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Guadalupian (Middle Permian) solitary rugose corals from the Degerböls and Trold Fiord formations, Ellesmere and Melville islands, Canadian Arctic Archipelago

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ABSTRACT:

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The sparse, Wordian rugose coral fauna of the Degerböls and Trold Fiord formations consists exclusively of nondissepimental, solitary taxa and includes the youngest Permian corals in the Sverdrup Basin. Similar, approximately coeval, Guadalupian coral assemblages are widespread in the youngest coral-bearing deposits of the *Calophyllum* Province in the northern Cordilleran-Arctic-Uralian Realm. The described Sverdrup Basin fauna includes eight species (four new) belonging to the genera *Allotropiochisma*, *Calophyllum*, *Euryphyllum*, *Lytvolasma*, *Soshkineophyllum*, and *Ufimia*. Revision of several previously described corals from East Greenland clarifies their taxonomy and emphasizes the similarity between that fauna and others in the *Calophyllum* Province. The distribution and relative abundance of solitary species in Svalbard, East Greenland and the Sverdrup Basin confirms the geographic proximity of those areas and open marine communication between them during Guadalupian time. Contrasting, low diversity in the Central European Basin and the Eastern European Platform indicates scarcity of favourable marine habitats and a low level of faunal exchange with the remainder of the *Calophyllum* Province.

Key words: Guadalupian, Permian, Solitary Rugosa, Arctic, Canada.

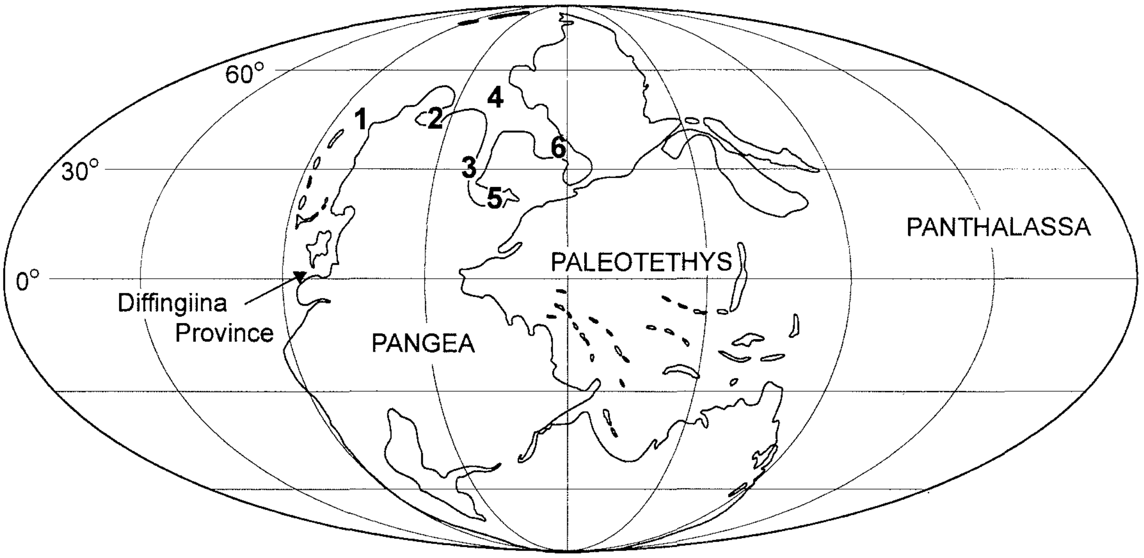
CONTENTS

INTRODUCTION

Guadalupian rugose coral faunas of the Tethys and Cordilleran-Arctic-Uralian (CAU) realms differ greatly in abundance and taxonomic diversity. In contrast to the well developed, highly diversified faunas of the Tethys Realm, those in the CAU Realm consist almost entirely of solitary, nondissepimental taxa. The distribution and the paleogeographic and biostratigraphic significance of the latter have been discussed in detail elsewhere by the authors (FEDOROWSKI & BAMBER, in press). In that paper, we recognized two distinct biogeographic provinces – the previously established Diffingiina Province to the south and the newly named *Calophyllum* Province in the northern part of the realm, the latter extending from the Eastern European Platform to Alaska and including the Sverdrup Basin in the Canadian Arctic Archipelago (Text-figs 1, 2). We wish to add the following comments to clarify our use of the name *Calophyllum* Province: 1) We are aware that, through time, *Calophyllum* was widely distributed beyond the limits of the province, but this genus and its species *C. columnare* were the most abundant and representative corals in the northern part of the CAU Realm during the Middle Permian time interval we are dealing with. We therefore feel justified in using this name for the temporally restricted area shown in Text-figs 1, 2). The province name was presented orally during the XIV International Congress on the Carboniferous and Permian, held in Calgary, 1999, and will be published in the proceedings of that Congress. Thus, it predates the name North Cool Water Province, suggested by HENDERSON & MEI (2000) in the informal newsletter Permophiles for a much larger area that includes and extends far beyond our province in time and space.

The present paper is the first monographic study of the Middle Permian (i.e., the youngest) Rugosa in the Sverdrup Basin. The first record of this fauna is that by THORSTEINSSON (1974, p. 70), who listed *Soshkineophyllum* sp., based on a collection of two incomplete specimens from the lower Trold Fiord Formation, near its type section (Text-fig. 2, locality 3) on Ellesmere Island. Most of the specimens included in our study were collected from the type section of the Degerböls Formation (Text-figs 2, 3). All others are from lateral equivalents of the Degerböls Formation in the lower Trold Fiord Formation at the remaining localities shown in Text-fig. 2.

The Sverdrup Basin fauna shows obvious similarities to corals described from various northern areas by earlier authors (SCHLOTHEIM 1813, HOWSE 1848, KING



1 - Alaska
2 - Sverdrup Basin
3 - East Greenland
4 - Svalbard Archipelago
5 - Central European Basin
6 - East European Platform

Fig. 1. Wordian-Capitanian palaeogeographic map (after ZIEGLER & *al.* 1996, Fig. 8; GOLONKA & *al.* 1994, Fig. 37) showing coral localities (1-6) in *Calophyllum* Province and location of Diffingiina Province (after FEDOROWSKI & BAMBER, in press, Fig. 1)

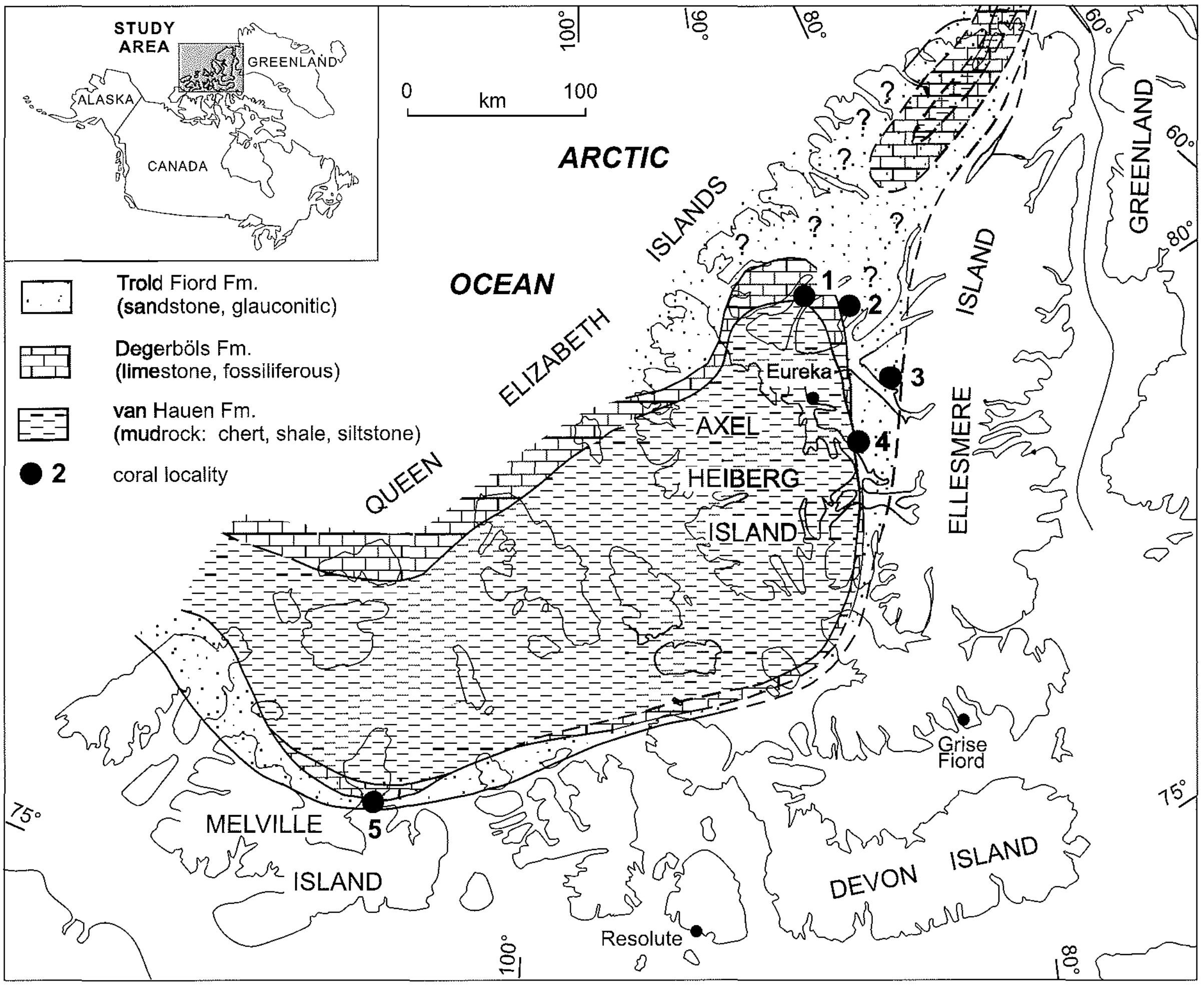


Fig. 2. Map of Sverdrup Basin, Canadian Arctic Archipelago, showing Wordian facies relationships and coral localities (after FEDOROWSKI & BAMBER, in press, Fig. 4): 1 – van Hauen Pass, type section of Degerböls Formation; 2 – north of McKinley Bay; 3 – East Cape River, north side of Canyon Fiord; 4 – Notch Lake, Sawtooth Range; 5 – Tigmisut Lake, Sabine Peninsula. For locality details, see Appendix

1848, 1850, NECHAEV 1894, SOSHKINA 1928, SOSHKINA & *al.* 1941, HERITSCH 1939, SCHINDEWOLF 1942, IVANOVSKY 1972, 1989, TIDTEN 1972, FLÜGEL 1973a, WEYER 1979, 1982, 1984, 1997, WEYER & ILINA 1979, FEDOROWSKI 1982, ILINA 1984, EZAKI & KAWAMURA 1992). For some of the taxa described by those authors, however, the morphology and the taxonomic positions and relationships require futher study and clarificataion. We have therefore included descriptions and illustrations of some previously studied corals from East Greenland and Vestspitsbergen.

Our general remarks on the age, distribution and analysis of the *Calophyllum* Province fauna are restricted to a minimum, because these topics have been discussed elsewhere by us (FEDOROWSKI & BAMBER, in press). In the present paper, we emphasize the systematics of these corals and the mutual relationships within several possible phylogenetic lineages. Uncertainties in this regard led to wide discussion of several genera. Nevertheless, we intend to restrict the discussion on the taxa present outside the CAU Realm because our paper is specifically devoted to those within it. Thus, not all occurrences are listed in the generic synonymies, which are restricted to taxa described by earlier authors from that realm and to those occurrences outside the CAU Realm that are important for taxonomic, evolutionary and palaeogeographic considerations. Our attitude to the question of insertion of initial septa and its taxonomic implications differs from that expressed recently by some authors. General considerations on this subject are therefore introduced as a part of the discussion on the genus *Tachylasma*.

AGE AND DISTRIBUTION OF CORALS IN *CALOPHYLLUM* PROVINCE

The fauna of the *Calophyllum* Province is the youngest autochthonous rugose coral fauna described from the CAU Realm. In Canada, it has been collected, to date, only from Wordian strata outcropping along the eastern and southern margins of the Sverdrup Basin (Text-fig. 2). Locality data and stratigraphic information for our collections are given in the appendix under Geological Survey of Canada (GSC) locality numbers referred to in the descriptive text. A brief summary of the lithology, stratigraphic relationships, age and environments of deposition was given for the Degerböls and Trold Fiord formations by FEDOROWSKI & BAMBER (in press). For further details, the reader is referred to the original descriptions of these units by THORSTEINSSON (1974) and to subsequent papers by BEAUCHAMP & *al.* (1989), BEAUCHAMP (1995) and BEAUCHAMP & DESROCHERS (1997).

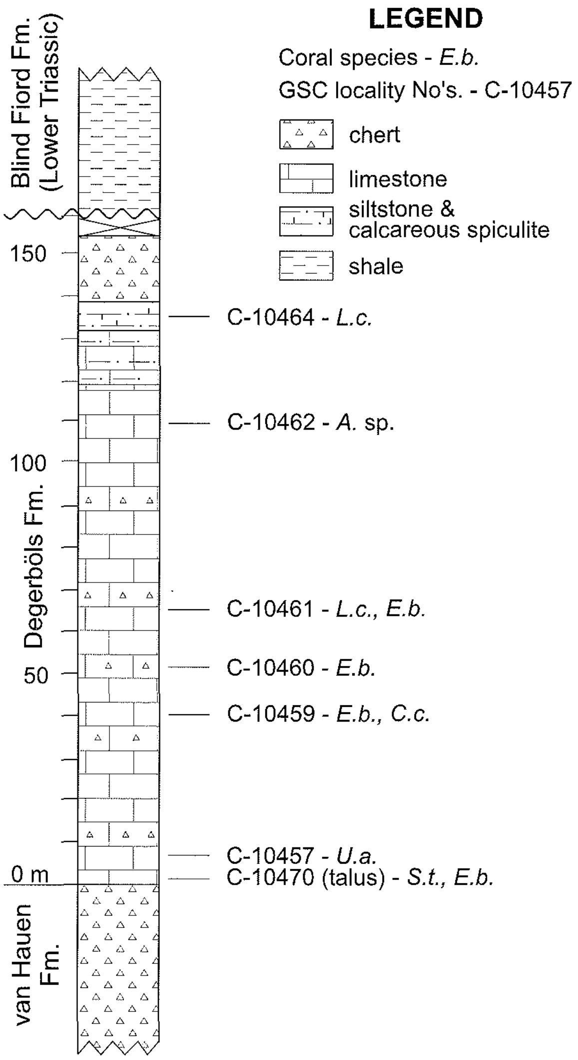


Fig. 3. Type section of Degerböls Formation, van Hauen Pass, Ellesmere Island (Text-fig. 2, locality 1); coral species: *A.* sp. – *Allotropiochisma* sp.; *C.c.* – *Calophyllum columnare* (SCHLOTHEIM, 1813); *E.b.* – *Euryphyllum boreale* sp. n.; *L.c.* – *Lytvolasma canadense* sp. n.; *S.t.* – *Soshkineophyllum turgidiseptatum* (Tidten, 1972); *U.a.* – *Ufimia arctica* sp. n.

The age and distribution information presented by FEDOROWSKI & BAMBER (in press) for the rugose corals of the *Calophyllum* Province is summarized below and in Tables 1 and 2, which show the regional distribution of individual taxa, the age and stratigraphic occurrence of the fauna in different regions and the zone fossils with which it is associated. Six of the eight species found in the Sverdrup Basin also occur in one or more of the other localities within the province (Table 1). Biostratigraphic data derived from associated fossil groups from the Degerböls and Trold Fiord formations indicates a Wordian age for all of the Canadian occurrences (Table 2). The total age range of the Sverdrup Basin species cannot yet be precisely determined, however, because their upper stratigraphic range is unknown with respect to overlying Capitanian conodont faunas (MEI & *al.* 1999, Table 1) and the solitary corals of the underlying, Roadian Assistance Formation have not been studied. At other localities within the *Calophyllum* Province, a Wordian (early Kazanian) age may be assigned to at least part of the coral fauna. In addition, as noted elsewhere (FEDOROWSKI & BAMBER, in press), the occurrence of *Calophyllum columnare* (SCHLOTHEIM, 1813) throughout the province and the presence of several other species at more than one locality (Table 1) suggests that the coral occurrences are approximately coeval and may form a single biozone of Wordian age. Such a biozone cannot presently be named or precisely defined, however, because of insufficient information on the exact stratigraphic and geographic distribution of these corals. The possibility of a wider age range, possibly including Roadian or early Capitanian, cannot be excluded, because of uncertainties concerning inter-regional correlations and local stratigraphic ranges.

Since completion of the summary paper by FEDOROWSKI & BAMBER (in press), a new interpretation of the correlations and age relationships for arctic Permian successions has been presented by HENDERSON & MEI (2000) in an article outlining a preliminary, cool water conodont zonation for northern Pangea. Although their article is informal and lacks detailed biostratigraphic and taxonomic data, it is dis-

CORAL SPECIES	CANADIAN ARCTIC ARCHIPELAGO	SVALBARD ARCHIPELAGO	EAST GREENLAND	CENTRAL EUROPEAN BASIN	EAST EUROPEAN PLATFORM
Allotropiochisma birkenmajeri Fedorowski			x		
Allotropiochisma longiseptata (Flügel)	x		x		
Allotropiochisma sp.	x	x			
Allotropiochisma excentrica (Flügel)			x		
Allotropiochisma pustulosa (Flügel)			x		
Calophyllum columnare (Schlotheim)	x	x	x	x	x
Calophyllum quadrifidum (Howse)			x		
Euryphyllum boreale sp. nov.	x	x			
Euryphyllum troldfiordense sp. nov.	x				
Leonardophyllum? sp.			x		
Lophophyllidium? sp.		x			
Lytvolasma canadense sp. nov.	x				
Tachylasma variabilis (Soshkina)			x		x
Soshkineophyllum turgidiseptatum (Tidten)	x	x			
Soshkineophyllum? sp.			x		
Tachylasma rhizoides Soshkina			x		
Ufimia arctica sp. nov.	x		x		

Table 1. Occurrence of solitary coral species in *Calophyllum* Province

Locality	Age of Corals	Associated Zone Fossils	Coral-bearing Units
Canadian Arctic Archipelago	Wordian	ammonoids brachiopods conodonts palynomorphs	Trold Fiord Fm. (lower) and Degerböls Fm.
Svalbard Archipelago	late Roadian to early Capitanian	brachiopods	Kapp Starostin Fm.
East Greenland	Wordian to early Capitanian	brachiopods conodonts foraminifers	Foldvik Creek Group
Central European Basin	Wordian to early Capitanian	brachiopods conodonts	Zechstein 1 (lower)
East European Platform	early Kazanian (Wordian)	brachiopods palynomorphs	lower Kazanian (Kamyshla and Baytugan beds)

Table 2. Age, faunal associations and stratigraphic distribution of solitary corals in *Calophyllum* Province

cussed below, because their ages and correlations conflict with those previously well established for the area, which were derived from studies of several microfloral and faunal groups, including conodonts.

The Trold Fiord Formation of the Sverdrup Basin was assigned a Capitanian through Wuchiapingian age by Henderson & Mei (2000, Table 1; *Mesogondolella bitteri* to *M. rosenkrantzi* zones). In contrast, an older, mid-Guadalupian, Wordian age is indicated for that formation by biostratigraphic evidence derived from brachiopods [Thorsteinsson, 1974, p. 69, 70, Kazanian (Wordian); Waterhouse *in* Bamber & Waterhouse, 1971, p. 182, 183, table 6, Gc fauna, Kazanian (late Wordian); Waterhouse & Waddington, 1982, p. 8, Table 1, Gc fauna, early Kazanian] and ammonoids (Nassichuk 1995, p. 218). From unpublished conodont and brachiopod evidence, Nakamura & *al.* (1992, p. 83, Fig. 3) suggested a slightly younger, early Capitanian age for the upper part of the formation. Conodonts, apparently from the upper part of the Trold Fiord Formation were assigned a Capitanian to earliest Wuchiapingian age by Mei & *al* (1999, Table 1; *Mesogondolella bitteri*, *M. rosenkrantzi*). Palynomorphs of the *Ahrensisporites thorsteinssonii* – *Scutasporites nanuki* Zone, which occur throughout the Trold Fiord and Degerböls formations, have been assigned a Wordian and possibly younger age by Utting (1994, p. 22, 31). The solitary corals described herein occur mainly in the lower part of the Trold Fiord Formation. Their upper range has not been established with respect to the conodont and palynomorph zone boundaries (Fedorowski & Bamber, in press).

The coral bearing Wegener Halvø and Ravnefjeld formations of East Greenland were assigned to the Lopingian (Wuchiapingian) by HENDERSON & MEI (2000, p. 18, Table 1), based on conodont faunas which, according to them, are associated with the ammonoid *Cyclolobus kullingi* (FREBOLD). In a summary of the ammonoid biostratigraphy of that area, however, NASSICHUK (1995, p. 229, 230; see also, FEDOROWSKI & BAMBER, in press) lists several early Djulfian (=early Wuchiapingian) ammonoid species, including *C. kullingi*, from beds stratigraphically above the conodont bearing units, within the Schuchert Dal Formation and its equivalents in the uppermost Foldvik Creek Group. The conodont faunas, which occur in gravity flow beds within the Ravnefjeld Formation, were dated as late Wordian to early Capitanian by RASMUSSEN & *al.* (1990, p. 315, Fig. 3) and Wordian to Capitanian conodonts have been reported at other localities in the area, from beds occuring stratigraphically below the ammonoids (HENDERSON, pers. com. *in* NASSICHUK, ibid., p. 230, 231). The precise stratigraphic level of the coral faunas within the Ravnefjeld and Wegener Halvø formations is not known with respect to the conodont-bearing beds, but an upper age limit of late Wordian to early Capitanian is indicated by the conodont and ammonoid age determinations listed above. Also associated with the East Greenland corals at several localities is a rich fauna of brachiopods considered by DUNBAR (1955) to be equivalent in age to the Zechstein brachiopod fauna of the Central European Basin. The reader is also referred to correlations between these two areas shown by STEMMERIK (1995, Figs 2, 3). In their study of the Tahkandit Formation of Alaska, BRABB & GRANT (1971, p. 13) assigned a Wordian age to the brachiopod fauna from the upper part of that formation and noted its similarity to the East Greenland fauna and that of the Trold Fiord Formation in the Sverdrup Basin.

From conodont evidence and the relative position of the Illawarra Reversal, HENDERSON & MEI (ibid., p. 18, Table 1) assigned Unit 1 of the Zechstein Formation a latest Capitanian to Wuchiapingian age. This is in disagreement with ages previously assigned to conodonts and brachiopods from that unit (RASMUSSEN & *al.*, ibid., p. 315; FEDOROWSKI & BAMBER, in press). Pending resolution of this and the other discrepancies listed above, between the ages presented by HENDERSON & MEI (2000) and those of previous authors, we have adopted the older, well-documented Wordian/Capitanian age determinations for coral faunas of the *Calophyllum* Province.

SYSTEMATIC PALAEONTOLOGY

Names of institutions are abbreviated in the text and plate descriptions as follows:

GSC – Geological Survey of Canada, Ottawa.
MMH – Mineralogical Museum of the University of Copenhagen.

Type specimens from the Sverdrup Basin are in the type collection of the Geological Survey of Canada, Ottawa.

Order Stauriida VERRILL, 1865
Suborder Stereolasmatina HILL, 1981
Family Hapsiphyllidae GRABAU, 1928
Subfamily uncertain
Genus *Euryphyllum* HILL, 1938

TYPE SPECIES: *Euryphyllum reidi* HILL, 1938

1938. *Euryphyllum* HILL, 1938, p. 25.
1939. *Bradyphyllum* HERITSCH, p. 82, *non* GRABAU, 1928, p. 35.
? 1975. *Lytvolasma* WU, p. 92, *non* SOSHKINA, 1925, p. 82.
? 1980. *Zaphrentites* GUO, p. 117, *non* HUDSON, 1941, p. 309.
? 1980. *Allotropiophyllum* GUO, p. 118, *non* GRABAU, 1928, p. 130.
? 1982. *Duplophyllum* WANG & LIU, p. 64, *non* KOKER, 1924, p. 21.
? 1982. *Lytvolasma* WANG & LIU, p. 64, *non* SOSHKINA, 1925, p. 82.
? 1986. *Lytvolasma* WANG & YU, p. 659, *non* SOSHKINA, 1925, p. 82.

EMENDED DIAGNOSIS: Hapsiphyllidae with major septa extending to axis and pinnately grouped about long, closed cardinal fossula, commonly bisected by long cardinal septum that may be slightly shortened below calice floor; counter septum commonly equal in length to adjacent major septa, may be slightly longer; axial structure formed by joined axial edges of major septa; septa trabecular; trabeculae closely spaced, approximately 0.04 mm in width.

DISCUSSION: For a comprehensive discussion of *Euryphyllum*, the reader is referred to the analysis by FEDOROWSKI (1987). The following additional remarks deal only with those occurrences that were not considered in that paper. We also briefly discuss the position of *Euryphyllum* within the Hapsiphyllidae, the length and variability of the cardinal septum, the septal microstructure and the distribution and relationships of the genus.

The generic content adopted by HILL (1981) for the families Hapsiphyllidae GRABAU, 1928, Zaphrentoididae SCHINDEWOLF, 1938 and Antiphyllidae ILINA, 1970 is difficult to accept. Various morphological characteristics occur in different combinations in the three families.

These include: consistent elongation and grouping of major septa at the corallite axis *versus* abaxial withdrawal during different growth stages; consistent elongation *versus* early shortening of the cardinal septum; slight elongation of the counter septum with respect to adjacent major septa *versus* equivalence in length or even slight shortening [e.g., *Zaphrentites disjunctus* (CARRUTHERS, 1910)]; presence or absence of biform morphology in the tabularium; and the construction of the cardinal fossula and its position with respect to corallite curvature. In addition, the microstructure of septa is unknown for most type species of the assigned genera, including the type genera. Establishment of the true generic content of the families listed above and the firm assignment of *Euryphyllum* to one of them requires more material than we have available and a thorough revision of the type species of most of the constituent genera. Thus, our acceptance of *Euryphyllum* within the Hapsiphyllidae is based on tradition, rather than indisputable data. Setting aside the question of the independent status of the family Zaphrentoididae (a possible synonym of the Hapsiphyllidae) we have reduced the taxonomic rank of the Antiphyllidae and accept its inclusion as a subfamily within the Hapsiphyllidae. The slight elongation of the counter septum in *Euryphyllum* may well indicate a relationship with the Antiphyllinae

Only limited discussion on the relationship between *Euryphyllum* and other genera of the Hapsiphyllidae has been included. It was discussed by FEDOROWSKI (1987) and has not been questioned since. Very few specimens similar to *Euryphyllum* have been described and illustrated from the Guadalupian or Lopingian of the northwestern shelves of Pangea. They belong to the following species: *Clisiophyllum geinitzi* TOULA, 1875, redescribed as *Bradyphyllum geinitzi* (TOULA 1875) by HERITSCH (1939); *Euryphyllum* sp. A and B of EZAKI & KAWAMURA (1992); and *Lytvolasma* (?) sp. cf. *L. geinitzi* (TOULA, 1875) of FLÜGEL (1973a). *"C." geinitzi* and *Euryphyllum* sp. B of EZAKI & KAWAMURA are discussed further under *Euryphyllum boreale* sp. n., below. The Svalbard coral *Euryphyllum* sp. A of EZAKI & KAWAMURA (1992) has long Km septa, the orientation of which indicates a biform tabularium. This character is typical for *Allotropiochisma*, rather than for *Euryphyllum*. Thus, their specimen will not be discussed further. The corallite from Greenland, referred to by FLÜGEL (1973a, Fig. 13A-E) as *Lytvolasma* (?) sp. cf. *L. geinitzi* (TOULA 1875), is slightly irregular and confusing in the arrangement and length of its major septa. It was re-studied and re-drawn by FEDOROWSKI (1982, Fig. 2.2), who showed the counter septum shortened and the alar and counter-lateral septa elongated. These characteristics, which are constant during ontogeny, led FEDOROWSKI (*Ibid.*) to place FLÜGEL's specimen in synonymy with *Tachylasma rhizoides* SOSHKINA, 1925. The holotype of *Clisiophyllum geinitzi* TOULA 1875, however, was not included by FEDOROWSKI *in* SOSHKINA's species.

The variability in the cardinal septum shown by the specimens described below is similar to that in the type species of the genus (HILL 1938, 1942). In the holotype of *E. boreale* sp. n., studied from very early ontogeny to the middle or upper part of the calice, the cardinal septum remains long, but withdraws slightly from the corallite axis fairly early in the ontogeny (Text-fig. 4.1d, e, Pl. 1, Figs 1h, i). This was implied for *E. reidi* by HILL (1938, 1942, 1981), who did not discuss the relationship between the length of the cardinal septum, its position above or beneath the calice floor and the adaxial extension of the cardinal fossula. In contrast to the holotype of *E. boreale* sp. n., the cardinal septum in some paratypes (e.g., Text-fig. 4. 2c, Pl. 1, Figs 4b, c, 6c) reaches the corallite axis up to the calice floor. Morphological features other than the length of the cardinal septum are similar in specimens included by us in that species. Therefore, we accept some variation in the length of the cardinal septum in *Euryphyllum*, even though it is constant in other hapsiphyllid genera.

The septal microstructure of *Euryphyllum* has not been established in the type species and has been described only by SORAUF (1984) in *Euryphyllum cainodon* KOKER, 1924 from the Middle Permian of Timor. SORAUF (ibid., p. 300) included this species in a group showing trabecular septa and discussed the micro-architecture of the septa rather than the morphology and sizes of individual trabeculae. His only statement in that respect is: "...the trabeculae are broad and show clear fanning within the trabeculae." Thus, the remarks that follow should be treated as characteristic only for the Canadian species described in this paper.

In both species described by us, the septal microstructure is trabecular and the size and spacing of the trabeculae are similar, although not identical (Pl. 6, Figs 1-4) in particular septa or parts of septa. Some of the differences that do exist in the trabeculae are diagenetic in origin (e.g. Pl. 6, Fig. 1a), whereas others are perhaps original (Pl. 6, Figs 3a, 4). There is almost invariably a single row of trabeculae, but individual trabeculae are often not arranged exactly in line (Pl. 6, Figs 3a, 4). The resulting wavy arrangement may, in some parts of the septa, be advanced to the extent that it resembles the zig-zag arrangement that we have described in *Ufimia*. In such instances, additional trabeculae may be present (Pl. 6, Fig. 4). In contrast to the zig-zag structure of the external wall, correctly interpreted by OEKENTORP (1980) as secondary, we consider the zig-zag arrangement of trabeculae in *Ufimia* and

Euryphyllum to be a primary feature. This problem is more widely discussed below, under *Ufimia* because the zig-zag arrangement is more clearly demonstrated in that genus.

Individual trabeculae are small (0.03-0.04 mm) and are mostly very closely packed. In the holotype of *E. boreale* sp. n. they appear to lie in the medial planes of the septa and to be consistently arranged in line (Pl. 6, Fig. 1a, b). This cannot be determined with certainty, however, because of diagenetic alteration in this specimen. The paratypes exhibit generally the same arrangement of trabeculae as the holotype, although the spaces between trabeculae may be wider (Pl. 6, Fig. 2). In most of the septa in this paratype (GSC 117155), the trabeculae near the periphery differ slightly in shape from those near the axial part of the cardinal septum (Pl. 6, Fig. 2). This may have been caused by diagenetic alteration or it may reflect more oblique orientation of individual trabeculae. By comparison with the holotype of *E. troldfiordense* sp. n. (Pl. 6, Fig. 3a, b) we consider the second alternative most likely. One of the paratypes of *E. troldfiordense* sp. n. (Pl. 6, Fig. 4) shows an arrangement of trabeculae similar to that described in this paper for *Ufimia*. Unfortunately, preservation of this specimen is poor and we cannot exclude the possibility that this structure is secondary.

Differences between the septal microstructure of our two new species of *Euryphyllum* are slight and may have resulted from diagenesis, which is more advanced in the holotype of *E. boreale* sp. n. (Pl. 6, Fig. 1b). Individual trabeculae are perhaps more closely packed in the peripheral parts of the septa in the latter species than in *E. troldfiordense* sp. n. (Pl. 6, Fig. 3b). In the periaxial parts of septa in both species, the trabeculae are so closely packed that they seem to form a solid line.

It is not quite certain that a direct lineage exists between the Australian Lower Permian (Artinskian?) type species of *Euryphyllum* and the species of that genus from the western hemisphere. The latter include only the uppermost Carboniferous (Virgilian) species described by FEDOROWSKI (1987) from the *Uddenites*-bearing Member of the Gaptank Formation in S.W. Texas and the new species described in this paper. Older Carboniferous taxa of intermediate morphology, although generally similar, do not belong to this genus. The Upper Moscovian (= Westphalian D) *Euryphyllum hispanicum* DE GROOT, 1963, from the Sierra Corisa limestone of the Cantabrian Mountains (Spain), which was included by FEDOROWSKI (1987) in *Allotropiochisma* because of its biform tabularium, cannot be considered as an intermediate taxon, but it indicates the existence of common roots for these two genera. "*Thecophyllum*" FOMICHEV, 1953, placed in synonymy with *Barytichisma* MOORE & JEFFORDS, 1945 by WEYER (1965), may perhaps approximate an intermediate taxon. It has a fairly long range, from Lower Bashkirian (Morrowan) to Lower Stephanian (Missourian), and occurs in intermediate areas (Donets Basin and midwestern North America). Shortening of its major septa late in its ontogeny – a character appearing in the phylogenetically advanced lineages of the Hapsiphyllinae – is the main reason for caution in considering *Barytichisma* ancestral to *Euryphyllum*. Thus, we refer to it only as a possibility. The Kasimovian *Allotropiophyllum*, from the Cantabrian Mts. (especially *Allotropiophyllum* sp. of RODRIGUEZ 1984), is the possibility best matching the demands for an ancestor of both *Euryphyllum* and *Allotropiochisma*. We do not suggest this particular species as a direct ancestor of those genera, but we consider its morphology indicative of a close relationship. Thus, the linkage between the Texan and Arctic species of *Euryphyllum* on the one hand and the Australian type species of this genus on the other is fully realistic, although the species migration routes leading to their established Permian distribution cannot be reconstructed on the basis of existing data.

Among the Asiatic taxa most probably belonging to *Euryphyllum* those listed in the synonymy with a question mark should be discussed briefly. They are included here only tentatively because their documentation is inadequate for definite identification. None of the specimens from the lower Permian Selung Group of the Qomolangma region, included in *Lytvolasma* by WU (1975, p. 92, Pl. 1, Figs 4-11), belongs in that genus, from which they have already been excluded by FEDOROWSKI (1987). The inconspicuous cardinal fossula, intersected by a long cardinal septum, the almost radial arrangement of their major septa and the probable lack of biform morphology in the tabularium demonstrate similarity (relationship?) between those specimens and *Euryphyllum*, to which we provisionally assign them.

