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On the genus *Bothrophyllum* Trautschold, 1879 (Anthozoa, Rugosa)

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ABSTRACT:

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The rugose coral genus *Bothrophyllum* Trautschold, 1879 is revised on the basis of data from the literature and the author's personal investigation of both topotypes of its type species *B. conicum* and related and/or similar taxa from other areas. The intraspecific variability of the type species, its neotype, the intra-generic framework and a new generic diagnosis are established. Many more than 100 taxa related and/or similar to *Bothrophyllum* were analyzed and the most important of them are discussed. Detailed analysis of the type species based on the neotype and supported by additional topotype specimens illustrated here, allows restriction of both the type species and the genus, and leads to the proposition that *Bothrophyllum*-like taxa with a shortened cardinal septum should be considered of subgeneric (not named) status. Detailed analysis of the specimens and species described and illustrated from the type site (Myachkovo Quarry, Moscow Basin) form the basis for further considerations. On the basis of that analysis and characters established for the type species, taxa from all other European, African, Asiatic and North American areas either named *Bothrophyllum* or bearing characters of that genus were analyzed. The supposed origin and discussion of the relationships conclude the paper. A list of synonyms and exclusions from *Bothrophyllum* and lists of species included, excluded, or possibly belonging to *Bothrophyllum* and *Bothrophyllum*-like corals with a shortened cardinal septum are presented.

Key words: Carboniferous *Bothrophyllum*; Morphological frames; Origin; Distribution; Relationships.

INTRODUCTION

Solitary dissepimental rugose corals are very important components of Carboniferous and Permian faunas. They were and still are commonly described, but seldom investigated to the extent of making them important for stratigraphy and palaeogeography. Taxa belonging, related, and/or morphologically similar to the genus *Bothrophyllum* Trautschold, 1879, common in Carboniferous and/or Permian strata, are among these corals.

Taxa of those corals when studied in adequate detail show large morphological variability and also inconsistency of several features not only between different corallites, but also during growth of a single corallite. Moreover, several features overlap one another in various combinations. Such variability causes difficulties in their classification. Thus, these corals have been assigned many specific names and described under several different generic names (see lists below), starting with the monograph of Fischer von Waldheim (1830=1837) and his new species *Turbinolia conica*. The reason for the application of double dates of the monograph is explained below.

The generic name *Bothrophyllum* has been widely applied, suggesting both the apparent cosmopolitism of the genus and its continuous occurrence in the palaeontological record for approximately 80–100 million years. That long period of occurrence, especially considering the dramatic geographical changes that took place between the Tournaisian (first appearance of the *Bothrophyllum* morphotype) and the late Cisuralian, seems unlikely.

The difficulties mentioned above are amplified by the very incomplete investigations of many formally introduced taxa, based on fragmentary specimens, and often illustrated by only one transverse and one longitudinal thin section or even a single transverse section taken from a random position in a corallite. Some of such taxonomically useless 'taxa' have been accepted by subsequent authors increasing the mess in classification. An overview of the literature and the study of material in preparation for this paper (see 'Material and Methods' chapter below) leave no doubt that complete studies of the neanic, the early mature and the later mature growth stages of corals are absolute keys to the correct taxonomic identification of taxa so variable as those discussed here. That approach is not new. Dobrolyubova (1948a) demonstrated the role of ontogeny in the correct classification of some Rugosa and in the recapitulation of their phylogenetic lineages. Fomichev (1953, p. 332), commenting on *Bothrophyllum*-like taxa with axial areas free from major septa, i.e., those reaching the so called caninoid growth stage, wrote: "…investigation of the ontogeny is absolutely necessary for a correct classification of caninoid corals." [Translated by the Author from Russian]. Unfortunately, only a few rugose coral students have followed those apparently obvious requirements.

The very inconsistent approach to the genus *Bothrophyllum* by various authors may have resulted from the imprecise diagnosis of *Bothrophyllum* and diagnoses of taxa morphologically close to *Bothrophyllum*, such as *Caninophyllum* Lewis, 1929, *Pseudotimania* Dobrolyubova and Kabakovich, 1948 and *Bothroclisia* Fomichev, 1953. Position of *Yakovleviella* Fomichev, 1953, which may be a younger synonym of *Bothrophyllum,* remains uncertain (see chapter *Bothrophyllum* and *Bothrophyllum*-like corals in Europe (including the Urals) and in North Africa.). The misuse of the generic name *Pseudozaphrentoides* Stuckenberg, 1904, mentioned in a separate *Note* below, has increased the nomenclatorial confusion.

Keeping in mind all doubts mentioned above, an analysis of *Bothrophyllum*-like corals, which does not presently exist, is badly needed. The analysis that follows fulfils that gap only in part. It first attempts to establish a reasonable framework for the genus *Bothrophyllum*. Species other than *B. conicum* are not revised. Taxa described outside the Moscow Basin and outside the Myachkovskyi Substage, i.e., outside the area and age typical for the type genus, are divided into two groups. Representatives of the first group, those from the Donets Basin, i.e., from the area located closest to the type area and belonging to the same Eastern European Province, are discussed in more detail as being potentially related to those from the Moscow Basin. Taxa from the second group, those described from other areas are subdivided again. "Genera" inadequately investigated, but potentially belonging to *Bothrophyllum* are included in the synonymy of that genus with a double question mark, but "species" belonging to such "genera" are omitted from the discussion and are not included in the lists of species. Taxa investigated to an extent that allows a suggestion that they may be co-generic with *Bothrophyllum s.s.* or ?*Bothrophyllum,* all with a shortened cardinal septum, are included in the lists of species and are briefly discussed in the chapter "*Bothrophyllum*-like corals with a shortened cardinal septum".

Only features of the holotype constitute the basis for a species classification. Such an approach directs the potential reader to the data from the literature utilized in the present paper and allows the readers to arrive at their own opinions. Also, it omits revisions of species, which are necessary but impossible to do in the present paper. All papers dealing with the *Bothrophyllum*-like corals and known to me were taken into account in the analysis that follows. Their number is large, but I am aware of the possible incompleteness of this list.

The microstructure of septa, important for the complete diagnosis of the type species and, consequently, for the genus *Bothrophyllum* and the family Bothrophyllidae, is omitted from this analysis. The advanced diagenetic alterations of all specimens derived from the type area and the type stratum, available for the present study, preclude such an analysis, whereas only data derived from topotypes are reliable.

The analysis starts from a discussion of the type species for the genus, i.e., *Turbinolia conica* Fischer von Waldheim, 1830=1837. Those remarks are supplemented by an analysis of the ontogenetic morphology of the neotype and a similar discussion on specimens from the type area accepted here as co-specific with the type specimen. That discussion is followed by remarks on the morphology of specimens included in *B. conicum*, but derived from outside the type area and stratum. Also, several species incorrectly included in *Bothrophyllum* and several other ones that bear characters diagnostic for that genus, but classified as different genera, are discussed. In that discussion only the taxa derived from the Moscovian and Gshelian strata of the Donets Basin, are discussed in detail. Taxa from remote areas, most from China, are discussed very briefly and only as examples. The commonly inadequate level of their investigation precludes a confident classification.

Following Hudson (1936) and Fedorowski (1997a) only the cardinal and the counter major septa are considered the protosepta.

Note. The question of the genus *Pseudozaphrentoides* and its type species *P. jerofeevi* Stuckenberg 1904 must be briefly discussed here as influencing the taxonomy of *Bothrophyllum* and *Bothrophyllum*-like corals. That type species was briefly restudied by myself during my visit to the VSEGEI Museum in 1969. Cutting of new sections was not permitted at that time. Thus, only its obliquely broken and partly ground lowermost surface and the existing section made beneath the calice were peeled and illustrated (Fedorowski 1975, fig. 1b, c). The ontogenetically earliest growth stage, although incomplete, leaves no doubt as to its short septal, amplexoid character. The morphology of the late neanic and earliest mature growth stages is unknown. The morphology of the ontogenetically most advanced growth stage of the specimen is pathologic. This is suggested by disordered shortening of some major septa and by the asymmetrical arrangement of sclerenchymal thickening of the major septa. Only the following characters can be accepted as characteristic for that growth stage: the cardinal septum is not shortened, but is equal in length to most of the longest major septa; the cardinal fossula is narrow and open, marked by the underdevelopment of the last pair of major septa in cardinal quadrants and by the curvature of sections of tabulae; the counter septum is either equal to adjacent major septa or shortened, if a very asymmetrical arrangement of the major septa is accepted; the dissepimentarium is narrow. A single specimen constituting the basis for that genus and species precludes its use in taxonomy. Thus, I repeat my forty-year-old suggestion (Fedorowski, 1975, p. 33), to let the name *Pseudozaphrentoides* fall into oblivion until complete data from a topotype collection is available. To my knowledge such a study has not yet been accomplished. The result has been that subsequent students of corals have placed any species with dissepiments and an axial area free from the major septa in the “genus” *Pseudozaphrentoides*. This has made this “genus” a waste basket and leading directly to an erroneous taxonomy, phylogeny and palaeogeography.

MATERIAL AND METHODS

Facts and interpretations included in the analysis that follows are supported by both data from the literature and by my personal acquaintance with several coral collections. References to the well documented achievements of earlier authors are applied as an easy method to illustrate the facts discussed. However, data from the literature are supported in this discussion by my detailed studies on the *Bothrophyllum* and *Bothrophyllum*-like corals (Fedorowski 1965, 1967, 1973 [in Fedorowski and Goryanov; this statement is omitted in citations below], 1975; Stevens *et al*. 2012). Also, the following early collections were re-investigated by myself with many specimens peeled: Stuckenberg (1888, 1895, 1904, 1905), Dobrolyubova (1937, 1940, 1948b, 1970), Dobrolyubova and Kabakovich (1948), Kabakovich (1937), Fomichev (1953), Gorsky (1938, 1951), Vassilyuk (1960). Those re-investigations, although mostly unpublished, allow a direct comparison of taxa described from various regions and strata of Russia and Ukraine, including the type area. Further help for the discussion on the question of the Bothrophyllidae are: (1) The acquaintance with Chwieduk’s (2009, 2013) collections from Vestspitsbergen, and (2) The preliminary identifications of specimens in the collections from the Canadian Arctic Archipelago, housed in the Institute of Sedimentary and Petroleum Geology, Canadian Geological Survey, Calgary, including my own collection from the Belcher Channel Formation of Devon Island, accomplished during a 1987 expedition.

SYSTEMATIC PALAEONTOLOGY

Subclass Rugosa Milne Edwards and Haime, 1850
Order Stauriida, Verrill, 1865
Suborder Caniniina, Wang, 1950
Family Bothrophyllidae, Fomichev, 1953
Genus *Bothrophyllum* Trautschold, 1879

TYPE SPECIES: *Turbinolia conica* Fischer von Waldheim, 1837, p. 153, by original designation of Trautschold (1879, p. 30).

SYNONYMY: Abbreviations in brackets: As – Aselian, Cis – Cisuralian, C short – cardinal septum shortened, B – Bashkirian, G – Gshelian, K-G – Kasimovian-Gshelian, KMM – Kasimovian Stage, Moscow Basin, LG – lower Gshelian, LM – lower Moscovian, LP – lower Permian, LS – lower Sakmarian, M – Moscovian, MB - Moscow Basin, MC – middle Carboniferous, MM – middle Moscovian, MMM – Myachkovskyi Substage, Moscow Basin, MW – middle Warnantian, Na – Namurian, P – Podolskian Substage, PMM Podolskian Substage, Moscow Basin, S – Sakmarian, S-B – Serpukhovian-Bashkirian, UB-LM – upper Bashkirian-lower Moscovian, UC – upper Carboniferous, UM – upper Moscovian, US – upper Serpukhovian, UV – upper Viséan, UV-LN – upper Viséan-lower Namurian, UV-M – upper Viséan-Moscovian, V – Viséan, WC – Westphalian C, WD – Westphalian D, ? – cardinal septum shortened, ?? – inadequately investigated; identification doubtful, but with some main features recognizable. Identifications as aff., cf., sp. and taxa inadequately investigated and poorly illustrated are not listed.

1837. *Turbinolia*; Fischer von Waldheim, p. 153. (MMM).
part 1861. *Campophyllum*; Eichwald, p. 142. (MMM).
1879. *Cyathophyllum* (*Bothrophyllum*) Trautschold, p. 30. (MMM).
1888. *Rossophyllum* Stuckenberg, p. 11. (MMM).
1888. *Pseudocaninia* Stuckenberg, p. 12. (MMM).
? 1895. *Bothrophyllum*; Stuckenberg, p. 56. (Cis. C. short.).
?? 1905. *Bothrophyllum*; Stuckenberg, p. 15. (?UC).
non 1934. *Bothrophyllum*; Heritsch, p. 152.
?? 1936. *Bothrophyllum*; Dobrolyubova, p. 105. (?UC).
1937. *Caninophyllum*; Dobrolyubova, p. 19. (MMM).
part 1937. *Bothrophyllum*; Dobrolyubova, p. 24. (PMM).
1937. *Timania*; Kabakovich, p. 95. (KM).
1937. *Bothrophyllum*; Kabakovich, p. 99. (KM).
part 1938. *Bothrophyllum*; Gorsky, p. 46. (MC).
?? 1938. *Caninella* Gorsky, p. 40. (age uncertain).
1939. *Bothrophyllum*; Fomichev, p. 55. (MC, UC).
part 1940. *Bothrophyllum*; Dobrolyubova, p. 24. (KMM).
?? 1941a. *Bothrophyllum*; Heritsch, p. 194. (?M).
non 1941b. *Bothrophyllum*; Heritsch, p. 152.
non 1944. *Bothrophyllum*; Easton, p. 122.
part 1948b. *Bothrophyllum*; Dobrolyubova, pls 2–4, pl. 5, figs 1–3. (MC, UC).
part 1948. *Bothrophyllum*; Dobrolyubova and Kabakovich, p. 10. (PMM, MMM).
non 1951. *Bothrophyllum*; Gorsky, p. 31.
part 1953. *Caninophyllum*; Fomichev, p. 235. (UB-LG).
part 1953. *Bothrophyllum* Fomichev, p. 330 (UM).
non 1957. *Bothrophyllum*; Kostić-Podgorska, p. 53. (UV).
non 1958. *Bothrophyllum*; Kostić-Podgorska, p. 55. (UV).
? 1960. *Bothrophyllum*; Vassilyuk, p. 64. (US).
part 1961. *Caninia*; Fontaine, p. 143. (S).
1962. *Bothrophyllum*; Dobrolyubova, p. 331. (MMM, PMM).
non 1962. *Bothrophyllum*; Wu, p. 332 (UC).
? 1963. *Pseudozaphrentoides*; de Groot, p. 71. (UB-LM, C. short.).
? 1963. *Bothrophyllum*; de Groot, p. 73. (WD, C. short.).
non 1963. *Bothrophyllum*; Flügel, p. 378.
?? part 1964. *Bothrophyllum*; Wu, p. 69. (UV, pl. 16, figs 11–14 only).
? 1965. *Bothrophyllum*; Fedorowski, p. 29. (LS, C. short.).
non 1967. *Bothrophyllum*; Ivanovsky, p. 59.
?? 1967. *Bothrophyllum*; Fedorowski, p. 15. (LS, C. short.).
? part 1969. *Bothrophyllum*; Rowett, p. 69. (LP, pl. 10, fig. 5a only).
non 1972. *Bothrophyllum*; Tidten, p. 31.
1973. *Bothrophyllum*; Fedorowski (in Fedorowski and Goryanov) p. 49. (MMM).
non 1974. *Bothrophyllum*; Semenoff-Tian-Chansky, p. 139.
?? 1974. *Bothrophyllum*; Wu and Zhao, p. 272. (UC).
? 1975. *Bothrophyllum*; Fedorowski, p. 57. (UC, C short.).
1975. *Bothrophyllum*; Gorsky, Degtyarov, Kachanov, Rakshin, Simakova, p. 83. (M).
non 1976. *Bothrophyllum*; Guo, p. 90.
non 1977. *Bothrophyllum*; Khoa, p. 376.
non 1977. *Bothrophyllum*; Jia *et al*., p. 173.
? part 1978. *Caninia*; Gorsky, p. 76 (MC, pl. 5, fig. 10 only).
part 1978. *Bothrophyllum*; Gorsky, p. 95 (MC,UC, non pl. 14, figs 9–12).
?? 1978. *Bothrophyllum*; Wang, p. 121 (UV= Wu 1964, pl. 16, figs 11,14).
?? 1978. *Pseudotimania*; Wu and Zhao (in Wang), p. 122 (UC).
?? 1979. *Bothrophyllum*; Degtyarov, p. 41. (LM, MM).
non 1979. *Bothrophyllum*; Li and Liao, p. 30
1981. *Bothrophyllum*; Hill, p. F346
? part 1981. *Bothrophyllum*; Poty, p. 47. (MW, pl. 22, fig. 1 only).
?? part 1982. *Bothrophyllum*; Jiang, p. 108. (non. pl. 66, fig.12).
?? 1983. *Bothrophyllum*; Boll, p. 34 (WC).
?? part 1983. *Bothrophyllum*; Ou, Yangxuan (in Cao *et al*.), p. 128.
1983. *Bothrophyllum*; Yu *et al*. p. 82.
? 1984. *Bothrophyllum*; Rodríguez, p. 286. (P).
?? 1984. *Bothrophyllum* (*Bothroclisia*); Rodríguez, p. 294. (P).
non 1985. *Bothrophyllum*; Xu, p. 187.
?? 1985. *Bothroclisia*; Wu and Zhang, p. 127 (same as in 1982).
non 1985. *Bothrophyllum*; Duan, p. 262.
?? part 1986. *Bothrophyllum*; Kossovaya, p. 67. (G, As).
non 1986. *Bothrophyllum*; Wang (in Xiao *et al*.), p. 205.
1987. *Bothrophyllum*; Ivanovsky, p. 10. (MMM).
?? 1987. *Pseudozaphrentoides*; Yu and Wang, p. 49. (LP).

?? 1987. *Caninophyllum*; Yu and Wang, p. 50. (LP).
?? 1987. *Pseudocaninophyllum*; Yu and Wang, p. 50. (LP).
?? 1987. *Timania*; Yu and Wang, p. 51. (LP).
?? 1987. *Bothrophyllum*; Yu and Wang, p. 51. (LP).
?? 1987. *Bothroclisia*; Yu and Wang, p. 51. (LP).
?? 1987. *Koninckophyllum*; Yu and Wang, p. 51. (LP).
non 1988. *Bothrophyllum*; Yu and Zhu, p. 91.
?? 1989. *Bothrophyllum*; Kato and Gupta, p. 406. (UV-LN).
?? 1989. *Pseudotimania*; Kato and Gupta, p. 407. (UV-LN).
1989. *Bothrophyllum*; Wu and Zhao, p. 53 (MC-UC).
?? part 1989. *Timania;* Wu and Zhao, 1989, p. 56. (UB-UC).
?? 1989. *Bothroclisia*; Wu and Zhao, p. 62 (UB-M).
?? 1989. *Pseudozaphrentoides*; Yu, p. 360. (M).
?? part 1989. *Timania*; Yu, p. 360. (M).
?? 1992. *Caninophyllum*; Wu and Lin, p. 87. (B).
?? 1992. *Taiziheophyllum*; Wu and Lin, p. 88. (B).
?? part 1992. *Yakovleviella*; Wu and Lin, p. 89. (B).
?? part 1992. *Bothroclisia*; Wu and Lin, p. 101. (B).
? 1992. *Bothrophyllum*; Peng, Lin and Li, p. 141. (UC).
?? part 1992. *Gshelia*; Peng, Lin and Li, p. 143. (UC).
1992. *Bothroclisia*; Peng, Lin and Li, p. 144. (UC).
?? 1993. *Gshelia*; Ding and Xu, p. 701 (LP).
non 1993. *Bothrophyllum*; Flügel, p. 53.
1995. *Bothrophyllum*; Lin Baoyu *et al*., p. 477. (MMM).
? part 1997. *Amandophyllum*?; Rodríguez *et al*., p. 211. (M).
? 2000. *Bothrophyllum*; Igo and Adachi, p. 47 (?S-B, K-G, C short).
2001. *Bothrophyllum*; Kossovaya, p.154. (MB).
? 2004. *Bothrophyllum*; Fedorowski, p. 96. (UB-LM, C short).
? 2009. *Bothrophyllum*; Chwieduk, p. 62 (LS, C. short).
? 2009. *Bothrophyllum*; Ogar, p. 63. (MC-UC, C. short).
non 2011. *Bothrophyllum*; Aretz, p. 607.
?? 2012. *Bothrophyllum*; Stevens, Fedorowski and Kawamura (UC).
? 2013. *Bothrophyllum*; Chwieduk, p. 57. (LP, C. short).

