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A revision of the Devonian rugosan phillipsastreid genus *Smithicyathus*

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The rugose coral genus *Smithicyathus* is diagnosed in this paper as massive to phaceloid phillipsastreid, with common horseshoe dissepiments and major septa that are very short in the tabularium. Revised taxonomy of this genus is based on analysis of over 20 numerical characters measured in sections and/or extracted from the literature data. Species are distinguished either by morphometric non-overlap in at least one, key feature or by geographic–stratigraphic isolation. The earliest possible representatives of the genus are known from the Eifelian of Angara (*S.*? *emendatus* and *S.*? *russakovi*). In the Upper Frasnian *Smithicyathus* is represented by seven species; in western Euramerica occur *S. cinctus* and *S. mcleani* sp. nov.; south-eastern Euramerican shelf area is with *S. lacunosus*, *S.* cf. *lacunosus*, *S. smithi*, *S.* cf. *smithi*, and *S. lubliniensis*; one probable species is recorded in Angara: *S.*? *belkovskiense*. The genus did not survive the Frasnian–Famennian crisis. *Smithicyathus* lived in tropical and sub-tropical shallow-marine carbonate environments, with the possible exception of the northern mid-latitudes species from Siberia. In the Holy Cross Mountains, *S. lacunosus* and *S. smithi* show a preference for restricted-marine facies. They may make up over 90% of all rugosan colonies collected in such locations, whereas in the more open-marine settings they are rare both in numbers and in proportion to other rugosan species.

Key words: Rugosa, Phillipsastreidae, *Smithicyathus*, variability, Devonian, Frasnian.

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Introduction

Many fossil corals are known exlusively from the holotype and thus, subsequent recognition of these species is hindered by poorly known intraspecific variation, especially since overlap of variability ranges can be expected in related species. This problem is clearly shown in the predominantly Frasnian (Upper Devonian) phillipsastreid genus *Smithicyathus* Różkowska, 1980. In the present paper, the database of measured massive and submassive phillipsastreids is analyzed, to (1) re-diagnose the genus *Smithicyathus* and thus separate its representatives from other phillipsastreids, and (2) distinguish species within this genus. Furthermore, (3) analysis of variability, quintile analysis, is used to investigate similarity or lack of similarity between various species of *Smithicyathus* and establish typical and outstanding colonies within its most abundantly represented species.

Institutional abbreviations.—GIUS, Department of Earth Sciences (University of Silesia), Sosnowiec, Poland; GSC, Geological Survey of Canada, Ottawa, Canada; UAM, Adam Mickiewicz University, Poznań, Poland.

Other abbreviations.—CO, ratio of space filling in a colony; D1, D2, maximum thickness of major and minor septa, respectively; DIC, calculated corallite diameter; L1, L2, length of major and minor septa within tabularium, respectively; L/T, ratio of length of major septum to tabularium radius; IN1, internal septotheca as percent of tabularium margin; IN2, ratio of expanded part of septum to its total length; MU, intercorallite wall type; N, sample size; PP, proportion of horseshoe dissepiments; SC, ratio of septal continuity between neighboring corallites; TM, TW, tabularium diameter as measured in transverse and in longitudinal section, respectively. More explanation and additional abbreviations are presented in Appendix 1.

Material and methods

The material for the present study has been selected from over 350 massive colonies taken from the literature and representing the Devonian World. They range in age from Eifelian to Famennian and were described from what is today central and western Europe, North Africa and North America (Fig. 1). Only a few specimens (and species) are known from China, Australia, and Russia (and countries of the former USSR). This reflects the practice of illustrating only selected specimens (usually holotypes) in the literature, rather than a lack of coral-bearing deposits in these areas. Added were about 550 colonies of mostly unpublished massive and phaceloid Devonian phillipsastreids from the Holy Cross Mountains, Poland (Figs. 2, 3). These colonies

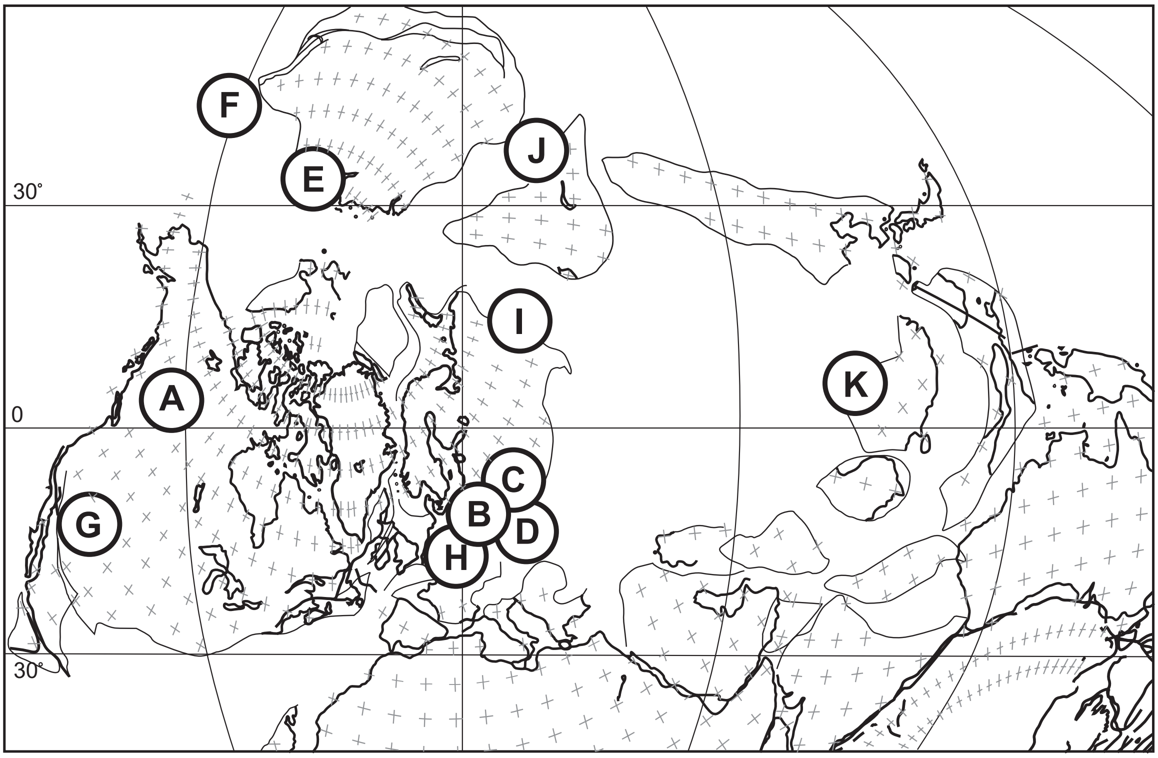


Fig. 1. Geography of the Devonian World, after Scotese and McKerrow (1990: fig. 15) with locations, yielding material for the present study. Locations with *Smithicyathus*: A, Western Canada; B, Holy Cross Mountains (see Figs. 2, 3); C, Lublin area; D, Moravia. Locations with dubious *Smithicyathus*: E, New Siberian Islands; F, NE Siberia. Additional locations with comparative material: G, New Mexico; H, Harz Mountains; I, Urals; J, Kuzbass; K, South China.

were measured, either directly from thin sections or from the photographed material, and the data obtained assembled into a database. This, along with published information, has provided a "hunting ground" for *Smithicyathus*.

Scanned thin sections of the original material used for the present study and numerical data of all material is available at the web-page of the Chair of Ecosystems Stratigraphy of the Earth Sciences Department at Sosnowiec (http://kse.wnoz.us.edu.pl/), sub-page of the Virtual Paleontological Museum (accessible also at: http://www.rugosa.wnoz.us.edu.pl).

Database.—Massive and submassive (i.e., densely packed phaceloid) phillipsastreid colonies have been measured; mean values were calculated, usually from measurements of five transverse and three longitudinal sections of "adult" corallites, i.e. those displaying stable size and morphology in each colony. The data were arranged in a Microsoft Access database. Each colony (record) in the database contains data from a single colony, or a morphologically distinct part of a colony and columns contain data corresponding to particular characteristics of individual specimens. Each colony is with sample location, collection storage information, and a suggested genus and species. The numerical data are either of ordinal type, i.e., with numerical values referring to discrete states as e.g., septal carination, or continuous values, with actual measurements and counts of various parameters, as well as some quantified estimates of gradational characteristics. Numerical data are presented and briefly explained in Appendix 1. Wherever possible, care has been taken to represent characters rather as continuous numerical variables, and not as discrete nominal values. This is the case with presentation of colony types. Gradation from protocorallites, through dendroid, phaceloid, cerioid, astreoid (pseudocerioid), thamnasterioid to aphroid colonies is non-continuous. Instead of using a single parameter, three separate characters were recorded for each colony of *Smithicyathus* to describe the observed variability. These are: CO (ratio of space filling in a colony), MU (type of intercorallite wall), and SC (ratio of septal blade development between neighboring corallites). This appears to be a more suitable way to describe otherwise hard to quantify structures, as in some massive astreoid *Smithicyathus smithi* (Różkowska, 1953) having peripheral atrophy of septa. This would be a combination corresponding to a peculiar "pseudocerioid-aphroid" colony.

The database thus formed can be considered an open system, available for correction of individual entries and also for adding or removing both records (colonies) and columns (features).

Taxonomic decisions.—These were made with multi-step analysis of data; recognized distribution patterns allowed for verification and correction of the earlier, usually intuitive, identifications of taxa. In the first step (1) the database was assembled, as described above, with data on over 900 measured massive and phaceloid phillipsastreid colonies obtained; (2) then, ca. 760 "complete" colonies were selected

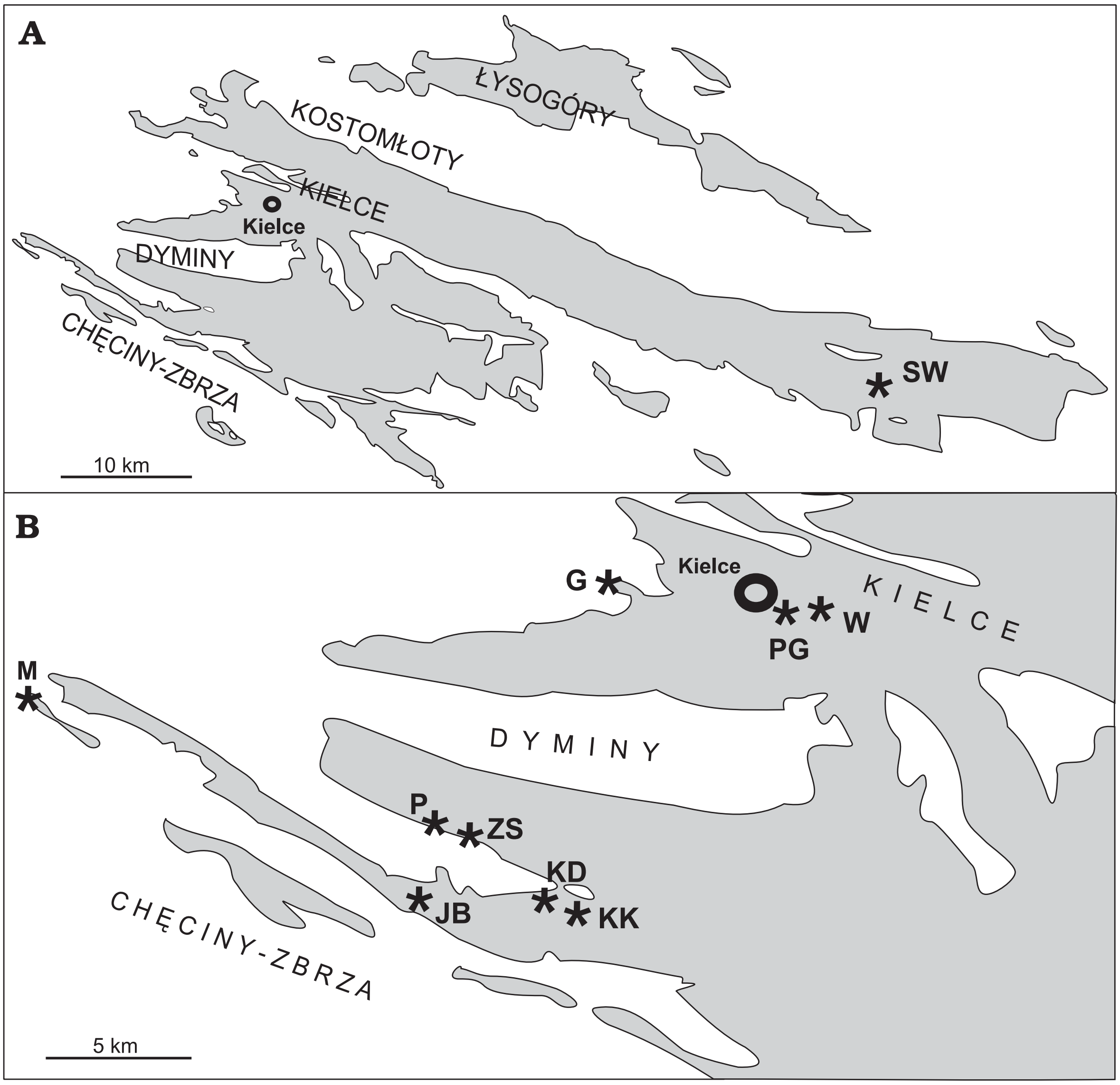


Fig. 2. Schematical geological map of the Devonian outcrop (shaded) in the Holy Cross Mountains, central Poland (after Dzik 2002: fig. 1A), with the main marine Devonian facies belts marked and with indicated coral-bearing sites mentioned in this paper: G, Grabina; JB, environs of Jaźwica quarry; KD, Kowala road cutting; KK, Kowala quarry; M, Miedzianka; P, Panek; PG, Psie Górki; SW, Sobiekurów; W, Wietrznia; ZS, Zgórsko.

