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Vojnovskytesidae – a new family of Mississippian Rugosa (Anthozoa)

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ABSTRACT:

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Two new species of the genus *Vojnovskytes* Fedorowski, 2009, namely *V. marcinowskii* and *V. arcuatus,* and a new genus, *Vojnimitor*, based on the new species *V. proiectus*, all from Mississippian strata of northern Spain, are described. *Vojnovskytes variabilis* (Vojnovsky-Krieger, 1934), the type species for the genus from the lowermost Viséan strata of southern Urals, also is discussed and illustrated. Characters displayed by the taxa mentioned permit introduction of a new family Vojnovskytesidae.

Key words: Rugosa (Anthozoa); New family Vojnovskytesidae; Taxonomy; Mississippian; Spain.

INTRODUCTION

Specimens selected from a collection of Mississippian rugose corals from northern Spain (Text-figs 1, 2) are described in the present paper for two reasons. First they are unique in that their morphology combines features which alone are common in a number of other remotely related and/or unrelated high level taxa. Second, similar sets of characters recognized by Vojnovsky-Krieger (1934) and Fedorowski (2009a) in specimens from the southern Urals were found in the currently described specimens from correlative and younger strata in northern Spain. These widespread occurrences suggest that the palaeogeography of the Mississippian was such that it allowed animals as sensitive to environmental conditions as corals to migrate long distances. This paper is supplemented by additional remarks and new illustrations of specimens from the Ural Mts.

The co-authors share the responsibility for the content of the paper as follows: The senior author completed and is responsible for the introductory part of the paper, the systematic part, illustrations, and the conclusions. All of those parts were approved and agreed upon by the junior author who is responsible for description of the coral-bearing localities and the stratigraphic position of all specimens. The Geological Setting was completed by Professor Sergio Rodríguez under his own authorship. As the paper is restricted to a small group of corals, detailed geological considerations and general remarks, including the succession of coral faunas in the area, are postponed to be included in another paper concerning the remaining parts of the collection.

MATERIAL AND METHODS

Most of the specimens described here were collected by the junior author during many years of field studies in the northern Spain. Other specimens numbered in the field with the letter 'K' were collected and several of them thin sectioned by Dr. J. Rinklef for his unpublished 1994 Ph.D. thesis completed under the supervision of the junior author. However, no part of the present work was taken from Dr. J. Rinklef's thesis. Additional specimens were also given to the junior author by his students and some German geologists working on Mississippian deposits of northern Spain.

The material collected by the junior author was identified and briefly described by the senior author in 1987 based on peels and *camera lucida* drawings made by him at that time. Unfortunately the application of that method resulted in a loss of large parts of some specimens without thin section documentation. Those early peels are utilized here, but the precision of the *camera lucida* drawings are inadequate. Thus, they have been replaced here by digital photographs and computer drawings made by the senior author, and by thin sections and additional peels made by his technician.

The collection described is housed in the Senckenberg Museum in Frankfurt Main. Both the Museum numbers (acronym SMF) and the field numbers are indicated in the Material section of particular species descriptions.

GEOLOGICAL SETTING

(by Sergio Rodriguez, Departamento de Paleontologia, Facultad de Ciencias Geológicas, Universidad Complutense y Consejo Superior de Investigaciones Cientificas, 28040 Madrid, Spain; e-mail sergrodr@geo.ucm.es)

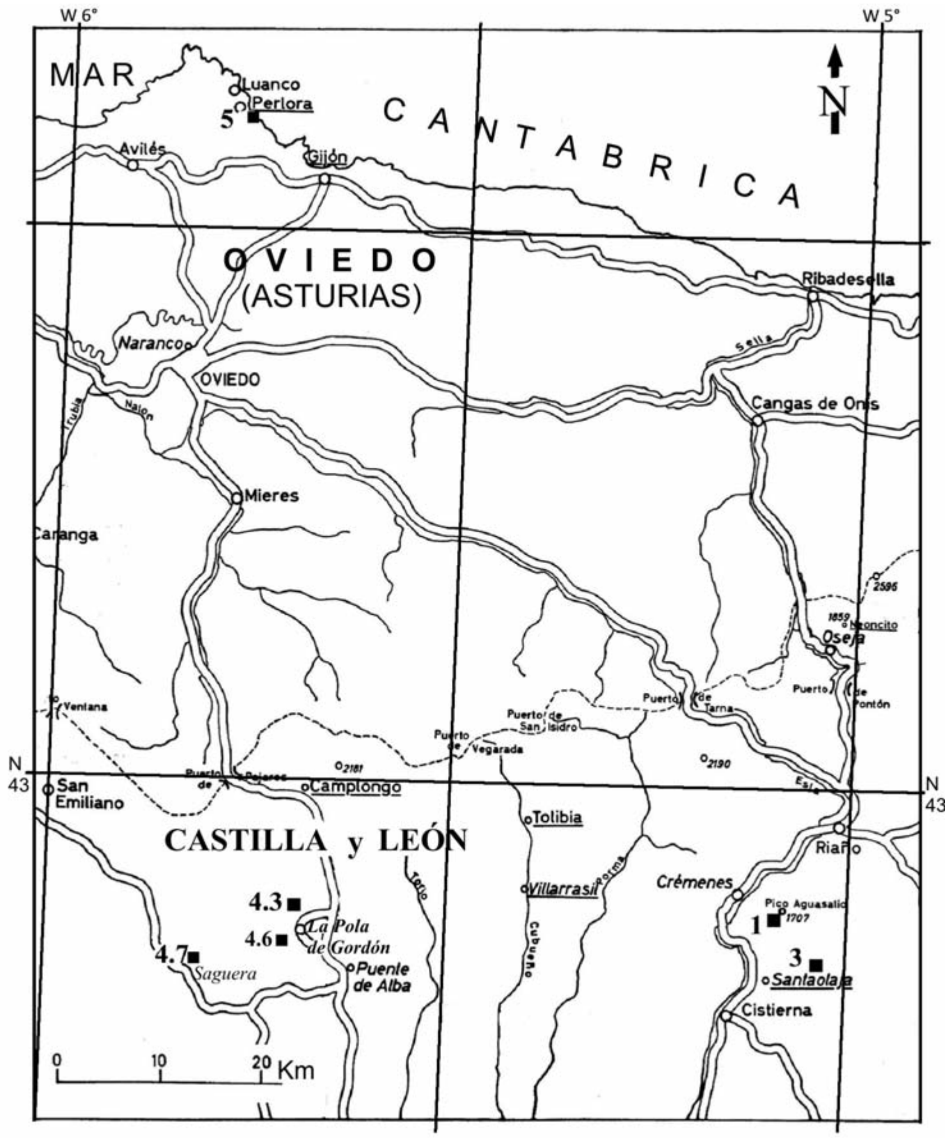
All corals included in this research were collected in the Alba Formation, also called Genicera Formation in some areas of Eastern Cantabrian Mountains. It has been also called in old papers and in minning articles as the "Carboniferous Griotte Limestone" (Suárez del Río *et al*. 2003). It overlies the Ermita Formation (Upper Devonian and lowermost Tournaisian sandstones), the Baleas Formation (Tournaisian white limestones) and the Vegamian Formation (Tournaisian black shales). It occurs throughout the Cantabrian Mountains, being a very characteristic unit. It is composed of 10 to 30 m of red to pink nodular limestones that pass progressively at the top into the well-bedded, black, laminated limestones of the Barcaliente Formation. In some areas of the Cantabrian Mountains this formation contains interbedded red shales, marls and radiolarites in its middle part. It represents a condensed sedimentation in a deep marine basin from the upper Tournaisian to the lowermost Serpukhovian (Menéndez-Álvarez 1978; Sánchez de la Torre *et al.* 1983; Sánchez de Posada *et al.* 1990; Sanz-López *et al*. 2007). It contains common ammonoids, crinoids, brachiopods, conodonts and locally rugose solitary, non-dissepimented corals. The corals occur mainly in the middle and upper parts of the Alba Formation, corresponding to the upper Viséan and lowermost Serpukhovian.

Text-fig. 1. Sketch map of Spain. The study area outlined

LOCALITIES

Locality 1. PICO AGUASALIO, León Province, NW section (42°53´19.87"N , 5°06´58.93" W). About 5 km SE of Crémenes. Alba Formation, composed of red nodular limestones and marls (see Belka and Korn 1994, fig. 2; Belka and Lehmann 1998, fig. 4). Basal layers do not contain cephalopods and corals. The main sedimentary sequence of red nodular marls include beds containing the conodont *Siphonodella anchoralis* and others (Higgins and Wagner-Gentis 1982). For this interval of the lower part of the Alba Formation, Raven (1983, p. 314, fig. 19) replaced the *anchoralis* Zone by the *anchoralis-latus* Zone. Late lower Viséan ammonoids and isolated rugose corals are characteristic of this zone (Kullmann 1961, p. 243).

Locality 3. PICO AGUASALIO SOUTH, León Province (42°50´04.23"N 5°05´23.48"W), South section of Pico Aguasalio and NE Santaolaja de la Varga, red nodular marls. Important outcrop of corals in the Alba Formation ("Marbre griotte"), see Kullmann, 1961, p. 243. Age: *Goniatites granofalcatus*, wide-spread, "*Goniatites*" stage .



Text-fig. 2. Map of study area with localities marked by black quadrangels

Locality 4. NE of LA POLA DE GORDON, León Province (42°51´17.92"N 5°40´12.73"W). Old abandoned quarry Las Baleas, E-NE of La Pola de Gordón, at Bernesga River. Alba Formation, Upper Viséan in age. Red nodular limestones with interbedded red marls. Contains *Merocanites* sp. and conodonts. Diverse Upper Viséan ammonoids and non-dissepimented rugose coral faunas occur mainly in the marl beds. The ammonoids are frequently badly preserved.

Locality 4.3. LA POLA DE GORDON, León Province. Top of the Alba Formation. Red to grey nodular limestones. Lowermost Serpukhovian in age.

Locality 4.6. BEBERINO, León Province (42°51'53.89"N, 5°40'51.52"W). Alba Formation. "Marbre griotte" localities below Barcaliente Formation, probably Serpukhovian.

Locality 4.7. SAGUERA, León Province (42°50´31.61"N 5°49´26.23"W), Red nodular limestones. Lower Viséan.

Locality 5. PERLORA Oviedo Province (43°34´46.47"N 5°44´47.49"W), Carranques Beach. Alba Formatrion. About 25 m of red nodular limestones and marls. Corals occur in the upper red nodular limestones, below grey limestones of Serpukhovian age (Kullmann 1962, p. 266; Budinger and Kullmann 1964, p. 425).

PALAEONTOLOGY

Order Stauriida Verrill, 1865
Suborder Cyathaxoniina Spassky, 1977
Family Vojnovskytesidae fam. nov.

TYPE GENUS: *Vojnovskytes* Fedorowski, 2009

DIAGNOSIS: Solitary, non-dissepimented; inner part of external wall septothecal, peripheral sclerenchyme with low costae-like structures possible; cardinal septum at convex side, slightly shortened in most; counter septum slightly to strongly elongated, may form pseudocolumella; aulos in early ontogeny of most; circulotheca always present, but may appear at different growth stages; minor septa contratingent; tabularium biform.

GENERA ASSIGNED: *Thuriantha* Weyer, 1981; *Vojnovskytes* Fedorowski, 2009; *Vojnimitor* gen. nov., ?*Silesamplus* Fedorowski, 2009.

DISCUSSION: All genera here included in the Family Vojnovskytesidae contain both a circulotheca and contratingent minor septa. However, these genera differ substantially from one another in several morphological features occurring in all growth stages. Therefore, when more specimens are studied these genera eventually may be placed in different subfamilies.

Morphologic details of species assigned to *Vojnovskytes* and *Vojnimitor* are given below, whereas those in *Thuriantha muelleri* were described and illustrated by Weyer (1981, pl. 1, figs 1–6, pls 2, 3). Unfortunately, both specimens representing *T. muelleri*, the genotype of this monotypic genus, lack the tips, so the early ontogeny of this species is unknown. Also, the microstructure of septa, described by Weyer (*ibid.*, p. 115) as lamellar, should be considered unknown until illustrated in a photograph.

