

# Lower Carboniferous solitary rugose corals from the Flett Formation of the Liard Basin, northwestern Canada vs. European and Asian Rugosa of the same geological age

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## ABSTRACT:

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The paper focuses on the taxonomic description of the lower Carboniferous (uppermost Tournaisian to middle Viséan) solitary rugose corals from bedded limestone and shale units in the Flett Formation in the Jackfish Gap (eastern Liard Range), northwestern Canada. The corals described herein include 12 species representing the genera *Ankhelasma* Sando, 1961, *Bradyphyllum* Grabau, 1928, *Caninophyllum* Lewis, 1929, *Cyathaxonia* Michelin, 1847, *Ekvasophyllum* Parks, 1951, *Enniskillenian* Kabakovich in Soshkina *et al.*, 1962, *Vesiculophyllum* Easton, 1944 and *Zaphrentites* Hudson, 1941. Two of these species are new (*Ankhelasma canadense* sp. nov. and *Ekvasophyllum variabilis* sp. nov.) and 6 taxa are described in open nomenclature. The distribution and relative abundance of solitary Rugosa in Europe and the Liard Basin confirm the geographical proximity of those areas and the open marine communication between them during the early Carboniferous. It therefore represents an important contribution to the determination of the time of isolation of the western Laurussia shelf fauna from that of southeastern Laurussia, as well as the time of the possible emergence of species from southeastern Laurussia into the western Laurussia seas. Of particular importance here are cosmopolitan taxa and the timing of their disappearance from the fossil record.

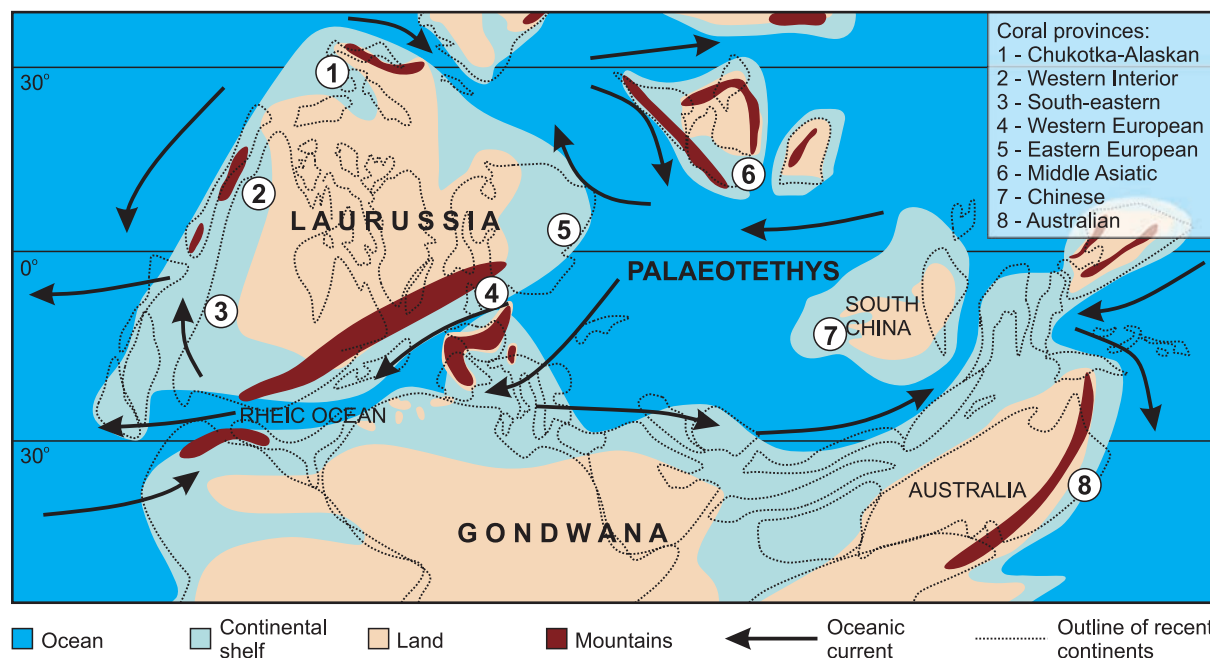
**Key words:** Rugosa; Taxonomy; Palaeogeography; Lower Carboniferous; Canada.

## INTRODUCTION

The lower Carboniferous in the SW Mackenzie District (Liard Basin), northwestern Canada, forms a thick, upward shallowing succession of continental terrace wedge deposits. This succession consists of terrigenous clastics, carbonates, chert, and a small amount of coal. It was deposited on the downwarped western margin of the North American Plate and is broadly exposed in the southern part of the Mackenzie Fold Belt (Richards 1989). Samples for this study were taken from limestone and shale, which are particularly rich in rugose corals. These

corals are important because they belong to one of several zoogeographic provinces occurring in the early Carboniferous (Fedorowski 1981; Sando and Bamber 1985; Text-fig. 1).

The results presented in this article are based on lower Carboniferous data from the Jackfish Gap outcrop, located in the Liard Basin of the southwestern Northwest Territories (Text-fig. 2). This paper discusses the taxonomy of the solitary Rugosa, and the sedimentary environments and palaeogeographic position of the region. These are important issues because the early Carboniferous was a period of important palaeogeographic transformations associ-



Text-fig. 1. Mississippian coral provinces (after Fedorowski 1981) against the background of the schematic arrangement of continents in the Viséan (after Somerville *et al.* 2020, modified).

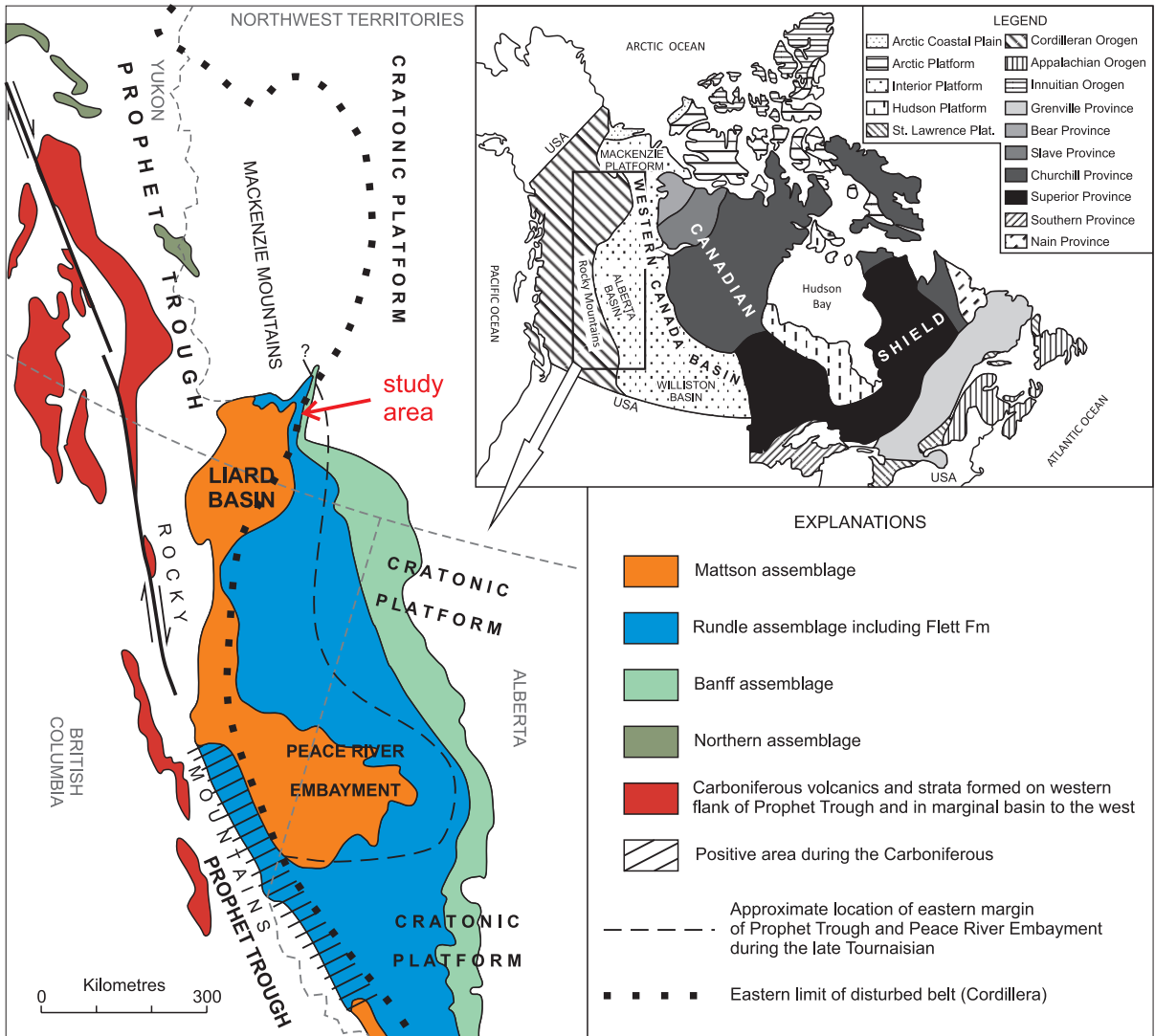
ated with the progressive collision of Gondwana and Laurussia. These transformations are documented, among others, by rugose corals, which responded to these changes more clearly than eurytopic organisms. This sensitivity, combined with the relatively rapid speciation, abundance and worldwide prevalence of the Rugosa, place these corals among the best environmental and geographical indicators of the Carboniferous. They also prove to be a good stratigraphic indicator, especially when orthostratigraphic fossils are not available. However, corals, like many other animal groups, exhibit zoogeographic provincialism, making it difficult to establish the interregional correlation of individual stratigraphic units and their boundaries between distant regions and continents. The problem is further complicated by the morphological similarity of many unrelated taxa (morphotypes), which can easily lead to erroneous conclusions.

## GEOLOGICAL SETTING

The Liard Basin is located west of the central part of the Canadian Shield, in a zone known as the Western Canada Basin (WCB), which includes the Williston and Alberta basins and the Mackenzie Platform (Text-fig. 2). The WCB forms the north-

western part of the North American Platform. Here, essentially flat-lying Phanerozoic sedimentary rocks extend from the Precambrian rocks of the Canadian Shield edge to the eastern boundaries of the Cordillera Orogen (Rocky Mountains), where they are faulted and folded, and locally weakly metamorphosed (Stott and Aitken 1993). Due to varying tectonics, several sub-basins existed in the WCB area throughout most of the Phanerozoic (Richards 1989). These are characterized by variable subsidence and uplift, as indicated by the lateral variation in the rocks present (Stott and Aitken 1993). In the Phanerozoic, in the Liard Basin covering the southern part of the Mackenzie Mountains (south-eastern Yukon–southwestern Northwest Territories), sedimentation developed on carbonate platforms and in intracratonic basins. The succession of upper Palaeozoic rocks from the uppermost Devonian to the upper Permian deposited on the margin of the North American Platform is well documented (Text-fig. 3) (Richards *et al.* 1993). During the Carboniferous, the growth of the ice sheet on southern Gondwana, in addition to the progressive collision of Laurussia and Gondwana, had significant impact on sea level and environmental development in the Liard Basin (Fielding *et al.* 2008).

The Flett Formation, which is the main unit of interest, as moderately weathered, is exposed in the



Text-fig. 2. Geological setting of the Liard Basin in Western Canada. The distribution of Carboniferous rock assemblages according to Richards *et al.* (1994).

Mackenzie Fold Belt region mainly along narrow strips at the limbs of several synclines and anticlines. It outcrops on the northern Tlogotsho Plateau to the west of the study area and is mainly a subsurface unit in the platform interior to the east. South of the study site it occurs mainly at the limbs of the Flett Anticline in the Liard Range.

**LITHOSTRATIGRAPHY**

The lithostratigraphic scheme of the Tournaisian and Viséan in the Jackfish Gap area, starting with the oldest rocks, includes the Besa River, Yohin,

Clausen, Prophet, Flett, Golata and Mattson formations (Richards 1989; Text-fig. 3). The last four formations are documented at Jackfish Gap. The Prophet Formation chiefly contains spiculites, spicule-rich limestones, and shales. The thickest section is 766 m thick, interpreted as having been deposited chiefly on the lower slopes of carbonate buildups (ramps grading into platforms) and as slope-related tongues in an adjacent shale basin. The age of the basal Prophet Formation is uncertain. Microfossils collected from the Prophet, Flett, and Besa River formations indicate that the Prophet Formation ranges in age from the middle(?) Tournaisian to the uppermost middle Viséan (Tn2 to V2). The Prophet and Flett

System and Subsystem		Series/Stage	Conodont zones	Foraminiferal zones	S. Mackenzie Fold Belt		
Carboniferous	Pennsylvanian	Bashkirian	unzoned		Permian / Lower Cretaceous		
			<i>minutus</i>				
			unzoned				
	Mississippian	Visean	Waramanian	<i>muricatus</i>	19		
				<i>girtyi-simplex</i>	18		
				<i>girtyi-collinsoni</i>	17		
				cf. <i>texasus</i>	16-S		
					16-I		
		Tournaesian	Middle (V2)	Livian			15
							14
			Lower (V1)	Moliniacian	<i>texasus</i>		13
							12
							11
	D. U. D.	Famennian (part)	TN3	<i>anchoralis-latus</i>	10		
				<i>typicus</i>	9		
				<i>U. crenulata-isosticha</i>	8		
			TN2	Haastarian	<i>L. crenulata</i>	7	
					<i>sandbergi</i>	pre 7	
			TN1	Haastarian	<i>duplicata</i>		
					<i>sulcata</i>		
			unzoned				

Text-fig. 3. Scheme of lower Carboniferous lithostratigraphic units in SW District of Mackenzie, modified from Richards (1989) and Richards *et al.* (1994), with standard conodont division. Foraminiferal zones after Mamet and Skipp (1970). Dashed lines indicate nature of contact uncertain, question marks indicate position of line uncertain (modified from Richards *et al.* 1994).

formations form the Rundle Group, which is known throughout the Mackenzie Fold Belt.

The upper Viséan and Serpukhovian (Text-fig. 3) are represented by sandstones with interbedded limestones with a total thickness of over 1300 m, classified as part of the Mattson Formation (Harker 1963;

Bamber and Mamet 1978; Richards 1989; Richards *et al.* 1993). The carbonate rocks of this formation also contain fossils, including corals. The two formations (Flett and Mattson) are separated by the relatively thin middle Viséan Golata Formation, which consists of shales and mudstones with subordinate dolostones and sandstones.

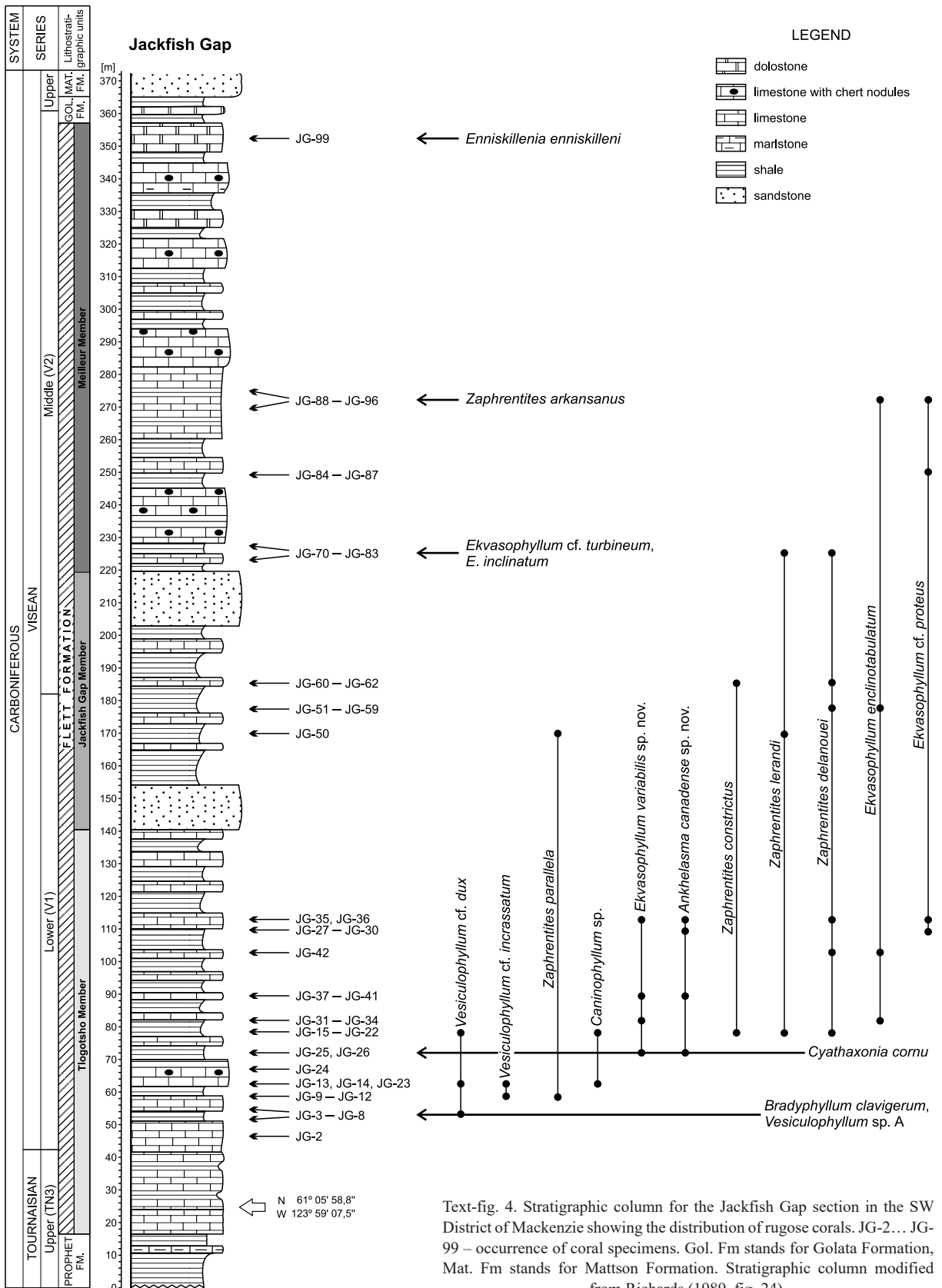
The Mattson and Golata formations were deposited in deltaic and shelf environments (Richards 1989). The lithostratigraphic scheme of the Flett and Mattson formations was proposed by Harker (1963) and modified by Richards (1989). In contrast, the conodont biostratigraphy of the lower Carboniferous of the WCB has not been described in detail, and there are few publications on this subject. Baxter (1972) and Baxter and von Bitter (1979) used a modified zonation proposed by Collinson *et al.* (1971) based on sections from the Mississippi Valley. Lower Carboniferous siphonodellid strata were zoned according to Sandberg *et al.* (1978), and lower Carboniferous post-siphonodellid strata were zoned according to Lane *et al.* (1980). In the present study, the subdivision proposed by Sandberg *et al.* (1972, 1978) and Sandberg and Poole (1977), supplemented by Richards (1989), and the foraminiferal scheme of Mamet and Skipp (1970) are used. Most biostratigraphers accept the recommended subdivisions.

Since the described collection of *Rugosa* is from the Flett Formation, only this formation will be discussed more widely herein. It represents the upper part of the first-order mega-sequence presented by Richards (1989). With a few exceptions, this megasequence upward becomes coarser-grained, more resistant and proximal in aspect (Pl. 1).

### Flett Formation

The stratotype of the Flett Formation studied at the Jackfish Gap (N 61°05'58.8"; W 123°59'07.5", eastern Liard Range) is composed of Tournaisian–Viséan rocks (Text-figs 3 and 4). It consists of lime packstones and grainstones with subordinate lime wackestones, dolostones, spiculites, siltstones, sandstones, shales and mudstones. Fossils (crinoid, bryozoans, brachiopods, and corals) occur mainly in carbonate rocks and shales. The thickness of the stratotype is 341 m (Text-fig. 4) and it contains no gaps in sedimentation (Richards 1989). These sediments are assumed to have formed in a neritic and carbonate ramp environment.

In the Jackfish Gap region, the Flett Formation is formally subdivided into three members (Text-figs 3 and 4; Pl. 1), from oldest to youngest: Tlogotsho,



Jackfish Gap and Meilleur. The thickness of these members in the Jackfish Gap is: 123.6 m for Tlogotsho, 80.4 m for Jackfish Gap, and 137.0 m for Meilleur. In the study area, in Jackfish Gap, the contacts between the Flett Formation and the underlying Prophet Formation, and between the Flett Formation and the overlying Golata Formation are gradational. According to Richards (1989), mixed-skeletal lime packstone lithofacies, lime wackestone and lime grainstone lithofacies are the most significant in the Flett Formation in the Jackfish Gap area. In addition, siltstones, sandstones, shales and mudstones are important with regard to their thickness. Dolostones and spiculites are subordinate. The lime packstones and wackestones in the Flett Formation are mainly bryozoan-pelmatozoan with occasional brachiopods. Pelmatozoan ossicles, bryozoans and spicules are generally the main allochems, but brachiopods, foraminifers, pellets and intraclasts are also present and locally dominate. Calcareous algae, ostracods, molluscs and corals are also present, but are rarely abundant. Spiculites are common in the upper part of most strata in the Flett Formation. The major component of the spiculites is authigenic chert, limestone and dolostone. Chert occurs mainly as isolated, greyish black to light grey nodules.

Although most of the allochems range in size from silt to small pebble, coarser material including brachiopods, corals, pelmatozoan ossicles, bryozoans and intraclasts is moderately common. Well-preserved macrofossils occur only in some strata. Bryozoans and pelmatozoans are common in most lime grainstone rocks of this formation. Brachiopods occur in most strata, but rarely in large clusters. Most of the macrofossils occur as fragments, crushed and abraded due to transport, compaction and pressure solution.

Dolostones occur in fairly small quantities in most of the Flett Formation. This is generally the main rock type in the upper part of the Meilleur Member. Sandstones and siltstones occur only in the Jackfish Gap Member, where they are the main rock types. The sandstones are mainly very fine to fine-grained. Shales and mudstones, which occur throughout most of the Flett Formation as thin, alternating inserts reaching up to several metres in thickness, are most abundant in the upper part of the Tlogotsho Member, in the Jackfish Gap Member, and in the lower and upper parts of the Meilleur Member. In the Flett Formation, the shales and mudstones are calcareous or non-calcareous, usually fossiliferous. The shales contain both well preserved and fragmented and abraded macrofossils.

The boundary between the Prophet and Flett formations has remained unclear for many decades. The first to document it was Harker (1961, 1963). Harker's concept of the Flett Formation was adopted by Douglas (1976), Douglas and Norris (1976a, b, c), Richards (1978), and Bamber *et al.* (1980). Foraminifers indicate the age of the Prophet Formation, depending on location. In the Jackfish Gap area, the Prophet/Flett boundary is dated to the latest Tournaisian (Tn3; upper foraminiferal zone 9; Mamet and Skipp 1970, 1971). The upper boundary of the Flett Formation falls within the uppermost middle Viséan (V2; upper foraminiferal zone 13) and is highlighted by a moderately abrupt change in lithology from dolostone and limestone with subordinate shale to clay shale with subordinate dolostone and minor argillaceous sandstone, which is classified as the Golata Formation (Richards 1989).

#### *Tlogotsho Member*

The Tlogotsho Member consists of lime grainstones, well stratified mixed-skeletal packstone limestones with subordinate crystalline limestones, shales and mudstones. Limestone wackestones, spiculites and dolostones are subordinate. In the Jackfish Gap outcrop, the contacts between the Prophet Formation and the Tlogotsho Member, and between the Tlogotsho Member and the Jackfish Gap Member are gradational. The contact between the Tlogotsho Member and the Jackfish Gap Member is defined by the appearance of siltstones and sandstones at the base of the Jackfish Gap Member (Richards 1989). The upper part of the Tlogotsho Member and the base of the Jackfish Gap Member belong to the lower Viséan (V1; lower foraminiferal zone 11).

#### *Jackfish Gap Member*

The type section comprises, proceeding from the base, an 18.0 m thick unit composed of planar-laminated to cross-bedded siltstones and sandstones, a 45.2 m thick middle unit, composed of shales, mudstones, with subordinate rhythmically-bedded limestones, and an upper, 21.2 m thick unit consisting mainly of cross-bedded siltstones and sandstones. In the study area, the contacts between the Tlogotsho Member and the Jackfish Gap Member, and between the Jackfish Gap Member and the Meilleur Member are gradational (Richards 1989). The upper part of the Jackfish Gap Member and the base of the Meilleur Member belong to the middle Viséan (V2; 12/13 foraminiferal zones).

### *Meilleur Member*

The Meilleur Member is the most weathered unit in the Flett Formation, consisting of rhythmically bedded to cross-bedded lime grainstones and packstones with subordinate dolostones, shales and mudstones. In the study area, the contacts between the Jackfish Gap Member and Meilleur Member, and between the Meilleur Member and the Golata Formation are gradational.

## MATERIAL AND METHODS

Fieldwork was carried out in the summer of 2018, during a scientific expedition to Canada. The Jackfish Gap outcrop, located within the Liard Basin, was selected in conjunction with Dr Barry Richards of the Geological Survey of Canada. The section was measured in detail and samples were collected. A total of 150 palaeontological samples from the Flett Formation were brought to Poland, of which 100 containing well-preserved rugose corals were selected for taxonomic study. The collected rugose corals were not in growth position, and were worn and apparently redeposited from their original neritic setting. In some specimens, compression during compaction and diagenesis had crushed the corallites. Laboratory studies were carried out using traditional palaeontological methods. More than 300 thin sections and a dozen celluloid peels were made from mechanically dissected or cut corals. Based on these materials, 18 taxa were identified, of which 12 were assigned at species level.

All specimens are housed in the Institute of Geology, Adam Mickiewicz University, Poznań (prefix UAM.IG). Individual numbers of coral specimens consist of: (1) collection prefix; (2) Tc – tetracorals; (3) C – first letter of the collector's surname [C – Chwieduk]; (4) outcrop symbol [JG – Jackfish Gap]; and, after a hyphen, (5) the sample and corallite number [e.g.: 15, 37(1), the number in parentheses refers to the subsequent specimen from a given sample]. The full coral specimen number is, for example, UAM.IG.Tc.C.JG-15 or UAM.IG.Tc.C.JG-37(1).

## SYSTEMATIC PALAEOLOGY

Despite the efforts of many specialists, the systematics of Rugosa has not yet been satisfactorily worked out, and there are differences of opinion on many issues. The present study bases its taxonomy of

lower Carboniferous corals on the classifications of Hill (1981) and Fedorowski (1991). Therefore, Rugosa Milne-Edwards and Haime, 1850 and Dividocorallia Fedorowski, 1991 are treated as subclasses of the Class Anthozoa Ehrenberg, 1834. An alternative subdivision, used e.g., by Oliver (1996) and Scrutton (1997), classifies Rugosa and Heterocorallia as separate orders of the Anthozoa. The reason for the different treatment of the major taxa is the ambiguous identification of Calyxcorallia Fedorowski, 1991, a taxon included by some authors in the Order Rugosa rather than in the Subclass Dividocorallia. Following Hudson (1936) and Fedorowski (1997), the term 'protosepta' is used in this article only to refer to cardinal and counter septa; thus, it is not applied to alar and counter-alar septa. Following Hill (1981), the term 'corallite' is used here to refer to the skeleton of solitary polyps and that of a single individual in a colony.

### Abbreviations:

n:d – septal index,  
 n – ratio of the number of major septa,  
 d (mm) – diameter of the corallite, diameter of the alar in case of oval corallite,  
 C – cardinal septum,  
 K – counter septum,  
 KL – counter-lateral septa,  
 Km – minor septa in loculi between counter and counter-lateral septa.

**Note:** All images in the text-figures and plates are from thin-sections, except when stated otherwise; transverse sections are oriented with the cardinal septum at the base, except when stated otherwise; scale bars located between two adjacent images correspond to both. The superscript ' next to the main number means that this image shows an enlarged fragment of the image with the main number.

Class Anthozoa Ehrenberg, 1834  
 Subclass Rugosa Milne-Edwards and Haime, 1850  
 Order Stauriida Verrill, 1865  
 Suborder Stereolasmatina Hill, 1981  
 Family Zaphrentoididae Schindewolf, 1938  
 Genus *Ankhelasma* Sando, 1961

TYPE SPECIES: *Ankhelasma typicum* Sando, 1961.

DIAGNOSIS (modified from Hill 1981): Small, solitary, ceratoid or trochoid corals; calyx deep; well-developed fossula long, extending beyond the axis, deep, adaxially gradually widening, bounded later-

ally by tall, fused axial segments of septa of cardinal quadrants and axially by fused ends of counter septum and septa of counter quadrants; alar pseudo-fossulae notable; in late stages counter-lateral and alar septa, and older metasepta retreating from fossula wall; some minor septa may be contralingent; dissepiments absent; tabular floor concave, tabulae complete; cardinal septum stunted in early stages, relatively short in late stages.

*Ankhelasma canadense* sp. nov.

(Pl. 2, Figs 1–5; Text-fig. 5)

HOLOTYPE: UAM.IG.Tc.C.JG-36(1), three transverse thin sections (Pl. 2, Figs 1a–c) were studied.

TYPE LOCALITY: Jackfish Gap (N 61°05'58.8"; W 123°59'07.5"), SW District of Mackenzie, Canada.

TYPE HORIZON: Flett Formation (middle part of Tlogotsho Member); lower Viséan (Text-fig. 4).

ETYMOLOGY: Latin *canadense* – the name of the species refers to the country where it has been sampled.

MATERIAL: Nine paratypes: UAM.IG.Tc.C.JG-26(1), UAM.IG.Tc.C.JG-26(3), UAM.IG.Tc.C.JG-28(2), UAM.IG.Tc.C.JG-29(2), UAM.IG.Tc.C.JG-29(3), UAM.IG.Tc.C.JG-29(5), UAM.IG.Tc.C.JG-37(1), UAM.IG.Tc.C.JG-37(2), UAM.IG.Tc.C.JG-37(3); lower Flett Formation (Tlogotsho Member); lower Viséan (Text-fig. 4).

DIAGNOSIS: *Ankhelasma* with 21–24 major septa at 6–7 mm corallite diameter in late mature growth stage; tabular floor concave, tabulae complete.

DESCRIPTION: Delicately curved, trochoid corals of small size (Pl. 2, Fig. 3b), reaching a maximum length of nearly 16 mm (Pl. 2, Fig. 4b) and a maximum diameter in calyx of nearly 7 mm (Pl. 2, Fig. 2b); calyx 10–15 mm deep; shallow growth rings (Pl. 2, Fig. 4b) and septal furrows on external wall surface. Septal index n:d from 9:2 to 23:7, 24:6 (Text-fig. 5). Major septa of various sizes (Pl. 2, Figs 1a–c, 2a, 3a, 4a, 5a). In mature growth stages, septal plan characterized by the retraction of most of major septa, leaving five plates bounded by counter septum, two counter lateral septa and by a fusion of the axial ends of the cardinal lateral septa (Pl. 2, Figs 2a, 3a, 4a, 5a). One specimen, UAM.IG.Tc.C.JG-29(3), is distinguished by the presence of carinae, clearly visible on

the septa only in the calyx (Pl. 2, Fig. 5b). Major septa of equal length in the calyx, reach 1/3 of the length of the corallite radius (Pl. 2, Fig. 2b). Cardinal fossula well-developed, on convex side; bounded laterally by fused axial ends of adjacent major septa and axially by fused ends of counter and counter lateral septa. Minor septa short, in calyx reaching the length of the major septa (Pl. 2, Fig. 2b). Tabular floor concave, tabulae complete, declined towards the external wall (Pl. 2, Fig. 2c).

REMARKS: The specimens of *Ankhelasma* studied were collected from the lower Viséan strata of the middle Tlogotsho Member in the lower Flett Formation (Text-fig. 4). Therefore, they extend the range of the genus to an older stratigraphic interval, which was previously known from upper Viséan Meramecian substage dolomites and limestones of northeastern Utah and northwestern Montana (Sando 1961). In addition, specimens from Jackfish Gap differ from those described by Sando (1961) primarily in the presence of tabulae, and in their smaller size and fewer major septa (Text-fig. 5). *Ankhelasma typicum* reaches more than 22 mm in length, has between 38 and 42 major septa in the mature growth stages, and 12.0–12.5 mm in corallite diameter. Specimens from USA are thus much larger than those from Canada. They are also characterized by a flattening of the convex side, which was not observed in the Canadian specimens. While the latter feature may be regarded as ecologically variable (factors related to the maintenance of negatively geotropic growth and stability after toppling from an erect, apically attached position – Sando 1961), features such as the smaller size of the specimens and the specific septal indices of the Canadian specimens, and in one case also the presence of carinae, indicate a different species.

OCCURRENCE: Western Canada (Jackfish Gap) – lower Viséan.

Family Stereophrentidae Fomichev, 1953

Genus *Zaphrentites* Hudson, 1941

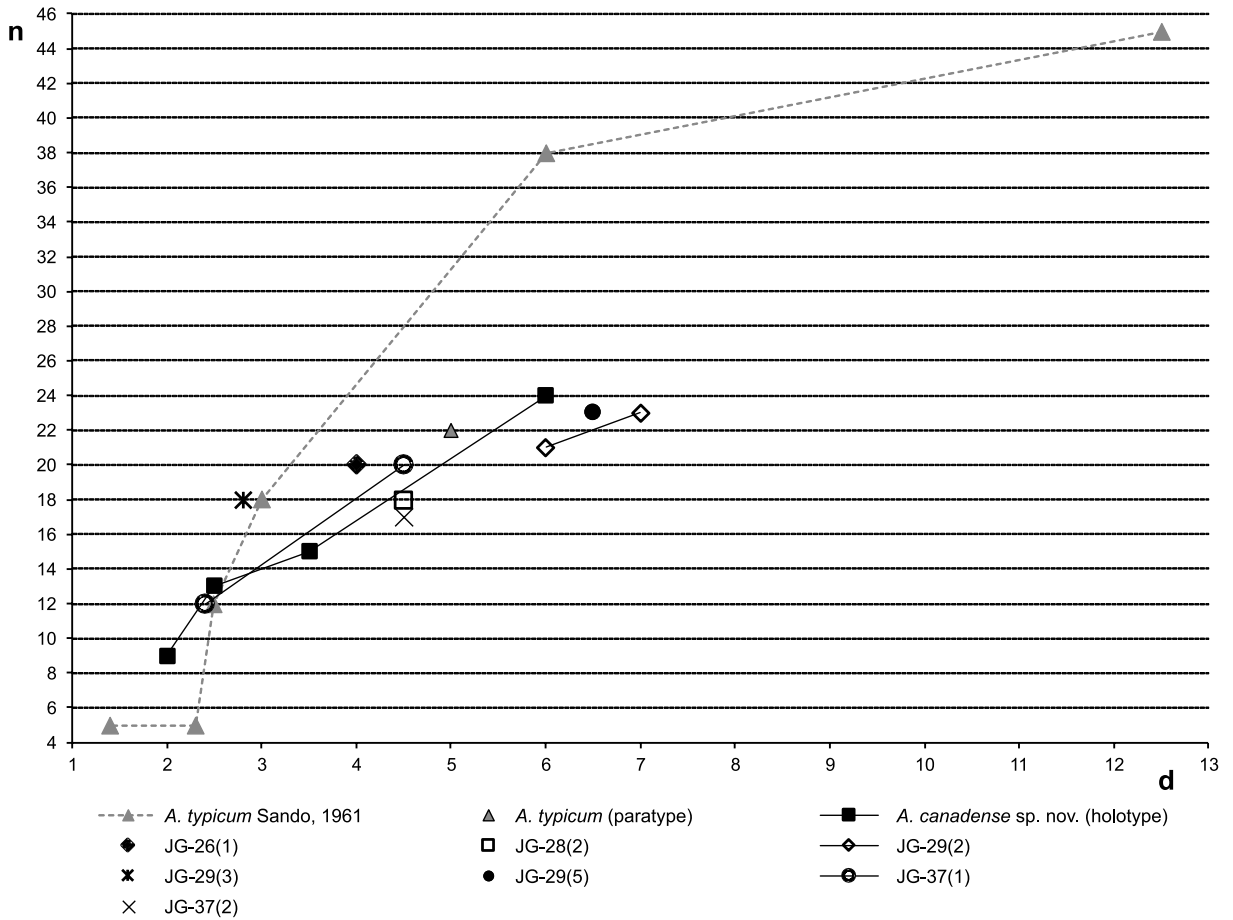
TYPE SPECIES: *Zaphrentis parallela* Carruthers, 1910.

