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Early Bashkirian Rugosa (Anthozoa) from the Donets Basin, Ukraine. Part 2. On the genera *Axisvacuus* gen. nov. and *Falsiamplexus* Fedorowski, 1987

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ABSTRACT:

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Five species belonging to two genera: *Falsiamplexus* Fedorowski, 1987 and *Axisvacuus* gen. nov. are described in detail and their species content and relationships are discussed. Both genera are perhaps related to *Rotiphyllum* and were probably derived from it, but relationship of *Falsiamplexus* to *Bradyphyllum* Grabau, 1928 cannot be excluded. The new genus *Axisvacuus* is represented by four species, of which three are new: *A. verus* (type species), *A. extendus* and *A. semicirculatus*. Stratigraphic ranges of species described are compared to the western European and Russian standards (Table 1). Some possible palaeogeographic implications of the occurrence of *Axisvacuus postumus* (Smith, 1931) and *Falsiamplexus reductus* Fedorowski, 1987 are briefly discussed.

Key words: Rugosa (Anthozoa); *Axisvacuus*; *Falsiamplexus*; Systematics; Early Bashkirian; Donets Basin; Ukraine.

INTRODUCTION

The present paper is the second in a series devoted to Early Bashkirian rugose corals from the Donets Basin, Ukraine. Thus all general data, such as the history of investigation, geological setting and methods applied, are to be found in the first paper of the series (Fedorowski 2009a). The location maps (Text-figs 1–4) were taken from that paper. Also, the distribution in the stratigraphic column of the *Axisvacuus* species (Table 1) was demonstrated on the basis of the stratigraphic table taken from that paper. The table shows the ranges of individual taxa described herein as well as their local stratigraphic positions, indicated in the occurrences, against the Russian and western European standards. Thus, the detailed discussion, published in the first paper of the series, is not repeated. It should only be mentioned that all Ukrainian specimens described herein are restricted in age to the early, but not the earliest Bashkirian. They were derived from Feninian to Zujevian strata, corresponding to the Kinderscoutian to Lower Langsettian in western European standards and to Krasnopolyanian to Lower Cheremshanskian strata in the Russian standards.

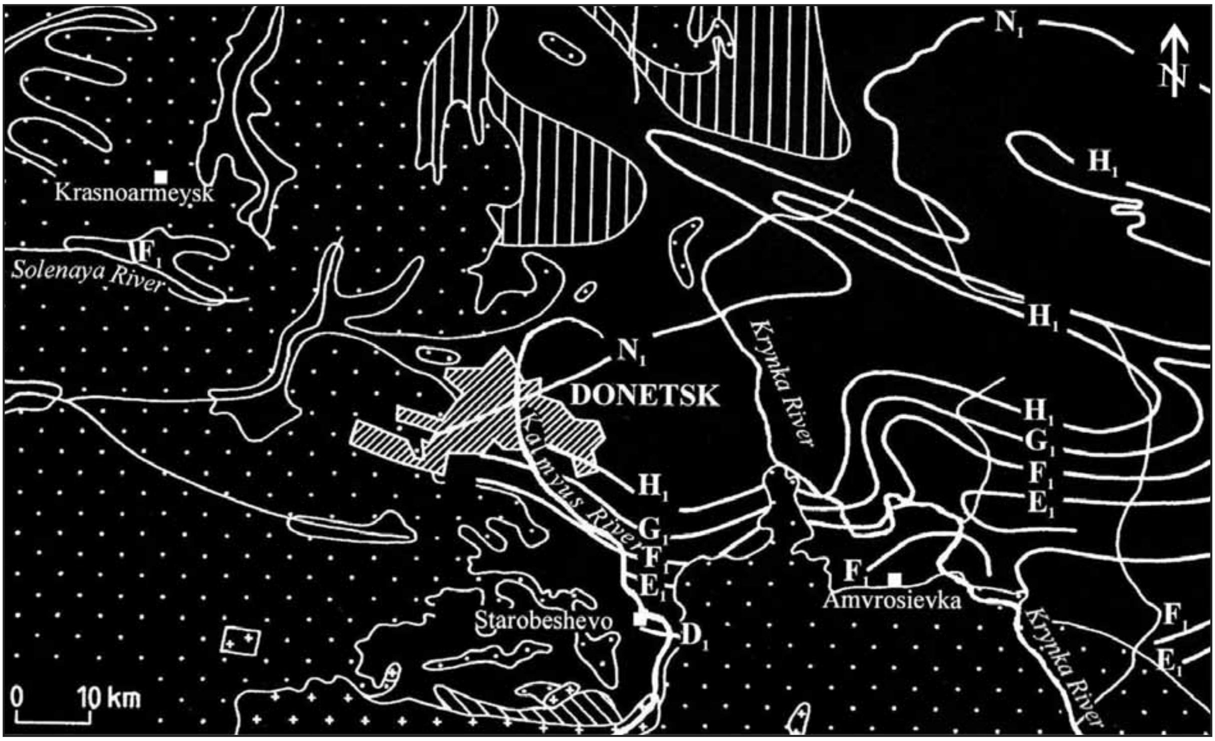
It should be made clear that the exact collecting sites of individual specimens cannot be firmly indicated. Rugose corals are very uncommon in the strata treated herein and were collected one by one by Dr. N.P. Vassilyuk during many years of collecting. As a

Text-fig. 1. General map of Ukraine showing approximate position of the study area

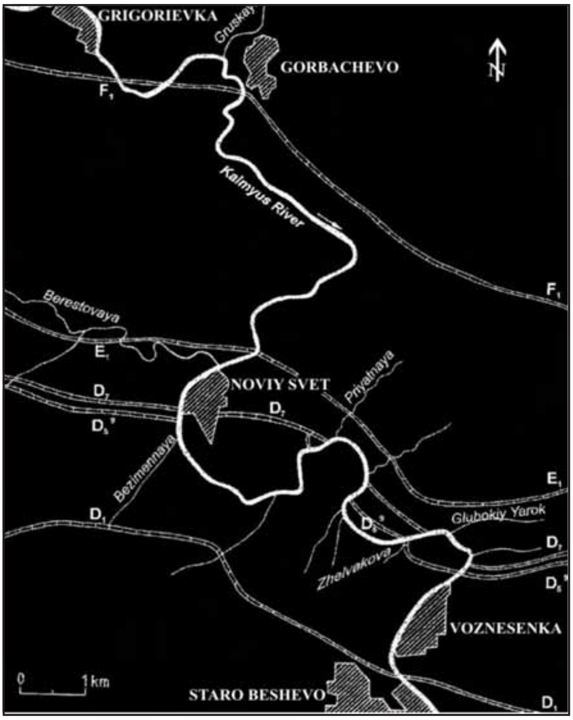
result, in the occurrences of individual species, it is possible to indicate only a given limestone intercalation, exposed in a named ravine (balka) in the vicinity of a given village, but not the exact collecting point. This is also the reason why exact localities are not specified in Text-figs 3 and 4. However, limestone intercalations are not repeated in particular ravines, making the stratigraphic positions of specimens clear enough. Since sequential positions of individual limestone intercalations appear more consistent than other stratigraphic subdivisions (see Fedorowski, 2009*a* for more details), the ranges of species in Table 1 are based on named Limestones.

Specimens of the species established earlier from other areas are stratigraphically younger. "*Zaphrentis*" *postuma* (= *Axisvacuus postumus)* occurs in the *Donetzoceras aegiranum* Zone in western Europe, while *Falsiamplexus reductus* was first described from strata of the Gaptank Formation (Kasimovian) in SW Texas, USA (Fedorowski 1987). Such a large difference between these occurrences may cast doubt on the identifications of the Ukrainian specimens, but their taxonomic assignment is supported by a close morphological similarity in both early and mature growth stages.

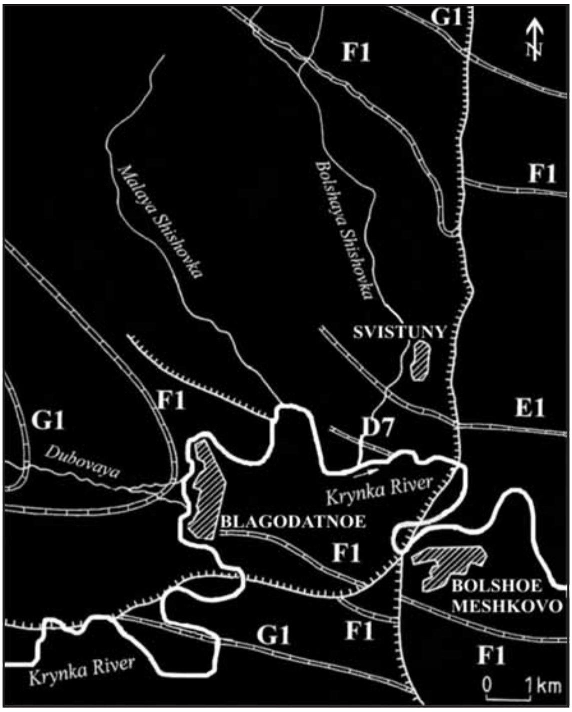
The main part of the present paper is devoted to systematics. Discussion of the family Antiphyllidae Ilina, 1970, covered in the first paper of the series, is omitted, but *Axisvacuus* and *Falsiamplexus* are discussed in detail, including their possible relationships. The synonymy lists for both genera should be treated as provisional. They are based mainly on macrostructural similarities because the septal microstructure is unknown from most taxa and studies of their ontogeny are commonly incomplete. The most controversial items are indicated by question marks and not all identifications by authors of individual specimens within species are accepted. Most of the latter items are treated in the discussion sections. The presence of one species in



Text-fig. 2. Vicinity of the town of Donetsk. Generalized positions of individual Limestone Groups (D to N). Carboniferous deposits left in white. Provided by Dr. N.P. Vassilyuk



Text-fig. 3. Outcrops in the area near the village of Staro Beshevo, south of the town of Donetsk, along the Kalmyus River and its tributaries. The most important ravines (balka) are named. Distribution of Limestone Groups D to F drawn as bands with brick ornaments. Provided by Dr. N.P. Vassilyuk



Text-fig. 4. Outcrops along Krynka River and its tributaries, east of the town of Donetsk. The most important ravines (balka) are named. Tectonically affected Limestone Groups D to G drawn as bands with brick ornaments. Provided by Dr. N.P. Vassilyuk

common with western Europe and another with the southwestern United States led to some preliminary palaeogeographic remarks in the summary chapter.

Order Stauriida Verrill, 1865
Family Antiphyllidae Ilina, 1970
Genus *Axisvacuus* gen. nov.

TYPE SPECIES: *Axisvacuus verus* sp. nov.

DERIVATION OF NAME: Composed of *lat*. “*axis*” – axis and *lat. vacuus, a, um* – empty. Named for open axial area, free from major septa at maturity.

SYNONYMS:

1890. *Amplexus* Worthen, 1890, p. 82 *non* Sowerby 1814, p. 165.
partim 1908. *Zaphrentis* Carruthers, p. 24 *non* Rafinesque and Clifford 1820, p. 234.
partim 1908. *Zaphrentis* Vaughan, p. 456 *non* Rafinesque and Clifford 1820, p. 234.
1929. *Cyathaxonia* Dutertre, p. 127 *non* Michelin 1847, p. 257.
1931. *Zaphrentis* Smith, p. 3 *non* Rafinesque and Clifford 1820, p. 234.
1931. *Caninia* Smith, p. 6 *non* Michelin 1840, p. 485.
? 1932. *Meniscophyllum* Gorsky, p. 11 *non* Simpson 1900, p. 199.
? 1933. *Amplexocarinia* Heritsch, p. 43 *non* Soshkina 1928, p. 379.
1934. *Meniscophyllum* Vojnovsky-Krieger, p. 12 *non* Simpson 1900, p. 199.
partim 1938-1941. *Zaphrentis* Hill, p. 135 *non* Rafinesque and Clifford 1820, p. 234.
partim 1942. *Rotiphyllum* Hudson; Hudson and Fox, p. 106.
partim 1944. *Rotiphyllum* Hudson, p. 356.
partim 1945. *Amplexus* Easton, p. 627 *non* Sowerby 1814, p. 165.
partim 1953. *Stereolasma* Fomichev, p. 96 *non* Simpson 1900, p. 205.
partim 1953. *Bradyphyllum* Fomichev, p. 120 *non* Grabau, 1928, p. 35.
partim 1953. *Stereophrentis* Fomichev, p. 141.
partim 1953. *Allotropiophyllum* Fomichev, p. 167 *non* Grabau 1928, p. 130.
partim 1953. *Thecophyllum* Fomichev, p. 175.
? 1961. *Allotropiophyllum* Fontaine, p. 63 *non* Grabau 1928, p. 130.
partim 1963. *Bradyphyllum* De Groot, p. 11, *non* Grabau 1928, p. 35.

? 1976. *Bradyphyllum* Guo, p. 67 *non* Grabau 1928, p. 35.
partim 1982. *Hapsiphyllum* Song, p. 24 *non* Simpson 1900, p. 203.
? 1984. *Bradyphyllum* Rodriguez, p. 132 *non* Grabau 1928, p. 35.
partim 1984. *Allotropiophyllum* Rodriguez, p. 214 *non* Grabau 1928, p. 130.
partim 1984. *Allotropiophyllum* Xu, p. 182 *non* Grabau 1928, p. 130.
? 1985. *Bradyphyllum* Zhao, p. 167 *non* Grabau 1928, p. 35.
partim 1986. *Eoamplexocarinia* Wang and Yu, p. 662.
partim 1986. *Rotiphyllum* Wu and Zhao, p. 658 *non* Hudson 1942, p. 257.
1989. *Amplexocarinia* Wu and Zhao, p. 39 *non* Soshkina 1928, p. 379.
1989. *Zaphrentites* Wu and Zhao, p. 41 *non* Hudson 1941, p. 309.
? 1992. *Bradyphyllum* Peng *et al*., p. 129 *non* Grabau 1928, p. 35.
1992. *Barrandeophyllum* Peng *et al*., p. 133 *non* Počta 1902, p. 190.
? 1999. *Neaxon* Rodriguez and Kullmann, p. 40 *non* Kullmann 1965, p. 81.
? 1999. *Zaphrentoides* Rodriguez and Kullmann, p. 76 *non* Stuckenberg 1895, p. 38.
partim 2003. *Pseudoamplexocarinia* Fan and Zhu, p. 229.
partim 2003. *Groenlandophyllum* Fan, p. 241 *non* Flügel 1973, p. 12.
2003. *Thecophyllum* Fan, p. 280 *non* Fomichev 1953, p. 175.

SPECIES ASSIGNED (in alphabetical order of species names: *Amplexus adnatus* Easton, 1945; ?*Bradyphyllum allotropiophylloidea* Peng *et al*., 1992; *Rotiphyllum cavum* Hudson 1944; *Zaphrentites crassus* Wu and Zhao, 1989 *non* Hudson, 1944; *Amplexus dilatus* Easton, 1945; *Zaphrentites* cf. *eniskilleni* Wu and Zhao 1989 *non* Milne- Edwards and Haime 1851; *Axisvacuus extendus* sp. nov.; *Stereophrentis fischeri* Fomichev; 1953; *Barrandeophyllum fuchengense* Peng *et al*., 1992; *Amplexus geniculatus* Worthen, 1890; *Stereolasma grande* Fomichev, 1953; *Rotiphyllum granulate* (Thomson) of Hudson and Fox, 1943; *Bradyphyllum kamyschnense* Fomichev, 1953; *Thecophyllum lebedevi* Fan 2003 non Fomichev 1953; ?*Stereophrentis mandrykinensis* Fomichev, 1953; *Hapsiphyllum meniscophylloides* Song, 1982; ?*Allotropiophyllum meniscophylloides* Xu (*In* Jia *et al*.), 1984; ?*Bradyphyllum minor* Xu, 1977; ? *Rotiphyllum monophylloides* Wang and Yu, 1986; *Neaxon*? *multitabulatus* Rodriguez and Kullmann, 1999; *Zaphrentis postuma* Smith, 1931; *Axisvacuus semicirculatus* sp. nov.; *Meniscophyllum uralicum* Vojnovsky-Krieger, 1934; *Axisvacuus verus* sp. nov.; *Amplexocarinia weiningensis* Wu and Zhao, 1989; ?*Groenlandophyllum xizangense* Fan, 2003; ?*Pseudoamplexocarinia yunnanensis* Fan and Zhu, 2003.

DIAGNOSIS: Antiphyllidae with rotiphylloid arrangement of major septa in early growth stages. Axial area permanently free from major septa in maturity, with cardinal protoseptum equal in length to remaining major septa. Tabularium normal. Microstructure of septa probably finely trabecular.

DISCUSSION: Microstructure is one of the most important diagnostic characters of species and genera of corals. Unfortunately, diagenetic alteration is advanced in most of the available corallites included in *Axisvacuus*, precluding direct and undisputable documentation of trabeculae. This is especially important in the type species of the genus. Diagenetic alterations and a reconstruction of the original microstructure are therefore discussed under *A. verus*. Arguments presented in that discussion and the occurrence of remnants of trabeculae in septa of other species allowed the diagnosis that the microstructure in *Axisvacuus* was probably trabecular.

Species name	N:d values	Major septa	Minor septa	Counter septum	Cardinal fossula	Free axial area	External wall
verus sp.nov.	25-30: 9-14	Thin, short	At calice margin	Equal to Cl in most	Inconspicous	1/4-1/2 radius	1/4-1/3 radius
postumus Smith, 1931	20-23: 4.5-7.5	Some rhopaloid	Absent*	Equal to Cl in most	Inconspicous	1/5-1/4 radius	1/3-1/9 radius
extendus sp.nov.	20-22: 5.5	Long rhopaloid	Short in lumen	Slightly elongated	Distinct wide	1/10-1/8 radius	1/18 radius
semicirculatus sp.nov.	24-25: 8.5-10	Rhopaloid	Absent*	Equal to Cl	Key hole	1/7-1/5 radius	1/6-1/5 radius

* Absent means that calice margin is not preserved and minor septa are absent from corallite lumen

Main characters of particular species of *Axisvacuus* studied

Several taxa resembling *Rotiphyllum* Hudson, 1942 in their most important diagnostic characters are distinguished from that genus by their axial areas being free from major septa. The possibility of differentiating, at the genus level, those with their major septa united at the corallite axis from those in which the inner margins of the major septa are never united at maturity, has already been mentioned (Fedorowski 2004, p. 77). However, the single specimen available for that study, described earlier by De Groot (1963, p. 14) as *Bradyphyllum* sp. no. 2, was inadequate for the introduction of a new taxon. Indeed, such taxa can easily be confused with *Bradyphyllum* Grabau, 1928, if the length of the cardinal protoseptum is not considered. In the latter genus, the cardinal protoseptum is shortened in transverse sections cut below the calice floor but consistently equal to adjacent major septa in *Rotiphyllum*. That character is strikingly constant in both of those genera despite their almost cosmopolitan distribution and long history. The oldest known representative of *Bradyphyllum*, i.e. *B. differentiatum* Fedorowski, 1973, was collected from the *Wocklumeria* or *Gattendorfia* Biozone of the Holy Cross Mountains, Poland (Fedorowski 1973). Its identification may be considered doubtful and hence this earliest appearance is omitted. Nevertheless the genus or bradyphylloid morphotypes are common in the Lower Carboniferous, and range into the Lower Permian of southwestern Texas, USA (Fedorowski 1987), while type species was described from Middle Carboniferous strata of China (Grabau 1928). Its zaphrentoid neanic growth stage and shortened cardinal protoseptum suggest derivation from taxa similar to or belonging to *Zaphrentites* Hudson, 1941. On the other hand, the long stratigraphic range and wide geographic distribution of *Bradyphyllum* may be indicative of a polyphyletic status, rather than the monophyletic relationships between species currently included in that genus.

