On three rugose coral genera from Serpukhovian strata in the Upper Silesian Coal Basin, Poland

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ABSTRACT:


The rugose coral specimens included by Schindewolf (1952) in the genera Claviphyllum Hudson, 1942, Fasciculophyllum Thomson, 1883 and Pentaphyllum (Tachylasma) Grabau, 1922 are revised on the basis of the original collection. The first two taxa are included in Antiphyllum Schindewolf, 1952, either in its original sense or in its newly introduced subgenus Antiphyllites. The new genus Effigies is introduced for Pentaphyllum (Tachylasma) silesiacum Schindewolf, 1952. The reasons for placing individual genera within given families and sub-orders are discussed. New, detailed descriptions of species are supplemented by text-figures in order to document their intraspecific variability and phylogenetic relationships.

Key words: Rugosa genera; Serpukhovian; Poland; Revision.

INTRODUCTION

The rugose coral fauna from the Serpukhovian strata of the Upper Silesian Coal Basin was first described roughly by Schwarzbach (1937) in his paper on the stratigraphy of that basin. Schindewolf (1942) introduced one new species (Ufimia schwarzbachi) as a partial revision of Zaphrentis sp. a of Schwarzbach, 1937. Ten years later Schindewolf (1952) monographed the entire Schwarzbach’s (1937) collection derived from the Polish part of the basin (Text-figs 1, 2). Most species and subspecies names introduced by Schindewolf (1952) remain valid, but this is not true for the genera in which those species were included. Also, several specimens of Schwarzbach’s collection were only superficially studied by Schindewolf (1952), and require taxonomic revision. Weyer (1974) has already re-oriented the holotype and only specimen of Antiphyllum inopinatum Schindewolf, 1952 and suggested the synonymy of that genus with Claviphyllum Hudson, 1942. He then further developed this idea (Weyer 1975) with a comprehensive discussion on several genera related to Claviphyllum as potential members of the subfamily Antiphyllinae Illina, 1970. His most recent attitude (Weyer 2005) to the question of the synonymy of Antiphyllum with Claviphyllum differs from his earlier one, as discussed in more detail below with the remarks on the genus Antiphyllum.

The revisions, re-descriptions and new descriptions of most Serpukhovian rugose coral taxa from the Upper Silesian Coal Basin, already completed by Fedorowski (2009a, 2010a, in press), allow a new approach to the taxonomy and relationships of those taxa. The present paper is devoted to the revision of the corals included by Schindewolf (1952) in the genera Claviphyllum Hudson, 1942, Fasciculophyllum Thomson, 1883 and Tachylasma Grabau, 1922, in order to bring them in line with the taxa revised so far. All specimens attributed by Schindewolf (1952) to those were collected from the Polish side of the Upper Silesian Coal Basin (Text-figs 1, 2 respectively). Considerations of the biostratigraphy of the
Serpukhovian deposits in the Upper Silesian Coal Basin based on the rugose corals, the possible phylogeny of those corals, and their relationships, would be misleading without such revision. Also, a more detailed investigation of many specimens in the Humboldt Museum collection, which were superficially treated by Schindewolf (1952), has allowed new taxonomic interpretations, proposed in this paper.

High resolution biostratigraphy for the taxa described in the present paper cannot be introduced for several reasons. The most important of these is the lack of the bed by bed collections of orthofossil goniatitids and the absence of index Conodonta and Foraminifera. As a result, the stratigraphy of the deposits yielding the rugose coral fauna is only superficially treated here (Table 1). All ‘Beds’ mentioned in the table belong to the Paralic Series (Text-fig. 2). The remaining series are barren from corals.

All specimens were derived from the upper part of the Roemer Marine Horizon (1b), which lies within the Poruba Beds of the local lithostratigraphy and corre-

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<th>Stage</th>
<th>Substage</th>
<th>‘Beds’</th>
<th>‘Horizons’</th>
</tr>
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<tbody>
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<td>Serpukhovian</td>
<td>Arnsbergian</td>
<td>Poruba (Porębskie) Beds</td>
<td>Roemer Ib (underlying &amp; overlying units omitted)</td>
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<td>(E₂ Zone)</td>
<td>Jaklově (Jaklowieckie) Beds</td>
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<td>Pendleian</td>
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Table 1. Simplified stratigraphy of the deposits yielding the rugose coral fauna
sponds to the Middle Arnsbergian or middle part of the upper *Eumorphoceras* Biozone (E2). These are the stratigraphically youngest marine beds in the Basin that yield rugose corals. Also, the rugose coral fauna of those beds is the richest and most diversified fauna present, as previously documented by Weyer (1977) and Fedorowski (2009a, 2010a, in press).

It should be mentioned that, following Hudson (1936) and Fedorowski (1997), only the cardinal and the counter septa are accepted as protosepta. The remaining major septa, including the alars and counter-laterals, are treated as metasepta.

**MATERIAL AND METHODS**

All specimens included by Schindewolf (1952) in genera mentioned in the introduction were restudied using the remnants of specimens along with original and new thin sections. All thin sections were digitally photographed with computerized Olympus microscope. Also most cuts were ground, treated with the immersion oil and photographed. Computer drawings based on digital photographs were prepared whenever necessary to augment the documentation.

Preservation varies among the specimens studied. The macro-morphology of the neanic and early mature growth stages is well preserved in most corallites, but the calices are commonly compressed. Also, the microstructure of septa is inadequately known because it has been almost entirely altered by diagenesis.

All re-studied specimens are housed in the Museum of Natural History, Department of Palaeontology of Humboldt University (Acronym MB.K). The repositories of individual specimens are not repeated in the figure captions.

**SYSTEMATIC PALAEONTOLOGY**

Subclass Rugosa  Milne Edwards and Haime, 1855
Order Stauriida Verrill, 1865
Suborder Stereolasmatina Hill, 1981
Family Antiphylliidae Ilina, 1970

**EMENDED DIAGNOSIS:** Small, solitary, non-dissepimented corals with cardinal septum located on convex side of coralite; early ontogeny rotiphiyloid; cardinal septum shortened late in ontogeny or only on calice wall; counter septum commonly elongated, never shortened; stereocolumn of early ontogeny often replaced by free axial area in maturity.

Remarks: Ilina (1970) introduced the family Antiphylliidae for taxa having the cardinal septum apparently elongated, i.e., she followed the mistake of Schindewolf (1952) in considering such a character to be present in the genus *Antiphyllum* Schindewolf, 1952. Weyer (1974) re-oriented the type species of *Antiphyllum* inopinatum Schindewolf, 1952, placed *Antiphyllum* in synonymy with *Claviphyllum* Hudson, 1942, and mentioned several potentially related genera. Later he emended the family Antiphylliidae, reduced it to the subfamily level and included that subfamily in the Hapsiphyllidae Grabau, 1928 (Weyer 1975). He also discussed several genera potentially belonging to that subfamily, introduced the new genus *Clavilasma*, and proposed a subfamily diagnosis.

Fedorowski (1987) accepted Weyer’s (1974, 1975) concepts of both the synonymy of *Antiphyllum* with *Claviphyllum* and the position of the subfamily Antiphylliidae within the family Hapsiphyllidae. Also, he offered a comprehensive discussion on the genera potentially belonging to the Antiphyllinae and introduced a subfamily diagnosis slightly different from the original one (Fedorowski 1987, p. 32). Most of his conclusions concerning genera, except for the synonymy of *Antiphyllum* with *Claviphyllum* are accepted here. Also, an emended diagnosis is introduced combining the main characters of both earlier diagnoses, and the Antiphyllidae are treated as an independent family both here and in earlier papers (Fedorowski, 2009b, c, 2010a, in press).

Subfamily Antiphyllinae Ilina, 1970

**DIAGNOSIS and REMARKS:** As for the family.

Genus *Antiphyllum* Schindewolf, 1952

**TYPE SPECIES:** *Antiphyllum* inopinatum Schindewolf, 1952.

**EMENDED DIAGNOSIS:** Antiphylliidae with cardinal septum slightly shortened in late ontogeny or long up to and including calice floor; counter septum strongly dominant; alar septa in early ontogeny long, in advanced mature growth stage amplexoid, shortened at least beneath tabulae; minor septa underdeveloped, free.

Remarks: For the following reasons the synonymy of the genus *Antiphyllum* with *Claviphyllum* is not recommended:

1. The holotype and only specimen included by Schindewolf (1952, p. 206, text-fig. 19a-d) in *Antiphyl-
Claviphyllum inopinatum, is poorly preserved, with its tip missing and its skeleton diagnostically altered to the extent that the microstructure of the septa is unrecognizable. That alteration is mentioned by Weyer (1974, p. 348) and is clear from his photographs (Weyer 1974, pl. 1, figs 1-3). Both of those factors hinder the comparison of other potential members of the genus to that specimen. Nevertheless, the careful revision by Weyer (1974) fully supports the position of Antiphyllum within the family Antiphylidae and the mature morphology of A. inopinatum allows some further considerations at the genus and species level.