Specimens included by GUO (1980) in *Allotropiophyllum* GRABAU, 1928 and *Zaphrentites* HUDSON, 1941 do not exhibit the main characteristics of those genera, but have several characters of *Euryphyllum* HILL, 1938 [see diagnosis by HILL (1981, p. F315), emended by FEDOROWSKI (1987, p. 23)] The same is true for all species described by WANG & LIU (1982) as *Duplophyllum* KOKER, 1924 and *Lytvolasma* SOSHKINA, 1925 and by WANG & YU (1986) as *Lytvolasma*.

Euryphyllum boreale sp. n.
(Text-figs 4, 5; Pl. 1, Figs 1-6; Pl. 2, Figs 3, 5; Pl. 6, Figs 1, 2)

1992. *Euryphyllum* sp. B. EZAKI & KAWAMURA, Pl. 4, Fig. 2.

HOLOTYPE: GSC 117159 (14 thin sections, 4 acetate peels), from GSC locality C-10460 (see appendix).

TYPE LOCALITY: GSC locality C-10460, type section of Degerböls Formation, van Hauen Pass, Ellesmere Island (Text-fig. 2).

TYPE HORIZON: Degerböls Formation, 52.7 m above base of type section (Text-fig. 3), Wordian.

ETYMOLOGY: Latin, *boreus* – northern; for occurrence in boreal (northern) area.

MATERIAL: Paratypes – GSC 117150 (3 thin sections), 117151 (1 thin section, 2 acetate peels), 117153 (1 thin section), 117154 (2 thin sections, 1 acetate peel), 117155 (2 thin sections, 2 acetate peels), 117156 (2 thin sections, 6 acetate peels), 117157 (11 acetate peels), 117158 (2 thin sections, 4 acetate peels), 117160 (1 thin section), 117161 (4 thin sections), 117163 (three thin sections), 117164 (1 thin section, 4 acetate peels), 117168 (2 thin sections, 6 acetate peels), from GSC localities C-10459, C-10460, C-10461, and C-10470.

In addition to the holotype and paratypes listed above, four unfigured, incomplete specimens were studied, using thin sections and acetate peels. Two of these specimens, with only the upper parts of their calices preserved, are conditionally included in this species.

DIAGNOSIS: *Euryphyllum* with deep, narrow calices containing very high stereocolumn extending almost up to calice rim; cardinal septum varies in length, both in and beneath calice; minor septa appear in septotheca near calice floor; n:d range 30:12 – 36:15.5 in middle of calice (33:14 in holotype).

DESCRIPTION OF HOLOTYPE: In terms of its morphology, this corallite (GSC 117159) represents the minority within the collection, but it was chosen as holotype because of its completeness. It was studied beginning with its very early ontogeny: 0.8 mm in diameter and 8 septa, 6 of which (cardinal, counter, 2 alars and 2 counter-laterals) join at axis (Pl. 1, Fig. 1a); first intervening septa appeared next to counter-lateral septa, establishing slight acceleration of septal insertion in counter quadrants – a feature observed throughout ontogeny; at this very early growth stage, corallite surface partly but not substantially corroded and next three sections, at 0.4 mm intervals, show thick, smooth, well preserved wall (Pl. 1, Figs 1b-d); also, small but obvious attachment structure (Text-fig. 4.1b, Pl. 1, Fig. 1d) preserved; corallite surface at this stage has no septal furrows, thus similar in this respect to young corallites of this genus investigated in detail from etched material (FEDOROWSKI 1987). Later in ontogeny, immediately above attachment (Pl. 1, Fig. 1e), corallite surface becomes deeply ribbed, with development of septal furrows corresponding to both major and minor septa, although minors not evident either in corallite lumen or in microstructure of corallite wall (Text-fig. 4.1a-c, Pl. 1, Figs 1a-h) until fairly late in ontogeny (Text-fig. 4.1d, e, Pl. 1, Figs 1i-k).

Arrangement of major septa zaphrentoid throughout early ontogeny, up to lower part of calice (Text-fig. 4.1a-d, Pl. 1, Figs 1a-i), with cardinal and alar fossulae almost equally well developed, narrow and closed. Cardinal septum varies slightly in length at different levels, generally long, but does not always reach corallite axis (e.g. Text-fig. 4.1d, e, Pl. 1, Figs 1h, j). In middle part of calice (Text-fig. 4.1f, Pl. 1, Fig. 1k) alar fossulae disappear because of rearrangement of major septa, which become almost radially arranged in counter quadrants and successively shortened towards cardinal septum in cardinal quadrants. Cardinal fossula remains narrow, but reaches inner margins of major septa of counter quadrants as in all earlier growth stages studied (Text-fig. 4.1d-f, Pl. 1, Figs 1d-k). Counter septum slightly longer than adjacent counter-lateral septa, but this slight elongation seen only in calice (Text-fig. 4.1f, Pl. 1, Fig. 1k). Alar septa are longest septa in cardinal quadrants during entire zaphrentoid stage, but become indistinguishable from other major septa in middle of calice, where cardinal septum becomes distinctly shortened. Minor septa become distinguishable in microstructure of external wall only near calice floor (Pl. 1, Figs 1i, j) and clearly evident in calice as component of septotheca (Pl. 1, Fig. 1k). They do not extend freely into calice in preserved part of corallite.

INTRASPECIFIC VARIABILITY: Although the number of specimens included in this species is the largest within our collection, it is inadequate for reliable statistics (Text-fig. 5). Therefore, our discussion of the intraspecific variability for the species is incomplete and our decisions subjective in some instances. All well preserved corallites exhibit a zaphrentoid septal arrangement early in their ontogeny, but in some, the major septa are much shorter in the counter quadrants than in the cardinal quadrants (e.g., Pl. 1, Figs 6a-d). In this respect, they resemble *Allotropiochisma*. The septal pattern in GSC paratype 117153 (Pl. 1, Fig. 5) is similar to that in some sections of the holotype (Pl. 1, Figs 1h, i), but the cardinal septum is longer. Thus, in this respect, the specimen is intermediate between the holotype and the paratypes discussed below.

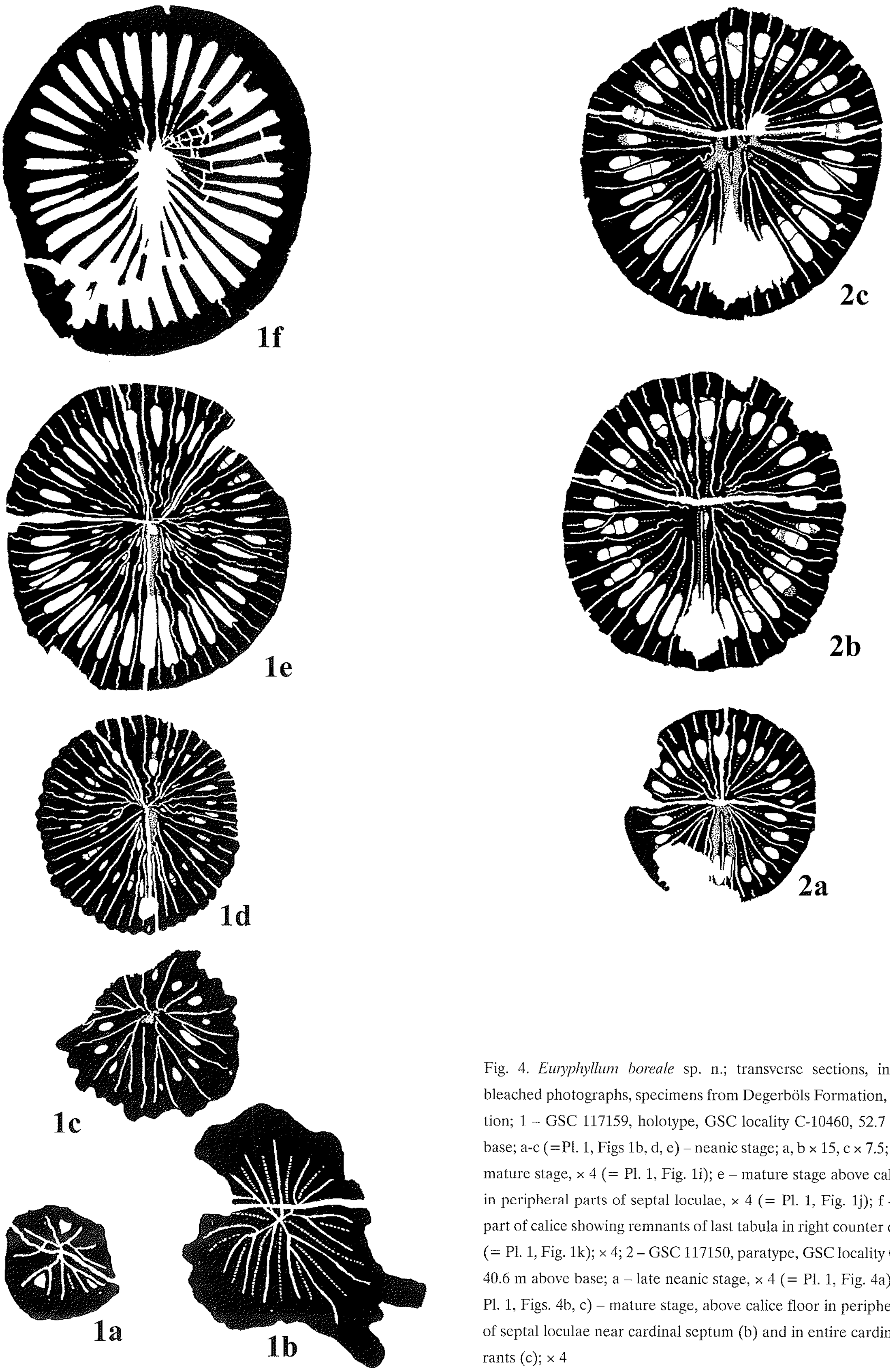


Fig. 4. *Euryphyllum boreale* sp. n.; transverse sections, inked and bleached photographs, specimens from Degerböls Formation, type section; 1 – GSC 117159, holotype, GSC locality C-10460, 52.7 m above base; a-c (=Pl. 1, Figs 1b, d, e) – neanic stage; a, b × 15, c × 7.5; d – early mature stage, × 4 (= Pl. 1, Fig. 1i); e – mature stage above calice floor in peripheral parts of septal loculae, × 4 (= Pl. 1, Fig. 1j); f – middle part of calice showing remnants of last tabula in right counter quadrant (= Pl. 1, Fig. 1k); × 4; 2 – GSC 117150, paratype, GSC locality C-10459, 40.6 m above base; a – late neanic stage, × 4 (= Pl. 1, Fig. 4a); b, c (= Pl. 1, Figs. 4b, c) – mature stage, above calice floor in peripheral parts of septal loculae near cardinal septum (b) and in entire cardinal quadrants (c); × 4

Elongation of the counter septum suggests that, in rare specimens, it could be distinct enough in some sections for comparison with the genus *Actinophrentis* (e.g., Pl. 2, Figs 3a, b). Similar elongation of the counter septum occurs in a specimen having minor septa biformly reduced (WEYER 1974) in the calice (Pl. 2, Fig. 5). The identification of this paratype (GSC 117160) as *Euryphyllum boreale* sp. n. is slightly doubtful, because its early ontogenetic stages are not preserved but, pending further study, we tentatively consider it to be most extreme variant of the species.

In most specimens in the collection the cardinal septum extends to the corallite axis up to the level of the calice floor (e.g., Text-fig. 4.2b, c, Pl. 1, Figs 4a-c, 5). Such corallites also show stronger elongation of the counter septum than is observed in typical *Euryphyllum*, indicating a fairly close relationship to *Allotropiochisma* or *Actinophrentis*. Our specimens are distinguished from both of those genera by a long cardinal septum and are further separated from *Allotropiochisma* by the presence of a tabularium without biform morphology.

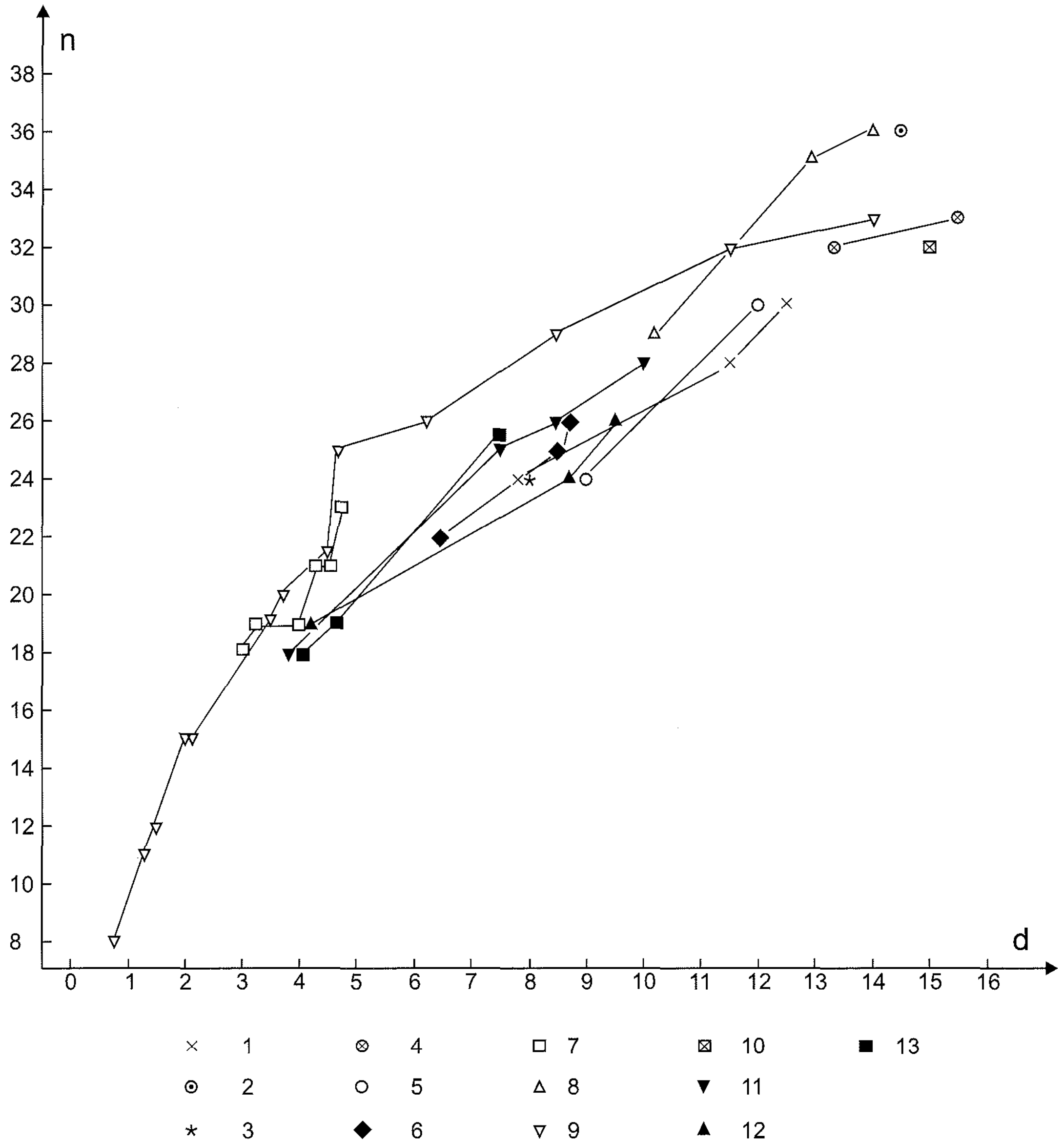


Fig. 5. *Euryphyllum boreale* sp. n.; number of major septa *vs.* diameter; n – number of major septa, d – diameter (mm). 1, 2 – GSC paratypes 117150, 117151; 3-8 – GSC paratypes 117153-117158; 9 – GSC holotype 117159; 10, 11 – GSC paratypes 117160, 117161; 12 – GSC paratype 117163; 13 – GSC paratype 117168. Symbols joined by lines represent values taken from individual specimens

In contrast to all other corallites included in *E. boreale* sp. n., one corallite from our collection (Text-fig. 4.2a-c, Pl. 1, Figs 4a-c) shows better development of its alar fossulae above the calice floor than below it. Also, in a section near its calice floor (Text-fig. 4.2c, Pl. 1, Fig. 4c, Pl. 6, Fig. 2) the cardinal septum is divided into two parts, with the inner one attached to the axial end of the cardinal fossula, thus proving the elongation of the cardinal septum along the calice floor.

In addition to the variants discussed above, our collection contains four specimens that are much smaller than the others, but are otherwise similar to them in their main morphological characteristics (Pl. 1, Figs 2, 3a, b). The small specimens have very deep, narrow calices and we cannot exclude the possibility that they belong to a separate species. We have included them as extreme variants of *E. boreale* sp. n., however, to avoid taxonomic splitting based on inadequate material.

DISCUSSION: Most described species of *Euryphyllum* are Cisuralian in age. Although they are generally similar to *E. boreale* sp. n. in their generic characteristics, they are clearly distinguished from it at the species level by the relationship between their septal number and corallite diameters, the development of the cardinal fossula, the thickness of their major septa and their trend toward shortening of the cardinal septum.

There appears to be a close relationship between "*Clisiophyllum*" *geinitzi* TOULA, 1875 and *Euryphyllum boreale* sp. n. We were unable to locate and study the originals of F. TOULA (1875), which were probably lost during the second world war, together with the remainder of the collection investigated by HERITSCH (1939). The illustrations of the holotype of "*Clisiophyllum*" *geinitzi*, presented by TOULA (1875) and HERITSCH (1939, Pl. 12, Fig. 7, Pl. 20, Figs 4, 5) are inadequate for determination of the diagnostic characters of that species, particularly with regard to the counter septum. HERITSCH (1939, p. 84) stated that the counter septum is very thin, but this cannot be seen in his figure (Pl. 12, Fig. 7), which, on the contrary, shows rhopaloid thickening of the counter septum and a long, thin cardinal septum, barely distinguishable from other major septa, as in our specimens of *Euryphyllum boreale* sp. n. Unfortunately, these important characters cannot be definitely established from HERITSCH 's illustration, and rather than refer to his ambiguous species, we have introduced a new species name, based on our more completely described and illustrated material. This was done despite several similarities between *E. boreale* sp. n. and TOULA's species, including those mentioned above, similar values for septal number and diameter, the union of the major septa at the corallite axis, and a similar development of the minor septa, which form a septotheca (epitheca of HERITSCH, 1939, p. 84).

We have assigned the Svalbard species *Euryphyllum* sp. B of EZAKI & KAWAMURA (1992) to *E. boreale* sp. n. on the basis of published illustrations only, because no description was provided. Although no calicular section of their specimen was shown, all of the illustrated characters closely match those of the Canadian specimens, especially the holotype.

OCCURRENCE: Vestspitsbergen, Kapp STAROSTIN Formation, Unit 1 (EZAKI & KAWAMURA, 1992, Table 2), probably Roadian (less probably latest Kungurian) or Wordian; Sverdrup Basin, Ellesmere Island, Degerböls Formation, type section (Text-fig. 3, GSC localities C-10459 – C-10461, C-10470, Wordian.

Euryphyllum troldfiordense sp. n.
(Text-fig. 6; Pl. 2, Figs 1, 2)

HOLOTYPE: GSC 117170 (5 thin sections, 8 acetate peels), from GSC locality C-82314 (see appendix).

TYPE LOCALITY: GSC locality C-82314, Notch Lake, Sawtooth Range, Ellesmere Island (Text-fig. 2).

TYPE HORIZON: lower Trold Fiord Formation, between 127 m and 142 m above base of formation, Wordian.

ETYMOLOGY: Named for Trold Fiord Formation, which yielded specimens.

MATERIAL: Paratypes: GSC 117171 (4 thin sections), 117174 (3 thin sections, 1 peel), from GSC locality C-82314. Three incomplete specimens were available for study, but only the holotype and one paratype (GSC 117171) were preserved well enough for adequate description. In the holotype, the calice and much of the early growth stages are preserved, but the calice has been diagenetically flattened, so that its middle and upper part cannot be studied.

DIAGNOSIS: *Euryphyllum* with major septa approximately equally thickened in mature growth stage, almost meet at corallite axis; in calice, major septa first thin in cardinal quadrants; cardinal fossula indistinct; cardinal septum slightly shortened below calice floor; minor septa evident only near or within calice; 37 major septa at corallite diameter of 20 mm, immediately above calice floor.

DESCRIPTION OF HOLOTYPE: Ontogenetically earliest preserved growth stage has n:d = 25:7 (Text-fig. 6.1a, Pl. 2, Fig. 1a) and shows typically zaphrentoid septal arrangement with cardinal septum crossing closed, distinct, parallel-walled cardinal fossula and almost reaching corallite axis; counter septum slightly longer than counter-lateral septa; alar septa are longest septa in cardinal quadrants, but only one alar fossula well developed; all major septa strongly thickened at periphery to form septotheca, periaxial ends of most majors in lateral contact, but not truly rhopaloid; minor septa absent from this growth stage, but their furrows can be recognized (Text-fig. 6.1a, Pl. Fig. 1a).

Mature growth stage (Text-fig. 6.1b, c; Pl. 2, Figs 1b-d) differs from juvenile stage by rearrangement of major septa into almost radial pattern, further thickening of majors around periaxial area and slight withdrawal from corallite axis, slight shortening of cardinal septum and appearance of minor septa in peripheral part of external wall. Most important morphological changes observed in holotype along approximately 14 mm of mature growth (i.e., up to calice floor) include variation in morphology of cardinal fossula and changes in n:d ratio from 35:14.6x12.0 to 37:18x16. Cardinal fossula differs in each section observed (Text-fig. 6.1b, c, Pl. 2, Figs 1b-d). Apparent morphological differences in axial area mainly reflect damage by recrystallization, which altered inner margins of several major septa to various degrees.

Transverse section cut partly above calice floor (Text-fig. 6.1d, Pl. 2, Fig. 1e) illustrates morphology of this important part of holotype – calice floor elevated much more in periaxial part of counter quadrants than in cardinal quadrants, as demonstrated by sections of tabulae present in counter quadrants, but absent from cardinal quadrants, where interseptal loculi filled with matrix; narrow ring of matrix fills peripheral parts of interseptal loculi in counter quadrants, indicating steep slope of calice floor; degree of septal thickening distinctly differs in cardinal and counter quadrants, caused

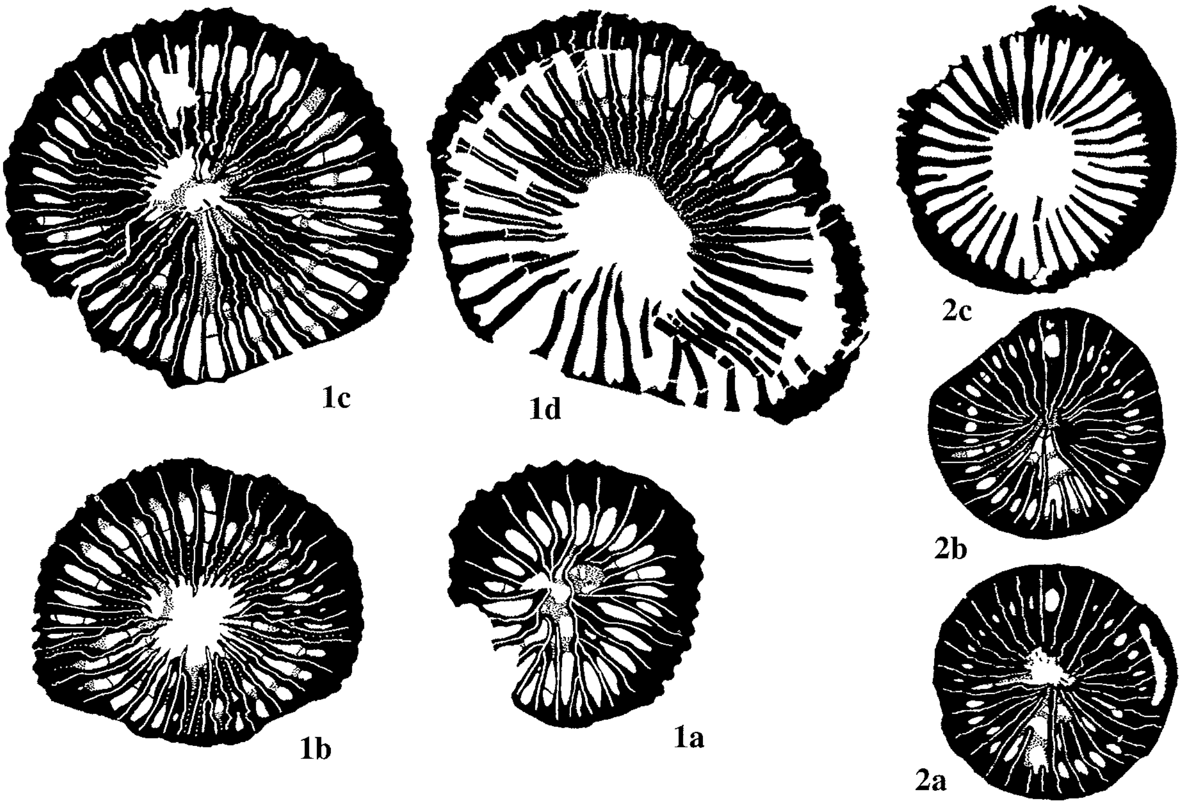


Fig. 6. *Euryphyllum troldfiordense* sp. n.; transverse sections, × 3 unless stated otherwise, inked and bleached photographs, specimens from Trold Fiord Formation at GSC locality C-82314, collected between 127 m and 142 m above base ; 1 – GSC 117170, holotype; a - neanic stage (= Pl. 2, Fig. 1a), × 5; b, c (= Pl. 2, Figs. 1b, d) – mature stage (c from acetate peel), d - middle part of calice beneath last tabula in inner parts of counter quadrants (= Pl. 2, Fig. 1e); 2 – GSC 117171, paratype;. a, b – mature stage (a = Pl. 2, Fig. 2b); b – from acetate peel); c – middle part of calice above last tabula (= Pl. 2, Fig. 2d), from acetate peel

at least in part by the position of the latter below the last tabula and the former above it; minor septa protrude slightly from external wall only in calice, but remain short and indistinct in preserved lower part of calice; rhopaloid character of septa in counter quadrants additionally emphasized by diagenetic alterations affecting their inner margins.

INTRASPECIFIC VARIABILITY: In contrast to holotype, best preserved paratype (GSC 117171; Text-fig. 6.2a-c, Pl. 2, Figs 2a-d) has thick, wedge-shaped major septa meeting at corallite axis and touching laterally, except for short breaks between their peripheral parts; majors radially arranged, with cardinal fossula inconspicuous and alar fossulae absent; cardinal septum reaches corallite axis along most of corallite length (Text-fig. 6.2a,b, Pl. 2, Figs 2a-c), becoming slightly shortened immediately below calice floor; specimen much smaller than holotype, with n:d = 31:12.5 below calice.

Second paratype (GSC 117174) incompletely preserved, more than 15 mm in diameter immediately above calice floor, number of septa unknown at this level; similar to holotype in morphology, length and reduction in thickening of major septa, development of minor septa and uniform tabularium.

DISCUSSION: *E. troldfiordense* sp. n. bears the greatest similarity to *E. boreale* sp. n., but is distinguished from the latter by a slighty larger corallite diameter, more numerous septa, an inconspicuous cardinal fossula, an absence of alar fossulae, and a radial arrangement of the major septa.

OCCURRENCE: Sverdrup Basin, Ellesmere Island, Trold Fiord Formation, GSC locality C-82314, Wordian.

Genus *Allotropiochisma* FEDOROWSKI, 1982

TYPE SPECIES: *Amplexizaphrentis longiseptata* FLÜGEL, 1973.

1939. ? *Hapsiphyllum* HERITSCH, p. 87, *non* SIMPSON, 1900, p. 203.
1973a. *Amplexizaphrentis* FLÜGEL, p. 32, *non* VAUGHAN, 1906, p. 315.
1973a. *Bradyphyllum* FLÜGEL, p. 40, *non* GRABAU, 1928, p. 35.
? *partim* 1977. *Allotropiophyllum* GRABAU, 1928, p. 130; XU, p. 130.
1982. *Allotropiochisma* FEDOROWSKI, p. 78.
? partim 1982. *Allotropiophyllum* GRABAU, 1928; YAN & CHEN, p. 117.
1987. *Allotropiochisma* FEDOROWSKI, p. 10.
1991. *Allotropiochisma (Alligia)* cf. *flabellum* FEDOROWSKI, 1987; KORA & MANSOUR, Fig. 3b.
1992. *Allotropiochisma* EZAKI & KAWAMURA, p. 72.
1992. *Pseudoallotropiophyllum* PENG, LIN & LI, p. 131.
1997 ? *Allotropiochisma* KOSSOVAYA, p. 67.

SUBGENERA ASSIGNED: *Allotropiochisma* FEDOROWSKI, 1982; *Alligia* FEDOROWSKI, 1987; *Abeophyllum* FEDOROWSKI, 1987.

DIAGNOSIS: Medium to large solitary corals without dissepimentarium; counter and alar septa slightly elongated in early ontogeny; cardinal septum shortened from early maturity or earlier; major septa arranged as in *Allotropiophyllum*, having axial ends joined directly or by stereocolumn at axial margin of long, closed cardinal fossula; minor septa present in corallite lumen below calice floor; tabulae hemispherical, sagging axially, with incipient biform morphology at periphery; septa trabecular, aseriate. (After FEDOROWSKI, 1987, p. 10, corrected).

DISCUSSION: A comparison of *Allotropiochisma* to the most similar and/or related genera was given by FEDOROWSKI (1982, 1987). Only three papers dealing with taxa assigned to *Allotropiochisma* have been published since (see synonymy). We accept the generic status of the undescribed specimen illustrated by EZAKI & KAWAMURA (1992, Pl. 4, Fig. 4), although their assignment of this specimen to *A. svalbardicum* (HERITSCH 1939) cannot be confirmed because of the inadequate description and illustration given by HERITSCH (1939).

KOSSOVAYA (1997) described and illustrated a new species of *Allotropiochisma* and illustrated another, including both in the subgenus *Alligia* FEDOROWSKI, 1987. The generic designation of neither species is convincing. In *A.* (*A.*) *mirus* KOSSOVAYA, 1997 the tabularium does not show biform morphology. *A.* (*A.*) *flabellum* FEDOROWSKI, 1987, illustrated by KOSSOVAYA (*ibid.*, Pl. 14, Fig. 3a-g), belongs to *Allotropiochisma* if the morphology of the counter septum has been pathologically changed and it is not shortened. The morphology of this specimen and its n:d values differ to such an extent from those of the Texan specimens described by FEDOROWSKI (1987) that they cannot belong to the same species.

Several taxa described from China may in fact belong to *Allotropiochisma*. Among three species described by XU (1977, pp. 130-131) only *Allotropiophyllum sinense heteroseptatum* belongs to that genus. We will not discuss *A. hunanense* XU, 1977 because its morphology does not correspond to either *Allotropiophyllum* or *Allotropiochisma*.

Several features of *A. hubaiense* XU, 1977, from the lower Maokouan of South China (XU 1977, Pl. 44, Figs 5a-c), fit the diagnosis of *Allotropiochisma* (*Alligia*). These include its clearly biform tabularium, the arrangement of its major septa (short in the counter and long in the cardinal quadrants) and its narrow cardinal fossula intersected by the cardinal septum until early maturity. Its well developed alar pseudofossulae and the lack of information on the microstructure of its septa, however, prevents its definite inclusion in that genus.

YAN & CHEN (1982) described four species of *Allotropiophyllum*, two or three of which display a fairly clearly developed biform tabularium and an arrangement of septa typical for *Allotropiochisma*, without alar pseudofossulae. These species, i.e., *A. anfuense* ZHU, *A. wuweiense* YAN & CHEN, and in particular *A. jiangxiense* YAN & CHEN, may belong in *Allotropiochisma*. None of them is described or illustrated in detail adequate for definite generic assigment.

The Upper Carboniferous specimen illustrated by KORA & MANSOUR (1991, Fig. 3b) as *Allotropiochisma* (*Alligia*) cf. *flabellum* FEDOROWSKI, from the western side of the Gulf of Suez, Egypt, may well belong to that genus and subgenus. Its generic affinites remain uncertain, however, becouse no description was provided and the illustrations are inadequate. This is very unfortunate because the rugose coral assemblage of the lower member of the Aheimer Formation fairly closely resembles that described by FEDOROWSKI (1987) from the Gaptank Formation of SW Texas and would have provided important palaeogeographical information if completely documented.

The Upper Carboniferous specimens from the southern part of the North Chinese Platform described and illustrated by PENG & *al.* (1992, p. 131, Pl. 13, Figs 8, 9) as *Pseudoallotropiophyllum huabaiense* exhibit all the main characteristics of *Allotropiochisma* and are included by us in that genus.

SUBGENUS *Allotropiochisma* FEDOROWSKI, 1982

TYPE SPECIES: As for genus.

1973a. *Amplexizaphrentis* FLÜGEL, p. 32, *non* VAUGHAN, 1906, p. 315.
1973a. *Bradyphyllum* FLÜGEL, p. 40, *non* GRABAU, 1928, p. 35.
1982. *Allotropiochisma* FEDOROWSKI, p. 78.
1987. *Allotropiochisma* (*Allotropiochisma*) FEDOROWSKI, p. 10.
1992. *Allotropiochisma* EZAKI & KAWAMURA, p. 72.

DIAGNOSIS: *Allotropiochisma s.s.* having major septa withdrawn early from corallite axis, axial ends joined eccentrically towards counter quadrants after further growth; minor septa "biformly reduced" (After FEDOROWSKI 1987, p. 10).

Allotropiochisma (Allotropiochisma) longiseptata (FLÜGEL 1973)
(Text-fig. 7.1, Pl. 3, Fig. 1)

1973a. *Amplexizaphrentis longiseptata* FLÜGEL, p. 39, Pl. 4, Fig. 2, Text-fig. 18.
1982. *Allotropiochisma longiseptata* (FLÜGEL 1973); J. FEDOROWSKI, Fig. 2.2a, b.
1987. *Allotropiochisma (Allotropiochisma) longiseptata* (FLÜGEL, 1973); J. FEDOROWSKI, Fig. 2.4.

MATERIAL: GSC hypotype 117176 (2 thin sections). Peels of holotype re-examined for comparison.

EMENDED DIAGNOSIS: *Allotropiochisma* with major septa of counter quadrants short and thickened at calice floor; n:d up to 38:18.

DISCUSSION: The single available specimen from Ellesmere Island is poorly preserved and incomplete. Its main morphological characteristics, especially the arrangement and length of the major septa in different quadrants, were easily recognizable and closely similar to those of the holotype. The Canadian specimen has more septa than the holotype (38 vs. 33) at a similar corallite diameter near the calice floor. We considered this numerical difference less important than the close similarity in other morphological features.

OCCURRENCE: East Greenland, Kap Stosch, Wegener Halvø Formation, Foldvik Creek Group ["*Productus* limestone" (FLÜGEL 1973a)], Wordian or early Capitanian; Sverdrup Basin, Ellesmere Island, Trold Fiord Formation, GSC locality C-82473, Wordian.