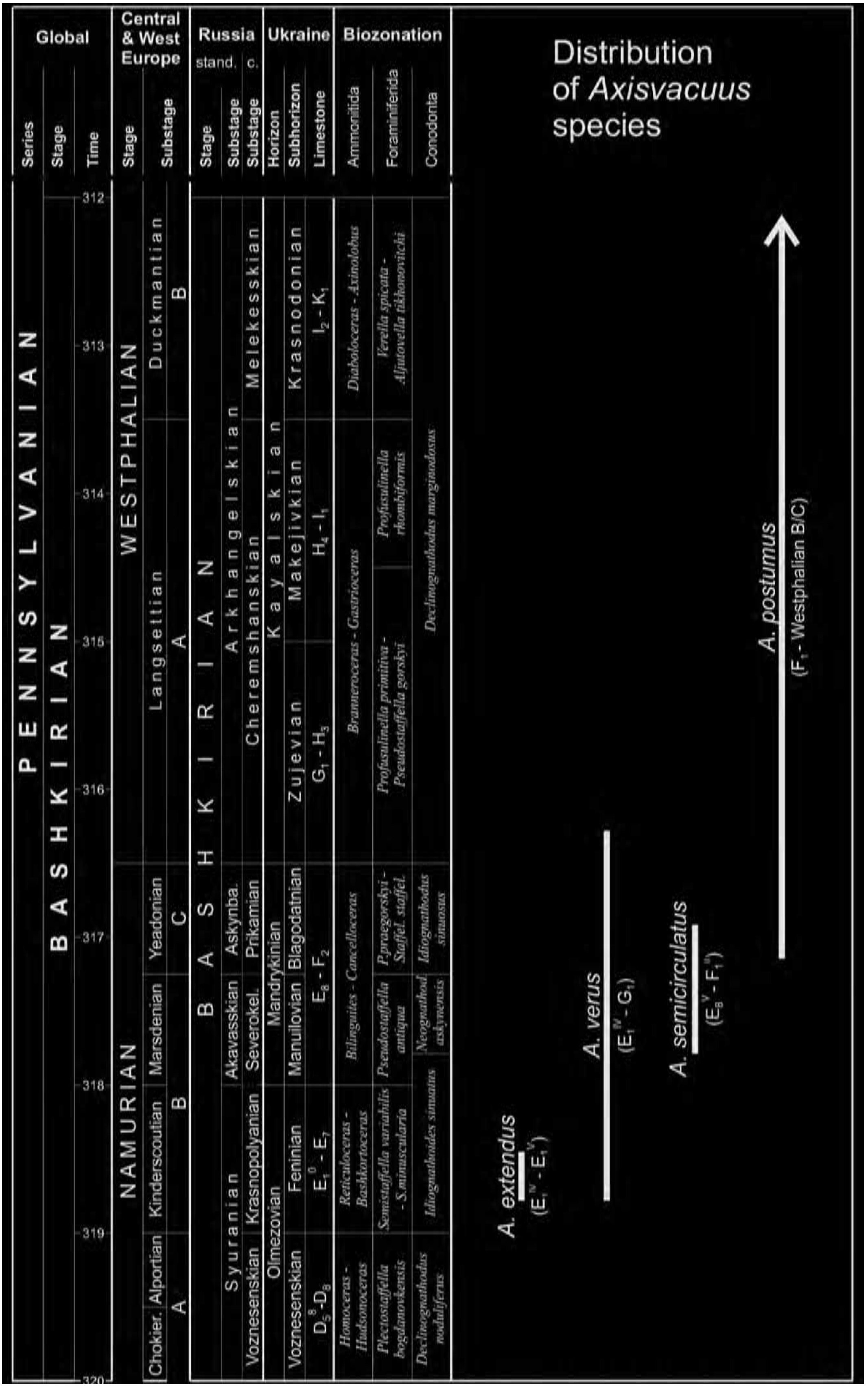
The stratigraphic range and geographic distribution of *Axisvacuus*, although narrower than those of *Bradyphyllum*, are wide enough to suggest a possible polyphyletic origin. That objection has already been raised in the remarks on *Rotiphyllum* (Fedorowski, 2009*a*). *Axisvacuus* may have been derived several times from one or several *Rotiphyllum*-like lineages. However, that option requires the introduction of several genera characterized by almost identical diagnostic skeletal features, and is therefore considered as a most improbable scenario for the fossil record. At present, the best procedure appears to be grouping together species having a rotiphylloid early ontogeny and a cardinal protoseptum equal in length to other amplexoidally shortened major septa at maturity.

An alternative method is to ignore the amplexoid morphology of some species and to consider them equal at the genus level with those having their major septa permanently united axially. This is, in my opinion, contrary to general taxonomic practice in the study of rugose corals, based on their predicted genetics and physiology. First of all, permanent and equal shortening of the protosepta and major septa at maturity requires genetic control. Secondly, such a shortening would cause changes in the physiology of the polyp, which must be genetically controlled as well. Such a double genetic control, although only predicted, cannot be ignored when the taxonomy of fossil animals is reconstructed.

Rotiphyllum may have appeared in the Late Tournaisian and was probably derived from an ancestor in common with *Zaphrentites* Hudson, 1941. This may have been *Zaphrentoides* (*Hapsiphyllum*) of Kullmann, 1965 but that is an open question. That taxon, described from Eifelian strata of northern Spain (Kullmann 1965), is so isolated in time from the occurrence of Carboniferous *Zaphrentites* that a direct relationship between them is doubtful.

The close similarity in the early neanic growth stages of *Zaphrentites* and *Rotiphyllum* is indisputable. In *Rotiphyllum*, however, the cardinal protoseptum remains long, thus retaining its neanic character up to and including the mature calice floor, whereas in *Zaphrentites* it shortens in the late neanic or early mature growth stage. Two opposite trends in the development of the counter protoseptum support separation of the lineages of these genera. The counter protoseptum in the *Rotiphyllum* lineage either remained equal to the counter-lateral septa or became elongated, leading towards *Monophyllum* Fomichev, 1953, whereas it tended to shorten in the phylogenetically advanced representatives of the *Zaphrentites* lineage. The disintegration of the inner margins of septa was a trend common to both *Zaphrentites* and *Rotiphyllum*. From *Zaphrentites* it led to *Ufimia*-like taxa (Fedorowski, in preparation) and, perhaps, to *Ufimia* Stuckenberg, 1895; and from *Rotiphyllum* it led to *Axisvacuus*.

Detailed study of *Axisvacuus verus* (see below) has shown that not only *Bradyphyllum* but also *Amplexocarinia* Soshkina, 1928, *Barytichisma* Moore and Jeffords, 1945 and *Pseudoamplexocarinia* Fan and Zhu, 2003 should be theoretically taken into account when the relationships *vs*. homeomorphy of the genus *Axisvacuus* are discussed. The advanced mature growth stage of *A. verus* can apparently be correctly identified as *Amplexocarinia*. The same is true for many Middle Devonian to Late Permian species that were


Global
Series
Stage
Time
Central & West Europe
Stage
Substage
Russia
stand.
c.
Stage
Substage
Substage
Ukraine
Horizon
Subhorizon
Limestone
Biozonation
Ammonitida
Foraminiferida
Conodonta
Distribution of *Axisvacuus* species
312
313
314
315
316
317
318
319
320
PENNSYLVANIAN
BASHKIRIAN
WESTPHALIAN
NAMURIAN
Duckmantian
B
Langsettian
A
Yeadonian
C
Marsdenian
Kinderscoutian
B
Alportian
A
Chokier.
BASHKIRIAN
Arkhangelskian
Askynba.
Akavasskian
Syuranian
Melekesskian
Cheremshanskian
Prikamian
Severokel.
Krasnopolyanian
Voznesenskian
Kayalskian
Mandrykinian
Olmezovian
Krasnodonian
Makejivkian
Zujevian
Blagodatnian
Manuilovian
Feninian
Voznesenskian
I_2 - K_1
H_4 - I_1
G_1 - H_3
E_8 - F_2
E_1^0 - E_7
D_5^8-D_8
Diaboloceras - Axinolobus
Branneroceras - Gastrioceras
Bilinguites - Cancelloceras
Reticuloceras - Bashkortoceras
Homoceras - Hudsonoceras
Verella spicata - Aljutovella tikhonovichi
Profusulinella rhombiformis
Profusulinella primitiva - Pseudostaffella gorskyi
P. praegorskyi - Staffel. staffel.
Pseudostaffella antiqua
Semistaffella variabilis - S. minuscularia
Plectostaffella bogdanovkensis
Declinognathodus marginodosus
Idiognathodus sinuosus
Neognathod. askynensis
Idiognathoides sinuatus
Declinognathodus noduliferus
A. extendus
(E_1^{IV} - E_1^{V})
A. verus
(E_1^{IV} - G_1)
A. semicirculatus
(E_8^{V} - F_1^{0})
A. postumus
(F_1 - Westphalian B/C)

identified as *Amplexocarinia* by many authors [e.g., Heritsch (1937, 1939), Moore and Jeffords (1945), Fomichev (1953), De Groot (1963), Fedorowski (1965), Różkowska (1969), Rodriguez (1984), Rodriguez and Kullmann (1999), Fan *et al.* (2003)]. Their identifications were based on a comparison of mature morphological features with the existing information on *Amplexocarinia muralis* Soshkina, 1928, whereas the microstructure of septa and external walls and the ontogeny of their corals were either unknown (in most instances) or ignored.

The grouping together of superficially similar specimens has been almost classic in rugose coral studies. It was repeated in many 'genera', including such widely known ones as *Amplexus* Sowerby, 1814, *Zaphrentis* Rafinesque and Clifford, 1820, *Cyathophyllum* Goldfuss, 1826, and *Caninia* Michelin, 1840. Individual components of those 'genera' were not only separated afterwards, but were sometimes included in different suborders when thoroughly studied. This will most probably be the future fate of *Amplexocarinia*, which has currently replaced *Amplexus* in the role of 'waste basket'. The inclusion by De Groot (1963, pl. 2, figs 1–3) of very different specimens in the same species of *Amplexocarinia* is a good example.

The revision by Fedorowski (1986a, text-fig. 18.1) of the type collection of *A. muralis* Soshkina, 1928 has shown that exclusively mature fragments of three specimens are present in that collection. Thus, the early ontogeny of the type species of the genus remains unknown. Nevertheless, the following important data have become available since that revision (Fedorowski 1986a, p. 217): 1. The microstructure of the primary septa is finely trabecular, 2. The protosepta are indistinguishable from the other major septa in length and thickness and no cardinal fossula exists, 3. The 'aulos', seen in transverse section, is composed mainly of deflected inner margins of septa supplemented by peripherally-dipping tabulae. Thus, it differs substantially from the 'aulos' composed of a continuous series of downturned axial tabellae, attributed to that genus by Soshkina (1928) and most authors dealing with *Amplexocarinia*-like corals. A new name for the latter kind of circumaxial structure was recently proposed by Fedorowski (2009b).

Some coral specialists (e.g., Rodriguez and Kullmann 1999) have already expressed their doubts concerning the existing species content of *Amplexocarinia*. In this paper the next step forward is made. It is here proposed to abandon the generic name *Amplexocarinia* Soshkina, 1928 until a well established Permian topotype collection of *A. muralis* is thoroughly studied in all the aspects required for a complete definition of the genus. The possibility of *Axisvacuus* being a junior synonym of the re-interpreted *Amplexocarinia* is not excluded here. However, it seems more logical to introduce a new genus, based on a completely studied type species rather than duplicating very probable errors.

Barytichisma Moore and Jeffords, 1945 is mentioned herein because Weyer (1965) considered *Thecophyllum* Fomichev, 1953 to be its junior synonym, whereas the latter taxon bears some characters in common with specimens described below as *Axisvacuus verus*. The early ontogeny of the type species of *Barytichisma* was adequately studied and illustrated by Moore and Jeffords (1945) and Sando (1965). The diagnosis by Hill (1981) can therefore be accepted with minor changes. Shortening of the cardinal protoseptum in transverse sections made well beneath the calice floor is one of the most important characters of *Barytichisma* in the present context. Thus, the difference at the genus level between *Barytichisma* proper and *Axisvacuus* is obvious and cannot be questioned.

The inclusion of *Thecophyllum* Fomichev, 1953 in synonymy with *Barytichisma* was accepted by Hill (1981), but an alternative interpretation, i.e., a close relationship between *Thecophyllum* and *Axisvacuus* cannot be excluded. The cardinal protoseptum in the holotype of *Thecophyllum lebedevi* Fomichev, 1953, the type and only species included in *Thecophyllum*, remains equal in length to the adjacent major septa during most of its ontogeny (Fomichev 1953, pl. 7, fig. 15a-v). In the late neanic or early mature growth stage illustrated by that author (pl. 7, fig. 15g) it is shortened, but equal to the two adjacent major septa, whereas it seems to be strongly shortened in the fully mature growth of the holotype (pl. 7, fig. 15d). However, that short major septum could be either the cardinal protoseptum, as suggested by Fomichev, or simply the last septum inserted in the left cardinal quadrant. Only the first option places *Thecophyllum* in synonymy with *Barytichisma*, whereas *Thecophyllum* should be accepted as valid, if its cardinal protoseptum remains long up to and including the calice floor. If the latter is true, *Axisvacuus* may be a younger synonym of *Thecophyllum*.

Table 1. Litho- and biostratigraphic schemes of the Bashkirian Stage in Eastern Ukraine with references to the Russian and western European standards, and the vertical ranges of the *Axisvacuus* species studied. Abbreviations: Chokier. – Chokierian, *Neognathod. – Neognathodus, P – Pseudostaffella, S. – Semistaffella,* Severokel. – Severokeltmenian, *Staffel. staffel. – Staffelleformes staffelleformis*

Unfortunately, very little is left of the holotype of *T. lebedevi* after thin sectioning. Thus, those remnants, examined by myself years ago, do not allow a firm solution to the question. Taking into account both Weyer's (1965) opinion and data available from the holotype of *T. lebedevi*, that specimen, and thus the species, is accepted as a representative of *Barytichisma*. Consequently, *Thecophyllum* was included in synonymy with the latter genus. However, in some paratypes of *Thecophyllum lebedevi* (Fomichev 1953, pl. 7, figs 13, 18), the cardinal protoseptum is long in the amplexoid mature growth stage, suggesting a possible synonymy with *Axisvacuus*.

The genus *Eoamplexocarinia* Wang and Yu, 1986 may also have priority over *Axisvacuus*, but a rotiphylloid early growth stage and a long cardinal protoseptum, equal to the remaining major septa at maturity, were not documented in that Chinese taxon. Specimens from the same collection, included by Wang and Yu (1986) in *Rotiphyllum* Hudson, 1942 and *Meniscophyllum* Simpson, 1900 have long cardinal septa. These may be immature individuals of *Eoamplexocarinia*, but such an option cannot be proven on the existing data. They were therefore included in *Rotiphyllum* (Fedorowski, 2009a).

Wu and Zhao (1989) described the new species *Amplexocarinia weiningensis* but did not mention *Eoamplexocarinia*. That species is included here in *Axisvacuus* together with two species identified by Wu and Zhao (1989) as belonging to European species of *Zaphrentites*. All diagnostic characters of those three species correspond to the diagnosis of *Axisvacuus*.

Fan *et al*. (2003) introduced the new genus *Pseudoamplexocarinia* from the Upper Carboniferous of western Yunnan Province, southern China, and included two species in that genus. *Pseudoamplexocarinia elegans*, the type species of the genus, was diagnosed as having 'two alar septa long, thick and prominently rhopaloid'. This character can be distinguished in one thin section (Fan *et al*. 2003, pl. 13, fig. 1b), but is absent from both the earlier and later ontogeny of that specimen. Besides this, a large middle area of the corallite is diagenetically altered and has lost all original structures. The true taxonomic position of such a poorly preserved specimen is impossible to establish. A better preserved holotype and the only corallite of *P. yunnanensis* displays several characters of *Axisvacuus* and is provisionally included in that genus.

The holotype of *Groenlandophyllum xizangense* Fan, 2003 from the Viséan Yunzhug Formation of Tibet (Xizang) bears all the main characters of *Axisvacuus*, including major septa equally shortened in maturity and a long cardinal protoseptum (Fan *et al*. 2003, pl. 16, fig. 1a–d). It is included in *Axisvacuus* questionably because its characters look too complex for such a phylogenetically early species. The paratype of that species, illustrated from a probably immature growth stage (Fan *et al*. 2003, pl. 16, fig. 2a–c) has an elongated counter protoseptum and probably represents a different species and genus.

The corallite identified by Fan (in Fan *et al*. 2003, p. 280, pl. 13, fig. 7a,b) as *Thecophyllum lebedevi* Fomichev bears all the main diagnostic characters of early and late maturity of *Axisvacuus*. It differs from most species included here in the latter genus in a long-lasting axial connection of its major septa, thus resembling *Rotiphyllum*.

In addition to the genera discussed above with regard to their similarity to *Axisvacuus* there are several species, originally included by authors in various genera that may belong to that genus. '*Zaphrentis*' *ambigua* Carruthers, 1908 from the Lower Viséan of Britain is one of the oldest representatives of *Axisvacuus*. In contrast to '*Densiphyllum*' (=*Rotiphyllum*) *rushianum* Vaughan, 1908 and '*Zaphrentis*' (=*Rotiphyllum*) *omaliusi* Milne Edwards and Haime, 1851 *'Z.' ambigua* has seldom been mentioned in the literature. Also, it remains uncertain from Carruthers' (1908, pl. 4, fig. 6) illustration whether the disintegration of the septa is permanent or temporary. Nevertheless, characters available from the literature data support its assignment to *Axisvacuus*. It is well documented that *Rotiphyllum rushianum cavum* Hudson, 1944 (pl. 57, fig. 1), elevated here to species level as *R. cavum*, has a permanent 'aulos' and biformly reduced (Weyer's 1974 term) minor septa. It resembles '*Permia*' *caverna* (Hudson, 1944, pl. 56, fig. 3) in most characters except for the free minor septa in the latter. The occurrence of a biform tabularium, demonstrated by sections of peripheral parts of tabulae in the latter species, may indicate a relationship between those two species. However, the biform tabularium eliminates them from the *Rotiphyllum – Axisvacuus* lineage.

Cyathaxonia of Dutertre (1929, p. 127, pl. 2, figs 7, 8) was illustrated by two polished surfaces of its mature growth stage. Thus, its synonymy with *Axisvacuus* can only be suspected. The absence of a columella and contratingent minor septa eliminates Dutertre's (1929) specimens from *Cyathaxonia*, whereas the cardinal and the counter protosepta, equal in length to the remaining major septa and withdrawn from the corallite axis, point towards *Axisvacuus.*

'Zaphrentis' postuma Smith, 1931 and ?*Caninia cornucopiae* Michelin of Smith (1931) are the only

representatives of *Axisvacuus* known so far from the *Donetzoceras aegiranum* Biozone (Westphalian B/C, Bashkirian) of northwestern and central Europe. The morphological similarity of both those taxa to the Donets Basin specimens described in this paper is discussed below in the remarks on *Axisvacuus postumus*. *Zaphrentis* aff. *postuma* Smith of Demanet (1938), represented by two corallites and briefly revised for the purpose of this paper (the complete, illustrated revision will be published separately), belongs to *Bradyphyllum* Grabau, 1928.

