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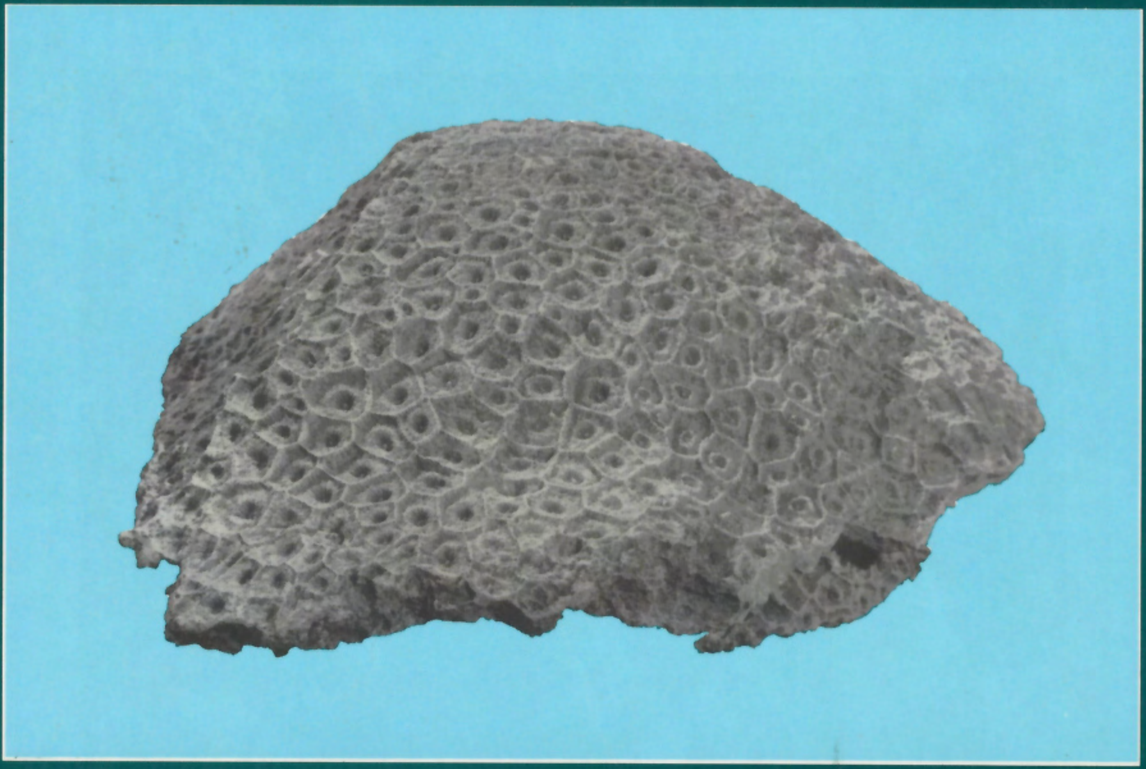
BIOSTRATIGRAPHY AND SYSTEMATICS OF UPPER CARBONIFEROUS CERIOID RUGOSE CORALS, ELLESMERE ISLAND, ARCTIC CANADA

E.W. Bamber and J. Fedorowski



1998

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BIOSTRATIGRAPHY AND SYSTEMATICS OF UPPER CARBONIFEROUS CERIOID RUGOSE CORALS, ELLESMERE ISLAND, ARCTIC CANADA

E.W. Bamber and J. Fedorowski
(with appendices by L. Rui and S. Pinard)

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Cover illustration
Well preserved colony of upper Moscovian *Petalaxis thorsteinssoni* sp. nov. (holotype, GSC 109653).

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PREFACE

Fossil corals have long been recognized as having major significance for the recognition of the geological age and ancient environments of Paleozoic sedimentary rocks, because of their abundance and because of the short time span and restricted, shallow-marine environmental conditions in which many species lived. More recently, they have become primary tools in interpreting climatic conditions, and locating the continents and oceanic connections for particular time periods within the Paleozoic. However, few Late Carboniferous corals have been described previously from Canada. In this report one of the two major groups of corals that occur in Upper Carboniferous strata in Arctic Canada, including the first Canadian recognition of many coral species, is described. Because the information derived from these corals is placed into the context provided by other fossil groups and by the rocks themselves, an unprecedented level of confidence in the new biostratigraphic data presented makes this report particularly important for extrapolation of the results nationally and internationally. This approach sets high standards for studies in fossil corals, from which future workers in many countries will benefit.

Not only is this report a major contribution to Canada's biostratigraphic time scale, to our knowledge of Canada's fossil heritage, and to Arctic Canada's geoscience knowledge base, but many of the results can be applied as well in western North America, Europe, and the Arctic, so that new levels of precision can be achieved in correlating sedimentary strata between these areas. Precise correlations and accurate knowledge of the depositional environments of sedimentary rocks allow our natural resource endowments to be exploited efficiently and effectively, and our geological maps and thematic studies in sedimentary rocks to be truly reliable.

M.D. Everell
Assistant Deputy Minister
Earth Sciences Sector

PRÉFACE

Les coraux fossiles sont considérés depuis longtemps comme des indicateurs importants de l'âge géologique et des paléoenvironnements des roches sédimentaires du Paléozoïque, en raison de leur abondance, de leur court intervalle d'existence et des conditions de milieu de mer peu profonde à circulation restreinte dans lesquelles de nombreuses espèces ont vécu. Depuis peu, ils sont devenus des outils de première importance quant à l'interprétation des conditions climatiques et à la localisation des continents et des liens océaniques à différents moments précis du Paléozoïque. Cependant, peu de coraux du Carbonifère tardif au Canada ont été décrits jusqu'à ce jour. Dans le présent bulletin, on trouvera la description de l'un des deux principaux groupes de coraux présents dans les strates du Carbonifère supérieur de l'Arctique canadien, auquel appartiennent de nombreuses espèces dont la présence au Canada est attestée pour la première fois. Puisque dans la présente étude les informations sur les coraux sont mises en relation avec celles tirées d'autres groupes de fossiles et des roches elles-mêmes, le degré de certitude sans précédent qu'offrent ces nouvelles données biostratigraphiques font de ce bulletin un outil particulièrement important pour l'extrapolation des résultats obtenus tant à l'échelle nationale qu'internationale. La méthode utilisée a permis d'établir d'excellents critères pour l'étude des coraux fossiles, sur lesquels pourront s'appuyer les chercheurs de nombreux pays.

En plus d'affiner de façon importante l'échelle biostratigraphique du Canada, d'approfondir notre compréhension de l'héritage fossilifère canadien et d'enrichir la base des connaissances géoscientifiques sur l'Arctique canadien, plusieurs des données contenues dans le présent bulletin peuvent être appliquées aussi bien à l'ouest de l'Amérique du Nord, qu'à l'Europe et à l'Arctique, de sorte qu'il est possible d'accroître le niveau de précision atteint dans la corrélation des successions sédimentaires entre ces diverses régions. Des corrélations précises et une connaissance exacte des milieux de dépôt des roches sédimentaires nous permettent d'envisager une exploitation efficace de nos richesses naturelles et d'accroître la fiabilité de nos cartes géologiques et de nos études thématiques sur les roches sédimentaires.

M.D. Everell
Sous-ministre adjoint
Secteur des sciences de la Terre

CONTENTS

Figures

Tables

BIOSTRATIGRAPHY AND SYSTEMATICS OF UPPER CARBONIFEROUS CERIOID RUGOSE CORALS, ELLESMERE ISLAND, ARCTIC CANADA

Abstract

The rugose coral genera ***Petalaxis*** *and* ***Cystolonsdaleia*** *occur at several stratigraphic levels in Moscovian to Gzhelian strata of the Sverdrup Basin. They are found in shelf carbonates of the middle and upper Canyon Fiord, lower Nansen and lower Belcher Channel formations, and in correlative debris flow deposits and shallow-water, reef-associated carbonates within the basinal Hare Fiord Formation. Lower to Upper Moscovian [Kashirian–lower(?)Podolskian] species include:* ***Petalaxis crassicolumnus*** *sp. nov.,* ***P. donbassicus*** *Fomichev,* ***P. ellesmerensis*** *sp. nov.,* ***P. mcoyanus*** *(Milne Edwards and Haime),* ***P. multilamellatus*** *sp. nov.,* ***P.*** *sp., and* ***Cystolonsdaleia*** *sp. Upper Moscovian (Podolskian–Myachkovian) strata have yielded the new species* ***P. beauchampi, P. thorsteinssoni*** *and* ***C. arctica.*** *These are succeeded by the Kasimovian species* ***P. baculatus*** *sp. nov. and* ***P. parvus*** *sp. nov., and the Kasimovian or lower Gzhelian species* ***P.*** *sp. cf.* ***P. elyensis*** *(Wilson and Langenheim),* ***C. carteri*** *sp. nov. and* ***C.*** *sp. aff.* ***C. carteri.***

Petalaxis *and* ***Cystolonsdaleia*** *have a broad geographic range in the Carboniferous of Europe, North America, Asia and North Africa. Several of the Ellesmere Island species are closely comparable to or identical with corals of similar age from Spain (Cantabrian Mountains), Ukraine (Donets Basin), Russia (Moscow Basin and the northern Ural Mountains), Spitsbergen and western U.S.A. (Nevada and California).*

Skeletal features characterizing both ***Petalaxis*** *and* ***Cystolonsdaleia*** *include four-layered corallite walls, biform tabularia, a variable, transeptal dissepimentarium, and variable axial structures containing median and lateral lamellae (new term) that originate as thickened, adaxial extensions of the cardinal septum.* ***Cystolonsdaleia*** *is further distinguished by the addition to its axial structure of short series of axial tabellae, accompanied by periaxial cones (new term) incorporating elongated axial tabellae and elevated, vertically extended axial parts of tabulae.*

Résumé

Des coraux rugueux des genres ***Petalaxis*** *et* ***Cystolonsdaleia*** *sont présents à plusieurs niveaux stratigraphiques dans la succession sédimentaire du Moscovien–Gzhélien du bassin de Sverdrup. Ils sont présents dans les roches carbonatées de plate-forme continentale des parties intermédiaire et supérieure de la Formation de Canyon Fiord, de la partie inférieure de la Formation de Nansen et de la partie inférieure de la Formation de Belcher Channel, ainsi que dans les unités corrélatives formées de coulées de débris et de roches carbonatées récifales d'eau peu profonde au sein des faciès de bassin de la Formation de Hare Fiord. Les espèces observées dans les strates du Moscovien inférieur-supérieur [Kashirien–Podolskien inférieur(?)] incluent :* ***Petalaxis crassicolumnus*** *sp. nov.,* ***P. donbassicus*** *Fomichev,* ***P. ellesmerensis*** *sp. nov.,* ***P. mcoyanus*** *(Milne Edwards et Haime),* ***P. multilamellatus*** *sp. nov.,* ***P.*** *sp. et* ***Cystolonsdaleia*** *sp. Les strates du Moscovien supérieur (Podolskien–Myachkovien) ont livré les nouvelles espèces* ***P. beauchampi, P. thorsteinssoni*** *et* ***C. arctica.*** *À celles-ci, succèdent les espèces* ***P. baculatus*** *sp. nov. et* ***P. parvus*** *sp. nov. du Kasimovien et les espèces* ***P.*** *sp. cf.* ***P. elyensis*** *(Wilson et Langenheim),* ***C. carteri*** *sp. nov. et* ***C.*** *sp. aff.* ***C. carteri*** *du Kasimovien ou du Gzhélien infèrieur.*

__Petalaxis__ et __Cystolonsdaleia__ montrent une vaste étendue géographique, se rencontrant dans le Carbonifère de l'Europe, de l'Amérique du Nord, de l'Asie et de l'Afrique du Nord. Plusieurs espèces récoltées dans l'île d'Ellesmere sont très comparables ou identiques à des coraux d'âge équivalent en Espagne (monts Cantabriques), en Ukraine (bassin de Donets), en Russie (bassin de Moscou et nord de l'Oural), au Spitzberg et dans l'ouest des États-Unis (Nevada et Californie).

Les éléments squelettiques qui caractérisent à la fois les genres __Petalaxis__ et __Cystolonsdaleia__ sont notamment des corallites montrant des parois à quatre couches, des tabularia biformes, un dissépimentarium transeptal variable et des structures axiales variables contenant des lamelles médianes et latérales (nouveau terme) qui ont pris naissance sous forme de prolongements adaxiaux épaissis du septum cardinal. __Cystolonsdaleia__ se distingue particulièrement par l'ajout à sa structure axiale de courtes séries de tabellae axiales, accompagnées de cônes périaxiaux (nouveau terme) incorporant des tabellae axiales allongées et des parties axiales élevées de tabulae prolongées dans le sens vertical.

INTRODUCTION

This is the first in a series of publications dealing with Upper Carboniferous rugose corals of the Sverdrup Basin. The cerioid specimens described below range in age from early Moscovian (Kashirian) to Kasimovian or early Gzhelian. They were collected, with associated foraminifers, conodonts, ammonoids and other invertebrate fossils, from measured stratigraphic sections and isolated outcrops in the western part of Ellesmere Island (Fig. 1, Table 1). At many of these localities, the coral fauna consists almost entirely of cerioid colonies, most of which belong to *Petalaxis*. Representatives of *Cystolonsdaleia* also occur locally, as do several fasciculate rugose genera. Solitary corals are locally numerous and tabulates are rare.

PREVIOUS WORK

With the exception of those dealt with herein, the Upper Carboniferous coral faunas of Canada are almost entirely undescribed, and little has been published on their nature and distribution. Several small, undescribed faunas have been reported from the western and northern mainland, and larger, more diverse assemblages are known from the northern Arctic Islands.

Western and northern mainland

Nelson (1982) described a Lower Pennsylvanian(?) tabulate coral, *Sinopora pascuali*, from the Kamloops area in southern British Columbia, and a Moscovian tabulate, *Michelinia harkeri*, from the upper part of the Ettrain Formation in northern Yukon Territory (Nelson, 1962).

Undescribed tabulate and rugose coral faunas of Late Carboniferous (Bashkirian and Moscovian) age are known from the Stikine assemblage of northwestern British Columbia (Brown et al., 1991; Nelson and Payne, 1984; Gunning, 1992) and are present in collections made by the British Columbia Geological Survey from the Lay Range Formation of the Aiken Lake map area of east-central British Columbia. Several species of *Fedorowskiella*, *Fomichevella*, *Heintzella*, and *Eastonastraea* from the Stikine assemblage were assigned a Permian age by Stevens and Rycerski (1989); this age has not been confirmed with data from other faunal groups. Corals and foraminifers recently collected from Stikinia suggest that the species described by Stevens and Rycerski originated from unnamed Upper Carboniferous (Bashkirian) carbonate units that are widespread in the area. A few undescribed Bashkirian and Moscovian rugose corals from the Lisburne Group of the Ogilvie, Richardson, and British mountains in northern Yukon Territory are contained in Geological Survey of Canada collections.

In neighboring northern Alaska, the Lisburne Group has yielded a small fauna of Bashkirian colonial rugose corals from the Wahoo Formation (Armstrong, 1972). A second small fauna, consisting of Middle Pennsylvanian tabulate and rugose corals, was reported and partly described from the Alaska Range of east-central Alaska by Rowett (1969, p. 15, 38, 74, 118).

Arctic Archipelago

In the Sverdrup Basin of the northern Canadian Arctic Islands (Fig. 1), corals occur at several stratigraphic levels ranging in age from Bashkirian to Gzhelian. Occurrences have been reported from the Canyon Fiord, Otto Fiord, Hare Fiord, and Nansen formations (Tozer and Thorsteinsson, 1964, p. 100; Nassichuk, 1975, p. 178, 179; Beauchamp, 1987, p. 41, 47; Nassichuk and Davies, 1980, p. 15; Mayr, 1992, p. 84-86, 105, 106).

ACKNOWLEDGMENTS

We wish to acknowledge the help and advice received while collecting corals for this study during the field seasons of 1971, 1985, 1989 and 1990. We are particularly grateful to W.W. Nassichuk and B. Beauchamp, who generously arranged logistical field support and provided essential information on stratigraphy and regional relationships in the study area. Welcome collecting assistance was given by C.M. Henderson, P. Thériault, R.H. Heise, and B. Olchowy. In addition to corals collected by the authors, this study also includes specimens from collections made by G.F. Bonham-Carter, G.R. Davies, P. Harker, U. Mayr, W.W. Nassichuk, and R. Thorsteinsson. Locality and stratigraphic data for several collections from the Blue Mountains were provided by G.F. Bonham-Carter and F.R. Brunton.

R.D. Michie prepared the numerous, high quality thin sections needed for this study, and N.N. Robinson and B.W.B. Tsang prepared serial acetate peels used for detailed morphological descriptions. Photographs for text figures and plates were produced by B.C. Rutley and W.B. Sharman. Digital drafting and processing of text figures and plates were completed by

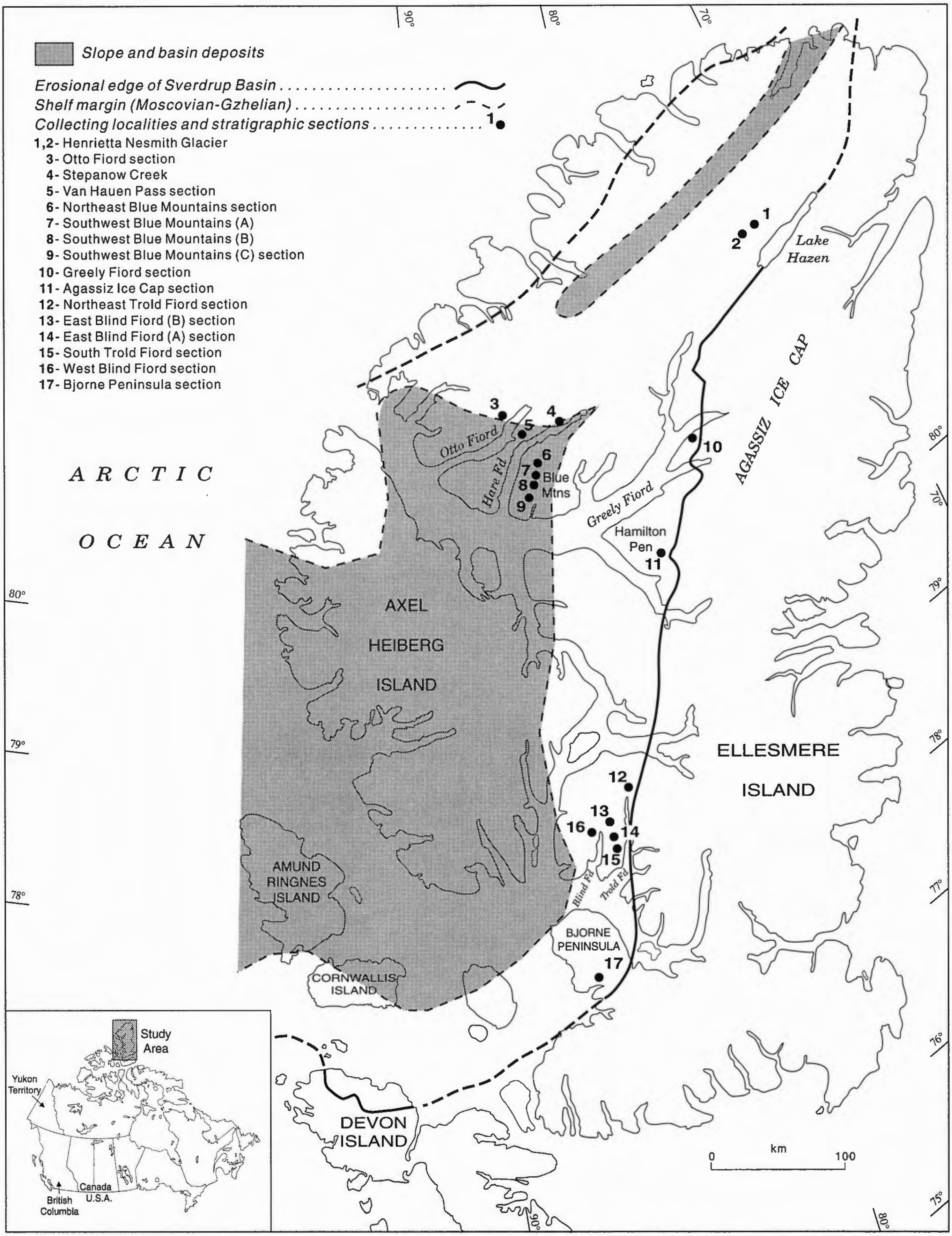

Figure 1. Eastern Sverdrup Basin, showing location of stratigraphic sections and collecting localities.