LISTS OF SPECIES [Species derived from the Moscow Basin marked by (M)]:

Species included here in *Bothrophyllum* (generic names original; arranged in accordance to date of introduction; question mark when incompletely studied): *Turbinolia conica* Fischer von Waldheim, 1830=1837 (M); *Pseudocaninia trautscholdi* Stuckenberg, 1888 (M); ?*Bothrophyllum volgense* Stuckenberg, 1905 (M); *Caninophyllum bothrophylloides* Dobrolyubova, 1937 (M); *Bothrophyllum pseudoconicum* Dobrolyubova, 1937 (M); *Bothrophyllum kashiricum* Kabakovich, 1937 (M); *Timania stuckenbergi* Kabakovich, 1937 (M); *Bothrophyllum simplex* Gorsky, 1939 (in Fomichev 1939); *Bothrophyllum robustum* Dobrolyubova, 1940 (M); ?*Bothrophyllum rareseptatum* Dobrolyubova, 1940 (M);?*Bothrophyllum flexuosum* Dobrolyubova and Kabakovich, 1948 (M); *Caninophyllum domheri* (forma a) Fomichev, 1953; ?*Caninophyllum dobrolyubovae* Fomichev, 1953; *Caninophyllum kalitvense* Fomichev, 1953; *Bothrophyllum aequalum* Fomichev, 1953; ?*Bothrophyllum berestovensis* Vassilyuk, 1960; *Pseudozaphrentoides rabanaliensis* de Groot, 1963; *Bothrophyllum pseudoconicum* Dobrolyubova, 1937 of Gorsky 1978; ?*Bothrophyllum tolstikinae* Gorsky, 1978; ?*Caninia vacua* Gorsky, 1978 (holotype only); ?*Bothrophyllum concentricum* Wu and Zhao, 1989; *Bothrophyllum okense* Kossovaya, 2001 (M);

Species accepted as possibly belonging to *Bothrophyllum* (generic names original; arranged in accordance to date of introduction; question mark when incompletely studied): ?*Caninophyllum kalitvense* Fomichev, 1953; *Bothrophyllum longiseptatum* (Lewis) of Wu, 1964; *Bothrophyllum pseudoconicum* Dobrolyubova of Wu and Zhao, 1974; *Caninia regularis* Gorsky, 1978; ?*Pseudotimania delicata* Wu and Zhao, 1978; ?*Bothrophyllum filigranum* Boll, 1983; ?*Pseudozaphrentoides cishanensis*; Yu, 1989;?*Bothrophyllum heterodisseptum* Wu and Zhao, 1989; ?*Bothroclisia sinensis* Wu and Zhao, 1989;? *Bothroclisia poriferoides* Fomichev of Peng, Lin and Li, 1992; ?*Gshelia yuanophylloides* Peng, Lin and Li, 1992; ?*Gshelia yishanensis* Xu et Ding, 1993.

Species with a shortened cardinal septum (generic names original; arranged in accordance to date of introduction; question mark when incompletely studied): *Bothrophyllum baeri* Stuckenberg, 1895; ?*Bothrophyllum formosum* Gorsky, 1938; ?*Bothrophyllum superbum* Gorsky, 1938; ?*Caninella pulchra* Gorsky, 1938; *Bothrophyllum pseudoconicum conicum* Dobrolyubova and Kabakovich, 1948 (M); ?*Bothrophyllum irregulare* Dobrolyubova and Kabakovich, 1948 (M); ?*Caninophyllum gurovi* Fomichev, 1953; ?*Bothrophyllum permicum* Fedorowski, 1965;?*Bothrophyllum orvini* Fedorowski, 1967; *Bothrophyllum timanioides* Fedorowski, 1975; *Bothrophyllum pseudoconicum* Dobrolyubova of Rodríguez, 1984; *Bothrophyllum volgense* Stuckenberg of Kossovaya, 1986 (M); *Timania huanglongensis* Yu, 1989; ?*Bothrophyllum conicum* of Wu and Zhao, 1989; ?*Bothrophyllum cystotabulatum* Wu and Zhao, 1989; ?*Timania planotabulata* Wu and Zhao, 1989; ?*Timania elegans* Wu and Zhao, 1989; ?*Bothrophyllum jiyuanense* Peng, Lin and Li,1992; *Bothrophyllum conicum*

Trautschold of Peng, Lin and Li, 1992; ?*Taiziheophyllum kongjiabuziense* Wu and Lin, 1992.

Potential members of different genera or subgenera from the type area (question mark when incompletely studied): *Bothrophyllum complexum* Dobrolyubova, 1937 (+*B. conicum* var.1 Dobrolyubova, 1940 + *B. pseudoconicum* Dobrolyubova and Kabakovich, 1948); ?*Bothrophyllum novlinskoi* Dobrolyubova and Kabakovich, 1948; ?*Bothrophyllum conicum conicum* of Kossovaya 2001.

Note. Lists include only formally introduced and reasonably studied taxa. Species are listed with original generic names with the dates of their introduction. Subsequent authors using those species names are not listed unless the specimens described by them do not fit the original species characteristics and differences are well documented. The list is divided into four categories reflecting different level of credibility. Taxa listed with a question mark are incompletely studied, but their main illustrated characters correspond at least in part to the diagnosis of *Bothrophyllum*.

EMENDED DIAGNOSIS: Solitary Bothrophyllidae; axial septum present during entire neanic growth stage; inner margins of several major septa approach corallite axis up to early maturity; in late maturity axial area may be free of septa; cardinal septum length equal to average major septa or longer counter septum long up to early mature growth stage, may be equal to other major septa in advanced maturity; cardinal fossula indistinct; loose indistinct axial structure composed of inner margins of major septa and axial tabellae may be gradually reduced during growth; tabularium biform and/or disstabularium.

NEW TERM: *Disstabularium* – an area intermediate between dissepimentarium and tabularium composed of basal skeletal structural elements: tabellae and/or long dissepiments making the boundary between those two structural zones indefinite (Text-fig. 1E).

ANALYSIS OF THE STATUS QUO

Recognition of the type species for the genus

Fischer von Waldheim = Fischer de Waldheim (1830 =1837, p. 153, pl. 30, fig. 6) introduced the new species *Turbinolia conica* from the Middle Carboniferous strata of the Moscow area. The two dates of publication resulted from two editions of that paper. The date 1837 is followed here for two reasons: (1) It was used by Trautschold (1867) when he introduced the new subgenus *Bothrophyllum*; (2) Only the second edition was at the present author's disposal.

The drawing by Fischer von Waldheim (1837, pl. 30, fig. 6) shows a corroded specimen with major septa meeting at the corallite axis, with the minor septa and part of the dissepimentarium lacking. Two other specimens included by that author in *Turbinolia* with the new species names *T. arietina* and *T. ibicina* (Fischer von Waldheim 1837, pl. 30, figs 4, 5, respectively) are corroded as well, but the arrangement of their major septa is similar to that of *T. conica*. Also, long minor septa are drawn in *T. arietina*. All specimens of those species may belong to the same species. Unfortunately, the collection was lost. Kossovaya (2001, p. 155) stated: "The collection serving as a basis for the description of that species [i.e., *Turbinolia conica*] by G. I. Fischer got lost during the 1812 war" [Translated herein from Russian]. She did not explain how the collection lost in 1812 could have served for a publication 25 years later.

The formal recognition of a new species by Fischer von Waldheim, supported by his illustration, allows consideration that that species name is valid despite the loss of the collection. As selection of a holotype was not required by law at that time, the species identification by Trautschold (1879, p. 30) as "*Bothrophyllum conicum* Fisch. sp." should be considered correct and valid. His footnote on the same page: "*Turbinolia conica* Fisch. Oryctographie de Moscou 1837, pag. 153, t. 30, f. 6" leaves no doubt about his approval of Fischer von Waldheim's authorship of *conica*. That authorship also was indicated by other 19th Century authors (Eichwald 1861 and Stuckenberg 1895). The rich topotype material studied by subsequent authors (Dobrolyubova 1937, 1948b; Dobrolyubova and Kabakovich 1948; Fedorowski 1973; Ivanovsky 1987; Kossovaya 2001) is also a factor apparently supporting Fischer von Waldheim's (1830=1837) authorship. However, the morphological differences of the specimens derived from the Myachkovskiy Horizon of the Moscow Basin (see discussion below), leading to the recognition of more than one species in the type area, put that authorship in doubt.

It is impossible to recognize which one of the existing species should bear the name *conica* introduced by Fischer von Waldheim (1837). Hill (1981, p. F346) stated: "[**Turbinolia conica* Fischer von Waldheim, 1830, explanation of pl. 30, fig. 6 *sensu* Trautschold, 1879, p. 30…]". Ivanovsky (1987, p. 10) accepted Fischer von Waldheim's authorship without mentioning the date of publication. However, the formal selection by him of a neotype derived from the type area made that morphotype representative for *Bothrophyllum conicum* Fischer von Waldheim. Kossovaya (2001, p. 155) and Ogar (2009, p. 63) accepted both the authorship by Fischer von Waldheim and the date of publication (1837) as pointed out by Trautschold (1879).

That authorship was not accepted by Heritsch (1934, 1944), Dobrolyubova (1937, 1940, 1948b, 1962), Dobrolyubova and Kabakovich (1948) Fedorowski (1973, 1975, 2004), Hill (1981) and Peng, Lin and Li (1992). All those authors attributed the authorship of *B. conica* to Trautschold (1879), but did not explain why they took that position. However, that approach will remain incorrect unless the name *Turbinolia conica* Fischer von Waldheim, 1837 is cancelled by the *International Commission of Zoological Nomenclature*. Wu and Zhao (1989, p. 54) attributed the species name *conicum* to Dobrolyubova (1937) and cited only her paper in the synonymy.

In the situation discussed above, the characters of the neotype (see below) illustrated by Ivanovsky (1987, pl. 1, figs 1a–v in Russian alphabet) must be accepted as typical for the type species of *Bothrophyllum*. It is a pity he did not select a well preserved specimen from Eichwald's (1861) collection, housed in the St. Petersburg University (Fedorowski in Fedorowski and Goryanov 1973), or one of the specimens identified by Stuckenberg (1888) as *Pseudocaninia conica* Fischer, housed in the VSEGEI Museum in St. Petersburg. However, Ivanovsky's (1987) decision is formally correct and must be followed. Peels taken from the surfaces of some of Stuckenberg's (1888) specimens are included in the present paper (Text-figs 1, 2) as supportive data**.** Like the neotype, those specimens belong to the second oldest collection derived from the Myatchkovo Quarry, i.e., the type site for *Turbinolia conica* Fischer von Waldheim, 1830=1837. They supplement the comprehensive study by Dobrolyubova (1937). All those collections provide a set of data allowing consideration of the morphology and the intraspecific variability of *B. conicum.*

The original basis for the genus

Trautschold (1879) was the first author to recognize a separate taxonomic status of the specimen from the Myachkovo Quarry, identified by Fischer von Waldheim (1830=1837) as *Turbinolia conica*. He introduced the new subgeneric name *Bothrophyllum* placing this taxon under the genus *Cyathophyllum* Goldfuss, 1826, based on several specimens included by him in that species. Unfortunately, his collection has been lost. However, his descriptions and illustrations, very precise for his time, allow recognition of the following characters:

(1) The number of septa (44×2) at possibly 20–25 mm corallite diameter (p. 31). Those data correspond to his illustrations (pl. 5, figs 1c, 1e). The largest diameter at a calice margin (5 cm), mentioned by him, was not confirmed by subsequent authors and is here omitted from consideration.

(2) The irregularity of a corallite growth with the external wall thin and almost smooth (p. 31, pl. 5, figs 1a, b) with only weak growth lines marked.

(3) The cardinal fossula located at convex side of the corallite (p. 31) with the cardinal septum mostly indistinguishable by length from the remaining major septa seen both in the section and the calice (pl. 5, figs 1c, 1e respectively).

(4) Length of major septa (15–17 mm) and minor septa (6–7 mm) (p. 31) correspond to the mean data established by Dobrolyubova (1937) in her revision and to other specimens from the type area illustrated previously and in this paper (see above).

(5) The possibility of rejuvenation (pl. 5, fig. 1a) confirmed by Dobrolyubova (1937) and Rozhnov (1974, 2014).

(6) Features of the early ontogeny which can be established with some confidence (pl. 5, fig. 1b, lowermost): major septa arranged in weakly recognizable quadrants, longest approaching and/or reaching corallite axial area; two major septa perhaps cardinal and counter septa located opposite each other at concave and convex corallite sides meeting axially to form an axial septum; minor septa and dissepimentarium absent at that growth stage, most probably neanic.

(7) Such features of mature morphology as: major septa thin, not differentiated by thickness in tabularium, most approaching, but not reaching corallite axis; minor septa long, mostly entering tabularium; dissepimentarium approximately 1/3 corallite radius wide (pl. 5, fig. 1c).

(8) In longitudinal section (p. 31, pl. 5, fig, 1d) tabulae incomplete; in axial part either flat and horizontal, or elevated (middle and upper of picture respectively). Peripheral tabellae downturned. Axial column absent.

(9) Calices of two specimens illustrated (figs 1e, 1f) similar in possessing thin major septa, mostly reaching corallite axis and long minor septa entering tabularium. However, first of those specimens (fig. 1e) possesses major septa almost radially arranged, cardinal septum indistinguishable from remaining major septa, cardinal fossula indistinct, and dissepimentarium approximately 1/3 corallite radius wide. In the calice of the second specimen (fig. 1f) major septa arranged in distinguishable quadrants, cardinal septum shortened, cardinal fossula distinct and dissepimentarium approximately ¼ corallite radius. Dobrolyubova (1937, p. 35)

included the calice of the second specimen in the list of Trautschold's (1879) illustrations accepted by her as the lectotype. Kossovaya (2001, p. 155) and Ogar (2009, p. 63) omitted that illustration from the synonymies of that species. Neither of those authors listed explained their positions. In the context of the intraspecific variability established so far, it remains unclear whether this specimen should or should not be excluded from the genus discussed, but it does not belong to the same species as the former one.

Most of the data listed above allow the conclusion that the specimens utilized by Trautschold (1879) to characterize the type species of his new genus *Bothrophyllum* are closely comparable to those of the neotype (Ivanovsky 1987, pl. 1, fig. 1a–v in Russian alphabet) and to the topotype specimens illustrated and described by Dobrolyubova (1937, 1948b) and Fedorowski (1973) and to specimens illustrated in the present paper (Text-figs 1A–D, 2A, B, D).

Neither the descriptions nor figure captions of Trautschold (1879, pp. 30, 31, 78 respectively) indicates the number of specimens illustrated by him as collection numbers for his specimens were not published. Also, the expression "Derselben Koralle" was only used once by Trautschold (1879, p. 78) in the captions. That phrase referred to figures 1b (incorrectly printed as 2b) and 1c. Thus, illustrations of three specimens (if figs 1b–e illustrate the same corallite) or five specimens (if figs 1d, 1e belong to different corallites) is possible. This means that Kossovaya (2001, p. 155) was correct in rejecting Dobrolyubova's (1937) selection of the lectotype. First, only one specimen can serve as a type and second, Dobrolyubova (1937, p. 35) was aware of the loss of Trautschold's (1879) collection. She wrote: " Since illustrations and descriptions by Trautschold clearly expose diagnostic characters of that species [*conicum*], I consider it possible to accept Trautschold's form as the lectotype although his originals are not preserved." [Translated herein from Russian]. That loss was confirmed by Ivanovsky (1987, p. 10).

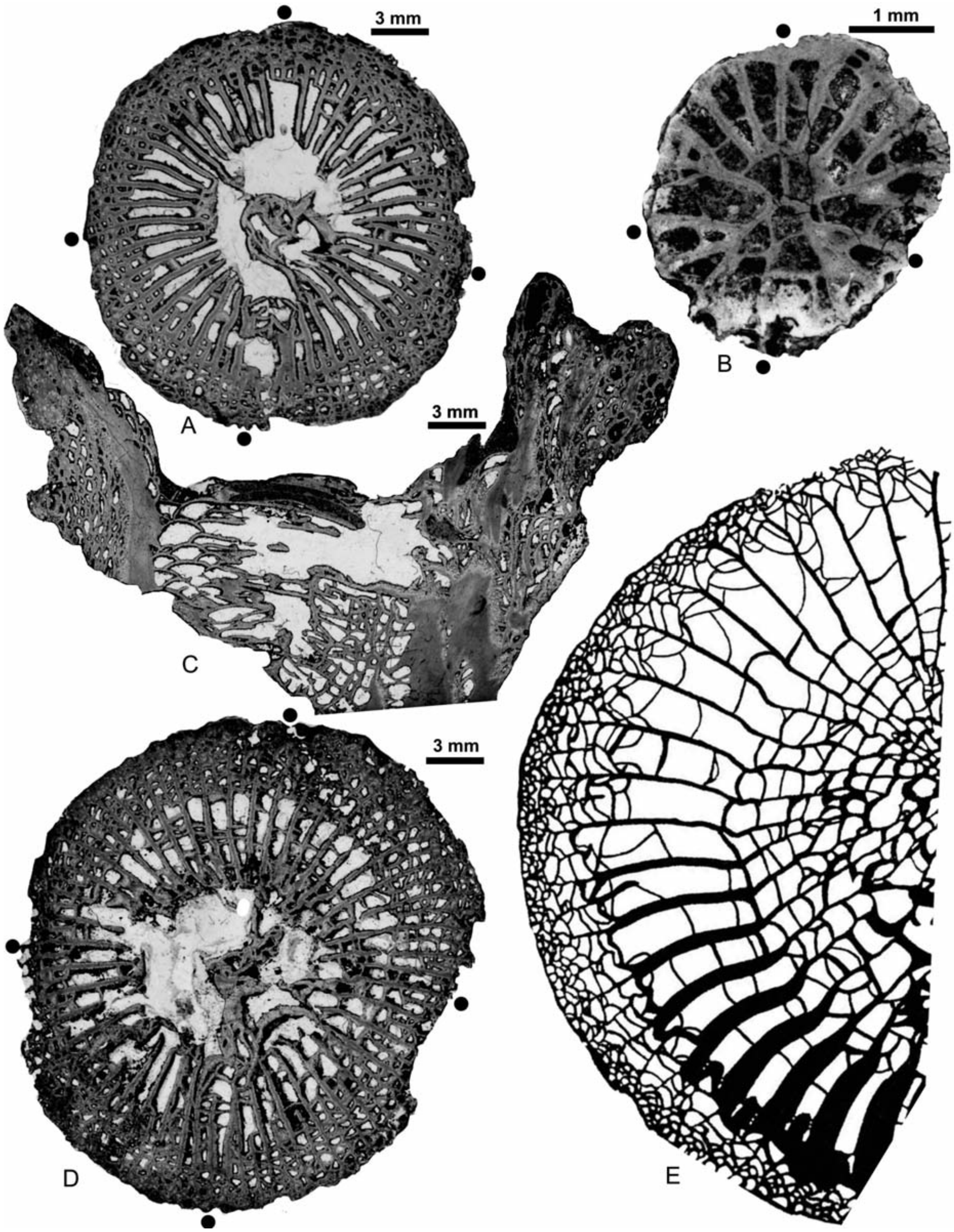
The type for the type species

The holotype of the type species was not selected by older authors, i.e., Fischer von Waldheim (1837), Eichwald (1861), Trautschold (1879) and Stuckenberg (1888, 1895, 1904), whereas Dobrolyubova's (1937, p. 35) selection was invalid as mentioned above. Kossovaya (2001, p. 155) put in doubt Ivanovsky's (1987) selection of the syntype (neotype). She wrote: "The specimen illustrated by Stuckenberg is incomplete and it differs from specimens described by T.A. Dobrolyubova in smaller size and simpler dissepimentarium. It probably belongs to the subspecies *B. conicum moribundum* Kossovaya subsp. nov. rather than to the nominative subspecies" [Translated here from Russian]. Judging from the phrase cited, Kossovaya (2001) did not question the formal correctness of Ivanovsky's (1987) selection of the syntype (neotype), only emphasizing its poor preservation and its morphological difference compared to the specimens described by Dobrolyubova (1937, 1940, 1948b) as *B. conicum* Trautschold. Such an approach by Kossovaya (2001) cannot be accepted. The valid syntype (neotype) introduced by Ivanovsky (1987, pl. 1, fig. 1a–v in Russian alphabet) with its morphology rather than those specimens identified by Dobrolyubova (1937) as *B. conicum*, must be accepted by law as the basis for any discussion on *Turbinolia conica* Fischer von Waldheim, 1837 and on the genus *Bothrophyllum* Trautschold, 1879. Also, its poor preservation is not a formal obstacle. Only a clear decision by the ICZN, declaring that selection invalid, can change the *status quo* of the neotype. Fortunately, the neotype was collected from the Myachkovo Quarry increasing its credibility irrespective of the incompleteness.

Ivanovsky (1987, p. 10, pl. 1, fig. 1a–v in Russian alphabet) offered only formal remarks and illustrations of three thin sections of the corallite when introducing the neotype of *B. conicum*. Thus, a brief description of that specimen, based on Ivanovsky's (1987) illustrations, seems necessary as an introduction to a further discussion of both *B. conicum* as the type species for the genus *Bothrophyllum* Trautschold, 1879 and for that genus itself.