DIAGNOSIS: See Bamber *et al.* (2017, p. 30).

*Zaphrentites arkansanus* (Girty, 1910)

(Pl. 3, Figs 1–3; Text-fig. 6)





Text-fig. 5. *Ankhelasma* Sando, 1961 – plot of the number of major septa (n) vs. diameter in mm (d). Symbols joined by lines represent values taken from individual specimens.

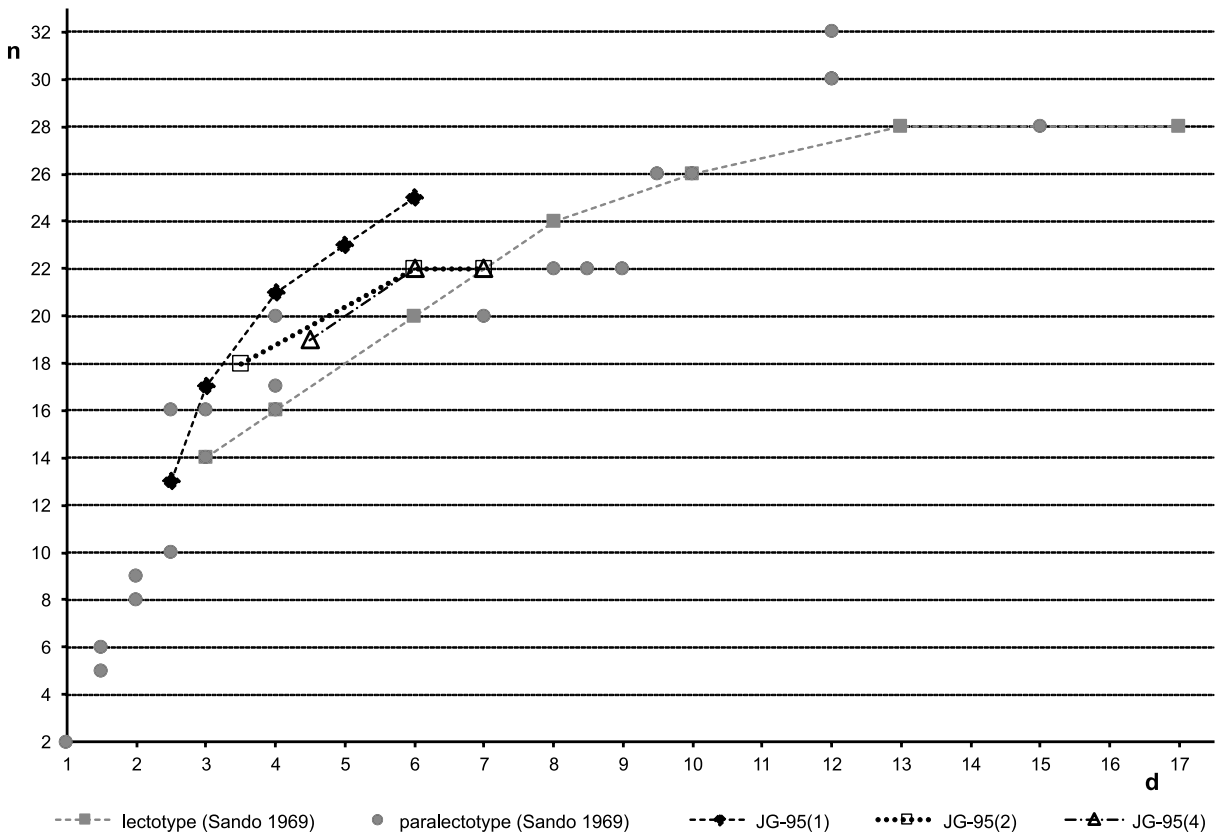
1910. *Menophyllum excavatum* var. *arkansanum* Girty, p. 190.

1969. *Zaphrentites arkansanus* (Girty); Sando, pp. 9–12, pl. 1, figs 1–17.

**DIAGNOSIS:** According to Sando (1969, pp. 9–12), corallite small, conical; calyx deep; maximum n:d ratio 28:13–17, 32:12; major septa long, thickened by stereoplasm, interseptal loculi almost closed; cardinal, counter and alar septa reaching corallite axis; above calyx floor, cardinal septum short, on concave side of corallite; minor septa short, may form low ridges on corallite wall; cardinal and alar pseudofossulae distinct.

**MATERIAL:** Three specimens, UAM.IG.Tc.C. JG-95(1), UAM.IG.Tc.C. JG-95(2), UAM.IG.Tc.C. JG-95(4); upper Flett Formation (middle Meilleur Member); middle part of middle Viséan (Text-fig. 4).

**DESCRIPTION:** Straight corallites, about 2 cm long (Pl. 3, Figs 2f, 3e), oval in transverse section. Calyx about 8 mm deep; the bottom of the fossula reaches another 2 mm below the calyx floor. In the calyx, the inner ends of septa erect, reaching almost to the edge of the calyx (Pl. 3, Figs 3c, d). Shapes of transverse sections through the corallites oval, compressed perpendicularly to the cardinal-counter (C-K) plane (Pl. 3, Figs 1–3). The septal index in the adult growth stage is: 22–25:6.0×11.0 (Text-fig. 6). Cardinal and counter septa long; cardinal septum remains long at the calyx floor (Pl. 3, Fig. 2d). Major septa, except the short cardinal septum, long and mostly of equal length in the calyx (Pl. 3, Figs 1d, 2e, 3c, d). Counter septum longer and thicker than the other major septa (Pl. 3, Figs 1c, d, 2e, 3d). Minor septa occur as short crests in the upper part of the calyx (Pl. 3, Figs 2e, 3d). Alar pseudofossulae more (Pl. 3, Figs 1a, b, 2a, b) or less (Pl. 3, Figs 2d, 3a, b) distinct. Wall of external corallite is thick.



Text-fig. 6. *Zaphrentites arkansanus* (Girty, 1910) – plot of the number of major septa ( $n$ ) vs. diameters ( $d$ ). Symbols joined by lines represent values taken from individual specimens.

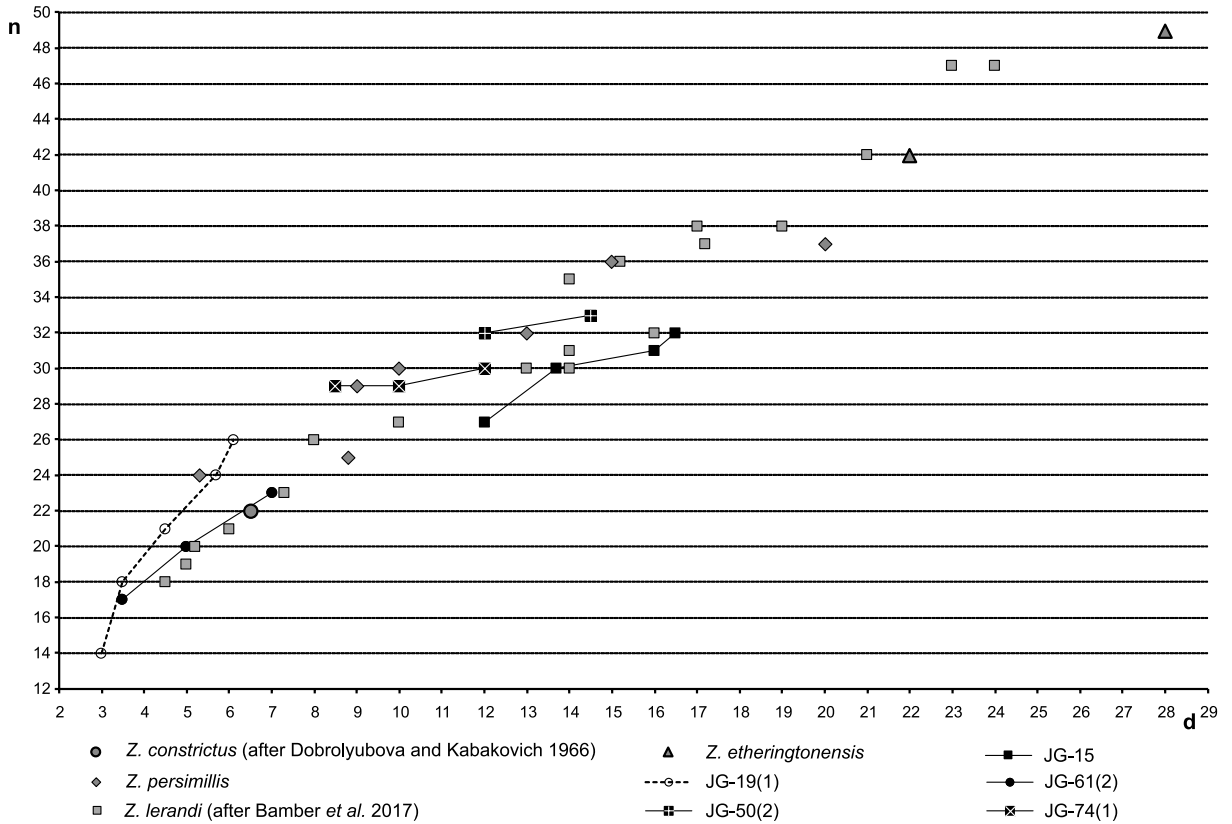
The earliest section studied (Pl. 3, Fig. 2a) shows 13 major septa with alar diameter of 2.5 mm and C-K diameter of 3.0 mm. All septa are thickened and occupy most of the space inside the corallite. Cardinal, counter, two counter laterals and alar septa are the longest, one extending to the axis of the corallite; alar pseudofossulae indistinct.

A thin section (Pl. 3, Fig. 2b, c), cut at alar diameter of 3 and 4 mm shows 17 and 21 major septa; alar pseudofossulae distinct; other internal details are very similar to those of the earlier growth stage. A thin section (Pl. 3, Fig. 2d), cut partially above the floor of the cardinal fossula, at alar diameter of 5 mm shows 23 major septa, most of them (also cardinal, counter and alar) extending to the axis of the corallite; cardinal septum thinner and counter septum thicker than major septa; alar pseudofossulae indistinct.

In a section made partially above the calyx floor (Pl. 3, Fig. 2e), the septal index  $n:d$  is 25:6×9.5. Major septa long and thinner than in previous stages; in the corallite axis – erect and interconnected, forming a peculiar axial structure (Pl. 3, Figs 3c, d), clearly

projecting above the calyx bottom. Septa of cardinal quadrants may be withdrawn (Pl. 3, Fig. 2e) or not (Pl. 3, Fig. 3c, d) from the corallite axis. Counter septum thicker than the major septa and the longest, reaching corallite axis (Pl. 3, Figs 1d, 2e, 3d). Cardinal septum very short. Minor septa seen for the first time, confined to corallite wall, locally absent (Pl. 3, Fig. 2e).

REMARKS: The *Zaphrentites* specimens studied herein were collected from the upper part of the middle Viséan strata of the upper Flett Formation. They are therefore stratigraphically older than the specimens described by Sando (1969) from the Fayetteville Formation (upper Viséan, Middle Chesterian Series), but the general appearance and most morphological elements of the Flett specimens make them similar to the Fayetteville specimens. The only feature that distinguishes the Fayetteville specimens from the Flett fauna is size. The specimens described by Sando (1969) reach 29.5 mm in length and 17.2 mm in calyx diameter, in which the number of major septa is 28 (lectotype); for the paralectotype the  $n:d$  ratio is



Text-fig. 7. *Zaphrentites* Hudson, 1941 – plot of the number of major septa (n) vs. diameters (d). Symbols joined by lines represent values taken from individual specimens.

30–32:12 (Text-fig. 6); their calyces are also proportionally deeper, reaching 14 mm. I presume that the generally smaller dimensions of the specimens from the Flett Formation were more diagnostic than other features. Another feature reported by Sando (1969), which can probably be regarded as an ecological variability, is the shape of transverse sections through the corallites, which changes from circular in the earliest preserved stage to oval, compressed perpendicular to the C-K plane, in intermediate stages, to become circular again in the calyx. Specimens from Canada are oval along their entire length.

OCCURRENCE: USA, Arkansas and Oklahoma – upper Viséan (Middle Chesterian); Western Canada, Mackenzie Mts. – middle Viséan (Livian, ?Upper Meramecian or Middle Chesterian), Jackfish Gap – middle Viséan.

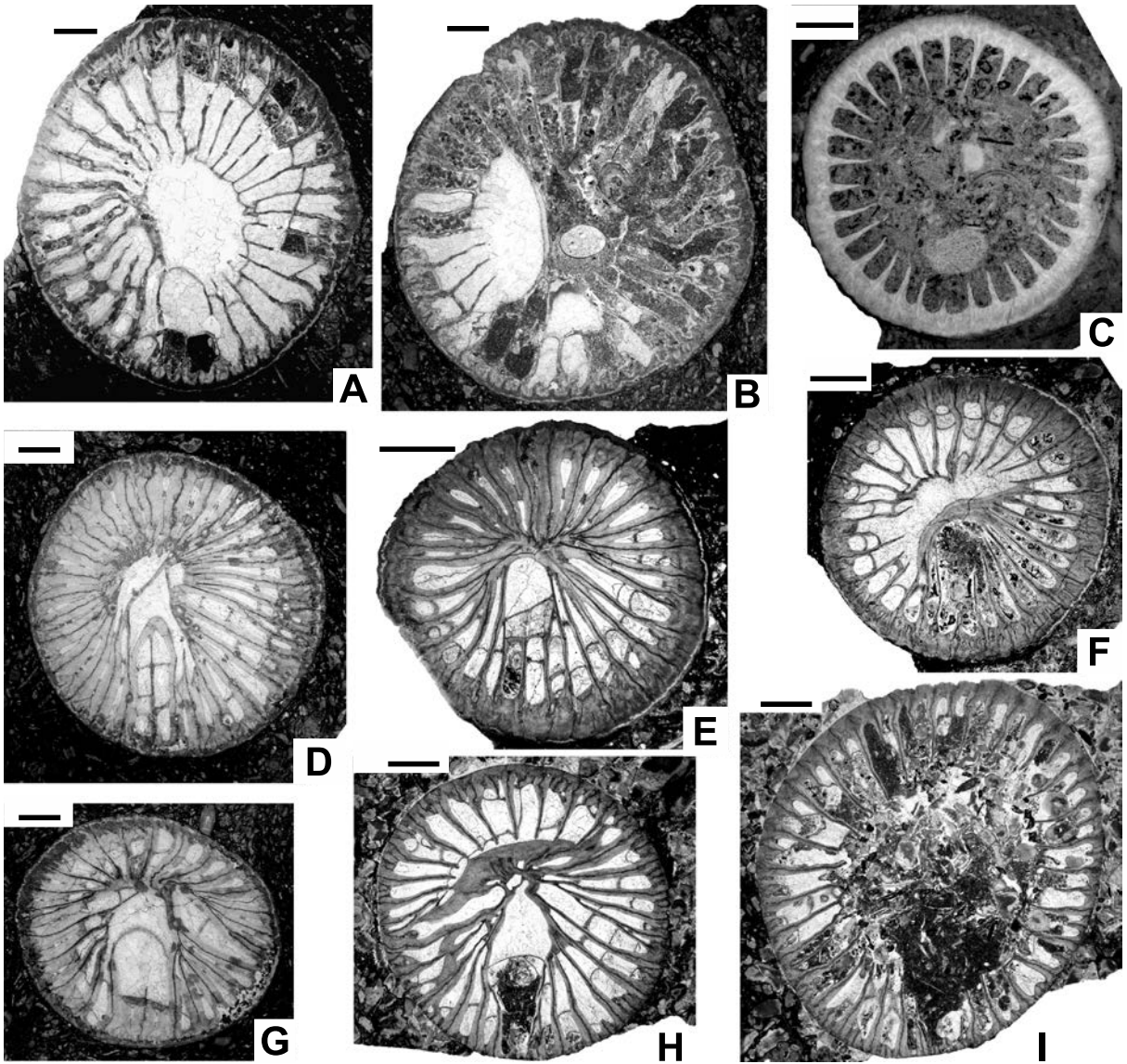
*Zaphrentites lerandi* Bamber and Rodríguez in Bamber *et al.* 2017 (Text-figs 7, 8)

2017. *Zaphrentites lerandi* Bamber and Rodríguez in Bamber *et al.* 2017, pp. 35, 36.

DIAGNOSIS: See Bamber *et al.* (2017), p. 35.

MATERIAL: Three specimens, UAM.IG.Tc.C.JG-15, UAM.IG.Tc.C.JG-50(2), UAM.IG.Tc.C.JG-74(1); Flett Formation (middle part of Tlogotsho Member to lower part of Meilleur Member); lower–middle Viséan (Text-fig. 4).

DESCRIPTION: Specimens with calyces preserved (30 mm depth), without proximal ends. At mature stage septal index n:d = 30:12.0, 32:16.5, 33:14.5 (Text-fig. 7). Major septa slightly thickened; under the calyx floor pinnate in cardinal and counter quadrants (Text-fig. 8D, E); in section taken partially above the calyx floor (Text-fig. 8A, F, H) weakly pinnate in cardinal quadrants and radially arranged in counter quadrants; in the central part of the calyx changing to radial in all quadrants (Text-fig. 8C, I). Major septa varied in length, the longest ones join on the coral-



Text-fig. 8. *Zaphrentites lerandi* Bamber and Rodríguez in Bamber *et al.*, 2017 from the Flett Formation (middle part of Tlogotsho Member–lower part of Meilleur Member), lower–middle Viséan. A, B, D, G – UAM.IG.Tc.C.JG-15: A, B – mature growth stage; D, G – immature growth stage. C, E, F – UAM.IG.Tc.C.JG-74(1), mature growth stage, C – made in dark-field microscopy. H, I – UAM.IG.Tc.C.JG-50(2), mature growth stage. Scale bars equal to 2 mm.

lite axis. At 10 mm diameter, in the mature stage, septa withdraw from axial region in both cardinal and counter quadrants, becoming amplexoid. In the mature stage, counter septum may be slightly thicker and longer than the other major septa (Text-fig. 8F). Alar septa reach the axial region in the early mature stage (Text-fig. 8E, H) and then withdraw, becoming approximately equal in length with the adjacent major septa in the cardinal quadrants (Text-fig. 8A, B, I). Minor septa incorporated into the wall (Text-

fig. 8E, F) or form low ridges on the corallite wall (Text-fig. 8A, H, I). Cardinal fossula conspicuous, slightly expanded in the youngest stages examined. Cardinal septum, except for amplexoid elongations just above tabulae (Text-fig. 8D, G), reaching half the length of major septa, located in deep cardinal fossula surrounded by major septa of cardinal quadrants, distinctly shortened in calyx (Text-fig. 8A, I). Alar pseudofossulae well-developed in the young stage examined (Text-fig. 8G).

REMARKS: Characteristic features for this species include amplexoid septa, slightly expanded cardinal fossula with shortened cardinal septum, and septal index n:d. The preserved corallite fragments from the Mackenzie Mts. do not differ from most specimens of *Z. lerandi* from the upper Viséan of the Canadian Rocky Mountains, described by Rodríguez in Bamber *et al.* (2017). The presence of several larger specimens with proportionally more major septa (Text-fig. 7) in the collection of Bamber (Rodríguez *et al.* 2017), may indicate a younger growth stage of the specimens from the Mackenzie Mountains.

OCCURRENCE: Canadian Rocky Mountains, upper Mount Head Formation, lower Etherington Formation, *Siphonodendron* Zone, Foraminifer Zone 16i, upper Viséan; Northwestern Canada (Jackfish Gap) – lower–middle Viséan.

*Zaphrentites constrictus* (Carruthers, 1910)  
(Text-figs 7, 9)

1910. *Zaphrentis constricta* Carruthers, p. 534, pl. 37, figs 5a–d.  
1962. *Zaphrentites constrictus* (Carruthers); Dobrolyubova and Kabakovich, p. 119, pl. C-4, figs 11, 12.  
1966. *Zaphrentites constrictus* (Carruthers); Dobrolyubova *et al.*, pp. 28, 29, pl. 1, figs 8, 9.

DIAGNOSIS: See Dobrolyubova *et al.* (1966), p. 28.

MATERIAL: Two specimens, UAM.IG.Tc.C. JG-19(1), UAM.IG.Tc.C.JG-61(2); lower–middle Flett Formation (middle part of Tlogotsho Member to middle part of Jackfish Gap Member); lower Viséan (Text-fig. 4).

DESCRIPTION: Specimens 20 mm long, with damaged calyx (about 15 mm depth), without proximal ends. In the youngest identified ontogenetic stages (Text-fig. 9I), the septal index n:d is 17:3.5. Cardinal, counter, alar and KL-1 septa join at the corallite axis; the remaining major septa vary in length. Cardinal fossula distinct, oval in outline, closed, bordered by adjacent major septa. Minor septa absent. In the middle part of the corallite (Text-fig. 9E), the septal index n:d is 20:5.0×5.5. The longest septa, reaching the corallite axis, are the same as in the previous section. Cardinal fossula narrow, closed, parallel-walled, reach the corallite axis; cardinal septum reaches the axis. At mature stage (Text-fig. 9C) septal index n:d is 23:7.0; initially zaphrentoid arrangement of septa changes to almost radial; cardinal septum shortened

to half the corallite radius, in a closing, V-shaped fossula. Minor septa very short, incorporated into the wall.

The second specimen included in this species (Text-fig. 9A, B, D, G, H) differs from the first in having a shorter cardinal septum, reaching 3/4 (Text-fig. 9G, H) or 1/2 (Text-fig. 9A, B, D) of the corallite radius and thinner major septa.

REMARKS: In such major features as septal arrangement, very short minor septa, ontogenetic changes in the shape of the fossula, short cardinal septum, and n:d index (Text-fig. 7), this specimen closely resembles *Z. constrictus*. The Canadian specimen is very similar in all essential details to specimens of *Z. constrictus* from Kuznetsk described by Dobrolyubova *et al.* (1966). However, the Canadian specimens have a much longer cardinal septum (in the holotype, on the calyx floor, it is shortened to 1/4 of the corallite radius). A cardinal septum longer than in the holotype (up to 1/3 of the corallite radius) is also documented by Dobrolyubova *et al.* (1966) in specimens from Kuznetsk. Compared to *Z. persimillis* (Easton and Gutschick, 1953), *Z. lerandi* or *Z. etheringtonensis* Bamber and Rodriguez, 2017, the described specimens are clearly smaller (Text-fig. 7).

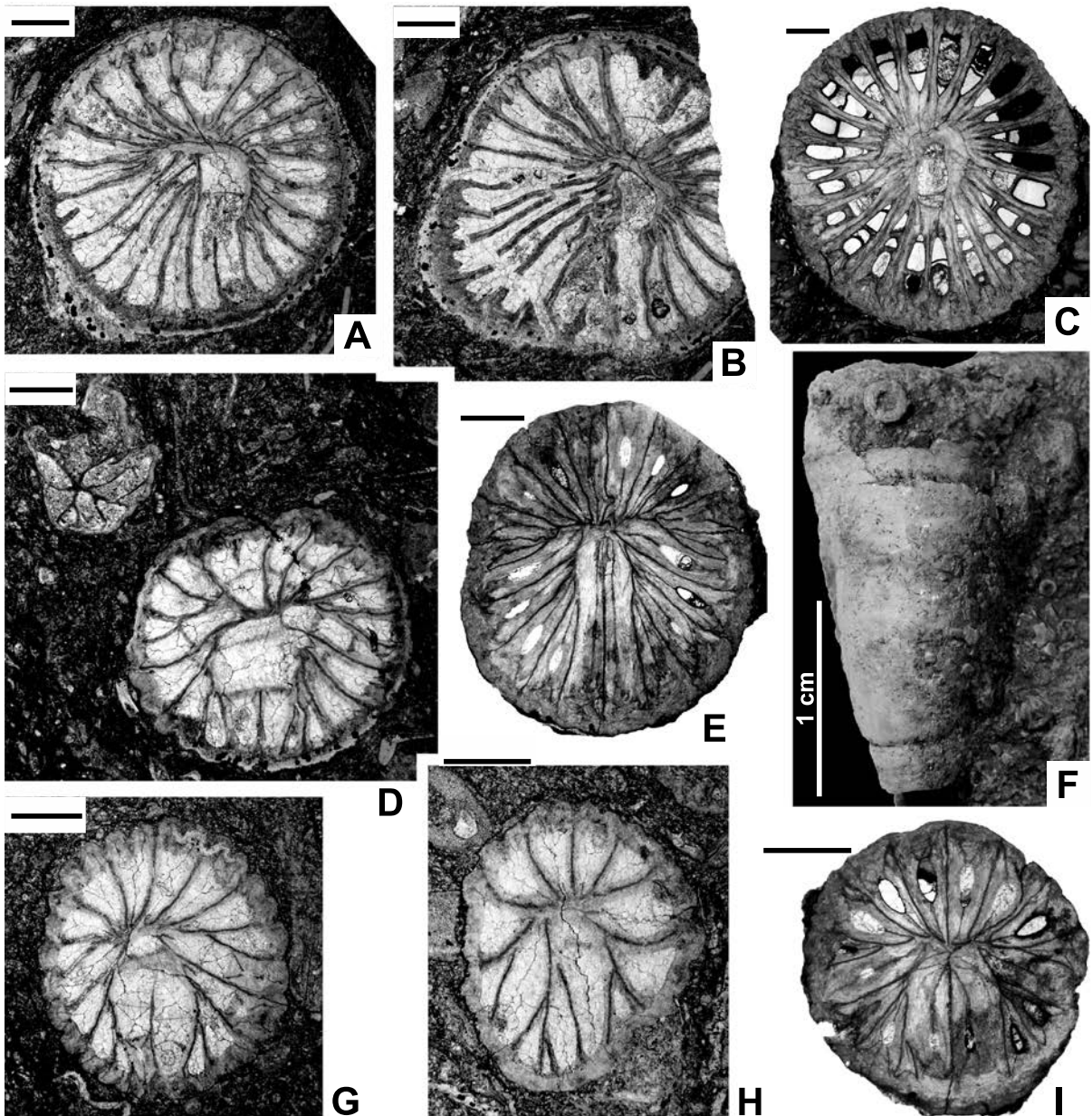
OCCURRENCE: Ural, Kuznetsk Basin – upper Tournaisian; Western Europe, Russian Platform – upper Tournaisian–upper Viséan; Scotland – upper Viséan–Serpukhovian; Northwestern Canada (Jackfish Gap) – lower Viséan.

*Zaphrentites parallela* (Carruthers, 1910)  
(Text-figs 10, 11A–G)

1910. *Zaphrentis parallela*; Carruthers, p. 533, pl. 37, figs 4a–d.  
1941. *Zaphrentis parallela* Carruthers; Hudson, p. 292.  
1962. *Zaphrentites parallelus* (Carruthers); Dobrolyubova and Kabakovich, p. 119, pl. C-4, figs 8, 10.  
1966. *Zaphrentites parallelus* (Carruthers); Dobrolyubova *et al.*, pp. 26–28, pl. 1, figs 4–7.  
2005. *Zaphrentites parallelus* (Carruthers); Chwieduk, pp. 427, 428, pl. 15, fig. 6.

DIAGNOSIS: See Hudson (1941, p. 292).

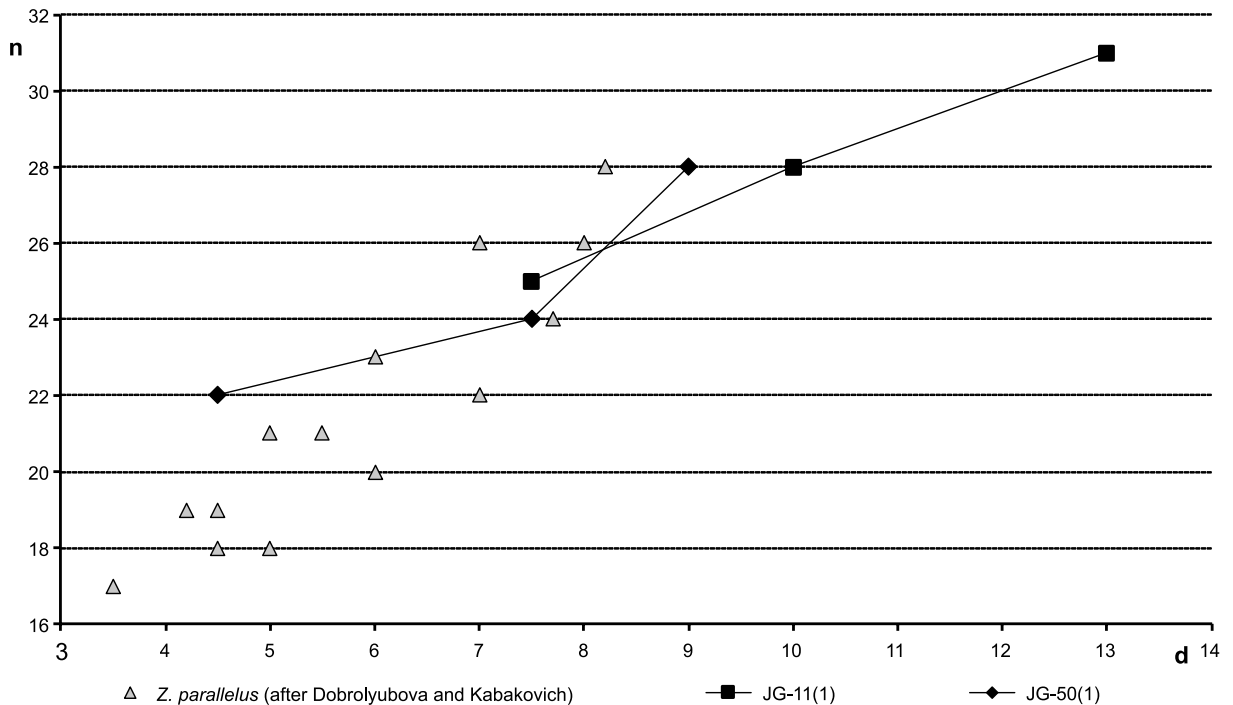
MATERIAL: Two specimens, UAM.IG.Tc.C. JG-11(1), UAM.IG.Tc.C.JG-50(1); lower Flett Formation (middle part of Tlogotsho Member to lower part of Jackfish Gap Member); lower Viséan (Text-fig. 4).



Text-fig. 9. *Zaphrentites constrictus* (Carruthers, 1910) from the lower-middle Flett Formation (middle part of Tlogotsho Member to middle part of Jackfish Gap Member), lower Viséan. A, B, D, G, H – UAM.IG.Tc.C.JG-19(1): A, B – mature growth stage; D, G, H – immature growth stage. C, E, F, I – UAM.IG.Tc.C.JG-61(2): C – mature growth stage; E, I – immature growth stage; F – corallite surface. Scale bars for A–E and G–I equal to 1 mm.

DESCRIPTION: Specimens about 3.0 cm long, with deep calyxes occupying 2/3 of corallite length; diameters at the edge of the calyxes 2.0 and 2.5 cm; main fossula deep, reaching 3.0 mm below calyx floor. At mature stage, 31 major septa 13 mm in diameter (Text-figs 10 and 11C); septa thick and laterally adjacent to the corallite axis, up to the calyx (Text-fig. 11A, C, F,

G). At all stages, major septa pinnately arranged in cardinal quadrants, radially arranged in counter quadrants (Text-fig. 11A, C–G); abaxial withdrawn during late mature stage (Text-fig. 11B). Septa first begin to withdraw from the axial part of the cardinal quadrants. Long cardinal septum (Text-fig. 11E) begins to shorten at about 7.5 mm in diameter (Text-fig. 11A,



Text-fig. 10. *Zaphrentites parallela* (Carruthers, 1910) – plot of the number of major septa (n) vs. diameters (d). Symbols joined by lines represent values taken from individual specimens.

D, F) to become very short in mature stages (Text-fig. 11B, C, G). In mature stages, counter septum usually slightly thicker and shorter than the other septa of counter quadrants (Text-fig. 11A, C). Alar septa usually approach or reach axial area. Minor septa very short in all stages. Cardinal fossula distinct, expanded with parallel margins in mature growth stages. Alar pseudofossulae well-marked.

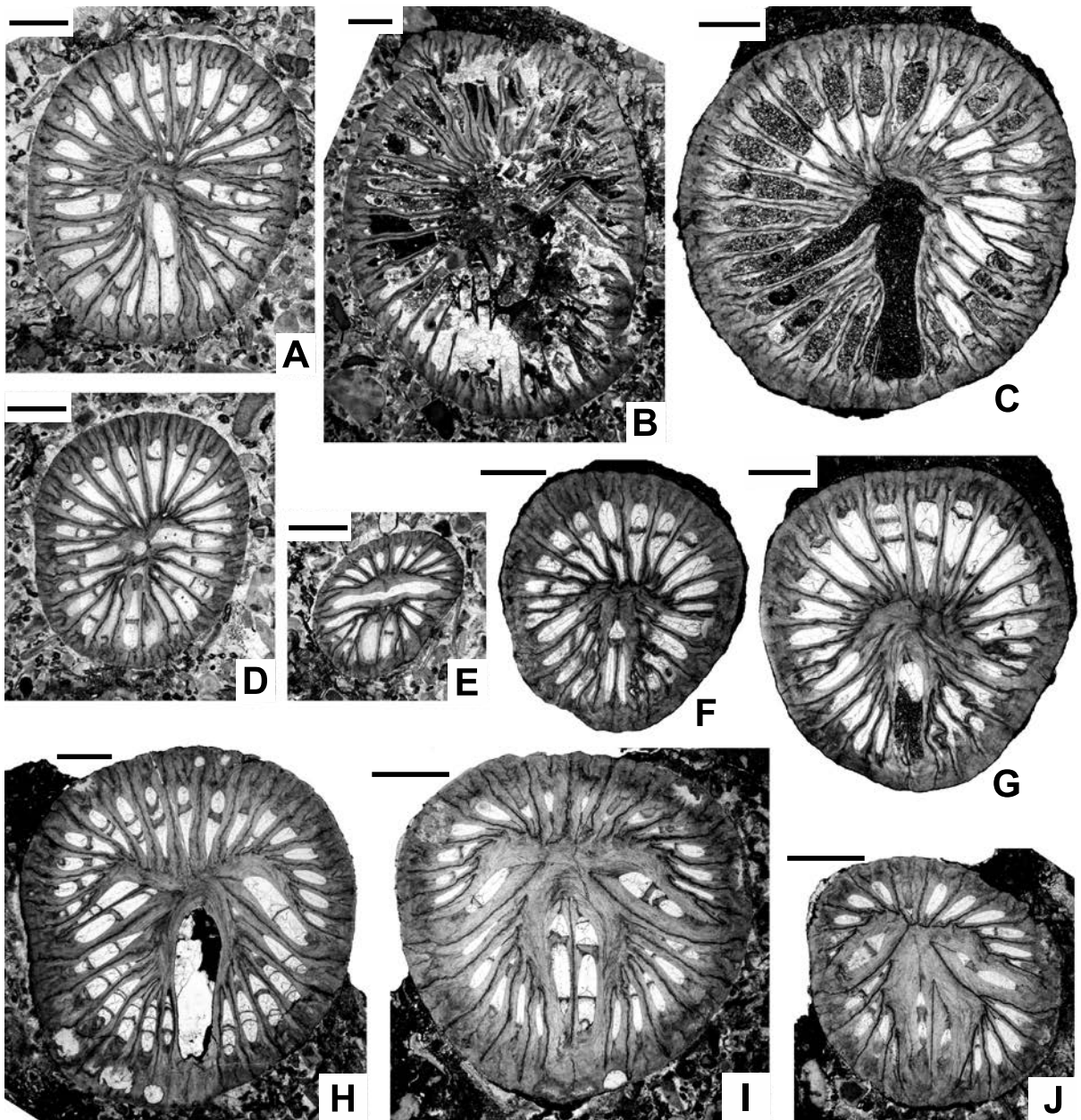
In the youngest observed section, with alar diameter of 4.5 mm, the number of septa 22; in each cardinal quadrant and in counter quadrants, major septa form 3 groups/fascicles (Text-fig. 11E), separated from each other by distinct cardinal and alar pseudofossulae. Major septa long, but do not reach corallite axis. Cardinal septum long, as long as cardinal fossula. Counter septum slightly thicker than other septa and the same length as adjacent major septa. Alar septa approach axial area. Minor septa very short, incorporated into the wall.