Table 1

Location of collecting sites

Section or Locality		Latitude Longitude	Formation Yielding Corals				Depositional Setting	
			Canyon Fiord	Belcher Channel	Nansen	Hare Fiord	Shelf	Basin/slope
1	Henrietta Nesmith Glacier	81°55′30″N 73°02′W	x				x	
2	Henrietta Nesmith Glacier	81°56′N 73°13′W	x				x	
3	Otto Fiord	81°17′N 85°58′W			x		x	
4	Stepanow Creek	81°07′N 84°06′W			x		x	
5	Van Hauen Pass	81°03′30″N 85°29′W				x		x*
6	Northeast Blue Mountains	80°50′N 85°03′10″W				x		x**
7	Southwest Blue Mountains (A)	80°45′50″N 85°31′0″W				x		x**
8	Southwest Blue Mountains (B)	80°45′N 85°37′W				x		x**
9	Southwest Blue Mountains (C)	80°44′30″N 85°45′W				x		x*
10	Greely Fiord	80°46′38″N 78°25′W	x				x	
11	Agassiz Ice Cap	80°08′30″N 80°50′W		x			x	
12	Northeast Trold Fiord	78°36′25″N 84°31′W	x				x	
13	East Blind Fiord (B)	78°23′52″N 85°25′W	x				x	
14	East Blind Fiord (A)	78°21′43″N 85°23′W	x				x	
15	South Trold Fiord	78°15′50″N 85°13′W	x				x	
16	West Blind Fiord	78°21′N 85°54′N			x		x	
17	Bjorne Peninsula	77°25′N 86°48′W	x				x	

Locality 18 - quarry near Leninskie Gorki, approximately 35 km south of Moscow, Russia (55°32′N, 37°38′E) (Belskaya et al., 1975, p. 37, locality 9); Novlinskaya Formation, base of Myachkovski “horizon”.

Locality 19 - Golubovka (formerly Kirovsk) Village, right bank of Lugan River, Luganskaya region, Ukraine (48°39′N, 38°40′E); Limestone L_5, early Moscovian (Kashirian).

* - Debris flow bed
** - Reef crest

Glen Edwards, Denise Then and Elizabeth Macey. Pat Greener and Hilde King were responsible for final word processing and document composition. We wish to express our appreciation for all of this excellent technical support.

We thank N.P. Vasilyuk for donating a specimen of the type species of *Cystolonsdaleia* from the Donets Basin, and gratefully acknowledge T.I. Nemirovskaya for her help in sending the specimen to us. We appreciate the time and effort generously given by W.J. Sando, who arranged the loan of type specimens, provided copies of publications and gave useful advice on the content and preparation of our paper. Helpful comments for improvements in the manuscript were kindly provided by E.C. Wilson. Specimens of *Petalaxis mcoyanus* (Milne Edwards and Haime) from its type area in the Moscow Basin were kindly donated to us by W.J. Sando and M. Kato. S. Rodriguez made specimens from his collection available for study, and contributed valuable information on the ages of coral-bearing strata in Spain.

We wish to draw special attention to the invaluable discussions with A.E.H. Pedder on many aspects of coral description and taxonomy, and to the foraminiferal studies of L. Rui and S. Pinard, who determined the ages of coral-bearing strata from many localities. Helpful observations and suggestions were given by the critical readers, B. Beauchamp, S. Rodriguez and W.J. Sando.

STRATIGRAPHY

A thick succession of Carboniferous and Permian marine sedimentary rocks, associated with minor nonmarine rocks and volcanics, is exposed in the Sverdrup Basin, a northeast-trending rift basin underlying the northern islands of the Canadian Arctic Archipelago (Fig. 1). The succession includes three laterally gradational facies assemblages that vary considerably in content and extent: a marginal clastic facies, a platform carbonate and clastic facies, and a basinal shale, evaporite and chert facies with local development of algal and bryozoan reefs (Thorsteinsson, 1974, Fig. 2; Nassichuk and Wilde, 1977; Nassichuk and Davies, 1980; Nassichuk, 1984; Beauchamp, 1987, 1992; Beauchamp et al., 1989b; Davies and Nassichuk, 1991; Mayr, 1992). From recent stratigraphic and sedimentological studies, eight upper Paleozoic transgressive–regressive sequences were recognized within the Sverdrup Basin (Beauchamp, 1994, 1995; Beauchamp and Henderson, 1994; Beauchamp and Thériault, 1994). The Upper Carboniferous succession of Ellesmere Island is included in the third and fourth of these sequences, which represent a major marine transgression that culminated in mid-Moscovian time, followed by a regression that ended near the Kasimovian–Gzhelian boundary (Beauchamp et al., 1989a, b; Beauchamp, 1995; Henderson et al., 1995). Figure 2, adapted from Beauchamp and Thériault, 1994, p. 202, Fig. 2), shows the stratigraphic relationships and depositional settings of formations within this interval in the southern part of the basin. The shallow-shelf siliciclastics and carbonates of the Canyon Fiord Formation grade laterally into shelf carbonates of the Antoinette and Nansen formations. Toward the axis of the basin, the shelf carbonates pass into the subaqueous evaporites and carbonates of the Otto Fiord Formation and the overlying algal and bryozoan reef buildups and slope-to-basin, thin bedded limestone and shale of the Hare Fiord Formation.

Species of *Petalaxis* and *Cystolonsdaleia*, described herein, were collected mainly from shallow-shelf limestone of the Canyon Fiord Formation near the southern basin margin. They were also found in shelf carbonates of the Nansen Formation on both the north and south sides of the basin, in limestone mapped by Thorsteinsson (1969) as part of the lower Belcher Channel Formation on Hamilton Peninsula (Agassiz Ice Cap section, Fig. 1, locality 11) and in basinal deposits of the Hare Fiord Formation (Fig. 1, Table 1). Those in the basinal deposits, however, occur only in shallow-water carbonates associated with local reef buildups ("Tellevak" limestone of Bonham Carter, 1966) in the lower part of the Hare Fiord Formation, and in debris-flow beds originating from upper slope or shelf settings. With few exceptions, the ages of the coral species were determined or confirmed from their association with several other marine invertebrate groups, including foraminifers, ammonoids, and conodonts. Most species of *Petalaxis* and *Cystolonsdaleia* are of Early and early Late Moscovian (Kashirian–Podolskian) age, but the collection also contains a few uppermost Moscovian (Myachkovian) and younger Carboniferous (Kasimovian to ?lowest Gzhelian) representatives of these genera (Figs. 3-15).

BIOSTRATIGRAPHY

Foraminifers, ammonoids and conodonts ranging in age from Bashkirian to Early Permian occur in all of the four formations (Canyon Fiord, Nansen, Hare Fiord, Belcher Channel) that have yielded cerioid corals in the study area (Table 2). The Upper Carboniferous faunas are briefly discussed below (Fig. 3).

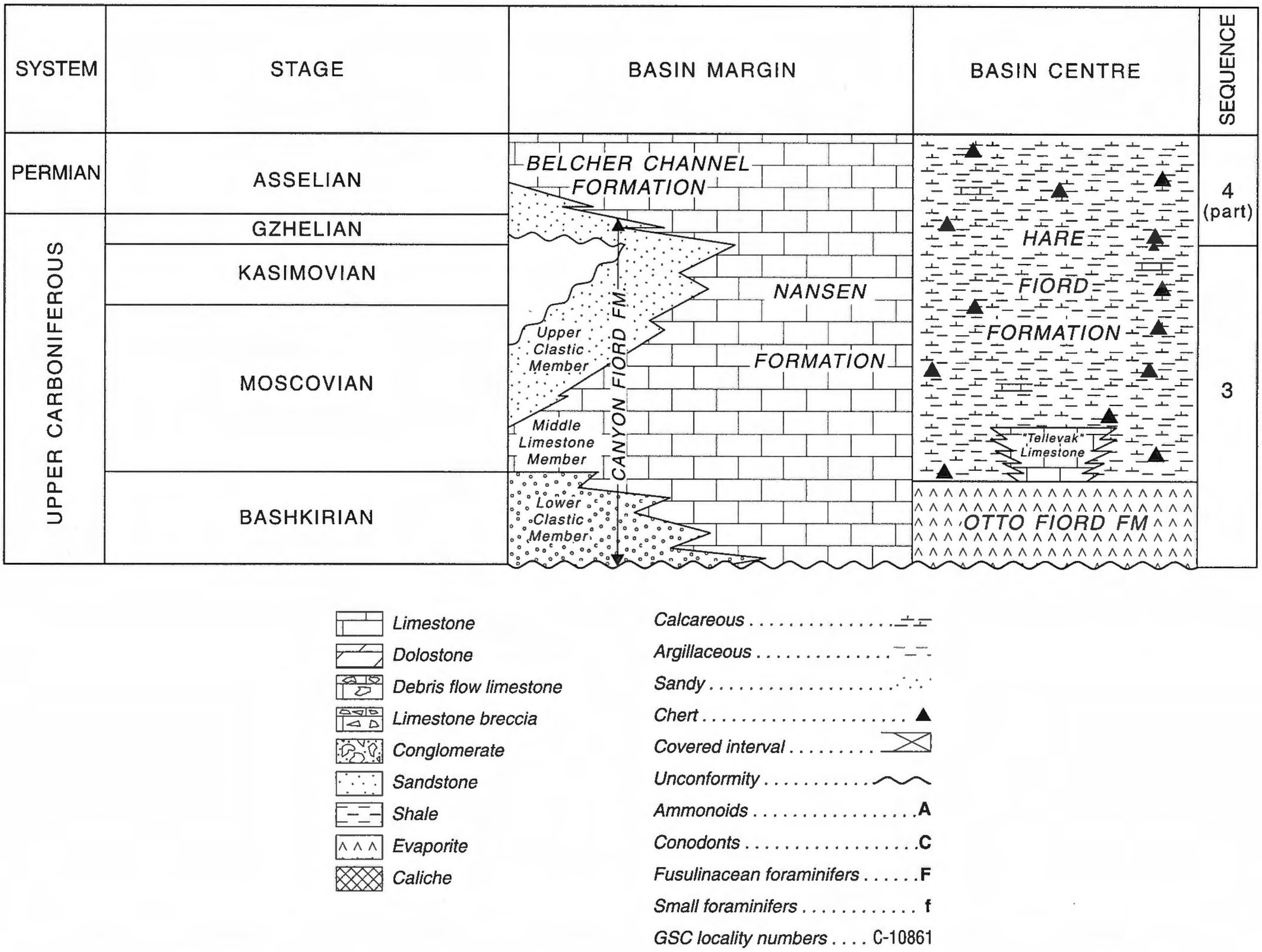

***Figure 2.** Stratigraphic relationships of Upper Carboniferous formations, southeastern side of Sverdrup Basin; modified after Henderson et al. [1995, Fig. 3, transgressive–regressive sequences 3 and 4 (part)].*

The stratigraphy and age relationships of the entire upper Paleozoic succession of Axel Heiberg Island and western Ellesmere Island were described initially by Thorsteinsson (1974). He based his Carboniferous age determinations on data from ammonoids, fusulinaceans and other foraminifers (Mamet, *in* Thorsteinsson, 1974, p. 87-95). In a comprehensive account of the Carboniferous ammonoids of the Sverdrup Basin, Nassichuk (1975) described species from the study area ranging in age from Bashkirian to Kasimovian. He later presented the known distribution and age significance of ammonoids and foraminifers in a summary of the stratigraphy and biostratigraphy of Atokan (upper Bashkirian and lower Moscovian) formations in the basin (Nassichuk, 1984). Bashkirian and lower Moscovian conodonts from the Hare Fiord and Nansen formations in the vicinity of Hare Fiord were described by Bender (1980). Henderson (1988) recognized five Upper Carboniferous and nine Permian zones in a study of the upper Paleozoic conodont faunas of the Blind Fiord–Trold Fiord area of southern Ellesmere Island. His investigations were co-ordinated with the stratigraphic work of Beauchamp (1987) and a study of the associated foraminifers by Pinard (1989). Henderson later combined his Carboniferous data with that of Bender (*ibid.*) to establish seven Upper Carboniferous assemblage and range zones (C2–C6a), to which he assigned ages from Bashkirian to Gzhelian (Beauchamp et al., 1989a). As a result of more recent foraminiferal and conodont studies in the area (Nassichuk and Rui, 1992; Henderson, 1992; Henderson et al., 1995, p. 231), he now considers the overlying zone P1 and at least part of P2, originally dated as Permian, to be latest Carboniferous in age. The Bashkirian and Moscovian foraminiferal biostratigraphy of the Nansen Formation in its type area was presented by Rui et al. (1991) and Groves et al. (1994). Non-fusulinacean foraminiferal faunas from the Nansen of this area and its correlatives in the Blind Fiord–Trold Fiord area were described by Pinard

Table 2

Locality register

GSC Locality	Section or Locality	Formation	Stratigraphic Position
47866	5	Hare Fiord	162 m above base
47867	5	Hare Fiord	27 m above base
52445	11	Canyon Fiord	46 m above base
57728	17	Canyon Fiord	275 m above base
58924	7	Hare Fiord	Top of “Tellevak” Lst.
58967	17	Canyon Fiord	Unknown, talus
60190	8	Hare Fiord	1.2 m above top of “Tellevak” Lst.
60192	9	Hare Fiord	173 m above top of “Tellevak” Lst.
60193	9	Hare Fiord	174 m above top of “Tellevak” Lst.
C-1877	4	Nansen	Lower part of formation, position uncertain
C-2082	1	Canyon Fiord	Approx. 267 m above base
C-10811	6	Hare Fiord	46.5 m below top of “Tellevak” Lst.
C-10812	6	Hare Fiord	27.5 m below top of “Tellevak” Lst.
C-10813	6	Hare Fiord	6.5 m above top of “Tellevak” Lst.
C-10814	6	Hare Fiord	12.2 m above top of “Tellevak” Lst.
C-10815	6	Hare Fiord	16.5 m above top of “Tellevak” Lst.
C-10861	5	Hare Fiord	81 m above base
C-10866	5	Hare Fiord	233 m above base
C-10872	13	Canyon Fiord	Base of middle limestone member
C-10873	13	Canyon Fiord	48 m above base of middle limestone member
C-10877	13	Canyon Fiord	Talus, 74 m above base
C-10881	13	Canyon Fiord	135 m above base
C-10884	13	Canyon Fiord	172 m above base
C-10885	13	Canyon Fiord	195 m above base
C-10886	13	Canyon Fiord	Rubble, 200 m above base
C-10888	13	Canyon Fiord	2.5 m above base of upper clastic member
C-10891	13	Canyon Fiord	Rubble, 60.5 m above base
C-10892	13	Canyon Fiord	98.5 m above base
C10893	13	Canyon Fiord	161.5 m above base
C-11402	14	Canyon Fiord	145.5 m above base of middle limestone member
C-11403	14	Canyon Fiord	150.1 m above base
C-27950	13	Canyon Fiord	Base of middle limestone member
C-27962	13	Canyon Fiord	137 m above base
C-27964	13	Canyon Fiord	163 m above base
C-27968	13	Canyon Fiord	172 m above base
C-27977	13	Canyon Fiord	231 m above base
C-27978	13	Canyon Fiord	232 m above base
C-27982	13	Canyon Fiord	242 m above base
C-27984	13	Canyon Fiord	245 m above base
C-27985	13	Canyon Fiord	246 m above base
C-27988	13	Canyon Fiord	259 m above base
C-27997	13	Canyon Fiord	331 m above base
C-28059	14	Canyon Fiord	49.5 m above base
C-28063	14	Canyon Fiord	68.5 m above base
C-28064	14	Canyon Fiord	80 m above base
C-28065	14	Canyon Fiord	83 m above base
C-28066	14	Canyon Fiord	85.5 m above base
C-28067	14	Canyon Fiord	96 m above base
C-31216	3	Nansen	161 m above faulted base of section
C-31217	3	Nansen	166.8 m above base
C-31218	3	Nansen	168 m above base
C-31219	3	Nansen	171 m above base
C-31223	3	Nansen	177 m above base
C-31226	3	Nansen	196 m above base
C-31227	3	Nansen	201 m above base
C-69857	2	Canyon Fiord	Uncertain, approx. middle of formation
C-99027	9	Hare Fiord	194.5 m above top of “Tellevak” Lst.
C-99028	9	Hare Fiord	195 m above top of “Tellevak” Lst.
C-99035	9	Hare Fiord	208 m above top of “Tellevak” Lst.
C-99052	9	Hare Fiord	285 m above top of “Tellevak” Lst.
C-99432	9	Hare Fiord	12 m above top of “Tellevak” Lst.
C-99436	9	Hare Fiord	24.75 m above top of “Tellevak” Lst.
C-147456	17	Canyon Fiord	361 m above base

Table 2 (cont.d')

GSC Locality	Section or Locality	Formation	Stratigraphic Position
C-179719	12	Canyon Fiord	67.5 m above base
C-179721	12	Canyon Fiord	Rubble at 94 m above base, probably derived from GSC loc. C-179722
C-179722	12	Canyon Fiord	96.5-97 m above base
C-179723	12	Canyon Fiord	Rubble near outcrop, at 97.5 m above base
C-179724	12	Canyon Fiord	99 m above base
C-179726	12	Canyon Fiord	100 m above base
C-179727	12	Canyon Fiord	103 m above base
C-179728	12	Canyon Fiord	102.5-103 m above base
C-179729	15	Canyon Fiord	249.2 m above base
C-179731	15	Canyon Fiord	286.5 m above base
C-179732	15	Canyon Fiord	299.5 m above base, rubble near outcrop
C-179734	16	Nansen	792 m below top
C-188241	16	Nansen	557 m below top
C-188642	15	Canyon Fiord	35 m above base
C-188644	15	Canyon Fiord	87 m above base
C-188645	15	Canyon Fiord	111 m above base
C-188646	15	Canyon Fiord	116 m above base
C-188649	15	Canyon Fiord	181 m above base
C-188650	15	Canyon Fiord	186.5 m above base
C-188651	15	Canyon Fiord	190.5 m above base
C-188652	15	Canyon Fiord	194 m above base
C-188653	15	Canyon Fiord	195 m above base
C-188654	15	Canyon Fiord	196 m above base
C-188655	15	Canyon Fiord	200 m above base
C-188656	15	Canyon Fiord	205.5 m above base
C-188658	15	Canyon Fiord	216 m above base
C-188660	15	Canyon Fiord	225 m above base
C-188661	15	Canyon Fiord	230.5 m above base
C-188662	15	Canyon Fiord	238 m above base
C-188663	15	Canyon Fiord	242.5 m above base
C-188664	15	Canyon Fiord	250.5 m above base
C-188665	15	Canyon Fiord	256.5 m above base
C-188666	15	Canyon Fiord	260 m above base
C193087	11	Belcher Channel	1.5-1.7 m above base
C193088	11	Belcher Channel	Rubble near outcrop, 25.8 m above base
C193090	11	Belcher Channel	Rubble near outcrop, 28.2 m above base
C193091	11	Belcher Channel	33.2 m above base
C193094	11	Belcher Channel	Talus, 87 m above base
C193095	11	Belcher Channel	Talus, 95 m above base
C193096	10	Canyon Fiord	176.5 m above base
C193097	10	Canyon Fiord	179.6 m above base
C193100	10	Canyon Fiord	270 m above base
C193105	10	Canyon Fiord	387 m above base
C193106	10	Canyon Fiord	387 m above base
C193107	10	Canyon Fiord	455 m above base

GSC loc. C-222965 - quarry near Leninskie Gorki, approximately 35 km south of Moscow, Russia (55°32′N, 37°38′E) (Belskaya et al., 1975, p. 137, locality 9); Novlinskaya Formation, base of Myachkovski "horizon"; collector, M. Kato, September 19, 1975.

GSC loc. C-147802 - Golubovka (formerly Kirovsk) Village, right bank of Lugan River, Luganskaya region, Ukraine (48°39′N, 38°40′E); Limestone L_5, Kashirian, early Moscovian; specimen provided by Dr. N.P. Vasilyuk, 1993.