The key characteristics of the family Vojnovskytesidae, a circulotheca and contratingent minor septa, also occur in some other families. It is only the combination of these and other structures in the Vojonovskytesidae and the microstructure of the external wall that should be considered diagnostic. The slight elongation of the counter septum in *Thuriantha* may be compared to that in *Vojnovskytes variabilis, V. arcuatus,* and an early growth stage of *Vojnimitor* and treated as the next feature in common.

Weyer (1981) suggested that septal costae occur in *Thuriantha*. This important character was not demonstrated by him in magnified photographs and is uncertain in *Vojnovskytes* and *Vojnimitor* because the surfaces of the available specimens are not perfectly preserved. However, growth lines in preserved peripheral parts of the external walls of corallites in the latter two genera are either concave towards the peripheral margins of the septa, incorporated in the wall, or nearly straight, but not convex as they would have been if septal costae were developed (Text-figs 5N, O; 8M, N; 9H; 10G, H). Thus, only secretion of the peripheral sclerenchyme first, followed by the introduction of septa, but not the occurrence of septal costae, suggested by Weyer (1981) for *Thuriantha*, is demonstrated so far in *Vojnovskytes* and *Vojnimitor*.

An overview of genera potentially related to the Vojnovskytesidae points only to *Silesamplus* Fedorowski, 2009, which displays some characters in common with *Thuriantha*. A possible relationship of that genus to both *Thuriantha* and *Vojnovskytes* has already been discussed and rejected by Fedorowski (2009a). Here we follow that position, although a relationship at the family level cannot be excluded. Features common for all three genera: a circulotheca, a slightly elongated counter septum, a triad, and a shallow dip of peripheral margins of septa into the sclerenchymal external wall suggest such a relationship. The position of *Silesamplus* in the Family Laccophyllidae Grabau, 1928, questionably accepted by Fedorowski (2009a), is less probable than in the Vojnovskytesidae when all similarities are considered.

Genus *Vojnovskytes* Fedorowski 2009

TYPE SPECIES: *Stereolasma variabilis* Vojnovsky-Krieger, 1934, p. 16, pl. 2, figs 7–12.

EMENDED DIAGNOSIS: Vojnovskytesidae with cardinal septum slightly shortened in maturity; counter septum rhopaloid, variably elongated, does not form pseudocolumella; calice floor deeper at concave corallite side.

SPECIES ASSIGNED: *Stereolasma variabile* Vojnovsky-Krieger, 1934 (partim); ?*Baritichisma*? *permica* Schouppè and Stacul, 1959; *Zaphrentoides*? n. sp. (aff. *Stereolasma variabile* Vojnovsky-Krieger, 1934) of Weyer 2002; *Vojnovskytes* sp. of Fedorowski 2009a; *Vojnovskytes marcinowskii* sp. nov., *V. arcuatus* sp. nov.

DISCUSSION: No papers dealing with representatives of *Vojnovskytes* have been published since the introduction of the genus by Fedorowski (2009a). Thus, most remarks and conclusions of that paper are considered valid and are not repeated here. The wide morphological variability of corallites, recognized earlier by Vojnovsky-Krieger (1934) in the type species, *Stereolasma variabile*, and followed by Fedorowski (2009a), is confirmed herein, although both of those authors expanded that variability too far. Some specimens included by Vojnovsky-Krieger (1934) in that species belong to *Rotiphyllum* and some others may represent *Weyerelasma* Kullmann and Liao, 1985 or a taxon related to that genus (See remarks on *V. variabilis* below for further discussion). Despite the large variability of the type species, some sets of characters exhibited by the Spanish specimens allow their grouping into new species as described below. An extreme morphological variant among the Spanish material, shown by specimens that developed an elevated pseudocolumella, are here separated into a new genus, *Vojnimitor*.

Some details suggested by Fedorowski (2009a) for *V. variabilis* appeared incorrect when photographs of thin sections and specimen surfaces, supplied by Dr. O.L. Kossovaya to the senior author, were studied. Thus, that species is additionally illustrated and discussed here.

Vojnovskytes variabilis (Vojnovsky-Krieger, 1934) (Text-fig. 3 A–G)

partim 1934. *Stereolasma variabile* Vojnovsky-Krieger, p. 16, pl. 2, fig. 10a–c only.

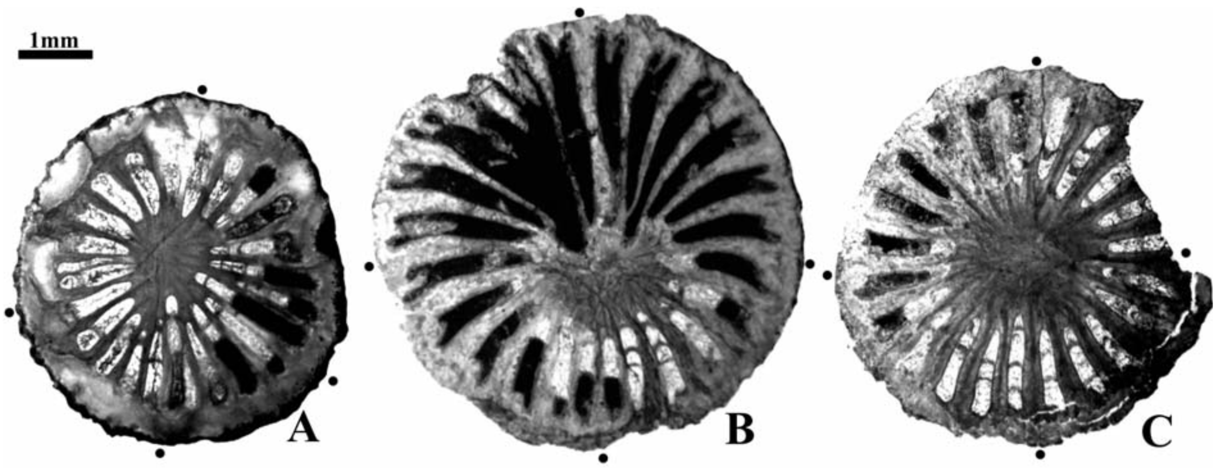
partim 2009a. *Vojnovskytes variabilis* (Vojnovsky-Krieger, 1934); Fedorowski, p. 305, text-fig. 3A–D only.

EMENDED DIAGNOSIS: *Vojnovskytes* with 19–20 major septa closely approaching corallite axis and up to 10 mm diameter at calice floor; cardinal septum slightly shortened, counter septum indistinctly elongated; short lasting circulotheca appears late in ontogeny; contratingent minor septa, reaching 1/3 length of major septa near calice floor, appear in corallite lumen late in ontogeny.

FORMAL REMARKS: Errors made by Fedorowski (2009a) should be clarified first. The lectotype possesses 19 rather than 21 major septa as pointed out in the original diagnosis (Fedorowski 2009a, p. 307). Two other errors resulted from the imprecise data accumulated by him during his visit to the former Soviet Union in 1968. The collection number is 1988 not 1980, and the repository is the VSEGEI Museum in St. Petersburg not the Institute of Paleontology, Russian Academy of Sciences in Moscow (Fedorowski 2009a, p. 305). Those errors were corrected thanks to the help of Dr. O.L. Kossovaya, VSEGEI, St. Petersburg. Also, the length of the counter septum, which was incorrectly drawn and described on the basis of peels taken from the lectotype (Fedorowski 2009a, text-fig. 3B, C), and some other details in those drawings, were corrected by using digital photographs of the thin sections and polished surfaces provided by Dr. O.L. Kossovaya in March 2012.

DISCUSSION: Vojnovsky-Krieger (1934, pl. 2, figs 7–12) illustrated mostly random thin sections and polished surfaces of five corallites. Only those thin sections, supplemented by peels, pictures of the corallite surfaces, and two thin sections of specimens not illustrated by Vojnovsky-Krieger (1934), are considered herein. Thus, remarks that follow should not be treated as a revision of the original collection, but only as corrections of the earlier descriptions.

Fedorowski (2009a) followed the broad concept of *Stereolasma variabile* by Vojnovsky-Krieger (1934),



Text-fig. 3. *Stereolasma variabile* 'Forma' A Vojnovsky-Krieger, 1934 = *Rotiphyllum* sp. Transverse thin sections, mature growth stage. Ala Tau Mine, Arkhangelsky Factory, Southern Urals. Perhaps lowermost Viséan. A – Specimen 72/1988 (= Vojnovsky-Krieger, 1934, pl. 2, fig. 7a). B – Specimen 74/1988 (= Vojnovsky-Krieger, 1934, pl. 2, fig. 8). C – Specimen 75/1988 but that conclusion is modified here. 'Forma' A of Vojnovsky-Krieger (1934, pl. 2, figs 7a, b, 8), showing a morphology typical for the genus *Rotiphyllum* (Text-fig. 3A–C), is excluded from *Vojnovskytes*. Neither details in the morphology nor the exact taxonomic position at a species level of the specimens belonging to that 'Forma' are discussed here as that is beyond the scope of the present paper.

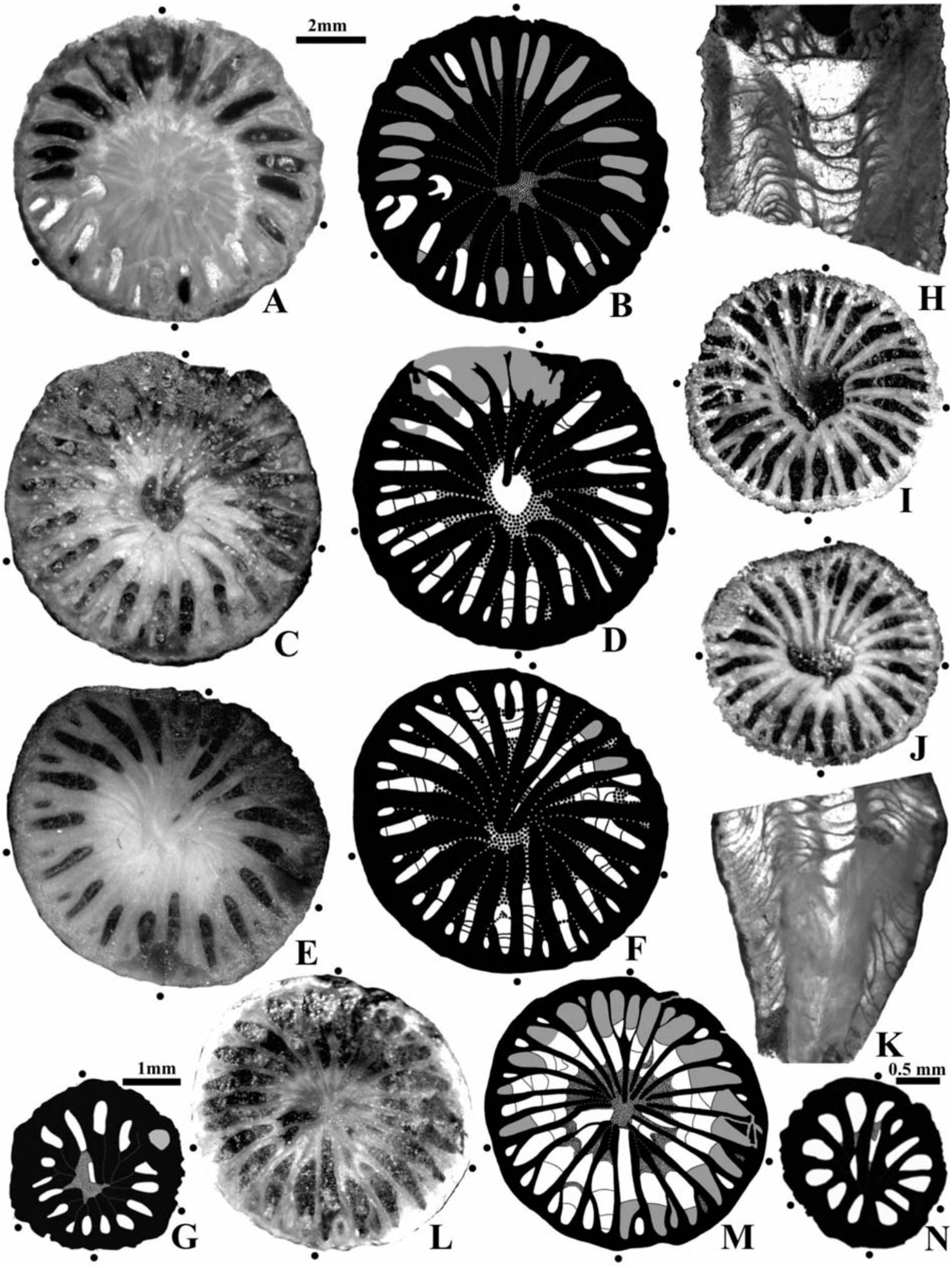
'Forma' B Vojnovsky-Krieger, 1934 was accepted by Fedorowski (2009a) as typical for the species and genus. The first of the corallites illustrated by Vojnovsky-Krieger (1934, pl. 2, fig. 10) was chosen by Fedorowski (2009a, text-fig. 3A–D; Text-fig. 4C–G here) as the lectotype, a position accepted in this paper. The second corallite of that 'Forma' originally illustrated in its rejuvenating calice (Vojnovsky-Krieger 1934, pl. 2, fig. 11) is temporarily not accepted as a paralectotype because its morphology at early growth stages is unknown. One of two specimens (Text-fig. 4A, B) not illustrated by Vojnovsky-Krieger (1934), but included by him in his 'Forma' B, was sectioned at an early mature growth stage. Its counter septum is stronger than in the lectotype, and its major septa are semi-bilaterally arranged. Both of those characters resemble features of *Vojnovskytes marcinowskii* sp. nov., but a firm identification cannot rely on a single, random thin section. Thus, a position of that specimen as a possible paratype of *V. variabilis* is accepted for the time being. The second specimen not illustrated by Vojnovsky-Krieger (1934) possesses an early growth stage (Text-fig. 4N) similar to that in the lectotype, but its mature growth stage differs significantly (Text-fig. 4L, M). Its major septa are thin and non-rhopaloid, a circulotheca is either absent or was not excavated by the cuts available for the study, the counter septum is only slightly longer than the remaining major septa, which are arranged in a manner characteristic of *Rotiphyllum* or *Weyerelasma* rather than *Vojnovskytes*, and the minor septa are short. All those characters suggest a distinct taxonomic position for that specimen at least at a species level.