Vojnovsky-Krieger (1934) described a rich rugose coral fauna from the lowermost Viséan of the South Urals. *Meniscophyllum uralicum aperta* Vojnovsky-Krieger, 1934 probably belongs to the genus *Axisvacuus*, as suggested by its long cardinal protoseptum, the rotiphylloid arrangement of its major septa in early growth stages and their permanent withdrawal from the corallite axis in maturity. The sclerenchymal arch connecting the inner margins of major septa in the counter quadrants, resemble that of *Meniscophyllum*, but other characters of *M. uralicum aperta* follow the diagnosis of *Axisvacuus*. Also, this arch closely resembles that in the holotype of *Axisvacuus verus* (see below). Thus, Vojnovsky-Krieger's (1934) specimens are included in that genus as one of the stratigraphically oldest species.

Schindewolf (1952) described several species from the Lower Namurian (*Eumorphoceras* Biozone) marine 'horizons' present in the Polish Upper Silesia mines. Two of those species, or some specimens included in them, resemble *Axisvacuus*. That morphological similarity is discussed by Fedorowski (in preparation) in a paper on Late Serpukhovian rugose corals from the Czech Republic side of the Upper Silesian Coal Basin.

There are several new species or specimens of individual species, included by Fomichev (1953) in *Allotropiophyllum* Grabau, 1928, *Bradyphyllum* Grabau, 1928, *Stereolasma* Simpson, 1900 and *Stereophrentis* Fomichev, 1953, that exhibit characters of *Axisvacuus*. Only those species illustrated to the extent of allowing recognition of the immature morphology are here included in the new genus. Species illustrated by Fomichev (1953) by single transverse sections were omitted from the discussion, although some of them may belong to *Axisvacuus*.

In the order described by Fomichev (1953), the reidentified species are: *Stereolasma*? *tripoliense*, the holotype of which has major septa that are strongly rhopaloid, but free axially beginning with the late neanic or early mature growth stage. In early ontogeny its axial area is filled in with sclerenchyme (Fomichev 1953, pl. 4, fig. 3b,v). The rhopaloid character of the major septa in that corallite depends on their position with respect to the tabulae; they thin just below a tabula and are thickest along its upper surface. An effect similar to that is described below with *A. verus*. Elongated, but not contratingent minor septa adjacent to the counter protoseptum form the next peculiarity of Fomichev's (1953) specimen. They persist up to the calice, where they flank the thin counter septum on both sides (Fomichev 1953, pl. 4, fig. 3zh). The character makes the holotype of '*Stereolasma*'? *tripoliense* different not only from other species here included in *Axisvacuus*, but also from the paratypes of that species, which resemble *Axisvacuus postumus* and probably belong to that species (see below).

Three new species of *Bradyphyllum*, namely *B. oppositum, B.*? *slavianovi* and *B. kamyshnense* of Fomichev (1953), have doubtful generic affinities. The first species was recently discussed by Fedorowski (2004) and left in *Bradyphyllum* with a question mark. That opinion is not changed herein, although a slight shortening of the cardinal protoseptum in the holotype of that species is recognizable in a single transverse section (Fomichev 1953, pl. 5, fig. 6v).

The holotype of *B.*? *slavianovi* closely resembles *B. oppositum* and may represent an early mature growth stage of that species. However, its cardinal protoseptum remains equal to other major septa, which fall short of the corallite axial area. Thus, a relationship to *Axisvacuus* is equally possible. The latter option is supported by the morphology of the paratype of *Bradyphyllum*? *slavianovi* (Fomichev 1953, pl. 5, fig. 9), which closely resembles transverse sections of "*Stereophrentis*" *postuma* forma *mandrykinensis* Fomichev, 1953, here included in *Axisvacuus*.

Two illustrated paratypes of *Bradyphyllum kamyshnense* Fomichev, 1953 have shortened cardinal protosepta (Fomichev 1953, pl. 5, figs 11, 13) and most probably belong to *Bradyphyllum*, but the holotype and one paratype have those protosepta equal to other major septa (Fomichev 1953, pl. 5, figs 10, 12) and are here included in *Axisvacuus*.

Probably none of the species included by Fomichev (1953) in *Allotropiophyllum* Grabau, 1928 belongs to that Chinese Permian genus. *Allotropiophyllum sniatkovi* Fomichev, 1953, with the cardinal protoseptum shortened in maturity and the corallite axial area free from major septa (Fomichev, 1953, pl. 7, fig. 8a–zh), belongs to *Bradyphyllum*. The same may be true for the holotype and one illustrated paratype of *A. irregulare* Fomichev (1953, pl. 7, figs 9, 11), whereas the other two paratypes (Fomichev, 1953, pl. 7, figs 10, 12) show the main characteristics of *Axisvacuus* in the illustrated transverse sections. Unfortunately, illustrations are restricted to one per specimen. Such incomplete documentation allows only conditional inclusion of those specimens in *Axisvacuus*.

A large number of specimens, grouped into several species, were included by Fomichev (1953) in his new genus *Stereophrentis*, with "*Zaphrentis*" *delanouei* Milne Edwards and Haime, 1851 as the type species. That designation allowed Hill (1981, p. F316) to correctly synonymize *Stereophrentis* with *Zaphrentites* Hudson, 1941. As with species discussed in the preceding paragraphs, Fomichev (1953) did not draw enough attention to the length of the cardinal protoseptum in transverse sections made below and above a calice floor, i.e., he did not specify whether that protoseptum extended to the corallite axis along the cardinal fossula or not. As a result, some species included by him in *Stereophrentis* fulfill the diagnosis of *Zaphrentites*, whereas the others follow the diagnosis of either *Rotiphyllum* or *Axisvacuus*. Discussion of the latter is included below with the remarks on *A. verus* sp. nov.

The above discussion may suggest either (a) low diagnostic value for the length of the cardinal protoseptum; or (b) a close similarity between the mature morphology of some different species and genera, difficult to recognize without a careful study of specimens based on many sections. The second option is accepted here although recognition of relationships of some fossil taxa may remain disputable and decisions subjective.

The length of the cardinal protoseptum is correctly accepted as diagnostic for many genera and is characteristic at the family level in the suborder Plerophyllina. I see no reason to ignore that character as a generic indicator in other suborders of the order Stauriida Verrill, 1865 when it is constant in the mature morphology of specimens.

Rodriguez (1984, text-fig. 43, pl. 1, figs 8, 9) followed De Groot (1963) in identifying two specimens from Asturias (northern Spain) as *Bradyphyllum oppositum* Fomichev. He illustrated only the corallite from the Upper Bashkirian and only that is considered here. Fedorowski (2004) questioned the generic status of all Spanish specimens included in *B. oppositum*. All those specimens have their cardinal protosepta permanently equal in length to the other major septa and are here included in *Axisvacuus*. This is obvious from the illustration by Rodriguez (1984, text-fig. 43) and was confirmed by Fedorowski (2004) who corrected De Groot's (1963) opinion regarding slight shortening of the cardinal protoseptum in her specimen. That shortening took place only above the calice floor and cannot be considered diagnostically important as such. The long-lasting axial connection of the major septa and the narrow axial area free from septa reached in late maturity of the specimen illustrated by Rodriguez (1984, text-fig. 43) are characters distinguishing the Spanish specimens from the type species of *Axisvacuus*. The microstructure of the Spanish specimens is unknown. That illustrated by Rodriguez (1984, text-fig. 42) cannot be considered primary. The arrangement of calcite fibrils oblique to the septum surface indicates diagenetic alteration.

Also, characters described and illustrated by Rodriguez (1984) in his *Allotropiophyllum* cf. *irregulare* Fomichev, 1953 and *A. sniatkovi* Fomichev, 1953 correspond to those of *Axisvacuus*, in which they are here included. *Allotropiophyllum* sp. of Rodriguez, 1984, with its long septa**,** corresponds to *Rotiphyllum.*

Jia *et al*. (1984) described several species, which they included in *Allotropiophyllum* Grabau, 1928. Illustrations of most of those species are either incomplete or inadequate for a reliable identification or exhibit characters other than those accepted for *Axisvacuus*. Such specimens are omitted from this discussion. Only *Allotropiophyllum meniscophylloides* Xu, illustrated in the early and mature growth stages and in the lower part of the calice (Jia *et al*. 1984, pl. 18, fig. 5a–c), exhibits characters typical of *Axisvacuus* and is here included in that genus.

Several specimens described by Peng *et al*. (1992) as *Amplexocarinia, Bradyphyllum* and *Barrandeophyllum* may belong in *Axisvacuus*. Their *Amplexocarinia asturia* Rodriguez is most doubtful among those species and is not included in the synonymy above. *Bradyphyllum allotropiophylloidea* was better documented, although some doubts remain concerning the length of the cardinal protoseptum. Thus, it is included in the synonymy with a question mark. Data concerning *Barrandeophyllum fuchengense* are considered convincing enough (Peng *et al*. 1992, pl. 13, figs 13, 14) to include this taxon in synonymy with *Axisvacuus* and in the list of species above.

Axisvacuus verus sp. nov.
(Text-figs 5–9)

HOLOTYPE: Specimen UAM-Tc.Don.1/42, illustrated in Text-fig. 7$A_{1\text{-}13}$. Six thin sections and nine peels were studied.

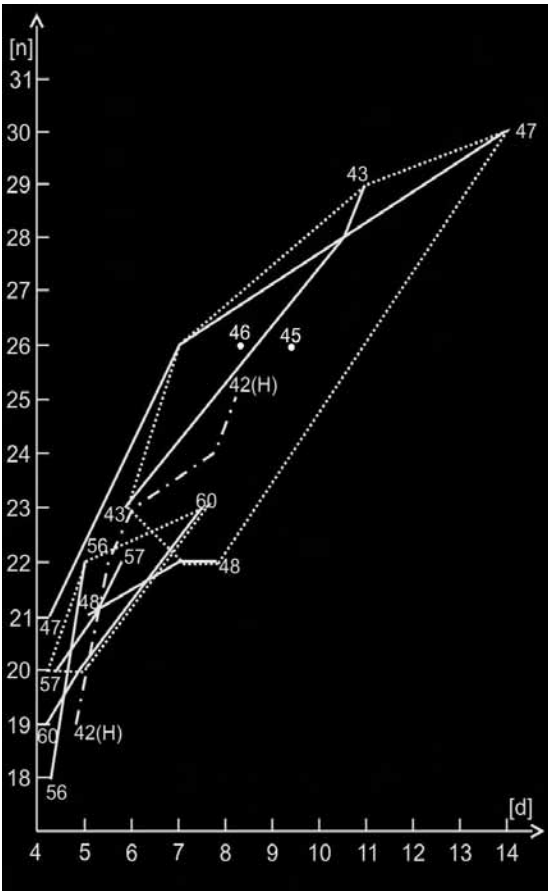
TYPE LOCALITY: Solenaya River Area, Novo Troitskoe Village, Sazanova Ravine (Balka).

TYPE HORIZON: Limestone F$_1$, Mandrykinian Horizon, upper Lower Bashkirian.

ETYMOLOGY: *Lat. verus, a, um* – true, reliable – typical representative of the genus.

MATERIAL: Holotype (UAM-Tc.Don.1/42) and thirteen paratypes (UAM-Tc.Don.1/43–1/55). Several specimens almost complete and well preserved except for diagenetically altered microstructure. Most of those specimens were illustrated in Text-figs 6, 8, 9. Forty-four thin sections and eighty-eight peels were available for study. Number of major septa vs. corallite diameter in representative specimens shown in Text-fig. 5.

DIAGNOSIS: *Axisvacuus* with n:d values of 25:9.0 mm (holotype) to 30:14.0 mm near calice floor; external wall 1/4-1/3 corallite radius in thickness with shallow septal grooves and growth striae; major septa rhopaloid in late neanic growth stage; at maturity thin, equally shortened, radially arranged; minor septa seen only close to calice margin; tabulae complete, flat-topped, highly elevated from periphery.



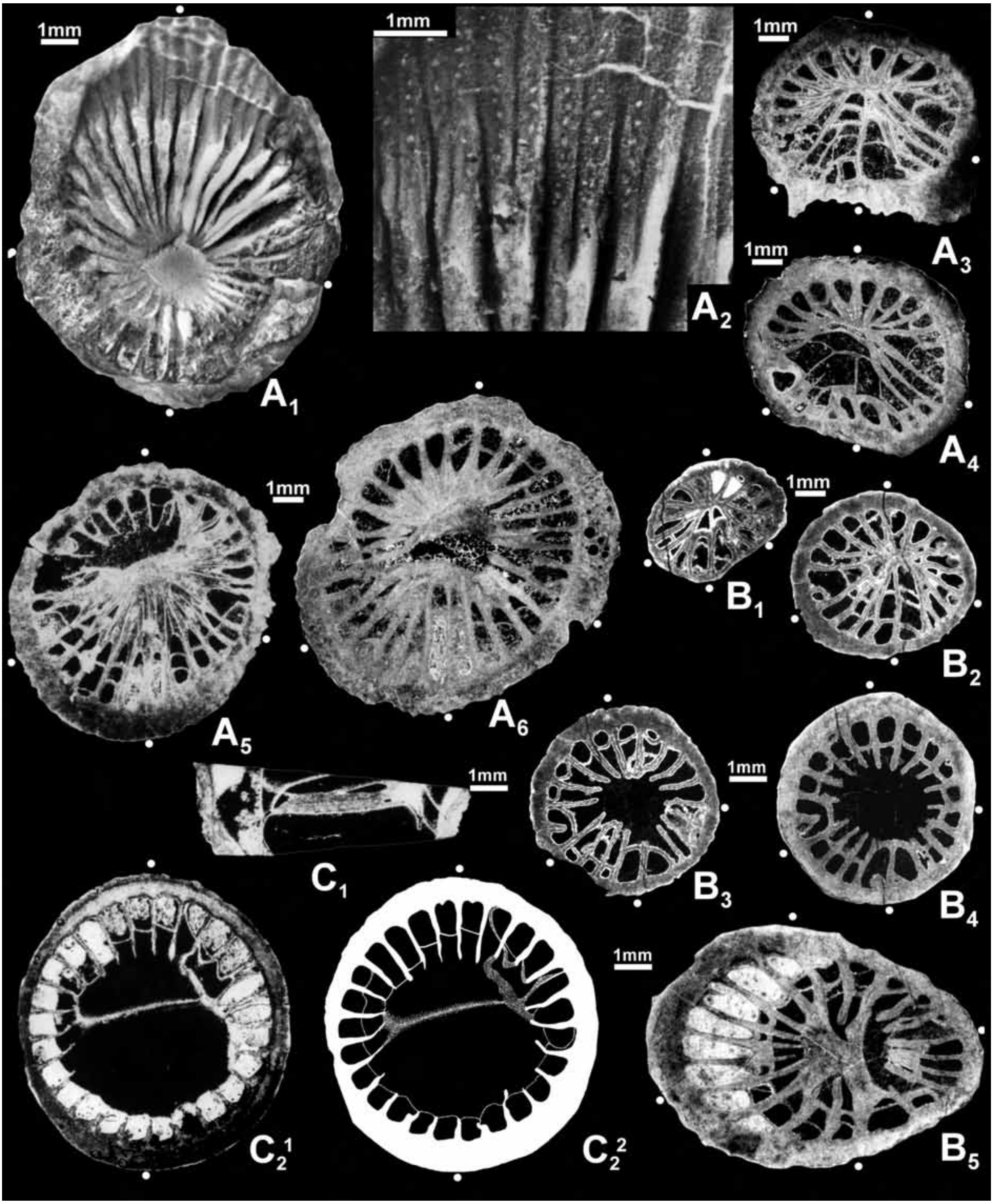
Text-fig. 5. *Axisvacuus verus* sp. nov. (numbers 42–48) and *Axisvacuus postumus* (Smith 1931) (numbers 56–60). Number of major septa (n) *vs.* corallite diameter in mm (d). Lines join values taken from individual transverse sections of specimens. Numbers at both ends of each line = number of the measured specimen. Extreme mature n:d values contoured by dotted lines to show differences in measurements between *A. verus* and *A. postumus*

DESCRIPTION OF CALICE: The extraordinarily well preserved fragments of the calice in one paratype (Text-fig. 6A$_{1,2}$) allow documentation of the most important characteristics of the genus *Axisvacuus*. It also shows desmocyte scars (see below). Its morphology is therefore described separately and is considered characteristic of the species and genus, albeit it shows major septa longer than those of the holotype of the type species.

The inner surface of the uppermost part of the calice is folded into almost equally developed, laterally contiguous bases of the major and minor septa, suggesting development of a septotheca. Septal bases of both cycles pass gradually into the septal blades, with those of the minor septa forming only low and short-lived ridges in the upper part of the calice (Text-fig. 6A$_{1,2}$). Blades of the almost radially arranged major septa are comparatively short along the calice wall, making the calice large and empty. Their thin inner margins either elongate slightly along the horizontal and flat axial parts of tabulae or terminate abruptly at their border. The cardinal protoseptum is equal to the remaining major septa and is barely recognizable. The morphology of the calice precludes the occurrence of an aulos, albeit a temporary "aulos"-like structure may occur in transverse sections of some species of *Axisvacuus* (e.g. Text-figs 6C$_2$, 7A$_{12}$, 8B$_5$).

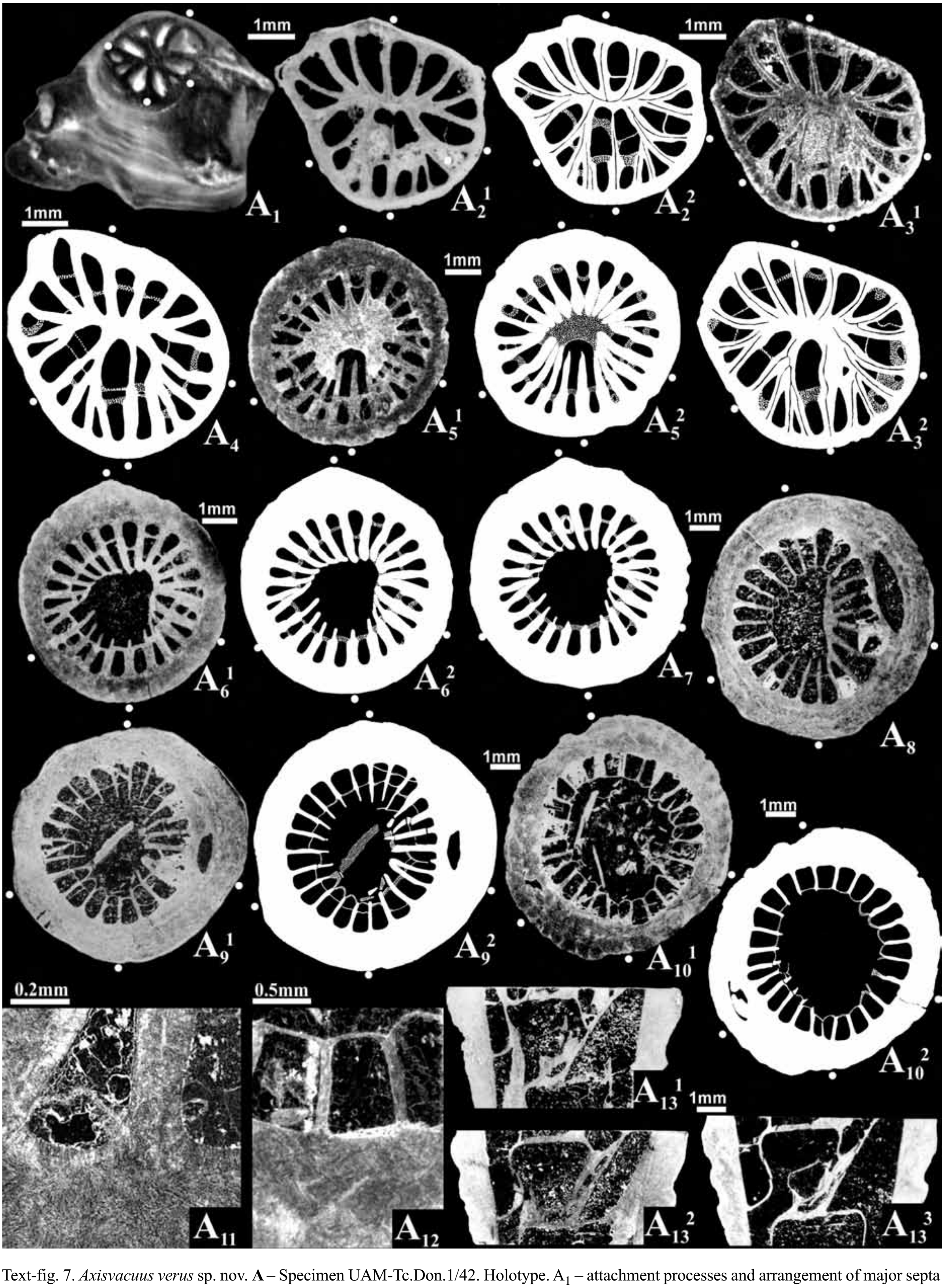
Rows of small depressions or holes (Text-fig. 6A$_2$), occurring between septal bases and blades of both cycles, are interpreted as desmocyte scars, similar to those described by Ilina (1984) as impressions of trabeculae and first re-interpreted by Fedorowski (1986b) as scars. This character, seldom observed in the Rugosa, confirms the occurrence of mesenteries corresponding to both septal cycles.