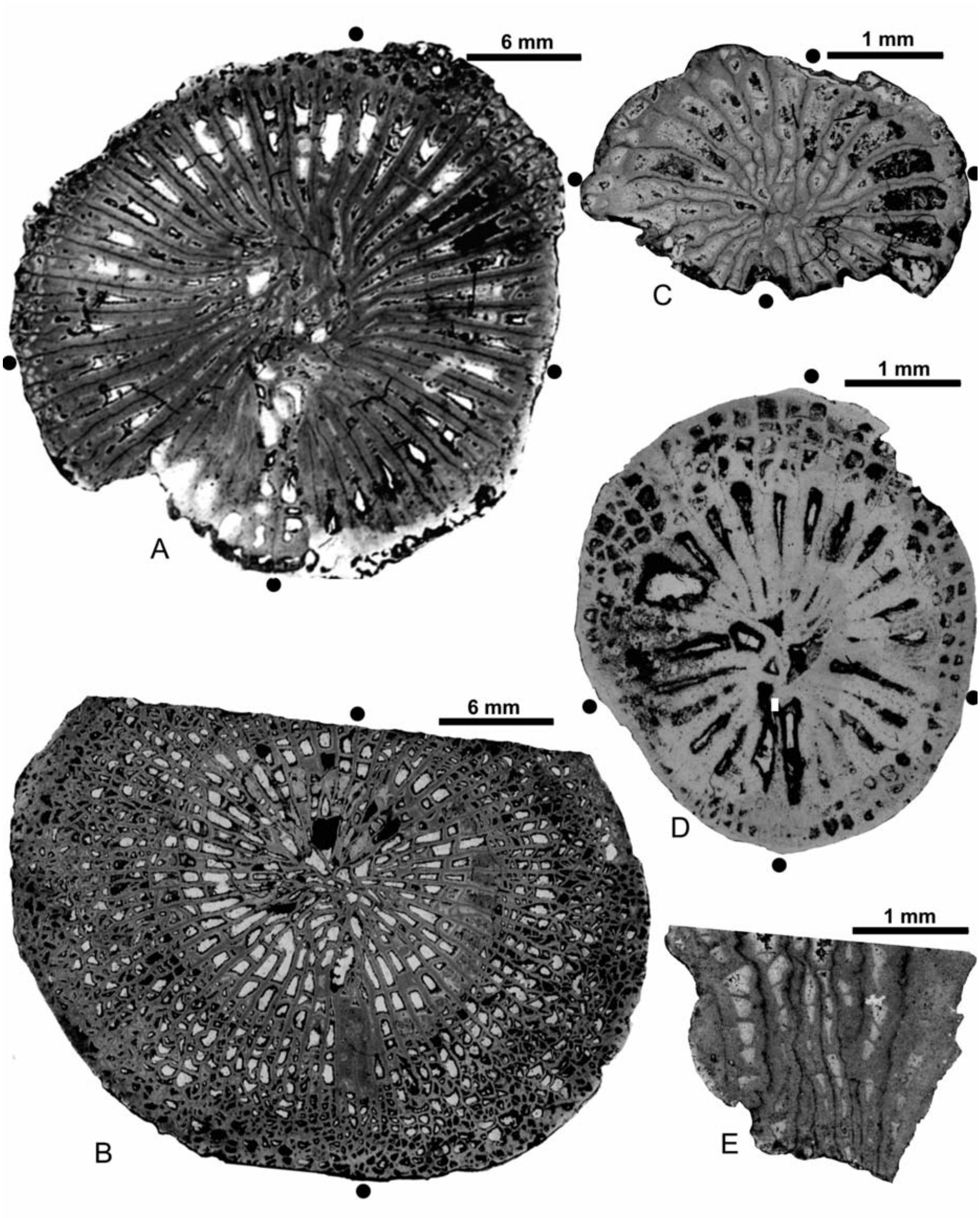
(1) The main features of the neanic growth stage of the neotype, with n:d value 24:4.0×4.8 mm (Ivanovsky 1987, pl. 1, fig. 1b) are: lack of minor septa and dissepiments; pinnate arrangement of thin major septa, several of which meet distinct axial septum; septal and tabular cardinal fossula present, the latter suggested by sections of tabulae more numerous next to cardinal septum than in adjacent septal loculi.

(2) The ontogenetically most advanced growth stage (Ivanovsky 1987, pl. 1, fig. 1a), here considered as advanced early mature, with 15.5×18.0 mm in diameter, partly destroyed, perhaps by recrystallization. Exact number of major septa unknown; possibly over 40 judging from number of preserved ones (35) and an area of corallite from which major septa have been eliminated by diagenesis. All preserved major septa in cardinal quadrants and most in counter quadrants thickened in tabularium, strongly tapering in axial parts. Major septa



Text-fig. 1. **A–D** – *Pseudocaninia conica* Fischer of Stuckenberg, 1888. Transverse cuts, except when stated otherwise; all peels. A, B – specimen 31_321. A – mature growth stage, B – neanic growth stage. C – specimen 28_321, longitudinal section. D – specimen 30_321 – mature growth stage. All housed in the VSEGEI Museum, St. Petersburg. **E** – *Bothrophyllum pseudoconicum* Dobrolyubova, 1937. Copied from Dobrolyubova 1937, pl. 14, fig. 2. Housed in the Paleontologicheskyi Institut, Russian Academy in Sciences, Moscow. Biform tabularium in cardinal quadrants replaced by disstabularium in counter quadrants. Magnifications indicated by scale bars.

Note. All specimens from Stuckenberg's (1888) collection are diagenetically altered by dolomitization. This and incomplete infillings in some loculi has resulted in apparent shortening of some septa major



Text-fig. 2. **A, B** – *Pseudocaninia conica* Fischer of Stuckenberg, 1888. Transverse cuts with peels. Mature growth stage. A – specimen 36_321, B – specimen 32_321. **C-E** – *Rossophyllum novum* Stuckenberg, 1888. C – specimen 26_321 – transverse cut with peel, late neanic growth stage, D – specimen 25_321 – transverse section with peel – late neanic/early mature growth stage, E – specimen 27_321 – eccentric longitudinal section with peel. Magnifications indicated by scale bars. All specimens housed in the VSEGEI Museum in St. Petersburg.

Note. All specimens from Stuckenberg's (1888) collection are diagenetically altered by dolomitization. This and incomplete infillings in some loculi resulted in apparent shortening of some septa. Incompleteness of figure B is artificial, resulted from narrow film available for me in 1969 when peels were taken.

in cardinal quadrants create tent-shaped structure by being inclined towards cardinal septum, with oldest septa in those quadrants being the longest and those adjacent to cardinal septum being shorter. Inner margins of three pairs of major septa unite to close indistinct cardinal fossula. Cardinal septum in tabularium equal in thickness to corresponding parts of adjacent major septa at its 4/5 length, abruptly tapering in its innermost part. Its length slightly less than that of other major septa, except for adjacent pair, but it is not truly shortened. Counter septum thin, slightly elongated. Minor septa penetrate tabularium; their tabular parts in cardinal quadrants thickened. Dissepimentarium occupies 1/5 corallite radius in cardinal quadrants and 1/7 in counter quadrants where it may be partly corroded. Dissepiments in cardinal quadrants regular; their remnants in counter quadrants small and irregular.

(3) Longitudinal section (Ivanovsky 1987, pl. 1, fig. 1v in Russian alphabet) taken from early growth stage. Section of continuous septum near corallite axis is either a long-lasting axial septum or elongation of one of the protosepta (probably counter). The continuous septum in that section is accompanied by a few short sections of additional septa and by convex inner tabellae to form a loose axial structure. Tabularium biform in recognizable parts of longitudinal and transverse sections. All tabulae incomplete, differentiated in length and arrangement, but generally dome-shaped, either horizontal or slightly elevated in axial parts. Shape of peripheralmost parts of tabulae depends on their position. In position I of Sutherland (1965) downturned (Ivanovsky 1987, pl. 1, fig. 1v, middle left side between sections of major and minor septa). In position II tabulae nearly horizontal or slightly elevated next to dissepimentarium, later upturned. In transverse thin section biformity of tabularium confirmed best by sections of tabulae in left cardinal quadrant. Dissepiments small, vertically arranged.

The specimens identified by Stuckenberg (1895) as his new species *Carcinophyllum indigae* and *Caninia lonsdalei*, included by Ivanovsky (1987, p. 39, pl. 6, fig. 5; pl. 8, fig. 2 respectively) in *B. conicum* are not discussed in detail. Both pictures by Ivanovsky probably are from immature parts of specimens. *C. indigae* possesses a short cardinal septum, located in a deep closed cardinal fossula and the counter septum is elongated. Both those characters and the arrangement of the major septa thickened in the tabularium suggest an early growth stage of *Timania* Stuckenberg, 1895. The transverse thin section of *C. lonsdalei* suggests it may belong to *Bothrophyllum*, but the short minor septa exclude it from *B. conicum*.

CONSIDERATIONS

Bothrophyllum conicum from the Myachkovian Substage of the Moscow Basin; variability and exclusions

Only corals derived from the type horizon and from the type site (preferably) or the area occurring close to that site ensure a credible recognition of characters diagnostic for the type species of *Bothrophyllum* and its probable intraspecific variability. Specimens described by Trautschold (1879), Eichwald (1861), Stuckenberg (1888) and most specimens illustrated by Dobrolyubova (1937) were derived from that type site, i.e., the Myachkovo Quarry. Some other specimens are from the sites situated in the Moscow Basin close to that type locality. Thus, the analysis is based on the specimens following that precondition. Also, only well illustrated specimens derived from the Myachkovian Substage and identified by authors as '*conicum*' are considered. They are discussed here without mentioning the generic names applied to that species by various authors (*Turbinolia* by Fischer von Waldheim 1830=1837, *Campophyllum* by Eichwald 1861*, Pseudocaninia* Stuckenberg 1888).

The analysis, supported by my personal acquaintance with several collections (see material and methods), is based mainly on the comprehensive study by Dobrolyubova (1937). Papers by Trautschold (1879), Stuckenberg (1888), Dobrolyubova (1948b), Dobrolyubova and Kabakovich (1948), Fedorowski (1973), Ivanovsky (1987) and Kossovaya (2001) are treated as additional sources of data. Those data are supplemented by illustrations (Text-figs 1, 2) and brief descriptions of specimens from Stuckenberg's (1888) collection as mentioned above.

Drawings by Dobrolyubova (1937) and her descriptions, supported by tables of measurements, suggest that most specimens illustrated by her are small but complete corallites. Dobrolyubova (1937) seems to have treated all those specimens as mature individuals. Her illustrations demonstrate some similarity in the early neanic growth stages of most corallites studied, documenting at the same time a large variation in the morphology, size and n:d values at advanced growth stages. The morphology at advanced growth stages of the small corallites commonly do not compare with either the morphology of the advanced growth stages of the large corallites or with the morphology of the growth stages of large corallites, corresponding in size to that of the small corallites.

The following facts should be kept in mind in that context: (1) Complete skeletons with calices preserved do not prove a mature growth stage; (2) Mortality among young creatures commonly exceeds the mortality of fully mature ones. Therefore it is not surprising that small corallites are prevalent in Stuckenberg's (1888) and Dobrolyubova's (1937) collections; (3) Mature morphological characteristics may be achieved by different specimens of different sizes and with different n:d values (n – number of septa, d – corallite diameter); (4) In rugose coral taxonomy the differences in the n:d values are as a rule accepted as quantitative features allowing discrimination at the species level.

Two approaches to the corals derived from the type area and analyzed in this paper are possible:

(1) The approach represented by Dobrolyubova (1937), suggesting an extremely wide intraspecific variability in almost all features. That broad approach was slightly reduced by Dobrolyubova and Kabakovich (1948) who named the new subspecies *B. conicum novlinskoi*. However, Ogar (2009) made the species definition even broader by putting not only the subspecies introduced by earlier authors from the Moscovian strata of the Moscow Basin, but also those in the Donets Basin and some Chinese specimens in the synonymy with *B. conicum*.

(2) The much narrower approach is proposed here. This latter approach is supported by the following premises: 1) Up to now rugose coral taxonomy has followed points 1–4 noted above. 2) The large variation at the generic and family level of corals derived from the Myachkovskyi Substage of the type area and vicinity. 3) The lack of a step by step analysis of the distribution and sequence of corals occurring in that Substage of the Myachkovo Quarry. These premises make differentiation at the species level acceptable and that solution is proposed here. The narrow approach applied in this paper allows exclusion of one specimen of Trautschold (1879; see above), several specimens described by Dobrolyubova (1937, 1940, 1948b), Dobrolyubova and Kabakovich (1948), Kossovaya (2001) from the type area, specimens described by Wu and Zhao (1989), Peng, Lin and Li (1992) from China and by Ogar (2009) from the Donets Basin, Ukraine from *B. conicum*. Several characters of the specimens excluded are beyond the limits of intraspecific variability. Some of those characters are qualitative and proper for the distinction at a subgeneric or a generic level (see for details below).

In order to avoid comparison of possibly different species from the type area described under the same name '*conicum*', only characteristics of the largest specimens described by Dobrolyubova (1937, 1948b), comparable in size to the corallites described and illustrated by Trautschold (1879), are considered in establishing the intraspecific variability of *B. conicum*. Small specimens are accepted as co-specific with *B. conicum* only when their morphology corresponds to morphology at a similar size in large corallites. Such an approach minimalizes the subjectivity in the evaluation and allows recognition of characteristics typical for *B. conicum* proper.

Changes during growth

The early growth stage

The brephic and earliest neanic growth stages remain unknown. The following neanic characters, however, are documented: The arrangement of major septa in distinct quadrants are clearly recognizable in some, but hardly exist in other corallites (Dobrolyubova 1937, pl. 7, figs 2, 9 and pl. 10, fig. 4 respectively). The axial septum is invariably present. It is most clearly seen in the neotype (Ivanovsky 1987, pl. 1, fig. 1b), in the earliest growth stage of the corallite present in Stuckenberg's (1888) collection (Text-fig. 1b; see below for description), and in the holotype of *B. conicum moribundum* Kossovaya, 2001 illustrated in her pl. 32, fig. 8. The cardinal fossula is recognizable in all specimens except the specimen illustrated by Dobrolyubova (1937, pl. 10, fig. 4). Sclerenchymal thickening is weak in the early neanic growth stage but increases considerably during corallite growth. Minor septa first become recognizable in a corallite lumen at a diameter of 4 to 10 mm and first dissepiments appear at a corallite diameter of 4–14 mm (Dobrolyubova 1937, p. 32). Unfortunately, most of those measurements were not related to clearly specified corallites. Dissepiments and minor septa elongated into a corallite lumen appear at approximately 10 mm in most corallites illustrated. In the neotype those features may appear at a diameter of 10 mm as suggested by the lowermost part of its longitudinal section (Ivanovsky 1987, pl. 1, fig. 1v in Russian alphabet). Two small specimens illustrated by Dobrolyubova (1937, pl. 7, fig. 3; and pl. 10, figs 3, 4) show development of minor septa and the dissepimentarium at a very small corallite diameter (4–4.6 mm). Also, the more advanced morphology of those corallites cannot be compared to corresponding growth stages (or to corresponding n:d values) of large corallites, typical for *B. conicum*. The first of those small corallites also exhibits an axial area free from major septa at a very small corallite diameter (4.5 mm). That kind of neanic morphology with the dissepimentarium becoming narrower during further corallite growth, and with minor septa short in most, but absent from some septal loculi (Dobrolyubova 1937, pl. 7, figs 1–7) eliminate that specimen from *B. conicum*. Both those corallites were included by Kossovaya (2001) in her new subspecies *Bothrophyllum conicum moribundum*. That question is discussed in the subchapter "Variety of other specimens from the Myachkovo Quarry" below.

Late neanic/early mature growth stage

It is difficult to characterize the growth stages that follow the growth stage characterized above. This difficulty is the result at least in part from the unfortunate decision by Ivanovsky (1987) to make a longitudinal thin section from the entire remnants of the neotype left after making two transverse thin sections (Ivanovsky 1987, pl. 1, fig 1v in Russian alphabet). The late neanic/early mature growth stage has not been illustrated by Trautschold (1879), Dobrolyubova and Kabakovich (1948) and Fedorowski (1973). The best illustrations of this part of the ontogeny are those by Dobrolyubova (1937, pl. 3, figs 4–6; pl. 8, figs 3–5, 11, 12; pl. 10, figs 5–9, pl. 11, fig. 1) and Kossovaya (2001, pl. 32, figs 1–3). However, the morphology of this and further growth stages (if studied) of the specimens listed above differs, sometimes considerably. In fact, only the late neanic/early mature growth stage of one of them (Dobrolyubova 1937, pl. 3, figs 4–6) can be considered as representing *B. conicum* proper as characterized in this chapter. The mature morphology of the remaining specimens listed differs considerably from the neotype and from the specimens morphologically close to it. Those specimens are here proposed to be excluded from *B. conicum* (see below for details).

The main characters of the late neanic/early mature growth stage, accepted here as typical, are: (1) Major septa long; in cardinal quadrants inclined towards cardinal septum, some united by their inner margins, making cardinal fossula temporarily closed; (2) Cardinal septum intersects cardinal fossula. Its thin wavy inner margin approaches and temporarily meets counter septum; (3) Counter and a few other major septa meet and/or unite near corallite axis; (4) Minor septa penetrate tabularium; (5) Peripheral tabularium biform as documented by unequal position of innermost dissepiments and asymmetrical sclerenchymal thickening of inner margins of minor septa, imitating a contrajunct character in some loculi.

The most advanced growth stage

The illustration of the thin section of the neotype (Ivanovsky 1987, pl. 1, fig. 1b) probably represents the advanced early mature growth stage. Such a conclusion is supported by its close morphological similarity to sections of the corresponding growth stage illustrated by Dobrolyubova (1937, pl. 3, figs 1–8; pl. 4, figs 1, 2; pl. 5, fig. 1; Dobrolyubova 1948b, pl. 2, figs 4–11, repeated from her 1937 paper). The similarity of both specimens includes: the closely comparable tent-shaped arrangement of the major septa in the cardinal quadrants; the length and thickening of the major septa, including the cardinal septum; the cardinal fossula closed by the thin inner margins of 2–3 pairs of the major septa; the counter septum elongated, with its inner section very thin; the minor septa penetrating deeply into the tabularium with their inner margins thickened; biformity of the peripheral tabularium demonstrated by sections of the peripheral parts of tabulae located left and right of the minor septa. The transverse section of Dobrolyubova's (1937, pl. 3, fig. 8) specimen is larger (n:d value 44:21.5×24 mm) than that of the neotype (±40: 15.5×18 mm), and it differs in having minor septa extending farther into the tabularium and a wider dissepimentarium. The latter character may be the result of corrosion of peripheral parts of the neotype. The differences listed are unimportant when close similarities are considered. Thus, both specimens are considered co-specific. That conclusion allows use of the morphology of the most advanced growth stage of Dobrolyubova's (1937, pl. 4, figs 1, 2; pl. 5, fig. 1) specimen to supplement information from the neotype and to consider that morphology typical for *B. conicum*.

The morphology of the most advanced growth stage of the specimen derived from the Myachkovian Substage of Novlinskoe Village (Dobrolyubova 1937, pl. 8, fig. 12) differs from the neotype and from the specimens considered typical for *B. conicum*. That specimen possesses a cardinal septum elongated to the corallite axis and slightly thickened near its inner margin, whereas its counter septum is equal in length to the adjacent major septa. Dobrolyubova and Kabakovich (1948, pl. 7, figs 5–7) did not mention that corallite when they introduced a new subspecies *Bothrophyllum pseudoconicum conicum*. Indeed, the holotype of that new subspecies (Dobrolyubova and Kabakovich 1948, pls 5, 6, pl. 7, fig. 1) derived from the Myachkovo Quarry differs considerably from it. However, the corallite derived from the Podolskian Substage of the Vasilkovo Village at the Volga River (Dobrolyubova and Kabakovich 1948, pl. 7, figs 5–7) exhibits a striking morphological similarity to the specimen from Novlinskoe Village. Both of them are here considered co-generic and possibly co-specific and are excluded from both the genus *Bothrophyllum* and from *B. pseudoconicum conicum*. Both of them closely resemble the mature morphology of *B.* aff. p*seudoconicum* Dobrolyubova of Fomichev (1953, p. 332, pl. 22, fig.

1) and are mentioned below, together with the Donets Basin specimens (see chapter "*Bothrophyllum* and *Bothrophyllum*-like corals in Europe (including the Urals) and in North Africa"). The specimen from the Vasilkovo Village was included by Kossovaya (2001, p. 155) in synonymy with *B. conicum*, a position accepted and followed here.

The holotype of *B. pseudoconicum conicum* (see above for details) with a shortened cardinal septum in the mature growth stage, the counter septum equal in length to the adjacent major septa, a biform tabularium penetrated by the minor septa and a disstabularium developed in other corallite areas (Dobrolyubova and Kabakovich 1948, pl. 6, figs 1, 2) is here included in the list of species with a shortened cardinal septum (see above). Although considered here a separate species, it is listed as a subspecies because the name *conicum* is preoccupied and formal new names are not proposed in this paper.

The third specimen included by Dobrolyubova and Kabakovich (1948, pl. 7, figs 2–4) in *B. pseudoconicum conicum* was derived from the Myachkovskyi Substage of the Tashenka Village near Kasimov City at the Oka River. This specimen is here included in *B. conicum*. In this respect, but exclusively in the case of that specimen, the suggestion of Ogar (2009, p. 63) is followed.

Variety of other specimens from the Myachkovo Quarry

Corallites described by Eichwald (1861) as *Campophyllum conicum* Fischer and redescribed by Fedorowski (1973) as *Bothrophyllum conicum* Trautschold 1879 represent long septal variants of *B. conicum*. Their morphology can be treated as intermediate between that of the neotype and the specimens collected from the Kasimovian strata at the Moskva River bank and identified by Dobrolyubova (1940, p. 30) as her new subspecies *Bothrophyllum conicum robustum*. That question is discussed below in the chapter "*Bothrophyllum conicum* outside the type area and/or age".

