Some peculiar rugose coral taxa from Upper Serpukhovian strata of the Czech Republic

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ABSTRACT:

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Two genera from Upper Serpukhovian strata in the Czech Republic part of the Silesian Coal Basin are described and figured. *Ostravaia* gen. nov., included in Ostravaiainae subfam. nov., may belong to the Family Antiphyllidae Ilina, 1970. It is represented by one, morphologically variable new species, *O. silesiaca*. Two other species, conditionally included in that genus, are left in open nomenclature. *Variaxon* gen. nov., included in Variaxoninae subfam nov. of an undetermined family, is represented by two species, one of which, *V. radians,* is new.

Key words: *Ostravaia, Variaxon*; New rugose genera; Upper Serpukhovian; Czech Republic.

INTRODUCTION

The Ostrava mining area in the Czech Republic constitutes the southern part of the Upper Silesian Coal Basin (Text-fig. 1). Similar to the Polish part of the Basin to the north, several marine "horizons", yielding invertebrate marine faunas, occur in the Upper Serpukhovian succession in the Czech part. The Czech faunas were monographed by Řehoř and Řehořova (1972), but the very few rugose coral specimens included in that monograph were treated superficially. Their identifications on both the generic and specific levels were either incorrect, weakly supported, or both.

In contrast to the Czech part of the Upper Silesian Coal Basin, the rugose corals from the Polish part of the Basin have been treated in several papers. Schwarzbach (1937) identified and described some of them at a superficial level. Schindewolf (1942) first studied one species ('*Ufimia*' *schwarzbachi* Schindewolf, 1942) and then compared it to *Pentaphyllum* n.sp. (Schindewolf 1944). The latter species was named by him *Pentaphyllum* (*Tachylasma*) *silesiacum* when he described the entire existing collection in detail (Schindewolf 1952). That

collection was partly revised and/or commented on by Weyer (1974, 1977). Some species introduced by Schindewolf (1952) were revised and re-defined by Fedorowski (2009a, in press)*,* and one species is re-defined here on the basis of the original collection.

Weyer (1977) discussed the stratigraphic positions of several marine "horizons" in the Polish side of the Basin and mentioned the occurrence of additional marine "horizons". He analyzed the ammonoid faunas used in correlation of these "horizons" and pointed out the rather weak support for them. His doubts were further augmented by Machłajewska (2003). She pointed out the difficulty in correlating most "horizons" because of the complex tectonics of the area and a scarcity or absence of index fossils in most collections, derived mostly from cores.

As a result of these difficulties and uncertainties, as well as the lack of any modern Czech revision of the strata discussed, traditional names of "horizons" from which the corals were collected follow the names given by the original collectors. All of the corals studied for the present paper apparently were derived from the Gaebler Marine Horizon, the stratigraphically highest corals in

Text-fig. 1. Map of Czech Republic and Poland with the approximate location of the study area

the collection. Weyer (1977, p. 462), following Bojkowski (1967), Řehoř (1970)) and Matl (1971), suggested a middle Arnsbergian age (E$_2$b) for that horizon. That suggestion is followed here.

Claystone beds of the Gaebler Marine Horizon belong to the thick series of deposits that constitute the paralic Upper Silesian Coal Basin. They are underlain and covered with mudstones transferred into sandstones. Being less resistant against compaction resulting from both the large thickness of the overlying deposits and the strong tectonic impacts, the claystone of the Gaebler Marine Horizon offered a limited protection to the enclosed fossils. Thus, several rugose coral skeletons are to some extent affected by compaction. They were not abraded, excluding the *post mortem* transportation.

MATERIAL AND METHODS

The collection studied here comprises all corallites from the Upper Silesian Coal Basin housed in the Ostrava Museum other than the *Ufimia*-like corals. All specimens were collected long ago from cores and the search for new specimens has not continued. Thus, enrichment of the collection cannot be expected. This is one reason why the new taxa are based on so few specimens. However, all the main characteristics of those specimens were investigated in detail and their morphology has been found to differ in qualitative features from all previously described taxa. The morphological peculiarity of the corals investigated here is a second reason and a very restricted number of Serpukhovian rugose corals known from central Europe for comparison

is a third. In spite of the limited number of specimens, these corals should be named to enrich our knowledge of that specific fauna, allowing more precise phylogenetic and palaeogeographic reconstructions, and stratigraphic correlations.

In addition to specimens from the Ostrava Museum, the holotype of '*Fasciculophyllum*' *repressum* Schindewolf, 1952, is re-described here. It is housed in the Bundesanstalt für Geowissenschaften und Rohstoffe, Aussenstelle Berlin (acronym ZGI-X) and was collected from the Polish side of the Upper Silesian Coal Basin.

An ultra-thin wire (0.05 mm) was used for cutting most slabs for thin sections or peels. The completeness of specimens is commonly satisfactory enough to allow ontogenetic studies, but re-crystallization has restricted microstructural study. Diagenetic alteration has also resulted in a poor quality of some photographs, so drawings on those digital photographs are used to augment the documentation.

All specimens, other than that from the German Museum listed above, are housed in the Ostrava Museum, town of Ostrava, Czech Republic.

SYSTEMATIC PALAEONTOLOGY

Subclass Rugosa Milne Edwards and Haime, 1855
Order Stauriida Verrill, 1865
Family ?Antiphyllidae Ilina, 1970
Subfamily Ostravaiainae subfam. nov.

DIAGNOSIS: Solitary, non-dissepimented. Rotiphylloid arrangement of major septa early in ontogeny replaced by stereocolumn first and circulotheca later. Counter protoseptum and alar septa slightly elongated, at least in late neanic/early mature growth stage. Cardinal protoseptum at mature growth stage shortened slightly; it is distinctly shortened above middle part of calice. Minor septa underdeveloped. Tabularium uniform. Microstructure of septa finely trabecular.

DISCUSSION: The microstructure of septa is considered by the author one of the most important characters for distinguishing between genera and families. Unfortunately, all specimens investigated in this paper were strongly affected by the diagenesis. Thus, that feature is mostly deduced from the rudiments. Nevertheless, a width of the so called "middle dark lines" allows to reconstruct an original width of the primary septa, whereas the arrangement of crystalline fibrils in the more or less distinct bunches suggest their original positions within trabecular rods. Both those characters combined allow

to suggest the finely trabecular microstructure of septa, accepted for the genus discussed.

Several families should be considered for placement of *Ostravaia* gen. nov. The rotiphylloid early ontogeny and the slightly elongated counter protoseptum at maturity point towards the Family Antiphyllidae Ilina, 1970 and to the genus *Axisvacuus* Fedorowski, 2009 in particular. Thus, the present genus is tentatively placed in that family. Some features of *Axisvacuus*, such as shortening of the major septa in the mature growth stage and their rhopaloid character at the upper surfaces of tabulae (Fedorowski 2009b, text-figs 6A5,6; 7A5; 8A5; 9A8,9, C3,4), also resemble fragments of transverse sections of *Ostravaia*. However, the circulotheca of Fedorowski (2009c) is not formed in *Axisvacuus* and its cardinal protoseptum is not shortened all the way up to the calice floor. The microstructure of septa, most probably finely trabecular, is similar in both genera discussed.

A circulotheca replacing a stereocolumn generally is accepted as typical for the Family Laccophyllidae Grabau, 1928. In *Ostravaia* a circulotheca appears in the late neanic/early mature growth stage as either a temporary morphological episode or as a character lasting up to the mature calice floor. When only the macro-morphology shown in random transverse sections is exposed, this genus can be easily confused with the late Devonian genus *Neaxon.* However, the coarsely trabecular microstructure of the latter genus (e.g., Różkowska 1969; Weyer 1971) differs distinctly from the finely trabecular microstructure in *Ostravaia*. The difference exceeding an order of magnitude cannot be confused. Also, the early ontogeny of Neaxon (Kullmann 1965; Różkowska 1969; Weyer 1984) does not resemble that character in *Ostravaia*. Thus, a close relationship between the two genera, based only on their morphological similarity shown at some growth stages, is not accepted here.

Hudson (1944, 1945) described a few Early Carboniferous non-dissepimented species from Britain, as *Permia* Stuckenberg, 1895. However, the contratingent minor septa and biform tabularium, developed in most British specimens, that also lack the dissepimentarium, suggest a different taxonomic position on the generic and family level. Some may belong to *Ostravaia*, but they should not be included in that genus without a careful revision.

Both the rotiphylloid early ontogeny of the Lower Devonian genus *Adradosia* Birenheide and Soto, 1977 and the development of circulotheca, present in that genus at the late neanic/early mature growth stage, closely resemble those characters in *Ostravaia*. The so called "naked tips" in the former genus, suggested by Birenheide and Soto (1977) as one of the most important diagnostic features of *Adradosia* was considered by Weyer (1985) and Berkowski (personal communication, 2009) as taxonomically unimportant. That approach is followed here. However, the microstructure of the septa in *Adradosia* (Kullmann 1965; Berkowski 2008), with regularly arranged "Knopfen" (the term introduced by Kullmann 1965) and the approximately 80 Ma difference between the occurrence of *Adradosia* and *Ostravaia,* precludes a relationship of *Ostravaia* to that Emsian genus. Thus, a relationship between *Ostravaia* and *Adradosia* at the family level is not suggested here.

A slight elongation of the counter protoseptum, accompanied by elongation of the alar septa, a slight shortening of the cardinal protoseptum and the finely trabecular microstructure of septa (Ilina 1984; Fedorowski and Bamber 2001) in *Sochkineophyllum* Grabau, 1928 from the family Polycoeliidae de Fromentel, 1864, may suggest a relationship to *Ostravaia*. However, *Sochkineophyllum* possesses a calophylloid arrangement of major septa at the early ontogeny, its rhopaloid major septa are differentiated in length and it lacks a circulotheca at any growth stage. Thus, some similarities between those two genera exist, but this does not suggest a relationship.

Genus *Ostravaia* gen. nov.

TYPE SPECIES: *Ostravaia silesiaca* sp. nov.

ETYMOLOGY: Named after the town of Ostrava, capital of the Czech Republic part of the Silesian Coal Basin.

DIAGNOSIS: As for the subfamily (Monotypic).

DISCUSSION: The species content of *Ostravaia* has not been established in this paper, but two species from the Polish side of the Silesian Coal Basin may belong to this genus. These are *Fasciculophyllum simplex* Schindewolf, 1952 and *Claviphyllum pauperculum* Schindewolf, 1952. Both species will be revised in a paper dealing with new material collected from the Polish part of the basin (Fedorowski and Machłajewska, in preparation).

Ostravaia silesiaca sp. nov.
(Text-figs 2–5)

HOLOTYPE: Specimen B-11411 (Text-figs 2A–O, 3A–I).
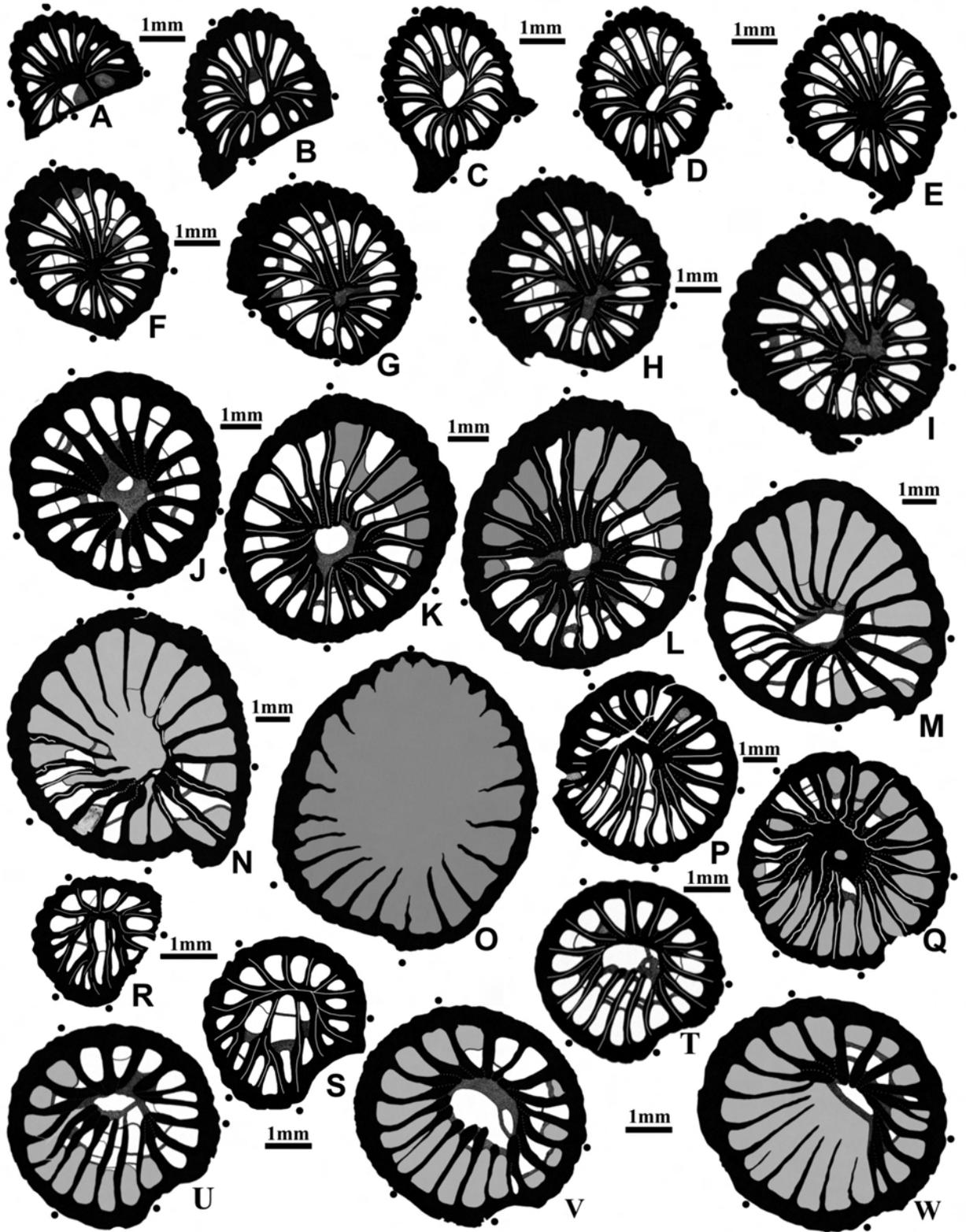
TYPE LOCALITY: Town of Doubrava, Doubrava mine, borehole Cr 106, depth 251.2 m.

TYPE HORIZON: Ostrava Formation, Gaebler Marine Horizon, E_2b biozone, Upper Serpukhovian.

ETYMOLOGY: After the area of the occurrence.

MATERIAL: Holotype (B-11411) and four paratypes (B-1066, B-9378, B-10181, B-11411A). Sixteen thin sections and twenty-nine acetate peels were available for study.

DIAGNOSIS: *Ostravaia* with n:d value near calice floor of 18–21:5.5–8.2mm; major septa irregularly arranged depending on corallite curvature; circumaxial structure narrow; cardinal protoseptum shortened slightly only in late maturity; blades of minor septa absent from corallite lumen.

DESCRIPTION OF THE HOLOTYPE: The corallite was flattened by the attachment to the substrate at the cardinal protoseptum and the right alar septum, i.e., its concave side (Text-fig. 2A–D). The cardinal protoseptum in this growth stage is indistinguishable by length from the adjacent major septa, and the cardinal fossula is absent. A false fossula appears next to the counter protoseptum as a result of the peculiar arrangement of major septa. That growth stage ends with a short-lasting axial opening that can neither be called an aulos nor a circulotheca. It resembles the aulos at the beginning (Text-fig. 2B, C) when inner margins of almost all 'middle dark lines'(= primary major septa) are either united or closely approach each other and the circulotheca later (Text-fig. 2D). Those 'middle dark lines' are shown as white lines in the cited and all remaining drawings.

Growth in the holotype at the next stage (Text-figs 2E–H, 3A) is characterized by the slightly rhopaloid major septa, that are axially connected to a strong stereocolumn, and by the domination of the counter protoseptum that is both the longest and the thickest of all major septa. The cardinal protoseptum, located on the concave corallite side, is one of the shortest, although not necessarily the shortest septum in the cardinal quadrants.

The latest neanic growth stage (Text-figs 2I; 3B) remains similar to the previously described morphology, except for a slight and inconsistent shortening of both protosepta. The earliest mature growth stage, sectioned entirely beneath the calice floor (Text-figs 2J, 3C), differs from the later growth stages in possessing major septa grouped in quadrants, with the inner margin of the counter protoseptum being connected to the right counter-lateral septum. A narrow circulotheca forms an opening in the stereocolumn. The cardinal protoseptum and the last major septum of the left cardinal quadrant, are the shortest septa in those quadrants. The thin, curved inner margin of the cardinal protoseptum joins the last inserted major septum in the right cardinal quadrant and retains that position during later growth stages, although its length changes (Text-figs 1K,L; 2D–F).

Peripheral parts of most septal loculi in the mature growth stage described in the preceding paragraph are sectioned above the calice floor. The counter protoseptum and the counter-lateral septa dominate in length and thickness. A cardinal fossula is either absent or very shallow, because the loculi adjacent to the cardinal protoseptum remain elevated above the calice floor. A circulotheca is best developed and complete at that growth stage (Text-fig. 3F). The inner margins of all major septa are laterally contiguous.