DESCRIPTION OF HOLOTYPE: This corallite was attached by strong attachment protrusions or tubes to a hard substrate (Text-fig.7A$_1$). The counter protoseptum is located between those protrusions and the cardinal protoseptum occurs on the slightly convex side of the corallite (upper right in the picture). Septal fur-



Text-fig. 6. *Axisvacuus verus* sp. nov. **A** – Specimen UAM-Tc.Don.1/43. Paratype. A_1 – calice. A_2 – upper part of calice; very short blades of minor septa and desmocyte scars between them and major septa, A_3 – late neanic growth stage, A_4 – late neanic/early mature growth stage (peel), $A_{5,6}$ – mature growth stage. **B** – Specimen UAM-Tc.Don.1/44. Paratype. $B_{1,2}$ – neanic growth stage, $B_{3\text{-}5}$ – mature growth stage. Note diagenetically shortened cardinal protoseptum in B_3. **C** – Specimen UAM-Tc.Don.1/45. Paratype. C_1 – longitudinal section, C_2 – mature growth stage.

Remarks to Text-figs 6-14: Transverse thin sections, except where stated. Scale bars common for two or more adjacent photos. Protosepta and alar septa marked by dots. Cardinal protoseptum at the bottom, except when stated. Computer drawings added to photographs when necessary. Both bear the same main numbers, but are distinguished by superscripts 1 and 2. Occurrences of individual specimens, listed after corresponding description of species in text, are not repeated in figure captions



Text-fig. 7. *Axisvacuus verus* sp. nov. **A** – Specimen UAM-Tc.Don.1/42. Holotype. A_1 – attachment processes and arrangement of major septa in early ontogeny (cardinal protoseptum upward), $A_{2\text{-}4}$ – neanic growth stage (A_2 – peel), $A_{5\text{-}10}$ – early to advanced mature growth stage, all below calice floor ($A_{8,\ 9}$ peels), A_{11} – diagenetically altered external wall and major septa, A_{12} – sections of tabulae imitate aulos, A_{13} – successive longitudinal sections from eccentric ($A_{13}{}^1$) to exactly axial ($A_{13}{}^3$) ($A_{13}{}^{1,2}$ peels). See Remarks at Text-fig. 6 for further explanations rows and interseptal ridges are absent from this stage, but growth striae are recognizable.

The external wall occupies no more than 1/6 of the corallite radius over the first 3.5 mm of preserved corallite growth. It increases in width immediately above the last attachment process. Thus, a mutual relationship between strength of attachment processes and thickness of the external wall can be accepted. Only major septa are seen in the corallite lumen throughout its ontogeny (Text-fig. 7A$_{1-10}$). Peripheral margins of those septa penetrate the external wall slightly (Text-fig. 7A$_{11, 12}$).

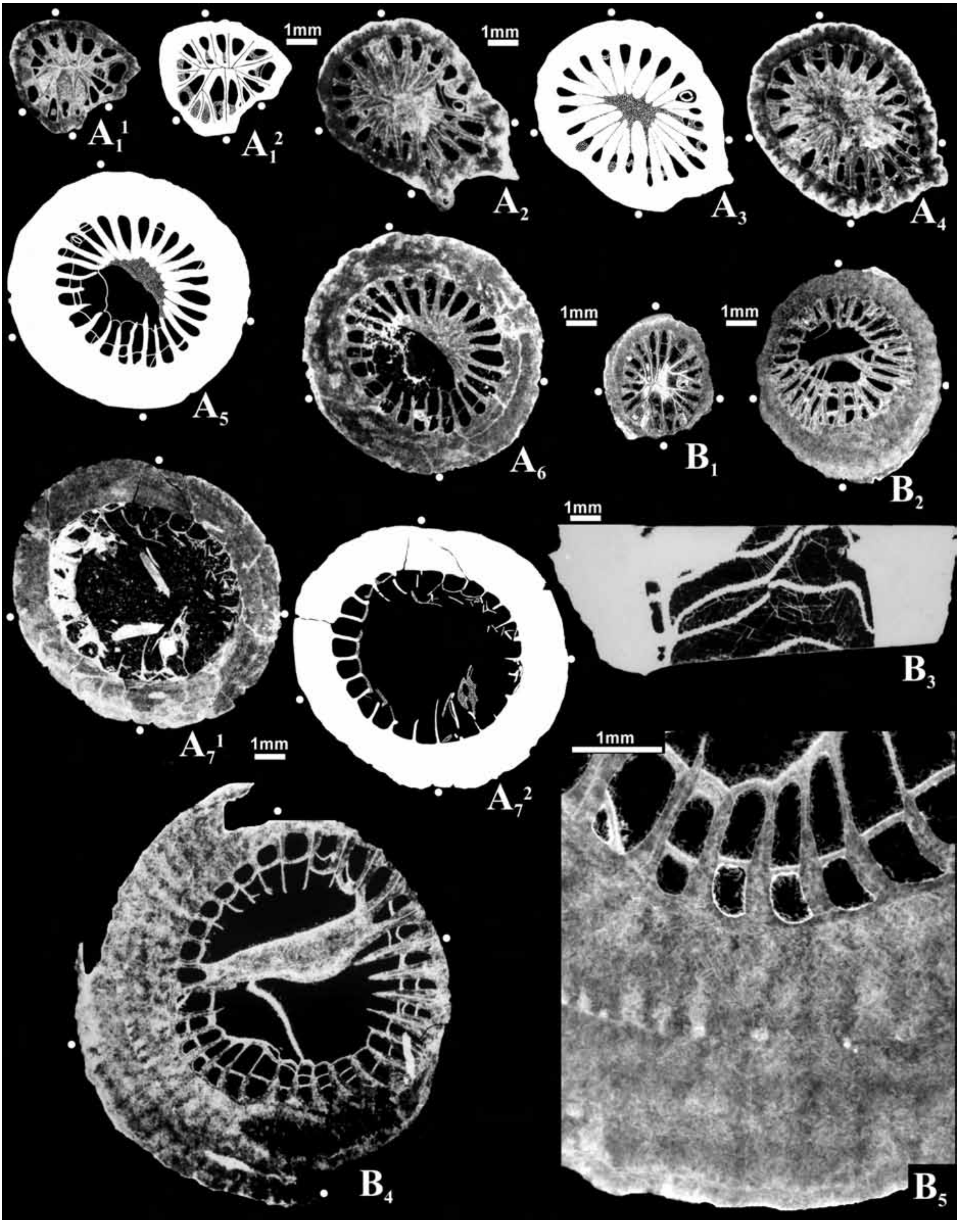
The broken surface of the earliest growth stage observed (Text-fig. 7A$_1$), with n:d value 10:1.6 mm shows accelerated septal insertion in the counter quadrants and an asymmetry in the development of the major septa. Two major septa occur in the right counter quadrant and three in the left one, whereas only the alar septum is present in the right cardinal quadrant and two major septa in the left one (For convenience in arranging the figures on the plate the cardinal protoseptum is located upward in Text-fig. 7A only). Asymmetry in septal insertion almost disappears 1.8 mm above, with n:d value 18:5.0 × 4.2 mm (Text-fig. 7A$_2$). The arrangement of the major septa in this and slightly more advanced neanic growth stages (Text-fig. 7A$_{3, 4}$) closely resembles that in *Rotiphyllum omaliusi* (Milne Edwards and Haime, 1851) in the pinnate pattern of the major septa in all quadrants, the slightly shorter major septa in the counter quadrants, the greater length of the cardinal protoseptum and alar septa, the distinct expression of the cardinal fossula, which is widest in its middle part, and the strong development of the alar pseudofossulae.

The neanic arrangement of the major septa changes 1.5 mm above the previously described transverse section, when measured along the convex side, and 1.0 mm above it along the concave side of the corallite, i.e., with n:d value 22:5.6 mm (Text-fig. 7A$_5$). The major septa in the counter quadrants are rearranged into an arch, with their inner margins connected by sclerenchyme. Only the alar septa and the longest adjacent major septa in the cardinal quadrants enter that circumaxial sclerenchymal arch, whereas the cardinal protoseptum and the major septum on its left become free. The morphology of this growth stage resembles that of *Meniscophyllum* Simpson, 1900, demonstrating how misleading information may be provided by single and random coral sections. The external wall thickens quickly from that growth level upward.

The sclerenchymal thickening, rhopaloid character and length of major septa decrease parallel to an increase in the number of major septa to six in each counter quadrant (Text-fig. 7A$_{6, 7}$), whereas four major septa remain in each cardinal quadrant. This early mature growth stage is the last growth level in which the alar pseudofossulae are recognizable, defined by the underdevelopment of the last pairs of major septa inserted in the counter quadrants. The major septa become almost equally shortened and thin above that growth level, making recognition of the protosepta and individual quadrants difficult. The cardinal fossula disappears in the more advanced mature growth stage (Text-fig. 7A$_{8-10}$) and the arrangement of major septa becomes radial. The thickness of the external wall continues to increase and the mature growth stage ends with *Amplexocarinia*-like morphology, expressed in transverse sections cut well beneath the calice floor (Text-fig. 7A$_{9, 10}$).

Longitudinal sections 5 mm in length were made from eccentric to exactly axial surfaces (Text-fig. 7A$_{13}^{1-3}$ respectively) and were oriented slightly obliquely to the cardinal-counter protosepta symmetry plan in order to show the relationship of tabulae to both free and united inner margins of the major septa. Unfortunately, the tabulae are very widely spaced, separated by 3 mm. Thus, only one is complete in the section. It is highly elevated in the periaxial part, with peripheral margins slightly concave and the top almost horizontal and flat. Slightly elevated tabellae occur at the periphery and an additional tabella imitating the tabula in shape occurs in the axial part of the corallite (Text-fig. 7A$_{13}^{3}$). The shape and completeness of tabulae demonstrate the lack of a true aulos. They are not divided into inner segments resting on each other (linked axial tabellae of Fedorowski *et al.* 2007) and do not form an axial tabular column. However, the inner margins of most major septa terminate on vertical parts of tabulae. Such a relationship between those two skeletal elements (Text-fig. 7A$_{10, 12}$) imitates the columnotheca, described recently by Fedorowski (2009*b*).

MICROSTRUCTURE AND DIAGENESIS: Both the external wall and the major septa (Text-fig. 7A$_{11, 12}$) of the holotype have been diagenetically altered. The 'middle dark lines' of septa (i.e., the primary major septa), almost continuous during early growth stages (Text-fig. 7A$_{2, 3}$), disappeared step by step in the mature part of the holotype, being almost completely replaced by fans of crystalline fibrils. Remnants of those 'lines' occurring in some mature septa prove the consistent nature of the microstructure in all growth stages, but indicate inconsistency in the diagenesis. A similar, but not identical pattern in the disappearance



Text-fig. 8. *Axisvacuus verus* sp. nov. **A** – Specimen UAM-Tc.Don.1/46. Paratype. A_1 – neanic growth stage, $A_{2\text{-}4}$ – late neanic growth stage, $A_{5,\,6}$ – early mature growth stage, A_7 – mature growth stage. **B** – Specimen UAM-Tc.Don.1/47. Paratype. B_1 – neanic growth stage, B_2 – early mature growth stage, B_3 – longitudinal section, B_4 – mature growth stage, B_5 – enlarged fragment of B_4, rudiments of minor septa in microstructure of external wall and inner margins of some major septa and section of tabula imitating aulos. See Remarks at Text-fig. 6 for further explanations of ‘middle dark lines’ occurs in all corallites investigated in detail. ‘Middle dark lines’ are always very thin and do not exhibit details allowing their original microstructure to be deciphered (Text-figs 7$A_{11, 12}$, 8B_5, 9A_{10}, C_6). They may either disappear from some segments of septa (Text-fig. 9A_{10}) or may be twisted and fragmented (Text-fig. 9C_7). The observed diagenetic alterations are comparable to those established recently in some Devonian specimens (Fedorowski 2009b, fig. 4B), showing trabeculae in some parts of septa and a solid dark line in others. Since microstructure is here considered to be constant for the specimen and the species, the differences mentioned must be diagenetic in nature. Thus, by analogy, finely trabecular septal microstructure is proposed here for *A. verus*.

Diagenesis, if not recognized**,** may in some instances result in dramatically false interpretation of structures. The combination of the basal crystalline film of the tabulae, the inner margin of the primary major septum (= ‘dark middle line’) to which that film is attached and the sclerenchyme secondarily covering both those structures (Text-fig. 9A_{10} upper) can well be interpreted as axial splitting of the primary septum. The apparent disappearance of a tabula from one septal loculus is another diagenetic alteration, but of much lesser diagnostic consequence.

The primary pattern in the arrangement of crystalline fibrils is not possible to establish in the external wall of the early growth stage of the holotype. Only the zig-zag pattern was observed above the late neanic stage (Text-fig. 7A_{11}). However, in the section made just beneath the calice floor (Text-fig. 7$A_{10}{}^1$) folds rather than zig-zags occur, suggesting their derivation from the bases of both major and minor septa. This character is best demonstrated in the very thick external wall of one paratype (Text-fig. 8:$B_{4, 5}$) and the proposed interpretation is supported by the morphology of the calice margin described above.

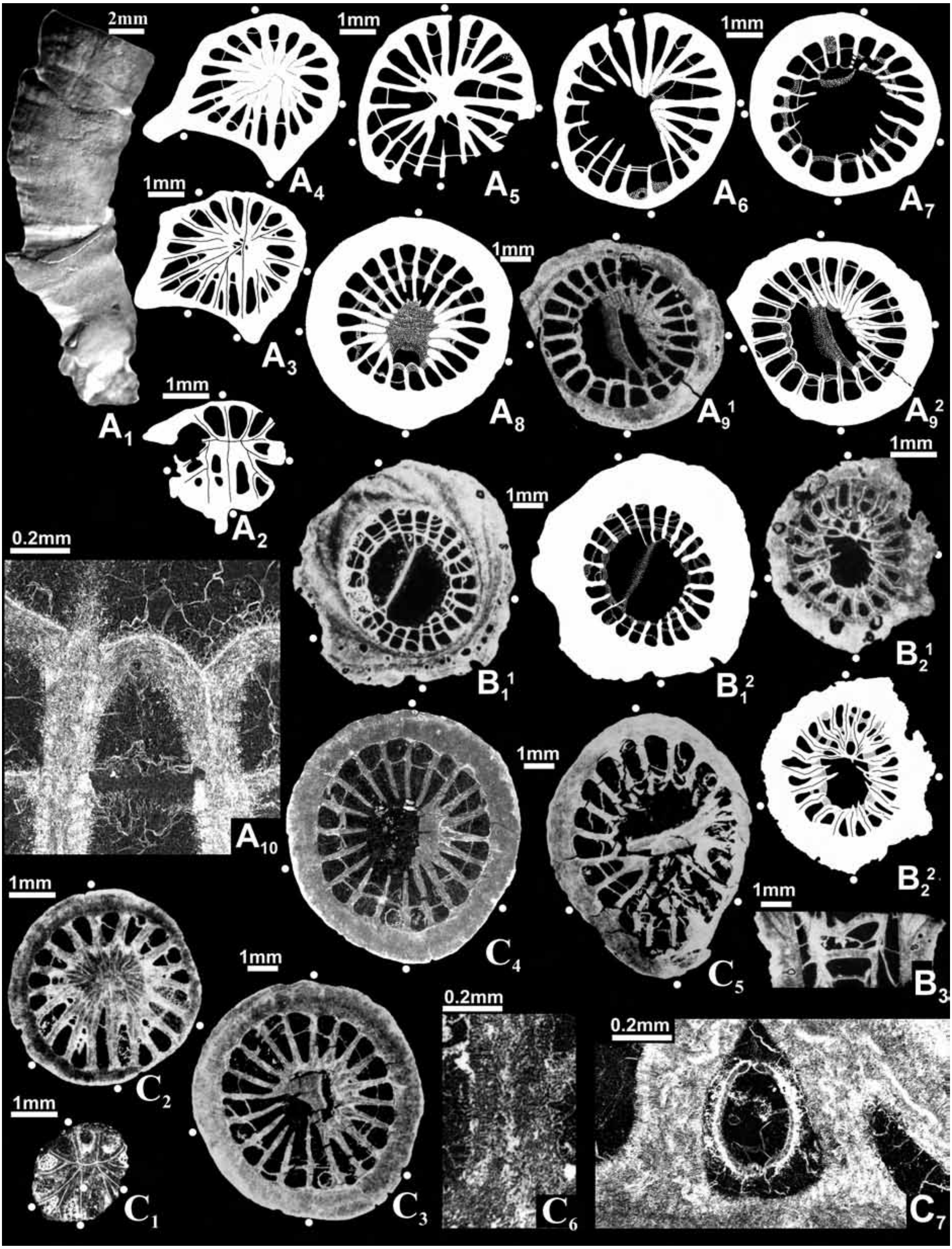
INDIVIDUAL VARIABILITY: Substantial morphological changes in the ontogeny of the holotype, discussed above (Text-fig. 7$A_{1\text{-}13}$), indicates wide individual variability in *A. verus*. The rotiphylloid pattern of major septa, with the cardinal fossula well developed, was noted in all corallites with their early growth stages preserved (Text-figs 6$A_{3, 4}$, $B_{1, 2}$; 8A_1, B_1; 9$A_{2\text{-}5}$, C_1). In that growth interval, the middle part of the cardinal fossula is widened in the holotype and in some paratypes (Text-figs 7$A_{2\text{-}4}$; 8A_1), but it may be rather triangular (Text-fig. 6A_3; $B_{1, 2}$) or parallel-walled (Text-figs 8B_1; 9$A_{2\text{-}4}$) in the others. The transition from the late neanic to the early mature growth stage is most variable. Some specimens demonstrate a strong thickening of inner margins of major septa and a nearly radial septal arrangement (Text-figs 8$A_{2\text{-}4}$; 9C_2). In other corallites most major septa are shortened with only slight reorganization of the general pattern (Text-figs 6:B_3; 8B_2) or an ’*omaliusi*’-like pattern of the early growth stage becomes asymmetrical (Text-fig. 9$A_{5, 6}$).