for further analysis. These were colonies with both transverse and longitudinal sections of corallites that could be measured and described. The subsequent step (3) was to divide the database into "homogenous" subunits: those which seemed to represent either geographically and/or stratigraphically and/or morphologically, well-constrained groups of colonies. This analysis allowed for recognition of 8 species groups within this database, as summarized in Wrzołek (2005: 164–166). One group is interpreted in the present paper as the genus *Smithicyathus*. Here belong approximately 130 colonies (as listed in Appendix 2) characterized by three characters in combination: frequent horseshoe dissepiments, i.e., PP ≥0.6 and short septa within tabularium: L/T <0.335 (where L/T = 2L1/TM and indicates ratio of major septal length to tabularium radius). Classification was continued as far as reliable criteria could be found to restrict the material as much as possible to discrete paleophena (Dzik 1990), that is, groups of specimens thought to represent individual, numerically well-constrained species, usually without bi- or poly-modal distribution of their principal characters. In some cases, different nominal species fall within a single morphometrically defined group. In such a case the younger species (here a subspecies) must be regarded as a junior synonym of the older one, as *Phillipsastrea lacunosa mariae* Wrzołek, 1993 and *Pachyphyllum lacunosum* Gürich, 1896 (see Table 1). In other cases, however, there is some morphometric overlap between two distinct groups of specimens, as is the case with *Medusaephyllum variabile* Sorauf, 1988 and massive species of the genus *Smithicyathus*; in the former species about 1/3 of the sample studied (N = 12) is characterized by low L/T values, similar to those occurring in the "typical" *Smithicyathus*; separation of *Medusaephyllum variabile* from

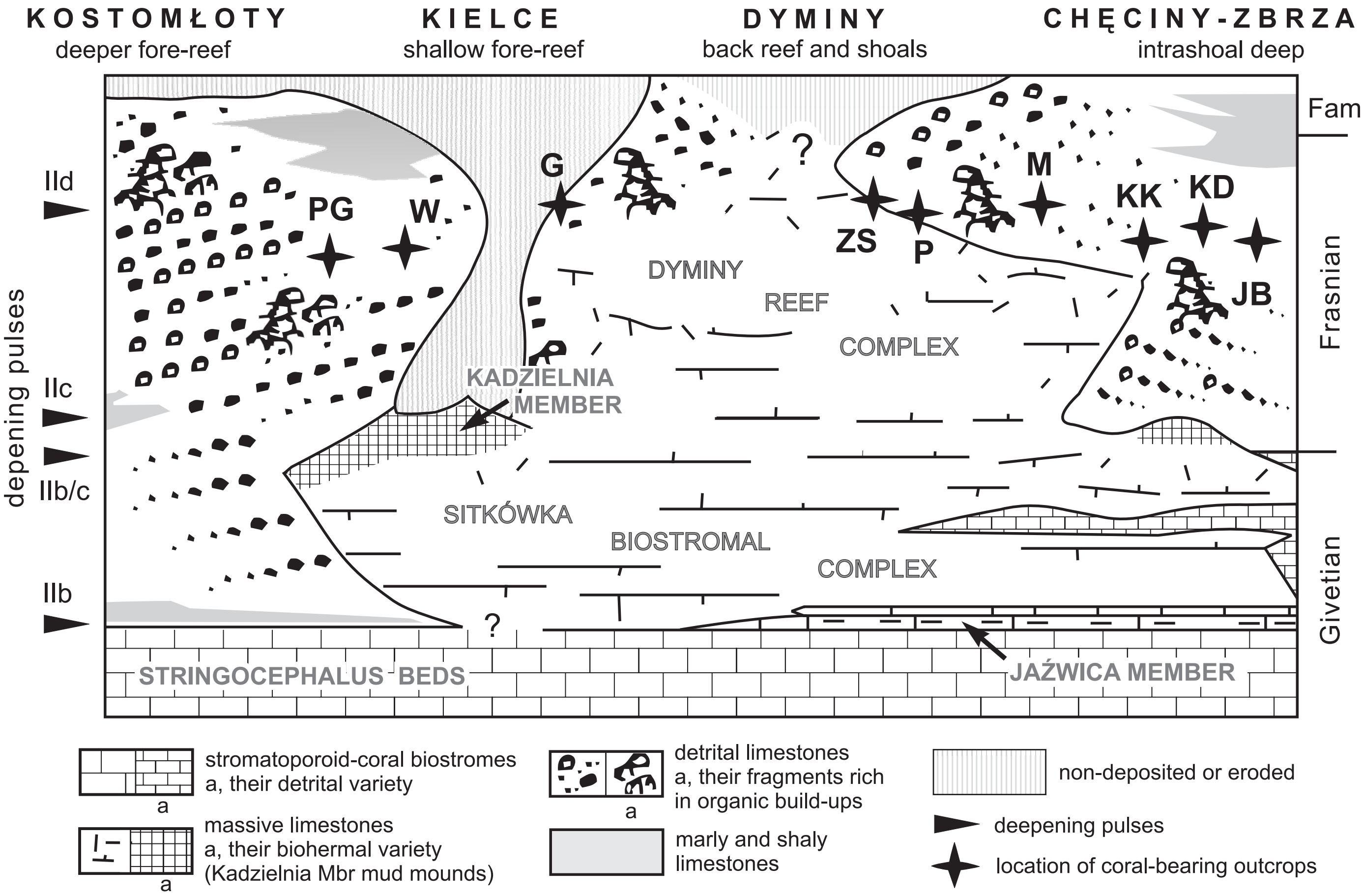


Fig. 3. Stratigraphy of the *Smithicyathus*-bearing deposits in the western part of the Holy Cross Mountains, central Poland; simplified and modified from Racki (1993: fig. 3, in part), G, Grabina; JB, environs of Jaźwica quarry; KD, Kowala roadcut; KK, Kowala quarry; M, Miedzianka; P, Panek; PG, Psie Górki; W, Wietrznia quarry; ZS, Zgórsko. Facies setting of Sobiekurów (SW) not marked here, would correspond to Upper Frasnian occurrence of shales and marls, as indicated above PG or KD in this scheme.

Smithicyathus is based on the presence of isolated trabeculae between neighboring corallites and the absence or scarcity of intercorallite walls in the former taxon. However, *M. variabile* apparently has a very broad range of variability and thus some of its specimens may be morphologically indistinct from *Smithicyathus*.

Still another analytical procedure, namely multi-factor analysis (4), can be applied for suspect species (taxa) having significant overlap of ranges of variability in many characters studied. To be as meaningful as possible, such an analysis requires a large volume of data for each species considered, and this is not the case for many of the species studied here.

Analysis of variablity.—Two groups of *Smithicyathus* specimens were analyzed, representing phaceloid and massive material (numerically dominated by *Smithicyathus lacunosus* and *S. smithi* respectively, but with other species added, as listed by Tables 1 and 2). Distribution of specimens within these samples was reviewed, character by character and registered were extreme or atypical records for each parameter, representing 5 intervals for original distribution (outlying low, low, medium, high and outlying high values); in case of some parameters, their distribution was normal and records could be placed in three median, and occasionally also in some extreme quintiles, in some examples distribution was skewed and colonies were listed as typical and atypically high (or low) or outstanding. The “typicality” (or “atypicality”) of a given colony (record of the database) has been evaluated by summarizing its occurrences in outlying up or down quintiles (each presence valued 3 points), extreme low or high (valued 1 point), with zero value given to presence in median quintile. The sum of these values for a given colony represents measure of its atypicality or atypicality index; these indices are presented in Tables 1 and 2, and the taxonomical decisions presented here are primarily based on them. This quintile analysis is a simple way to distinguish typical and atypical specimens in large collections, not only of fossil corals. Of course I can imagine one might construct a similar analysis based on the other values ascribed to outstanding and extreme occurrences in quintiles, one might also consider distribution of specimens within more than five intervals, thus having deciles or centiles rather than quintiles—this I leave for the other workers. In the present study, quintile analysis suggests distinction between the phaceloid species *Smithicyathus lacunosus* from the Holy Cross

Table 1. Atypicality indices in 73 phaceloid colonies of *Smithicyathus*: *Smithicyathus lacunosus* (N = 67), *Smithicyathus* cf. *lacunosus* (N = 3) and in *Smithicyathus mcleani* sp. nov. (N = 3). Asterisks (*) mark colonies illustrated in the literature (Różkowska 1953—UAM A73,6; Wrzołek 1993; McLean 1994b—GSC); *italics* for those of *Phillipsastrea lacunosa mariae* Wrzołek 1993; ***boldface italics*** for 3 colonies of *Smithicyathus* cf. *lacunosus*; **boldface** for 3 colonies of *Smithicyathus mcleani* sp. nov.

Atypicality index	Colonies	Interpretation
10–17	***P173a P173b P147a*** **GSC98207*** **GSC98208***	outstanding
7–9	KD41B P166b PG41B PG90A	extremal
4–6	G155-1 G169 KD25 KD39 KK27* KK158 MS01E P121 P159 ZS08 **GSC13826**	
2–3	*G11* G152-1 *KK24** *KK29** KK55* KK156A KK264B KK288 *PG09** ZS13	typical
1	G16B KK52 KK60 KK129 P22 P30 P57 P96 P108 P132 *PG27** UAM A73,6* ZS07 ZS11 ZS15B*	
0	KK278A P06 P08 P09 P21 P29 P41 P54 P65 P72A P89 P105 P109 P160 P163 P164 P166a P172 P178 PG29 *PG31* PG51B UAM324 UAM325a UAM342 UAMKorcz1891B ZS12A* ZS17	

Table 2. Atypicality indices in 52 massive colonies of *Smithicyathus*: *Smithicyathus smithi* (N = 45), *Smithicyathus* cf. *smithi* (N = 2), *Smithicyathus lubliniensis* (N = 2), and in *Smithicyathus cinctus* (N = 3). Asterisks (*) mark colonies illustrated in the literature (Różkowska 1953—UAM A61-3; Różkowska 1980—the holotype of *S. lubliniensis*; Wrzołek 1993; GSC specimens—Smith 1945 and McLean 1994b); ***boldface italics*** for 2 colonies of *S.* cf. *smithi*; **boldface** for 3 colonies of *Smithicyathus cinctus* (prefixed GSC) and 2 colonies of *Smithicyathus lubliniensis* (prefixed UAM).

Atypicality index	Colonies	Interpretation
15–20	P165a **GSC 9244*** **GSC98205*** **GSC98206***	outstanding
9–10	***P101*** **UAMroz80*** **UAMKorcz1891A** ***ZS05***	
6	P27B P39 P74 PG35B	extremal
4–5	P58 P104a P174A UAMKorcz1951c	
2–3	KD12* P01 P28* P49 P97 P104b P175 P176 P177A UAM310A	typical
1	P32 P50 P53* P55A P55B P56 P61 P162 P165b P168 P179 P180A UAM A61-3* UAM310B ZS14*	
0	P27A P43* P51 P66 P69 P107 P112 P153 P158 P161 P167	

Mountains and the phaceloid *S. mcleani* sp. nov. from Western Canada. It also suggests a lack of distinction between the Holy Cross species *S. lacunosus* and *S. mariae* (Table 1); in massive material there is morphometric distinction between *S. cinctus* (Smith, 1945), *S. smithi*, and *S. lubliniensis* Różkowska, 1980 (Table 2). Such an analysis is of limited value, however, for isolated specimens, as there is no way to tell how typical or atypical they are (were) within their populations.

The material studied contains a few colonies with marked polymorphism. These distinct morphs were analyzed as separate records and are indicated by lower case letters at the end of their collection number. Although they will be analyzed separately, they should be noted here as they indicate phenotypic plasticity, and thus very broad variability range to be expected in these corals (see also systematic part below). Modern and Neogene examples of this phenomenon in Scleractinia are described by Budd (1993).

Paleogeographical and geological setting

Smithicyathus and comparative material, as presented here, comes from the following areas (Fig. 1):

(1) South-eastern shelves of Devonian Euramerica (presently Holy Cross Mountains, Poland—details will be given below, also Lublin area subsurface—Upper Frasnian Modryń Formation: see Różkowska 1980; Miłaczewski 1981).

(2) Western shelves of Euramerica (Upper Frasnian of western Canada: McLean 1994b, Upper Frasnian of New Mexico: Sorauf 1988; also material of the author from western Alberta, the Mount Hawk Formation, ?Ronde Member, collected at Cinquefoil Mountain, see Geldsetzer 1987: 39–43).

(3) Shallow marine settings within the oceanic realm to the south of Euramerica (Moravia—Sumbera rocks near Brno, Czech Republic, see Hladil and Kalvoda 1993: 38–40, a single colony collected by the author, and Harz-Iberg limestone at Winterberg quarry, material of Pickett 1967: pl. 1: 3–5).

(4) Shallow marine settings within the Uralian oceanic realm (Russia) to the east of Euramerica (Soshkina 1952: pl. 20: 74).

(5) Southern shelves of Angara and shallow marine settings within the oceanic realm (Indigiro-Kolyma area) to the south-west of Angara (presently located in northern and in north-eastern Siberia, Russia respectively; details on corals' locations are in Besprozvannykh et al. 1975).

(6) North-eastern margins of Angara (presently Kuzbass area in south-central Siberia, Russia; Famennian Kurunduss beds; detail on corals given by Bulvanker 1958).

(7) Marginal seas of the south China craton (presently Sichuan; corals published by Hou 1988).

The Holy Cross Mountains of central Poland (Figs. 1–3), provided material of *Smithicyathus* chiefly from the Panek and Zgórsko quarries at Bolechowice (73 + 9 records) representing shallow-marine, possibly back-reef environments, whereas Grabina (5 colonies), Kowala quarry (12 colonies), Psie Górki (8 colonies), Wietrznia (1 colony) and road cutting at Kowala (4 colonies) display sediments of more and more offshore fore-reef settings (Figs. 2, 3). The stratigraphic data for these locations (Fig. 3) has been modified from Racki (1993).

The comparative material from the Holy Cross Mountains is *Phillipsastrea progressa* (Różkowska, 1953) with 28 colonies from the Upper Frasnian (Psie Górki, Domaszowice, Jaźwica quarry set R, Śluchowice quarry), and *Ph. dybowskii* (Różkowska, 1953) with 12 colonies, mostly from Upper Frasnian marly limestones of Sobiekurów, eastern Holy Cross Mountains. Another species is *Ph. samsonowiczi* (Różkowska, 1953), known only from two colonies, reported by Różkowska (1953: 54, 55) from the Upper Frasnian of Kowala and Psie Górki.

Systematic paleontology

Family Phillipsastreidae C.F. Roemer, 1883.

Genus *Smithicyathus* Różkowska, 1980.

Type species: *Phillipsastrea cincta* Smith, 1945, designed by Różkowska 1980: 18, Upper Frasnian, District of Mackenzie, Redknife River, Canada.

Emended diagnosis.—*Smithicyathus* Różkowska, 1980, is a massive to submassive phillipsastreid with (1) L/T index 0.335 or lower, i.e., its major septa do not reach deeper into tabularium than 0.335 of its radius; (2) numerous horseshoe dissepiments (PP = 0.6 or more, typically 1.0, i.e., continuous series) sometimes obscured by expanded septa.

