colony, and enclosing it as far as the calicinal edges, also by the constant shape of colonies in a fixed environment.

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[4] After Schouppé (1958, p. 235) *Phillipsastraea hennahi* (Lonsd.) is provided with horse-shoe dissepiments, hence, the genus *Phillipsastraea* d'Orb. is an older synonym of the genus *Pachyphyllum* E. & H.

A hexacoral colony is markedly different. Polyps of one colony are closely interconnected, the epitheca is lacking, there is only a pseudotheca which may be synapticular, dissepimental (paratheca) or septal. Moreover, a peritheca is developed, characteristic of hexacorals.

Similar interconnection of corallites in one colony is observable in a family of Palaeozoic tetracorals, the Thamnophyllidae. Soshkina (1951) mentions them as displaying hexacoralloid character. Here also a pseudotheca only (septal or dissepimental) is formed to separate the corallites. In cerioid colonies the wall separating the corallites arises from the septal bifurcation, while in plocoid colonies corallites are interconnected either by septa or by dissepiments. The wall is lacking here. During the ontogeny of Thamnophyllidae the bud does not produce an epitheca, but it is in intimate contact with the budding corallite, e.g. in the genera *Peneckiella* and *Sudetia*, as well as in *Phillipsastraea*.

2. *Individual variation in colonial corallites*

a) *Ontogenetic changes of the bud.* A colony may be considered as a pure animal population. In them the palaeontologist can investigate the extent and intensity of variations, and at the same time study the evolutionary mechanism in chronologically different forms.

Every colonial corallite is subject to modification during blastogeny, analogously as the individual coral has to pass through certain ontogenetic stages. The morphological stages of development are usually uniform in buds of the same colony. E. g. every corallite of a massive colony of *Hexagonaria laxa* begins its development within the dissepimentarium. Isolated by the epitheca it passes through the diaphragmatophoric and later — the pleonophoric stages. Finally, in mature individuals, laminar septa may become lonsdaleoid. The ontogeny of the first corallite, i.e. the oozoid, from which the colony originates, has not been established. The development of the oozoid may differ from that of the blastozooid. For example, the oozoid of *Thamnophyllum trigeminum* Pen. passes the bilateral symmetry stage in early ontogeny, while no such stage is noted in buds. Populations of individual corallites have their own, specifically characteristic n/d ratio curve. The value of this ratio varies during ontogeny since the increase of the number of septa may be either allometrically negative or positive. In the same way colonial corallites display their own n/d or n/t ratio curves, and allometric intensity during blastogeny is likewise different.

Disphylloid and thamnophylloid buds may be distinguished already during ontogeny. Moreover, each of the four here considered genera displays peculiar blastogeny. In *Disphyllum* the bud, arising in the dissepimental part of the parent corallite, becomes disphylloidally lateral during further evolution. In *Hexagonaria* it is disphylloidally intermural; in *Peneckiella* — thamnophylloidally lateral; in *Sudetia*[5] — two types of budding occur: thamnophylloidally lateral and syringoporoidal. Hence, on the basis of blastogeny, we may include each of these genera into higher systematic units and, moreover, secure a new diagnostic generic character. The presence within one genus of two types of blastogeny may, on the other hand, probably indicate generic divergence.

b) *Variability of mature colonial corallites.* The ontogeny of corallites in one colony is identical, but polymorphism of the mature corallites may be very strong. It displays a notable intensity range, depending on the phylogenetic stage of the given lineage, as well as on environment. This has been previously ascertained by the writer in colonial corallites and will be discussed here below.

Disphyllum geinitzi, which had probably lived in quiet deeper waters, is nearly stable. Slight variations only are noted in mature individuals. Corallite structure is not complicated. The particular skeletal elements are fully developed. No traces of reduction observable: septa laminar, without carinae and without peripheral regression. All this is suggestive of phylogenetic youth („phylojuvenile" forms). Colonial corallites are excellently adapted to the rather constant environmental conditions.

Modifications are unimportant and seemingly represent direct reaction against the internal environment factors within the colony, as well as those of external environment outside the colony. The internal environment factors probably reflect the „struggle" for space and food for the polyps. Corallites of a phaceloid colony, growing upward and having sufficient space available, are circular in section and only sporadically develop connecting processes (fig. 4). Closely spaced corallites touch each other by their walls and are irregular.

The dissepimentarium width, as compared with the tabularium, varies to a small extent. Rapid sedimentation is probably responsible for the appearance of larger dissepiments and more widely spaced complete tabulae.

Hexagonaria laxa displays a completely different variation range, as is also the case in its mutation *H. laxa jurkowicensis*. It seems that they represent two distinct ecological types within the studied reefs: a) *H. laxa* from Dziewki developed within a reef-facies, but, most likely, this part of the reef has not been exposed to the action of strong waves; b) the Jurkowice mutation, on the other hand, had probably lived on the surf-side of the reef.

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[5] In recent *Hexacoralla* a diagnostic feature may be one type of budding, though exceptions are noted too: in *Barabattoia mirabilis* Yabe & Sugiyama (1941, p. 72) together with intermural buds intracalicinal are also encountered within one colony.

Adaptation of skeletal elements is expressed by thick septa (2-3 times thicker than those in *H. laxa*), massive trabecules (0.2 mm thick) and a massive wall.

Space available in the colony and easily gained food may have been decisive factors in differences of growth and budding of adjacent corallites. With the same number of septa (36-38) and diameter of tabularium (4.5—5.5 mm) some corallites have a broad dissepimentarium with large peripheral vesicles and they produce buds, while others are not capable of budding.

In mature corallites dissepimentarium width variations depend on the amount of space available and on budding. The size and spacing of vesicles may possibly be a function of external environment and rate of sedimentation, but it may also be associated with the budding process.

Development of septa which display every sign of degeneration, is a feature subject to strongest variations. Together with complete septa others occur in the same corallite, which are peripherally regressive and disintegrated into radiating segments. Carinate septa occur together with nearly smooth ones. The strong variability of reducing organs has been ascertained as early as in 1859 by Darwin. It was also confirmed by Simpson (1955). In the phylogerontic phase tetracorals vary strongly too.

Variability of mature corallites never exceeds here the limits of intraspecific variations. They are merely modifications within a population which is still genetically homogeneous. The individual colonial corallites may be arranged into a succession of continuous variation series, both in the above species and in *D. geinitzi*.

In recent colonial hexacorals, strong phenotypic variability is likewise encountered. Yabe & Sugiyama describe calicinal dimorphism and even trimorphism, as commonly reoccurring within the same colony of *Leptosera columna* (1941, p. 75) and in *Astraeaopora tayama* (p. 84). Strong morphological variations have been also pointed out by Wells (1954) in *Stylocoenella armata* (Ehrenberg), *Acropora formosa* (Dana) and *A. polymorpha* Brook. They include shape of colony, depth and spacing of calices, length of septa and size of trabeculae. These variations are a function of water depth. The differences may be so great that fragments of two colonies may appear assignable to two distinct species if it were not for the occurrence of a number of forms linking the extreme variants.

Peneckiella minor kunthi — the colonies here are fasciculate, made up of straight, parallel corallites. In appearance they resemble *D. geinitzi* except that the particular corallites are thinner. Here, similarly as in *D. geinitzi*, short epithecal processes have developed to insure greater compactness of colonial structure.