Allotropiochisma (*Allotropiochisma*) sp.
(Text-fig. 7.2; Pl. 2, Fig. 4; Pl. 7, Fig. 3)

MATERIAL: Upper part of one incomplete specimen, including calice [(GSC hypotype 117165 (2 thin sections, 2 acetate peels)], from GSC locality C-10462. Inner morphology and septal microstructure well preserved.

DESCRIPTION : External wall 0.8-1.2 mm thick, septothecal on its inner side, but lamellar at periphery; expanded peripheral margins of minor septa penetrate external wall less deeply than similarly expanded peripheral parts of major septa. Major septa long but do not meet at corallite axis, leaving open axial area 3-4 mm wide (when measured perpendicular to cardinal septum); inner halves of major septa thickened to join laterally around axial part of corallite; resulting ring of septa opens only at axial margin of cardinal fossula (Text-fig. 7.2a, b; Pl. 2, Figs 4a, b); axial margins of major septa thin adaxially (best seen on and immediately above tabula – Text-fig. 7.2b), thus, major septa not truly rhopaloid; no major septa elongated. Underdevelopment of last septa in counter quadrants indicates great acceleration of septal insertion in those quardants (10:6, excluding alars and counter-laterals). N:d = 38:26.5 in lower part of calice, 38:23.7 at calice floor.

Cardinal fossula very deep, narrow, but slightly widened toward periphery and axis; cardinal septum in preserved part of corallite probably did not exceed 2 mm in length, but was observed only at a level well above last tabula in fossula (Text-fig. 7.2a, b; Pl. 2, Figs 4a,b) and therefore true length unknown. In youngest preserved part of corallite, cardinal fossula bordered along most its length by two major septa adjacent to cardinal septum, but closed axially by inclined inner margins of all major septa of cardinal quadrants, including alar septa. Some major septa connected by intercepts of tabulae (Text-fig. 7.2a, b; Pl. 2, Fig. 4a), which indicate depth of tabular fossula. Major septa surrounding cardinal fossula above last tabula join axial depression of calice surrounded by inner margins of remaining major septa, showing true shape and relationship of cardinal fossula to both tabulae and major septa. Calcitic fabric present between inner parts of major septa bordering axial depression contrasts with clastic matrix inside axial depression and near periphery of corallite showing adaxial elevation of tabulae; comparison of sequential transverse sections documents higher position of calice floor in counter quadrants than in cardinal quadrants, as well as depression of calice floor toward cardinal fossula (Text-fig. 7.2b; Pl. 2, Figs 4a,b).

Biform reduction (WEYER 1974) of minor septa,

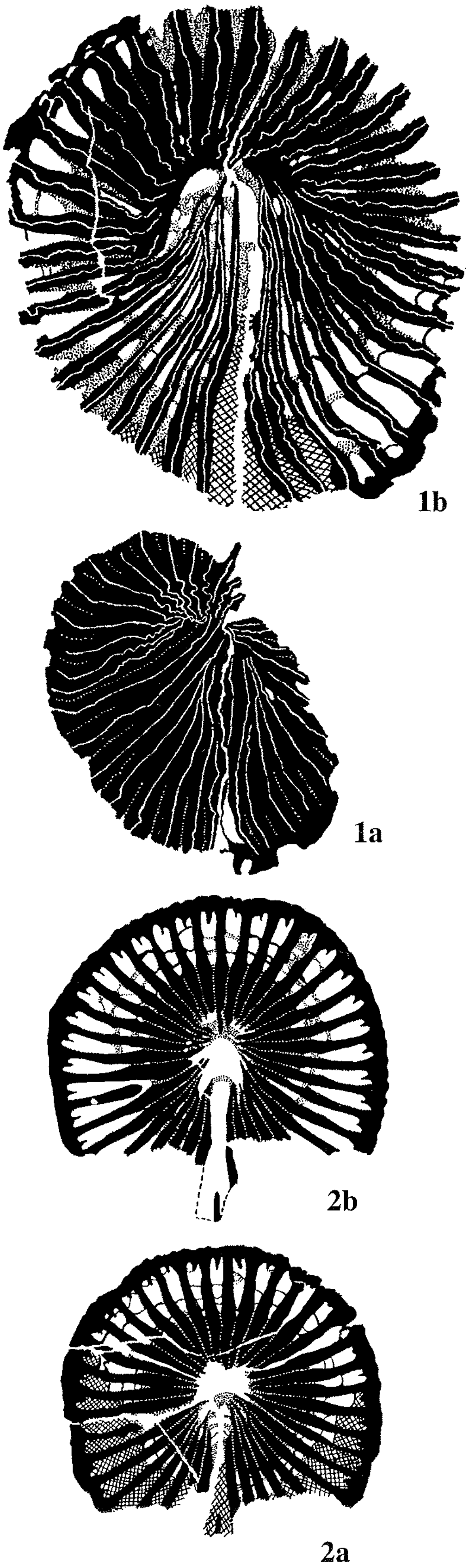


Fig. 7. *Allotropiochisma* (*Allotropiochisma*); transverse sections, inked and bleached photographs; 1 – *Allotropiochisma* (*Allotropiochisma*) *longiseptata* (FLÜGEL 1973a), GSC 117176, hypotype; GSC locality C-82473, Trold Fiord Formation, 33 m above base; a – late neanic stage (= Pl. 3, Fig. 1a); b – early mature stage (= Pl. 3, Fig. 1b); × 4; 2 – *Allotropiochisma* (*Allotropiochisma*) sp., GSC 117165, hypotype, GSC locality C-10462, Degerböls Formation, type section, 109.2 m above base; mature stage, a – partly above calice floor at periphery (shaded) (from acetate peel); b – almost entirely above calice floor at periphery and in cardinal fossula (= Pl. 2, Fig. 4a); × 2

shape of outermost parts of tabulae, and appearance of matrix on cardinal side of some minor septa indicate biform morphology in peripheral part of the tabularium.

Septal microstructure trabecular (Pl. 7, Figs 3a, b), with individual trabeculae among the largest (0.7-0.1 mm) of all those in taxa described in this paper. Arrangement of trabeculae varies along transverse sections of individual septa (i.e., during their growth). They form a single row through major parts of septa, are most closely packed near periphery and in middle parts of septa, and are most widely spaced between these two areas and near axial margins of septa. Apparent arrangement of trabeculae may be artificial to some extent, conditioned by shape of upper and inner margins of septa and corresponding changes in directions of growth of trabeculae; in some parts of almost all septa sectioned, arrangement of some trabeculae close to aseriate in aspect .

DISCUSSION: The corallite described is very incomplete, but its main morphological characteristics match those of *Allotropiochisma* (*Allotropiochism*a) and allow comparison with other representatives of that subgenus. Its description is included here to give the fullest possible treatment of the sparse coral fauna from the Degerböls and Trold Fiord formations. According to the emended diagnosis of FEDOROWSKI (1987, p. 10) only aseriate septal microstructure is typical for the genus. The material available for our study is too limited to allow general conclusions to be drawn concerning the microstructure of its septa.

Specimens illustrated by EZAKI & KAWAMURA (1992) as *Allotropiochisma svalbardicum* (HERITSCH) are morphologically most similar to our specimen, with the following characters in common: thickening of the major septa, strong acceleration of septa in the counter quadrants, similar shape of the cardinal fossula, biform reduction of the minor septa and a biform tabularium. The Svalbard specimens are distinguished by more strongly accentuated alar fossulae and, perhaps, slightly elongated counter septa, but the latter character cannot be confirmed because no description of the specimen was published by EZAKI & KAWAMURA (*ibid.*) and their illustrations are not quite clear. Nevertheless, we consider our specimen to be conspecific with the Svalbard specimen. We have left it in open nomenclature, rather than assigning it to HERITSCH's species, for the following reasons: 1) The precise nature of *"H." svalbardicum* HERITSCH, 1939 cannot be determined, because HERITSCH's original material has been lost (see below). 2) The intraspecific variability and septal microstructure of the Svalbard specimens are unknown. 3) Without data from other collections, a new species name cannot be established on the basis of our single, incomplete specimen.

OCCURRENCE: Svalbard, Kapp Starostin Formation, units 5, 7 (EZAKI & KAWAMURA 1992, Table 2), probably Roadian or Wordian; Sverdrup Basin, Ellesmere Island, Degerböls Formation, GSC locality C-10462, Wordian.

Subfamily Antiphyllinae ILINA, 1970
Genus *Lytvolasma* SOSHKINA, 1925
(Emended WEYER, 1975; FEDOROWSKI 1987)

TYPE SPECIES: *Lytvolasma asymmetrica* SOSHKINA 1925)

? 1980. *Lytvolasma* SOSHKINA, 1925, p. 82; GUO, p. 118.
non 1982. *Lytvolasma* SOSHKINA, 1925; WANG & LIU, p. 64.
non 1986. *Lytvolasma* SOSHKINA, 1925; WANG & YU, p. 659.
1991. *Lytvolasma* FEDOROWSKI, 1987; KORA & MANSOUR, Fig. 2c.
non 1987. *Lytvolasma* SOSHKINA, 1925; ZHAO & ZHOU, p. 487.

REMAINING SYNONYMY: See FEDOROWSKI (1987, p. 57)

DIAGNOSIS: Antiphyllinae with deep key-hole cardinal fossula, often bordered by half-aulos in counter quadrants; cardinal septum shortened late in ontogeny; counter septum slightly elongated; arrangement of major septa semi-radial; calices deeper in cardinal quadrants; minor septa very short; microstructure of septa trabecular. (after FEDOROWSKI 1987, p. 57, slightly modified).

DISCUSSION. The genus *Lytvolasma* SOSHKINA, 1925 was discussed in detail and emended by FEDOROWSKI (1987), whose conclusions were based on information from a review of the holotype, some specimens described by FOMICHEV (1953a) from the Donets Basin, and a collection from southwestern Texas. No further discussion of the occurrence of the genus in the CAU Realm is presented here, because no new data have since been obtained. *Lytvolasma* is currently known to range from the Kasimovian to the Artinskian in the CAU Realm, but has not previously been described from Wordian or younger strata. The identification by FLÜGEL (1973a) of *Lytvolasma* (?) sp. cf. *L. geinitzi* (TOULA, 1875) was questioned by FEDOROWSKI (1987) and is referred to above in the discussion of *Euryphyllum boreale* sp. n.

Some species described from the Tethys Realm may belong to *Lytvolasma*. In contrast to FEDOROWSKI

(1987, p. 57) we can see the possibility that some specimens described by GUO (1980, p. 118) may be included in that genus. This concerns first of all the specimen illustrated by that author in his plate 65, figure 5. Unfortunately, poor preservation and the absence of illustrations of its early ontogenetic stages make a final decision on his specimen impossible.

The morphology in the single transverse and longitudinal sections of the mature part of a corallite from Egypt shown by KORA & MANSOUR (1991), resembles that of the North American species of *Lytvolasma* closely enough to be accepted at the genus level at least. Lack of description and more complete illustrations precludes acceptance of his species identification, which is unfortunate for the purposes of paleogeographical reconstruction.

We were unable to confirm the presence of characters diagnostic for *Lytvolasma* in either of the two transverse sections of the poorly preserved specimen illustrated by ZHAO & ZHOU (1987, Pl. 1, Figs 4, 5). In addition, long major septa, twisting at the corallite axis do not occur at any known growth stage of *Lytvolasma*. Thus, we do not accept their identification.

Lytvolasma canadense sp. n.
(Text-fig. 8, Pl. 3, Fig. 2, Pl. 5, Fig. 5)

HOLOTYPE: GSC 117166 (4 thin sections, 4 acetate peels), from GSC locality C-10464 (see appendix).

TYPE LOCALITY: GSC loc. C-10464; type section of Degerböls Formation, van Hauen Pass, Ellesmere Island (Text-fig. 2).

TYPE HORIZON: Degerböls Formation, 136.6 m above base of type section (Text-fig. 3), Wordian.

ETYMOLOGY: named for occurrence in Canada.

MATERIAL: Paratype – GSC 117162 (2 thin sections, 2 acetate peels), from GSC locality C-10461. Two specimens available for study are incomplete, partly corroded and slightly silicified; three thin sections and four peels prepared from holotype, two thin sections and two peels from paratype.

DIAGNOSIS: *Lytvolasma* with cardinal septum distinctly shortened; counter septum elongated beneath and above calice floor; major septa slightly rhopaloid; minor septa protrude from corallite wall only in calice; trabeculae up to 0.1 mm in diameter; up to 30 major septa at corallite diameter of 12.5 mm, near calice floor.

DESCRIPTION OF HOLOTYPE. External wall 0.6 mm thick, wavy at periphery, indicating presence of septal furrows corresponding to major and minor septa; in earliest preserved growth stage (Text-fig. 8a, Pl. 3, Fig. 2a) minor septa not seen in corallite wall, except possibly in loculi adjacent to slightly elongated counter septum; minor septa more strongly developed in more mature growth stages, where they combine with major septa to form septotheca (Text-figs 8b-d; Pl. 3, Fig. 2b-d). Major septa, which are arranged asymmetrically in earliest growth stage (Text-fig. 8a; Pl. 3, Fig. 2a), become radially arranged, rhopaloid and almost equal in length in more mature stage (Text-fig. 8b; Pl. 3, Fig. 2b); only counter septum slightly but permanently elongated and cardinal septum distinctly shortened; last major septa inserted in quadrants are shorter and thinner than other major septa, but alar fossulae not developed. Cardinal septal fossula triangular, but open adaxially, bordered by two pairs of major septa with last pair underdeveloped and other major septa of cardinal quadrants slightly but successively shorter toward cardinal septum. In calice (Text-figs 8c, d; Pl. 3, Figs 2c, d) major septa lose rhopaloid thickening, but remain radially arranged with counter septum clearly elongated. Biform morphology weakly expressed (Text-figs 8b, d). Successive n:d values as follows: 24:8.4; 26:10.7; 26:12.6 (near calice floor). Microstructure comprises single row of large trabeculae (Pl. 5, Fig. 7) up to 0.1 mm in diameter; trabeculae situated in medial plane of septum, growing perpendicular to its axial margin and fairly widely spaced over entire length of septum.

INTRASPECIFIC VARIABILITY: Not established; single paratype distinguished from holotype by slightly higher number of septa at comparable diameters: 26 at 12.6 mm (holotype), 30 at 12.4 mm (paratype); also, major septa thicker in paratype; combination of these characters caused greater crowding of septa in corallite lumen of paratype than in holotype.

DISCUSSION: *Lytvolasma canadense* sp. n. is distinguished from other species of *Lytvolasma* by its dimensions, the stronger elongation of its counter septum, the persistent shortening of the last major septa in all quadrants and in the underdevelopment of its minor septa. In early maturity, the holotype shows asymmetrical thickening of its major septa, very similar to that in the type species of the genus. No comparison of the septal microstructure in *L. canadense* sp. n. can be made, because that feature has not been described in the type species or in other species included in *Lytvolasma* by earlier authors.

Although our collection of this species is limited to only two specimens, their unique morphology appears

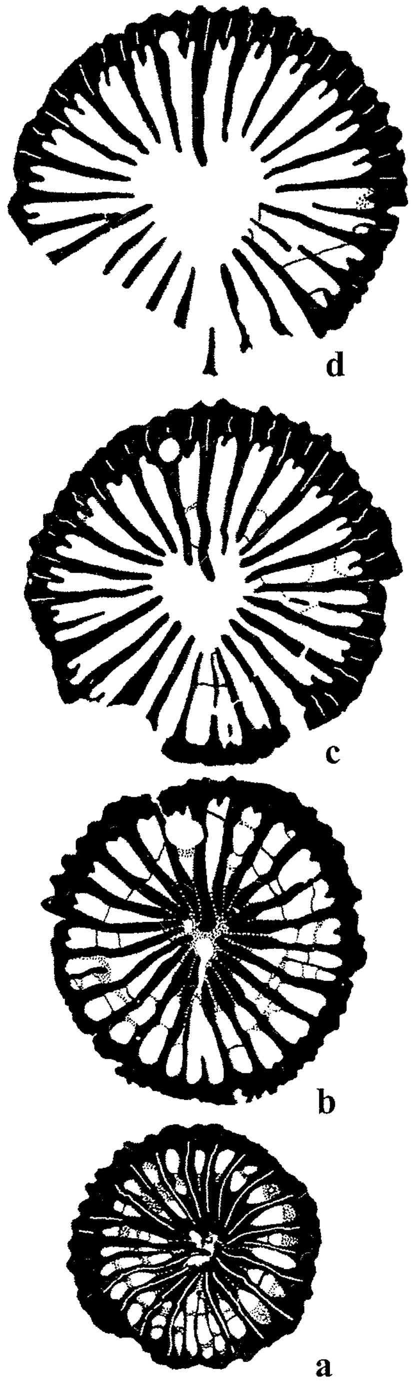


Fig. 8. *Lytvolasma canadense* sp. n.; transverse sections, inked and bleached photographs, GSC 117166, holotype; GSC locality C-10464, Degerböls Formation, type section, 136.6 m above base; a – late neanic stage (= Pl. 3, Fig. 2a); b – mature stage (= Pl. 3, Fig. 2b); c – above calice floor at periphery (= Pl. 3, Fig. 2c); d – middle part of calice, mostly above its floor (= Pl. 3, Fig. 2d); × 4

to justify the establishment of a formal species. Also, the Canadian species is geographically isolated from other species of *Lytvolasma* and is the youngest species known. It is unlikely that more specimens will be obtained from this isolated region.

OCCURRENCE: Sverdrup Basin, Ellesmere Island, Degerböls Formation, GSC localities C-10461, C-10464, Wordian.

Family Plerophyllidae Koker, 1924
Genus *Ufimia* Stuckenberg, 1895

TYPE SPECIES: *Ufimia carbonaria* Stuckenberg, 1895

partim 1922. *Tachylasma* Grabau, p. 34.
1936a. *Rhopalolasma* Hudson, p. 93.
1940. *Rhopalelasma* Lang, Smith & Thomas, p. 115.
1942 ? *Prionophyllum* Schindewolf, p. 209 (see also *Tachylasma*).
1944. *Zaphrentites* Hudson, p. 45; non Hudson, 1941, p. 309.
1966. *Meniscophylloides* Kullmann, p. 452.

DIAGNOSIS: Small Plerophyllidae with four septa (alar and counter-lateral) longer, taller, thicker and more rhopaloid than others in late stages; early stages zaphrentoid; rhopaloid axial ends of major septa commonly conjunct in axial region in middle stages of development, withdrawing and becoming free axially in late stages with smooth distal edges; longest and strongest septa commonly midquadrant; counter and cardinal septa shorten progressively; minor septa rudimentary to short; tabular floors tall, axially depressed domes; no dissepiments. (After Hill, 1981, p. F328, with minor changes).

DISCUSSION: In this paper we follow several earlier authors (e.g. Schindewolf 1942, Fedorowski 1973, Hill 1981) in distinguishing between *Ufimia* Stuckenberg, 1895 and *Tachylasma* Grabau, 1922 at the family level, although we do not exclude the separation at the suborder level proposed by Fedorowski (1973, p. 113). In contrast to the opinion of Ilina (1984, p. 101), we consider the distinct underdevelopment of the counter septum in the corallite lumen of *Tachylasma* to be an important character, in spite of the fact that its septal furrow may appear fairly early in the ontogeny. This problem has been discussed by several authors (e.g. Weyer 1974, Ilina1984, Fedorowski 1991) and is discussed below, in a more general sense, in the remarks on

Tachylasma. The lectotype of *U. carbonaria*, selected by FEDOROWSKI (1973) from STUCKENBERG'S (1895) originals was redrawn by ILINA (1984, Fig. 40) with no indication of its source. It clearly shows the zaphrentoid early ontogeny noted by HILL (1981) in her generic diagnosis, with both the cardinal and the counter septum long (FEDOROWSKI 1973, Fig. 11.1a; ILINA 1984, Fig. 40v). These septa became shortened in succeeding stages, but their original length should be considered an important genus and family characteristic.

SCHINDEWOLF (1942, p. 209) introduced the new subgenus *Prionophyllum* within the genus *Pentaphyllum* DE KONINCK 1872. The single, incomplete specimen studied by SCHINDEWOLF (*ibid.*), with its apical part destroyed, does not provide information adequate for its identification on the family, genus or even the species level. Strong thickening of major septa, particularly the alar and counter-lateral septa, is its main distinguishing character. In our opinion, such a character, developed at an unknown growth stage, has no taxonomic value. Three incomplete corallites included in that subgenus by NIERMANN (1975, p. 191) show amplexoid, thin septa and do not resemble SCHINDEWOLF'S (*ibid.*) corallite, except for slight elongation of some major septa, typical for a form of *Tachylasma* having short septa. The nature of the septa led NIERMANN (*ibid.*, p. 192) to compare his specimens closely to *Plerophyllum variabile* SOSHKINA, 1941 and to include one of his corallites in that species as a new subspecies. Neither the illustration nor the description by NIERMANN (*ibid.*) is adequate for drawing final conclusions.

The generic name *Ufimia* has been applied many times in papers dealing with solitary non-dissepimental corals at various stratigraphic levels and geographic locations. Species more or less correctly included in this genus are known to occur from Lower Devonian to Upper Permian. Also, the name has sometimes been used as a substitute for the genus *Tachylasma* and *vice versa*. In this paper we do not intend to revise this complex genus and we restrict our synonymy and also our remarks to the taxa most obviously belonging to it.

Ufimia arctica sp. n.
(Text-fig. 9; Pl. 5, Figs 1, 2; Pl. 7, Fig. 4;
Pl. 8, Figs 1, 2)

1973a. *Cryptophyllum (Tachylasma?)* sp.? FLÜGEL, p. 24, Pl. 4, Fig. 5; Text-figs 11A, B.

HOLOTYPE: GSC 117149 (6 thin sections, 2 acetate peels), from GSC locality C-10457 (see appendix).

TYPE LOCALITY: GSC locality C-10457, type section of Degerböls Formation, van Hauen Pass, Ellesmere Island, Sverdrup Basin (Text-fig. 2).

TYPE HORIZON: Degerböls Formation, 7.9-10 m above base of type section, Wordian.

ETYMOLOGY: Named for occurrence in Arctic.

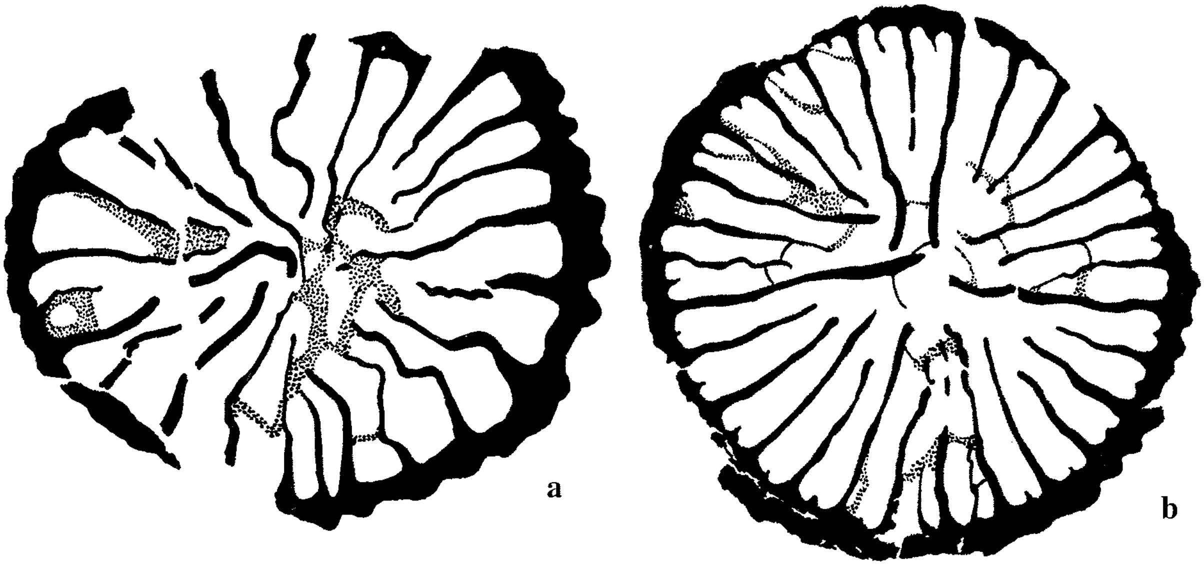


Fig. 9. *Ufimia arctica* sp. n.; transverse sections, inked and bleached photographs, GSC 117149, holotype; GSC locality C-10457, Degerböls Formation, type section, collected between 7.9 m and 10 m above base; a – neanic stage (= Pl. 5, Fig. 1a), × 10; b – mature stage (= Pl. 5, Fig. 1b); × 6

MATERIAL: Only two specimens available for study. Holotype fairly complete, length of preserved segment 33 mm, estimated from corallite shape that approximately 7 mm of early growth stages absent; upper part of calice slightly flattened and partly corroded but preserved almost to periphery.

Paratype (designated herein): No. MMH 11940, from East Greenland, first described by FLÜGEL (1973a) as *Cryptophyllum* (*Tachylasma?*) sp.?; calice crushed (FLÜGEL 1973a, Pl. 4, Fig. 5) and earliest growth stage absent, but inner morphology well preserved; three thin sections prepared for our study, in addition to two peels made earlier by FLÜGEL (1973a).

DIAGNOSIS: *Ufimia* with deep calice; number of septa equal or almost equal in all quadrants; cardinal septum long in early growth stages, shortened at maturity; counter septum shortened less than cardinal septum; major septa long, with only a few slightly rhopaloid; minor septa very short; n:d up to 32:13 immediately beneath calice.

DESCRIPTION OF HOLOTYPE: Corallite conical with slightly convex cardinal side. Calice approximately 16 mm deep; in its uppermost preserved part, major and minor septa almost equal in length, majors thicker than minors; septotheca 1.2 mm thick, formed by lateral union of major and minor septa at periphery. At level 2.5 mm below calice margin, major septa become differentiated from minor septa by length, but length of majors uniform; in upper part of calice, all major septa, including cardinal septum, of equal length (counter septum corroded); 7 mm lower in corallite, individual major septa became fully differentiated in length (Pl. 5, Fig. 1d); in some, secondary thickening and rhopaloid shape remain indistinct down to lower part of calice; alar septa more prominent and thicker than all others; cardinal septum only slightly shortened and cardinal fossula indistinct (Pl. 5, Figs 1c, d); septal furrows best preserved near calice floor on 0.8 mm-thick external wall.

In lowermost part of calice (where all charcters fully developed; Pl. 5, Fig. 1c) and immediately below calice floor (Text-fig. 9b, Pl. 5, Fig. 1b; n:d = 31:12.6), major septa clearly differentiated in length, with alars and counter-laterals longest and showing most rhopaloid thickening; this thickening remains generally light, however, so corallite lumen not crowded with septa. Cardinal and counter septa remain fairly long (Text-fig. 9b; Pl. 5, Figs 1b, c); length of counter septum in calice unknown because of corrosion on counter side of corallite. Minor septa appear as low ridges on external wall.

In earliest preserved ontogenetic stage (n:d ratio 23:7.8x5.8) differentiation in length of major septa, typical for *Ufimia*, is already distinguishable, although counter septum only slightly shorter than counter-lateral septa (Text-fig. 9a; Pl. 5, Fig. 1a); cardinal septum does not reach corallite axis, but is longer than one adjacent major septum on the right and two on the left; differentiation in length not clear for major septa other than alars and counter-laterals, only second pair in cardinal quadrants slightly elongated; all major septa thin and non-rhopaloid. Minor septa not evident – external wall thick (up to 0.5mm), but does not show waviness that would indicate presence of furrows representing minor septa.

Microstructure of septa investigated in early (Pl. 8, Fig. 1a) and mature (Pl. 7, Fig. 4; Pl. 8, Figs 1b, c) growth stages of holotype, where secondary sheets of septa are thin or absent, allowing comparison between the two levels; slight and unequally distributed re-crystallization has slightly obscured individual calcite fibres, but trabecular nature of septa and distribution of individual trabeculae sufficiently distinct and recognizable.

During certain growth stages and within individual septa, width of trabeculae varies – from approximately 0.035 mm to 0.05 mm in early growth stage and from approximately 0.05 mm to 0.08 mm at maturity (error in measurements caused by diagenetic alterations probably does not exceed 0.01 mm.). Distribution of trabeculae within septa at individual growth stages and in different parts of septa is similar; single row of trabeculae present at axial margin of septum (Pl. 8, Fig. 1a), whereas more than one row develops toward periphery – i.e., during growth of septum (Pl. 7, Fig. 4; Pl. 8, Figs 1b, c); single rows of trabeculae also present over short intervals in older growth stages of septa.

Arrangement and orientation of trabeculae also varies; they may be located in middle of septum and grow exactly along its medial plane towards its axial margin, with transverse sections of such trabeculae best seen in almost vertically growing septum (Pl. 8, Fig. 1a); similarly arranged trabeculae that were located near the curved edge of a septum would have been cut obliquely and would form half-moon structures. In mature growth stage trabeculae most commonly arranged in two or three irregular rows, with individual trabeculae inclined at different angle to medial plane of septum; some trabecule grow almost perpendicular to medial plane of septum, such that lateral surface of septum becomes nodular and its transverse section wavy (Pl. 8, Fig. 1c); in such parts of septa most trabeculae arranged in zig-zag pattern because, in addition to those inclined towards periphery, others follow medial plane of septum more or less exactly.

Secondary septal sheets present in several septa or parts of septa (Pl. 7, Fig. 4, Pl. 8, Fig. 1b), but thin and locally incomplete, thus leaving primary microstructure partly unmasked so that its characteristics may be distinguished. Plate 8, Figure 1c, which demonstrates zig-zag arrangement of trabeculae and their deviation from median plane of septum, shows secondary septal sheet on left, only slightly altered diagenetically; alterations shown mostly as cracks intersecting some structures and delicate rearrangement of crystals in the secondary septal sheet (Pl. 7, Fig. 4). Degree of diagenetic alteration varies within corallite – more strongly altered at periphery (Pl. 8, Fig. 1b) with many fibres of individual trabeculae destroyed and dense mosaic of cracks.

The zig-zag structure considered primary by SCHINDEWOLF (1942) was shown to be secondary by OEKENTORP (1980). We fully agree with OEKENTORP's interpretation, but this does not apply to the microstructure of septa described above. Some of the diagenetic alterations that we have briefly described affect the trabeculae contemporaneously with the remaining septal material without changing their arrangement. The best proof for the original arrangement of trabeculae is the regular, wavy peripheral outline of the primary septum, evident where it is not covered by stereoplasmic sheets. Such an outline is caused by peripheral protrusions of individual trabeculae that were not growing directly upwards, but towards the lateral periphery of a septum. It is always seen in the upper margins of septa constructed from large trabeculae. Those protrusions, which are a lateral analogy of marginal trabecular protrusions, are masked by secondary stereoplasmic sheets in most septa, which do not show waviness of that kind. Secondary (i.e., diagenetic) re-arrangement of trabeculae in the primary septum into a zig-zag pattern would not have been possible, however, without being evident and most probably continuous within the stereoplasmic sheets.This has not been observed. Thus, the primary arrangement of trabeculae described above appears certain to us.

INTRASPECIFIC VARIATION: Paratype MMH 11940 from East Greenland, described by FLÜGEL (1973a) as *Cryptophyllum* (*Tachylasma?*) sp.? and chosen by us as paratype of *U. arctica* sp. n., is more altered diagenetically than Canadian specimen, but shows same general morphological characteristics (Pl. 5, Figs 2a-c) and septal microstructure (Pl. 8, Fig. 2). Paratype distinguished from holotype by more regular arrangement of septa in early ontogeny (Pl. 5, Fig. 2a) and slightly more rhopaloid thickening of some major septa in mature growth stage, particularly alar and counter-lateral septa (Pl. 5, Figs 2b, c). Other characteristics, including dimensions at maturity, almost identical with those of holotype. Complete intraspecific variability of species cannot be established from limited material.

DISCUSSION: The genus *Ufimia* has been reported over the interval from Devonian (Eifelian) to Permian (upper Changhsingian), but its Devonian occurrence (KULLMANN 1965) is questioned by us (see discussion of *Tachylasma*). Nevertheless, it is represented by many species, several of which are inadequately studied. Also, the concept of the genus has varied among authors, with an extreme view held by ILINA (1984). We consider the list of species included by ILINA (1984, pp. 102, 103) to be unsupported and do not accept it. Only those species most similar to our new species are discussed here.

The considerable length of the counter septum in the holotype of *U. arctica* sp. n. indicates that it was not totally underdeveloped in earliest growth stages, as it is in all Tachylasmatidae that have been investigated in adequate detail. Thus, it appears likely that the septal arrangement in early ontogeny was zaphrentoid, which is characteristic for *Ufimia*, but not for *Tachylasma*. Therefore, our specimen has been assigned to *Ufimia*. In addition, our species resembles the type species of that genus, *U. carbonaria* STUCKENBERG, 1895, in the arrangement of septa in the cardinal quadrants and the similarly long cardinal and counter septa throughout the growth stages studied. The two species show the greatest similarity in the morphology of their calices. Our species has a larger corallite diameter than *U. carbonaria* and has its major septa much less thickened and equally numerous in the cardinal and counter quadrants.

The description by ILINA (1984) of the septal microstructure in *Ufimia carbonaria* STUCKENBERG, 1895 indicates that the microstructure described for *U. arctica* sp. n. is characteristic for the genus. Although ILINA (1984, p. 104) began her description by stating that small, simple trabeculae (0.04 mm across) are "arranged in a single row", she added that "sclerodermites... are sometimes developed along almost the whole septum on both sides". This is confirmed by her illustrations, especially plate 11, figures 4g and 5, which show septal microstructure similar to that described above. The local construction of septa from a single row of trabeculae may well be a species character. Thus, we propose to consider the septal microstructure described for our new species to be a diagnostic character for *Ufimia*. Such microstructure is somewhat similar to that described by FEDOROWSKI (1974) for *Timorphyllum* and termed "aseriate" by HILL (1981), but is distinguished from the latter by the local development of more trabeculae, especially in the calice, and by a resulting increase in complexity. We propose herein to call such trabeculae "alternate".

Plerophyllum (= *Ufimia*) *exceptatum* SOSHKINA, 1928, which is characterized by only slight thickening of its major septa beneath the calice, bears the closest similarity to *U. arctica* sp. n., but has much smaller corallite diameters and shows acceleration of the major septa in its counter quadrants. *Tachylasma sophiae* HERITSCH, 1939 is also morphologically close to *U. arctica* sp. n., but is much larger and lacks minor septa (HERITSCH 1939, p. 87). These differences are small and the two species may well be synonyms, but *T. sophiae* is known only from a single section made in an unknown part of the calice and the type specimen is missing, so its relationship to our new species cannot be established.

WEYER & ILINA (1979) tentatively assigned *Cryptophyllum* (*Tachylasma*?) sp.? of FLÜGEL (1973a) (designated herein as the paratype of *U. arctica* sp. n.) to *Paracaninia*. Although the immature growth stages of some species included by those authors in *Paracaninia* are strikingly similar to *Ufimia* in the arrangement of their major septa (e.g., WEYER & ILINA 1979, Fig. 7:3, WEYER 1982, Pl. 1, Figs 4-8, Pl. 3, Figs 6-8), FLÜGEL's specimen lacks two important characters of *Paracaninia* – equal shortening of the major septa below the calice floor, and a biform tabularium.