This combination of features seems rare if not unique within the family Phillipsastreidae; it can be observed also in some (but not all) colonies of *Ph. variabilis* (Sorauf, 1988) which, however, can be distinguished by degradation of peripheral septal blades to isolated spines combined with reduction of intercorallite walls (Fig. 4A), and rarely in *Ph. progressa* (Różkowska, 1953; see Fig. 4B), which is predominantly thamnasterioid (*versus* astreoid or phaceloid *Smithicyathus*) and with corallites larger than in the species of *Smithicyathus* and in *Medusaephyllum variabile*.

Species assigned.—*Pachyphyllum lacunosum* Gürich, 1896 (including *Phillipsastrea lacunosa mariae* Wrzołek, 1993), *Phillipsastrea cincta* Smith, 1945, *Smithicyathus mcleani* sp. nov. (included into *Smithicyathus cinctus* by McLean 1994b), *Pachyphyllum smithi* Różkowska, 1953, and *Smithicyathus lubliniensis* Różkowska, 1980; also, *Smithicyathus* cf. *lacunosus* (Gürich, 1896) and *Smithicyathus* cf. *smithi* (Różkowska, 1953) as presented below.

Doubtful species.—Here belong the three species described by Spasskiy and Kravtsov (in Besprozvannykh et al. 1975): *Phillipsastrea emendata*, *Frechastraea russakovi*, and *Stellatophyllum belkovskiense* (but not: *S. belkovskiense* of Hou 1988). These species are discussed below.

Most probably not to this genus should be assigned the two other colonies, originally identified as representing the species of *Smithicyathus*, but with high L/T indexes, as listed in Appendix 3 (columns "o" and "p"). They are *Pachyphyllum cinctum* as illustrated by Soshkina (1952: pl. 20: 74), classified as *Chuanbeiphyllum* by McLean (1994b), with a narrow tabularium and broad aphroid dissepimentarium, and *Pseudoacervularia* cf. *smithi* of Pickett (1967: pl 1: 3–5) having marked lateral septal expansion, and possibly close to *Phillipsastrea ranciae* Coen-Aubert, 1987. More material would possibly allow for better justification of taxonomical decisions, both at genus and species level, in case of these two taxa.

Comparative material.—Here belong over 50 colonies listed in Appendix 3, which represent 4 species of *Phillipsastrea* that are morphologically close to *Smithicyathus*. Among them are two colonies of *Ph. progressa* (Różkowska, 1953) from the Holy Cross Upper Frasnian with atypically short major septa (see column "l" of Appendix 3; one of them is illustrated in Fig. 4B), whereas a majority of colonies of this species (26 out of 28 studied) have septa that are significantly longer in the tabularium. This suggests only minor morphological overlap between *Smithicyathus* and *Ph. progressa*.

The other comparable species is *Ph. variabilis* (Sorauf, 1988) from the Upper Frasnian of western North America, with a very broad range of variability (Appendix 3: columns "m" and "n"), especially with respect to septal length in the tabularium, septal development between tabularia (very frequently only occurring as isolated spines in this area), and also the frequency of horseshoe dissepiments. Five out of 12 colonies measured might be "numerically" included into *Smithicyathus*, among them also the specimen shown in Fig. 4A, but review of all the material allows for interpretation of *Ph. variabilis* as a distinct species, with significant morphological overlap with *Smithicyathus*. Occurrence of isolated spines (trabeculae) in outer septal regions may be the most conspicuous diagnostic feature of *Ph. variabilis*. According to McLean (personal communication, 2004) these two species (*S. cinctus* and *Ph. variabilis*) can occur together in the Upper Frasnian of western Canada.

Two very similar species, *Ph.*? *dybowskii* (Różkowska, 1953) and *Ph.*? *samsonowiczi* (Różkowska, 1953), thus far only illustrated by two colonies, are peculiar submassive/cerioid species: *Ph.*? *dybowskii* has longer septa in the tabularium and larger corallites (Fig. 4C, see also Appendix 3, column "q") than *Ph.*? *samsonowiczi*. Multiserial tabularia with distally convex profile and variable but generally poor development of horseshoe dissepiments testify against including these two species into *Smithicyathus*. Possibly they are related to astreoid *Ph. ananas* (Goldfuss, 1826) *sensu* Różkowska (1953).

Discussion.—The genus was introduced by Różkowska (1980: 18), who diagnosed it as containing massive to subphaceloid phillipsastreids, with an epithecate (three-layered) intercorallite wall commonly surrounding more than one corallite. In the Devonian of Poland, Różkowska (1980) recognized two species of the genus: *S. lacunosus* and *S. lubliniensis*. Wrzołek (1993) classified the species recognized in the present paper as *Smithicyathus* into *Phillipsastrea*, as four subspecies of *Ph. lacunosa*, i.e., *Ph. lacunosa lacunosa*, *Ph. l.*

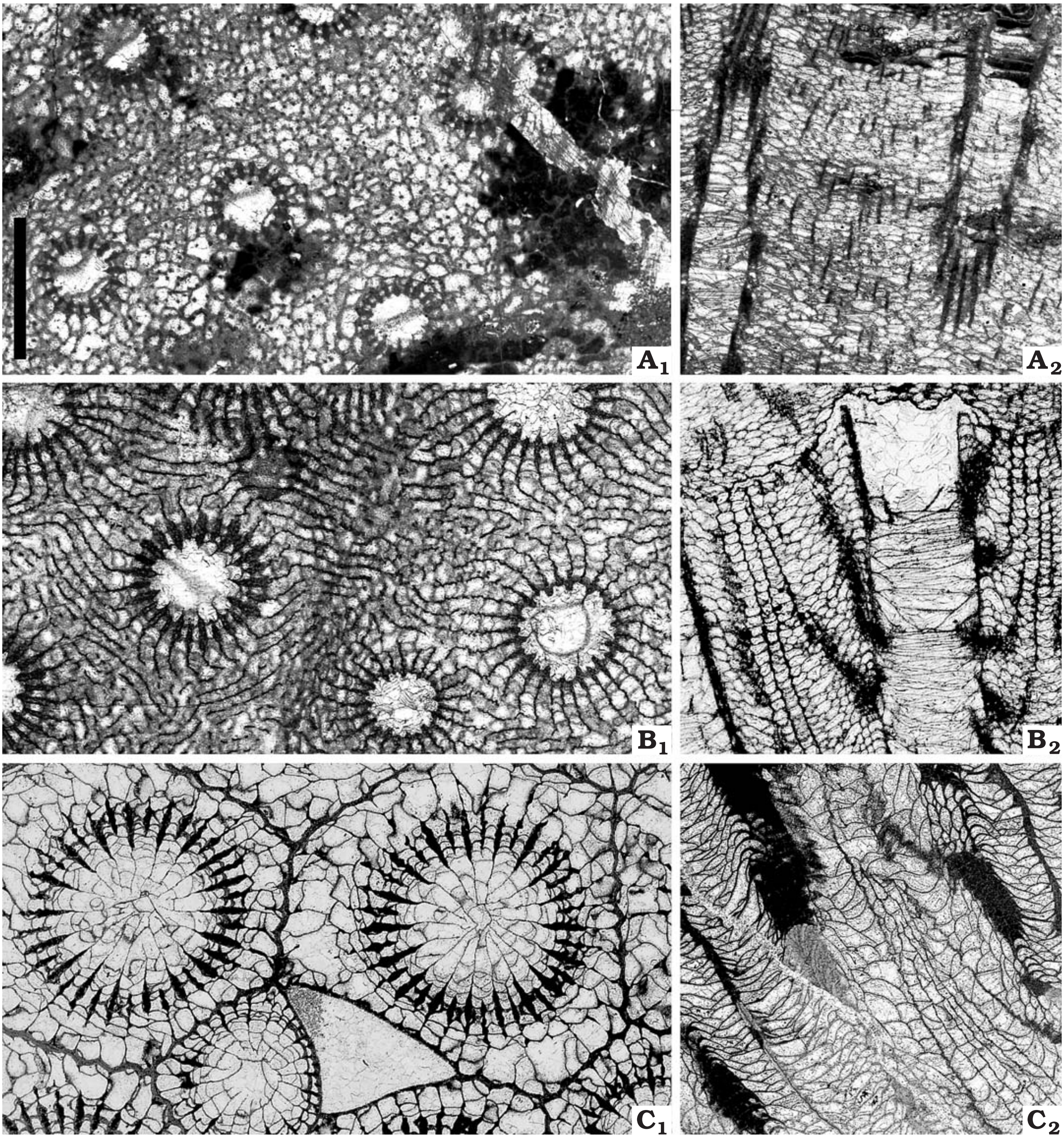


Fig. 4. Upper Frasnian tetracorals more or less similar to *Smithicyathus*. **A**. *Phillipsastrea variablis* (Sorauf, 1988), Western Canada, GIUS1531CD 09, a colony with short septa in tabularium, see text for exact location (A_1 transverse, A_2 longitudinal section). **B**. *Phillipsastrea progressa* (Różkowska, 1953), fields to the South of Bolechowice village, GIUS 402JB 01, colony with septa atypically short in the tabularium; the thamnasterioid species, with weak lateral septal expansion and numerous horseshoe dissepiments (B_1 transverse, B_2 longitudinal section). **C**. *Phillipsastrea dybowskii* (Różkowska, 1953), Sobiekurów quarry, GIUS 373SW 10, a typical colony with phaceloid to massive habit, ceriod (tripartite) walls seen in places without secondary silification, with long septa, and variable development of horseshoe dissepiments; (C_1 transverse, C_2 longitudinal section). Scale bar 4 mm for all items.

smithi, *Ph. l. mariae* ssp. nov. and *Ph. l. lubliniensis*. McLean, in a monograph of Canadian phillipsastreids (1994b: 79–80) followed the diagnosis of Różkowska (1980) and discussed possible synonymy of *Smithicyathus* with *Paramixogonaria* Liao and Birenheide 1985, which remains dubious in his opinion. He also described in detail new Canadian material of the type species and discussed several species of the genus, among them *Pseudoacervularia samsonowiczi* Różkowska, 1953 from the Holy Cross Devonian. Fedorowski (2003), in a review of rugose corals from the Polish Devonian, re-illustrated and re-classified the Polish material of, among others, Różkowska (1953, 1980) and Wrzołek (1993). In his opinion *Smithicyathus* is represented in Poland, in addition to *S. lacunosus lacunosus* and *S. lacunosus mariae*, by *S. dybowskii* and *S. samsonowiczi*, but not by *Phillipsastrea smithi*.

Review of the intercorallite wall structure (see also Fig. 5) allows for revision of the generic concept of *Smithicyathus*. Both the literature and the author's material indicate that the walls in the species considered here as belonging to *Smithicyathus* can be either pseudocerioid or, rarely cerioid or both structures can be seen in the same colony.

(1) Pseudocerioid walls. These can be seen in massive colonies and also in the holotype of *S. cinctus* (Smith 1945: pl. 22: 4, re-illustrated here in Figs. 5A, 6A) and in the topotypic material, illustrated by McLean (1994b: pl. 3: 1–4). In the latter case pseudocerioid wall is indicated by local occurrence of vertically non-continuous wall, formed by isolated and short wall segments (seen in longitudinal section in Fig. $5A_2$). Contrary to the opinion of McLean (1994b), pseudocerioid walls can be seen in massive *S. smithi* (Różkowska, 1953) and also in its submassive colonies, with intracolony voids bordered by epithecate walls (Fig. 5C). Additionally, review of material of *S. lubliniensis* Różkowska, 1980, indicates the presence of pseudocerioid walls in this submassive species.

(2) Cerioid (tripartite) walls. These typically are present in submassive–phaceloid colonies of *S. mcleani* sp. nov. (see Fig. 6B, C) and of *S. lacunosus* (Gürich, 1896; see Fig. 5B). These species are characterized by generally phaceloid form with isolated epithecate corallites, but with significant massive segments of colonies, with cerioid walls dominating. On the other hand pseudocerioid wall segments can also occur there, especially in newly formed partitions between parent and offset corallites (Fig. $5B_2$), but also between some adult corallites, as in Fig. $5B_1$.

Occurrence of multiple corallites within a single wall, considered to be an important characteristic of the genus *Smithicyathus* (Różkowska 1980: 18; McLean 1994b: 80) does not occur as commonly as suggested in the literature. It can be clearly seen only in the type material of *S. cinctus*, from western Canada. In other material it seems that only juvenile multiple offsets are associated with their parent corallite to give the impression of this structure (as in *S. mcleani* sp. nov. in Fig. 6B).

From the other massive Phillipsastreidae, as reviewed by McLean (1994b, see also McLean 1994a), *Trapezophyllum* and its possible synonym *Stellatophyllum* are massive and cerioid, with numerous horseshoe dissepiments. Non-cerioid and commonly with the horseshoe dissepiments are: *Phillipsastrea* (its possible synonym *Pseudoacervularia*), *Chuanbeiphyllum*, *Pachyphyllum*, and *Smithicyathus*. Within these *Chuanbeiphyllum* can be distinguished by large corallites and septal degeneration between the tabularia, whereas *Phillipsastrea* and *Pachyphyllum* are with medium-sized corallites. The former genus is with typically massive habit, the latter is massive and transitory to dendroid habit, with few corallites in a colony, highly elevated above its massive part. *Smithicyathus* and its probable synonym *Paramixogonaria* is with small corallites and short septa in tabularium. *Frechastraea* is with small-sized corallites and without horseshoe dissepiments.

Some representatives of the predominantly dendroid genus *Thamnophyllum* also develop the phaceloid arrangement of corallites and thus are similar to some species assigned to *Smithicyathus* by me. For example in western Canada phaceloid and short-septate *Th. tructense* (McLaren, 1959) is more similar to *S. mcleani* sp. nov. than dendroid and also short-septate *Th. pedderi* McLean, 2005 (both species illustrated by McLean 2005).

Smithicyathus cinctus (Smith, 1945)

Figs. 5A, 6A.

1945 *Phillipsastrea cincta* sp. nov; Smith: 43, pls 22: 4a–c, 23.
non 1952 *Pachyphyllum cinctum* (Smith); Soshkina 1952: 86, pl. 20: 74 (possibly to *Chuanbeiphyllum*)
non 1962 *Phillipsastrea cincta* Smith; McLaren and Norris 1962: pl. 11: 28, 29 (to *Smithicyathus mcleani* sp. nov., see Fig. 6C)
1986 *Smithicyathus cinctus* (Smith); Sorauf and Pedder 1986: pl. 5: 1, 4.
1994 *Smithicyathus cinctus* (Smith, 1945); McLean 1994b: 80–82 (partim), pl. 3: 1–4 (non pl. 2: 2–5 = *S. mcleani* sp. nov.).