2. Among the potential members of the genus Antiphyllum are species such as Claviphyllum hillae Hudson and Fox, 1943 that have a zaphrentoid early ontogeny, no pseudofossula at the counter septum, the major septa differentiated in length within all quadrants of septa, the cardinal septum and the alar septa permanently shortened starting from at least the early mature growth stage, and the counter-lateral septa shorter than the next major septa in the sequence of insertion. Such a set of characters is absent from the holotype of A. inopinatum, although its cardinal septum is shortened in a comparatively early growth stage and the length of one or both of its counter lateral septa is less in its early growth stage than that of the next major septa inserted (Weyer 1974, text-fig. 1:2, 3). The major septa in the cardinal quadrants of the holotype of A. inopinatum are not differentiated in length, but they are differentiated in part of the mature growth stage of ‘Claviphyllum’ magnificum Schindewolf 1952 (Text-fig. 16e; Text-fig. 31, J herein), which is here questionedly included in the former species. All of the similarities listed above are weakly developed. The differences are possibly sufficient for isolating that group of species into a separate new genus or a subgenus of Antiphyllum, but this is not proposed here in a formal way.

3. Another group of species exhibit characteristics which are opposite to those in the corals discussed above and are either absent or hardly recognizable in A. inopinatum. The main differences from Antiphyllum include the lack of shortening of the cardinal septum throughout the entire ontogeny up to the mature calice floor and the development of a circumaxial structure comparable to a circulotheca or an incomplete aulos. This group can further be subdivided into subgroups – one with a very well developed counter pseudofossula and another in which that feature is hardly recognizable or not developed. The first subgroup, represented by ‘Claviphyllum’ pauperculum Schindewolf 1952 (= Antiphyllites pauperculus), exhibits some similarity to the immature growth stage of ‘Claviphyllum’ magnificum, whereas the second was included by Schindewolf (1952) in Fasciculophyllum and by Weyer (1977) in Rotiphyllum. Those subgroups are here treated together, but that approach is the result of scarcity of material rather than from the conviction that they are identical at the genus or subgenus level. This combined group is here distinguished as the new subgenus Antiphyllites.

The proposed subdivision may be treated as an instance of excessive splitting. My attitude to that question is supported by two reasons: (A) Skeletal elements available for animals so primitive as corals are very limited. Thus, variants of those elements are commonly repeated across the phylogeny of particular lineages. The elongated counter protoseptum in Soshkineophyllum Grabau 1928 (Plerophyllinae Sokolov, 1960) and Claviphyllum (Stereoelasmatinae Hill, 1981) can serve as one example. The aulos and the columnotheca may be taken as another example; they appear very similar in general morphology and are similar in their functions, but are completely different in origin (Fedorowski 2009d). (B) According to the regulations of the International Code of Zoological Nomenclature qualitative characters have at least a generic rank. Having nothing but skeletons available for the taxonomy of rugose corals, we must be especially sensitive to any differences in morphology. The question of morphological similarity and functional analogy as factors bearing on rugose coral taxonomy is more widely treated elsewhere (Fedorowski 2010b).

The correction of the orientation of the holotype of A. inopinatum by Weyer (1974, 1975, 1977) allowed him to include that species in Claviphyllum. That option was followed by Fedorowski (1987, 2001), as mentioned above in the remarks on the family. However, those two taxa may be separated at the genus level, because clearly contralating minor septa are present in Cyathopsis erica McCoy, 1851, the type species for the genus Claviphyllum, whereas the underdeveloped minor septa in A. inopinatum are very short and free when present. Separation of A. inopinatum from Claviphyllum validates the name Antiphyllum although not in the sense proposed by Schindewolf (1952). Weyer (2005, p. 8) presented a similar conclusion by using the name Antiphyllum for both species originally included by Schindewolf (1952) in Claviphyllum. The validity of the name Antiphyllum was also suggested in one of my earlier papers (Fedorowski 2010a, p. 181).

In addition to the group of species discussed above in item number 1 as being represented by Claviphyllum hillae, only Clavilasma Weyer, 1975 should be discussed as bearing features comparable to either Claviphyllum or Antiphyllum. Metriophyllloid flanges present on the major septa in Clavilasma distinguish it from the last two genera mentioned, although its contralating minor septa point towards the first genus.
Both of those characters are weakly developed, but their occurrence must be treated as qualitative, thus indicating generic rank. The pinnate, Zaphrentites-like arrangement of major septa, persisting in that genus up to the calice floor, may be considered an auxiliary character allowing its distinction from Antiphyllum and pointing towards Claviphyllum ss., as originally proposed by Weyer (1975). Thus, Clavilasma is here considered as either an independent genus as originally erected by Weyer (1975) or a subgenus of Claviphyllum. Its synonymy with the latter is also a possible option.

Actinophrentis Fomichev, 1953 and Monophyllum Fomichev, 1953, both revised by Fedorowski (1987), are characterized by an elongated counter septum, and are similar to Antiphyllum in several morphological aspects. However, their alar septa are never shortened and are commonly elongated. That character alone is adequate for their distinction from Antiphyllum. Other genera of the family Antiphyllidae bear much more distinct characteristics and do not require detailed discussion.

Subgenus Antiphyllum Schindewolf, 1952

TYPE SPECIES: As for the genus

DIAGNOSIS: Antiphyllum with a cardinal septum shortened beginning in early maturity or earlier; counter pseudofossula may occur early in ontogeny.

Antiphyllum ?inopinatum Schindewolf, 1952
(Text-fig. 3)

1952. Antiphyllum inopinatum Schindewolf, p. 206, text-fig. 19a–d.

?1952. Claviphyllum magnificum Schindewolf, 1956, text-fig. 16a–f, pl. 1, fig. 4, pl. 2, fig. 6.


1977. Claviphyllum inopinatum (Schindewolf, 1952); Weyer, pl. 1, fig. 3.

EMENDED DIAGNOSIS: Antiphyllum with n:d value 16:20:6.0:10.0 mm; cardinal fossula weakly accentuated, triangular; counter septum strong, rhopaloid, reaches corallite axis; shortening of alar septa inconspicuous, obvious only immediately beneath tabulae.

MATERIAL. Two specimens designated by Schindewolf (1952, pp. 196 and 206) holotypes of a) Claviphyllum magnificum Schindewolf, 1952 (MB.K. 795) and b) Antiphyllum inopinatum Schindewolf, 1952 (MB.K. 78) respectively. Both specimens are slightly incomplete, with the earliest ontogenetic growth stage missing but with part of the neanic growth stage preserved. The microstructure of the septa is strongly diagenetically altered in both corallites. Only the thin sections prepared from the holotype of 'C. magnificum were restudied here, whereas the comparison to the holotype of A. inopinatum is based on the careful restudy of that species by Weyer (1974).

REMARKS: This section is restricted to a comparison of the holotypes of A. inopinatum and Claviphyllum magnificum. Detailed descriptions of both species were given by Schindewolf (1952, pp. 196–199 and 206–208). Unfortunately, his incorrect orientation of the former specimen made his description misleading in several points. Thus, the re-description of A. inopinatum by Weyer (pp. 346–350) is used here for the comparison of the holotypes. Weyer (1974, p. 350) has already suggested the possible synonymy of C. magnificum and C. pauperculum with A. inopinatum. Only his suggestion concerning C. magnificum is accepted here with some restrictions.

The holotype of A. inopinatum is much smaller and possesses fewer major septa than the holotype of 'C. magnificum. Those small values in A. inopinatum have either resulted from its death in the early mature growth stage, or are typical for the species. Paucity of material prevents a plausible choice between these alternatives. Several characters of both specimens are comparable (Schindewolf 1952, text-fig. 19a–d; Weyer 1974, text-fig. 1:1–5; this paper, Text-fig. 3A–L). These are:

1) The comparatively early and constant shortening of the cardinal septum.

2) The strong, permanently elongated, non-amplexoid and rhopaloid counter septum. Its elongation well above the calice floor is established only in the holotype of A. inopinatum since the calice in 'C. magnificum was not sectioned.

3) The permanent elongation of the alar septa during the immature growth stage. They may vary slightly in length during the neanic growth stage, but are generally the longest in the cardinal quadrants during that growth stage (Text-fig. 3A–H; Weyer 1974, text-fig. 1:1). The alar septa became amplexoid and variable in length during the mature growth stage of both specimens, i.e., their length depends partly on the position against tabulae. However, that relationship, i.e., shortening of the alar septa just beneath tabulae, is better demonstrated in the holotype of 'C. magnificum (Text-fig. 3I–L), whereas one of those septa in the holotype of A. inopinatum is long in the calice, i.e., well above the last tabula (Schindewolf 1952, text-fig. 19d, left; Weyer 1974, text-fig. 1:4, right).

*Note:* Scale bars located between two adjacent pictures apply to both; those to right of picture apply only to that picture. Scale bar at bottom of figure applies to remaining pictures. Protosepta and alar septa marked by black dots. Cardinal septum at bottom. Transverse thin sections, except where stated. Drawings follow corresponding photographs where necessary. Septal loculi sectioned above last tabula (= calice floor) shadowed in drawings. For occurrence see descriptions of species.
(4) The great elevation of the peripheral parts of tabulae, resulting in the comparatively large number of tabular intercepts seen in transverse sections.

The taxonomic value of the similarities listed above, which are not always close, as in the alar septa, is further reduced by the following differences: The diameter and number of septa in the holotype of *C. magnificum* are much larger than in the holotype of *A. inopinatum* (maxima in the diagnosis). The amploexoid character of major septa is more strongly accentuated in *C. magnificum* (Text-fig. 3I, J vs 3K, L) than in *A. inopinatum* (Weyer 1974, text-fig. 1:2−4). *C. magnificum* has counter pseudofossulae in its neanic growth stage (hardly if at all distinguishable in *A. inopinatum*), and its cardinal fossula is inconspicuous or absent from that growth stage (Text-fig. 3A−G). The variable length of the counter-lateral septa in particular growth stages is much better demonstrated in the holotype of *C. magnificum* than in *A. inopinatum*. Those septa are clearly elongated in the early ontogeny of *C. magnificum* (Text-fig. 3A−H), with one of them being as strong and long as the counter septum (Text-fig. 3G, H), whereas in *A. inopinatum* both of the counter-lateral septa are shorter than the counter septum (Weyer 1974, text-fig. 1:1). In the mature growth stage of the holotype of *C. magnificum* the counter-lateral septa are permanently shortened, whereas they are not shortened in the calice of the holotype of *A. inopinatum* and are inconsistent in length beneath the calice floor, where one of them is long (Weyer 1974, text-fig. 1:4 and 2, 3 respectively).