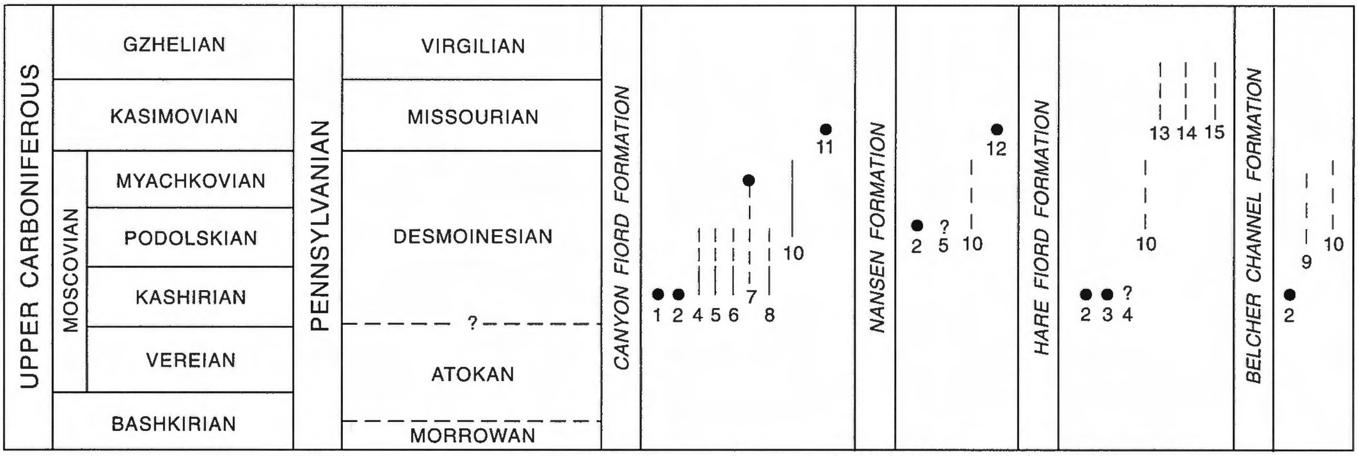

*Figure 3. Age ranges of **Petalaxis** and **Cystolonsdaleia** in the Canyon Fiord, Nansen, Hare Fiord, and Belcher Channel formations, Ellesmere Island. (Age definite, ●, ——; age indefinite, ?,– – –) (Ages of corals derived from associated foraminifers, ammonoids, and conodonts.)* **Coral Species:** *1,* ***Petalaxis mcoyanus*** *(Milne Edwards and Haime); 2,* ***P. donbassicus*** *(Fomichev); 3,* ***P.*** *sp.; 4,* ***P. crassicolumnus*** *sp. nov.; 5,* ***P. ellesmerensis*** *sp. nov.; 6,* ***P. multilamellatus*** *sp. nov.; 7,* ***P. beauchampi*** *sp. nov.; 8,* ***Cystolonsdaleia*** *sp.; 9,* ***C. arctica*** *sp. nov.; 10,* ***Petalaxis thorsteinssoni*** *sp. nov.; 11,* ***P. baculatus*** *sp. nov.; 12,* ***P. parvus*** *sp. nov.; 13,* ***P.*** *sp. cf.* ***P. elyensis*** *(Wilson and Langenheim); 14,* ***Cystolonsdaleia carteri*** *sp. nov.; 15,* ***C.*** *sp. aff.* ***C. carteri.***

(1989), who recently presented detailed distribution data and faunal illustrations as part of an Upper Carboniferous biostratigraphy and sequence stratigraphy study in the Blind Fiord area (Henderson et al., 1995). A comprehensive fusulinacean study by L. Rui is in progress, dealing with the Carboniferous and Permian faunas of western Ellesmere Island and Axel Heiberg Island, including those associated with the coral faunas described here (Appendix 1). His work includes a re-evaluation (discussed below) of the faunas near the Carboniferous–Permian boundary in the West Blind Fiord section (locality 16, Fig. 1; Nassichuk and Rui, 1992).

Nansen Formation

Foraminifers, ammonoids and conodonts

Age assignments for Carboniferous foraminifers from the shelf carbonates of the Nansen Formation range from Serpukhovian (latest Early Carboniferous) to Gzhelian (Thorsteinsson, 1974; Mamet *in* Nassichuk, 1975; Beauchamp, 1987; Pinard, 1989; Rui et al., 1991; Ross *in* Mayr, 1992; Nassichuk and Rui, 1992; Henderson et al., 1995). In a recent, detailed study of the fusulinacean zones in the lower part of the Nansen in its type area near the head of Hare Fiord, Groves et al. (1992, 1994) favour an early Bashkirian, rather than Serpukhovian, age limit for the basal beds of the formation. Nassichuk (1975, p. 43) described ammonoids of Atokan (Bashkirian, pers. comm., 1993) age from the type section of the Nansen and also reported a single Kasimovian (Missourian) specimen from the formation at locality 4 (Fig. 1) to the southwest (*ibid.*). Morrowan and Atokan (Bashkirian and lower Moscovian) conodonts were described by Bender (1980) from the lowest 431 m of the type Nansen (conodont zones 1-3 of Henderson *in* Beauchamp et al., 1989a).

Until recently, all but the lowest beds of the Nansen Formation in the west Blind Fiord section (locality 16, Figs. 1, 14) were assigned to the Permian, based on the distribution of foraminifers, conodonts and ammonoids (Nassichuk and Wilde, 1977; Nassichuk and Henderson, 1986; Beauchamp, 1987; Henderson, 1988; Pinard, 1989). From new biostratigraphic data, however, Nassichuk and Rui (1992) now place the base of the Permian 327 m above the base of this section and have reassigned the underlying strata to the Kasimovian and Gzhelian stages (Fig. 14). Their interpretation is based on a new discovery of the exclusively Upper Carboniferous ammonoid genus *Dunbarites* (GSC loc. C-188241, Fig. 14), 235 m above the base of the section, coupled with a detailed restudy of the fusulinaceans. The base of the Permian was tentatively drawn by these authors to correspond with the lowest occurrence of *Pseudofusulina plana* Skinner and Wilde. Foraminifers and conodonts found with *Petalaxis parvus* sp. nov., 4 m above the base of this section, indicate a Kasimovian [possibly early(?)

Kasimovian] age (Fig. 14, Table 3, GSC loc. C-179734; Henderson et al., 1995).

Corals

Few collections of cerioid corals from the Nansen Formation are available for study. In the Otto Fiord section (locality 3, Figs. 1, 4), the lower part of the formation has yielded *Petalaxis ellesmerensis* sp. nov. and *P. donbassicus* (Fomichev) associated with foraminifers of late Moscovian (Podolskian) age. *Petalaxis parvus* sp. nov., one of the two species from the study area, firmly dated as Kasimovian, occurs in the lower part of the Nansen Formation, 4 m above the base of the west Blind Fiord section (Fig. 14, Table 3). The evidence from microfossils and ammonoids for the age of the lower part of the formation in this section is discussed above.

Hare Fiord Formation

Foraminifers, ammonoids and conodonts

The lowest part of the type section of the Hare Fiord Formation (Van Hauen Pass section, locality 5, Fig. 1; Fig. 5) has yielded lower Atokan (Bashkirian) conodonts (Bender, 1980; Zone C3, Beauchamp et al., 1989a). These are overlain by Atokan [=Bashkirian to lower Moscovian (Vereian), Nassichuk, 1984, p. 160] ammonoids, which occur approximately 28 m above the base of the formation at this section (GSC loc. 47867) and in the "Tellevak" limestone, approximately 30 m above the base of the Hare Fiord Formation to the east, near locality 4 (Fig. 1) (Thorsteinsson, 1974, p. 31; Nassichuk, 1975, p. 27). South of the type area of the Hare Fiord Formation, Nassichuk (1975, p. 27-29; pers. comm., 1993) reported a similar, but slightly younger, Atokan [Bashkirian to lower Moscovian (Vereian), Nassichuk, 1984, p. 160, pers. comm., 1993] ammonoid fauna from several localities in the "Tellevak" limestone of the Blue Mountains and a still younger Atokan (Bashkirian to lower Moscovian) fauna from that unit in the Krieger Mountains to the northeast (Nassichuk, 1984, p. 166).

The lowest part of the Hare Fiord Formation, overlying the "Tellevak" limestone, contains lower Moscovian (Kashirian) fusulinaceans in the northeast Blue Mountains section (locality 6, Fig. 1; Fig. 6), and upper Moscovian (Podolskian or Myachkovian) fusulinaceans in the southwest Blue Mountains (C) section (locality 9, Fig. 1; Fig. 7). Higher in the latter section, foraminifers of Kasimovian or earliest Gzhelian age were collected by G.F. Bonham-Carter, 173–174 m above the top of the "Tellevak" limestone (GSC locs. 60192, 60193, Appendices 1, 2). These are overlain by Gzhelian foraminifers, 21 m higher in this section (GSC loc. C-99027, C-99028). Zhigulevian (Kasimovian-lower Gzhelian) fusulinaceans were reported by Thorsteinsson (1974, p. 30, 31) from the lower part of the type section of the Hare Fiord Formation.

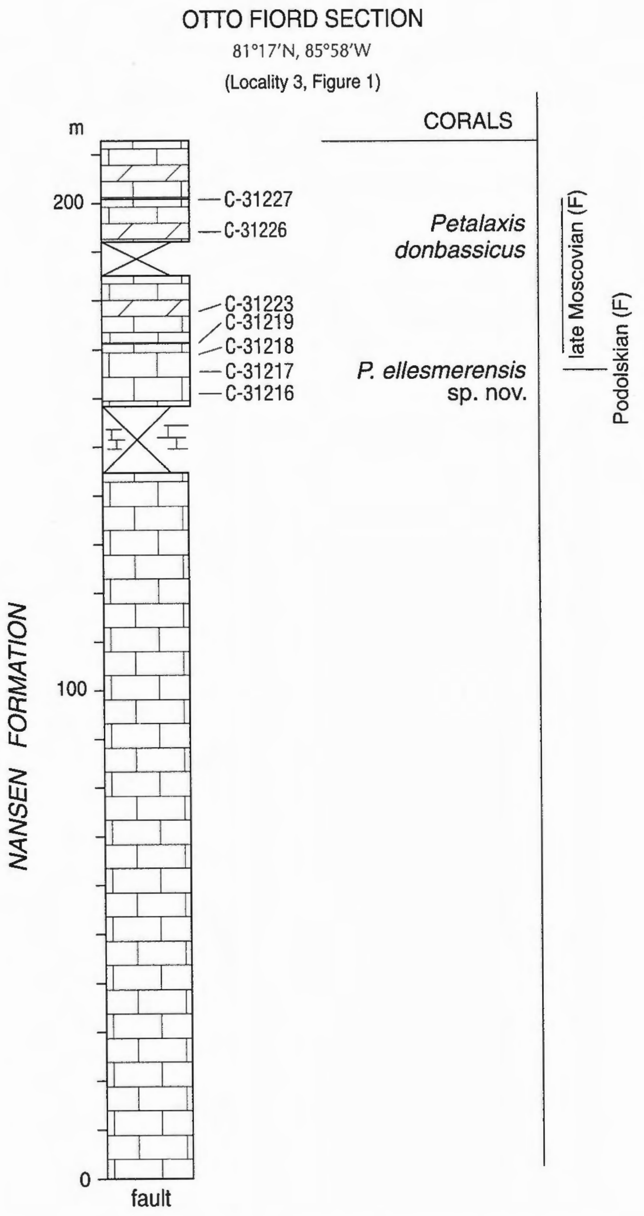

Figure 4. *Otto Fiord section (locality 3, Fig. 1, Table 1); data from section measured by W.W. Nassichuk and G.R. Davies in 1974; age from fusulinaceans(F). See Figure 2 legend for explanation of symbols.*

Corals

In the axial part of the Sverdrup Basin (Fig. 1), within the slope-to-basin deposits of the Hare Fiord Formation, lower Moscovian (Kashirian) representatives of *Petalaxis* are abundant in shallow-water carbonates associated with reef buildups ("Tellevak" limestone). Kasimovian or lowest Gzhelian debris-flow beds originating from slope or shelf settings yielded both *Petalaxis* and *Cystolonsdaleia*. A specimen of *Petalaxis thorsteinssoni* sp. nov., the most widespread cerioid species in the study area, was collected in the Van Hauen Pass section (locality 5, Fig. 1; Fig. 5) from a limestone clast within a debris-flow bed, 81 m above the base of the Hare Fiord Formation (GSC loc. C-10861). The debris-flow bed also contains upper Moscovian (Podolskian or Myachkovian) foraminifers. Kasimovian or lower Gzhelian fusulinaceans were reported by Thorsteinsson (*ibid.*, p. 30, 31; GSC loc. 47866) approximately 81 m above the coral occurrence. To the south of the Van Hauen Pass section, *Petalaxis donbassicus* (Fomichev), *P.* sp., and *P. crassicolumnus*? sp. nov. were collected by W.W. Nassichuk and G.R. Davies from Kashirian limestone overlying the "Tellevak" limestone (GSC locs. C-10813–C-10815) in the northeast Blue Mountains section (locality 6, Fig. 1; Fig. 6). *P. donbassicus* also occurs at localities 7 and 8, where it was collected by G.F. Bonham-Carter from the top of the "Tellevak" limestone and 1.2 m above that unit, respectively (Tables 1-3, GSC locs. 58924, 60190). The youngest Carboniferous cerioid corals known from the study area are Kasimovian to lowest Gzhelian specimens, also collected by Bonham-Carter, from debris-flow limestone of the Hare Fiord Formation in the southwest Blue Mountains (C) section (locality 9, Fig. 1; Fig. 7, GSC locs. 60192, 60193). These collections, at 173 and 174 m above the top of the "Tellevak" limestone, contain foraminifers of Kasimovian or earliest Gzhelian age. Gzhelian foraminifers were identified by S. Pinard 21 m higher in this section (GSC loc. C-99028). These are overlain by Permian fusulinaceans, at 208 m above the top of the "Tellevak" limestone (GSC loc. C-99035). The lower collection from the debris-flow (GSC loc. 60192) yielded *Petalaxis* sp. cf. *P. elyensis* and *Cystolonsdaleia* sp. aff. *C. carteri*, and the upper collection (GSC loc. 60193) yielded *C. carteri* sp. nov.

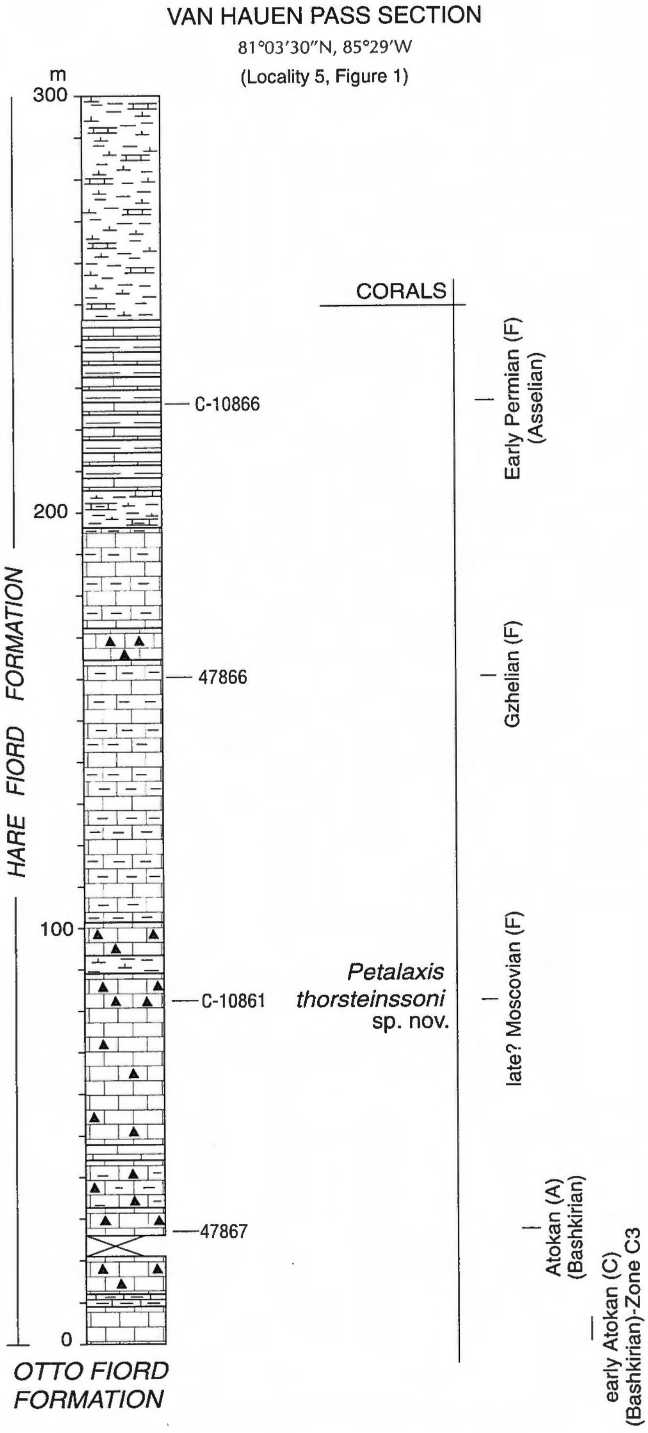

Figure 5. *Van Hauen Pass section (locality 5, Fig. 1, Table 1); data from section measured by W.W. Nassichuk and E.W. Bamber in 1971 (type section of Hare Fiord Formation = section 69 of Thorsteinsson, 1974, Fig. 9); age from fusulinaceans(F), ammonoids(A) and conodonts(C). See Figure 2 legend for explanation of symbols.*

Belcher Channel Formation

In the Agassiz Ice Cap section on Hamilton Peninsula (locality 11, Fig. 1; Fig. 9), the lower part of a thick limestone succession assigned to the Belcher Channel Formation (Thorsteinsson, 1974, Fig. 9, section 74;

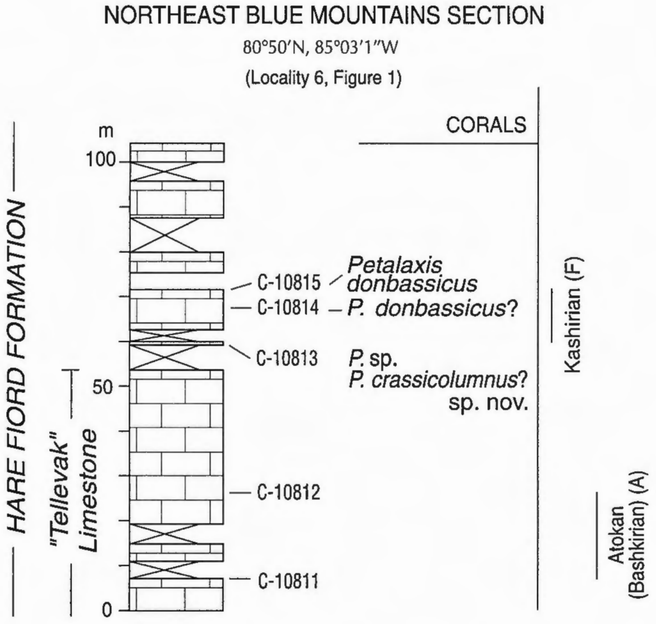

Figure 6. Northeast Blue Mountains section (locality 6, Fig. l, Table 1); data from section measured by W.W. Nassichuk and G.R. Davies in 1971; age from fusulinaceans(F) and ammonoids(A). See Figure 2 legend for explanation of symbols.

Thériault and Beauchamp, 1991, Fig. 2, section 4) contains middle to upper Moscovian corals and fusulinaceans. The lowest limestone unit has not been dated with microfossils. It contains *Petalaxis donbassicus* (GSC loc. C-193087), which is mid-Moscovian (Kashirian to Podolskian) at other Ellesmere Island localities (Fig. 3). Higher in the section, *Cystolonsdaleia arctica* (GSC locs. C-193090, C-193091) and *Petalaxis thorsteinssoni* (GSC locs. C-193094, C-193095) are associated with upper Moscovian (Podolskian or Myachkovian) fusulinaceans.

Canyon Fiord Formation

Foraminifers, ammonoids and conodonts

Thorsteinsson (1974) and Mamet (*in* Thorsteinsson, 1974) reported fusulinacean and other foraminifers ranging in age from early Bashkirian to Zhigulevian (=Kasimovian–early Gzhelian) from the Canyon Fiord Formation. Foraminifers within this age range have since been widely reported within the formation (Nassichuk, 1975; Beauchamp, 1987; Pinard, 1989; Mayr, 1992). Those identified for this study by L. Rui and S. Pinard are listed in Appendices 1 and 2, and Table 3.