At alar diameters 7.5 and 9.0 mm (Text-fig. 11A, D), number of septa 24 and 28, cardinal fossula distinctly V-shaped, becoming narrow with parallel margins, extending to the axial area (Text-fig. 11F). Cardinal septum shortened to 1/2 of the corallite radius. Alar pseudofossulae well-developed. Counter

septum of the same length as the adjacent major septa (Text-fig. 11D, F) or slightly shortened (Text-fig. 11A). Minor septa very short, incorporated into wall. Little over succeeding interval, at alar diameter 10.0 mm, with 28 septa (Text-fig. 11G); cardinal septum shortened to 1/4 of corallite radius; cardinal fossula narrow with parallel margins; alar pseudofossulae well-developed. Minor septa short, forming low ridges on inner side of wall.

REMARKS: The Canadian specimens are very similar to those described by Dobrolyubova *et al.* (1966) from the Kuznetsk Basin. The V-shaped fossula in one growth stage is referable to *Z. crassus*. However, the smaller size of the examined corallites and the presence of cardinal fossula with parallel walls in adult growth stages, as well as a longer cardinal septum, and distinct alar pseudofossulae argue for *Z. parallela*.

OCCURRENCE: Ural, Kuznetsk Basin, Donbas – upper Tournaisian. Poland (Western Pomerania) – Tournaisian. Russian Platform, Western Europe – upper Tournaisian–upper Viséan. Northwestern Canada (Jackfish Gap) – lower Viséan.



Text-fig. 11. A–G – *Zaphrentites parallela* (Carruthers, 1910) from the lower Flett Formation (middle part of Tlogotsho Member to lower part of Jackfish Gap Member), lower Viséan. A, B, D, E – UAM.IG.Tc.C.JG-50(1): A, B – mature growth stage; D, E – immature growth stage. C, F, G – UAM.IG.Tc.C.JG-11(1), mature growth stage. H–J – *Zaphrentites delanouei* (Milne-Edwards and Haime, 1851) from the Flett Formation (middle part of Tlogotsho Member to lower part of Meilleur Member), lower–middle Viséan; UAM.IG.Tc.C.JG-42(1): H, I – mature growth stage; J – immature growth stage. Scale bars equal to 2 mm.

*Zaphrentites delanouei*  
(Milne-Edwards and Haime, 1851)

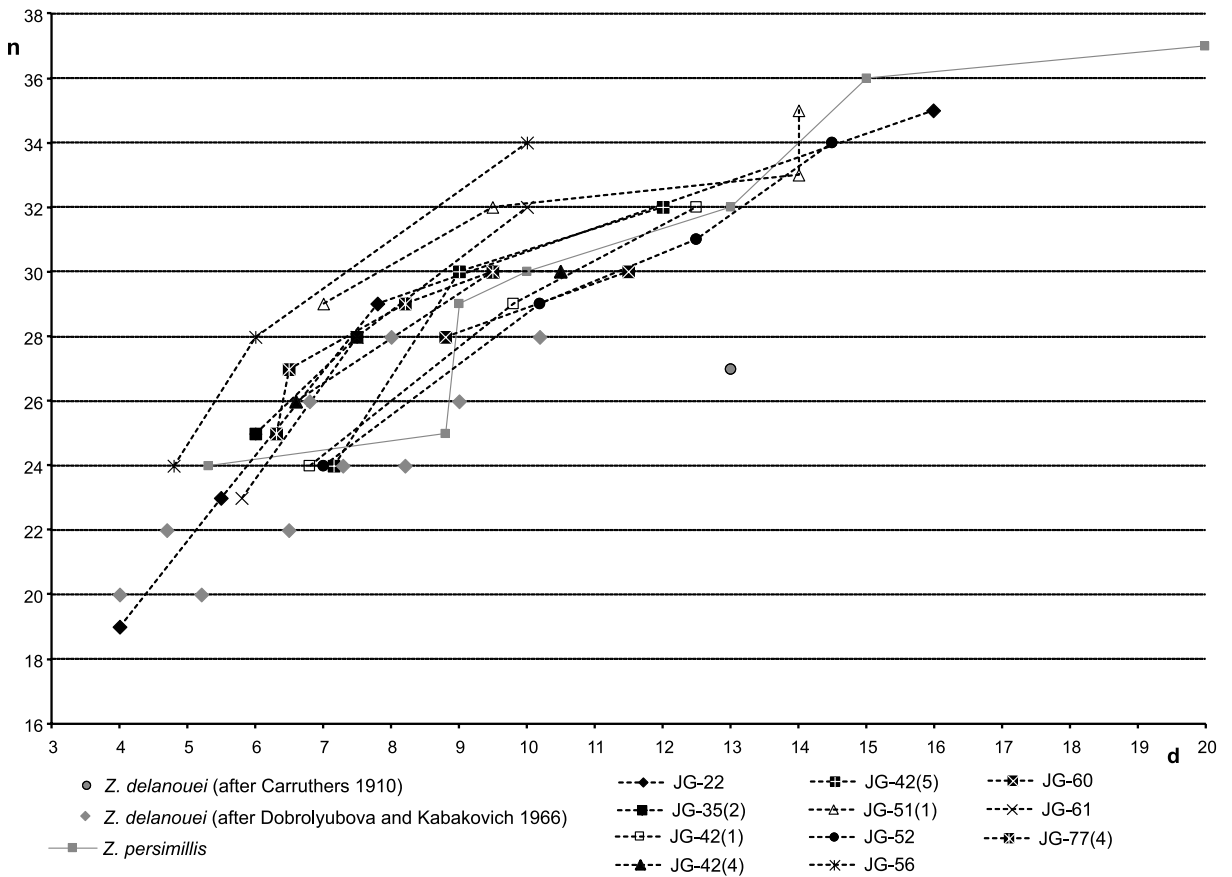
(Pl. 4, Figs 1–4, Pl. 5, Figs 1–4; Text-figs 11H–J, 12)

2015. *Zaphrentites delanouei* (Milne-Edwards and Haime);  
Denayer, p. 377, figs 3B, 3C (cum synon.).

DIAGNOSIS: See Dobrolyubova *et al.* (1966, p. 25).

MATERIAL: 14 specimens, UAM.IG.Tc.C.JG-19(2),  
UAM.IG.Tc.C.JG-22, UAM.IG.Tc.C.JG-35(2), UAM.  
IG.Tc.C.JG-42(1), UAM.IG.Tc.C.JG-42(4), UAM.  
IG.Tc.C.JG-42(5), UAM.IG.Tc.C.JG-51(1), UAM.IG.





Text-fig. 12. *Zaphrentites* Hudson, 1941 – plot of the number of major septa (n) vs. diameters (d). Symbols joined by lines represent values taken from individual specimens.

Tc.C.JG-51(3), UAM.IG.Tc.C.JG-52, UAM.IG.Tc.C.JG-56, UAM.IG.Tc.C.JG-60, UAM.IG.Tc.C.JG-61(1), UAM.IG.Tc.C.JG-73(1), UAM.IG.Tc.C.JG-77(4); Flett Formation (middle part of Tlogotsho Member to lower part of Meilleur Member); lower–middle Viséan (Text-fig. 4).

DESCRIPTION: Short fragments with a deep calyx only partially preserved, without proximal ends (Pl. 4, Figs 1d, e, 3d, 4d), reaching a length of 12 to 25 mm and a maximum diameter of 16 mm (Pl. 5, Fig. 1d). In mature stages, 30–35 major septa, 10–16 mm in diameter (Text-figs 11H and 12, Pl. 4, Figs 1c, 2c, 3c; Pl. 5, Figs 1d, 2d, 3c, d). Cardinal fossula distinct, very deep on the concave side of the coral (Pl. 4, Figs 1d, e, 3d). Alar pseudofossulae distinct, deep (Pl. 4, Fig. 1c; Pl. 5, fig. 3c). Major septa long; the longest, including cardinal, counter, alar, KL1-2 extend to the corallite axis; their thickened inner ends join in the corallite

axis to form fascicles, one formed from the septa of the cardinal quadrants and one with the septa of the counter quadrants (Text-fig. 11H–J; Pl. 4, Figs 1a–c, 2a–c, 3a–c, 4a–c; Pl. 5, Figs 2a–c, 3a–c). Cardinal fossula and alar pseudofossulae distinct, long, closed, extending towards corallite axis. Cardinal septum thinner than other major septa, as long as the main fossula, shortens only at calyx floor (Text-fig. 11H; Pl. 5, Figs 2c, 3c). Counter septum does not differ from the adjacent major septum. Minor septa very short, visible only in mature stages.

In the youngest section observed (Pl. 5, Fig. 1a), septal index n:d is 19:4.0. The arrangement of septa is zaphrentoid; major septa of different lengths, the longest including alar, counter and cardinal septa reaching the corallite axis. Main fossula oval, alar pseudofossulae narrow; minor septa absent. In sections of the higher parts of the specimens, with n:d = 23:5.5, arrangement of major septa similar to that of

previous sections; main fossula elongate with almost parallel walls, alar pseudofossulae narrow. In section with corallite diameters of 6–9 mm, the numbers of septa range from 24 to 30 (Pl. 4, Figs 1b, 2b, 3a, b, 4b; Pl. 5, Figs 1c, 2c, 4a); the arrangement of major septa is zaphrentoid, the cardinal fossula extends towards corallite axis; the cardinal septum reaches the corallite axis along the cardinal fossula, except for a young specimen (Pl. 5, Fig. 2c), in which at this diameter occurs calyx floor with shortened cardinal septum. At diameters of 7–8 mm very short minor septa appear (Pl. 4, Fig. 2b; Pl. 5, Fig. 3a). In the sections with corallite diameters of 10–12 mm, the number of major septa range from 29 to 34; usually the sections pass through the bottom of a deep main fossula (Pl. 4, Figs 1c, 3c, 4c; Pl. 5, Figs 3b, 4b) with a shortened cardinal septum. Septal indices n:d of adult stages range from 31–32:12.5 to 33–35:14.0–16. Above the calyx floor (Pl. 5, Fig. 3d), the previously distinct 3 septal bundles disintegrate. Cardinal septum differs little from the very short minor septum.

The largest specimen of this species (Pl. 5, Fig. 1a–d), 16 mm in diameter, has 35 major septa. In this section, taken just below the bottom of the calyx, cardinal septum slightly shorter than the adjacent major septa; reaching the axis, the main fossula of the corallite attains a key-hole shape. Minor septa, with the exception of the long Km septum, very short.

The corals described here were transported or possibly redeposited before deposition. Most specimens lack epitheca, distal ends and calyx and are water damaged in appearance.

REMARKS: What distinguishes the studied specimens from those documented by Carruthers (1910) and Dobrolyubova *et al.* (1966) is primarily the larger number of septa at similar corallite diameters (Text-fig. 12). However, the arrangement of septa, the ontogenetic development, the characteristic shape of the main fossula (although variable in young stages), which always extends towards the corallite axis in adult stages, the long cardinal septum in young stages, and the distinct alar pseudofossulae are typical features of *Z. delanouei*. The specimens described above are very similar to those from Kuznetsk described by Dobrolyubova *et al.* (1966); one specimen (UAM.IG.Tc.C.JG-56, Pl. 4, Fig. 4) is distinguished by a slightly higher number of septa at similar corallite diameters (Text-fig. 12); in turn, three other specimens [UAM.IG.Tc.C.JG-22, UAM.IG.Tc.C.JG-51(1), UAM.IG.Tc.C.JG-52; Text-fig. 12; Pl. 5, Figs 1, 3] are distinguished by slightly larger corallite diameters. However, these specimens have

all the features of *Z. delanouei*, and the larger size in the adult stages (Text-fig. 12) makes them similar to *Z. persimillis*. This species, however, differs from the Canadian specimens by its elliptical cross-section. The examined specimens, with the exception of an oblique section (Pl. 5, Fig. 1c), have a circular cross-section and not an elliptical one as in *Z. persimillis*. Also puzzling is the presence of one elongated counter minor septum (Km) in specimen UAM.IG.Tc.C.JG-22 (Pl. 5, Fig. 1d). Elongated Km septa are present in *Enniskillenina* Kabakovich in Soshkina *et al.*, 1962, a specimen of similar age and occurrence in Canada. However, the absence of elongated Km septa in the younger growth stage and the presence of only one elongated Km septum, as well as the smaller size and smaller number of major septa and shorter minor septa, do not allow the assignment of the studied specimen to *Enniskillenina*. Perhaps the presence of one elongated Km septum is a pathological feature of this representative of *Z. delanouei*. It is a pity that the upper part of the corallite and calyx were not preserved (they are crushed). Had they not been crushed, it would be possible to check the possible continuation of the long Km septum, or the appearance of a second long Km septum.

Some doubt was also raised by specimens UAM.IG.Tc.C.JG-42(4), UAM.IG.Tc.C.JG-42(5), and UAM.IG.Tc.C.JG-61(1) (Pl. 4, Figs 1–3) and the unillustrated specimens UAM.IG.Tc.C.JG-35(2) and UAM.IG.Tc.C.JG-73(1), which resemble *Rotiphyllum* Hudson, 1942 due to what appears to be a long cardinal septum at the calyx floor (Pl. 4, Figs 1b, 2c, 3b). Careful analysis of the corallites, however, revealed that sediment may have entered the fossula through damage to the calyx bottom and walls, falsifying the image. Such suspicions were based on the fact that all other morphological features correspond to those of *Zaphrentites*.

*Zaphrentites delanouei* is mainly known from the Tournaisian, but is also documented in the Viséan (Asbian) of SW Spain (Rodríguez *et al.* 2016). Its presence in the Viséan of Canada, would therefore be an ecological appearance of this species in this area.

OCCURRENCE: Russian Platform, Ural, Kuznetsk Basin, Donbas, Donets Basin, Western Europe, Poland, Turkey, Iran – upper Tournaisian; SW Spain (Cordoba) – Viséan; Northwestern Canada (Jackfish Gap) – lower–middle Viséan.

Genus *Enniskillenina* Kabakovich  
in Soshkina *et al.*, 1962

TYPE SPECIES: *Zaphrentis enniskilleni* Milne-Edwards and Haime, 1851.

DIAGNOSIS: See Bamber *et al.* (2017, p. 37).

*Enniskillenia enniskilleni* (Milne-Edwards and Haime, 1851)  
(Text-figs 13–15)

1851. *Zaphrentis enniskilleni* Milne-Edwards and Haime, p. 334.  
 1852. *Zaphrentis enniskilleni* Milne-Edwards and Haime, p. 170, pl. 34, fig. 1.  
 1881. *Zaphrentis enniskilleni* Milne-Edwards and Haime; Thomson, p. 218 (25), pl. 3, fig. 1.  
 1881. *Zaphrentis curvulena (curvulina)* Thomson, p. 223 (30), pl. 4, fig. 4.  
 1904. *Amplexus cornutus* Stuckenberg, p. 13, pl. 4, fig. 3.  
 1904. *Anisophyllum carbonicum* Stuckenberg, p. 19, pl. 6, fig. 4.  
 1906. *Zaphrentis* aff. *enniskilleni*; Vaughan, p. 315, pl. 29, fig. 2.  
 1930. *Zaphrentis enniskilleni* Milne-Edwards and Haime; Lewis, p. 277, pl. 23, figs 1–8.  
 1931. *Zaphrentis delanouei* var. *kusnetzkenis*; Fomichev, p. 21, pl. 1, fig. 6.  
 1931. *Zaphrentis* cf. *enniskilleni*; Fomichev, p. 23, fig. 7.  
 1935. *Zaphrentis enniskilleni* Milne-Edwards and Haime; Lewis, p. 123, pl. 5, figs 1–8.  
 1940. *Zaphrentis enniskilleni* Milne-Edwards and Haime; Hill, p. 140.  
 1940. *Zaphrentis curvilinea* Hill, p. 142, pl. 7, fig. 73, pl. 8, figs 1–3(?), 4–10.  
 1966. *Enniskillenia enniskilleni* (Milne-Edwards and Haime); Dobrolyubova *et al.*, pp. 33–35, pl. 1, figs 12, 13.

DIAGNOSIS: (modified from Dobrolyubova *et al.* 1966). Major septa varied in length, the longest reaching the corallite axis, in counter quadrants may be thicker than in cardinal quadrants, pinnately arranged in cardinal quadrants, radially arranged in counter quadrants, zaphrentid septal arrangement in young stages; septal indexes n:d in mature growth stages 38–40:15–20; cardinal septum long in young stages, shortened in mature growth stages; counter septum usually slightly shorter than adjacent major septa; minor septa, except Km septa, short; Km septa form a triad with counter septum; cardinal fossula on concave side, distinct, deep, of varying shape, extends to corallite axis.

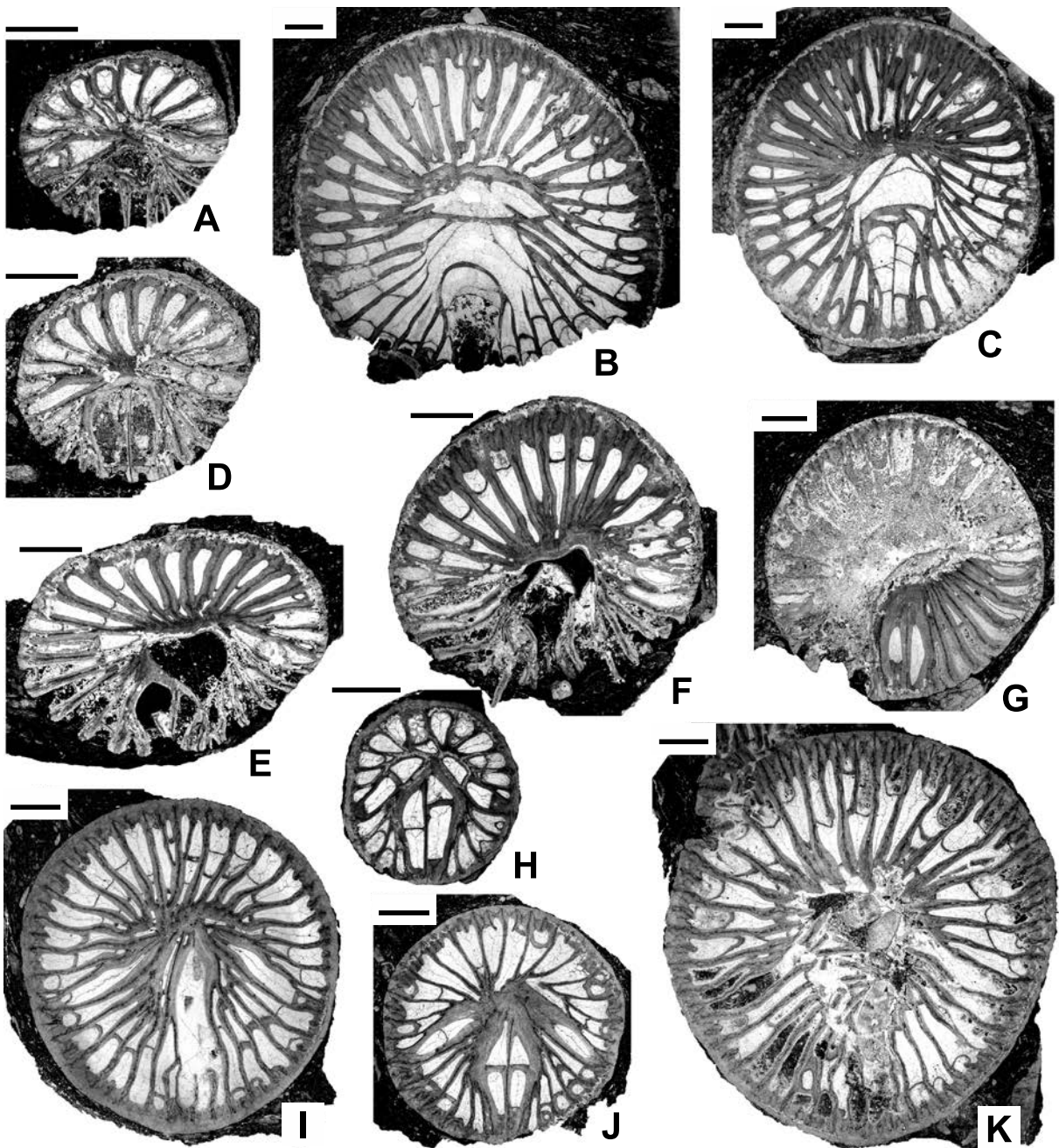
MATERIAL: Three specimens, UAM.IG.Tc.C.JG-99, UAM.IG.Tc.C.JG-99(1), UAM.IG.Tc.C.JG-99(2); up-

per Flett Formation (upper part of Meilleur Member); upper part of middle Viséan (Text-fig. 4).

DESCRIPTION: Corallites about 4 cm long; preserved calyx 20.5 mm in diameter and about 10 mm deep. Major septa of varying length and thickness; the longest extends to corallite axis (Text-figs 13A, D, H–J and 14A–E); thickness of major septa in ontogeny variable; usually in counter quadrants thicker than in cardinal quadrants (Text-fig. 13C, E, F, K). The n:d index of the septum in adult growth stages is 38–40:16–20 (Text-fig. 15). Cardinal septum thin; in young stages it is the longest septum (Text-figs 13H, J and 14B); in adult stages it shortens (Text-figs 13B, C, I and 14A, D, E); at the calyx floor it is either confined to the external wall or becomes visible as a septal rib (Text-figs 13K and 14E). Main fossula distinct, of different shape in different growth stages and in different specimens (Text-figs 13A–G, H–J and 14A–E); may be narrow, widened in corallite axis, or widened in the middle of its length. Counter septum usually slightly shorter than the longest major septa (Text-fig. 13B, C). Alar septa as long as the longest major septa. Alar pseudofossulae distinct in young stages (Text-fig. 13J), faint in older stages. Minor septa very short, or confined to external wall. In adult stages Km septa elongated, with counter septum forming a triad (Text-figs 13C, I, K and 14A). External wall with distinct septal furrows (Text-fig. 14F).

REMARKS: The Canadian specimens are very similar to those described by Dobrolyubova *et al.* (1966). Comparable are both the sizes (Text-fig. 15; Russian specimens reach 50–60 mm in length, usually 40 mm in length and 15–20 mm in calyx diameter in adult stages) as well as the skeletal structures of the corallites – different lengths and variable thicknesses of the major septa, which in the counter quadrants are greater than in the cardinal quadrants; cardinal fossula variable in shape; counter septum may be shortened; alar septa long; alar pseudofossulae distinct in young stages. The only difference is that in the specimens described herein, both Km septa are elongated and contratingent, whereas in the specimens described by Dobrolyubova *et al.* (1966), both or only one Km septum may be elongated and combined with the counter septum.

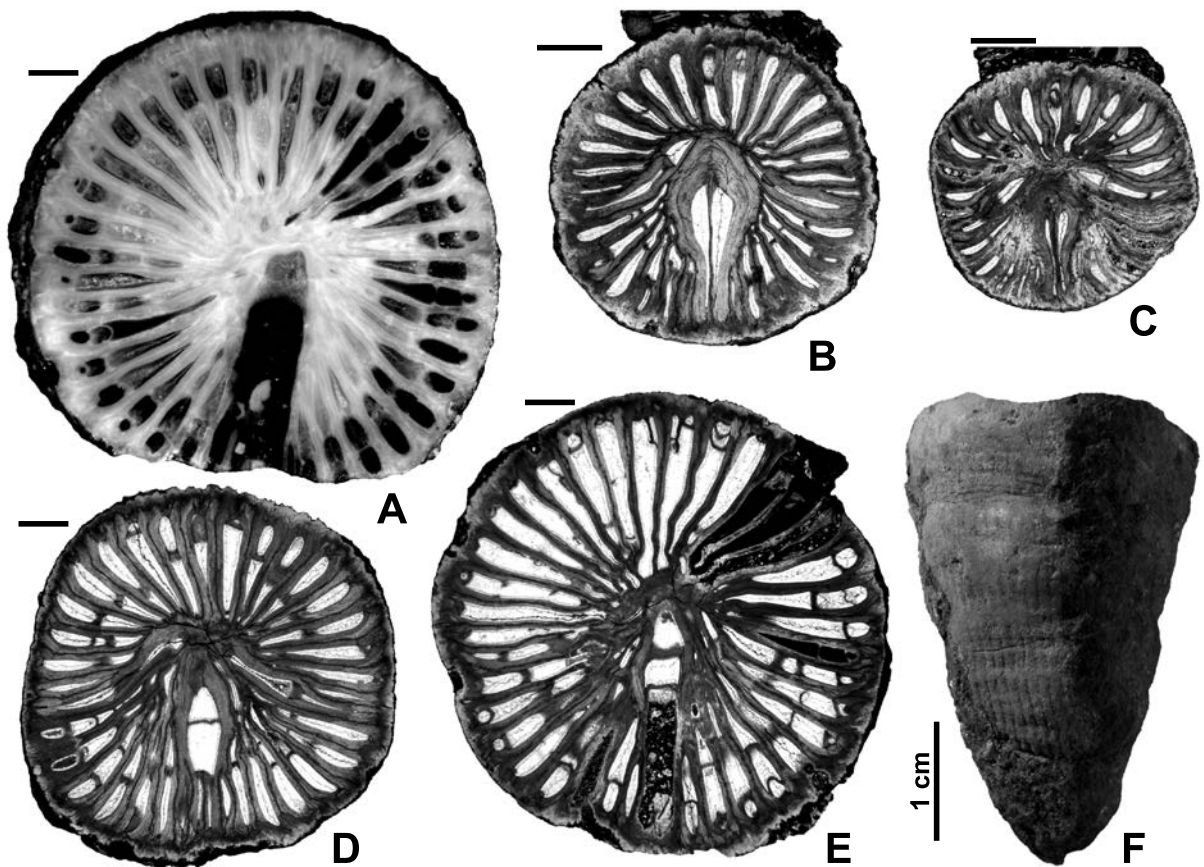
In the details of the internal structures, specimens from Canada are also very similar to specimens of the type species from the Viséan of Britain and Ireland (Lewis 1935). In both cases the major septa are usually straight, slightly flexed or convex towards the fossula, the alar pseudofossulae are conspicuous,



Text-fig. 13. *Enniskillenia enniskilleni* (Milne-Edwards and Haime, 1851) from the upper Flett Formation (upper part of Meilleur Member), upper part of middle Viséan. A–G – UAM.IG.Tc.C.JG-99(1): A, D, E, F – immature growth stage; B, C, G – mature growth stage. H–K – UAM.IG.Tc.C.JG-99(2): H, J – immature growth stage; I, K – mature growth stage. Scale bars equal to 2 mm.

the cardinal fossula extends to or beyond the corallite axis, and may expand inwards broadly at the neanic stage, but narrows inwards or attains subparallel walls at later stages. Some differences can be seen in the size of the specimens. Although the n:d ratios of the compared specimens are similar, the specimens

from Britain are longer, reaching a length of 8 cm (specimens from Canada reach 4 cm). Furthermore, in the British specimens the minor septa appear when about 24 major septa are present, whereas in the Canadian specimens, minor septa appear only when 31–32 major septa are present (Text-fig. 13F, J). It also



Text-fig. 14. *Enniskillenia enniskilleni* (Milne-Edwards and Haime, 1851) from the upper Flett Formation (upper part of Meilleur Member), upper part of middle Viséan. A–F – UAM.IG.Tc.C.JG-99: A, D, E – mature growth stage, A – image in reflected light; B, C – immature growth stage; F – corallite surface. Scale bars for A–E equal to 2 mm.

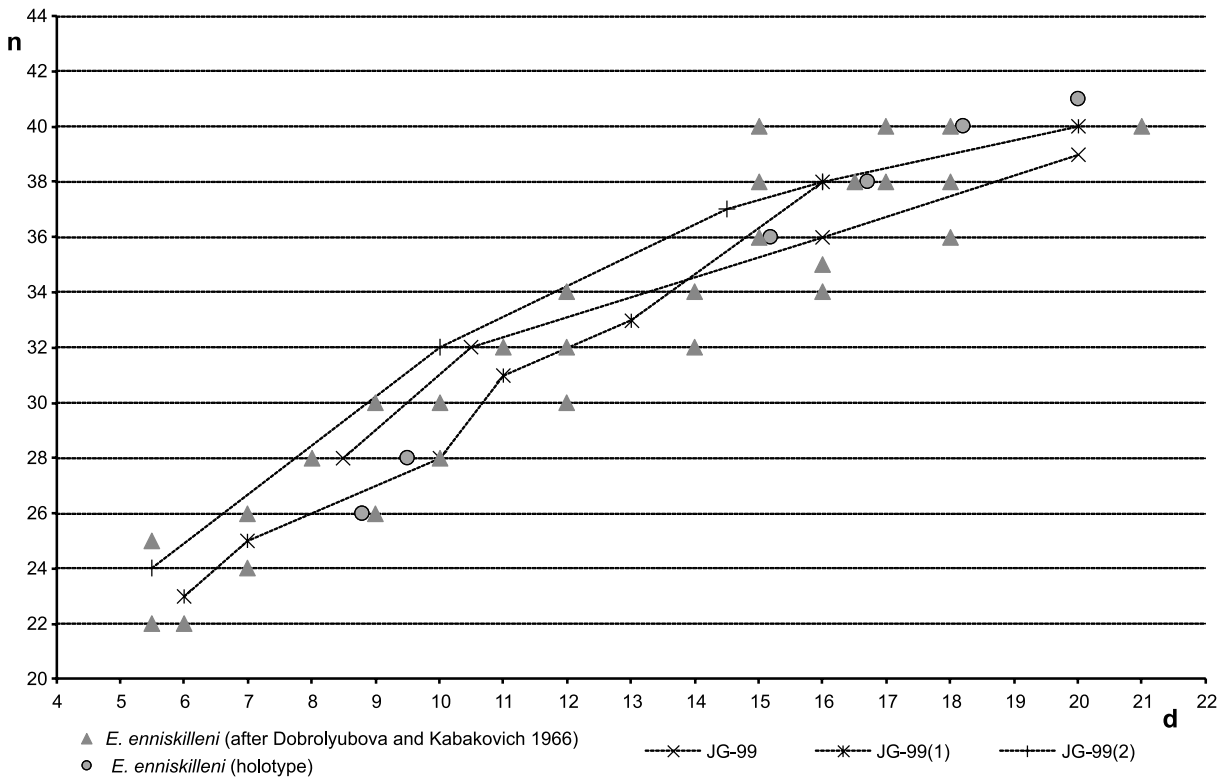
appears that elongation of the Km septa is not a rule in British specimens, as indicated by Lewis (1935, p. 124): “In many individuals the minor septa flanking the counter septum are much longer than the rest of the minor septa”.

In comparison with *Zaphrentis curvilinea* from Scotland (Hill 1940, 1981), the Canadian specimens are related to them by: the development of the cardinal fossula; the cardinal septum, which at first bisects the fossula, but becomes very short early in ontogeny; the counter-lateral and alar septa, which are usually very long, and may be slightly thickened at their inner margins; minor septa, which in both cases are visible with a diameter of c. 16–17 mm and a number of major septa 36–38. The Scottish specimens, however, differ from the Canadian ones in their deep calyx and larger size, as they reach a length of 9.0 cm, and a diameter 4.0 cm at the calyx. And although at a diameter of 17 mm they have similar numbers

of major septa, at diameters of 25–35 (not reached by the Canadian specimens) they have 49–53 major septa. Furthermore, the Km septa, although they may be longer than the other minor septa, do not form a typical triad (not seen in the illustrations in Hill 1940, pl. 7, fig. 73; pl. 8, figs 1–10).

Relative to the abundant Canadian *Enniskillenia multiseptata* Bamber and Rodríguez in Bamber *et al.*, 2017 (upper Viséan, lower Etherington Formation), specimens from Jackfish Gap differ by being more than twice as small in size (specimens from the Etherington Formation reach 8–10 cm in length) and more than twice as small in n:d.

OCCURRENCE: Kuznetsk Basin – middle Tournaisian–lower Viséan; Russian Platform, Donbas, Western Europe, Canada, USA – Viséan (after Dobrolyubova *et al.* 1966); Northwestern Canada (Jackfish Gap) – upper part of middle Viséan.



Text-fig. 15. *Enniskillenia enniskilleni* (Milne-Edwards and Haime, 1851) – plot of the number of major septa (n) vs. diameters (d). Symbols joined by lines represent values taken from individual specimens.

Family Antiphyllidae Ilina, 1970  
Genus *Bradyphyllum* Grabau, 1928

TYPE SPECIES: *Bradyphyllum bellicostatum* Grabau, 1928.

DIAGNOSIS: See Fedorowski (1973, p. 105).

*Bradyphyllum clavigerum* Easton, 1962  
(Text-fig. 16)

1962. *Bradyphyllum clavigerum* Easton, p. 31, pl. 3, figs 9–17.

DIAGNOSIS: See Easton (1962, p. 31).

MATERIAL: One specimen, UAM.IG.Tc.C.JG-8(1); lower Flett Formation (Tlogotsho Member); lower part of lower Viséan (Text-fig. 4).