Mature forms display notably strong variations expressed in every skeletal element. Two variation types are distinguishable: 1) somatic modifications reflecting the action of environment factors within the colony, and of environment factors outside the colony. These are slight quantitative changes varying in extent, but present in all corals. They constitute continuous variability involving thickness of septa, spacing of tabulae and dissepiments, also appearance of colony. The per cent variation curves of these characters are one-topped; 2) genetically conditioned variations expressed in the different phenotypes by qualitative changes suggestive of commencing divergence of features, leading perhaps to a new genus; here dissepiments and septa change structurally.

In our species dissepiments show strong diversity, since they may be horse-shoe like, peneckielloid, horizontal or sigmoidal. Such diversity is associated with regression of horse-shoe dissepiments. These may be small or large, numerous or completely lacking. Their extinction is accompanied by that of horizontal vesicles; sigmoidal dissepiments have originated from the fusion of horse-shoe like and horizontal dissepiments. The variability of the horse-shoe number ratio/number of peneckielloid dissepiments is not continuous.

Septa are usually strongly thickened by a stereoplasm layer which surrounds the inner zigzag trabecular line. In some places the septa lose the superimposed stereoplasm layer thus revealing the carinae. Minor septa may vary in length so much so as to become rudimentary.

Sudetia lateseptata forms dendroid colonies. Minute, irregularly twisted individuals are closely intertwined and connected by extremely numerous connecting processes. Very strong variations are exhibited in the shape of the corallites. In cross section they may be circular, elliptic, or extremely irregular. Such variability is due to scarcity of space available within the colony, syringoporoid budding and numerous connecting processes.

In mature forms the particular skeletal elements are considerably thickened owing to the superimposition of stereoplasm, so much so that septa touch laterally. Corallites, as well as whole colonies thus augment their resistivity against the action of water. Dissepiments are large, tabulae very distant, indicating rapid reaction to accumulation of sediments.

The structure of dissepiments here differs from that in the ancestral species *Peneckiella minor kunthi*. The great diversity of shape has disappeared, the vesicles are all uniformly peneckielloid, differences are slight, quantitative.

Genetic changes are those of septal structure. Septa are here the disappearing element. This is expressed in the number of minor septa which are fully developed in some corallites, while in others several or nearly all will disappear. Similarly as in *P. minor kunthi*, a thick stereoplasm layer surrounds the inner zigzag trabecular line. On some septa trabecular processes are set free through the reduction of stereoplasm. Septa are then provided with a new feature, i.e. with carinae which do not make their appearance before the maturity of forms. A new feature, which is not continuous, consists in syringoporoid budding.

3. *Genomorphs*

The appearance within *Peneckiella* and *Sudetia* colonies of new qualitative features together with others characterizing the genus *Thamnophyllum* which is their ancestral form, puts forward the problem of genomorphs so frequently discussed in literature. In 1905, Vaughan was the first to ascertain „diphyphylloid and lonsdaleoid modifications" in the genus *Lithostrotion.* In 1930, Lang and Smith (in Hill, 1934, p. 88) designated that phenomenon with the name of genomorphs. These authors have described the dimorphic genus *Lithostrotion* which, in the same colony, displays the structural pattern of the genus *Diphyphyllum* along with its own generic features. This new type in *Lithostrotion* colonies, corresponding to the genus *Diphyphyllum*, was by them called a genomorph. In the more recent papers by Dobroljubowa (1952, 1958), McLarren & Sutherland (1949), and Sutherland (1958) this problem is discussed at large.

Genomorphs are apparently recorded in greater abundance from Carboniferous coral colonies only. Smith (1945, p. 7) quotes the Devonian genus *Phacelophyllum* as a genomorph within the species *Disphyllum caespitosum* (Goldf.). More recent papers have, however, revealed the clearly distinct microstructure of these two genera which makes them probably referable to two suborders. Moreover, they never occur together in the same colony, hence they are not genomorphs.

Genomorphs occur in some corallites of both fasciculate and massive colonies, but the dimorphic structure scheme may likewise occur in one corallite.

At Mokrzeszów, in the Upper Frasnian *Peneckiella minor kunthi*, similarly as in *P. minor* (figured by Schouppé and in the thin slide of the Grund specimen), two structural patterns are observable, the thamnophylloid and the peneckielloid. In the same corallite horse-shoe dissepiments, accompanied by horizontal ones, may occur side by side with peneckielloid vesicles which are dominant.

Peneckiella minor kunthi is an objective subspecies, displaying its own characteristic curve of the growth n/d ratio and variable features ratio, placed symmetrically in relation to the dominant mean (thickness of septa, major/minor septal length ratio). Together with the here dominating generic features of *Peneckiella,* the occurrence is noted also of receding thamnophylloid characters. The number of new dissepiments is on the average seven times that of the horse-shoe dissepiments. New qualitative features diagnostic for genomorphs do not display typical continuity, but are distinctly predominant driving out the conservative fêatures. These features are not associated with the age of the corallite, neither do they indicate maturity as do the lonsdaleoid septa of *Hexagonaria laxa,* but they appear in every ontogenetic stage of blastogeny. A peculiar feature is the early disappearance of horse-shoe dissepiments, while horizontal dissepiments still persist for some time, underlying the peneckielloid vesicles. Locally, the horizontal dissepiments disappear as well, and then the peneckielloid dissepiments are in direct contact with the wall. Thus *Peneckiella* loses this aspect of its hexacoral character.

Peneckiella minor kunthi occurs in the reef together with *Sudetia lateseptata.* Hence, colonies of these two species lived side by side and corallites of one genus coalesced frequently with those of the other one. In 24 thin slides *Sudetia* corallites are coalescent with those of *Peneckiella.*

Sudetia lateseptata now displays only few thamnophylloid features. Dissepiments are of uniform structure. The predominant syringoporoid buds occur together with a few only of those produced similarly as in *P. minor kunthi.* Outside of this, microstructure is thamnophylloid.

Peneckiella minor kunthi and *Sudetia lateseptata* are two species differing in their degree of adaptation to reef environment. They are very closely allied and linked by direct phyletic connections. They do not, however, represent species owing their formation to progressive divergence due to geographical isolation. The Mokrzeszów species must have developed through rapid evolution. They represent two stages of phylogenetic evolution: *Thamnophyllum* — *Peneckiella* and *Peneckiella* — *Sudetia.* As has already been ascertained by Sutherland (1958), evolution in the Carboniferous genus *Lithostrotion* is associated with neotenia. The simplified, regressive, terminal forms of *Sudetia lateseptata* must have been formed in this manner, too.

P. minor kunthi is very near to the phyletic end of the Thamnophyllidae lineage. In this stage the morphological diversity of conspecific forms may be markedly strong. It does not, however, usually exceed intraspecific limits, as has been ascertained by the present writer in species of the Upper Frasnian genus *Phillipsastraea* (Rozkowska, 1953). In Mokrzeszów species, on the other hand, similarly as in the Carboniferous *Lithostrotion* forms, new qualitative features appear along with phenotypic variations, characteristic of the species *P. minor. Peneckiella,* in addition to thamnophylloid characters, realizes simplified dissepiments. *Sudetia* is already provided with peneckielloid dissepiments only and realizes a new, simple mode of budding along with the peneckielloid type. Aseptal buds in *Sudetia* resemble the nepionic stage in *Protomacgeea dobruchnensis,* where the oozoidal pedicillum is nearly aseptal too (Różkowska, 1957).