OCCURRENCE: East Greenland, Kap Stosch, Wegener Halvø Formation, Foldvik Creek Group ["*Productus* limestone" (FLÜGEL 1973a)], Wordian or early Capitanian; Sverdrup Basin, Degerböls Formation, 7.9-10 m above base of type section, Wordian.

Family Polycoeliidae ROEMER, 1883
Genus *Calophyllum* DANA, 1846

TYPE SPECIES: *Turbinolia donatiana* KING, 1848

SYNONYMY: See SCHINDEWOLF (1942, p. 64. *Polycoelia*), WEYER (1979, p. 982; generic names listed by him under *Calophyllum profundum* and *C. quadrifidum*) and ILINA (1984, p. 139). *Pycnocoelia* SCHINDEWOLF, 1942 (Synonymy see ILINA 1984, p. 156).

EMENDED DIAGNOSIS: Small Polycoeliidae; cardinal, counter and two alar septa almost equally spaced, longer and thicker than other major septa, but in upper third of calice shortened so that all septa appear equal; immature stages zaphrentoid; metaseptal insertion accelerated slightly in counter quadrants; tabulae complete, flat axially, with downturned margins; microstructure of septa trabecular; trabeculae 0.03-0.1 mm in diameter, arranged in single row. (from HILL 1981, p. F321; ILINA 1984, p. 139 and our study).

DISCUSSION: The genus *Calophyllum* is widely distributed in time and space and the species that have been assigned to it are very numerous. Its type species is among the earliest described rugose corals. Revision of such a genus is a task in itself requiring revision of specimens and the literature data from most of the world. The main purpose of this paper is to describe the unknown rugose coral fauna from the Sverdrup Basin, not to present a complete revision of the genera in which our species are included. Thus, we restrict ourselves to taxa resembling or related to *Calophyllum columnare* (SCHLOTHEIM, 1813). The reader is referred to the discussion of that species given below.

Calophyllum columnare (SCHLOTHEIM, 1813)
(Text-figs 10, 11; Pl. 3, Figs 3-6; Pl. 5, Fig. 6)

1813. *Coralliolites columnaris* SCHLOTHEIM, p. 59.
1842. *Cyathophyllum profundum* GERMAR *in* GEINITZ, p. 579, Pl. 10, Figs 14, 14a.
1894. *Petraia permiana* NECHAEV, p. 106, Pl. 1, Figs 16, 18, Pl. 2, Fig. 19.
1939. *Gerthia heintzi* HERITSCH, p. 78, Pl. 16, Fig. 5, Pl. 20, Figs 2, 3.
1942. *Polycoelia (Polycoelia) profunda* (GEIN.); O.H. SCHINDEWOLF, p. 67, Pl. 19, Figs 1a-c, 2, Text-figs 18, 23a-f.
partim 1942. *Polycoelia (Polycoelia) compressa* (LDWG.); O.H. SCHINDEWOLF, p. 72, Pl. 17, Fig. 1, Pl. 19, Figs 3a-c, Text-figs 25a,b.
1973a. *Hapsiphyllum* sp. FLÜGEL, p. 28, Pl. 3, Fig. 2, Text-fig. 12.
1973b. *Calophyllum profundum* (GEINITZ, 1842); H.W. FLÜGEL, Fig. 3.
1979. *Calophyllum profundum* (GEINITZ, 1842); D. WEYER, p. 982, Text-figs 3, 4, Pl. 3, Figs 9, 10, Pl. 4, Figs 1-3 (*cum synon.*).
1982 *Calophyllum profundum* (GEINITZ, 1842); J. FEDOROWSKI, p. 73, Pl. 1, 2, Pl. 3, Figs 1, 2, 6, 7, Pl. 4, Fig. 5, Text-fig. 2:4a, b (*cum synon.*, except for *C. punctata* FLÜGEL, 1973).
1984. *Calophyllum profundum* (GERMAR in GEINITZ, 1842); T.G. ILINA, 1984, p. 142, Pl. 22, Figs 2-8, Text-fig. 57 (*cum synon.*, except for species introduced by LUDWIG, which were suppressed).
1984. *Calophyllum columnare* (SCHLOTHEIM, 1813); D. WEYER, Figs. 8:1-3, photo 6:8-10.
1989. *Calophyllum profundum* (GERMAR in GEINITZ,

1842); A. B. IVANOVSKY, p. 33, Pl. 3, Fig. 1, Pl. 5, Fig. 2, Pl. 6, Figs 1, 2.

1989. *Amplexocarinia muralis* SOSHKINA, 1928; A.B. IVANOVSKY, p. 32, Pl. 1, Figs 1, 2.

partim 1989. *Paralleynia permiana* SOSHKINA, 1936; A.B. IVANOVSKY, p. 32, Pl. 1, Figs 3, 4, 6.

1989. *Groenlandophyllum teicherti* FLÜGEL, 1973; A.B. IVANOVSKY, p. 34, Pl. 2, Figs 2-4.

1989. *Groenlandophyllum variabile* (SOSHKINA, 1941); A.B. IVANOVSKY, p. 35, Pl. 3, Figs 2, 3, Pl. 4, Figs 2-5.

1989. *"Gerthia"* sp. IVANOVSKY, p. 36, Pl. 5, Figs 1, 3.

1989. *Sassendalia bashkirica* IVANOVSKY, p. 36, Pl. 1, Fig. 5.

1989. *Pentaphyllum hexaseptatum* (SOSCHKINA, 1928) (sic.); A.B. IVANOVSKY, p. 37, Pl. 4, Fig. 1 (*non synon.*).

1989. *Euryphyllum minor* FONTAINE, 1961; A.B. IVANOVSKY, p. 38, Pl. 2, Fig. 1, Pl. 4, Fig. 6.

1992. *Calophyllum profundum* (GEINITZ, 1842); Y. EZAKI & T. KAWAMURA, Pl. 4, Fig. 3.

1997. *Calophyllum permianum* (NECHAEV, 1894); D. WEYER, p. 91, Pl. 1, Text-figs 2-6 (*cum synon.*).

MATERIAL: Hypotypes – GSC 117152 (1 thin section, 11 acetate peels), 117172 1 thin section, 1 acetate peel), 117173 (5 thin sections, 1 acetate peel), 117175 (2 thin sections, 3 acetate peels), from GSC localities C-10459, C-82314 and C-82471; MMH11942 from East Greenland (see occurrence). All specimens incomplete, two with calices and one with fairly early growth stage preserved; internal structures slightly recrystallyzed and silicified.

DIAGNOSIS: *Calophyllum* with thick external wall not penetrated by septa; counter quadrants clearly dominate in volume; counter and alar septa approach corallite axis, cardinal septum commonly slightly withdrawn; remaining major septa differentiated in length with those in middle parts of quadrants commonly longest; minor septa absent from corallite lumen beneath calice. n:d highly variable, ranges from 20:7 to 35:14.5 [data from lectotype (WEYER 1984, Fig. 8:1), SCHINDEWOLF (1942), WEYER (1979) and our studies].

DISCUSSION: The lectotype of *C. columnare*, chosen by WEYER (1984, Text-fig. 8.1) has never been described in detail. Nevertheless, the morphology of the species has been quite well established by WEYER's illustration of the lectotype, his illustrations of other lower Zechstein specimens (WEYER 1979, Text-figs 3, 4; Pl. 4, Figs 1-3) and detailed description and illustrations of *Polycoelia (Polycoelia) profunda* by SCHINDEWOLF (1942, Text-figs 18, 23; Pl. 19, Figs 1, 2), also based on a lower Zechstein collection. For this study, we do not have access to the type material and we have not presented a new description of *C. columnare*, because our Sverdrup Basin specimens yielded little new morphological information, other than details of septal microstucture, dimensions and septal number.

In most of the Sverdrup Basin specimens, the microstructure of the septa is difficult to recognize or has been diagenetically destroyed. Where the septa are best preserved, they are trabecular (e.g., Pl. 5, Fig. 6). The trabeculae are consistently arranged in a single row, which agrees with the observation by ILINA (1984, p.139), who included that character in the diagnosis of the genus. We agree with her concept, because all available observations seem to confirm the presence of a single row of small trabeculae in the middle parts of the septa. The width of trabeculae observed by us, however, differ from those considered by ILINA (1984) to be diagnostic (i.e., 0.05-0.1 mm). All Canadian specimens and those that we have observed from Greenland have much smaller trabeculae, not exceeding 0.03 mm in width and less commonly as small as 0.015 mm. In some specimens the small trabeculae are so closely packed that they are barely recognizable. Thus we propose to accept width of trabeculae as a species character and to consider very narrow trabeculae (0.01-0.03 mm) diagnostic for *C. columnare* (SCHLOTHEIM, 1813).

Three of the four specimens from the Sverdrup Basin and the specimen from Greenland (Pl. 3, Figs 5a-c) are of medium size, compared to other specimens in the species, but have large numbers of septa (Text-fig. 10) (n:d = 24:9.0 in the lectotype; measured from WEYER 1984, Text-fig. 8:1); one shows an extreme n:d ratio (3.5, i.e. 32:9.0). The Greenland specimen has an even larger n:d ratio (3.7, i.e., 32:8.5) contrasting with most of the corallites described by WEYER (1979, 1984), which have n:d ratios of 2.2 to 3.3 (i.e. 27:12.0 to 26:8.0). The morphology of all these corallites is very similar in other respects and all are similar to the lectotype, in which the cardinal septum tends to shorten (WEYER, *Ibid.*). One of the corallites in our collection, preserved only in the late mature growth stage (Text-fig. 11.3, Pl. 3, Fig. 6) has its cardinal septum almost equal in length to the three other longest major septa, thus resembling *"Tetralasma"* SCHINDEWOLF, except for the greater length of the remaining major septa. Also, this specimen is strikingly similar to that illustrated by EZAKI & KAWAMURA (1992, Pl. 4, Fig. 3) from Unit 5 of the Kapp Starostin Formation. Our specimen also bears a slight resemblance to *C. quadrifidum* HOWSE, 1848 in the strong elongation of four septa up to the calice, but is distinguished from that species by size and other characteristics. The variation in the morphology and

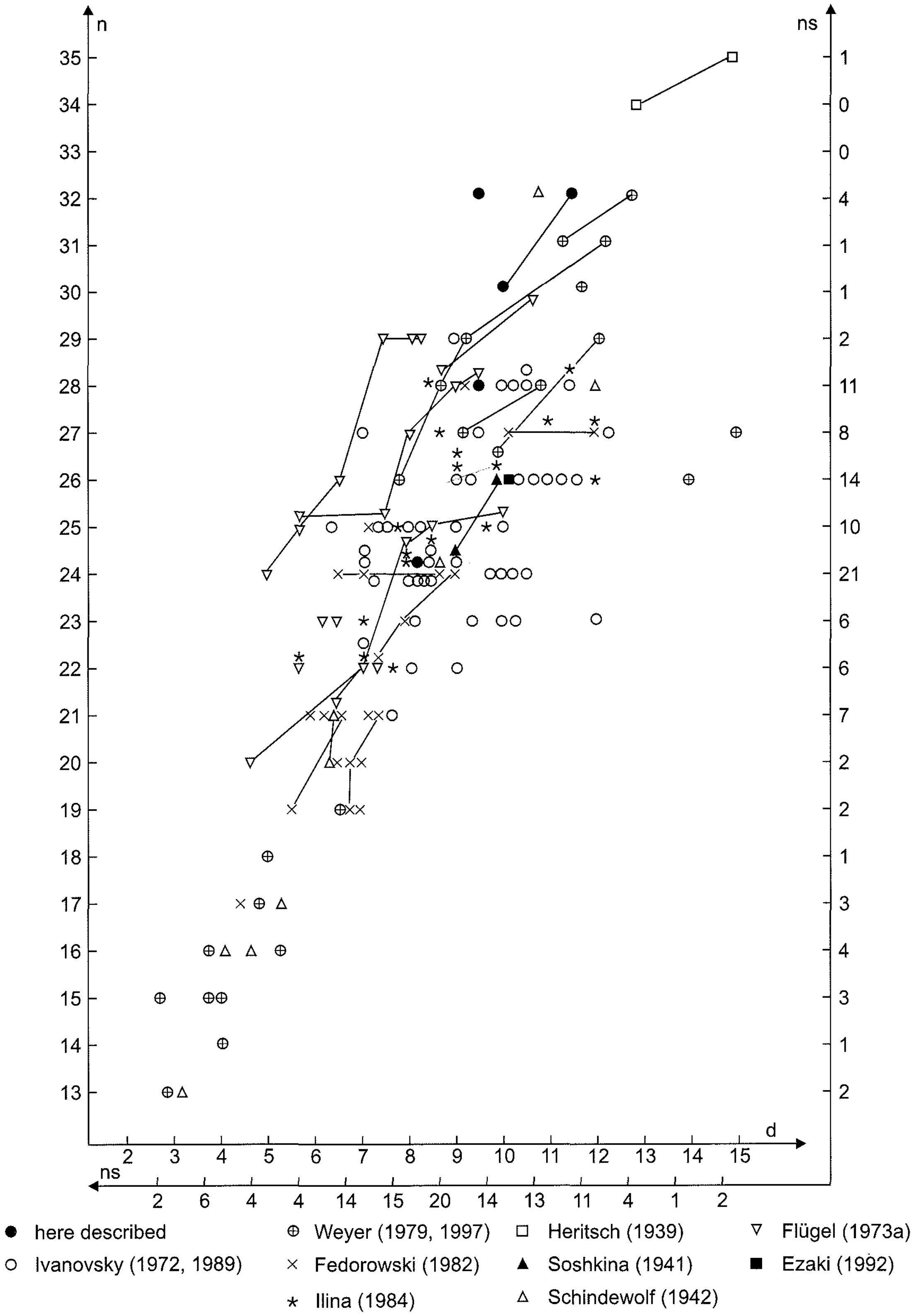


Fig. 10. Number of major septa *vs.* diameter for taxa placed in synonymy with *Calophyllum columnare* (SCHLOTHEIM 1813) and *C. quadrifidum* (HOWSE 1848); n – number of major septa, d – diameter (mm), ns – number of studied specimens having corresponding diameters (values listed horizontally) and septal numbers (values listed vertically); symbols joined by lines represent values taken from individual specimens

measurements of our specimens, however, are closely comparable, in all respects, with individual specimens from the Central European Basin, East European Platform, East Greenland and Vestspitsbergen; thus, the Canadian specimens are not described in detail.

Calophyllum columnare (SCHLOTHEIM, 1813) has been studied for more than 180 years, during which time a great deal of controversy has developed concerning its taxonomic treatment. These difficulties have arisen because of the enormous variation in its morphology, which has been treated as intraspecific variability by some authors, but has been used to establish numerous species within different genera by others. The best example of the latter approach is the publication by IVANOVSKY (1989, see below). Also, the descriptions of corals belonging to the species have been further complicated by inaccurate terminology and misinterpretation of morphology – e.g., the description of septal insertion as occurring in "sextants" and the use of the term "fibro-normal trabeculae" (IVANOVSKY 1972). FEDOROWSKI (1982, p. 73) discussed the last two problems briefly. In view of these difficulties, we have included the following, fairly broad discussion of the various studies of *Calophyllum*, which supplements a recent summary by WEYER (1997).

FLÜGEL (1973b) restudied the type material and reconsidered the taxonomic position of the genus *Calophyllum* DANA, 1846. According to him, the name *quadrifida* has not been used since its introduction by HOWSE (1848) and should be considered a *nomen oblitum*. Thus, he proposed *Turbinolia donatiana* KING, 1848 as the type species for the genus *Calophyllum* (questioned by WEYER 1979 – see below) and chose a neotype for the latter. Unfortunately, his neotype is so badly preserved that its morphology, ontogeny and microstructure cannot be accurately determined. With this in mind, we question the description by ILINA (1984, p. 142) of *Calophyllum donatianum* (KING, 1848). From her study of a single, strongly corroded specimen derived from KING's collection, she described the early ontogeny, the septal formula and the arrangement of the major septa at maturity, but illustrated only an external view (ILINA 1984, Pl. 22, Fig. 1). Her description is, therefore, unsupported and is not acceptable to us, especially in view of the brevity of the description by FLÜGEL (1973b, p. 62), which is restricted mainly to the dimensions and septal number of the poorly preserved neotype.

In his regional analysis of the European Zechstein corals and related faunas, WEYER (1979) pointed out several citations of "*Caryophyllia*" *quadrifida* HOWSE, 1848, published since the original introduction of the species, and questioned FLÜGEL's (1973b) proposal to consider it a *nomen oblitum*. WEYER's (1979) opinion is in agreement with the International Code of Zoological Nomenclature and we accept it here. We do not accept the usage by ILINA (1984, p. 142) of the name *Calophyllum donatianum* (KING, 1848), which contravenes the international rules. Also, we refer the reader to the thorough discussion of nomenclatural details presented by WEYER (1979) and to his most comprehensive description and illustrations of "ampleximorphic", small representatives of that genus, included by him in *C. quadrifidum* (HOWSE, 1848). In his more recent papers, WEYER (1984, 1997) considered *C. profundum* (GEINITZ, 1842) to be a junior synonym of *C. columnare* (SCHLOTHEIM, 1813). His illustrations of specimens are convincing. Thus, we follow his suggestions concerning the priority of the name "*columnare*" despite the fact that a formal revision of SCHLOTHEIM's species has not yet been published. WEYER (1979, 1984, 1997) favours a relatively narrow species concept for representatives of *Calophyllum* in the CAU Realm, thus accepting 3 separate species: *C. columnare, C. quadrifidum* and *C. permianum* (NECHAEV, 1894). In contrast, FEDOROWSKI (1982, p. 73) introduced a broader concept for *C. profundum* (= *C. columnare*), considering all "taxa" described from the northern part of the CAU Realm (*Calophyllum* Province of FEDOROWSKI & BAMBER, in press) to be synonyms. This concept may be questioned with respect to small "ampleximorphs" if WEYER's (1979) assignment of that morphotype to a separate species – *C. quadrifidum* – is accepted. However, there is no doubt that various morphotypes occur together, not only in the same bed, but even in a single small hand sample or thin section, as shown by WEYER (1979, Pl. 1) and FEDOROWSKI (1982, Pl. 2, Fig. 8). Also, the occurrence of many forms with intermediate morphology and dimensions, in local areas and regionally throughout the province, is obviously related to facies variations [(e.g., large and small specimens in Greenland, derived from carbonate and shale-dominated facies, respectively (FEDOROWSKI 1982, Pl. 1, 2; Pl. 3, Figs 1, 2)]. However, certain morphotypes are prevalent among small specimens, but almost non-existent among large ones. This is true of the "ampleximorphs", which are prevalent among the "*quadrifidum*" group, but very rare among the "*columnare*" group. The corallite illustrated by IVANOVSKY (1989, Pl. 4, Fig. 5) as *Groenlandophyllum variabile* (SOSHKINA, 1941) is perhaps the most typical published example of an "ampleximorph" in the "columnare" group. A second example was kindly reported to us by Dr. Dieter WEYER (written communication, October 2000), who possesses a typical "ampleximorph" of *C. columnare* in his undescribed collection.

Also, the analysis of the n:d values for more than one hundred specimens in the published illustrations (Text-fig. 10) may indicate some dimensional distinction of the smallest corallites. As with the morphology, however, this distinction is vague when compared to the total distribution of specimens (Text-fig. 10). Thus, we are not certain if *Calophyllum* was represented by only one, or by two species on the shallow marine shelves of the *Calophyllum* Province. Therefore, we have not placed the small, amplexoid "taxa" in synonymy with *C. columnare* and will not consider them further, but provisionally accept them as synonyms of *C. quadrifidum* (Howse, 1848) in the sense of Weyer (1979). In doing so, we do not exclude the possibility that *C. columnare* and C. *quadrifidum* are no more than ecotypes, in which instance, the former would have priority. From existing data, however, is it not possible to recognize more than two species of *Calophyllum* in the *Calophyllum* Province, because only two groups can be distinguished on their morphological and dimensional characteristics.

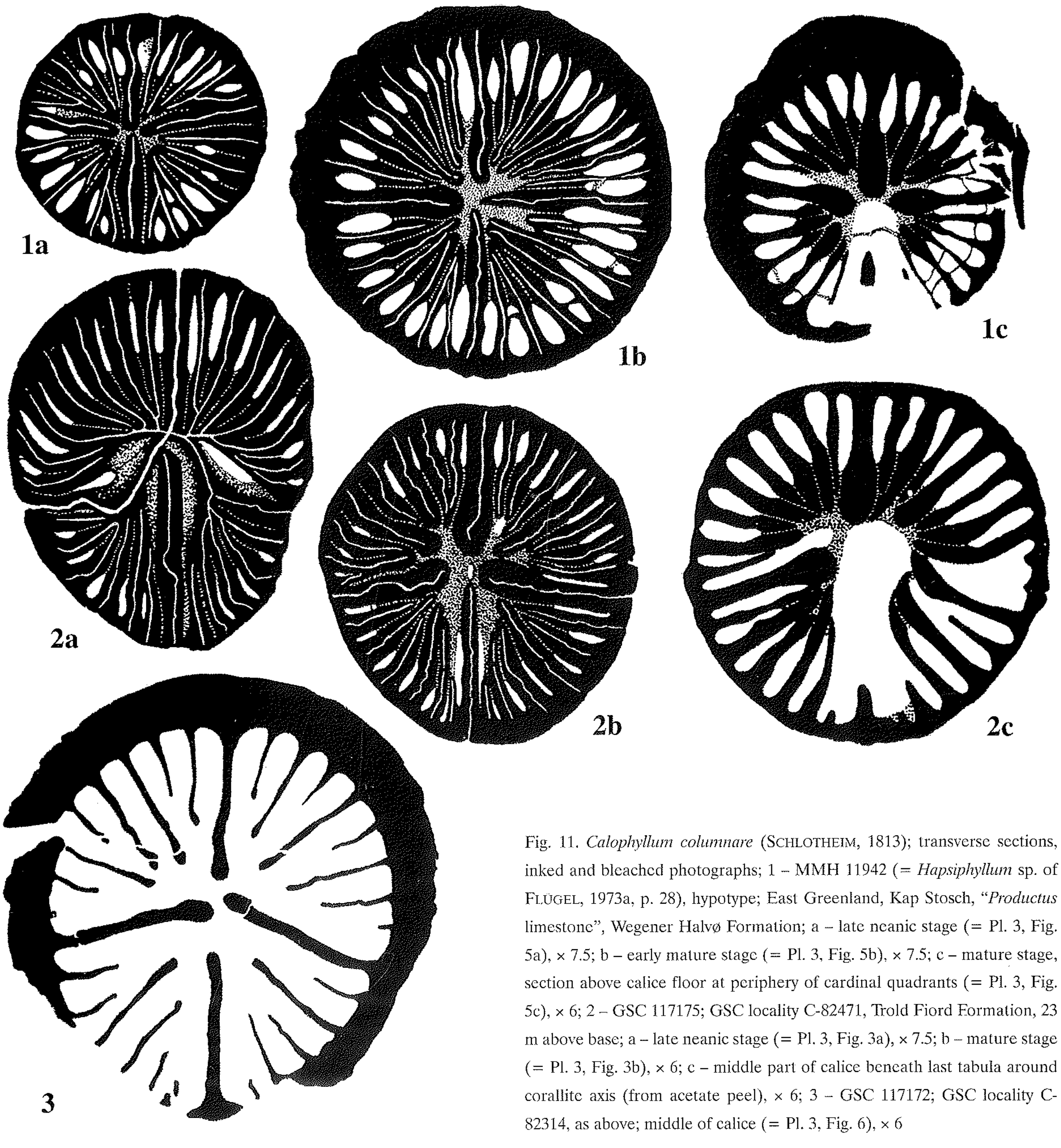


Fig. 11. *Calophyllum columnare* (Schlotheim, 1813); transverse sections, inked and bleached photographs; 1 – MMH 11942 (= *Hapsiphyllum* sp. of Flügel, 1973a, p. 28), hypotype; East Greenland, Kap Stosch, "*Productus* limestone", Wegener Halvø Formation; a – late neanic stage (= Pl. 3, Fig. 5a), × 7.5; b – early mature stage (= Pl. 3, Fig. 5b), × 7.5; c – mature stage, section above calice floor at periphery of cardinal quadrants (= Pl. 3, Fig. 5c), × 6; 2 – GSC 117175; GSC locality C-82471, Trold Fiord Formation, 23 m above base; a – late neanic stage (= Pl. 3, Fig. 3a), × 7.5; b – mature stage (= Pl. 3, Fig. 3b), × 6; c – middle part of calice beneath last tabula around corallite axis (from acetate peel), × 6; 3 – GSC 117172; GSC locality C-82314, as above; middle of calice (= Pl. 3, Fig. 6), × 6

Thus, we do not accept *Petraia permiana* NECHAEV, 1894 as an independent species, but include it within *C. columnare*.

SCHINDEWOLF (1942) described several species of *Calophyllum* under the generic name *Polycoelia* KING, 1849, with the type species *Cyathophyllum profundum* GEINITZ, 1842. The legality of SCHINDEWOLF's approach was discussed by FLÜGEL (1973a) and ILINA (1984) and will not be repeated here. Also, ILINA (1984), following FEDOROWSKI (1982), placed *Polycoelia rossica* SCHINDEWOLF, 1942 and *P. baytuganense* SOSHKINA, 1941 in synonymy with *Calophyllum profundum*. Of the two other species described by SCHINDEWOLF (1942) from the German Zechstein deposits – *Polycoelia compressa* (LUDWIG, 1865) and *Polycoelia gracilis* SCHINDEWOLF, 1942 – the second was placed by WEYER (1979) in synonymy with *Calophyllum quadrifidum*. We have provisionally followed WEYER's decision and omitted SCHINDEWOLF's species from the synonymy of *C. columnare*. We placed (see synonymy) part of *P. compressa* (LUDWIG, 1865) of SCHINDEWOLF, 1942 in synonymy with *C. columnare*. The corallite illustrated by SCHINDEWOLF (1942, Pl. 19, Fig. 4a-f, Text-fig. 24) may belong to *C. quadrifidum* – a possibility previously considered by WEYER (1979) – or may be taken as evidence of the identity of *C. columnare* and *C. quadrifidum*.

In his description of the genus *Calophyllum* from East Greenland, FEDOROWSKI (1982) reviewed the interpretation by IVANOVSKY (1972) of the mode of septal insertion in the genus and its microstructure, and also rejected *Groenlandophyllum* FLÜGEL, 1973a as a valid subgeneric name. We agree with his decision, despite the recognition by HILL (1981) of *Groenlandophyllum*. The very specific phenomenon of asexual reproduction producing corallites with naked tips could possibly be evaluated as a character of subgeneric value distinguishing this group of corals. We maintain, however, that in comparing these corals to other representatives of *Calophyllum*, this single, ecologically controlled character should be evaluated much lower than others, such as the identical early (but not the earliest) ontogeny, the microstructure of the septa, the morphology of mature corallites and the similar intraspecific variability. For further information on this question, the reader is referred to the discussion by FEDOROWSKI (1982).

HERITSCH (1939) described the new species *Gerthia heintzi*, based on a single specimen from Permian strata of Vestspitsbergen. He illustrated an external view and two thin sections, most probably cut through the lower part of the calice. The arrangement of septa matches that of Zechstein representatives of *C. columnare*, although HERITSCH's corallite is larger. He did not mention *C. columnare* in his discussion, which deals mainly with Tethyan taxa. From the illustrations presented by HERITSCH (*ibid.*, Pl. 20, Figs 2, 3), the morphology of the Vestspitsbergen specimen appears to be very similar to that of specimens described in this paper and of other representatives of *C. columnare*. Therefore, we have reassigned it to that species despite its larger size and the probability that the type material may have been lost along with the remainder of the collection studied by HERITSCH, as discussed previously.

We accept the synonymy and statements by ILINA (1984, p. 139-146) for the genus *Calophyllum* and the species *C. profundum*, except for the references in her synonymy lists to names introduced by LUDWIG (1865-1866), which were suppressed in 1971 by ICZN Opinion 946 and should not be cited. The illustrations and descriptions by ILINA (1984) do not require further discussion. They fit well with our material and with specimens of other published species that we have placed in synonymy with *C. columnare*.

As discussed by WEYER (1997, p. 97), IVANOVSKY (1989) assigned specimens collected in the northeastern part of the East European Platform to three superfamilies, four families, eight genera and nine species (one new and one in open nomenclature). In agreement with WEYER (*ibid.*), but using a different species name, we have reassigned all of these "taxa" to *Calophyllum columnare*, except for one specimen illustrated by IVANOVSKY (*ibid.*, Pl. 6, Fig. 3a-v) and identified by him as *Paralleynia permiana* SOSHKINA, 1936. This specimen may belong to *C. columnare* as well, but it was not illustrated clearly enough for a final assignment to be made. Also the cardinal, counter and alar septa are only slightly elongated in the specimen identified and illustrated by IVANOVSKY (1989, Pl. 1, Figs 2a-v) as *Amplexocarinia muralis* SOSHKINA, 1928, but they are long enough, in our opinion, for this specimen to be included as a peripheral variant of *C. columnare*. The calophylloid elongation of four septa and the zaphrentoid arrangement of the remaining major septa in this and also in the corallite illustrated by IVANOVSKY (1989) on his plate 1, figure 1a are closely comparable to these features in several specimens of *C. columnare* from elsewhere. Both of IVANOVSKY's specimens are closely comparable with the corallite identified by him as *Groenlandophyllum teicherti* (IVANOVSKY 1989, Pl. 2, Fig. 4a). The same is true for his "*Euryphyllum minor*" and especially for the transverse section illustrated in his Plate 2, figure 1a. This section is difficult to relate to those illustrated in figures 1b and 1v, which according to IVANOVSKY (ibid., p. 153), were derived from the same corallite. Both of the latter sections show the arrangement and differentiation of major septa typical for *Calophyllum columnare*.

The specimens assigned by IVANOVSKY (1989, Pl. 1, Figs 3, 4, 6) to *Paralleynia permiana* are all differently oriented. In those shown in figures 3a and 3b, the cardinal septum is located at the lower left, in figure 4a – at the right, in figure 6a – at the upper right, in figure 6b – at the top center, and in figure 6v – at the right. Some of the sections illustrated (e.g., Figs 3b, 4a, 6a) have circumaxial stereoplasmic thickenings that may give the impression of an aulos, but the cardinal, counter and alar septa are clearly rhopaloid and dominant, as in other specimens of *C. columnare*. The arrangement of the remaining septa is also typical for this species.

The holotype of *Sassendalia bashkirica* IVANOVSKY, 1989 – the only specimen representing the species – shows transverse sections entirely typical for the lowermost part of the calice in *C. columnare* and need not be discussed further.

Comments on *Pentaphyllum hexaseptatum* of IVANOVSKY (1989), reassigned by us to *C. columnare*, indicate acceleration of the insertion of metasepta in the counter quadrants very similar to that illustrated by WEYER (1984) in the lectotype of *C. columnare*. Also, other characteristics of IVANOVSKY's specimens are typical for *C. columnare* and have nothing in common with either the genus *Pentaphyllum* DE KONINCK, 1872 or with the species "*Tachylasma*" *hexaseptatum* SOSHKINA, 1928.

The comments by IVANOVSKY (1989) on species of *Groenlandophyllum* and *Gerthia* – genera considered by FEDOROWSKI (1982) and ILINA (1984) to be synonyms of *Calophyllum* – and his comments (*ibid.*) on *C. profundum* can be attributed to the intraspecific variability of *C. columnare* without further discussion. We do not recognize the distinction between *Calophyllum* and *Groenlandophyllum*, proposed by IVANOVSKY (1989) on the suspected presence of a zaphrentoid versus a non-zaphrentoid early ontogeny, because this has not been demonstrated. The only possible distinction between these two taxa is the presence or absence of naked corallite tips, which was not mentioned by IVANOVSKY (*ibid.*).

Rare specimens (e.g., IVANOVSKY 1972, Pl. 4, Fig. 2; IVANOVSKY 1989, Pl. 2, Fig. 2), which are very similar to other representatives of *C. columnare* in most of their morphological characteristics, show biform morphology in their tabularia. We cannot confirm this feature or evaluate its significance, because such specimens were not available to us for re-study. Thus, we provisionally consider them as extreme variants of *C. columnare*, but the presence of biform morphology may well justify the establishment of a separate species.

We have restricted our discussion to the taxa occurring within the *Calophyhllum* Province, in the northern part of the CAU Realm, although there are some representatives of *Calophyllum* from the Tethys Realm that are very similar morphologically to *C. columnare* – e.g., *Polycoelia pennata* and *P. clausa intermissa*, both described by NIERMANN (1975). This morphological similarity may indicate a truly close relationship between the species in these two groups of corals, or it may represent convergence. The latter is suggested by the wide separation of the Tethys Realm from the *Calophyllum* Province during Permian time (Text-fig. 1).

OCCURRENCE: Central European Basin, lower Zechstein [lower Werra Cycle (= Zechstein 1)], Wordian or early Capitanian; East European Platform, lower Kazanian, Wordian; Vestspitsbergen, lower Kapp Starostin Formation, probably Wordian or early Capitanian; East Greenland, Kap Stosch and Jameson Land, Foldvik Creek Group, Wegener Halvø and Ravnefjeld formations ("*Productus* limestone", "*Posidonia* shale", "*Martinia* limetone") (FLÜGEL 1973a, FEDOROWSKI 1982), Wordian or early Capitanian; Sverdrup Basin, Degerböls and Trold Fiord formations, GSC localities C-10459, C-82314, and C-82471, Wordian.

Genus *Soshkineophyllum* GRABAU, 1928

TYPE SPECIES: *Pleurophyllum artiense* SOSHKINA, 1925

partim 1925. *Pleurophyllum* SOSHKINA, p. 91.
partim 1928. *Tachylasma* SOSHKINA, p. 350; E.D. SOSHKINA & al., 1941, p. 47.
partim 1941. *Plerophyllum* SOSHKINA, p. 73; E.D. SOSHKINA & al., 1941, p. 73.
1941. *Timorphyllum* SOSHKINA, p. 110; E.D. SOSHKINA & al., 1941, p. 110.
non 1941. *Soshkineophyllum* GRABAU, 1928; MOORE & JEFFORDS, p. 102.
1972. *Sassendalia* TIDTEN, p. 28.
partim 1986. *Amplexizaphrentis elliptica* (WHITE); KORA & JUX; Fig.3e.
1992. *Sassendalia*; TIDEN; Y. EZAKI & T. KAWAMURA, Pl. 5, Figs 1, 2

DIAGNOSIS: Plycoeliidae with cardinal septum shortened at or near floor of deep cardinal fossula in calice; counter septum elongated most distinctly, alar septa less so; microstructure of septa finely trabecular with closely spaced centers.