A slight downward curvature of the tabula, i.e., the occurrence of a true cardinal fossula, is documented only in the next two sections by the infilling with dark strange matrix (Text-figs 2M, N; 3H, I), whereas the adjacent loculi remain completely (left) or partly (right) white, i.e., are elevated above a calice floor. The circumaxial structure seen in the ontogenetically advanced mature growth stage (Text-figs 2M, 3H) resembles again a mixed aulos-circulotheca type. The strongly curved inner margins of most major septa in the counter quadrants only touch each other. Also, a direct connection of 'middle dark lines' of major septa in the cardinal quadrants is only suggested by their curvature, but not documented. The separation of the inner margins of major septa in counter quadrants first (Text-figs. 2N; 3I) may have resulted from the slight obliqueness of the section. Precise orientation of the specimen was impossible because it was encased in matrix. The cardinal pro-

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Text-fig. 2. *Ostravaia silesiaca* sp. nov. A-O, B-11411. Holotype. A-I – early to late neanic growth stage (H = Text-fig. 3A), J – late neanic/early mature growth stage (= Text-fig. 3C), K-M – mature growth stage (=Text-fig. 3D, E, H), N – mostly just above calice the floor (= Text-fig. 3I), O – slightly oblique transverse section; near calice margin in upper part. P-Q, B-1066. Paratype. P – late neanic growth stage, Q – early mature growth stage. R–W, B-9378. Paratype. R–S – neanic growth stage (=Text-fig. 3J, K), T-V – mature growth stage (U,V = Text-fig. 3L, M), W – mature growth stage; mostly above calice floor (=Text-fig. 3N). *Note*. Transverse thin sections, except when stated. Protosepta and alar septa marked by dots. Cardinal protoseptum at the bottom of figures. Parts cut above calice floor shadowed in drawings. "middle dark lines' (primary septa) shown as white ines in drawings. Scale bars between two pictures corresponds to both; bar at upper right of a picture corresponds to that picture only. For occurrences see descriptions of species
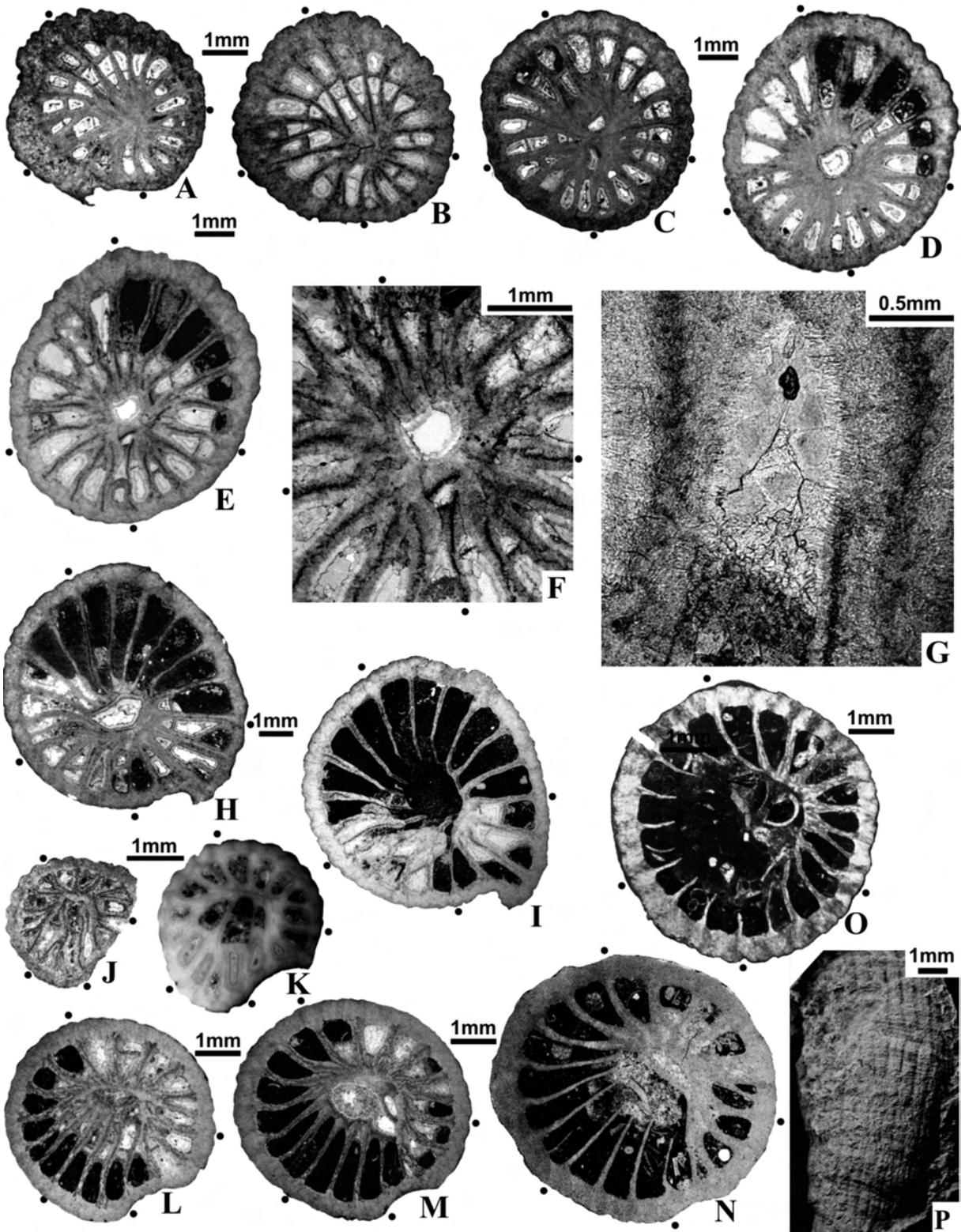
Text-fig. 3. *Ostravaia silesiaca* sp. nov. A-I, B-11411. Holotype. A-B – late neanic growth stage (A = Text-fig. 2H), C – late neanic/early mature growth stage (= Text-fig. 2J), D, E, H– mature growth stage (=Text-fig. 2 K-M), F – Middle part of text-fig. 3E enlarged to document morphology of circulotheca, G – diagenetically altered microstructure of major septa, I –mostly just above calice floor (= Text-fig. 2N). J-P, B-9378. Paratype. J-K – neanic growth stage (=Text-fig. R-S), L-M – mature growth stage (= Text-fig. 2 U,V), N-O – mature growth stage; mostly above calice floor (N =Text-fig. 2W), P – exterior of corallite. See *Note* following description of Text-figure 2 for further explanations

toseptum at that growth stage is the thinnest and the shortest septum in the cardinal quadrants.

Minor septa do not extend from the external wall to form blades, but protuberations on the inner side of the external wall suggest their occurrence within the external wall that is also induced by differences in the arrangement of crystalline fibrils. The very poor state of preservation does not allow a photographic documentation.

INTRASPECIFIC VARIABILITY: One of the paratypes is an immature specimen (not illustrated). Its identification is based on the close morphological similarity at comparable growth stages of the holotype and its position in the rock next to the holotype. The remaining two paratypes (Text-figs 2P–W; 3J–P) exhibit substantial morphological differences in some aspects of their early ontogeny and mature growth stage.

The earliest preserved growth stage, perhaps late neanic, of one corallite displays the morphology different from the holotype (Text-fig. 2P *vs* 2E, F). The longest major septa are in the cardinal quadrants and are asymmetrical; only the left alar septum is elongated. The upper surface of the slab of that paratype (Text-fig. 2Q) shows a comparable morphology to the early mature growth part of the holotype in possessing a circumaxial structure opened at the axis. However, the inner margins of many of the major septa are connected by 'middle dark lines' (=primary septa). The cardinal protoseptum is slightly shorter than adjacent major septa in cardinal quadrants, but is not truly shortened, and the counter protoseptum is indistinguishable by length or thickness. Most peripheral parts of the corallite and the circumaxial structure, were sectioned above the calice floor. Thus, the transverse section described bears a mixture of mature and juvenile characters with the latter present above the calice floor. Its n:d value (20:6.3 mm) is larger than that at a comparable growth stage in the holotype.

The arrangement of major septa in the neanic growth stage of another paratype (Text-figs 2R, S; 3J, K) resembles rotiphylloid, except for the position of the long cardinal protoseptum on the concave corallite side, i.e., like in the holotype. However, unlike in the latter specimen, the inner margins of the major septa in the paratype discussed are shorter in the counter than in the cardinal quadrants and all are united by their 'middle dark lines' (=primary septa). That morphology gradually evolves into a wide circulotheca by separation of major septa in counter quadrants and a reduction in length of the longest major septa in the cardinal quadrants. The cardinal protoseptum has become shorter than the adjacent major septa, but elongates again in the slightly more advanced growth stage (Text-figs 2T *vs* 2U). The

circumaxial structure is irregular during the further corallite growth (Text-figs 2U, V; 3L, M). In contrast to the holotype, the inner margins of major septa in the left cardinal quadrant separate first, whereas the inner margins (but not the primary septa) of those in the counter quadrants and the right cardinal quadrant unite to form an arch over the free and rhopaloid major septa of the left cardinal quadrant. That connection of the inner margins of major septa remains well above the calice floor (Text-figs 2W; 3N, O). Minor septa do not extend from the external wall to form blades, but their occurrence within the external wall is suggested by differences in the arrangement of crystalline fibrils, best seen in the middle part of the calice (Text-fig. 3O) where they alternate with wide peripheral margins of major septa to form a septotheca. The external surface of the paratype discussed (Text-fig. 3P) displays the comparatively deep and narrow septal furrows and the wide, almost flat interseptal ridges with very shallow wrinkles of 'hyposepta' of Weyer (1980).

The horn-shaped corallite B-10181, with the surface of the external wall bearing moderately deep furrows of the major and minor septa and shallow wrinkles of "hyposepta" (Text-fig. 5A) differs from the holotype most distinctly and may belong to a separate species. Thus, it was described and illustrated in detail. During corallite growth, the thickness of the external wall increases from 0.2 mm in the earliest growth stage preserved to 1.4 mm in the middle part of the calice, occupying in the latter case 1/4-1/3 of the corallite radius.

The arrangement of the major septa in the earliest neanic growth stage preserved (Text-figs 4A–C; 5B–E) is very irregular. A slit present between the last two underdeveloped major septa inserted in the left counter quadrant imitates a cardinal fossula. The presence of that false fossula is further illustrated by the inner margins of the remaining septa, both protosepta included, arching above that slit. The protosepta are hardly recognizable. The cardinal protoseptum imitates the last inserted major septum in the right cardinal quadrant. The counter protoseptum does not differ from the adjacent major septa. Its inner margin is bent towards the inner margin of the adjacent counter-lateral septum. A cardinal fossula is absent at this growth stage.

The late neanic/earliest mature growth stage (Text-figs 4D, E; 5F, G) is marked by the first steps in the rearrangement of the major septa into a bilateral appearance, best seen in the next illustrated growth stage (Text-fig. 4F). Their inner margins become separated and the alar septa slightly elongated without being truly rhopaloid (Text-fig. 5G). All the inner margins of septa end in the sclerenchyme forming a conspicuous stereocolumn. At this growth stage the two last pairs of ma-
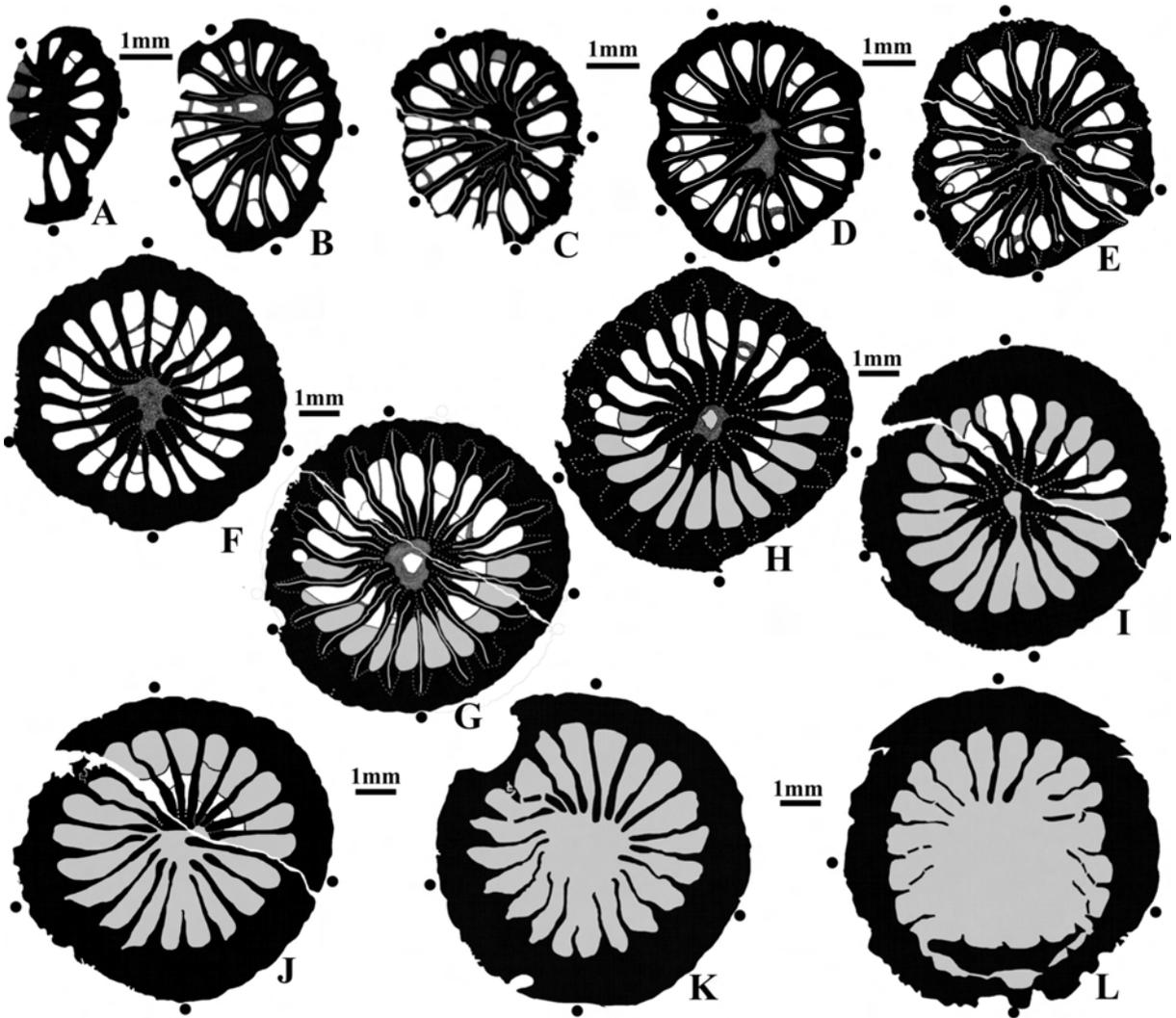
Text-fig. 4. *Ostravaia silesiaca* sp. nov. B-10181. Paratype. A-C – early to late neanic growth stage (= Text-fig. 5B-D), D-F – early mature growth stage (D= Text-fig. 5F), G-I – mature growth stage; calice floor and circulotheca elevated highest at counter protoseptum (= Text-fig. 5H, J, L). J-K – lower part of calice (K = Text-fig. 5N). L – highest part of calice preserved. See *Note* following description of Text-figure 2 for further explanations

jor septa are inserted. Their number then remains constant (20) up to the end of growth of the specimen.

The early mature growth stage is here arbitrarily placed where thinning and further shortening of the cardinal protoseptum and formation of the clearly triangular cardinal fossula occurs (Text-fig. 4F). Most major septa in the cardinal quadrants become rhopaloid, the elongated alar septa most distinctly, but the stereocolumn continues to occur. That growth stage is the last one illustrated by the transverse section made entirely beneath the calice floor.

The morphology accepted here as completely mature (Text-figs 4G, H; 5H–K) is achieved near the calice floor. The rhopaloid major septa are radially arranged, and the circulotheca is strong and complete,

with the axial duct surrounded by both the inner margins of the major septa and the sclerenchyme. The thin, straight cardinal protoseptum is slightly shorter than adjacent major septa, but it reaches the outer periphery of the circulotheca, where the triangular cardinal septal fossula is terminated. The length of the counter protoseptum is uncertain, but it probably equals that of the counter-lateral septa.

The calice floor in the mature growth stage is elevated highest at the counter protoseptum and counter-lateral septa, whereas the cardinal fossula forms the deepest part of the calice. This is documented by the infillings of a strange fabric in the cardinal fossula and peripheral parts of interseptal loculi in cardinal quadrants (Text-figs 4G, H, shadowed; 5H–K, dark). Also, the cir-
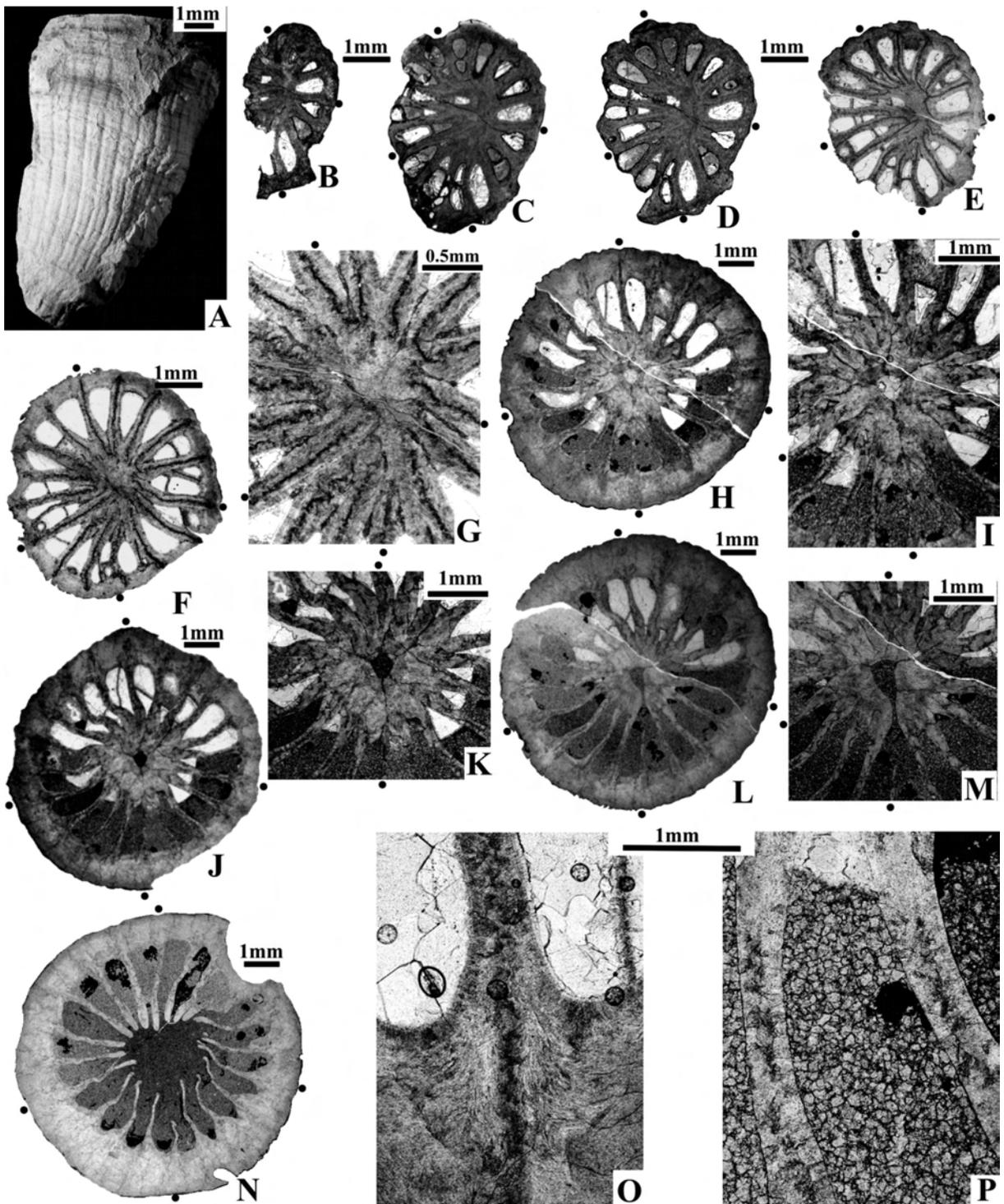
Text-fig. 5. *Ostravaia silesiaca* sp. nov. B-10181. Paratype. A – exterior view of corallite, B-E – early to late neanic growth stage (B-D = Text-fig. 4A-C), F – early mature growth stage (= Text-fig. 4D), G – axial part of Text-fig. 5F enlarged to show stereocolumn and inner margins of major septa, H, J, L – mature growth stage; sections above calice floor at periphery of cardinal quadrants (= Text-fig. 4G-I), I, K, M – enlarged circulotheca of Text-figure 5H, J, L, N – lower part of calice with inner margins of all major septa free (=Text-fig. 4K), O – basal part of major septum embedded in external wall, P - remnants of trabeculae in middle parts of diagenetically altered major septa. See *Note* following description of Text-figure 2 for further explanations

culotheca is elevated as documented by the occurrence of sclerenchyme between the inner margins of major septa. The separation of the circulotheca begins opposite to the inner margin of the cardinal fossula and is accompanied by a distinct shortening of the cardinal protoseptum (Text-figs 4I; 5L, M). That separation of the inner margins of major septa then proceeds towards the counter protoseptum. The counter protoseptum, the few inner margins of major septa closest to it, and the inner parts of loculi between them lasted longest above the calice floor (Text-fig. 4J, loculi left in white). This is the most advanced growth stage with the alar septa elongated distinctly.

