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SEPTAL DEVELOPMENT OF OLIGOPHYLLOIDES PACHYTHECUS FROM THE FAMENNIAN OF POLAND

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The septal development of Oligophylloides pachythecus Różkowska, the type species for the genus, has been studied by means of closely spaced serial sections. It has been observed that four original septa were secreted on a basal plate with two sets of adjacent septa joining before the two resulting axial septa each join. The result is a symmetrical double 'Y', with the bases of the letters joined at the axis. Subsequently each of these four may split peripherally, producing eight septa. Next, two additional septa were added pinnately on each side on one of the open fossulae, but not within the adjacent enclosed loculae. The specimens studied have a total of only 10 septa each. The resulting septal pattern, which produces a bilateral symmetry with open fossulae in the plane of symmetry, is at marked variance with the previously assumed septal insertion plans described from Lower Carboniferous heterocorals.

Key words: corals, Heterocorallia, ontogeny, septal pattern, Upper Devonian, Poland.

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INTRODUCTION

The coelenterate Order Heterocorallia has traditionally been known from only two genera, *Heterophyllia* and *Hexaphyllia*, and their confirmed occurrences known only from the Carboniferous Upper Tournaisian, Viséan and Lower Namurian, from various parts of Europe, Asia and Australia (Sutherland and Mitchell, in press). However, Różkowska (1969) described a new heterocoral genus Oligophylloides from the Upper Devonian, Famennian, of Poland. We are indebted to Prof. Różkowska for the loan of several specimens of its type species O. pachythecus Różkowska, 1969 and for permission to section them. Closely spaced serial sections have been made of two of these specimens by Forbes, on a special Capco Saw, located in the Sedgwick Museum at Cambridge University, England. These sections average one-third millimeter in spacing. They have been studied by Sutherland and are here described.

GENERAL CHARACTERISTICS

The general characteristics of Oligophylloides pachythecus have already been described by Różkowska (1969). The purposes of this paper are to clarify the nature of the early septal insertion pattern based on serial sections and to compare it with other insertion patterns that have been postulated by several authors for Carboniferous species of heterocorals.

O. pachythecus differs most strikingly from all described Carboniferous species of heterocorals by the occurrence, at the base of the thin, cylindrical coral, of a large tent-shaped basal talon-like structure, which is as much as 11 mm in maximum diameter (Różkowska 1969: 163). Różkowska records the maximum observed length of a specimen that preserves the talon at 13 mm. The diameter of the cylindrical, distal end of such a specimen is 3 by 3.5 mm.

The large talon formed subsequently to the development of the original basal plate and developed as extensions of tabulae, which grew outward and downward, well below the level of the basal plate and apparently extended into the underlying sediment. O. pachythecus has no external epitheca and the growing surface, certainly at the time of development of the talon, extended from the small central area, where septa were being secreted, laterally down the outward sloping surfaces of the tabulae. Septal ridges commonly extended some distance down these tabular surfaces (pl. 40: 5, 6) and appear in cross-section as discontinuous septa (pl. 40: 1—6). These septal extensions, seen in a particular transverse section (such as, pl. 40: 5) reflect the nature and number of septa at a distinctly higher (later) position in the development of the coral. For example, in figures 4 and 5 of plate 40 the central area shows only 3 and 5 septa but the peripheral tabularium of the talon, secreted later, shows a full compliment of 10 septa.

SEPTAL INSERTION PATTERN

The lowest serial sections show matrix in the area of the central column (pl. 40: 1; pl. 41: 1). This is overlain by the basal plate, which varies in diameter from 0.375 mm to 0.8 mm in the two examples illustrated. Figures 2 and 3 on plate 40 intersect the basal plate obliquely, thus showing partly matrix and partly basal plate. In these figures the basal plate appears to have no structure but in figures 2 and 3 in plate 41 the basal plate shows what appears to be radiating fibers. These are presumed to represent recrystallization.