Material.—Besides the holotype (GSC 9244) there are two other, possibly topotypical colonies listed by McLean (1994b: 81) from the Uppermost Frasnian of Alberta, Canada: GSC 98205, 98206.

Diagnosis.—The massive species of *Smithicyathus* with septa present only at the inner boundary of the dissepimentarium, i.e., in the vicinity of the vertical series of horseshoe dissepiments, with very large corallites (DIC is over 7.7 mm), commonly with more than one tabularium within a single intercorallite wall.

Discussion.—This species is geographically isolated from others of the genus. Two morphotypes: massive and phaceloid, were included into the species by McLean (1994b), with massive specimens indicated as topotypic. Measurements and the numerical analysis by me (Tables 1, 2 and Appendix 2) suggest that; (1) massive and phaceloid colonies should be regarded as separate species (different CO and DIC parameters); and (2) comparison with the other species (Appendix 2) indicates that the tabularium diameter (TM and TW), and consequently L1 and L2, are larger in the Canadian material (both in massive *S. cinctus* and in phaceloid *S. mcleani* sp. nov.), than in any other species of *Smithicyathus*, with the exception of the two Siberian species *S.*? *emendatus* and *S.*? *russakovi*. Further comparison with the two latter species will be possible when more Siberian material is available. Among the best-known species of the genus, *S. cinctus* is morphometrically and morphologically most similar to *S. smithi* and its closely related species, *S. lubliniensis*, but the

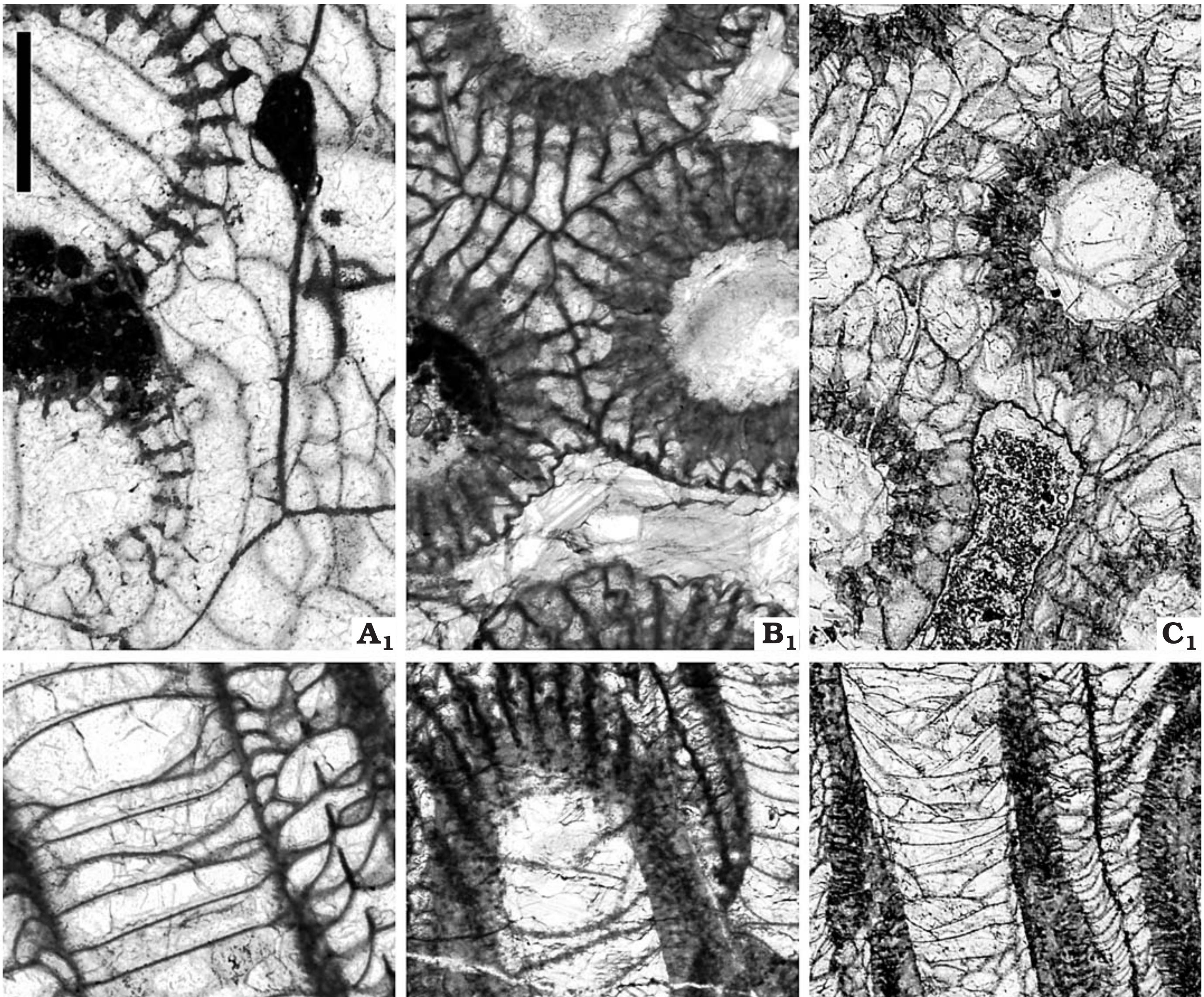


Fig. 5. Wall and septal microstructures in the Upper Frasnian *Smithicyathus*. **A**. The holotype of massive *Smithicyathus cinctus* (Smith, 1945), Western Canada, GSC 9244, with non-cerioid, locally discontinuous intercorallite walls; for details of sampling location see McLean 1994b: 80, 81 (A_1 transverse, A_2 longitudinal section). **B**. *Smithicyathus lacunosus* (Gürich, 1896), Panek quarry, GIUS 384P 54, densely phaceloid colony with cerioid (tripartite) intercorallite walls predominating, but also with pseudocerioid segments, mainly between parent and offset corallites close to offsetting area, note also presence of 3rd order septa at some corallite peripheries (B_1 transverse, B_2 longitudinal section). **C**. *Smithicyathus smithi* (Różkowska, 1953), Zgórsko quarry, GIUS 382ZS 14, massive pseudocerioid colony with occasional intercorallite voids, bordered by epithecate walls (C_1 transverse, C_2 longitudinal section). Scale bar 2 mm for all items.

latter two typically have smaller corallites (lower values of DIC, TM, lower septal number). *Pachyphyllum cinctum* of Soshkina (1952; mentioned under "dubious species" above; see also Appendix 3, column "o") possibly represents a distinct species of the phillipsastreid genus *Chuanbeiphyllum* He, 1978 (as suggested by McLean 1994b: 81).

Stratigraphic and geographic range.—Uppermost Frasnian of the District of Mackenzie, western Canada: Kakisa Formation (McLean 1994b: 81).

Smithicyathus mcleani sp. nov.

Fig. 6B, C.

1962 *Phillipsastrea cincta* Smith; McLaren and Norris 1962: pl. 11: 28, 29 (colony re-illustrated here in Fig. 6C)

1994 *Smithicyathus cinctus* (Smith, 1945); McLean 1994b: 80–82 (partim), pl. 2: 2–5 (non pl. 3: 1–4 = *S. cinctus*).

Derivation of the name: In honour of Ross McLean, student of Devonian Rugosa.

Holotype: GSC 98208 (illustrated by McLean 1994b, pl. 2: 4, 5 and re-illustrated here in Fig. 6B), a colony.

Type locality: NW flank of Mount Mackenzie (Amoco Loc. 11411), Alberta, Canada (McLean 1994b: 81).

Type horizon: Uppermost Frasnian (the top of Simla Formation).

Material.—Besides the holotype there are 2 other colonies listed by McLean (1994b: 80, 81) from the Uppermost Frasnian of Alberta, Canada: GSC 98207 from Eagle's Nest Pass (Amoco Loc. 15255) and GSC13826 probably from Simla Fm of Cardinal Mountain (GSC Loc. 24398).

Diagnosis.—Submassive (phaceloid) colonies of *Smithicyathus*, commonly with cerioid walls in their massive fragments, and with well developed peripheral dissepimentaria. Corallites are large: their diameter is from 5.5 to 5.8 mm, tabularium diameter is from 2.99 to 3.5 mm.

Description.—The colonies are phaceloid, densely packed with corallites (Fig. 6B_1, C_1). Cerioid walls between the neighboring corallites are common, although pseudocerioid (septal) walls can also occur and in places walls are totally absent, possibly between parent–offset (Fig. 6C_1). Septa of both orders barely enter tabularium, they may be to a various degree withdrawn from the corallite periphery. The horseshoe dissepiments are developed in a single series at the tabularium–dissepimentarium boundary (Fig. 6B_2, C_2), locally they can be replaced by peneckielloid dissepiments in narrower fragments of corallites (Fig. 6B_2). At the corallite periphery there are typically one or two rows of peripheral, globose dissepiments. Tabularium is with mostly complete, usually flat tabulae.

Discussion.—Although McLean explicitely noted (1994b: 81) that high intracolony variation speaks for both phaceloid and massive colonies being included in a single species, namely *Smithicyathus cinctus*, the current re-examination of available material from the Upper Frasnian of Western Canada (6 colonies) suggests there are in fact two distinct species present there. The first is a massive species (presented as *S. cinctus* above), the other, *S. mcleani* sp. nov., is phaceloid and has large tabularia. The new species is numerically very close to *S. lacunosus* from the Holy Cross Devonian (described below); in fact comparison of most measured parameters (see Appendix 2: columns "b" and "c") shows either very close or overlapping variability ranges of the two species. Generally, however, the separate species status of *S. mcleani* sp. nov. is indicated by: (1) larger tabularia, combined with (2) the morphometrical similarity of corallites to those of massive *S. cinctus*, and (3) analysis of variability of the total sample of phaceloid colonies indicating high "atypicality" of the Alberta material (Table 1, prefixed GSC), in relation to "typical" colonies representing *Smithicyathus lacunosus*.

Stratigraphic and geographic range.—Uppermost Frasnian of Alberta, western Canada: Simla Formation and probable Simla Formation. More details on sampling locations are in McLean (1994b: 81, listed by him among the material of *S. cinctus*).

Smithicyathus lacunosus (Gürich, 1896)

Figs. 5B, 7A–C, 8A.

1896 *Pachyphyllum lacunosum* sp. nov; Gürich 1896: 183–184, pl. 4: 6a–c.

1953 *Pachyphyllum lacunosum* Gürich; Różkowska 1953: 45, fig. 26, pl. 6: 3, 4.

1978 *Frechastraea*? *lacunosa* (Gürich, 1896); Birenheide: 104–105, fig. 55.

1993 *Phillipsastrea lacunosa lacunosa* (Gürich, 1896); Wrzołek: 295, fig. 1.1–1.5.

1993 *Phillipsastrea lacunosa mariae* ssp. nov.; Wrzołek: 295–297, figs. 2.1–2.6, 3.3, 3.4.

2003 *Smithicyathus lacunosus lacunosus* (Gürich, 1896); Fedorowski: 113, pls 53: 4,5, 54:1.

2003 *Smithicyathus lacunosus mariae* (Wrzołek, 1993); Fedorowski: 113, pl. 54:2.

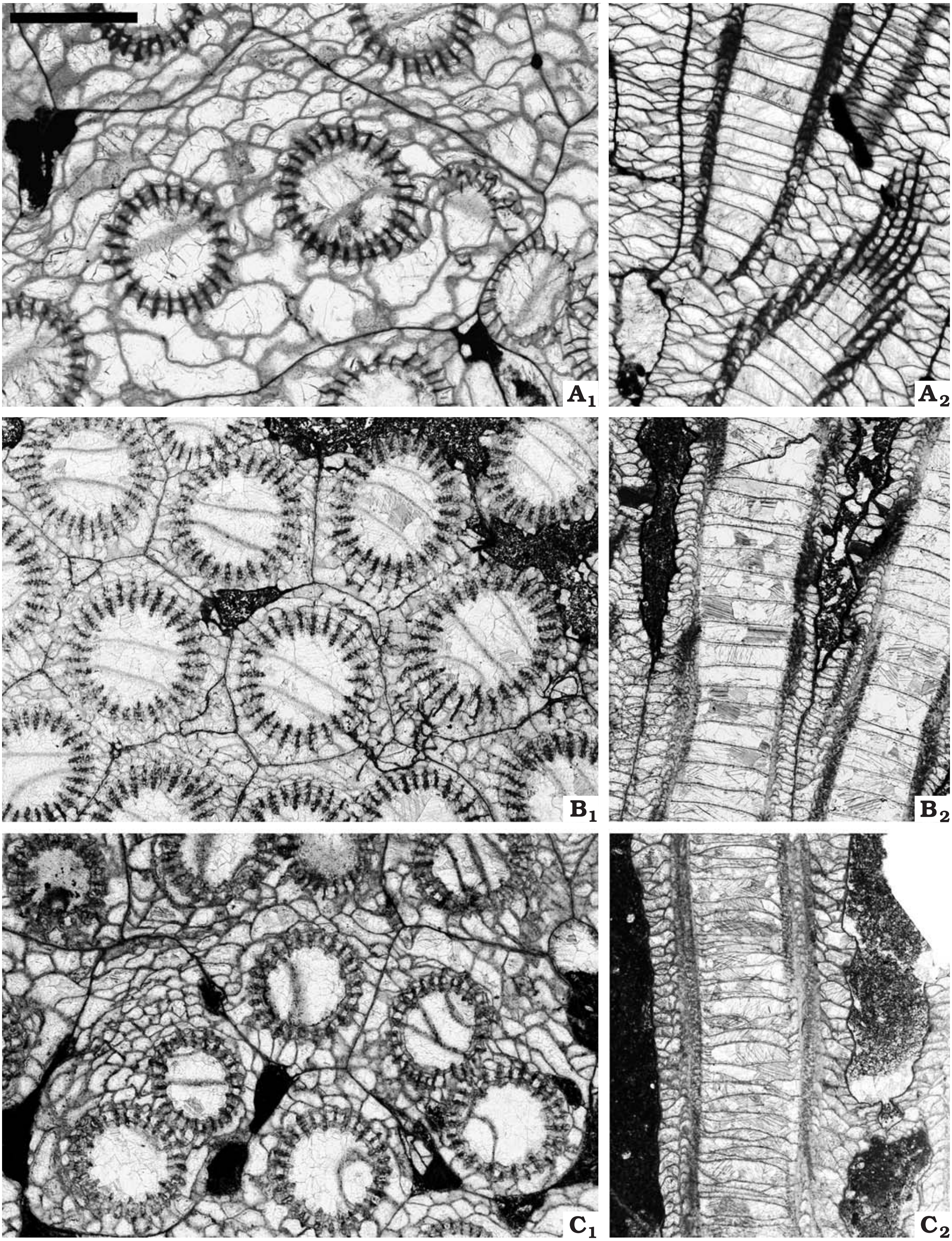
Neotype: GIUS 401PG 51B, fragment of a phaceloid colony (illustrated in Fig. 7A).