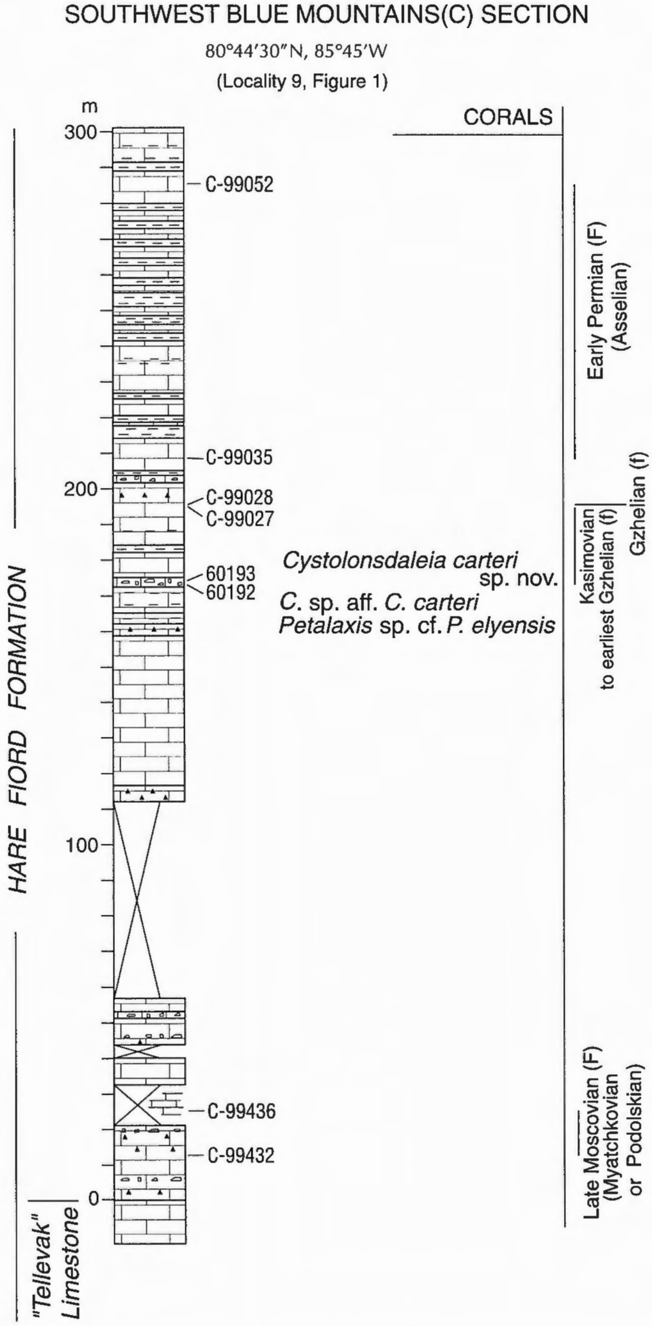

Figure 7. Southwest Blue Mountains(C) section (locality 9, Fig. 1, Table 1); data from section measured by J. Utting and W.W. Nassichuk in 1982 and F.R. Brunton in 1992; age from fusulinaceans(F) and small foraminifers(f). See Figure 2 legend for explanation of symbols.

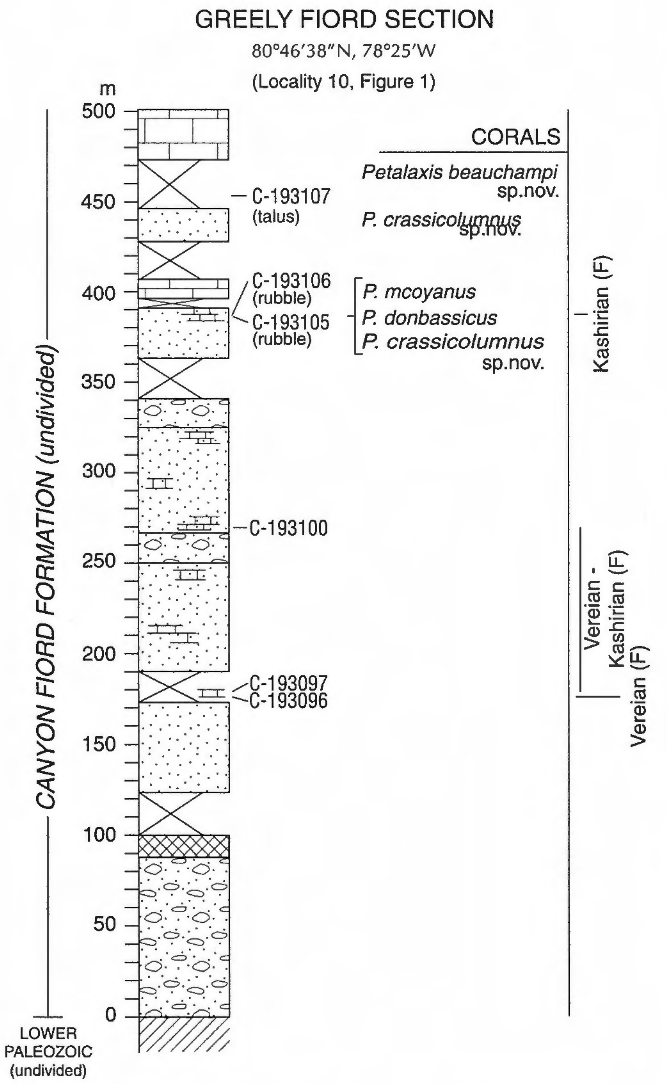

Figure 8. *Greely Fiord section (locality 10, Fig. 1, Table 1); data from section measured by P. Thériault and E.W. Bamber in 1990 (= section 82 of Thorsteinsson, 1974, Fig. 10); age from fusulinaceans(F). See Figure 2 legend for explanation of symbols.*

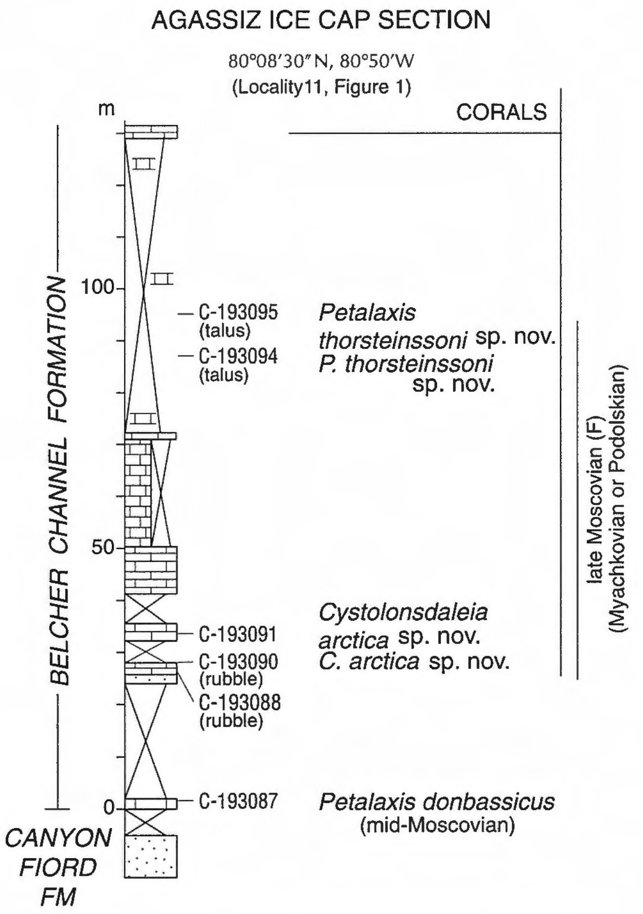

Figure 9. *Agassiz Ice Cap section (locality 11, Fig. 1, Table 1); data from section measured by P. Thériault and E.W. Bamber in 1990 (= section 74 of Thorsteinsson, 1974, Fig. 9); age from fusulinaceans(F). See Figure 2 legend for explanation of symbols.*

Nassichuk (1975, p. 30, 47–49) reported a lower Atokan (=upper Bashkirian) ammonoid species from the lower part of the Canyon Fiord Formation in the Agassiz Ice Cap section (locality 11, Fig. 1, GSC loc. 52445, Table 3, in pocket). These are underlain by lower Bashkirian foraminifers reported from this section near the base of the formation (Mamet *in* Thorsteinsson, 1974, p. 89, 90). Nassichuk (*ibid.*, p. 38, 49) assigned a late Moscovian age to several ammonoid species associated with foraminifers and corals from the upper part of the formation at the East Blind Fiord (B) section (locality 13, Figs. 1, 11, GSC locs. C-10885, C-10891, Table 3). Concerning two of these species, however, he noted that *Metapronorites pseudotimorensis* (Miller) typically occurs in the Missourian (Kasimovian) of West Texas, and *Somoholites bamberi* Nassichuk closely resembles *S. sholakensis* Ruzhencev from the Zhigulevian (Kasimovian–lower Gzhelian) of the southern Ural Mountains in Russia (Nassichuk, 1975, p. 67, 119). Fusulinaceans, identified by L. Rui for the present study, occur in the East Blind Fiord (B) section at several levels within the interval containing ammonoids. They include species of *Pseudofusulinella* (e.g., GSC locs. C-10886, C-27984, Fig. 11, Table 3), indicating a Kasimovian or Gzhelian, rather than a late Moscovian age for the two ammonoid occurrences. However, an upper age limit of Kasimovian is indicated by the presence of *Bisatoceras* sp. among the

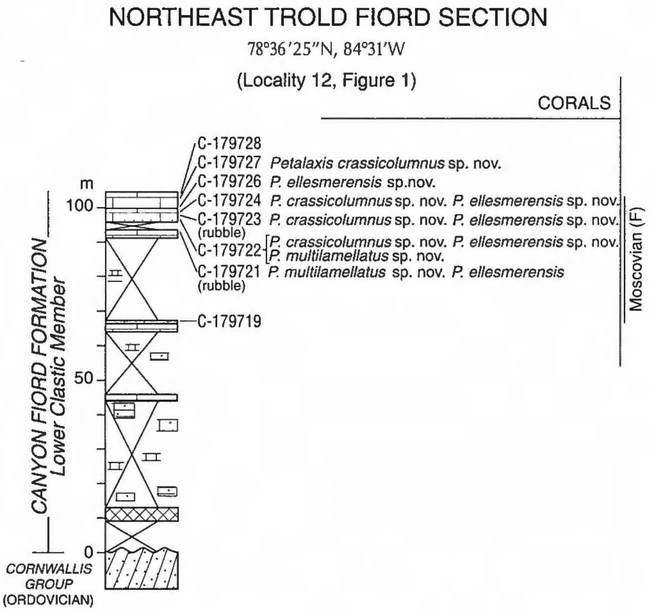

Figure 10. *Northeast Trold Fiord section (locality 12, Fig. 1, Table 1); data from section measured by P. Thériault and E.W. Bamber in 1989; age from fusulinaceans(F). See Figure 2 legend for explanation of symbols.*

ammonoids. A tentative Kasimovian age was assigned by S. Pinard to associated foraminifers from GSC loc. C-10891 (Appendix 2). The age of these faunas is particularly important because of its implications for the age range of the genus *Petalaxis* in the Canadian Arctic, discussed below.

Five Upper Carboniferous conodont zones were recognized by Henderson (1988; *in* Beauchamp et al., 1989a) in the middle and upper parts of the Canyon Fiord Formation in the Trold Fiord–Blind Fiord area of southwestern Ellesmere Island. He assigned a Moscovian age to faunas from the lower part of the middle limestone member of Beauchamp et al. (1989b) (Fig. 2) and dated those from the upper part of this member and the lower part of the overlying upper clastic member of Beauchamp et al. (*ibid.*) as Kasimovian and Gzhelian. Similar age assignments were presented by Henderson et al. (1995).

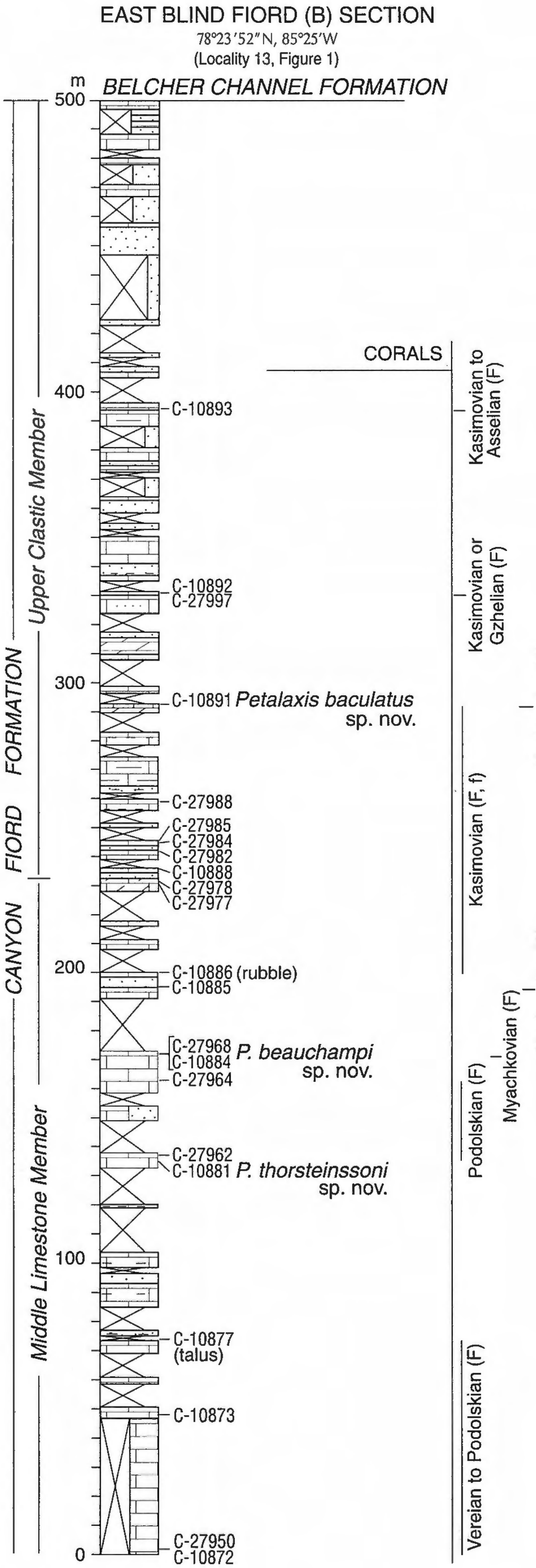

Figure 11. *East Blind Fiord (B) section (locality 13, Fig. 1, Table 1); data from section measured by W.W. Nassichuk and E.W. Bamber in 1971; age from fusulinaceans(F), small foraminifers(f) and ammonoids(A). See Figure 2 legend for explanation of symbols.*

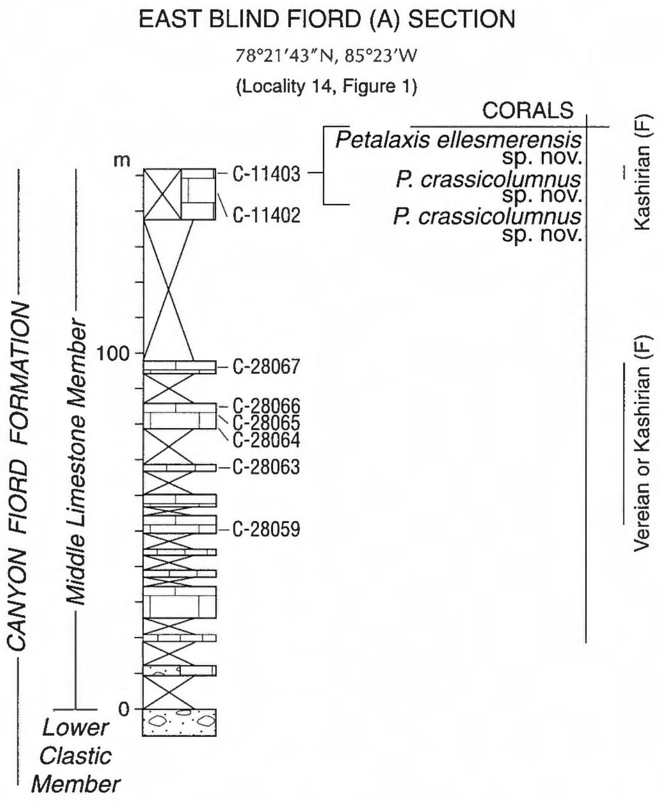

Figure 12. *East Blind Fiord (A) section (locality 14, Fig. 1, Table 1); data from section measured by W.W. Nassichuk and E.W. Bamber in 1971; age from fusulinaceans(F). See Figure 2 legend for explanation of symbols.*

Corals

Cerioid corals are abundant and widespread in the Moscovian carbonates of the middle Canyon Fiord and occur rarely in the Kasimovian to (?)lowest Gzhelian part of the overlying upper clastic member (Figs. 3, 8-13, 15). Kashirian to lower(?) Podolskian faunas are best developed in the Trold Fiord-Blind Fiord and Greely Fiord areas (Fig. 1, sections 10, 12, 14, 15), where *Petalaxis ellesmerensis* sp. nov., *P. crassicolumnus* sp. nov. and *P. multilamellatus* sp. nov. are locally very abundant. Other species of this age include *P. mcoyanus* (Milne Edwards and Haime), *P. donbassicus* (Fomichev), and *P. beauchampi* sp. nov. *Cystolonsdaleia* sp. occurs with Kashirian or Podolskian fusulinaceans near Henrietta Nesmith Glacier (locality 2, Fig. 1). Younger Moscovian cerioid corals are relatively rare in the carbonates of the middle Canyon Fiord Formation, but the distinctive species *Petalaxis thorsteinssoni* sp. nov. is widely distributed in upper Moscovian (Podolskian and Myachkovian) strata from Bjorne Peninsula to Hamilton Peninsula (Fig. 1, sections 11, 13, 17).

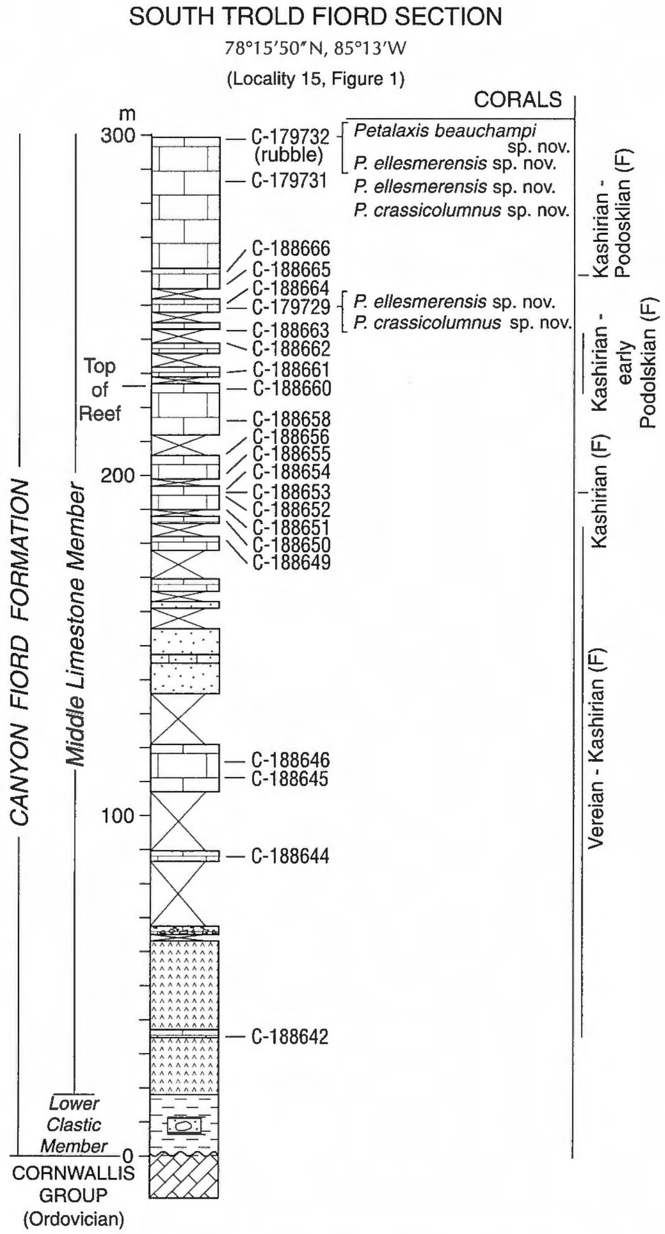

Figure 13. *South Trold Fiord section (locality 15, Fig. 1, Table 1); data from sections measured by B. Beauchamp, E.W. Bamber and C.M. Henderson in 1989; see Thorsteinsson (1974, p. 41, 99, Pl. 5, locality 137); age from fusulinaceans(F). See Figure 2 legend for explanation of symbols.*

The youngest cerioid corals collected from the Canyon Fiord Formation belong to the Kasimovian species *Petalaxis baculatus* sp. nov. It is known from only one locality within the lower part of the upper clastic member at section 13 [East Blind Fiord(B) section, Figs. 1, 11, GSC loc. C-10891], where it occurs with Kasimovian ammonoids (see above) and foraminifers. *Petalaxis baculatus* and other

Kasimovian to (?)lowest Gzhelian species of *Petalaxis* occurring elsewhere in the study area [*P. parvus* sp. nov., *P.* sp. cf. *P. elyensis* (Wilson and Langenheim)] are the only post-Moscovian representatives of the genus reported from arctic North America.