DISCUSSION: The genus *Soshkineophyllum* was introduced by GRABAU (1928) to include two species described by SOSHKINA (1925) from the Lower Permian of the western slope of the Urals. In the original descriptions, the characteristics of neither species were completely or accurately established and no type or topotype material was re-investigated. According to SOSHKINA (*ibid.*, p. 91), the type species, *P. artiense*, is represented by three specimens. We did not have access to those type specimens. Of the two drawings presented by SOSHKINA (1925, Pl. 2, Fig. 12, 12a), one illustrates an oblique and eccentric longitudinal section and the other, a transverse section cut somewhere below the calice. Neither the early ontogeny nor the septal microstructure of the type species is known. Biform morphology is weakly expressed in the peripheral parts of some tabulae shown (SOSHKINA, *ibid.*, Pl. 2, Fig. 12) in the transverse section of the holotype of *P. artiense*. This character is not obvious in all loculi and its presence cannot be confirmed from the longitudinal section (*ibid.*, Pl. 2, Fig. 12a), possibly because of its incorrect orientation. Thus, we are not entirely certain that a biform tabularium is present in the holotype of *P. artiense*. The same is true for *P. tenuiseptatum* (SOSHKINA, 1925). Other species included in *Soshkineophyllum* by ILINA (1984) and *S. internectum* FEDOROWSKI, 1973 either lack this character or it is expressed so weakly that its presence cannot be definitely established. Thus, we propose to include within *Soshkineophyllum* species with weakly expressed biform morphology and also those without this feature.

The level, with respect to the calice floor, at which the cardinal septum becomes shortened is another fairly important character of *Soshkineophyllum* but again, we cannot establish the level at which shortening occurs in the holotype. It may well have taken place above the last tabula, which is depressed to form the cardinal fossula. In the original transverse section (SOSHKINA 1925, Pl. 2, Fig. 12), intercepts of tabulae indicating the presence of a cardinal fossula are shown only in the periaxial area, in a position contrasting with that of tabula intercepts in other loculi. The peripheral part of this section lies above the last tabula, where the calice floor is depressed and the cardinal fossula is enclosed laterally by the axial margins of major septa. A specimen illustrated by ILINA (1984, Pl. 28, Fig. 4a) as *S. artiense*, however, clearly shows the cardinal septum shortened below the calice floor. Unfortunately, her specimen is not a topotype but was derived from a distant locality and cannot serve as a morphological and ontogenetic standard for the genus. Although all other morphological features of ILINA's specimen are consistent with its assignment to the genus *Soshkineophyllum*, we are not certain that her species identification is correct. Therefore, we tentatively accept the assignment to *Soshkineophyllum* of species showing variation in the level at which the cardinal septum becomes shortened.

ILINA (1984) re-described *S. artiense* (SOSHKINA, 1925) from a collection of 28 specimens. Unfortunately, she did not re-illustrate the holotype, but only mentioned its diameter and septal number (*ibid.*, p. 153), thus resolving none of the uncertainties mentioned above. In the same description, ILINA noted the presence of finely trabecular septal microstructure in the type species. This feature is also evident in specimens from the Sverdrup Basin (Pl. 7, Fig. 2) and the Svalbard Archipelago (Pl. 7, Figs 1a, b), and thus appears to be typical for the genus. Also, we accept as typical for the type species and the genus, the zaphrentoid arrangement of major septa early in the ontogeny, shown by ILINA (1984, Pl. 27, Fig. 2a), and the calophylloid elongation of the cardinal, counter and alar septa, best seen in her Plate 27, Figure 2b. No specimen illustrated by ILINA (1984) shows biform morphology in its tabularium and she did not mention the occurrence of that character in any of the species of *Soshkineophyllum* dealt with in her paper.

When introducing the genus *Soshkineophyllum* and discussing its characteristics, GRABAU (1928) redescribed SOSHKINA's (1925) species, using her descriptions and illustrations. He also established a new species, but the latter has an axial structure and a dissepimentarium, features excluding it from *Soshkineophyllum*. Nevertheless, this genus is known to occur in the Tethys Realm (see below).

TIDTEN (1972, p. 28) conditionally included his proposed new genus *Sassendalia* within the family Lophophyllidiidae MOORE & JEFFORDS, 1945. He attached particular importance to the elongated counter septum and its relationship to the columella or, strictly speaking, to its ability to form that structure. Many rugose coral taxa have an elongated counter septum, but this does not always lead to the development of a columella extending into the calice. The presence or absence of a columella may, in fact, be more important for taxonomy than the differentiation in length of the major septa, commonly considered to occur only in the plerophyllids. Such differentiation may also occur in lophophyllidiids (see discussion below), but members of the latter family have a columella, which *Sassendalia* does not. Thus, we maintain that *Sassendalia* should be excluded from the Lophophyllidiidae MOORE & JEFFORDS, 1945.

The early ontogeny of specimens included in *Sassendalia* has not been previously investigated. Additional sections cut from two paratypes of TIDTEN's (1972) type species show the cardinal septum elongated in the early growth stages so as to become dominant along with the counter septum and the alar septa in the manner typical for the Polycoeliidae (Text-figs. 13.3a-c; Pl. 3, Figs 7a,b). In view of the structural features discussed above and the shortening of the cardinal septum at maturity in Tidten's type species, we consider *Sassendalia* to be a synonym of *Soshkineophyllum*.

Among the other species that have been assigned to *Soshkineophyllum* (e.g., MOORE & JEFFORDS 1941, FOMICHEV 1953b, SOKOLOV 1960, DE GROOT 1963) only the oldest (*S. internectum* FEDOROWSKI, 1973), from the *Wocklumeria* or *Gattendorfia* Biozone in Poland, has been almost completely studied in terms of its early ontogeny (FEDOROWSKI 1973, p. 102-105, Text-fig. 7). It developed typical zaphrentoid morphology in its early growth stage, followed by a calophylloid septal pattern with the axial area filled by stereoplasm but the major septa withdrawn from the corallite axis. Shortening of the cardinal septum occurs only above the last tabula and the tabularium is regular with convex tabulae. Of the other species listed above, those described by SOKOLOV (1960) are the most doubtful representatives of *Soshkineophyllum*, whereas the species investigated by FOMICHEV (1953b) seem to be closely comparable to those described in detail by ILINA (1984). None of these species shows a biform tabularium.

It should be noted that, despite the differentiation in the length of its major septa, *S. mirabile* MOORE & JEFFORDS, 1941 has the main characteristics of *Lophophyllidium* and should be transferred to that genus. Such septal differentiation is fairly common among North American lophophyllids (e.g., MOORE & JEFFORDS 1945, FEDOROWSKI 1987).

The type species of *Empodesma* MOORE & JEFFORDS, 1945, assigned by FEDOROWSKI (1973) to the genus *Soshkineophyllum*, has a regular but concave tabularium (MOORE & JEFFORDS 1945, Figs 10d, 12c, 13, 14) through most of its ontogeny, in contrast to the convex tabularium in the holotype of *S. artiense*. Thus, in spite of the striking similarity in the septal arrangement of these two species, we do not follow the earlier decision by FEDOROWSKI (*ibid*., p. 102), but accept *Empodesma* as an independent genus. The early ontogeny of the type species, *E. imulum* MOORE & JEFFORDS, 1945, is known only from the calophylloid stage to maturity but is similar over that interval to specimens described by FEDOROWSKI (1973) and ILINA (1984) as *Soshkineophyllum* and should be included in the same family.

As noted above, there are specimens in the Tethys Realm that almost certainly should be included in the genus *Soshkineophyllum*. Despite their poor preservation, we accept the generic designation of specimens described as *Soshkineophyllum japonicum* by IGO (1959) from the lower Permian of Hida Massif (Central Japan) and those by YAMAGIWA (1960) as *Soshkineophyllum* sp. indet. from the probable upper Permian of southwestern Japan. Both of those species display distinct differentiation in the length of their major septa, with the counter septum dominating and the cardinal septum shortened.

GUO (1976, Pl. 40, Fig. 8) described and illustrated a single transverse section through the middle (?) part of the calice as *Soshkineophyllum artiense* (SOSHKINA). We cannot acknowledge the species identification of this corallite. Also, the documentation presented by GUO (*ibid.*) is inadequate for a final decision as to the genus. Nevertheless, the clear differentiation in length and thicknes of major septa, the slight elongation of the counter septum and the distinct shortening of the cardinal septum indicates that this specimen probably belongs in *Soshkineophyllum.*

Soshkineophyllum longyiense WU & ZHAO (1989, p. 39, Pl. 1, Figs 2a, b) exibits morphology typical for the genus, thus indicating the presence of *Soshkineophyllum* in southwestern China.

KORA & JUX (1986, Fig. 3f) illustrated *Soshkineophyllum* sp. from the Viséan deposits of Sinai (Egypt). Unfortunately, there are no descriptions of species or illustrations of early ontogenetic stages in their paper. Thus, a more comprehenive discussion is precluded. It seems probable that such characters as the rhopaloid thickening and differentiation in length of major septa, the elongation of the counter septum and the shortening of the cardinal septum shown by some specimens are adequate for identification of the genus *Soshkineophyllum*. If this and the stratigraphic position is confirmed, their species would be the third oldest representative of *Soshkineophyllum* after those from Germany (SCHINDEWOLF, 1942) and Poland (FEDOROWSKI, 1973). It is possible that some other species of *"Amplexizaphrentis"* described by KORA & JUX (1986) and by KORA (1989) from Egypt may belong to *Soshkineophyllum*.

Soshkineophyllum turgidiseptatum (TIDTEN, 1972)
(Text-figs 12, 13; Pl. 3, Figs 7, 8; Pl. 4, Figs 1, 2; Pl. 7, Figs 1, 2)

1972. *Sassendalia turgidiseptata* TIDTEN, p. 30, Pl. 5, Figs 1-7, Pl. 10, Fig. 8; Pl. 11, Figs 11-14, Pl. 12, Figs 1, 2, Pl. 15, Figs 11, 12.
1974. *Sochkineophyllum* sp. BAMBER *in* R. THORSTEINSSON, p. 70.
1992. *Sassendalia turgidiseptata* TIDTEN; Y. EZAKI & T. KAWAMURA, Pl. 5, Figs 1, 2.

MATERIAL: Four paratypes from type collection restudied (B 2.130, B 2. 131, B 2.133, B 2.142); hypotypes – three large, fairly well preserved corallites [GSC 117148 (2 thin sections, 1 acetate peel), 117167 (6 thin sections), 117169 (6 thin sections, 3 acetate peels), from GSC localities 73156, C-32504 and C-10470.

DIAGNOSIS: *Soshkineophyllum* with axial margins of major septa contiguous laterally; rhopaloid thickening and differentiation in length of septa best expressed near calice floor; minor septa evident only in calice; near calice margin, n:d = 60:45.

INTRASPECIFIC VARIABILITY: Text-fig. 12 shows variation in size and n:d values within acceptable limits for a single species. The same is true for the variation in

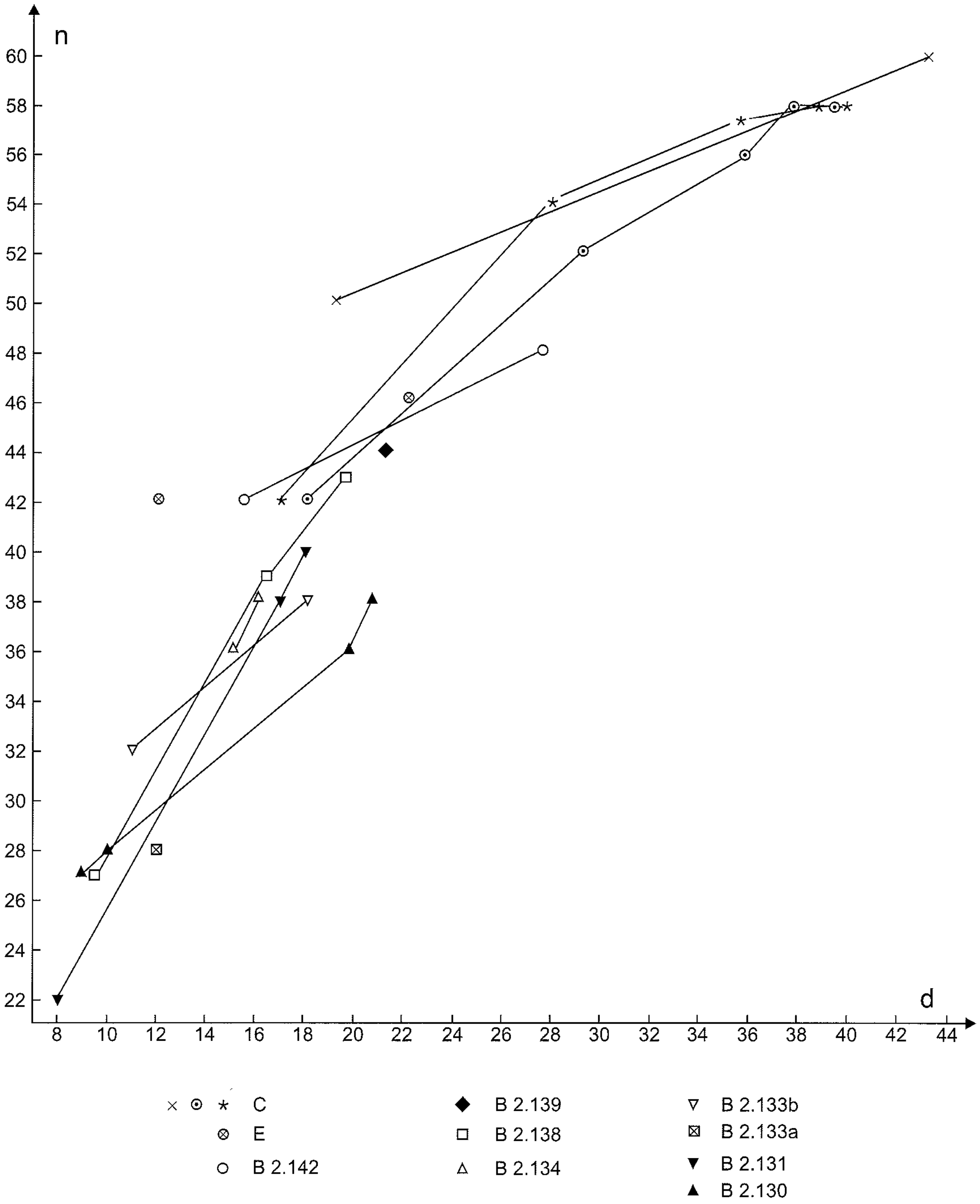


Fig. 12. *Soshkineophyllum turgidiseptatum* (TIDTEN 1972); number of major septa *vs.* diameter for specimens described in the literature and in this paper; n – number of major septa, d – diameter (mm), C – specimens studied for this paper, E – specimens from EZAKI & KAWAMURA (1992, Pl. 5), all other symbols represent values from TIDTEN (1972, p. 30); symbols joined by lines represent values taken from individual specimens

other morphological characteristics, especially when compared at corresponding growth stages, rather than in randomly situated sections of different specimens. Some of the observed differences between corallites are as follows: In some corallites (e.g., Pl. 4, Fig. 1d), minor septa appear within the corallite wall below the calice, whereas in others (e.g, the holotype), they appear only in the highest part of the calice; the shape of the cardinal fossula remains lense-like above the calice floor in some corallites (Tidten 1972, Pl. 15, Figs 11, 12) but much more commonly the fossula walls became parallel fairly early in the ontogeny (Pl. 3, Fig. 8a; Pl. 4, Figs 1a-c); the thickening of major septa may be slightly reduced earlier or later in the ontogeny. These and others are truly small, individual differences and we do not consider them to be substantial for separating species. They occur in specimens from both the Svalbard Archipelago and the Sverup Basin, among which no two individuals are identical. The Canadian specimens are larger than those from Vestspitsbergen, but fit well with n:d values shown in Text-fig. 12.

DISCUSSION: The original description of this species by Tidten (1972, p. 30, 31) is fairly complete and needs only to be supplemented with a few additional remarks. We agree that the relationship between the diameter and number of septa in this species is highly variable, but not to the extent expressed by Tidten (1972, p. 30), who

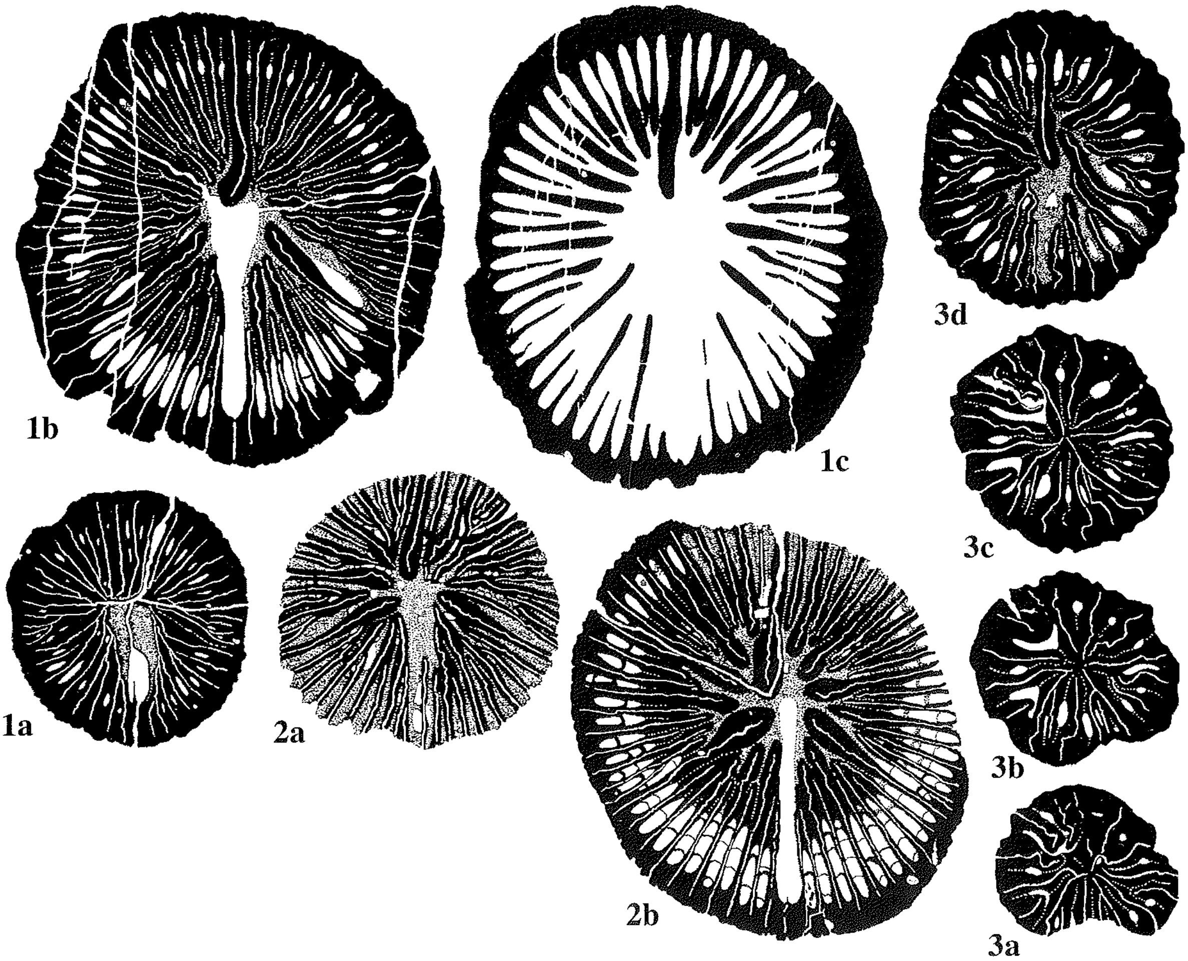


Fig.13. *Soshkineophyllum turgidiseptatum* (Tidten, 1972); transverse sections, inked and bleached photographs; 1 – GSC 117167, hypotype; GSC locality C-10470, Degerböls Formation, type section, talus from lower 3 m; a – late neanic stage (= Pl. 4, Fig. 2a), × 2; b – mature stage, peripheral interseptal loculae in cardinal quadrants above last tabula (= Pl. 4, Fig. 2b), × 2; c – middle part of calice (= Pl. 4, Fig. 2d), × 1.5; 2 – GSC 117148, hypotype; GSC locality 73156, Trold Fiord Formation, 130 m above base; a – late neanic stage (= Pl. 3, Fig. 8a), × 2; b – mature stage, cardinal fossula above calice floor (= Pl. 3, Fig. 8b), × 1.5; 3 – B 2.130 (Tidten 1972, p. 30), paratype; Sassendalen, central Vestspitsbergen, probably from Kapp Starostin Formation or its equivalents; a-c – neanic stage (b = Pl. 3, Fig. 7a; c = Pl. 3, Fig. 7b), × 5; d – late neanic/early mature stage (= Pl. 3, Fig. 7c), × 4

saw no evident relationship between the two values. All available measurements were plotted (Text-fig. 12) to compare data for separate corallites of the species and for individual growth stages of particular corallites. Two tendencies, independent of corallite diameter, are evident throughout the ontogeny: one toward rapid increase and the other toward slow increase in the number of septa in relation to the diameter. Comparisons between the most distinctive specimens, with the holotype showing rapid septal increase, reveals no substantial differences in morphology (TIDTEN 1972, Pl. 5, Figs 1-5; Pl. 11, Figs 11-14). Comparison of n:d values for individual corallites shows that most of them can well be placed along a fairly stable curve (Text-fig. 12). Thus, we consider that the differences in size of individual corallites and their n:d values show a gradual increase to be expected within a species.

The early ontogeny of *S. turgidiseptatum* has not been previously described. Two new series of thin sections cut from the paratypes show a typically zaphrentoid early ontogeny with the cardinal, counter and alar septa meeting at the corallite axis. The middle dark lines of the counter-lateral septa show that they may reach the axis as well (Text-fig. 13.3a-c). In contrast to other, thoroughly investigated species of *Soshkineophyllum*, the length of the cardinal septum in the paratypes of *S. turgidiseptatum* and also in our specimens from the Sverdrup Basin (Text-fig. 13.1a, b, 2b; Pl. 3, Figs 8a,b; Pl. 4, Figs 1a-d, 2a, b) is reduced early in the ontogeny – i.e., at a diameter of approximately 10 mm or less. In one specimen (Text-fig. 13.1a; Pl. 4, Fig. 2a) the cardinal septum barely protrudes from the corallite wall, even at such an early growth stage. This reduction occurs below the calice floor but is to some extent related to the extreme depth of the cardinal fossula. The latter may be filled with matrix even into the lower 1/3 of the corallite (Text-fig. 13.1a; Pl. 4, Fig. 2a).

In the early growth stage, the cardinal fossula is completely or almost completely infilled with stereoplasm. This strong stereoplasmic infilling obscures the arrangement of the septa surrounding and forming the cardinal fossula. They become successively shorter, beginning with the alar septa or the first pairs of major septa adjacent to the alars. As a result of this regular shortening and the deposition of sheets of stereoplasm, the walls of the cardinal fossula are always parallel, as is best shown in transverse sections cut near the calice floors (Text-fig. 13.2b, 3d; Pl. 3, Fig. 8b; Pl. 4, Figs 1c, d, 2b). The inner margin of the consistently narrow cardinal fossula may either remain narrow (Text-fig. 13.2b, 3d; Pl. 3, Fig. 8b; Pl. 4, Figs 1d, 2b) or become slightly widened (Text-fig. 13.1b; Pl. 4, Fig. 2b).

Both the differentiation in length and the rhopaloid thickening of the major septa are greatly obscured by stereoplasm in *S. turgidiseptatum*, but close inspection shows (e.g. Text-fig. 13.1b, 2a, b; Pl. 3, Fig. 8a; Pl. 4, Figs 1a-c, 2a) that the major septa are differentiated in length fairly early in the ontogeny and that the shorter ones are non-rhopaloid or only weakly rhopaloid. They are almost equally thickened along their entire length, except in the outer tabularium, where all interseptal loculi become open fairly early in the ontogeny (Text-fig. 13.1a, 3a, b; Pl. 4, Figs 1a-c, 2a). Some major septa become distinctly non-rhopaloid only in the calices, where most of the shorter septa become thinner and shorten to the extent that they resemble minor septa (e.g. Text-fig. 13.1c; Pl. 4, Figs 2c, d). This character was first illustrated by TIDTEN (1972, Pl. 11, Fig. 14) in the holotype. The counter septum is clearly dominant in all better preserved corallites, including the holotype. This is evident both beneath the calice and within it, where the stereoplasmic sheets on the counter septum are reduced distally, as in other rhopaloid major septa (Text-fig. 13.1c; Pl. 4, Figs 2c, d).

We studied the septal microstructure of this species in paratype B 2.130 of "*Sassendalia*" *turgidiseptata* TIDTEN, 1972 from the Svalbard Archipelago (Pl. 7, Figs 1a, b) and in Canadian Arctic specimens (Pl. 7, Fig. 2). It has been altered diagenetically in all of these specimens (especially in the paratype), but is consistent in character and strongly resembles that in *Soshkineophyllum artiense* (SOSHKINA, 1925), the type species of the genus (ILINA 1984, p. 154). In all instances, the microstructure consists of a single row of small (width 0.03-0.05 mm), simple trabeculae. Unfortunately, ILINA (*ibid.*) described the microstructure from new material, rather than from the holotype of *S. arteinse*. Thus, we can only assume that the microstructure of the type material matches that described by her. The consistency of data from specimens collected from several widely separated areas, however, suggests that the microstructure described above is characteristic for the genus.

OCCURRENCE: Svalbard Archipelago, Central Vestspitsbergen: Sassendalen, possibly Kapp STAROSTIN Formation or its equivalents, possibly Wordian or early Capitanian. TIDTEN (1972, p. 30) assigned an Artinskian age to this species and placed it within the *Parafusulina* zone. The reasons for his age and zonal assignments are unclear, however, because no fusulinaceans are known from the area at that biostratigraphic level. We have assumed a Wordian or early Capitanian age for his specimens, from the age established for this species by EZAKI & KAWAMURA (1992) (see following); Festningen, Kapp Starostin Formation, units 5-8, probably Wordian or early Capitanian.

Sverdrup Basin: Melville Island, Trold Fiord Formation, GSC locality 73156, Wordian; Ellesmere Island, Trold Fiord Formation (GSC locality C-32504) and type section of Degerböls Formation (C-10470), Wordian.

Soshkineophyllum ? sp.
(Text-fig. 14; Pl. 4, Figs 3a-c; Pl. 8, Figs 3a, b)

1973a. *Sinophyllum* sp. FLÜGEL, p. 43, Text-fig. 20.

MATERIAL: Specimen MMH 11938, illustrated by FLÜGEL (*Ibid.*).

DISCUSSION: The morphology of the specimen illustrated by FLÜGEL (*Ibid.*, Text-fig. 20) as *Sinophyllum* was checked from newly made thin sections and also from its partly preserved calice (Pl. 4, Fig. 3c), which was not described by FLÜGEL (*Ibid.*). The corallite is incomplete and partly crushed, but its fairly well-preserved surface shows septal furrows and growth striae. Only the upper part of the calice (Pl. 4, Fig. 3c) is destroyed. It is shallow, with its axial part elevated by the union of the axial margins of most major septa. The cardinal septum is shortened in a narrow, slit-like cardinal fossula, which may have been diagenetically reduced in size, but was originally elongate rather than triangular. The counter septum is strongly elongated to reach the cardinal fossula, but is not axially elevated to form a columella.

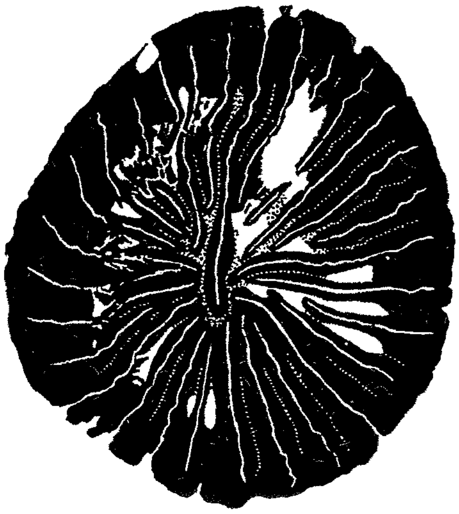


Fig.14. *Soshkineophyllum*? sp. (= *Sinophyllum* sp. of FLÜGEL 1973a, p. 43), MMH 11938, transverse section, mature stage, inked and bleached photograph (= Pl. 4, Fig. 3b); East Greenland, Kap Stosch, "*Productus* Limestone", Wegener Halvø Formation; × 4

In transverse sections cut beneath the calice (Text-fig. 14, Pl. 4, Figs 3a, b) the morphology is similar to that within the calice, except that all septa are thick and most of them are rhopaloid and differentiated in length, as are those in other representatives of the genus *Soshkineophyllum*. Minor septa are absent from both the corallite lumen and the preserved part of the calice, although furrows corresponding to them are present. Also, a delicate waviness, suggesting their presence, is evident in the outermost part of the external wall.

The septal microstructure is trabecular with individual trabeculae mainly forming a single row in the medial plane of the septum (Pl. 8, Figs 3a, b). This arrangement indicates that the trabeculae grew directly toward the upper and inner edges of the septa. Locally, the trabeculae may be directed slightly outward toward the periphery and/or form more than a single row (Pl. 8, Fig. 3a). Such outwardly directed trabeculae are cut obliquely in transverse section. Wide "half-moons" of fibres (Pl. 8, Fig. 3a) are here interpreted to represent obliquely sectioned trabeculae arranged in double rows. We disagree with the opinions of SCHINDEWOLF (1942) and OEKENTORP (1980) that such structures are growth lamellae, rather than trabeculae. This distinction has been more widely discussed by FEDOROWSKI (1974). Both of the above trabecular arrangements occur during the growth of a single septum. The size of the trabeculae varies, but they are generally large, with a width reaching 0.11 mm (Pl. 8, Fig. 3b). Large, similarly arranged trabeculae are also typical for *Lophophyllidium*, but the differentiation in length and thickness of the major septa, the lack of a columella, the shape of the cardinal fossula and other characteristics of FLÜGEL's (1973a) specimen match those of *Soshkineophyllum* rather than *Lophophyllidium*. Incomplete preservation and diagenetic alteration of this specimen preclude ontogenetic studies and prevent more precise identification.

OCCURRENCE. East Greenland, Kap Stosch, Wegener Halvø Formation, Foldvik Creek Group "*Productus* Limestone" (FLÜGEL 1973a, p. 43), Wordian or early Capitanian.

Genus *Tachylasma* GRABAU, 1922

TYPE SPECIES. *Tachylasma cha* GRABAU, 1922

1942 ? *Prionophyllum* SCHINDEWOLF, p. 209 (see *Ufimia* for discussion).

DIAGNOSIS: Plerophyllina with pentaphylloid early ontogeny; in maturity cardinal and counter septa shortened, alar and counter-lateral septa elongated or equal to other major septa; microstructure of septa finely trabecular.

DISCUSSION: Differentiation in the length of its major septa is the main feature characterizing the suborder Plerophyllina, whereas the differentiation between individual families and genera within the suborder are based on the elongation and/or shortening of the cardinal, counter, alar and counter-lateral septa, which occur in various combinations and result from at least two different patterns of ontogenetic development. In this discussion we wish to express our views concerning the mutual relationships of several nondissepimental taxa within the Plerophyllina in relation to species described herein.

We begin our discussion with *Paracaninia* CHI, 1937, because most of the controversial questions and uncertainties are best discussed with reference to that genus. The systematic position and content of the European and Arctic representatives of *Paracaninia* has not been discussed since the studies by WEYER & ILINA (1979), WEYER (1981, 1982) and ILINA (1984). All of their studies were based on Upper Carboniferous and Permian specimens from Russia, with references to other areas and to the type species of the genus, but without revision of the latter based on type or topotype material. Also, no such revision has been done elsewhere, although several species of *Paracaninia* were reported from China (e.g. ZHAO, 1976, 1981, GUO 1980; YAN & CHEN, 1982 [*in* ZHU & *al.*], WU & ZHAO, 1982 [*in* ZHU, & *al.*], CAO & *al.* 1983, XU, 1984 and others). Most of those species display adult morphology closely resembling that described by CHI (1937) in the type species, but none deals with early ontogeny. As a result, information on the early ontogeny and septal microstructure of the type species is lacking for both the original type material (CHI, 1937, Pl. 4, Fig. 1a-f.) and more recently described specimens included by Chinese authors in the type species or its new subspecies (e.g. ZHAO, 1976, YAN & CHEN, 1982 [*in* ZHU & *al.*], CAO & *al.* 1983). In the absence of adequate published data on Chinese species assigned to *Paracaninia* by authors subsequent to CHI (1937), we will restrict our discussion mainly to the European and Arctic species that have been included in that genus.

CHI (*ibid.*, Pl. 2, Figs 3c, d and Pl. 3, Fig. 3c) illustrated the late? neanic stage for two taxa, included by ILINA (1984) in *P. sinense*. We accept her synonymy and consider both the late(?) neanic and mature morphology of all specimens included by CHI (1937) in *Paracaninia* and *Allotropiophyllum* to be typical for *Paracaninia* within the limits of intraspecific variability. This approach allows at least the late(?) neanic stage of *P. sinensis* to be considered as zaphrentoid. For the purpose of this paper and until it is re-appraised by further study of the type or topotype collection, we propose to assume a zaphrentoid septal arrangement for the earliest ontogeny of *Paracaninia sinensis*.

As with our treatment of *Ufimia vs. Tachylasma* (see discussion of *Ufimia* above) our approach to the taxonomy of corals included by WEYER (*ibid.*), WEYER & ILINA (*ibid.*), and ILINA (*ibid.*) in *Paracaninia* is based mainly on differences in their early ontogeny. We distinguish clearly between the zaphrentoid and pentaphylloid or tachylasmatid ontogeny (see below). Thus, despite the morphological similarity of their mature growth stages, we cannot accept the inclusion within a single genus of *"Pseudobradyphyllum" nikitini* (STUCKENBERG, 1888), with its zaphrentoid early growth stage (DOBROLYUBOVA, 1940; WEYER 1981) and *"Plerophyllum" variabile* SOSHKINA, 1941, with its pentaphylloid early ontogeny (SOSHKINA & *al.* 1941; WEYER 1982).