New type locality: Psie Górki, abandoned quarries in the city of Kielce, Holy Cross Mountains, Poland.

New type horizon: Set F, micritic limestones with intraformational conglomerates, Uppermost Frasnian.

Material.—67 colonies with both transverse and longitudinal sections studied (Table 1, Appendix 2: column "c"). From the Holy Cross Mountains is the following material (points 1–10 below). (1) Original holotype: illustration of a fragment of a single colony by Gürich (1896: pl. 4: 6). (2) Topotypic (neotopotypic) material: besides the neotype (GIUS 401PG 51B), also the colonies GIUS 401PG 41B, 90A. (3) Possibly topotypic (either from set E or from set F of Psie Górki) are UAM A73,76 (Różkowska 1953: pl. 6: 3,4) and unnumbered UAM specimen (labelled 324 in collection of Różkowska 1953). (4) From the set E of Psie Górki are: GIUS 401PG 09, 27, 29, 31.

Fig. 6. Upper Frasnian *Smithicyathus* from Western Canada. **A**. The holotype of *Smithicyathus cinctus* (Smith, 1945), GSC 9244, the same colony as in Fig. 4A, with some little lacunae within the colony, and non-cerioid walls commonly surrounding more than one tabularium (A_1 transverse, A_2 longitudinal section). **B**, **C**. *Smithicyathus mcleani* sp. nov. with subphaceloid habit, from the collection of McLean (1994b); **B**. The holotype, GSC 98208, (B_1 transverse, B_2 longitudinal section); **C**. Another colony, GSC13826, (C_1 transverse, C_2 longitudinal section), with occasional grouping of few corallites within common wall. Scale bar 4 mm for all items. →


A1
A2
B1
B2
C1
C2

(5) From Grabina quarry set C are: GIUS 356G 11, 16B, 152-1, 155-1, 169. (6) From road cutting at Kowala are: GIUS 376KD 25, 39, 41. (7) From Zgórsko quarry at Bolechowice are: GIUS 382ZS 07, 08, 11, 12A, 13, 15B, 17. (8) From Panek quarry at Bolechowice (set B) are: GIUS 384P 06, 08, 09, 21, 22, 29, 30, 41, 54, 57, 65, 72A, 89, 96, 105, 108, 109, 121, 132, 159, 160, 163, 164, 166a, 166b, 172, 178. (9) From Kowala quarry at Kowala (set G) are: GIUS 388KK 24, 27, 29, 52, 55, 60, 129, 156A, 158, 264B, 278A, 288. (10) From Wietrznia quarry is an unnumbered UAM specimen (labelled 325 in collection of Różkowska 1953), possibly from the Uppermost Frasnian (point "19" of Różkowska 1953: 46). Non-Holy Cross Mountains material is from the Lublin area (unnumbered UAM specimen from Korczmin borehole, depth 1891m, collection Różkowska 1980) and from Sumbera near Brno, Czech Republic (GIUS1690MS01E).

Emended diagnosis.—Submassive (phaceloid) colonies of *Smithicyathus*, commonly with cerioid walls in their massive fragments, and with peripheral dissepimentaria either narrow or absent; corallites are smaller (DIC typically from 4.0 to 4.75 mm), and tabularia are narrower (typically 1.75 to 2.75 mm) than in *Smithicyathus mcleani* sp. nov. from western Canada (see above).

Remarks.—The holotype of Gürich (1896; see above), was noted as collected at Karczówka Hill in the Kadzielnia range, presumably from the Upper Frasnian; this material is reportedly lost in Wrocław in the final days of World War II; moreover the original location of Gürich could not be re-investigated in strongly overgrown Karczówka, nota bene with the legal status of a natural monument protected area and thus inaccessible for sampling. Due to these circumstances, the present author suggests selection of Psie Górki in Kielce as the new type locality, the Uppermost Frasnian set F of this quarry as a new type horizon, and the specimen illustrated in the present paper in Fig. 7A as the neotype. In all characters the neotype is similar to and conspecific with the colony (fragment) from Karczówka illustrated by Gürich (1896; see synonymy above). Unfortunately, although Różkowska (1953) also illustrated material from Psie Górki (Różkowska, 1953: pl. 6: 3, 4; re-illustrated by Fedorowski 2003: pl. 53: 4, 5; sections UAMTc4/17 and UAMTc4/18), her data are insufficient to indicate precisely the horizon where her specimen has been collected and thus should not be selected as neotype. At Psie Górki, both in set E and in set F, *S. lacunosus* is rather uncommon component of diversified assemblage of mostly colonial (*Phillipsastrea*, *Frechastraea*) but also solitary (*Tabulophyllum*, *Hankaxis*) rugosans.

Variability.—As presented in "material and methods–intraspecific variability", and summarized in Table 1, review of 73 phaceloid colonies of *Smithicyathus* reveals that 53 of them have atypicality indices valued 3 or lower. As the neotype of *S. lacunosus* (GIUS 401PG 51B) belongs to this group, this may indicate that the "53" represent the "typical" *S. lacunosus* (see Fig. 7, Table 1). Also all of the colonies formerly designated as *Phillipsastrea lacunosa mariae* belong to this group, therefore there are no sound reasons for distinguishing the two subspecies. The colonies with atypicality indices valued 4 to 9 (15 records) are considered "extreme", most of them possibly represent morphologically extreme representatives of *S. lacunosus*, but also one colony of *S. mcleani* sp. nov. falls into this group. As "outstanding" are qualified the colonies (5 records) with atypicality indices from 10 to 17. Here belong the remaining two colonies of *S. mcleani* sp. nov., but also two colonies from the Panek quarry (one of them dimorphic, and thus three records), which are so outstanding in their morphology, that they are described separately, as *S.* cf. *lacunosus* (below).

Discussion.—*S. cinctus* and *S. mcleani* sp. nov. have broader tabularia than *S. lacunosus*. Another similar species, *S. smithi*, never displays the tripartite (cerioid) walls; some of its colonies, namely those with isolated corallites (CO <1), are otherwise very similar to *S. lacunosus*.

Paleoecology.—In the Holy Cross Mountains *S. lacunosus* (Gürich, 1896) occurs in various paleoenvironments. In the Kadzielnia chain of hills, the species is reported from Karczówka (1 colony), from Grabina quarry, set C (5 colonies), Psie Górki, sets E and F (8 colonies) and from Wietrznia quarry, set E (1 colony). These locations represent fore-reef environments (see Fig. 3), shallower at Grabina (set C) becoming deeper and deeper at Wietrznia (set E) and at Psie Górki (sets E and F). In all these locations *S. lacunosus* (Gürich, 1896) is accompanied by numerous other species of Rugosa. Limestones of Karczówka were probably deposited in back-reef settings, but this is only a supposition as the outcrop is strongly overgrown there. In the southwestern Holy Cross Mountains the species is known from the northern limb of the Chęciny syncline, mostly from the quarries of Panek (set B: 39 colonies) and Zgórsko (7 colonies) at Bolechowice, but also from the Kowala quarry, set G (12 colonies) and road cutting Kowala (3 colonies). In the southern limb of the Chęciny anticline it occurs at the southern slopes of Miedzianka hill at Miedzianka (fragmentary material, not measured). These southern *Smithicyathus*-bearing locations represent the shallow-marine, back-reef facies (Panek and Zgórsko) with *Smithicyathus* being the numerically dominating tetracoral species. The more open-marine settings occur at Miedzianka and in the Kowala quarry, set G, Still deeper, marly facies with intercalated flat-pebble conglomerates is present at road cutting Kowala. In the Lublin area, eastern Poland, *S. lacunosus* is recored from the Korczmin 2 borehole (1 colony), from dark marly and detrital limestones of the Modryń Fm, from depth 1891m, i.e., the same depth and horizon as the holotype of *S. lubliniensis* Różkowska, 1980. In Moravia, eastern Czech Republic, *S. lacunosus* (1 colony) has been sampled from Sumbera rocks near Brno (Hladil and Kalvoda 1993: 38–40), from dark detrital limestones deposited in the deeper fore-reef settings. As it seems *S. lacunosus* (Gürich, 1896) is a species indicating shallow-marine, back-reef settings or their proximity.

Stratigraphic and geographic range.—Upper Frasnian of the Holy Cross Mountains and the Lublin area in Poland, and

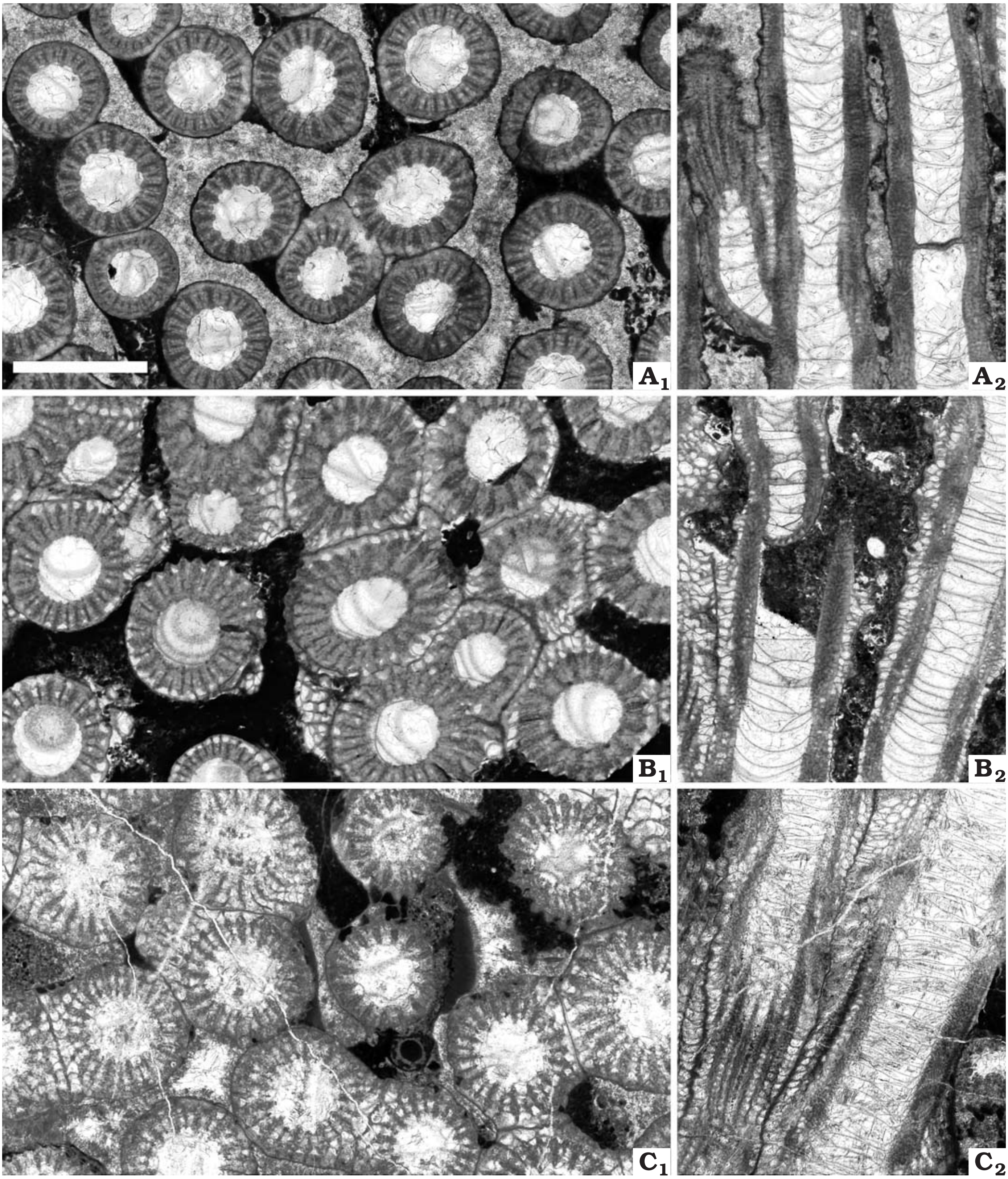


Fig. 7. Typical colonies of the Upper Frasnian *Smithicyathus lacunosus* (Gürich, 1896). **A**. Neotype of *S. lacunosus*, Psie Górki, set F, GIUS 401PG 51B, with small corallites, thick septa, and the lateral offset in A_2, (A_1 transverse, A_2 longitudinal section). **B**. Zgórsko quarry, GIUS 382ZS 13, with large corallites and with thick septa; although lateral offsets predominate, note the marginal parricidal offset in B_2, (B_1 transverse, B_2 longitudinal section). **C**. Sumbera near Brno, Moravia, Czech Republic, GIUS1690MS 01E, with large corallites and with relatively thin septa, (C_1 transverse, C_2 longitudinal section). Scale bar 4 mm for all items.

Moravia (Czech Republic), the southeastern Euramerican shelf and the eastern margin of the Bohemian microcontinent, respectively.

Smithicyathus cf. *lacunosus* (Gürich, 1896)

Fig. 8B, C.

Discussion.—Here belong two colonies from the Upper Frasnian set B of Panek, with the highest atypicality indices within the sample of over 70 phaceloid colonies measured. They may represent either morphologically outstanding colonies of *Smithicyathus lacunosus*, or another species (or two other species, to be exact). The first of them (Fig. 8B) has very thin septa and a very broad dissepimentarium, externally to the periphery of the zone of horseshoe dissepiments. The other (Fig. 8C) is the dimorphic colony with larger and smaller corallites present, the former with broader dissepimentarium, the latter with very narrow dissepimentarium and the occasional replacement of horseshoe dissepiments by peneckielloid ones. Apparently, smaller corallites result from suppression of growth, caused by local re-orientation of corallites' growth direction from normal, outwardly orientated, with resulting fan-shaped corallites' arrangement, to inwardly-orientated, with resulting deficiency of available space and suppression of growth of some, but not of all, corallites.

Smithicyathus smithi (Różkowska, 1953)

Figs. 9, 10.

1953 *Pachyphyllum smithi* sp. nov.; Różkowska 1953: 40, figs. 22, 23, pl. 5: 1–3.

non 1967 *Pseudoacervularia* cf. *smithi* Różkowska 1953; Pickett 1967: 52, 53, pl. 1: 3–5 (possibly close to *Phillipsastrea hennahi ranciae* Coen-Aubert, 1987).