The above discussion does not support an unequivocal synonymy of the specimens discussed. Several details in their morphology differ to the extent that a distinction at the species level is possible. Paucity of material available for re-study does not allow an adequately supported decision to be made. Thus, *C. magnificum* is only questionably included in the synonymy of *A. inopinatum*, but may in fact represent a separate species as described by Schindewolf (1952).

**OCCURRENCE:** Sośnica Mine (Oehringen Grube in German). Gaebler marine horizon, upper Roemer (Ib) marine band, Serpukhovian (middle Amsbergian), ammonoid Zone E3b.

**Type Specie:** *Claviphyllum pauperculum* Schindewolf, 1952

**Name derivation:** *Antiphyllites* after close relationship to *Antiphyllum.*

**Diagnosis:** *Antiphyllum* with cardinal septum long up to and including mature calice floor; cardinal fossula absent or very inconspicuous; either united inner margins of major septa form counter pseudofossula that persists up to calice floor, or long-lasting circumaxial structure occurs.

**Remarks:** The main characters distinguishing corals included here in the new subgenus *Antiphyllites* derived from the nominative subgenus are the permanent equality of the cardinal septum with the adjacent major septa and the underdevelopment or absence of the cardinal fossula. They indicate that the polyp’s life habits were different from polyps of the nominative subgenus and should be treated as being genetically determined, thus constituting a taxonomically important difference. Several aspects of the physiology of rugose corals were discussed earlier (Fedorowski 1997) and are mentioned here to point out the taxonomic value of those reconstructed features, commonly forgotten to consider.

The occurrence of a circumaxial structure, lasting throughout most of the ontogeny is the next important character of *Antiphyllites*, distinguishing it from *Antiphyllum*. That structure, in the form of either the counter pseudofossula (Text-figs 4C–K; 5J, Q, R; 6F) or an almost complete or entirely complete circulotheca (Text-figs 8G–J; 9F, G, K, T; 10H–M), is elevated well above the calice floor. Neither of those structures occurs in the holotype of *A. inopinatum*. The counter pseudofossula occurring in the holotype of *Claviphyllum* *magnificum* is short-lasting and restricted to the neanic growth stage. However, that character is here interpreted as proof of the close relationship of both subgenera.

The shape of the tabularium, as deciphered from the arrangement of tabular intercepts seen in the transverse sections, is the next distinguishing character. Numerous tabulae seen in both specimens included here in *Antiphyllum inopinatum* are in contrast to the rare sections of tabulae seen in all specimens included here in *Antiphyllites*. From those differences it is interpreted that the former has a highly elevated tabularium with densely packed tabulae and the latter specimens have widely spaced tabulae. The taxonomic value of that feature is less important than those discussed earlier, and is treated only as an auxiliary factor. Summing up arguments given here and in the remarks on the genus, the distinction at the subgenus level between *A. inopinatum* on the one hand and *Claviphyllum* *pauperculum* on the other seems to be adequately supported.

Note on the genus ‘*Fasciculophyllum*’ of Schindewolf 1952
This note is introduced as a separate part of the discussion in order to briefly demonstrate in the approach of some scientists to Fasciculophyllum and to explain my own approach to that genus in the context of ‘F.simplex’ Schindewolf, 1952, questionably transferred here to the subgenus Antiphyllites. The approach of individual researchers to the generic name Fasciculophyllum and to the taxonomic content of the genus varies considerably since it was introduced by Thomson (1883). That only in part resulted from the loss of all syntypes of F. dybowskii, chosen as the type species by Gregory (1917, p. 238), and of all other specimens illustrated by Thomson and Nicholson (1876) and by Thomson (1883) (Hill, 1938–1941, pp. 130 and 133 respectively). Differences in the evaluation of the taxonomic value of individual features and/or the disregard of some of them by particular authors, are perhaps the most important reasons. That is already obvious from the discussion by Hill (1938–1941, pp. 130–132), who revised the Scottish coral taxa introduced by Thomson and Nicholson (1876) and by Thomson (1883) and also from her synonymy and description of Fasciculophyllum eruca (McCoy). Her statement (p. 133): ‘the alar septa and their neighbours in the cardinal quadrants are long’ means that she did not recognize the true alar septa, whereas the shortening or underdevelopment of those septa allowed Hudson (1942) to introduce the genus Claviphyllum. Both Hill (1938–1941) and Hudson (1942) either did not recognize or did not accept the taxonomic value of the difference between contratant and short, free minor septa. Also, that difference was not recognized by Schindewolf (1952), Weyer (1974, 1975, 1977, 1982) or Fedorowski (1987, 2004), who discussed Fasciculophyllum, Rotiphyllum, Antiphyllum and several other genera that were considered by them to be either related or only similar to each other. The above aspects are omitted from this discussion and the reader is referred to the papers cited.

Species included by Schindewolf (1952) in Fasciculophyllum differ considerably from one another, as partly documented in earlier revisions by Fedorowski (2009a, 2010a) of the types of Fasciculophyllum tritus Schindewolf, 1952 and F. repressum Schindewolf, 1952. The first of those species was selected as the type species of the new genus Silesamplus Fedorowski, 2009a, whereas the second was accepted as the type species of the new genus Variaxion Fedorowski, 2010a, belonging to the new subfamily Variaxioninae Fedorowski, 2010a. Also Fasciculophyllum simplex Schindewolf, 1952, revised in this paper, does not belong in the genus Fasciculophyllum (see below). It was re-identified by Weyer (1977, p. 460) as Rotiphyllum. However, that generic identification, which was accepted in my earlier paper (Fedorowski 2004), cannot be accepted here. This conclusion was drawn from my subsequent studies of the type collection of Schindewolf (1952), the additional Czech Republic and Polish collections of the Serpukhovian Rugosa from the Upper Silesian Coal Basin (Fedorowski, 2009a, 2010a, in press), and the Lower Bashkirian Rugosa of the Donets Basin, Ukraine (Fedorowski 2009b, c). Although similar to Rotiphyllum in some characteristics, specimens of ‘F. simplex’ differ from the type and other species of that genus in several characters specified below. Thus, none of the species identified by Schindewolf (1952) as Fasciculophyllum belongs to that genus.

Antiphyllum (Antiphyllites) pauperculus (Schindewolf, 1952)
(Text-figs 4−7)

1937. Zaphrentis aff. postuma Smith; Schwarzbach, p.433, pl. 15, figs 1, 3, 6; text-fig. 5.
1952. Claviphyllum pauperculus Schindewolf, p. 200, pl. 1, figs 3, 5–9; pl. 2, figs 3–5; text-figs 17, 18.

MATERIAL: Schindewolf (1952, p. 202) mentioned the holotype and 24 specimens of this species as being at his disposal. From that original collection only the holotype (MB.K. 796) and 18 paratypes and hypotypes (MB.K. 797, 799–803, 5458–5463A–E, 5464, 5465), were available for the present re-investigation. The remaining six specimens were not found. Most specimens are partly destroyed by compaction in their mature parts. This concerns first of all the holotype, the original illustrations of which were idealized (Schindewolf 1952, text-fig. 17a−e vs Text-fig. 4A−K herein). Some specimens have been corroded and the tips of almost all are lacking. Also, the diagenetic alteration of the septa is advanced to the extent that reliable reconstruction of their microstructure is impossible in most instances. Forty one thin sections were available for study. Fourteen of them were newly made for the purpose of this paper.

EMENDED DIAGNOSIS: Antiphyllum with n:d value 16−18:4.5–5.3 mm; inner margins of major septa in cardinal quadrants and most of counter quadrants unite to form arch open towards counter pseudofossa; cardinal septum equal in length to adjacent major septa, may be very slightly shortened only in advanced mature growth stage; counter septum elongated; alar septa slightly shortened beneath tabulae.

INTRODUCTORY REMARKS: Despite dealing with five thin sections prepared by Schindewolf (1952) for his
study, my recognition of individual growth stages of the holotype, the details of its morphology, and the state of its preservation differ from those of Schindewolf (1952, pp. 200–202). Those differences are so numerous that a completely new description rather than a discussion of individual details is more practical. Thus, I will point to particular statements of Schindewolf only when necessary.

The poor state of preservation of the holotype, not mentioned by Schindewolf (1952) in his description, should be pointed out first. The partial crushing of the skeleton may have resulted in the infillings with strange fabric of the interseptal loculi. Those infillings suggest an apparently deep calice, extending down to the neanic growth stage. Such an extension may not be true, as indicated by the occurrence of a tabula in a loculum completely filled with fabric in the earlier growth stage (Text-fig. 4E, G vs. C, D, upper left, white). Thus, the true depth of the calice remains unknown.

The idealized drawings by Schindewolf (1952, text-fig. 17a–e) are misleading in some aspects, the most important of which is the shortening of the cardinal protoseptum in the late mature growth stage. That septum is longitudinally broken near its inner margin (Text-fig. 4J, K, lower) and is in fact only slightly shorter than the major septum, adjacent to it on its left side, but it is as long as its neighbouring major septum on the right. Thus, the depression toward the periphery of the axial area is shallower than was drawn by Schindewolf (1952). Also, his statement that the holotype reaches 10 mm across is not confirmed. The tip of the corallite is missing.