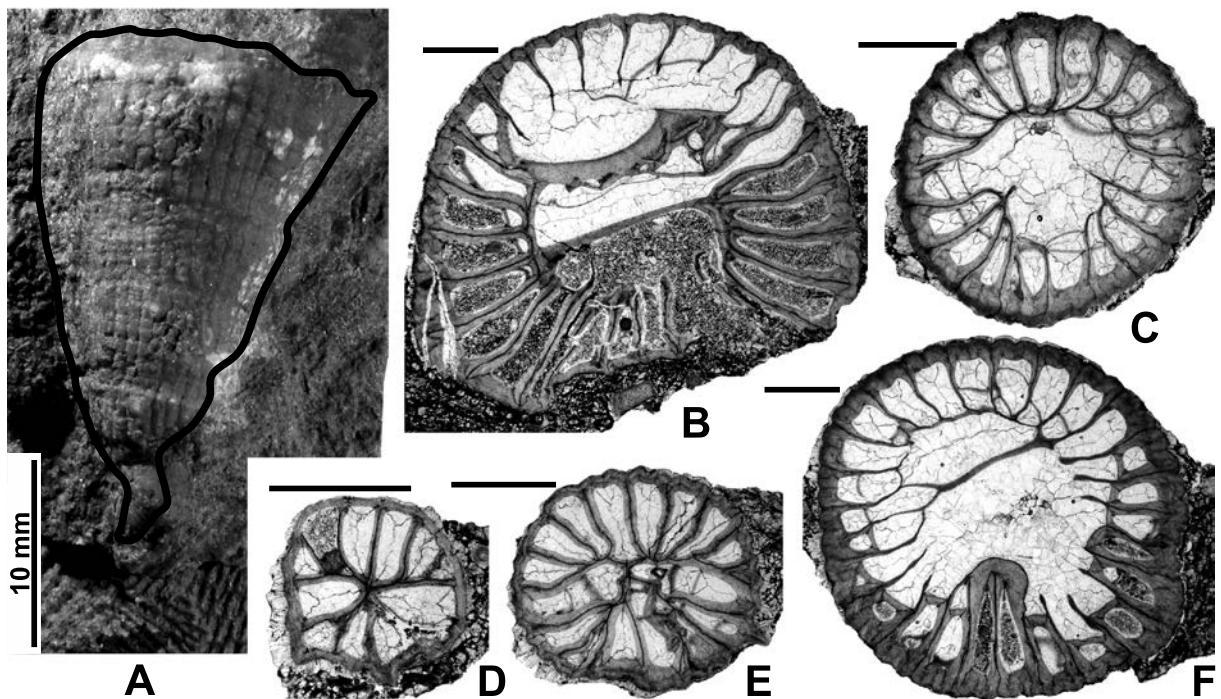
DESCRIPTION: Small, ceratoid, reaching maximum preserved length of nearly 30.0 mm (Text-fig. 16A) and maximum mature diameter of about 15.0 mm.

External wall with well-preserved septal furrows. Calyx 15 mm deep.

The earliest stage observed (Text-fig. 16D) has 12 major septa at alar diameter of 2.6 mm. Cardinal, counter, alar and the two major septa of counter quadrants meet axially. Cardinal fossula well-developed, closed. Alar and counter pseudofossulae distinct. Corallite external wall 0.1–0.2 mm thick, smooth in outline, indicating absence of septal furrows.

In the late neanic stage (Text-fig. 16E), there are 17 major septa, subradially arranged in counter quadrants and pinnately arranged in cardinal quadrants, with 3 in each cardinal quadrant and 10 on the counter side of the section, and the corallite is 4.6 mm in diameter. Cardinal septum crosses wide cardinal fossula. Alar pseudofossulae well-developed. External wall of corallite 0.2 mm thick, with poorly developed septal furrows.

In the transverse section at n:d index = 23:6.2 – early maturity (Text-fig. 16C), major septa shortened to 1/2 of the corallite radius, form 3 groups/fascicules, separated from each other by cardinal and alar pseudofossulae. Cardinal quadrants contain 4



Text-fig. 16. *Bradyphyllum clavigerum* Easton, 1962 from the lower Flett Formation (Tlogotsho Member), lower part of lower Viséan. A-F – UAM.IG.Tc.C.JG-8(1): A – corallite surface; B, F – mature growth stage; C–E – immature growth stage. Scale bars for B–F equal to 2 mm.

and 5 septa. Cardinal septum shortened to 3/4 of the length of the major septa in broad, open fossula. Counter septum as long as other major septa. External wall of corallite 0.5 mm thick, with well-developed septal furrows.

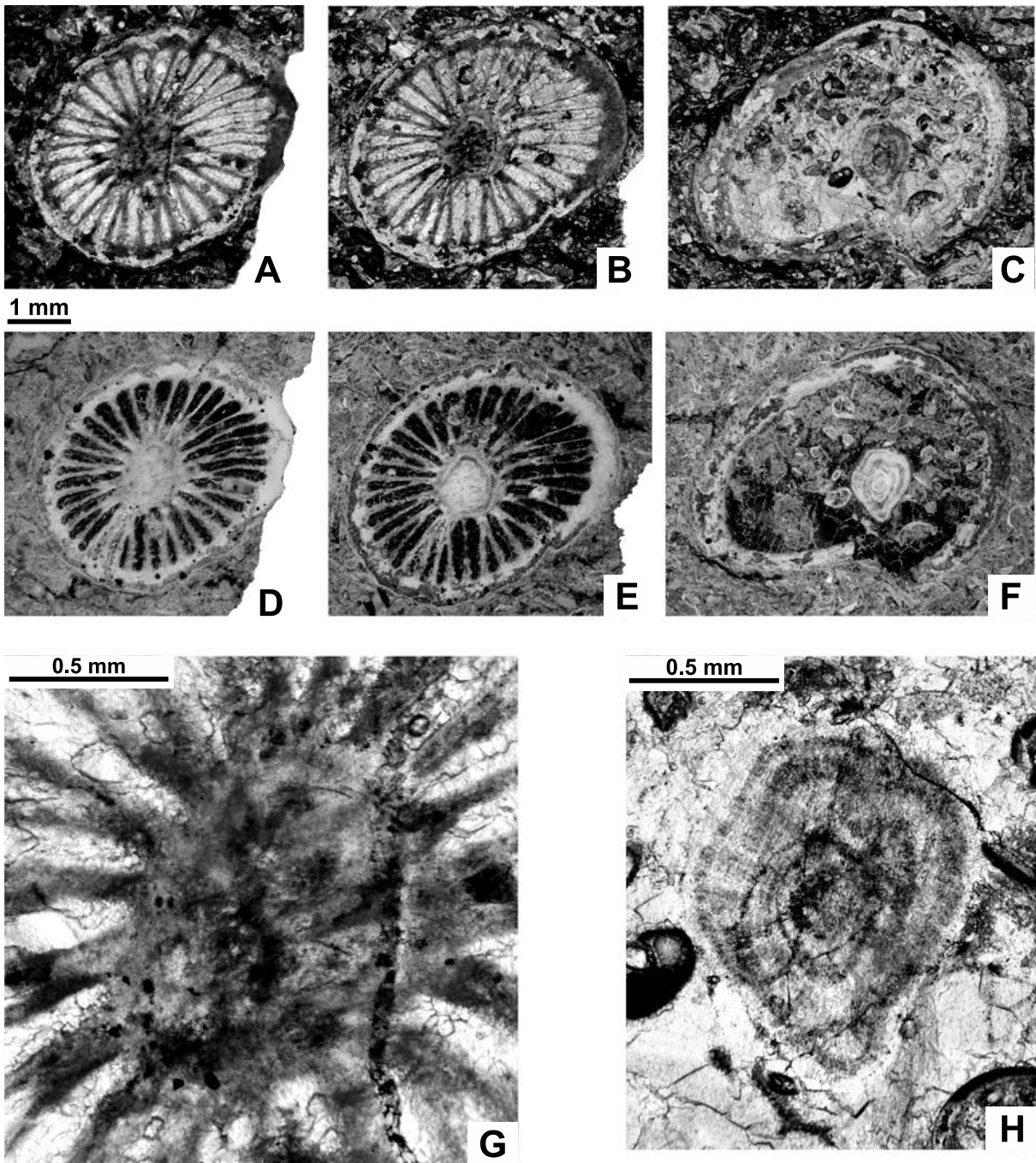
In further growth (partially above calyx floor) with n:d = 26:10, major septa shortened up to 1/2 of the corallite radius in length (Text-fig. 16F). Cardinal septum long, slightly rhopaloid in well-defined fossula, partially filled with stereoplasm deposited on the fossular wall, bordered by two almost parallel major septa. Alar pseudofossulae indistinct. Counter septum as long as other major septa. Minor septa are usually absent or rudimentary, incorporated into the wall. External wall of corallite 0.5 mm thick, with well-developed septal furrows.

A section taken partially above the calyx floor (Text-fig. 16B, oblique section) shows 26 major septa at alar diameter of 12.0 mm. Major septa of different length, withdrawn from the axial area, much longer and thicker in the calyx than in the part slightly below the calyx floor.

REMARKS: The examined specimen shows many features in common with *B. clavigerum*. Particularly

high similarity can be observed at the level of early growth stages. The earliest stage of the holotype of *B. clavigerum* has an n:d index of 13:2.3 (vs. 12:2.6 in the Canadian specimen). In both specimens the cardinal, alar and counter septa meet axially. Alar pseudofossulae are discernible. In stage 18:4.0, the septa are arranged subradially, 3 in each cardinal quadrant and 11 on the counter side of the section (Easton 1962); in the Canadian specimen, the numbers are 3 and 10, respectively. In both specimens, the cardinal septum crosses the wide cardinal fossula, and the alar pseudofossulae are well-developed. At early growth stages in both specimens, the major septa are long and mostly reach the corallite axis. At these growth stages, the differences between the specimens compared are visible in the holotype where the major septa are dilated and meet along their sides for most of their length, the counter fossula is indicated by extra-wide loculi only at n:d = 20:4.7, and the counter septum is slightly rhopaloid. In the Canadian specimen the counter septum is not rhopaloid, and the counter pseudofossula is already visible at n:d = 12:2.6.

At mature growth stages, the n:d septal indices are 22:7.9 in the holotype and 23:6.2 in the Canadian

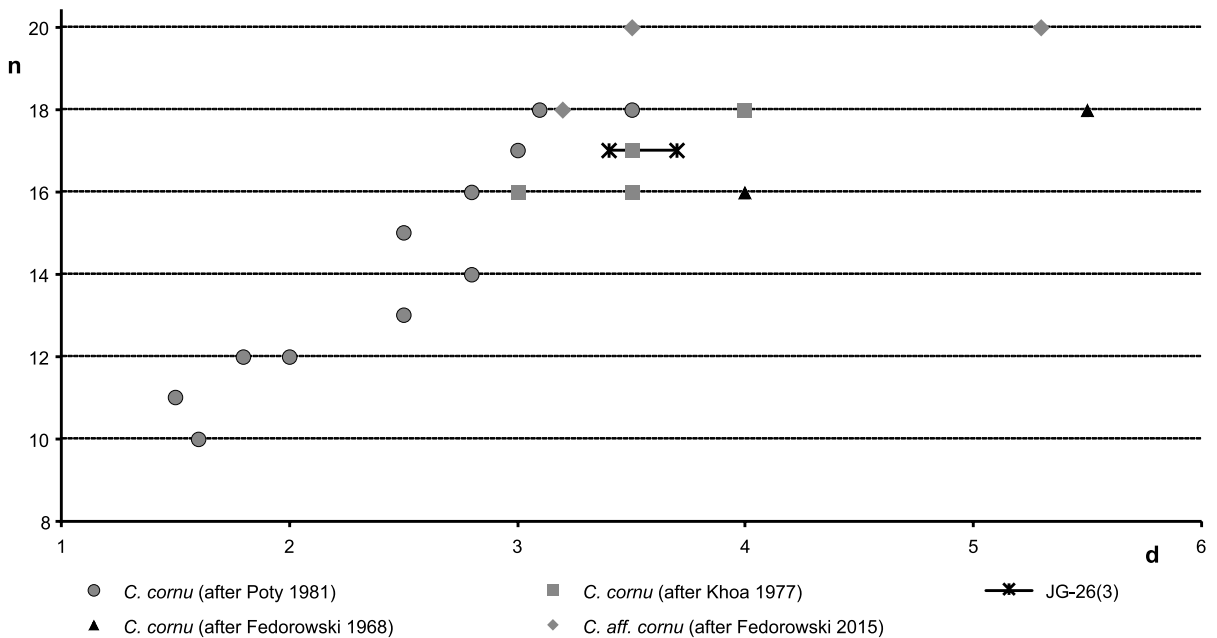


Text-fig. 17. *Cyathaxonia cornu* Michelin, 1847 from the lower Flett Formation (middle part of Tlogotsho Member), lower Viséan. A–H – UAM.IG.Tc.C.JG-26(3): A–C – mature growth stage, in transmitted light microscopy; D–F – same section, in dark-field microscopy; G – enlarged fragment from A; H – enlarged fragment from C.

specimen. In both specimens, major septa are arranged radially, shortened to about 1/2 of the coralite radius, equally short, deep cardinal fossula with shortened cardinal protoseptum; minor septa poorly developed, restricted to the external wall. A section

taken at the calyx floor (Text-fig. 16F) with shortened major septa ( $n:d = 26:10$ ) and a slightly longer rhopaloid cardinal septum, suggests that the septa are amplexoid. This can also be seen in the illustration of the paratype made by Easton (1962, pl. 3, fig. 12b;  $n:d$





Text-fig. 18. *Cyathaxonia cornu* Michelin, 1847 – plot of the number of major septa (n) vs. diameters (d). Symbols joined by lines represent values taken from individual specimens.

= 24:10). This specimen, in general, is very similar to the Canadian specimen.

The main difference between the compared specimens, therefore, is that the examined specimen does not have thickened septa in the young stage and that the major septa (except for the cardinal septum) are not rhopaloid. However, although Easton (1962) claims that the major septa are rhopaloid, this is not apparent in all illustrations (Easton 1962, pl. 3, figs 9d, 12b). It is possible that the thickened major septa in the young growth stages of *B. clavigerum* express the ecological variability of this species.

OCCURRENCE: USA (central Montana) – upper Mississippian or lower Pennsylvanian; Northwestern Canada (Jackfish Gap) – lower Viséan.

Order Stauriida Verrill, 1865  
 Suborder Metriophyllina Spasskiy, 1965  
 Family Cyathaxoniidae Milne-Edwards and Haime, 1850  
 Genus *Cyathaxonia* Michelin, 1847

TYPE SPECIES: *Cyathaxonia cornu* Michelin, 1847.

DIAGNOSIS: See Hill (1981, p. F186).

*Cyathaxonia cornu* Michelin, 1847  
 (Text-figs 17, 18)

1847. *Cyathaxonia cornu* Michelin, p. 258, pl. 59, figs 9a, b.  
 1909. *Cyathaxonia cornu* Michelin; Faurot, p. 75 (7).  
 1913. *Cyathaxonia cornu* Michelin; Carruthers, p. 53, pl. 3, figs 4–7.  
 1941. *Cyathaxonia cornu* Michelin; Hill, p. 195.  
 1953. *Cyathaxonia archangelskyi* Fomichev, p. 60, pl. 1, figs 6–9.  
 1953. *Cyathaxonia kapustini* Fomichev, p. 57, pl. 1, figs 1, 2.  
 1960. *Cyathaxonia cornu* Michelin; Vassilyuk, p. 157, pl. 12, fig. 8.  
 1964. *Cyathaxonia cornu* Michelin; Vassilyuk, p. 87, pl. 7, fig. 1.  
 1968. *Cyathaxonia cornu* Michelin; Fedorowski, p. 210, pl. 1, figs 4a–d.  
 1977. *Cyathaxonia cornu* Michelin; Khoa, p. 319, text-fig. 4, pl. 1, figs 1–6.  
 1978. *Cyathaxonia cornu* Michelin; Poty in Kimpe *et al.*, pl. 5, fig. 5.  
 1981. *Cyathaxonia cornu* Michelin; Poty, p. 17, text-fig. 8, pl. 2, figs 2–5.  
 1999. *Cyathaxonia cornu* Michelin; Liao and Rodríguez, p. 541, fig. 3.6a–c.

DIAGNOSIS: See Fedorowski (1968, p. 210).

**MATERIAL:** One specimen, UAM.IG.Tc.C.JG-26(3); lower Flett Formation (middle part of Tlogotsho Member); lower Viséan (Text-fig. 4).

**DESCRIPTION:** Small, partially silicified corals, reaching maximum preserved length of nearly 7.0 mm and maximum mature diameter of about 4.0 mm. The sections examined (Text-fig. 17A–C) show 18 major septa at C-K diameter of 3.7 mm. The arrangement of the septa corresponds to that of *Cyathaxonia cornu*. Major septa slightly rhopaloid, thickened at the periphery, reach the columella. Cardinal septum thinner than the others. Minor septa contratingent, somewhat thinner and shorter than the major septa; sometimes longer and joining the major septa at the columellar margin; they are as much or less thickened than the major septa. Columella oval (Text-fig. 17G), occupies about one-fourth of the diameter of the corallite, thickened by stereotheca adhering to it in concentric lines (Text-fig. 17H). External walls of the corallites are about 0.3 mm thick, smooth in outline, indicating absence of septal furrows.

**REMARKS:** The preserved growth stages are morphologically very similar to *C. cornu* described by Carruthers (1913), Grabau (1922), Fedorowski (1968), Khoa (1977) and Poty (1981). Also its septal n:d indices (Text-fig. 18) are comparable with the septal n:d index of the specimen examined in this study.

**OCCURRENCE:** Poland (Lublin region and Holy Cross Mts.) – upper Viséan; Western Europe (Great Britain, Belgium, France, Ireland) – Tournaisian–Viséan; Western Sahara – Tournaisian; Russia (Urals, Moscow Basin, Donets Basin) – lower Carboniferous; Northwestern Canada (Jackfish Gap) – lower Viséan.

Suborder Aulophyllina Hill, 1981  
Family Ekvasophyllidae Hill, 1981  
Genus *Ekvasophyllum* Parks, 1951

**TYPE SPECIES:** *Ekvasophyllum inclinatum* Parks, 1951, p. 175.

**DIAGNOSIS:** See Hill (1981, p. F373).

*Ekvasophyllum inclinatum* Parks, 1951  
(Pl. 6, Fig. 1; Text-figs 19, 20)

1951. *Ekvasophyllum inclinatum* Parks, p. 175, pl. 29, figs 1, 3.

**DIAGNOSIS:** See Parks (1951, p. 175).

**MATERIAL:** Two specimens, UAM.IG.Tc.C.JG-71, UAM.IG.Tc.C.JG-78, one partially recrystallized; upper Flett Formation (lower part of Meilleur Member); middle Viséan (Text-fig. 4).

**DESCRIPTION:** Trochoid, slightly curved corals (Pl. 6, fig. 1g; Text-fig. 19A), partially silicified (Pl. 6, Figs 1a–f). Corallite 5.5 cm long on convex side and 3.0 cm long on concave side, without proximal ends. Calyx diameter is 21.5 and 25.0 mm. Septal index n:d of mature growth 49:21.5 and 48:25.0 (Text-fig. 20). Cardinal septum on convex side. Tabulae incomplete, in the section perpendicular to the C-K line, slightly upturned at margins, slope upward toward axis where they join the columella at a large angle (Text-fig. 19F). Tabellae visible in this illustration flatly reaching the columella are the result of a slightly oblique section.

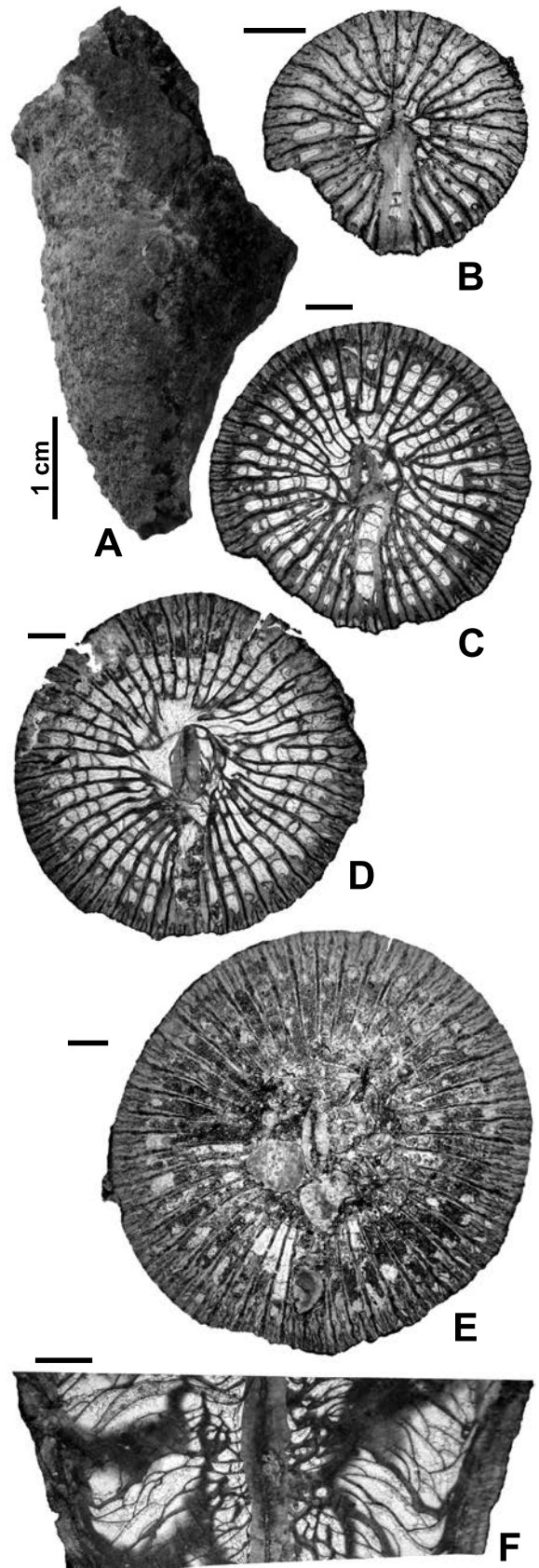
The earliest section examined (Pl. 6, Fig. 1a), late neanic/early mature growth stage, shows 26 major septa at alar diameter of 6.0 mm. All septa are thickened and occupy most of the space in the corallite interior. Major septa tend to have radial symmetry except around the cardinal fossula, where they tend to be pinnately arranged. Cardinal septum shortened to 1/4 of the corallite radius. Narrow, parallel-sided, long cardinal fossula is on the convex side of the corallite, enclosed by a central column (Pl. 6, Fig. 1a, a'). Cardinal fossula almost completely filled by the stereoplasm deposited on the fossular wall. Central column distinct, connected to but not continuous with the longest major septa. Minor septa very short, incorporated into the wall. The earliest stage of the second specimen (UAM.IG.Tc.C.JG-78, Text-fig. 19B) shows 30 major septa at alar diameter of 8.2 mm. All septa are thickened. Major septa arranged pinnately in cardinal quadrants and radially in counter quadrants, of varying length. Cardinal septum also shortened to 1/4 of the corallite radius, and narrow, parallel-sided, long cardinal fossula, is also almost completely filled by stereoplasm deposited on the fossular wall. Counter septum slightly thinner than the other major septum. Alar pseudo-fossulae indistinct. Central column oval, with distinct median lamella. Minor septa short, 1/6 of the corallite radius.

In the section taken 5.0 mm above section 1a (illustrated in Pl. 6, Fig. 1b), the septal index is 33:9. Apart from the septal index, other features of morphological structure are similar to those observed on the transverse section.

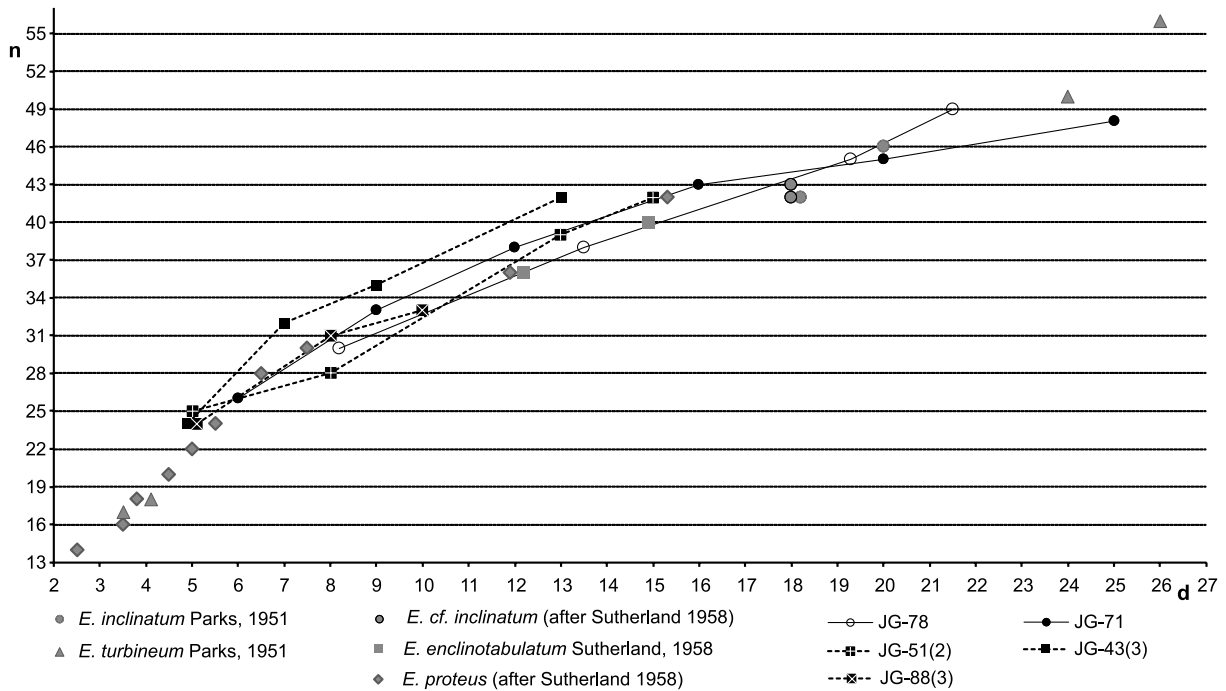
The higher sections (Pl. 6, Fig. 1c, d; Text-fig. 19C), taken every 5.0 mm relative to the previous sections, have septal indices of 38:12, 43:16 and 38:13.5, respectively. Compared to the previous sections, these sections differ in the disappearance of the columellar axial structure. In its place, either the ends of the longest major septa (Pl. 6, Fig. 1d) or a single lamella (Text-fig. 19C) remain, which, together with the sections through the traverses of the tabulae form an irregular axial structure. Initially narrow, main fossula may widen or curve slightly in the corallite axis. Main septum is of equal length with the longest minor septa, which slightly penetrate into the tabulae. Most minor septa are limited to about 1.0 mm thickness of the external septothecal wall.

Subsequent sections, made below the calyx floor (Pl. 6, Fig. 1e; Text-fig. 19D), with septal indices n:d 45:20 and 45:19.3 are characterized by the reappearance of the columellar axial structure (Pl. 6, Fig. 1e') and the presence of dissepiments. Dissepimentarium poorly visible in specimen UAM.IG.Tc.C.JG-78 (Text-fig. 19D), well-developed in specimen UAM.IG.Tc.C.JG-71 (Pl. 6, Fig. 1e), 2.0 mm wide, composed of interseptal, concentrically arranged dissepiments. Major septa arranged pinnately in counter quadrants and radially in cardinal quadrants, of different length. The longest major septa connect to the axial structure. Cardinal septum and minor septa confined to dissepimentarium. Cardinal fossula elongated, reaching the corallite axis. External wall 0.2 mm thick.

A transverse section near the calyx floor (Pl. 6, Fig. 1f) shows a very short cardinal septum in a well-defined fossula; septal index n:d = 48:25. Most of the major septa extend to the axis. Minor septa straight, about 1/4 of the corallite radius. Dissepimentarium 1/4–1/3 of the corallite radius in width, dissepiments interseptal. External wall thin. Due to significant recrystallization of calyx, axial structure and inner ends of the septa are not visible. Axial structure is also not visible in the upper part of the calyx (Pl. 6, Fig. 1h). However, the section illustrated in Text-fig. 19E (specimen UAM.IG.Tc.C.JG-78) shows the presence of the axial structure at least in the mid-depth of the calyx. This section also reveals the shortening of all the major septa (49 in number) to about 2/3 to 1/2 of the corallite radius; they are radially arranged.



Text-fig. 19. *Ekvasophyllum inclinatum* Parks, 1951 from the upper Flett Formation (lower part of Meilleur Member), middle Viséan. A–F – UAM.IG.Tc.C.JG-78: A – corallite surface; B – immature growth stage; C–E – mature growth stage; F – longitudinal thin section, perpendicular to the C–K line. Scale bars for B–F equal to 2 mm.



Text-fig. 20. *Ekvasophyllum* Parks, 1951 – plot of the number of major septa (n) vs. diameters (d). Symbols joined by lines represent values taken from individual specimens.

REMARKS: Due to the creation of *E. inclinatum* by Parks (1951) on the basis of one transverse section and one longitudinal section from the adult holotype, and one transverse section from the adult paratype, it is not clear whether the features observed in the development of the specimens described above may be present in *E. inclinatum*. According to the diagnosis, this species has a “solid, slightly laterally compressed, rod-like columella” (Parks 1951, p. 175). In the Canadian specimens the columella (axial structure) changes during ontogeny. From a series of transverse sections, only one (Pl. 6, Fig. 1e, e’) shows features similar to those described by Parks (1951), including a similar axial structure. Finally, the affiliation of the studied specimens to this species was determined by shape of the tabularium (Text-fig. 19F), which is very similar in shape to that described and illustrated by Parks (1951, pl. 29, fig. 1b). The small fragment of the columella, seen in the longitudinal thin-section of the Canadian specimen also shows that, at least in the higher part of the corallite, it is solid and of similar thickness to that of the holotype.

The variable axial structure of the examined specimens makes them similar to *Ekvasophyllum proteus* Sutherland, 1958. However, representatives of this species are smaller. The diameters of their

calyxes are 12–15 mm, and the number of septa is 36–42 (Text-fig. 20); they also have a narrower dissepimentarium, and the axial structure is still visible at the calyx floor. The last two features are observed in specimen UAM.IG.Tc.C.JG-78 (Text-fig. 19E), but because of its larger size (n:d = 49:21.5) this specimen cannot belong to *E. proteus*.

Many features, including the septal index of the adult stages, the length and arrangement of the major septa, the structure and width of the dissepimentarium, and the axial structure in adult stages, make the specimens studied similar to specimens described by Sutherland (1958) from the Liard River region, designated by him as *Ekvasophyllum cf. inclinatum*. However, the disappearance of the columnar axial structure in the early mature growth stages in the specimens studied differs from Sutherland’s (1958) specimens, in which the columnar axial structure is visible in sections of all growth stages. Furthermore, the specimens described by him differ from *E. inclinatum* in having much more steeply inclined tabulae. It is therefore not possible to identify Sutherland’s (1958) specimens with those described in this article.

OCCURRENCE: Northwestern Canada (Jackfish Gap) – middle Viséan.

*Ekvasophyllum enclinotabulatum* Sutherland, 1958  
(Pl. 7, Figs 1, 2; Text-figs 20, 21)

1958. *Ekvasophyllum enclinotabulatum* Sutherland, pp. 81–83, pl. 27, figs 1–4; pl. 28, figs 1, 2.

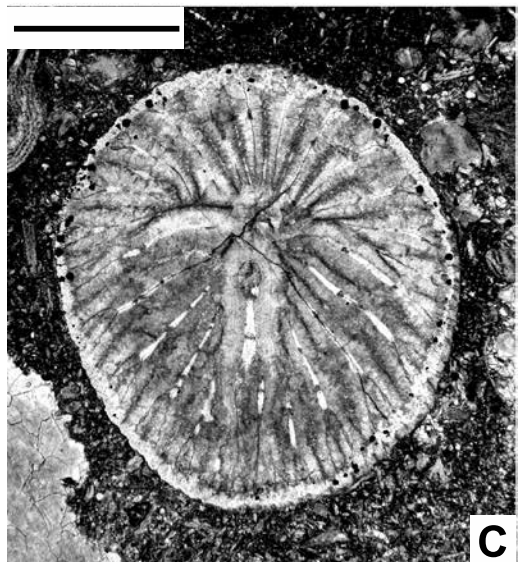
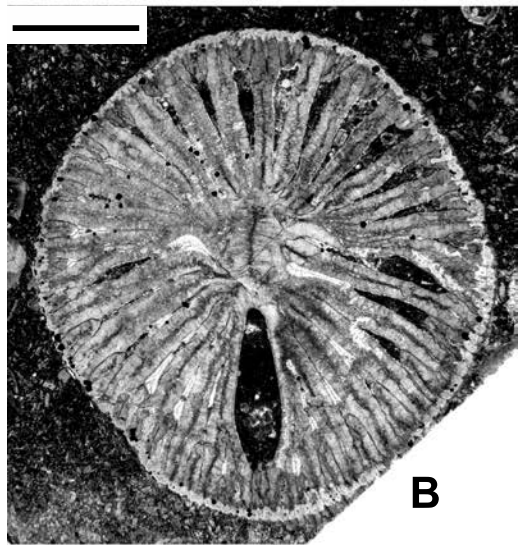
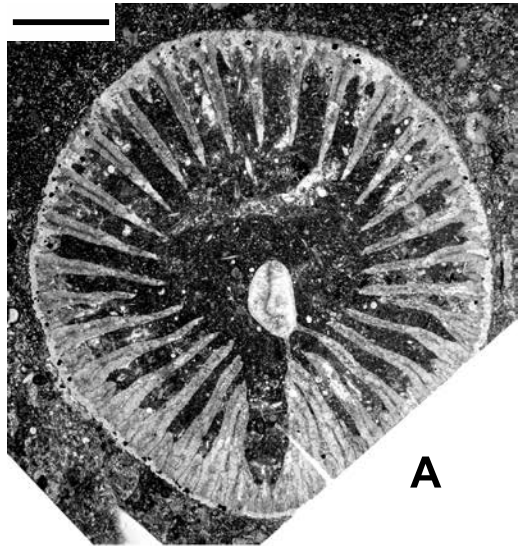
DIAGNOSIS: See Sutherland (1958, p. 81).

MATERIAL: Six specimens, partially recrystallized, UAM.IG.Tc.C.JG-34, UAM.IG.Tc.C.JG-42(3), UAM.IG.Tc.C.JG-43(3), UAM.IG.Tc.C.JG-51(2), UAM.IG.Tc.C.JG-88(2), UAM.IG.Tc.C.JG-88(3); Flett Formation (middle part of Tlogotsho Member to middle part of Meilleur Member); lower–middle Viséan (Text-fig. 4).

DESCRIPTION: Trochoid, slightly curved (Pl. 7, Fig. 2e), partially silicified. Corallite 15–20 mm long, without proximal ends. Calyx 10–15 mm in diameter. Septal index n:d of mature growth 42:15 (Text-fig. 20). Cardinal septum on convex side. Cardinal fossula narrow, closed, extends to axis, marked by a depression in the tabulae. Simple axial column protrudes in the floor as a knob (Pl. 7, Fig. 2f).

The earliest section examined, an early mature growth stage (Pl. 7, Fig. 2a; Text-fig. 21C), shows 24 major septa at 5.0 mm alar diameter. All septa are thickened and occupy almost the entire space in the corallite interior. Major septa, arranged pinnately in the cardinal quadrants and radially in the counter quadrants, vary in length. Cardinal septum shortened to 1/2 of the corallite radius. Narrow, parallel-sided, long cardinal fossula is located on the convex side of the corallite, enclosed by axial structure. Cardinal fossula is almost completely filled by stereoplasm deposited in the fossular wall. Central column distinct, connected to but not continuous with the longest major septa. Counter septum not distinct from the other major septa of the counter quadrants. Alar pseudo-fossulae distinct. Central column oval, with distinct median lamella. Minor septa straight, short, 1/4 of the corallite radius in length, incomplete.

A thin section cut at 8.0–9.0 mm alar diameter shows 28–35 major septa (Pl. 7, Figs 1a, 2b, c). All septa are thickened and occupy almost the entire space in the corallite interior. Major septa arranged pinnately in cardinal quadrants and radially in counter quadrants, of different length. Cardinal sep-



Text-fig. 21. *Ekvasophyllum enclinotabulatum* Sutherland, 1958 from the Flett Formation (middle part of Tlogotsho Member – middle part of Meilleur Member), lower–middle Viséan. A–C – UAM.IG.Tc.C.JG-88(3), mature growth stage. Scale bars equal to 2 mm.

tum shortened to half the corallite radius. Cardinal fossula narrow, parallel-sided, long, enclosed by axial structure. Central column distinct, connected to but not continuous with longest major septa. Counter septum not distinct from other major septa. Alar pseudofossulae indistinct. Central column oval, with distinct median lamella. Minor septa straight, short, 1/5 of the corallite radius in length.