Both that inclusion and the introduction of a new subspecies by Kossovaya (2001) raise two questions: formal and substantial. She selected and illustrated as the holotype (Kossovaya 2001, pl. 32 [incorrectly mentioned by her as 33 in p. 157], fig. 8) an immature specimen, probably representing a neanic growth stage. Such a selection of a type specimen contradicts the ICZN recommendation, making the formal conditions doubtful despite a similarity in morphology of that growth stage to the earliest known growth stage of the neotype (Ivanovsky 1987, pl. 1, fig. 1b).

The substantial doubts are of two kinds. First they concern the inclusion of specimens illustrated by Dobrolyubova (1937, pl. 7, figs 1–13) by Kossovaya (2001, p. 157) in her new subspecies. That inclusion is not supported by the morphology at any growth stage of Dobrolyubova's (1937) specimens. Besides, the early ontogeny and the mature morphology of those specimens differ considerably, precluding their position within a single species. Neither of those specimens resembles Kossovaya's (2001) corallites in either the early or mature growth stage. The taxonomic position of these specimens is left as an open question, but they are excluded from both the nominative species and the subspecies *B. conicum moribundum*.

The second substantial doubt deals with a need for the introduction of the new subspecies '*moribundum*'. This doubt arises from the similarity of the early growth stage of its holotype (Kossovaya 2001, pl. 32, fig. 9) to the corresponding growth stage of the neotype of *B. conicum* (Ivanovsky 1987, pl. 1, fig. 1a) and from the similarity of some morphological features of the paratype of *B. c.* '*moribundum*' to the comparable growth stage in the neotype of *B. conicum*. That similarity was previously mentioned by Kossovaya (2001, p. 155).

Characters of the holotype of '*moribundum*' (Kossovaya 2001, p. 157, pl. 32, figs 8) are unknown since only an early growth stage was illustrated by her. The paratype specimen (Kossovaya 2001, pl. 33, fig. 9) differs considerably from both specimens illustrated by Dobrolyubova (1937), being at the same time comparable to the neotype of the nominative species, as already pointed out by Kossovaya (2001, p. 155). Unfortunately the thin section illustrated is partly damaged, making a close comparison impossible. This first of all concerns the length of the cardinal septum, stated as shortened by Kossovaya (2001, p. 157). Judging from the close similarity of other features, that septum may be similar in length to that in the neotype, whereas an open cardinal fossula mentioned by Kossovaya (l. c.) is doubtful. Remnants of the thin inner margins of the major septa adjacent to the cardinal septum are bent towards it like in the neotype. Similarities discussed allow one to synonymize those two specimens, making baseless the introduction of the subspecies *B. conicum moribundum*. However, only the holotype selected by Kossovaya (2001, p. 157) but not Dobrolyubova's (1937, pl. 7, figs 1–13) specimens belong to *B. conicum*. Ogar (2009) has already proposed the synonymy of *B. c. moribundum* with the nominative subspecies, but without distinguishing between the specimens included by Kossovaya (2001) in her new subspecies.

Some specimens included by Stuckenberg (1888) in *Pseudocaninia conica* Fischer and *Rossophyllum novum* Stuckenberg, 1888, housed in the VSEGEI Museum were for some unknown reason omitted by Ivanovsky

(1987) from his re-identifications of corals described by Stuckenberg (1888, 1895, 1904, 1905). Since all data derived from old collections of corals from the type site are important for increasing the documentation of the type species, short descriptions and illustrations of those specimens (Text-figs 1A–D, 2A–E) are included to supplement and confirm data derived from the sources discussed above. The new data are incomplete because the present author was given permission by the VSEGEI Museum Custodian in 1969 to peel only existing surfaces of sections of the specimens reinvestigated.

The earliest growth stage investigated (Text-fig. 1B) closely resembles the typical morphology of *B. conicum* illustrated by Dobrolyubova (1937; see above). The cardinal and counter septa are united by their "middle dark lines" although their connection does not form a straight line. Thus, an axial septum occurs in this growth stage. The occurrence of that protoseptum cannot be documented in the incomplete, ontogenetically more advanced growth stage identified by Stuckenberg (1888) as *Rossophyllum novum* (Text-fig. 2C). Thus, the identification of this corallite as *B. conicum* remains uncertain. Another specimen of that genus and species (Text-fig. 2D) in Stuckenberg's (1888) collection exhibits the morphology typical for a late neanic/early mature growth stage of *B. conicum*. The very eccentric longitudinal section (Text-fig. 2E) adds little to the knowledge of *Bothrophyllum*, except for the opposite directions of some sections of tabulae (left in the picture) that may confirm the biform tabularium.

The morphology in the transverse sections of specimens, accepted here as mature, differs in several details. Specimens 30_321 and 31_321 (Text-fig. 1D, A respectively) closely resemble the neotype and the corallite illustrated by Dobrolyubova (1937, pls 3, 4, pl. 5, fig. 1) and accepted here as typical. Shortening of the cardinal septa in those specimens apparently is the result of diagenetic alteration. The longitudinal section, typical for the genus and species, is diagenetically altered as well (Text-fig. 1C).

Two remaining specimens (Text-fig. 2A, B) differ both from each other and from the previously mentioned ones. The first of those two corallites, with the major septa equally thick in the tabularium, very long and twisted axially, may either represent a variant of *B. conicum*, not described so far or a different species. Its bothrophyllid characters, with a long cardinal septum and a biform tabularium are obvious. The second specimen (Text-fig. 2B) is one of the largest corallites of *Bothrophyllum* reported so far. Its incompleteness in the counter quadrants is artificial, resulting from the too narrow film for peeling I possessed at that time. Its large size and the minor septa restricted mainly to the very wide dissepimentarium resemble the corallite illustrated by Dobrolyubova and Kabakovich (1948, pl. 5, fig. 5) from early Kasimovian strata. Unfortunately, the latter specimen is axially incomplete, precluding a closer comparison to Stuckenberg's (1888) corallite, the major septa of which approach and/or reach the corallite axis with some joining one another. Its cardinal septum is long – a character camouflaged by the cardinal fossula infilling. The specimen described may represent a new species of *Bothrophyllum*.

Variation in individual skeletal structures

The major septa are amplexoid. The length and thickness of the septa are different at different growth stages, and also are different in different corallites irrespective of the growth stage. Their tent shaped arrangement with some approaching and others reaching the corallite axis are here considered typical for the late early mature growth stage of *B. conicum* (Dobrolyubova 1937, pl. 3, fig. 8, n:d value 44:21.5×24 mm; Fedorowski 1973, text-fig. 17b, c, n:d value 46:22×26 mm; Ivanovsky 1987, pl. 1, fig. 1a, n:d value ±40: 15.5×18 mm). All major septa are thickened in the tabularium to various degrees, being thicker in the cardinal quadrants. They are very thin in the dissepimentarium. That kind of differentiated thickening may in some specimens persist long during ontogeny, accompanying the tent-like arrangement of major septa (Fedorowski 1973, text-fig. 17b, c). In the specimen suggested here as supplementary to the neotype (Dobrolyubova 1937, pl. 4, fig. 1, n:d value 44:22.5×27.5 mm) the major septa remain long, with several meeting at the corallite axis, but their thickness is only slightly reduced. Comparatively thin major septa persist in the latter specimen up to advanced maturity (Dobrolyubova 1937 pl. 5, fig. 1, n:d value 44:30×33 mm).

Length of the cardinal septum may cause doubts. Dobrolyubova (1937, p. 31) characterized the cardinal septum as follows: "The cardinal septum is not well expressed in all thin sections, but sometimes clearly differs from the other major septa by less thickening and being shorter or on the contrary, by being longer." [Translated here from Russian]. Permanent shortening of the cardinal septum was not established in any specimen of *B. conicum* from the Myachkovskyi Substage, although it may appear shortened in some of them (e.g., Fedorowski 1973, fig 17b, c). Actually the thin inner margin of that septum remains connected to transverse sections of the tabulae within the cardinal fossula. Thus, there is a low extension above the cardinal fossula floor of the cardinal septum**.** The apparent shortening of the major septum appears when a given cross section cuts the cardinal fossula above the upper margin of the cardinal septum. This may be why Hill (1981, p. F346) wrote: "thickened part of cardinal septum may be short". Although not truly shortened, the cardinal septum may be slightly shorter than most septa in the cardinal quadrants when the cardinal fossula is closed (Dobrolyubova 1937, pl. 3, figs 7, 8; Ivanovsky 1987, pl. 1, fig. 1a; Kossovaya 2001, pl. 32, fig. 3).

The cardinal septum is almost invariably long in the mature growth stage. It may either meet the inner margin of the counter septum (Dobrolyubova 1937, pl. 4, figs 1, 2; pl. 5, fig. 1) or the protosepta may be isolated from one another (Fedorowski 1973, fig. 17b, c; Ivanovsky 1987, pl. 1, fig. 1a). The long cardinal septum may be disconnected from the counter septum in some specimens excluded here from *B. conicum* (Dobrolyubova 1937, pl. 11, fig. 1; Kossovaya 2001, pl. 32, fig. 6).Thus, the shortening of the cardinal septum in *B. conicum* and other species derived from the Myachkovskyi Substage of the type area is apparent in most specimens. The apparent shortening results from its low elevation above the cardinal fossula floor. Only one specimen from the Myachkovo Quarry possesses a shortened cardinal septum in the advanced growth stage (Dobrolyubova and Kabakovich (1948, pl. 6, figs 1, 2) in their new subspecies *B. pseudoconicum* var. *conicum*. That occurrence favors a close relationship of species with the cardinal septum either long or shortened. Should the difference be interpreted as important at the subgenus or genus is a question that remains open for the time being.

The counter septum is elongated in the early growth stages of most corallites studied in adequate detail. It may remain elongated throughout corallite growth (Dobrolyubova 1937, pl. 5, fig. 1), or it may be long, but equal to the adjacent major septa (Fedorowski 1973, fig. 17b, c). Shortening of the counter septum has not been traced in *Bothrophyllum*-like any specimen from the type area investigated so far.

Length of the minor septa compared to the length of the major septa was the main criterion used by Dobrolyubova (1937) for distinguishing her new species *Bothrophyllum pseudoconicum* from *B. conicum*. Neither that identification nor the taxonomic value of the length of the major septa is contested here. However, not a simple major/minor septa length ratio is important. First, the major septa are amplexoid, making that ratio different within the same specimen depending on the position of the thin section (just below or immediately above a tabula). Second, the minor septa change length during growth, being commonly correlated to the width of the dissepimentarium. Third, only the minor septa penetrating the tabularium may result in the occurrence of the biformity in the peripheral tabularium whereas the normal *vs* the biform tabularium is commonly treated as a qualitative feature, i.e., characterizing a taxonomic level higher than species.

All specimens from the Myachkovskyi Substage identified as *B. conicum* possess minor septa entering the tabularium with their inner margins thickened. In most corallites those septa are free axially at all growth stages. The corallites illustrated by Dobrolyubova (1937, pl. 11, fig. 2) and Kossovaya (2001, pl. 32, figs 1–6) form important exceptions. Their minor septa are free axially at early growth stages, but some of those septa (Dobrolyubova 1937, pl. 11, fig. 2) or most of them (Kossovaya 2001, pl. 32, figs 4 and 6) become contrajunct and contratingent at the mature growth stage. This is an important qualitative character that excludes those specimens from *B. conicum*. Dobrolyubova and Kabakovich (1948, p. 11) selected Dobrolyubova's (1937) corallite the type specimen for their new subspecies *B. conicum novlinskoi* (see chapter '*Bothrophyllum conicum* outside the type area and/or age' below).

The cardinal septal fossula in the late neanic to the early mature growth stage of particular corallites differs. It commonly is hardly distinguishable or not developed (Dobrolyubova 1937, pl. 7, figs 3–7, 10–12; pl. 8, figs 3–5; pl. 10, figs 8, 9; pl. 11, fig. 1). All those specimens have already been excluded from *B. conicum* (see above). The cardinal fossula is easily distinguishable in the transverse sections of specimens accepted as typical for *B. conicum* (Dobrolyubova 1937, pl. 3, figs 3–6). The possibility of recognition of the cardinal fossula increases parallel to the thinning of tabular parts of the major septa and development of the dissepimentarium, into which it dips slightly. This concerns both the typically constructed corallites and some of those excluded from *B. conicum* (Dobrolyubova 1937, pl. 3, fig. 8; pl. 4, figs 1, 2; pl. 5, fig. 1; pl. 10, fig. 10; pl. 11, fig. 2; Fedorowski 1973, fig. 17b, c; Ivanovsky 1987, pl. 1, fig. 1a; and Text-figs 1A, B, D; 2A, B, D here). In the neotype and in the specimens accepted here as co-specific with the neotype, the cardinal fossula is closed at the neanic growth stage, but is open in more advanced growth stages. It commonly is bordered by two major septa arranged parallel to one another. The cardinal tabular fossula is commonly shallow and extends towards the corallite axis at less than ½ corallite radius. Those characters are indicated by sections of tabulae within the fossula. They are only slightly more numerous than those in the adjacent septal loculi.

The axial structure in early corallite growth was compared by Dobrolyubova (1937, p. 33) to the genus *Dibunophyllum* and to the "Clisiophyllina group". She pointed to “corallite No. 1” when making that comparison, but did not illustrate that corallite, making her comparison unsupported. None of the corallites illustrated by her possesses the dibunophylloid septal lamellae in the transverse section and, what is more important, none possesses lateral tabellae, bordering an axial column in the longitudinal section. Both those characters are typical for the *Dibunophyllum* Thomson and Nicholson, 1876. Thus, Dobrolyubova’s (1937, p. 33) comparison of *Bothrophyllum* to the Aulophyllidae is not followed here either in the case of the early or in the fully mature corallite growth stages of *B. conicum*.

The length of the major septa and the occurrence or absence of an axial septum in advanced maturity are reflected in the morphology of the axial structure in the growth stages older than neanic. In a transverse section of the ontogenetically most advanced growth stage of the neotype, considered early mature (see above), a part of the corallite axial area is damaged diagenetically (Ivanovsky 1987, pl. 1, fig. 1a). Remnants suggest weakness of the axial structure and its restriction to thin inner margins of some major septa and axial parts of the incomplete tabulae. The morphology of the axial part of a larger, perhaps a fully mature corallite, illustrated by Fedorowski (1973, fig. 17b, c) resembles that kind of axial structure, suggesting continuity of such a morphology in some corallites. Diagenetic alteration may have resulted in the appearance of the axial structure apparently isolated from the major septa (Text-fig. 1A, B). Also, numerous major septa may reach the corallite axial area with their inner margin either twisted or straight (Text-fig. 2A, B respectively). In the longitudinal section of the neotype, the thin, irregular axial septum, locally accompanied by sections of inner margins of rare major septa, extends along the entire longitudinal section illustrated (Ivanovsky 1987, pl. 1, fig 1v). A discontinuous axial septum or an elongated counter septum occurs in most longitudinal sections of specimens from the Myachkovskyi Substage attributed to *B. conicum* by Dobrolyubova (1937, pl. 1, fig. 15; pl. 8, figs 8, 16, 20; pl. 10, fig. 11). Only the first of the corallites listed is here accepted as belonging to that species, the remaining ones perhaps belonging to the genus *Bothrophyllum*. The elongated counter septum or an axial septum occurs in the lower part of the longitudinal section of the corallite illustrated by Fedorowski (1973, fig. 17a).

The slightly shortened major septa with the corallite axial area intersected by the axial septum occur in the mature growth stage of the specimen proposed here supplementing the neotype (Dobrolyubova 1937, pl. 5, fig. 1). Three specimens (Dobrolyubova 1937, pl. 8, figs 9–13; pl. 10, figs 1–11; pl. 11, figs 1–3) differ in the axial structure and in the morphology of some other characters from the neotype and from each other. All were derived from localities outside the Myachkovo Quarry and are discussed in the next chapter. Their position outside the *Bothrophyllum conicum* species group is suggested.

Morphology of tabularium requires special attention. Sutherland (1965) established different positions of two peripheral parts of a tabula in *Ditoecholasma lawrencense* Sutherland, 1965 located left and right of the contratingent minor septum (Sutherland 1965, text-fig. 21). He called those positions I and II respectively. Weyer (1972) expanded Sutherland’s idea by establishing the occurrence of a biform tabularium (Weyer’s 1972 term) not only in taxa possessing contratingent minor septa, but also in those with the inner margins of the minor septa free. Neither of those authors nor their followers discussed and considered the possibility (?) of the occurrence of a biform tabularium in specimens possessing minor septa restricted to the dissepimentarium. Only an incomplete biform tabularium, i.e., absent from some septal loculi and occurring in the other loculi, has been established so far (Fedorowski *et al.* 2014).

Normal *vs* biform tabularium should be treated as an important diagnostic character. In transverse sections of *B. conicum* the occurrence of the biform tabularium is proven by the different number of sections of tabulae left and right of the invariably long minor septa. It is confirmed by the arrangement of peripheral parts of tabulae in several longitudinal sections previously published, including the neotype (Dobrolyubova 1937, pl. 1, fig. 15; pl. 6, fig. 2; pl. 10, fig. 11; pl. 11, fig. 3; Fedorowski 1973, fig. 17a; Ivanovsky 1987, pl. 1, fig. 1v). That character is not always clear. In some transverse sections of a given corallite sections peripheral parts of tabulae may be attached to the inner margins of minor septa at almost the same level on both sides, whereas their positions differ clearly in adjacent septal loculi. Besides, the permanently greater length of the minor septa, i.e., the condition necessary for a biform tabularium to develop, cannot be accepted as diagnostic for the entire genus *Bothrophyllum*. Several obvious bothrophyllids would be eliminated from that genus if such a restriction is accepted. Also, there are species, such as *Bothrophyllum pseudoconicum* Dobrolyubova, 1937 with minor septa long up to early maturity and the tabularium biform at that growth stage (Dobrolyubova 1937, pl. 13, figs 3–6), but in more advanced ontogeny those septa become shortened and the biformity of the tabularium may be absent (Dobrolyubova 1937, pl. 14, fig. 2). Thus, two questions arise: 1. Can a biform tabularium be developed when minor septa do not penetrate a tabularium? 2. Should such a qualitative difference as presence or absence of a biform tabularium be neglected in the diagnosis of the genus *Bothrophyllum*? Both those questions should be discussed and clarified despite their irrelevance with regard to the type species for that genus.

The differentiation in length of the minor septa in *B. pseudoconicum* mentioned above and the inconsistent status of its tabularium, motivates such a discussion. Those phenomena either put in doubt a rigid distinction between a normal *vs* a biform tabularium, or suggests the possibility of an occurrence of a third type of a peripheral tabularium. The occurrence of such a third type would legitimize the morphology of a tabularium to be one of the qualitative premises for the distinction at a genus level.

The morphogenesis of dissepiments and tabulae closely resembles each other. Both were secreted by flat, continuous ectoderm of a polyp floor (see Schouppé and Stacul 1955, 1959; Wells 1969; Sorauf 1970; Fedorowski 1997a for details). Thus, the difference between those structural elements can be reduced to their position: down oriented in the case of dissepiments, horizontal to strongly upward oriented in the normal tabularium and scissors-like at the periphery in the biform tabularium. Boundaries between a dissepimentarium and both kinds of tabularia are sharp when sclerenchymal thickenings at the innermost dissepiments are secreted. A boundary lacking a sclerenchymal thickening remains easily distinguishable in many taxa, but in some it is not (see below). Sharp and easily recognizable dissepimentarium/tabularium boundaries can commonly be present in different parts of the same transverse section of a specimen and are easily distinguishable in longitudinal sections of phylogenetically distant taxa such as Aulophyllidae Dybowski, 1873 or Cyathopsidae Dybowski, 1873. This means that the characters discussed are useless for the taxonomy at a higher taxonomic level and are not discussed. They may in some circumstances be treated as supplementary diagnostic features at the specific level.

However, the dissepimentarium/tabularium boundary sharp in the early growth stages of some taxa, e.g., *Bothrophyllum pseudoconicum* Dobrolyubova, 1937 (pl. 13, figs 2–6; pl. 15, figs 5–8) loses that sharpness during corallite growth. That process is parallel to shortening of the minor septa and reduction of the sclerenchymal thickenings (Dobrolyubova 1937, pl. 14, figs 1, 2; pl. 16, figs 1–3). An intermediate zone, best recognizable in transverse section, is developed (Text-fig. 1E, copied from Dobrolyubova 1937, pl. 14, fig. 2). Dissepiment-like skeletal elements, attached to one another and/or to the major septa, present in that intermediate dissepimentarium/tabularium area, can be interpreted either as peripheral tabellae or as strange dissepiments. Their disorderly arrangement makes the tabularium/dissepimentarium boundary hardly distinguishable. Such an undefined intermediate zone is proposed here to be called the *disstabularium* (a new term defined above). Easily recognizable in transverse sections, the disstabularium may not be clearly recognized in random longitudinal sections, except for the occurrence of strange looking dissepiment-like bodies (e.g. Dobrolyubova 1937, pl. 15, fig. 1, right). The complete morphology of the disstabularium will be known when series of well oriented longitudinal sections are made. Such a study is in preparation.