An arch of rhopaloid inner margins of the major septa, supplemented by sclerenchymal axial deposits, occurs in several corallites (Text-figs 6$A_{4\text{-}6}$; 8$A_{5, 6}$; 9$A_{8, 9}$). However, neither the sequence shown by the holotype nor the position of the arch is constant. Moreover, the appearance and location of such an arch is related to the position of a given transverse section in relation to the top part of a tabula. Major septa cut below a tabula are thin, whereas the same septa cut just above its upper surface are thick and rhopaloid (Text-fig. 6$A_{5, 6}$ upper, respectively) Thus, the position of the sclerenchymal arch is perhaps of limited diagnostic value, whereas the permanent presence of long major septa at maturity is provisionally accepted as an extreme variant of this species for the time being. Specimens of that morphology may represent a different species, not introduced here because of their scarcity. In some corallites the radial arrangement of comparatively long major septa lasts through most of their mature growth stage (Text-figs 6$A_{1, 5, 6}$, $B_{3\text{-}5}$; 9$C_{3\text{-}5}$). However, this phase may be rapidly replaced by one characterized by very short septa near the calice floor (Text-fig. 8A_7).

Extreme thickness of the external wall, accompanied by the ontogenetically early disintegration of the inner margins of septa, was established in two corallites (Text-figs 8$B_{1, 4}$; 9$B_{1, 2}$). The presence of major septa shorter than the width of the external wall is the main feature differentiating those specimens from the holotype and the remaining paratypes.

Text-fig. 9. *Axisvacuus verus* sp. nov. **A** – Specimen UAM-Tc.Don.1/48. Paratype. A_1 –external view of specimen showing rejuvenation on three occasions. $A_{2\text{-}5}$ – early to late neanic growth stage (peels), A_6 – late neanic/early mature growth stage (peel), $A_{7\text{-}9}$ – mature growth stage ($A_{7, 8}$ peels), A_{10} – tabula imitates aulos (upper right), inner margin of major septum extends through ‘aulos’ (upper left) and tabulae variously altered by diagenesis (middle). **B** – Specimen UAM-Tc.Don.1/49. Paratype. B_1 – mature growth stage, B_2 – peculiar arrangement of major septa in early mature growth stage, B_3 – longitudinal section. **C** – Specimen UAM-Tc.Don.1/55. Paratype. C_1 – early neanic growth stage, C_2 – late neanic growth stage, $C_{3\text{-}5}$ –mature growth stage, C_6 – diagenetically altered microstructure of major septum, C_7 – lower part of C_4 enlarged to demonstrate diagenetic alterations of microstructure and ostracode shell trapped in septal loculus. See Remarks at Text-fig. 6 for further explanations

Longitudinal sections of the corallites mentioned above differ in detail from the holotype and from each other (Text-figs 7A_{13}; 6C_1; 8B_3; 9B_3, respectively), but mostly as a result of their different orientation with respect to the cardinal/counter protosepta symmetry plan and their slightly eccentric position. The section oriented parallel to the protosepta (Text-fig. 8B_3) demonstrates both the slightly higher elevation of the calice



floor next to the counter protoseptum (right in the picture) and the curvature of tabulae identical to that in the holotype. The eccentric longitudinal section (Text-fig. $9B_3$) suggests the occurrence of an aulos-like circumaxial structure. However, a closer examination of the extension of individual tabulae confirms either their contiguity or the lack of linked tabellae. This section, cut beneath the transverse section illustrated in Text-figure $9B_2$, corresponds to the ontogenetically early growth stage with skeletal elements thickened. The corallite with mature morphology in transverse section (Text-fig. $6C_2$) similar to that in the holotype, is also similar to it in longitudinal section (Text-fig. $6C_1$) and is distinguished only by more closely spaced tabulae with flat axial parts.

The diameter and septal number of corallites (Text-fig. 5) varies as well. Unfortunately, the number of specimens available for the study limits the statistical results. Nevertheless, two important characters can be demonstrated: 1) The sequence in n:d values in the ontogeny of individual corallites is not linear. The increasing diameter may not cause an increase in septa in some corallites, whereas in others, the insertion of several septa may accompany a limited increase in the diameter. Substantial differences in n:d values may appear when random transverse sections of individual corallites, rather than series are compared. Thus, a more careful application of n:d data as a diagnostic character is suggested. 2) Similar directions of lines connecting measured growth stages of individual corallites are commonly accepted as diagnostically important. However, similar directions, but dissimilar positions within a diagram may occur. Moreover, segments of lines reflecting the immature growth of one species may correspond to those of mature growth in another. This is well demonstrated by data from *A. verus* and *A. postumus* in Text-fig. 5. These species should be combined if all extreme n:d values in this figure were connected to contour the field of occurrence. However, their distinction becomes clear when only points corresponding to mature morphology, i.e., the truly diagnostic ones, are connected. Such a method may be used to demonstrate a close relationship between species on the one hand and distinction between them on the other.

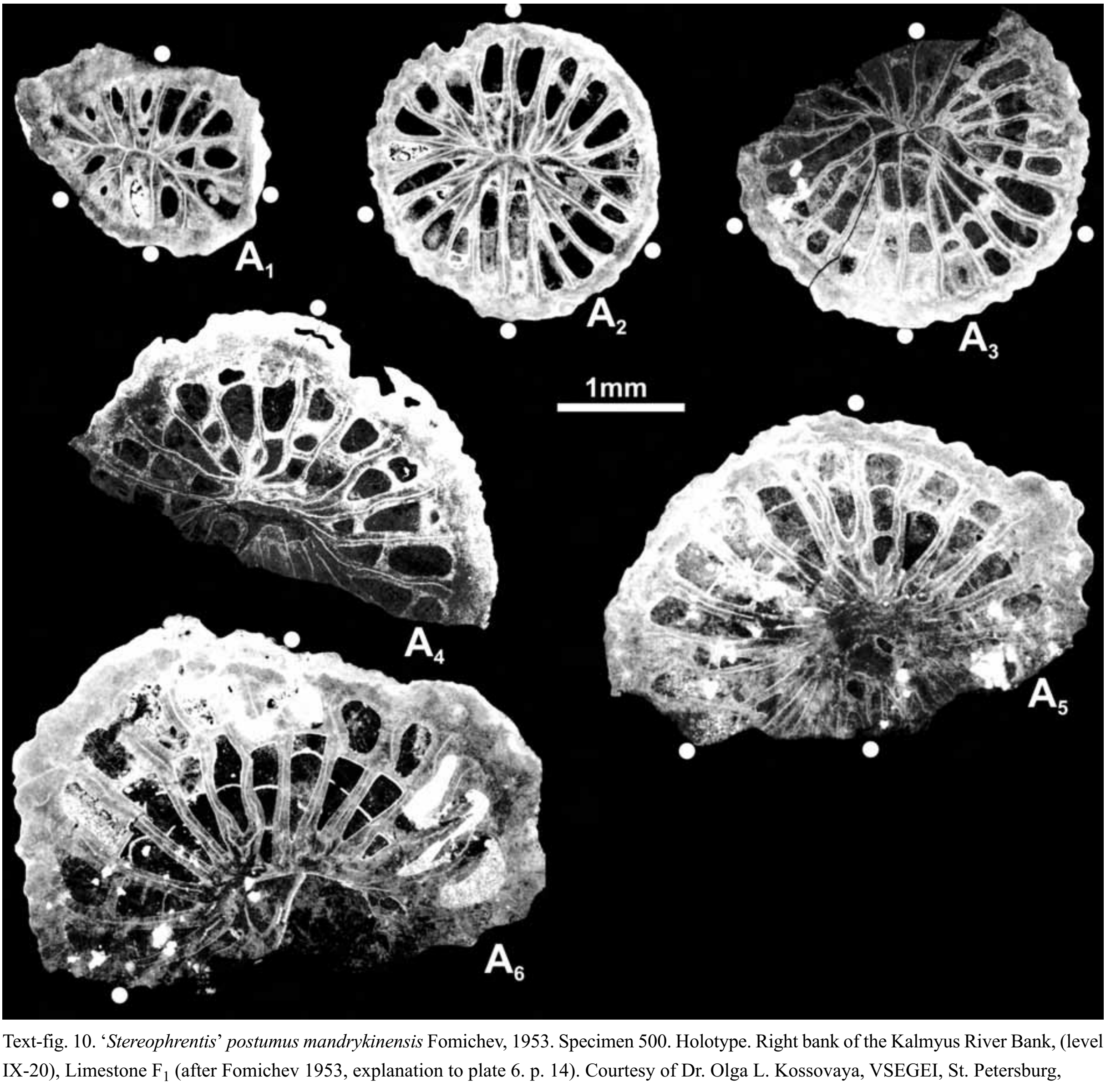
Rejuvenation is perhaps another factor causing changes in morphological characters. This is demonstrated by a specimen that was rejuvenated three times (Text-fig. $9A_1$), It exhibits increase and decrease in its diameter accompanied by a constant number of septa (Text-fig. 5) and a non-sequential pattern and length of the major septa (Text-fig. $9A_{6-9}$). A very shallow and local rejuvenation occurred also in the holotype (Text-fig. $7A_{8,\ 9}$), but it did not cause morphological changes.

Despite some characters that may be considered as intermediate, specimens included in *A. verus* may be grouped into two or even three groups, perhaps representing separate species. Lack of sharp morphological boundaries between those groups, however, prevents their formal distinction as species for the time being. This contrasts with other groups of specimens, distinguished at the species level despite their small number.

DISCUSSION: Most specimens included here in *A. verus* were derived from Limestone F_1, which yielded the holotype and two paratypes of '*Stereophrentis*' *postuma* (Smith) forma *mandrykinensis* Fomichev, 1953. Four other paratypes of that 'forma' were derived from limestone $G_1{}^1$, which also yielded some specimens from the collection described here. For those reasons the comparison that follows begins with that 'forma', since its elevation to the species level and the recognition of its priority would have been a logical procedure if its morphology matched that of the specimens treated herein. Unfortunately, the thin sections of the holotype of '*S.*' *postuma mandrykinensis* (Text-fig. $10A_{1-6}$) do not allow definite identification of its diagnostic features, although those representing the immature growth stage (Text-fig. $10A_{1-3}$) show the indisputable rotiphylloid arrangement and length of the major septa. The thin sections of the mature growth stage (Text-fig. $10A_{4-6}$) are not complete enough for confirmation of indisputable *Axisvacuus*-like morphology. The cardinal quadrants were destroyed in the thin sectioning process, precluding recognition of the true length of the cardinal protoseptum, whereas the fragment of the holotype remaining from thin sectioning is restricted to the partly crushed calice. An axial area free from major septa in the mature growth stage is the only diagnostic character of *Axisvacuus* shown by thin sections of the holotype of '*Stereophrentis*' *postuma mandrykinensis*. This is not enough for the identification at the species and genus levels. Moreover, sclerenchymal infilling of the axial area may appear between two growth levels in which that area is free from major septa (Text-fig. $10A_5$ vs. $10A_{4,\ 6}$). Such a sclerenchymal infilling may be considered as incidental, resulting from the section cutting the upper surface of the thickened axial part of a tabula, and should not be called a stereocolumella. Its appearance cannot be ignored, however, in the discussion at the species level. The narrow opening of the axial area in Fomichev's specimen differs strongly from the wide axial area, free from septa, that is present in the holotype of *A. verus*.

The holotype of '*S.*' *postuma mandrykinensis*, along with two other specimens (Fomichev 1953, pl. 6, figs 1, 2, 5), may with some restrictions be compared to the specimens with long septa of *A. verus* (Text-fig. 6A$_{1-6}$, B$_5$; 9C$_{1-5}$). The major septa are similarly long and slightly rhopaloid in both groups of specimens, but that single character in common is not sufficient for assignment of Fomichev's (1953) 'forma' in *A. verus*; especially when the morphology of the mature growth stage of the 'forma' is so uncertain, as described above. Besides, the specimens described here do not have an elongated counter protoseptum present in the holotype of '*S.*' *postuma mandrykinensis* (Text-fig. 10A$_6$). Also their external wall is thicker than in '*S.*' *postuma mandrykinensis* and is almost smooth externally. Thus, the characters of long septal specimens included in *A. verus* in common with the holotype of that species are here considered more important than those in common with '*S.*' *postuma mandrykinensis*.

Amplexus ? *tschigariensis* Fomichev, 1953 from Limestone H$_6^1$, is another potential species to consider. Specimens included in that species by Fomichev (1953, pl. 2, figs 18, 19) have thick external walls and very short major septa, thus closely resembling the mature morphology of *A. verus*. However, neither of those two corallites, illustrated by a single section each, exhibit a set of characters allowing its certain



Text-fig. 10. '*Stereophrentis*' *postumus mandrykinensis* Fomichev, 1953. Specimen 500. Holotype. Right bank of the Kalmyus River Bank, (level IX-20), Limestone F$_1$ (after Fomichev 1953, explanation to plate 6. p. 14). Courtesy of Dr. Olga L. Kossovaya, VSEGEI, St. Petersburg, Russia. A$_{1-3}$ – early to late neanic growth stage, A$_{4-6}$ – mature growth stage identification at the genus and species level. Thus, that species is not included in the synonymy of *A. verus*.

OCCURRENCE: Kalmyus River Area: Razsypnaya Village, Limestone E_1^{IV}, Lower Feninian Horizon (Specimen UAM-Tc.Don.1/43). Gorbachevo Village, Limestone F_1^2, Mandrykinian Horizon (Specimen UAM-Tc.Don.1/50), Limestone G_1^1, Lower Kayalskian Horizon, Zujevian Subhorizon (Specimens UAM-Tc.Don.1/47, 51). Menchugovo Village, shales just above Limestone F_2^0, Mandrykinian Horizon (Specimen UAM-Tc.Don.1/52), Limestone G_1^1, Lower Kayalskian Horizon, Zujevian Subhorizon (Specimen UAM-Tc.Don.1/44). Solenaya River Area: Novo Troitskoe Village, Sazanova Ravine (Balka), Limestone F_1, Mandrykinian Horizon (Specimens UAM-Tc.Don.1/42, holotype and UAM-Tc.Don.1/45, 46, 48, 49, 53, 54, paratypes).

Axisvacuus postumus (Smith, 1931)
(Text-figs 5, 11)

1931. *Zaphrentis postuma* Smith, p. 4, pl. 1, figs 1–9.
1931. ? *Caninia cornucopiae* Michelin; Smith, p. 7, pl. 1, fig. 10.
partim 1953. *Stereolasma*? *tripoliense* Fomichev, p. 106 (*non* the holotype)
? *partim* 1953. *Stereophrentis fischeri* Fomichev, p. 147, pl. 6, figs 8–10, *non* pl. 6, fig. 11.

MATERIAL: Eight corallites (UAM-Tc.Don.1/56-1/63), some with almost entire proximal parts preserved. In one corallite the longitudinally broken, 12 mm deep calice retained. Inner morphology of corallites mostly well preserved, but microstructure of septa and external wall diagenetically altered. For n:d values see Text-fig. 5. Nine thin sections and eighteen peels were available for study.

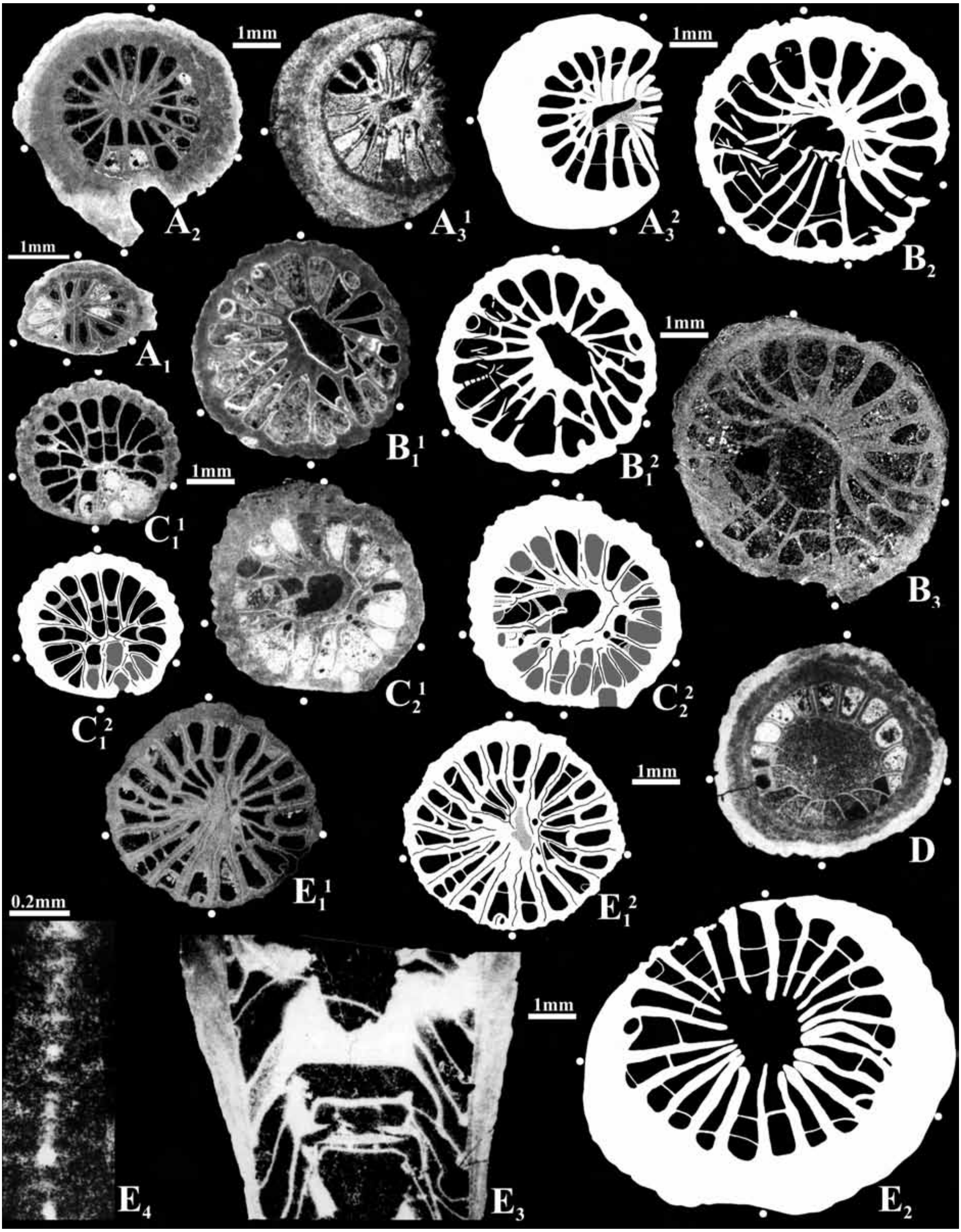
DIAGNOSIS: *Axisvacuus* with up to 23 major septa and 7.5 mm maximum diameter immediately below calice floor; in early maturity major septa long and in part rhopaloid; they thin and shorten to 1/2-2/3 corallite radius near calice floor; minor septa absent from corallite lumen; tabulae trapezoid, highly elevated.