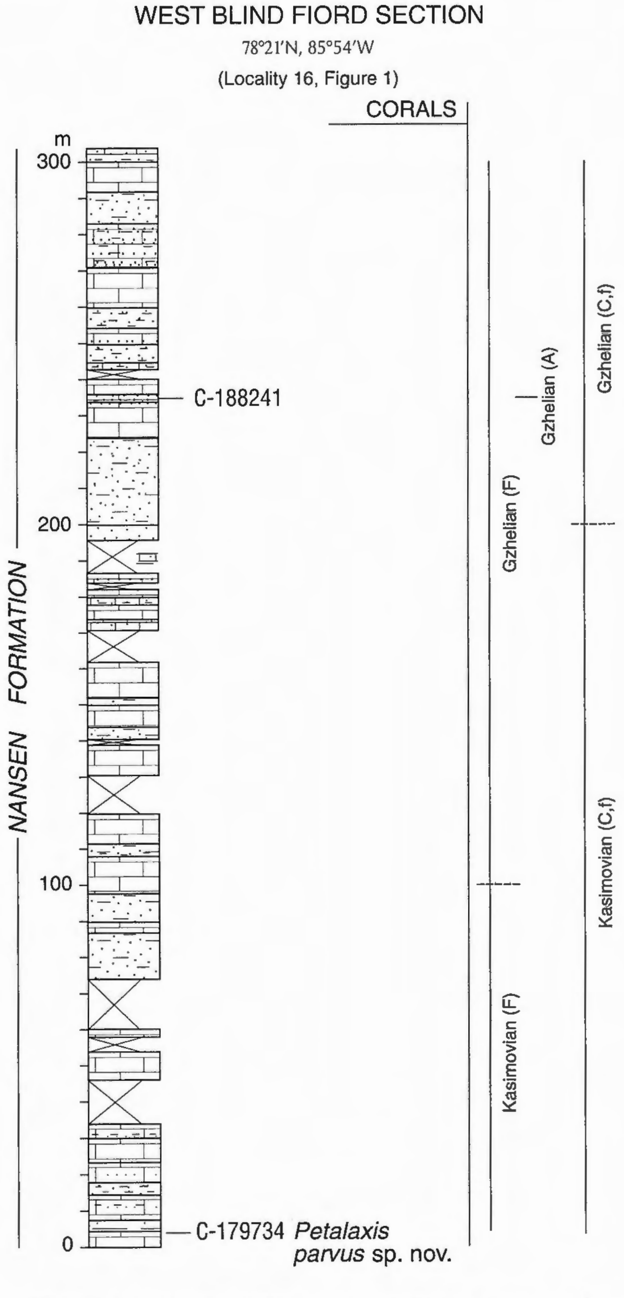

Figure 14. *West Blind Fiord section (locality 16, Fig. 1, Table 1); data from section measurements by W.W. Nassichuk, B. Beauchamp, C.M. Henderson, S. Pinard, and E.W. Bamber from 1971 to 1989; see Beauchamp (1987, Fig. 31, section 2), Nassichuk and Rui (1992), Henderson et al. (1995); age from fusulinaceans(F), small foraminifers(f), conodonts(C) and ammonoids(A). See Figure 2 legend for explanation of symbols.*

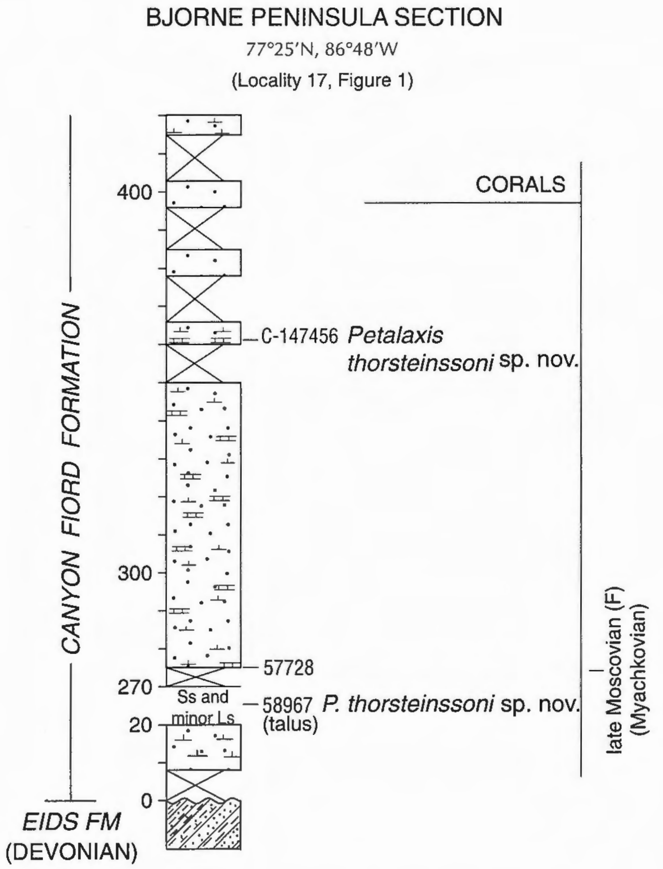

Figure 15. *Bjorne Peninsula section (locality 17, Fig. 1, Table 1); data from Thorsteinsson (1974, Fig. 7, section 50); age from fusulinaceans(F). See Figure 2 legend for explanation of symbols.*

COMPARISON WITH RELATED CORAL FAUNAS

Of the fifteen species of *Petalaxis* and *Cystolonsdaleia* described from Ellesmere Island, 10 are new and 5 are closely comparable or identical with species from other regions. Detailed comparisons and age ranges are given for each species in the systematic paleontology section.

The Moscovian (Kashirian to Myatchkovian) corals in our collection appear to be most closely related to those described from the Moscovian of the Cantabrian Mountains of Spain (de Groot, 1963; Rodriguez, 1984), the Donets Basin of Ukraine (Fomichev, 1953) and the Moscow Basin and Ural Mountains of Russia (Dobrolyubova, 1935a, b, 1936b; Kachanov, 1971). *Petalaxis donbassicus* (Fomichev), which occurs in Kashirian strata of the Donets Basin, ranges from the Kashirian into the Podolskian on Ellesmere Island. *Cystolonsdaleia* sp., from the Kashirian or Podolskian of Ellesmere shows some features in common with the upper Moscovian species *C. densiconus* (de Groot), from Spain. Species described from Russia that closely resemble Ellesmere species include *P. mcoyanus* (Milne Edwards and Haime), from the Myachkovian of the Moscow Basin, and *P.* sp. aff. *P. stylaxis* (Trautschold), described by Dobrolyubova (1936b, p. 127) from the northern Ural Mountains. The latter species, for which a late Moscovian age was suggested (*ibid.*, p. 81), may belong to our new Kashirian to Podolskian species *P. ellesmerensis*.

The upper Moscovian species *Cystolonsdaleia arctica* sp. nov. resembles several Moscovian species described from China (Yu and Wang, 1987; Wang, 1989; Wu and Zhao, 1989). In the western U.S.A., the axial structure of *Petalaxis yosti* Stevens (1995), from Desmoinesian (middle or upper Moscovian) strata of eastern California, displays the well developed lateral lamellae (new term; see below) typical of Moscovian species from Ellesmere Island.

The Kasimovian to lowest Gzhelian species of *Petalaxis* and *Cystolonsdaleia* from Ellesmere Island are morphologically distinct from those of similar age in western China and Mongolia (Guo, 1983; Luo et al., 1989b). No other occurrences of these genera are known from Kasimovian or Gzhelian strata. The only species of comparable age that appears to be closely related to the youngest Carboniferous Ellesmere corals is *Petalaxis elyensis* (Wilson and Langenheim) from the lowest part of the Permian succession in Nevada, western U.S.A. It closely resembles *Petalaxis* sp. cf. *P. elyensis* from the Hare Fiord Formation of the Blue Mountains (locality 9, Fig. 1; Fig. 7).

TERMINOLOGY AND LABORATORY PROCEDURES

Morphological terms used in the following coral descriptions are mainly those recommended by Hill (1981). The new terms "lateral lamella" and "periaxial cone" are used for distinctive axial elements — the former being thickened extensions of the cardinal septum and the latter formed from vertically extended tabulae and axial tabellae (see sections on skeletal morphology). Lateral lamellae occur in both *Petalaxis* and *Cystolonsdaleia*, whereas periaxial cones are found only in *Cystolonsdaleia*. Under the name "septal lamellae" we have included all radially disposed ridges and vertically discontinuous plates that form part of the axial structure and are attached to median and lateral lamellae. These may vary considerably in thickness and length and locally may be joined to major septa. The mean diameters of corallites were determined in transverse section by taking the average of the greatest and least corallite diameters, measured through the axis from the approximate mid-points of opposing sides; measurements from the corners of corallites were avoided. All drafted textfigures and some of the coral illustrations in the text were digitally prepared, but most textfigures of corals were drawn by hand from enlarged photos or digital images.

For consistency in morphological observations and comparisons, longitudinal thin sections of individual corallites were cut approximately perpendicular to the counter-cardinal plane, as close to the centre of the axial structure as possible. Illustrated sections or parts of sections that are slightly eccentric or oblique to the counter-cardinal plane are identified in textfigures or plate captions. Two or more serial thin sections were cut through many specimens to determine vertical variations in structural elements. Blastogeny studies were carried out mainly by the use of closely spaced peels taken on clear acetate film from finely ground, transverse surfaces, prepared with 1000-grade carborundum powder and lightly etched with dilute hydrochloric acid. Closely spaced, serial thin sections were cut to determine the details of the nature and development of corallite walls.

SYSTEMATIC PALEONTOLOGY

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

GSC - Geological Survey of Canada, Ottawa.
USNM - United States National Museum of Natural History, Washington, D.C.

Type specimens of corals described below are in the type collection of the Geological Survey of Canada, Ottawa. Associated reference collections are at the Geological Survey of Canada (Calgary).

Phylum COELENTERATA Frey and Leuckart, 1847

Class ANTHOZOA Ehrenberg, 1834

Subclass RUGOSA Milne Edwards and Haime, 1850

Order STAURIIDA Vervill, 1865

Family PETALAXIDAE Fomichev, 1953

Genus *Petalaxis* Milne Edwards and Haime, 1852

Stylaxis Milne Edwards and Haime, 1851, p. 452 (part); non McCoy, 1849, p. 119.

Petalaxis Milne Edwards and Haime, 1852 (part). Milne Edwards, 1860, p. 440 (part); Roemer, 1883, p. 387, 388 (part); Lindstrom, 1883, p. 12; Stuckenberg, 1888, p. 20 (part); Etheridge, 1900, p. 17; Grosch, 1909, p. 5; Yabe and Hayasaka, 1915, p. 94 (32); Bolkhovitinova, 1915, p. 63(?); Dobrolyubova, 1935b, p. 10; Fomichev, 1953, p. 449; Soshkina et al., 1962, p. 339; de Groot, 1963, p. 81; Onoprienko, 1970; Fedorowski and Gorianov, 1973, p. 58; Kozyreva, 1974, p. 24 (part); Sutherland, 1977, p. 185; Kozyreva, 1978, p. 75; Wilson, 1982, p. 65; Sando, 1982, p. 238 (part), 1983, p. 23 (part); Rodriguez, 1984, p. 348; Yu Xue-guang, 1984, p. 107; Boll, 1985, p. 41; Sando and Bamber, 1985, p. 25; Semenoff-Tian-Chansky, 1985, Pl. 15, figs. 5a, b; Wilson, 1985, p. 10; Zheng Chun-zi, 1986, p. 34, 35; Luo et al., 1989a, p. 120, 121; Wang Zhi-gen, 1989, p. 535; Wu and Zhao, 1989, p. 131 (part); Yu Xue-guang, 1989, p. 366; (?)Luo and Qi, 1990, p. 705, Pl. 5, figs. 1a, b; Fontaine et al., 1991, p. 60; Yamagiwa et al., 1991, p. 752; Sutherland and Grayson, 1992, p. 90, Pl. 3, figs. 17, 18; Ding and Xu, 1993, p. 701 (part), Pl. 3, figs. 1-3; Stevens, 1995, p. 787; Goreva and Kossovaya, in press, Pl. 2, figs. 1a, b; Somerville, 1997, Pl. 1, figs. 1-6; Sutherland, 1997, Pl. 1, figs. 1-5, Pl. 2. non Barrois, 1882, p. 305; non Stuckenberg, 1895, p. 74; non Yanishevsky, 1900, p. 89; non Gabunia, 1919, p. 39; non Heritsch, 1939, p. 18; non Hill, 1940, p. 165; non Lang, Smith and Thomas, 1940, p. 97; non Kolosvary, 1951, p. 39; non Hill, 1956, p. F282; non Minato and Kato, 1974, p. 68; non Cotton, 1973, p. 152; non Semenoff-Tian-Chansky and Nudds, 1979, p. 255; non Cotton, 1984, p. 128; non Stevens and Rycerski, 1989, p. 178; non Ding and Xu, 1993, p. 701 (part), Pl. 2, fig. 2.

Hillia de Groot. Wang et al., 1978, p. 139 (part); Yu et al., 1978, p. 29(?); Wu et al., 1982, p. 124; Guo, 1983, p. 224; (?)Zheng and Cai, 1983, p. 159; Rodriguez, 1984, p. 354.

Grootia Yu, 1984, p. 104, 112; Zheng Chun-zi, 1986, p. 33; Wu and Zhao, 1989, p. 133.

Lithostrotion Fleming. Eichwald, 1861, p. 149 (part); Trautschold, 1879, p. 35 (part); Heritsch, 1939, p. 29; Bassler, 1950, p. 222 (part).

Lithostrotion (*Lithostrotionella*) Merriam, 1942, p. 377 (part); Bassler, 1950, p. 220 (part), 222, 235, 252 (part); Easton, 1960, p. 578.

non *Lithostrotion* (*Petalaxis*) Fomichev, 1931, p. 44.

Lithostrotionella Yabe and Hayasaka. Yu, 1933, p. 101(?); Dobrolyubova, 1935a, p. 10; 1935b, p. 10, 12; 1936a, p. 28 (part)(?); 1936b, p. 127; Hayasaka, 1936, p. 69 (part), 70; Heritsch, 1937, p. 164; 1939, p. 30; 1940, p. 72(?); Fomichev, 1939, p. 60; Kelly, 1942, p. 351 (part); Minato, 1955, p. 87 (part); Yokoyama, 1957, p. 78; Nelson, 1960, p. 114 (part); 1961 (part), p. 24, 25, Pl. 14, figs. 1, 2, Pl. 18, figs. 1-3; Yamagiwa, 1961, p. 102 (?); de Groot, 1963, p. 80 (part); Wu *in* Yu Chang-min et al., 1963, p. 86 (part)(?); Wilson and Langenheim, 1962, p. 512; Sutherland, 1966, p. 178; Minato and Kato, 1974, p. 67 (part); Wu and Zhao, 1974, p. 271; Sutherland, 1975, p. 36; Onoprienko, 1976, p. 29 (part); Yu Xue-guang, 1976, p. 225; Xu, 1977, p. 201 (part); Fan, 1978, p. 182 (part); Gorsky, 1978, p. 150; Wang (*in* Wang et al.), 1978, p. 133 (part); Kato et al., 1979, p. 140, Pl. 33, fig. 19, Pl. 34, fig. 3, Pl. 35, fig. 1; Yan, 1981, p. 68 (part); Zheng and Cai, 1983, p. 152(?) (part), 153; Yu Xue-guang, 1984, p. 109(?); Yu and Wang, 1987, p. 81; Huang, 1988, p. 30; Yu Xue-guang, 1989, p. 362; Luo et al., 1989a, p. 120.

Lithostrotionella (*Thysanophyllum*) Nelson, 1960, p. 115.

Lithostrotionella (*Hillia*) de Groot, 1963, p. 86.

Diphyphyllum Lonsdale. Warren, 1927, p. 44.

Thysanophyllum Nicholson and Thomson. Crickmay, 1955, p. 13; Bamber, 1966, p. 23; Bamber and Copeland, 1970, Pl. 13, figs. 2a, b; Kachanov, 1971, p. 72; (?)Kozyreva, 1978, p. 78 (part), Pl. 2, figs. 2a-g; Sando, 1983, p. 36; Sando and Bamber, 1985, p. 30 (part); Yu Xue-guang 1989, p. 362.

Acrocyathus (d'Orbigny). Ivanovsky, 1987, p. 12.

Eastonoides Wilson and Langenheim, 1962, p. 511.

Beshanophyllum Yu, 1982, p. 10.

Type species. Stylaxis M'Coyana Milne Edwards and Haime, 1851, p. 453, Pl. 12, figs. 5, 5a (designated by Roemer, 1883, p. 387, 388), Upper Carboniferous, Moscovian (Myatchkovian), Moscow Basin, Russia (Sutherland, 1977, p. 185).

Diagnosis (*emended*). Cerioid, rarely subcerioid in part of colony; corallite walls fibrous, trabecular to four-layered, may be discontinuous in early growth stages. Septa of two orders, finely trabecular, thickened at corallite wall, generally discontinuous in dissepimentarium. Major septa commonly long and slightly sinuous, several may join axial structure. Minor septa usually well developed, rarely weakly developed as septal crests and ridges on corallite walls. Axial structure joined to cardinal septum; varies from simple median lamella formed by axial thickening of cardinal septum to complex structure consisting of median lamella, septal and lateral lamellae and rare axial tabellae. Tabularium biform; tabulae complete or incomplete, subhorizontal to adaxially elevated or depressed, usually concave to subplanar. Dissepiments ordinarily transeptal, but in some species mainly regular. Increase lateral.

Taxa assigned to genus

Milne Edwards and Haime, 1851: *Stylaxis M'Coyana.*
Eichwald, 1861: *Lithostrotion portlockii.*
Trautschold, 1879: *Lithostrotion stylaxis, L. flexuosum.*
Warren, 1927: *Diphyphyllum astraeiforme.*
Yu, 1933: *Lithostrotionella kueichouensis*(?), *L. spiniformis*(?).
Dobrolyubova, 1935b: *Lithostrotionella vesiculosa.*
Dobrolyubova, 1936a: *Lithostrotionella* sp.(?).
Dobrolyubova, 1936b: *Lithostrotionella* aff. *stylaxis* Trautschold.
Hayasaka, 1936: *Lithostrotionella tabulata, L. simplex.*
Fomichev, 1939: *Lithostrotionella donbassica* Fomitchev (in litt.)
Merriam, 1942: *Lithostrotion* (*Lithostrotionella*) *occidentalis.*
Fomichev, 1953: *Petalaxis maccoyana* forma *orlovkensis* [probable synonym of *P. donbassicus* (Fomichev, 1939)], *P. maccoyana* var. *belinskiensis, P. maccoyana* var. *multiseptata* [probable synonym of *P. donbassicus* (Fomichev, 1939)], *P. mohikanus, P. vesiculosa* var. *lisitschanskensis.*
Minato, 1955: *Lithostrotionella* sp. indet.(?), *L. kitakamiensis, L.* cfr. *tingi* Chi(?).
Yokoyama, 1957: *Lithostrotionella taishakuensis.*
Easton, 1960: *Lithostrotion* (*Lithostrotionella*) *mokomokensis, L.* (*L.*) *dilatata*(?).
Nelson, 1960: *Lithostrotionella bailliei.*
Yamagiwa, 1961: *Lithostrotionella* sp. indet.(?).
Wilson and Langenheim, 1962: *Lithostrotionella brokawi, Eastonoides elyensis.*
de Groot, 1963: *Lithostrotionella maccoyana* f. *major, L. monocyclica, L. orboensis, L. sexangulata, L.* (*Hillia*) *cantabrica, L.* (*H.*) *intermedia, L.* (*H.*) *parapertuensis, L.* (*H.*) *radians, L.* (*H.*) *santaemariae, L.* (*H.*) *wagneri.*
Sutherland, 1966: *Lithostrotionella* sp.
Kachanov, 1971: ?*Thysanophyllum petrovi.*
Kozyreva, 1974: *Petalaxis confertus, P. evidens, P. exilis, P. immanis, P. korkhovae, P. mirus, P. persubtilis.*
Minato and Kato, 1974: *Lithostrotionella* sp.
Onoprienko, 1976: *Lithostrotionella tchucotica.*
Fan, 1978: *Lithostrotionella awenggouensis*(?), *L. orboensis regularis, L. vesiculosa vesiculosa*(?), ?*L.* sp.
Gorsky, 1978: *Lithostrotionella stylaxis* (Traudschold) subsp. *uralica.*
Kozyreva, 1978: *Thysanophyllum tenuiforme*(?).
Wang (*in* Wang et al.), 1978: *Lithostrotionella kueichouensis magna, L. multivesiculata.*
Yu et al., 1978: *Hillia* cf. *santaemariae* Groot(?).
Yan, 1981: *Lithostrotionella planitabulata, L. planitabulata shijianpuensis, L. rarivesicula.*
Wilson, 1982: *Petalaxis allisonae, P. besti, P. kennedyi, P. pecki, P. sutherlandi.*
Wu et al., 1982: *Hillia irregularis.*
Yu, 1982: *Beshanophyllum simplex.*
Guo, 1983: *Hillia formosa, H. languida.*
Sando, 1983: *Petalaxis exiguus, P. fomichevi* [objective synonym of *P. donbassicus* (Fomichev, 1939)], *P. grootae* [synonym of *P. mcoyanus* (Milne Edwards and Haime, 1851)], *P. major, P. wyomingensis.*
Zheng and Cai, 1983: *Lithostrotionella kitakamiensis breviseptata, Hillia* cf. *santaemariae* Groot(?), *H. regularis*(?).
Rodriguez, 1984: *Petalaxis penduelensis.*
Yu Xue-guang, 1984: *Petalaxis gigantea, Lithostrotionella breviseptata, Grootia longhuoensis, Beshanophyllum petalaxoidea.*
Yu, 1984: *Grootia longhuoensis.*
Semenoff-Tian-Chansky, 1985: *Petalaxis* aff. *exilis* Kozyreva, 1974
Zheng Chun-zi, 1986: *Petalaxis laticystatum, P. rosicum, Grootia tenuis.*
Ivanovsky, 1987: *Acrocyathus portlocki* (Stuck.).
Yu and Wang, 1987: *Lithostrotionella mokomokensis tenuepitheca, L. crassoseptata.*
Huang, 1988: *Lithostrotionella gudingziensis.*
Wang, Zhi-gen, 1989: *Petalaxis grootae breviseptatus, P. nandanensis, P. sinensis.*
Wu and Zhao, 1989: *Petalaxis* cf. *flexuosis* (Trautschold), *P.* cf. *stylaxis* (Trautschold).
Yu Xue-guang, 1989: *Petalaxis curvata, P. provecta, Lithostrotionella gorskyi.*
Yamagiwa et al., 1991: *Petalaxis hangzhouensis.*
Sutherland and Grayson, 1992: *Petalaxis* n. sp.
Ding and Xu, 1993: *Petalaxis guiensis, P. wuguilingensis.*
Stevens, 1995: *Petalaxis yosti.*
Goreva and Kossovaya, in press: *Petalaxis vesiculosus major* Kossovaya.
Kossovaya, in press: *Petalaxis orboensis* (de Groot), *P. persubtilis* Kozyreva, *P. vesiculosus* (Dobrolyubova), *P.* sp. ex. gr. *P. vesiculosus* (Dobrolyubova).
Somerville, 1997: *Petalaxis* sp. C, *Petalaxis* sp. E, *Petalaxis* sp. B.
Sutherland, 1997: *Petalaxis* n. sp.