A thin section (Pl. 7, Figs 1b, 2d), cut partially above cardinal fossula floor, at alar diameter of 13 mm shows 39 and 42 major septa, most of them extending to the corallite axis, all slightly thinner than those in the transverse sections. Cardinal septum as short as minor septa (Pl. 7, Fig. 1b) or reaches 1/2 of the corallite radius (Pl. 7, Fig. 2d, d'), thinner than major septa. Cardinal fossula narrow, extending to central column. Counter septum as long as the longest major septa, extends to central column, but is not continuous with it. Alar pseudofossulae indistinct. Minor septa well developed, short, 1/5 of the corallite radius in length.

A transverse section near the calyx floor (Pl. 7, Fig. 1c) shows a very short cardinal septum in well-defined fossula; n:d index 42:15. Most of the major septa reach the axis. Minor septa straight, about 1/5 of the corallite radius. Dissepimentarium narrow, composed of 1–2 rows of interseptal dissepiments, 1/5 of the corallite radius in width.

Specimen UAM.IG.Tc.C.JG-88(3) (Text-fig. 21A–C) differs slightly from the others. This is probably due to the fact that it is a young specimen of this species, as may be evidenced by the absence of a developed dissepimentarium, which appears late in ontogeny. On the transverse section, at 5.0 mm in diameter, it does not differ from the specimens described above. However, at 8.0 mm in diameter (Text-fig. 21B) the calyx floor can be observed in this specimen; the number of major septa is 31, and the major septum is very short, equal in length to the minor septa. A section taken slightly higher passes through the middle part of the calyx (Text-fig. 21A). The septal index n:d is 33:10. Major septa withdraw from the axis of the corallite, their lengths are 1/2 to 3/4 of the corallite radius (slightly oblique section, the central part is dominated by an oval columella.

REMARKS: Despite the lack of a longitudinal section, the features observed on transverse sections are closer to *E. enclinatorulatum* than to the very similar *E. proteus* with similar septal indices n:d (Text-fig. 20), which, however, is distinguished by having a variable axial structure, which may be lath-like, kidney-shaped or irregular in cross-section. The specimens examined,

on the other hand, have a regular central columella, a narrower dissepimentarium, and smaller corallites, maximally reaching 20 mm in length. Corallites of *E. proteus* reach 25–35 mm in length.

OCCURRENCE: Western Canada (British Columbia, Prophet Formation) – middle Mississippian, (Jackfish Gap) – lower–middle Viséan.

*Ekvasophyllum* cf. *turbineum* Parks, 1951  
(Text-figs 22, 23)

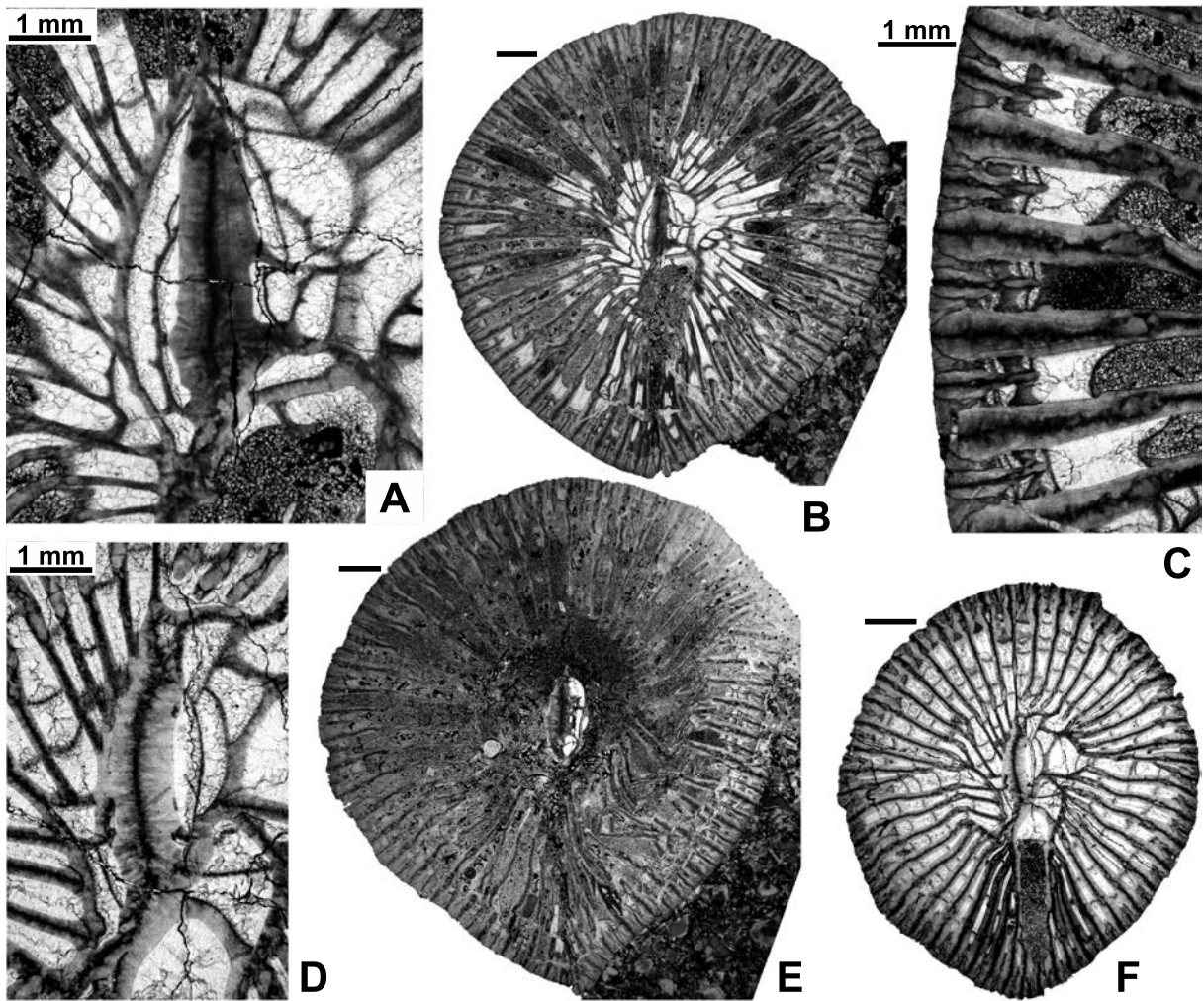
MATERIAL: One specimen, UAM.IG.Tc.C.JG-72; upper Flett Formation (lower part of Meilleur Member); middle Viséan (Text-fig. 4).

DESCRIPTION: Trochoid, slightly curved corals. Calyx 23.0 mm in diameter; 53 major septa in mature growth stage. Minor septa about 1/6 of the length of the major septa, confined to dissepimentarium composed of 1–4 rows of small, interseptal dissepiments (Text-fig. 22C). Columella very laterally compressed (Text-fig. 22B, E, F), projecting above the calyx floor (Text-fig. 22E). Cardinal septum very short in open fossula on the side of convex curvature.

The earliest section examined (Text-fig. 22F), cut partially above the floor of the cardinal fossula, shows 48 major septa at alar diameter of 14.0 mm. All septa are slightly thickened. Major septa arranged pinnately in cardinal quadrants and radially in counter quadrants of varying length. Cardinal septum shortened up to 1/6 of the corallite radius. Cardinal fossula narrow, parallel-sided, long, bounded by fused axial ends of adjacent pinnate major septa. Central column distinct, connected to but not continuous with the longest major septa. Counter septum long, thinner than other major septa, reaching central columella. Alar pseudofossulae distinct. Central column elongated, with distinct median lamella. Minor septa short, about 1/6 of the corallite radius in length.

Above the calyx floor (Text-fig. 22B), at a diameter of 22.0 mm, the number of major septa is 53. Major septa varied in length, mostly not reaching corallite axis, weakly pinnate in cardinal quadrants and radially arranged in counter quadrants. Axial structure composed of spindle-shaped central columella, axial tabellae and several septal lamellae. Minor septa very short, cardinal septum as long as minor septa. Counter septum reaches the central columella, but is not continuous with it.

In the central part of the calyx (Text-fig. 22E), length of major septa about 3/4 of the radius, extending radially in all quadrants, not reaching the axial



Text-fig. 22. *Ekvasophyllum* cf. *turbineum* Parks, 1951 from the Flett Formation (lower part of Meilleur Member), middle Viséan. A-F – UAM. IG.Tc.C.JG-72: A – columella (enlarged fragment from B); B, E, F – mature growth stage; C – peripheral margin with major and minor septa and dissepiments; D – columella (enlarged fragment from F). Scale bars for B, E, F equal to 2 mm.

structure. The clearly visible axial structure resembles that of the preceding section. Cardinal septum very short, counter septum slightly shorter than the other major septa.

REMARKS: The examined specimen shows a mosaic of features of different *Ekvasophyllum* species (Table 1). The size of the corallites, the n:d indices, the cardinal fossula and the extremely laterally compressed columella look like *E. turbineum*. However, the examined specimen has short minor septa, which in *E. turbineum* reach 1/2 of the length of the major septa, and a narrow dissepimentarium, which in *E. turbineum* occupies almost 1/2 of the corallite radius. Short minor septa and narrow dissepimentaria occur

in *E. inclinatum*, *E. enclinotabulatum* and *E. proteus*. However, these species have fewer septa with similar corallite diameters compared to the examined specimen (Text-fig. 23). They also differ in having a less laterally compressed columella.

OCCURRENCE: Northwestern Canada (Jackfish Gap) – middle Viséan.

*Ekvasophyllum* cf. *proteus* Sutherland, 1958  
(Text-figs 23, 24)

MATERIAL: Four specimens UAM.IG.Tc.C. JG-29(1), UAM.IG.Tc.C.JG-35(1), UAM.IG.Tc.C.JG-84, UAM.IG.Tc.C.JG-96(2); Flett Formation (upper part

Species	<i>Ekvasophyllum inclinatum</i>	<i>Ekvasophyllum enclinotabulatum</i>	<i>Ekvasophyllum turbineum</i>	<i>Ekvasophyllum proteus</i>	<i>Ekvasophyllum variabilis</i> sp. nov.
<b>n:d values</b>	42:18 46:20	20:4 36:12 40:15	50:24 56:26	20:4.5 24:5.5 30:7.5 38:12 42:16	22:5.5 32:10 36:12 37:15
<b>major septa</b>	some reach corallite axis, slightly dilated	most reach corallite axis, near cardinal fossula pinnately arranged and radial elsewhere, dilated in all growth stages	3/4 corallite radius in length	form fascicles, some reach corallite axis, near cardinal fossula pinnately arranged	thick, long, most reach axial column, pinnately arranged in cardinal and radially in counter quadrants
<b>minor septa</b>	1/4 corallite radius in length	very short	1/2 of major septa length	short	1/3–1/4 of major septa length
<b>C septum</b>	shortened early in ontogeny	shortened early in ontogeny	short	shortened early in ontogeny	long, shortened only at the calyx floor
<b>K septum</b>	equal in length to adjacent major septa, may be connected to columella	as long as major septa	as long as adjacent major septa, not attached to columella	long, connected to columella	as long as other major septa, permanently connected to axial column
<b>cardinal fossula</b>	open, bounded by fused axial ends of adjoining pinnate major septa	closed, narrow, extended to corallite axis	prominent, open, bounded by fused axial ends of adjoining pinnate major septa	open or closed, extended to, or almost to, the axis	closed, narrow, extended to axial column
<b>axial structure</b>	columella solid, slightly laterally compressed, rod-like	columella prominent, spindle- or kidney-shaped, simple or may contain occasional tabellae, develops very early in the ontogeny	columella solid, extremely laterally compressed, rod-like, projects above floor of calyx	axial column lath-like, kidney-shaped or irregular, simple or contains sparse tabellae, protrudes as a knob in the floor of calyx	simple, spindle-shaped, or lens-shaped, projects to upper part of calyx
<b>tabularium</b>	tabulae incomplete, slightly upturned at margins, slope upward toward axis where they join the columella at a large angle	tabulae flat or gently inclined upward towards the axis where they join the columella	tabulae very steeply inclined upward near axis, merge smoothly into columella at a low angle	tabulae incomplete, moderately to steeply inclined upward, join the column at a very low angle	tabulae gently inclined upward towards the axis where they join the columella
<b>dissepiments</b>	small, elongate, steeply inclined, dissepimentarium narrow	absent or sparsely developed in the late epehebic stage	small, elongate, steeply inclined; dissepimentarium up to 1/2 corallite radius in width	narrow ring of dissepiments, commonly present in epehebic stage	absent

Table 1. Main characters of particular species of *Ekvasophyllum* studied.

of Flogotsho Member to middle part of Meilleur Member); lower–middle Viséan (Text-fig. 4).

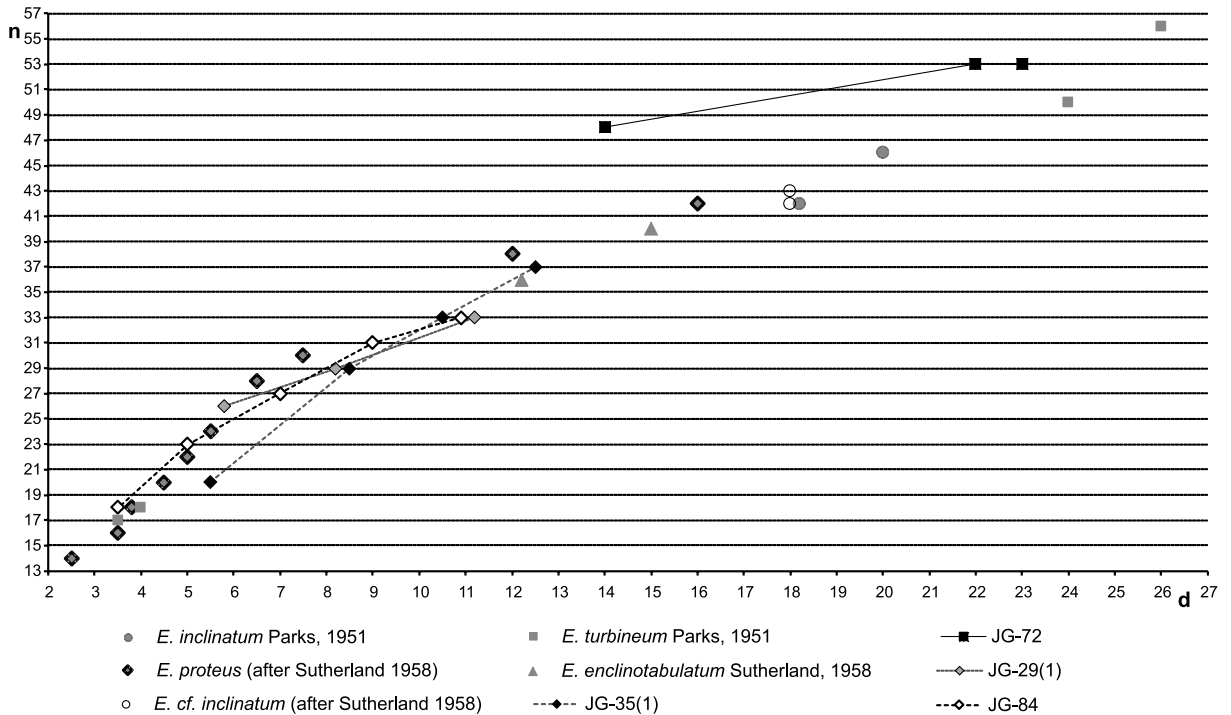
**DESCRIPTION:** Trochoid, slightly curved corals (Text-fig. 24N). Corallite about 20 mm long, without proximal ends, with the calyx 8.0 mm deep. Calyx diameter 10.5–12.5 mm. Septal index n:d of mature growth 37:12.5 (see Text-fig. 23). Major septa dilated, tend to be pinnate near cardinal fossula and radial elsewhere. Minor septa very short. Cardinal fossula distinct, narrow, on convex side extends to axis. Axial column protrudes as distinct spikes in calyx floor.

At alar diameter of 3.5 mm (Text-fig. 24E), in the youngest observed section, septa quite thick, varied in length, number of septa 18. Alar septa longest, joined

at the corallite axis. Cardinal septum shortened to 1/2 of the length of the corallite radius, located in distinct cardinal fossula. Counter septum slightly shortened.

The early mature growth stage (Text-fig. 24D) shows 23 major septa at alar diameter of 5.0 mm. All septa thickened and occupy almost the entire space in the corallite interior. Major septa, arranged pinnately in the cardinal quadrants and radially in the counter quadrants, varied in length. Cardinal septum shortened to 1/2 of the length of the corallite radius. Narrow, parallel-sided, long cardinal fossula, situated on the convex side of the corallite, almost completely filled by stereoplasm deposited on the fossular wall. Central column and short minor septa visible in this section.





Text-fig. 23. *Ekvasophyllum* Parks, 1951 – plot of the number of major septa (n) vs. diameters (d). Symbols joined by lines represent values taken from individual specimens.

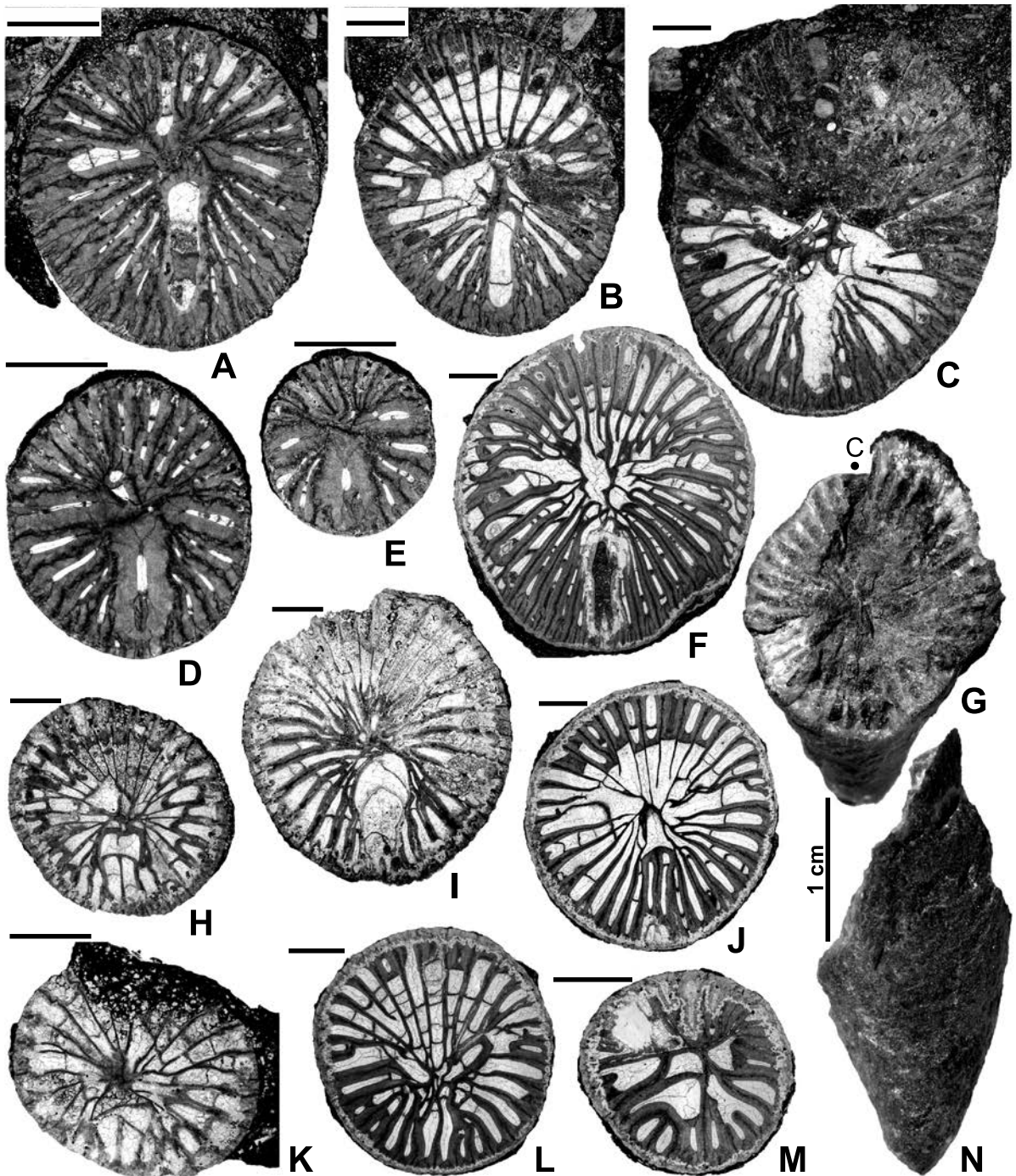
In the transverse section at n:d index = 27:7 (Text-fig. 24A), major septa thickened, of varied length. Minor septa usually absent or rudimentary. At this stage of growth, cardinal septum very short, counter septum somewhat shortened, axial structure already well-developed. Below the calyx floor (Text-fig. 24B, slightly oblique section), i.e., 4 mm above the section illustrated in Text-fig. 24A, major septa of different lengths, thicker in the cardinal quadrants than in the counter quadrants. Minor septa very short. Cardinal septum as long as minor septa. Cardinal fossula remains prominent. Counter septum slightly shorter and thinner than other major septa in counter quadrants. Central column elongated, consists of medial lamella flanked by layers of fibrous tissue; for the first time shows a distinct outline with several ends of the septum touching but not continuous with it.

A section taken partially above the calyx floor (Text-fig. 24C, oblique section) shows 33 major septa at alar diameter of 11.0 mm. Major septa of different lengths, withdrawn from the axial area. Central column distinct, its outline becoming irregular, containing irregular internal lamellae and axial tabellae.

Some differences are displayed by the following two specimens (illustrated in Text-fig. 24F–N).

The first is generally characterized by thinner major septa in all accessible growth stages and by the major corallite fossula extending towards the axis, which attains a keyhole shape. The second specimen is distinguished in the young stages by a long cardinal septum reaching the corallite axis. This septum shortens slightly at corallite diameter of 10.5 mm (Text-fig. 24J), and is clearly shortened only at calyx floor (Text-fig. 24F).

REMARKS: A characteristic feature of *E. proteus* is the presence of an irregular central columella, variable during individual growth. The examined specimens are related to this species by this feature. They also have similar septal indices n:d (Text-fig. 23) and similarly developed septa. Unfortunately, the examined specimens did not show the dissepiments, which can appear singly in *E. proteus* quite early in ontogeny, the narrow ring of dissepiments generally appearing in the middle or late mature growth stage. However, Sutherland (1958, p. 79) notes that “in some specimens they are not observed until late mature growth stage. Thus in immature specimens no dissepiments will be seen”. A certain, general similarity and the fact that the septal ends merge into irregular groups before reaching the axis (Text-fig. 24A, D, E,

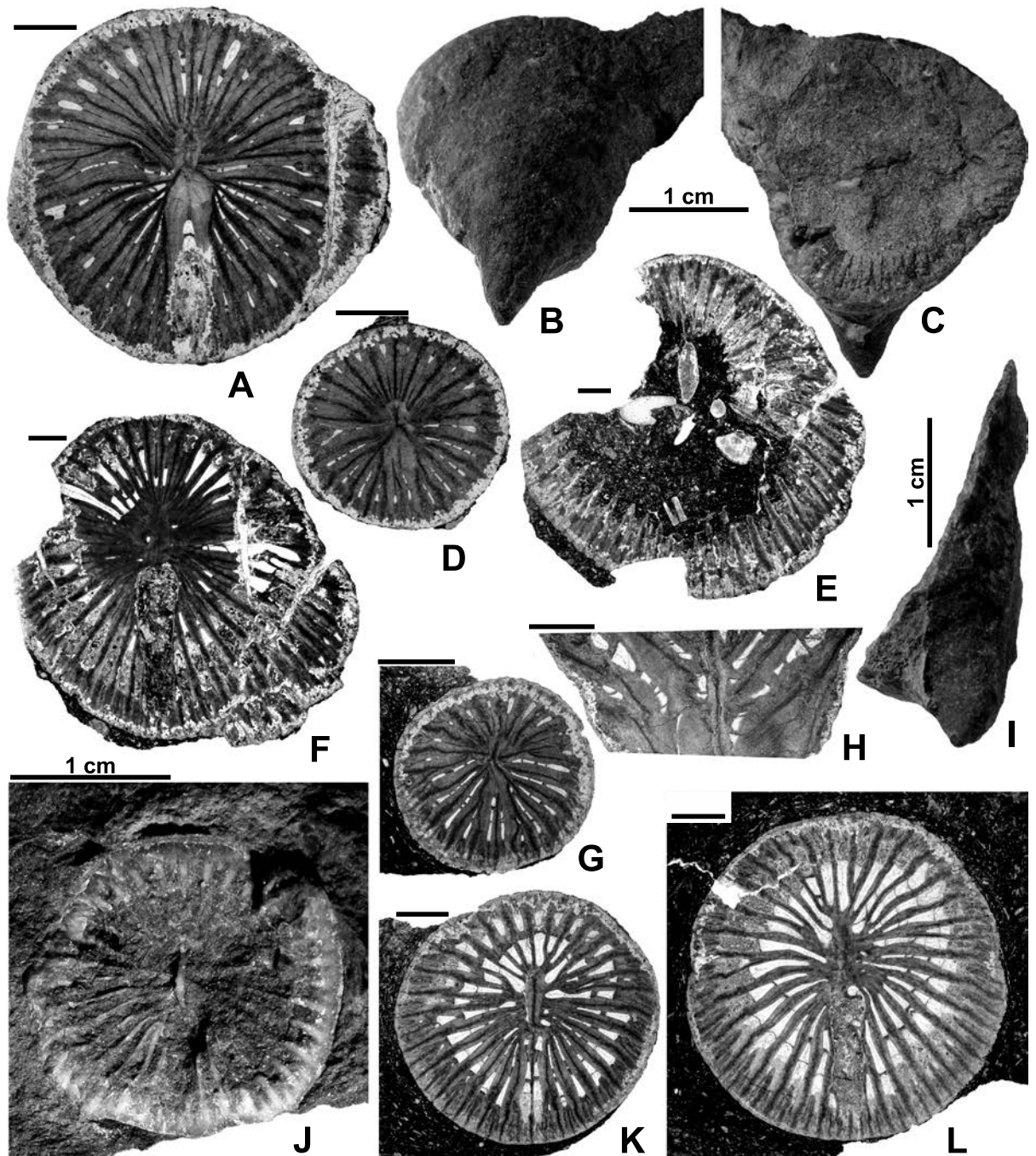


Text-fig. 24. *Ektvasophyllum* cf. *proteus* Sutherland, 1958 from the Flett Formation (upper part of Tlogotsho Member – middle part of Meilleur Member), lower–middle Viséan. A–E – UAM.IG.Tc.C.JG-84: A–C – late mature growth stage; D – early mature growth stage; E – late neanic growth stage. H, I, K – UAM.IG.Tc.C.JG-29(1): H, K – immature growth stage; I – mature growth stage. F, G, J, L–N – UAM.IG.Tc.C.JG-35(1): F – late mature growth stage; G – external view of mature growth stage (partially preserved calyx filled with sediment); J, L – early mature growth stage; M – neanic growth stage; N – corallite surface. Scale bars for A–F and H–M equal to 2 mm.

J, L) make the examined specimens similar to *E. enclinotabulatum*. However, the examined specimens differ from it by an irregular columella, which in *E.*

*enclinotabulatum* is regular in shape and develops very early in the ontogeny of the coral.

The classification of the examined specimens as



Text-fig. 25. *Ekvasophyllum variabilis* sp. nov. from the lower Flett Formation (middle part of Tlogotsho Member), lower Viséan. A–F, I – paratype, UAM.IG.Tc.C.JG-25: A, E, F – late mature growth stage; B – corallite surface; C – external view of mature growth stage (preserved calyx filled with sediment); D – early mature growth stage; I – corallite surface (side view). G, H, J–L – holotype, UAM.IG.Tc.C.JG-33(3): G – early mature growth stage; H – longitudinal thin section, perpendicular to the C–K line; J – external view of mature growth stage (preserved calyx filled with sediment); K, L – late mature growth stage. Scale bars for A, D–H, K and L equal to 2 mm.

*E. cf. proteus* was based on the assumption that the absence of dissepiments is due to the fact that they are young. Their n:d indices at the calyx floor are 33:10.5,

33:11.0, 37:12.5, while the adult *E. proteus* described by Sutherland (1958), having a distinct dissepimentarium, have n:d indices of 38–42:12–16 (Text-fig. 23).

Specimen UAM.IG.Tc.C.JG-35(1) (Text-fig. 24F, G, J, L–N), distinguished by a long cardinal septum in early growth stages, was retained in this taxon because the occurrence of such a long cardinal septum in paratype G.S.C. No. 10623, described by Sutherland (1958, pl. 22, fig. 2), while maintaining the other features of the species (except for the absence of the dissepimentarium), may confirm the affiliation of this specimen to *E. proteus*. In contrast, the disputed specimen UAM.IG.Tc.C.JG-29(1) (Text-fig. 24H, I, K), distinguished by the peculiar shape of the main fossula (keyhole-shaped), which has not been documented in *E. proteus*, may suggest variability of this feature for this species, especially since the other features of *E. proteus* have been preserved in this specimen.

OCCURRENCE: Northwestern Canada (Jackfish Gap) – lower–middle Viséan.

*Ekvasophyllum variabilis* sp. nov.  
(Text-figs 25–28)

HOLOTYPE: UAM.IG.Tc.C.JG-33(3), three transverse and one longitudinal thin sections (Text-fig. 25G, H, J–L) were studied.

TYPE LOCALITY: Jackfish Gap (N 61°05'58.8"; W 123°59'07.5"), SW District of Mackenzie, Canada.

TYPE HORIZON: Flett Formation (middle part of Tlogotsho Member); lower Viséan (Text-fig. 4).

ETYMOLOGY: Latin *variabilis* – variable – after variously developed internal structures, which, in varying degrees of development, also occur in other species of the genus *Ekvasophyllum*.

MATERIAL: Four paratypes, partially recrystallized, UAM.IG.Tc.C.JG-25, UAM.IG.Tc.C.JG-31, UAM.IG.Tc.C.JG-35, UAM.IG.Tc.C.JG-38(2); lower Flett Formation (middle part of Tlogotsho Member); lower Viséan (Text-fig. 4).

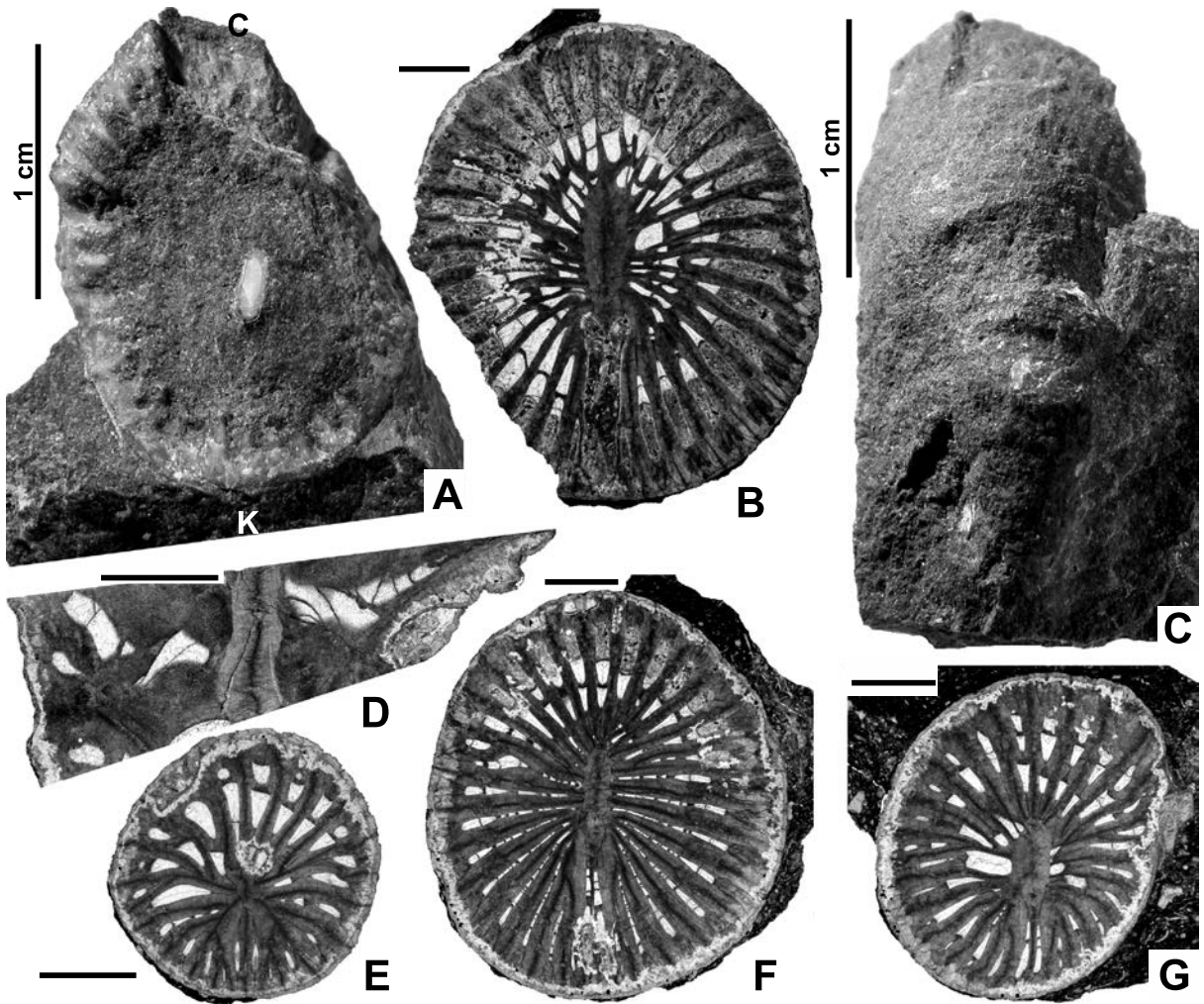
DIAGNOSIS: Broadly conical, strongly curved *Ekvasophyllum* with 34–36 major septa and 11.6–12.0 mm corallite diameter at calyx floor; major septa long, pinnately arranged in cardinal quadrants and radially in counter quadrants; cardinal septum long, reaching corallite axis, shortens at calyx floor; cardinal fossula narrow; counter septum connected with axial column; minor septa 1/3–1/4 of major septa length; axial column lens-shaped; tabulae gently inclined upward towards axial column; dissepiments absent.

DESCRIPTION: All specimens broadly conical or turbinate, curved (Text-fig. 25B, C, I), apex of cone eccentric (= semipatellate), partially silicified. Corallite length 35 mm on the convex side and 10 mm on the concave side. Calyx diameter 20–25 mm (Text-fig. 25C, J). Calyx wide and deep, occupying about 20 mm on the convex side, 8 mm on the concave side. Flattened central column projects to the upper part of the calyx (Text-figs 25J and 26A). Septal index n:d of mature growth 35–37:12–15 (Text-figs 25L, 26B and 27B). Major septa thick, long, of slightly varied length, generally connected to axial column (Text-figs 25A, D, F, K, L; 26B, F, G and 27A, C, D). Cardinal septum on the convex side, in early growth stage long and thick, reaching the corallite axis (Text-fig. 25G, K), shortens only at calyx floor (Text-figs 25L and 27A). Cardinal fossula narrow, closed, extending to axis, deep (to about 3.0 mm below the calyx floor), marked by a depression in the tabulae. Counter septum of the same length as the other major septa, permanently connected to the axial column (Text-figs 25E and 26B, F, G). Minor septa reaching 1/3 of the length of the major septa and free (Text-fig. 25K). Simple axial column protruding into the floor as a knob or lamella (Text-figs 25E, J, 26A and 27B). Strongly thickened septa make the tabulae weakly visible in longitudinal thin section (Text-figs 25H and 26D). Nevertheless, it can be seen that the tabulae are gently inclined upward towards the axis where they join the columella.