The early ontogeny of *P. sinensis*, illustrated by CHI (1937, Pl. 2, Figs 3c, d; Pl. 3, Fig. 3c), is not similar to any growth stage of *Paracaninia variabilis* (SOSHKINA & *al.* 1941, Pl. 7, Figs 1-3; WEYER 1982, Pl. 1-5) but shows considerable similarity to the well preserved early ontogeny of *Zaphrentis nikitini* STUCKENBERG, 1888 (DOBROLYUBOVA 1940, Pl. 2, Figs 3, 4, 11-15, 20-23, 26, 27; WEYER, 1981, Pl. 3, Fig. 3-5; Pl. 4, Figs 1, 3, 7, 8; Pl. 5, Fig. 9; Pl. 7, Figs 3-5, 8, 9). The unusual morphology of the early ontogeny of *P. nikitini*, illustrated by ILINA (1984, Text-fig. 49), cannot be ascribed to either the zaphrentoid or the pentaphylloid type. From ILINA's illustration (*ibid.* Text-fig. 49a) one can assume the presence of an aseptal cup at the very beginning of the skeletogenesis. Within this cup, the first septum then developed on its floor and walls, as postulated by FEDOROWSKI (1991). Sections of the upper parts of this septum (the future cardinal and counter septa) appear as intercepts attached to the external wall, indicated by ILINA (*ibid.* Text-fig. 49a) as "G" (= cardinal) and "P" (= counter). Her next three drawings (*ibid.*, Text-fig. 49 b-g – transliterations of the Russian alphabet are used in this and in all subsequent citations of Russian papers) differ greatly from each other, from her next drawings (*Ibid.*, Text-fig. 49d-k) and from the early ontogeny of all other well preserved specimens illustrated by ILINA (*Ibid.*), WEYER (*ibid.*) and other authors dealing with Plerophyllina. Therefore, we prefer not to regard text-figures 49b-g of ILINA (*ibid.*) as indicative of any particular type of early ontogeny for this species, but suggest that they may have been affected by pathologic or diagenetic alterations in morphology.

Of the two amplexoid genera, *Pleramplexus* and *Pentamplexus*, introduced by SCHINDEWOLF (1940), only the latter has been shown to have a pentaphylloid young stage (WEYER & ILINA 1979, Text-fig. 5.1-3). The early ontogeny of the holotype of *Pleramplexus similis* SCHINDEWOLF, 1940, the type species of the genus, will never be investigated because the tip of this specimen was destroyed (SCHINDEWOLF 1942, Pl. 28, Fig. 1d). Thus, we can only assume that the persistent elongation of its cardinal septum and the considerable length of its counter septum (SCHINDEWOLF 1942, Text-fig. 67a, b, Pl. 28, Fig. 1a, b) indicates that the early ontogeny is not pentaphylloid. Nevertheless, we follow SCHINDEWOLF (1942) in placing his species in the Plerophyllinae lineage – i.e., we tentatively consider the early ontogeny of *Pleramplexus* to be zaphrentoid and accept its synonymy with *Paracaninia*, as proposed by WEYER & ILINA (1979, p. 1332).

The new, re-orientated drawings of SCHINDEWOLF's original thin sections, presented by WEYER & ILINA (1979, Text-fig. 5:1-3), strongly suggest a pentaphylloid ontogeny for *Pentamplexus simulator* SCHINDEWOLF, 1940, the type species of the genus. Unfortunately, this cannot be fully substantiated from the single, incomplete specimen on which this species is based. Nevertheless, we agree with WEYER & ILINA (1979) that *Pentamplexus* differs morphologically from *Paracaninia*. The question of the feasibility of recognizing both genera is addressed near the end of this discussion, along with the short-septal mature growth proposed by WEYER & ILINA (*ibid.*) as a third generic character of *Pentamplexus*. First we will discuss two items in the diagnosis of *Pentamplexus* proposed by WEYER & ILINA (*Ibid.*, p. 1334) – the pentaphylloid ontogeny and the long cardinal septum at maturity.

The interpretation of pentaphylloid ontogeny by WEYER & ILINA (*ibid.*), followed by each of those authors in their subsequent papers, does not take into account the underdevelopment of the counter septum early in the ontogeny, but stresses elongation of the cardinal, alar and counter-lateral septa and assigns particular importance to the elongation of the cardinal septum. In our interpretation, following SCHINDEWOLF (1942) and FEDOROWSKI (1973), the underdevelopment of the counter septum early in the ontogeny is the most substantial feature, whereas the length of the cardinal septum may vary irrespective of the length of the counter septum (see below). Permanent underdevelopment of the counter septum is a widespread and consistent feature that can perhaps first be seen in the Upper Silurian *Anisophyllum*. Drawings by ILINA (1984, Text-fig. 30) of the early ontogeny of the topotypes of *A. agassizi* MILNE EDWARDS & HAIME, 1850 from the Brownsport Formation, Tennessee, strongly support this possibility. The early ontogeny in *Oligophyllum kullmanni* WEYER (1973, Pl. 2), from the Lower Emsian of Germany, closely resembles the typical pentaphylloid pattern. The latter certainly occurs in the Emsian species of *Oligophyllum* and *Pentaphyllum*, described by KULLMANN (1965) from the Cantabrian Mountains of northern Spain. The same type of early ontogeny has been established for the uppermost Devonian or lowermost Carboniferous *Pentaphyllum, Commutia* and *Dalnia* from Poland (FEDOROWSKI 1973) and the Tournaisian and Viséan *Pentaphyllum*, described as *Cryptophyllum hibernicum* by CARRUTHERS (1919, Pl. 11). Pentaphylloid ontogeny in younger taxa can be traced into the Serpukhovian, where it occurs in a single specimen distinguished by ILINA (1984) as the new species *Pentaphyllum uralicum*. There are no confirmed occurrences in younger Carboniferous rocks, but pentaphylloid ontogeny again appears in the Permian, where it is known as high as the Changhsingian, in Chinese species of *Tachylasma*. These Permian taxa may be descendents of those in the Lower Carboniferous, or pentaphylloid ontogeny may have developed independently in these two groups of taxa (see short discussion below).

Following SCHINDEWOLF (1942) and FEDOROWSKI (1973) we wish to point out the contrast between the retarded development of the counter septum in the pentaphylloid ontogeny and that seen in *Ufimia*. In the latter genus, the counter septum is united with the cardinal septum over a considerable interval of growth and the remaining major septa have a zaphrentoid arrangement. Either the cardinal septum or the counter septum, or both, may then become shorter. The stratigraphically lowest appearance of zaphrentoid ontogeny in the Plerophyllina is uncertain. It almost certainly does not occur in the early ontogeny of the Eifelian *Ufimia prius* KULLMANN, 1965, for the ontogenetically earliest morphology of which KULLMANN, (*Ibid.*, Text-fig. 12a) indicates a pentaphylloid rather than a zaphrentoid ontogeny. Thus, we would eliminate that species from the genus *Ufimia*. Two specimens of another Eifelian species, *Oligophyllum soshkinae* ILINA, 1980, from the eastern slope of the Central Urals (ILINA 1984, Text-fig. 28a-f) demonstrate substantial differences in their early ontogeny. One of them (*Ibid.*, Text-fig. 28 a-e) can, with some reservation, be considered zaphrentoid. Unfortunately, illustrations of the more mature growth stages of this specimen are lacking. The second specimen is dubious but exhibits more characteristics of a pentaphylloid ontogeny. Although included by ILINA (*ibid.*) in *Oligophyllum*, the specimen does not exhibit the main characteristics of that genus. The nature of the early ontogeny of *Ufimia*, demonstrated by RÓŻKOWSKA (1969) from the Upper Famennian of Poland, is slightly unclear, although the elongation of the cardinal and counter septa in the ontogenetically earliest transverse section available for *U. supradevonica* RÓŻKOWSKA, 1969 is obvious (RÓŻKOWSKA, *Ibid.*, Text-fig. 50A). Unquestionable illustrations of zaphrentoid ontogeny developed by *Ufimia*-like corals are those of HUDSON (1936a, Pl. 4) in "*Rhopalolasma*" *tachyblastum* HUDSON, 1936 and "*R.*" *symplecta* HUDSON, 1936 from the Upper Tournaisian of Britain. Thus, we tentatively consider the zaphrentoid early ontogeny characteristic for *Ufimia* to have been derived from a nondissepimental taxon with a zaphrentoid septal arrangement and its protosepta (i.e., the cardinal and counter septa) united in the neanic stage. The zaphrentoid arrangement seems to be most common in the Rugosa, occurring in the early ontogeny of many nondissepimental and dissepimental taxa since Middle Ordovician time, but it has not been documented below the Tournaisian or perhaps the Upper Famennian for taxa showing the differentiation in the length of their major septa that is characteristic for the Plerophyllina.

Variation in the length of the cardinal septum occurs in the Plerophyllina, irrespective of the degree of development of the counter septum, and can be observed in almost all possible combinations with the latter. For example, most Devonian and Lower Carboniferous taxa developing a pentaphylloid ontogeny have a long cardinal septum, with *Dalnia* FEDOROWSKI, 1973 being the only known exception. Thus, we consider this character and the retarded development of the counter septum to be primitive characteristics of the early Plerophyllina. Shortening of the cardinal septum in species with a pentaphylloid ontogeny is unknown below the appearance of the genus *Tachylasma* GRABAU, 1922 in the Lower Permian. Also, this genus is, in fact, the only known bearer of that character among all Pentaphyllidae. Species of *Tachylasma* reported from older deposits (e.g., KABAKOVICH 1952, FOMICHEV 1953a, VASSILYUK 1960) either show zaphrentoid ontogeny or their early ontogeny has not been illustrated. Thus, shortening of the cardinal septum occurs in only the second stratigraphic interval (Permian) in which the counter septum is shortened (see above).

The situation is different for the Plerophyllina with a zaphrentoid ontogeny. This type of ontogeny appeared late (if the strange *Oligophyllum soshkinae* ILINA, 1984, discussed above, is not considered) and was the basis for different combinations involving elongation of the cardinal, counter, alar and counter-lateral septa. That from the upper Devonian or lowest Carboniferous strata of Poland is the oldest documented occurrence (RÓŻKOWSKA 1969, FEDOROWSKI 1973). The early ontogeny of the late Silurian or early Devonian *Amandaraia* was not illustrated and cannot be considered, although LAVRUSEVICH (1968, p. 108) pointed out the permanent elongation of four septa in all growth stages of that coral. FEDOROWSKI (1973) demonstrated the occurrence of zaphrentoid ontogeny in *Calophyllum* and *Soshkineophyllum*, but not in *Plerophyllum*. The ontogeny of specimens included by him in *Plerophyllum* is pentaphylloid, rather than zaphrentoid. Thus, true *Plerophyllum* does not appear below the *Eumorphoceras* biozone (SCHINDEWOLF 1952, KULLMANN 1966).

The development of a zaphrentoid early ontogeny in the Plerophyllina is fairly common in the Viséan and Serpukhovian but rare in younger strata. Rare documented taxa with a zaphrentoid ontogeny and elongated alar and counter-lateral septa include: *Plerophyllum (Ufimia) alternans* DE GROOT, 1963, from the Westphalian D (= Upper Moscovian) Sierra Corisa Limestone of the Cantabrian Mountains, northern Spain; and "*Tachylasma*" *elongatum* GRABAU of FOMICHEV (1953a), from the Kasimovian limestones "M" to "O" in the Donets Basin [questionably included by WEYER & ILINA (1979) in *Paracaninia*]. In contrast to the occurrence of pentaphylloid ontogeny (see above), however, zaphrentoid ontogeny is present in several taxa, such as *Actinophrentis*, *Stereophrentis*, *Barytichisma* (= *Thecophyllum* of FOMICHEV 1953a), *Bradyphyllum*, *Monophyllum* and *Lophophyllidium*, that occur either throughout or in various intervals of the Bashkirian, Moscovian and Gshelian of the Donets Basin (FOMICHEV 1953a). The exact stratigraphic position and taxonomy of *Tachylasma crassum* GORSKY, 1951 from the "Barents Series" of Novaya Zemlya cannot be established, but it should be noted that its major septa are differentiated in length and it has a slightly elongated counter septum. *Barytichisma*, *Stereocorypha* and *Lophophyllidium* show a zaphrentoid ontogeny in the Pennsylvanian of North America (e.g., MOORE & JEFFORDS 1945, JEFFORDS 1947, ROWETT & SUTHERLAND 1964, FEDOROWSKI 1987). We do not suggest that any particular genus of those listed above is related to or, even less likely, has given rise to the Permian Plerophyllina, but we wish to draw attention to the continuous occurrence of the zaphrentoid ontogeny and the absence of corals with a pentaphylloid ontogeny in the interval between Serpukhovian and Asselian or Sakmarian.

The most comprehensive ontogenetic studies of Permian Plerophyllina are those by ILINA (1965, 1984).

Thus, our remarks that follow are based on her work and on the discussion above, with some references to older species discussed and illustrated by KULLMANN (1965, 1966), FEDOROWSKI (1973, 1991, 1997a) and WEYER (1981, 1982). The available data allows the reconstruction of the early ontogeny of some representatives of the suborder Plerophyllina. It begins with an aseptal cup, comparable to that postulated by FEDOROWSKI (1991) for other rugose coral taxa. Its presence was established by ILINA (1984, Text-figs 9, 30?, 45, 49?, 63). In such a cup there is either an initial, axial septum forming a continuous ridge on the floor and walls of the cup, or two initial protosepta, with the appearance of the counter septum delayed and retarded during further development. In the first instance, the cardinal and counter septa are derived from the axial septum through retarded upward growth of its middle part. In the second instance, the two protosepta were distinct from the very beginning of their development. FEDOROWSKI (1997a, p. 13) considers the cardinal and the counter septum to be the only septa secreted in exocoels between the directive mesentheries – i.e., the only protosepta. HUDSON (1936b) was the first student to reduce the number of protosepta in the Rugosa to only two.

The substantial delay in the upward growth of the middle part of the axial septum and the short upper margins of this septum located next to the wall are represented by short intercepts in transverse section (e.g. ILINA 1984, Text-figs 9v, g; 30a; 45b; 49a). Elongation of those intercepts may result in them being temporarily connected, and in some instances joined to other major septa to form a zaphrentoid pattern (e.g., ILINA 1984, Text-figs 91, 34a-g, 45v, g). In other instances (ILINA 1984, Text-fig. 9v-zh, m-o, 33, 42), the intercepts of the counter septum apparently remain short. Such variability in the length of the counter septum allowed ILINA (1984) to disregard the difference between the pentaphylloid and zaphrentoid ontogenies in the sense accepted here and to supress the genera *Plerophyllum, Tachylasma, Commutia, Dalnia* and several others.

The two morphogenetic possibilities for the development of the cardinal and counter septa can be extended farther to the genus *Verbeekiella* PENECKE 1908. FEDOROWSKI (1986, Pl. 1, Figs 1a-c, 2a, b) documented the absence from that genus of an axial septum and the retarded development of both the cardinal and counter septa. This demonstrates that the independent development of the two protosepta is not unique and is not restricted to the family Pentaphyllidae. Nevertheless, the difference between the pentaphylloid and zaphrentoid ontogenies is as substantial as postulated by SCHINDEWOLF (1942), FEDOROWSKI (1973, 1986, 1991, 1997a) and in this discussion.

Differentiation between a truly pentaphylloid and an advanced zaphrentoid ontogeny is not always simple and easy. The "classic" version of the pentaphylloid ontogeny, found in Devonian to Serpukhovian species, is constant and easy to recognize. As discussed below, however, the two types of ontogeny cannot be so readily separated in some of the Permian taxa investigated by ILINA (1965, 1984). Development of a zaphrentoid ontogeny depends on the division, during growth, of the axial septum into separate parts and may be expressed in several different ways in transverse section. Among these, the discontinuity between two opposing intercepts of septa very early in the septogenesis is perhaps the most intriguing. In some instances (e.g. ILINA 1984, Text-fig. 45), it is possible to demonstrate that such isolated septal intercepts in fact represent only the upper margins of an axial septum that is continuous but only very slightly elevated above the calice floor. The upward and inward growth of such an axial septum may be so retarded that its continuity may be seen only in an etched calice or in a transverse section immediately above a tabula. In calicies in which the axial septum has grown a considerable amount, it protrudes high above the calice floor and the connection between the cardinal and counter septa is, or appears to be, constant (e.g. ILINA 1984, Text-fig. 34). For further discussion of early skeletogenesis, the interpretation of features seen in transverse sections and the morphology shown by calices, the reader is referred to FEDOROWSKI (1991, 1997a).

After several major septa have been inserted, the length of the counter septum and its relationship with the cardinal septum are significantly affected by the shape of the tabulae and/or the development of amplexoid *vs.* non-amplexoid septa. Also, these characters may cause variation in the length of the counter septum during further growth of the corallite. In such instances, persistent shortening of the counter septum may be mistakenly interpreted as an indication that the early ontogeny is pentaphylloid. Such an interpretation would be inaccurate, however, because abaxial withdrawal of the counter septum did not occur until late in the ontogeny. In corallites in which the counter septum is not amplexoid, the latter may be permanently retarded in growth and separated from the cardinal septum. This condition seems to have been illustrated by ILINA (1984) in her Text-fig. 9a-zh. Separation may also occur when the tabulae are highly elevated, as shown by ILINA (*Ibid.*, Text-fig. 36zh) and/or the counter septum is only weakly amplexoid, so that it is slightly elongated next to a tabula but does not extend far enough to meet the cardinal septum. Such amplexoid variation in the length of the counter septum is well documented in *Pentamplexus minimus* (ILINA 1984, Text-fig. 45d-i) and *Pentaphyllum dombaricum* (ILINA, *Ibid.*, Text-figs 36b, v, 37).

To conclude this part of our discussion, we wish to state that we can well accept the persistent underdevelopment of the counter septum and its separation from the cardinal septum in pentaphylloid ontogeny of Silurian to Serpukhovian taxa, but we would rather see such morphology in several of the Permian taxa investigated by ILINA (1965, 1984) as an extreme variation of zaphrentoid ontogeny. For instance, what appears to be the best example of a pentaphylloid ontogeny in the taxa illustrated as *Pentaphyllum* by ILINA (1984, Text-fig. 9) can equally well be considered as such a variant. This is, to some extent, supported by the elongation of six septa that meet at the corallite axis of another specimen (*Ibid*., Text-fig. 91). Such an interpretation, however, may not apply to all Permian corals with a pentaphylloid ontogeny. The early ontogeny in *Tachylasma*, illustrated by SCHINDEWOLF (1942, Text-figs 81, 82, 85, 86), and that in *Paracaninia variabilis* (SOSHKINA, 1941) of WEYER (1982, Pl. 2, Figs 1, 2; Pl. 3, Figs 1-5; Pl. 4, Fig. 6) are strikingly similar to the Devonian-Lower Carboniferous taxa discussed above.

The question of validity of amplexoid morphology as a generic character was left to the end of this discussion, because the answer depends on preferences in taxonomic procedure and cannot be rigidly adhered to. For instance, to what extent must the length of the major septa be uniform in order to be accepted as a new generic character? The specimens of *"Paracaninia" variabilis* illustrated by WEYER (1982) provide a good example. Why does the corallite illustrated by that author in his Plate 5, figures 1-8 belong to *Paracaninia*, but not to *Tachylasma*, if the elongation of its alar and counter-lateral septa is recognizable and all remaining major septa are long? Also, the holotype of *"Plerophyllum" variabilis* SOSHKINA (1941, Pl. 7, Fig. 1a, b) and the paratypes (*Ibid*., Pl. 7, Figs 2, 3) have elongated alar and counter-lateral septa. Furthermore, the two truly amplexoid specimens of *"P". variabilis* illustrated by WEYER (1982, Pls 1-3) may well be considered to represent an extreme morphotype, connected to the main stock of the genus *Tachylasma* by a series of intermediate morphotypes. The situation is similar with *Pleramplexus minimus* ILINA (1965), which was later included by her in *Pentamplexus* (ILINA 1984, p. 114). Five septa in the specimen illustrated in her text-figure 45 are clearly longer than the others, whereas the septa are almost equal in the corallite illustrated by her in 1965 (Pl. 14, Fig. 8). We have given these examples to stress the gradational boundaries between species included in amplexoid, as opposed to non-amplexoid, genera.

At the beginning of this discussion we pointed out the taxonomic value of retarded development of the counter septum as opposed to variability in the length of the cardinal septum. Among the nondissepimental Plerophyllina, elongation of the cardinal septum may be accompanied by elongation of the alar septa (*Amandaraia, Calophyllum*), or by elongation of both the alar and the counter-lateral septa (*Pentaphyllum, Plerophyllum*). The latter combination occurs in the ampleximorphic *Pentamplexus*. In fact, among all illustrations of ampleximorphs only those of *Pentamplexus simulator* SCHINDEWOLF, 1940 are fully convincing as ampleximorphs with a pentaphylloid early ontogeny. All other fully investigated species or specimens attributed to the genus *Pentamplexus* (see WEYER & ILINA 1979, p. 1334, 1335 for synonymy) are either incompletely documented (*Amplexus cristatus* WAAGEN & WENTZEL, 1886; *Pentaphyllum* (*Pentaphyllum*) n. sp. b of NIERMANN 1975) or 5 septa are clearly elongated, but are variably shortened at different levels in the corallite (*Amplexus leptoconicus* Abich, 1878 [WEYER & ILINA 1979, Fig. 4]; *Pleramplexus minimus* ILINA, 1965 [ILINA 1984, Text-fig. 45]). Some specimens in both *"A." leptoconicus* and *"P." minimus* seem to attain almost a true amplexoid morphology (e.g., ILINA 1965, Pl. 12, Fig. 2b; Pl. 13, Fig. 4v; Pl. 14, Fig. 8g), but in most specimens, even with such short septa as those illustrated by ILINA (1965, Pl. 13, Fig. 3), the elongation of 5 septa is clearly recognizable. In our opinion, the development of ampleximorphic morphology is so variable within individual species that it cannot be used as a diagnostic character for distinguishing between genera. Also, the single, incomplete corallite on which SCHINDEWOLF (1940) based his new genus *Pentamplexus* is inadequate for the complete definition of a genus. Considering the wide intraspecific variability in *"A." leptoconicus* and *"P." minimus*, we would expect a similar variability within the type species, *Pentamplexus simulator* SCHINDEWOLF, 1940, if the collection had been large enough. Thus, we consider the holotype of the latter species to probably represent an extreme variant that was selected as the type. Consequently, in contrast to WEYER & ILINA (1979) and ILINA (1984), we synonymize *Pentamplexus* with *Pentaphyllum*. EZAKI (1991) maintains a similar position by including in *Pentaphyllum* several species considered to belong in *Pentamplexus* by ILINA (1984). Also, we propose to synonymize *Pleramplexus* with either *Ufimia* or *Paracaninia*, because the early ontogeny of the two ampleximorph taxa differ, as discussed above, and neither of them can be proven to have constant, diagnostic generic characters.

We do not propose placing *Paracaninia* and *Ufimia* in synonymy at this time, because the ontogeny and microstructure of *Paracaninia* are inadequately known and it has an obviously biform tabularium, which does not occur in the type species of *Ufimia*. *Pseudobrady-*

phyllum DOBROLYUBOVA, 1940 would thus be an independent genus.

We will not discuss the phylogenetic lineage proposed by WEYER & ILINA (1979, p. 1330), except to state that we distinguish between the early ontogeny of *Ufimia* and that of *Tachylasma*, as discussed above. Therefore, we do not agree with placing *Ufimia* as an intermediate genus between *Pentaphyllum* and *Paracaninia*. We can see more or less well documented lineages leading from *Anisophyllum* through *Oligophyllum* to Lower Carboniferous representatives of *Pentaphyllum* but not to the Permian species of *Pentaphyllum*. In fact, the latter may be unrelated to the Lower Carboniferous type species, if we have correctly interpreted the early ontogeny of the Permian corals included in that genus by ILINA (1965, 1984). The long, Upper Carboniferous gap in the occurrence of taxa showing a pentaphylloid ontogeny cannot be ignored, although the possibility of their survival in a Bashkirian-Gshelian refuge cannot be excluded. We cannot propose a single lineage for genera with a zaphrentoid early ontogeny but we can see the *Calophyllum-Soshkineophyllum* lineage in some way connected to the Antiphyllinae ILINA, 1970. A direct connection between *Plerophyllum* and *Ufimia*, as proposed by SCHINDEWOLF (1940), cannot be excluded but derivation of *Plerophyllum* and *Ufimia* from different ancestors seems more likely. The *Zaphrentites delanouei-Z. shunnerensis* line, proposed by HUDSON (1944), may be considered an example of transformation of *Zaphrentites*-like corals to *Ufimia*, although the very probable occurrence of *Ufimia* in the upper Famennian excludes *Z. delanouei* (MILNE EDWARDS & HAIME 1851) as a direct ancestor of *Ufimia*. It is difficult to choose any particular genus or species as an ancestor for *Plerophyllum*. The Viséan *Claviphyllum* HUDSON, 1942 or *Rotiphyllum* HUDSON, 1942 would be good candidates if a polyphyletic origin of the Plerophyllina is accepted.

Although neither *Tachylasma* nor *Leonardophyllum* is known from the Middle Permian of the Sverdrup Basin, we have briefly revised some of the inadequately known East Greenland specimens of those genera, described by FLÜGEL (1973a), to clarify their morphology and/or confirm their occurrence elsewhere in the *Calophyllum* Province.

Tachylasma variabilis (SOSHKINA, 1941)
(Pl. 5, Fig. 4)

1941. *Plerophyllum variabile* SOSHKINA; SOSHKINA, DOBROLYUBOVA & PORFIRIEV, 1941, p. 83, Pl. 7, Figs 1-3.

1973a. *?Pentamplexus schindewolfi* FLÜGEL, p. 18, Pl. 2, Fig. 5, Text-fig. 8.

1973a *?Cryptophyllum (Tachylasma?) ponderosum* SCHINDEWOLF, 1942; H.W. FLÜGEL, p. 20, Pl. 2, Fig. 4, Text-fig. 9.

1973a. *Amplexocarinia* sp. FLÜGEL, p. 26, Pl. 3, Fig. 1.

1979. *Paracaninia variabilis* (SOSHKINA, 1941); D. WEYER & T.G. ILINA, Pl. 7.

1982. *Paracaninia variabilis* (SOSHKINA 1941); D. WEYER, p. 66, Pl. 1-5, Text-figs 1, 2. (*cum synon.*).

1984. *Paracaninia variabilis* (SOSHKINA, 1941); T.G. ILINA, p. 126, Pl. 19, Fig. 1; Text-fig. 50.

1997. *Paracaninia variabilis* (SOSHKINA, 1941); D. WEYER, p. 96 (*cum synon.*)

MATERIAL: The type material for several taxa described by FLÜGEL (1973a) and here re-assigned to *T. variabilis* (see synonymy above) was reviewed for this paper; two new thin sections cut from specimens MMH 11941.

DIAGNOSIS: *Tachylasma* with alar and counter lateral septa in mature stage slightly longer than or equal to other major septa; minor septa restricted to external wall; up to 38 major septa at corallite diameter of 20 mm.

DISCUSSION: The specimens described by FLÜGEL (1973a) from East Greenland were re-studied by FEDOROWSKI (1982) and were also reviewed for this paper. *Amplexocarinia* sp. of FLÜGEL (1973a) was described from a single, incomplete, unsectioned specimen (MMH 11941). Two thin sections, prepared for this paper from the lower and upper parts of the remaining fragment of the specimen, cut the mature growth stage. The main tachylasmatid characteristics (i.e., shortening of the counter septum and slight elongation and rhopaloid thickening of the alar and counter-lateral septa) are best shown in the lower of these sections (Pl. 5, Fig. 4a); weakly developed biform morphology in the tabularium is evident in individual loculi of both sections. This specimen closely matches some variants of *P. variabilis* in morphology, but is slightly larger, reaching a diameter of 20 mm with 38 major septa. We do not consider such a difference sufficient for distinguishing a separate species. The same appears to be true for *Pentamplexus schindewolfi* FLÜGEL, 1973a and *Cryptophyllum* (*Tachylasma?*) *ponderosum* SCHINDEWOLF, 1942 of FLÜGEL (1973a). Neither their main morphological characteristics nor their measurements exceed the limits of wide intraspecific variability established for "*Paracaninia*" *variabilis* by WEYER & ILINA (1979) and WEYER (1982), who revised and broadly discussed its type material and additional specimens and proposed its assignment to *Paracaninia* CHI, 1931. We acknowledge WEYER's revision of the species but we do not follow his generic assignment (see discussion of the genus).

The septal microstructure has not been studied in the type and other Russian specimens of "*P*". *variabilis* and is unknown for the type species of the genus. Thus, neither the descriptions by ILINA (1984) of the trabecular microstructure in some species assigned by her to *Ufimia* (i.e., the older synonym of *Tachylasma*, according to her), nor the microstructure described here can be taken as fully characteristic for the genus. In almost all of the better preserved septa in specimens from Greenland, there is a single row of moderately spaced trabeculae, 0.07-0.09 mm in diameter, growing perpendicular to the axial margin of the septum, along its medial plane (Pl. 5, Fig. 4c). This arrangement is similar to that recognised by ILINA (1984, p. 104) in *Ufimia carbonaria*, but the size of the trabeculae and the spaces between them are much larger (0.04 mm in *U. carbonaria vs.* 0.07-0.09 mm in the specimen that we investigated). The septal microstructure investigated by ILINA (*Ibid*., pp. 109-112) in other species included by her in *Ufimia* is trabecular, with individual trabeculae 0.05-0.06 mm in diameter. Some of those species (e.g., *Tachylasma elongata* GRABAU, 1922, *Tachylasma alternata* HUANG, 1932) most probably belong to the genus as originally described.

OCCURRENCE: East European Platform, early Kazanian; East Greenland, Kap Stosch, "*Productus* limestone", "*Martinia* limestone" (FLÜGEL 1973a, p. 18, 20, 26), Foldvik Creek Group, Wordian or early Capitanian.

Family Lophophyllidae GRABAU, 1928
Genus *Leonardophyllum* MOORE & JEFFORDS, 1941

TYPE SPECIES: *Leonardophyllum distinctum* MOORE & JEFFORDS, 1941

Leonardophyllum? sp.
(Pl. 5, Fig. 3)

1973a. *Leonardophyllum* sp. FLÜGEL, p. 44, Text-fig. 21.

MATERIAL: Original three peels and one eccentric longitudinal section, supplemented by two new transverse thin sections prepared for this paper, all from single specimen (MMH 11939), illustrated by FLÜGEL (1973a, Text-fig. 21).

DISCUSSION. The higher of the two new transverse sections (Pl. 5, Fig. 3b) shows several intercepts of the inner parts of tabulae, indicating that they are fairly steeply elevated – a feature characteristic for *Leonardophyllum*. This is confirmed, to some extent, by the eccentric longitudinal section (Pl. 5, Fig. 3c), despite its inaccurate orientation. The tentative generic assignment is also supported by the few free septal lamellae that join the medial lamella and the axial tabellae attached to them. It should be noted, however, that the abaxial declination of tabulae is much less pronounced in FLÜGEL's specimen than in the type species of *Leonardophyllum*, and more closely resembles that shown by some species of *Lophophyllidium*. The nature of its tabularium and the absence of early growth stages for this specimen prevent a definite generic assignment. Nevertheless, it is the only representative of either *Lophophyllidium* or *Leonardophyllum* known from such a high stratigraphic level in the Arctic.

OCCURRENCE: East Greenland, Kap Stosch, "*Productus* limestone" (FLÜGEL 1973a, p. 44), Wegener Halvø Formation, Foldvik Creek Group, Wordian or early Capitanian.

ANALYSIS OF THE FAUNA

In the CAU Realm, autochthonous, post-Artinskian, Permian rugose coral faunas are sparse and are restricted to solitary, non-dissepimental taxa, with the exception of rare occurrences of cerioid corals of probable Kungurian age, recently discovered in autochthonous rocks of the western U.S.A. (FEDOROWSKI & BAMBER in press). Post-Artinskian, solitary non-dissepimental corals from the southern part of the realm (western North America and South America) are almost unknown and have been omitted from this analysis. Our discussion is devoted, instead, to the best known, more northerly faunas from the Urals, the northeastern and central parts of the East European Platform, the Central European Basin, the Svalbard Archipelago, central East Greenland and the Sverdrup Basin, all of which were included in the *Calophyllum* Province by FEDOROWSKI & BAMBER (in press).

Stratigraphic correlations within the *Calophyllum* Province, discussed at the beginning of this paper, indicate a mainly Wordian or early Capitanian age for strata containing rugose corals comparable to those from the Degerböls and Trold Fiord formations of the Sverdrup Basin. Related coral faunas range at least as low as the Middle Artinskian, and all genera to which these corals are assigned have long stratigraphic ranges, rarely extending into the Lower Carboniferous (e.g., *Ufimia*).

The most diversified and abundant non-dissepimental Rugosa were described from the Urals and adjacent areas to the west and southwest. Those investigations, summarised by SOSHKINA *& al.* (1941), remain the most complete contribution to our knowledge of Artinskian and Kazanian corals of that area. Although their paper (*Ibid.*) contains many taxonomic misinterpretations, their illustrations allow modern classification of the fauna. Some of the Uralian taxa were restudied by ILINA (1984) but her approach to the taxonomy, especially on the generic level, is mostly unacceptable to us (see discussion of *Tachylasma*). The new information provided by her, however, especially on the septal microstructure and early ontogeny of many taxa, supplements our knowledge of those taxa and aids in their re-interpretation. WEYER (1982) revised "*Plerophyllum*" *variabile* SOSHKINA, 1941, summarised data from all rugose coral occurrences in the "Kazanian Sea" (WEYER 1997) and critically discussed all Kazanian taxa from the northern and eastern part of the East European Platform.

Most rugose coral faunas from the Urals and adjacent areas to the west disappeared before the end of the Artinskian, and no corals have been reported from strata of the overlying, strongly regressive Kungurian stage. Thus, a direct, overall comparison of the corals of this area with the other faunas mentioned above is impossible. In the earlier papers on the area, beginning with the classic study by NECHAEV (1894), the following species names have been applied: *Polycoelia profunda* (GEINITZ 1842) (first identified by NECHAEV, 1894 under that name); *Petraia permiana* NECHAEV, 1894; *Polycoelia baytuganense* SOSHKINA, 1941; *Polycoelia negativa* SOSHKINA, 1941; *Polycoelia rossica* SCHINDEWOLF, 1942; *Plerophyllum variabile* SOSHKINA, 1941 and several other taxa, commonly left in open nomenclature. Subsequently, several authors (FOMICHEV 1953a, b; IVANOVSKY 1972, 1989; WEYER 1979, 1982, 1984, 1997; WEYER & ILINA 1979; FEDOROWSKI 1982; ILINA 1984) have proposed various synonymy schemes at the species and genus level. From their descriptions and discussions and from our own observations, we conclude that only two or three species truly occur in the lower Kazanian of the area. These are: *Calophyllum columnare* (SCHLOTHEIM 1813), with *P. permiana, P. baytuganense* and *P. rossica* as its synonyms; the inadequately known *Calophyllum negativum* (SOSHKINA 1941), which may be treated as either a separate species or as a synonym of *C. columnare* and *Tachylasma variabilis* (SOSHKINA 1941). Our revision of some inadequately described specimens from the FLÜGEL (1973a) collection (see above) shows that the latter species occurs in East Greenland as well. Thus, of the species occurring on the Eastern European Platform, *T. variabilis* appears to rank next to *C. columnare* as a stratigraphic and paleogeographical marker for the *Calophyllum* Province (Table 1, Text-fig. 1) (FEDOROWSKI & BAMBER, in press).