Discussion. Petalaxis was established as a valid genus by Roemer (1883, p. 387, 388), who chose *Petalaxis mcoyanus* (Milne Edwards and Haime) as its type species (Sando, 1983, p. 24; Hill, 1981, p. 401). The genus was subsequently recognized in several of the older publications (e.g., Stuckenberg, 1888; Fomichev, 1953) and has more recently received wider recognition through descriptions of new species from Ukraine (Kozyreva, 1974) and specimens of the type species from its type locality (Fedorowski and Gorianov, 1973; Sutherland, 1977). A thorough review of the taxonomic history of *Petalaxis* prior to 1978, was given by Sando (1982; 1983, p. 23-25) in his revision of *Lithostrotionella*. He clearly demonstrated that many species formerly included in *Lithostrotionella* belong in *Petalaxis* and concluded that *Lithostrotionella* is probably a junior synonym of *Acrocyathus* (Sando, 1983, p. 4, 16). He provided a diagnosis of *Petalaxis*, discussed its systematic relationships and distribution, provided comprehensive information on its species content, and described and illustrated its morphology. He also gave descriptions and/or diagnoses for all species that he included in *Petalaxis* and arranged them into five species groups.

Stylastraea inconferta Lonsdale, the type species of the genus *Stylastraea*, was tentatively referred to *Petalaxis* by Yanishevsky (1900, p. 89). The type specimen of this species, which was redescribed by Smith and Lang (1930, p. 185) and has recently been restudied by the authors, does not possess the features of *Petalaxis*. It differs from the latter in having consistently convex tabulae, numerous regular dissepiments and a discontinuous, highly irregular axial structure consisting of a curved to sinuous median lamella bearing irregularly developed septal lamellae. No lateral lamellae are present. In addition, a biform tabularium was not observed in the type specimen. *Lithostrotionella uralica* Dobrolyubova (1936a, p. 28), which appears to possess similar features, is also excluded by the authors from *Petalaxis* and may belong in *Stylastraea*.

Gabunia (1919, p. 40) described the tabulae of *Petalaxis sibiricus* as convex toward the calice, rather than concave, as they generally are in *Petalaxis*. This species was redescribed and referred to *Lithostrotion* (*Petalaxis*) by Fomichev (1931, p. 44), who included within it three species previously assigned by Tolmachev (1924) to *Lithostrotion* and *Stylophyllum*. Fomichev (*ibid.*, p. 45, Pl. 1, figs. 12d, e) described and illustrated convex, strongly curved, split tabulae that are steeply elevated adaxially and are commonly elevated in the outer tabularium to join the dissepimentarium. He also (*ibid.*, p. 45) described the axial structure as a discontinuous, simple plate or lens joined to one or both of the cardinal and counter septa. Tolmachev (1933) proposed the name *Stelechophyllum* to replace the preoccupied name *Stylophyllum* and designated as its type species *S. venukoffi*, one of the three species formerly included in *Lithostrotion* (*Petalaxis*) *sibiricus* by Fomichev (1931, p. 44). Fomichev (1955, p. 303) later used the name *Lithostrotion* (*Eolithostrotionella*) *sibiricum* for this species. All of the corals referred to as *sibiricus* by Gabunia and Fomichev were finally reassigned to *Stelechophyllum* Tolmachev by Dobrolyubova and Kabakovitch (1966, p. 130, 131). Their descriptions and illustrations of *S. venukoffi* and its subspecies confirm those of Fomichev (1931) and clearly show the differences between the axial structures and tabulae of these corals and those of *Petalaxis*.

The species referred to *Petalaxis* by Heritsch (1939, p. 18-28) have regular dissepiments, steeply elevated tabulae (where illustrated - Pl. III, fig. 1), and a variable axial structure consisting of a median lamella, septal lamellae and axial tabellae (*ibid.*, Pl. 21, figs. 8-16). They resemble *Kleopatrina* and are here excluded from *Petalaxis*.

In an uppermost Carboniferous species from Guangxi Province, China, described as *Petalaxis difformis* by Ding and Xu (1993), the corallite wall is discontinuous and locally appears to be completely absent between adjacent, mature corallites (*ibid.*, p. 709, Pl. 2, fig. 2a). The authors have therefore not included that species in the genus *Petalaxis*, which has a continuous wall in all but the earliest growth stages.

Two species of cerioid corals from the Stikine assemblage of northwestern British Columbia were included in the genus *Petalaxis* by Stevens and Rycerski (1989, p. 178, 179). Both species possess periaxial cones, typical of *Cystolonsdaleia*, and are here assigned to that genus. The age and structure of the Stikine specimens are discussed below, under *Cystolonsdaleia*.

The following species, which were assigned to *Petalaxis* by Sando (1983) and included within his *Petalaxis maccoyanus* group (*ibid.*, p. 25), are here excluded from the genus and referred to *Cystolonsdaleia* because of the nature of their axial structures: *Lithostrotionella celadensis* de Groot (1963, p. 82), *Petalaxis dobrolyubovae* Sando [= *Lonsdaleia portlocki* (Stuckenberg) Dobrolyubova (1935b, p. 29)], *Petalaxis donetsensis* Sando [= *Cystolonsdaleia portlocki* (Dobrolyubova) Fomichev (1953, p. 457)], and *Lonsdaleia ivanovi* Dobrolyubova (1935b, p. 31). These species possess numerous axial tabellae, and the periaxial cones (defined below) typical of *Cystolonsdaleia* appear to be present in the illustrations of longitudinal sections of all four.

In addition to the diagnosis given by Sando (1983, p. 24), diagnoses for *Petalaxis* have recently been published by Hill (1981, p. F401), Rodriguez (1984, p. 348), Sando and Bamber (1985, p. 25), Wang (1989, p. 535) and Luo and Qi (1990, p. 704). In his analysis of lithostrotionelloid corals, Wang (1989, p. 527-530, 535, 536) discussed the systematic relationships of *Petalaxis* and expressed general agreement with Sando (1983) on the content of the genus. Wang (*ibid.*, p. 528, 530) described and illustrated five major types of axial structure in *Petalaxis* and compared its axial structures and tabulae with those of related genera.

As a result of the clarification of its skeletal structure and systematic position (Fedorowski and Gorianov, 1973; Sutherland, 1977; Sando, 1983; Wang, 1989), *Petalaxis* is now generally accepted and used as a valid genus (e.g., Yu, 1984, 1989; Wilson, 1985; Semenoff-Tian-Chansky, 1985; Wang, 1989; Wu and Zhao, 1989; Luo and Qi, 1990; Yamagiwa et al., 1991). Continued use of the name *Lithostrotionella* for corals with the skeletal structure of *Petalaxis* (see synonymy list, above) is inadvisable because of uncertainty concerning the nature of the type species, *Lithostrotionella unica* Yabe and Hayasaka, and the published evidence that *Lithostrotionella* may be a junior synonym of *Petalaxis* or *Acrocyathus* d'Orbigny (Easton, 1973; Hill, 1981, p. F403, F404; Sando, 1983, p. 4; Wang, 1989, p. 535; Luo and Qi, 1990, p. 705; Wang et al., 1989, p. 120). It is interesting to note that the single, obliquely oriented thin section, designated as lectotype of *L. unica* (Minato and Kato, 1974, p. 72, 73; Hill, 1981, p. F403, Fig. 264.1), shows several features found in *Petalaxis* and *Cystolonsdaleia*. Biform morphology is clearly evident in the tabularium of the corallite in the upper left corner of the published figure *(ibid.)*. The vertical axial element lying to the left of the median lamella in this corallite may be either a lateral lamella or a septal lamella, separating the tabulae from the median lamella. A periaxial cone (new term), typical of corals assigned by us to *Cystolonsdaleia*, may be represented by a vertical element on the right side of the axial structure, but this cannot be verified from the published figure. The exact nature of the axial structure in *L. unica* must be clarified by investigation of additional material from its type locality, before the true generic affinities of *Lithostrotionella* can be determined.

Grootia was proposed by Yu (1984) to replace the preoccupied name *Hillia* de Groot (1963) and was subsequently used by Wu and Zhao (1989, p. 133) for Moscovian corals from western Guizhou Province, southwestern China. *Hillia* was proposed by de Groot (*ibid.*, p. 86) as a subgenus of *Lithostrotionella* to include corals having subhorizontal, concave tabulae, relatively few, inconsistently developed transeptal dissepiments, and an axial structure continuous with the cardinal septum. The connection between the axial structure and the cardinal septum is a feature of *Petalaxis*, as discussed below, and the number of transeptal dissepiments developed is a feature too highly variable to be used independently for separating de Groot's species from *Petalaxis*. We therefore agree with several previous authors (Hill, 1981, p. F401; Sando, 1983, p. 25; Boll, 1985, p. 41; Wang, 1989, p. 535), who placed *Grootia* (= *Hillia* de Groot) in synonymy with *Petalaxis*.

Morphology. *Petalaxis* is distinguished by its generally concave, biform tabulae and by the nature of its axial structure from similar cerioid corals having transeptal dissepiments (e.g., *Acrocyathus* d'Orbigny, *Actinocyathus* d'Orbigny, *Cystolonsdaleia* Fomichev, *Porfirievella* Minato and Kato, *Stelechophyllum* Tolmachev). Considerable variation occurs in the tabulae, axial structure, and other skeletal components of *Petalaxis* (discussed in detail below and summarized in Table 4) and the genus contains a wide diversity of species (Sando, 1983, p. 25). These range in structure from relatively simple forms with mainly complete tabulae and a simple, lath-like or lens-shaped axial structure, to more complex forms characterized by incomplete, vesicular tabulae and thick axial structures with axial tabellae and numerous vertical lamellae.

Wall structure. The walls in *Petalaxis* vary only slightly in thickness throughout a colony, but commonly have a denticulate or beaded appearance in transverse section, caused in part by addition of the trabecular tissue of attached septa or septal crests. The median planes of the corallite walls are approximately planar or slightly curved where the septa of adjacent corallites are inserted opposite each other (Fig. 16a), but may be slightly to strongly sinuous where the positions of these septa are offset (Fig. 16b; Wang, 1989, p. 523, Textfig. 4). Septal thickening of the wall occurs to some degree in all species of *Petalaxis*, and is particularly evident in some of those having few transeptal dissepiments, assigned to *Hillia* by de Groot (1963) and included by Sando (1983, p. 25) in his *Petalaxis wagneri* species group.

In the early growth stages of some specimens, the wall is incompletely developed between offsets that grow adjacent to each other in the same parent corallite. Rarely, this condition may persist, and the dissepimentaria of such offsets may remain partly or completely joined into maturity.

For this study, the structure of the corallite walls was investigated with the light microscope only. The

Table 4

Characteristic features of species of *Petalaxis* from Ellesmere Island. DT/DC, ratio of tabularium diameter to corallite diameter (most commonly occurring values for number of major septa, mean corallite diameter and DT/DC given in brackets.)

Species	Mean Corallite Diameter (mm)	Number of Major Septa	Septa	Axial Structure	Median Lamellae	Septal Lamellae	Lateral Lamellae	Axial Tabellae	Tabulae	Dissepimentarium	DT/DC
Petalaxis baculatus sp. nov.	5.5-11.5 (6-10)	14-24 (15-22)	Thin; majors short; minors very short, as septal crests and ridges on wall	Discontinuous, generally narrow	Lens-shaped to circular, commonly isolated rod	Absent	1 or 2, lens-shaped or circular, commonly isolated rods	Rare	Concave, subhorizontal to adaxially elevated, 7-8 in 5 mm	Continuous, transeptal; dissepiments large, in 1 or 2 rows	0.61-0.82 (0.67-0.75)
P. beauchampi sp. nov.	5-11 (5.5-6.5)	14-22 (18-21)	Thin and sinuous; majors long, minors medium to long	Discontinuous, thin	Thin, curved or sinuous	Absent	One, vertically discontinuous, thin	Rare	Mainly complete, concave, generally subhorizontal, 9-12 in 5 mm	Continuous, transeptal; dissepiments convex, large, in 1 or 2 rows	0.54-0.80 (0.63-0.75)
P. crassicolumnus sp. nov.	6-13 (7-11)	18-27 (19-24)	Long, commonly thick and wedge-shaped, locally weakly naotic	Continuous, thick	Thick, commonly lens-shaped	Rare to numerous	1-4	Rare	Variable, commonly incomplete, vesicular, adaxially depressed to elevated, 11 or 12 in 5 mm	Continuous, transeptal; dissepiments small to medium, in 3-5 rows	0.60-0.80 (0.65-0.73)
P. donbassicus (Fomichev)	3.5-7.5 (4-7)	13-23 (14-19)	Generally thin, variable; majors long, minors medium to long	Continuous, fairly thick	Thick, locally forms thick lens	Short, rare to numerous	1, rarely 2	Rare, locally form short series	Numerous, commonly complete, concave, subhorizontal to depressed, 9-16 in 5 mm	Rarely discontinuous, transeptal; dissepiments of medium size, in 1 or 2 rows	0.61-0.82 (0.68-0.75)
P. ellesmerensis sp. nov.	4.2-11.75 (5-9.5)	15-23 (16-21)	Majors long, minors medium to long	Generally thin, rarely discontinuous	Normally thin, tabular to lens-shaped	Normally few, short	1 rarely 2	Rare, locally form short series	Mainly incomplete, concave, slightly to moderately elevated adaxially, 9-13 in 5 mm	Continuous, transeptal; dissepiments small to medium, in 2-4 rows	0.64-0.78 (0.67-0.75)
P. sp. cf. *P. elyensis* (Wilson and Langenheim)	2.35-5.75 (3.5-4.5)	12-16 (13-14)	Thick and wedge-shaped to thin and sinuous; majors long; minors very short, form ridges on wall	Generally thick and continuous, locally thin and discontinuous	Mainly thick, lens-shaped, locally thin and sinuous	Short, normally 1 or 2	Rarely present	Absent	Commonly complete, adaxially depressed to subhorizontal, 7-9 in 5 mm	Discontinuous; dissepiments small, globose, mainly regular, locally transeptal, in one row	0.66-0.88 (0.72-0.78)
P. mcoyanus (Milne Edwards and Haime)	4-8	14-19 (15-17)	Thin, majors long, minors medium to long	Continuous, fairly thick	Moderately to strongly thickened	Short, locally numerous	Rarely more than one	Rare	Mainly incomplete, subhorizontal to depressed, locally elevated adaxially, 5-12 in 5 mm	Continuous, transeptal; dissepiments of medium size, in 1 or 2 rows	0.65-0.73
P. multilamellatus sp. nov.	4-9 (5.5-8.5)	16-23 (17-21)	Thin to moderately thick, majors long, minors medium to long	Continuous, fairly thick	Thickened, tabular to lens-shaped	Variable in length and shape, locally numerous	Strongly developed, commonly 2 or 3 present	Widely spaced, locally form series of 3 or 4	Generally incomplete, concave, adaxially depressed or horizontal, 9-13 in 5 mm	Continuous, transeptal; dissepiments small to medium, in 1-3 rows	0.62-0.78 (0.64-0.75)
P. parvus sp. nov.	3.4-7.2 (4.5-7)	14-18	Thin; majors short; minors very short, as ridges on wall and rare septal crests	Continuous, fairly thick, lens-shaped	Lens-shaped rod of variable thickness	Rare, thick	Rare	Absent	Mainly complete, concave, horizontal to axially elevated	Locally discontinuous, transeptal; dissepiments medium to large, in 1 or 2 rows	0.64-0.89 (0.66-0.77)
P. thorsteinssoni sp. nov.	6-18.5 (8-16)	17-27 (18-24)	Thin; majors long; minors medium to long	Locally discontinuous, thin to moderately thick	Thin to thick, curved	Few, short	One, inconsistently developed	Rare, but locally form series	Mainly complete, concave, strongly depressed, 6-10 in 5 mm	Continuous, wide, transeptal; dissepiments medium to large, in 1-7 rows	0.43-0.74 (0.50-0.65)
P. sp.	3-6 (4.5-5.5)	15-18	Thin; majors long; minors short	Continuous, thin	Thin to moderately thick	Short, thick, rarely more than one	One, inconsistently developed	Absent	Mainly incomplete, concave, subhorizontal to axially elevated, 10-12 in 5 mm	Locally discontinuous, narrow; dissepiments almost all regular, small to medium, in 1 or 2 rows	0.69-0.85 (0.73-0.82)

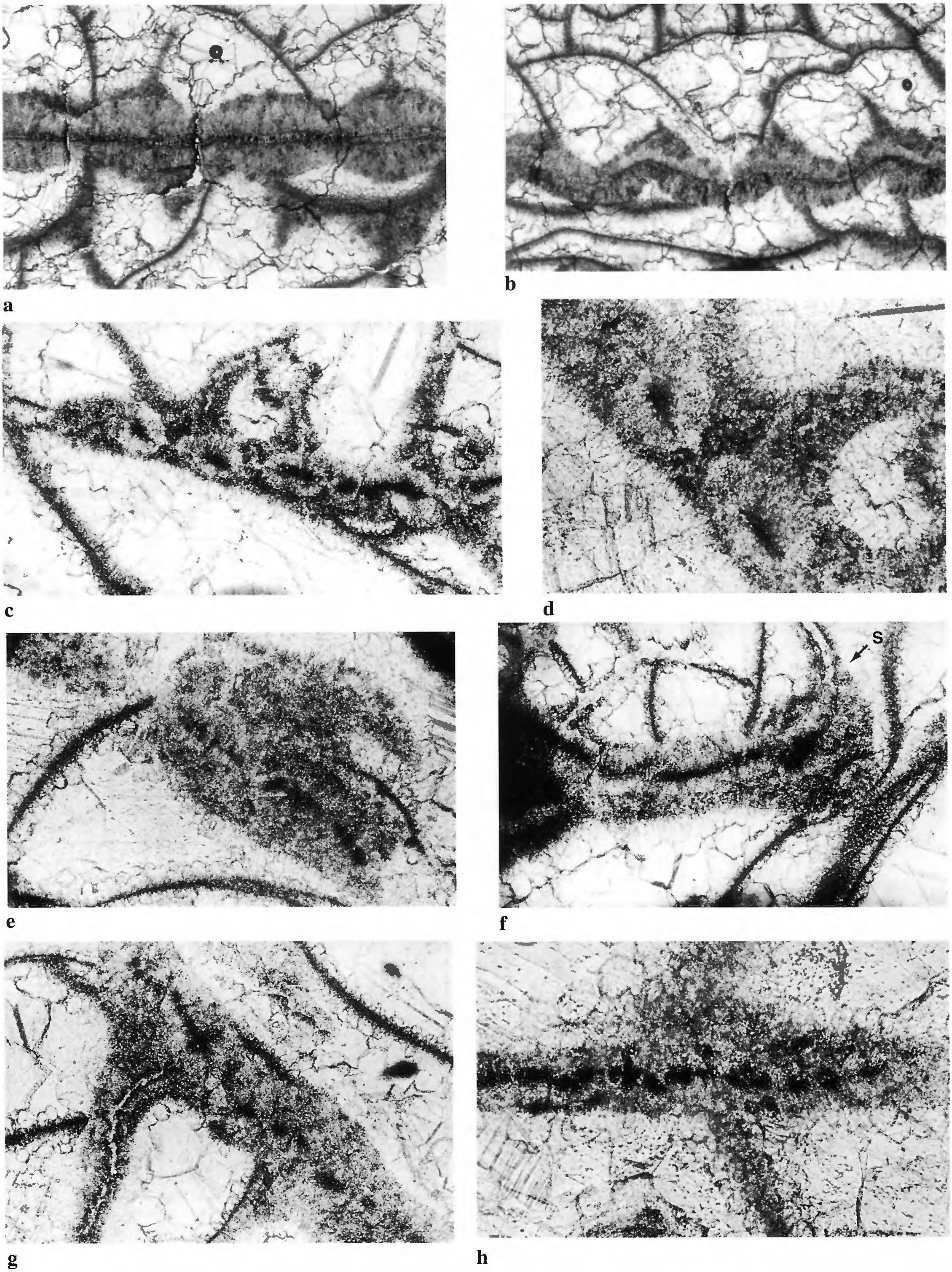

Figure 16a-h.