The earliest section examined, the late neanic stage (Text-fig. 27E), shows 21 major septa at alar diameter of 4.5 mm. All septa thickened and occupy almost the entire space in the corallite interior. Major septa form 3 groups/fascicules, separated by cardinal and alar pseudofossulae. Cardinal septum long. Narrow, parallel-sided, long cardinal fossula situated on the convex side of the corallite. Cardinal fossula almost completely filled by a stereoplasm deposited on the fossular wall. Central column indistinct. Counter septum as long and thick as the other major septa.

In the early mature growth stage (Text-figs 25D, G, 26E, G and 27D), the central column may be visible for the first time and shows distinct outline with the ends of the septa touching but not continuous with it. Septal index n:d is 22–27:5.3–7.3. Cardinal septum long reaching the corallite axis, in distinct fossula with narrow, almost parallel walls. Counter septum of the same length as the other major septa in counter quadrants.

In the next growth stage (Text-figs 25K, 26F and 27C) there are 31–32 major septa and the corallite



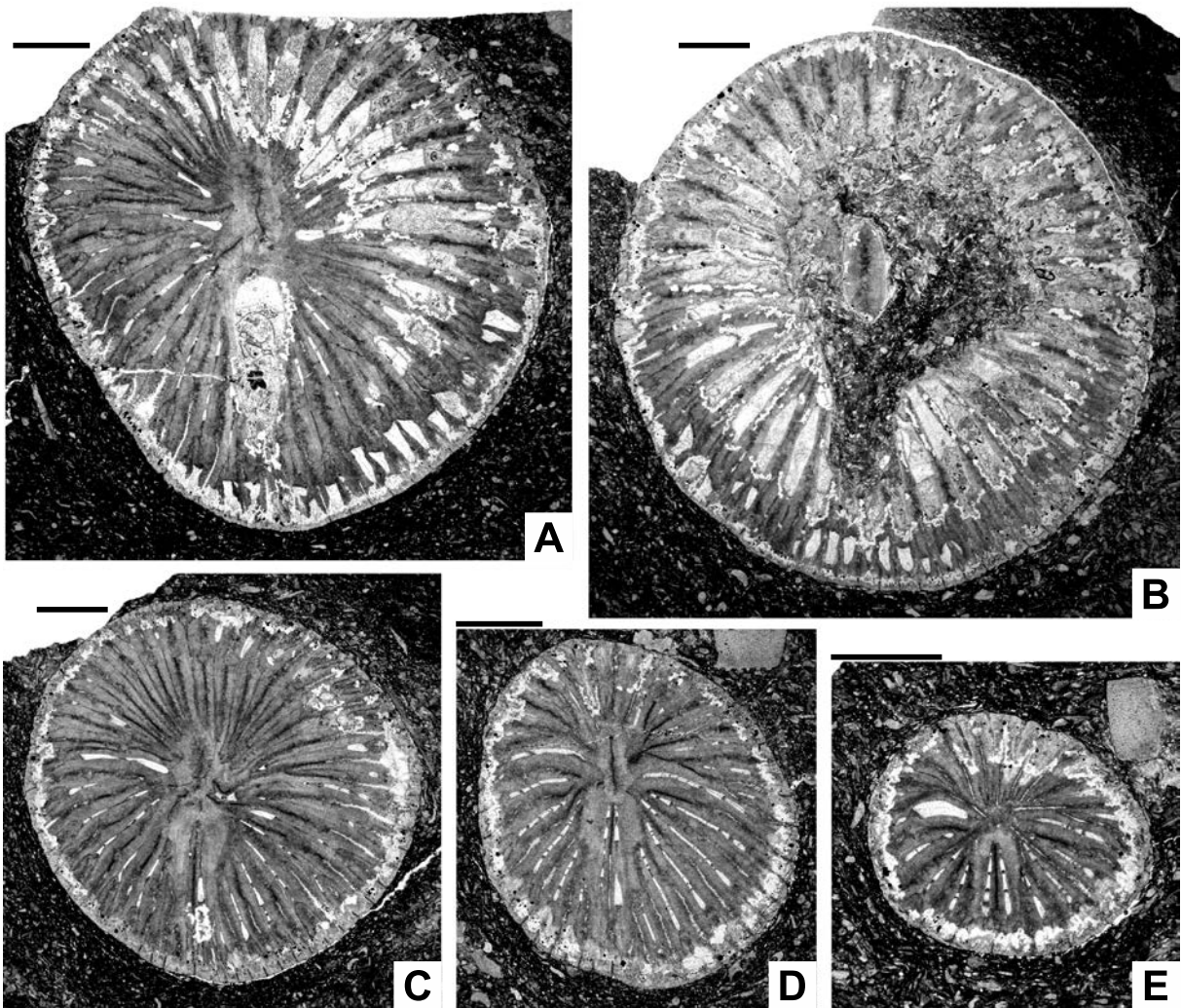
Text-fig. 26. *Ekvasophyllum variabilis* sp. nov. from the lower Flett Formation (middle part of Tlogotsho Member), lower Viséan. A–G – paratype, UAM.IG.Tc.C.JG-35: A – partially preserved calyx filled with sediment; B, F – late mature growth stage; C – corallite surface; D – longitudinal thin section, perpendicular to the C–K line; E, G – early mature growth stage. Scale bars for B and D–G equal to 2 mm.

is 10.0–10.8 mm in diameter. All septa thickened and more or less occupy almost all the space in the corallite interior. Major septa long, arranged pinnately in cardinal quadrants and radially in counter quadrants. Cardinal septum remains long, reaching the axial column, thinner than other major septa, in distinct fossula with narrow, almost parallel walls. Central column distinct, oval in outline, connected to but not continuous with the longest major septa. Counter septum not distinct from other major septa. Alar pseudofossulae indistinct. Minor septa straight, short, 1/4 to 1/3 of the length of the corallite radius.

A thin section cut partially above the floor of the cardinal fossula (Text-fig. 27A) or the calyx floor (Text-figs 25F, L and 26B), at alar diameter

of 12.0–15.5 mm shows 35–36 major septa, most of them extending to the corallite axis. Cardinal septum shortened to 1/4–1/5 of the length of the corallite radius. Cardinal fossula narrow, elongated, reaching central column. Counter septum approximately equal in length to other major septa. Alar pseudofossulae indistinct. Minor septa well developed, 1/5 of the length of the corallite radius.

A transverse section cut in the upper part of the calyx (Text-figs 25E and 27B), at alar diameter of 15.0–20.5 mm shows 37 major septa, which are shortened to 1/2 of the corallite radius and free. Minor septa straight, extending to 1/2 of the length of major septa. Cardinal septum as long as minor septa. Counter septum may be slightly elongated (Text-

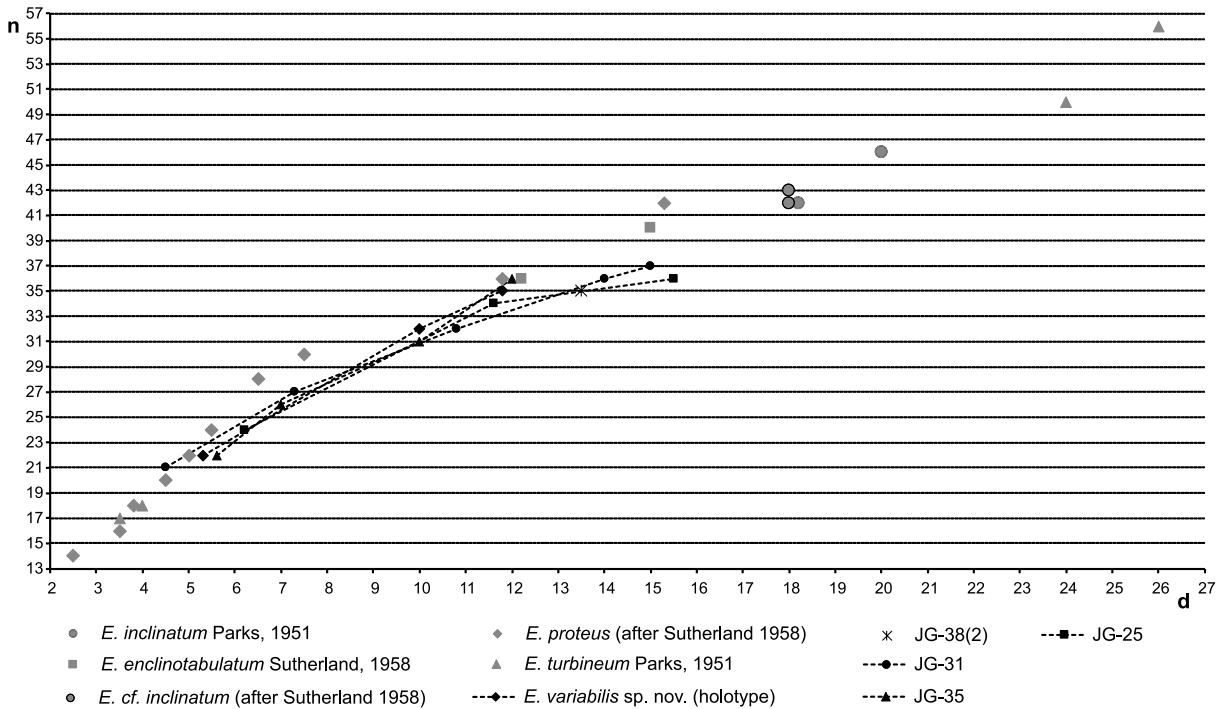


Text-fig. 27. *Ekvasophyllum variabilis* sp. nov. from the lower Flett Formation (middle part of Tlogotsho Member), lower Viséan. A–E – paratype, UAM.IG.Tc.C.JG-31: A–C – late mature growth stage; D – early mature growth stage; E – late neanic growth stage. Scale bars equal to 2 mm.

fig. 25E) and reaches a distinct, lens-shaped central column. No longitudinal section was made, but based on the illustrated sections (Text-figs 25L and 26B) it can be inferred that, at least in the calyx, the bottoms in the axial part of the corallite are considerably elevated, forming a convexity in the corallite axis.

REMARKS: The examined specimens are morphologically similar to most species of *Ekvasophyllum* (Table 1), from which they differ by the semipatellate corallite, the long cardinal septum, which clearly shortens only in the calyx floor, and a regular, central columella. The examined specimens also differ from other *Ekvasophyllum* species in lacking a disseptimentarium.

The regular axial column and septal arrangement of the specimens described herein corresponds to *E. enclino-tabulatum* and *E. inclinatum*. With *E. enclino-tabulatum* they also share similar septal indices  $n:d$  (Text-fig. 28). However, both species (*E. enclino-tabulatum* and *E. inclinatum*) have straight to slightly curved corals and a shortened cardinal septum in early ontogenetic stages. Besides, *E. inclinatum* has higher septal  $n:d$  indices. Compared to *E. proteus*, the examined specimens have smaller numbers of septa at similar corallite diameters, long minor septa, always closed fossula extending to axial column, and tabulae reaching the columella at a greater angle. This may be due to the fact that the longitudinal thin-sections illustrated herein are perpendicular to the C-K line, while



Text-fig. 28. *Ekvasophyllum variabilis* sp. nov. in comparison with other taxa of *Ekvasophyllum* Parks, 1951 – plot of the number of major septa (n) vs. diameters (d). Symbols joined by lines represent values taken from individual specimens.

those illustrated by Sutherland (1958) are parallel to the C-K line (set by cardinal and counter septa).

Focusing on the morphological features of *E. enclinotabulatum*, *E. proteus* and *E. inclinatum*, Sutherland (1958) noticed that *E. proteus* is morphologically more advanced than *E. enclinotabulatum* because of the better developed dissepimentarium, and *E. inclinatum* more advanced than *E. proteus*. According to Sutherland (1958), this may be related to the stratigraphic appearance of these species. It is a fact that *E. cf. inclinatum* from the Liard River area appears in slightly higher horizons than those where *E. proteus* has been found. Following this line of reasoning, *E. variabilis* sp. nov. lacking dissepiments, as suggested by Sutherland (1958), may be the oldest species of this genus. Unfortunately, the exact stratigraphic ranges of all *Ekvasophyllum* species are not known to confirm this supposition.

OCCURRENCE: Northwestern Canada (Jackfish Gap) – lower part of lower Viséan.

Suborder Caniniina Wang, 1950  
 Family Uraliniidae Dobrolyubova in Dobrolyubova  
 and Kabakovich, 1962

Genus *Vesiculophyllum* Easton, 1944

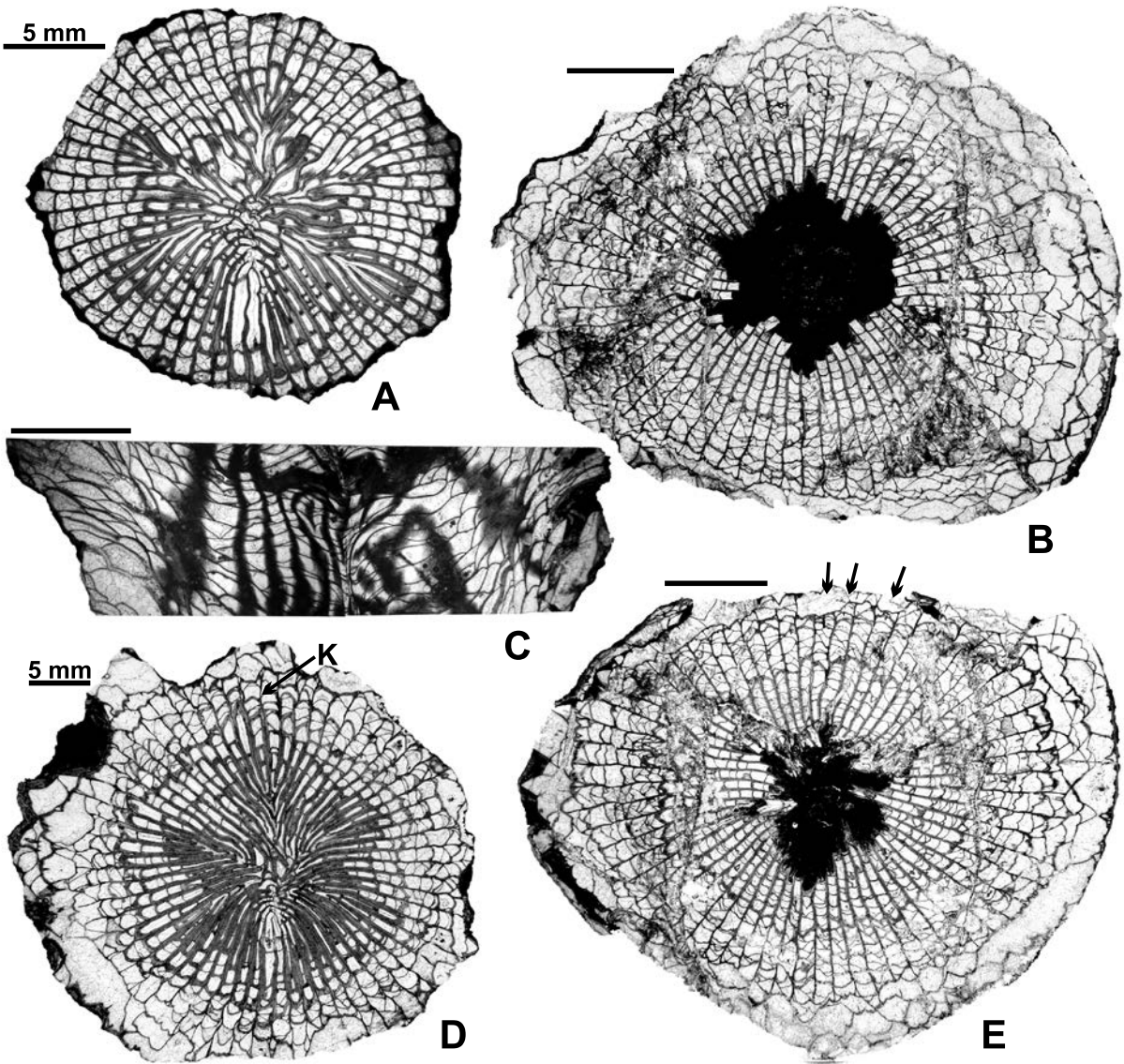
TYPE SPECIES: *Chonophyllum sedaliense* White, 1880.

DIAGNOSIS: See Sando (1969, p. 298).

*Vesiculophyllum* cf. *dux* (Sutherland, 1954)  
 (Text-figs 29, 30, 31A, C, 32)

MATERIAL: Four specimens, UAM.IG.Tc.C.JG-6, UAM.IG.Tc.C.JG-14, UAM.IG.Tc.C.JG-17, UAM.IG.Tc.C.JG-17(1); Flett Formation (lower part of Tlogotsho Member); lower Viséan (Text-fig. 4).

DESCRIPTION: Specimens partially abraded, representing a cylindrical stage, 7 cm long; calyxes and early stages absent. A transverse section at a diameter of 48–60 mm reveals 62–64 major septa present (Text-figs 29B, E and 31C). Major septa of various lengths, the longest approaching the axis of the corallite but not fusing with it; dilated within the tabularium. Cardinal septum long, in narrow fossula bordered by two major septa. Counter septum slightly shorter than the other major septa. Short crestal minor septa developed on dissepiments (Text-fig. 29E,



Text-fig. 29. *Vesiculophyllum* cf. *dux* (Sutherland, 1954) from the lower Flett Formation (lower part of Tlogotsho Member), lower Viséan. A–E – UAM.IG.Tc.C.JG-17: A, D – early mature growth stage; B, E – late mature growth stage (B – lower part of calyx, E – base of calyx), arrows show minor septa; C – longitudinal thin-section, perpendicular to the C-K line. Scale bars for B, C, E equal to 10 mm.

black arrows; 31C, white arrows). As the specimens are variously abraded (Text-figs 29, 30), the dissepimentarium is fragmentarily preserved or completely destroyed. Usually only a few rows of concentric dissepiments are visible, and lonsdaleoid dissepiments are clearly visible only in the undestroyed parts of the specimens (Text-figs 29B, D, E and 31A, C). In longitudinal thin section (Text-fig. 29C), dissepiments vary in size, globose; tabulae incomplete, deeply inclined toward the corallite axis and form a concave floor in the axial region.

A transverse section at a diameter of 40–48 mm reveals 62–63 major septa present (Text-figs 29D and 31A, C); those in the cardinal and counter quadrants show a pinnate arrangement. Major septa of various length, the longest approaching the corallite axis but not fusing with it; dilated within the tabularium. Cardinal septum slightly shorter than the other major septa, in narrow fossula bordered by two major septa. Counter septum slightly longer than the adjacent two major septa, and shorter than the other major septa (Text-fig. 29D) or distinctly shorter (Text-fig. 31C).

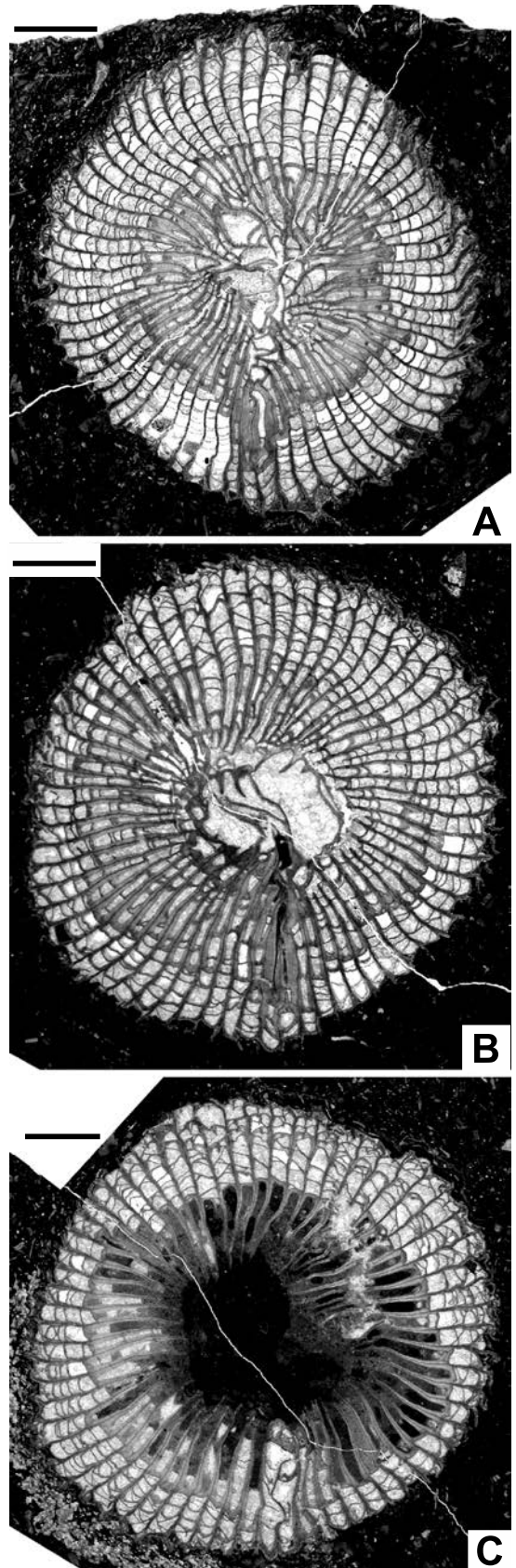


Minor septa are absent. Dissepimentarium occupies about 1/2 of the corallite radius. Two zones of dissepiments present. Inner dissepimentarium consists of 3 to 6 rows of globose, interseptal dissepiments, rarely heringbone, inner row of dissepiments thickened; outer dissepimentarium formed by a wide zone of lonsdaleoid dissepiments, present alongside the epitheca.

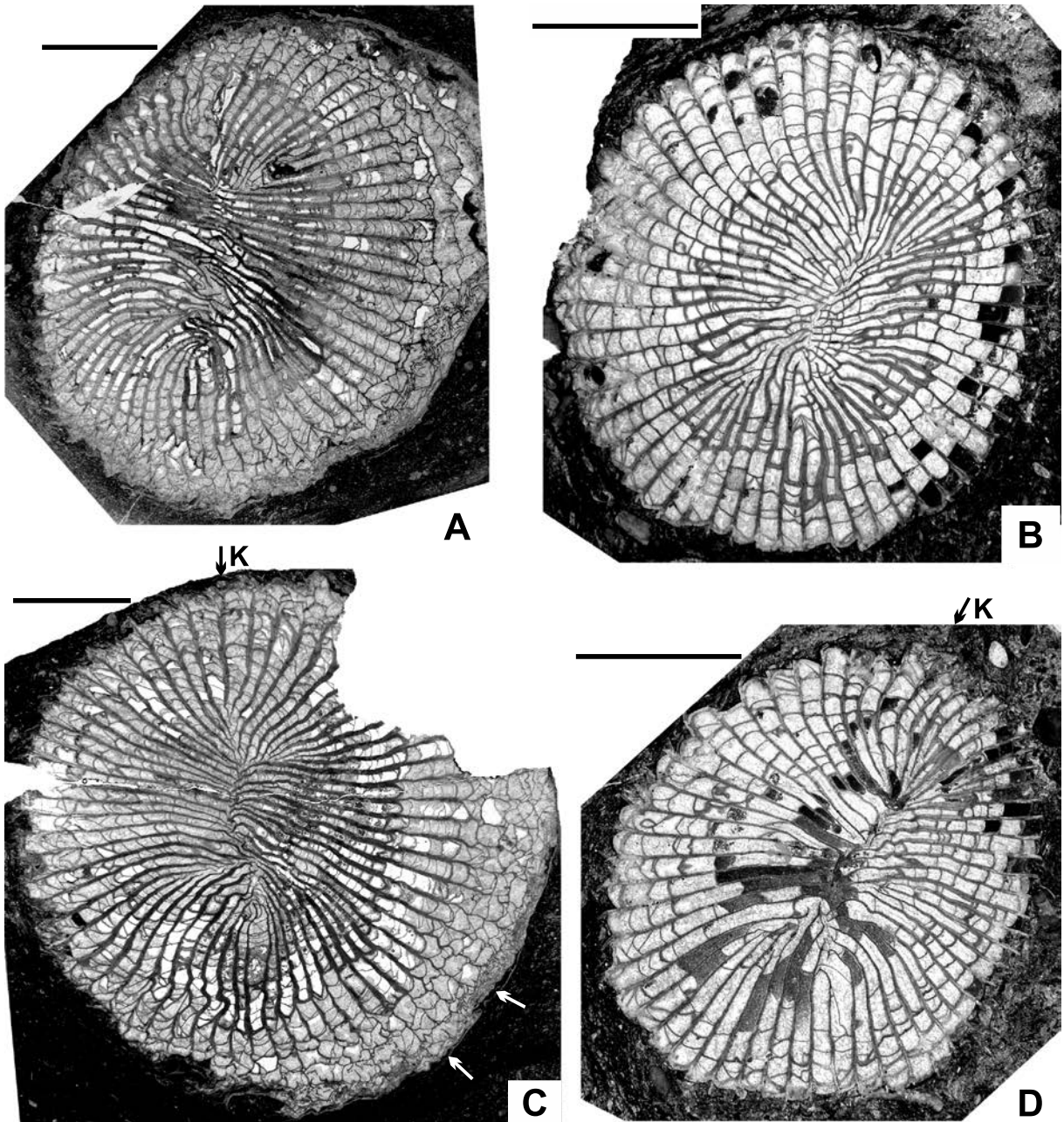
At a diameter of 60 mm, 63–64 major septa are present that do not extend to the axis (Text-fig. 29B, E). Septal plan radial. Major septa thin, with dilated peripheral ends, withdrawn from axis, leaving a free area 10–15 mm in diameter. Cardinal and counter septa slightly shorter than other major septa. Minor septa, if present, are very short and not continuous through the zone from dissepiments to the epitheca (Text-fig. 29E, see arrows). Dissepimentarium broad, very similar to those of the earlier growth stage. External corallite wall 0.2–0.4 mm thick.

The specimen in Text-fig. 30A–C, compared to the other specimens (Text-figs 29 and 31A, C), is characterized by smaller corallite diameters with a constant number of septa (n:d = 64:27–30). Smaller corallite diameters are due to the loss of some external skeletal elements. This is evidenced by the absence of the external wall and part of the dissepimentarium. The fine structures visible in the sediment surrounding the corallite are probably fragments of lonsdaleoid dissepiments, part of the inner dissepimentarium and the external wall. Such close proximity of the corallite and its remains may indicate little transport in the dynamically moving sediment – abraded during burial. Assuming that a well-preserved dissepimentarium is about half the corallite radius, the diameters of the illustrated sections should be almost twice as large. The n:d indices would then be similar to the specimen illustrated in Text-fig. 29. Due to other features of morphological structure (number of major septa, their formation, shortened septa cardinal and counter, poorly developed minor septa), it is highly probable that the specimen illustrated in Text-fig. 30 also belongs to *Vesiculophyllum* cf. *dux*.

REMARKS: The examined specimens represent mature growth stages. Their septal indices of 63–64:41–60 make them similar to *V. dux*, described by Stensaas and Langeheim (1960), whose n:d is 55–65:30–70 (Text-fig. 32). The examined specimens are also similar to *V. dux* due to the long, generally thin



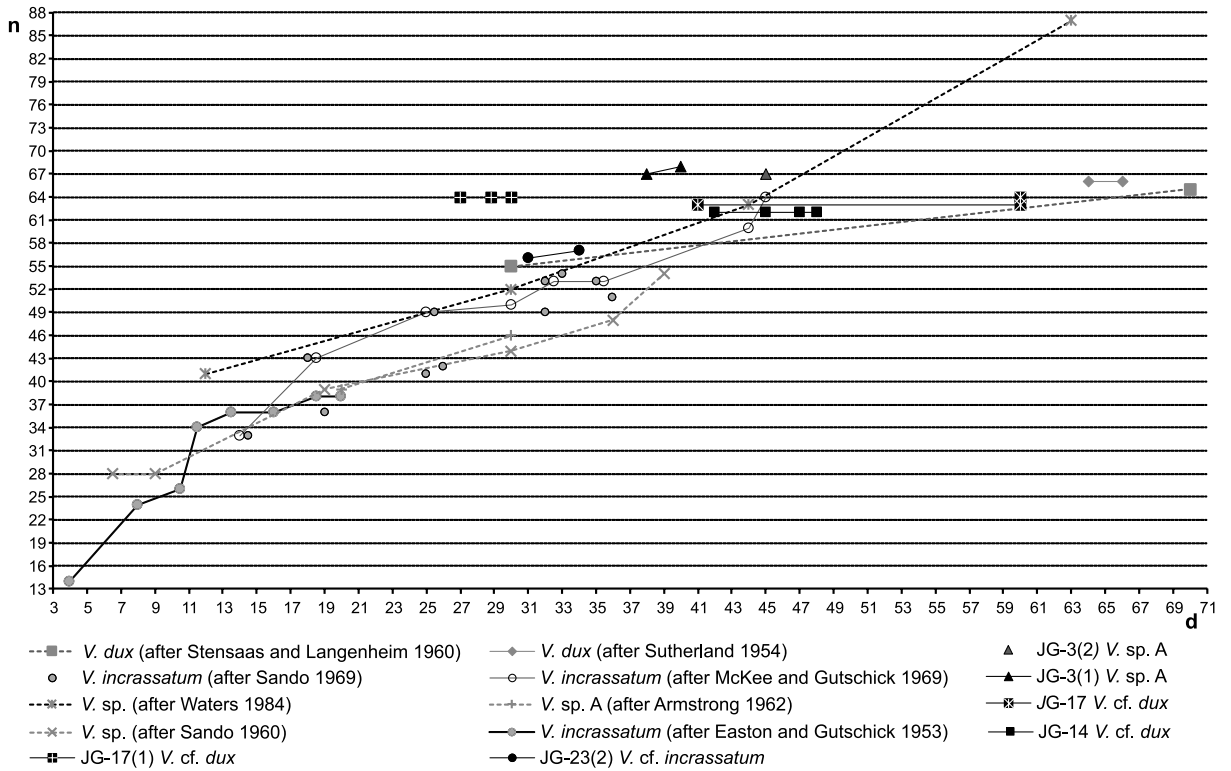
Text-fig. 30. *Vesiculophyllum* cf. *dux* (Sutherland, 1954) from the lower Flett Formation (lower part of Tlogotsho Member), lower Viséan. A–C – UAM.IG.Tc.C.JG-17(1), mature growth stage (B – at the calyx floor, C – upper part of the calyx). Scale bars equal to 5 mm.



Text-fig. 31. **A, C** – *Vesiculophyllum* cf. *dux* (Sutherland, 1954) from the lower Flett Formation (lower part of Tlogotsho Member), lower Viséan; UAM.IG.Tc.C.JG-14 – mature growth stage. **B, D** – *Vesiculophyllum* cf. *incrassatum* (Easton and Gutschick, 1953) from the lower Flett Formation (middle part of Tlogotsho Member), lower Viséan; UAM.IG.Tc.C.JG-23(2) – mature growth stage. Scale bars equal to 10 mm.

major septa, which in the tabularium may be dilated, a radial symmetry (Text-fig. 29B, E), or major septa grouped into series by shortening and bunching (Text-fig. 29A, D), irregularly developed minor septa, the dissepimentarium consisting of two parts, equal to approximately half the corallite radius, and tabular

floor depressed adaxially – generally similarly shaped to the specimens described by Sutherland (1954). The difference is that the studied specimen has a narrower zone with lonsdaleoid dissepiments. It covers about 1/4 of the corallite radius, while in the case of *V. dux* it occupies more than 1/3 of the corallite radius. The



Text-fig. 32. *Vesiculophyllum* Easton, 1944 – plot of the number of major septa (n) vs. diameters (d). Symbols joined by lines represent values taken from individual specimens.

cardinal fossula, which is usually absent in *V. dux*, is also distinct in the studied specimens.

According to Stensaas and Langeheim (1960), *V. dux* occurs in three localities along the Canadian Rockies between Banff, Alberta and the Liard River and apparently ranges stratigraphically from the upper Banff Formation to the upper Flett Formation. Thus, stratigraphically and geographically, the specimens studied correspond to *V. dux*. It is also possible that the features described above indicate intraspecific variability. However, this requires confirmation on larger material.

OCCURRENCE: Northwestern Canada (Jackfish Gap) – lower Viséan.

*Vesiculophyllum cf. incrassatum* (Easton and Gutschick, 1953)  
(Text-figs 31B, D, 32)

MATERIAL: Two specimens, UAM.IG.Tc.C.JG-10, UAM.IG.Tc.C.JG-23(2); lower Flett Formation (middle part of Tlogotsho Member); lower Viséan (Text-fig. 4).

DESCRIPTION: The fragments examined are up to 5 cm long and represent advanced growth stages. Both examined specimens were abraded before burial, and surface details of the epitheca and outer dissepimentarium were usually destroyed; calyces and early stages are missing. At a diameter of 31–34 there are 56–57 major septa (Text-fig. 31B, D). The original bilateral septal plan is evident. Major septa are long, their axial ends occupy most of the axial area of the corallite. Cardinal septum short and located in a distinct fossula. Counter septum slightly shorter than the adjacent major septa (Text-fig. 31D). Minor septa absent. Dissepimentarium 1/3–1/2 of the corallite radius in width, composed of 4 to 10 rows of interseptal dissepiments, rarely herringbone, inner row of dissepiments thickened; outer dissepimentarium abraded.

REMARKS: Sando's (1969) description of the topotypes shows that the most variable characteristics of *V. incrassatum* do not lend themselves well to quantification. However, compared to *V. cf. dux* described above, *V. cf. incrassatum* has smaller corallite diameters and fewer major septa, similar to what is

observed in the paratypes (Easton and Gutschick 1953) and topotypes (Sando 1969) of *V. incrassatum* (Text-fig. 32). While the smaller diameters of the examined corallites are due to their obtuseness (lack of lonsdaleoid dissepiments), the smaller number of septa, compared to *V. dux*, is characteristic of *V. incrassatum* and may indicate this species.

OCCURRENCE: Northwestern Canada (Jackfish Gap) – lower Viséan.

*Vesiculophyllum* sp. A  
(Text-figs 32, 33)

MATERIAL: Two specimens, UAM.IG.Tc.C.JG-3(1), UAM.IG.Tc.C.JG-3(2); lower Flett Formation (lower part of Tlogotsho Member); lower Viséan (Text-fig. 4).

DESCRIPTION: Partially weathered, crushed and eroded specimens about 6 cm long, with the upper part of the calyx and early stages missing. The specimen from Jackfish Gap (Text-fig. 33A–D) has a septal index n:d = 67–68:38–45. Major septa of varying lengths, wavy and thickened in tabularium, clustered in 5–6 fascicles; the longest major septa extend to the axis of the corallite, but are not fused into an axial structure. In the lower part of the calyx, major septa withdrawn from the axis, leaving a free area of 11 mm in diameter (Text-fig. 33B). Cardinal septum short, reaching 9.0 mm in length, counter septum slightly shorter than the other major septa (Text-fig. 33A, C, D). Cardinal fossula distinct, closed below the calyx floor. Minor septa are usually missing or rudimentary, incomplete, forming low ridges on dissepiments. Poorly preserved dissepimentarium (markedly weathered) occupies about 1/2 of the corallite radius, and consists mostly of relatively large, irregular, lonsdaleoid dissepiments, interrupting 2 to 4 major septa. The inner dissepimentarium consists of 3 to 8 rows of interseptal, globose and herringbone dissepiments.