DESCRIPTION: The external wall of *A. postumus* is commonly thick, reaching almost 1/3 corallite radius in extreme specimens (e.g. Text-fig. 11:A_3). Septal grooves and growth striae in such thick-walled corallites are weakly marked, but better accentuated in two thinner walled corallites. The ontogenetically earliest parts are missing from all corallites. The neanic growth stage is typically rotiphylloid with the cardinal fossula bisected by the cardinal protoseptum, which reaches the corallite axis. Alar pseudofossulae are not prominent, but are recognizable (Text-fig. 11:$A_{1,\,2}$, C_1). The increase in septa in the cardinal and counter quadrants is almost equal, with the counter quadrants accelerated by one septum in some specimens.

The transition from immature to mature morphology is rather rapid but manifested differently. In one instance (Text-fig. 11$A_{2,\,3}$, $E_{1,\,2}$) the major septa are radially arranged prior to the reduction of sclerenchyme in the axial part of the corallite. In the second instance observed, the rotiphylloid neanic morphology passes directly into the mature one, with the ‘middle dark lines’ of the inner margins of most major septa connected around an open axial area (Text-fig. 11$C_{1,\,2}$).

The following features of mature morphology can be distinguished in both the type collection (Smith 1931, pl. 1, figs 1–10) and the corallites described here (Text-fig. 11A-E): 1) Corallites with long septa and an inconsistent, aulos-like, circumaxial structure formed by the inner margins of the major septa (Smith 1931, pl. 1, figs 6, 8a,b and Text-fig. 11:A_3, $B_{1,\,2}$, C_2 in this paper. Those corallites resemble the Upper Serpukhovian taxa from the Upper Silesian Coal Basin (Fedorowski, in preparation); 2) Corallites with long septa, without the aulos-like structure (Smith, 1931 pl. 1, fig. 8b and Text-fig. 11E_1 in this paper); 3) Long-lasting neanic morphology (Smith 1931, pl. 1, figs 3-5 and Text-fig. 11$A_{1,\,2}$ in this paper); 4) Corallites with short septa (Smith 1931, pl. 1, figs 9, 10 and Text-fig. 11D in this paper). The combination of all those characters in common suggests a relationship between the British (South Wales) and Ukrainian (Donets Basin) corals close enough to be accepted as conspecific in spite of the time difference in the occurrence (see below). Another alternative is the occurrence of more than one species in each area that were either directly related or only closely comparable in morphology. This alternative is supported by the large morphological variability in almost all characters, discussed above. Only the acquisition of much larger collections from both areas will solve that dilemma.

The morphology in longitudinal section was not investigated by Smith (1931) and was observed in only one specimen of the collection studied here. In this axially sectioned corallite (Text-fig. 11E_3), the tabulae are trapezoid, elevated in their periaxial, horizontal parts up to 3 mm above their attachments to the external wall. The upper surfaces of axial parts of



Text-fig. 11. *Axisvacuus postumus* (Smith, 1931). **A** – Specimen UAM-Tc.Don.1/ 56. A_1 – early neanic growth stage, A_2 – late neanic growth stage, A_3 – mature growth stage. **B** – Specimen UAM-Tc.Don.1/ 57. $B_{1\text{-}3}$ – successive sections of mature stage (B_3 peel). **C** – Specimen UAM-Tc.Don.1/ 58. C_1 – late neanic growth stage, C_2 mature growth stage. **D** – Specimen UAM-Tc.Don.1/ 59. mature growth stage; major septa very short. **E** – Specimen UAM-Tc.Don.1/60. E_1 – late neanic/early mature growth stage, E_2 – mature stage; above calice floor in the axial part, E_3 – longitudinal section, E_4 – remnants of trabeculae in major septum. See Remarks at Text-fig. 6 for further explanations some tabulae bear a stereoplasmic cover when the section approaches amplexoid septa.

The microstructure of the septa and the external wall is diagenetically altered. Thus, only the zig-zag pattern in the external walls and the solid 'middle dark lines' of the septa remain in most corallites (not illustrated). Remnants of separate bodies, interpreted here as diagenetically altered trabeculae present in rare fragments of septa, suggest original trabecular microstructure (Text-fig. $11E_4$).

DISCUSSION: The relationship of the Donets Basin '*Stereophrentis*' *postuma mandrykinensis* to '*Zaphrentis*' *postuma* Smith has already been postulated by Fomichev (1953, pp. 146, 147). That relationship is here extended to ?*Caninia cornucopiae* of Smith (1931), placed in synonymy with *A. postumus*. The main difference between specimens included by Smith (1931) in those two species can be confined to the ontogenetically early disintegration of the inner margins of the major septa in his ?*C. cornucopiae*. This character is discussed above as one of the intraspecific variants. At this point it should be remembered that *Caninia cornucopiae* Michelin, 1840 is a Tournaisian dissepimental rugose coral, belonging to a different suborder, and thus having nothing in common with specimens under discussion here.

The holotype of '*Zaphrentis*' *postuma* was not illustrated. Thus, a direct comparison to it of the specimens described here is possible only by analogy. The only information on its morphology can be derived from the following sentence by Smith (1931, p. 5): 'Sections M810 and M811, and more particularly the latter, although not identical with it, resemble the holotype, which has been cut, but not sectioned.' The morphology of the sections listed is convincing enough to consider '*Z.*' *postuma* a representative of *Axisvacuus*.

The large variability of specimens described and illustrated by Smith (1931, pl. 1, figs 1–10) resulted in part from the disappearance of the stereocolumn at different sizes and growth levels of individual corallites. It may disappear as early as in his ?*Caninia cornucopiae* or as late as in his thin sections M814a and b (Smith 1931, pl. 1, fig. 5a,b). The presence of the stereocolumn cannot be equated with the axial union of the inner margins of the major septa because the origins of those two characters differ. Axial parts of the 'middle dark lines' of the major septa are clearly disconnected in section M814b cited above. Reduction of the sclerenchyme from between such septa results in the immediate opening of the axial area, i.e. achieving a generic character in the corallite.

The similarity between the Donets Basin corallites and the type collection is emphasized above. Both the British and Donets Basin specimens of *A. postumus* are most closely related to *A. verus*. The main features distinguishing these two species are the much smaller diameters and numbers of septa and the longer major septa compared to the diameter in all but one corallite of *A. postumus* in the collection studied. The n:d values (Text-fig. 5) are perhaps another distinguishing factor, but the number of specimens measured is inadequate for a final conclusion in this respect.

Stereophrentis fischeri Fomichev, 1953, considered by that author (Fomichev 1953, p. 150) to be most similar to '*Zaphrentis' postuma* Smith, 1931, exhibits several characters in common with both *A. verus* and *A. postumus*, but probably belongs to the latter species if the presence of a permanently long cardinal protoseptum in its holotype and paratypes can be confirmed. Unfortunately, the ontogenetically most advanced morphology of the holotype (Fomichev 1953, pl. 6, fig. 8g) is uncertain. The illustrated section may expose the cardinal septal fossula above the last tabula and the statement by Fomichev (1953, p. 149) 'The cardinal septum strongly shortened, hardly distinguishable from the external wall' (translated herein from Russian) may refer to the shortening of that septum above the calice floor. Only the occurrence of a long cardinal protoseptum up to and including the calice floor will allow the assignment of that specimen to *Axisvacuus* and probably to *A. postumus*.

OCCURRENCE: Cefn Coed Colliery, South Wales (Britain), *Donetzoceras aegiranum* Zone, i.e. Westphalian B/C (Duckmantian/Bolsovian). Donets Basin. Solenaya River Area: Novo Troitskoe Village, Sazanova Ravine (Balka), Limestone F_1, Mandrykinian Horizon (Specimens UAM-Tc/Don.1/56-63).

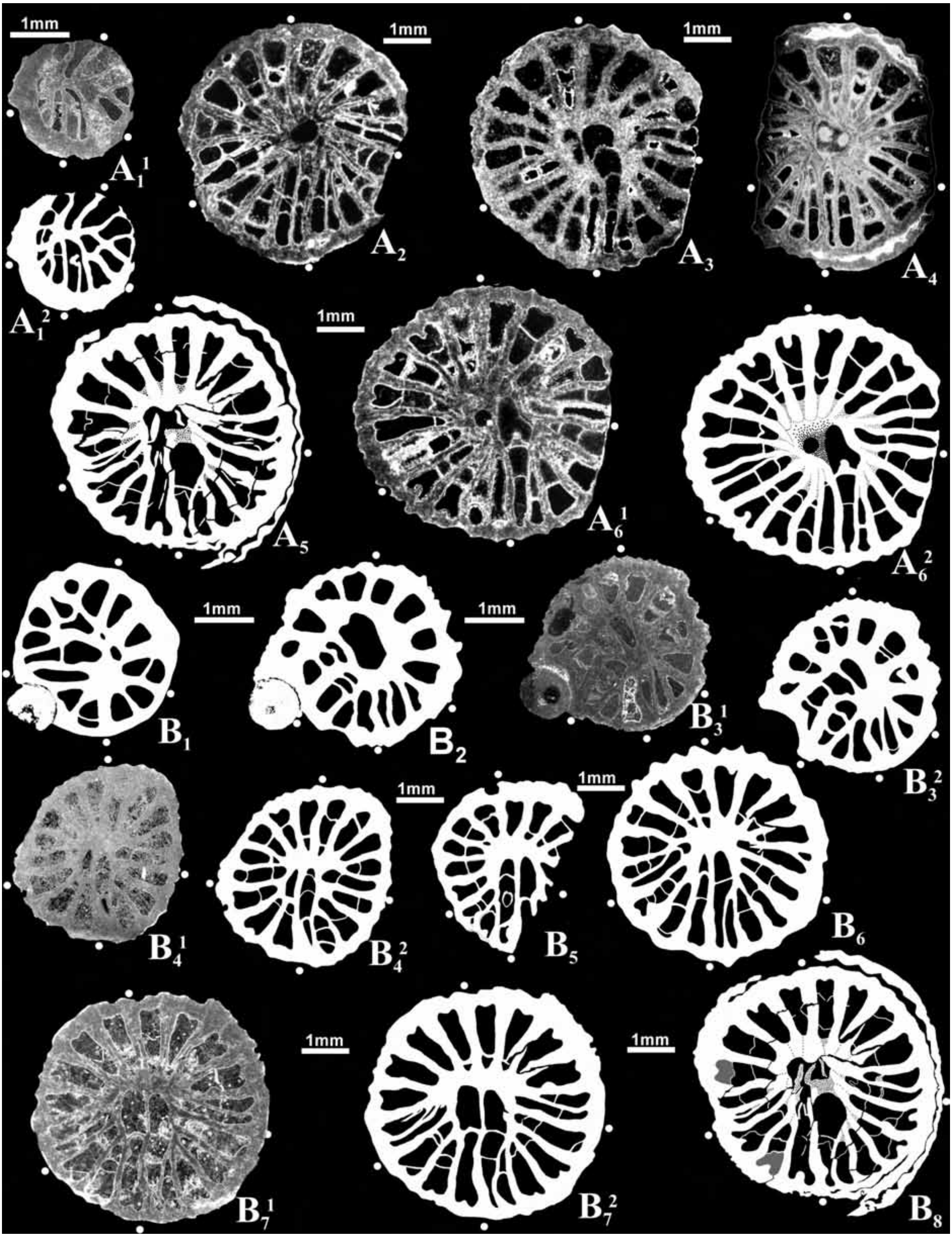
Axisvacuus extendus sp. nov.
(Text-fig. 12)

HOLOTYPE: Specimen UAM-Tc.Don.1/64, illustrated in Text-fig. $12A_{1\text{-}6}$. Seven thin sections and six peels were studied.

TYPE LOCALITY: Kalmyus River Area, Grigorievka Village, Shirokaya Ravine (Balka).

TYPE HORIZON: Shale between Limestones $E_1{}^{IV}$ and $E_1{}^{V}$, Lower Feninian Horizon.

ETYMOLOGY: *Lat. extendo, tendi, tendum* – prolonged – after long lasting axial connection of major septa.



Text-fig. 12. *Axisvacuus extendus* sp. nov. **A** – Specimen UAM-Tc.Don.1/64. Holotype. A_1 – early neanic growth stage, $A_{2\text{-}6}$ – early to late mature growth stage. **B** – Specimen UAM-Tc.Don.1/65. Paratype. $B_{1\text{-}3}$ – neanic growth stage ($B_{1,\ 2}$ peels); arrangement of major septa deformed by attachment to crinoid ossicle, $B_{4\text{-}7}$ – late neanic to early mature growth stage ($B_{4,\ 6}$ peels), B_8 – shallow rejuvenation of mature growth stage. See Remarks at Text-fig. 6 for further explanations

MATERIAL: Three almost complete corallites, the holotype (UAM-Tc.Don.1/64) and two paratypes (UAM-Tc.Don.1/65, 66). The holotype and the paratype UAM-Tc.Don.1/65 with inner morphology below calices well preserved, but calices flattened by compaction. The second paratype deformed by the long-lasting attachment to the substrate. Thirteen thin sections and fifteen peels are available for study.

DIAGNOSIS: *Axisvacuus* with 20–22 major septa at 5.5 mm corallite diameter; open axial area, 0.5–0.7 mm wide, appear only in advanced maturity; short minor septa present in corallite lumen; external wall 0.3 mm thick with septal furrows well developed.

DESCRIPTION OF HOLOTYPE: Major septa in the earliest preserved growth stage (Text-fig. $12A_1$) are rotiphylloid, but irregularly arranged. The protosepta approach the corallite axis, but their inner margins do not terminate exactly against one another. The mature morphology shown by particular transverse thin sections and peels depends to some extent on their position in relation to the tabulae. In sections cut just beneath the top part of a tabula (Text-fig. $12A_{2,\,4}$) an aulos-like circumaxial structure appears. The inner margins of the major septa reach elevated parts of tabulae and became both rhopaloidally thickened and laterally contiguous with some sclerenchyme between them. In a section cut just above the top part of a tabula (Text-fig. $12A_{3,\,5}$) and another cut almost exactly at the top of a tabula (Text-fig. $12A_6$) the aulos-like circumaxial structure disappears although the inner margins of most major septa remain connected. Those sections show a deep cardinal fossula extending beyond the corallite axis. The arrangement of the major septa is similar although not identical in all transverse sections. They are semi-radially arranged in the counter quadrants and more or less clearly pinnate in the cardinal quadrants. Alar pseudofossulae are marked by the underdeveloped and/or thin last major septa in the counter quadrants.

The cardinal protoseptum is permanently longer and thicker than the last pair of major septa in the cardinal quadrants, but its inner margin is either straight (Text-fig. $12A_5$) or slightly curved (Text-fig. $12A_{2,\,3,\,4,\,6}$). The counter protoseptum is permanently but only slightly thicker than other major septa of the counter quadrants. In some growth intervals (Fig. $11A_{3,\,5}$) it may also be longer than the counter-lateral septa. The alar septa are indistinct, being recognizable mainly because of the underdevelopment of the last pairs of major septa in the counter quadrants.

In the earliest growth stage known (Text-fig. $12A_1$), minor septa are absent from the corallite lumen and its external wall. They became recognizable in the external wall early in maturity (Text-fig. $12A_{2,\,3}$), but expand into the corallite lumen only in the further growth, near the end of a shallow rejuvenation (Text-fig. $12A_{4,\,5}$). However, they remain short up to the section made just beneath the calice floor (Text-fig. $12A_6$), being mostly seen as low ridges or small protuberances on the inner surface of the external wall.

INTRASPECIFIC VARIABILITY: The morphology of the paratype UAM-Tc.Don.1/66 is strongly disturbed by its attachment to the substrate and is not discussed. The early neanic growth stage of the second paratype UAM-Tc.Don.1/65 was deformed by an attachment to a crinoid ossicle (Text-fig. $12B_{1\text{-}3}$). The earliest growth observed with long septa (Text-fig. $12B_1$) is followed by a short-lasting aulos-like circumaxial structure (Text-fig. $12B_{2\text{-}3}$). The arrangement of major septa in the late neanic growth stage above the attachment becomes regular and closely comparable to the holotype (Text-fig. $12B_{4,\,5}$). The prominent cardinal protoseptum extends beyond the corallite axis to meet the slightly thickened counter protoseptum. The remaining major septa are long, pinnately arranged in the cardinal quadrants and semiradially arranged in the counter quadrants (Text-fig. $12B_{4\text{-}8}$), thus closely resembling some growth intervals in the holotype. The cardinal fossula (septal and tabular) is well developed, but the alar pseudofossulae are barely recognizable or absent. The main features of this specimen that differentiate it from the holotype can be reduced to: (a) a longer cardinal protoseptum that bisects the cardinal fossula, meeting the counter protoseptum (Text-fig. $12B_{7,\,8}$); (b) major septa withdrawn from the axial area late; and (c) peripheral thickening of major septa similar to that characteristic for such Viséan taxa as *Rotiphyllum rushianum* (Vaughan, 1908) or *R. omaliusi* (Milne Edwards and Haime, 1851). Minor septa occur in all septal loculi, but mostly as short ridges on the inner surface of the external wall.

The microstructure of the septa in all the specimens has been diagenetically altered to such an extent that meaningful consideration is impossible. Irregular bunches of calcite fibrils occurring in the middle parts of most septa and irregularly distributed fragments of 'middle dark lines' do not provide information adequate for the direct recognition of the original septal microstructure.

The probability of the presence of trabecular microstructure may be implied only by the same analogy as that mentioned in the above discussion on the microstructure in *A. verus*. The microstructure of the external wall has been altered into zig-zag structures.

DISCUSSION: *A. extendus* is morphologically close to the genus *Rotiphyllum* and to *R. voznesenkae* Fedorowski (2009a) in particular. Amplexoid major septa in the latter species are temporarily disconnected beneath the tabulae, making such sections comparable to *A. extendus*. However, shortening of the major septa in *A. extendus* is permanent and does not depend on the position of a section with respect to a tabula. It may be predicted, however, that those species are related. The slightly subsequent occurrence of *A. extendus* supports such an idea. That, in turn, may renew the discussion on the taxonomic validity of the ampleximorphs. This question, widely discussed by Fedorowski (2009c), is omitted from the present paper. It should only be mentioned that the relationships between the genus *Rotiphyllum* and individual species of the genus *Axisvacuus* may follow relationships characteristic for iterative evolution.

The long lasting sclerenchymal connection of the major septa, the slightly elongated counter protoseptum and the comparatively thin external wall with septal furrows well accentuated are characters of *A. extendus* in common with the holotype of '*Stereophrentis*' *postuma* forma *mandrykinensis* Fomichev, 1953. The much smaller diameter and septal number (20-22:5.5mm *vs.* 26:8.5 mm) and the presence of short minor septa in the corallite lumen of the former *vs*. the absence of minor septa in the latter are the main differences between those two taxa. Both of them as well as *A. semicirculatus* bear some characters in common with the Late Serpukhovian taxa from the Upper Silesian Coal Basin (Fedorowski, in preparation).

Some characters of *A. extendus*, such as the long-lasting rotiphylloid arrangement of septa, long cardinal septum and small open axial area resemble those in *Neaxon*? *multitabulatus* Rodriguez and Kullmann, 1999, included here in the genus *Axisvacuus*. The thick external wall, the absence of minor septa and the slightly smaller number of septa at slightly larger corallite diameters in the Spanish species constitute a set of differences between those two taxa. Both of them as well as *A. semicirculatus* bear some characters in common with the Late Serpukhovian taxa from the Upper Silesian Coal Basin (Fedorowski, in preparation).