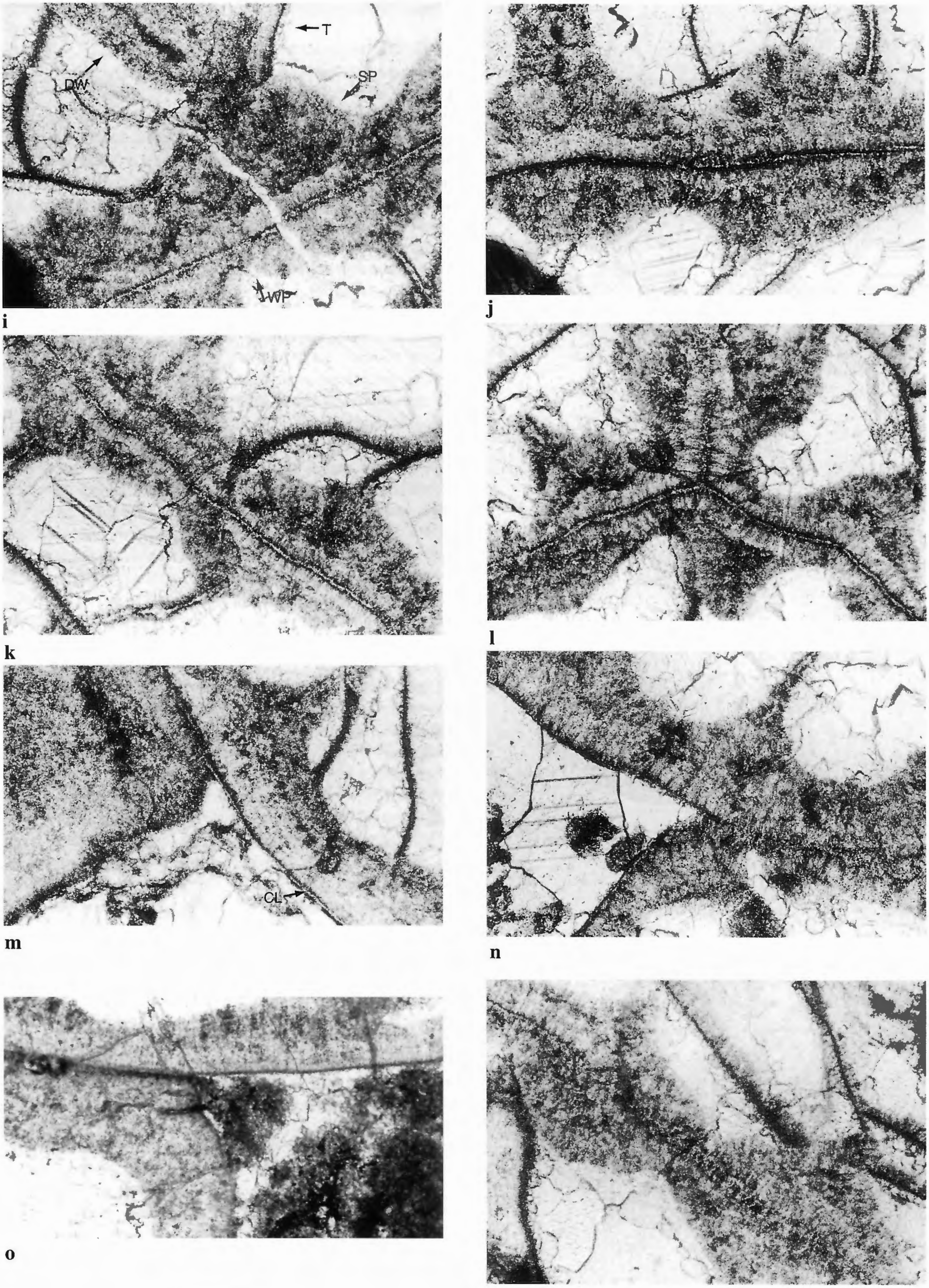

Figure 16i-p.

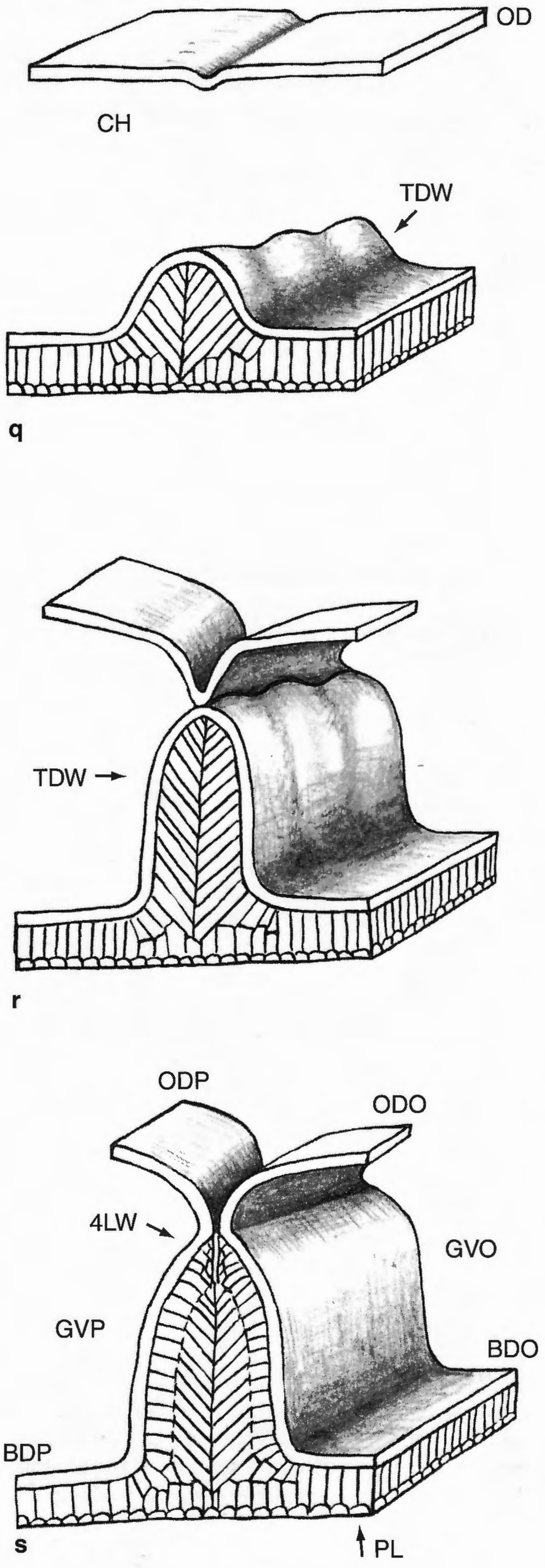

*Figure 16. Wall structure and development in **Petalaxis**; **a** and **b**, denticulate, four-layered wall in **Petalaxis mcoyanus** (Milne Edwards and Haime) (hypotype, GSC 109630), in part thickened by peripheral parts of septa, x30; **a**, wall approximately planar, bearing opposing septa of adjacent corallites; **b**, wall sinuous, septa of adjacent corallites offset; **c-n**, development of dividing wall in holotype of **P. multilamellatus** (GSC 109646), x70 unless otherwise indicated; **c**, dividing wall containing a chain of trabeculae or groups of trabeculae; **d**, two trabeculae or groups of trabeculae within secondary fibrous layer of wall illustrated in Figure 16c, x140; **e**, pinnacle of dividing wall with chain of trabeculae, almost attached to septum of parent (upper left); **f**, margin of dividing wall with septum (S) attached to it; **g**, dividing wall in advanced stage of development, but still showing trabecular microstructure; **h**, dividing wall showing well developed trabecular structure; **i**, margin of dividing wall (DW) attached to tabula (T) and to base of parent septum (SP), WP - four-layered parent wall; **j**, four-layered, mature wall bearing three septal bases and a septum with trabecular microstructue; **k**, four-layered mature wall showing two dark layers and two light layers with attached septal bases; **l**, junction of three four-layered mature walls; **m**, walls of two partly isolated corallites, joined near centre of photograph; peripheral layer of light calcite (CL) of uncertain origin; **n**, walls of two partly isolated corallites, as in Figure 16m, but bordered by dark layers of small calcite crystals; **o**, **Petalaxis baculatus** sp. nov. (holotype, GSC 109657), walls of corallites separated by matrix (on right), consisting of very thin, dark, outer layer and thick, lighter coloured inner layer; four-layered intercorallite wall present on left, where corallites joined (x100); **p**, **P. multilamellatus** sp. nov. (holotype, GSC 109646), wall with four-layered or, possibly, fibronormal microstructure (upper left) passing into trabecular microstructure (lower right); **q-s**, interpretation of three main steps in development of wall dividing parent from offset polyp; **q**, pinnacles with septal microstructure appear in epidermal pocket beneath basal disc; oral disc shown with initial, downward infolding parallel to incipient dividing wall; wide channel connecting gastrovascular cavities of parent and offset allows free fluid exchange; **r**, dividing wall with septal microstructure grows upward to meet downward fold in oral disc; connecting channel closed in area shown, but may remain open and functioning nearby; secondary sheets may have already developed in dividing wall (not shown here); communication between parent and offset polyp occurs through united soft parts; **s**, body walls between parent and offset polyps separate along zone of contact between down-folded oral disc and elevated part of basal disc covering dividing wall; process leads to complete separation of polyps, closely resembles separation and subsequent healing of soft parts observed during strobilation in Sphinctozoa; beginning at this stage, each of the separated polyps begins to form its own wall and composite, four-layered wall develops; BDO - basal disc of offset, BDP - basal disc of parent, CH - channel, GVO - gastrovascular cavity of offset, GVP - gastrovascular cavity of parent, OD - oral disc of offsetting individual, ODO - oral disc of offset, ODP - oral disc of parent, PL - primary layer, TDW - trabecular dividing wall, 4LW - four-layered wall.*

development of the wall separating adjacent corallites was studied in detail in the holotype of *Petalaxis multilamellatus* sp. nov. (GSC 109646), using serial thin sections cut at intervals of approximately 0.3–0.4 mm. Although this specimen has been partly altered by recrystallization, its morphological details are sufficiently well preserved for the following observations to be made.

1. The formation of the dividing wall separating a parent corallite from its offset begins with the upward growth of small crystals, secreted by the flat epidermis of the basal disc of the polyp. This layer closely resembles the external layer of a tabula, composed of minute, closely spaced crystals. Remnants of these, and also of larger crystals, are still recognizable in the next stage of development, described below (Fig. 16c, d), in which the upward-growing pinnacles of the dividing wall are clearly recognizable.

2. Unlike the initial, tabular layer of crystals, the microstructure of the succeeding pinnacles, mentioned above, is analogous with that of the septa in this specimen (Fig. 16c, d). Such structures could have been formed only by upward folding of the epidermis of the basal disc. Identical structures were described by Fedorowski (1978) in etched specimens of *Heritschioides* sp. from southwestern Texas. Pinnacles forming the early phases of the dividing wall may be small, consisting of few trabeculae (Fig. 16c, d) or may form fairly large bodies, composed of many trabeculae surrounded by secondary sheets (Fig. 16e). Our observations suggest that the first appearance of pinnacles is consistently located near the middle of the future wall, approximately midway between the walls of the parent corallite to which the new wall will be attached.

3. The coalescence of pinnacles within the dividing wall is normally followed by closer spacing of the trabeculae, which eventually form an almost continuous, solid layer, identical in microstructure with the closely comparable "median dark layer" of the septa (Fig. 16f). In some instances (Fig. 16g) individual trabeculae and/or groups of trabeculae within the middle part of the dividing wall remain widely spaced, so that the wall resembles a well preserved mature septum (Fig. 16h). Most of the septa, including the new septa attached to the dividing wall, are poorly preserved, exhibiting only an irregular "zigzag", partly recrystallized median layer of indefinite structure (Figs. 16a, b, g), which has diagenetically replaced the original trabeculae.

4. After the dividing wall becomes continuous, it grows laterally along both of its margins toward the walls of the parent. During this stage, which is of considerable duration, the parent and the offset polyps remain connected through channels located next to the parent walls. The new dividing wall eventually joins the wall of the parent or a septal base formed on that wall (Fig. 16i), but this attachment does not necessarily imply division of the soft parts of the two polyps. On the contrary, continued connection between the parent and offset is indicated by the arrangement of crystals in the dividing wall and in the septal base, which continue to grow toward each other (Fig. 16i). The tabula attached to the right side of this septal base was formed by a local part of the basal disc, common to the parent and offset polyps. Direct connection between these polyps eventually was terminated by the upper tabula shown in Figure 16i.

5. Along the median plane of almost all mature corallite walls observed, there is a clear discontinuity which, in our opinion, indicates true division between the bodies of the living polyps. This implies that most, or all of, the adjacent, mature polyps in the colonies studied were in contact, but had no connecting tissue in common. The medial break in the wall separates two narrow, dark layers consisting of very small crystals, which grew adaxially, away from the median plane. This indicates that the two dark layers were secreted independently by the two neighbouring polyps. The dark layers are flanked by contrasting, thick, light layers consisting of relatively large calcite crystals, which constitute most of the corallite wall (Fig. 16j). The combined dark and light layers thus form a four-layered wall separating adjacent corallites. Commonly, the surfaces of the wall bear secondary sheets of crystals, which are locally grouped into bundles, especially where the peripheral margins of septa join the wall (Fig. 16k, l). In the subcerioid species *P. baculatus* sp. nov., the wall in corallites separated by matrix consists of a thin, dark outer layer and a thicker, light inner layer (Fig. 16o), as described above for *P. multilamellatus* sp. nov.

In rare instances, there is variation from the normal, mature wall structure described above. Locally, the median layer of the wall may consist of grouped crystals forming a series that closely resembles the trabecular microstructure of a septum or the analogous microstructure of the early growth stages of a dividing wall (Fig. 16p, lower right). This trabecular microstructure extends for only a short distance laterally, beyond which the median layer of the wall appears to have the normal mature microstructure, with two dark layers separated by a fairly distinct, clear calcite layer (Fig. 16p, upper left). Such a transition, from trabecular to normal wall structure, is interpreted as representing a lateral transition from fully connected to totally divided parts of adjacent polyps.

Several conclusions can be drawn from the observations listed above. The trabecular microstructure of the wall in its early stages of development indicates that this part of the wall was deposited beneath an upward fold in the epidermis of the basal disc, as outlined above. It is our opinion that the structure of the mature, four-layered wall has not been greatly altered by diagenetic processes, although some minor diagenetic changes are obvious. The pattern of wall development and the arrangement of calcite crystals in the mature wall, perpendicular to the median plane, indicate that the wall was originally secreted by the flat epidermis of the lateral polyp walls in a manner typical for all corals, solitary and colonial, in which the polyps are totally independent. We interpret the development of the wall, from an initial septum-like phase to a mature four- layered phase, to have occurred through parallel changes taking place on the oral and basal discs. During this process, upward growth of the dividing wall beneath a septum-like pocket of the basal disc was accompanied by a corresponding, parallel, downward infolding of the oral disc (Fig. 16q). This eventually led to contact and fusion between the basal and oral discs (Fig. 16r), followed by lateral separation into parent and daughter polyps above the median plane of the new wall (Fig. 16s). This process began in the middle part of the new wall, where the mature, four-layered wall structure first appeared, and then progressed laterally in both directions toward the wall of the parent corallite, as outlined above.

The main features of wall development found in *P. multilamellatus* sp. nov. were also observed in serial sections through a specimen of *P. crassicolumnus* sp. nov. (Paratype GSC 109640), but minor differences between these species are also evident. The most important features common to these two species are the initial, trabecular structural phase of the new wall and the subsequent transition to a four-layered structure, beginning in the middle of the wall and extending laterally. In *P. crassicolumnus*, however, this transition progressed much more rapidly than in *P. multilamellatus*, extending farther at an earlier stage and almost reaching the margins of the new wall before it joined the parent wall (Figs. 17a, b). Thus, separation of the main parts of oral and basal discs of the parent and the offset polyps took place in *P. crassicolumnus* much earlier and proceeded more rapidly than in *P. multilamellatus*. Channels remained open, however, at one or, more commonly, at both ends of the dividing wall, providing communication between the parent and offset through connecting passages between their gastrovascular cavities and by means of the continuous soft parts of their oral and basal discs bordering the channels. From analogy with the channel development seen in the genus *Heritschioides* (Fedorowski, 1978, p. 186), it appears probable that these channels remained open for a considerable length of time, before being bridged by tabular and/or dissepimental tissue. The reason for such early separation of parent and offset polyps is not clear. Perhaps early separation was possible because of better skeletal support of the young polyp, allowing stronger development of tentacles and mesenteries.

Another feature observed in *P. crassicolumnus*, but absent from *P. multilamellatus* is the insertion of new septa at the free margins of the dividing wall, with alternate development of major and minor septa (Figs. 17b, c). In some instances, the new septa appear to be natural continuations of the dividing wall (Fig. 17d) and in others they are laterally attached to it (Fig. 17c). Serial sections show that a new septum, after its insertion at the margin of the dividing wall, shifts to the lateral surface of the dividing wall as the latter grows toward the parent wall (Fig. 17b). This type of insertion and early septal development has not been described in other species, and therefore may be a characteristic feature of *P. crassicolumnus*.

Septa. *Petalaxis* has two orders of finely trabecular, wedge-shaped septa that are thickened in the outer tabularium and become thinner adaxially and toward the periphery. They are moderately to strongly thickened along their peripheral edges, where they join the wall. In the dissepimentarium of most species, the septa are vertically discontinuous and are represented by septal crests on the surfaces of transeptal dissepiments, but may be almost continuous in a few species having mostly regular dissepiments. Septal crests in the outer dissepimentarium of some colonies (e.g., *Petalaxis crassicolumnus* sp. nov., Figs. 30a, 32b, c) are highly sinuous and may break up into the peripheral septal plates or irregular papillae of weakly naotic septa. Such irregularly formed septal crests may rest on large, transeptal dissepiments or on smaller, more highly convex plates resembling regular dissepiments.