To sum up: The tabularium in the type species of the genus *Bothrophyllum* is biform. A transition from the biform tabularium in the early ontogeny to the disstabularium in the mature growth stage, observed within specimens of *B. pseudoconicum* occurs as well. That occurrence is here interpreted in the classic approach: the character of the species appears in maturity. However, the difference between the biform tabularium and the disstabularium is qualitative, i.e., generic. Thus, *B. pseudoconicum* with development of both types of tabularia and with the cardinal septum temporarily shortened may form an intermediate evolutionary step, leading towards bothrophyllids lacking a biform tabularium and having the cardinal septum permanently shortened.

The first dissepiments appear at 4–14 mm (Dobrolyubova 1937, p. 32). The earlier discussion, pointing to the possibility of the taxonomic variability greater than proposed by Dobrolyubova (1937, 1940, 1948a, b) reduces reliability of such large differences. The first appearing dissepiments are mostly regular. They may remain regular in the inner dissepimentarium up to the mature growth stage (Dobrolyubova 1937, pl. 4, figs 1, 2; pl. 5, fig. 1; Ivanovsky 1987, pl.1, fig. 1a), but may be irregular and densely packed after a comparatively early growth stage (Dobrolyubova 1937, pl. 10, figs 6–10; pl. 11, fig. 1). The latter specimens have already been excluded from *B. conicum* for another reasons (see above), but a rather complex dissepimentarium may occur in the otherwise typical *B. conicum* from the type area (Fedorowski 1973, fig. 17b, c). The peripheral part of the dissepimentarium is always composed of small dissepiments, commonly forming pseudonaotic structures.

Offsetting

Stuckenberg (1888), Dobrolyubova (1937), Yakovlev (1965), Semenoff-Tian-Chansky (1974) and Rozhnov (1974, 2014) described and illustrated offsetting corallites attributed by them to the genus *Bothro-*

phyllum. Those corals differ from one another in both the kind of offsetting and their geographic and stratigraphic distribution.

Specimens from the Moscow Basin (Late Moscovian stage, Myachkovian Substage to early Kasimovian Stage) were all derived from the type area and most of them were included in the type species, thus requiring attention in this review. Stuckenberg (1888, p. 16) described that phenomenon as follows: "Some corallites of that species reproduced by offsetting to form complex and elongated skeletons since offsets appeared exclusively at the upper ridge of a calice" [Translated here from Russian]. He illustrated external characters of a specimen with an intracalicinal offset dead shortly after its appearance, and another one documenting a very deep and successful rejuvenation (Stuckenberg 1888, pl. 2, figs 33, 35 respectively). The second one evidently illustrates his statement cited above. Both of those specimens were included by Stuckenberg (1888) in his new genus and species *Pseudocaninia trautscholdi*. The generic name *Pseudocaninia* was synonymized with *Bothrophyllum* by himself (1895, p. 56) and by most of the subsequent authors, but his species name remains valid. Offsets in that species closely resemble offsets in the type species, illustrated by Dobrolyubova (1937, pl. 9, figs 8–16; pl. 23, fig. 7). In both species the offsets are ontogenetically underdeveloped and hidden within or only slightly elevated above the parent's calice ridge, thus being treated here as multiply rejuvenations.

Dobrolyubova (1937, pp 27–30) distinguished between offsetting and rejuvenation. According to her opinion, the shape of the corals studied by her was affected by the rejuvenation which was dependent on the environment. All structures called offsets by her and "epimorphosis", "morphallaxis" and "compensatory regeneration" of Rozhnov (2014) are here considered as environmentally caused phenomena (see below). There are two types of offsets distinguished by Dobrolyubova (1937) in her collection**:** lateral observed in one corallite and intracalicinal occurred in the remaining 11 offset corallites. She considered the lateral offsetting uncertain and wrote: "The young corallite may in this case appear not from a bud of the old corallite, but developed from a larva that used the latter only as a hard substrate to attach to" [Translated here from Russian]. That second option, supported by her illustration (Dobrolyubova 1937, pl. 9, figs 6, 7), is accepted here. All remaining corallites in her and other collections from the type area offset peripherally and none of the illustrated ones achieved mature size and morphology. The largest of the offsets illustrated (Dobrolyubova 1937, pl. 23, fig. 7) reached a little more than two centimeters in length and approximately 1.2 cm in width at its calice margin, i.e., its growth was terminated at approximately ½ of the mature corallite size. Its sister offsets, produced close to the long one, died shortly after appearing.

The transverse sections of one offset was illustrated by Dobrolyubova (1937, pl. 8, figs 6, 7) and a few by Rozhnov (1974, figs 1a, b, 2–5; most of them repeated by him later: Rozhnov 2014, figs 5, 7–9). All offsets illustrated by Rozhnov (1974, 2014) appear to be a response of the polyp to severe extrinsic factors, leading eventually to its death in most cases observed. That question has been discussed by the present author several times previously and will not be repeated here (e.g., Fedorowski 1970, 1978, 1981, 1987; Fedorowski and Jull 1976; Fedorowski *et al*. 2012, Fedorowski and Ogar 2013). Similar offsetting as a response to the extrinsic factors is not unique (e.g. Webb 1987, figs 1–6; Gómez-Herguedas and Rodríguez 2005, pl. 3, fig. 1)

Rozhnov (2014) distinguished three types of the development within the lateral offsets he studied, calling them "epimorphosis", "morphallaxis" and "compensatory regeneration". Neither his illustrations nor description based on them are convincing, but the discussion on that subject is not developed here, being outside the topic of this review. The most important in the context of this paper is the absence of true colonies or protocolonies in the specimens he described and illustrated and in all other specimens of the *Bothrophyllum* species from the type area described so far. Thus it seems correct to sum up this question as follows: Rare representatives of *Bothrophyllum* can produce peripheral offsets when severe environmental conditions appear. Most of those offsets do not reach maturity. They can be either considered as multiply rejuvenations or lost structures. Several offsetting specimens (Dobrolyubova 1937, pl. 23, fig. 6; Rozhnov 2014, fig. 6) show changes in the direction of growth, followed by the production of peripheral offsets. This means the corallite was overturned and partially buried. A polyp surviving from the burial may rejuvenate and/or produce offset-like structures from the energy accumulated in its body. This is well illustrated by Rozhnov (20014, fig. 6) with several offsets, the morphologically most advanced of which rejuvenated again.

Specimens from the Limestone bands N_3 (early Gshelian) of the Donets Basin (Ukraine), were identified by Yakovlev (1965) as his new species *Bothrophyllum dobrolyubovae*. The incorrectness of that authorship was established by Ogar (2009, p. 62). Yakovlev (1965, pl. 14) illustrated both corallites attached to larger ones and possible lost structures. Unfortunately, neither his illustrations nor description is adequate for any final conclusions to be made in the kind of offsetting. Fomichev (1953, p. 242) included that species in *Caninophyllum* (generic identification rejected by both Ogar (2009) and herein) and mentioned in the diagnosis: "Solitary (sometimes with repeated offsetting)" [Translated herein from Russian]. That phrase may suggest an occurrence in his material of regular colonies with *Bothrophyllum*-like morphology. However, neither the illustrations nor the description by Fomichev (1953) demonstrates the formation of a true colony, i.e., a sequence of at least two generations that were asexually produced and reached mature characteristics. Thus, the colonial growth form of "*Caninophyllum*" [= *Bothrophyllum*] *dobrolyubovae* is here rejected. The description and illustration of that process (Fomichev 1953, pl. 13, fig. 3a–z in Russian alphabet) suggest a successful and complete rejuvenation rather than formation of a colony.

Specimens described by Semenoff-Tian-Chansky (1974) from the early Bashkirian strata of the Bechar Basin in Algeria are protocolonial (Fedorowski and Ogar 2013 term) and are here excluded from the genus *Bothrophyllum*. It is briefly discussed below in the chapter "*Bothrophyllum* and *Bothrophyllum*-like corals in Europe (including the Urals) and in North Africa".

***Bothrophyllum conicum* and corals included in it from outside the type area and/or age**

Taxa somehow connected to B. conicum from the type area and/or age

Dobrolyubova (1940) described the new subspecies *Bothrophyllum conicum robustum* from the Kasimovian deposits (Khamovnicheskyi Substage) of the Moskva River Bank near Voskresensk. Kossovaya (2001, p. 156) accepted that identification, whereas Ogar (2009, p. 63) included *B. c. robustum* within the synonymy of *B. conicum*. Contrary to the opinion of the latter author, that subspecies is elevated here to the species level. The following characters of *B. robustum* distinguish it from both the neotype of *B. conicum* and other species undoubtedly belonging to that genus: n:d value in maturity 40:25×27 mm, thickening of the major septa in the tabularium strong and long lasting, well developed cardinal fossula with the cardinal septum long, but clearly two partite: strongly thickened at the periphery and thread-like thin in the inner sector, minor septa very long, contrajunct, some contratingent. Some of the characters listed allow comparison of *B. robustum* with the most advanced growth stage of the specimen from the Myachkovo Quarry, re-described by Fedorowski (1973, fig. 17c). The similarity is best seen in the thickening of the major septa, morphology of the cardinal septum and the cardinal fossula. Also, the minor septa in both specimens look similar in length and thickness. However, a close examination of those septa in the specimen redescribed by Fedorowski (l. c.) documents both their arrangement parallel to the major septa and their strong, slightly asymmetrical thickening in the tabularium. Such a distribution of sclerenchyme reduces the distance between the minor septa and the adjacent major septa to almost none, making them similar to contratingent.

The corallite from the Myachkovskyi Substage of the Peski Quarry, illustrated by Kossovaya (2001, pl. 32, figs 1–6) and identified by her as *B. conicum conicum* possesses n:d value in the mature growth stage (44:20 mm) different from that in *B. robustum* but closely resembles that species in the length and arrangement of the minor septa. Most of the septa are free in the early growth stage studied (Kossovaya 2001, pl. 32, figs 1, 3) [morphology and size of her figures 2 and 3 suggest an incorrect sequence in pictures]. The minor septa in the specimen discussed became contratingent in the late neanic/early mature growth stage and continue that arrangement in the mature growth stage (Kossovaya 2001, pl.32, figs 4–6). That character is important enough to exclude Kossovaya's (2001) specimen from *B. conicum*, as suggested here although a formal new species name is not proposed. That specimen is added to the list above as a separate taxon.

Also, the corallite from Kasimovian strata, included by Dobrolyubova (1940, pl. figs 1–9) in *B. conicum conicum* exhibits characters of *B. robustum* and is here transferred to that species. Keeping all the above remarks in mind, an appearance in the Moscow Basin (late Moscovian and early Kasimovian) of specimens with long, contrajunct and/or contratingent minor septa is established. It is premature to recognize a separate evolutionary lineage, but an important separate evolutionary trend within the genus *Bothrophyllum* in the type area is suggested.

Dobrolyubova (1937, p. 36; 1940, p. 29) described as *Bothrophyllum conicum* Trd var. 1 and illustrated two specimens: first from the Myachkovskyi Substage of the "second Quarry" in Peski and second from the Kasimovian Stage ("Teguliferinovyi" Horizon) from Voskresensk at the Moskva River Bank. Both those specimens are characterized by a peculiar axial structure. A similar structure occurs in *Bothrophyllum complexum* Dobrolyubova, 1937, derived from the Myachkovian Substage of the "second Quarry" in Peski and in two specimens included by Dobrolyubova and Kabakovich (1948, pl. 3, figs. 11, 12 and fig. 13) in *Bothrophyllum pseudoconicum*. The first of those two specimens was collected from the Podolskian Substage deposits near the Myamlino Village at the Volga River and the second one from the Kasimovian Stage deposits near the Kasimov City at the Oka River. Dobrolyubova and Kabakovich (1948, p.

14) mentioned an inclination of those specimens towards the genus *Aulophyllum*, an observation followed here in the sense of morphological similarity, but not relationship. The easily recognizable morphological differences shown by particular specimens listed suggest an occurrence of at least two different species in addition to the named species *B. complexum*, but new species names are not proposed here. Also, a very important character – the occurrence of extra septal lamellae in the axial structure, easily recognizable in the specimen illustrated by Dobrolyubova (1940, pl. 6, figs 5, 6), are not established for sure in the remaining corallites. Nevertheless, an obvious trend leading towards formation of the complex, *Aulophyllum*-like axial structure, is here suggested. It is not clear at the moment whether all specimens discussed should be excluded from *Bothrophyllum* or that some of them should be left within that genus as intermediate taxa leading towards a new genus**.** Some, however, certainly should be excluded. Following a general approach in this paper to avoid an introduction of new taxa, the new species and genus names, based on the specimen illustrated by Dobrolyubova (1940, pl. 6, figs 1–7) are not proposed.

Dobrolyubova and Kabakovich (1948, p. 11) grouped together three specimens characterized by the development of lateral-cystose dissepiments. Two of those specimens were collected from the Myachkovskyi Substage of the Novlinskoe Village. The first of them, selected as the holotype of the new subspecies *B. conicum novlinskoi* Dobrolyubova and Kabakovich, 1948, was described and illustrated by Dobrolyubova (1937, p. 30, pl. 11, figs 1–3) in her earlier monograph. It is characterized by n:d value in the mature growth stage 36:18.5×21.5, the major septa thick but leaving the corallite axial area free and several of the minor septa contrajunct. The second specimen from Novlinskoe (Dobrolyubova and Kabakovich (1948, p. 11, pl. 3, figs 7–10) with n:d value 30:15 mm possesses shortened major septa, equally thin around, the cardinal septum and the cardinal fossula unrecognizable, the minor septa free ended, and the lateral-cystose dissepiments in one half of the corallite strongly developed, but almost lacking from its opposite side. The third specimen, derived from the Kasimovian Stage near the Kasimov City, resembles first specimen mentioned above in the thickening of the major septa and the second specimen in the development of abundant lateral-cystose dissepiments**.** Its major septa, however, are long and its n:d value (36: approximately 12×15 mm) differs from both specimens derived from the Myachkovskyi Substage. All those specimens are here excluded from *B. conicum*. They bear some characters in common, but may represent different species. The material available is too restricted for a final decision. Thus, only the holotype specimen is proposed to be retained in *B. novlinskoi*, elevated here to the species rank. Taxonomic position of the remaining two specimens is not suggested.

Taxa from outside the type area described as Bothrophyllum conicum

Heritsch (1941b, p. 152, fig. 10) described and illustrated as *Bothrophyllum conicum* Trautschold a single transverse thin section of the specimen derived from the late Carboniferous strata in Bosnia. He compared that thin section to the plate 3, figure 6 of Dobrolyubova (1937). However, none of the major characters of his specimen, perhaps immature, fits those of the Russian specimen pointed out by him. The major septa leave the corallite axial area free, the shortened cardinal septum is located in a distinct cardinal fossula, and the counter septum is equal to adjacent major septa. All those characters preclude a position of that specimen not only in *B. conicum*, but also in the genus *Bothrophyllum*.

Wu and Zhao (1989, p. 54, pl. 6, figs 3, 6) included two incomplete specimens in *B. conicum*. Each of them is represented by one transverse thin section, probably taken from a mature part of a corallite, and one longitudinal thin section, poorly preserved or oblique. The shortened cardinal septum and the minor septa restricted to the dissepimentarium eliminate those specimens from *B. conicum*. None can be with adequate credibility included in the genus *Bothrophyllum*, or in its probable subgenus with the shortened cardinal septum since their early growth stages remain unknown.

Peng *et al*. (1992, p. 141) identified as *Bothrophyllum conicum* Trautschold a single, incomplete specimen from the late Carboniferous deposits of China. Its late neanic/early mature growth stage (Peng *et al*. 1992, pl. 15, fig. 5a) resembles the comparable growth stage of *B. conicum* in having the major septa in the cardinal quadrants bent above the cardinal septum with the inner margins of some united. Also, the cardinal septum of that growth stage reaches the inner limit of the cardinal fossula. The length of the counter septum is uncertain. It seems to be elongated in the mature (?) growth stage (Peng *et al*. 1992, pl. 15, fig. 5c), but the cardinal septum in the latter growth stage is shortened and located in an open cardinal fossula. The major septa remain bent above the cardinal septum but their inner margins are free. The shortened cardinal septum and the minor septa restricted to the dissepimentarium eliminate the specimen discussed from *B. conicum*, but its relationship at the subgenus level to the genus *Bothrophyllum* seems real.

Ogar (2009, p. 63, synonymy) proposed extremely wide species framework for *B. conicum*, not followed here, as mentioned above. Most taxa synonymized by him are discussed in the preceding sections of the present paper. *Caninophyllum dobrolyubovae* Fomichev, 1953 is discussed below, together with other species of *Bothrophyllum*-like corals described by Fomichev (1953). *Caninophyllum* cf. *dobrolyubovae* Wu and Lin, 1992 the last species synonymized by Ogar (2009) with *B. conicum* and not discussed elsewhere in this paper, belongs to an abundant group of *Bothrophyllum*-like, poorly investigated Chinese taxa of uncertain taxonomic positions. Several examples of those taxa are discussed below in the chapter "Some examples of the Chinese *Bothrophyllum*-like taxa". Thus, only specimens collected by Ogar (2009) himself from the Limestone bands O_6 and O_6^1 (early Gshelian) of the Donets Basin are briefly commented upon here.

Three morphotypes can be distinguished on the basis of illustrations published by Ogar (2009). The first morphotype, illustrated in his pl. 1, figs 1–7 with maximum n:d value 36:18 mm, resembles most closely the corallite illustrated by Fedorowski (1973, fig. 17b, c; n:d value 45:25 mm) in morphology. The arrangement of the major septa in the cardinal quadrants of both specimens, their cardinal septum apparently shortened, but with thin strips "hanging" on sections of tabulae proving their great length with only a slight elevation above the tabula floor, and positions of their minor septa towards the major septa are the most important characters in common. Placement of both of those corallites in the *B. conicum* group of specimens inclined towards *B. robustum* is suggested here.

The specimen illustrated by Ogar (2009, pl. 1, figs 8–11) probably belongs to *Bothrophyllum* although its direct inclusion in *B. conicum* is doubtful. Illustrations of its early growth stages are lacking and other data are incomplete as a result of its poor preservation. Its minor septa in counter quadrants are restricted to the dissepimentarium – a character absent from *B. conicum* as emended in the present paper. However, its tabularium is biform when minor septa are long and a disstabularium occurs in the corallite sector where they are restricted to the dissepimentarium.

The second morphotype (Ogar 2009, pl. 1, figs 12–15 and 16) lacks illustrations of early growth stages, making these remarks incomplete. The early mature and mature growth stages exhibit a shortened cardinal septum which is located in a closed cardinal fossula, closely resembling *Siedleckia* Fedorowski, 1975, in that particular detail. Also, the counter septum appears shortened in the second corallite illustrated. That septum is thin in the earliest growth stage of the first corallite illustrated by Ogar (2009, pl. 1, fig. 12), but its length is uncertain. Nevertheless, a potential position of the morphotype discussed in *Siedleckia* should be kept in mind. *Pseudotimania* Dobrolyubova and Kabakovich, 1948 should be the second option, whereas the position of that corallite within *Bothrophyllum* is here excluded.

***Bothrophyllum* and *Bothrophyllum*–like corals in Europe (including the Urals) and in North Africa**

The Donets Basin is located closest to the type area for *Bothrophyllum* and bears the most abundant and carefully studied corals belonging and/or related to *Bothrophyllum* (Fomichev 1953; Vassilyuk 1960; Ogar 2009). Thus, special attention is paid here to the Donets Basin corals, especially those described by Fomichev (1953). Corals described by Ogar were commented upon in the preceding subchapter, whereas *Bothrophyllum berestovensis* Vassilyuk, 1960 is reinvestigated and other *Bothrophyllum*-like Rugosa are described in a separate paper dealing with the early Bashkirian Rugosa from the Donets Basin (Fedorowski in preparation).

Fomichev (1953, p. 339) did not accept the intraspecific variability of the type species of *Bothrophyllum* established by Dobrolyubova (1937, 1940, 1948b) and included some of her subspecies in *Bothroclisia*. Also, species names suggesting a relationship of his specimens to those from the Moscow Basin are applied as *affinis* (*B. pseudoconicum* Dobrolyubova, 1937) or *conformis* (*B. kashiricum* Kabakovich, 1937). Indeed, most of the Donets Basin specimens illustrated by Fomichev (1953) can hardly, if at all, be compared to the Moscow Basin types. *B.* cf. *kashiricum* is represented in his collection by three incomplete, possibly immature specimens (Fomichev 1953, pl. 20, figs 11–13) that do not provide data suitable for any fruitful discussion. *B.* aff. *pseudoconicum* is illustrated and described (Fomichev 1953, p. 332, pl. 22, figs 1a–g [in Russian alphabet], 2, 3) on the basis of one specimen illustrated by three transverse and one longitudinal thin section and two random transverse thin sections of mature growth stages of two specimens (one partly crushed is omitted from further consideration). The mature morphology of the more completely investigated specimen, derived from Limestone K_7 (perhaps an equivalent of the Kashirskyi Substage), closely resembles two specimens from the Moscow Basin as mentioned above (see discussion on the specimens included by Dobrolyubova and Kabakovich (1948) in *B. conicum novlinskoi*). The elongated cardinal septa and the counter septa equal to adjacent major septa present in all three specimens require special attention as that points towards *Bothroclisia*. The immature morphology of the Donets Basin specimen (Fomichev 1953, pl. 22, fig. 1a, b) more closely resembles the typical morphology of the late neanic/early mature growth stage of *Bothrophyllum conicum* than those of the remaining Moscow Basin species. This may have resulted from its older stratigraphic position, suggesting derivation of *Bothroclisia* from *Bothrophyllum*. That derivation is questionably contested by Fomichev (1953, pp. 339, 340) despite his ultimate decision to consider *Bothroclisia* a subgenus of *Bothrophyllum*.