The holotype was almost completely thin-sectioned. Thus, the reader is referred to Schindewolf (1952, p. 200) for the description of the external characteristics of that specimen.

Text-fig. 4. *Antiphyllum (Antiphyllites) pauperculus* (Schindewolf, 1952). Specimen MB.K. 796. Holotype. A, B – neanic growth stage (=Schindewolf 1952, text-fig. 17a), C-K – early to late mature growth stage (=Schindewolf 1952, text-fig. 17b–e respectively). Photographs by courtesy of Dr. Dieter Weyer, Berlin. See Note following description of Text-fig. 3 for further explanations.
EMENDED DESCRIPTION OF THE HOLOTYPE:
The cardinal and counter septa are long, but their ‘middle dark lines’ (the primary septa) do not meet in the ontogenetically earliest preserved growth stage, which has an n:d value 13:2.4 mm (Text-fig. 4A, B; Schindewolf 1952, text-fig. 17a). All of the primary major septa (‘middle dark lines’) in the cardinal quadrants are in direct contact. The inner margin of the cardinal septum curves towards and is united with the left primary major septum. That arrangement can be described as leading towards the arch that is present in the next thin section of the series. The primary major septa of the individual counter quadrants are directly connected, but the resulting sets are isolated from those of the cardinal quadrants and from the primary counter septum. The latter septum is already slightly thicker than the counter-lateral major septa, but it is longer than only one of them and almost equal in length to the other.

The morphology shown in the next thin section of the series (Text-fig. 4C, D; Schindewolf 1952, text-fig. 17b) is closely comparable to that described above and is here considered as the more advanced neanic growth stage with an n:d value 16:3.6 mm. The major septa are now arranged in a complete arch, typical for the species discussed. The arch is open towards the counter pseudofossula, which is occupied by the counter septum, the longest and thickest of all major septa. The inner margin of that septum extends beyond the corallite axis, reaching the inner margin of the arch next to the cardinal septum. Only some primary major septa in particular quadrants remain in direct contact. An axial bifurcation of the primary cardinal septum is apparent in this thin section and the next one in the series. It illustrates the inner margin of the cardinal primary septum curved toward the right and a segment of one of the left primary major septa, perhaps the alar septum, diagnostically isolated from its peripheral part, but united with the cardinal septum. Both counter-lateral septa became the longest in the counter quadrants, whereas the alar septa remain longest in the cardinal quadrants.

The third thin section in the series (Text-fig. 4E, G; Schindewolf 1952, text-fig. 17c) exhibits a mixture of immature and mature features and is here considered to represent either the very advanced neanic or very early mature growth stage. The number of major septa (18), reached at a corallite diameter of 4.4 mm remains constant in the remaining part of the corallite growth, although the corallite diameter increases. The inner margins of the primary major septa became isolated at that growth stage and some of them became rhopaloid. However, the cardinal septum remains distinctly longer than the newly inserted septa in the cardinal quadrants, the inner margin of the counter septum remains in a direct contact with the septal arch, and the alar and the counter-lateral major septa remain the longest in their quadrants. All of the characters listed are immature.

The length and apparent axial splitting of the cardinal primary septum and the attachment of the counter septum to the arch with its thinning inner margin are immature characters persisting in the fourth thin section (Text-fig. 4H, I; Schindewolf 1952, text-fig. 17d). However, all major septa reach their mature, rhopaloid character. Their arch is now comparable to an incomplete circulotheca of Fedorowski (2009d). The alar septa and the left counter-lateral septum became slightly shortened and the first minor septa become visible in the corallite lumen next to the counter septum and in septal loculi of the counter quadrants adjacent to it. Those characters allow that growth stage to be considered as early mature.

In the last thin section of the series (Text-fig. 4J, K; Schindewolf 1952, text-fig. 17e) the counter septum the counter-lateral septa and all major septa in the left counter quadrant are free axially and comparatively thin. The inner margins of the remaining major septa are in direct contact. Those of the cardinal quadrants remain rhopaloid and in lateral contiguity. An inner fragment of the cardinal protoseptum, diagnostically separated from its more peripheral part, remains attached to the inner margin of the last major septum in the left cardinal quadrant which is slightly longer. However, that separated fragment of the cardinal protoseptum is equal to the adjacent major septum on its right side. Thus, the shortening of the cardinal protoseptum may be described as very indistinct or absent. Shortening of the alar septa is slightly better accentuated. The left counter-lateral septum remains long, whereas the right one became slightly shortened only at this growth stage.

The morphology described above allows the following statements to be made: 1. The calice floor is perhaps differentiated in depth with the circumaxial area, i.e. the septal arch, being elevated well above its floor. 2. That elevation is greater in the cardinal quadrants than in the counter quadrants and is especially great next to the cardinal septum. That may suggest that the cardinal tubaral fossula is either absent or very shallow. 3. In contrast, the development of a true tabular counter fossula may occur or at least the depth of the calice may be most advanced next to the counter septum. This is suggested by the opening of the arc towards the counter septum since early ontogeny and the separation of the counter septum and the counter-lateral septa from the arch earlier than that of the remaining major septa.

INTRASPECIFIC VARIABILITY: The external wall of the specimens (Text-figs 6A, 7A; Schindewolf 1952, pl. 1, figs 3, 5–9) bears shallow septal furrows, wide and al-
most flat interseptal ridges, delicate growth striae and irregularly spaced growth bands. Some differences in that sculpture may have resulted from the preservation. The cardinal septum is almost invariably located on the convex side of the corallite. Its slight lateral shifting resulted perhaps from the oblique settlement of a larva and does not have taxonomic value.

The ontogenetically earliest growth stage available for study (Text-figs 5A, B, K; 6B, C) is already at the neanic level. The arrangement of the major septa is regularly rotiphylloid with both protosepta reaching the corallite axis, with their 'middle dark lines' (the primary septa) either in contact or closely approaching each other. Some asymmetry in the arrangement of the ma-

JOR SEPTA, WHICH APPEARS DURING THE FURTHER NEANIC GROWTH OF THE CORALLITES MAY BE EITHER ARTIFICIAL, RESULTING FROM OBLIQUE SECTIONING (TEXT-FIG. 6D), OR NATURAL AND COMPARATIVELY LONG-LASTING (TEXT-FIGS 5C–G, S, T), RESULTING IN THE ASYMMETRICAL POSITION OF THE SEPTAL ARCH.

The arrangement and shape of the major septa is most differentiated in the transitional late neanic/early mature and early mature growth stages (Text-figs 5L–N; 6E, G, H; 7B, E–H, J, O, P). Although most of the specimens developed a septal arch, that structure varies in several details, such as the width of the counter

pseudofoosula, the length and thickness of the counter septum, the length of the counter-lateral septa and the symmetry in the arrangement of the major septa. It is worth mentioning that the cardinal septum may be attached to the septal arch asymmetrically, but neither that septum nor the alar septa is shortened in that growth stage.

Two corallites having fully mature growth stages closely comparable to each other (Text-fig. 5J vs Q, R) and to the holotype (Text-fig. 4J, K) pass through the early mature growth stage in a manner extremely different from all remaining specimens of the collection, including the holotype. One of them produced a very strong, pendulum-like counter septum (Text-fig. 5H, I), resembling some growth stages of the genus Lophophyllidium Grabau, 1928. The second formed a circulotheca-like axial opening (Text-fig. 5L–M), being in that growth stage similar to the genus Ostravaia Fedorowski, 2010a.

The mature growth stage of individual corallites within the collection varies in both the morphology and the dimensions at which it was achieved. The smallest specimens (Text-fig. 7I) attain mature characteristics with an n:d value of 16:4.0 mm, i.e., when it is only slightly wider than the holotype in the neanic growth stage. It should be pointed out, however, that only very few corallites produced more than 16 major septa. Thus, that number rather than the corallite diameter is most typical for the species, in addition to the arch of the major septa. That arch may be symmetrical (Text-figs 5J, O–R, U; 6I, J, 7C, D, O, P) or asymmetrical (Text-figs 6F; 7G, H, M, N). The identification of one specimen is conditional because of its asymmetry and is based mainly on the morphology of its early mature growth stage (Text-fig. 7K, L). The asymmetry is seen in both its late neanic and mature growth stages (Text-fig. 7J and N, M respectively) and its n:d value at maturity (19:5.5 mm), differs slightly from the largest established in other specimens of A. (Antiphyllites) pauperculus. Perhaps this corallite represents a different species, not proposed here for a single specimen.

One corallite (Text-fig. 6G–L) should be mentioned as having the septal arch and counter pseudofoosula well developed in its early mature growth stage, but developing a stereocolum immediately below the calice floor. The circunaxial part of this corallite is highly elevated, as indicated by strange fabric accumulated in peripheral parts of all septal loculi.

OCCURRENCE: Sośnica Mine (Oehringen Grube in German). Gaebler Marine Horizon, Upper Roemer (Ib) Marine Band, Serpukhovian (Middle Amsbergian), ammonoid zone E3b.

?Antiphyllum (?Antiphyllites) simplex (Schindewolf, 1952) (Text-figs 8, 9, 10N–Q)

1937. Zaphrentis aff. postuma Smith; Schwarzbach, p. 433, pl. 15, fig. 5.
1952. Fasciculophyllum simplex Schindewolf, 1952, p. 190, pl. 1, fig. 2, text-figs 13, 14.
1977. Rotiphyllum simplex (Schindewolf 1952); Weyer, pl. 1, fig. 1.