P. minor kunthi is the synthetic form linking characters of the conservative lineage *Thamnophyllum* with the terminal form *Sudetia lateseptata.*

Among recent hexacorals, *Porites lichen* Dana (Wells, 1954, p. 453) displays marked variations of qualitative character. Corallites assignable to various species may occur within the same colony, since corallites provided with a columella may occur with others lacking the columella; pali may be well developed or absent. In this connection Wells has ascertained the lack of a stabilized ecological form characteristic of the corresponding environment. *Porites lichen* may possibly be an example of living genomorphs. We do not, however, know whether the new, rapidly developing qualitative characters, accompanied by simplified structure (atrophy of columella and pali) will predominate in the future and eliminate the ancestral characters giving rise to a new genus.

The following inferences may be drawn on the above observations of the Mokrzeszów forms.

a) The appearance of genomorphs is a real fact. Individuals with distinctly different structural scheme make their appearance among corallites of one colony displaying specific ancestral characters. The occurrence of new features takes place during various ontogenetic stages. In the first phase they still have to "struggle" for predominance with the receding characters, e. g. peneckielloid dissepiments in *P. minor kunthi.*

b) The evolution of the colonial tetracorals, in which genomorphs occur, is orthogenetic since during the following stages conservative characters are completely eliminated by the new features, e.g. peneckielloid dissepiments in *Sudetia lateseptata.*

c) Phylogenetic development here progresses rapidly, as has been observed in the succession *Thamnophyllum* — *Peneckiella* — *Sudetia.* New genera of *Peneckiella* and *Sudetia* are formed.

d) The appearance of genomorphs is associated with the phenomenon, of simplification, since the new structural pattern is of regressive nature, structure becomes simplified, as is shown in e.g. peneckielloid dissepiments, reducing minor septa and aseptal buds.

e) Genomorphs occur towards the close of the evolution of a lineage, as is the case in *Thamnophyllum* from the Upper Devonian.

f) Species of colonial tetracorals in which genomorphs occur may be of stratigraphic significance. Such is *Peneckiella minor,* widely spread in the Upper Frasnian (the Sudeten, Harz and Antitaurus Mountains), also *Sudetia.* The latter form has so far been recorded from the Upper Frasnian of the Sudeten only. It is possible that some species, likewise provided with aseptal buds, and by Soshkina described as *Peneckiella*, are assignable here.

4. *Generic and specific diagnostic characters in Devonian colonial tetracorals*

In connection with notable difficulties encountered in the identification of colonial tetracorals the writer will here try, perhaps still too early, to interpret some of her own observations. Different reasons may account for difficulties met during specific delimitation of colonial corals.

a) Phenotypic variability occurs in all the colonies, similarly as in the most homogeneous populations; its range may be very slight within one species, notably great in another. The extreme variants may then be regarded as distinct species.

b) Phylogenetic adaptation of various lineages to similar environmental conditions leads to convergency. It may be ascertained by detailed investigation of the ontogeny and microstructure, also of the structural scheme of a given lineage. The polyphyletic genus *"Hexagonaria"* is here an unquestionable illustration. It is an adaptative form, showing power of adaptation to the reef facies. The assignment of the genus *"Hexagonaria"* to various phyletic lines is confirmed by varying microstructure; i.e. trabecules may have a fan-like arrangement as in suborder Phillipsastraeacea Roemer (comp. Schouppé, 1958, p. 217), or be parallel as in the disphylloid group; dissepimental blastogeny may be of the thamnophylloid or disphylloid type, structure scheme disphylloid or stenophylloid.

Representatives of the genus *Hexagonaria* enter into various reef niches, hence they form various species and subspecies adapted to more limited ecological habitat. Specific characters here are adaptative and of a quantitative type. Every species exhibits variability in its own limits. In *Hexagonaria laxa* e.g. the maximum tabularium diameter is 6 mm, with 38 major and minor septa; while in *H. laxa jurkowicensis* this is 7 mm, with 40 septa. Similarly, septal thickness is limited too: in *H. laxa* — 17 per cent of corallites attain 0.4 mm, while in *H. laxa jurkowicensis* — 23 per cent of the corallites in one colony attain the figure of 1.3 mm.

In tetracorals, species are established on morphological characters, structure of septa, mode of budding, and on correlations such as the n/d allometry growth curve, length ratio of major septa to that of the minor, septal length range, the dissepimentarium/tabularium width ratio. Since variability of morphological characters occurs everywhere and is of continuous nature, species is characterized by one-topped biometric curves of the various features.

A species differs from a subspecies in features of quantitative nature only. Hence the n/d or n/t allometry line has the same style, being only slightly displaced into the direction of that character which is allometrically predominant. E.g. the difference between *H. laxa* and *H. laxa jurkowicensis* is indicated by the allometrically positive increase of the number of septa during phylogeny. Biometrical curves partly coincide, e.g. that of the tabularium/dissepimentarium variability ratio.

Thamnophyllum trigeminum Pen.[6] (= *Th. trigemme* (Quenst.)) (in Różkowska, 1957), is a good illustration of the intraspecific variability and value of the above quoted criteria. This is a conservative species, which has persisted in the Devonian of Poland from the Givetian through the Frasnian. Throughout that period it retains the same structural pattern, analogous ontogeny, parricidal blastogeny, and the same type of allometry. It may, however, be separated into several varieties which, in 1956 and 1957, were by Różkowska incorrectly assigned to distinct species. Their biometrical curves partly coincide, unless they are separated by the incompleteness of material or a sedimentary gap. All these „species" may be reasonably considered as subspecies of *Thamnophyllum trigeminum* Pen. Hence, upwards from the Lower Givetian to the Frasnian the following mutations will be encountered within *Thamnophyllum trigeminum: Th. trigeminum* Pen. *skalense* Rozk., *Th. trigeminum trigeminum* Pen., *Th. trigeminum* Pen. *pajchelae* Rozk., *Th. trigeminum* Pen. *kozlowskii* Rozk. and *Th. trigeminum* Pen. *superius* Rozk.

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REFERENCES

ALLOITEAU, J. 1955. Contribution à la systématique des Madréporaires fossiles. 1-462, Paris.

BULVANKER, E. Z. 1958. Devonskie četyrechlučevye korally okrain Kuzneckogo bassejna. — *VSEGEI, Min. geol. ochr.*, 1-212, Leningrad.

DAMES, W. 1869. Herr Dames an Herrn Kunth. — *Ztschr. deutsch. geol. Ges.*, **21**, 699, Berlin.

DARWIN, K. 1859 (1955). O powstawaniu gatunków drogą doboru naturalnego, czyli o utrzymaniu się doskonalszych ras w walce o byt. — *Kom. Ewol. PAN, Bibl. klas. biol.*, Warszawa.

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[6] H. Flügel (1959, p. 117) has proved the priority of the specific name *Thamnophyllum trigeminum* Penecke in respect to the name *Th. trigemme* Pen. The species *trigemme* Quenstedt has by Flügel been included into the genus *Favistella* Dana.

DOBROLJUBOVA, T. A. 1952. Formoobrazovanie u nižnekamennougolnych korallov Lithostrotion i Lonsdaleia v svete mičurinskogo učenja. — *Izv. Akad. Nauk. SSSR, ser. biol.*, 6, 95-110, Moskva.