Corrections of and supplements to the original description of the lectotype specimen are as follows: 1. Domination of the protosepta and the alar septa in the earliest preserved growth stage (Text-fig. 4G), pointed out by Fedorowski (2009a), only slightly exceed that common for early growth stages of taxa passing through rotiphylloid or zaphrentoid stages in early ontogeny. 2. The arrangement and length of the major septa and other details of the early mature growth stage drawn by Fedorowski (2009a, text-fig. 3B *vs* Text-fig. 4E, F herein) are mostly correct. Only the counter septum is slightly shorter than previously drawn. That error resulted from the axial sclerenchymal growth lines arranged in bands which appeared in peels to be part of the counter septum. The same is true for the peel taken from another fragment of the lectotype discussed below. 3. A thin section of the mature growth stage (Text-fig. 4C, D) intermediate between the previously illustrated two stages (Fedorowski 2009a, text-fig. 3B, C) documents occurrence of the circulotheca, an important character missing from previously illustrated growth stages, which were based exclusively on peels taken from the corallite surfaces above and below the level of its skeleton cut for the thin section. That short-lasting and late-appearing feature is important in the context of the Spanish specimens. The counter septum in that thin section (Text-fig. 4C, D) is only slightly longer than the adjacent major septa in the counter quadrants, and the counter-lateral septa are not elongated. The apparent elongation of all of those septa in an ontogenetically more advanced growth stage, sectioned partly above the calice floor (Fedorowski 2009a, text-fig. 3C), may have resulted from a diagenetic re-arrangement of crystals, imitating extensions of septa. Elongation of major septa within a calice greater than at its floor is contrary to the general trend in the Rugosa.

'Forma' C was illustrated by Vojnovsky-Krieger (1934) with only one specimen. The early ontogeny of that specimen is unknown. Two longitudinal thin sections taken from its upper and lower fragments, are oriented in the cardinal/counter septa plan (Vojnovsky-Krieger 1934, pl. 2, fig. 12c; Text-fig. 4H, K herein). One surface of the middle fragment of that specimen was illustrated by Vojnovsky-Krieger (1934, pl. 2, fig. 12a), whereas both surfraces of that middle fragment were peeled and photographed for this paper (Text-fig. 4I, J). Based on this material (Text-fig. 4H–K) the following statements can be made: 1. A circulotheca appears early in the ontogeny, as it is already present at the earliest growth stage preserved (Text-fig. 4K, lower). 2. The inner mar-

Text-fig. 4. *Stereolasma variabile* Vojnovsky-Krieger, 1934. 'Forma' B = *Vojnovskytes variabilis* (Vojnovsky-Krieger, 1934). A, B – specimen 84/1988. Paralectotype? Early mature growth stage. C-G – specimen 77-79/1988. Lectotype. C, D – mature growth stage with short-lasting circulotheca, E, F – early mature growth stage (= Fedorowski 2009a, text-fig. 3B, corrected; polished surface and peel), G – neanic growth stage (=Fedorowski 2009a, text-fig. 3A, corrected; polished surface and peel). H-K – 'Forma' C = *Vojnovskytes* sp. nov. 1. Specimen 88-90/1988. H, K – longitudinal thin sections, I, J – transverse cuts located between the previous two (polished surfaces and peels). L-N – intermediate between 'Forma' A and B = ?*Vojnovskytes* sp. nov. 2. Specimen 83/1988. L, M – mature growth stage, N – neanic growth stage (polished surface)

Note: Scale bar between figures A and B corresponds to all figures except where marked at upper right of a picture. Black dots indicate cardinal, counter and alar septa on this and all following illustrations. Cardinal septum at the bottom. Transverse thin sections except where stated. Occurrences of individual specimens, listed after corresponding description of species, are not repeated in figure captions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1mm
0.5 mm
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gins of the major septa remain permanently short of the corallite axis, but are weakly united by circumaxial sclerenchyme up to maturity to form a circulotheca (Text-fig. 4K, upper; 4J). The major septa lose their lateral contiguity in advanced mature growth stages, but remain arranged around the circumaxial area (Text-fig. 4I). It remains an open question whether such a structure can bear the name circulotheca as accepted here or should be given a different name. Fewer axial tabellae occurring in the axial part of the corallite than in its peripheral part, and development of the intermediate tabularium composed of densely packed, bubble-like tabellae, restricted to the circumaxial area, support the first option. Those bubble-like tabellae replace interseptal sclerenchyme that fills spaces between inner margins of major septa in the typical 'incomplete circulotheca' (term introduced by Fedorowski 2009b). Thus, both structures participate in the formation of a belt that borders the axial tube. Also, shape of those tabellae indicate that the circumaxial area was elevated above the calice floor higher than the peripheral and axial parts of the calice. This is another character of a circulotheca.

The characters mentioned above and the shortened cardinal septum developed comparatively early in the ontogeny are characters obviously different from those present in the 'Forma' B, i.e., *V. variabilis s.s*. Thus, 'Forma' C belongs to a different new species of *Vojnovskytes*. It was illustrated here to show why the present approach to *V. variabilis* differs from that of Fedorowski (2009a).

Vojnowskytes marcinowskii sp. nov.
(Text-figs 5–7)

HOLOTYPE: Specimen 3403 = SMF 75745.

TYPE LOCALITY: Locality 1. Pico Aquasalio, León Provine, NW section (42°53´19.87"N , 5°06´58.93" W). About 5 km SE of Crémenes.

TYPE HORIZON: Alba Formation. Member A. The *anchoralis-latus* Zone, late Lower Viséan.

ETYMOLOGY: Named in honor of the late Professor Ryszard Marcinowski from Warsaw University.

MATERIAL: Holotype 3403 = SMF 75745 and eight paratypes (3355, 3371, 3403A, 3403B, 3405, K-42, K-70, K-85 = SMF 75746 – SMF 75753 respectively). Most specimens almost complete, except for the earliest growth stages. Skeletons strongly diagenetically altered. 17 thin sections and 152 peels were available for study.

DIAGNOSIS: *Vojnovskytes* with n:d value near calice floor 16:6.5 mm to 19:8.8 mm; major septa bilaterally arranged, extend close to corallite axis; cardinal septum slightly shortened in advanced maturity; counter septum permanently elongated, including lower part of calice, commonly extends to corallite axis.

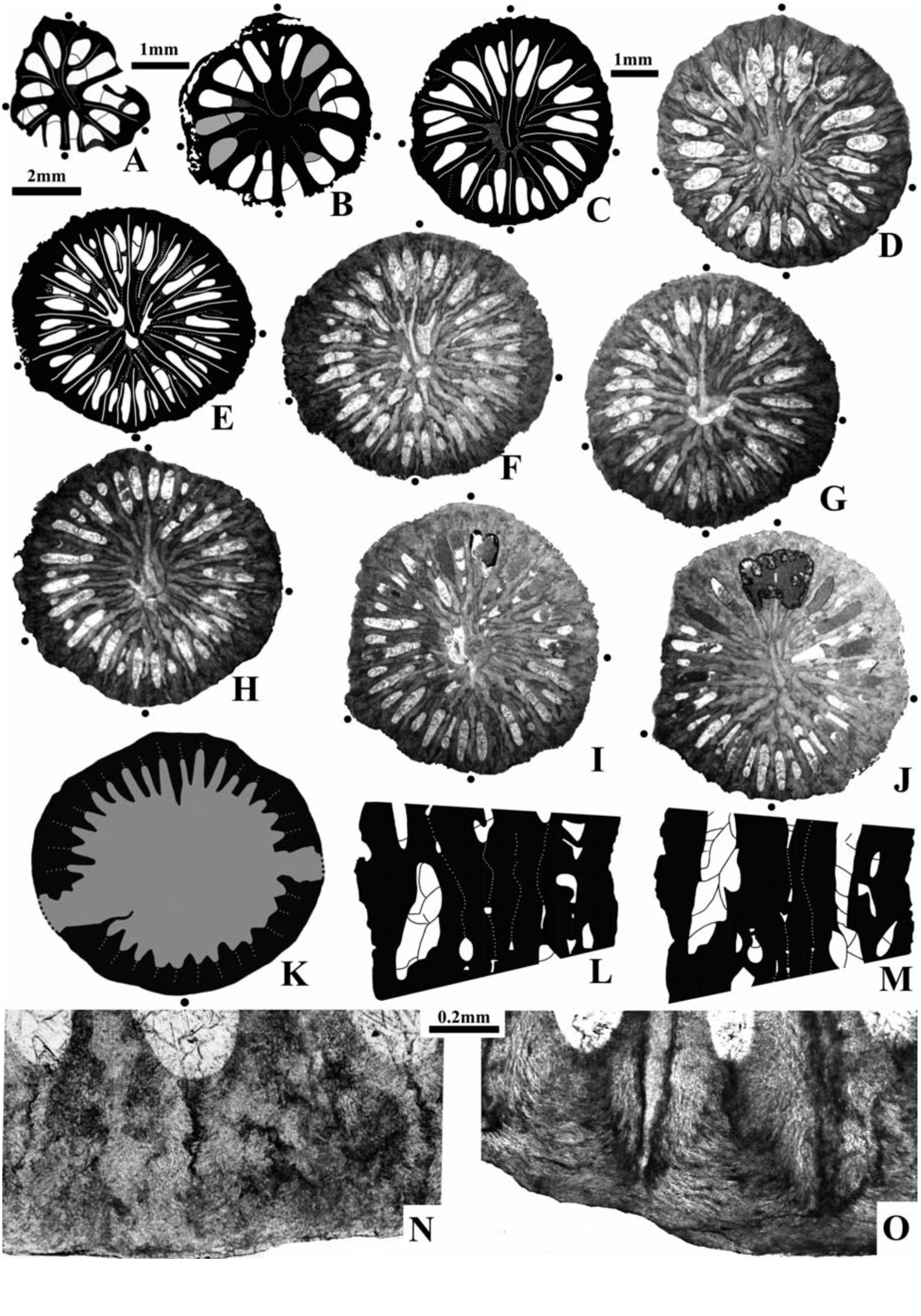
DESCRIPTION OF THE HOLOTYPE: The holotype is slightly over 30 mm long, ceratoid but almost cylindrical in its upper part. At an early growth stage the external wall was damaged by corrosion and/or by boring organisms (Text-fig. 5B); thus its exact thickness and morphology are uncertain. The wall is mostly sclerenchymal, with only peripheral margins of the major septa incorporated. At maturity the wall is approximately 1.2 mm thick and is divided into an inner septothecal and a peripheral sclerenchymal part (Text-fig. 5N, O). The surface of the mature external wall bears very shallow growth striae.