Among the rugose coral faunas of the *Calophyllum* Province, that of East Greenland is perhaps the richest and most diversified. *Calophyllum columnare*, first described and dominant in the Central European Zechstein (See WEYER 1979 for summary of occurrence), was also the dominant species in East Greenland and on the East European Platform, if the synonymies proposed by FEDOROWSKI (1982) and herein are accepted. Also, this species is present in the Svalbard Archipelago and the Sverdrup Basin, thus being the most widely distributed and commonly the most abundant species in the middle part of the Guadalupian of the *Calophyllum* Province. Thus, *C. columnare* is characteristic at this stratigraphic level over a broad area beginning in the mid-eastern and northeastern parts of the East European Platform and extending through the Central European Basin, the Svalbard Archipelago, central East Greenland and into at least the Sverdrup Basin and perhaps Alaska (FEDOROWSKI & BAMBER, *Ibid.*; FEDOROWSKI *& al.* 1999, p. 168, 169). It has not been possible, however, to establish the precise age limits of this species within the middle Guadalupian, as discussed in the biostratigraphy section of this paper.

The genera *Allotropiochisma* and *Euryphyllum* are widespread from the Svalbard Archipelago through central East Greenland to the Sverdrup Basin. They are represented by a diversified group of species, mostly restricted to individual basins. Both genera are present in the Diffingiina Province of southwestern Texas, but occur only in Lower Permian strata. Thus, the connection between the southern species and those to the north in the *Calophyllum* Province is uncertain. The problem of a direct relationship between Australian and North American/Greenland euryphylla has been discussed above in the remarks on the genus *Euryphyllum*, where we indicate the possibility of the existence of common roots for species included in this genus from both realms.

Allotropiochisma, reported by EZAKI & KAWAMURA (1992) from Unit 11, near the top of the Kapp Starostin Formatin, is the youngest Permian rugose coral in Vestspitsbergen. The relative ages of the genera reported from East Greenland is not evident. Most of the taxa described from that area by FLÜGEL (1973a), including *Allotropiochisma* (= *Amplexizaphrentis* and *Bradyphyllum* of FLÜGEL 1973a) were derived from the so-called "*Productus* Limestone", a unit of coquina beds approximately two meters thick within the Wegener Halvø Formation. It has been established, however, that the species listed by FLÜGEL (1973a) (revised, in part, by FEDOROWSKI (1982) and in this paper) constitute the youngest Permian coral fauna present in Greenland. Also, *Allotropiochisma* and associated genera in the Sverdrup Basin (Table 1) comprise the youngest Permian coral fauna known from arctic Canada.

The palaeogeographic implications of the uneven distribution pattern shown by species within the *Calophyllum* Province were briefly discussed by FEDOROWSKI & BAMBER (in press) and are summarized here. As discussed above, the strongest development of the mid-Guadalupian coral fauna occurs in East Greenland, with comparable diversity and taxonomic content in Svalbard and the Sverdrup Basin (Table 1). Similarity between the faunas of these three areas is predictable from their geographic proximity shown in several paleogeographic reconstructions of the area (e.g., Text-fig. 1; GOLONKA & *al.* 1994, Figs 37, 78) and the resulting likelihood of open marine communication between them.

In contrast to the three areas discussed above, the more isolated Central European Basin and Eastern European Platform show very low coral diversity, probably strongly influenced by episodic natural coral occurrences and by the mid-Guadalupian paleogeography of the area (Table 1, Text-fig. 1). Only *Calophyllum columnare* (SCHLOTHEIM, 1813) and possibly one other species of that genus occur in the Central European Basin. Such unusually low diversity reflects two factors: the mainly restricted marine conditions represented by evaporitic deposits overlying the thinner, coral-bearing, normal marine carbonates of the lower Zechstein; and the severe limitations on faunal exchange with other marine areas of the province, caused by the relative isolation of the Zechstein Sea. Slightly higher diversity is shown by the fauna of the Eastern European Platform, where *C. columnare* is accompanied by *Tachylasma variabilis* (SOSHKINA, 1941) and possibly very few other, poorly understood taxa in the Kazanian succession, which contains abundant siliciclastic deposits. For more detailed distribution data, the reader is referred to papers by WEYER (1979, 1997). The taxonomic poverty of this area, as in the Central European Basin to the west, indicates scarcity of favourable marine habitats and a low level of faunal exchange with more open marine areas to the west (Text-fig. 1).

Of the more numerous species living in the open marine areas, it appears that only those few with the most persistent, long-lived larvae were able to reach the peripheral embayments in which the Zechstein and Kazanian successions were deposited. There, they developed morphologically variable, local populations that were rich in individuals but taxonomically monotonous. *Calophyllum columnare*, which occurs throughout the province, was the most successful of these species and was the most plastic, genetically. It produced numerous morphotypes showing variation in the arrangement and thickness of their septa, different corallite dimensions and n:d values and, most importantly, a very specific mode of asexual reproduction in response to the muddy areas in which some of them lived. FLÜGEL (1973a) assigned the latter ecotype to his new genus *Groenlandophyllum*, which we do not recognize [See our discussion of *Calophyllum*, above, and that by FEDOROWSKI (1982)]. *Tachylasma variabilis* may have displayed genetic plasticity similar to *C. columnare* (e.g., WEYER 1982, Pls 1-5), but was less widespread geographically. It may well be another reliable stratigraphic marker for the Wordian-lower Capitanian (= lower Kazanian) within the area from the eastern margin of the East European Platform to East Greenland. Other species are of more local value because of their restricted geographical distribution.

APPENDIX

Geological Survey of Canada (GSC) collecting localities, Sverdrup Basin.

GSC locality 73156 – approximately 6.5 km northwest of Tingmisut Lake, Sabine Peninsula, Melville Island, 76°00'20"N, 108°00'00"W; Text-figure 2, locality 5; middle part of Trold Fiord Formation, 130 m above base.

GSC locality C-10457 – Van Hauen Pass, Ellesmere Island, 81°04'N, 85°40'W. Text-fig. 2, locality 1; 7.9-10 m above base of Degerböls Formation, type section.

GSC locality C-10459 – location as for GSC locality C-10457, 40.6 m above base of Degerböls Formation.

GSC locality C-10460 – location as for GSC locality C-10457, 52.7 m above base of Degerböls Formation.

GSC locality C-10461 – location as for GSC locality C-10457, 66.5 m above base of Degerböls Formation.

GSC locality C-10462 – location as for GSC locality C-10457, 109.2 m above base of Degerböls Formation.

GSC locality C-10464 – location as for GSC locality C-10457, 136.6 m above base of Degerböls Formation.

GSC locality C-10470 – location as for GSC locality C-10457, talus from lower 3 m of Degerböls Formation.

GSC locality C-32504 – East Cape River, north side of Canyon Fiord, Ellesmere Island, 80°02'15"N, 81°47'30"W. Text-fig. 2, locality 3; lower Trold Fiord Formation, type section, 57.3 m above base.

GSC locality C-82314 – Notch Lake, Sawtooth Range, Ellesmere Island, 79°31'N, 83°21'W. Text-fig. 2, locality 4; lower Trold Fiord Formation, collected between 127 m and 142 m above base.

GSC locality C-82471 – North of McKinley Bay, Ellesmere Island, 81°10'N, 79°08W. Text-fig. 2, locality 2; lower Trold Fiord Formation, 23 m above base.

GSC locality C-82473 – location as for GSC locality C-82471, lower Trold Fiord Formation, 33 m above base.

REFERENCES

BAMBER, E.W. & WATERHOUSE, J.B. 1971. Carboniferous and Permian stratigraphy and paleontology, northern Yukon Territory, Canada. *Bulletin of Canadian Petroleum Geology*, **19**, 29-250. Calgary.

BEAUCHAMP, B. 1995. Permian history of Arctic North America. *In*: P.A. SCHOLLE, T.M. PERYT & D.S. ULMER-SCHOLLE (*Eds*), The Permian of northern Pangea, vol. 2, Sedimentary basins and economic resources, 1-22. *Springer-Verlag*; Berlin – Heidelberg.

BEAUCHAMP, B. & DESROCHERS, A. 1997. Permian warm- to very cold-water carbonates and cherts in northwestern Pangea. *In*: N.P. JAMES & J.A.D. CLARK (*Eds*), Cool-water carbonates, *Society of Sedimentary Geology, Special Publication* **56**, 327-347. Tulsa.

BEAUCHAMP, B., HARRISON, J.C. & HENDERSON, C.M. 1989. Upper Paleozoic stratigraphy and basin analysis of the Sverdrup Basin, Canadian Arctic Archipelago: Part 2, transgressive-regressive sequences. *In*: Current Research, Part G, *Geological Survey of Canada, Paper* **89-1G**, 115-124. Ottawa.

BRABB, E.E. & GRANT, R.E. 1971. Stratigraphy and paleontology of the revised type section for the Tahkandit Limestone (Permian) in east-central Alaska. *United States Geological Survey Professional Paper*, **703**, 26 pp. Washington.

CAO X.-DUO, OUYANG X. & JIN T.-A. 1983. Rugosa. *In*: Paleontological Atlas of northwest China. Shaanxi, Gansu and Ningxia volume. Pt. II. Upper Palaeozoic. *Geological publishing House*, pp. 46-179. Beijing. [*In Chinese*]

CARRUTHERS, R.G. 1919. A remarkable Carboniferous coral. *The Geological Magazine*, **6** (1), 436-441. London.

CHI, Y.S. 1937. Simple corals from the Permian of Yungsin, Kiangsi. *Bulletin of the Geological Society of China*, **17** (1), 83-109, Nanking.

DOBROLYUBOVA, T.A. 1940. Rugose corals of the Upper Carboniferous of the Moscow Basin. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, **9** (3), 1-87. Moskva. [*In Russian*]

DUNBAR, C.O. 1955. Permian brachiopod faunas of central East Greenland. *Meddelelser om Grönland*, **110**, 1-169. Copenhagen.

EZAKI, Y. 1991. Permian corals from Abadeh and Julfa, Iran, West Tethys. *Journal of the Faculty of Sciences, Hokkaido University*, **23** (1), 53-146. Sapporo.

EZAKI, Y. & KAWAMURA, T. 1992. Carboniferous-Permian corals from Skansen and Festningen, Central Spitsbergen: their faunal characteristics. *In:* K. Nakamura (*Ed.*), Investigations on the Upper Carboniferous-Upper Permian Succession of West-Spitsbergen by Japanese-Norwegian Research Group. *Hokkaido University*, pp. 59-75. Sapporo.

FEDOROWSKI, J. 1973. Rugose corals Polycoelaceae and Tachylasmatina subord. n. from Dalnia in the Holy Cross Mts. *Acta Geologica Polonica*, **23** (1), 89-133. Warszawa.

— 1974. The Upper Palaeozoic tetracoral genera *Lophophyllidium* ad *Timorphyllum*. *Palaeontology*, **17** (3), 441-473. London.

— 1982. Some rugose corals from the Upper Permian of East Greenland. *Rapport Grønlands geologiske Undersøgelse*, **108**, 71-91. Copenhagen.

— 1986. Permian rugose corals from Timor (Remarks on SCHOUPPE & STACUL's collections and publications from 1955 and 1959). *Palaeontographica Abt. A*, **191**, 173-226. Stuttgart.

— 1987. Upper Palaeozoic rugose corals from southwestern Texas and adjacent areas: Gaptank Formation and Wolfcampian corals. part 1. *Palaeontologia Polonica*, **48**, 1-271. Warszawa.

— 1991. Principles of early ontogeny in the rugose corals: a critical review. *Hydrobiologia*, **216/217**, 413-418. Dordrecht.

— 1997a. Remarks on the palaeobiology of Rugosa. *Geologos*, **2**, 5-58. Wrocław.

— 1997b. Diachronism in the development and extinction of Permian Rugosa. *Geologos*, **2**, 59-164. Wrocław.

FEDOROWSKI, J., BAMBER, E.W. & STEVENS, C.H. 1999. Permian corals of the Cordilleran-Arctic-Uralian Realm. *Acta Geologica Polonica*, **49** (2), 159-173. Warszawa.

FEDOROWSKI, J. & BAMBER, E.W. in press. Paleogeographic and biostratigraphic significance of Guadalupian (Middle Permian) solitary corals, Sverdrup Basin, arctic Canada. XIV International Congress on the Carboniferous and Permian, Proceedings, Calgary 1999.

FLÜGEL, H.W. 1973a. Rugose Korallen aus dem oberen Perm

Ost-Grönlands. *Verhandlungen der geologischen Bundesanstalt*, **1**, 1-57. Wien.

— 1973b. Zur Kenntnis des Typus von *Calophyllum* DANA, 1846: *Turbinolia donatiana* KING 1848 (Anthozoa). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2**, 61-66. Stuttgart.

FOMICHEV, V.D. 1953a. Rugose corals and stratigraphy of Middle and Upper Carboniferous and Permian deposits of the Donets Basin. *Trudy Vsesoyuznogo Nauchno-Issledovatelskogo Geologicheskogo Instituta (VSEGEI)*, pp. 1-622. Moskva. [*In Russian*]

— 1953b. Permian rugose corals from the Far-East. *Trudy Vsesoyuznogo Nauchno-Issledovatelskogo Geologicheskogo Instituta (VSEGEI)*, pp. 1-71. Moskva. [*In Russian*]

GEINITZ, H.B. 1842. Über einige Petrefakte des Zechsteins un Muschelkalks. *Neues Jahrbuch für Mineralogie, Geologie und Petrefacten-Kunde*, pp. 578-579. [*Not seen*]

GOLONKA, J., ROSS, M.I. & SCOTESE, C.R. 1994. Phanerozoic paleogeographic and paleoclimatic modeling maps. *In*: A. F. EMBRY, B. BEAUCHAMP & D.J. GLASS (*Eds*), Pangea: global environments and resources. *Canadian Society of Petroleum Geologists Memoir*, **17**, 1-47. Calgary.

GROOT, G.E., DE. 1963. Rugose corals from the Carboniferous of northern Valencia (Spain). *Leidse Geologische Mededelingen*, **29**, 1-123. Leiden.

GRABAU, A.W. 1922. Palaeozoic corals of China, Part 1, Tetraseptata. *Palaeontologia Sinica*, B, **2** (1), 1-76. Peking.

— 1928. Palaeozoic corals of China. part 1. Tetraseptata. *Palaeontologia Sinica*, B, **2**, 1-175. Peiping.

GUO S.-Z. 1976. Tetracoralla. *In*: Paleontological atlas of the north China region, Inner Mongolia. Paleozoic volume. *Geological Publishing House*, pp. 63-101, Beijing. [*In Chinese*]

— 1980. Tetracoralla. In: Paleontological atlas of northeast China. Paleozoic volume. *Geological Publishing House*, pp. 106-153. Beijing. [*In Chinese*]

HENDERSON, C.M. & MEI SHI-LONG. 2000. Preliminary cool water Permian conodont zonation in North Pangea: a review. *Permophiles*, **36**, 16-23. Boise.

HERITSCH, F. 1939. Die Korallen des Jungpaläozoikums von Spitsbergen. *Arkiv för Zoologi*, **31A**, **16**, 1-138. Stockholm.

HILL, D. 1938. *Euryphyllum*: A new genus of Permian zaphrentoid rugose corals. *Proceedings of the Royal Society of Queensland*, **49**, 23-28. Brisbane.

— 1943. Further Permian corals of Western Australia. *Journal of the Royal Society of Western Australia*, **27**, 57-75. Perth.

— 1981. Coelenterata, Supplement 1, Rugosa and Tabulata. *In*: C. TEICHERT (*Ed.*), Treatise on Invertebrate Paleontology, Part F. *Geological Society of America and University of Kansas Press*, pp. F1-F762. Lawrence.

HOWSE, R. 1848. Catalogue of fossils; Permian System of the Counties of Northumberland and Durham. *Transactions of the Tyneside Nature Field Club*, **1**, 1-47. Newcastle-upon-Tyne. [*Not seen*]

HUDSON, R.G.S. 1936a. On the Lower Carboniferous corals *Rhopalolasma*, gen. nov. and *Cryptophyllum* CARR. *Proceedings of the Yorkshire Geological Society*, **23** (2), 1-12. Warfield.

— 1936b. The development and septal notation in the Zoantharia, Rugosa (Tetracoralla). *Proceedings of the Yorkshire Geological Society*, **23**, 68-78, Warfield.

— 1941. On the Carboniferous corals: *Zaphrentis carruthersi* sp. nov. from the Mirk Fell Beds and its relation to the *Z. delanouei* species group. *Proceedings of the Yorkshire Geological Society*, **23** (4), 290-311. Warfield.

— 1944. On the Lower Carboniferous corals: *Zaphrentites crassus* and *Z. tenuis* spp. n. *The Annals and Magazine of Natural History*, 11, **75**, 145-154, Hertford.

IGO, H. 1959. Note on some Permian corals from Fukuji. Hida Massif, Central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan*,**34**, 79-85. Tokyo.

ILINA, T.G. 1965. Late Permian and early Triassic Tetracoralla from Transcaucasus. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **107**, 1-104. Moskva. [*In Russian*]

— 1984. Historical development of corals. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **198**,1-184. Moskva. [*In Russian*]

IVANOVSKY, A.B. 1972. Intraspecific variability, morphology and ontogeny of the skeleton of *Calophyllum profundum* (Rugosa). *In*: A.S. DAGIS & A.B. IVANOVSKY (*Eds*), Morphological and phylogenetic questions of paleontology. *Trudy Instituta Geologii i Geofiziki*, **112**, 4-9. Moskva. [*In Russian*]

— 1989. Solitary Rugosa from the Upper Permian of eastern Russian Platform. *In*: A.S. DAGIS & V.N. DUBATOLOV (*Eds*), Upper Paleozoic and Triassic of Siberia. *Trudy Instituta Geologii i Geofiziki im. 60-letya Soyuza SSR*, **732**, 31-39. Novosibirsk. [*In Russian*]

JEFFORDS, R.M. 1947. Pennsylvanian lophophyllid corals. *The University of Kansas Paleontological Contributions.* **1** (Coelenterata 1), 1-84. Lawrence.

KABAKOVICH, N.V. 1952. New species of the genus *Tachylasma* from the Lower Carboniferous of the Moscov Basin.*Trudy Paleontologicheskogo Instituta AN SSSR*, **40**, 115-126. Moskva. [*In Russian*]

KING, W. 1848. A catalogue of the organic remains of the Permien rocks of Northumberland and Durham. 1-16. Newcastle-upon-Tyne. [*Not seen*]

— 1850. A monograph of the Permian fossils of England. *Palaeontographical Society of London*, **3**, 1-258. London.

KORA, M. 1989. Lower Carboniferous (Viséan) fauna from Wadi Budra west-central Sinai, Egypt. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **9**, 523-538. Stuttgart.

KORA, M. & JUX, U. 1986. On the early Carboniferous macrofauna from the Um Bogma Formation, Sinai. *Neues*

Jahrbuch für Geologie und Paläontologie, Monatshefte, **2**, 85-98. Stuttgart.

Kora M. & Mansour, Y. 1991. Late Carboniferous solitary rugose corals from the western side of the Gulf of Suez, Egypt. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **10**, 597-614. Stuttgart.

Kossovaya, O.L. 1997. Rugosa of the typical sections of the Gzhelian-Artinskian stages of northern Timan and the western slope of the Urals. *In*: G.A. Stukalina (*Ed.*), Atlas of standard complexes of Palaeozoic benthonic fauna of northeastern European Russia. *P. Karpinskyi All-Russian Scientific-Research Geological Institute (VSEGEI)*, pp. 53-96. St. Petersburg. [*In Russian*]

Kullmann, J. 1965. Rugose Korallen der Cephalopodenfazies und ihre Verbreitung im Devon des südöstlichen Kantabrischen Gebirges (Nordspanien). *Akademie der Wissenschaften und der Literatur. Abhandlungen der matematisch-wissenschaftlichen Klasse*, **2**, 1-136. Wiesbaden.

— 1966. Goniatiten-Korallen-Vergesellschaftungen im Karbon des Kantabrischen Gebirges (Nordspanien). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **125**, 443-466. Stuttgart.

Lang, W.D., Smith, S. & Thomas, H.D. 1940. Index of Palaeozoic coral genera. *British Museum*, pp. 1-231. London.

Lavrusevich, A.I. 1968. Rugosa of Post-Ludlov deposits of the Zarawshan River Valley (Central Tadzhykistan). *In*: B.S. Sokolov & A.B. Ivanovsky (*Eds*), Biostratigraphy of Silurian/Devonian boundary deposits. *Nauka*, pp. 102-128. Moskva. [*In Russian*]

Ludwig, R. 1865-1866. Korallen aus paläolitischen Formationen. *Palaeontographica*, **14**, 133-244, Stuttgart.

— 1869. Korallenstöcke aus paläolitischen Formationen. *Palaeontographica*, **17**, 129-135. Stuttgart.

Mei Shi-Long, Henderson, C.M. & Jin Yu-Gan. 1999. Permian conodont provincialism, zonation and global correlation. *Permophiles*, **35**, 9-16. Boise.

Moore, R.C. & Jeffords, R.M. 1941. New Permian corals from Kansas, Oklahoma, and Texas. *State Geological Survey of Kansas Bulletin*, **38**, 65-120. Lawrence.

— & — 1945. Description of Lower Pennsylvanian corals from Texas and adjacent states. *University of Texas Publication*, **4401**, 77-208. Austin.

Nakamura, K., Tazawa J. & Kuman, F. 1992. Permian brachiopods of the Kapp Starostin Formation, west Spitsbergen. *In*: K. Nakamura (*Ed.*), Investigations on the Upper Carboniferous-Upper Permian succession of West Spitsbergen 1989-1991. Hokkaido University, 77-95. Sapporo.

Nassichuk, W.W. 1995. Permian ammonoids in the arctic regions of the world. *In*: The Permian of northern Pangea, P.A. Scholle, T.M. Peryt & D.S. Ulmer-Scholle (*Eds*), vol. 1: Paleogeography, Paleoclimates, Stratigraphy, 210-235. Springer-Verlag. Berlin – Heidelberg.

Nechaev, A.N. 1894. Fauna of Permian deposits of eastern part of European Russia. *Trudy Obshchestva Estestvie-ispytatelei Imperatorskogo Kazanskogo Universiteta*, **27**, 1-503. Kazan. [*In Russian*]

Niermann, H.T. 1975. Polycoeliidae aus dem Oberperm von Basleo auf Timor. *Münstersche Forschungen zur Geologie und Paläontologie*, **37**, 131-225. Münster.

Oekentorp, K. 1980. Aragonit und Diagenese bei jungpaläozoischen Korallen. *Münstersche Forschungen zur Geologie und Paläontologie*, **52**, 119-239. Münster.

Peng, X.-D., Lin, Y.-D. & Li, Y., 1992. The Late Carboniferous strata and coral fauna in southern part of North platform of China. *In:* Lin, Y.-D., Huang, Z.-X., Wu, S.-Z. & Peng, X.-D. (*Eds*) Professional papers of Carboniferous corals of China. *Jilin Science and Technology Press*, pp.113-151. Jilin. [*In Chinese with English summary*]

Rasmussen, J.A., Piasecki, S., Stemmerik, L. & Stouge, S. 1990. Late Permian conodonts from central East Greenland. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **178**, 309-324. Stuttgart

Rodriguez, S. 1984. Corales Rogosos del Carbonifero del Este de Asturias. Ph.D. thesis, published by *Departmento de Paleontologia, Universidad Complutense de Madrid*. Doctoral thesis collection no. 109/84, 1-328.

Rowett, C.L. & Sutherland, P.K. 1964. Biostratigraphy and rugose corals of the Lower Pennsylvanian Wapanuka Formation in Oklahoma. *Oklahoma Geological Survey Bulletin*, **104**, 1-124.

Różkowska, M. 1969. Famennian tetracoralloid and heterocoralloid fauna from the Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica*, **14** (1), 5-187. Warszawa.

Schindewolf, O.H. 1940. "Konvergenzen" bei Korallen und bei Ammoneen. *Fortschrift für Geologie und Palaeontologie*, **12** (41), 389-492. Berlin.

— 1942. Zur Kenntnis der Polycoelien und Plerophyllen. Eine Studie uber den Bau der "Tetrakorallen" und ihre Beziehungen zu den Madreporarien. *Abhandlungen des Reichsamtes für Bodenforschung*, **204**, 1-324. Berlin.

— 1952. Korallen aus dem Oberkarbon (Namur) des oberschlesischen Steinkohlen-Beckens. *Akademie der Wissenschaften und der Literatur. Abhandlungen der matematisch-naturwissenschaftlichen Klasse*, **4**, 143-227. Wiesbaden.

Schlotheim, E.F. von. 1813. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. *In*: C.C. Leonhard: Taschenbuch für die gesamte Mineralogie mit Hinsicht auf die neuesten Entdeckungen, Frankfurt a. M., Jahrgang **7** (1), 3-134. Frankfurt am Main.

Sokolov, B.S. 1960. Permian corals of the southeastern part of the Omolon Massif (with special attention to plerophyllid Rugosa). *Trudy Vsesoyuznogo neftyanogo nauchno-*

geologicheskogo Instituta (VNIGRI), 154, 38-77. Leningrad. [*In Russian*]

Soshkina, E.D. 1925. Les coraux du Permien inférieur (étage d'Artinsk) du versant occidental de l'Oural. *Bulletin de la Société des Naturalistes de Moscou, Section Géologique*, **33**, 76-104. Moskva.

Soshkina, E.D., Dobrolyubova, T.A. & Porfiriev, G.S.. 1941. Permian Rugosa of the European part of the USSR. *Paleontologia SSSR*, **5**, 3, 1, 1-304. Moskva-Leningrad. [*In Russian*]

Sorauf, J. 1984. Upper Permian corals from Timor and diagenesis. *Palaeontographica Americana*, **54**, 294-302.

Stemmerik, L. 1995. Permian history of the Norwegian-Greenland Sea area. *In*: P.A. Scholle, T.M. Peryt & D.S. Ulmer-Scholle (*Eds*.), The Permian of northern Pangea, vol. 2, Sedimentary basins and economic resources, pp. 88-118. *Springer-Verlag*; Berlin – Heidelberg.

Stuckenberg, A.A. 1895. Corals and bryozoans from the Carboniferous deposits of the Urals and Timan. *Trudy Geologicheskogo Komiteta*, **10**, 1-244. St. Petersburg. [*In Russian and German*]

Thorsteinsson, R. 1974. Carboniferous and Permian stratigraphy of Axel Heiberg Island and western Ellesmere Island, Canadian Arctic Archipelago. *Geological Survey of Canada, Bulletin*, **224**, 1-115. Ottawa.

Tidten, G. 1972. Morphogenetisch-ontogenetische Untersuchungen an Pterocorallia aus dem Permo-Karbon von Spitzbergen. *Palaeontographica*, **A**, **139**, 1-63. Stuttgart.

Toula, F. 1875. Permo-Karbon-Fossilien von der Westküste von Spitzbergen. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* (for 1875), *225-264*. Stuttgart.

Utting, J. 1994. Palynostratigraphy of Permian and Lower Triassic rocks, Sverdrup Basin, Canadian Arctic Archipelago. *Geological Survey of Canada, Bulletin* **478**, 1-106. Ottawa.

Vassilyuk, N.P. 1960. Nizhnekamennougolnye korally Doneckogo Basseina. *Trudy Instituta Geologicheskikh Nauk Akademii Nauk Ukrainskoi SSR*, **13**, 1-179. Kiev. [*In Russian*]

Vaughan, A. 1906. Faunal lists and account of the faunal succession and correlation. *In*: C.A. Matley & A.Vaughan, The Carboniferous rocks at Rush (County Dublin). *Quarterly Journal of the Geological Society of London*, **62**, 295-322. London.

Wang, Z.-J. & Liu, S.-K. 1982. Early Lower Permian rugose corals from the Saga, Zhongba and Namuco areas of Xizang. In: Contribution to the geology of the Qinghai – Xizang (Tibet) Plateau, **7**, 59-85. *Geological Publishing House*, Beijing.

Wang, Z.-J. & Yu, X.-G. 1986. Early Late Carboniferous corals from Jinghe of Xinjiang. *Acta Palaeontologica Sinica*, **25**, 6, 657-662, Nanjing.

Waterhouse, J.B. & Waddington J. 1982. Systematic descriptions, paleoecology and correlations of the Late Paleozoic subfamily Spiriferellinae (Brachiopoda) from the Yukon Territory and the Canadian Arctic Archipelago. *Geological Survey of Canada, Bulletin*, **289**, 1-72, Ottawa.

Weyer, D. 1965. Über *Amplexus zaphrentiformis* White, 1876 Pterocorallia, Oberkarbon, Pennsylvanian). *Geologie*, **14** (4), 449-463. Berlin.

— 1973. Einige Rugose Korallen aus der Erbslochgrauwacke (Unterdevon) des Unterharzes. *Zeitschrift für geologischen Wissenschaften*, **1**, 45-65. Berlin.

— 1974. Der Rugosa-Genus *Antiphyllum* Schindewolf, 1952 (Unternamur, Oberschlesisches Steinkohlenbecken). *Časopis pro mineralogii a geologii*, **19** (4), 345-365. Praha.

— 1979. Korallen-Funde im europaischen Zechstein-Meer. *Zeitschrift für geologische Wissenschaften*, **7** (8), 981-1021. Berlin.

— 1981. Revision von *Pseudobradyphyllum* Dobrolyubova, 1940 (Anthozoa, Rugosa; Oberkarbon). *Abhandlungen und Berichte für Naturkunde Vorgeschichte (Kulturisches Museum Magdeburg)*, **12** (3), 3-21. Magdeburg.

— 1982. *Paracaninia variabilis* (Soshkina, 1941) aus dem Kazanian der Russischen Platform (Anthozoa, Rugosa, Mittelperm). *Abhandlungen und Berichte für Naturkunde Vorgeschichte (Kulturisches Museum Magdeburg)*, **12** (4), 65-78. Magdeburg.

— 1984. Korallen im Paläozoikum von Thüringen. *Hallesches Jahrbuch für Geowissenschaften*, **9**, 5-33. Gotha.

— 1997. Korallen im oberpermischen Kazan-Meer von Russland. *Freiberger Forschungsheft*, **C** **466**, 85-107. Freiberg.

Weyer, D. & Ilina, T.G. 1979. Die permischen Rugosa-Genera *Pleramplexus* und *Pentamplexus*. *Zeitschrift für geologische Wissenschaften*, **7** (11), 1315-1341. Berlin.

Wu, W.-S. 1975. The coral fossils from the Qomolangma Feng region. *In*: Qomolangma (Mt. Everest) Scientific Reports. Part I. Palaeontology. *Scientific Press*, 83-113, Beijing. [*In Chinese*]

— & — 1989. Carboniferous and early early Permian Rugosa from western Guizhou and eastern Yunnan, SW. China. *Palaeontologia Sinica*, **177**, 24, 1-230, Beijing. [*In Chinese with English summary*]

Xu, S.-Y. 1977 In: Jia H.-Z., Xu, S.-Y, Kuang, G.-D, Zgang, B.-F., Zhao, Z.-B. & Wu, J.-Z. Anthozoa. *In*: Palaeontological Atlas of central-south China. Pt. 2, Upper Palaeozoic. *Geological Publishing House,* pp. 109-241, Beijing. [*In Chinese*]

Xu, S.-Y. 1984. Coelenterata, Anthozoa. *In*: Biostratigraphy of the Yangtze Gorge area. **(3)** Late Palaeozoic area. *Geological Publishing House*, 177-203, Beijing. [*In Chinese*]

Yamagiwa, N. 1960. The Late Palaeozoic corals from Maizuru zone, Southwest Japan. *Memoirs of the Osaka University of Liberal Arts and Education. B. Natural Science,* **9**, 72-81, Osaka.

Zhao, J.-M. 1976. Late Permian rugose corals from Anshun, Luzhi and Quinglong, Guizhou Province. *Acta Palaeontologica Sinica*, **15**, 2, 213-222, Nanjing. [*In Chinese with English summary*]

— 1981. Permian corals from Beichuan and Jiangyou of Sichuan and from Hanzhong of Shaanxi. *Memoirs of Nanjing Institute of Geology and Palaeontology, Academia Sinica*, **15**, 233-274, Nanjing. [*In Chinese with English summary*]

ZHAO, J.-M. & ZHOU, G.D. 1987. Discovery of *Lytvolasma* fauna from western section of eastern Kunlun Mountains. *Acta Palaeontologica Sinica*, **26** (4), 486-491, Nanjing. [*In Chinese with English summary*]

ZHU, Z.-G., REN., R.-S, QI, D.-R., WU, W.-S., YAN, Y.-Y., YU, C.-M., YU, X.-G., ZHAO, J.-M, CHEN, H.-C, CHEN, M.-J. & LIAO, W.-H. 1982. Anthozoa, pp. 108-179. *In*: Palaeontological atlas of east China, 2. Late Paleozoic Era. *Geological Publishing House*, Beijing. [*In Chinese*]

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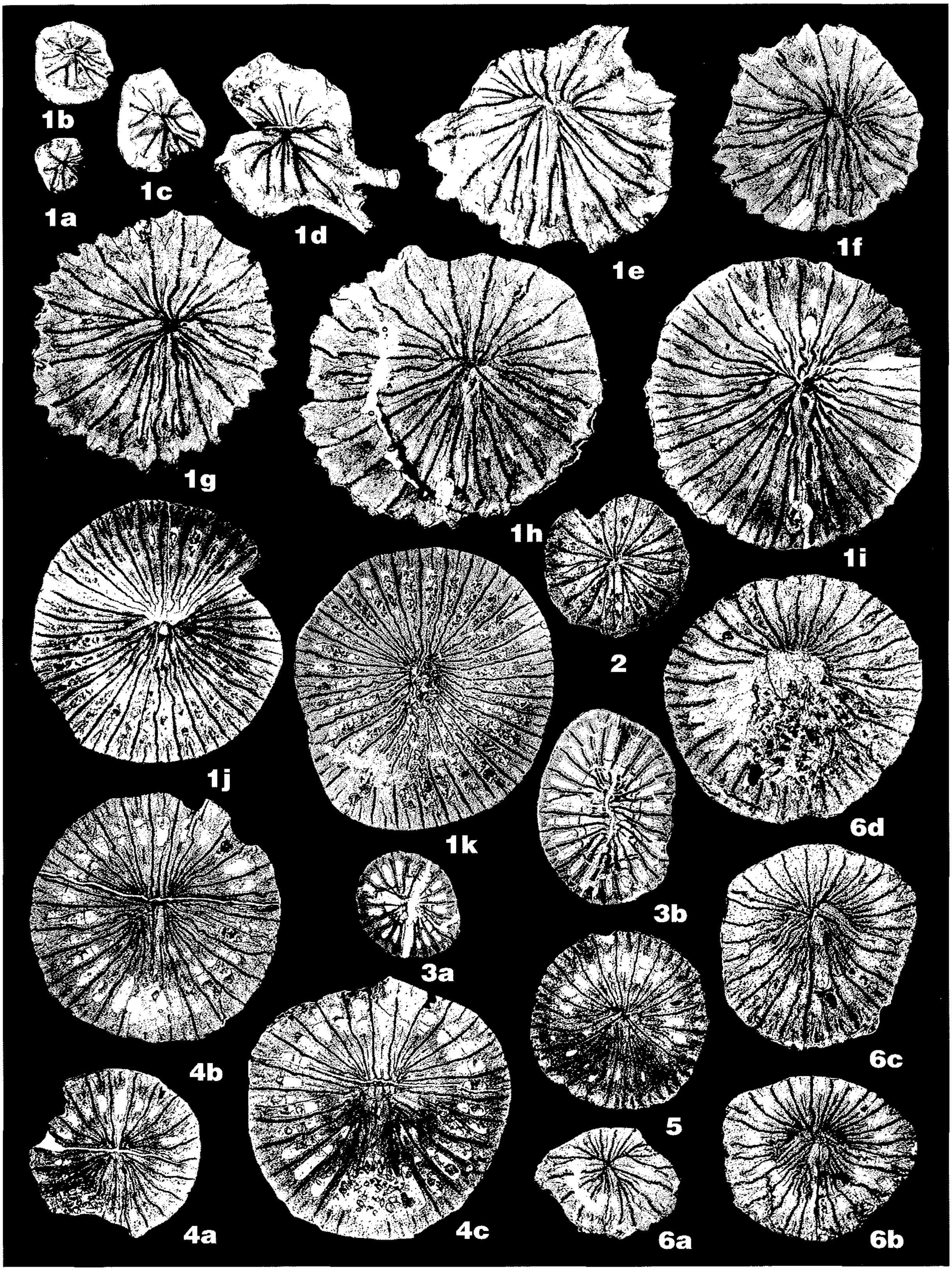
PLATE 1

Euryphyllum boreale sp. n.; transverse sections
(specimens from Degerböls Formation)

1 – GSC 117159, holotype; GSC locality C-10460, 52.7 m above base; a-d – early neanic stage (b = Text-fig. 4.1a; d = Text-fig. 4.1b), × 12; e-h – neanic stage, e × 12 (= Text-fig. 4.1c), f-h × 8, i – early mature stage, × 6 (= Text-fig. 4.1d), j – mature stage, sectioned above calice floor at periphery, × 4 (= Text-fig. 4.1e), k – lower part of calice, × 4 (= Text-fig. 4.1f).
2 – GSC 117164, paratype; GSC locality C-10461, 66.5 m above base; neanic stage, lower part of calice; × 4.
3 – GSC 117168, paratype; GSC locality C10470, talus from lower 3 m; a, b – early and late mature stages; × 4.
4 – GSC 117150. Paratype. GSC locality C-10459, 40.6 m above base, a - neanic stage (= Text-fig. 4.2a), b, c - mature stage, all x4 (= Text-figs. 4.2b, c).
5 – GSC 117153, paratype; GSC locality C-10459, 40.6 m above base; late neanic stage; × 4.
6 – GSC 117161, paratype; GSC locality C-10460, 52.7 m above base; a – neanic stage, × 6; b, c – early mature and mature stages, × 4; d – lower part of calice, × 4.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4c
6a
6b

PLATE 2

(Specimens from Degerböls Formation, unless stated otherwise)

1-2 – *Euryphyllum troldfiordense* sp. n.; transverse sections; GSC locality C-82314, Trold Fiord Formation, collected between 127 m and 142 m above base. 1 – GSC 117170, holotype; a – neanic stage (= Text-fig. 6.1a), × 6; b-d – mature stage, successive sections, with d immediately beneath calice (b = Text-fig. 6.1b; d = Text-fig. 6.1c) all × 3; e – lower part of calice (= Text-fig. 6.1d), × 3. 2 – GSC 117171, paratype; a-c – successive sections, early to late mature stage (b = Text-fig. 6.2a), d - middle part of calice (= Text-fig. 6.2c; from acetate peel); all × 4.