— 1958. Nižnekamennougolnye kolonjalnye četyrechlučevye korally Russkoj Platformy. — *Tr. Paleont. Inst. Akad. Nauk SSSR*, **70**, 1-224. Moskva.

DYBOWSKI, W. N. 1873. Beschreibung zweier aus Oberkunzendorf stammenden Arten der Zoantharia Rugosa. — *Ztschr. deutsch. geol. Ges.*, **25**, 402-408, Berlin.

FLÜGEL, H. 1956. Kritische Bemerkungen zum Genus Peneckiella Soshkina. — *N. Jb. Geol. Paläont.*, **8**, 335-365, Stuttgart.

— 1959. Zur Kenntnis der Typen von Favistella (Dendrostella) trigemme trigemme (Quenst., 1881) und Thamnophyllum trigeminum trigeminum Penecke 1894. — *Ibidem*, **3**, 113-120.

FRECH, F. 1885. Die Korallenfauna des Oberdevons in Deutschland. — *Ztschr. deutsch. geol. Ges.*, **37**, 21-130, Berlin.

GLINSKI, A. 1955. Cerioide Columnariidae (Tetracoralla) aus dem Eiflium der Eifel und des Bergischen Landes. — *Senckenberg. Lethaea*, **36**, 73-114, Frankfurt a. M.

GOGOLCZYK, W. 1956. Rodzaj Amphipora w dewonie Polski (Amphipora dans le Dévonien de Pologne). — *Acta Palaeont. Pol.*, **1**, 3, 211-240, Warszawa.

— 1959. Rodzaj Stachyodes (Stromatoporoidea) w dewonie Polski (On the stromatoporoid genus Stachyodes in the Devonian of Poland). — *Ibidem*, **4**, 4, 353-388.

GÜRICH, G. 1896. Das Palaeozoicum im Polnischen Mittelgebirge. — *Verh. russ. kais. min. Ges.*, **32**, 1-539, St. Petersburg.

— 1908—1909. „Leitfossilien". II: Devon, 97-199, Berlin.

HALLER, W. 1936. Einige biostratigraphische Untersuchungen in der Rohrer Mulde unter besonderer Berücksichtigung der Keriophyllen. — *Jb. preuss. geol. Landesanst.*, **56**, 590-632, Berlin.

HILL, D. 1934. The Lower Carboniferous corals of Australia. — *Proc. Roy. Soc. Queensland*, **45**, 12, 63-115, Brisbane.

— 1935. British terminology for Rugose corals. — *Geol. Mag.*, **72**, 857, 481-619, London.

KÜHN, O. 1926. Variationsuntersuchungen an rezenten Korallen und ihre Anwendbarkeit auf die Fossilen. — *Verh. zool. bot. Ges* 1924-1925, 74/75, Wien.

LANG, W. D. & SMITH, S. 1935. Cyathophyllum caespitosum Goldfuss, and other Devonian corals considered in a revision of that species. — *Quart J. Geol. Soc.*, **91**, 538-590, London.

LANG, W. D., SMITH, S. & THOMAS, H. D. 1940. Index of Palaeozoic coral genera. — *Brit. Mus.*, 1-231, London.

LECOMPTE, M. 1954. Quelques données relatives à la genèse et aux caractères écologiques des "récifs" du Frasnien de l'Ardenne. — *Vol. Jub. Vict. v. Straelen*, **1**, 151-181, Bruxelles.

McLAREN, D. J. & SUTHERLAND, P. K. 1949. Lithostrotion from Northeast British Columbia and its bearing on the genomorph concept. — *J. Paleont.*, **23**, 625-634, Menasha.

PAWLIK, D. 1939. Zur Stratigraphie des südlichen Freiburger Oberdevongebietes. — *N. Jb. Min.* etc., **81**, B, 23-60, Stuttgart.

Regionalna Geologia Polski. 3: Sudety, 1. Utwory przedtrzeciorzędowe. 1-300, Kraków, 1957.

RÓŻKOWSKA, M. 1956. Pachyphyllinae from the Middle Devonian of the Holy Cross Mts., I (Pachyphyllinae ze środkowego dewonu Gór Świętokrzyskich, I). — *Acta Palaeont. Pol.*, **1**, 4, 271-330, Warszawa.

— 1957. Considerations on Middle and Upper Devonian Thamnophyllidae Soshkina in Poland, II (Rozważania ogólne dotyczące rodziny Thamnophyllidae Soshkina w środkowym i górnym dewonie Polski, II). — *Ibidem*, 2, 2/3, 81-153.

SAMSONOWICZ, J. 1917. Utwory dewońskie wschodniej części Gór Świętokrzyskich. — *Prace T.N.W.*, wydz. mat. przyr., 3, 20, 1-69, Warszawa.

SCHLÜTER, C. 1881. Über einige Anthozoen des Devon. — *Ztschr. deutsch. geol. Ges.*, 33, 75-105, Berlin.

SCHOUPPÉ, A. v. 1949. Die "Thamnophyllen" und ihre Beziehung zur Gruppe des "Cyathophyllum caespitosum". — *Palaentographica*, 97, A, 99-180, Stuttgart.

— 1958. Revision des Formenkreises um Phillipsastraea d'Orb., "Pachyphyllum" E. & H., Macgeea (Webst.), "Thamnophyllum" Pen., Peneckiella Soshk. und verwandter Formen. — *N. Jb. Geol. Paläont.*, Abh., **106**, 2, 139-224. Stuttgart.

SIMPSON, G. G. 1955. The major features of evolution. 1-434, New York.

ŚLIWIŃSKI, S. 1956. O występowaniu wapieni i dolomitów dewońskich koło Siewierza oraz o możliwościach ich użytkowania. — *Zesz. nauk. A.G.H., geol.*, 9, 1, 91-117, Kraków.

SMITH, F. G. WALTON. 1948. Atlantic reef corals. 1-110, Miami.

SMITH, S. 1945. Upper Devonian corals of the Mackenzie river region Canada. — *Geol. Soc. America, Spec. pap.*, 59, 1-126, New York.

SMITH, S. & LANG, W. D. 1930. Descriptions of the type-specimens of some Carboniferous corals of the genera "Diphyphyllum", "Stylastraea", Aulophyllum, and Chaetetes. — *Ann. Mag. Nat. Hist.*, 10 ser., 5, 26, 177-194, London.

SOSHKINA, E. D. 1939. Verchnedevonskie korally Rugosa Urala. — *Tr. Paleont. Inst. Akad. Nauk SSSR*, 9, 1-88, Moskva.

— 1951. Pozdnodevonskie korally Rugosa, ich sistematika i evolucija. — *Ibidem*, 34, 1-122.

— 1954. Devonskie četyrechlučevye korally Russkoj Platformy. — *Ibidem*, 52, 1-74.

STASIŃSKA, A. 1958. Tabulata, Heliolitida et Chaetetida du Dévonien moyen des Monts de Sainte-Croix (Tabulata, Heliolitida i Chaetetida z dewonu środkowego Gór Świętokrzyskich). — *Acta Palaeont. Pol.*, 3, 3/4, 161-282, Warszawa.

SUTHERLAND, P. K. 1958. Carboniferous stratigraphy and Rugose coral faunas of northeastern British Columbia. — *Geol. Surv. Canada, Mem*, 295, 1-177, Ottawa.