1978 *Medusaephyllum*? *smithi* (Różkowska, 1953); Birenheide 1978: 117.

1993 *Phillipsastrea lacunosa smithi* (Różkowska, 1953); Wrzołek 1993: 297, figs. 3.1, 3.2, 3.5, 3.6, 4.1–4.5.

2003 *Phillipsastrea smithi* (Różkowska, 1953); Fedorowski 2003: 105, pl. 48: 4.

Type material, type location: The holotype of Różkowska (1953, see synonymy above; UAM A61-3 = UAM Tc 4/11), from the Upper Frasnian of Bolechowice (presumably the Panek quarry, set B, backreef limestones).

Remarks.—In the collection of Różkowska in Poznań, as the holotype labeled are the two colony fragments from "Bolechowice", numbered 310 and designated as UAM310A and UAM310B in Table 2 of the present paper. The two fragments are somewhat different from each other, but they may be derived from the same colony, and it is quite possible, in light of their numerical data that also the illustration of Różkowska (1953: pl. 5: 1–3) is from the same specimen. As of the 3 quarries in close vicinity of the village of Bolechowice only Panek is with *S. smithi* and was accessible for sampling in late forties–early fifties of 20th century (when Różkowska gathered her collection), therefore I am fairly sure that the original sampling location of *S. smithi* for Różkowska is at Panek quarry.

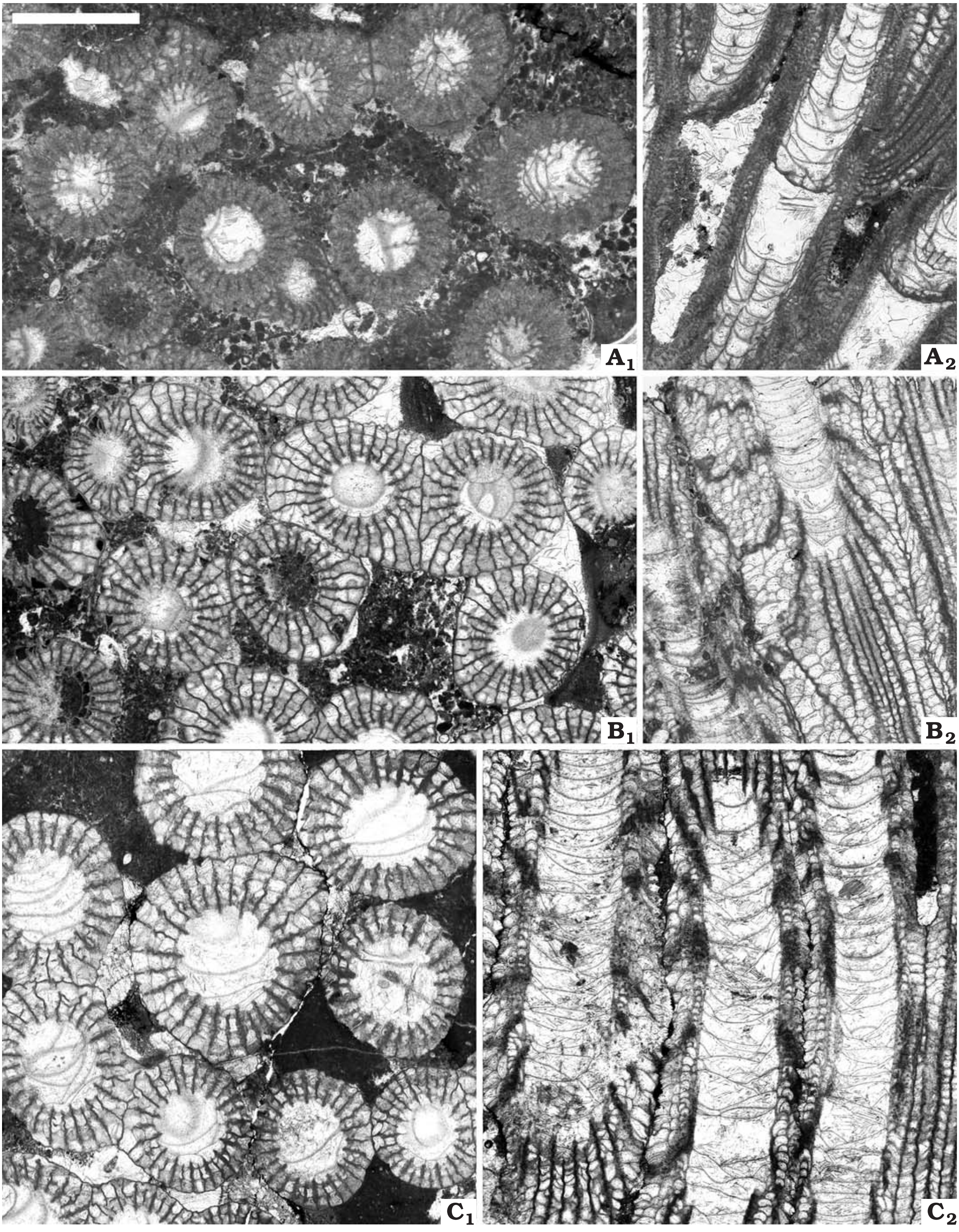
Material.—45 colonies with transverse and longitudinal sections measured, as listed in Table 2 and in Appendix 2 (column "e"). The known material is, with exception for a single colony, from the Holy Cross Mountains, from the following locations (points 1–5 below). (1) The holotype: (UAMA61-3), from Panek quarry, set B, in Bolechowice; for documentation purposes as the holotype listed are also unnumbered specimens from Różkowska 1953 collection (labelled 310A and 310B). (2) Topotypic material: besides the holotype from Panek are also the colonies GIUS 384P01, 27A, 27B, 28, 32, 39, 43, 49, 50, 51, 53, 55A, 55B, 56, 58, 61, 66, 69, 74, 97, 104a, 104b, 107, 112, 153, 158, 161, 162, 165a, 165b, 167, 168, 174A, 175, 176, 177A, 179, 180A. (3) Single colony from road cutting in Kowala: GIUS 376KD 12. (4) Single colony from Zgórsko quarry in Bolechowice: GIUS 382 ZS14. (5) Single fragmentary colony from Psie Górki (set F) in Kielce: GIUS 401PG 35B. Outside of the Holy Cross Mountains *S. smithi* is so far known from Lublin area, Korczmin 2 borehole, depth 1951 m (unnumbered UAM specimen from Różkowska 1980 collection).

Emended diagnosis.—Massive (astreoid) *Smithicyathus* with marked septal expansion partly masking the horseshoe dissepiments, and with slight tendency towards reduction of septal blades at corallite periphery. Smaller diameter of corallites (and tabularium) distinguish this species from the Canadian *S. cinctus*.

Variability.—Appendix 2 (column "e") presents the variability ranges. Results of the quintile analysis (for the massive colonies, with *S. cinctus* and *S. lubliniensis* included) is given in Table 2. As it becomes obvious *Smithicyathus smithi* is numerically distinct from *S. cinctus* and *S. lubliniensis*. Within the studied material two other colonies, as numerically outstanding (GIUS 384P101 and GIUS 382ZS 05), are described as *S.* cf. *smithi* below.

Among more than 40 colonies classified as *S. smithi*, the two from Panek represent polymorphic characteristics. The colony P104 (GIUS 384P104; see Fig. 9C) is with local degradation of intercorallite walls and without septa in these local areas. The two morphs within this colony were measured separately (listed as P104a and P104b in Table 2), and besides the above mentioned peculiarities both seem to represent quite typical *S. smithi*. Possibly some environmental factors were responsible for these local alterations. The other colony is

Fig. 8. Upper Frasnian phaceloid tetracorals from Panek quarry, set B. **A**. *Smithicyathus lacunosus* (Gürich, 1896), GIUS 384P166, a dimorphic colony, with some corallites with short septa (measured as P166a) and the other with long septa (P166b), in longitudinal sections long septa can be traced as appearing and disappearing in the same corallite (A_1 transverse, A_2 longitudinal section). **B**, **C**. *Smithicyathus* cf. *lacunosus* (Gürich, 1896): **B**. GIUS 384P147a, with relatively thin septa and numerous peripheral dissepiments (B_1 transverse, B_2 longitudinal section). **C**. GIUS 384P173, a dimorphic colony, with larger (P173a) and smaller (P173b) corallites side by side, both morphotypes with relatively thin septa (C_1 transverse, C_2 longitudinal section). Scale bar 4 mm for all items. →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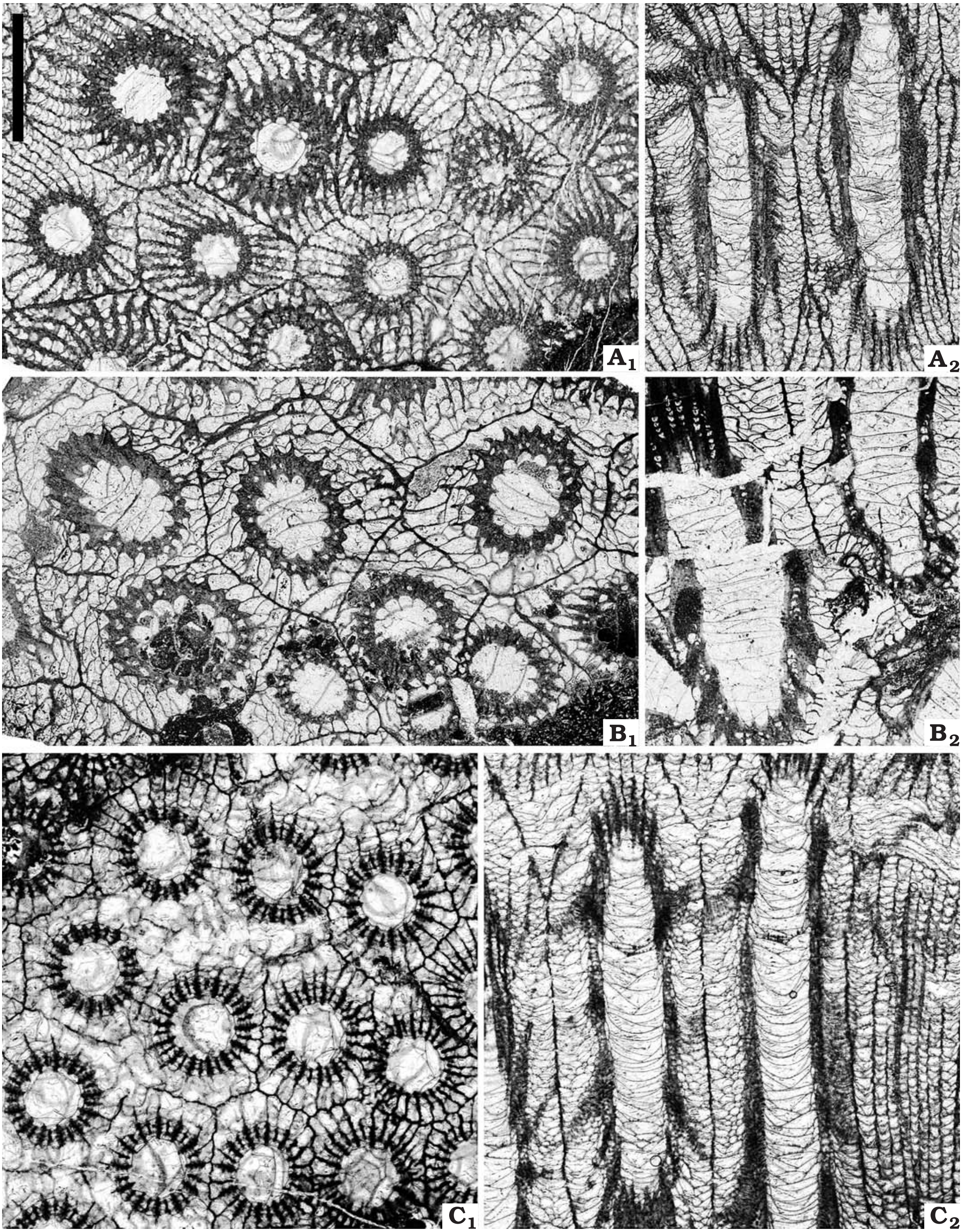
C2


A1
A2
B1
B2
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C2

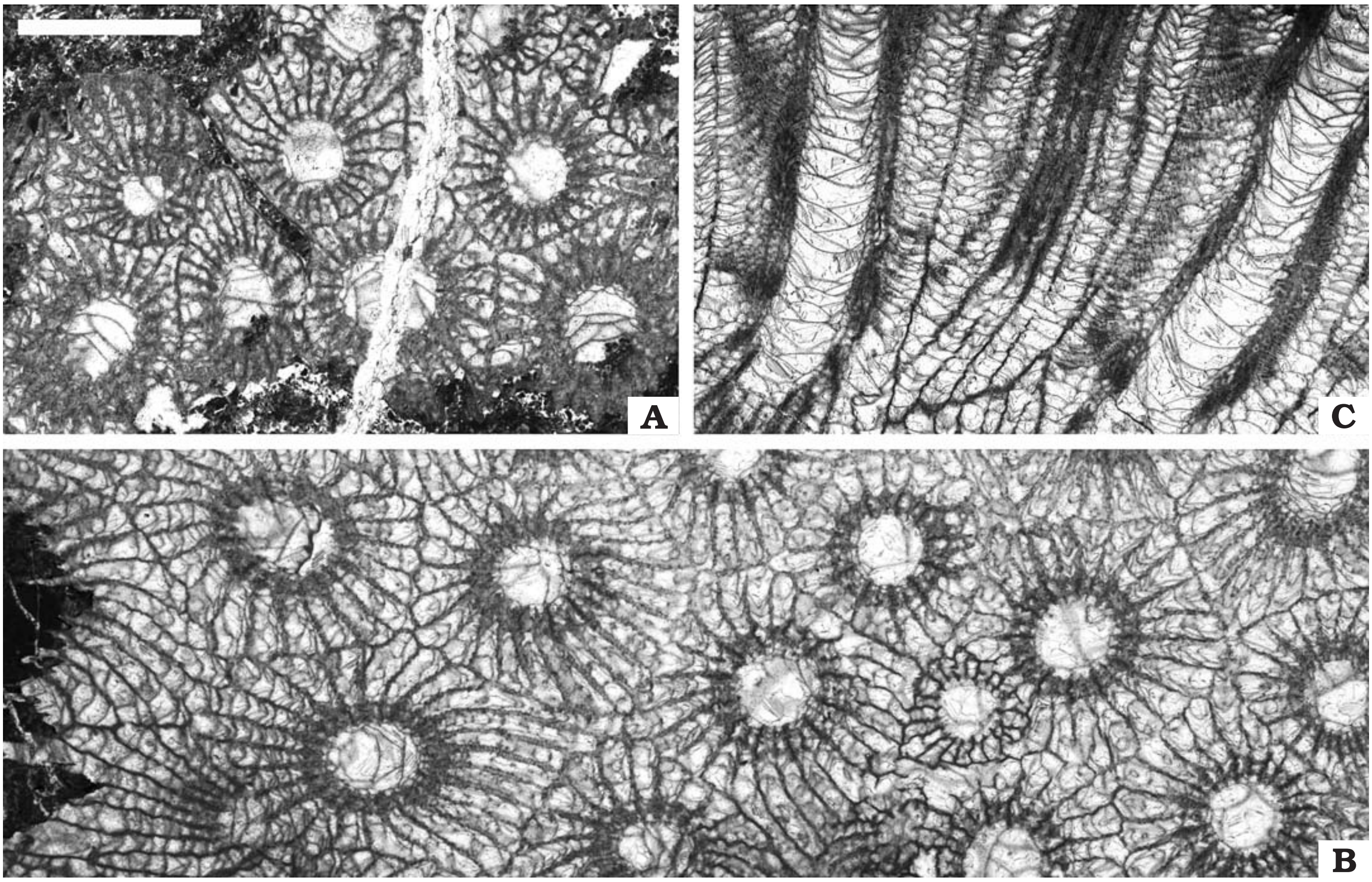

Fig. 10. Effect of corallite age for corallite morphology and thus classification, in *Smithicyathus smithi* (Różkowska, 1953), Upper Frasnian, Panek quarry, set B, colony GIUS 384P165. **A**, **B**. Transverse sections. **A**. Group of very small, evidently juvenile corallites with thin skeletal elements (measured as P165a). **B**. Large and thick-septate, adult corallites from another section (measured as P165b). **C**. Longitudinal section. Scale bar 4 mm for all items.