The ontogenetically earliest skeleton of the corallite is missing. The arrangement of the major septa in the earliest growth stage preserved (n:d value 13: 2.5 mm) is rotiphylloid (Text-fig. 5A). Most major septa, the cardinal septum included, approach the corallite axis. The last major septa in all quadrants are underdeveloped. The strongly elongated counter septum approaches one of the major septa in the right cardinal quadrant. The alar septa are slightly longer than remaining major septa in the cardinal quadrants. The right counter-lateral septum is slightly shorter and the left counter-lateral septum is slightly longer than the next major septa in these quadrants. The first appearing minor septa are represented by a strong thickening of the peripheral margin of the counter septum.

At 1.4 mm of corallite growth, the major septa are radially arranged. Their rhopaloid, laterally contiguous inner margins have become incorporated into the stereocolumn (Text-fig. 5B). That lateral contiguity of the major septa is here considered to represent a circulotheca , closely comparable to the typically developed immature circulotheca of Fedorowski (2009b, fig. 4A–C). Absence of a hollow pipe in the corallite axis in *V.*

Text-fig. 5. *Vojnovskytes marcinowskii* sp. nov. 3403 = SMF 75745. Holotype. A, B – neanic growth stage (peels), C – early mature growth stage (peel), D-J – mature growth stage (E – peel), K – upper part of calice (peel), L, M – longitudinal sections (peels); L – eccentric, M – axial, N, O – relationship of peripheral margins of septa to external wall and arrangement of sclerenchyme growth lines

Note: Scale bar between figures A and E corresponds to all figures except where marked between two pictures. For further explanations see *Note* at Text-fig. 4 (except first sentence)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O

marcinowskii is the only difference between that structure and a typical mature circulotheca. The cardinal septum is equal in length and morphology to completely developed major septa. The counter septum is much longer and its inner margin is much thicker than in the major septa, but it is considerably shorter than in earlier growth stage. The alar septa are not elongated, whereas the counter-lateral septa become slightly shortened. The minor septa which are contratingent to the counter septum, are the only minor septa in the corallite lumen.

The length of the major septa in the mature part of the corallite remains almost constant, although their arrangement changes step by step from irregularly radial (Text-fig. 5C, D) to bilateral (Text-fig. 5E–J). The cardinal septum is slightly shortened, reaching only the peripheral limit of the circulotheca, whereas the counter septum either reaches the corallite axis or extends slightly beyond it (Text-fig. 5E, J). This septum is so strongly rhopaloid early in maturity (Text-fig. 5D) that its inner margin occupies the entire axial part of the corallite. Later it is reduced in thickness step by step eventually becoming equal to the inner margins of other major septa (Text-fig. 5J). The amount of sclerenchymal infilling of the corallite axial area changes from section to section, probably being dependent on their position against axial tabellae. In the upper part of the calice (Text-fig. 5K), most major septa are almost equal in length, with only the counter septum being slightly elongated.

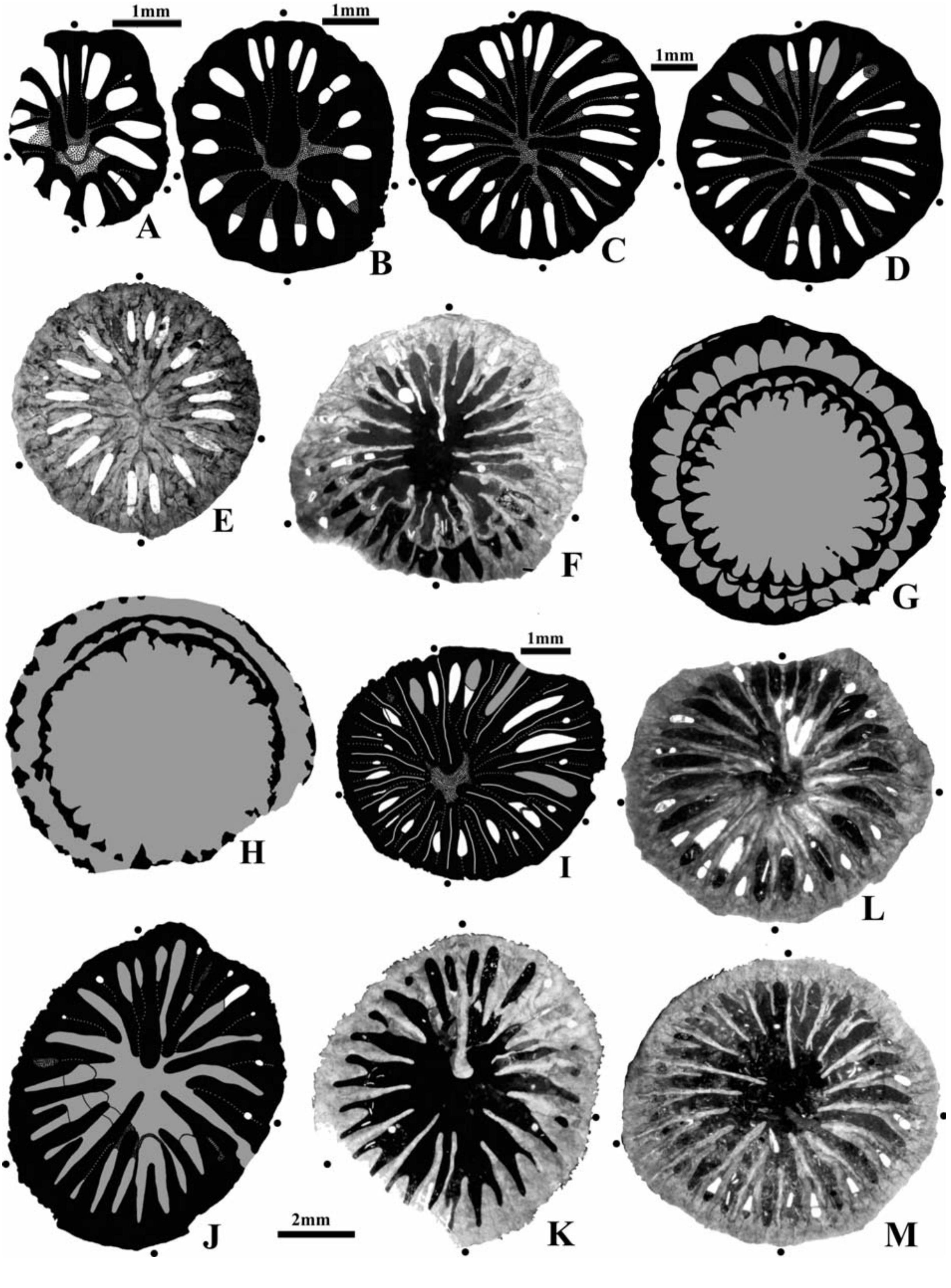
The minor septa become recognizable in the corallite lumen beginning in the early mature growth stage (Text-fig. 5C, D). They resemble peripheral swellings on the major septa when they first appear within the corallite lumen, being recognizable mainly by a different arrangement of crystalline fibrils. That lateral contiguity with the adjacent major septa disappears step by step in later growth stages (Text-fig. 5E–H) and the minor septa become typically contratingent. However, their middle dark lines (primary septa) remain isolated from those of the adjacent major septa. The length of the minor septa increases during the course of the corallite growth, with their inner margins eventually penetrating the peripheral part of the circulotheca (Text-fig. 5F–J).

The cardinal tabular fossula probably is absent. It was not documented either by sections of tabulae next to the cardinal septum or by the longitudinal section (Text-fig. 5L, M). Peripheral tabulae are incomplete with individual tabellae long and bubble-like. The latter character is best demonstrated by the eccentrically sectioned part of the corallite (Text-fig. 5L). In the precisely axial longitudinal section (Text-fig. 5M) tabellae are widely spaced, elevated towards the corallite axis, and very thin. They obviously play a subordinate supportive role for the polyp. A circulotheca is well documented by narrow axial lumina with sections of axial tabellae appearing in some.

INTRASPECIFIC VARIABILITY: The immature morphology of most paratypes resembles that of the holotype (Text-figs 6A, B; 7B, I). Only one paratype (Text-fig. 6A) resembles an early growth stage of *V. arcuatus* sp. nov. in the presence of a half-aulos of major septa in the cardinal quadrants. However, at further growth stages that corallite (Text-fig. 6B–E) closely resembles corresponding stages of the holotype. All paratypes differ from the holotype in possessing calices deepest at the concave side of the corallite. That difference appears at various growth stages, as demonstrated by sediment present in the interseptal lumina (Text-figs 6D, I; 7C, D, I). Different depths of the peripheral parts of calice floors, observed in all corallites, are the result of their biform tabularium. It is demonstrated by calcitic infillings in position I of Sutherland (1965) and the occurrence of sediment in the septal loculi containing tabulae in position II. That difference persists up to the middle and/or upper parts of calices (Text-figs 6L, M; 7G, H). Some corallites (Text-figs 6D; 7C, D) possess calice floors that differ irregularly in depth in position II as demonstrated by the infillings mentioned above. Axial parts in the paratypes are elevated as shown by sclerenchymal infillings within the circulotheca (Text-figs 6D, I; 7C, D, I, J). In some corallites the inner margins of the major septa in the cardinal quadrants remain elevated even when the axial area of the corallite is depressed (Text-figs 6L; 7E). Such characteristics point towards *V. arcuatus*. One corallite possesses a counter septum that is reduced in length step by step down to the size of the counter lateral septa (Text-fig. 7B–H). In other paratypes that protoseptum may stay long up to the middle part of the calice (Text-fig. 7K), where it may be rhopaloid (Text-fig. 6K). The minor septa may be shorter or longer than in the holotype. This set of characters in some specimens (e.g. Text-figs 6A–H, I-K; 7A–H) may eventually result in placing them in separate species.