The species concept in palaeontology. The systematics association. 2, 1-145, London, 1956.

VOYNOVSKIJ-KRIGER, K. G. 1956. O dinamike razwitja septalnogo apparata v ontogeneze četyrechlučevych korallov. — *Bjul. Mosk. Obšč. Isp. Prir.*, otd. geol., 29, 5, 51-64, Moskva.

WEDEKIND, R. 1921. Zur Kenntniss der Stringophyllen des Oberen Mitteldevon. — *Sitzber. Ges. Förd. Naturwiss.*, **1**, 1-16, Marburg.

— 1925. Das Mitteldevon der Eifel. Eine biostratigraphische Studie. 2: Materialien zur Kenntniss des Mittleren Mitteldevon. — *Ibidem*, **14**, 4, 1-85.

WELLS, J. W. 1954. Recent corals of the Marshall Islands. Bikini and nearby Attols. 2: Oceanography (biologic). — *Geol. Surv., Prof. Pap.*, **260**, 1, 385-486, Washington.

YABE, H. & SUGIYAMA, T. 1941. Recent reef-building corals from Japan and the South Sea Islands under the Japanese mandate, **2**, 67-91, Tokyo.

YOH SEN-SHING. 1937. Die Korallenfauna des Mitteldevons aus der Provinz Kwangsi, Südchina. — *Palaeontographica*, **87**, A, 45—76 Stuttgart.

MARIA RÓŻKOWSKA

BLASTOGENEZA I ZMIENNOŚĆ OSOBNICZA W KOLONIACH TETRACORALLA Z DEWONU POLSKI

Streszczenie

W pracy opisana została morfologia, blastogeneza oraz zmienność osobnicza wewnątrzkolonijna u pięciu przedstawicieli Tetracoralla z dewonu Gór Świętokrzyskich i Sudetów. Materiał ten pozwolił poczynić ogólne obserwacje, dotyczące zagadnienia kolonijności, procesu blastogenezy, zmienności osobniczej w kolonii oraz cech diagnostycznych gatunkowych i rodzajowych.

Istnieją grupy korali nie przejawiających zdolności pączkowania, obok innych, mających te zdolności. Do tych ostatnich należą Thamnophyllidae z rodzajami *Peneckiella, Sudetia* i *Phillipsastraea*. Kolonie ich, żyjące równocześnie, są faceloidalne, krzaczaste i masywne. Pokrój kolonii jest funkcją środowiska, a nie stadium filogenetycznego danego szczepu. Kolonie u Hexacoralla są bardziej progresywne, niż u Tetracoralla. U Tetracoralla osobniki oddzielone są epiteką i zachowują silną indywidualność; u Hexacoralla zmniejsza się indywidualność osobników, gdyż łączy je wspólna pseudoteka i pojawia się peryteka. Wśród Tetracoralla tylko rodzina Thamnophyllidae (Soshkina, 1951) przejawia charakter heksakoraloidalny, gdyż brak tu epiteki, osobniki zaś połączone są pseudoteką.

Ontogeneza oozoida jest u form kolonijnych mało znana. Przechodzi on przez stadium symetrii bilateralnej. Blastogeneza jest mniej prawidłowa. Początek wszystkich pączków jest intrakalicynalny. Dalszy jego rozwój jest różny u zbadanych tutaj rodzajów. Wśród nich wyróżnić można dwa typy pączkowania, zależnie od wytwarzania epiteki między pączkiem a koralitem pączkującym: typ disfyloidalny i typ tamnofyloidalny. Rozwój pączka może się odbywać w kolonii cerioidalnej między ścianami (pączki intermuralne), jak u *Hexagonaria laxa,* lub może wyjść poza kielich osobnika macierzystego, odchylając się odeń, zabierając jednak część jego septów, które się zachowują po stronie zewnętrznej pączka. Jest to pączkowanie lateralne, jak u *Disphyllum geinitzi.* U form tamnofyloidalnych pączek lateralny zachowuje septa kielicha pączkującego po swojej stronie zewnętrznej i przyosiowej (*Peneckiella minor kunthi*). Przy pączkowaniu syringoporoidalnym (*Sudetia latiseptata*) pączek rozwija się jako wyrostek boczny, nie mający w ogóle septów w fazie najmłodszej.

Zmienność osobnicza w obrębie kolonii jest bardzo różnorodna: najmniejsza u form filojuwenilnych, u których istnieją struktury filogenetyczne młode, a najbardziej urozmaicona u filogerontycznych, u których pewne elementy ulegają atrofii. Zmienność morfologiczna jest także nie tylko funkcją stadium filogenetycznego, lecz również środowiska. Polimorfizm bowiem jest niewielki w facji głębszego, cichego morza, natomiast znaczny w facji rafowej.

Pojęcie genomorfu wprowadzone zostało przez Langa i Smitha (1930) dla dymorficznego rodzaju *Lithostrotion*, który w tej samej kolonii, obok osobników o bu-

dowie charakterystycznej dla *Lithostrotion*, zawiera inne, o budowie takiej, jak u *Diphyphyllum*. *Diphyphyllum* jest tutaj genomorfem. Genomorfy rozpowszechnione są u form karbońskich; szerzej zostały opisane przez Sutherlanda (1958) i Dobrolubową (1949, 1958). Genomorfy występują w *Peneckiella minor kunthi*, gdzie obok planu budowy *Thamnophyllum* (dissepimenta horyzontalne i podkowiaste oraz wachlarze trabekul) zaznacza się nowa cecha, jaką stanowią dissepimenta penekielloidalne; wypierają one dissepimenta tamnofyloidalne, przewyższając je liczbowo aż siedmiokrotnie. Obie struktury występują w jednym koralicie w różnych stadiach blastogenezy. U *Sudetia lateseptata* występują już tylko pęcherze penekielloidalne, lecz pojawia się nowy typ pączkowania intrakalicynalnego: syringoporoidalne pączki aseptalne; natomiast blastogeneza taka, jak u *Peneckiella*, występuje już tylko sporadycznie. Oba gatunki żyjące tuż obok siebie spokrewnione są bezpośrednio i powstały zapewne w drodze szybkiej ewolucji; odpowiadają one dwu etapom rozwoju filogenetycznego: od *Thamnophyllum* do *Peneckiella* i od *Peneckiella* do *Sudetia*.

Rozwój i powstawanie genomorfów połączone jest prawdopodobnie ze zjawiskiem neotenii (Sutherland, 1958). Genomorfy są to uproszczone formy regresywne, pojawiające się przy końcu rozwoju szczepu, jak np. *Peneckiella* i *Sudetia* przy końcu ewolucji szczepu *Thamnophyllum*.