MATERIAL: The holotype MB.K.817, three paratypes (MB.K. 83, 818, 5473) out of six mentioned by Schindewolf (1952, p. 192), one specimen (MB.K. 5474) labeled as Fasciculophyllum cf. simplex and one specimen (MB.K.802) originally identified as a paratype of Claviphyllum pauperculum were included in this species. The corallite illustrated by Schindewolf (1952, text-fig. 15) under the number 875 is most probably lost and is omitted from the discussion.

All specimens are diagenetically altered and perhaps each of them was differently advanced in its ontogeny when it died. Thus, the main differences discussed below in the Intraspecific Variability section may have resulted from those two factors. Diagenetic alterations are described in more detail in the Microstructure and Diagenesis section.

EMENDED DIAGNOSIS: Antiphyllidae with cardinal septum long up to and including the mature calice floor; counter septum longer and thicker than remaining major septa; alar septa slightly shortened in mature calice or earlier; circunaxial structure variable; cardinal fossula inconspicuous; counter pseudofoosula absent; biformly shortened minor septa appear in mature calice.

EMENDED DESCRIPTION OF THE HOLOTYPE: The earliest growth stage is missing. The ontogenetically earliest skeleton preserved, with n:d value 9:1.7 mm, shows an asymmetrically rotiphylloid arrangement of major septa with the counter septum positioned obliquely to the cardinal septum and all major septa in the counter quadrants thinner than those of the cardinal quadrants (Text-fig. 8A, B). The original arrangement of major septa in the succeeding growth stage with n:d value 13:2.8 mm (Text-fig. 9C, D, M) is diagenetically altered to an extent that precludes its detailed and credible description (see Microstructure and Diagenesis, below). All major septa are strongly thickened and, except for the strongly elongated right alar septum, their length is almost uniform.

The late neanic growth stage, with n:d value 15:3.6 mm (Text-fig. 8E, F), is diagenetically altered to a much
lesser septa of the counter quadrants join each other short of the corallite axial area and form an arch over the cardinal septum, which is equal in length and thickness to the major septa of the cardinal quadrants. All septa remain short of the corallite axis. One before the last major septum in the left counter quadrant is strongly and temporarily elongated. Its inner part remains in lateral continuity with the inner part of the left alar septum. The inner margin of the right alar septum joins the arch formed by the major septa of the counter quadrants. The corallite axis, which is free from major septa, is intersected only by a tabula.

The level at which the inner margins of all primary major septa are separated, at an n:d value 16:4.1 mm, is here considered the early mature growth stage. Almost all of those septa, except for the last inserted major septa of the counter quadrants approach, but do not reach the corallite axis; those on the left side of the corallite approach it more closely. That side of the axial area is filled with sclerenchyme, whereas the opposite side is empty and is intersected only by a tabula. The cardinal septum is equal in length to the major septa of the right cardinal quadrant, but is slightly shorter than those in the left cardinal quadrant. The counter septum is slightly longer and thicker than the counter-lateral septa. Alar septa are the longest in the cardinal quadrants. Minor septa remain absent from the corallite lumen, but two of them were traced in the external wall of the corallite next to the counter protoseptum in a form referred to by Weyer (1974, p. 350) as biformly reduced minor septa.

The holotype reaches its mature characteristics at the level of the calice floor with an n:d value 18:5.2 mm (Text-fig. 8I, J). Most septal loculi in that cross section were cut above the calice floor, as indicated by their infillings with strange fabric. Druzy dolomite crystals have filled the corallite axial area that is free from septa (Text-fig. 8L). Such an infilling suggests the position of the corallite axial area below the last tabula. Only such a position would allow the crystallization of dolomite crystals. The arrangement of the major septa became almost semi-circular in that growth stage with the counter septum dominating in thickness and (slightly) in length and the cardinal septum being slightly longer than the last pair of major septa in the cardinal quadrants (Text-fig. 8L, arrow). The alar and counter-lateral septa are very slightly longer than the major septa inserted next to them. The remaining major septa are not differentiated in length. Protrusions of the ‘biformly reduced’ minor septa appear in several septal loculi. The narrow and shallow cardinal fossula is recognizable by the arrangement of the major septa and by the shape of the tabula, arching to form its inner limit (Text-fig. 8I, J, L). Neither a true, tabular cardinal fossula nor alar pseudofossulae can be credibly identified in the earlier growth stages.

The lower surface of the remaining fragment of the holotype, with n:d value 18.9:5 mm, corresponds perhaps to the lower/middle part of the calice (Text-fig. 8K). It was not described or illustrated by Schindewolf (1952). The arrangement of the major septa exposed on that surface is almost radial with free inner margins of some of them curved towards the counter septum. The counter septum continues to dominate in length and thickness over the remaining major septa. Its peripheral part is barrel-like in shape, i.e., it narrows toward the external wall. Such a shape occurs in the major septa of Densiphyllum rushianum Vaughan, 1908 (pl. 49, fig. 2), the type species of the genus Rotiphyllum Hudson, 1942. The cardinal septum is shortened to approximately ½ the length of the longest major septa in the cardinal quadrants. Both alar septa are slightly shortened. The lengths of the remaining major septa differ slightly, but not in an orderly fashion. All septa, except for the counter septum, are wedge-shaped. Minor septa expand into the calice, but only in the form of semicircular protuberances on the external wall.

INTRASPECIFIC VARIATION: The number of specimens in the collection is too small and the differences between them too large for the intraspecific variability to be credibly established. Differences shown by individual corallites seem to exceed the framework acceptable for a species. However, that may be apparent as a result of two factors: 1) the death of particular specimens at different stages in their ontogeny and 2) poor preservation camouflaging the original morphology.

The diameters and morphology of only two specimens in the collection approach closely enough to those of the holotype, whereas the other three are here considered to be immature. The first of those two corallites (Text-fig. 9A–G) shows the arrangement of its major septa in the immature growth stages and an n:d value in its mature growth stage (18:5.1 mm) similar to those in the holotype. It differs from the holotype in that its axial area free of septa is wider and resembles a circulotheca more clearly. Its rhopaloid cardinal septum extends to and participates in the formation of that circumaxial structure, but is slightly shorter than the adjacent major septa. The counter septum is elongated more distinctly in the late neanic/early mature growth stage of that specimen than in the holotype (Text-fig. 9E vs Text-fig. 8G, H), but is comparable to the holotype in more advanced maturity. It also differs from the holotype in that its left alar septum is shortened beneath the mature calice and the right one is elongated in the same transverse thin section. Minor septa are absent from the
corallite lumen, but the specimen is sectioned beneath the calice floor and its compressed calice precludes further investigation.

Only a previously unknown part of the mature growth stage, with n:d value 16:7.0 mm (Text-fig. 9T), is available from the second of the specimens mentioned above as being morphologically similar to the holotype. However, it has fewer septa than the holotype, whereas its diameter is larger than that of the holotype beneath the calice and smaller than that in its calice. The major septa of this paratype form a regular, narrow circulotheca. The narrowed inner margin of the cardinal septum is in-

cluded in the circulotheca. The counter septum is thicker and slightly longer than the other major septa so that it penetrates the circulotheca with its inner margin. However, the lateral surfaces of that septum are in lateral contiguity with the adjacent major septa, leaving the circulotheca unbroken. The barrel-like peripheral part of the counter septum closely resembles that in the holotype, as seen in the calice. Recognition of the alar septa is slightly uncertain, but they are perhaps shortened a little. The wedge-shaped minor septa extend into the corallite lumen in all loculi, but remain attached to outermost parts of the major septa in some, documenting their biformly reduced origin.

One of the remaining three immature corallites (Text-fig. 9H–K), included by Schindewolf (1952, pl. 1, fig. 7a,b) in Claviphyllum pauperculum, resembles the holotype of ?A.(C.) simplex comparatively closely. Only a closer connection between the inner margins of its major septa than is seen in those adjacent to the counter septum should be mentioned as a distinguishing feature of this immature specimen, pointing at the same time towards A.(A.) pauperculus.

The skeleton of the second of the three immature corallites (Text-fig. 9L–S) has been altered, partly by recrystallization (Text-fig. 9L–O) and partly by shallow rejuvenation (Text-fig. 9R, S). However, the arrangement of major septa in its less altered part (Text-fig. 9P, Q) is opposite to that in the type species for the subgenus, i.e. neither a septal arch nor a counter pseudofossula is formed. Its counter septum is long and thick, approaching the inner margin of the elongated cardinal septum through the sclerenchymal infilling of the axial area. In the ontogenetically most advanced growth stage studied (Text-fig. 9R, S), the major septa twist around the free axial area rather than forming a typical circumaxial structure. That specimen is included in ?A.(C.) simplex with reservation.