Four original septa are secreted (pl. 41: 4) but one specimen shows only three at first (pl. 40: 4). The four form a symmetrical double "Y", with the bases of the letter joined at the axis (fig. 1 A), forming an axial cross-bar. Subsequently, each of these four may split peripherally, producing eight septa but this happens irregularly and not as a single cycle. Typically, two, not of the same "Y", split peripherally (fig. 1 B), giving a total septal number of 6, followed later by the other two splitting (fig. 1 C), giving a septal number of 8.

Next, in both of the specimens for which a long sequence of serial sections are available, two septa are added in one of the open fossulae between the double "Y" (fig. 1 D). At first these are erect and not pinnate (pl. 40: 10; fig. 1 D). Subsequently they tend to lean away from each other and become pinnate, against the sides of the adjacent closed loculae (pl. 40: 12; pl. 41: 10).

This completes the total compliment of 10 septa normally found in O. pachythecus (fig. 1 E). The structure produced is one with bilateral symmetry formed through the two broadest fossulae. In particular it should be noted that no septa were added within any of the four closed loculae.



Fig. 1. Steps in the septal insertion of Oligophylloides pachythecus.

The described structure is clearly shown in both of the specimens for which serial sections are available although one (pl. 41: 1-14) is about half the diameter of the other (pl. 40: 1-17). There would however, be uncertainties in interpretation if the sections were not in an oriented sequence. Problems result from the fact that



Fig. 2. Irregular septal developments observed in Oligophylloides pachythecus. Compare: "A" with pl. 40: 17; "B" with pl. 41: 15; "C" with pl. 41: 16.

the septa once secreted within the axial region may "disappear" due to subsequent withdrawal from the axial region. Such septa may continue as discontinuous septa in the peripheral tabularium (compare pl. 40: 10, 11). The full compliment of septa is completed at or shortly above the upper limit of the large basal talon, near the beginning of the cylindrical position of the corallite. Above this point the axial ends of the septa do not necessarily maintain their original inserted relationships (fig. 2). It is thus impossible in most cases to take an isolated section from the cylindrical portion of a corallite and identify with certainty the four original septa (pl. 41: 15, 16).

The insertion pattern described above for *O. pachythecus*, based on two specimens, needs to be extended and supported with the serial sectioning of additional specimens.

COMPARATIVE INSERTION PATTERNS

At least three distinctly different septal insertion patterns have been postulated for Lower Carboniferous species of *Heterophyllia*. Regretfully, in each of these cases the postulations have of necessity been based on the comparison of mostly isolated sections from specimens of different sizes because of the nonavailability of specimens showing early growth states.

The first, by Yabe and Sugiyama (1940), postulated 6 protosepta identical in formation to that seen in *Hexaphyllia* (fig. 3 A). They attempted to relate the pattern as closely as possible to the Order Rugosa and identified cardinal (C) and counter (C') septa. They postulated that all subsequent septa were inserted serially within the two lateral, closed loculae (fig. 3 B, 3 C). We agree with Schindewolf (1941: 232) that their isolated section, illustrated here as figure 3 A, is probably a specimen of *Hexaphyllia* and not an early state of *Heterophyllia*.

The second described pattern, by Schindewolf (1941), is much better known and has been widely given in paleontology references. Schindewolf postulated a division of septa into four groups formed by four original septa each of which subsequently split peripherally, forming a basic pattern of 8 septa. He postulated that all subsequent septa were inserted within the four closed loculae (fig. 4) in an alternating



Fig. 3. Septal development postulated in *Heterophyllia kitakamiensis* Yabe and Sugiyama (1940: fig. 1), from the Lower Carboniferous of Japan, as refigured by Schindewolf (1941: figs 1-3).



Fig. 4. Septal development postulated for *Heterophyllia*, based on a study of Lower Carboniferous specimens from Germany, by Schindewolf (1941: fig. 30).

pinnate fashion, but not inserted in a regular cyclic or serial pattern. He stressed that no septa were added in the four open fossulae.