Wielkie trudności wyłaniają się przy oznaczaniu gatunkowym form kolonijnych z następujących przyczyn: 1) amplituda zmienności jest różna, zwłaszcza duża u form filogerontycznych, a więc warianty krańcowe można mylnie uważać za oddzielne gatunki; 2) zjawisko konwergencji występuje często u gatunków kolonijnych i jest powodem, że gatunki należące do różnych szczepów filogenetycznych bywają włączane do jednego rodzaju. Klasycznym przykładem jest polifiletyczny rodzaj *Hexagonaria*. Przy oznaczaniu gatunku należy uwzględnić cechy morfologiczne osobników dojrzałych i rozwój ontogenetyczny szeregu skorelowanych cech. Ważne jest też zbadanie zmienności fenotypowej, gdyż dla gatunku charakterystyczne są jednowierzchołkowe krzywe biometryczne. Podgatunek ma taki sam co gatunek plan budowy, jednakową mikrostrukturę i blastogenezę. Różnice ilościowe występują w przesunięciach linii allometrycznych oraz w krzywych biometrycznych, pokrywających się częściowo z krzywymi osobników typowych. Przykładem tego jest *Thamnophyllum trigeminum* Penecke, występujący w Polsce od żywetu do górnego franu i tworzący w tym czasie 5 podgatunków. Cechy diagnostyczne rodzaju są jakościowo bardziej uogólnione, zaś jego zasięg geograficzny duży. Obok cech charakteryzujących rodzinę, do której należy, ma on zarówno swoistą ontogenezę oozoidu, jak i blastogenezę oraz właściwy sobie pokrój kolonii.

Zagadnienia te zbadane zostały na podstawie przeprowadzonej analizy morfologicznej 4 gatunków i 1 podgatunku, które scharakteryzować można jak następuje.

Disphyllum geinitzi L. & S. (fig. 2-8), z Sitkówki k. Kielc (żyweckie wapienie zoogeniczne), tworzy kolonie faceloidalne. Blastogeneza jest na początku intrakalicynalna, jak u wszystkich Tetracoralla. Pączek już wcześnie w ontogenezie oddziela się epiteką od koralita macierzystego. Gatunek ten ma budowę prostą, bez śladów uwstecznienia. Żył on zapewne w nieco głębszym morzu. Zmienność osobnicza jest niewielka; przejawia się tylko w umieszczeniu tabul, w wielkości dissepimentów, w proporcji długości septów I i II rzędu oraz w grubości septów.

Hexagonaria laxa Gürich (fig. 9-16), z Dziewek k. Siewierza (żyweckie rafy stromatoporoidowo-tabulatowe), tworzy kolonie cerioidalne, przy czym poszczególne osobniki oddzielone są od siebie zwartą epiteką. Zmienność morfologiczna jest bardzo duża, gdyż forma ta znajduje się w stadium filogerontycznym i rozwijała się w środowisku niespokojnym, rafowym. Pączek pojawia się w narożach o silnie uwstecznionych septach lonsdaloidalnych, gdzie istnieją ponadto duże, lecz rzadkie dissepimenta. Już wcześnie pączek oddziela się od osobnika macierzystego epiteką, otoczoną po obu stronach pseudoteką. Przyrost liczby septów jest allometrycznie ujemny. Zmienność osobnicza przejawia się też w stosunku tabularium do dissepimentarium i w gęstości tabul i dissepimentów (jako reakcja na szybkość sedymentacji). Największą zmienność wykazują septa: zmienny jest stosunek długości septów I rzędu do II-go, ich grubość, liczba listewek, ich stopień rozpadu na kolce. Potwierdza się tu obserwacja Darwina (1859) i później Simpsona (1955), według której największa skala zmienności występuje w redukujących się organach.

Hexagonaria laxa jurkowicensis n. subsp. (fig. 17-19), z Jurkowic pod Opatowem (górno-żywecka rafa stromatoporoidowo-tabulatowa), tworzy kolonie cerioidalne. Ten nowy podgatunek różni się od formy typowej nieco większymi rozmiarami kielichów (16 × 18 mm), tabulariów (7 mm), większą liczbą septów (do 20-tu I rzędu) i dalej posuniętą atrofią septów. Septa II rzędu są nieco dłuższe, niż u formy typowej. Blastogeneza — jak u gatunku *H. laxa*, z tą różnicą, że pączki wyrastają promieniście z kielicha. Współczynnik n/d ma większą wartość, niż u formy z Dziewek, gdyż liczba septów jest większa, wobec czego linia allometrii jest nieco przesunięta w porównaniu z linią tą u formy typowej. Polimorfizm osobników jest bardzo duży, podobnie jak u formy typowej, lecz septa nie rozpadają się na kolce, ale na poprzeczne bryłki. Mikrostruktura septów jest disfyloidalna. Trabekule grube (0,2 mm). Elementy strukturalne grube, o dużej zmienności. Forma ta rozwijała się w strefie kipieli.

Peneckiella minor (Roemer) *kunthi* (Dames) (fig. 20-29), z Mokrzeszowa, D. Śląsk (górno-frańska rafa koralowa), tworzy kolonie faceloidalne. Blastogeneza jest tamnofyloidalna, tzn. pączek nie oddziela się od osobnika macierzystego epiteką, lecz łączy się z nim pseudoteką. Grube trabekule septalne (0,16 mm) tworzą niesymetryczne wachlarze. Przyrost septów podczas ontogenezy jest allometrycznie dodatni, w stadium efebicznym — ujemny. Polimorfizm jest bardzo duży, przejawiając się zwłaszcza w septach, które i tutaj ulegają uwstecznieniu. Poza tym ustępują charakterystyczne dla *Thamnophyllum* dissepimenta horyzontalne i podkowiaste, wypierane przez nowe, bardzo proste dissepimenta penekielloidalne. Od formy z Grund, której amplituda zmienności nie jest znana, odmiana z Mokrzeszowa różni się większą liczbą septów.

Sudetia lateseptata n. gen., n. sp. (fig. 30-33, szlify mikroskopowe nr 12 i 15), z Mokrzeszowa, D. Śląsk.

Diagnoza holotypu: kolonia krzaczasta, o nieregularnie powyginanych koralitach, mających — przy średnicy 3,0-4,6 mm — 32-36 septów I i II rzędu. Gruba epiteka; na pograniczu dissepimentarium i tabularium — pseudoteka wewnętrzna. Kielich głęboki, o płaskim dnie i stromych ścianach. Septa I rzędu krótkie, szerokie, z listewkami zasłoniętymi przeważnie stereoplazmą; septa II rzędu na ogół uwstecznione zupełnie. Jeden szereg dissepimentów penekielloidalnych; tabule przeważnie kompletne, wklęsłe; niesymetryczne wachlarze trabekul; beleczki grubości 0,06-0,18 mm. Pączkowanie dwojakie: rzadziej lateralne, tamnofyloidalne, często syringoporoidalne, w najwcześniejszych zaś stadiach — aseptalne (fig. 30-43).

Gatunek ten występuje w rafie wespół z *P. minor kunthi*. Osobniki obu form przyrastają do siebie. Krzaczaste kolonie i elementy szkieletowe silnie pogrubiałe odzwierciadlają przystosowanie do życia w rafie. Pączki są dwojakie: lateralne, tamnofyloidalne — jak u *P. minor kunthi* oraz syringoporoidalne. Mają one budowę cystifyloidalną i są aseptalne. Po stadium aseptalnym następuje stadium brewiseptalne, kiedy pojawiają się septa krótkie, cienkie. U form dojrzałych septa są grube aż do zetknięcia się, septa zaś II rzędu wypadają prawie wszystkie. Podobne pączki aseptalne z budową cystifyloidalną opisała Soshkina (1955) u *Peneckiella jevlanensis* Bulvanker. Polimorfizm jest bardzo duży, widoczny w pokroju koralitów i budowie septów. Nowe dissepimenta penekielloidalne są natomiast bardzo jednolite. Przyrost liczby septów n/d i stosunek średnicy wolnej od septów przestrzeni osiowej (c) do średnicy koralita — są podobne jak u *P. minor kunthi*. Uwidocznione to jest na fig. 43.