My orientation of corallites is 180° opposite to that applied by Schindewolf (1952), which should be kept in mind in this paragraph. His drawing in text-figure 14a corresponds to that in text-figure 10N here. The number and the arrangement of major septa are similar in both drawings, but I was not able to establish shapes of individual major septa within the sclerenchyme, whereas Schindewolf omitted the sclerenchyme from his drawing and drew a rather imaginative shape for the septa. It should only be mentioned that the cardinal septum is not shortened, although its total length is uncertain. Schindewolf’s (1952) text-figure 14b (= Text-fig. 100) is here turned 90° left. Shortening of one major septum in the counter quadrant is temporary as shown by the preceding and following thin sections. The cardinal septum is long, with its inner margin deflected to the left to join the circumaxial structure, which is completed by the section of the tabula right of that septum. The counter septum is the thickest septum in its peripheral part, but thins within the circumaxial structure. Its inner margin does not cross that structure. The recognition of the protosepta in the ontogenetically most advanced growth stage (Text-fig. 10P, Q; Schindewolf 1952, text-figure 14c) is identical in both instances, but the interpretation of its morphology differs. The counter septum is not elongated as was drawn by SCHINDEWOLF. It is only slightly longer than the right counter-lateral septum, but was artificially elongated by Schindewolf at the cost of the sclerenchyme that covers the inner margins of the major septa on the right side of the circumaxial area and is diagnostically isolated from those margins (Text-fig. 10P, Q). Thus, the ontogeny of this specimen ends with an almost closed circulotheca, composed of all septa, barely distinguishable by length.

**MICROSTRUCTURE AND DIAGENESIS:** Strong diagenetic alteration, not mentioned by Schindewolf (1952), is of special significance in establishing the generic position of specimens included in the species discussed above. The holotype and one paratype are most advanced in those alterations. The axial area of the holotype is differently altered in its various growth stages. The large empty axial area (Text-fig. 8C, D, M) in the early growth stage resulted perhaps from recrystallization, as documented by the presence of large druzy dolomite crystals. Inner margins of the major septa may have been dissolved during that process. Thus, perhaps neither their length nor shape is original. The process of dissolution and later crystallization was less advanced in the late neanic/early mature growth stage (Text-fig. 8E–H). Remnants of sclerenchyme in that growth stage and better preservation of the primary septa confirm such a suggestion. The druzy dolomite crystals appeared again at the beginning of the fully mature growth stage, i.e., when the inner margins of major septa became separated (Text-fig. 8I, J, L). Those druzy crystals may have slightly deformed the free axial area, but most probably did not cause its secondary appearance. This is suggested by the shape and length of the counter septum, by the shape of the inner margins of the remaining major septa and by the arrangement of the tabula closing the cardinal septal fossula. A section of the inner margin of that tabula is convex towards the corallite axis and is not deformed by druzy crystals.

Several major septa in the mature growth stage of the holotype have been broken by compaction. That damage is slight and does not obscure the original mor-
The corallite MB.K. 5474, labelled Fasciculophyllum cf. simplex Schindewolf (1952) shows a strange morphology, resulting from the diagenetic alteration of the original skeleton. Those alterations are especially advanced in the early growth stage (Text-fig. 9L-O), leading to the disintegration of the inner margins of the major septa. In contrast to the holotype, those inner margins became thin and thread-like and hardly distinguishable from the tabulae attached to them. The dissolved and re-crystallized axial sclerenchyme and possibly parts of the inner margins of the major septa are observed in the next thin section (Text-fig. 9N, O). The late neanic growth stage (text-fig. 9P, Q) was described above as suffering much less from diagenetic changes.

The examples described permit the following final conclusion to be made: 1. Diagenetic alteration varies in its advancement irrespective of the advancement in corallite ontogeny. 2. Stronger ontogenetic alterations in early rather than in mature growth stages does not necessarily indicate correlation between alteration and corallite growth. 3. Some kinds of diagenetic alteration, especially those connected with recrystallization, may cause substantial changes in the arrangement of major septa and may bias taxonomy. Such secondary alterations must be recognized and should not be described as original morphology. That question was already mentioned in one of my earlier papers (Fedorowski 2003).

**OCCURRENCE:** Sośnica Mine (Oehringen Grube in German). Gaebler Marine Horizon, Upper Roemer (Ib) Marine Band, Serpukhovian (Middle Amsbergian), ammonoid zone E$_5$b.

**DESCRIPTION:** In the earliest growth stage studied, with an n:d value 14:1.4 mm (Text-fig. 10A, B), the inner margins of several primary major septa (‘dark middle lines’), including the counter septum, are either united around the axial area or are free, but terminate within the axial sclerenchyme prior to reaching the corallite axis. The free inner margin of the cardinal septum points towards the counter septum. The structural element intersecting the corallite axis is septal in its microstructure, corresponding either to the middle part of the axial septum or to the elongated counter septum.

During approximately 0.8 mm of further corallite growth the n:d value (14:1.55 mm) remains similar to the previous one, but the morphology changes considerably (Text-fig. 10C, D). The initial stage of formation of the counter pseudofossula and the circumaxial structure are observed. The former is marked by the separation of the primary counter-lateral septa from the primary counter septum and by their right and left curvature to become attached to or closely approach the primary septa of the adjacent major septa in the counter quadrants. The circumaxial structure is formed by all septa, including the long counter septum. That septum penetrates the axial area free from both sclerenchyme and the inner margins of septa, but its inner margin is connected to the inner margins of the major septa adjacent to it from the right side. Also, the inner margin of the primary cardinal septum is included in the circumaxial structure. It appears to split axially, but one arm of that apparent split belongs to the right major septum, being diagenetically separated from it. The circumaxial structure is completed by a body, which is septal in microstructure, attached to the counter septum on its left side. Such a circumaxial structure would be called an aulos in the sense of Fedorowski (2009d) if the inner margins of all primary septa were in direct contact, but they are not. That separation may be either primary, resulting from elongation of the inner margins of some of the primary septa more than others, or secondary, i.e. caused diagenetically. That question remains open.

The n:d value and the morphology exposed on the polished surface (Text-fig. 10E) resembles that seen in the thin section described in the preceding paragraph, but some details differ. The polished surface shows the primary cardinal septum not split, but long, penetrating the free axial area with its narrow inner margin. Also, there are sections of tabulae but not the inner margins
of septa attached to both sides of the cardinal septum. Those tabula sections, supplementing the circumaxial structure, correspond perhaps to the most highly elevated peripheral parts of tabulae. A similar section of the tabula has replaced the septal body present previously next to the counter septum. The distance between the thin section described in the preceding paragraph and the surface described here is not greater than 0.2 mm. Thus, either the image exposed by the polished surface does not provide all morphological and microstructural details or the 0.2 mm distance was adequate for the morphological changes discussed. The next polished surface (Text-fig. 10F, G), exposed by ½ millimeter of grinding, seems to suggest the second alternative. The presence of two sections of tabulae rather than the one exposed earlier, and a slight shortening of the cardinal septum are the main morphological differences between those two surfaces, in addition to a slightly larger n:d value (14:1.75 mm) and a slightly better developed counter pseudofossula for the second.

Within 2.1 mm of further corallite growth all inner margins of the primary septa become separated and all major septa but one that is newly inserted in the left cardinal quadrant become radially arranged and slightly rhopaloid with the inner margins of most of them contiguous laterally around the free axial area. Thus, the complete circulotheca is formed at that growth stage. Lack of material for a longitudinal section precludes an indisputable confirmation of the latter, but sections of tabulae located outside that structure and the elevation of the inner part of the corallite support such a suggestion to some extent. Both the thin section (Text-fig. 10H, I) and the closely spaced polished surface (Text-fig. 10J, K) document those characters. The counter septum is thicker and slightly longer than the remaining major septa but one that is newly inserted in the left cardinal quadrant, is the most important character of this growth stage. The cardinal septum is slightly thinner, but remains equal in length to the adjacent major septa. The counter-lateral major septa thin adaxially, but are not shortened. The left alar septum is the only major septum slightly shorter than the remaining ones. That slight shortening is additionally expressed by the abaxial depression of the circulotheca. Minor septa are well seen in all loculi, but they remain short with ‘middle dark lines’ absent from most.

DISCUSSION: The described specimen is one of the smallest in the studied collection. Also, it bears characters both typical and atypical for Antiphyllum. Shortening of the alar septa, elongation of the counter septum, and formation of a counter pseudofossula in early ontogeny should be pointed out as typical for Antiphyllum. The formation of the circulotheca points towards Ostravaia Fedorowski, 2010a from correlative strata of the Ostrava area, Czech Republic and to Ostravaia sp. 1 in particular. The latter species, represented by a single specimen, exhibits a similar mixture of characters, discussed by Fedorowski (2010a, p. 177), but it is larger and possesses more numerous septa (n:d value 19:9x7 mm) than the specimen described here. Also, its circulotheca is better developed, although short-lived, and its cardinal septum is shortened in the calice, whereas in ?Antiphyllum (?Antiphyllites) sp.1 it remains long up to and including the calice floor (Text-fig. 10L, M). The latter character occurs in Fasciculophyllum simplex Schindewolf, 1952, here conditionally included in Antiphyllites. Paucity of material precludes a firm identification of the above mentioned specimen and a reliable discussion of their mutual connections (relationships ?). It was described in order to make the taxonomic variability of the Upper Silesian Coal Basin coral fauna more complete.

OCCURRENCE: Sośnica Mine (Oehringen Grube in German). Gaebler Marine Horizon, Upper Roemer (Ib) Marine Band, Serpukhovian (Middle Amsbergian), ammonoid zone E2b.

?Antiphyllum (?Antiphyllites) sp. 2
(Text-fig. 11)

MATERIAL: Single, incomplete specimen MB.K. 816. Paratype of ‘Fasciculophyllum’ simplex, Schindewolf
1952. The only surfaces studied were those exposed by the original cutting and grinding of the specimen into two fragments. Thin sections were not prepared. The surface of the ontogenetically earliest growth stage was ground obliquely by Schindewolf’s technician. The remaining surfaces almost correspond to the coralite growth lines. All photographs were taken from the polished surfaces.