Text-fig. 6. *Vojnovskytes marcinowskii* sp. nov. A-H – 3405 = SMF 75750. Paratype. A, B – late neanic growth stage (peels), C-E –mature growth stage (E- peel), F – lower part of calice; beginning of rejuvenation and very long minor septa, G, H – middle part of calice – rudiments of unsuccessful rejuvenation (polished surfaces). I-K – K-42 = SMF75751. ?Paratype. I – late neanic/early mature growth stage (peel), J – mostly above calice floor, except where white (peel), K – middle part of calice. L-M – K-85 = SMF 75753. Paratype. L — mature growth stage above calice floor in most loculi, M – above calice floor, except for some loculi in Position I (white)

Note: Scale bar between J and K at the bottom corresponds to all figures except for A-D and I marked specifically. For further explanations see *Note* at Text-fig. 4 (except first sentence)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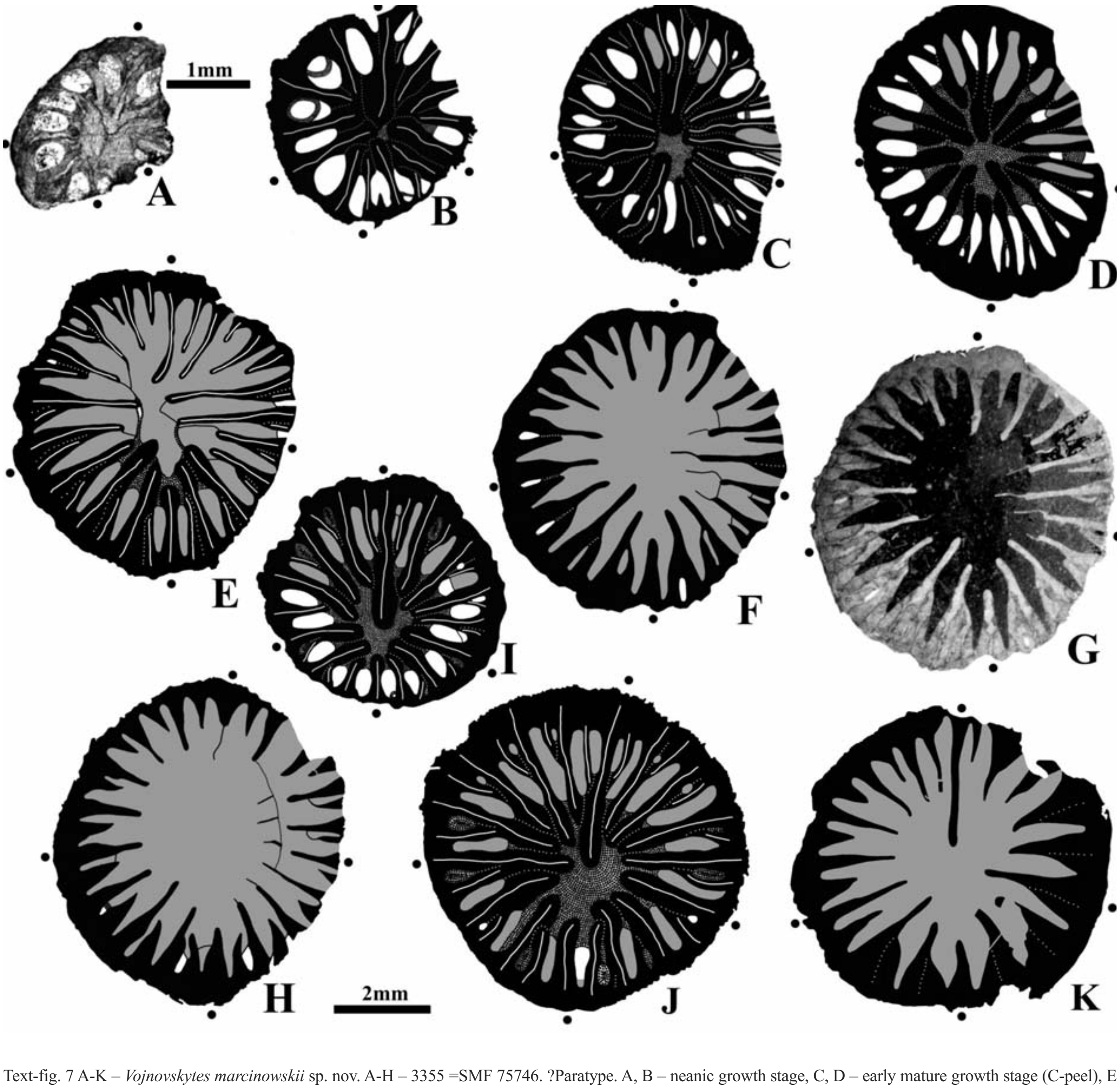
Rejuvenation in the paratype (Text-fig. 6F–H) led to the equalization in length of the major septa, including the protosepta, and in reduction in length of most of them to the size and thickness of the minor septa. At the initial stage of the rejuvenation (Text-fig. 6F) a few minor septa become elongated so as to almost reach the length of the adjacent major septa. Those septa adjacent to the cardinal septum may in fact be transformed later into major septa. Unfortunately, that phenomenon cannot be studied in detail. The calice of another specimen (Text-fig. 6K) shows that that phenomenon also occurs in normally developing specimens.

MICROSTRUCTURE AND DIAGENESIS: The original microstructure of the primary septa in the holotype and paratypes has been diagenetically altered to the extent that any reconstruction is impossible (Text-fig. 5N, O). Only the relationship of the very narrow primary septum to its sclerenchymal cover is known. It should be pointed out in this moment, that only the primary septa, i.e., the innermost parts of septa, secreted prior to any sclerenchymal sheets are formed, must be taken in mind when the microstructure of septa is described. This fact has been suggested already by Schouppé and Stacul (1955) and further discussed by Fedorowski (1978), who recognized as secondary the lamellar mi-



Text-fig. 7 A-K – *Vojnovskytes marcinowskii* sp. nov. A-H – 3355 =SMF 75746. ?Paratype. A, B – neanic growth stage, C, D – early mature growth stage (C-peel), E – mature growth stage immediately above calice floor (peel), F-H – successive cross sections through calice; note reduced length of counter septum (F, H-peels). I, J – 3403A = SMF 75748. Paratype. Early mature growth stage (peels). K – 3371 = SMF 75747. Paratype. Lower part of calice (peel)

Note. Scale bar in lower part of text-figure corresponds to all figures except for A, B marked separately. For further explanations see *Note* at Text-fig. 4 (except first sentence) crostructure of septa *sensu* Schindewolf (1942). The septal sclerenchymal sheets were secreted when septal pockets became too wide for secretion of trabeculae. Restriction of the primary microstructure to the primary septa in the modern Scleractinia was documented by Stolarski (2003), although nomenclature proposed by him differs from that applied here and is not followed. Almost nothing of the microstructure of the septa can be reconstructed from their peripheral parts (Text-fig. 5N). Only the limits of the peripheral margins of septa and a continuity of their sclerenchymal cover growth lines to the sclerenchyme of the external wall is recognizable (Text-fig. 5O).

DISCUSSION: The thin termination of the counter septum, located in a counter pseudofossula (Fedorowski 2009a, text-fig. 3A; Text-fig. 4G herein) of the lectotype of *V. variabilis* (Vojnovsky-Krieger, 1934), the type species of the genus, constitutes one of the differences when compared to early growth stage of the holotype of *V. marcinowskii.* Otherwise there is a similar arrangement of major septa in one of its paratypes (Text-fig. 6A). The cardinal septum in the lectotype of *V. variabilis* remains long up to the calice, becoming slightly shortened close to and at its floor, whereas it reaches only the peripheral margin of the circulotheca in *V. marcinowskii*. On the other hand the counter septum in the holotype and all undoubted paratypes of *V. marcinowskii* is much longer than in the lectotype of *V. variabilis*. Only one of the possible paralectotypes of *V. variabilis* restudied (Text-fig. 4A, B) possesses both elongation of the counter septum and the arrangement of the major septa similar to that in *V. marcinowskii*. That specimen differs slightly in having a greater number of septa at smaller corallite diameters, but it may provisionally be accepted as closely related with the Spanish specimens. The specimen from 'Forma' C of Vojnovsky-Krieger (Text-fig. 4H-K) differs from specimens described here in its smaller diameter, much shorter minor septa and the early appearing and long-lasting circulotheca, replaced in the advanced maturity by a circulotheca-like structure discussed above. The corallite identified by Vojnovsky-Krieger (1934) as "intermediate between Forma A and B" (Text-fig. 4L–N) differs distinctly from all remaining specimens making detailed discussion unnecessary.

OCCURRENCE: Locality 1: Holotype 3403 = SMF 75745 and paratypes 3355 = SMF 75756, 3403A = SMF 75748, 3403B = SMF 75749, 3405 = SMF 75750. Locality 4.6: Paratype 3371 = SMF 75747. Locality 4.7: Paratypes K-70 = SMF 75752, K-85 = SMF 75753. Locality 5: Paratype K-42 = SMF 75751. See chapter LOCALITIES for details.

Vojnovskytes arcuatus sp. nov.
(Text-figs 8–10)

HOLOTYPE: 1359 = SMF 75754.

TYPE LOCALITY: Locality 3. South section of Pico Aguasalio, León Province (42°50´04.23"N 5°05´23.48"W), NE Santaolaja de la Varga.

TYPE HORIZON: *Goniatites granofalcatus* Biozone, Lower Visèan.

ETYMOLOGY: *Lat. arcuatus* – arcuate. Named after long lasting rudiments of the circulotheca opposite the counter septum.

MATERIAL: Holotype (1359 = SMF 75754) and 12 paratypes (1456, 3311, 3352, 3356, K-61, K-68, K-75, K-84, K-87, K-1372, K-1454, K-1455A = SMF 75755 – SMF 75766 respectively). The ontogenetically youngest parts of skeletons are missing from all specimens, but the neanic growth stage is present in some. The microstructure of the septa has been diagenetically affected to various degrees: destroyed in most. 30 thin sections and 53 peels were available for study.

DIAGNOSIS: *Vojnovskytes* with n:d value 17:6.0 mm to 20:6.6 mm near calice floor; calice deepest at counter septum side of corallite; cardinal septum slightly shortened; counter septum slightly to distinctly longer than counter-lateral septa; long lasting arch-like structures similar to circulotheca opposite counter septum; contratingent minor septa reach or approach circulotheca.

DESCRIPTION OF THE HOLOTYPE: The inner margins of almost all major septa in the ontogenetically youngest growth stage preserved (n:d value 13:2.3 mm) are bent towards the cardinal septum, and reach the sclerenchymal sheets of adjacent septa (Text-fig. 8A). The primary septa ('middle dark lines') do not meet. The circumaxial structure is completely filled with sclerenchyme closely resembling, but not completely equivalent, to aulos, as re-defined by Fedorowski (2009b). The cardinal and counter septa are equal in length to the remaining major septa and participate in a circumaxial structure, but their inner margins are not bent. Contratingent minor septa occur only at the counter septum.

The thin section made approximately 1 mm above the previously described one (Text-fig. 8B), with n:d value 16:3.8 mm, exhibits a mixture of juvenile and early mature characteristics. Inner margins of some major septa remain bent, but most are straight and rhopaloid. The cardinal septum remains equal to the adjacent major septa. The counter septum is longer and thicker than the counter-lateral septa. The minor septa appear in most septal loculi, but almost all of them stay in lateral contiguity with the adjacent major septa. The circulotheca remains infilled with sclerenchyme.

The next thin section (Text-fig. 8C) made 1.2 mm above the previous one and the drawing made from a peel taken 0.4 mm higher (Text-fig. 8D), with n:d values 16:4.5 mm and 17:5.1 mm, respectively, illustrate the mature morphology immediately below the calice floor. The major septa are all rhopaloid, forming a strong circulotheca lacking sclerenchymal infilling. The counter septum remains the thickest, but it is only slightly longer than the remaining major septa. The cardinal septum, equal to the adjacent major septa in the thin section mentioned, becomes slightly shortened 0.4 mm above it. Also, some septal loculi in the counter quadrants and the inside of the circulotheca, were sectioned above the calice floor at that level, as indicated by dark infillings of those loculi (Text-fig. 8D). Most contratingent minor septa remain in lateral contact with their adjacent major septa, but some are disconnected from them at the periphery.

The deterioration of the circulotheca started next to the counter septum at n:d value 17:7.0 mm (Text-fig. 8E). The counter septum looses its rhopaloid character, but remains longer than the counter-lateral septa. The arch formed by the inner margins of the major septa, typical for the species, is clearly developed. The remaining characters exposed by a transverse section made partly above the calice floor (dark infillings) and partly below it closely resemble those described above.

The presence of rejuvenated parts of the holotype (Text-fig. 8F–H) allows comparison of that process to the ontogeny. The new skeleton, almost completely isolated from the old skeleton (Text-fig. 8F), is smaller than the regular ontogeny at corresponding growth stages (Text-fig. 8C, D), but it is morphologically close to them. The most advanced rejuvenation studied (Text-fig. 8G, H) also repeats the arrangement of major septa typical of the advanced ontogeny in the holotype (Text-fig. 8E) and similar growth stages in the paratypes (e.g. Text-fig. 8Q).