In the transverse section cut entirely above the calice floor (Text-figs 4K; 5N) the cardinal protoseptum remains distinctly shortened, whereas the counter protoseptum is the longest of all septa. The remaining major septa in the counter quadrants are thicker than the thin and wavy major septa in the cardinal quadrants. The strongly thickened peripheral parts of all major septa are apparently laterally touching, making it improbable that minor septa are present in this part of the external wall (Text-fig. 5N). The counter protoseptum and counter-lateral septa remain the longest and thickest septa up to the middle part of the calice (Text-fig. 4L).

MICROSTRUCTURE AND DIAGENESIS: The original trabecular microstructure of primary septa in the holotype, which were perhaps less than 0.02 mm wide, as indicated by fan-shaped crystalline fibrils (Text-fig. 3G), can only be deduced from the diagenetically altered remnants. Those fibrils continue partly into the fibrils of sclerenchymal sheets of septa that reach the limits of the septa at narrow angles. This suggests that advanced diagenetic alteration of the microstructure has occurred.

The microstructure is best demonstrated in some septa of the paratype specimen B-10181 (Text-fig. 5G, O, P). Segments of the primary septa both embedded in the external wall (Text-fig. 5O) and free (Text-fig. 4P), show small clusters of fibrils, either almost continuous in the first instance or obviously isolated from one another in the second. Both are remnants of fine trabeculae that resisted diagenesis, but alteration of the latter was less advanced.

DISCUSSION: The arrangement of the major septa in the neanic growth stage of the holotype and the paratypes, investigated in an adequate detail, closely resemble rotiphylloid, except for the position of the cardinal protoseptum at the convex side of the corallite. Thus application of the term 'rotiphylloid' is not quite accurate despite the elongation of the cardinal protoseptum. Position of that protoseptum on the convex

corallite side in '*Zaphrentis*' (= *Rotiphyllum*) *omaliusi* Milne Edwards and Haime, 1851 was first established by Carruthers (1908) and discussed by Fedorowski (2009d). Also, the arrangement of major septa in the early growth stage of the holotype (Text-fig. 2B–D) only superficially resembles that in *R. omaliusi*, but is in fact a mirror image to it. Growth in the holotype at the next stage (Text-figs 2E–H; 3A) is typical for the genus *Rotiphyllum* in the general arrangement of slightly rhopaloid major septa, in their axial connection to a strong stereocolumn, and domination of the counter protoseptum that is both the longest and the thickest of all major septa. The inconstant length of the cardinal protoseptum, which is one of the shortest, although not necessarily the shortest septum in the cardinal quadrants, and its position on the concave corallite side, are the main differences from *Rotiphyllum*. Those characters and the similarity in the microstructure of septa were elevated to support an earlier suggestion of a probable derivation of *Ostravaia silesiaca* from *Rotiphyllum*.

The corallite B-10181 differs from the holotype in three ways: 1. Regular, typically built and comparatively long-lasting circulotheca, opened first towards the cardinal fossula and later disappearing by a simple reduction of interseptal sclerenchyme. 2. Obvious, although not distinct, elongation of the counter protoseptum and alar septa in advanced maturity. 3. Absence of minor septa from both the corallite lumen and the thick external wall up to the upper part of the calice.

OCCURRENCE: B-11411 (Holotype) and B-11411A, Doubrava Village, Doubrava mine, borehole Cr 106, depth 251.2 m. B-9378, Orlová Village, Zápotocky mine, borehole 960/XXXVIII, depth 399.7m. B-1066, Town of Karviná, borehole NP. 473, depth 1148.8 m. B-10181, Karvina ČSA mine, borehole E5, depth 105,9m. All from Ostrava Formation, Gaebler Marine Horizon, E_2b biozone, Upper Serpukhovian.

?*Ostravaia* sp. 1
(Text-figs 6, 7)

MATERIAL: One almost complete specimen B-8899 slightly damaged diagenetically in the mature growth stage. Three thin sections and eight peels were available for study.

DESCRIPTION: The corallite was approximately 15 mm long, narrow (8.0×5.3 mm diameter near the flattened calice margin), horn-shaped in the early growth stage, but erect at maturity, with the cardinal protoseptum on the convex side. Rigid growth striae dominate

over shallow septal furrows on its external surface (Text-fig. 7K). The external wall of the septotheca–type (Text-fig. 7F–H) is 0.6–0.8 mm thick at maturity as measured between major and minor septa.

In the earliest growth stage investigated (Text-figs 6A, B; 7A) the major septa of the cardinal quadrants are connected to each other by their 'middle dark lines' (= primary septa). The cardinal protoseptum is longer than the adjacent major septa and its inner margin is bent to the right, joining the inner margin of the adjacent major septum. The arrangement described closely resembles an aulos (Fedorowski 2009c). The arrangement of the major septa in the counter quadrants is different. The axially free counter protoseptum and the counter-lateral septa are the longest septa in those quadrants, extending beyond the corallite axis and pointing into an arch formed by the major septa of the cardinal quadrants. The inner margins of the last pairs of septa in the counter quadrants are united. The relationships between the inner margins of

the septa in the late neanic growth stage (Text-figs 6C, D; 7C) is more typically zaphrentoid than in the earlier stages. The inner margins of some major septa in the counter quadrants become re-united and the counter protoseptum varies in length, being slightly shortened first (Text-figs 6C; 7C) and slightly elongated again soon after (Text-fig. 6D, E). The major septa become nearly symmetrically arranged, with the cardinal fossula and the alar pseudofossulae well accentuated by the newly inserted major septa. These are the last major septa inserted in this corallite. The constant number of septa (19) with increasing corallite diameter results in n:d values rising from 19:4.0 mm in the late neanic growth stage to 19:8.0×5.7 mm in the middle part of the calice. The difference points to the necessity of precise comparison of corresponding growth stages when the n:d values of potentially different species are compared.

Approximately 2.7 mm above the previously described growth stage when measured at the concave
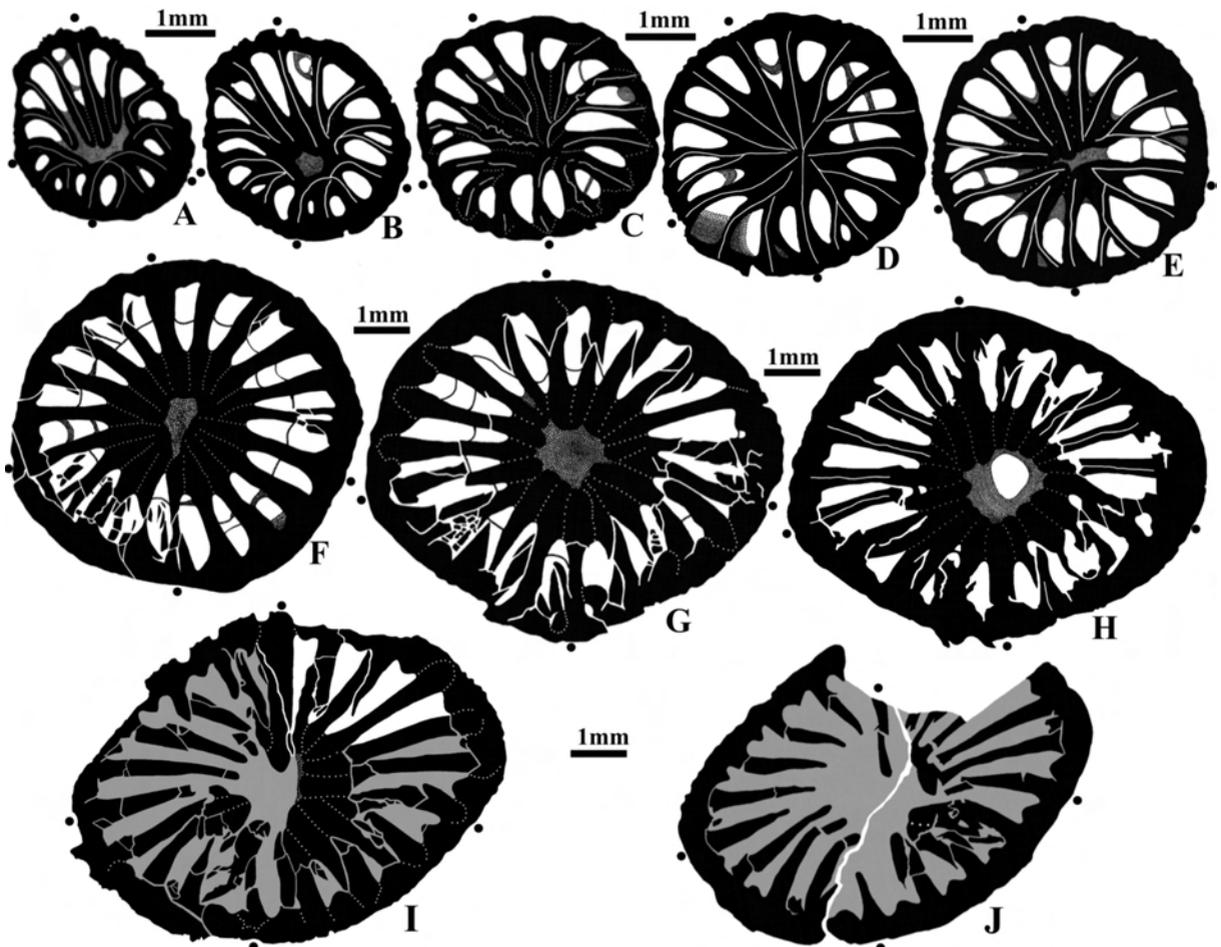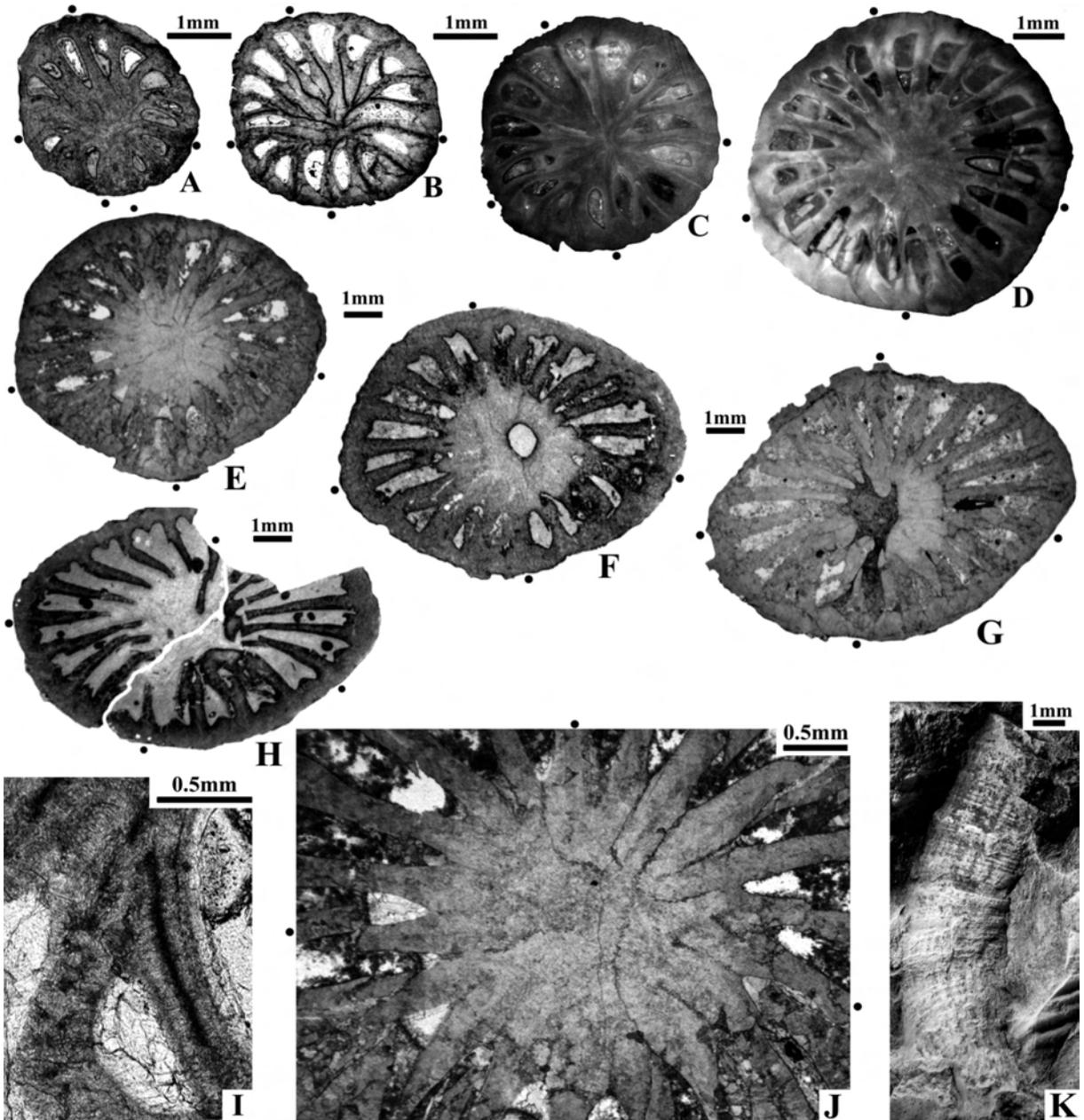

Text-fig. 6. ?*Ostravaia* sp. 1. B-8899. A-E – early to late neanic growth stage (A, C, D = Text-fig. 7A-C), F-G – early mature growth stage (=Text-fig. 7D, E), H – mature growth stage (=Text-fig. 7F), I – mature growth stage; cut mostly above calice floor (=Text-fig. 7G), J – lower part of calice (=Text-fig. 7H). See *Note* following description of Text-figure 2 for further explanations

corallite side and 5.2 mm at its convex side, all major septa become radially arranged, rhopaloid, and laterally contiguous in their inner margins that terminate in a strong stereocolumn (Text-figs 6F, G; 7D, E, J). This growth stage is arbitrarily considered early mature. The cardinal protoseptum becomes slightly shorter than the adjacent major septa at this growth stage and during the short time when a complete cir-

culotheca is present (Text-figs 6H; 7F). It becomes distinctly shortened only in the calice (Text-figs 6I, J; 7G, H). The length of the counter protoseptum begins to increase in early maturity eventually reaching the corallite axis in the lower part of the calice (Text-figs 6H–J; 7F–H).

During the main part of the mature growth stage the alar and the counter-lateral septa do not differ in length

Text-fig. 7. ?*Ostravaia* sp. 1. B-8899. A-C – early to late neanic growth stage (= Text-fig. 6A, C, D), D-E– early mature growth stage (= Text-fig. 6F-G), F – mature growth stage (=Text-fig. 6H), G – mature growth stage; cut above calice floor in most part (=Text-fig. 6I), H – lower part of calice (Text-fig. 6J), I – two neighboured major septa showing different diagenetic alterations; possible remnants of trabeculae seen in left septum, J – inner part of E enlarged to document arrangement of inner margins of major septa, K – external view of corallite. See *Note* following description of Text-figure 2 for further explanations

or thickness from the remaining major septa. Temporary shortening of the right alar septum (Text-figs 6G; 7E) may be the result of a peripheral break. However, true shortening of the alar septa is established in the advanced mature growth stage, i.e., in the transverse section made mostly above the calice floor (Text-figs 6I; 7G). That trend of shortening is confirmed by the transverse section in the lower part of the calice (Text-figs 6J; 7H). The counter-lateral septa in that part of the corallite seem to be slightly shortened as well. Unfortunately, the major septa in the mature growth stage (Text-figs 6F–I; 7D–G) have been broken by compression, making drawings imprecise.

Thickenings at the bases of the counter protoseptum and the counter-lateral septa suggest the appearance of minor septa in a form called by Weyer (1974, p. 351) 'biformen Kleinseptenreduction' (biformly reduced) (Text-figs 6F, G; 7D–E). They lose that character in their further growth (Text-figs 6H, I; 7G), becoming typically underdeveloped minor septa.