The third pattern is that proposed by Poty (1978). In this system there are four original septa (fig. 5 A), of these, two opposing ones split peripherally, producing a basic septal number of 6 (fig. 5 B), in the pattern of the genus *Hexaphyllia*. The two opposing unsplit septa form what would be comparable to a cardinal-counter plane. Up to this point the system is identical to that of Yabe and Sugiyama (fig. 3 A). In the Poty plan, however, additional septa are added not in the lateral closed loculae but in the spaces between the outsides of those loculae and the cardinal and counter septa (fig. 5 C).



Fig. 5. Septal development postulated for Heterophyllia, based on a study of Heterophyllia ornata from the Lower Carboniferous of Belgium, by Poty (1978: fig. 2).

It is impossible to make precise comments about these three insertion patterns since none are based on serial sections but, of necessity, on deductive postulation. They all differ markedly from each other and from that recorded here based on closely spaced serial sections from two specimens of *O. pachythecus*. It is interesting to note that Schindewolf postulated insertion only within four closed loculae, Yabe and Sugiyama only within two closed loculae and Poty only outside of two closed loculae. It is concluded that the pattern of septal insertion in the Carboniferous *Heterophyllia* must be considered to be uncertain until specimens become available that allow serial sectioning of early stages.

It is impossible to postulate where additional septa might be added after the 10 observed in O. pachythecus. It is clear, however, that the only two septa added in addition to the basic pattern of 8 (fig. 1 C) were added in an open fossula, outside of the four closed loculae. It is hoped that additional specimens of the species can be collected from the type locality of O. pachythecus, in the Holy Cross Mountains of Poland, in order that additional serial sections can be made.

MATERIAL STUDIED

Sutherland has studied the entire Różkowska collection of specimens of Oligophylloides, in the Palaeozoological Institute of the Polish Academy of Sciences, Poznań Branch. The specimens (ZPAL P.Tc.3) are from Gałęzice, beds 1 and 2, in the Holy Cross Mountains, Central Poland (see Różkowska 1969; 19–20).

The three specimens here figured are all from Galezice, bed 2. Sizes and measurements of these specimens are as follows:

(1) No. 2394 (pl. 40: 1—17). This paratype of Oligophylloides pachythecus was more fully figured by Różkowska (1969: fig. 68 C₁, C₂; fig. 69 A₁-A₄) than any other specimen. The maximum dimensions of the specimen cannot be determined because Różkowska had taken four peels through the lower part of the talon and five peels at the top of the preserved portion of the cylindrical part of the coral. The diameter of the talon in the lowest peel is 8 mm (pl. 40: 1 shows axial region of this peel) and the diameter of the highest peel in the cylindrical portion is 3.2 mm in diameter (pl. 40: 17 shows axial region of the peel). The intervening middle fragment of the specimen, from which the transverse section illustrated in plate 40: 5—12 were cut, was 2.77 mm in length. The diameter of section 7 (pl. 40: 11 shows axial region), the approximate upper limit of the talon and beginning of the cylindrical portion of the coral, is 3.7 mm.

(2) No. 2469 (pl. 41: 1—14). The specimen was 6.8 mm in length, including a complete talon, but was broken in the cylindrical portion of the coral. The maximum diameter of the talon, near its base, was about 4.5 mm in diameter. The distance from the base of the talon up to the basal plate was 1.2 mm and from the basal plate to the approximate upper limit of the talon, 1.8 mm. Thus, the height of the talon was 3.0 mm. The preserved portion of the cylindrical part of the coral was 3.8 mm. The diameter of the coral at the approximate upper limit of the talon was 1.4 mm (pl. 41: 8) and at the highest preserved part of the coral about 1.3 mm in diameter. Note that the diameters in this specimen are only about half those found in specimen no. 2394 but the septal insertion pattern and septal number are closely similar.

(3) No. 2306 (pl. 41: 15—17). This specimen was a cylindrical fragment about 12 mm in length and 2.9 mm in diameter. The two transverse sections were taken from the base (pl. 41: 15) and the top (pl. 41: 16) of the fragment from which a longitudinal section was subsequently cut. The septal patterns in the two transverse sections cannot be related with certainty.