P165 (GIUS 384P165; see Fig. 10); in the first transverse-section which was available for measurements (Fig. 10A_1) corallites are small and with relatively thin septa. This resulted in very high atypicality index (see P165a in Table 2). Re-investigation and additional sectioning revealed the prevalence of larger corallites, with thicker septa in the new transverse-sections (Fig. 10A_2, measured as P165b), with typical appearance and low atypicality index (Table 2). This bimodality is interpreted as juvenile vs. adult corallites displayed in various portions of one colony. It is noteworthy that the juvenile characteristics are only seen in a very restricted area, not much larger than the one presented in Fig. 10A_1.

Discussion.—Massive *Smithicyathus smithi* (Różkowska, 1953) is most closely related to phaceloid *S. lacunosus* (Gürich, 1896). This point of view has been underlined by Różkowska (1953) at her presentation of supposed phylogeny of the Holy Cross Phillipsastreidae (Różkowska, 1953: fig. 40). Also Wrzołek (1993) considered *S. smithi* and *S. lacunosus* as subspecies of *Pachyphyllum lacunosum* Gürich, 1896. The other authors do not recognize such a close affinity: Birenheide (1978) distinguished *Medusaephyllum*? *smithi* and *Frechastraea*? *lacunosa*—he knew the species only from illustrations of Różkowska (1953) and did not recognize the presence of horseshoe dissepiments in the latter species; Różkowska (1980: table 1) changed her earlier opinion and listed the two species as *Phillipsastrea smithi* (Różkowska) and *Smithicyathus lacunosus* (Gürich); this distinction was repeated by McLean (1994b) and by Fedorowski (2003). In my opinion *S. smithi* (Różkowska, 1953) is related to *S. lacunosus* (Gürich, 1896) in a similar way as *S. cinctus* (Smith, 1945) is related to *Smithicyathus mcleani* sp. nov.. In both cases there is a pair of massive and phaceloid species, with some interme-

← Fig. 9. Upper Frasnian *Smithicyathus smithi* (Różkowska, 1953), with massive to somewhat lacunose habit. **A**. Possible holotype of the species, most probably from Panek quarry, set B, UAM colony marked as #310 in collection of Różkowska (1953), with septa very thick and spindle-shaped (in transverse section), (A_1 transverse, A_2 longitudinal section). **B**. UAM colony from the Korczmin borehole, marked as Korczmin 1951C in collection of Różkowska (1980), with septal expansion restricted mostly to zone of horseshoe dissepiments at the dissepimentarium–tabularium boundary. **C**. Colony from Panek quarry, set B, GIUS 384P104, with cyclomorphic pattern (?) recorded as zones with (P104b) and without (P104a) intercorallite walls, and, correspondingly, seen with and without septal continuity towards corallite periphery in transverse section (C_1) and with alternation of zones with septa and zones with presepiments in the longitudinal section (C_2). Scale bar 4 mm for all items.

diate material present, so there may be some doubts as for presence of two, and not one species, but no doubt at all as for the congeneric status of the Holy Cross and Canadian pairs of massive and phaceloid morphotype.

The species is known only from the Holy Cross Mountains. The Harz material (Pickett 1967, see synonymy above) has long septa in the tabularium (numerical data in Appendix 3, column "p") and is probably close to *Phillipsastrea ranciae* Coen-Aubert, 1987.

Morphologically and morphometrically close to *S. smithi* (Różkowska, 1953) are *S. cinctus* (Smith, 1945) and *S. lubliniensis* Różkowska, 1980. The former species is with septa strongly reduced at corallites' peripheries, with larger corallites (DIC and TM parameters). In quintile analysis of massive *Smithicyathus* atypicality index of colonies of *S. lubliniensis* (two colonies studied) is in 9–10 range (Table 2); in comparison to *S. smithi*, *S. lubliniensis* is with thinner septa (smaller IN1, IN2, D1 and D2 values) and more frequent and complete tabulae. Otherwise it could be classified as a colony of *S. smithi* with atypically thin septa and a rather large tabularium diameter and number of septa.

Another similar species is *S.*? *belkovskiense* from the Frasnian of New Siberian islands in Northern Siberia (Appendix 2, column "j", see also below), reported as cerioid, but possibly astreoid and also morphometrically close to *S. smithi.* Review of numerical data (Appendix 2, compare columns "e" and "j") demonstrates the specimen of Siberia is numerically indistinguishable from the Holy Cross *S. smithi*.

Paleoecology.—This species occurs in fewer locations than its phaceloid counterpart, *S. lacunosus*. As it seems it is of broadly similar ecological preferences to the latter species, i.e. it occurs mainly in back-reef settings, where it can be numerically abundant. In fore-reef settings it is rare.

Stratigraphic and geographic range.—Upper Frasnian of the Holy Cross Mountains, southeastern Euramerican shelf: Panek quarry (41 colonies) and Zgórsko quarry (1 colony) at Bolechowice; Psie Górki F (1 colony) in Kielce, Kowala road cutting (1 colony) in Kowala. In the subsurface of the Lublin area, it is recorded in the Upper Frasnian Modryń Fm. of the Korczmin 2 borehole, depth 1951m (1 colony).

Smithicyathus cf. *smithi* (Różkowska, 1953)

Fig. 11A, B.

Discussion.—The two Upper Frasnian colonies, one from Panek, the other from Zgórsko, are with high atypicality indices (GIUS 384P101 and GIUS382ZS05, listed as P101 and ZS05 in Table 2). Their septa are rather thin and with carinate appearance, short in tabularium (Fig. $11A_1$, B_1). Horseshoe dissepiments are present in the longitudinal sections (Fig. $11A_2$, B_2). The colony from Zgórsko is with much smaller corallites than in the specimen from Panek. Some similarity of this material to *Frechastraea carinata* Scrutton, 1968 from the Upper Frasnian of Devonshire (Scrutton 1968) can be noted, but the latter species is with stronger carination and without the horseshoe dissepiments.

Smithicyathus lubliniensis Różkowska, 1980

Fig. 11C.

1980 *Smithicyathus lubliniensis* sp. nov; Różkowska 1980: 19–20, pl. 1: 2, 3a–c.
1993 *Phillipsastrea lacunosa lubliniensis* (Różkowska, 1980); Wrzołek 1993: 297, 300.
2003 ?*Smithicyathus lubliniensis* Różkowska, 1979; Fedorowski 2003: 113, 114, pl. 54: 3.

Emended diagnosis.—Massive (astreoid) *Smithicyathus* with very narrow dissepimentarium, of one horseshoe series, of two peripheral series of dissepiments, and with thin septa.

Discussion.—The material illustrated herein is derived most probably from the holotype of the species, collected and described by Różkowska (1980: 18, 19; pl. 3a–c), and thus both records (one set of measurements taken from the illustrations of Różkowska, 1980, another one from additional thin sections supplied from Poznań) in the database may in fact belong to the same colony. This material displays a massive habit, with occasional lacunae. Walls are pseudocerioid. Septa are locally thickened at the zone of horseshoe dissepiments, and there is a marked tendency towards septal degeneration at the corallite periphery. As was noted above, this material might be interpreted as a highly atypical *S. smithi*. Anyway in all appearance it must be closely related to the Holy Cross representatives of the latter species. Possibly if I were to find such a material in Panek or in Zgórsko I would not hesitate to include it into *S. smithi*.

The material studied comes from the dark marly limestone (intercalation?), suggesting deeper offshore origin of this sample, if not for the species *S. lubliniensis* Różkowska, 1980.

Stratigraphic and geographic range.—Lublin subsurface Devonian (eastern Poland), Korczmin borehole, depth 1891 m; Upper Frasnian Modryń Formation, Zubowice Member (Miłaczewski 1981: 21–24).

Dubious species of *Smithicyathus*

Presented below are the three Siberian species, described by Spasskiy and Kravtsov (in Besprozvannykh et al. 1975), and illustrated by a single colony each. Due to scarcity of material and insufficient clarity of illustrations, but also due to paleogeographic if not stratigraphic isolation of these species, their taxonomic position must remain dubious, until more material and better illustrations become available.

Smithicyathus? *russakovi* (Spasskiy and Kravtsov in Besprozvannykh et al., 1975)

1975 *Frechastraea russakovi* sp. nov.; Spasskiy and Kravtsov (in Besprozvannykh et al. 1975): 63; pl. 15: 1.

Discussion.—This Eifelian species of Indigiro-Kolyma (Appendix 2: column "h") fits the numerical criteria for *Smithicyathus* established above and might possibly represent an ancestral species of the genus. On the other hand it is with large septal number, broad tabularium and lack of intercorallite walls. These parameters, but also geographical and stratigraphical isolation of this species suggest for *Smithicyathus*?

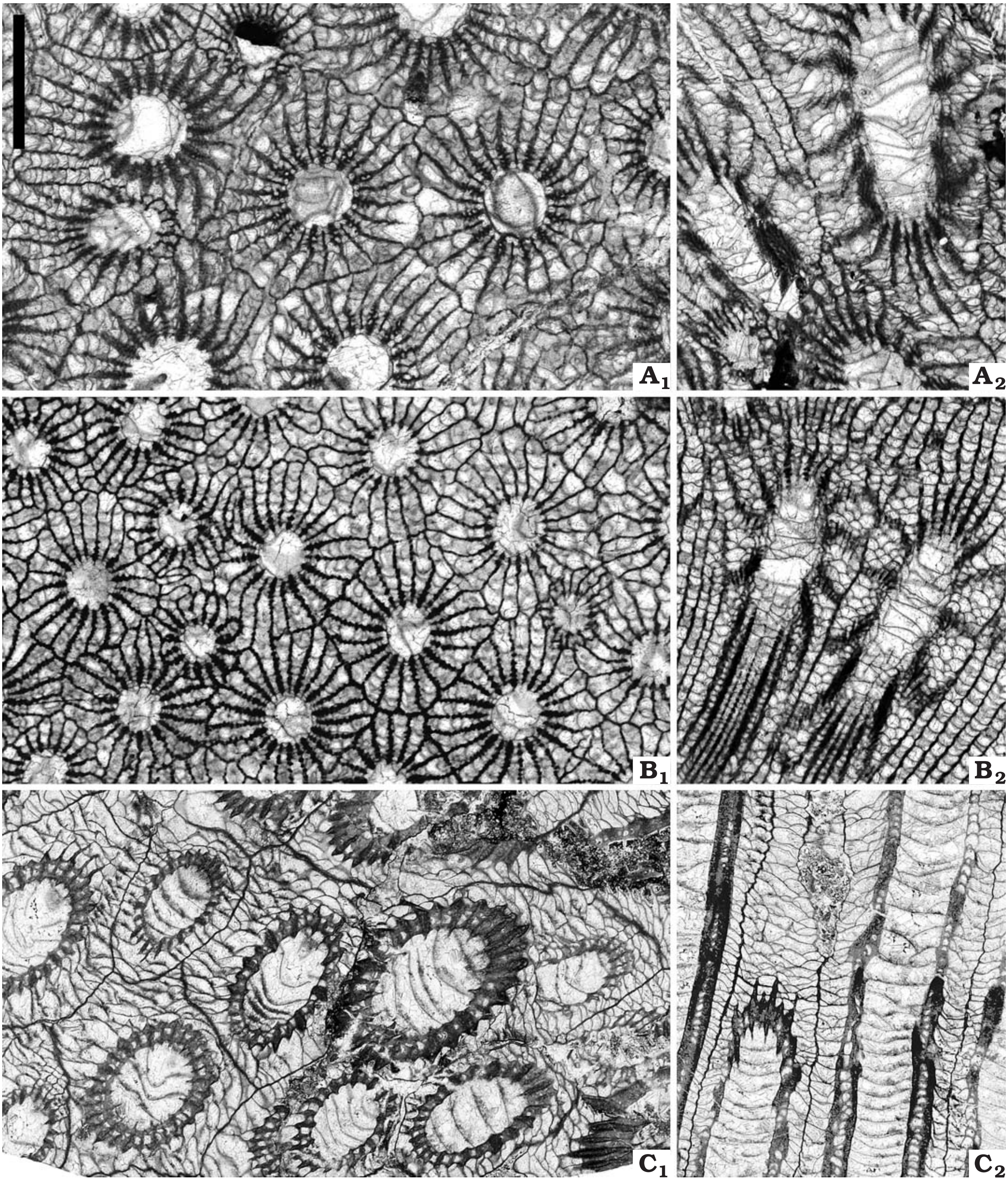

Fig. 11. Upper Frasnian massive material of *Smithicyathus* from the Holy Cross Mountains (**A**, **B**) and the Lublin area (eastern Poland) subsurface (**C**). **A**, **B**. *Smithicyathus* cf. *smithi* (Różkowska, 1953) with relatively thin septa. **A**. Panek quarry, set B, GIUS 384P101, with larger corallites and better development of horseshoe dissepiments (A_1 transverse, A_2 longitudinal section). **B**. Zgórsko quarry, GIUS 382ZS 05, with small corallites, carinated septa and relatively scarce horseshoe dissepiments (B_1 transverse, B_2 longitudinal section). **C**. *Smithicyathus lubliniensis* Różkowska, 1980, possibly cut from the holotype of the species, Korczmin borehole, depth 1891 m, UAM material marked as Korczmin 1891A, from collection of Różkowska (1980), with narrow zone of septal expansion, marked intercorallite non-cerioid walls and with narrow dissepimentaria, (C_1 transverse, C_2 longitudinal section). Scale bar 4 mm for all items.

russakovi a dubious status within *Smithicyathus*. A continuous series of horseshoe dissepiments excludes it from the genus *Frechastraea* Scrutton, 1968 (type species: *Cyathophyllum pentagonum* Goldfuss, 1826). McLean (1994a: 71) suggested it might belong either to the genus *Chuanbeiphyllum* He, 1978 or to its older homeomorph.