A circulotheca is a temporary character that replaces the stereocolumn without any obvious changes in the arrangement and morphology of the major septa (Text-figs 6H; 7F). It appears just beneath the calice floor and its rudiments extend slightly above it (Text-figs 6I; 7G, right).

Diagenetic alteration of all structural elements makes recognition of the original microstructure of septa almost impossible. Also, septa adjacent to one another (Text-fig. 7I) may be differently affected by the process. Most of the right major septum illustrated shows a solid 'middle dark line' surrounded on both sides by differently altered sclerenchymal sheets. Only in the lower part of the illustration is it replaced by secondary structures, involving both the primary septum and its sclerenchymal sheets. Crystalline fibrils in most of the left major septum form bunches, extending the entire width of the septum. Both the arrangement of fibrils and the dark centers of their bunches imitate large trabeculae. They may be altered fine or medium size trabeculae, enlarged by growth of their fibrils at the cost of the diagenetically molten sclerenchyme. The solid 'middle dark line' of that major septum appears only in the innermost part illustrated.

DISCUSSION: The specimen described bears a mixture of features that distinguishes it from all other specimens here included in *Ostravaia*. It differs from the corallite B-10181 of *Ostravaia silesiana*, the most similar specimen, in possessing a much longer counter protoseptum, an inconspicuous shortening of the cardinal protoseptum lasting almost up to the calice floor, slightly shortened alar and counter-lateral septa near and above the calice

floor, and easily recognizable minor septa. Some of these characters, the long length of the counter protoseptum, and slightly shortened alar septa in particular, suggest that a different generic assignment might be appropriate. It is morphologically close to the '*Claviphyllum*' *hillae* Hudson and Fox, 1943 group of species, as discussed below in the remarks on phylogeny. Its questionable placement in *Ostravaia* is based mainly on characters of the early growth stages that differ distinctly from '*C.' hillae*, belonging most probably to the genus *Antiphyllum* Schindewolf, 1952.

OCCURRENCE: Town of Karviná, ČSA mine, borehole 84/74, depth 202.6m. Ostrava Formation, Gaebler Marine Horizon, E_2b biozone, Upper Serpukhovian.

?*Ostravaia* sp. 2
(Text-figs 8, 9)

MATERIAL: Two specimens. B-1069 was earlier sectioned and identified by Řehoř and Řehořova (1972, pl. 2, fig. 9) as *Claviphyllum pauperculum* Schindewolf, 1952. Only a thick slab was left from that specimen. One thin section and one peel were prepared from it for the purpose of this paper (Text-figs 8O, P; 9O). The peripheral part of specimen B-10714 was destroyed during drilling. Six thin sections and eight peels from various growth stages were prepared. The earliest growth stage is strongly altered diagenetically. The original microstructure of septa is not preserved.

DESCRIPTION: Specimen B-10714 is horn shaped with the cardinal protoseptum on the concave side of the corallite. Its surface is mostly corroded, but shallow furrows of minor and major septa occur (Text-fig. 9C, D, F, I) in the better preserved part. The arrangement of major septa in the early growth stage is irregular, of a deformed zaphrentoid type (Text-figs. 8A, B; 9A, B). That irregularity (Text-figs 8C, 9C) continues for 2.7 mm of growth, measured along the concave corallite side, and 3.8 mm along the convex side. The inner margins of the major septa in the right cardinal quadrant and the cardinal protoseptum at that growth stage are united by their 'middle dark lines' (= primary septa), whereas those of the left cardinal quadrant are free (Text-figs 8C; 9C). The counter quadrants from this, as well as much of the remainder of the corallite (Text-figs 8C-J; 9C, D, F, I, J) were almost completely destroyed by drilling.

The arrangement of the major septa becomes more regular within approximately 1 mm of further growth (Text-figs 8D; 9D, E). The inner margins of all major septa at that growth stage terminate in the sclerenchyme
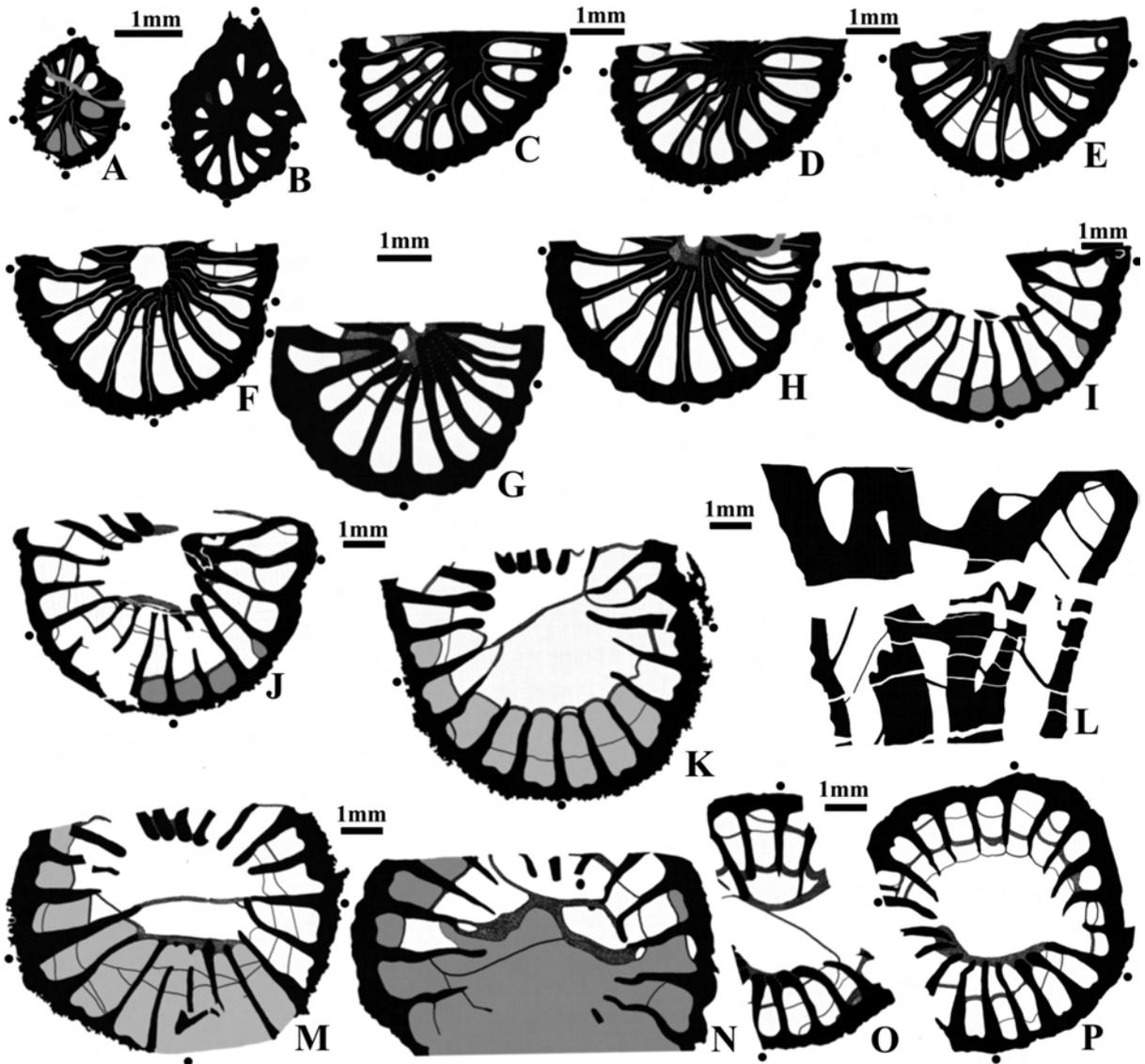
Text-fig. 8. ?*Ostravaia* sp. 2. A-N, B-10714. A-C – early to late neanic growth stage (=Text-fig. 9A-C; B, C – polished surfaces), D – late neanic/early mature growth stage (= Text-fig. 9D), E-H – early mature growth stage (F, H = Text-fig. 9F, I; E, G – peels, I – polished surface), I-K,M-N – mature growth stage (I, K, M, N = Text-fig. 9J-M), L – longitudinal section between H and I (=Text-fig. 9H; polished surface). O-P, B1069. Mature growth stage (P = Text-fig. 9O; peel). See *Note* following description of Text-figure 2 for further explanations

of the stereocolumn. The cardinal protoseptum is slightly shortened at this growth stage and at the beginning of the next growth stage (Text-fig. 8D, E). Such a morphology is here considered intermediate between the late neanic and early mature growth stages.

The previously described and next growth stage, during which a circulotheca is developed (Text-figs 8E–H; 9F, G, I), are typical for *Ostravaia*. The inner margins of the major septa that form the circulotheca terminate around the free axial tube, being laterally contiguous there, although some bend towards the adjacent major septa (Text-fig. 9G). The cardinal protoseptum reaches the length of the remaining major septa in the

cardinal quadrants and becomes indistinguishable from them in length and thickness. This is here considered to be an early mature growth stage.

The longitudinal section (Text-figs 8L, 9H) exposed by drilling, is 6.1 mm long. Its morphology confirms the occurrence of a circulotheca for approximately 1/3 the length of the specimen. The inner tabellae, almost horizontally arranged, are widely spaced, and some are strongly thickened by sclerenchyme. Peripheral tabellae, more numerous than inner ones, are elevated towards the circulotheca at approximately 45°.

The circulotheca disappeared just above the highest inner tabella exposed by the longitudinal section
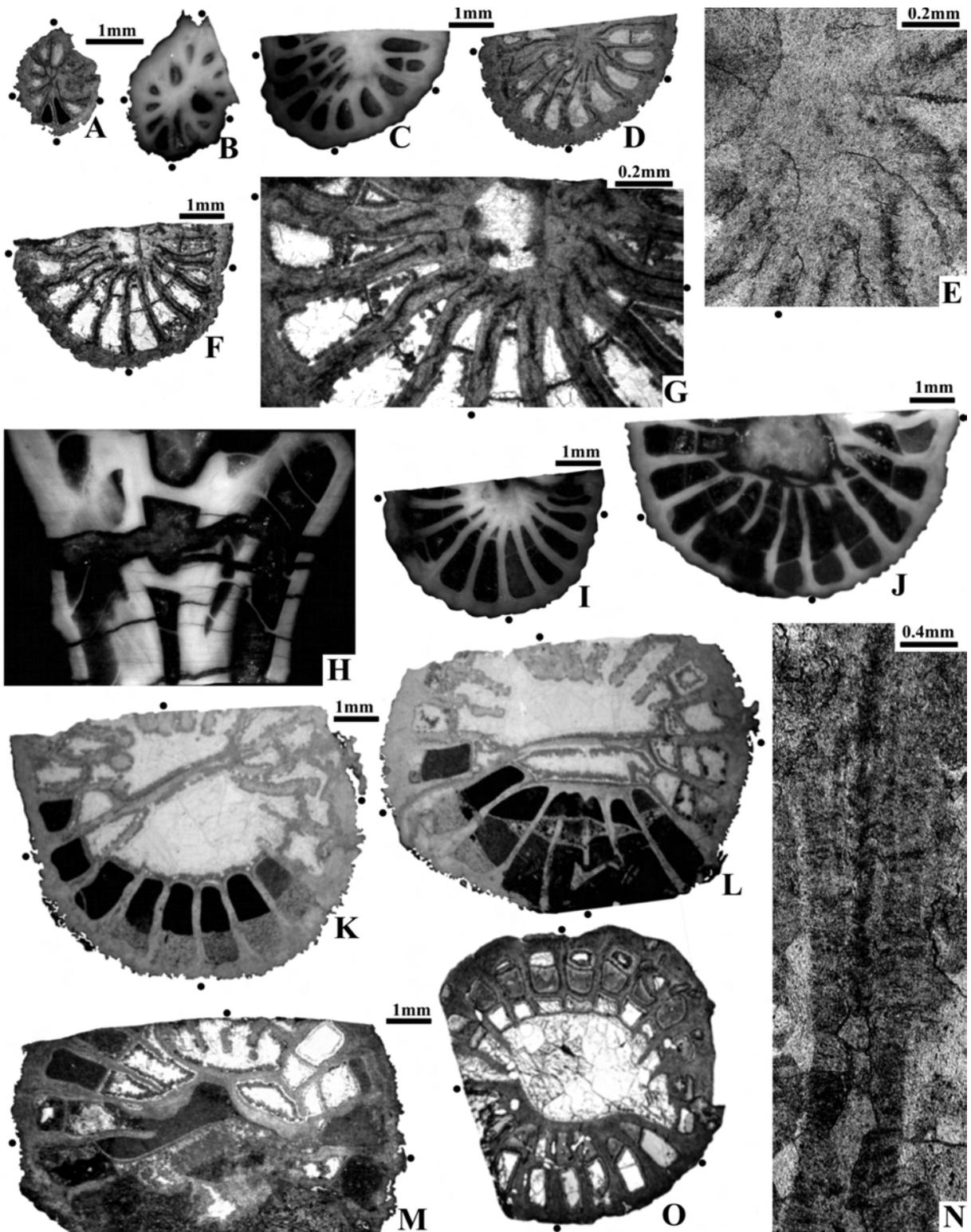
Text-fig. 9. ?*Ostravaia* sp. 2. A-N, B-10714. A-C – early to late neanic growth stage (=Text-fig. 8A-C; B, C – polished surfaces), D – late neanic/early mature growth stage (= Text-fig. 8D), E – middle part of D enlarged to show arrangement of inner margins of major septa, F, I - early mature growth stage (= Text-fig. 8F, H; I – polished surface), G – middle part of F enlarged to show inner margins of major septa, J-M – mature growth stage (=I, K, M, N; J – polished surface) H – longitudinal section between I and J (= Text-fig. 8 L; polished surface), N – differentiated diagenetic alteration of primary septum and its sclerenchymal cover. O, B1069. Mature growth stage (= Text-fig. 8P; peel). See *Note* following description of Text-figure 2 for further explanations

(Text-figs 8L, 9H, uppermost). The inner margins of the major septa at that growth stage (Text-figs 8I, 9J) are connected only by sections of tabulae, being otherwise free and equally shortened. The cardinal protoseptum remains indistinguishable. The free axial area widens during further corallite growth (Text-figs 8I–K, M, N; 9J–M). The ontogenetically advanced part of the corallite is more complete than the ontogenetically earlier growth. That resulted from the corallite curvature, which allowed the inner parts of major septa of the counter quadrants to survive destruction by drilling. Thus, a slightly rhopaloid character of some major septa in the counter quadrants and the length of the counter protoseptum equal to that of the counter-lateral and other major septa in those quadrants, can be documented although only inner-most parts of those septa survived from destruction of peripheral part of the counter quadrants. The cardinal protoseptum remains indistinguishable from the remaining major septa of the cardinal quadrants. The alar septa are temporarily elongated, but this resulted perhaps from their amplexoid character as indicated by their connection to tabulae. Most of the corallite at this growth stage was sectioned beneath the calice floor. Thus, both the shortening and alignment of all major septa and the protosepta must be treated as typical and constant for the mature growth stage of this specimen, lasting for approximately 7 mm of the corallite growth or longer. The cardinal quadrants in the uppermost part of the specimen are missing (Text-figs 8N, 9M). The very advanced diagenetic alterations preclude microstructural study of the specimen discussed. A narrow, irregular 'middle dark line' (Text-fig. 9N), seen in the best preserved major septum, is the only feature observed.

The morphology of the second specimen (Text-figs 8O, P; 9O) is similar to that of the mature morphology of the previously described corallite. Unfortunately, the lack of its early growth stage precludes its detailed description.

DISCUSSION: The more complete specimen described above displays a mixture of characters considered diagnostic for two genera. In its early growth stage it displays characters typical of *Ostravaia*, whereas its mature growth stage is closely comparable to the genus *Axisvacuus* Fedorowski, 2009. Some specimens of the latter genus, described from the Early Bashkirian strata of the Donets Basin, developed rudimentary structures similar to a circulotheca (Fedorowski 2009b, figs 11B$_1$; 12A$_{2,4}$, B$_2$; 13A$_4$, B$_2$). Thus, a link between ?*Ostravaia* sp. 2 and *Axisvacuus* is possible, but cannot be confirmed based upon so few specimens.

OCCURRENCE: B1069, Koukolná Village, borehole NP 720, depth 1200 m. B10714, Town of Karviná, ČSA mine, borehole D-11, depth 278.3 m. Both from Ostrava Formation, Gaebler Marine Horizon, E$_2$b biozone, Upper Serpukhovian.

Family *Incertae sedis*
Subfamily Variaxoninae subfam. nov.
Genus *Variaxon* gen. nov.

TYPE SPECIES: *Fasciculophyllum repressum* Schindewolf, 1952

DERIVATION OF NAME: Named after the inconsistent axial structure which is composed of various septal lamellae.

SPECIES INCLUDED: *Fasciculophyllum repressum* Schindewolf, 1952; *Variaxon radians* sp.nov.

DIAGNOSIS: Solitary, non-dissepimented. Early growth stage rotiphylloid. Cardinal protoseptum shortened at maturity. Cardinal fossula present; commonly inconspicuous. Minor septa free. Axial structure compact, derived from united septal lamellae of various major septa with neither of protosepta dominating. Tabularium uniform. Microstructure of septa finely trabecular.