The position of *Bothroclisia* requires re-consideration. Fedorowski (1975) synonymized that subgenus with *Bothrophyllum* keeping in mind Fomichev's (1953, p. 340) diagnosis. Several characters mentioned in that diagnosis are of a specific rather than of a generic rank. Two characters, earlier omitted from a more careful consideration are elevated here to contest that synonymy: (1) Domination of the cardinal septum in length and reduction of the counter septum to the length of the adjacent major septa; (2) The possibility of separation of the inner margin of the cardinal septum to form a median lamella in a weak axial structure. The components of the latter may be completely or in part free from inner margins of major septa. Those two characters are qualitative, i.e., of a generic rank. Other characters of *Bothroclisia*, such as the early ontogeny and the mature morphology point to *B. conicum*, the type species for the genus *Bothrophyllum*. Also, the cardinal septum in the latter species is not shortened at maturity, being at least equal to major septa of cardinal quadrants. The differences and similarities between *Bothroclisia* to *Bothrophyllum* mentioned allow acceptance of Fomichev's (1953) concept of the close relationship of those two taxa rather than to follow his doubts. *Bothrophyllum* is here accepted ancestral for *Bothroclisia* at a subgeneric level. Hill (1981, p. F346) considers *Bothroclisia* a probable synonym of *Bothrophyllum*.

Fomichev (1953, p. 235) accepted the independent position of the genus *Caninophyllum* Lewis, 1929. However, his comments leave no doubts about difficulties he met in trying to distinguish *Caninophyllum* from *Bothrophyllum* in his specimens. It is enough to cite parts of two of his comments to make that obvious (Fomichev 1953, p. 335, one to the last paragraph): "Sharp boundary between *Caninophyllum* and *Bothrophyllum* … does not exist. *Bothrophyllum* differs in possessing major septa accreted in the corallite axis at an early growth stage" and lower in the same paragraph: "long and even axially accreted major septa [occur] in young *Caninophyllum*…" [Both translated here from Russian]. Thus, most specimens illustrated by Fomichev (1953, pls 12, fig. 2; 13, figs 1–3, 5; 14, figs 2–5) are here included in *Bothrophyllum*. The remaining ones possess shortened cardinal septa and are included in the appropriate list above. Igo and Adachi (2000) included in *Bothrophyllum domheri* Fomichev, 1953 several Japanese specimens from the Kasimovian strata of Central Japan (Hida Massive). That close relationship (or morphological similarity?) is beyond the focus of the present paper and is not discussed here. Japanese specimens with a shortened cardinal septum belong perhaps to a new subgenus of *Bothrophyllum* suggested, but not introduced in this paper. Ogar (2009) included *Caninophyllum dobrolyubovae* but not *C. domheri* in the synonymy of *Bothrophyllum conicum*. That synonymy is not followed here as mentioned above, but both of Fomichev's (1953) species are here included in *Bothrophyllum*.

Fomichev (1953, p. 318) diagnosed his new genus *Yakovleviella* as possessing several features in common with *Bothrophyllum* and some similar to *Gshelia* Stuckenberg, 1888. The length and modification of the cardinal septum were described by him as follows: "The cardinal septum detaches from the counter; its long and thin inner sector occupies the axial part of a corallite; that inner sector of the cardinal septum detaches sometimes from its peripheral sector and continues to grow in the form of a separate median lamella, commonly lens-shaped thickened." [Translated here from Russian]. Keeping that apparent character in mind, Fomichev (1953, p.319) accepted a close relationship, or even a synonymy of *Yakovleviella* with *Gshelia*. Unfortunately, the modifications of the cardinal septum in *Yakovleviella* are not demonstrated in his illustrations (Fomichev 1953, pl. 19, figs 3, 4; pl. 20, figs 1–10; pl. 21, figs 1–9). Also, none of peels taken from his specimens and being at my disposal exhibits the feature most characteristic for *Gshelia*, i.e., the lens-shaped pseudocolumella, clearly demonstrated by Dobrolyubova (1940, pl. 13, figs 14–16; pl. 16, figs 7–9; pl. 17, figs 3–7). Thus, Fomichev's (1953) comparison to *Gshelia* is considered unsupported. Also, his comparison to other morphologically close genera (Fomichev, 1953, p. 32) is not convincing. The type species *Yakovleviella tschernyschewi* Fomichev, 1953 bears several features of *Bothrophyllum*, but differs from that genus by possessing the axial septum lasting up to the mature growth stage. Keeping all those doubts in mind, the genus *Yakovleviella* is here conditionally accepted as valid.

The middle Carboniferous to the early Cisuralian *Bothrophyllum*-like rugose corals of the Urals, the Timan Mountains and the Novaya Zemlya (Stuckenberg 1895; Dobrolyubova 1936; Gorsky 1938, 1951, 1978; Gorsky *et al*. 1975; Degtyarov 1979; Kossovaya 1986, 2001) are related to those of the Moscow Basin. Unfortunately, the level of the investigation of those faunas is not always adequate. Also, not all taxa introduced from those areas are suitable for a detailed analysis. Some are mentioned in preceding chapters. Thus, the discussion that follows is restricted to short comments. Only *Alekseevella* Kossovaya 2001 is more broadly treated below.

Gorsky (1938, pp. 47–49, pl. 6, figs 4–6, pl. 7, figs 1, 3–5) introduced two new species *Bothrophyllum superbum* and *B. formosum* from possibly late middle Carboniferous strata and a new genus and species *Caninella pulchra* from uncertain strata, possibly middle Carboniferous, of Novaya Zemlya. Both species of *Bothrophyllum* display such characters as an elongated counter septum and a disstabularium present in *Bothrophyllum*. However, the cardinal septum is shortened in both. One thin section included in *B. superbum* in addition to the type specimen and the specimen described as *Bothrophyllum* (?) (Gorsky 1938, pl. 7, figs 1, 2 respectively) may belong to *Pseudotimania.* Also, the cardinal fossula in *B. formosum* resembles the latter genus. Unfortunately, lack of early growth stages prevents indisputable identifications, although the original identifications of the named species were tentatively accepted and both are included in the list of *Bothrophyllum*-like species with a shortened cardinal septum. *Caninella pulchra* (Gorsky 1938, pl. 5, figs 7, 8) is illustrated by one transverse and one longitudinal thin section, derived from the subcylindrical, i.e., probably mature part of the corallite. Its inner morphology is partly crushed, but most of the features, except for the shortened cardinal septum, closely resemble *Bothrophyllum*.

Fomichev (1953, p. 399–401) restudied Gorsky's (1938) thin sections, and confirmed the poor preservation of the specimen with a squeezed axial area. However, he was able to distinguish wide axial tabellae, that are elevated axially and "… which may form an inconsistent, supplementary axial structure." [Translated here from Russian]. He accepted *Caninella* as an independent genus, introduced two new species, each represented by two poorly preserved specimens and described two additional, incomplete specimens left in the open nomenclature. All those specimens were derived from the Moscovian (Limestones K_5, L_5, M_2), but their morphologies differ to such an extent that a distinction higher than specific is suggested (compare Fomichev's 1953 holotypes, pl. 17, figs 14, 15a–v in Russian alphabet and pl. 18, fig. 2a, b). Fomichev (1953) included *Caninella* in his new family Neokoninckophyllidae. However, the incomplete documentation and poor preservation of the Donets Basin specimens precludes confidence in his identification. His new species *Caninella semperjuvenilis*, characterized by a wide and complex dissepimentarium, a shortened cardinal septum and an axial area possibly free from major septa, may be related to the specimens included by him in the Neokoninckophyllidae. However, his species *C. murchisoni*, with its peculiar axial structure, an absence of a cardinal fossula, and a narrow dissepimentarium suggests that a taxonomic position of that specimen within the Family Bothrophyllidae is possible. This, however**,** cannot be confirmed.

Hill (1981, p. F346) accepted all the Novaya Zemlya and the Donets Basin specimens as *Caninella* and questionably included that genus in the family Bothrophyllidae. In this paper, only the Novaya Zemlya holotype of *C. pulchra* is tentatively included in the list of *Bothrophyllum*-like species with a shortened cardinal septum.

Bothrophyllum pseudoconicum Dobrolyubova, 1937 and *B. simplex* Gorsky, 1939 [in Fomichev] from the Moscovian strata of the Urals are too poorly represented and inadequately illustrated to be included in any species. They may belong to *Bothrophyllum*, but are not included in the lists of species above.

Gorsky (1951, p. 31, pl. 8, figs 1, 2) introduced a new species *Bothrophyllum magnificum* from the late Viséan/early Namurian strata of Novaya Zemlya. Its mature morphology closely resembles *Caninophyllum*, but the lack of early ontogenetic data prevents confident identification. It is not included in the list of species above, but may be considered a candidate for an intermediate *Caninophyllum/Bothrophyllum* taxon when thoroughly revised. An unquestionable *Bothrophyllum* has not yet been described from the Novaya Zemlya.

Several species and subspecies of *Bothrophyllum* were described by Gorsky (1978) from various middle and possibly early late Carboniferous outcrops in the Urals. He identified *B. pseudoconicum* Dobrolyubova, 1937 and introduced the new subspecies *radialis, vesiculosa* and *crassa* of that species. None of his specimens corresponds to Dobrolyubova's (1937) species closely enough to be accepted as co-specific. All are based on inadequate material, sometimes on a single thin section taken from an unknown part of the corallite. However, they bear several characters of *Bothrophyllum* and are included in the list of species together with *B. tolstikinae* Gorsky, 1978. Inclusion of both of them is supported by specimens illustrated by Degtyarov (1979), included by him in Gorsky's (1978) species. Thus, *Bothrophyllum* undoubtedly occurs in the middle Carboniferous strata of the Urals but its species content requires substantial revision in most instances. Gshelian records are unknown to me, whereas the Cisuralian *B. baeri* Stuckenberg, 1895 and the specimen identified by Dobrolyubova (1936) as ?*Bothrophyllum baeri*, possess a short cardinal septum.

Kossovaya (2001) introduced a new genus *Alekseeviella* to include corals similar to *Bothrophyllum*, but commonly identified as *Caninia* Michelin in Gervais, 1840. A distinct genus or genera including several middle and late Carboniferous, dissepimental rugose coral species are undoubtedly needed. *Alekseeviella* would have solved some of the nomenclatorial questions connected to such taxa, if introduced in an acceptable way. Unfortunately, its introduction created problems instead of solving them. Thus, that genus is here treated as one of the morphotypes present among the corals mentioned, but not as the acceptable genus. The following objections concerning *Alekseeviella* are:

(1) Species of the morphotype discussed are much more numerous than the six listed by Kossovaya (2001, p. 152). Also, they are much more widespread in time and area than she mentioned. In addition to the middle and late Carboniferous strata of the Ural Mountains and the Moscow Basin in Russia, the Donets Basin in Ukraine and the Cantabrian Mountains in Spain which she mentioned, corals of similar morphotype are very abundant in China (see below), Laos and Vietnam (Fontaine, 1961) and North America (Cocke, 1970). Besides, they were included not only in *Caninia*, as Kossovaya (2001) stated, but also in *Bothrophyllum, Caninophyllum, Pseudozaphrentoides, Pseudocaninia* and *Timania*. Unfortunately, the level of the investigation of the overwhelming majority of those taxa is inadequate for their confident classification and comprehensive discussion.

(2) "*Caninia*" *irinae* Gorsky, in Fomichev (1939, pl. 6, figs. 10, 11) was selected by Kossovaya (2001, p. 152) as the type species of *Alekseeviella*. This species was rewritten and pictures mentioned were re-illustrated by Gorsky (1978, pl. 5, figs. 11, 12, 12a). He supplemented them with a few more pictures of specimens derived from various outcrops on the western slope of the Urals. The holotype is the only illustrated corallite collected from the "left bank of Kos'va River, near the railroad bridge" (Gorsky, 1978, p.199). [Translated herein from Russian], i.e. from the type locality. That illustration is restricted to a single transverse section cut from an unknown phase of a mature (?) growth stage. None of the specimens illustrated by Fomichev (1939) and Gorsky (1978) documents an ontogenetic development starting from a neanic to an unquestionable mature growth stage. Irrespective of the incompleteness of the specimens illustrated by Gorsky (1978) and variability in the morphology of these specimens not necessarily reflecting different growth stages, Kossovaya (2001, p. 153) accepted all of them as co-specific with the holotype. Moreover information by Kossovaya (2001, p. 153) that the specimen illustrated by Fomichev (1939) in plate 6, figure 11 shows the holotype, is incorrect. The latter specimen was derived from a distant locality, described by Gorsky (1978, p. 199) as "Left bank of the Tschussovaya River, Vysokaya Hill" [translated herein from Russian].

(3) The ontogeny of *Alekseeviella irinae*, shown by Kossovaya (2001, fig. 8:8–12) in a series of drawings, are based on a Moscovian specimen (Kashirskyi Substage) from the Moscow Basin, not on a topotype. The distance between the type area and age of the holotype and the specimens illustrated by Kossovaya: Suite C12 = Bashkirian, Prikamskyi Substage in the Urals *vs* Moscovian Stage (Kashirskyi and Podolskyi Substages) in the Moscow Basin, make doubtful the value of that ontogeny as typical for the species and genus. The incompleteness and poor preservation of the specimens investigated (Kossovaya 2001, pl. 30, figs 1–5, 10, 11, 14) increase those doubts. Specimens from the Moscow Basin would help in establishing an intraspecific and/or more probably, an intrageneric variability when the type is well investigated, but they cannot substitute for the type. With all doubts mentioned the genus *Alekseeviella* is here omitted from the discussion on the relationships of *Bothrophyllum*.

The Svalbard Archipelago area and its late Carboniferous to the Sakmarian rugose coral fauna was closely connected to the Timan Mountains and the Urals fauna (Fedorowski 1981, 1986, 1989; Fedorowski *et al*. 2007). *Bothrophyllum* has been reported from Spitsbergen (Fedorowski 1965, 1967; Chwieduk 2009, 2013) but all specimens recorded from that area so far possess a short cardinal septum. *B. permicum* Fedorowski, 1965 may belong to a new subgenus of *Bothrophyllum*. Its main characteristics demonstrated a mixture of characters both typical and strange for *Bothrophyllum*, such as: the cardinal septum shortened early in the ontogeny, the counter septum hardly distinguishable by length from other major septa in that growth stage, but extending to the corallite axis in maturity, the tabularium biform in the late neanic/early mature growth stage and a disstabularium developed in maturity. A specimen included in that species by Chwieduk (2013), incorrectly described as new in figure captions (p. 61), is represented by an immature part of one corallite. The morphology of that growth stage is similar to comparable growth stages of the holotype specimen. *B. orvini* Fedorowski, 1967 is represented by several fragments of corallites, but all are poorly preserved. A formal name should not have been given to such a collection of specimens. All specimens illustrated by Tidten (1972) exhibit characters of *Timania* and are here shifted to that genus. Thus, an indisputable *Bothrophyllum* does not occur in the early Cisuralian strata of the Svalbard Archipelago.

Species from western and central Europe and North Africa, i.e., from the Western European Province, similar to *Bothrophyllum* are not numerous. Most of them, except those from Spain (de Groot 1963; Rodríguez 1981; Fedorowski 2004) are not younger than Serpukhovian. Also, the level of the investigation of types of species, introduced commonly by 19th Century authors, is inadequate unless revised by subsequent authors on the basis of the type collections. *Caninophyllum* Lewis, 1929 exemplifies such a well revised taxon. Unfortunately, the original meaning and content of that genus underwent subjective modifications by many authors dealing with dissepimental corals, Carboniferous and Permian in age. Those modifications are too numerous to be discussed in detail. Thus, only my own very early paper (Fedorowski 1965) is mentioned as an example of an over interpretation. Neither of two species described in that paper has been investigated completely enough to be compared to particular growth stages of *Caninophyllum archiaci* (Milne Edwards and Haime, 1852), the type for the genus. Thus, the fundamental condition in the investigation of a morphotype like this is not followed. Both species were included in *Caninophyllum* mainly on the basis of the mature morphology similar to *C. archiaci*. Neither belongs to that genus. Of the two *C. belcheri magnum* Fedorowski, 1965 is better to cite as an example. It should have been either left in the open nomenclature or undescribed. A formal introduction of that subspecies increases nomenclatorial chaos in that group of corals instead of adding substantial information to the taxonomic diversification of the early Sakmarian coral fauna from Spitsbergen. Examples of that kind are numerous in the literature, but they are purposely omitted from citations.

Lewis (1929) included both *Cyathophyllum archiaci* Milne Edwards and Haime, 1852 and *Caninia patula* Michelin, 1846 in *Caninophyllum*. The latter species, well represented in the western European sites (e.g. Sale 1910; Monty 1964; Poty 1981; Poty and Hannay 1994) is either unknown from other areas or its identifications are not convincing. Besides, specimens of *C. patulum* described and illustrated so far, do not exhibit characters comparable to *Bothrophyllum*. Thus the taxonomic position of that species is not discussed and remarks that follow are restricted to *C. archiaci* as the type for the genus. Its revised type specimen was derived from the "*Dibunophyllum* Zone, Llanymynech, North Wales, collected by Sir Roderick Murchison" (Lewis 1929, p. 459). In addition to the typical or nominative taxon, included by Lewis (1929) in his "Halkynense" Type present in the D2 and D3 strata (= Brigantian, early Serpukhovian), he distinguished the "Monense" Type from several outcrops of S to D1 strata (= late Arundian-early Asbian) and "Bristolense" Type from S1 (= late Arundian) strata of the Avon Gorge, Bristol.

The morphology of the mature growth stage of all three "Types" resemble the type species of *Bothrophyllum* in possessing long major septa. Those septa more closely approach the corallite axis in the Monense Type than in the other two. "The minor septa may penetrate the intrathecal area [i.e., the tabularium] for a distance of 1 mm or more…" (Lewis 1929, p. 461). The dissepimentarium is well developed, but the pseudonaotic pattern, typical for *Bothrophyllum*, is restricted to a narrow belt at the periphery, or does not occur. The tabularium is biform as documented by the position and number of sections of peripheral parts of tabulae in the transverse sections. Opposite positions of some peripheral tabellae in the longitudinal section of one paratype (Lewis 1929, pl. 11, fig. 3) confirms that biformity. All the characters listed occur in *Bothrophyllum*. In contrast to the species considered here as unquestionable *Bothrophyllum*, the cardinal septum is shortened in all but one or two (?) transverse sections of *C. archiaci* illustrated (Lewis 1929, pl. 12, figs 2, 4a?) and the counter septum is equal to the adjacent major septa.

The early ontogeny of *C. archiaci* resembles that in *B. conicum* to a much lesser degree than the morphology of the mature growth stage. Lewis (1929, pp. 462, 463) characterized the earliest growth stage investigated by him as follows: "a zaphrentoid grouping" of major septa, "the cardinal septum long and the longer septa are united at their distal ends." He did not mention either the length of the counter septum or an occurrence or absence of an axial septum. This may have resulted from the incompleteness of that earliest growth stage studied by him (Lewis 1929, text-fig. 4; pl. 11, fig. 6c). The cardinal septum remains long in the more advanced growth stage of the specimen cited, but the counter septum is indistinguishable from the adjacent major septa. Thus, the axial septum is absent from the comparatively early growth stage of that specimen and from the comparable growth stage of the holotype and other paratypes (Lewis 1929, pl. 11, fig. 1c and fig. 2c, d; pl. 12, fig. 4c respectively).

Taking into account some differences in the mature growth stage, the absence of an axial septum after the advanced neanic growth stage, the cardinal septum shortened early in the ontogeny and the counter septum equal to the adjacent major septa in length, the synonymy of *Caninophyllum* with *Bothrophyllum* is now rejected (see also discussion in the chapter "The origin of *Bothrophyllum*" below). That synonymy was first postulated by Campbell (1957, p. 92) on the basis of his restudy of *C. archiaci*, but without a personal knowledge of the typical morphotype of *Bothrophyllum*. According to that author, the difference between the types of *Caninophyllum* and *Bothrophyllum* may be only specific. Rowett (1969, p. 70) expressed a similar opinion. Fedorowski (1975) placed *Caninophyllum* in the synonymy with *Bothrophyllum*. That synonymy was accepted (with a question mark) by Hill (1981) and by Igo and Adachi (2000), but was rejected by several authors (e.g., Poty 1981; Kossovaya 1989; Chwieduk 2013). The occurrence of an axial septum in the very early neanic growth stage of *Caninophyllum archiaci*, if documented by new studies of topotypes, will not change the situation. The axial septum occurs in very early growth stages of several families unrelated to Bothrophyllidae, such as the Family Aulophyllidae and in some taxa of the related Family Cyathopsidae. However, only a long-lasting occurrence of that character, persisting to the early mature growth stage as it does in the type species of the genus *Bothrophyllum*, can be considered diagnostic for that genus.