INTRASPECIFIC VARIABILITY: The morphology of most paratypes at similar growth stages closely resembles that of the holotype. In one paratype (Text-fig. 8I) the aulos, which lack sclerenchymal infillings, occurs in the ontogenetically earliest growth stage preserved. That growth stage is ontogenetically earlier than the youngest growth stage preserved in the holotype. The next growth stage of the same specimen closely resembles the corresponding growth stage of the holotype (Text-fig. 8J *vs* 8B) in the arrangement of the major and minor septa and in the sclerenchymal infilling of a typical circulotheca. A similar morphology occurs in all specimens possessing the preserved neanic growth stage (e.g. Text-fig. 9A–C, I, J).

The morphology of the mature growth stage of most paratypes (e.g. Text-fig. 8 K, L, O, Q, R) closely resembles the corresponding growth stage of the holotype, and in both the major septa in the cardinal quadrants plus at least the last inserted pairs of the major septa in the counter quadrants participate in an arch formed by their laterally contiguous inner margins. Also, all corallites included in this species possess calices deepest at the counter septum side (Text-figs 8J–L, O–P; 9K) closely resembling that in the holotype.

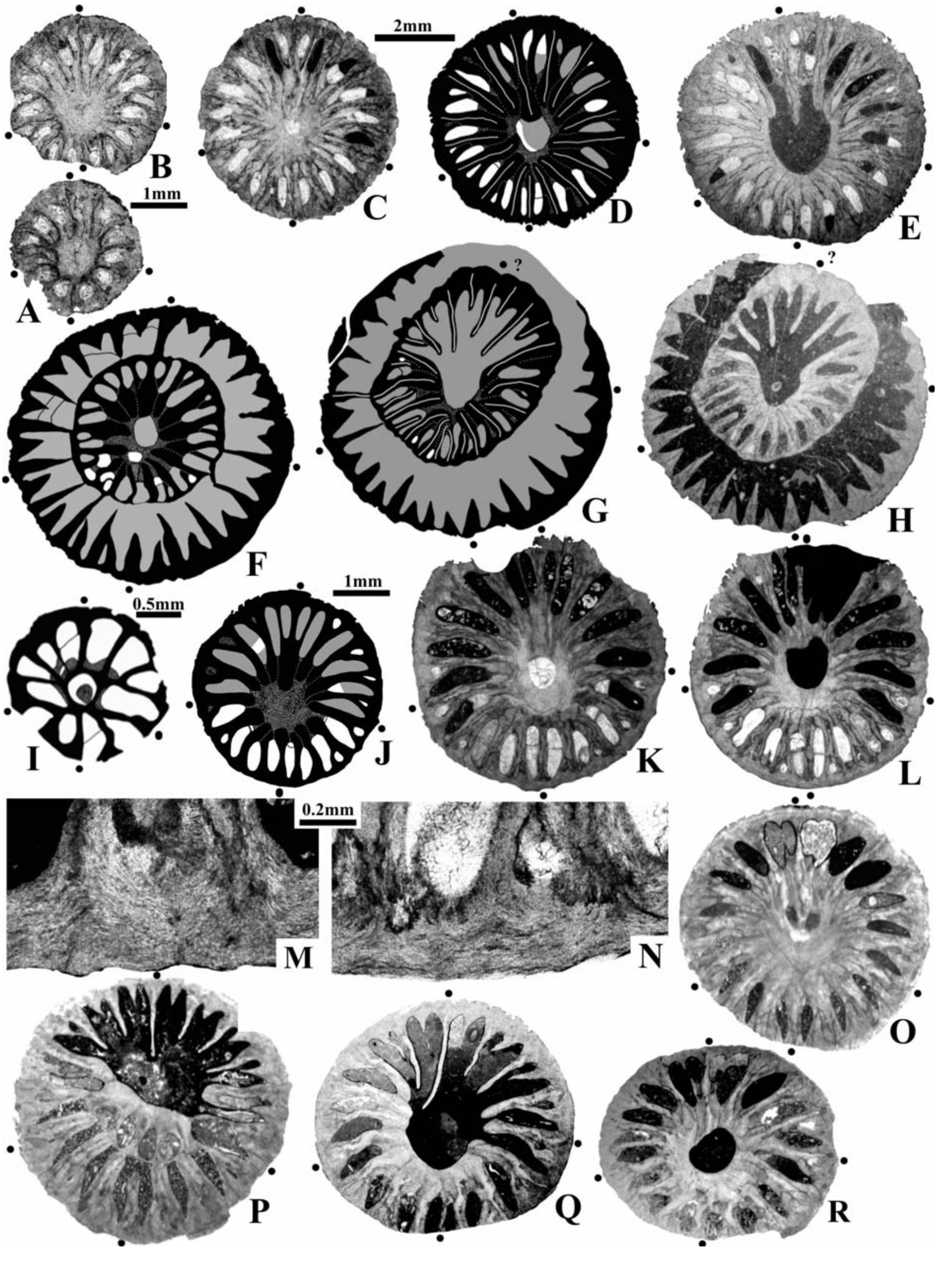
A group of three corallites displays sets of characters that may eventually serve as diagnostic for a new species. Their counter septa reach the corallite axes (Text-fig. 9F, G, K, M, N) and their alar septa are not longer, and sometimes are shorter than the last major septa in the counter quadrants. In those characters they resemble *V. marcinowskii.* However, the inner margins of the major septa in the cardinal quadrants, typical for *V. arcuatus,* form a long-lasting arch. The strange morphology of the otherwise typical fourth corallite (Text-fig. 8P, Q) resulted from the initial stage of the rejuvenation.

One corallite (Text-fig. 10A–H) differs from all specimens of *V. arcuatus* in possessing a short-lasting septal arch, temporarily replaced by an axial opening in the circulotheca in some transverse sections and camouflaged by heavy sclerenchymal cover in others. Also, its calice is almost equally deep all the way around, its minor septa are extremely long, and its n:d value (20:6.6 mm) is greater than that of all other corallites. That specimen almost certainly belongs to a separate species.

MICROSTRUCTURE AND DIAGENESIS: The microstructure of primary septa has been almost completely destroyed by the diagenesis. In spite of the sub-

Text-fig. 8. *V. arcuatus* sp. nov. A-H – K-1359 = SMF 75754. Holotype. A – neanic growth stage, B – late neanic growth stage, C, D – early mature growth stage (D-peel), E – mature growth stage sectioned above calice floor near counter septum, F – rejuvenation repeating early mature morphology (peel), G, H – rejuvenation repeating advanced mature morphology. I-N – 1456 = SMF 75755. Paratype. I – early neanic growth stage; aulos empty from sclerenchyme, J – late neanic/early mature growth stage (peel), K, L – mature growth stage, M, N – relationship of peripheral margins of septa to growth lines of external wall. O-P – K-84 = SMF 75762. Paratype. O – mature growth stage, P – very early stage of rejuvenation (lower). Q-R – 3356 = SMF 75758. Paratype. Mature growth stage. R – circulotheca elevated above calice floor, Q – fragment of circulotheca persists above calice floor (lower left)

Note. Scale bar between figures C and D corresponds to all figures except for A, I, J, M, N marked separately. For further explanations see *Note* at Text-fig. 4 (except first sentence)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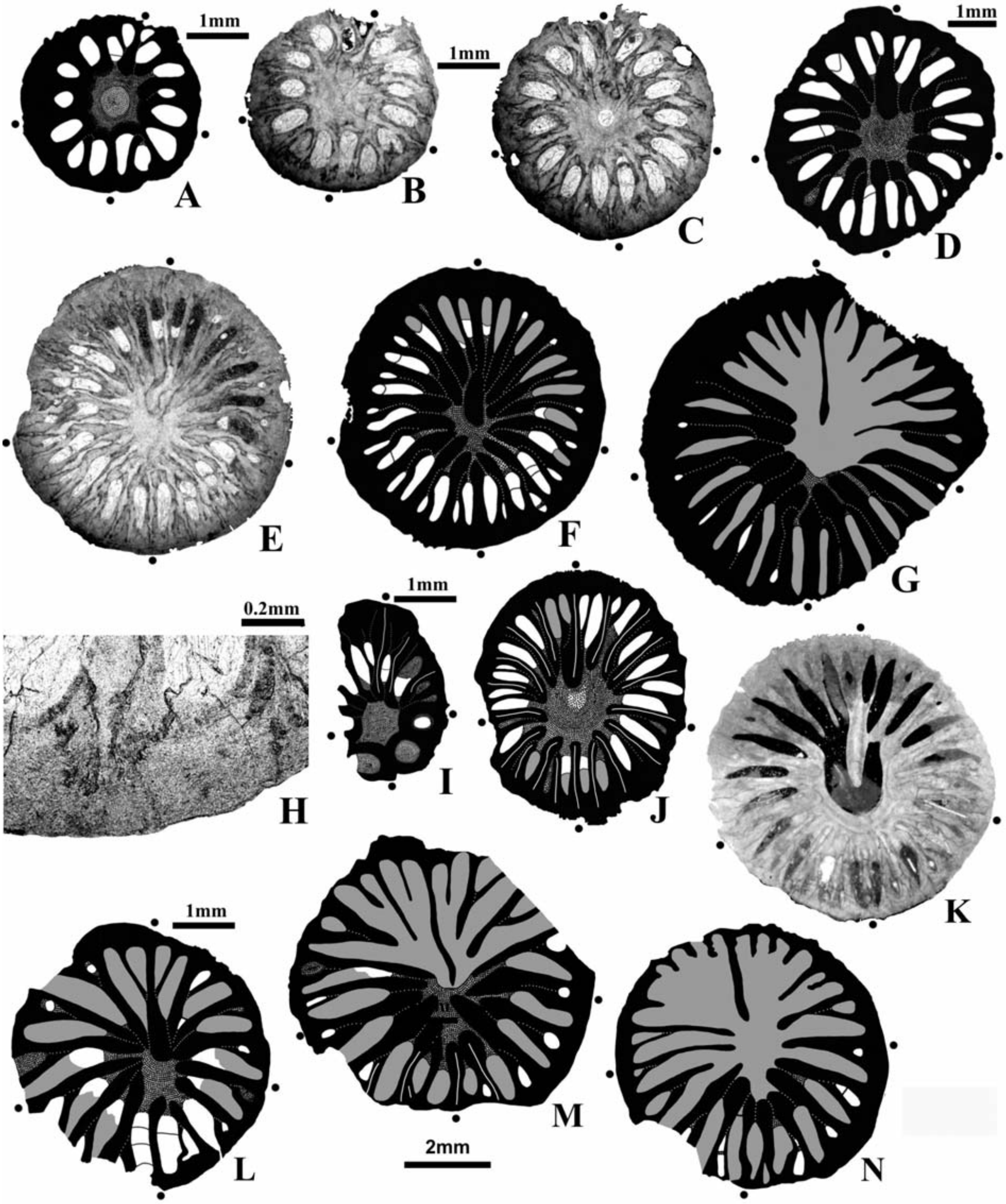
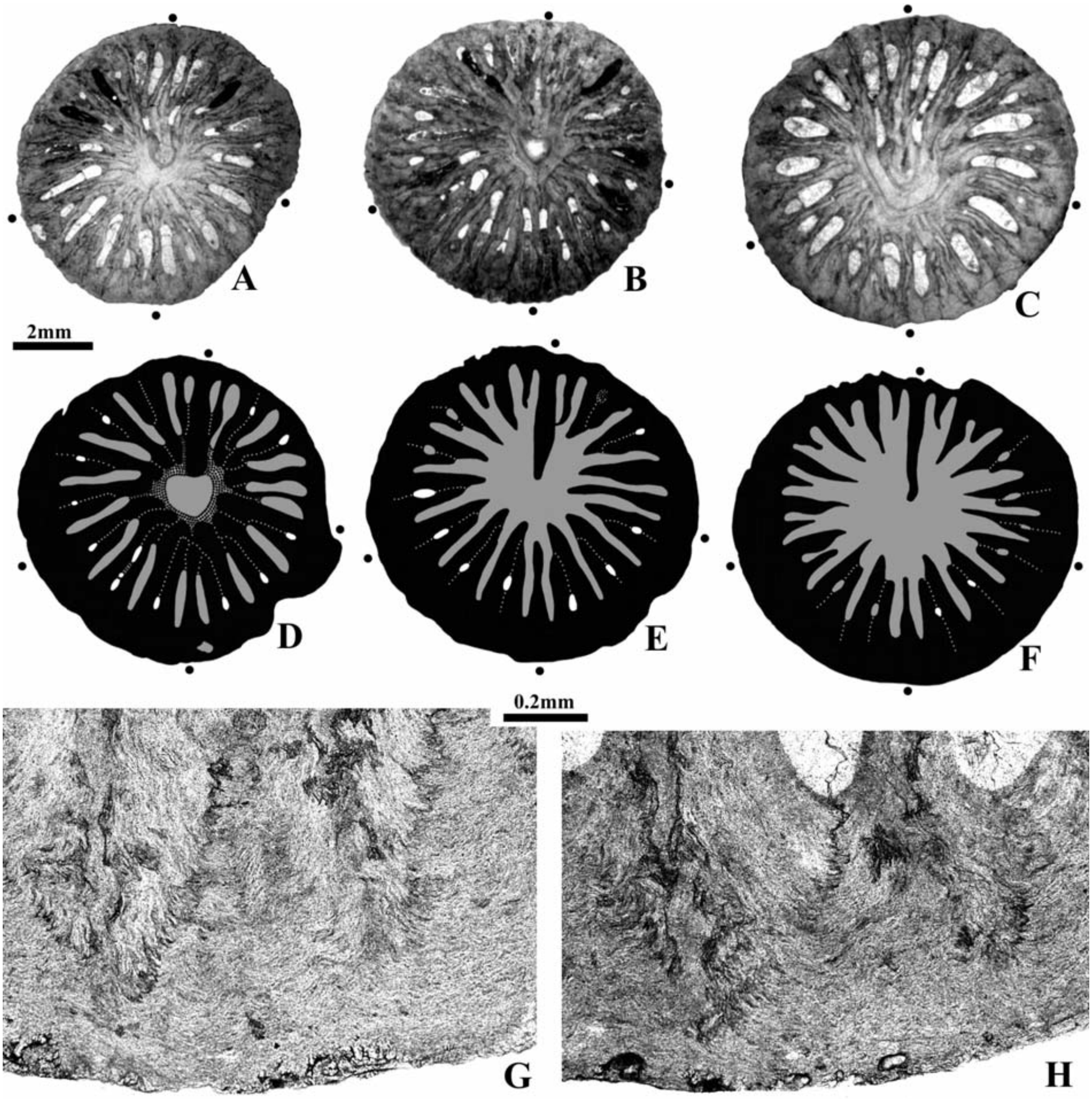