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 5)

Mapa rozmieszczenia miejscowości, z których pochodzą zbadane formy.

Fig. 2 (p. 8)

Disphyllum geinitzi Lang & Smith; Sitkówka, żywet. Przekrój poprzeczny koralitów.

Fig. 3 (p. 8)

Disphyllum geinitzi Lang & Smith; Sitkówka, żywet. Przekrój podłużny młodego osobnika, oddzielonego od macierzystego częściowo już powstałą nową epiteką (*e*).

Fig. 4 (p. 9)

Disphyllum geinitzi Lang & Smith; Sitkówka, żywet. Poprzeczny przekrój pączka w stadium nepionicznym; zaczątki nowej epiteki (*e*) i pseudoteki (*p*).

Fig. 5 (p. 10)

Disphyllum geinitzi Lang & Smith; Sitkówka, żywet. Przekrój poprzeczny pączka w stadium późnonepionicznym; epiteka i nowe septa częściowo utworzone.

Fig. 6 (p. 10)

Disphyllum geinitzi Lang & Smith; Sitkówka, żywet. Przekrój poprzeczny stadium wczesnoneanicznego; nowa epiteka prawie utworzona pomiędzy dwiema pseudotekami (p_1, p_2) u trzech osobników, ściśle ze sobą połączonych przez pączkowanie.

Fig. 7 (p. 11)

Disphyllum geinitzi Lang & Smith; Sitkówka, żywet. Przekrój podłużny pączka z epiteką (*e*), oddzielającą go w stadium neanicznym od koralita macierzystego.

Fig. 8 (p. 12)

Disphyllum geinitzi Lang & Smith; Sitkówka, żywet. Krzywa korelacji n/d; na osi odciętych — średnice koralitów (*d*), na osi rzędnych — liczba septów I rzędu (*n*).

Fig. 9 (p. 14)

Hexagonaria laxa Gürich; Dziewki, żywet. Przekrój poprzeczny kolonii cerioidalnej.

Fig. 10 (p. 14)

Hexagonaria laxa Gürich; Dziewki, żywet. Przekrój podłużny kolonii cerioidalnej.

Fig. 11 (p. 15)

Hexagonaria laxa Gürich; Dziewki, żywet. Przekrój poprzeczny koralita, przygotowującego miejsce na dwa pączki (*1*, *2*).

Fig. 12 (p. 15)

Hexagonaria laxa Gürich; Dziewki, żywet. Przekrój poprzeczny pączka w stadium nepionicznym; *e* nowa epiteka pączka.

Fig. 13 (p. 16)

Hexagonaria laxa Gürich; Dziewki, żywet. Przekrój poprzeczny pączka (*b*) w stadium późnonepionicznym; epiteka jeszcze niecałkowita.

Fig. 14 (p. 16)

Hexagonaria laxa Gürich; Dziewki, żywet. Przekrój poprzeczny pączka w stadium neanicznym.

Fig. 15 (p. 18)

Krzywa korelacji n/t; na osi odciętych — średnice tabulariów (*t*), na osi rzędnych — liczba septów I i II rzędu (*n*). Linia przerywana i kropki — dane dla *Hexagonaria laxa* Gürich (Dziewki, żywet); linia ciągła — *H. laxa jurkowicensis*Różk. (Jurkowice, żywet).

Fig. 16 (p. 19)

Krzywa korelacji t/diss; na osi odciętych — stosunek średnicy tabularium (*t*) do szerokości dissepimentarium (*diss*), na osi rzędnych — % osobników. Linia przerywana — *Hexagonaria laxa* Gürich (Dziewki, żywet); linia ciągła — *H. laxa jurkowicensis*Różk. (Jurkowice, żywet).

Fig. 17 (p. 24)

Hexagonaria laxa jurkowicensis Różk.; Jurkowice, żywet. Przekrój poprzeczny kolonii cerioidalnej.

Fig. 18 (p. 24)

Hexagonaria laxa jurkowicensis Różk.; Jurkowice, żywet. Przekrój podłużny kolonii cerioidalnej.

Fig. 19 (p. 24)

Hexagonaria laxa jurkowicensis Różk.; Jurkowice, żywet. Przekrój poprzeczny części koralita z pączkiem w stadium nepionicznym; brak jeszcze nowej epiteki.

Fig. 20 (p. 29)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Przekroje poprzeczne dojrzałych koralitów: *A* koralit przyrasta wydłużoną częścią brzeżną do sąsiada, *B* pączek w połączeniu z koralitem macierzystym.

Fig. 21 (p. 30)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Przekrój poprzeczny koralita z wyraźnymi listewkami na septach, często niezasłoniętymi stereoplazmą.

Fig. 22 (p. 30)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Przekrój podłużny koralita.

Fig. 23 (p. 30)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Przekrój poprzeczny koralita z pączkiem; septa koralita macierzystego wydłużając się wchodzą w pączek.

Fig. 24 (p. 31)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Przekrój pączka mającego już całkowitą pseudotekę.

Fig. 25 (p. 31)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Przekrój podłużny pączka; brak epiteki między obu osobnikami.

Fig. 26 (p. 32)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Krzywa korelacji łącznej liczby septów (*n*) i średnicy koralitów (*d*), oraz szerokości pola osiowego (*c*) wolnego od septów i średnicy koralitów (*d*); *c*, *d* — w mm.

Fig. 27 (p. 33)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Przekrój podłużny: widoczne podkówki, pęcherze penekielloidalne, horyzontalne i sygmoidalne; wachlarze trabekularne oparte na podkówkach lub na normalnych (penekieloidalnych) pęcherzach.

Fig. 28 (p. 33)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Przekrój podłużny przedstawiający różne dissepimenta.

Fig. 29 (p. 35)

Peneckiella minor kunthi (Dames); Mokrzeszów, górny fran. Przekrój podłużny przedstawiający różnorodne dissepimenta oraz gęste, poziome tabule.

Fig. 30 (p. 35)

Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Przekrój poprzeczny koralita; septa II rzędu prawie zupełnie zredukowane.

Fig. 31 (p. 36)

Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Przekrój podłużny.

Fig. 32 (p. 36)

Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Przekrój podłużny.

Fig. 33 (p. 37)

Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Przekrój podłużny przedstawiający pokrój osobnika z pączkiem syringoporoidalnym (*A*) i wyrostkiem czepnym (*B*).

Fig. 34 (p. 38)
Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Przekrój poprzeczny osobnika wraz z pączkiem aseptalnym.

Fig. 35 (p. 38)
Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Przekrój poprzeczny pączkującego koralita wraz z nieco ukośnie przekrojonym pączkiem aseptalnym.

Fig. 36 (p. 38)
Sudetia lateseptata Rożk.; Mokrzeszów, górny fran. Pączek z trzema septami, przylegający do koralita sąsiedniego; oba w przekroju poprzecznym.

Fig. 37 (p. 38)
Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Pączek nieco dalej rozwinięty, stadium brewiseptalne z wyrostkiem czepnym.

Fig. 38 (p. 39)
Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Młody osobnik w stadium neanicznym, przylegający do koralita sąsiedniego.

Fig. 39 (p. 39)
Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Osobnik pączkujący, wraz z pączkiem, w przekroju podłużnym nieco ukośnym.