REMARKS: The Canadian specimens described above clearly differ from *V. incrassatum* and *V. dux*. The most important distinguishing features of the examined specimens are the large differences in the length of the major septa, their bending and their formation into fascicles. In comparison with *V. incrassatum* and *V. dux* and the *Vesiculophyllum* taxa described above, the *V. sp. A* specimens described here have a larger number of septa with similar corallite diameter (Text-fig. 32). The specific arrangement of the major septa of the specimens studied, in general, resembles that found in *V. sp. A* from the middle

part of the Hachita Formation (Upper Osage) of New Mexico (Armstrong 1962, pl. 3, fig. 11). However, the Canadian specimens are larger than those and have a greater number of septa (n:d 67–68:38–40 and 67:45 vs. 39–46:20–30; Text-fig. 32) and poorly developed minor septa, which in the New Mexico specimens are present in full number and reach about 1/2 of the length of the major septa.

A precise comparison was not possible due to insufficient number of individuals to be sectioned and due to the poor state of preservation.

OCCURRENCE: Northwestern Canada (Jackfish Gap) – lower Viséan.

Family Bothrophyllidae Fomichev, 1953  
Genus *Caninophyllum* Lewis, 1929

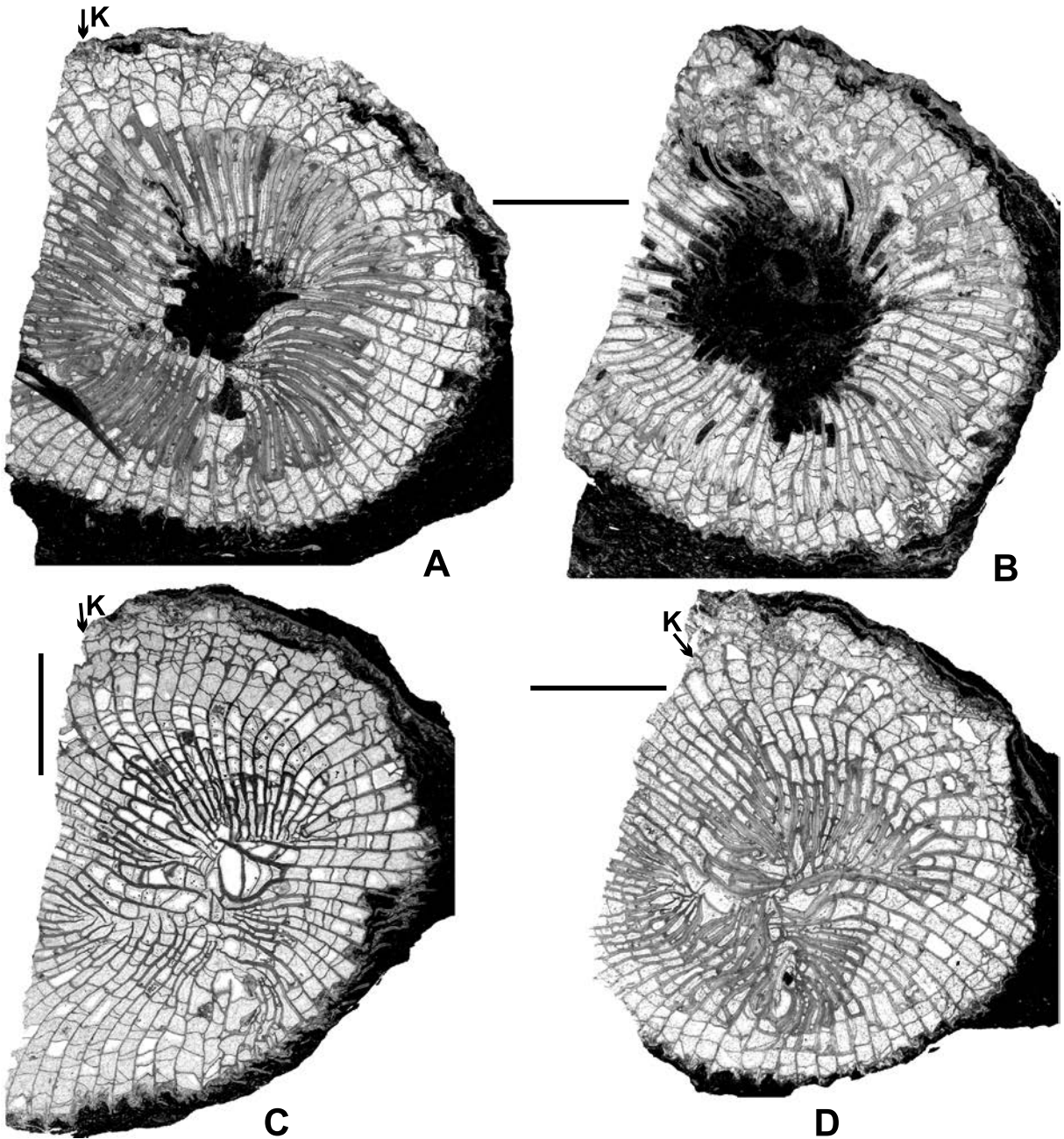
TYPE SPECIES: *Cyathophyllum archiaci* Milne-Edwards and Haime, 1852.

DIAGNOSIS: See Hill (1981, p. F346).

*Caninophyllum* sp.  
(Pl. 8, Figs 1, 2)

MATERIAL: Two specimens, UAM.IG.Tc.C.JG-17(2) and UAM.IG.Tc.C.JG-23(1); lower Flett Formation (middle part of Tlogotsho Member); lower Viséan (Text-fig. 4).

DESCRIPTION: The examined fragments are up to 6 cm long. The fragmentarily preserved external wall is very thin, only 0.2 mm maximum. The n:d ratio is 78–79:57–65 (Pl. 8, Fig. 1a, b), and 70:48 (Pl. 8, Fig. 2b). Major septa of various lengths, the longest reaching up to 3/4 of the corallite radius; and are mostly thin (Pl. 8, Figs 1, 2). Cardinal septum shortened, occurs always in an open, deep tabular fossula, which is not longer than 4/5 of the corallite radius (Pl. 8, Fig. 1). Fossula limited by shortening, adjacent major septa, connected in pairs to the traverses of the tabulae. Minor septa very short or absent. Dissepimentarium occupies up to half the corallite radius and is composed of up to 18 rows of globose and herringbone dissepiments, which are more common in the internal sphere of the dissepimentarium; sporadically lonsdaleoid. In longitudinal section (Pl. 8, Fig. 1c, d), dissepiments of various sizes, generally small, convex (Pl. 8, Fig. 1c) or nearly flat (Pl. 8, Fig. 1d). Tabulae, gently leaning towards the cardinal septum (Pl. 8, Fig. 1d, right side), forming a deep, tabular



Text-fig. 33. *Vesiculophyllum* sp. A from the lower Flett Formation (lower part of Tlogotsho Member), lower Viséan. A, B, D – UAM. IG.Tc.C.JG-3(1), mature growth stage (A – base of calyx, B – lower part of calyx). C – UAM.IG.Tc.C.JG-3(2), mature growth stage. Scale bars equal to 10 mm.

fossula there. In the axial part of the corallite, tabulae slightly concave, less frequently convex or flat and are relatively densely distributed (about 6 per 1 cm). Edges of the tabulae are bent down.

REMARKS: Specimens show no sign of long transport, and the absence of proximal ends must be due to

damage caused during their collection. The preserved growth stages (absence of calyx and earlier stages) do not allow for species identification. However, the preserved growth stages are morphologically very similar to *C. ovibos* (Salter, 1855) and *C. belcheri* (Harker, 1960) var. *magnum* from the lower Permian of Spitsbergen described by Fedorowski (1965) and

Chwieduk (2009, 2013) in the following features: the number of major septa (70–79 vs. 70–75), corallite diameters (48–65 vs. 40–63), a wide dissepimentarium occupying about 1/2 of the corallite radius, the length of the cardinal protoseptum, the shape and size of the cardinal fossula, the length of the major septa, and the structure of the tabularium. Differences are marked in the structure of the dissepimentaria, which in the Canadian specimens contain more numerous lonsdaleoid dissepiments and in the growth of minor septa, which in the Canadian specimens are very short and not fully developed, while in the Spitsbergen specimens are in full number, short and thin, reaching 1/4 to 1/3 of the dissepimentarium width.

Lower Carboniferous *Caninophyllum* is also known from Kuznetsk, the Russian Platform and the Urals (Dobrolyubova *et al.* 1966). Unfortunately, the lower Viséan *C. robustum* from Kuznetsk is much smaller in size and has a lower number of septa than the Canadian specimens; the septal indices n:d of the largest specimens from Kuznetsk are 40–48:23–29. In contrast, the Tournaisian *C. tomiense* (Tolmachev, 1931), found in Kuznetsk, the Urals and the Russian Platform, has septal indices (61–74:40–50) closer to the Canadian specimens. Particularly high similarity to *C. tomiense* is shown by the specimen illustrated in Pl. 8, Fig. 2. Unfortunately, the fragmentarily preserved specimens from Canada do not allow for their precise species designation.

Of similar age (lower Viséan) to the specimens described above is *C. patulum* (Michelin, 1846), known from Belgium (Poty 1981). However, the examined specimens are clearly different from *C. patulum* in the following features: a larger number of major septa (70–79 vs. 51–59), larger corallite diameters (48–65 vs. 22–40), shorter major septa (vs. up to corallite axis), shorter minor septa (vs. locally penetrating into tabularium), and less frequent tabulae (6 vs. 10, but also 30–35 per 1 cm).

**OCCURRENCE:** Northwestern Canada (Jackfish Gap) – lower Viséan.

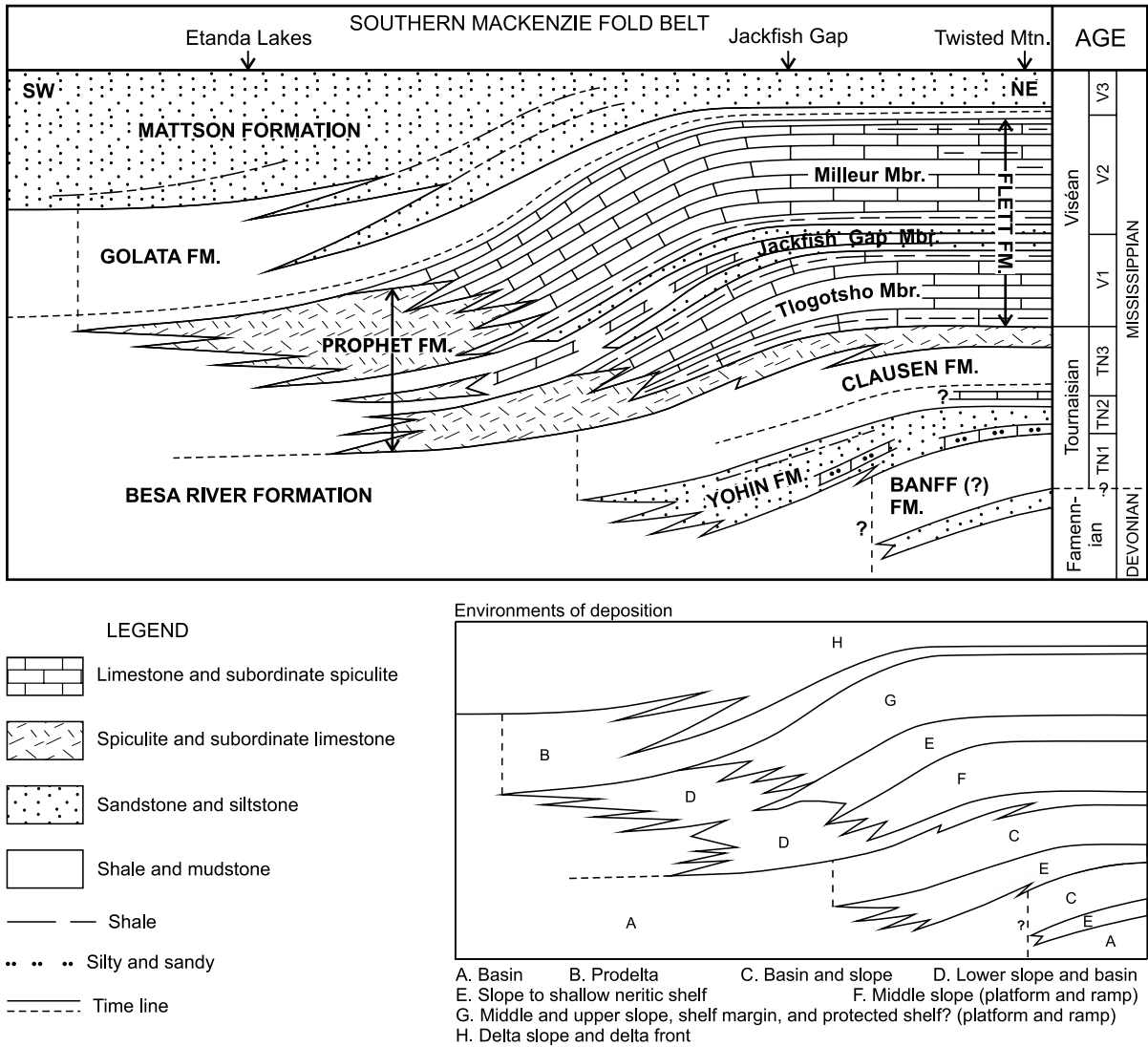
#### ENVIRONMENTAL ASPECTS

During the late Tournaisian to the middle Viséan (TN3 to V2; from late foraminiferal zone 9 to uppermost zone 13), two intervals of limestones interbedded with shales separated by sandstone and shale members with thin limestones developed in the study area (Richards 1989). They are documented in the Tlogotsho and Meilleur members, separated

by a thick interval dominated by terrigenous clastics (sandstones and shales) with thin marine limestones of the Jackfish Gap Member (Text-figs 4 and 34). As a whole they comprise the middle slope, slope to shallow-neritic, and middle to upper slope and shelf margin environments (Richards 1989). The rugose corals described in this paper are from both carbonates and shales in rhythmically bedded strata (Text-fig. 4). The vast majority are small-sized corals, representing the genera: *Ankhelasma*, *Zaphrentites*, *Enniskillenia*, *Bradyphyllum*, *Cyathaxonia* and *Ekvasophyllum*. Larger corals, *Vesiculophyllum* and *Caninophyllum*, were found in the limestone only in the lower part of the Flett Formation (Tlogotsho Member).

According to Richards (1989), deposition of the first carbonate-rich unit, which essentially constitutes the lower Tlogotsho Member (Text-fig. 4), took place during the initial phase of a major regional transgression. The corals found here are mainly large, dissepimented solitary forms of *Vesiculophyllum* and *Caninophyllum*, with a smaller contribution of *Zaphrentites*. With the rise of sea level in this area, in the higher part of the Tlogotsho Member marked by a greater accumulation of spicule-rich rocks and dark, shale-rich deposits (Text-fig. 4), large dissepimented Rugosa disappear from the depositional record. This part of the Tlogotsho Member is dominated by smaller corals, including *Cyathaxonia cornu*, considered an indicator of deep-water conditions (Hill 1938–41; Scrutton 1997; Somerville and Rodríguez 2007), and numerous representatives of *Ankhelasma*, *Ekvasophyllum* and *Zaphrentites*.

A large interval of carbonates is recorded in the rocks of the Jackfish Gap Member. A decrease in water depth, induced by regional regression (Macqueen and Bamber 1968), is indicated by the presence of siltstones and sandstones containing cross-bedded shallow-neritic sediments, forming the lower and upper parts of the Jackfish Gap Member (Text-fig. 4). Small-sized corals, mainly *Zaphrentites*, were found in the middle part of the Jackfish Gap Member, in layers with shales and rhythmically bedded strata (a period of alternating siliciclastic and carbonate deposits). These strata were probably deposited during relative sea-level changes. According to Rose (1976), this style of cyclic sedimentation results from changes in the proximity of the siliciclastic shoreline deposits in response to sea-level fluctuations, basin-subsidence changes and uplift of source areas for terrigenous clasts. The link between these changes, despite attempts to correlate them with eustatic events, is unclear, if only because of insufficient biostratigraphic resolution and an indeterminate Viséan definition. And while the cyclicity of



Text-fig. 34. Stratigraphic cross-section showing the lower Carboniferous in the eastern Cordillera of the SW District of Mackenzie (after Richards 1989).

sedimentation is well documented in many areas of the world, there are few attempts to understand its control on larger-scale patterns.

One major transgression in the study area followed the folding of the Jackfish Gap Member (Text-fig. 3) during the middle Viséan (V2; boundary 12/13 to middle zone 13; Richards 1989). Significant here is the rapid transition from shallow-neritic sandstone in the Jackfish Gap Member to mid-depth-water deposits in the overlying Meilleur Member (Text-fig. 4 and Pl. 1). The initial phase of the transgression is dominated by corals of the genera *Ekvasophyllum* and *Zaphrentites* (Text-figs 4 and 34). The last coral

occurrences, represented here by *Enniskillenella enniskilleni* (Text-fig. 4), collected from the lime grainstone lithofacies, probably indicate open-shelf settings. Carbonate deposits overlie basal deposits of siliciclastics of the Golata Formation (Text-figs 3 and 4; Pl. 1) devoid of rugose corals.

PROVINCES AND PALAEOZOOGEOGRAPHY

Current knowledge of Palaeozoic corals, especially their systematics, is still far from perfect. Due to the very different interpretations of the features

of their morphological structure, rugose corals are rarely used to interpret sedimentary environments and stratigraphy. Sometimes even the genera are uncertain, as the boundaries between them may be blurred by homeomorphism and poor interpretations. Thus, by careful use of literature data and taking into account individual research, it can be concluded that the rugose corals, widely distributed in the Viséan, appear to be strongly mixed worldwide (Tables 2 and 3) and are similar to each other, regardless of the region (the exception being the Australian province where they show a mixture of native – ‘endemic’ – and cosmopolitan genera and species; Table 3). This fact suggests that there must still have been a direct, marine connection between western Laurussia and the Palaeo-Tethys in the Viséan. This in turn makes it difficult to define and distinguish palaeozoogeographic provinces. In this context, North America is no exception. Previous studies of corals in this area have been conducted by, e.g., Sutherland (1958), Sando (1969), Sando *et al.* (1977), Bamber and Mamet (1978), and Bamber *et al.* (2017). The varying degrees of endemicity of different fossil groups, and differences in different authors’ opinions, make it impossible to clearly define the provincial position of western Canada throughout the Carboniferous (Richards *et al.* 1993). Nevertheless, some clues are emerging. Mamet and Skipp (1979) traced three Foraminifera Realms back to the lower Carboniferous: 1) The Tethys Realm extends from northern Africa through northern Europe, the East European Platform, Malaysia and Vietnam to north-western and probably south-eastern Australia. The Tethys fauna is abundant and of high quality and shows a high degree of endemism; 2) The Taymyr/Alaska Realm includes Taymyr, Lena, the Kolyma and Omolon massif areas and Arctic North America. The fauna of this second realm shows less qualitative differentiation and lower endemism than in the Taymyr Realm; and 3) The Realm of Kuznetsk/North America which is intermediate between the first two.

The distribution of other lower Carboniferous fauna in the WCB suggests that this region had relationships with the realms mentioned above. For example, Carter (1987) points out the high similarity of the brachiopods from the Banff Formation of the southern Rocky Mountains in Canada with the brachiopods of Kuznetsk. In contrast, Waterhouse (in Bamber and Waterhouse 1971) showed that upper Carboniferous brachiopods from the northern Yukon are more similar to those from the Ural Mountains than to those from North America.

Crasquin (1984), on the other hand, distinguished three provinces of lower Carboniferous ostracods. The widely distributed *Bairdia brevis* Province occurs in the eastern Cordillera and interiors of North America, northern Siberia, Kazakhstan and north-western Europe. The *B. brevis* Province is subdivided into 3 subprovinces: 1) extending through the Interior and eastern Cordillera of North America; 2) connecting northern Siberia and Kazakhstan; and 3) covering north-western Europe. The second province, *Graphiadactyllis*, is documented only in the Appalachians of North America. The third province, *Hollinella*, covers northern Africa, western Turkey and the Moscow Basin.

In contrast, the lower Carboniferous microflora of northern Yukon to south-western Mackenzie region is similar to that of Spitsbergen (Playford 1962, 1963) and points to the *Lophozotriletes* region according to Van del’Zwan (1981). This would be the tropical humid belt of northern Euramerica, extending from Russia to Spitsbergen. The microflora of Atlantic Canada has much in common with that of the western Europe (Utting 1980, 1987), later included in the *Vallatisporites* region by Van del’Zwan (1981), which includes the subtropical dry belt of southern Euramerica (eastern Canada, Ireland, Britain and Denmark).

In the case of conodonts, Carboniferous species are cosmopolitan along the equatorial belt. However, when the conodont assemblages of North America, Europe, North Africa, China, Russian Platform and Urals are compared, their diversity becomes evident. In areas outside the northern Yukon, the lower Carboniferous conodonts of North America are less diverse than on other continents. Upper Carboniferous conodonts of the Yukon have not been studied, but those of the Canadian Arctic Islands are closer in genera and species to those of the Russian Platform and Urals than to those of the rest of North America (Richards *et al.* 1993).

Global palaeogeographic reconstructions based on corals are fewer in number and more difficult to make. Among several works devoted to this issue, the work of Fedorowski (1981) is one of the most important and most frequently cited. Fedorowski separated two coral-based realms: the Cordilleran-Arctic-Uralian and the Palaeo-Tethys, and further divided these realms into zoogeographic provinces. In principle, these palaeogeographic and phylogenetic distinctions are not disputed to this day. The regional distribution of rugose corals was previously addressed by Sando *et al.* (1977). They recognized a Western Interior Coral Province that links the western United



Series/Stage Taxa	TOURNAISIEN							VISEAN							SERPUKHOV.		
	TN1	TN2	TN3	V1			V2			V3			17	18	19		
	pre7	7	8	9	10	11	12	13	14	15	16i	16s	Chesterian				
	Osagean							Meramecian									
<i>Ankhelesma canadense</i> sp. nov.					—												
<i>Zaphrentites arkansanus</i>							—	Mackenzie Mts.								—	USA
<i>Zaphrentites lerandi</i>																	Canadian Rocky Mts
<i>Zaphrentites constrictus</i>																	Scotland
<i>Zaphrentites parallela</i>																	
<i>Zaphrentites delanouei</i>																	
<i>Enniskillenia enniskilleni</i>																	
<i>Bradyphyllum clavigerum</i>																	
<i>Cyathoxonia cornu</i>																	
<i>Ekvasophyllum enclinatubulatum</i>																	
<i>Ekvasophyllum inclinatum</i>																	
<i>Ekvasophyllum cf. turbineum</i>																	
<i>Ekvasophyllum cf. proteus</i>																	
<i>Ekvasophyllum variabilis</i> sp. nov.																	
<i>Vesiculophyllum cf. dux</i>																	
<i>Vesiculophyllum cf. incrassatum</i>																	
<i>Vesiculophyllum</i> sp. A																	
<i>Caninophyllum</i> sp.																	

— taxa described in this work      — literature data, age limits definite      ..... literature data, age limits indefinite

Table 2. Distribution and zonation of lower Carboniferous solitary rugose corals known from Jackfish Gap, northwestern Canada.

A	Genera	CA	US	FR	BE	GB	PL	UR	UL	KU	RP
	<i>Bradyphyllum</i>	x									
	<i>Liardiphyllum</i>	x									
	<i>Ankhelasma</i>	x	x								
	<i>Canadiphyllum</i>	x	x								
	<i>Ekvasophyllum</i>	x	x								
	<i>Vesiculophyllum</i>	x	x								
	<i>Zaphriphyllum</i>	x	x								
	<i>Hapsiphyllum</i>	x	x				x				
	<i>Cyathaxonia</i>	x	x		x	x					
	<i>Rotiphyllum</i>	x	x		x		x				
	<i>Koninckophyllum</i>	x	x			x	x	x			
	<i>Zaphrentites</i>	x	x		x	x	x	x		x	
	<i>Caninia</i>	x	x			x	x	x		x	
	<i>Enniskillenia</i>	x	x			x		x		x	x
	<i>Lophophyllum</i>	x	x			x				x	
	<i>Dibunophyllum</i>	x	x					x	x		x
	<i>Sychnoelasma</i>	x	x	x	x	x	x	x	x		x
	<i>Caninophyllum</i>	x			x	x		x		x	
	<i>Rylstonia</i>		x		x	x		x	x	x	
	<i>Amygdalophyllum</i>				x						
	<i>Syringaxon</i>				x						
	<i>Corphalia</i>				x						
	<i>Hexaphyllia</i>				x	x					
	<i>Axophyllum</i>				x	x					
	<i>Carruthersella</i>				x	x					
	<i>Haplolasma</i>				x	x					
	<i>Spirophyllum</i>					x					
	<i>Merlewoodia</i>				x	x					
	<i>Cravenia</i>				x	x	x				
	<i>Palaeosmilia</i>				x	x	x	x	x	x	x
	<i>Siphonophyllia</i>				x	x	x	x	x	x	
	<i>Clisiophyllum</i>				x	x	x				x
	<i>Bifossularia</i>				x			x		x	
	<i>Ufimia</i>				x	x	x				x
	<i>Cyathoclisia</i>				x			x	x	x	
	<i>Keyserlingophyllum</i>				x				x	x	
	<i>Calmiussiphyllum</i>							x	x		

B	Genera	CA	US	FR	BE	GB	PL	UR	UL	KU	RP
	<i>Amygdalophyllum</i>				x						
	<i>Ankhelasma</i>	x	x								
	<i>Axophyllum</i>				x	x					
	<i>Bifossularia</i>			x				x		x	
	<i>Bradyphyllum</i>	x									
	<i>Calmiussiphyllum</i>							x	x		
	<i>Canadiphyllum</i>	x	x								
	<i>Caninia</i>	x	x			x	x	x		x	
	<i>Caninophyllum</i>	x			x	x		x		x	
	<i>Carruthersella</i>				x	x					
	<i>Clisiophyllum</i>			x	x	x					x
	<i>Corphalia</i>				x						
	<i>Cravenia</i>			x	x	x					
	<i>Cyathaxonia</i>	x	x		x	x					
	<i>Cyathoclisia</i>				x			x	x	x	
	<i>Dibunophyllum</i>	x	x					x	x		x
	<i>Ekvasophyllum</i>	x	x								
	<i>Enniskillenia</i>	x	x			x		x		x	x
	<i>Haplolasma</i>				x	x					
	<i>Hapsiphyllum</i>	x	x				x				
	<i>Hexaphyllia</i>				x	x					
	<i>Keyserlingophyllum</i>				x				x	x	
	<i>Koninckophyllum</i>	x	x			x	x	x			
	<i>Liardiphyllum</i>	x									
	<i>Lophophyllum</i>	x	x			x				x	
	<i>Merlewoodia</i>			x	x						
	<i>Palaeosmilia</i>			x	x	x	x	x	x	x	x
	<i>Rotiphyllum</i>	x	x		x		x				
	<i>Rylstonia</i>		x		x	x		x	x	x	
	<i>Siphonophyllia</i>			x	x	x	x	x	x	x	
	<i>Spirophyllum</i>					x					
	<i>Sychnoelasma</i>	x	x	x	x	x	x	x	x		x
	<i>Syringaxon</i>				x						
	<i>Ufimia</i>				x	x	x				x
	<i>Vesiculophyllum</i>	x	x								
	<i>Zaphriphyllum</i>	x	x								
	<i>Zaphrentites</i>	x	x		x	x	x	x		x	

Table 3. Distribution of lower and middle Viséan rugose coral genera in North America, Western and Central Europe, and Russia. CA – Canada, US – USA, FR – France, BE – Belgium, GB – Great Britain, PL – Poland, UR – Ukraine, UL – Ural, KU – Kuznets, RP – Russian Platform. Data mainly taken from Harker (1963), Dobrolyubova *et al.* (1966), Sando (1969), Fedorowski (1981, 2001), Hill (1981), Sando and Bamber (1985), and Rodríguez *et al.* (2020). A – Palaeozoogeographic distribution. B – Alphabetical listing.

States and western Canada, but excludes northern and south-eastern Alaska, the northern Yukon Territory, north-western Washington, central Oregon and northern California. They also showed that corals from the Western Interior Province are more closely related to corals from the northern Yukon and northern Alaska than to others in North America. However, Sando *et al.* (1977) did not make comparisons with areas outside North America. In contrast, the work of other authors (Hill 1981; Kossovaya 1996; Poty 1999) is deficient; it either fails to account for palaeogeographic reconstructions based on plate tectonics, or relies on inaccurate determinations of coral taxa, or is based on scarce and/or unrepresentative material. A significant cessation in the worldwide development of rugose corals began in the latest Viséan. This was probably due to orogenic movements, the reduction of shallow seas and, to a lesser extent, climate change (Fedorowski 1981; Bamber *et al.* 2017).

As can be seen from the data presented above, it is impossible to distinguish a single zoogeographic province for all of North America for the early Carboniferous. There is a certain unity of fauna only in the Eastern Cordillera and Western Interior (western parts of USA and Canada). This unity is indicated by: foraminifera, brachiopods, ostracods, conodonts and corals. However, these organisms show more affinity with the fauna of the Kuznetsk Basin, Europe or Kazakhstan than with the equatorial fauna of the Arctic and eastern Canada or the eastern USA.

## CONCLUSIONS

1. This study has shown that the assemblage of solitary rugose corals from the lower and middle Viséan in northwestern Canada is distinctly different from that of corals found in Western and Central Europe at that time (Table 3). The lower and middle Viséan rugose coral fauna from Europe is more diverse than that from North America.

2. Taking into account literature data and the results of this study, it is clear that in the early and middle Viséan, both 'endemic' and cosmopolitan genera and species are abundant in North America (Tables 2 and 3). The 'endemic' group here includes 7 genera: *Ankhelasma*, *Bradyphyllum*, *Canadiphyllum* Sutherland, 1954, *Ekvasophyllum*, *Liardiphyllum* Sutherland, 1954, *Vesiculophyllum*, *Zaphriphyllum* Sutherland, 1954 and species of *Zaphrentites* (*Z. arkansanus*, *Z. lerandi*), while the number of taxa shared, if only with the European area, is at least 12 (Table 3). This fact indicates zoogeographic links be-

tween these areas. Thus, the mechanism responsible for the limited occurrence of North American genera is not related to the lack of faunal communication along the southern shelf of Laurussia. The local occurrence of specific taxa cross North America (7 genera) and Europe (18 genera) during the studied time interval indicates rather the existence of specific environmental conditions that established such taxonomic composition. Also for this reason, new species are consciously not called endemic.

3. It is significant that the genera common for the two regions appeared earlier in Europe (data taken mainly from Hill 1981; see Table 3), e.g., *Hapsiphyllum* Simpson, 1900 and *Zaphrentites* (from the Middle Devonian), *Dibunophyllum* Thomson and Nicholson, 1876 and *Cyathaxonia* (from the Upper Devonian), *Enniskillenia* and *Rotiphyllum* (from the Tournaisian), *Koninckophyllum* Thomson and Nicholson, 1876 (from the lower Viséan). The same is true of *Clisiophyllum* Dana, 1846, *Siphonophyllia* Scouler, 1844, *Haplolasma* Semenoff-Tian-Chansky, 1974 and *Hexaphyllia* Stuckenberg, 1904 documented in Europe in the lower and middle Viséan; these genera in North America occur in younger strata, in the upper Viséan, uppermost Viséan, upper Mississippian and upper Mississippian–lower Pennsylvanian.

This fact may suggest that the complex region of Europe may have been the cradle of most Carboniferous genera. It was there that they appeared earliest and from there they spread eastwards to Russia and southwards to Africa (Fedorowski 1981), and westwards to North America.

4. *Ekvasophyllum* occurs in Canada in zone 10, while in USA in zone 13. The presence of this genus in USA in zone 13 would therefore be an ecological appearance of this species in this area.

5. One feature that can be discerned when analysing all the coral specimens is that many species have representatives that are smaller than their counterparts recorded in USA; this is true for all species of *Zaphrentites*, except *Z. delanouei*. Lower Viséan specimens of *Enniskillenia enniskilleni* from Jackfish Gap compared to the specimens of this species from upper Viséan from southern Canadian Rocky Mountains are also smaller and demonstrate close affinities with *E. enniskilleni* from the Tournaisian–lower Viséan of Kuznetsk.

6. *Ankhelasma* from Jackfish Gap lowers the stratigraphic range of this genus to the lower Viséan. *Ankhelasma canadense* sp. nov. is also smaller than the stratigraphically younger *Ankhelasma* known from the upper Viséan in the US.

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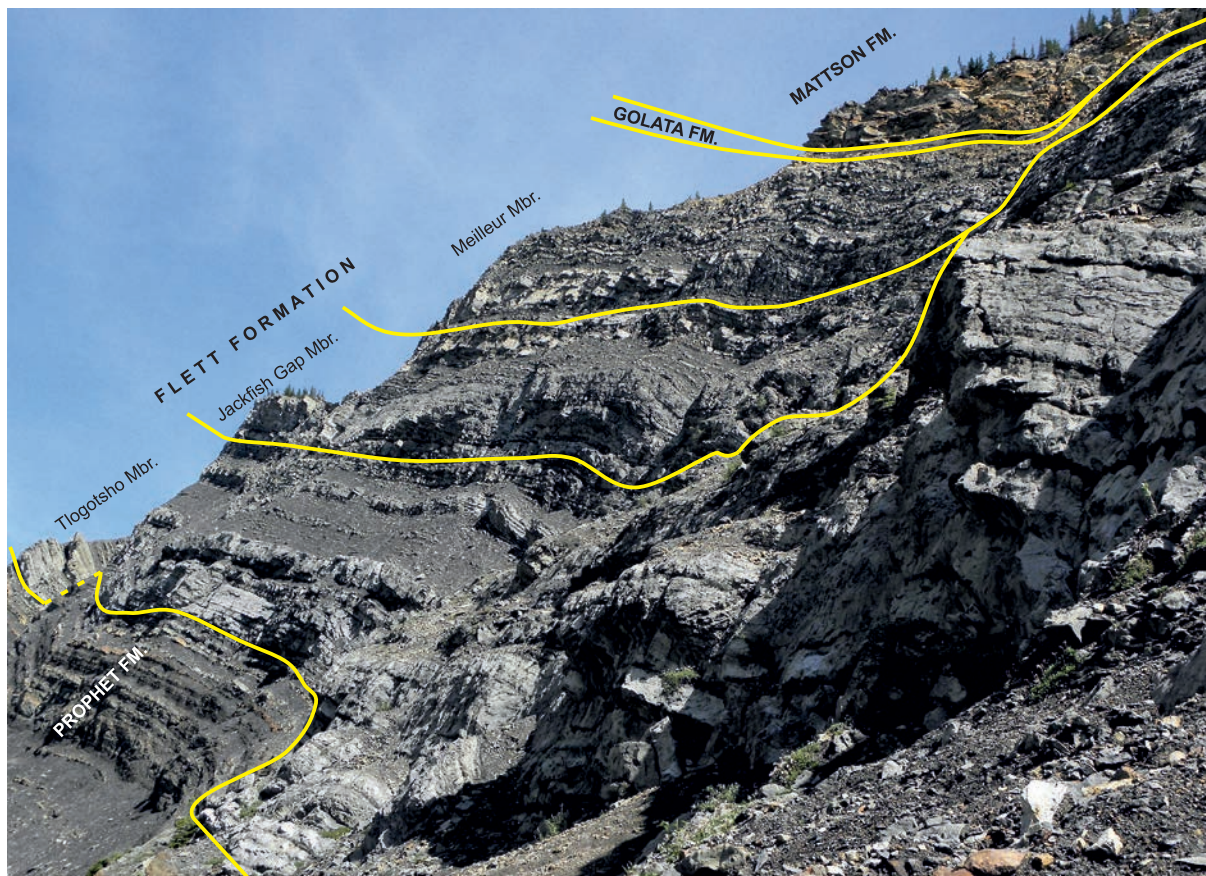
*Revised version accepted: 11<sup>th</sup> October 2021*



PLATES 1-8

PLATE 1

Photograph showing the distribution of lower Carboniferous rocks in Jackfish Gap, southwestern Mackenzie Mts., northeastern Liard Basin, northwestern Canada.