Text-fig. 9. *Vojnovskytes arcuatus* sp. nov. A-H – 3311 = SMF 75756. ?Paratype. A, B – neanic growth stage (A-peel); C, D – late neanic/early mature growth stage, E, F – mature growth stage (F-peel); G – mature growth stage; fragment of circulotheca and some loculi in Position I (white) above calice floor; minor septa very long (peel); H – relationship of peripheral margins of septa to growth lines of external wall. I-K – K-87 = SMF 75763. Paratype. I – neanic growth stage (peel), J – late neanic/early mature growth stage (peel), K – mature growthy stage. L-N – K-1372 = SMF 75764. ?Paratype. L – late neanic/early mature growth stage (peel), M, N – mature growth stage (peels)

Note. Scale bar at the bottom of text-figure corresponds to all figures except for A-D, H, I marked separately. For further explanations see *Note* at Text-fig. 4 (except first sentence)



Text-fig. 10. *Vojnovskytes arcuatus* sp. nov. 3352 = SMF 75757. ?Paratype. A-D – mature growth stage (D – polished surface), E, F – above calice floor except for some septal loculi in Position I (white) (peels), G, H - relationship of peripheral margins of septa to growth lines of external wall (enlarged from C)
Note. Scale bar between figures A and D corresponds to all figures except for G, H marked separately. For further explanations see *Note* at Text-fig. 4 (except first sentence)

stantial alterations, some characters, such as the arrangement of sclerenchymal growth lamellae in the external wall and position of the peripheral margins of the septa within the external wall, can be reconstructed. The peripheral margins of septa dip 2/3 to 3/4 into the external wall (Text-figs 8M–N, 9H, 10G, H). The sclerenchymal growth lamellae of these peripheral sectors of neighboring septa are sometimes united (Text-fig. 8M, upper). More commonly those lamellae are connected with the external wall lamellae (Text-figs 8M, lower; 9H right; 10G, middle, 10H, upper) or more or less clearly isolated from them by stylolitic-like structures (Text-figs 8N; 9H left; 10G, H, lower). The variety mentioned characterizes an unequal distribution of diagenetic alterations along short distances within the skeleton with the stylotites characterizing the most advanced diagenesis. Despite that alteration, the growth lamellae in the external wall are recognizable as not being convex opposite the peripheral margins of the septa. Thus, septal costae have not been recognized.

DISCUSSION: Only ?*Zaphrentoides* n. sp. of Weyer (2002, text-fig. 4:2a, b) from the Chadian of the Rhenish Slate Mountains closely resembles one atypical corallite of *V. arcuatus* (Text-fig. 9L–N) and to a lesser degree another one (Text-fig. 9A–G). Those two or three corallites could perhaps be grouped together as a separate species. *V. arcuatus* differs substantially in its diagnostic characteristics from all other species of *Vojnovskytes*, making closer comparison unnecessary.

OCCURRENCE: Locality 3: Holotype (1359 = SMF 75754). Locality 1: Paratypes 1456 = SMF 75755, 3356 = SMF 75758. Locality 4.3: Paratypes K68 = SMF 7560, K87 = SMF 75763. Locality 4.7: Paratypes 3311 = SMF 75756, K61 = SMF 75759, K84 = SMF 75762, K1372 = SMF 75764, K1454 = SMF 75765, K1455A = SMF 75766. Locality 4.8: 3352 = SMF 75757. Locality uncertain: K75 = SMF 75761. See chapter LOCALITIES for details.

Genus *Vojnimitor* gen. nov.

TYPE SPECIES: *Vojnimitor proiectus* sp. nov.

DERIVATION OF NAME: Combination of first syllable of the name *Vojnovskytes* and *lat*. *imitor* – to imitate, to mimic – after its similarity and relationship to that genus.

SPECIES ASSIGNED: Monotypic.

DIAGNOSIS: Vojnovskytesidae with most features like in *Vojnovskytes*, but with an elevated pseudocolumella.

DISCUSSION: *Vojnimitor* gen. nov. is strikingly similar to *Vojnovskytes* in its early ontogeny and, perhaps, in the microstructure of the septa. The latter conclusion is based on the identical diagenetic alterations in both genera. Also, the relationship of the peripheral margins of septa to the external wall in *Vojnimitor proiectus* closely resembles that in all species of *Vojnovskytes* investigated in this paper. Only one character, i.e., a very strong thickening of the inner margin of the counter septum first and its later transformation into a pseudocolumella projecting high above the calice floor later in the mature growth stage, forms a qualitative difference. Formation of that skeletal element must have altered the water circulation within the polyp's cavity, its physiology, and position of its body both when active and resting. That character is most similar to analogs represented in *Cyathaxonia*, as reconstructed by Fedorowski (1997, fig. 7A, B). Keeping in mind the similarities on the one hand and the differences on the other, either a subgeneric or a generic level should be applied to the bearers of that new diagnostic feature. We selected the second option, but treat the genus *Vojnimitor* as a direct descendent of *Vojnovskytes*.

The similarity of *Vojnimitor* to the Permian genus *Lophbillidium* Fedorowski, 1986 is superficial. Both of those genera appear especially similar when calicular transverse sections of the former, showing minor septa long and free, are compared to the transverse sections made beneath the calice floor of the latter. However, *Lophbillidium* differs in the microstructure of the pseudocolumella, composed of the median lamella and septal lamellae incorporated into it, versus the monoseptal pseudocolumella in *Vojnimitor*, in the lack of contratingent minor septa, and possession of a true, triangular cardinal fossula. In addition a circulotheca only occurs in *Vojnimitor* and the morphology of the very early growth stages and the morphology of the external wall of *Lophbillidium* (Fedorowski 1986, text-fig. 17:2a–c, 3a, b; pl. 12, figs 2a, b, 3, 5a, b [early growth stages], pl. 12, figs 1a–c, 4b, 6b [external wall]) are totally different from that in both *Vojnovskytes* and *Vojnimitor*.

Vojnimitor proiectus sp. nov.
(Text-figs 11, 12)

HOLOTYPE: 1471 = SMF 75767.

TYPE LOCALITY: Locality 5. Perlora, Province Oviedo (43°34´46.47"N 5°44´47.49"W), Carranques Beach.

TYPE HORIZON: Alba Formation, ?lower Serpukhovian (upper red nodular limestones, below grey limestones of Serpukhovian age).

ETYMOLOGY: Lat. *proiectus* – after elevated pseudocolumella.

MATERIAL: The holotype (1471 = SMF 75767) and four paratypes (1469, 1477, 3313, 3413 = SMF 75768 – SMF 75771 respectively). The brephic growth stages are missing from all corallites, but the neanic growth stage of two corallites and at least parts of calices of all corallites are preserved. The septal microstructure of all specimens is destroyed by advanced diagenesis. The main morphological features are exposed in the 9 transverse thin sections and 41 peels which were available for study.

DIAGNOSIS: *Vojnimitor* with n:d value near calice floor of 18:5.5 × 7.5 mm in the holotype and 16:5.8 mm to 19:10.0 mm in the paratypes.

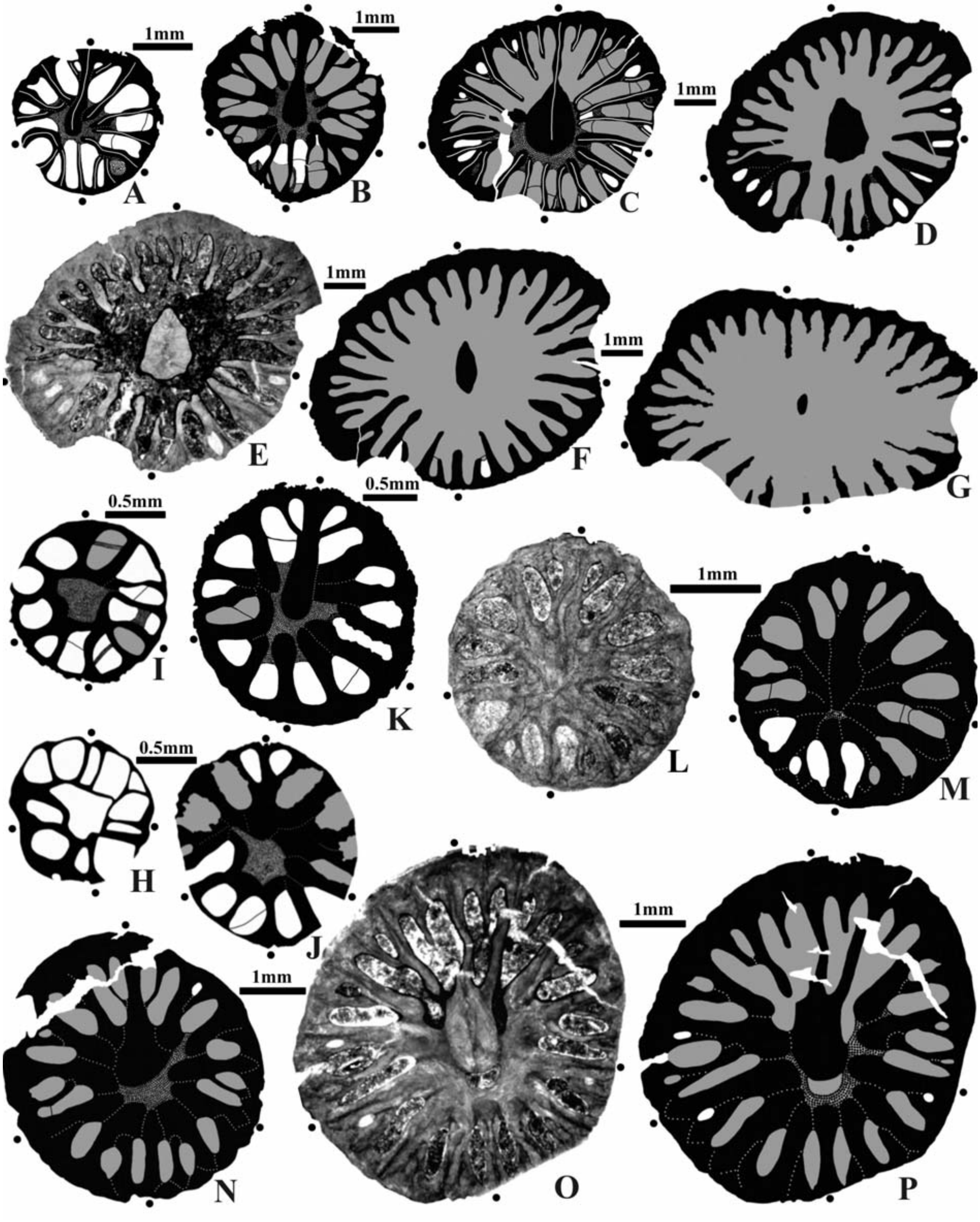
DESCRIPTION OF THE HOLOTYPE: A mixture of characters are observed in the earliest preserved growth stage of the holotype (Text-fig. 11A). Inner margins of some major septa are bent towards the adjacent major septa, suggesting development of an aulos in an earlier growth stage, whereas other major septa are already slightly rhopaloid. The long cardinal septum approaches the stereocolumn, but does not meet the axially thickened counter septum which projects beyond the corallite axis. Minor septa, except those contratingent to the counter septum, are not yet developed in the corallite lumen.