Poty (1981, p. 47) postulated a phylogenetic line leading from *Caninophyllum archiaci monense* through *C. archiaci halkynense* (both names applied by him with the question mark) to *Bothrophyllum*. Reduction of the axial structure was pointed out by him as the only criterion. In the case discussed, this reduction means a slight shortening of the major septa in the tabularium. Changes of one character observed in specimens of *Caninophyllum*, collected from a small western European area, distant in space and time from the type area of the genus *Bothrophyllum*, cannot form a basis for such a phylogenetic reconstruction. This question is discussed in more detail in the chapter “The origin of *Bothrophyllum*” in the conclusive part of the paper.

The occurrence of *Bothrophyllum* in Spain was first established by de Groot (1963) who described the new species *Pseudozaphrentoides rabanaliensis* from the Perapertu Formation (late Bashkirian-early Moscovian), *Bothrophyllum* sp. cf. *pseudoconicum* Dobrolyubova, 1937 from the lower part of the Sierra Corisa Limestone (Westphalian D) and *Bothrophyllum*? sp. from the same limestone. Fedorowski (2004) transferred the first of those species to *Bothrophyllum*. It is cited in the list of species above. He rejected the identification by Boll (1985) of *P. rabanaliensis* as unsupported (Fedorowski 2004, p. 97), but accepted a possibility of *Bothrophyllum filigranum* Boll, 1985 to be a member of that genus when restudied. All specimens described by Boll (1985) are fragmentary, lacking data necessary for a confident identification. *Bothrophyllum pseudoconicum* Dobrolyubova of Rodríguez (1984) possesses a shortened cardinal septum at maturity and was included in the list of species bearing that character. *Bothroclisia* sp. Rodríguez, 1984 lacks a free median lamella, but possesses a cardinal septum elongated or equal to the adjacent major septa. It may belong to *Bothrophyllum*, but the lack of early growth stages makes that possibility doubtful. Rodríguez *et al*. (1997) questionably identified several specimens from the early Moscovian strata of Ribadesella (Spain) as *Amandophyllum* Heritsch, 1941 and described them as a new species ?*A. etayum*. Indeed, the Spanish specimens bear some similarity to *Amandophyllum carnicum* (Heritsch, 1936) the type species of that genus, based on a single, incomplete specimen, examined by myself in 2003 (not published). However, most of those similarities are secondary characters and are not analyzed in detail. Most characters of the Spanish specimens point towards the Bothrophyllidae. The early stage of the holotype of *A.? etayum* (Rodríguez *et al*., 1997, pl. 1, fig. 5a) is especially convincing in this respect. Nevertheless, other characters of that species makes questionable its position within *Bothrophyllum*.

Bothrophyllum proteum Semenoff-Tian-Chansky, 1974 derived from the base of the Lower Member of the Hassi Kerma Formation, early Bashkirian strata of Bechar Basin (Algeria) forms protocolonies (Fedorowski and Ogar 2014 term) and is considered here as a representative of a new genus, not named. The original study by Semenoff-Tian-Chansky (1974), supplemented by Guillaume and Semenoff-Tian-Chansky (1991) does not contain such important data as the morphology of the early ontogenetic growth stages of protocorallites and the blastogeny. Aretz’s (2011) illustration of a single transverse section, did not add to a more comprehensive knowledge of that species and genus. The microstructure of septa, drawn by Semenoff-Tian-Chansky (1974, fig. 55) may characterize that specimen, but cannot be considered diagnostic for the genus. Its protocolonial growth form and the morphology of the mature growth stage which is different in several diagnostic characters from the type species of *Bothrophyllum* (compare Semenoff-Tian-Chansky 1974, pl. 29, figs 1–5; pl. 30, figs 1–5) exclude the north African specimens from the later genus. Offsetting discussed above as present in rare specimens of the type species does not indicate a close relationship between ‘*Bothrophyllum*’ *proteum* and *Bothrophyllum conicum*. Short lasting offsets in the latter species are environmentally caused peripheral rejuvenations, single and/or multiple, whereas ‘*B.*’ *proteum* produces verticils of lateral immature offsets, i.e., the lost structures of Fedorowski (1978).

The relationship of ‘*B*’. *proteum* remains uncertain even at a family level. A brief comment by Aretz (2011, p. 607, fig. 8G) did not support a solution. The lack of blastogenetic data precludes its close comparison to colonial species. Corallites or fragments of corallites of '*B*'. *proteum* that lack an axial structure resemble "*Craterophyllum*" *verticillatum* Barbour, 1911, but the occurrence of an axial structure in some fragments eliminates a close relationship between those two. Stuckenberg (1905 pl. 1, fig. 11b, c) illustrated and described similar verticils of offsets in his new species "*Campophyllum*" *volgense* derived from the late Carboniferous strata of the Samarian bend. Unfortunately, his illustrations lack details, precluding a close comparison to '*B*'. *proteum*. *Caninostrotion* Easton, 1944 with its supplementary study by Webb (1987, figs 6:1–15, 7:1–7) exhibits an enormous intraspecific variability in the morphology of the axial area starting from a dense axial structure to an axial area free of any skeleton, except for tabulae. Probable formation of lost structures (Webb 1987, fig. 9:9) in addition to rejuvenation and regular offsetting, increases the peculiarity of that species and genus. Its growth form is uncertain in the sense that it may form simple, but normal colonies, as well as protocolonies.

***Bothrophyllum* and *Bothrophyllum*-like corals from the Americas and Asia**

The generic name *Bothrophyllum* has been reported several times from North America, but specimens undoubtedly belonging to that genus have not been described and illustrated. *Bothrophyllum*-like specimens with shortened cardinal septa occur in the Belcher Channel Formation (early Sakmarian) of the Devon Island in the Canadian Arctic Archipelago (author's unpublished data). *Bothrophyllum* cf. *pseudoconicum* Dobrolyubova of Rowett (1969, p. 70), represented by seven incomplete corallites, are very different in morphology. Two corallites illustrated by the transverse thin sections (Rowett 1969, pl. 10, fig. 6c; pl. 11, figs 1a, b) resemble *Bothrophyllum* in their mature growth stage. Also, the late neanic/early mature growth stage of the second specimen listed (Rowett 1969, pl. 11, fig. 1c) possesses the cardinal and the counter septa united in the corallite axis up to this advanced growth stage, i.e., typical for *Bothrophyllum*. However, both specimens listed possess distinctly shortened cardinal septa. The first of them possesses an axial structure composed mainly of axial tabellae that are densely packed and very steeply elevated to form a narrow axial column (Rowett 1969, pl. 10, fig. 6a, b). This character excludes the Alaskan specimen from *Bothrophyllum*. The axial structure in the corallite illustrated only by a drawing of a longitudinal section (Rowett 1969, pl. 11, fig. 2a) resembles the *Bothrophyllum* morphology more closely than the previous one. One of two specimens identified as *Bothrophyllum* sp. A (Rowett 1969, pl. 10, fig. 5a) closely resembles *Bothrophyllum* in possessing the cardinal and the counter septum long. Unfortunately, the single transverse thin section, taken from an unknown part of the corallite, cannot prove its taxonomic position. Nevertheless, corals closely resembling or related to *Bothrophyllum* occur in the early Permian strata of Alaska

The incomplete investigation of ?*Bothrophyllum kansasense* (Miller and Gurley, 1894) of Easton (1944, p. 123, pl. 22, figs 8–10) does not allow for a comprehensive discussion on that taxon. Doubts concerning its taxonomic position was already mentioned by Easton (1944, p. 123), who wrote "This species is neither a *Campophyllum* nor a *Caninia*, but may represent a new genus closely related to *Bothrophyllum*…. The present tentative reference is suggested because adequate material to enable further study is not available yet…". Nothing has changed since that time, whereas the characters illustrated do not allow inclusion of that species in *Bothrophyllum*.

Dissepimental solitary corals resembling, related and/or belonging to the genus *Bothrophyllum* are abundant in China and were described by Chinese authors in numerous papers under various names, not always mentioned in the discussion that follows and in the list of synonyms above. Unfortunately, the level of the investigation, often documented by one transverse thin section taken from an unknown part of a corallite and one longitudinal thin section, or even a single transverse thin section, do not allow a confident identification of most of those taxa. Species bearing some characters indicating their possible relationship to *Bothrophyllum*, but leaving doubts, are omitted from the lists of species in order to avoid further nomenclatorial confusion on the species level. However, names of genera originally applied to those excluded species are included in the synonymy list of the genus *Bothrophyllum* when their most important diagnostic features are in common or resemble that genus. This approach and the corresponding papers cited in the references should facilitate finding and checking those species.

The identification as *Bothrophyllum* of almost all Chinese species included in the lists above is questionable. However, detailed analysis of taxa found in the Chinese literature available to me will add little to the knowledge of *Bothrophyllum* since the level of their investigation is inadequate. Restrictions and doubts mentioned reduces the remarks that follow to only a few papers discussed in accordance to their publication dates. Also, all species identified as *Yuanophyllum* Yu, 1931 and described by Yu (1933) are omitted from the discussion although some of them bear features resembling *Bothrophyllum* (in a broad sense) more closely than the type of *Yuanophyllum kansuense* Yu, 1931 (e.g. Minato and Rowett 1967, pl. 42; Fan *et al*. 2003, pl. 27, figs 4a, 5a). The presence of such *Bothrophyllum*- like "*Yuanophyllum*" species may indicate a different origin of Chinese "bothrophyllids", when thoroughly revised.

Bothrophyllum longiseptatum (Lewis) of Wu (1964) with a long cardinal septum, the counter septum equal to the adjacent major septa, and with a narrow dissepimentarium may belong to *Bothrophyllum*, but not to the species to which it was assigned. *B. pseudoconicum* Dobrolyubova of Wu and Zhao (1974) from the late Carboniferous of SW China possesses both protosepta shortened and may belong to either *Siedleckia* Fedorowski, 1975 or to a genus morphologically similar to it.

Ou Yangxuan (1983, in Cao *et al.*) identified several specimens as *Bothrophyllum tomiense* (Tolmachev), *B. longiseptatum* (Lewis), *B. pseudoconicum conicum* Dobrolyubova and Kabakovich and a new species *B. yuanophylloides*. All those species are inadequately studied. Thus, neither the apparently old nor the newly introduced species are included in the lists above. The name of the latter species suggests a similarity to the genus *Yuanophyllum* and some of its features support that suggestion. Some specimens included in the previously known species do not bear characteristics of those species. Some of their characters weakly resemble the type species of *Bothrophyllum*. However, all possess short minor septa.

Yu and Wang (1987) described several new species under various generic names (see synonymy). All those taxa bear several characters in common with the *Bothrophyllum*-like species possessing a shortened cardinal septum. Unfortunately, their early growth stages remain unknown and morphological data of the mature (?) growth stages are inadequate for confident identification. The disstabularium present in most transverse sections of the specimens illustrated and a bothrophylloid morphology in longitudinal sections of the tabularium, can be treated only as supportive indications, but not as characters determining a generic identification.

Yu and Zhu (1988) described several species they included in *Koninckophyllum, Neokoninckophyllum, Pseudotimania, Pseudozaphrentoides, Timania, Yuanophyllum* and *Bothrophyllum*. All were described on the basis of one transverse and one longitudinal section each. The morphology of the sections illustrated closely resembles one another making their co-specific status likely. Early growth stages of all remain unknown. None of the generic names mentioned is included in the list of synonyms of *Bothrophyllum* and none of new species is included in the list of potential bothrophyllids.

Two new species introduced by Yu (1989) under the names *Pseudozaphrentoides cishonensis* and *Timania huanglongensis* from Moscovian strata bear characters closely resembling *Bothrophyllum*. The first of them possesses a long cardinal septum in the early growth stage and a complex peripheral dissepimentarium in the mature growth stage. The second species possesses a shortened cardinal septum, but its counter septum is elongated and its tabularium is biform. The earliest growth stages of both species are unknown, but they may belong to *Bothrophyllum s.l.*

Wu and Zhao (1989) described several species, morphologically similar to one another, but included in different genera. Most of them were inadequately illustrated for confident identification, but some species included by those authors in *Bothrophyllum, Bothroclisia* and *Timania* are here accepted as possibly belonging to *Bothrophyllum* and/or to *Bothrophyllum*-like species with a shortened cardinal septum. Some specimens included by those authors in *Arctophyllum, Orygmophyllum* and *Zaphriphyllum* may be related to *Bothrophyllum* as well, but their illustrations are too limited to judge.

Wu and Lin (1992) described several species and included them in such genera as *Caninophyllum*, *Yakovleviella* and *Bothroclisia*. Some of those late Bashkirian specimens and the genus *Taiziheophyllum* were considered new taxa, and some were included in the Donets Basin taxa *Caninophyllum domheri, C.* cf. *dobrolyubovae,* and *Yakovleviella tschernyschevi*. Those species identifications are not accepted here. The morphology of the mature (?) growth stage of *C. domheri*, *C.* cf. *dobrolyubovae* and *Taiziheophyllum kongjiabuziense* illustrated by Wu and Lin (1992, pl. 6, figs 2, 5 and 10 respectively) are similar enough to possibly be treated as one species. All those taxa are conditionally included in the synonymy list of the genus *Bothrophyllum*. The same is true for some specimens of *Yakovleviella* and *Bothroclisia*. The corals discussed bear a closer similarity to eastern European taxa than does any other species from the other Chinese collections discussed above. This similarity may suggest an open marine connection between those two areas during the Bashkirian.

The rugose coral fauna described by Peng *et al.* (1992) from the *Pseudoschwagerina* Biozone of the southern part of the northern Chinese Platform, i.e., from the area supplying the Bashkirian fauna discussed in the preceding paragraph, also exhibits an eastern European character. That character is exaggerated by the morphologically and ontogenetically unsupported inclusion of the Chinese specimens in the Donets and/or Moscow Basins species of *Caninophyllum, Gshelia, Bothrophyllum* and *Bothroclisia*. Most of those Chinese taxa are illustrated exclusively by the mature parts of specimens, making their identifications uncertain. *Bothrophyllum conicum* of those authors has already been excluded from that Russian type species for the genus (see chapter "*Bothrophyllum conicum* and corals included in it outside the type area and/or age"), but a position of that species and two other species included by Peng *et al*. (1992) in *Bothrophyllum*, is here accepted as possible. Also, some taxa included by those authors in *Bothroclisia* and *Gshelia* may belong to *Bothrophyllum* (see lists of species above).

Two papers dealing with *Bothrophyllum*-like corals from remote, but paleogeographically important areas, require brief comments. Fontaine (1961, p. 147, pl. 31, figs 3, 4) described and illustrated a new species *Caninia laosensis* from the Sakmarian strata of Laos. Major septa of that species leave a wide axial area free, but its counter septum is elongated. Shortening of the cardinal septum may have resulted from the section of the cardinal fossula made above the calice floor. The muddy infilling of the fossula suggests such a possibility. The tabularium of that specimen is biform when the minor septa long. All those characters may suggest a relationship of that specimen to *Bothrophyllum*.

Contrary to that possibility, none of the specimens from Iran, identified by Flügel (1963, 1993) as *Bothrophyllum*, can be included in that genus. All of them exhibit characters of the Heterocaniniidae Hill, 1981 and should be included in that family. Thus, *Bothrophyllum* proper or corals related to that genus may occur in Laos, but they have not been recorded so far from Iran and/or adjacent areas.

DISCUSSION

The origin of *Bothrophyllum*

Caninophyllum Lewis, 1929 resembles *Bothrophyllum* closely enough to be considered its younger synonym (Campbell 1957; Fedorowski 1975; Hill 1981 with a question mark). Several authors, however, have distinguished between those two genera (Chwieduk 2013). Poty (1981) distinguished between them, but postulated a direct origin of *Bothrophyllum* from *Caninophyllum archiaci*. His suggestion seems unlikely as documented below, and is not followed. Rejection of that simplified approach does not contradict the possibility that *Bothrophyllum* descended from a species of *Caninophyllum* other than *C. archiaci*. On the contrary, that origin seems more likely than its derivation from any other known genus. The stratigraphic position of *Caninophyllum*, which is lower than the lowest occurrence of *Bothrophyllum,* and the similarity in morphology of the earliest growth stages known in the type species of both genera, support that idea. Some mature characters in common are less important, since many dissepimental Rugosa may reach a similar mature morphology. The microstructure of septa in the type species of both genera remains unknown. This weakens a support for their close relationship, but we cannot reject such a possibility until a substantial difference of that character is documented. Also, some other factors, not considered by Poty (1981), must be discussed in order to either accept or reject that relationship.

Similar trends in the development of at least some diagnostic characters should be documented in order to accept a synonymy of *Caninophyllum* with *Bothrophyllum*. Such trends are not observed when the western European, Viséan *Caninophyllum* species are compared to the Moscovian species from the Moscow Basin. At first, the progressive elongation of the minor septa in *Bothrophyllum* species from the Moscow Basin, well documented by Dobrolyubova (1937, 1940) and Dobrolyubova and Kabakovich (1948) is different from the long minor septa in *C. archiaci*. It is difficult to accept long septa in an ancestor, reduction in their length in an intermediate taxa and a repeated elongation in the final evolutionary phase. Opposite trends in the development of a character cannot appear in a single evolutionary lineage. Secondly, the cardinal septum in *Caninophyllum* becomes shortened in the neanic growth stage, whereas it remains permanently long in *Bothrophyllum s.s*. That character suggests a split into two genera during the early ontogeny of an ancestral species. Also, the major septa in *Bothrophyllum* do not follow a trend in shortening, suggested by Poty (1981). It is enough to point to the very long-septal specimens from the late Moscovian and early Gshelian strata of the Moscow Basin (Dobrolyubova 1937, pl. 14, figs 1, 2, pl. 17, fig. 1, pl. 18, figs 5, 6; 1940, pl. 7, figs 1, 2 respectively) to reject Poty's (1981) suggestion in this respect.

Rejection of *C. archiaci* as an ancestor for *Bothrophyllum* allows one to look for another candidate among the species morphologically close to the latter genus. "*Pseudocaninia*" *longiseptata* Lewis, 1931, studied to the extent of allowing a credible analysis, is the most promising species present in the western European coral faunas. Lewis (1931) accepted the generic name *Pseudocaninia* Stuckenberg, 1888 despite it being synonymized with the genus *Bothrophyllum* by Stuckenberg himself (1895, p. 56). That synonymy was accepted by Dobrolyubova (1937, p. 25) and majority of subsequent authors. Peels taken from Stuckenberg's (1888) originals (Text-figs 1A–D, 2A–E) confirm that synonymy.

"*P.*" *longiseptata* possesses an axial septum developed in the early neanic growth stage (Lewis 1931, pl. 8, fig. 2). However, comparatively early in the ontogeny that septum becomes divided into the cardinal and counter septa. The cardinal septum remains long whereas the counter septum becomes shortened to the length of the major septa in counter quadrants. All major septa, except perhaps the cardinal septum, are amplexoid. Thus the counter septum accompanies the other major septa of counter quadrants in their elongation along tabular surfaces, but it does not exceed those septa in length (Lewis 1931, pl. 7, figs 3b, c, 4b, c; pl. 8, fig. 1e, g–i – holotype). The cardinal septum, long at the neanic and early mature growth stage of the holotype, becomes permanently shortened at its advanced maturity (Lewis 1931, pl. 8, fig. 1h, i). The length of the cardinal septa in the paratypes varies. In one paratype it is shortened at an early mature growth stage, but is long at advanced maturity. The second paratype, illustrated only in advanced maturity, possesses a long cardinal septum (Lewis 1931, pl. 7, fig 4a–d *vs* 4e, f and 6a respectively). The minor septa in all specimens of "*P.*" *longiseptata* are restricted to the narrow dissepimentarium that consists of herringbone and regular dissepiments. Also, the tabularium is normal, clearly separated from the dissepimentarium by a thickened inner wall.

The characters mentioned resulted in a mixture of features present and absent from *Bothrophyllum conicum*. A well documented axial septum in early ontogeny and a long cardinal septum in the advanced ontogeny of both species are the most important features from a phylogenetic point of view. Specimens included by Lewis (1931) in "*P.*" *longiseptata* were collected by him from the type locality of *C. archiaci*. That collecting site was described as "Upper *Dibunophyllum* Zone of the Carboniferous Limestone of Llanymynech, N. Wales." (Lewis 1931, p. 226, lower). Thus, "*P.*" *longiseptata* rather than *C. archiaci* can be considered to be in the phylogenetic line leading towards *Bothrophyllum*, if the paleogeography did not make both those species difficult to accept as ancestral.

The paleogeography of a period analyzed (late Viséan to late Serpukhovian inclusively) was the next factor not taken in mind by Poty (1981). An easy communication between particular links of a phylogenetic lineage must be ensured in order to make a phylogenetic reconstruction credible. Such an easy communication between western and central European sites and the far Asiatic ones *via* eastern Europe, existed up to the early Brigantian (late Viséan) time inclusively (Fedorowski 1981, 1986, 1989), theoretically allowing the *Caninophyllum* species of that time to spread almost World-wide. However, dramatic changes in the paleogeography that begun in late Brigantian (*Goniatites granosus* Biozone), excludes western European species of *Caninophyllum* as ancestral for *Bothrophyllum*. The Sudetic Phase of the Variscan Orogeny uplifted the major part of western and central Europe, making impossible a direct communication between Serpukhovian sea remnants in southern Scotland that continued to host *Caninophyllum* species and the eastern European basins. Thus, only a well documented *Caninophyllum* species of late Viséan and/or early Serpukhovian age from the latter basins can play an ancestral role for *Bothrophyllum*. Such a species should display a *Caninophyllum*-like ontogeny well documented and a mature morphology not contradicting *Bothrophyllum* trends in its main characteristics. Unfortunately, such a species has not been established so far in the eastern European basins.