Smithicyathus? *emendatus* (Spasskiy and Kravtsov in Besprozvannykh et al., 1975)

1975 *Phillipsastraea emendata* sp. nov.; Spasskiy and Kravtsov (in Besprozvannykh et al. 1975): 61, 62; pl. 14: 2.

Discussion.—The species is reported from the Eifelian–Frasnian interval in Indigiro-Kolyma. It has large septal number and relatively broad tabularium (Appendix 2: column "i"). If confirmed, its stratigraphic range is peculiar in itself. Corallites are not so large as in *S.*? *russakovi* (see above), and thus it is closer in size to "typical" species of *Smithicyathus*. McLean (1994a: 58) classified this species into *Phillipsastrea*.

Smithicyathus? *belkovskiense* (Spasskiy and Kravtsov in Besprozvannykh et al., 1975)

1975 *Stellatophyllum belkovskiense* sp. nov.; Spasskiy and Kravtsov (in Besprozvannykh et al. 1975): 58, 59; pl. 13: 1.

non 1988 *Stellatophyllum belkovskiense* Spasskiy and Kravtsov; Hou 1988: pl. 34: 7 (possibly to *Phillipsastrea*).

Discussion.—The type species of the genus *Stellatophyllum* Spasskiy in Bulvanker et al., 1968, *S. lateratum* Spasskiy in Bulvanker et al., 1968, is cerioid and with rather long major septa in the tabularium. However, *Stellatophyllum belkovskiense* is astreoid (as can be judged from the illustrations) and has septa withdrawn from the axis, thus meeting the criteria established for *Smithicyathus* in the present paper. From the morphological and numerical point of view it would make an almost perfect *Smithicyathus smithi*, if it were found in the Holy Cross Mountains, although it displays slightly fewer horseshoe dissepiments and less septal dilatation (Appendix 2: column "j") than does the Holy Cross species. The Chinese material, as listed above, is with long septa in tabularium and most probably is not conspecific with the Siberian material, and it is still less probable that it belongs to *Smithicyathus*.

Conclusions

- *Smithicyathus* can be found in the Upper Frasnian deposits of western Euramerica (*S. cinctus* and *S. mcleani* sp. nov.) and south-eastern Euramerican shelf seas (*S. lacunosus*, *S.* cf. *lacunosus*, *S. smithi*, *S.* cf. *smithi*, and *S. lubliniensis*). Its probable Angaran representative may be *S.*? *belkovskiense*. The genus did not survive the Frasnian–Famennian crisis.
- The early history of *Smithicyathus* is obscure. Its probable early species from the Eifelian of Angara: *S.*? *emendatus* and *S.*? *russakovi*, may in fact represent early homeomorphs of the genus.
- *Smithicyathus* lived in tropical and sub-tropical shallow-marine carbonate environments, with the possible exception of the northern mid-latitudes species from Siberia mentioned above.
- In the Holy Cross Mountains the local species, *Smithicyathus lacunosus* and *S. smithi* show a preference for restricted-marine facies. They may make up over 90% of all rugosan colonies collected in such locations (e.g., Panek quarry), whereas in the more open-marine settings they are rare both in numbers and in proportion to other rugosan species.
- Frasnian species of the Holy Cross Mountains and Canada (to a lesser degree) are well-characterized numerically, with over 120 colonies measured to date. Quintile analysis has been used to characterize variability patterns within the massive and phaceloid material of *Smithicyathus*. This numerical method cannot be used for small samples or scarce species.
- As a new species described is *Smithicyathus mcleani* sp. nov. from the Uppermost Frasnian of western Canada.
- As the type material of *Smithicyathus lacunosus* (Gürich, 1896) is lost, selected is the neotype of this species.

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Appendix 1

Explanation of features presented in database of massive and submassive fossil Phillipsastreidae. Normal type indicates directly measured or counted parameters; *italics* indicate parameters calculated from those directly obtained.

Feature	Explanation
CO	ratio of space filling by corallites as deduced from transverse section; 0.1 assumed for protocorallites
MU	intercorallite walls: 1 individual epithecae, 2 juxtaposed epithecae (cerioid wall), 3 septal (pseudocerioid) wall, 4 wall absent
SC	ratio of septal continuity between the calicinal margins of neighboring corallites
IN1	internal wall as percent of tabularium margin—from 0.0 to 1.0
IN2	expansion of the major septa-ratio of expaneded part of septum to its total length
CA	septal carinae: 0 absent, 1 delicate, 2 significant
TB	tabularium profile: 0 concave, 1 flat, 2 mesa-shaped in axis, 3 domical
TC	proportion of complete tabulae: from 0.0 to 1.0
PP	proportion of horseshoe dissepiments: from 0.0 to 1.0
DIC	calculated corallite diameter (mm)
L/T	*2*L1/TM, i.e. ratio of length of major septa to tabularium radius*
N/D1	*#S1/TM*
N/D2	*#S1/DIC*
#S1	number of major septa
TM	tabularium diameter in transverse section (mm)
L1	length of the major septa in tabularium (mm)
L2	length of the minor septa in tabularium (mm)
D1	maximum thickness of the major septa (mm)
D2	maximum thickness of the minor septa (mm)
TW	tabularium diameter in longitudinal section (mm); essentially it must be close to TM
W	number of vertical series of internal dissepiments
Z	number of vertical series of external dissepiments
AZ	inclination of peripheral calicinal platform to corallite axis (degrees)
AW	inclination of internal dissepiments to corallite axis (degrees)
TT	mean distance between tabulae/tabellae (mm), along corallite axis
D/L	*number of peripheral dissepiments over width of marginarium*

Appendix 2

Range of variability observed in species of *Smithicyathus* (columns a–f) and in dubious species of *Smithicyathus* (columns h–j). *S.* = *Smithicyathus*; features as explained in Appendix 1; numerical data for more species are given in Appendix 3.

Species / Feature	*S. cinctus*	*S.mcleani* sp. nov.	*S. lacunosus*	*S.* cf. *lacunosus*	*S. smithi*	*S.* cf. *smithi*	*S. lubliniensis*	*S.? russakovi*	*S.? emendatus*	*S.? belkovskiense*
	a	b	c	d	e	f	g	h	i	j
CO	1	0.7–0.9	0.3–0.9	0.8–0.9	0.8–1	1	1	1	1	1
MU	3.5–4	1.5–2.5	1–2.5	1.5	2.5–4	3–3.5	3	4	3.5	3
SC	0.1–0.2	0.2 1	0.5–1	1	0.3–1	1	0.3 1	0.1	1	1
IN1	0.3–0.5	0.4–0.6	0.4–1	0.3–0.4	(0.5) 0.7–1	0.7 0.8	0.5	0.3	0.4	0.6
IN2	0.8	0.7–0.8	0.5–0.9	0.5–0.7	0.3–0.8	0.4 0.8	0.3 0.6	0.2	0.1	0.5
CA	0	0	0 (0.5)	0 0.5	0 (0.1; 0.3)	0.5 1	0	0	0	0
TB	1	1	0–1	0 0.7	0–1	0.5	0.5	0	0	1
TC	0.8–0.9	0.5 1	0–0.9	0.6–0.7	0–0.7	0.1 0.2	0.9	0.1	0	0.7
PP	0.8–0.9	0.6–1	0.8–1	0.6 1	1	0.4 1	0.8 1	1	1	0.6
DIC	7.7–8.4	5.5–5.8	2.8–7.7	4.1–5.9	3.7–7.6	4.4 8.7	4.8 5.2	8.7	8.2	4.1
L/T	0.2–0.33	0.12–0.28	0.04–0.32 (0.61)	0.16–0.2	0.08–0.3	0.2 0.25	0.15 0.19	0.31	0.18	0.3
N/D1	3.8–4.54	4.43–5.04	4.66–10.53	4.55–6.54	4.79–7.92	5.13 6.63	6.09 6.16	3.23	4.78	6.45
N/D2	1.55–1.84	2.36–2.62	1.78–4.04	2.34–3.22	1.71–3.43	1.41 2.41	2.69 2.88	1.86	1.95	3.37
#S1	13–14.2	13–15	11.3–15.2	13.2–13.8	11.2–14.3	10.6 12.3	13.8 14	16.2	16	13.8
TM	2.95–3.42	2.58–3.29	1.14–3.09	2.11–3.03	1.49–2.38	1.6 2.4	2.24 2.3	5.01	3.35	2.14
L1	0.33–0.54	0.16–0.46	0.04–0.37 (0.59)	0.2–0.28	0.08–0.31	0.2 0.24	0.17 0.21	0.77	0.3	0.32
L2	0.09–0.19	0.06–0.22	0–0.11	0.03	0–0.16	0.1 0.11	0.02 0.03	0.46	0.21	0.07
D1	0.2–0.25	0.2–0.28	0.22–0.63	0.1–0.23	(0.14) 0.23–0.55	0.22 0.3	0.23 0.28	0.27	0.18	0.23
D2	0.1–0.18	0.12–0.18	0.11–0.4	0.06–0.07	(0.06) 0.11–0.41	0.14 0.18	0.12 0.17	0.23	0.14	0.13
TW	3.13–3.21	2.99–3.5	1.1–3.05	2.27–3.08	1.47–2.48	1.6 2.1	2.2	5.25	3.14	1.96
W	0	0	0–1.3	0 0.8	0–1.6	0.7 1	0	1.3	0	0
Z	2.3–3.7	2–2.3	0–3	1–5	1.5–5.3	3	1.8 2	4.3	3	2.3
AZ	75–80	70–77	0–90	55–85	43–82	40 67	70 80	67	68	63
AW	0	0	0–20	0 13	0–18	13 15	0	40	0	0
TT	0.45–0.61	0.31–0.65	0.2–0.61	0.37–0.47	0.21–0.54	0.32 0.35	0.45 0.47	0.53	0.24	0.35
D/L	0.92–1.67	1.37–1.83	0.0–3.41	1.23–4.18	0.76–2.99 (3.94)	0.95 2.14	1.24 1.56	2.33	1.24	2.35
N = 128	**3**	**3**	**67**	**3**	**45**	**2**	**2**	**1**	**1**	**1**

Appendix 3

Range of variability observed in material compared to *Smithicyathus*. Continuation of Appendix 2; *Ch.* = *Chuanbeiphyllum*, *Ph.* = *Phillipsastrea*; features as explained in Appendix 1.

Species / Feature	*Ph. progressa*	*Ph. progressa* as *Smithicyathus*	*Ph. variabilis*	*Ph. variabilis* as *Smithicyathus*	*Ch.* quasi-*cinctum*	*Ph.* quasi-*smithi*	*Ph. dybowskii*	*Ph. samsonowiczi*
	k	l (ex k)	m	n (ex m)	o	p	q	r
CO	0.8–1	1	1	1	1	1	0.7–1	0.7
MU	3.5–4	4	4	4	4	3	1.5–2.5	1.5
SC	0.1–1	0.8 0.9	0.1–1	0.1–1	0	1	0.5–1	1
IN1	0.3–0.9	0.3 0.7	0.2–0.8	0.3–0.6	0.3	1	0.3–0.8	0.3
IN2	0.3–0.6	0.3	0.2–0.4	0.2–0.3	0.8	0.4	0.3–0.7	0.5
CA	0–2	0 0.5	0–1.5	0–1.5	0	0	0–0.5	0
TB	0–2	0.5 1	0–2	0–1	1	0	1.5–2	2
TC	0–0.8	0.1 0.2	0–1	0.1–1	0.9	0	0	0
PP	0.6–1	0.8	0.1–1	0.6–1	1	1	0–1	0.9
DIC	6–11.7	7.7	3.2–7.5	4.9–7	6.1	6.4	6.5–11.3	6.7
L/T	0.28–1.01	0.28 0.32	0.08–0.96	0.08–0.33	0.64	0.81	0.72–1	0.42
N/D1	3.37–5.7	4.5 4.98	5.15–8.42	5.8–8.15	6.78	4.37	3.19–5.02	4.05
N/D2	1.1–1.87	1.4 1.82	1.36–2.5	1.48–2.0	2.03	1.91	1.77–2.51	2.54
#S1	10.6–17	10.8 14	8–11.4	9.4–10.6	12.4	12.2	16.3–20.3	17
TM	2.38–4.13	2.4 2.81	0.95–1.98	1.3–1.69	1.83	2.79	3.25–5.27	4.2
L1	0.38–1.63	0.38 0.4	0.05–0.79	0.05–0.28	0.59	1.13	1.43–2.38	0.88
L2	0.08–0.36	0.14 0.15	0.04–0.18	0.05–0.12	0.09	0.06	0–0.6	0.38
D1	0.19–0.44	0.19 0.26	0.08–0.26	0.1–0.24	0.09	0.34	0.23–0.43	0.18
D2	0.13–0.32	0.14 0.18	0.06–0.18	0.06–0.16	0.06	0.17	0.15–0.32	0.09
TW	2.4–4.77	2.63 3.2	1.18–2.44	1.3–1.7	1.74	3	3.2–4.65	4.3
W	0–1.5	0	0	0	0	0	0–3	2
Z	3.3–7	4.3 5	1.7–6	1.7–5	4	4	2–5	3
AZ	40–80	53	53–87	75–87	68	55	57–85	65
AW	0–30	0	0	0	0	0	0–30	25
TT	0.18–0.49	0.22 0.24	0.16–0.33	0.2–0.33	0.22	0.4	0.24–0.46	0.27
D/L	0.85–2.62	1.62 2.04	0.81–3.11	0.81–2.55	1.87	2.22	0.98–2.01	2.4
N = 55	**28**	**2** (ex 28)	**12**	**5** (ex 12)	**1**	**1**	**12**	**1**