The corallite exhibits early mature characteristics (Text-fig. 11B) approximately 1.8 mm above the previously described growth stage. Inner margins of most major septa, except for the last inserted ones, are rhopaloid and terminate within the axial sclerenchyme. Not all of them are in lateral contiguity. Thus, the circulotheca as defined by Fedorowski (2009b) is incomplete. The cardinal septum remains long, approaching, but not reaching the counter septum, which is elongated and dilated axially. Contratingent minor septa are present within the corallite lumen. Almost all septal loculi in Position II of Sutherland (1965) are filled with sediment, proving an extreme depth of the calice (Text-fig. 11B). Only those loculi next to the cardinal septum, left white in the picture, are cut partly beneath the calice floor as suggested by its drusy calcite infilling. Thus, the commonly deepest area of a calice, occupied by a cardinal fossula, was elevated, opposite the general trend in the Rugosa. This interpretation is supported by a similar image in a comparable growth stage of one paratype (Text-fig. 11L, M), and in part by two other specimens (Text-fig. 12A, J). This character is definitely absent from the fifth specimen (Text-fig. 12E–I).

The axial part of the calice of the holotype (Text-fig. 11C) is occupied by a very strongly dilated inner margin of the counter septum. That septum remains surrounded by axial sclerenchyme at the cardinal septum side, by the inner margins of the major septa of the cardinal quadrants, and by the last major septa in the counter quadrants; the counter-lateral septa are already disconnected from the circulotheca at this stage. The arrangement and length of the major septa suggest that the axial area on the cardinal septum side of the corallite was elevated above the calice floor. Also, most septal loculi in the Position I of Sutherland (1965) remain elevated, as indicated by their infilling with calcite. Still higher in the calice (Text-fig. 11D–G) all inner margins of the major and minor septa become free. The counter septum separates from the pseudocolumella and remains similar in length to the counter-lateral septa, whereas the cardinal septum becomes slightly shortened. The pseudocolumella is elevated high above the calice floor and is sharply terminated, as suggested by its upwards thinning.

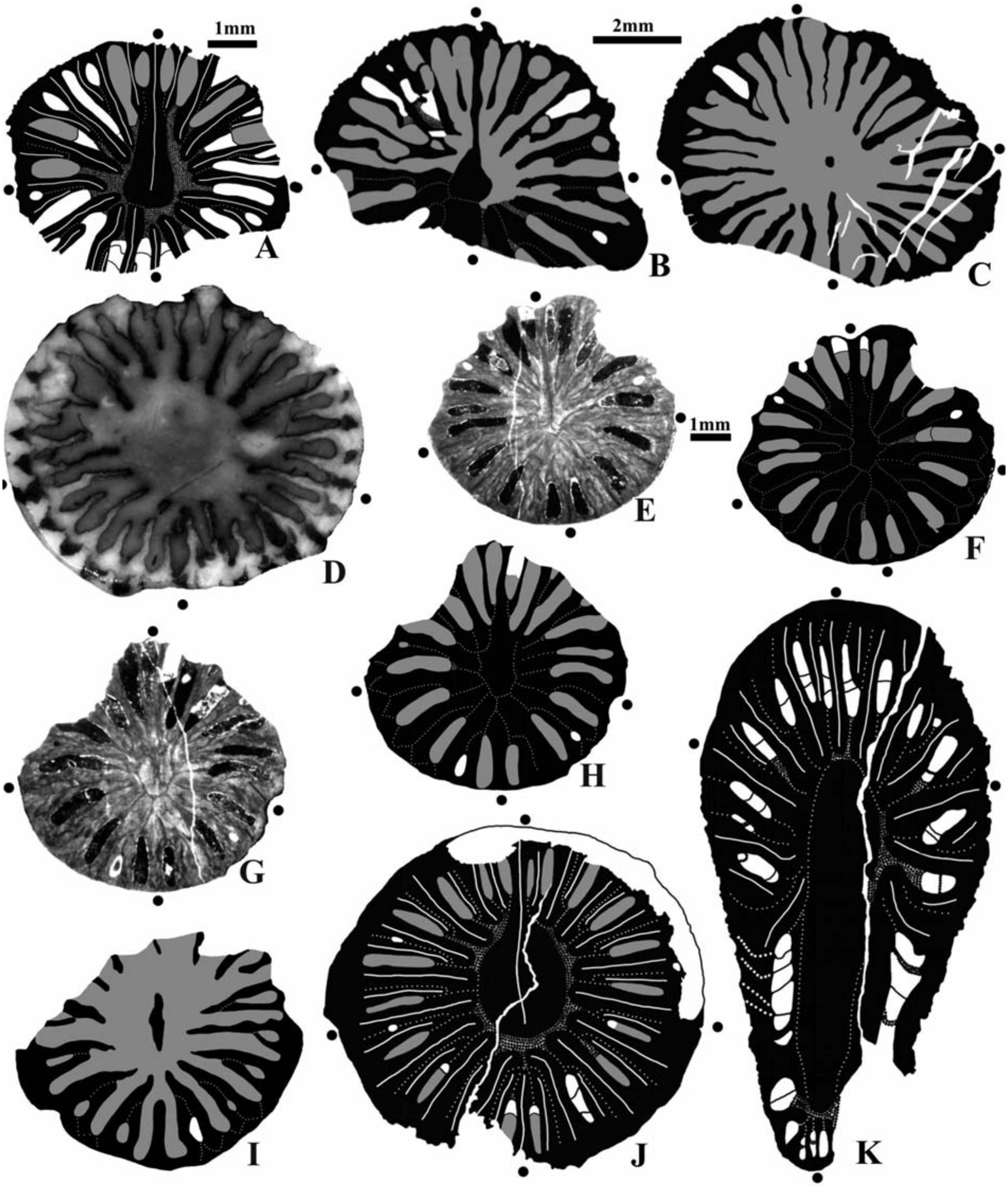
INTRASPECIFIC VARIABILITY: The ontogenetically youngest part of one paratype (Text-fig. 11H) documents a coral morphology earlier in the ontogeny than that preserved in the holotype. The axially hollow aulos occurs in that early neanic growth stage. The aulos becomes infilled with the sclerenchyme within 0.4 mm of additional growth of the corallite (Text-fig. 11I). The infilling may correspond to the position of the inner tabella being cut at that level. The peripheral dilation of the counter septum in that growth stage suggests the earliest stage of development of the triad. A further elongation and the axial dilation of the counter septum takes place within the next 0.4 mm of corallite growth of that paratype (Text-fig. 11J). The aulos or the aulos-like circumaxial structure is replaced by a circulotheca in the counter quadrants, but its remnants can be traced in the cardinal quadrants both in this and in the next thin section, made 0.6 mm higher in the corallite (Text-fig. 11J, K respectively). The morphology of the corallite in the next thin section is comparable to that preserved in the earlier growth stages of the holotype (Text-fig. 11K–M *vs* 11A, B). The major septa in the paratype are much thicker than those in the holotype in this growth stage, a feature which continues up to the lower part of the calice (Text-fig. 11K–P). This character is interpreted here as environmentally controlled. The paratype described is morphologically closest to the holotype. Unfortunately, it lacks the upper part of the calice.

Other specimens accepted as paratypes display wide morphological differences that could be adequate for separation at the species level if represented by a larger number of specimens. Very long minor septa are common in all three of them (Text-fig. 12A–K). However, the corallites differ from one another in their n:d values (16:5.8 mm, 16:8.0 mm, 19:10.0 mm) with first two measured in the upper part of the calice and the third one measured near the calice floor (calice is missing). These specimens also differ from one another in radial versus bilateral arrangement of septa (Text-fig. 12J *vs* 12E–G), in the length of the cardinal septum, in its shortening early in the ontogeny of one paratype (Text-fig. 12F–I), but not in the other two, and in the difference in the thickness and shape of the pseudocolumella. The incomplete specimen discovered in a random section (Text-fig. 12J, K) differs from both the holotype and the remaining paratypes. It is included in this species conditionally in order to show maximum morphological variability within the genus. The strongly oblique section of that corallite shows complete tabulae elevated at approximately 45° towards the pseudocolumella.



Text-fig. 11. *Vojnimitor proiectus* sp. nov. A-G – 1471 = SMF 75767. Holotype. A – late neanic growth stage (peel), B – late neanic/early mature growth stage (peel), C – mature growth stage; axial area elevated above and loculi left white sectioned below calice floor (peel), D-G – lower to upper middle part of calice; highly elevated, sharply ended pseudocolumella (D, F, G-peels) . H-P – 1477 = SMF 75769. Paratype. H-K – early to late neanic growth stage (peels), L-N early mature growth stage, O, P – mature growth stage

Note. Scale bar upper right of picture corresponds to that picture, middle between pictures corresponds to both. For further explanations see *Note* at Text-fig. 4 (except first sentence)



Text-fig. 12. *Vojnimitor proiectus* sp. nov. A-D – 3313 = SMF 75770. Paratype. A, B – mature growth stage (A- peel), C – lower part of calice (peel), D – shallow peripheral rejuvenation (polished surface). E-I – 1469 = SMF 75768. Paratype. E-H – mature growth stage, I – middle part of calice with rudiments of pseudocolumella. J-K –3413 = SMF 75771. ?Paratype. J – mature growth stage, K – Oblique section, mature growth stage (peels); cardinal septum at top

Note. Scale bar between figures B and C corresponds to all figures except for A, E, F marked separately. For further explanations see *Note* at Text-fig. 4 (except first sentence)

DISCUSSION: See discussion for genus.

OCCURRENCES: Locality 4.6: Paratype 3413 = SMF 75771. Locality 5: Holotype 1471 = SMF 75767. Paratypes 1469 = SMF 75768, 1477 = SMF 75769, 3313 = SMF 75770. See chapter LOCALITIES for details.

SUMMARY

1. Corals described in this paper belong to a group of unusual taxa present in early Mississippian time but bearing characters typical for taxa common in Devonian and Silurian strata.
2. The Family Vojnovskytesidae combines features of several Mississippian and older taxa thus constituting an unique mosaic of characteristics. This presence of such diagnostic features precludes recognition of its ancestor; no late Devonian specimens contain this combination of features.
3. The Family Vojnovskytesidae is widely distributed in the early Viséan, but continues up into Serpukhovian time. A possible Permian occurrence has already been questioned by Fedorowski (2009a), who tentatively had included *Barytichisma*? *permica* Schouppé and Stacul, 1959 in *Vojnovskytes*.

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