DISCUSSION: The application of the generic name *Fasciculophyllum* Thomson, 1883 to Carboniferous rugose corals was discussed earlier by Weyer (1974, 1975, 1982) and Fedorowski (1987, 2004), and does not require repetition in this paper. Weyer (1977, pp. 463, 464) not only rejected application of that name to corals described by Schindewolf (1952), but also transferred '*F.*' *repressum* to *Lophophyllidium* (with the question mark) and proposed a phylogenetic lineage for some of them, leading from *Rotiphyllum* through *Claviphylum* and *Stereostylus* to *Lophophyllidium*. His rejection of Schindewolf's identification is reasonable, but his phylogenetic reconstruction requires comment. The lineage proposed by Weyer (1977) groups together taxa possessing: (a) minor septa either free or contratingent, (b) a tabularium either normal or biform, (c) a cardinal protoseptum shortened either early in the ontogeny or permanently long and intersecting the cardinal fossula in calices, and (d) either possessing a pseudocolumella derived from the counter protoseptum and expanded highly above the calice floor (as in *Lophophyllidium* Grabau, 1928), or an elongated counter septum which does not expand upwards (as in *Claviphyllum eruca*

(McCoy, 1849); '*Claviphyllum*' *hillae*, Hudson and Fox, 1943; *Antiphyllum inopinatum* Schindewolf, 1952 and *Monophyllum sokolovi* Fomichev, 1953). Such mixed characteristics cannot form a monophyletic lineage. In addition, *Claviphyllum* needs revision as two distant morphotypes are grouped together in this genus. One, represented by the type species *Claviphyllum eruca*, possesses contratingent minor septa and a biform tabularium and the second one, represented by *Claviphyllum hillae* and *Antiphyllum inopinatum*, possesses minor septa short and free and the tabularium normal. Revision by Weyer (1974) has shown the error by Schindewolf (1952), who recognized the counter protoseptum in *Antiphyllum inopinatum* as the cardinal. The re-orientation of the corallite and the re-study of the early growth stage of that specimen, allowed Weyer (1974, p. 350) to synonymize *Antiphyllum* with *Claviphyllum*. He changed the latter opinion in the informal way, by using the name *Antiphyllum inopinatum* and including in that genus two other species, originally described by Schindewolf (1952) as *Claviphyllum* (see Weyer 2005, p. 8). That option is accepted in the present paper. It means, however, that differences between *C. eruca* on the one hand and '*C.*' *hillae/A. inopinatum* on the other are perhaps adequate for including those species in different families. Thus, Weyer's (1977) phylogenetic reconstruction is not accepted. However, several of his suggestions (pp. 463, 464) concerning '*Fasciculophyllum*' *repressum* are certainly correct and important. These are: "the counter septum is rather short and does not provide the columellar foundation…", and "…the holotype possessing a prominent axial boss similar to that visible in a conspecific specimen figured by Matl (1971, pl. 1, fig. 1)". Also, his statement: "enough information might be present to define a new genus" is certainly correct and the new name *Variaxon* gen. nov. is introduced here for '*Fasciculophyllum*' *repressum* and related corals.

The mixed characters observed in *Variaxon* both during its early ontogeny and mature growth stage make the family status of that new genus uncertain. The early ontogeny resembles *Rotiphyllum*, but that kind of morphology is common to many taxonomically distant taxa and cannot be considered adequate for their grouping together. The axial structure present in the specimens discussed precludes a close relationship to *Rotiphyllum* and to the Family Antiphyllidae Ilina, 1970, although *Rotiphyllum* may have been a distant ancestor of *Variaxon*.

The axial structure points to the Family Lophophyllidae Grabau, 1928 or Lophophylidiidae Moore and Jeffords, 1945. Those two may be synonyms as postulated by Fedorowski (2004, pp. 89–91). However, in the above family (or families) the axial structure is in-

variably derived from the counter protoseptum. It forms the monoseptal pseudocolumella in species traditionally included in *Stereostylus* Jeffords, 1947, synonymized by Fedorowski (1974) with *Lophophyllidium*, but its morphology varies considerably in many species (Fedorowski 1974; Webb 1984). Most lophophyllidia incorporate some septal lamellae in the pseudocolumella to make it complex (Jeffords 1942, 1947; Moore and Jeffords 1945; Schindewolf 1952; Fedorowski 1974, 1987; Webb 1984). That sequence ends with the complex pseudocolumella of *Pseudowannerophyllum* Flügel, 1975 (Flügel 1975; Fedorowski 1987). Besides, *Lophophyllidium* and *Pseudowannerophyllum*, i.e., genera morphologically closest to *Variaxon,* possess a cardinal protoseptum shortened early in the ontogeny, a cardinal fossula distinct and triangular in the maturity (in the former), and a biform tabularium (in the latter). All those differences taken together, exclude *Variaxon* from the family (or families) discussed.

The Family Wannerophyllidae Fedorowski, 1986, which possesses a strong axial structure, is the only other family, looking apparently appropriate for hosting *Variaxon*. However, a calophyllid early growth stage with four septa dominating (Fedorowski 1986, text-figs 4:1a, 2a,b; 5:4), a different morphology of the axial structure, and its different derivation preclude any relationship between *Wannerophyllum* Schouppé and Stacul, 1955 and *Variaxon*. Different ages and geographic occurrences of both groups of corals (Middle Permian of Timor Island *vs* Upper Serpukhovian of Europe) are supplementary reasons for their distinction at the family level.

The preceding discussion has shown that *Variaxon* is isolated at the family level. However, only a separate new subfamily is here proposed for that genus as a safer solution than the introduction of a new family. Derivation of that genus from *Rotiphyllum*-like genera, if firmly documented, would point to the Family Antiphyllidae. The subfamily level for taxa possessing an axial boss as opposed to those having a more or less clearly elongated counter protoseptum, which is not elevated axially, would in such a case be necessary. A similar solution, i.e., inclusion of *Variaxon* in the Lophophyllidae (or Lophophyllidiidae) would be possible if a different derivation and the inner morphology of the axial structure is proven less important than the characters in common. However, distinction of *Variaxon* at the subfamily level would remain necessary. Elevation to a separate family level is the third option possible when more genera related to *Variaxon* are introduced.

<div align="center">

Variaxon repressus (Schindewolf, 1952)
(Text-figs 10–13)

</div>

1952. *Fasciculophyllum repressum* Schindewolf, p. 185, text-fig. 12a–c

1971. *Claviphyllum pauperculum* Schindewolf; Matl, pl. 1, fig. 1.

non 1977. *Lophophyllidium* ? *repressum* (Schindewolf, 1952); Weyer, pl. 2, figs 4–13.

2001. ? *Rotiphyllum repressum* (Schindewolf, 1952); Fedorowski, p. 102, pl. 30, fig. 3.

MATERIAL: The holotype X-3652 consists of a small fragment of the longitudinally cut calice and three thin sections made from the immature part of the corallite. Judging from differences in size and morphology between the calice and the ontogenetically early corallite growth, the mature growth stage of the holotype is missing. This is, to some extent, confirmed by the almost complete corallite B-8857 from the Czech Republic collection. The specimen B-8799 from that collection is restricted to the calice. Eleven thin sections and five peels representing both B-8857 and B-8799 were available for study in addition to those taken from the holotype. Also, all ground surfaces were studied and some photographed.

EMENDED DIAGNOSIS: *Variaxon* with 22–24 major septa and 12.0–13. 0 mm corallite diameter near calice margin; major septa at pre-mature growth stage irregularly differentiated in length with longest meeting at corallite axis, radially arranged and shortened at maturity; axial structure at maturity composed of middle lens-like body, surrounded by several thick septal lamellae; short minor septa appear late in ontogeny.

DESCRIPTION OF THE HOLOTYPE: In the ontogenetically earliest growth stage preserved at a diameter of 4.5 mm, there are 20 major septa. The attachment flattening (Text-fig. 10A, E right) documents both the lateral attachment of the larva and the strong attachment by the polyp. The protosepta approach the corallite axis, but their "middle dark lines" do not touch. The remaining major septa form four distinct bunches corresponding to the quadrants. However, in contrast to the regular zaphrentoid arrangement of major septa, the middle or one before the last inserted major septa are the longest in particular quadrants. These septa meet at the corallite axis with a weak sclerenchyme secreted between them. The alar septa do not dominate in the cardinal quadrants, being shorter than the longest major septa in those quadrants. Neither the cardinal nor the counter protoseptum extend as far axially as the longest major septa and their inner margins are isolated from each other by those long septa (Text-fig. 10I). Thus, none of them can be considered as providing fragments in the axial structure. Minor septa are absent from the moderately thickened external wall, but their furrows occur between neighbouring major septa in the best preserved corallite surface (Text-fig. 10A, E lower left). The parallel-walled cardinal fossula is well developed. The number of tabulae, larger than in adjacent septal loculi, indicate the occurrence of true, i.e., tabular alar fossulae.

The morphology of the next growth stage (Text-fig. 10B, F) resembles that of the previously described one in general, but differs in several details. The protosepta remain long, but are clearly isolated from each other by the thick inner margin of the middle major septum of the left cardinal quadrant that extends beyond the corallite axis and meets major septa of the right counter quadrant (Text-fig. 10J). The arrangement of major septa and the morphology of the cardinal fossula remain similar to the earlier growth stage. However, not only the right alar fossula, but even the pseudofossula, disappear. Minor septa remain absent from the thick external wall.

The axial part of the corallite undergoes the most substantial changes. A curved bar appears in the corallite axis (Text-fig. 10J), positioned perpendicular to the protosepta. Its derivation is not clear, but it certainly was not derived from any of the protosepta. Two other bars, septal in microstructure, also appear. One of them corresponds to the cardinal protoseptum in its position (Text-fig. 10J, horizontal arrow) and may have been derived from it. The other one is perpendicular to that protoseptum, approaching its inner margin (Text-fig. 10J, vertical arrow). A thin layer of sclerenchyme supplements the inner margins of the major septa and the septal bars that constitute the ephemeral axial structure.

The ontogenetically most advanced growth stage represented by a thin section, was cut mostly above the calice floor at the periphery (Text-fig. 10C [dark], 10G [shadowed]) and beneath it in the middle part (Text-fig. 10C, G, white). The attachment flattening continued, demonstrating a demand of the corallite for a strong attachment and confirming its orientation. Such a confirmation is useful because the cardinal fossula and alar fossulae or pseudofossulae disappear and a false pseudofossula appears in the left counter quadrant. The slightly shortened cardinal protoseptum terminates within the thick tabula. The counter protoseptum meets the lateral side of the fourth inserted major septum of the right counter quadrant (Text-fig. 10C, G, K). That strongly elongated, rhopaloid major septum extends beyond the corallite axis, imitating the counter protoseptum of a simplified *Lophophyllidium* and replacing in its dominant role the major septum of the left cardinal quadrant, described above. The counter protoseptum and a few of the longest major septa from all quadrants meet or approach that dominating major septum, to
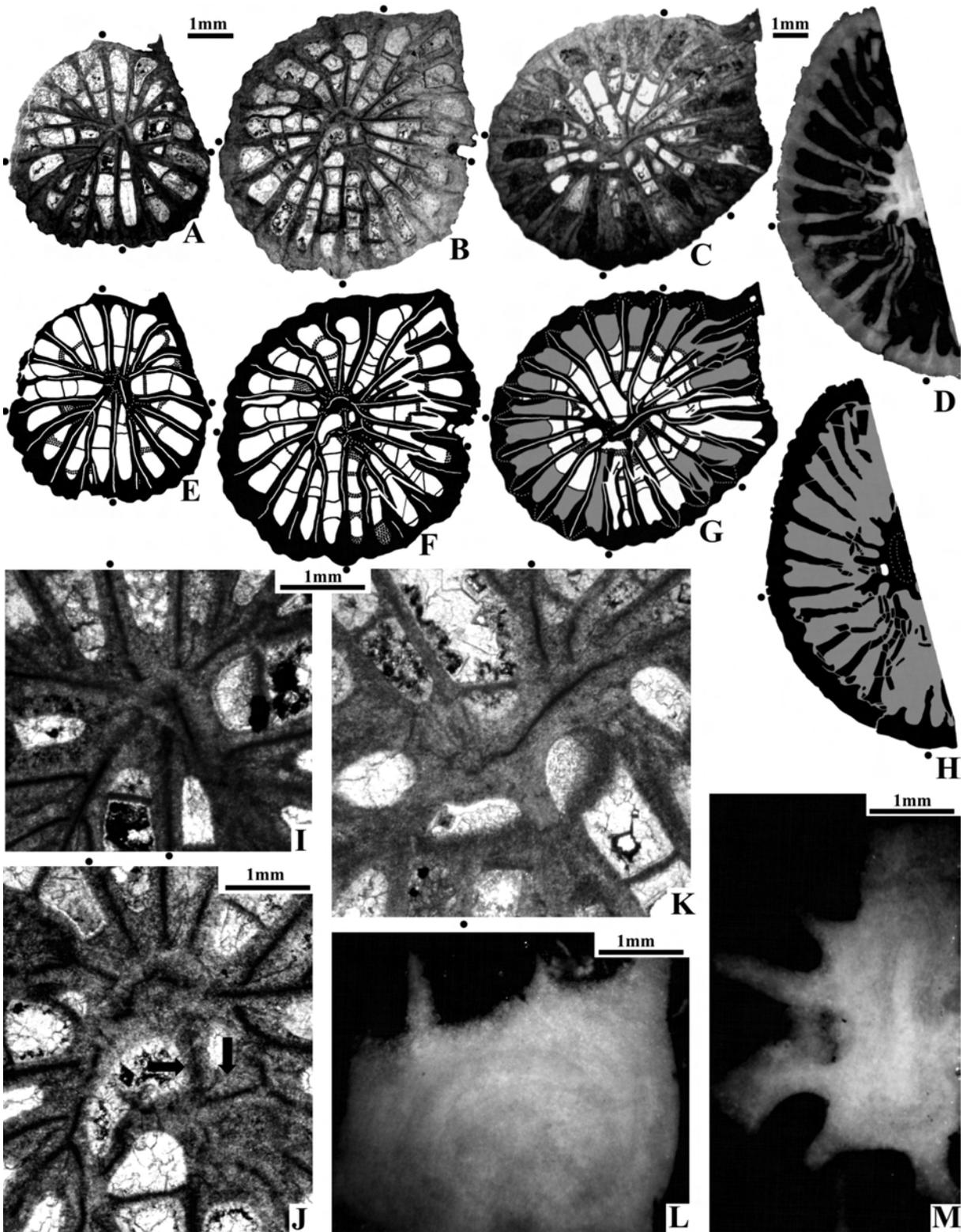
Text-fig. 10. *Variaxon repressus* (Schindewolf, 1952). Holotype, X-3652. A, E – late neanic growth stage, B, F – late neanic or early mature growth stage, C, G – early mature growth stage, D, H – Lower part of calice, I-K – axial parts of figures A-C enlarged to demonstrate isolation of proto-septa from axial extension of one of major septa, L – longitudinal section of axial structure, M – transverse section of axial structure showing lens-like axial body and septal lamellae. See *Note* following description of Text-figure 2 for further explanations

form an axial structure that is simpler than that of the preceding growth stage. Both counter-lateral septa are distinctly shorter in this growth stage than the next major septa inserted, whereas the alar septa are hardly distinguishable from the adjacent major septa (Text-fig. 10C, G). Short knobs of minor septa appear between major septa at the inner surface of the external wall.

In summary: 1. The protosepta do not dominate. However, they are not clearly shortened during the growth stage described although a slight shortening of the cardinal protoseptum is obvious. 2. The counter protoseptum is better developed than the cardinal protoseptum, but it does not produce any component of the axial structure. 3. The arrangement of septa in all quad-
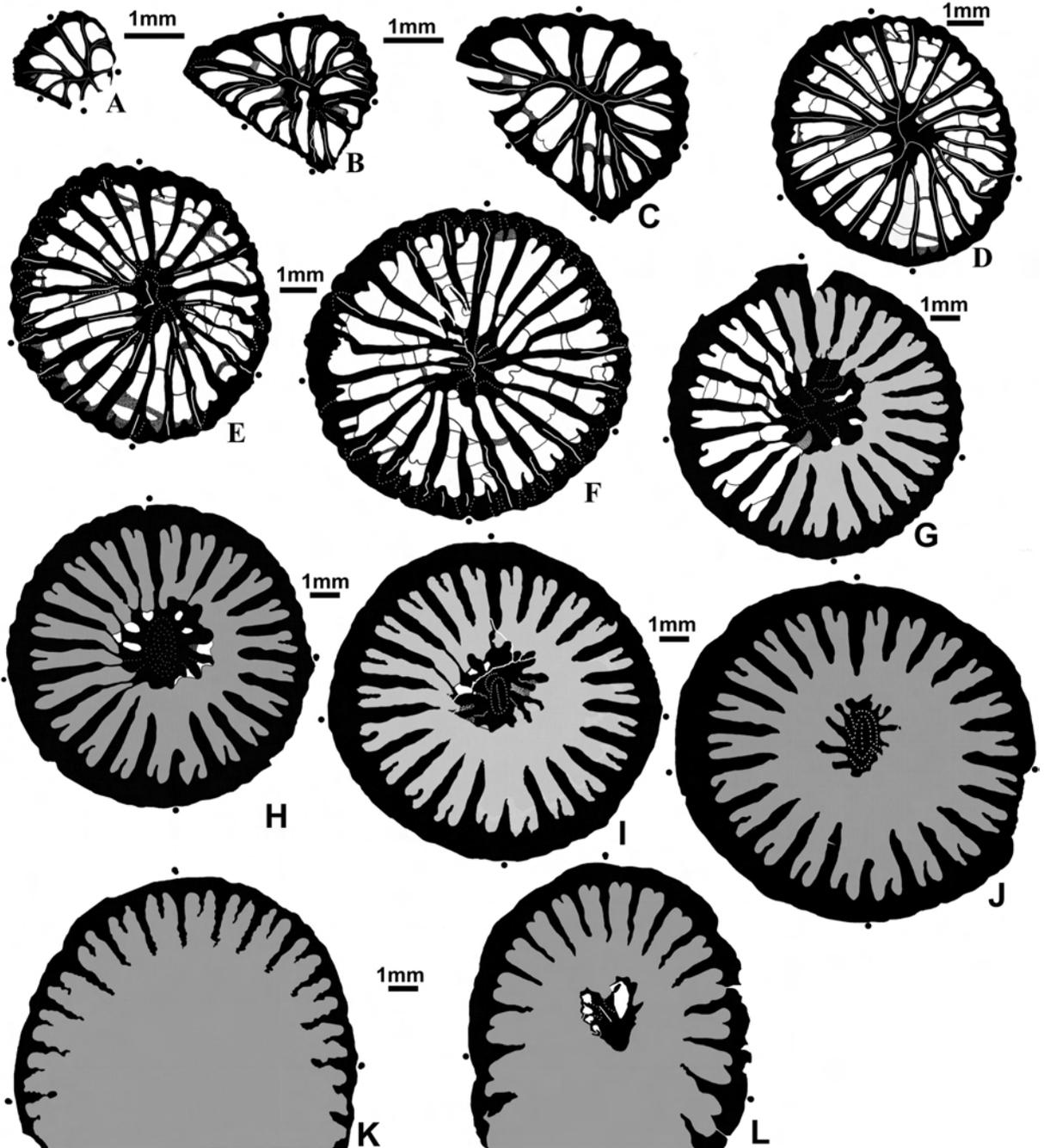
Text-fig. 11. A-K - *Variaxon repressus* (Schindewolf, 1952). B-8857. A-C – neanic growth stage (= Text-fig. 11D, E, G), D-F – early mature growth stage (E, F = Text-fig. 12I, L), G-J – mature growth stage; morphology exposed by subsequent sections of calice (= Text-fig. 13 A, D, E, G), K – upper part of calice. L – B-8799. Upper fragment of axial structure in calice. See *Note* following description of Text-figure 2 for further explanations

rants changes during the course of growth, but the middle septa in all quadrants are almost invariably the longest. 4. The counter-lateral septa are underdeveloped near the calice floor.