The arrangement of the major septa in *A. extendus* resembles that in *A. semicirculatus* sp. nov., but the other characters do not match. Differences in the mature morphology between *A. extendus* and *A. verus*, the type species of *Axisvacuus*, are so large that detailed discussion is unnecessary.

A summary of the comparisons of species discussed above is shown in Table on page 286, supporting the idea of the introduction of a new species despite the small number of specimens available for the study. The close morphological similarity of those specimens (Text-fig. 12A$_{1\text{-}6}$, B$_{1\text{-}8}$) documents their repeatable diagnostic characters, supporting the idea of their independent taxonomic status.

OCCURRENCE: Kalmyus River Area: Grigorievka Village, Shirokaya Ravine (Balka) (Specimens UAM-Tc.Don.1/64, holotype and UAM-Tc.Don.1/65, paratype). Krynka River Area: Svistuny Village, Bolshaya Shishovka Ravine (Balka) (Specimen UAM-Tc.Don.1/66, paratype). Both localities: shale between Limestones E_1^{IV} and E_1^{V}, Feninian Horizon.

Axisvacuus semicirculatus sp. nov.
(Text-fig. 13)

HOLOTYPE: Specimen UAM-Tc.Don.1/67, illustrated in Text-fig. 13$_{1\text{-}9}$. Four thin sections and one peel were studied.

TYPE LOCALITY: Solenaya River Area, Novo Troitskoe Village

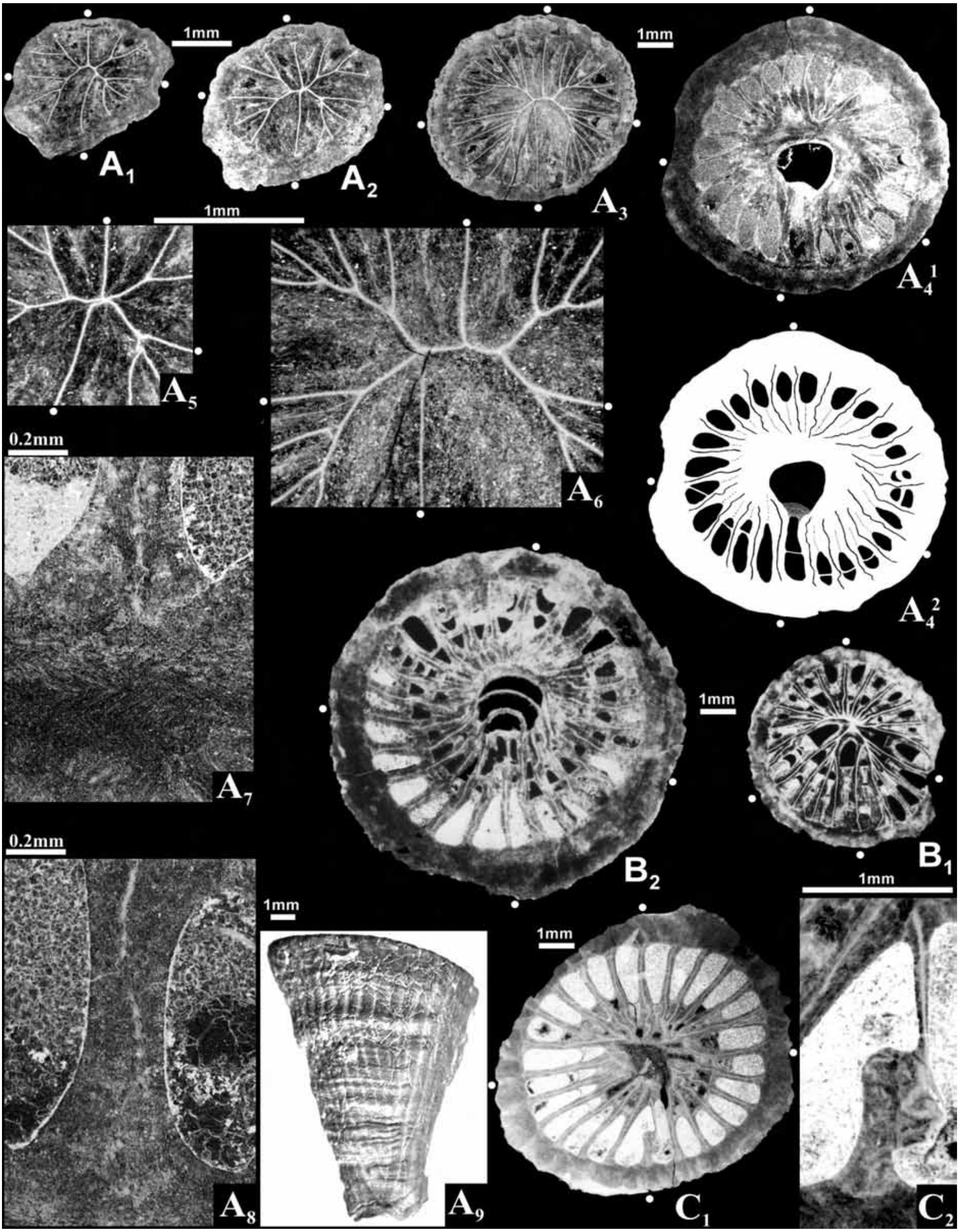
TYPE HORIZON: Limestone F_1, Mandrykinian Horizon.

ETYMOLOGY: *Lat. semicirculatus* – semicircular – after arrangement of inner margins of major septa around a corallite axis.

MATERIAL: Four corallites. The holotype UAM-Tc.Don.1/67 with inner morphology well preserved, but with the calice missing. Paratypes: UAM-Tc.Don.1/68 – cut into three thin sections with no material left. UAM-Tc.Don.1/69 – one thin section with no material left; provisionally included, see below. UAM-Tc.Don.1/70 – most parts missing, only calice preserved; provisionally included, see below. Nine thin sections and two peels are available for study.

DIAGNOSIS: *Axisvacuus* with 24 or 25 major septa, at 8.5–10.0 mm corallite diameter; rhopaloid inner margins of major septa and their sclerenchymal cover surround inner limit of key-hole cardinal fossula which extends beyond corallite axis; minor septa absent from corallite lumen; external wall 1/5–1/6 corallite radius in thickness.

DESCRIPTION OF HOLOTYPE: The specimen bears shallow but distinct septal furrows of both the



Text-fig. 13. *Axisvacuus semicirculatus* sp. nov. **A –** Specimen UAM-Tc.Don.1/67. Holotype. A_{1-3} – early to late neanic growth stage, A_4 – mature growth stage, $A_{5,\,6}$ – axial parts of A_2 and A_3 (respectively) enlarged to show peculiar arrangement of primary major septa, A_7 –attachment of major septum to external wall and diagenetic deformation of the latter, A_8 – Possible rudiments of trabeculae in major septum (lower), A_9 external view from alar septum side. **B** – Specimen UAM-Tc.Don.1/68. Paratype. B_1 – neanic growth stage, B_2 – mature growth stage. **C** – Specimen UAM-Tc.Don.1/69. Paratype (?). C_1 – early mature growth stage. C_2 – diagenetic deformation of cardinal protoseptum. See Remarks at Text-fig. 6 for further explanations major and minor septa, alternating in a regular sequence (Text-fig. 13A_9). The arrangement of the major septa in the neanic growth stage is almost regularly rotiphylloid with 'middle dark lines' (= primary major septa) united by their inner margins into distinct quadrants. In the early neanic growth stage (Text-fig. 13$A_{1, 2}$) the insertion of major septa in the cardinal quadrants is slightly accelerated. Also, those quadrants are larger than the counter quadrants. The axial protoseptum is already absent from the earliest growth stage available for study. The inner margins of the primary cardinal and counter protosepta do not meet directly (Text-fig. 13$A_{5, 6}$), but are indirectly joined through the union of alar and counter-lateral septa. That peculiar arrangement of the axial parts of major septa and protosepta is best exemplified in the late neanic growth stage (Text-fig. 13$A_{3, 6}$). Primary alar and counter-lateral septa join some distance short of the corallite axis. Thus, the axis is crossed by a single primary septum, perpendicular to the protosepta. They join that primary septum with a leftward shift of the cardinal protoseptum rather than opposite each other (Text-fig. 13$A_{3, 6}$). Such an arrangement, in which four septa are longest is peculiar, but it is not considered to be taxonomically important. That arrangement, together with the adaxial widening of the cardinal fossula, the grouping of major septa into quadrants and the shape of the alar pseudofossulae, characterize the morphology of the interval between the early neanic and mature growth stages.

Throughout early ontogeny (Text-fig. 13$A_{1\text{-}3}$) almost all septal loculi are completely filled with sclerenchyme. Small openings at the periphery are ephemeral, appearing in individual septal loculi over short intervals of corallite growth. Such openings are absent from the large space between the cardinal protoseptum and the last inserted major septa, i.e., the potential cardinal fossula, and from potential alar pseudofossulae, distinctly marked by the arrangement of primary major septa.

All the major septa in the mature growth stage (Text-fig. 13A_4), including the cardinal protoseptum, are rhopaloid and laterally contiguous in the circumaxial area. The inner margins of all are incorporated in the thick sclerenchyme that surrounds the slightly irregular, open axial area. The 'middle dark lines' of all the major septa became detached in that growth stage, with their length almost equal and their arrangement nearly radial. Thus, alar pseudofossulae disappear. The cardinal protoseptum is longer than the adjacent major septa, but its inner margin curves leftward to become incorporated in the circumaxial sclerenchymal arch. The strongly thickened tabula right of the cardinal protoseptum looks as if it were supplementing an aulos, but its curvature, almost parallel to the inner margin of the sclerenchymal arch, suggests that it belongs in the tabular cardinal fossula. That in turn allows the open axial area to be considered as a probable part of the deep cardinal fossula.

INTRASPECIFIC VARIABILITY: Only the calice is preserved from one of the two paratypes provisionally included in this species (UAM-Tc.Don.1/70, not illustrated). The occurrence of an arch of septa in the counter quadrants, persisting up to the lower part of the calice, is the main reason for its assignment to *A. semicirculatus* However, that specimen is much larger than the holotype, possessing 27 major septa at a corallite diameter of 11.2 mm in the lower part of the calice. That diameter increases to 14.3 mm at the calice margin. Also, the length of its cardinal protoseptum is uncertain.

The morphology of the other corallite, provisionally included in this species (Text-fig. 13C_1) is here interpreted as early mature. It exhibits strong diagenetic alteration of some structures, including the cardinal protoseptum, which is secondarily shortened, as indicated by its doubled peripheral part (Text-fig. 13C_2). Also, there may have been diagenetic deformation of the axial part of the corallite. The arch characteristic of the mature growth stage of the holotype and paratype UAM-Tc.Don.1/68 is not yet developed, but the arrangement of the major septa in the counter quadrants resembles that of the holotype and the typically constructed paratype (Text-fig. 13A_3, B_1 respectively). Also, the irregular axial area is directly connected to a triangular cardinal fossula in a manner characteristic of both the holotype and the more typical paratype, the major septa are rhopaloid, and the axial part of the calice is elevated. All of those characters suggest the proposed assignment to *A. semicirculatus*.

Morphological differences are slight between the holotype and the best preserved paratype (Text-fig. 13$B_{1, 2}$). Its cardinal quadrants in the earliest growth stage (Text-fig. 13B_1) contain four septa each, against six and five major septa in the counter quadrants. The latter quadrants are also larger. Light sclerenchymal cover reveals the alar pseudofossulae, which are perhaps both septal and tabular as suggested by the number of sections of tabulae. 'Middle dark lines' of major septa adjacent to the counter protoseptum are already detached in that early growth stage. Their arrangement suggests an early development of the arch typical of the species.

In the mature growth stage of this specimen (Text-fig. 13B$_2$) a direct connection between the narrow, triangular and inner, rounded parts of the cardinal fossula is best shown, supporting the interpretation proposed above for the holotype. The inner margin of that key-hole cardinal fossula extends beyond the corallite axis and its great depth is marked by two additional intercepts of tabulae. The inner margin of the long cardinal protoseptum is straight, rather than curved as it is in the holotype. It meets the tabula, arched between the inner margins of the last pair of major septa in the cardinal quadrants, i.e. on the border between the triangular and circular parts of the cardinal fossula (Text-fig. 13B$_2$), imitating that feature in *Hapsiphyllum* Simpson, 1900.

MICROSTRUCTURE AND DIAGENESIS: Advanced diagenesis has destroyed the microstructure of the external wall in all corallites included in *A. semicirculatus*. Only the zig-zag structure is left (Text-fig. 13A$_7$). Thus, the recognition of potential minor septa within the external wall is impossible.

The microstructure of the septa has been destroyed as well. Only solid and narrow 'middle dark lines' are seen in most instances. In very few septa of the holotype, isolated, very fine bunches of fibrils are recognized and interpreted here as trabeculae (Text-fig. 13A$_8$, middle). However, elsewhere in the same septa (Text-fig. 13A$_8$, upper) only a solid 'dark line' is seen.

DISCUSSION: *Axisvacuus semicirculatus* superficially resembles *Barytichisma* Moore and Jeffords, 1945 in its arrangement of septa (e.g. Moore and Jeffords 1945, text-figs 11–113, 123; Sando 1965, pls 2, 3; Weyer, 1965, pl. 1, figs 2b, 2f). In contrast to that genus, however, its cardinal protoseptum remains permanently long up to and including the calice floor. Also, external surfaces of all specimens of *Barytichisma* described to date lack distinct septal furrows.

None of the other species included here in *Axisvacuus* has a cardinal fossula comparable to *A. semicirculatus*. Only one transverse section of the holotype of *A. verus* (Text-fig. 7A$_5$) and the mature growth stage of one specimen of *A. postumus* (Text-fig. 11C$_2$) slightly resembles it. Arches are also developed in the holotypes of *Rotiphyllum latithecatum* Fedorowski, 2009a and *R. simulatum* Fedorowski, 2009a. However, those structures appearing in a different genus can be treated only as analogous. Thus, the arch bordering the inner part of the very deep key-hole cardinal fossula is here considered the main distinguishing character of *A. semicirculatus*.

OCCURRENCE: ?Amvrosievskyi Kupol, Limestone E$_8^5$, Lower Mandrykinian Horizon, Manuilovian Subhorizon (Specimen UAM-Tc.Don.1/70). Solenaya River Area: Novo Troitskoe Village, Limestone F$_1$, Upper Mandrykinian Horizon, Blagodatnian Subhorizon (UAM-Tc.Don.1/67, Holotype). Kalmyus River Area: Gorbachevo Village, Limestone F$_1^2$, Horizon and Subhorizon as above (UAM-Tc.Don.1/68, 69).

Genus *Falsiamplexus* Fedorowski, 1987

TYPE SPECIES: *F. elongatus* Fedorowski, 1987

? partim 1953. *Amplexus* Fomichev, p. 77 *non* Sowerby 1814, p. 165.
? 1984. *Amplexocarinia* Rodriguez, p. 149 *non* Soshkina, 1928, p. 379.
? 1992. *Amplexocarinia* Peng *et al*., p. 132 *non* Soshkina, 1928, p. 379.
? 2003. *Amplexocarinia* Fan *et al*., p. 228 *non* Soshkina, 1928, p. 379.
[Only taxa not placed in synonymy by Fedorowski (1987, p. 73) are listed above]

EMENDED DIAGNOSIS: Antiphyllidae with early ontogeny rotiphylloid; major septa short, amplexoid; cardinal protoseptum amplexoid, shortened beneath tabula, but almost equal in length to other major septa along its surface; counter protoseptum slightly longer than adjacent major septa; cardinal fossula inconspicuous; minor septa marked by furrows on external wall, occurring as short outgrowths inside calice, near its margin; tabulae complete, trapezoid; microstructure of septa trabecular.

SPECIES ASSIGNED: See Fedorowski (1987, p. 73, except for those transferred above to *Axisvacuus*) and probably *Amplexus* ? *romanovskyi* Fomichev, 1953; *Amplexus* ? *stuckenbergi* Fomichev, 1953; *Amplexocarinia tenuiseptata* Fan and Zhu, 2003.

DISCUSSION: The concept of the genus *Falsiamplexus* accepted in this paper differs in some details from the original (Fedorowski 1987, pp. 73–77) and hence the diagnosis has been emended. The occurrence of an 'incomplete aulos' early in ontogeny is the most important character deleted from the new generic diagnosis. Recent investigation of the structure commonly referred to as the 'aulos' demonstrated that it varies greatly in its morphogenesis (Fedorowski 2009b). The aulos proper, i.e., as originally understood by Smith (1928) and based on *Solenodendron furcatus* (Smith, 1925), is a permanent skeletal structure, consisting of curved and united inner margins of major septa secreted parallel to the corallite growth direction to form a tube, intersected by inner tabellae. Nothing like that structure occurs in the neanic growth stage of *Falsiamplexus*, although the inner margins of some of the major septa may curve toward each other (e.g. Fedorowski 1987, figs 28:1e, 33:1h). However, that structure results from the axial widening of the cardinal fossula, which is an intermediate step towards the final disintegration and shortening of the major septa.

Also, the 'aulos' formed from thickened inner margins of major septa (Fedorowski 1987, fig. 30:4a) results from the positioning of a transverse section coincidentally cut just above the upper surface of a tabula, where remnants of sclerenchymal cover remain. Thus, no type of 'aulos' occurs in the early ontogeny of *Falsiamplexus*.

The length of the cardinal protoseptum is the next question requiring consideration. A firm statement concerning the amplexoid character of that protoseptum is absent from the discussion by Fedorowski (1987, pp. 73–77), whereas that character caused the variability in the length of the cardinal protoseptum described in this paper and the earlier one cited above. Thus, the phrase 'long cardinal septum' in Fedorowski (1987) should be taken to mean an increase in the length of the cardinal protoseptum until it becomes temporarily almost equal to the major septa just above the upper surface of a tabula. It does not mean that the cardinal protoseptum is permanently lengthened.

Rotiphyllum was not mentioned in the earlier discussion (Fedorowski 1987) as ancestral to *Falsiamplexus*. That discussion was devoted mainly to the distinction of that genus from various ampleximorphs. Thus, the discussion that follows is focused mainly on that question and on the probable or possible relationship to *Falsiamplexus* of some earlier described ampleximorphs.

Indisputable representatives of the genus *Falsiamplexus*, other than those assigned to it by Fedorowski (1987, p. 73), remain unknown. The record by Kossovaya (1997, p. 57) of *F. delicatus* (Ross and Ross, 1963) from the Upper Gshelian deposits of Northern Timan was not illustrated and cannot be verified. The other probable synonyms, originally described as either *Amplexus* Sowerby, 1814 or *Amplexocarinia* Soshkina, 1928, are discussed below.

Fomichev (1953) critically discussed all important contributions dealing with the two genera mentioned above and included all his specimens in the genus *Amplexus*. However, he suggested a possible generic distinction between those specimens based on their differently oriented tabulae (Fomichev 1953, p. 80). Unfortunately, most specimens described and illustrated by that author were used for making thin sections, precluding additional studies, whereas his published data are inadequate for a firm re-identification of species and genera.

The holotype of '*Amplexus*' *stuckenbergi* Fomichev, 1953 has its major septa radially arranged and meeting at the corallite axis in the immature growth stage, but short and almost equal in length at maturity (Fomichev 1953, pl. 2, fig.10 a,b respectively), closely resembling '*Amplexus*' *corrugatus* Mather, 1915, included by Fedorowski (1987) in *Falsiamplexus*. An indistinct cardinal protoseptum occurs in one paratype of '*A.*' *stuckenbergi*, whereas it is clearly shortened in the other (Fomichev 1953, pl. 2, fig.11 a–v, 12 a–g respectively). Variation in the length of the cardinal protoseptum is analogous to that in '*A.*' *corrugatus*. Thus, '*A.*' *stuckenbergi* is provisionally included here in *Falsiamplexus*.