The remaining potential areas for yielding a taxon ancestral for *Bothrophyllum* are: the Urals, the Timan Mountains and Novaya Zemlja to the North and East, and the Lublin-Lvov Basin, Spain and northern African basins to the South and West. A communication between those areas, suggested by Fedorowski (1981, 1989, 2015) was confirmed by Rodríguez *et al*. (1986) and to some extend by Cósar *et al*. (2014a, b). Unfortunately, late Serpukhovian specimens, unambiguously belonging to *Caninophyllum*, and showing features pointing to *Bothrophyllum*, have not yet been described from any of the basins and areas mentioned. The existence of such a species in a refuge, unknown so far, cannot be excluded. A peculiar fauna, typical for the Brigantian strata in Europe and northern Africa, described recently (Fedorowski *et al*. 2012) from the middle and late Bashkirian deposits of the Sverdrup Basin suggests the possibility of such an option. However, *Caninophyllum* has not been listed by Cózar *et al*. (2014b) from the Tindouf Basin in northern Africa, considered by those authors a refuge for some Serpukhovian faunas. Other refuges of that time interval and in the areas listed, have not been mentioned in the literature.

Caninophyllum becharense Semenoff-Tian-Chansky, 1974 from the Tindouf Basin in North Africa, bears some similarity to *Bothrophyllum* and may perhaps be considered a *Bothrophyllum*-like coral with a shortened cardinal septum. However, its documentation is incomplete. Other dissepimental taxa, described from Spain as *Pseudozaphrentoides* (Gómez-Herguedas and Rodríguez 2005) and from Serpukhovian deposits of northern Africa as *Caninophyllum* (Aretz 2011) can be considered only as indicative of an intermediate *Caninophyllum/Bothrophyllum* species in those areas. Their documentation is inadequate for closer analysis.

The Donets or the Lvov-Lublin Basin are in my opinion the most promising areas for the occurrence of a *Bothrophyllum* ancestor. The following circumstances support that suggestion: (1) The occurrence in the Lublin area of late Brigantian dissepimental solitary corals resembling both *Caninophyllum* and *Bothrophyllum* from *Bothrophyllum* (Fedorowski 1968; Khoa 1977). Although excluded here, better preserved specimens of those genera, not met by drill cores, are possibly present. Rich coral fauna collected from drill cores of the Ukrainian part of the Lublin-Lvov Basin was lost prior to becoming investigated in detail (Dr. V. Ogar oral communication 2015); (2) Both the shape of the Lublin-Lvov Basin in the form of a sack opening eastwards, but locked westwards and its peculiar coral fauna (Fedorowski 2015), eliminates the connection with British Serpukhovian outcrops. An occurrence of diversified *Bothrophyllum*-like taxa in the latest Serpukhovian and earliest Bashkirian strata of the Donets Basin and possibly new species of *Bothrophyllum* in early/middle Bashkirian strata of that basin (Fedorowski, in preparation) point to both the eastern European basins yielding an ancestor of *Bothrophyllum*. The suggestion above is as yet unsupported by faunal findings, but is more probable than an origin of *Bothrophyllum* from western European or northern African taxa.

Options. The origin of *Bothrophyllum* by descent from *Caninophyllum*, accepted for the time being, requires at least three conditions to be fulfilled. Two of them: the similarity in the early ontogeny and suitable geographical conditions, were discussed in the preceding subchapter. The third of those conditions, i.e., a possible split of *Caninophyllum,* one part becoming *Bothrophyllum* is briefly discussed below.

The occurrence of an axial protoseptum in both genera, and modifications of the cardinal and counter protosepta derived from it, are in my opinion crucial for establishing both the relationship of those genera and the differences between them. As mentioned above, the axial septum in *Caninophyllum* is divided into the cardinal and the counter septa early in the ontogeny, whereas the axial septum in *Bothrophyllum* lasts up to early maturity. Also, the manner of modifications of the cardinal and the counter septa in both genera differs. Thus, either the split into *Bothrophyllum* took place early in the ontogeny of an ancestral species of *Caninophyllum*, i.e., prior to the division of the axial septum, or another genus, not yet described, is the ancestral for both *Caninophyllum* and *Bothrophyllum*. The last option, allows an explanation why the cardinal septum in *Caninophyllum*, the stratigraphically older genus, is shortened fairly early in the ontogeny, and its counter septum is equal to the adjacent major septa. Both those features look more advanced phylogenetically than the corresponding characters in *Bothrophyllum*. In the theoretical option discussed both *Caninophyllum* and *Bothrophyllum* would have split independently from that original hypothetical genus. Their characters in common would in this case illustrate common roots but not the direct relationship by descent. Unfortunately, that option is purely theoretical and cannot be proven by the taxa known so far.

The successive elongation of the minor septa and the increasing complexity of the peripheral dissepimentarium, but not changes in the protosepta, and the remaining major septa should be considered the main evolutionary stream, if the theoretical option mentioned above, is rejected. However, such an approach neglects the role of septa in the classification, i.e., one of the fundamental premises for the taxonomy of all corals. Modifications of the protosepta and some major septa proposed by Schindewolf (1942) in his classic study remains not only valid up to now for the suborder Plerophyllina, but may also serve as an example of the taxonomic value of that character. Thus, a complex approach, combining both modifications of major septa, the protosepta in particular, superimposed on changes of remaining skeletal structures, should be applied to the classification of the genus *Bothrophyllum* and the *Bothrophyllum*-like corals. The consequences of leaving modifications of the protosepta out of contention will result in acceptance of the recent nomenclatorial confusion.

***Bothrophyllum*-like corals with the cardinal septum shortened**

The length of the cardinal septum is perhaps the most important question, and one of the most troublesome factors in the classification of the *Bothrophyllum*. It seems reasonable to point out that the length of that septum is not necessarily correlated with its elevation above the cardinal fossula floor. Low elevated blades of cardinal septa may reach the inner limit of the cardinal fossula, thus being long, whereas a section made above upper limits of such septa gives the impression of them being shortened. Besides, peripheral parts of the cardinal septa in *Bothrophyllum* may be thickened, contrasting to their thread-like thin inner parts that may be identified as sections of tabulae and ignored. The cardinal septum in the type species of *Bothrophyllum* is long. Thus, such a septum must be considered typical for the genus. I cannot see any reason to neglect that factor in this particular genus only because there are numerous *Bothrophyllum*-like taxa with a shortened cardinal septum. To exclude such taxa from *Bothrophyllum* is the only way to make the framework of that genus precise. *Bothrophyllum*-like species with shortened cardinal septa may receive a subgeneric status, when they differ from the type genus by that single character, or should be separated at a genus level if their differences, including the neanic growth stage, are greater.

Despite several gaps in the record, resulting mostly from incomplete investigations (see discussion above), at least two periods can be distinguished in the occurrence of specimens with a shortened cardinal septa. The first period is limited to the early Carboniferous (late Tournaisian – Serpukhovian) and to the taxa included in or related to *Caninophyllum*. The incompleteness of data precludes a confident decision whether or not descendants of those early taxa continued into the Bashkirian and younger strata, up to the Cisuralian inclusively. Numerous dissepimental coral species present in those younger strata and identified by many earlier authors either as *Caninia* (e.g. Stuckenberg 1895, 1905; Chi 1931; Heritsch 1929, 1936, 1939; Gorsky 1938, 1978; Fomichev 1939, 1953; Harker 1960 [in Harker and Thornsteinsson]; Rowett, 1969), or as "*Caninia*" (Fedorowski 1975; Chwieduk 2013) do not answer that question. The same is true for the middle and late Carboniferous and/or Cisuralian taxa included in *Caninophyllum* (e.g., Fomichev 1953; Fedorowski 1965; Aretz 2011), or *Timanophyllum* Kossovaya, 1997. The lack of microstructural studies superimposed on commonly inadequate knowledge of the early ontogeny of those taxa, makes detailed discussion irrelevant. Nevertheless, the possibility of the extinction in Serpukhovian or earliest Bashkirian of the early Carboniferous evolutionary lineage is here suggested as more probable than its uninterrupted extension to the early Permian.

Specimens with the morphology of species identified previously as *Caninia* or *Caninophyllum* which were included by Kossovaya (1997) in *Timanophyllum* differ from *Bothrophyllum.* If she had given a new generic name and if her specimens were better documented by good quality and more complete illustrations, such a name might be acceptable. Unfortunately, the generic name *Timanophyllum*, based on the type species *Timania mosquensis* Dobrolyubova, 1937, was preoccupied by Fomichev (1953, p. 252). He introduced that generic name in his monograph which was ready for print in 1939, but which was delayed for publication 14 years for political reasons. In the meantime Dobrolyubova and Kabakovich (1948) proposed the name *Pseudotimania* based on the same type species. That latter name is valid according to the ICZN rules, pointing to dates of publications as decisive. The references in Fomichev's (1953) monograph (pp. 608–614) leave no doubt about his acquaintance with the paper by Dobrolyubova and Kabakovich (1948) and the Sovjet Union geological and palaeontological literature published after 1939. Thus, it will remain unknown why he kept the name *Timanophyllum* in the eventually printed version of his monograph.

The introduction by Kossovaya (1997) of the name *Timanophyllum* as new cannot be explained. Specimens included by her in that genus and those identified by her (Kossovaya 2001) as a new genus *Alekseeviella*, could have solved at least some of the nomenclatorial problems, if established correctly (see above for details concerning *Alekseeviella*). Unfortunately, the recent status of both of those genera only increases the existing nomenclatorial chaos.

The second period of the well documented occurrence of the *Bothrophyllum*-like species with a shortened cardinal septum began with some specimens of *Bothrophyllum pseudoconicum* Dobrolyubova, 1937 from the Moscow Basin**.** In one specimen illustrated from the Podolskian Substage (Dobrolyubova 1937, pl. 16, fig. 3), one from the Myachkovian Substage (Dobrolyubova and Kabakovich 1948, pl. 6, figs 1, 2; identified as *B. pseudoconicum conicum*) the cardinal septum is temporarily shortened. Also the cardinal septum seems to be permanently shortened in two Kasimovian specimens from the same basin (Dobrolyubova 1940, pl. 10, fig. 1; pl. 11, fig. 6). All remaining characters of the latter specimens listed are typical for *Bothrophyllum*. Their occurrence would have been treated here as a taxonomic split caught *in statu nascendi*, if the morphology of the peripheral dissepimentarium and the peripheral parts of septa in some Gshelian specimens (e.g., *Bothrophyllum conicum* of Ogar 2009, pl. 1, figs 12–15), are less advanced in development than those of the Kasimovian specimens illustrated by Dobrolyubova (1940). Also, in the Gshelian and/or early Sakmarian *Bothrophyllum*-like corals from the Urals (Stuckenberg 1895; Dobrolyubova 1936) and Spitsbergen (Fedorowski 1965, 1967; Chwieduk 2009, 2013), possessing shortened cardinal septa and the minor septa underdeveloped, the dissepimentaria are simple and commonly narrow. Those data may suggest two ways of phylogenetic development: (1) The appearance in the Kasimovian–early Gshelian in the Moscow Basin of a local, short-lasting morphological modification ended the *Bothrophyllum* lineage in the type area. Thus, the shortened cardinal septum is in this case considered a character that appeared parallel to the short-septal evolutionary lineage, but did not belong to that lineage. That option is here accepted as probable and supported by facts; (2) The appearance outside of the Moscow Basin of the lineage with the shortened cardinal septum. That lineage perhaps appeared in the Bashkirian or the early Moscovian, became widespread in the Eastern European Province and lasted possibly up to the Sakmarian inclusively. Whether or not that lineage was a direct offspring from a species of *Bothrophyllum*, remains an open question, but that option is here accepted as most probable. Potential candidates for the ancestor of that lineage are: species similar to those described by Gorsky (1938, 1978) as *Caninia* from the Novaya Zemlya and the Urals, species from the Donets Basin described by Fomichev (1953) as *Caninia* from the Moscovian strata, or taxa from the Urals and the Timan Mountains included by Kossovaya (1997, 2001) in her genera *Timanophyllum* and *Alekseeviella* when properly established (see discussion above). However, no species can be pointed out as unambiguously ancestral.

Chinese species are less probable as ancestral for the lineage discussed than those from the areas listed above, but cannot be excluded. Geographical isolation of the Chinese microcontinental shelves took place in the latest Kasimovian-early Gshelian time, making possible faunal exchange in the Bashkirian-Moscovian time. However, the level of knowledge of the Chinese fauna is inadequate for indisputable conclusions (see discussion above).

The lack in the literature of a completely investigated taxon, bearing characters typical for a *Bothrophyllum*-like taxa with a shortened cardinal septum, prevents the introduction here of a new genus or a subgenus needed for those corals. The long duration of that lineage (Bashkirian to Sakmarian inclusively) and the geographical widespread occurrence (northern Africa, SE Poland, Ukraine, Moscow Basin, the Urals, the Timan Mountains, the Novaya Zemlya, the Svalbard Archipelago, the Canadian Arctic Archipelago, Alaska, China and Japan) would make monophyletic relationships of taxa present in those areas acceptable only after their morphologies in all growth stages and the microstructure of their septa have been thoroughly studied and documented as common.

Phylogeny suggested by Kossovaya (1989)

All remarks in this chapter concern Kossovaya's (1989) paper. Thus citations below are restricted to pages and figures only. In this paper Kossovaya has made an attempt to reconstruct "the morphogenesis and phylogeny" of several dissepimental corals from late Carboniferous and early Cisuralian strata. She clearly distinguished between the phylogenetic lineages of Cyathopsidae and Bothrophyllidae. According to her, those two lineages existed parallel to one another from their very beginning in the early Carboniferous up to end of the Gshelian (Bothrophyllidae) and early Sakmarian (Cyathopsidae) (fig. 3). *Caninia* was indicated by her as ancestral for the Cyathopsidae, whereas a phrase "Loss of an amplexoid phase in ontogeny gave rise to *Caninophyllum*, the earliest representative of Bothrophyllidae" may mean either *Caninia* or an unnamed genus. The phrase cited is the only indication by her of an ancestor for the latter family (p. 112 and fig. 3).

Detailed analysis of that paper would be too long and unnecessary. Thus, only reasons for rejection of great majority of Kossovaya's conclusions are pointed out. I agree with her that the most important factor for studies involving the reconstruction of the phylogeny of this group of the rugose corals is the ontogeny and with her suggestion (possibly in this case) of the ancestral position of *Caninophyllum* within the family Bothrophyllidae. Both those subjects were discussed above. Points of disagreement, listed below, are much more numerous and have resulted from various reasons.

Methodological inaccuracies

1. Types (preferably), or topotypes if the former are lost, must form the basis for phylogenetic considerations. To replace the original specimens by specimens from remote areas and/or age, are methodologically incorrect. This has happened in part or in total for *Arctophyllum, Pseudotimania, Siedleckia* and *Timania*. Also, the ontogeny of the specimen derived from the Kasimovian deposits of the Samarian bend cannot replace the ontogeny of the true "*Caninophyllum*" *kokscharowi* Stuckenberg, 1895 collected from the early Permian deposits of the Urals.

2. The supposedly colonial genus *Ferganophyllum* of advanced mature morphology, but with the early growth stage of the protocorallite and the blastogeny unknown, cannot be placed as an intermediate link between the two morphologically simpler genera *Caninia* and *Arctophyllum*. Besides, shortening of the counter septum during the entire neanic growth stage in *Arctophyllum*, cannot be equated with the elongated counter septum in a corresponding growth stage of *Caninia* and there is no basis for comparing those two with *Ferganophyllum*, lacking any data of that growth phase. Besides, Ross and Ross (1962) identified their new species *Pseudozaphrentoides ordinatus* as solitary, and described only its cylindrical, i.e., mature growth stage. This means that the generic position of that species is unknown and does not support the decision by Kossovaya to include her colo-

nial corals into that solitary species. Growth form is generally accepted as a qualitative character for the overwhelming majority of rugose corals. Selection of that species as a representative of the genus in those circumstances is especially unconvincing.

3. Data may be derived either from completely investigated and well illustrated taxa published already, or from the precise author's illustrations. Methods by Kossovaya (figs 1, 2) are far from those demands. Her illustrations are simplified sketches rather than precise drawings. Such important characters as the long lasting axial septum in *Hornsundia* and *Bothrophyllum*, or shortening of the counter septum in *Siedleckia vs.* its elongation in *Caninia* are missing from those sketches.

4. Phylogenies, theoretically based on early growth stages of all taxa discussed, cannot omit those stages from some taxa (fig. 1).

Unsupported and/or incorrect statements

1. Specimens described by Gorsky (1978) as *Caninia* are based on incomplete corallites, and represented by random thin sections taken from their unknown parts. Thus, the statement "show vermicularis and nistiana (amplexoid) phases" (p. 109) is not supported by the facts. The same is true for the extension of that genus to the end of the Moscovian and for its largest taxonomic differentiation in the Bashkirian-Moscovian time. All that is unsupported, resulting perhaps from simple counting of the number of species names bearing the genus name *Caninia*. True *Caninia* may well be restricted to Tournaisian-Viséan time. Some of those Gorsky's (1978) 'caninias' were included by Kossovaya (2001) in her new genus *Alekseeviella* (see above).

2. There is a substantial difference between the terms 'amplexoid septa' and 'amplexoid growth stage' or 'amplexoid morphology'. The 'nistiana' phaze, i.e., the 'amplexoid growth stage' has been documented so far only in *Caninia ss*. That morphology requires the absence of dissepiments and all major septa to be short, thin and equal in length, i.e., closely comparable to the morphology of the genus *Amplexus*. Such a morphology apparently occurs in the early growth stage of the type and only specimen representing *Pseudozaphrentoides jerofeewi* Stuckenberg, 1905 (Fedorowski 1975, fig. 1b), which is not included by Kossovaya in her phylogenetic lineages. All other taxa compared by her possess only 'amplexoid'major septa. This makes the inclusion of *Hornsundia, Pseudotimania* and *Timania* in the Cyathopsidae unsupported. Position of *Arctophyllum* which lacks an elongated counter septum remains uncertain, whereas *Ferganophyllum* which lacks fundamental data necessary for identification must be left out of the discussion.

3. Any author who copies pictures to his/her paper is obliged not only mention the source as Kossovaya did, but is also obliged to either copy them exactly, or mention the simplification and sketchy character of his/her illustrations by comparison to the originals, what she did not at least in the case of *Arctophyllum, Caninia* and *Hornsundia*.

4. Incorrectness of the original diagnostic character does not have any explanation. The original diagnostic character of *Arctophyllum*: "…with particularly well developed alar septa…" (Fedorowski 1975, p. 43) cannot be replaced by "… increase in length of the counter-lateral septa." (p. 111). In the type species for the genus *Arctophyllum* the counter-lateral septa do not increase in length.

The methodological inaccuracies and incorrect statements listed above are important enough to reject as unsupported the phylogeny reconstructed by Kossovaya (1989). Also, that reconstruction is incomplete. In addition to *Pseudozaphrentoides* mentioned above, she omitted *Caninella* Gorsky, 1938, *Yakovleviella* and perhaps *Cystilophophyllum* both of Fomichev 1953. The level of investigation of those genera may be insufficient, but they should have been at least mentioned in the paper analyzed above.

CONCLUSIONS

The *status quo* in the study on the genus *Bothrophyllum* is established in terms of: (a) the authorship of its type species, (b) the morphology and status of the neotype, (c) the characteristics of the type species based on specimens from the type site (Myachkovo Quarry), supplemented by new illustrations of Stuckenberg's (1888) specimens, (d) a discussion on species from the type area (Moscow Basin) based on similarities and differences in particular growth stages and particular characters, leading to the precise recognition of the characters of the type species and other species of *Bothrophyllum* from the type area and to exclude some from both the type species and the genus, (e) discussion of species in *Bothrophyllum* and several other genera, belonging/related/named/similar to *Bothrophyllum* described from all areas, other than the type area i.e., from all continents except for Australia and South America, from which the *Bothrophyllum*-like taxa are unknown so far, (f) inclusion of new diagnoses for the type species and for the genus *Bothrophyllum*, (g) providing lists of synonyms of and exclusions from the genus *Bothrophyllum* with ages of their occurrences, and lists of species of *Bothrophyllum* included/excluded/possibly belonging/with shortened cardinal septa are compiled.

To sum up: (a) several options for the origin and relationships of the genus *Bothrophyllum* are discussed, (b) *Bothrophyllum*-like corals with a shortened cardinal septum are recommended to be included in that genus when their remaining morphology corresponds to the type species of the genus or to be distinguished as a new genus if that morphology differs in several important characters (no new name, however, is proposed here), (c) phylogeny of *Bothrophyllum*-like taxa proposed by Kossovaya (1989) is briefly discussed and rejected.

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