The reminder of the calice provides important data on the morphology of the axial structure (Text-fig. 10D, H, L, M). Previously Weyer (1977, p. 464) drew attention to the high extension of the axial structure above the cal-
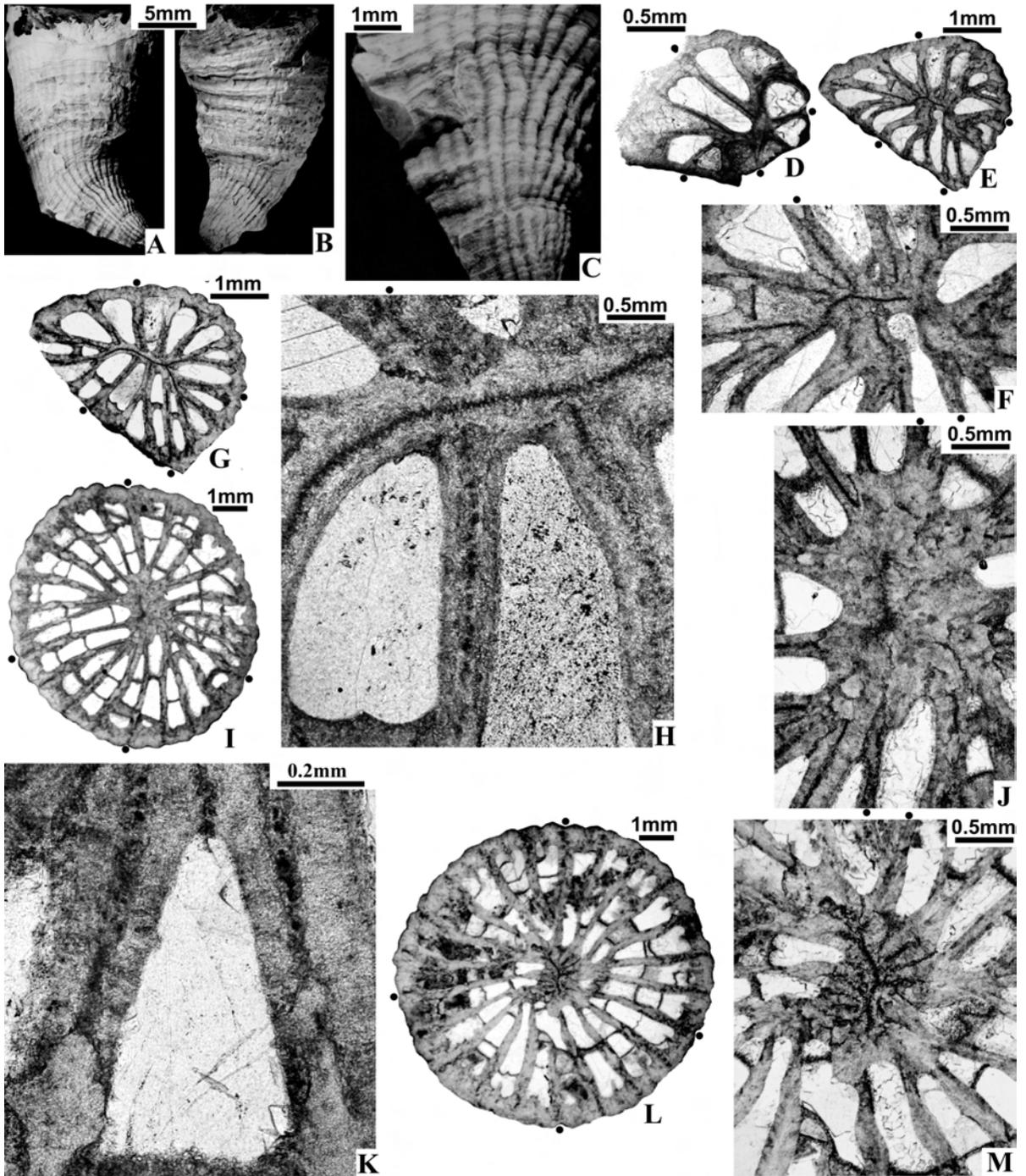
Text-fig. 12. *Variaxon repressus* (Schindewolf, 1952). B-8857. D, E, G – neanic growth stage (= Text-fig. 11A-C), F-H – middle parts of E and G enlarged to document separation of protosepta from septal body situated perpendicular to them; H documents remnants of fine trabeculae in left major septum, I, L– early mature growth stage (= Text-fig. 11E, F), J, M – middle parts of I and L enlarged to demonstrate formation of axial structure independent from protosepta, K – various advancement of diagenetic alterations of septal microstructure; total destruction in lower part of left septum and remnants of trabeculae in its upper part. See *Note* following description of Text-figure 2 for further explanations

ice floor and its separation from the major septa. Both of those characters are absent from *Fasciculophyllum*, but are typical for *Lophophyllidium* in which Weyer (1977, p. 463) conditionally placed '*F.*' *repressum*. He also considered the specimen illustrated by Matl (1971, pl. 1, fig. 1) conspecific with the latter species, an idea followed here. High magnification of the inner morphology of the holotype (Text-fig. 10L, M) shows an axial lens-like body with septal lamellae arranged around it, exactly the same way as in the almost complete corallite B-8857. This corallite, therefore, is included in *V. repressum* and data derived from it are considered complementary to those missing from the holotype.

SUPPLEMENTARY DESCRIPTION: The almost complete corallite B-8857 confirms the rotiphylloid early ontogeny of *V. repressum* and lack of connection of the axial structure to the protosepta in that species (Text-figs 11A–C; 12D, E, G). This is most obvious when the continuous 'middle dark line' (= united primary major septa), is observed at a higher magnification (Text-fig. 12F, H). It extends perpendicular to the cardinal-counter protosepta, the inner margins of which reach the sclerenchymal cover, but not those 'middle dark lines' (=primary septa). Such an arrangement proves the isolation of the protosepta from each other, and lack of their influence on the formation of the axial structure.

At a later growth stage (Text-figs 11D–F; 12I, L) the morphology differs from both that of the preceding development and that at the calice floor. It is similar to the comparable growth stage of the holotype in major characteristics, but differs in the better development of the axial structure. The long median lamella, probably derived from the axial part of the formerly united major septa, becomes re-oriented. It is not oriented perpendicularly as before, but obliquely to the cardinal-counter protosepta plan (Text-fig. 12J, M), remaining isolated from both of them. In contrast to the holotype, none of the major septa dominates at that growth stage, but the inner margins of several major septa approach the median lamella first (Text-fig. 12J) and later form septal lamellae (Text-fig. 12M). Such a morphology is more advanced than that exposed in the highest thin section of the holotype (Text-fig. 10C, G) in spite of the latter being cut partially above the calice floor. Nevertheless, the described growth stage of the holotype (Text-fig. 10B, C, F, G) and specimen B-8857 (Text-figs 11E, F; 12I, L) are considered early mature since they differ more from the neanic growth stage than from that exposed by the sections of calices. Besides, the number of major septa becomes constant since the growth stage discussed. Other differences between the holotype and the specimen B-8857 include better developed minor septa in the latter specimen, with some elongated slightly into the corallite lumen, a cardinal fossula hardly recognizable at this growth stage in B-8557, and the cardinal protoseptum more clearly shortened than in the holotype.

The complete mature characteristics are demonstrated only by the calicular sections of both specimens. Unfortunately, the incompleteness of the holotype precludes their close comparison. Thus, specimen B-8857 is described in detail, with reference to the holotype whenever possible. Shortening of the cardinal protoseptum is obvious in both corallites (Text-figs 10D, H,; 11G–J; 13A, D, E, G). However, a slightly longer-lasting connection of the counter protoseptum to its lamella than other septal lamellae to other major septa, and its slight elongation remaining up to the upper part of the calice (Text-fig. 11J; 13G), is recognized only in corallite B-8857. Also, the inner morphology of the axial structure in the lower part of the calice, composed solely of thick, irregular septal lamellae with a median lamella absent (Text-fig. 13B, C), is recognizable only in that specimen. This may have resulted from the incompleteness of the holotype. The lens-like body, located in the cardinal-counter protosepta plan, appeared higher in the calice and occurs in both specimens (Text-figs 10M; 13F–H). However, its development independent from both protosepta is better demonstrated in specimen B-8857. Concentric growth lines of that body isolate it clearly from septal lamellae (Text-fig. 13H).

An occurrence of the lens-like axial body is also recognized in the axial structure of the incomplete specimen (Text-fig. 10L) included in *V. repressum*. Thus, it should be considered as a constant, diagnostic character of that species. The microstructure of the lens-like axial body seems to be not trabecular, but fibro-lamellar and comparable to that in the genus *Cyathaxonia* Michelin, 1846. Such an axial structure as described would be different from all axial structures known in rugose corals so far, when confirmed by the study of more numerous and better preserved corallites.

The sculpture of the external surface of specimen B-8857, observed along almost the entire corallite except for the lost tip, is differentiated. Septal furrows are deeper in the early parts than in the most advanced stages (Text-fig. 12A, B), whereas the growth striae and the irregularly spaced growth bands are more pronounced during later growth. A closer view of the alar septal side of the corallite (Text-fig. 12C) shows an increase in the number of alternating major and minor septa towards that septum.

The microstructure of septa, demonstrated in the early growth stage of specimen B-8857 (Text-fig. 12H,

K) is much better preserved in some fragments than in the holotype, allowing documentation of a single, continuous row of fine trabeculae (Text-fig. 12H, left major septum). It also illustrates differences in the degree of diagenesis possible not only in adjacent major septa (Text-fig. 12H), but also within the same septum. In the left major septum shown in the Text-figure 12K (lower), a large crystalline body has replaced both the primary
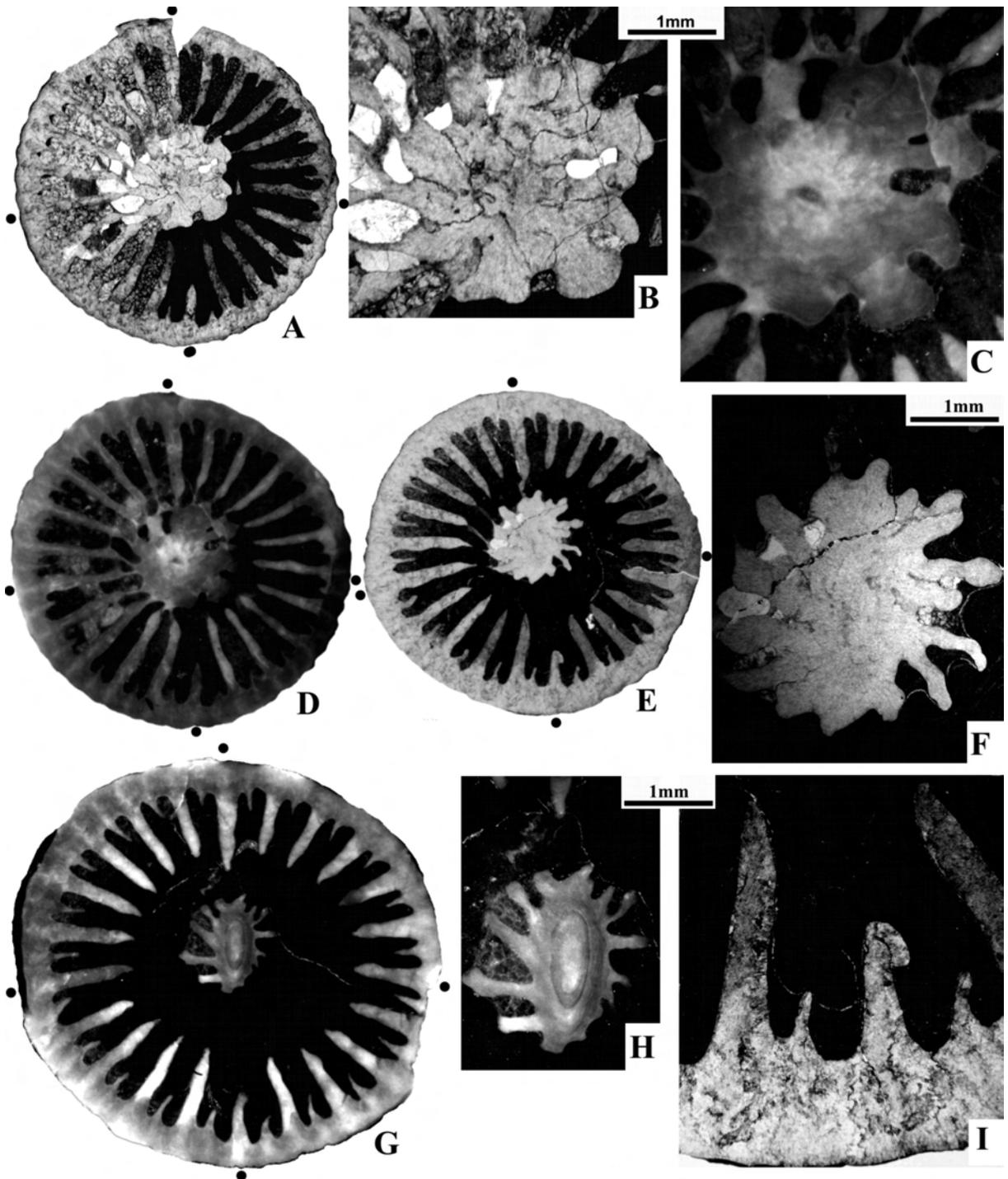
Text-fig. 13. *Variaxon repressus* (Schindewolf, 1952). B-8857. A, D, E, G - – mature growth stage; morphology exposed by subsequent sections of calice (= Text-fig. 11G-J), B, C, F, H – middle parts of figs A, D, E, G enlarged to document morphology of axial structure, I – strong diagenetic alterations of septa and external wall in high part of calice. See *Note* following description of Text-figure 2 for further explanations

septum and its sclerenchymal sheets. Immediately above that crystalline body, there is a continuous row of irregular bunches of fibrils of the primary septum, surrounded by differently arranged fibrils of altered sclerenchymal sheets (middle in the picture). That middle part of the major septum passes into a still less altered inner part, in which separate trabeculae remain. This part of the major septum is closely comparable to the left major septum shown in Text-fig. 12H. The microstructure and diagenetic alterations of septa illustrated in the Text-fig. 12H, K demonstrate the various degree of that alteration occurring next to each other in the same corallite and a possibility of microstructural reconstructions supported by comparatively weak data derived from the altered septa.

OCCURRENCE: The holotype X-3652, Szczęście Luizy (Louisenglück in German) coal mine, former Rożdzień Village, actually part of the town of Katowice (= Gutter Traugutt near Rosdzin, after Schindewolf 1952), Gaebler Marine Horizon, E_2b biozone, Upper Serpukhovian; B-8799, Dolni Sucha, Dukla Mine, borehole Nr.33; B-8857, locality as above, borehole D-32. Stratigraphic positions of both as for the holotype.

Variaxon radians sp. nov.
(Text-figs 14–17)

1977. *Lophophyllidium ? repressum* (Schindewolf 1952); Weyer, pl. 2, figs 4–13.

HOLOTYPE: Specimen B-12884 from which four thin sections and eleven peels were prepared.

TYPE LOCALITY: Dolni Suchá Village, Dukla mine, borehole D2182, depth 35.4 m.

TYPE HORIZON: Ostrava Formation, Gaebler Marine Horizon, E_2b biozone, Upper Serpukhovian.

ETYMOLOGY: Named after radially arranged sparse septal lamelle in axial structure.

MATERIAL: Five specimens, the holotype B-12884 and four paratypes B-496, B-6230, B-6821, B-9379. Most specimens nearly complete, but all crushed to some extent by compaction. Seventeen thin sections and twenty five peels were available for study.

DIAGNOSIS: *Variaxon* with 21–22 major septa at 7.0–8.0 mm corallite diameter near and just above calice floor; major septa connected to axial boss up to middle part of calice; axial structure consists exclusively of very few septal lamellae; minor septa very short.

DESCRIPTION OF THE HOLOTYPE: The external wall bears distinct septal furrows of major and minor septa but not the 'hyposepta'. The strong attachment of the corallite to the substrate (Text-fig. 15A) has deformed its morphology at an early growth stage (Text-figs 14A–G; 15B–D). Deformation resulted in: a) thinning of the sclerenchyme in the corallite axis so that it resembles a circulotheca (Text-figs 14 D, E; 15C), b) strange arrangement of 'middle dark lines (= primary septa) (Text-figs 14E; 15C), and c) irregular arrangement and thickness of major septa near the end of the early neanic growth stage (Text-figs. 14F, G; 15D). Nevertheless, the increase in major septa is rather regular. The diameter is extremely small during the entire early neanic growth stage.

At a diameter of 0.8 mm the septa consist of the axial protoseptum and the counter-lateral septa (Text-figs 14A; 15B). The alar septa appear next, followed by a pair of major septa in the cardinal quadrants (Text-fig. 14B–E). The strange arrangement of primary septa in the latter growth stage is mentioned above. The first major septa in the counter quadrants, other than the counter-lateral septa, appear only at the end of the early neanic growth stage (Text-figs 14G; 15D).

In the late neanic growth stage (Text-figs 14H; 15E), the deep cardinal fossula is intersected by the long cardinal protoseptum that reaches its inner margin beyond the corallite axis. The counter protoseptum equals the counter-lateral septa in length and thickness. Those three septa, and another three in each counter quadrant, form an arch ending at the alar pseudofossulae. The alar septa are the longest major septa in cardinal quadrants in each of which there are three major septa. The increase of major septa in the counter quadrants during the late neanic growth stage was rapid. In contrast to the earliest growth stages, the major septa become more numerous in the counter than in the cardinal quadrants after the late neanic growth stage and up to the calice (Text-figs 14 J–O; 15G, H, J, K).