3, 5 - *Euryphyllum boreale* sp. n.; transverse sections; 3 – GSC 117158; paratype; GSC locality C-10459, 40.6 m above base; a, b – successive sections, mature stage; × 4. 5 – GSC 117160, paratype; GSC locality C-10460, 52.7 m above base; lower part of calice; × 4.

4 – *Allotropiochisma* (*Allotropiochisma*) sp., GSC 117165; GSC locality C-10462, 109.2 m above base; transverse sections; a, b – mature stage, sections partly (a) and almost completely (b) above calice floor (a = Text-fig. 7.2b), both × 2.

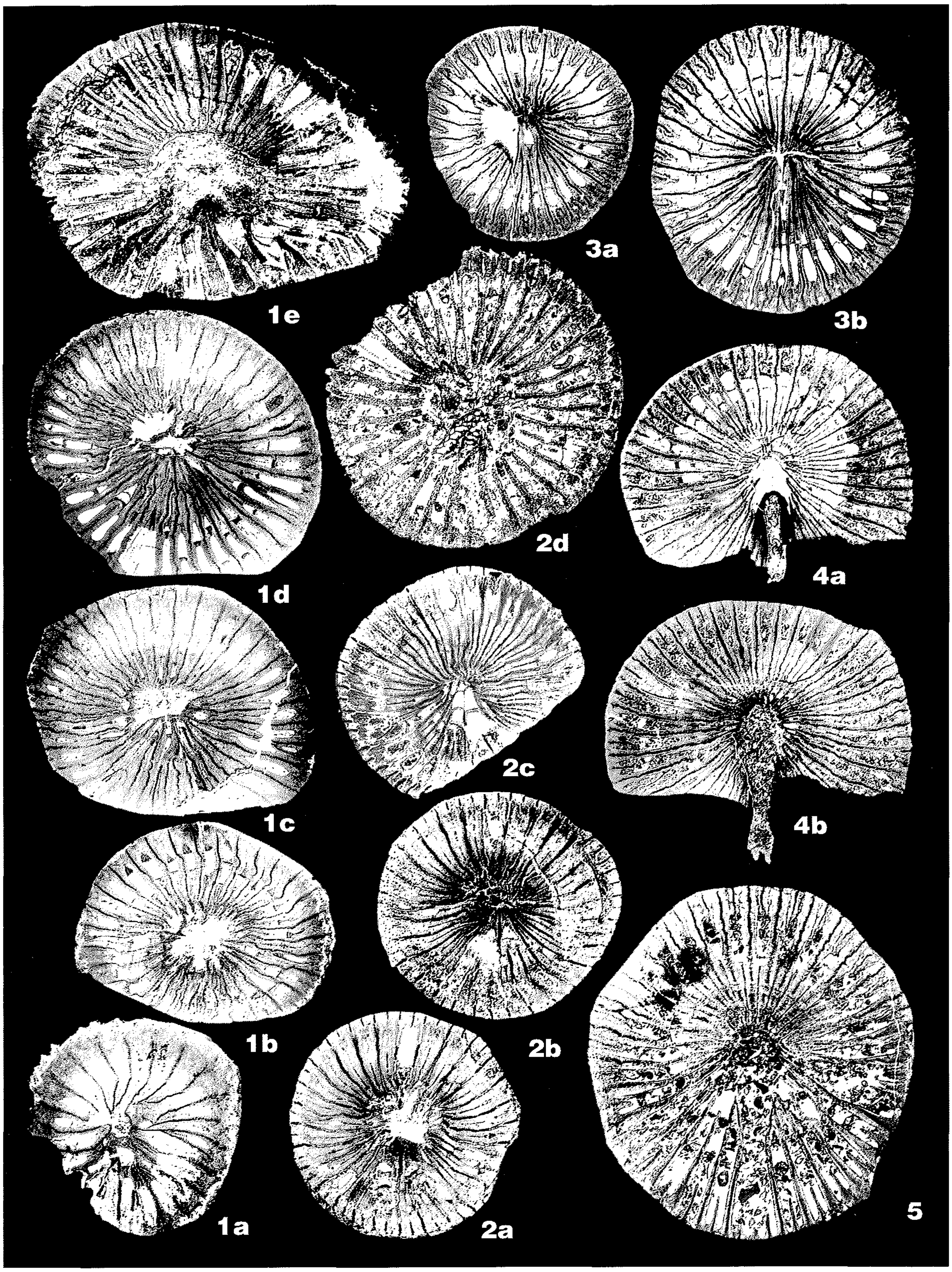
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PLATE 3

1 - *Allotropiochisma (Allotropiochisma) longiseptata* (FLÜGEL, 1973a), transverse sections, GSC 117176; GSC locality C-82473, Trold Fiord Formation, 33 m above base; a – late neanic stage (= Text-fig. 7.1a), b – early mature stage (= Text-fig. 7.1b), both × 3.
2 – *Lytvolasma canadense* sp. n., transverse sections, GSC 117166, holotype; GSC locality C-10464, Degerböls Formation, 136.6 m above base; a – late neanic stage; b – mature stage; c, d – calice (= Text-figs. 8.a-d); all × 4.
3-6 - *Calophyllum columnare* (SCHLOTHEIM 1813), transverse sections. 3 – GSC 117175; GSC locality C-82471, Trold Fiord Formation, 23 m above base; a – late neanic stage (= Text-fig. 10.2a), × 6; b – mature stage (= Text-fig. 10.2b), × 4. 4 – GSC 117173; GSC locality C-82314, Trold Fiord Formation, 127-142 m above base; mature stage, above calice floor, × 4. 5 – MMH 11942 (= *Hapsiphyllum* × sp. of FLÜGEL 1973a, p. 28), hypotype; East Greenland, Kap Stosch, "*Productus* limestone", Wegener Halvø Formation; a – late neanic stage (= Text-fig. 10.1a); b – early mature stage (= Text-fig. 10.1b); c – mature stage, above calice floor in cardinal quadrants (= Text-fig. 10.1c); all × 4. 6 – GSC 117172; GSC locality C-82314, Trold Fiord Formation, collected between 127 m and 142 m above base; mature stage, middle level of calice (= Text-fig. 10.3); × 4.
7, 8 - *Soshkineophyllum turgidiseptatum* (TIDTEN 1972), transverse sections. 7 – B 2.130, paratype; Sassendalen, central Vestspitsbergen, probably from Kapp Starostin Formation or its equivalents; a, b – neanic stage (= Text-figs. 13.3a, b), × 6; c – late neanic/early mature stage (= Text-fig. 13.3d), × 4. 8 – GSC 117148, hypotype; GSC locality 73156, Trold Fiord Formation, 130 m above base; a – late neanic stage (= Text-fig. 13.2a), × 3; b – mature stage (= Text-fig. 13.2b), × 2.

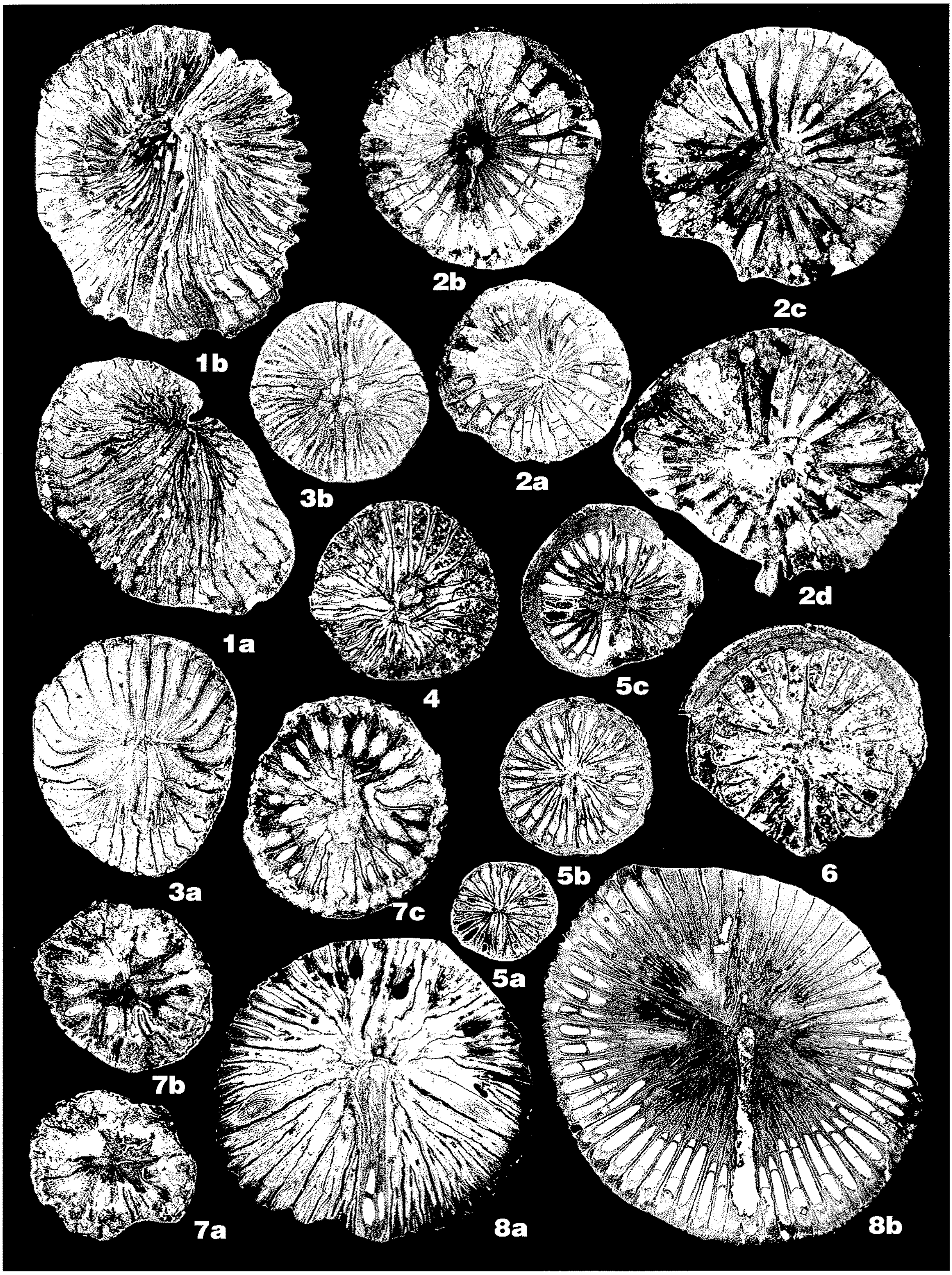
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PLATE 4

1-2 – *Soshkineophyllum turgidiseptatum* (TIDTEN 1972), transverse sections. 1 – GSC 117169, hypotype; GSC locality C-32504, Trold Fiord Formation, 57.3 m above base; a-c – neanic stage; a-b × 4; c × 3; d – mature stage, × 2. 2 – GSC 117167, hypotype; GSC locality C-10470, Degerböls Formation, talus from lower 3 m; a – late neanic stage (= Text-fig. 13.1a), ?3; b – mature stage, above calice floor in cardinal quadrants (= Text-fig. 13.1b), × 2; c, d – successive sections of calice (d= Text-fig. 13.1c), × 2.

3 – *Soshkineophyllum*? sp. (= *Sinophyllum* sp. of FLÜGEL 1973a, p. 42), MMH 11938, hypotype; East Greenland, Kap Stosch, "*Productus* limestone", Wegener Halvø Formation; a, b – transverse sections approximately 1.5 cm (a) and immediately (b) beneath calice floor (= Text-fig. 14); c – partly broken calice; all × 3.

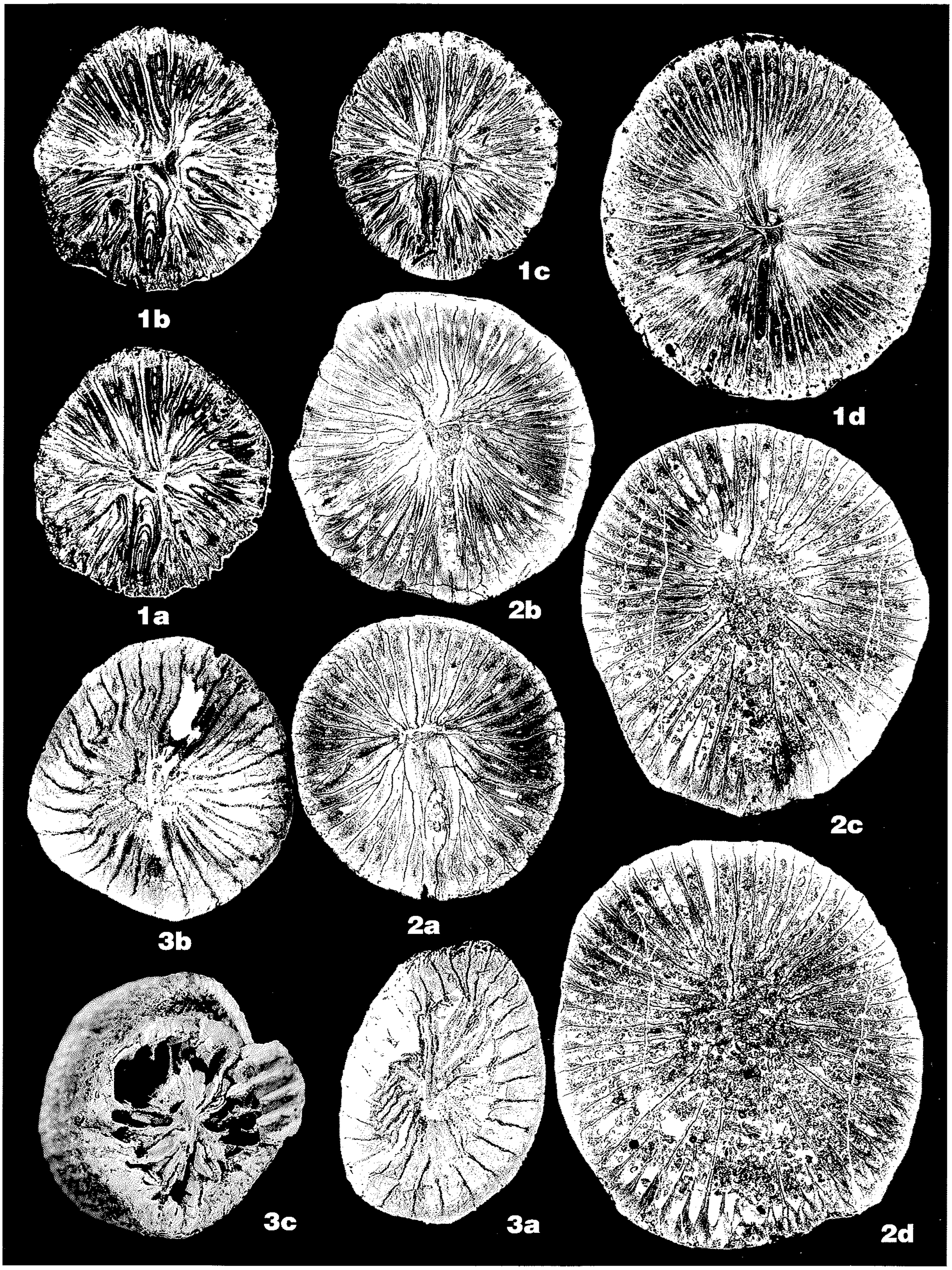
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PLATE 5

1-2 - *Ufimia arctica* sp. n., transverse sections. 1 – GSC 117149, holotype; GSC locality C-10457, Degerböls Formation, collected between 7.9 m and 10 m above base; a – neanic stage (= Text-fig. 9a), × 6; b-d – mature stage, b – approximately 1 cm beneath calice floor (= Text-fig. 9b), × 4, c – immediately beneath calice floor, × 3, d – immediately above calice floor, × 3. 2 – MMH 11940, paratype [= *Cryptophyllum* (*Tachylasma*?) sp. of FLÜGEL 1973a, p. 24]; East Greenland, Kap Stosch, River 1, "*Productus* Limestone" (FLÜGEL 1973a, p. 43) Wegener Halvø Formation, Foldvik Creek Group; a – late neanic stage; b, c – mature stage; all × 4.
3 – *Leonardophyllum* × sp., MMH 11939 (= *Leonardophyllum*? sp. of FLÜGEL 1973a, p. 44); East Greenland, Kap Stosch, River 1, "*Productus* Limestone" (FLÜGEL 1973a, p. 43) Wegener Halvø Formation, Foldvik Creek Group; a, b – transverse sections beneath (a) and partly above (b) calice floor; × 6; c – longitudinal section, × 4.
4 – *Tachylasma variabilis* (SOSHKINA, 1941), MMH 11941 (= *Amplexocarinia* sp. of FLÜGEL 1973a, p. 26, Pl. 3, Fig. 1); East Greenland, Kap Stosch, "*Productus* limestone", Wegener Halvø Formation; a,b – transverse sections separated by approximately 1.2 cm., mature stage, ?2; c – diagenetically altered microstructure of septum showing remnants of trabeculae, × 150.
5 – *Lytvolasma canadense* sp. n., GSC 117162, paratype; GSC locality C-10461, 66.5 m above base of Degerböls Formation; transverse section showing small trabeculae, × 75.
6 – *Calophyllum columnare* (SCHLOTHEIM, 1813), GSC 117172, hypotype; GSC locality C-82314, Trold Fiord Formation, collected between 127 m and 142 m above base; transverse section showing small trabeculae, × 75.
7 – *Lytvolasma canadense* sp. n., GSC 117166, holotype; GSC locality C-10464, Degerböls Formation, 136.6 m above base; diagenetically altered microstructure of septum showing remnants of large trabeculae, × 75.

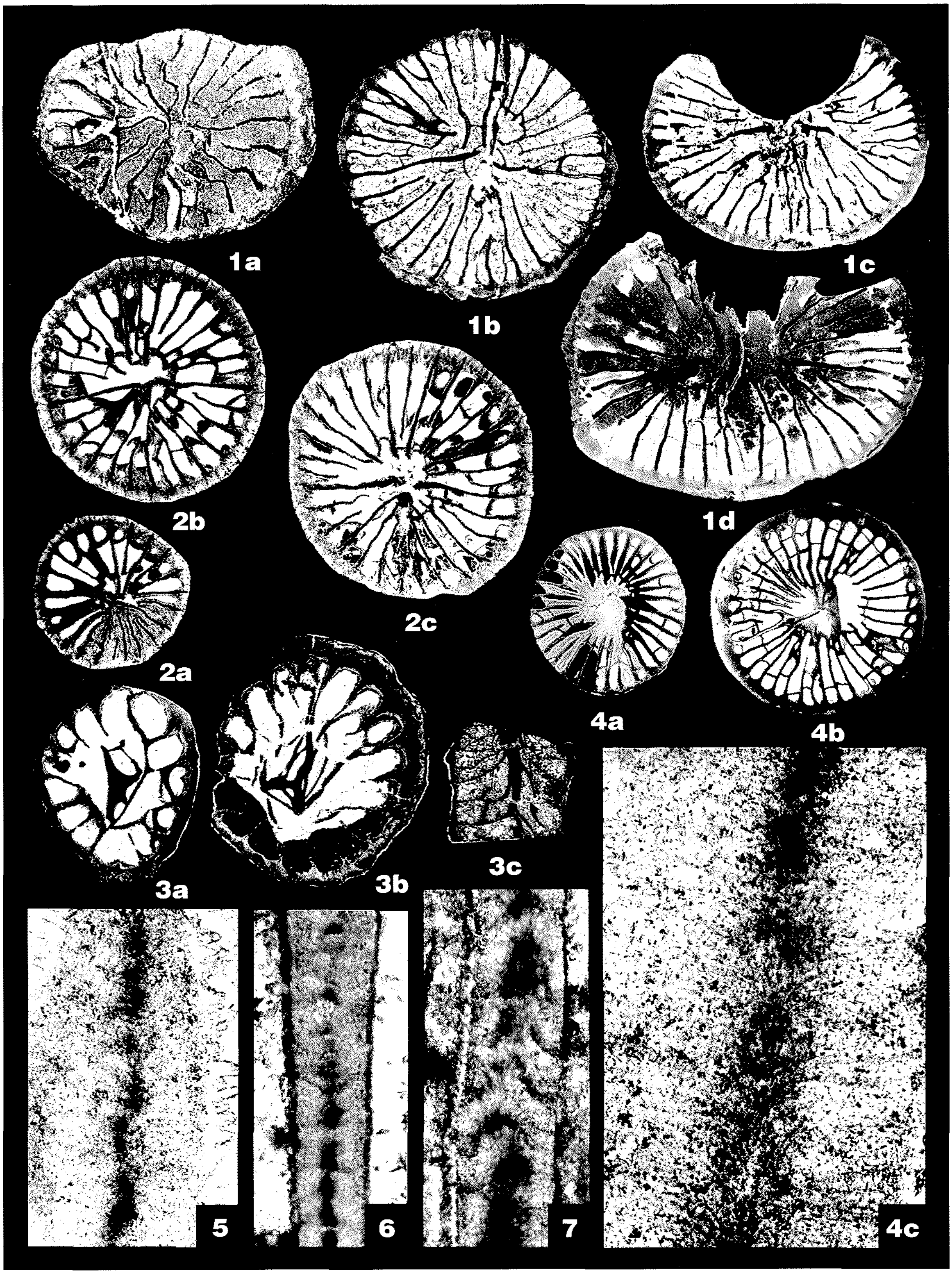
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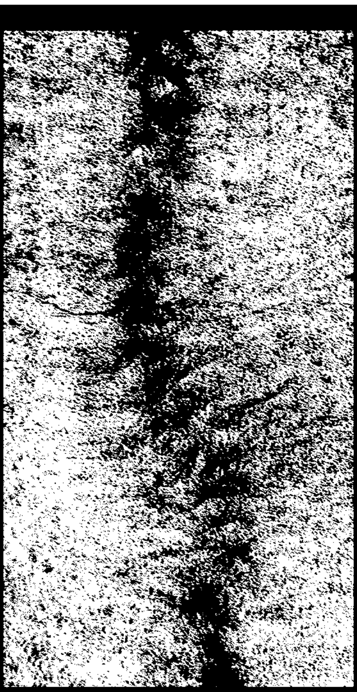
PLATE 6

1-2 – *Euryphyllum boreale* sp. n.; transverse sections. 1 – GSC 117159, holotype; Degerböls Formation, 52.7 m above base; microstructure of septa strongly altered diagenetically, probably finely trabecular; a × 75, b × 150. 2 – GSC 117155, paratype; GSC locality C-10459, Degerböls Formation, 40.6 m above base; diagenetically altered, small trabeculae along inner margin of cardinal septum, × 75.
3-4 – *Euryphyllum troldfiordense* sp. n., transverse sections; GSC locality C-82314, Trold Fiord Formation, collected between 127 m and 142 m above base. 3 – GSC 117170, holotype; a – remnants of trabeculae in middle part of major septum, × 75; b – trabecular microstructure in peripheral part of septum, × 150. 4 – GSC 117174, paratype; remnants of small trabeculae in mature growth stage, × 75.


1a


1b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3b

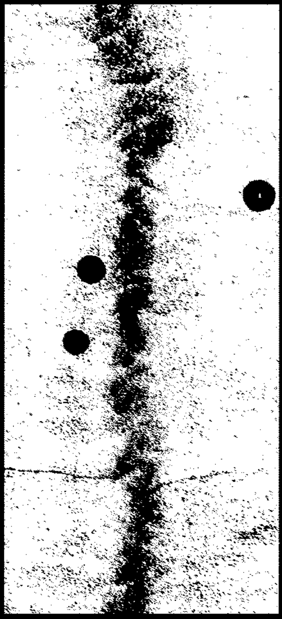
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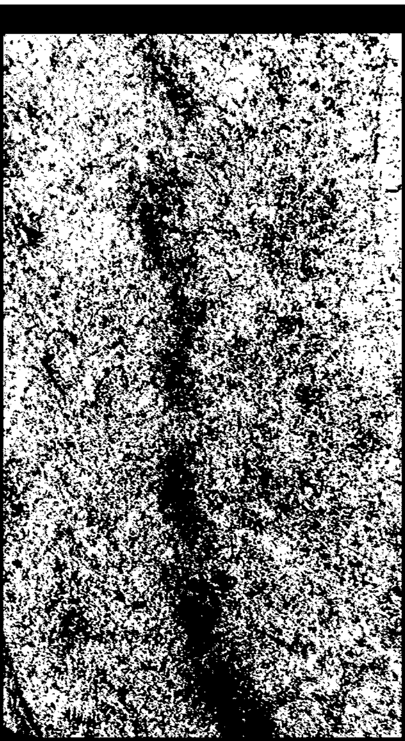
PLATE 7

1-2 – *Soshkineophyllum turgidiseptatum* (TIDTEN 1972); transverse sections. 1 – B 2.130, paratype; Sassendalen, central Vestspitsbergen, probably from Kapp Starostin Formation or its equivalents; diagenetically altered trabecular microstructure; a × 75, b × 150. 2 – GSC 117148, hypotype; GSC locality 73156, Trold Fiord Formation, 130 m above base; diagenetically altered microstructure with remnants of small trabeculae in the middle area and stereoplasmic growth layers altered to zig-zag structure, × 75.

3 – *Allotropiochisma (Allotropiochisma)* sp., GSC 117165, transverse sections, hypotype; GSC locality C-10462, Degerböls Formation, 109.2 m above base; remnants of large trabeculae; a × 75, b × 150.

4 – *Ufimia arctica* sp. n., GSC 117149, transverse section, holotype; GSC locality C-10457, Degerböls Formation, collected between 7.9 m and 10 m above base; remnants of small trabeculae arranged in scattered and zig-zag manner, × 75.

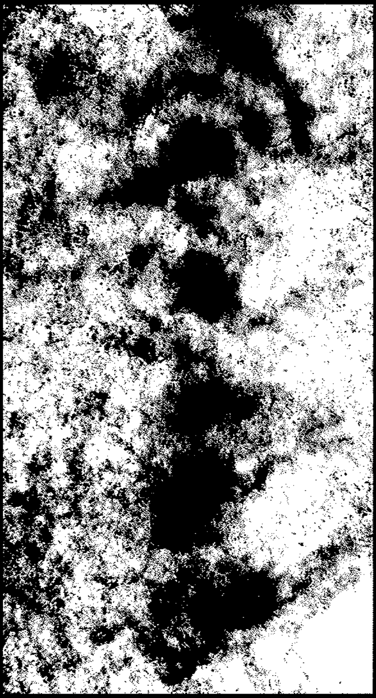
1a



1b

2

3a

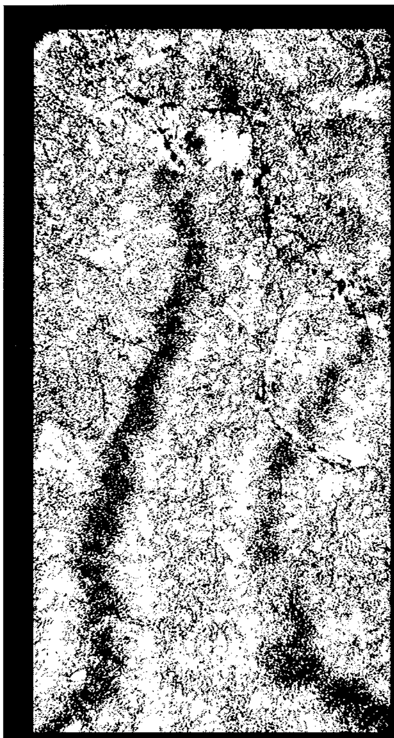


3b

4

PLATE 8

1-2 – *Ufimia arctica* sp. n.; transverse sections. 1 – GSC 117149, holotype; GSC locality C-10457, Degerbols Formation, collected between 7.9 m and 10 m above base; a – juvenile growth stage, inner parts of two major septa, × 75; b-c – mature growth stage, b – zig-zag pattern, stereoplasmic sheets strongly diagenetically affected, × 150, c – nodular shape of lateral surface of septum resulting from zig-zag arrangement of trabeculae, × 150. 2 – MMH 11940; East Greenland, Kap Stosch, "*Productus* limestone", Wegener Halvø Formation; mature growth stage trabeculae in zig-zag pattern and scattered, × 150.
3 – *Soshkineophyllum*? sp., MMH 11938; locality and formation as above; a, b – transverse sections, remnants of large trabeculae, × 150.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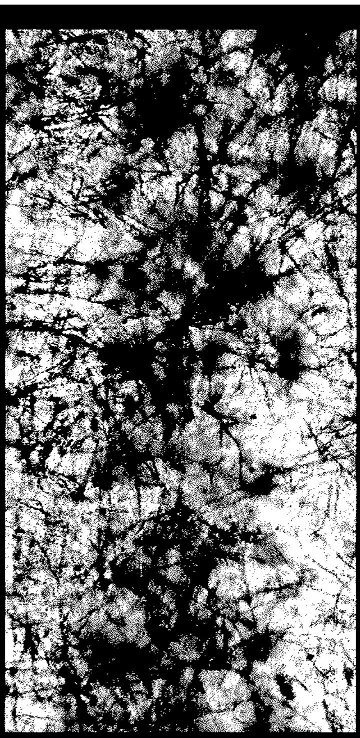
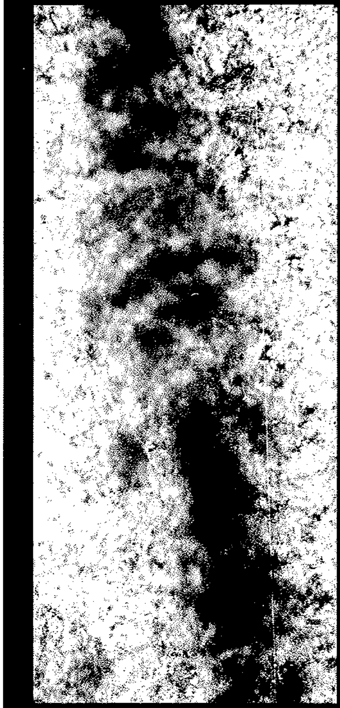

1b


1c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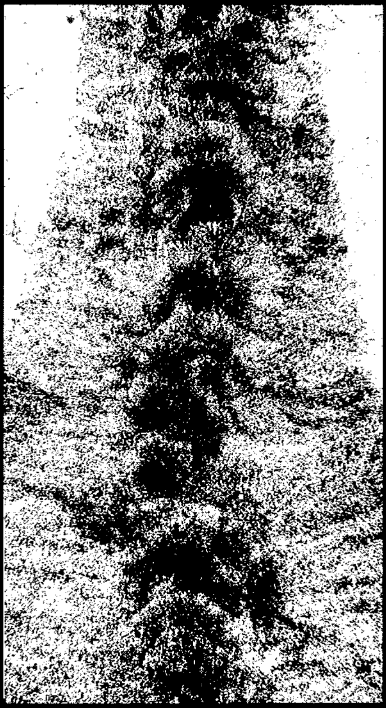
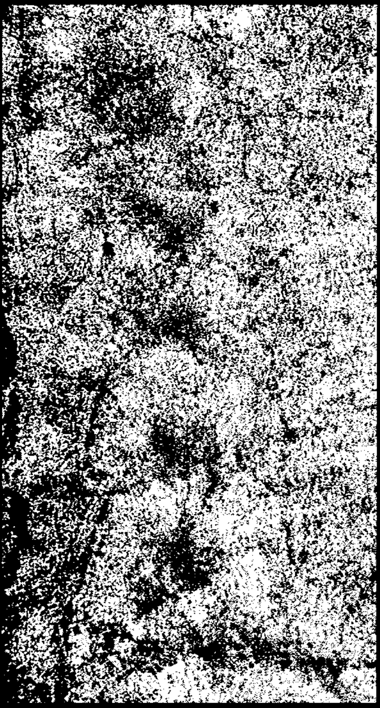

3a


3b