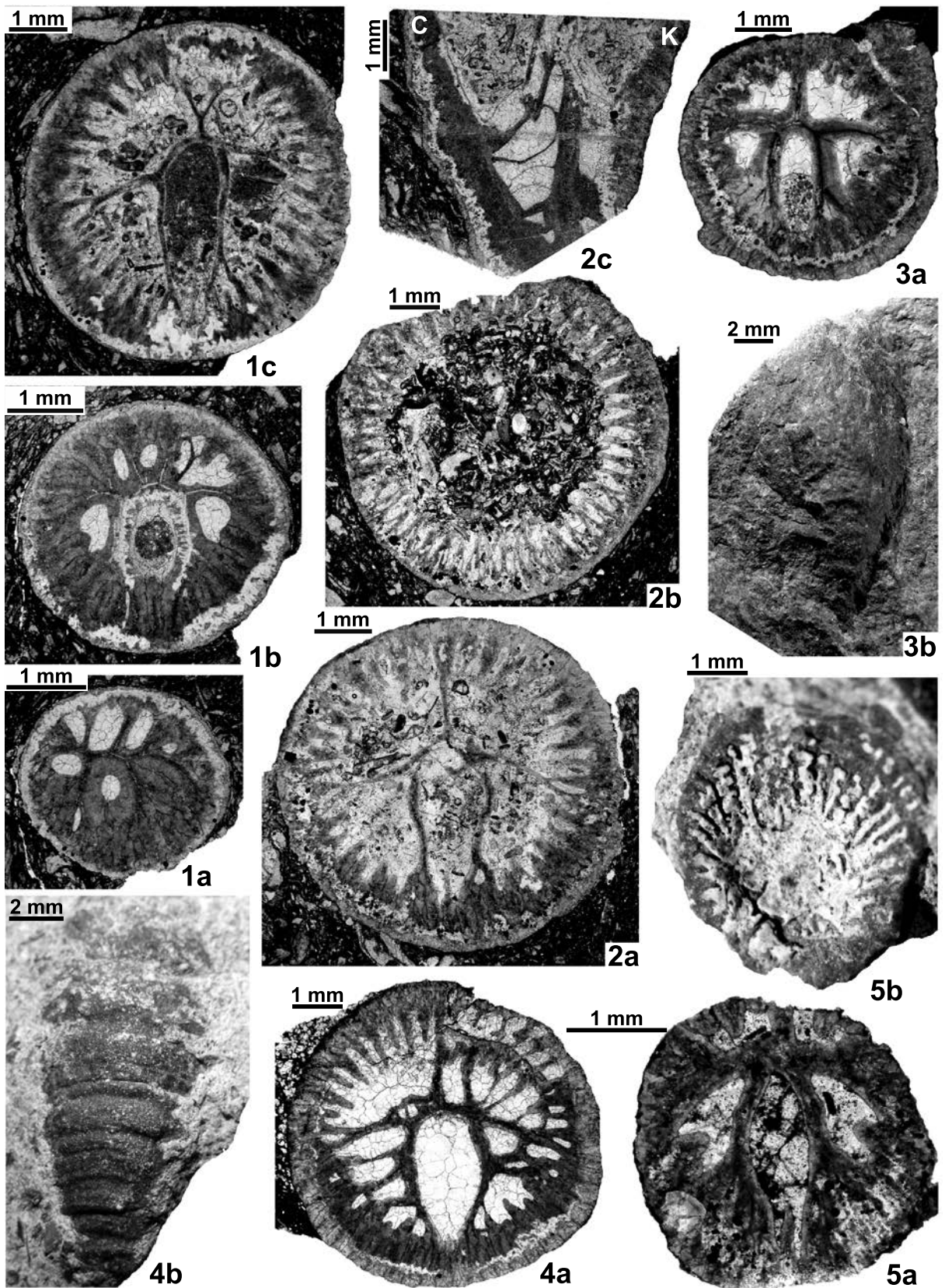


## PLATE 2

*Ankhelasma canadense* sp. nov.

1 – holotype, UAM.IG.Tc.C.JG-36(1); 1a – neanic growth stage; 1b – neanic/early mature growth stage, 1c – late mature growth stage. 2 – paratype, UAM.IG.Tc.C.JG-29(2); 2a, b – mature growth stage; 2c – longitudinal thin section along the C-K line. 3 – paratype, UAM.IG.Tc.C.JG-28(2); 3a – early mature growth stage; 3b – corallite surface. 4 – paratype, UAM.IG.Tc.C.JG-29(5); 4a – mature growth stage; 4b – corallite surface. 5 – paratype, UAM.IG.Tc.C.JG-29(3); 5a – early mature growth stage; 5b – partially preserved calyx filled with sediment.

All specimens are from the lower Flett Formation (Tlogotsho Member), lower Viséan.

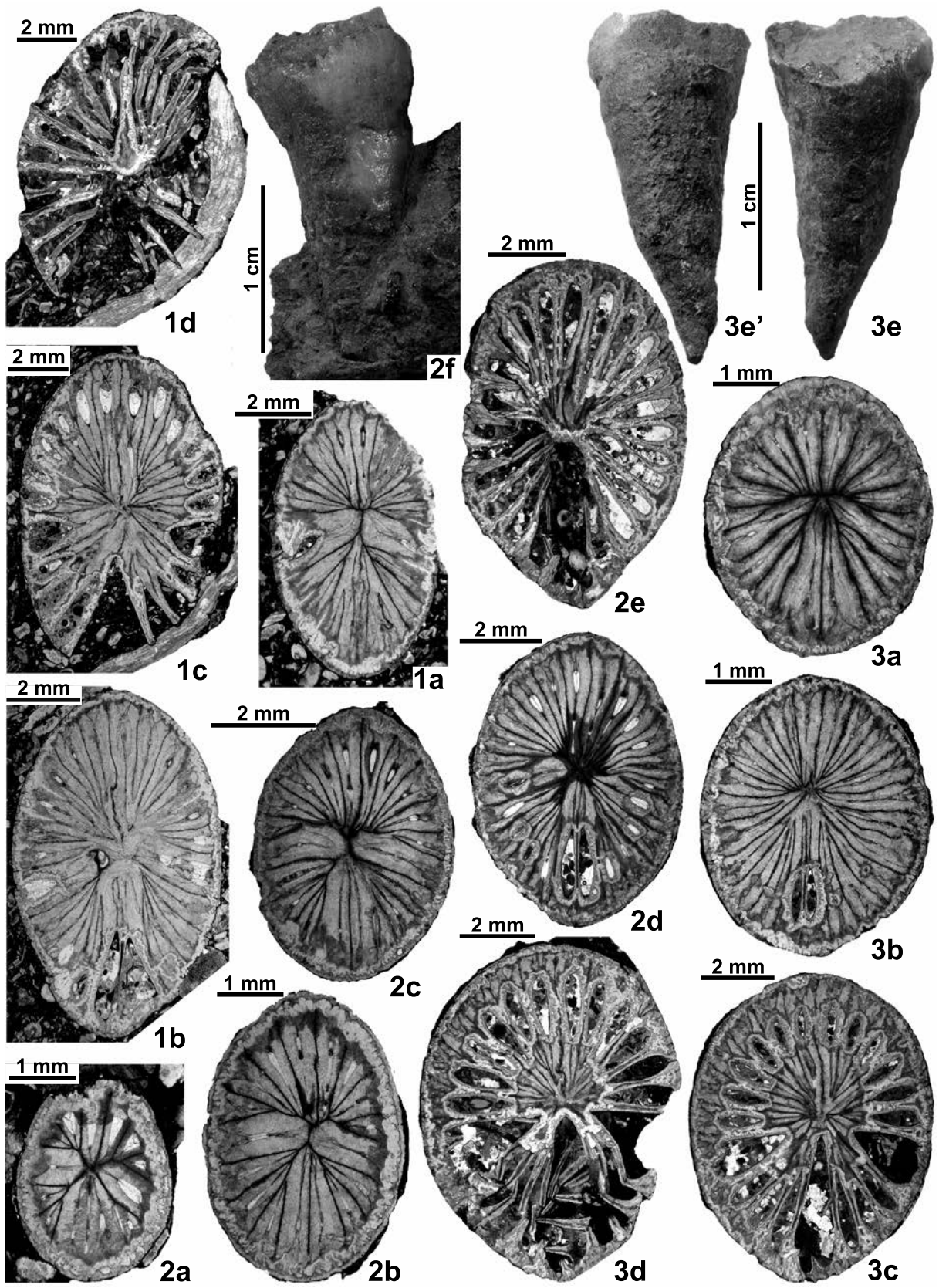


## PLATE 3

*Zaphrentites arkansanus* (Girty, 1910)

1 – UAM.IG.Tc.C.JG-95(4): 1a – late neanic growth stage; 1b–d – mature growth stage. 2 – UAM.IG.Tc.C.JG-95(1): 2a – early neanic growth stage; 2b, c – late neanic growth stage; 2d, e – mature growth stage; 2f – corallite surface. 3 – UAM.IG.Tc.C.JG-95(2): 3a – early mature growth stage; 3b–d – late mature growth stage; 3e, e' – corallite surface (3e concave side, 3e' convex side).

All specimens are from the upper Flett Formation (middle Meilleur Member), middle part of middle Viséan.



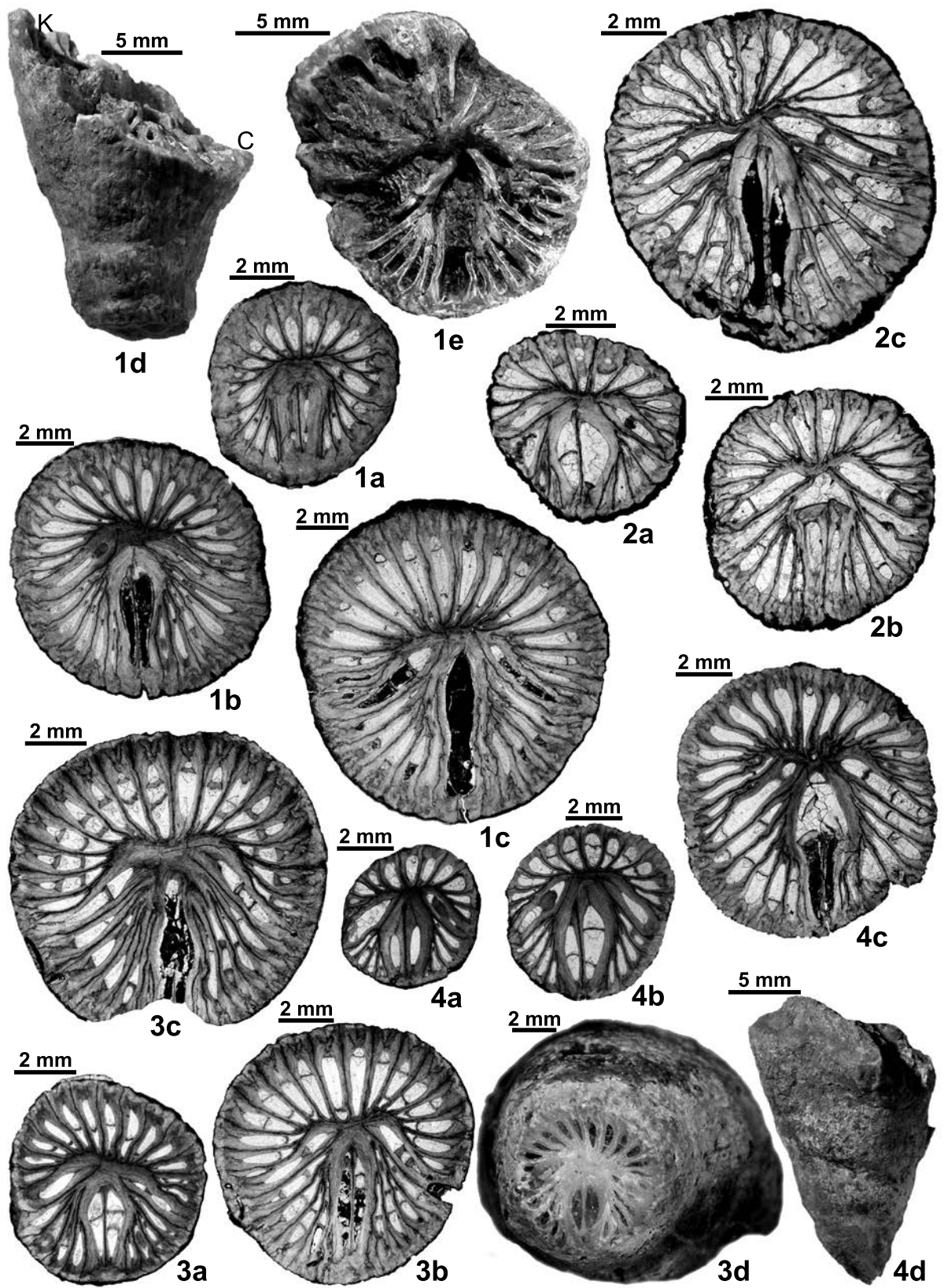
## PLATE 4

*Zaphrentites delanouei* (Milne-Edwards and Haime, 1851)

1 – UAM.IG.Tc.C.JG-42(5): 1a, b – early mature growth stage; 1c – late mature growth stage; 1d – corallite surface; 1e – partially preserved calyx filled with sediment. 2 – UAM.IG.Tc.C.JG-61(1): 2a – late neanic growth stage; 2b – early mature growth stage; 2c – late mature growth stage. 3 – UAM.IG.Tc.C.JG-42(4): 3a, b – early mature growth stage; 3c – late mature growth stage; 3d – early mature growth stage (weathered surface). 4 – UAM.IG.Tc.C.JG-56: 4a – late neanic growth stage; 4b – early mature growth stage; 4c – late mature growth stage; 4d – corallite surface.

All specimens are from the Flett Formation (middle part of Tlogotsho Member to lower part of Meilleur Member), lower–middle Viséan.





## PLATE 5

*Zaphrentites delanouei* (Milne-Edwards and Haime, 1851)

1 – UAM.IG.Tc.C.JG-22: 1a – late neanic growth stage; 1b, c – early mature growth stage; 1d – late mature growth stage. 2 – UAM.IG.Tc.C.JG-77(4): 2a, b – early mature growth stage; 2c, d – late mature growth stage. 3 – UAM.IG.Tc.C.JG-52: 3a – late neanic growth stage; 3b – early mature growth stage; 3c, d – late mature growth stage. 4 – UAM.IG.Tc.C.JG-60: 4a, b – late neanic/early mature growth stage.

All specimens are from the Flett Formation (middle part of Tlogotsho Member to lower part of Meilleur Member), lower–middle Viséan.

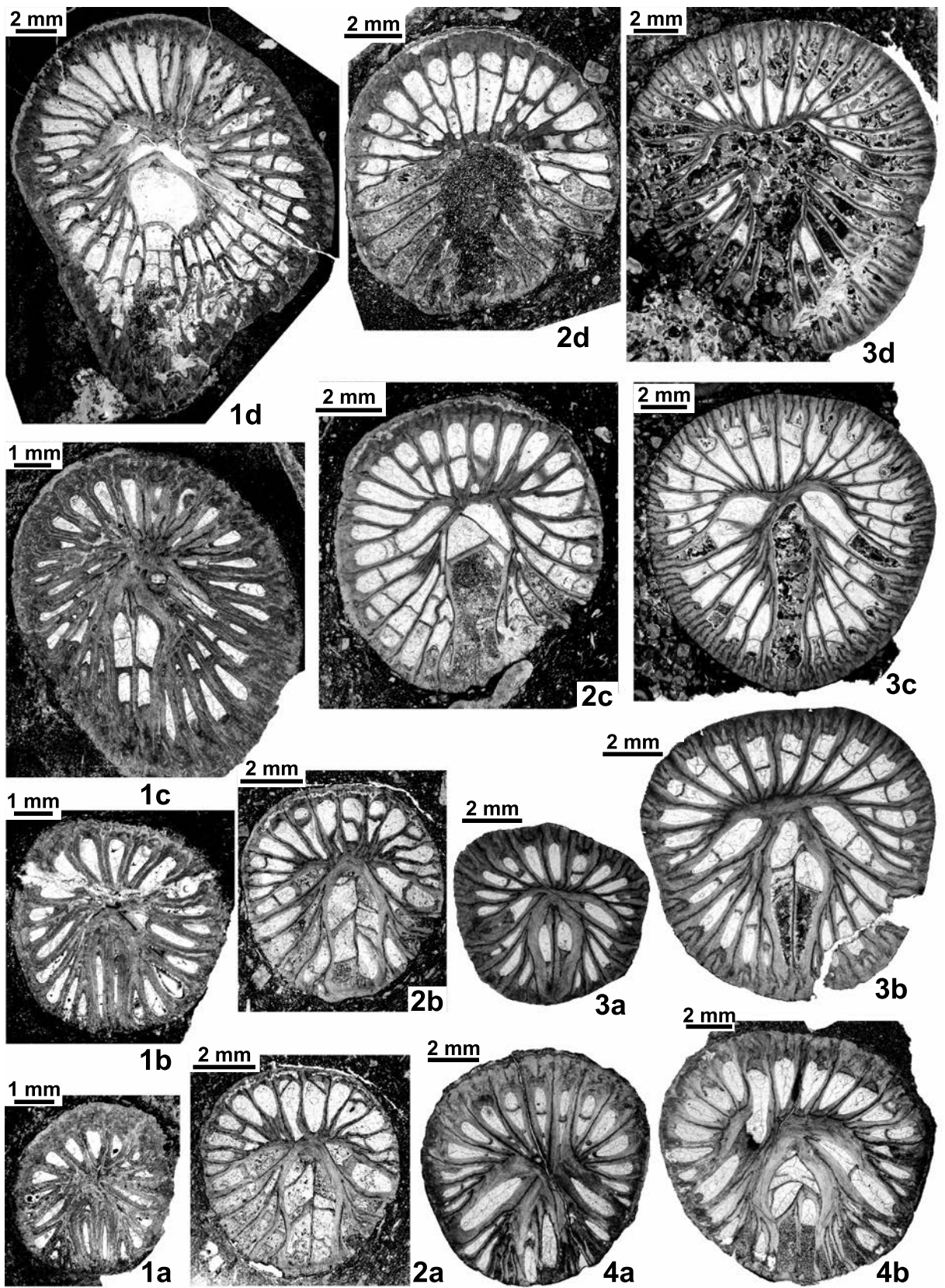
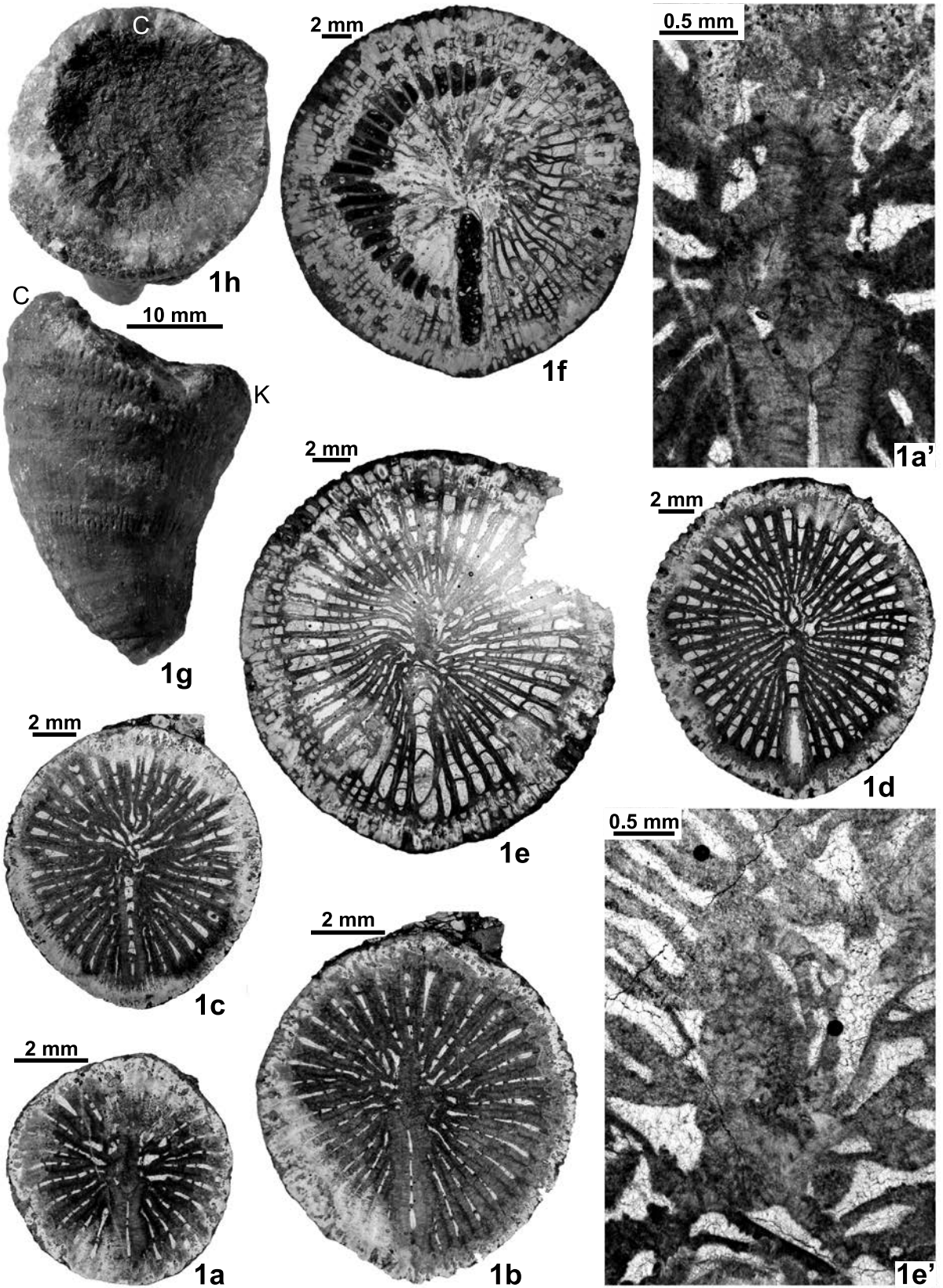


PLATE 6

*Ekvasophyllum inclinatum* Parks, 1951

UAM.IG.Tc.C.JG-71: 1a, 1b – late neanic growth stage; 1a' – columella (enlarged fragment from 1a); 1c, 1d – early mature growth stage; 1e, f – late mature growth stage; 1e' – columella (enlarged fragment from 1e); 1g – corallite surface; 1h – preserved calyx filled with sediment.

Specimen from the upper Flett Formation (lower part of Meilleur Member), middle Viséan.



## PLATE 7

*Ekvasophyllum enclinotabulatum* Sutherland, 1958

1 – UAM.IG.Tc.C.JG-51(2): 1a – early mature growth stage; 1b, c – late mature growth stage; 1b' – columella (enlarged fragment from 1b). 2 – UAM.IG.Tc.C.JG-43(3): 2a – early mature growth stage; 2b – early mature growth stage; 2c, d – late mature growth stage; 2d' – cardinal fossula (enlarged fragment from 2d); 2e – corallite surface; 2f – external view showing partially preserved calyx, long major septa and columella.

All specimens are from the Flett Formation (middle part of Tlogotsho Member – middle part of Meilleur Member), lower–middle Viséan.

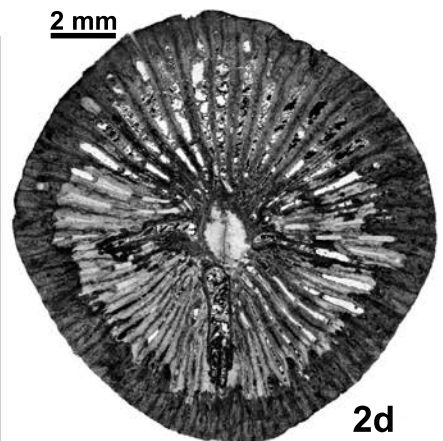
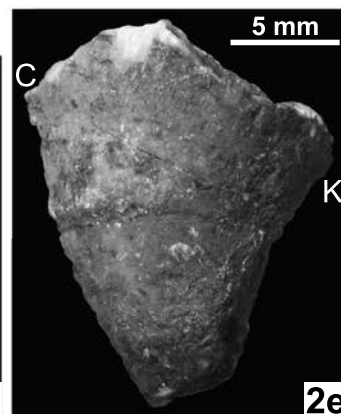
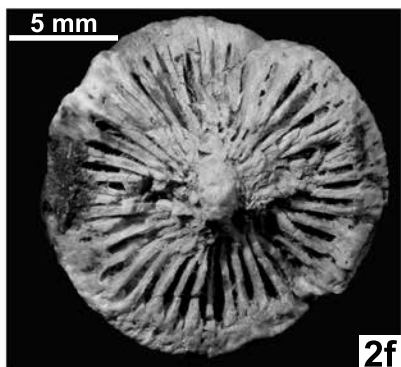
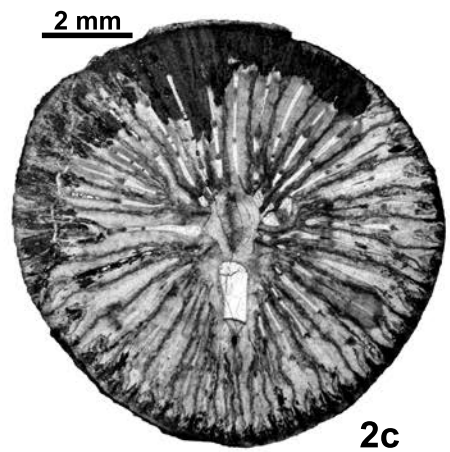
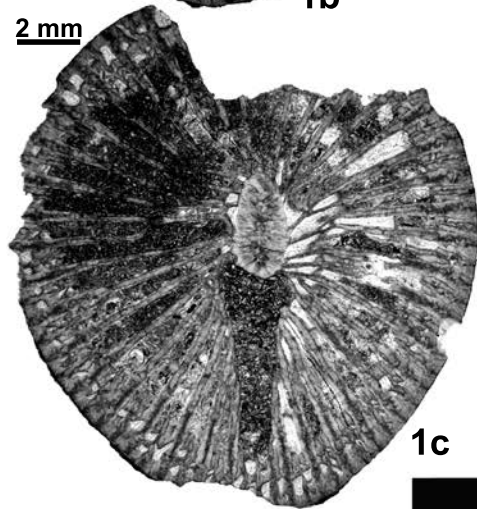
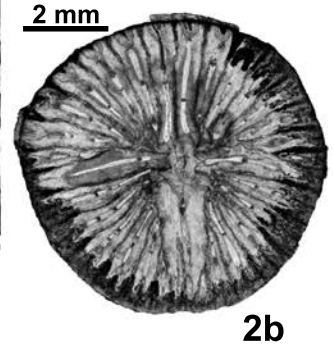
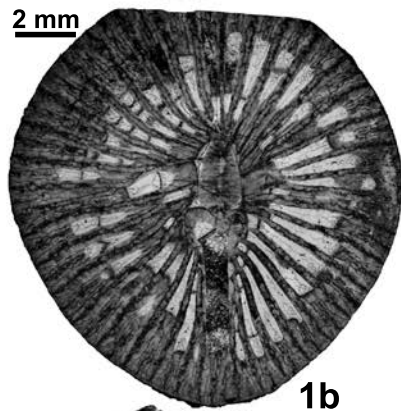
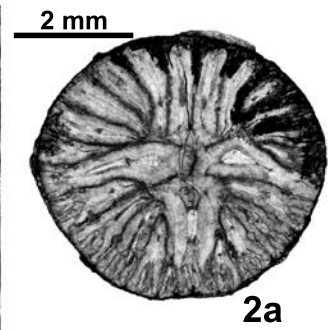
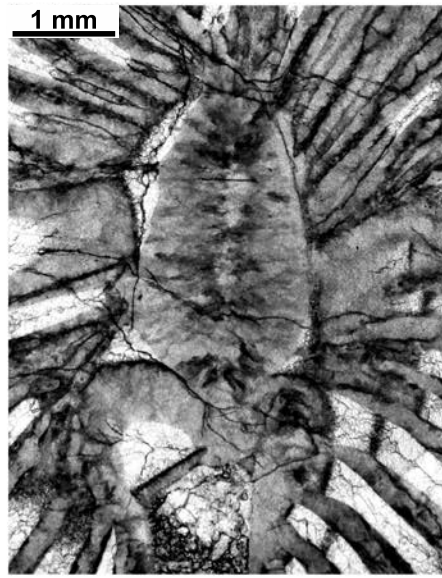
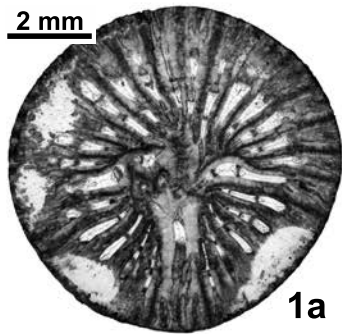


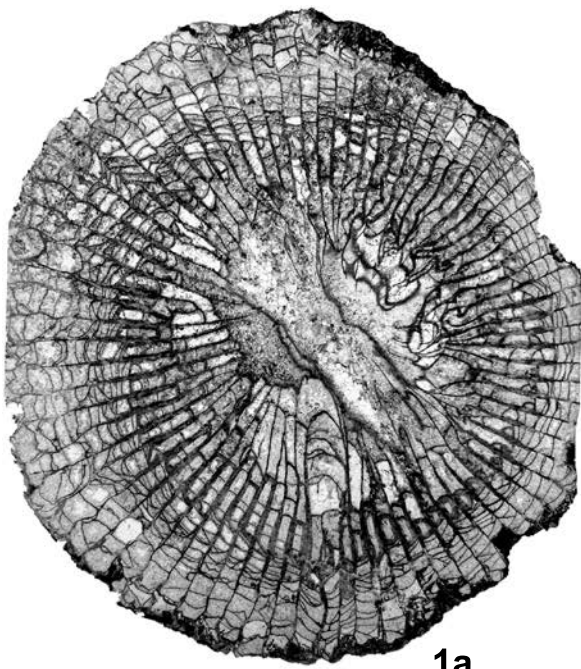
PLATE 8

*Caninophyllum* sp.

1 – UAM.IG.Tc.C.JG-17(2): 1a, b – mature growth stage; 1c – longitudinal section perpendicular to the C-K line, 1d – longitudinal section along the C-K line. 2 – UAM.IG.Tc.C.JG-23(1): 2a, b – mature growth stage.

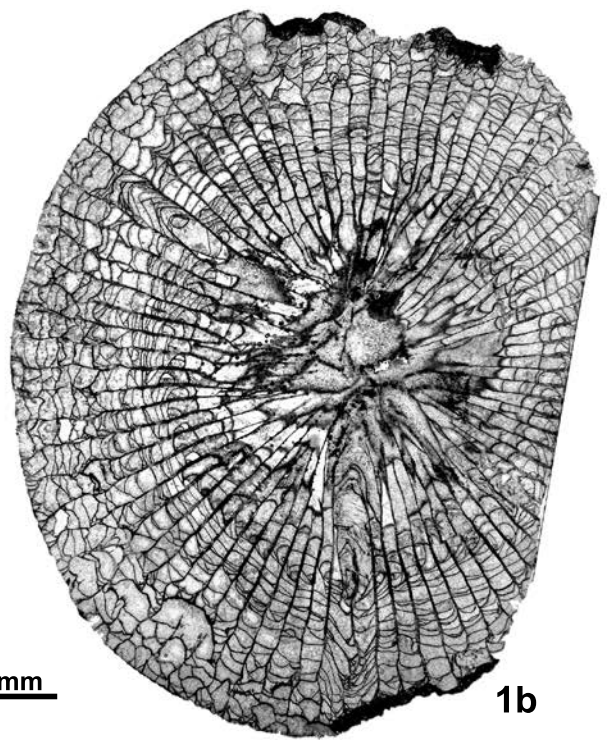
All specimens are from the lower Flett Formation (middle part of Tlogotsho Member), lower Viséan.





1a

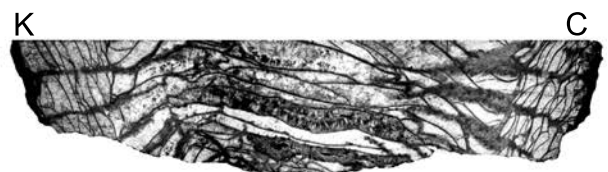
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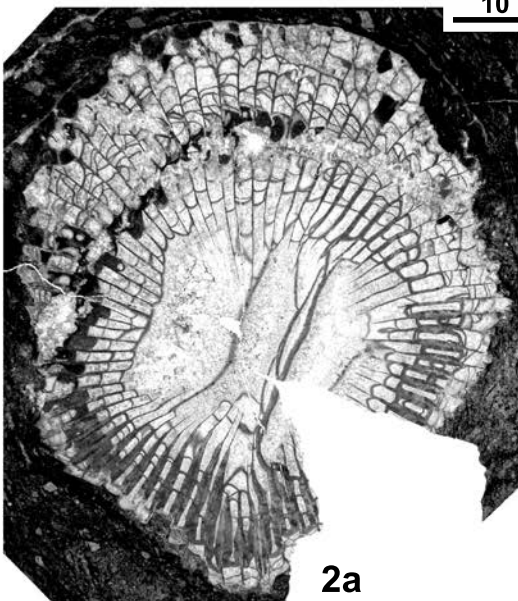
1b



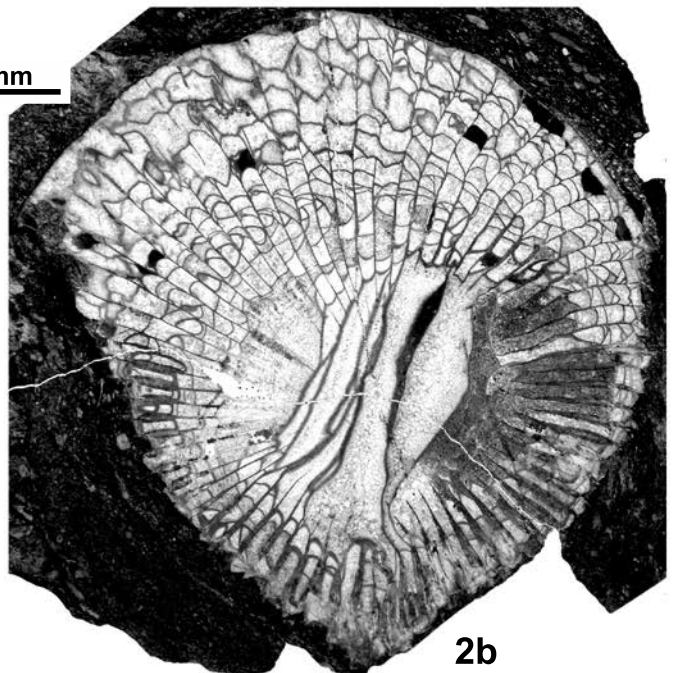
1c



1d



2a



2b

10 mm