The major septa in the cardinal quadrants were more affected by compaction than those in the counter quadrants, but their true length in the mature growth stage and up to the calice floor (Text-figs14J–L; 15G, H) is shorter than those of the counter quadrants. That change in length started in the intermediate late neanic/early mature growth stage when the cardinal protoseptum becomes slightly shortened (Text-fig. 14I; 15F), remaining as such up to the middle part of the calice (Text-figs. 14O; 15K). The counter protoseptum becomes slightly longer than the counter-lateral septa in the early mature
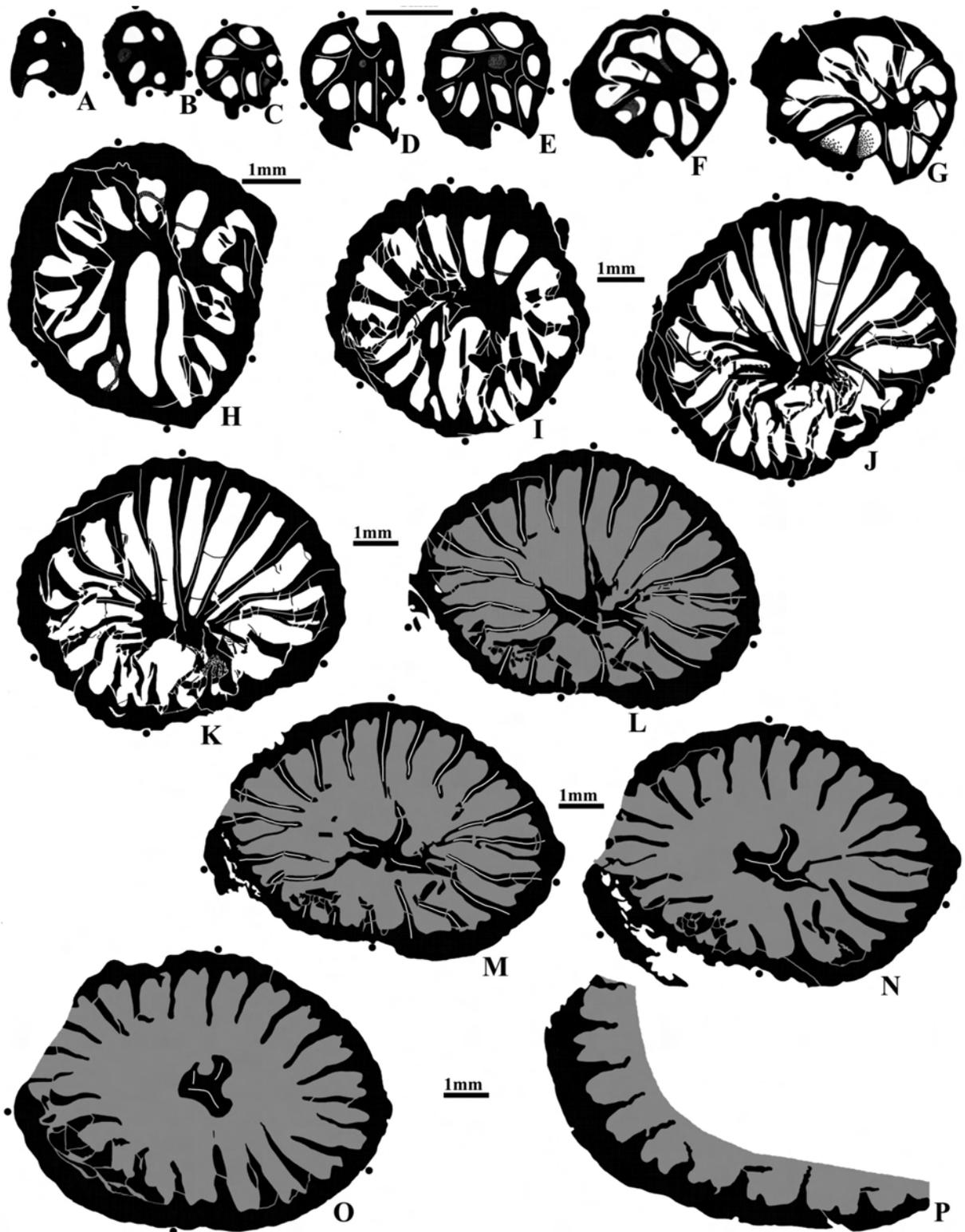
Text-fig. 14. *Variaxon radians* sp. nov. B-12884. Holotype. A-G – early to late neanic growth stage deformed by strong corallite's attachment (A, D, G = Text-fig. 15B-D), H-I – late neanic/early mature growth stage (= Text-fig. 15E, F; polished surfaces), J-K – early mature growth stage(J = Text-fig. 15G; K – polished surface), L-O – mature growth stage; successive sections through calice (N, O = Text-fig. 15 J, K; peels), P – fragment of calice's marginal part (peel). See *Note* following description of Text-figure 2 for further explanations
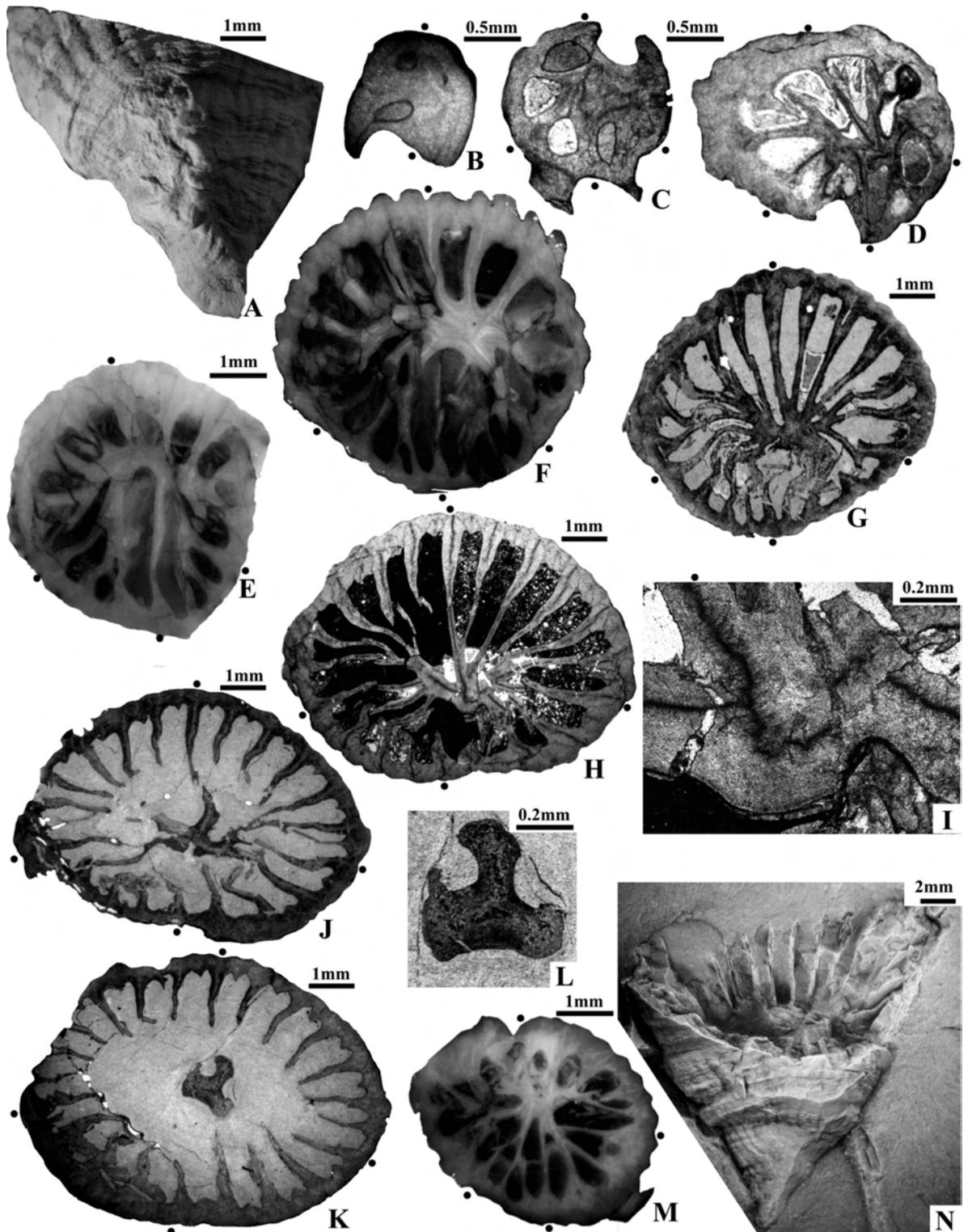
Text-fig. 15. *Variaxon radians* sp. nov. B-12884. Holotype. A – side view of corallite's early growth stage, B-D – early to late neanic growth stage deformed by strong attachment (= Text-fig. 14A, D, G), E-F – late neanic/early mature growth stage (= Text-fig. 14H, I; polished surfaces), G-H – early mature growth stage(G = Text-fig. 15J), I – middle part of H enlarged to demonstrate mutual relationships of primary septa in corallite axis, J-K – mature growth stage; successive sections through calice (= Text-fig. 14 N, O; peels), L – axial structure of K enlarged to document mutual relationships of 'middle dark lines' in septal lamellae (peel). B- 496. Paratype. M – late neanic growth stage, N – external view; upper part flattened making width of calice artificial. See *Note* following description of Text-figure 2 for further explanations

growth stage (Text-fig. 14J; 15G) and is temporarily dominant near the calice floor (Text-fig. 14K; 15H, I). The morphology at this growth stage most closely resembles that of the *Stereostylus*-like *Lophophyllidium.*

In the early mature growth stage most major septa, except for the last inserted ones, of all quadrants meet near the corallite axis (Text-figs 14J, K; 15G, H). The middle major septa of the right cardinal and the left counter quadrants become thickened in their periaxial parts and meet the thickened inner margin of the long counter protoseptum (Text-fig. 15H, I). Thus, the counter protoseptum participated in formation of the axial structure. Higher in the calice (Text-figs 14L–N; 15J), two elongated major septa, arranged almost perpendicular to the thickened inner margin of the counter protoseptum, are the sources for two septal lamellae, constituting the axial structure together with the septal lamella derived from the counter protoseptum. The middle dark lines of the lamellae of those two major septa become eventually united and form the single
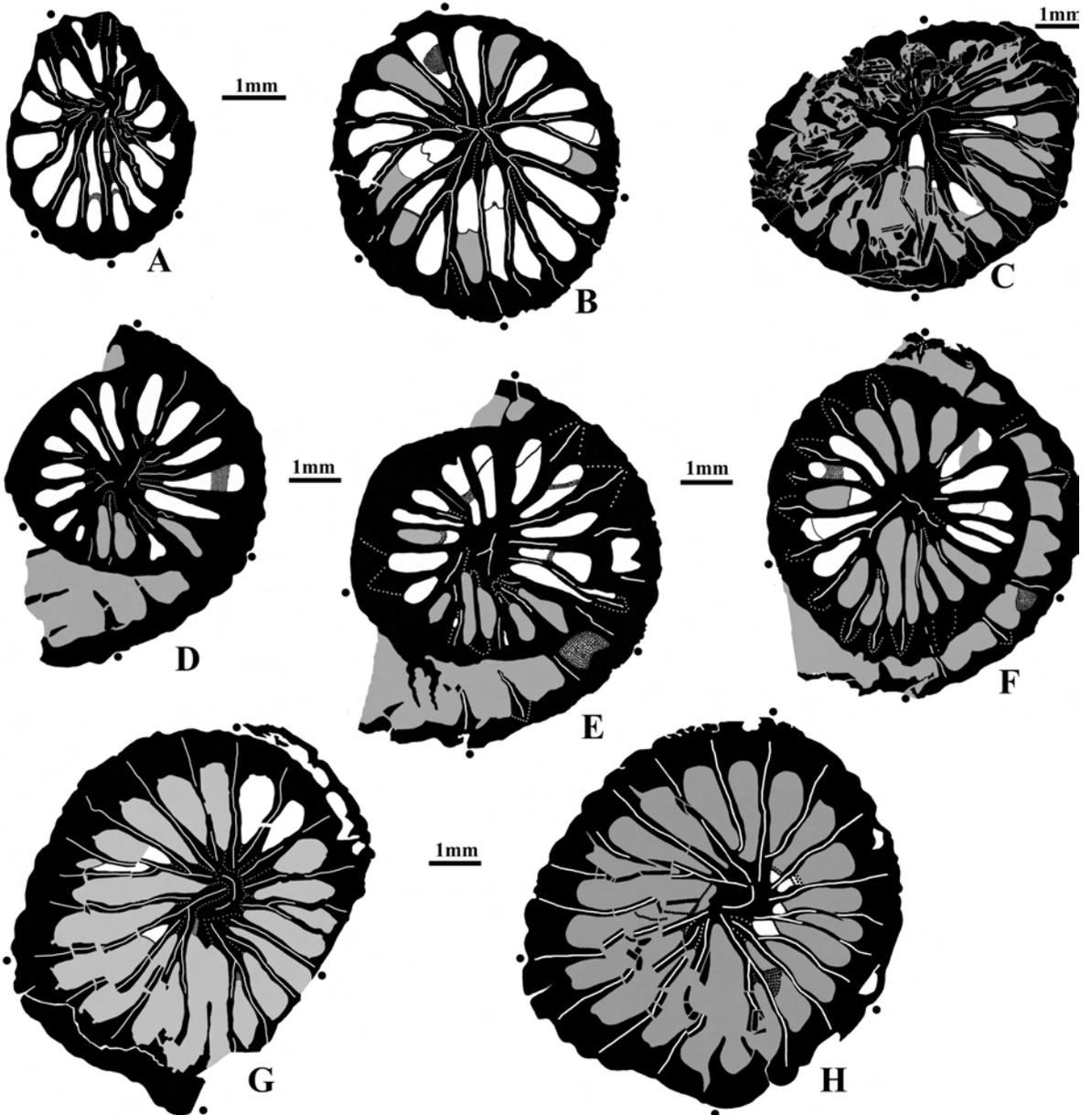
Text-fig. 16. *Variaxon radians* sp. nov. A-C, B-6281. Paratype. A – neanic growth stage, B – late neanic growth stage, C – early? mature growth stage; axial part cut above calice floor (A-C = Text-fig. 17J-L). D-H – B-6230. Paratype. D-F – rejuvenating corallite; perhaps late neanic/ early mature growth stage, (=Text-fig. 17 A, B, E), G-H – early(?) mature growth stage (=Text-fig. 17F, H). *Note*. Uppermost scale bar concerns all drawings in uppermost row. See also *Note* following description of Text-figure 2 for further explanations

lamella oriented perpendicular to the lamella derived from the counter protoseptum (Text-fig. 15K, L). Thus, the free axial structure was derived from the inner margins of three major septa, the counter protoseptum included, but not the latter lead in the final result of that process. Although the role of the counter protoseptum in the formation of the axial structure in *V. radians* is more important than in *V. repressus*, the arrangement of the septal lamellae and their derivation is comparable to the early mature growth stage of the latter. It differs from the derivation of the pseudocolumella in *Lophophyllidium* Grabau, 1928 and *Lophophyllum* Milne Edwards and Haime, 1851 (Schindewolf 1952; Lecompte 1955; Fedorowski 1974, 1990; Webb 1984). In those genera the leading role of the counter protoseptum in the formation of the pseudocolumella is obvious irrespective of the part of a corallite sectioned and complexity of that structure, whereas that protoseptum lead for only a short early mature period of growth in *V. radians*.

The minor septa are distinguishable in the external wall near the counter protoseptum and the counter-lateral septa after the late neanic/early mature growth stage. They appear in the wall developing progressively towards the cardinal protoseptum (Text-figs 14J–L; 15G, H, J), but appear in all septal loculi only in the lower part of the calice (Text-figs. 14L; 15H). They are short and wedge-shaped up to the upper part of the calice (Text-fig. 14P).

INTRASPECIFIC VARIABILITY: The advanced mature growth parts of all the paratypes are crushed (e.g. Text-fig. 17M), precluding detailed study of formation of the axial structure. However, fragmentary data allow a comparison to the holotype in its main features, i.e. the absence of an axial lens-like body and the position of a median lamella, if separated from inner margins of major septa (Text-fig. 17A–H) or an elongated major septum (Text-fig. 17L). Both those bodies are oriented obliquely and/or almost perpendicular to the protosepta in the early mature growth stage of the paratypes. The subordinated role of the protosepta in formation of the axial structure, is better accentuated in the paratypes than in the holotype. None of them possesses the counter pro-

toseptum elongated so much, as observed in the early mature growth stage of the holotype.

The earliest growth stages are absent from the paratypes. Their advanced neanic growth stage (e.g. Text-figs 15M; 16A, B; 17J, K) closely resembles that in the holotype in both the arrangement of the major septa, the length of the cardinal protoseptum that intersects the distinct cardinal fossula, a slight acceleration of major septa in the counter quadrants, and the lack of minor septa in the corallite walls. That similarity continues into the early mature growth stage. Thus, this species is rather uniform in both morphology and the value of the number of septa to the corallite diameter. The larger appearing paratype (Text-fig. 15N) is flattened so its width is deceiving. It was illustrated to demonstrate the depth of the calice which reaches almost ½ the corallite length, the short septal blades in most of the calice, and the absence of minor septa in its lumen. The strong underdevelopment of minor septa seems to be the most important difference between all of the paratypes and the holotype.