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EXPLANATION OF THE PLATES 40 AND 41

Plate 40

Oligophylloides pachythecus Różkowska

All figures are transverse serial peels and sections from a single specimen (ZPAL P.Tc. 3/2394), all are oriented in the same way, and all show axial region only except 6, which shows whole talon.

- 1. Lowest peel, matrix in axial region below basal plate; made by Różkowska 1969, same as her fig. 69A₄; ×15.
- Second and third peels, basal plate intersected obliquely, partly showing matrix; made by Różkowska 1969, same as her figs. 69A₃ and 69A₄; ×15.
 - 4. Fourth peel, three of 4 primary septa; made by Różkowska 1969, same as her fig. $69A_1$; $\times 15$.
 - 5. Serial section 1; 5 septa in axial region; note the presence of 10 discontinuous septa in peripheral tabularium; $\times 15$.
 - 6. Serial section 1; note steeply sloping peripheral tabulae that make up talon (same as 5); $\times 8$.
 - 7. Serial section 2; 6 septa; 0.67 mm above section 1; \times 24.
 - 8. Serial section 3; 7 septa; 0.97 mm above section 1; \times 24.
 - 9. Serial section 4; 7 septa; 1.27 mm above section 1; \times 24.
 - 10. Serial section 6; 9 septa; 1.87 mm above section 1; \times 24.
 - 11. Serial section 7; 8 septa (note withdrawal from axial region of one of new septa inserted in 10); 2.17 mm above section 1; \times 24. Coincides approximately with beginning of cylindrical portion of coral and upper limit of talon.
 - 12. Serial section 8; 8 septa (note septum at lower right is leaning sharply to right, toward closed loculus); 2.47 mm above section 1; \times 24.
- 13—17. Serial peels of cylindrical portion of coral with 17 being the highest; 13 and 14 have 8 septa, 15—17 have 9 septa; made by Różkowska 1969 and two of these five are the same as Róêkowska 1969, fig. 68C1 and 68C2. Note in 17 that the axial cross-bar is lost.

Plate 41

Oligophylloides pachythecus Różkowska

1-14 are transverse sections from a single specimen (ZPAL P.Tc. 3/2469) and all sections are oriented in the same way except possibly 14, for which the orientation was lost. All \times 24.

- 1. Serial section 16; lower part of talon, matrix in axial region below basal plate; approximately 0.6 mm above lowest extent of talon.
- 2. Serial section 14; intersection of basal plate showing preserved radiating fibrous structure; 0.6 mm above section 16.
- 3. Serial section 13; similar to section 14; 0.3 mm above section 14.
- 4. Serial section 12; 4 primary septa; 0.3 mm above section 13.
- 5, 6. Serial section 11 and 10; 6 septa; 0.3 mm and 0.6 mm above section 12.
- 7,8. Serial sections 9 and 8; 7 septa; 0.3 mm and 0.6 mm above section 10; section 8 marks approximate upper limit of talon and beginning of cylindrical portion of coral.
 - 9. Serial section 7; 8 septa, axial cross-bar lost; 0.3 mm above section 8.
- 10. Serial section 6; 10 septa and axial cross-bar reappears; 0.5 mm above section 7.
- 11. Serial section 5; 10 septa but one almost lost; 0.5 mm above section 6.
- 12. Serial section 4; 9 septa; 0.5 mm above section 5.
- 13. Serial section 3; 9 septa; 0.5 mm above section 4; axial cross-bar lost.
- 14. Serial section 1; 8 septa; 1.0 mm above section 3; axial cross-bar and septal pair at upper right disoriented; certain orientation of this section in relation to others was lost.
 - 15-17 are sections from a single specimen (ZPAL P.Tc 3/2306). All ×15.
- 15. Lower section, from base of 17; 10 septa; orientation uncertain.
- 16. Upper section, from top of 17; orientation in relation to 15 unknown.
- 17. Longitudinal section; what appears to be a thick outer wall is composed of thickened, steeply inclined, outward-sloping tabulae.