Fig. 40 (p. 39)
Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Pączkowanie tamnofylloidalne, wydłużone septa koralita pączkującego wchodzą do pączka.

Fig. 41 (p. 40)
Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Młodociany osobnik, prawdopodobnie oozoid, mający u samej już podstawy septa od najwcześniejszego stadium.

Fig. 42 (p. 40)
Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Młodociany osobnik, prawdopodobnie oozoid, w przekroju podłużnym nieco ukośnym, z pączkiem cystifyloidalnym na końcu dystalnym.

Fig. 43 (p. 41)
Sudetia lateseptata Różk.; Mokrzeszów, górny fran. Krzywa korelacji łącznej liczby septów (*n*) i średnicy koralitów (*d*), oraz szerokości pola osiowego wolnego od septów (*c*) i średnicy koralitów (*d*); *c*, d — w mm.

МАРИЯ РУЖКОВСКА

БЛАСТОГЕНЕЗ И ИЗМЕНЧИВОСТЬ ОСОБЕЙ В КОЛОНИЯХ ЧЕТЫРЕХЛУЧЕВЫХ КОРАЛЛОВ ИЗ ДЕВОНА ПОЛЬШИ

Резюме

В настоящей работе описано морфологию, бластогенез и изменчивость особей в колониях пяти представителей четырехлучевых кораллов из девона Свентокржиских Гор и Судетов. Этот материал дал возможность произвести

наблюдения касающиеся в особенности колониальности, изменений происходящих в бластогенезе и явления геноморфов.

В колониях *Disphyllum geinitzi* и *Hexagonaria laxa jurkowicensis*, как и у всех четырехлучевых кораллов, сильно подчеркнута индивидуальность отдельных особей, вполне отделенных друг от друга эпитекой. Вместо того у *Sudetia lateseptata* и *Peneckiella minor kunthi* преобладает индивидуальность колонии, потому что, будучи представителями гексакораллоидных Thamnophyllidae, имеют особи соединенные ложными стенками.

Изменения в бластогенезе сочетаются с формой колонии и ввиду этого являются функцией среды. Каждый род обладает собственным типом почкования, а в случае когда выступают два разных типа, так они связаны с явлением филетической дивергенции.

Автор обсуждает вопрос геноморфов. Понятие это введено Лангом и Смисом (Lang & Smith, 1930) для диморфного рода *Lithostrotion*, который в одной и той же колонии, рядом с особями со строением характерным для *Lithostrotion*, содержит особи обнаруживающие строение свойственное *Diphyphyllum*. *Diphyphyllum* является тут геноморфом. Геноморфы распространены среди карбонских форм; более широко описаны Сасерлендом (Sutherland, 1958) и Добролюбовой (1949, 1958).

Явление геноморфов проявляется в материале автора у *Peneckiella minor kunthi*, у которой наряду с тамнофиллоидной структурой (веера трабекул, горизонтальные и подковообразные диссепименты) встречается пенекиеллоидная структура (пенекиеллоидные диссепименты), а также у *Sudetia lateseptata*, у которой, рядом с тамнофиллоидной структурой (веера трабекул, боковое почкование как у *Peneckiella*), имеются цельные пенекиеллоидные диссепименты и сырингопороидные почки. Оба эти виды представляют две стадии быстрого развития от *Thamnophyllum* до *Peneckiella* и от *Peneckiella* до *Sudetia*.

Эти вопросы были исследованы на основании проведенного морфологического анализа 4 видов и 1 подвида, которые можно охарактеризовать следующим образом.

Disphyllum geinitzi Lang & Smith (фиг. 2-8) из Ситковки около Кельц (верхний живет), с фацеллоидными колониями, образует боковые почки, берущие свое начало в диссепиментариуме. Почки быстро отделяются посредством эпитеки, на которой возникают новые перегородки для обоих особей — материнского кораллита и почки; между тем часть перегородок почкующей особи сохраняется в почке на ее наружной стороне. Вид этот является филоювенильной формой живущей в спокойном море, что отражается в малой амплитуде морфологической изменчивости. Модификация в строении перегородок, густоте днищ и величине диссепиментов, являются тут функцией внешней среды.

Hexagonaria laxa Gürich (фиг. 9-16) из Дзевок около Севержа (средний живет) и его мутация *H. laxa jurkowicensis* n. subsp. из Юрковиц около Опатова (верхний живет), из рифовой фации с цериоидными колониями. Почки развиваются тут целиком в пределах диссепиментариума и рано отделяются эпитекой. Обе формы находятся на высоком уровне филогенетического развития, что проявляется в лонсдалоидном строении перегородок и в присутствии планочек. С явлением редукций связан широкий диапазон изменчивости в строении перегородок, а влияние подвижной морской среды становится видным по толщине элементов скелета и расположении днищ и диссепиментов.

Подвид *H. laxa jurkowicensis* (фиг. 17-19) отличается от типичной формы большим диаметром чашечки (16 × 18 мм), табуляриумов (7 мм), большим количеством перегородок (до 20-ти, I цикла) и более сильной атрофией перегородок. Перегородки II цикла несколько длиннее чем у типичной формы.

Peneckiella minor (Roemer) *kunthi* (Dames), (фиг. 20-29), из Мокржешова (Судеты, верхний фран), из кораллового рифа, с фацеллоидными колониями. Почкование тамнофиллоидное, т. е. почка не отделяется эпитекой от почкующего кораллита. Часть его перегородок входит в состав приосевой части чашечки почки. Большая амплитуда изменчивости проявляется в строении диссепиментов, так как горизонтальные и подковообразные диссепименты бывают вытеснены характерными для этого рода пенекиеллоидными. Большая изменчивость видна также в строении перегородок, их толщине и появлении септальных планок. Наряду с такими генетическими изменениями реакция на внешние импульсы проявляется в расположении днищ и величине пузырей.

Sudetia lateseptata n. gen., n. sp. (фиг. 30-43); микроскопические шлифы № 12 и 15). Диагноз голотипа: колония кустистая с неправильно изогнутыми кораллитами, обладающими при диаметре 3,0—4,6 мм от 32 до 36 перегородок I и II цикла. Под эпитекой толстая ложная стенка на границе между табуляриумом и диссепиментариумом. Чашечка глубокая, с плоским дном и отвесными стенками. Перегородки I цикла короткие, широкие, с планками прикрытыми по большей части стереоплазмой; перегородки II цикла часто полностью редуцированы; один ряд пенекиеллоидных диссепиментов; днища преимущественно полные, вогнуты; несимметрические веера трабекул (трабекулы толщиною 0,06—0,18 мм). Почкование двоякого рода: реже боковое как у *Peneckiella*, чаще сырингопороидное, а на наиболее ранних стадиях — асептальное.

Форма эта жила рядом с *P. minor kunthi* и зачастую прирастала к ее кораллитам. Рядом со спорадическими боковыми почками, как у *P. minor kunthi*, распространено почкование сырингопороидное. Тут можно выделить две более молодые стадии: асептальную (констатированную у *Peneckiella jevlenensis* Bulv. Сошкиной, 1954) и бревисептальную. Генотиповая изменчивость проявляется в строении перегородок, которые подвергаются атрофии, а влияние среды видно из расположения днищ и диссепиментов равно как и в общей форме нерегулярных кораллитов кустистой колонии.