One paratype (Text-figs 16D–G; 17A, B, E, F) rejuvenates, returning in its morphology to a deformed late neanic growth stage and later again reaching an early mature morphology. Formation of a strongly thickened but simple axial structure is a character of the rejuvenated part of that paratype, different from both the holotype and all other paratypes. 'Middle dark lines', i.e., remnants of primary septa in septal lamellae, are differently oriented in individual transverse thin sections of that specimen (Text-figs 16D–H; 17A–H), but they do not point directly to the protosepta at any growth stage investigated. In an earliest growth stage investigated the right counter-lateral septum points to the axial lamellae (Text-fig. 17A). The lamella corresponding to the left alar septum appears next (Text-fig. 17B, C). That orientation changes completely during the next 1.5mm of growth and the slightly wavy 'middle dark line' of that lamella points to the middle major septa in the right cardinal and the left counter quadrant (Text-fig. 17D, E). In the next step, the axial lamella arches over the inner margin of the strongly and temporarily elongated left alar septum (Text-fig. 17 F, G). In the ontogenetically most advanced growth stage observed (Text-fig. 16H; 17H)

Text-fig. 17. *Variaxon radians* sp. nov. A-I – B-6230. Paratype. A, B, E – rejuvenating corallite; perhaps late neanic/ early mature growth stage, (=Text-fig. 16D-F), C – middle part of B enlarged to demonstrate disconnection of 'middle dark lines' in thick axial structure and third 'line' pointing to left alar septum, D – middle part of E enlarged to demonstrate long, continuous 'middle dark line' located almost perpendicular to protosepta and short 'line' pointing towards cardinal fossula, F, H – early(?) mature growth stage (=Text-fig. 16G, H). G – middle part of F enlarged to show morphology of axial structure closely corresponding to comparable growth stage of holotype, I – diagenetically altered major septum with probable remnants of trabeculae in its upper part. J-M, B-6281. Paratype. J – neanic growth stage, K – late neanic growth stage, L – early? mature growth stage; axial part cut above calice floor (J-L = Text-fig. 16A-C), M – side view of corallite; crushed in fully mature growth stage. See *Note* following description of Text-figure 2 for further explanations
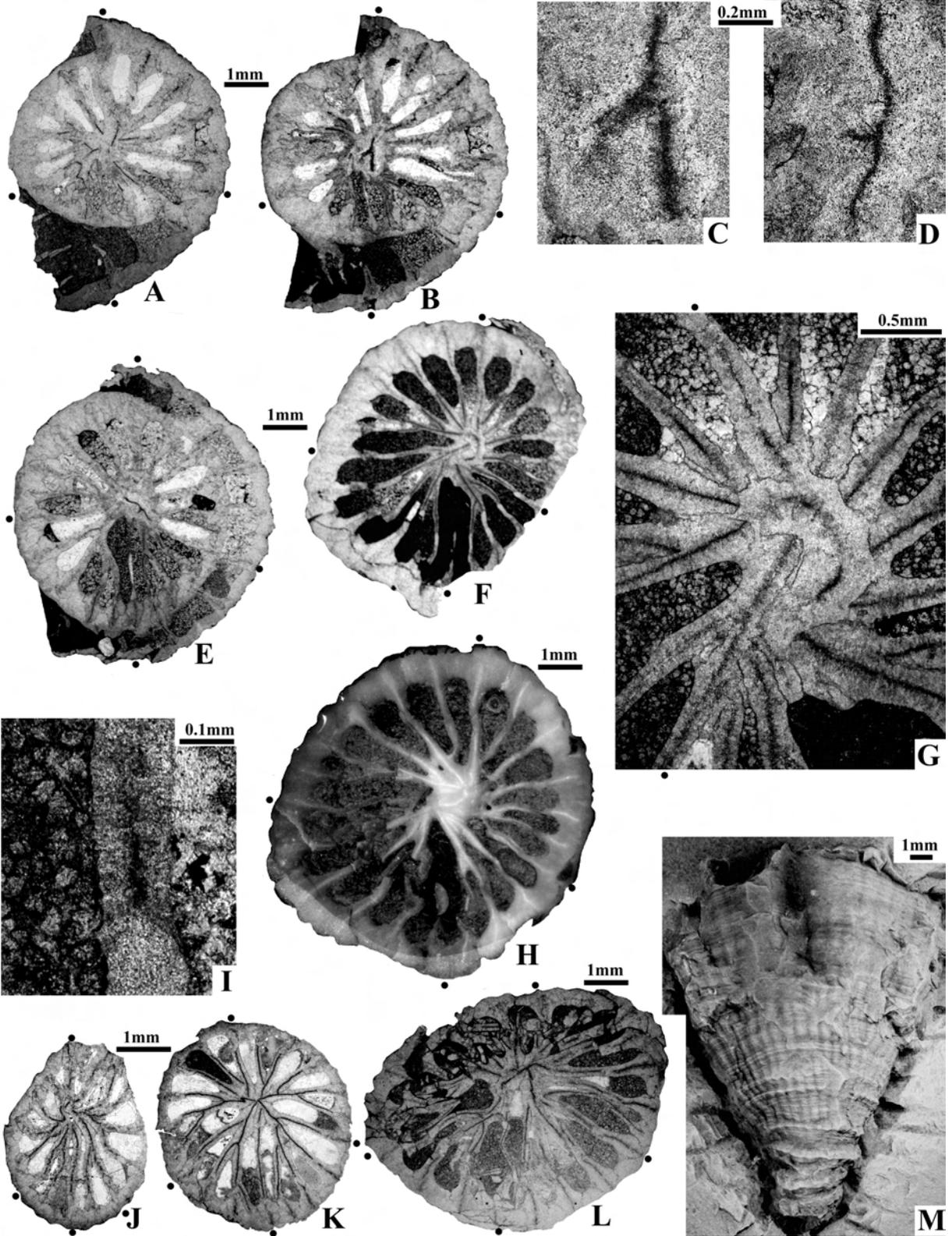
the median lamella continues to arch, but its 'middle dark line' points to an elongated major septum of the left counter quadrant on one side and to the left alar septum on the other. Thus, the position of septal lamellae is highly variable and their derivation uncertain. They almost certainly were not derived from either the cardinal or the counter protoseptum, following the holotype and other paratypes in that respect.

MICROSTRUCTURE OF SEPTA: The septal microstructure was strongly diagenetically altered in all specimens, including the holotype. In most instances the continuous, curved 'middle dark lines' are everything preserved. Fragmentation of the 'middle dark lines' (=primary septa) in some segments of major septa (e.g. Text-fig. 17G, I) may be interpreted as indicative of a finely trabecular microstructure. As in the other instances observed, diagenetic alterations of septa may differ, destroying part of a septum completely (Text-fig. 17I, lower), but leaving bunches of calcite fibrils, i.e., probable remnants of trabeculae, nearby (Text-fig. 17I, upper).

DISCUSSION: The differences between *V. repressum* and *V. radians* are small and can be reduced to: a) a much simpler axial structure in *V. radians,* with the lens-like axial body absent, b) smaller diameters with only a slightly smaller number of major septa in *V. radians* than in *V. repressum*, making their n:d values different. Unfortunately, the small number of specimens available for study precludes an application of statistics, thus making the last character uncertain. The early growth stages of *V. repressum* and *V. radians* are similar in their morphology and dimensions, suggesting a close relationship of both species.

Schindewolf (1952) described in detail and illustrated only the holotype specimen of '*F.*' *repressum*. He also described, but did not illustrate, one specimen from Huta Królewska (Königshütte in German) and two specimens from the borehole Książenice (Knieczenitz in German) near the town of Szczygłowice, Franciszka Marine Horizon, Hrushov Beds (upper Pendleian or Lower Arnsbergian). One of the latter specimens was investigated and illustrated by Weyer (1977, pl. 2 figs 4–13) as *Lophophyllidium* ? *repressum*. His questionable identification at the genus level resulted from both his correct recognition of differences in derivation of the axial structure between that specimen and *Lophophyllidium* and the absence of a genus appropriate to include it (Weyer 1977, pp. 463–464). That specimen exhibits the main characteristics of *V. radians* and is here transferred to that species.

Three characters of the specimen re-studied by Weyer (1977, pl. 2, figs 4–13) are of special value for more general considerations: 1) The wedge-shaped major septa in maturity, 2) The low upwards extension of the axial boss, which disappears from the corallite axis soon after separation from most major septa in the cardinal quadrants (Weyer 1977, pl. 2, figs 11, 12, and 3) The outline of the axial boss and the longest lasting connection of major septa to their lamellae suggests derivation of those lamellae from the middle major septa in all quadrants. Phylogenetic suggestions based on the characters listed and the stratigraphically early occurrence of the specimen re-investigated by Weyer (1977), are discussed in the section on Phylogeny.

OCCURRENCE: ZGI-X3514, Książenice (Knieczenitz in German) near the Town of Szczygłowice, Franciszka Marine Horizon, Hrushov Beds (upper Pendleian or Lower Arnsbergian). B-496, Orlová-Poruba, Žofie mine; B-6230, B-9379, B-12884 (Holotype), Dolni Sucha Village, Dukla mine, borehole numbers and depths respectively: Nr.21/72 and 113.2 m; D-22 and 191.1 m; D2182 and 35.4 m. B-6821, Karviná, 1. Máj mine, borehole Nr. 5046, depth 118.6 m. All from Ostrava Formation, Gaebler Marine Horizon, E_2b biozone, Middle Arnsbergian, Upper Serpukhovian.

SOME REMARKS ON THE PHYLOGENY

Both genera described in this paper provide data for consideration of the lineages to which they may belong and exclusion of some other possibilities based only on morphologic similarities. Some questions were already pointed out in the discussions on the subfamilies and genera.

In the case of the Ostravaiainae subfam. nov., its relationship to the Family Antiphyllidae Ilina, 1970 is possible. However, that possibility, supported by the rotiphylloid-like arrangement of the major septa and elongation of the counter protoseptum in *O. silesiaca* sp. nov. in early ontogeny, is rather weak. The cardinal protoseptum in that species is located on the concave corallite side and elongation of the counter protoseptum is slight and temporary, restricted to the immature growth stage of the holotype and is only slightly accentuated in the mature growth stage of one paratype. The lack of satisfactory morphologic support and the occurrence of a circulotheca, has resulted in the introduction of the new subfamily. Such a solution allows both the possibility of a distant relationship on the one hand and the possibility of development of a phylogenetic lineage different from the main stock of the Antiphyllidae on the other.

?*Ostravaia* sp. 1, in strong contrast to the type species, possesses an elongated counter protoseptum in

the lower part of the calice that reaches the corallite axis. This character negates to some extent its direct relationship to *O. silesiaca*, whereas the occurrence of a circulotheca and the symmetrical arrangement of the major septa could suggest that relationship. However, the alar septa in ?*Ostravaia* sp. 1 are obviously shortened in the advanced mature growth stage, making it similar to *Antiphyllum inopinatum* and '*Claviphyllum*' *hillae* Hudson and Fox, 1943, as mentioned above. A combination of clearly shortened alar septa, elongation of the counter protoseptum, and shortening of the cardinal protoseptum is rare among the Rugosa and should be considered important. Thus, *A. inopinatum* and/or '*C.*' *hillae* rather than *O. silesiaca* could be considered related to ?*Ostravaia* sp. 1 if the latter did not develop a circulotheca, a character absent from both species mentioned. With the existing data, evaluation of one character over the other is premature. However, the appearance of a circulotheca in several Devonian and Carboniferous families may suggest its lower taxonomic value than the rare combination of an elongated counter protoseptum and shortened alar septa. The well preserved and thoroughly investigated microstructure of septa not now available may be the key for establishing the monophyletic lineages of the taxa discussed. In summary: ?*Ostravaia* sp. 1 may be an intermediate *Antiphyllum/Ostravaia* taxon, but its true taxonomic position cannot be established on the basis of existing data.

The analysis of ?*Ostravaia* sp. 2 brings up another question: the taxonomic and phylogenetic value of the length of the cardinal protoseptum. Fedorowski (2009b, d) recently discussed that question exemplified by *Zaphrentites* Hudson, 1941 which has a shortened protoseptum in the cardinal fossula, and by *Rotiphyllum* Hudson, 1942 in which it permanently reaches the inner limit of a cardinal fossula, although not necessarily highly elevated. The ampleximorph *Axisvacuus* Fedorowski, 2009 from the Lower Bashkirian strata of the Donets Basin, Ukraine was suggested as directly related to *Rotiphyllum* on the basis of a permanent long cardinal protoseptum in addition to other characters in common for both of those genera (Fedorowski 2009b).

A comparison of the mature growth stage of ?*Ostravaia* sp. 2 to *Axisvacuus* and their earliest ontogeny would have left no doubt as to the synonymy of the former with the latter. However, the post-neanic and pre-late mature growth stage of ?*Ostravaia* sp. 2, during which a circulotheca is long-lasting, precludes this option. The longitudinal section of that species (Text-figs 8L; 9H) shows a typical circulotheca, closely comparable to that in the Silurian *Syringaxon*, Lindström 1886

and Devonian *Neaxon* Kullmann, 1965. The unnecessary assumption of the high taxonomic value of a circulotheca alone was already mentioned above. However, that character is certainly important when combined with other features. Also, an assumption of its environmentally caused development should be rejected. It would put in doubt the taxonomic value of several Upper Ordovician to Upper Carboniferous families. Thus, the true relationship of ?*Ostravaia* sp. 2 remains unknown and its morphological similarity to *Axisvacuus* in the mature growth stage does not indicate a direct relationship of those two taxa.

The preceding discussion leads to the conclusion that: 1. The rigid taxonomic position of *Ostravaia* on the family level is not established. 2. The inclusion in that genus of two species possessing only some characters in common with the type species of *Ostravaia* and left in open nomenclature, may be treated as creation of a taxonomic waste basket. That procedure was forced by both the very limited amount of material, impossible to augment in practice, and a lack of knowledge of the potential value of all morphotypes for phylogenetic reconstructions. Each character points to either earlier or later appearing genera or both. 3. A circulotheca, although considered valuable as a qualitative character, should be applied to the taxonomy with caution. It appears to have been an useful skeletal construction in many unrelated or distantly related families such as the Petraiidae De Koninck, 1872, the Laccophyllidae Grabau, 1928, the Protozaphrentidae Ivanovskiy, 1959, the Taralasmatidae Hill, 1981 and other families, extending over an enormous length of time, starting from the Upper Ordovician and ending with the Upper Carboniferous. The taxonomic and physiological value of that and other circumaxial skeletal structures was recently discussed by Fedorowski (2009*c*).

The so far monotypic Variaxoninae subfam. nov. poses another phylogenetic question: the taxonomic value of the axial structure in terms of its derivation. The suggestion by Weyer (1977, p. 463) concerning the 'possible series, *Rotiphyllum – Claviphyllum – Stereostylus – Lophophyllidium',* leading directly from the Subfamily Antiphyllinae to the Lophophyllinae has already been critically commented on in the discussion of the genus *Variaxon* and is here rejected. However, Weyer's (1977, p. 464) statement 'the construction of an everted axial structure in direct descendants of *Rotiphyllum'* is valuable in pointing to a probable ancestor of *Variaxon* and the derivation of its axial structure. In contrast to Weyer's (1977) concept, exemplified by his 'series' of genera, all genera with the counter protoseptum dominating over all other major septa are here eliminated as suspected ancestors of *Variaxon*. The

same is true for genera possessing one of the following pairs of opposing characters: a) cardinal protoseptum permanently reaching the inner margin of a cardinal fossula *vs.* shortened early in ontogeny, b) contratingent *vs* underdeveloped and free minor septa, c) a normal i.e., uniform *vs* biform tabularium and d) alar septa long *vs* shortened at any growth stage. These characters should be evaluated highly and their mixture should not appear in the same monophyletic lineages.

The morphology of the counter protoseptum during the entire ontogeny of *Variaxon repressus* does not confirm its leading role in spite of being slightly elongated in the calice of some specimens, perhaps as a result of the longer connection to its lamella (Text-figs 11I, J; 13E, G). Also, a temporary elongation of the counter protoseptum in *V. radians*, resembling the counter protoseptum in '*Stereostylus*' (Text-figs 14K; 15H, I) cannot be treated as proof of a relationship. Similar ephemeral elongation of one alar septum (Text-fig. 17F, G) and a middle septum in the right cardinal quadrant (Text-fig. 17L) documents the fortuitousness of that character. Thus, the counter protoseptum should be treated equal to other major septa that give rise to septal lamellae.

Weyer's (1977) suggestion that *Rotiphyllum* was ancestral to his ?*Lophophyllidium*, here included in *Variaxon*, is accepted with a restriction that *Variaxon* did not develop directly from *Rotiphyllum*, but there was a genus (or genera) intermediate in morphology between the two. Such a hypothetical genus is not known at present. It can only be stated that the stratigraphically lowest specimen included here in *Variaxon radians* sp. nov. and investigated by Weyer (1977, pl. 2, figs 4–13), exhibits the most primitive characters of the axial structure and the arrangement and shape of the major septa. These characters are comparable to both '*Densiphyllum*' *rushianum* Vaughan, 1908, i.e., the type species of the genus *Rotiphyllum,* and to '*Zaphrentis*' *omaliusi* Milne Edwards and Haime, 1851, one of the widely known species of that genus. Both of those species occur stratigraphically lower than any representative of *Variaxon* known so far. The axial structure of specimens included here in *V. radians* is not only simple, composed perhaps of five short septal lamellae. It also shows a very slight elevation above the inner margins of the major septa, pointing to a taxon possessing major septa that meet at the corallite axis, but are not elevated.

Both subfamilies discussed above pass through the rotiphylloid-like arrangement of major septa or rotiphylloid growth stage in their early ontogeny with some restrictions in the case of *Ostravaia*, pointed out earlier in this paper. That similarity brings up the question of the relationships of other taxa passing through the roti-

phylloid arrangement of the major septa in the neanic growth stage, but developing totally different morphologies in the intermediate late neanic/early mature and mature growth stages. Two approaches in such cases are possible:

1. To consider the rotiphylloid arrangement of septa fundamental for the neanic growth stage of many solitary non-dissepimented and some dissepimented rugose corals that possess nothing else or very little in common. The taxonomic and phylogenetic value of such a character would then be very low or none, suggesting no more than a similarity during early corallite growth, perhaps resulting from the usefulness of such an arrangement of major septa for the physiology of a young polyp.

2. To restrict an analysis to the taxa passing through the rotiphylloid growth stage, but possessing some other important characters in common. The close similarity in the microstructure of septa should be the most important among those characters. Unfortunately, diagenetic destruction of the microstructure is common, making that character of limited value. Thus, such morphological characters as the length of the protosepta and the alar septa, formation and derivation of the circumaxial and the axial structures, development of free *vs* contratingent minor septa, and normal *vs* biform tabularia appear to be the most important characters to consider when constructing phylogenetic lineages, starting with the rotiphylloid growth stage.

In conclusion:

1. The rotiphylloid early growth stage or the arrangement of major septa can be accepted as a common starting point for two or more lineages only if the immediate post- rotiphylloid growth stages in those lineages do not differ too much as, for instance, between those of *Ostravaia* and *Variaxon* described in this paper.

2. The taxa morphologically different in the mature growth stages, but passing through an early rotiphylloid growth stage may be related, but their relationship should be considered successively more distant when the morphologic differences appear in later growth stages. Nevertheless, the possible multidirectional phylogenetic radiation of the *Rotiphyllum*-like corals during the Tournaisian (and/or Late Famennian) – Viséan – Serpukhovian – Early Bashkirian time in Europe seems possible.

3. A credible phylogeny on the family level will not be possible until more data on the microstructure of septa, in particular, are gathered.

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