DESCRIPTION: The rotiphyllloid arrangement of the major septa, here considered to be neanic (Text-fig. 11A, B), persists through 3.05 mm of corallite growth, when measured between the most distant points of surfaces of the lower fragment. The n:d value of the lower surface is 16:3.5 mm, measured perpendicular to the protosepta in order to avoid inaccuracy resulting from the obliqueness of the surface. The n:d value of the upper surface is 16:4.8 mm measured parallel to the protosepta. The cardinal septum extends beyond the corallite axis, intersecting the cardinal fossula. The united inner margins of three major septa of the right cardinal quadrant are attached to an arch formed by inner margins of all remaining major septa, including the counter septum, which is indistinguishable from the counter-lateral septa by length and thickness. The left alar septum is long, but the right one is shortened at the end of this growth stage (Text-fig. 11B).

The distance is unknown between the surface described above and the lower surface of the upper coralite fragment, which has an n:d value of 16:5.4 mm and was measured parallel to the protosepta. A sort of a deformed incomplete aulos, consisting of the inner margins of most major septa and opening towards the cardinal fossula, appears in that growth stage (Text-fig. 11C). It is supplemented by a section of a tabula, attached to the free inner margin of a long major septum of the right cardinal quadrant. The thin cardinal septum intersects the long cardinal fossula and is attached to the opposing inner margin of that long major septum. The counter septum remains incorporated in the corallite arch, but its inner margin extends slightly farther towards the corallite axis and is slightly thicker than those of the counter-lateral septa. The left alar septum remains long and the right one remains shortened. Most septal loculi are already cut above the calice floor.

The uppermost preserved surface of the specimen is situated a maximum of 2.55 mm from the lower surface of this corallite fragment. It exposes the lower part of the calice with an n:d value of 17:5.7 mm measured...
parallel to the protosepta. Almost all inner margins of the major septa are free, but the main aspect of their arrangement remains the same, i.e., their inner margins still surround the axial area. The cardinal septum is now withdrawn to the peripheral part of the triangular cardinal fossula, bordered by two major septa of the cardinal quadrants. The counter septum is much thicker, but only slightly longer than most major septa of the counter quadrants, except for the counter-lateral septa. The right counter-lateral septum is clearly reduced in length and thickness, whereas the left one is missing. Its disappearance is perhaps diagenetic in origin. Protruberances of minor septa occur at the narrow external wall.

REMARKS: The described specimen bears a mixture of characters of different species and genera. The irregularly shortened counter-lateral septa resemble all species here included in the genus *Antiphyllum*, but were also described in *Ostravaia* sp. 1 of Fedorowski, 2010a. The deformed circumaxial structure, points to *Ostravaia* sp. 1, to *(A. (?A.) simplex, and to *A. (?Antiphyllum)* sp. 1. The shortening of the cardinal septum observed in the lower part of the calice resembles that in *Ostravaia silesiaca* Fedorowski, 2010a and *Ostravaia* sp. 1. Shortening of that septum occurs much earlier in the ontogeny of the nominative subgenus of *Antiphyllum*, but remains long in *Antiphyllites*. The slight domination of the counter septum in the specimen under discussion resembles only *A. (A.) pauperulum*, whereas reduction in the length of the counter-lateral septa resembles only *A. (A.) inopinatum*. The variation of characters, accumulated in the described specimen make its taxonomic position uncertain. Its description was added to the present paper as supplementary to the knowledge of the Upper Silesian Coal Basin coral fauna.

OCCURRENCE: Sośnica Mine (Oehringen Grube in German). Gaebler Marine Horizon, Upper Roemer (Ib) Marine Band, Serpukhovian (Middle Amsbergian), ammonoid zone E₁b.

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**Suborder Incerte sedis**

REMARKS: The suborder Tachylasmatina Fedorowski, 1973 would have been appropriate for taxa having a cryptophylloid (term from Fedorowski 2009c) early ontogeny if the early ontogeny of *Tachylasma inopinatum* Grabau, 1922 (the type species of the genus *Tachylasma* Grabau, 1922) were known and if its retarded counter protoseptum were absent from the corallite lumen in the earliest ontogeny. Unfortunately, those data are not available. Despite that defect, Schindewolf (1942) introduced the name tachylasmatoid ontogeny and suggested its close similarity to the early ontogeny of *Cryptophyllum hibernicum* Carruthers, 1919. This question is not discussed here in detail. The reader is referred to Fedorowski (2009c, 2010c) for a comprehensive discussion.

The name Tachylasmatina has not been widely accepted since the introduction. Its synonymy with the suborder Plerophyllina Sokolov, 1960 and questionably with the family Pentaphyllidae Schindewolf, 1942 was postulated by Hill (1981, pp. F320 and F330 respectively). Rejection of the difference between the zaphrentoid or rotiphyllloid ontogeny on the one hand and the cryptophylloid (tachylasmatoid at that time) on the other, was the second and most important reason. Disregard of that difference was expressed by several coral specialists, either directly in their remarks on particular taxa or by placing taxa of different early ontogeny under the same family name (e.g. Ilina 1965, 1984; Weyer 1972, 1975, 1994; Weyer and Ilina 1979; Ezaki 1991; Fan *et al.* 2003, Wang *et al.* 2004). My opinion strongly emphasizing the importance of that difference has been constant since publication of the first paper (Fedorowski 1973), till the latest ones dealing with that question (Fedorowski 2009c, 2010c, in press), and is again expressed here. Thus the use of the term *Incerte sedis* for the suborder does not reflect my hesitation in assigning corals with the cryptophylloid ontogeny to a separate suborder, but results from the unfortunate selection by Grabau (1922) of the type species for Tachylasma. If a completely studied species of Tachylasma or the genus Cryptophyllum had given its name for the family, the question would not have appeared.

At the moment it cannot be decided if the Early Carboniferous taxa with cryptophylloid ontogeny should be included in the suborder based on the Permian taxon Tachylasma or if they belong to a different lineage. The lack of occurrence of such taxa, especially long in the Palaeotethys area (Upper Viséan to Lower Permian) and the formation of Pangaea during that period of time, may preclude such a relationship. The occurrence of *Cryptophyllum striatum* Rowett, 1969 in the “post Morrowan-pre Missourian” strata of Alaska (Rowett 1969, p. 36) only allows that species to be considered as the last representative of the European/North American lineage known so far. Thus, the phylogenetic link between the corals bearing cryptophylloid ontogeny, which existed prior to and after the closure of the Pangaea landmasses, was most probably broken.
In contrast to that, the “cryptophylloid” Early Carboniferous corals from Euramerica and the Palaeotethys, may have been directly related. The open oceanic paths along shelves of islands and landmasses bordering the Rheic and the Palaeotethys Oceans, were at that time available for migration. Thus, a true relationship to European genera is accepted here for several Chinese species of Fan (In: Fan et al. 2003), included by Fedorowski (2009e, p. 582) in Cryptophyllum, as well as for the Viséan Commutia exoleta Wang et al. 2004 from the South China. Unfortunately, that recognition does not solve the question of whether or not the same suborder should be used for Early Carboniferous and Permian taxa.

Family Commutidae Fedorowski, 1973


DIAGNOSIS: Small, solitary, non-dissepimented Rugosa; length of cardinal septum characteristic for individual genera; counter septum distinctly retarded in appearance within corallite lumen; alar and counter-lateral septa dominate at least during late neanic-early mature growth stage; aulos-like circumaxial structure may be developed.


REMARKS: The family Commutidae was originally (Fedorowski 1973) erected as a subfamily of the family Tachylasmatidae. That concept is rejected here for two reasons discussed above with remarks on the suborder, i.e., the unknown early ontogeny of Tachylasma and the probable lack of a direct phylogenetic link between taxa from the Early Carboniferous and the Permian. Elevation to the family level is in such a situation a natural consequence of those statements, allowing the genera listed above to be placed within it. That opportunity was lost in my earlier paper (Fedorowski 1973, 1981, 2009e, 2010c, in press; Fedorowski and Bamber 2001; Fedorowski et al. 2007) for treatment of several questions potentially important for this discussion. These include the main cycles and phases of rugose coral evolution, the value of palaeogeography for taxonomy and phylogeny, the taxonomic value of the difference between the reduction and underdevelopment of the protosepta, and a discussion on the difference between the zaphrentoid and cryptophylloid ontogeny with a suggestion to avoid the term tachylasmatoid.

Effigies silesiacus (Schindewolf, 1952) (Text-figs 12–15)

e.p. 1937. Zaphrentis aff. postuma Schwarzbach, p. 433, text-fig. 5.


1952. Pentaphyllum (Tachylasma) silesiacum Schindewolf, p. 218, text-figs 3, 24–29; pls 1, figs 13–18; 2, figs 1–11.

1977. Tachylasma silesiacum (Schindewolf 1952); Weyer, pls 1, figs 5, 6; 2, figs 1–3.

MATERIAL: 15 specimens out of the 20 mentioned by Schindewolf (1952, p. 22) were restudied. The remaining ones were not found in the Humboldt Museum collection. Several specimens have most of their early on-
togeny preserved. The calices and late mature parts of most specimens have been affected by compaction to various degrees. That damage was not shown by Schindewolf in his drawings. The original arrangement and
morphology of septa are recognizable in all mature specimens. Silicification and/or dolomitization are advanced to the extent that the microstructure of the septa is unrecognizable in most. Twenty eight thin sections with forty slabs were available for study.