'Amplexus'? *romanovskyi* Fomichev, 1953 exhibits some characters similar to those of *F. reductus* but it is too poorly documented to allow a final identification. '*Amplexus*'? *schigariensis* Fomichev, 1953 may be conspecific with *Axisvacuus verus*, but its early ontogeny is missing. Both species of *Amplexus* left by Fomichev (1953) in open nomenclature are unidentifiable.

Two Chinese species, namely *Amplexocarinia muralis* of Peng *et al.* (1992) and *Amplexocarinia tenuiseptata* Fan and Zhu, 2003, are mentioned here as displaying the main diagnostic characters of *Falsiamplexus* and having very little in common with *Amplexocarinia* (compare with Soshkina 1928 and Fedorowski 1986a). Unfortunately, the immature growth stages of those specimens were not illustrated. Thus, they are only provisionally included in *Falsiamplexus*.

Most genera morphologically similar and possibly related to *Falsiamplexus* were discussed by Fedorowski (1987, pp. 73–77). Thus, only those showing similarity or relationship to *Axisvacuus* are discussed in this paper. The distinction between *Falsiamplexus* and *Axisvacuus* may be reduced to a single but important character: cardinal protoseptum amplexoid in the former and non-amplexoid in the latter. Thus, in *Axisvacuus*, that protoseptum, which is long in both genera during the immature growth stages, becomes permanently equal in length to other major septa in maturity, when all septa are shortened. The cardinal fossula disappeared in parallel with that shortening. In contrast, the amplexoid cardinal protoseptum in *Falsiamplexus* varies in length, depending on its position in relation to subsequent tabulae. That amplexoid character varies within individual species, being strongly accentuated in some specimens, but weakly in others. Species of *Falsiamplexus* having the cardinal protoseptum only slightly amplexoid, i.e., permanently shorter than adjacent major septa, have a deeper cardinal tabular fossula, and are thus easily distinguishable from *Axisvacuus*, but resembles *Bradyphyllum* Grabau, 1928. Specimens with a strongly amplexoid cardinal protoseptum and an underdeveloped cardinal fossula at maturity closely resemble *Axisvacuus* when transverse sections are cut just above the upper surface of a tabula. Also, shortening of the cardinal protoseptum may in some specimens be delayed in ontogeny (e.g. Text-fig. $14A_{5,\ 6}$). Thus, only a series of transverse sections allows the distinction between *Falsiamplexus* and *Axisvacuus*, whereas random transverse sections may easily be misleading. Consequently, difficulties in distinguishing between these two genera can be attributed to the technique applied, but not to true differences in morphology.

In contrast to the distinction between *Falsiamplexus* and *Axisvacuus* in the development of their cardinal protosepta, their counter protosepta vary in length to a similar extent. They are never truly elongated, but may either be equal to adjacent major septa or slightly longer than the counter-lateral septa. That slight elongation in early ontogeny, along with their finely trabecular microstructure, confirms both a close relationship between those genera and their inclusion in the family Antiphyllidae Ilina, 1970.

Three theoretical phylogenetic scenarios may be considered: 1) An independent derivation of both *Falsiamplexus* and *Axisvacuus* from *Rotiphyllum*; 2) Derivation of *Falsiamplexus* from *Axisvacuus*; 3) Parallel development of those taxa, derived from different members of the family.

The first scenario is the simplest and thus, most likely. *Rotiphyllum* is the stratigraphically oldest and morphologically simplest of the three genera in question. Its morphology shows characters typical of early growth stages of both *Falsiamplexus* and *Axisvacuus.* Thus, two slightly different mutations, both leading towards reduction in length of the major septa, are required to achieve genetic control on the main diagnostic differences mentioned above. Also, the stratigraphic level at which derivation occurred, which is critical for the second scenario, is unimportant in the first one. Both *Falsiamplexus* and *Axisvacuus* remain related to *Rotiphyllum* and to each other irrespective of the time of their derivation.

The second scenario requires precise dating of the oldest representatives of both *Falsiamplexus* and *Axisvacuus*. Also, representatives of both the ancestral genus and the oldest species of the descendant one should be present in a common geographic area. Otherwise, the possibility of migration of an apparently descendant species and genus could not be excluded. The data so far available apparently fulfill those criteria. *Axisvacuus* first appeared slightly earlier (Limestone E_1^{IV}) than *Falsiamplexus* (Limestone F_1) in the Donets Basin. Also, there are species of *Axisvacuus* much older than those from the Donets Basin (see list of species above). Thus, both the migration of *Axisvacuus* to that basin, and the resulting derivation of *Falsiamplexus* from that genus, can apparently be postulated. However, this scenario would be possible only if the Donets Basin representatives of *F. reductus* were the stratigraphically oldest of all remaining species included in that genus. Such evidence does not exist. On the contrary, '*Amplexus*' *expansus* Easton, 1945, from the Fayetville shale of Oklahoma, USA (Homburg or Elvira Group of Chesterian age) is certainly older than both the Texan (Fedorowski 1987; Gaptank Formation, Kasimovian) and Donets Basin (this paper; Early Bashkirian) representatives of *F. reductus*. Also, there are such species as '*Amplexus*' *geniculatus* Worthen, 1890 from the Lower Chesterian or '*A.*' *adnatus* and '*A.*' *dilatus*, both of Easton (1945) that exhibit characters of *Axisvacuus*. Those facts do not contra-indicate the second scenario, but point to the North American Chesterian as an area and time of the possible appearance of *Falsiamplexus*. It should be made clear, however, that the latter idea is of no more than a possibility based on the existing data.

The third scenario is purely theoretical at the moment because no taxa other than *Rotiphyllum* can be postulated as ancestors for either *Axisvacuus* or *Falsiamplexus*. The cardinal protoseptum in neither of those two taxa is shortened in the immature growth stage as it is in *Zaphrentites*. Thus, that genus should be excluded as ancestral despite being similar in some morphological features to early growth stages of both *Axisvacuus* and *Falsiamplexus*.

Bradyphyllum Grabau, 1928 is the genus most similar to *Falsiamplexus*, but the relationship between those two genera has not yet been discussed in adequate detail. Its status as a monophyletic genus, but not a morphotype, can be questioned. The latter is suggested by its very long stratigraphic range, covering at least the time span from Viséan to Early Permian. It may be even longer if *Bradyphyllum differentiatum* Fedorowski, 1973, from the *Wocklumeria* or *Gattendorfia* Biozone, is accepted as a member of that genus as originally suggested (Fedorowski 1973, p. 105). That assignment is not quite certain at the genus and family level. *B. differentiatum* is therefore excluded here from further consideration. Unfortunately, neither the early ontogeny nor the septal microstructure is known from the holotype of *Bradyphyllum bellicostatum* Grabau, 1928, the type species for the genus. Its cardinal protoseptum varies from being clearly shortened to equalling the adjacent major septa in length (Grabau 1928, pl. 2, fig. 11b–e), suggesting that it may be amplexoid. That feature, along with its slightly elongated counter protoseptum would be characters in common with *Falsiamplexus*. The morphology of the early growth stage is unknown in the type species, but detailed studies of Late Viséan (Fedorowski 1968) and Virgilian (Fedorowski 1987) species included in *Bradyphyllum* established a close similarity between the early growth stages of those species and to the early growth stage of *Falsiamplexus*. Thus, it may be shown that those two genera are synonymous if detailed study of the topotypes of *B. bellicostatum* documents a rotiphylloid early morphology and finely trabecular septal microstructure. The lack of such data and the uncertain monophyletic relationships within *Bradyphyllum* make distinction between those two genera more practical for the time being. Their close relationship seems undisputable.

Falsiamplexus reductus Fedorowski, 1987
(Text-fig. 14)

? 1953. *Amplexus*? *romanovskyi* Fomichev, p. 85, Pl. 2:16,17.
1987. *Falsiamplexus reductus* Fedorowski, p. 92, Pls 8: 16, 17; 10: 10, 13-15.

MATERIAL: Eight corallites (UAM-Tc.Don.1/72-78). Major parts of calices and/or proximal ends preserved in most. Calices very deep, narrow, following cylindrical mature growth of corallites; some flattened. Microstructure diagenetically altered, but macro-morphology well preserved. Fifteen thin sections and nineteen peels were available for the study.

DIAGNOSIS: *Falsiamplexus* with n:d = 16-20:4.0-6.0 mm; major septa short, thin; minor septa appear in upper part of mature calice; thin external wall bears shallow septal grooves; tabulae widely spaced, complete (after Fedorowski 1987, p. 92, modified).

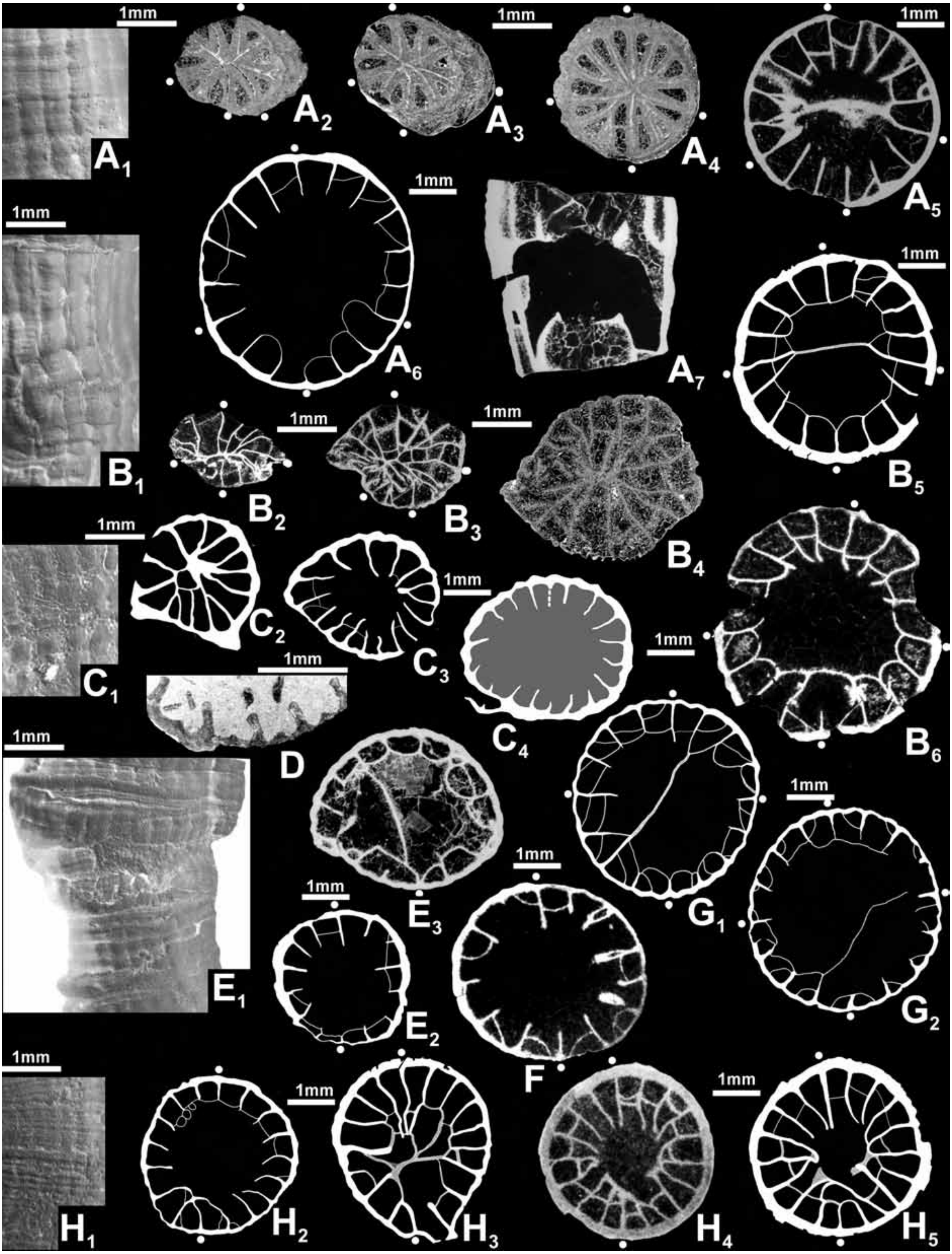
DISCUSSION: Despite differences in their stratigraphic position (Bashkirian to Kasimovian), and the great geographical separation between their occurrences, specimens from the Donets Basin are strikingly similar to those from SW Texas in their ontogeny and the morphology of their mature corallites. Also, the intraspecific variability in the two groups of specimens is closely similar.

The Donets Basin specimens are slightly smaller than those from Texas. Their septal numbers and corallite diameters vary from 14: 3.4 to 17:4.5 mm, but are not regularly sequential. Two specimens (Text-figs 14C_{1-4}, G_{1-5}) are differentiated from the others by n:d values of 18:3.2×2.8 mm and 18:3.9 mm respectively. Such a difference is insufficient for their separation at species level.

The morphology in the ontogenetically earliest observed growth stages of three corallites (Text-fig. 14A_{2-4}, B_{2-4}, C_2) differs mainly in the thickness of the septa and some secondary characters, caused in part by diagenesis (Text-fig. 14B_{2-4}). At the same time, they display a close similarity in all main diagnostic characters. Their cardinal protosepta reach the corallite axis and their rotiphylloid arrangement of the major septa is easily recognizable. The neanic morphology passes fairly rapidly into the mature morphology, characterized in general by a radial arrangement of short major septa with minor septa absent from both the corallite lumen and the thin external wall. However, the morphology exposed in individual transverse sections of that growth stage differs in the course of growth of individual corallites. That variation depends on two factors: the growth stage (early or late maturity) and the relationship of major septa to tabulae.

The first of the factors mentioned above results in the major septa being comparatively long where the cardinal protoseptum is not yet shortened (Text-fig. 14A_5, C_3). The second causes several changes, with development of an incomplete aulos-like structure being most common (Text-fig. 13B_5). That structure appears when the corallite is cut a short distance beneath a tabula. In that part of the corallite, the amplexoid major septa reach only the elevated peripheral parts of trapezoid tabulae (Text-fig. 14A_7), which span between their inner margins in the transverse sections (Text-fig. 14A_6, lower, $B_{5,\ 6}$ lower, F_1). Transverse sections cut in the parts of corallites with very underdeveloped major septa shows them to be free axially with sections of tabulae mainly or only at the periphery (Text-fig. 14D_2, E, F_2,). Transverse sections cut partly obliquely exposes amplexoid major septa partly above the flattened upper part of the tabula and partly beneath it (Text-fig. 14B_6 lower and upper respectively).

The identification of one corallite (Text-fig. 14H_{1-5}) as *F. reductus* is uncertain because its cardinal protoseptum was not identified with certainty. This possibly is the septum marked in the figure cited, but confirmation is impossible. The lengths of the major septa in this corallite are highly differentiated in individual growth intervals, being shortest in the earliest part studied (Text-fig. $14H_2$) and most differentiated in a slightly oblique section cutting some closely spaced tabulae (Text-fig. $14H_3$). Major septa in the advanced maturity of that specimen are much longer than those in typically developed specimens. Also, this specimen exhibits much shallower septal grooves and stronger



growth striae than the other corallites (Text-fig. 1H_1 and A_1, B_1, C_1, D_1).

A comparison of *F. reductus* to most other species included in the genus was made by Fedorowski (1987) and is not repeated here.

OCCURRENCE: SW Texas, locality USNM 700a, Gaptank Formation, Upper (?) Missourian (Kasimovian). Donets Basin, Solenaya River Area, Novo Troitskoe Village, Limestone F_1 Upper Mandrykinian Horizon, Blagodatnian Subhorizon **(**Specimens UAM-Tc.Don.1/72-78).

SUMMARY

Axisvacuus and *Falsiamplexus* exhibit close similarity to each other in such main diagnostic characteristics as the finely trabecular microstructure of septa, the rotiphylloid neanic structure and the amplexoid mature morphology. Thus, both are included in the family Antiphyllidae Ilina, 1970 and considered closely related to each other and to *Rotiphyllum* Hudson, 1942. The fact that the cardinal protoseptum is indistinguishable from other major septa in the mature growth stage of *Axisvacuus*, but is amplexoid and variable in length, albeit generally shortened along the cardinal fossula floor in *Falsiamplexus*, is accepted as a qualitative distinction adequate for the discrimination of separate genera.

Rotiphyllum is here considered ancestral to both genera, but only *Axisvacuus* is proposed above to have been derived directly from that genus. Two options are suggested for the derivation of *Falsiamplexus*: either directly from *Rotiphyllum* or with *Axisvacuus* as an intermediate taxon. The existing data do not indicate which option is more probable.

Rotiphyllum voznesenkae Fedorowski, 2009a and *Axisvacuus extendus* are examples of species barely distinguishable at genus level. In the first species the inner margins of the major septa have temporarily disintegrated, i.e., it temporarily exhibits the diagnostic character of *Axisvacuus*, whereas permanent disintegration of the inner margins of the major septa appears late in the ontogeny of the second species. Those examples emphasize the necessity for investigations to be based on a series of sections taken from all ontogenetically important parts of corallites. Studies based on one or two random transverse sections lead to misinterpretations at genus or even family level. Longitudinal sections are important in that they offer several pieces of information – primarily the presence or absence of the columnotheca of Fedorowski 2009b and the morphology of the tabularium (normal or biform). However, a careful study of the microstructure and mutual relationships of the septa and tabulae in well oriented transverse section will bring similar results. Thus, the lack of a longitudinal section, sometimes resulting from scarcity of material, does not reduce the accuracy of the description of a taxon, if transverse sections of its particular growth stages are thoroughly studied and distances between them are known.

The occurrence of specimens from the Donets Basin, identified here as *Axisvacuus postumus* (Smith, 1931), may suggests a marine transgression directed from the southeast in western Europe during *Donetzoceras aegiranum* time. *Falsiamplexus reductus* Fedorowski, 1987 may indicate that communication between the Ukrainian and southwestern Texan seas extended from Bashkirian to Kasimovian time.

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Text-fig. 14. *Falsiamplexus reductus* Fedorowski, 1987. Protosepta and alar septa marked by dots where their identification possible. **A** – Specimen UAM-Tc.Don.1/71. A_1 – surface of external wall, $A_{2\text{-}4}$ – neanic growth stage (peels), $A_{5,\,6}$ – mature growth stage, A_7 – longitudinal section. **B** – Specimen UAM-Tc.Don.1/75). B_1 – surface of external wall, $B_{2\text{-}4}$ – neanic growth stage, $B_{5,\,6}$ – mature growth stage; note differentiated length of strongly amplexoid cardinal protoseptum (B_4 peel, B_5 drawing). **C** – Specimen UAM-Tc.Don.1/76. C_1 – surface of external wall, C_2 – neanic growth stage, C_3 – early mature growth stage, C_4 –middle part of calice. **D** – Specimen UAM-Tc.Don.1/78 upper part of calice with short minor septa developed. **E** – Specimen UAM-Tc.Don.1/73. E_1 surface of external wall, $E_{2,\,3}$ mature growth stage. **F** – Specimen UAM-Tc.Don.1/77. Mature growth stage. **G**. Specimen UAM-Tc.Don.1/74. $G_{1,\,2}$ – mature growth stage. **H** – Specimen UAM-Tc.Don.1/72. H_1 – surface of external wall, $H_{2\text{-}5}$ – mature growth stage. See Remarks at Text-fig. 6 for further explanations

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