DIAGNOSIS: Effigies with n:d values of 16:4.4 mm (holotype) to 19:7.4-8.2 mm; alar and counter-lateral septa dominant since early ontogeny; commonly very strongly so; counter septum elongate during growth; cardinal septum variable in length, slightly shortened in most; minor septa recognizable in advanced maturity.

DESCRIPTION OF THE HOLOTYPE: This horn-shaped specimen is one of the smallest in the collection (see diagnosis). Its ontogenetically earliest skeleton is missing. Five major septa occur in the corallite lumen of the earliest preserved growth stage (Text-fig. 12A, B). The alar and counter-lateral septa dominate as indicated by their “middle dark lines” (i.e. the primary septa). The cardinal septum is the shortest and its “middle dark line” joins that of the right alar septum. Such an arrangement suggests a subordinate role of the cardinal septum since its appearance. The counter septum is not yet evident in the corallite lumen or its wall, but there is a shallow furrow on the wall, corresponding to that septum. An arrangement of major septa almost identical to that described in this paragraph is found in only one other specimen of the collection (Text-fig. 15A, B).

The arrangement of major septa remains similar in a slightly more advanced growth stage (Text-fig. 12C, D), the main difference being the insertion of one major septum in each quadrant. The cardinal septum is slightly longer here than in the earlier growth stage, but it does not reach the corallite axis, which is occupied by the thick inner margins of the alar and counter-lateral septa. The cardinal septum (Text-fig. 12C, D) and the newly inserted septum in the right counter quadrant are broken, whereas the newly inserted major septum in the left counter quadrant is underdeveloped. The counter septum is marked by a deep furrow and a low protrusion on the inner surface of the external wall.

The growth stages intermediate between that described above and the mature stage are missing. The third and last transverse thin section of the holotype was cut just above the calice floor in most septal loculi and just beneath it in others (Text-fig. 12E, F; beneath calice floor white). The counter-lateral septa and the left alar septum dominate strongly, with their rhopaloid inner margins joining each other. It is uncertain if the secondary septa of those septa fill the axial area or if it is occupied by sclerenchyme independent of those septa. The septal margins pass into that sclerenchymal mass without obvious boundaries (Text-fig. 12E, G). Such an image may have resulted from the diagenetic alteration, but it was drawn here as sclerenchyme (Text-fig. 12F). Schindewolf (1952, text-fig. 24c) left the corallite axial area white, suggesting that it is devoid of any skeletal material, but that is incorrect. The right alar septum is only slightly stronger than the remaining two major septa of the right cardinal quadrant. The cardinal septum is as long as the adjacent major septa of the cardinal quadrants, except for the alar septa. The counter septum is broken, but its inner margin is recognizable in the form of a knob attached to the right counter-lateral septum (Text-fig. 12E-G). Inner margins of all major septa in the counter quadrants, except for the counter-lateral septa, are free. Low protrusions of minor septa are recognizable in some septal loculi. Dark dots, recognizable in some primary septa (Text-fig. 12G, H) may be interpreted as remnants of small trabeculae, but the finely trabecular microstructure of septa can be only suggested, not proven.

PECULIARITY OF EARLY ONTOGENY: Three corallites were sectioned at a very early growth stage with diameters of 1.0×1.2 mm (Text-fig. 13A, B), 1.2×1.3 mm (Text-fig. 14A, B) and 1.4×0.9 mm (Text-fig. 14E, F = Weyer 1977, pl. 2, fig. 1). The arrangement of septa in all those specimens is similar in the sense that one or two septal bodies intersect the corallite lumen. Those bodies are here given the informal name ‘intersecting septa’ in order to avoid confusion in the discussion. The presence of an ‘intersecting septum’ at the beginning of the septogenesis would be normal for the Rugosa if it could be considered as the axial septum. Unfortunately, the retardation in the appearance of the counter septum excludes such an interpretation. As a result, those septal bodies become potential foundations for the alar and/or the counter-lateral septa. The following characters of those ‘intersecting septa’ allows such an interpretation:

1. The shape of ‘intersecting septa’ in two corallites (Text-figs 13A, B; 14A, B). Their peripheral thickening, corresponding to weakly marked dark lines that are interpreted as interseptal boundaries, allows them to be considered as the future counter-lateral and alar septa with the former dominating. That interpretation is supported by the presence of septal bodies perpendicular to the ‘intersecting septa’. These are a well developed septum in one specimen (Text-fig. 14A, B) and a protuberance in the external wall in the other one (Text-fig. 13A, B). Both of those septa are interpreted here as the cardinal septa.
2. In one corallite (Text-fig. 14E, F = Weyer 1977, pl. 2, fig. 1), not only a single, but two ‘intersecting septa’ occur. One of those septal bodies, not marked by dots in the picture, is here considered to be the common foundation of the counter-lateral septa, whereas the ‘intersecting septum’ marked by dots with question marks is interpreted as the common foundation of the alar septa. The latter interpretation is based on the barely recognizable septal body located parallel to the external wall and closely attached to it along most of its length, except for its inner margin, which joins the ‘intersecting septum’ at an angle (Text-fig. 14E, F, lower questioned dot). That underdeveloped septal body, not drawn by Weyer (1977, pl. 2, fig 1), is interpreted as the cardinal protoseptum. Further growth of the corallite (Text-fig. 14G-J = Weyer 1977, pl. 2, figs 2, 3) confirms this interpretation. The peculiarity of the corallite characterized by the ‘intersecting septum’ at an angle (Text-fig. 14E, F) is here considered to be the common foundation of the alar septa. The latter interpretation is based on the incompleteness of the specimen precludes recognition of the manner in which that morphology was achieved.

The length of the cardinal septum does not correlate with that of the counter septum. The latter may be inserted and elongated early in the ontogeny (Text-fig. 14G, H) or comparatively late (Text-figs 13G, H; 14C, 15C, D). It may quickly reach a great length or lengthen slowly during growth until it reaches the inner thickened margins of the counter-lateral septa (Text-fig. 13I–K; 15E–H, M). Shortening of the counter septum may be only apparent in some instances, resulting from diagenetic damage (Text-figs 131, J; 14D), but may also be original (Text-figs. 14R; 15I–K).

The strong thickening and axial union of the inner margins of the alar and counter lateral septa, typical for the holotype (Text-fig. 13E, F), occurs in several corallites. It appears mostly at a rather early growth stage and lasts up to the calice floor (Text-figs 13G–K; 14C, D, I–K, R, O). However, that character may appear comparatively late in the ontogeny and is only moderately strong (Text-fig. 15C–H, I, J, M, N). Also, the alar and counter-lateral septa may stop short of the corallite axis and be either clearly (Text-fig. 15M) or only slightly rhopaloid (Text-fig. 15K).

The minor septa became recognizable in the external wall late in the ontogeny and in all corallites, although their furrows occur along the entire corallite surface as shown by Schindewolf (1952, pl. 1, figs 13–16) and observed in the corallite fragments present in the restudied collection. Well-developed blades of those septa are absent from almost all specimens. Two short-lasing blades are present next to the counter septum in only one specimen (Text-fig. 15N–P).

The longitudinal thin section that was briefly described and illustrated by Schindewolf (1952, p. 221, pl. 2, fig. 11) was not found in the restudied collection. Thus, the reader is referred to the paper cited.

The morphological variability described and the maximum n:d values measured for individual specimens may have in part reflect the growth stages they achieved during their life time. Some of the latter are as follows: 16:4.3 mm (Text-fig. 14O) through 18:6.6×5.9 mm (Text-fig. 13K) and 18: 7.5×7.0 mm (Text-fig. 15I, J) to 19: 7.4 and 8.5×8.0 mm (Text-fig. 15N–P).
MICROSTRUCTURE AND DIAGENESIS: All corallites are strongly altered by diagenesis. Black dots present in rare primary septa may be interpreted as fine trabeculae, arranged in a single regular row (Text-figs 12G, H; 13M). Such an interpretation is weakly supported and cannot be considered proven. Diagenetic alterations, i.e., silicification and/or dolomitization affected nearly all septa. Dissolution in some
of them completely ruined the primary septa and their early sclerenchymal covering (Text-fig. 15L). Thus, the microstructure of the described species and the genus Effigies must be considered unknown.

OCCURRENCE: Sośnica Coal Mine (Oehringen Grube in German), Gaebler Marine Horizon, Upper Roemer (Ib) Marine Band, Serpukhovian (Middle Arnsbergian), ammonoid zone E2b.

CONCLUDING REMARKS

1. The recent approach to rugose coral taxonomy differs from that of the early and mid twentieth century. This and the importance of the Serpukhovian rugose coral faunas from the Upper Silesian Coal Basin for the phylogeny of that group of fossils and for paleogeography, make their revision a necessity. The present paper is the fourth in a series of revisions (Fedorowski 2009a, 2010a, in press) and there will be one more to come. Thus, general conclusions concerning the entire fauna are not proposed here.

2. All taxa revised here were derived from the same coal mine and the same stratigraphic level, but belong to different suborders. They are treated together in this same publication in order to avoid multiplication of papers.

3. One species is described with a question mark and two other are left in open nomenclature. That resulted from the small size of the collection, which prevented both a more precise study and the introduction of new species. Those incompletely studied species were included in the paper to show the total taxonomic range of the fauna.

4. The early ontogeny of some specimens exhibit a mixture of generic characteristics and may be treated either as proof for the synonymy of Ostravaiia with Antiphyllum (an option not accepted here) or as representatives of a new genus, intermediate between those two. That option is more probable, but is not formalized here because of the inadequate representation.

5. My approach to high level taxa (families and suborders) is discussed in the remarks for those taxa and is not repeated here.

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