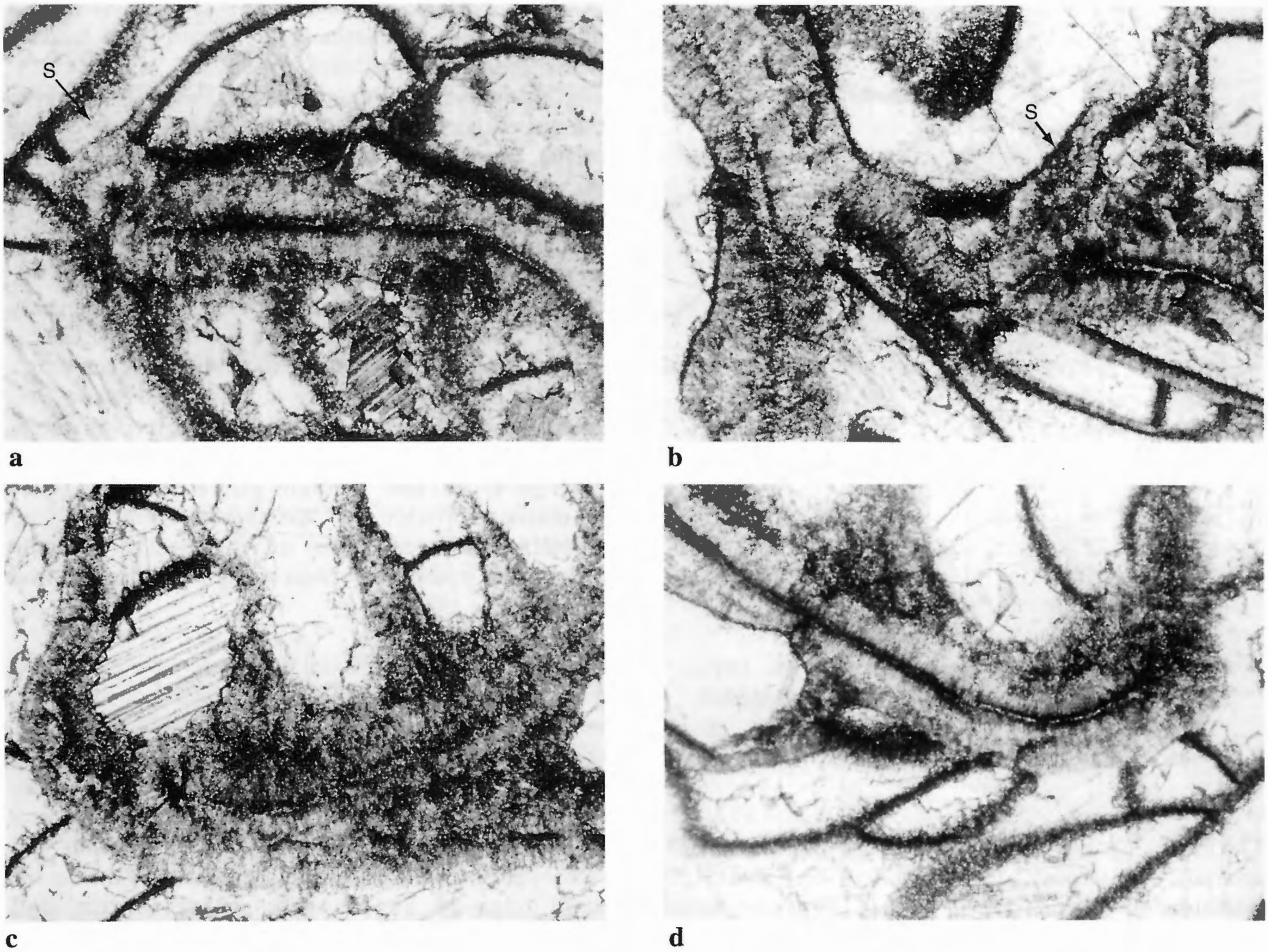

*Figure 17. Wall development in **Petalaxis crassicolumnus** sp. nov. (paratype, GSC 109640), x70; **a**, four-layered or, possibly, fibronormal wall with new septum (S), in very early stage of development, attached to its margin; **b**, as in Figure 17a, but developed farther, parent wall at left; **c**, **d**, as in Figures 17a and b, but with larger attached septum.*

There is considerable interspecific variation in the shape, thickness, and length of the major septa. They may be straight or gently curved to sinuous, and range from thin to very thick. The axial margins of major septa are commonly curved or sharply deflected laterally. Major septa are long in most species and vary in length vertically. Only rarely do they extend less than half the tabularium radius toward the axis. In many species they closely approach the axial structure and, commonly, a few of them join it. The cardinal septum, identified by the pattern of septal insertion in several Ellesmere species (see discussion of axial structure, below), is commonly slightly thicker than adjacent major septa (e.g., *P. thorsteinssoni* sp. nov., Pl. 5, fig. 10, Pl. 6, fig. 2, Figs. 18-20; *P. baculatus* sp. nov., Pl. 6, fig. 5, Fig. 41a; *P. parvus* sp. nov., Pl. 7, figs. 1, 2, Fig. 43a) and consistently joins the axial structure along much of its length. Along its axial margin, the cardinal septum is thickened to form the median lamella of the axial structure in early growth stages and subsequently forms one or more lateral lamellae (see discussion of axial structure, below) in some species. In species with weakly developed axial structures [e.g., *Petalaxis beauchampi* sp. nov., Pl. 5, fig. 5; *P. orboensis* (de Groot)], the cardinal septum may be locally shortened or deflected from the cardinal-counter plane, with the result that the axial area is left open or is occupied only by other long major septa. In these and other species, the counter septum is of normal thickness and rarely extends to the axial structure.

Minor septa are generally well developed and long in *Petalaxis*, but in some species they may be very short or expressed only as septal crests or as ridges on the corallite wall [e.g., *P. parvus* sp. nov. (Pl. 6, figs. 14,

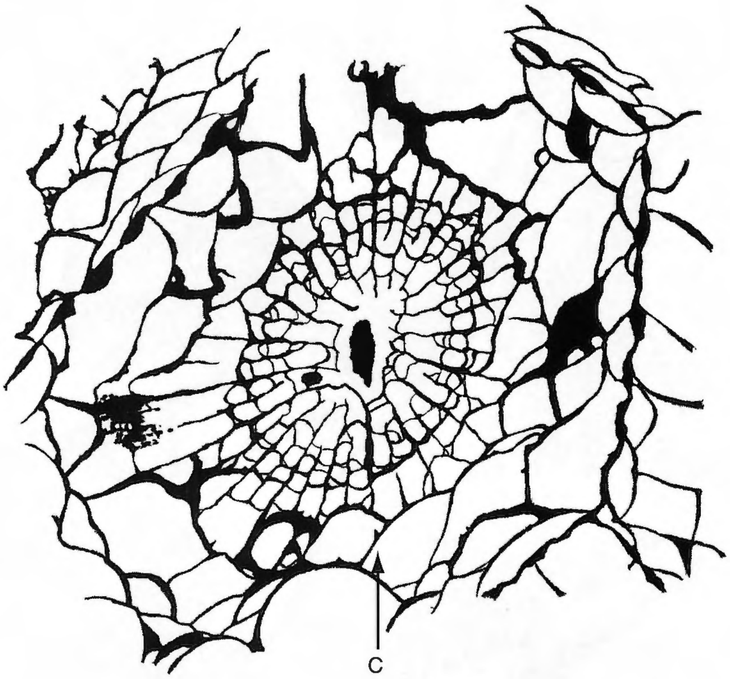

Figure 18. Petalaxis thorsteinssoni sp. nov., holotype GSC 109653. Thickened cardinal septum (C), slightly withdrawn from axial structure, x6, hand drawn from photograph.

17; Pl. 7, figs. 1, 2), *P. exiguus* Sando, *P. monocyclicus* (de Groot), *P. wyomingensis* Sando, *P. kitakamiensis* (Minato and Kato)]. *Petalaxis exilis* Kozyreva is the only described species that apparently lacks minor septa. Kozyreva (1974, p. 26, Pl. 1, fig. 1) stated that minor septa are not developed in this species.

The septal microstructure of *Petalaxis penduelensis* Rodriguez and *P. wagneri* (de Groot) was described as fibrous by Rodriguez (1984, p. 352, 359, figs. 185, 192). Minato and Kato (1974, p. 74) described that of *P. kitakamiensis* (Minato) as fibronormal and Sando (1983, p. 26, 28) used the same term for *P. simplex* (Hayasaka), *P. wyomingensis* Sando, and *P. exiguus* Sando. The type specimens of *P. exiguus* (USNM 162002A, B) were re-examined for this study. They are silicified and recrystallized to the extent that, in our opinion, the nature of their microstructure cannot be positively determined. We have not studied specimens of *P. kitakamiensis*, *P. simplex* or *P. wyomingensis*. With the kind co-operation of Professor S. Rodriguez, we examined the microstructure of *P. penduelensis* and *P. wagneri*, represented by well preserved specimens in his collection from the Cantabrian Mountains. In both of these species, as well as in species of *Cystolonsdaleia* from the same collection, the microstructure is finely trabecular, exactly as it is in all of the Ellesmere species in which septal microstructure is preserved. The septa of *Petalaxis* from Ellesmere Island possess a medial, finely monacanthine layer, composed of numerous, adaxially elevated, gently curved trabeculae. Flanking the trabecular layer are lateral layers consisting of fine calcite fibres, arranged perpendicular to the median planes of the septa. These features are best shown by thin sections from several specimens of *P. thorsteinssoni* sp. nov. and are also poorly expressed in a Myatchkovian specimen (GSC 109632) of *P. mcoyanus* from near Leninskie Gorki, approximately 35 km south of Moscow, Russia (GSC loc. C-222965). In *P. thorsteinssoni* sp. nov., individual trabeculae are clearly visible in transverse and longitudinal section (Figs. 19a, b). They are aligned with the median planes of the septa in the outer tabularium, but commonly diverge from the median planes in the inner tabularium. Within the dissepimentarium and on septally thickened parts of the wall, randomly distributed trabeculae form irregular papillae and crests (Figs. 19b, 20).

Axial structure. The axial structure in *Petalaxis* is normally strongly developed, vertically continuous, and ranges in shape from a thin lamella to a thick column of irregular oval or circular outline in transverse section. In a few corallites of many species, the axial structure is locally discontinuous. It shows a broad range of complexity, but is generally understood to consist of a median lamella, joined to the thickened, axial edge of an elongate major septum and complicated in many species by the development of septal lamellae and rare, vertically discontinuous series of axial tabellae. The septum forming the median lamella was identified as the cardinal septum by Minato and Kato (1974, p. 74, 75), in their description of *P. kitakamiensis* (Minato) (see also de Groot, 1963, p. 80; Hill, 1981, p. F401; Rodriguez, 1984, p. 348, 351, 356; Wang and Chen, 1989, p. 58; Stevens, 1995, p. 787; Figs. 21, 22, this paper).

In his analysis of topotypes of *P. mcoyanus*, the type species of the genus, Sutherland (1977, p. 187) described strong vertical and lateral variation in the axial structure, which may range within a single corallite from a simple axial plate to a more complex structure containing septal lamellae and axial tabellae. Sando (1983, p. 25) assigned the type species and seven others to his *P. maccoyanus* species group, characterized by complex axial structures and well developed transeptal dissepiments. He recognized four other species groups (*P. flexuosus*, *P. simplex*, *P. vesiculosis*, *P. wagneri*) that have simple axial structures. From published illustrations, however, it appears that several of the species assigned by Sando to his *P. flexuosus* group [e.g., *P. donbassicus*

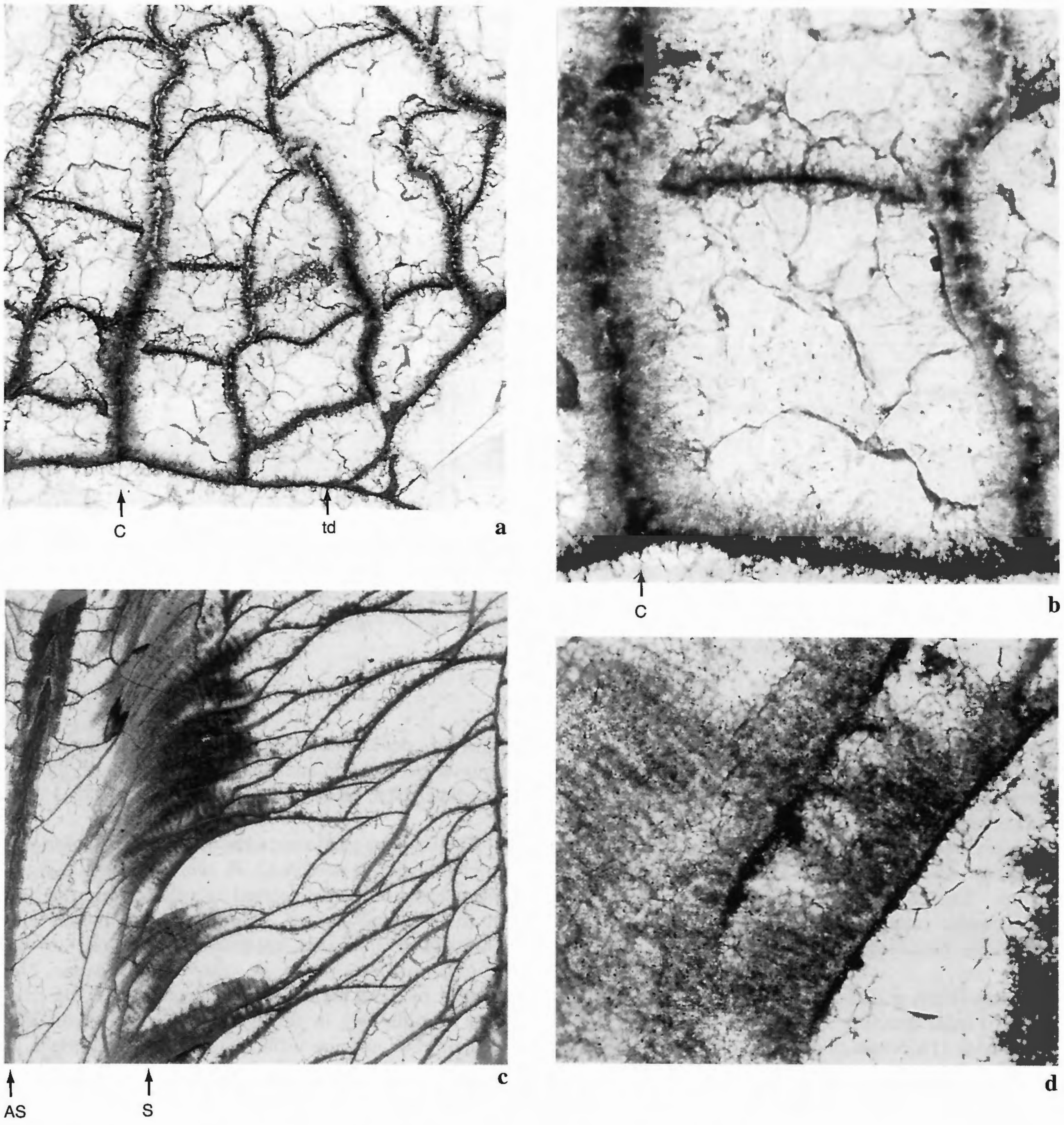

Figure 19. Petalaxis thorsteinssoni *sp. nov., holotype GSC 109653. Septal microstructure, showing medial, finely monacanthine layer and two lateral layers of fine calcite fibres;* **a**, *transverse section of thickened cardinal septum (C) and adjacent septa in tabularium and innermost dissepimentarium, x45, td - transeptal dissepiment;* **b**, *enlargement of Figure 19a, showing poorly preserved trabeculae in cardinal(C) and adjacent minor septum, x150;* **c**, *longitudinal section of axial structure (AS), tabularium and dissepimentarium, cut obliquely through septum (s), showing adaxially elevated trabeculae within septum, and papillae and septal crests formed by trabeculae on dissepiments, x10 (for complete section, see Pl. 5, fig. 13);* **d**, *enlargement of lowermost, central part of Figure 19d, showing poorly preserved trabeculae in septal crests, x100.*

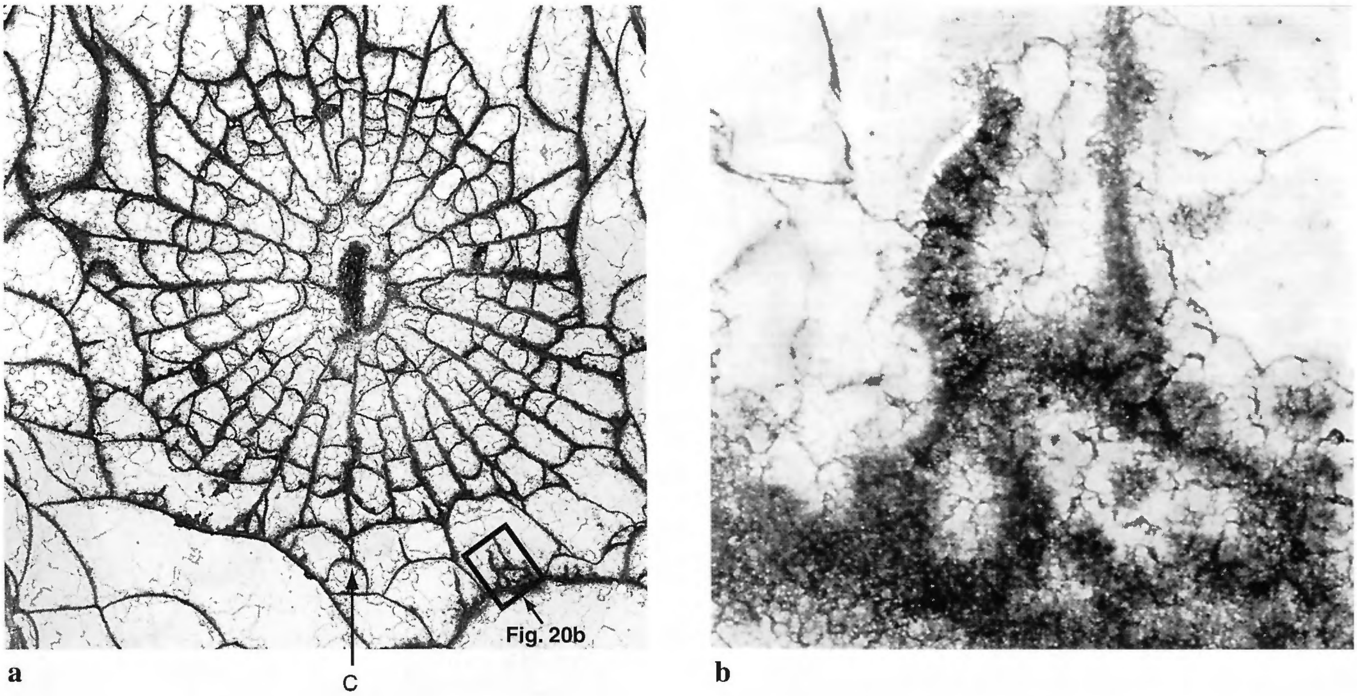

***Figure 20. Petalaxis thorsteinssoni** sp. nov., holotype GSC 109653. **a**, transverse thin section of mature corallite showing slightly thickened cardinal septum (C) and trabeculae in dissepimentarium forming septal crests and irregular papillae, x10; **b**, enlargement of small area in lower right of Figure 20a, showing trabecular septal crests and papillae, x110.*

(Fomichev) (= *P. fomichevi* Sando), *P. major* (Sando), *P. brokawi* (Wilson and Langenheim)] have complex axial structures bearing septal lamellae and/or lateral lamellae (new term, see below). These should probably be added to the *P. mcoyanus* group. With the exception of the Viséan to Serpukhovian *P. simplex* group, Sando's morphological groups have long stratigraphic ranges (Sando, loc. cit.) and appear to have little biostratigraphic application.

Wang (1989, p. 528-530, Fig. 13) distinguished five types of axial structure within *Petalaxis*, characterized as follows: 1) a simple, lamellar columella, 2) a median lamella with radial ridges (= septal lamellae, this paper), 3) a median lamella with radial ridges and a single, discontinuous series of inclined tabellae, 4) a solid, inflated, smooth columella, 5) an irregularly inflated plate with radial ridges, showing intersections of concave tabulae and inclined tabellae. These types have little taxonomic value, however, because two or more of them may appear in the same colony or even within the same corallite during its development. The axial structures in *Petalaxis* from Ellesmere Island show a range of variation similar to that described by Wang *(ibid.)*, but in most Ellesmere species, the axial structures are further complicated by additional lamellae developed approximately parallel to the counter-cardinal plane (see description of lateral lamellae given below and shown in Fig. 21).

The simplest axial structures in *Petalaxis* consist of a single, median lamella [e.g., *P. simplex* (Hayasaka), *P. mirus* Kozyreva]. It is formed as a thickened extension of the cardinal septum, is generally continuous and normally is elongated approximately parallel to the counter-cardinal plane in transverse section. The lamella may be planar, curved, or sinuous and may vary considerably in thickness. It is most commonly tabular, but may be inflated to form a thick lens in transverse section. Its connection with the cardinal septum is vertically discontinuous in most species. In species with more complex axial structures, including most of those from Ellesmere Island, the median lamella bears vertically discontinuous septal lamellae (columellar ridges of de Groot, 1963; column septa of Luo et al., 1989a, p. 120, 121). These commonly extend only a short distance abaxially, but in some species they occur as curved or sinuous plates of variable thickness, extending a considerable distance from the median lamella [e.g., *P. crassicolumnus* sp. nov. (Pl. 2, figs. 10, 11, Fig. 30a), *P. multilamellatus* sp. nov. (Pl. 4, fig. 3; Figs. 21, 22), *P. major* Sando].

In the present study, it was found that in the axial structures of many species, the median lamella is accompanied by one or more additional lamellae. Such lamellae (here named "lateral lamellae") are formed as thickened, adaxial extensions of the cardinal septum and are situated adjacent to the median lamella, ordinarily roughly parallel to it (Fig. 21q-z, a[1]-e[1], Pl. 2, figs. 10, 11; Pl. 4, figs. 3, 8-10). Lateral lamellae were described and illustrated in geyerophyllid corals by Rodriguez (1984, 1985), but have not been widely noted previously in *Petalaxis*. They are evident in published illustrations of several species [e.g., *P. cantabricus* (de Groot), *P. wagneri* (de Groot)], and have been described in *P. yosti* Stevens (1995) from Desmoinesian (Moscovian) strata in eastern California. In some species, they give the impression of local development of more than one columella in a corallite (*P. baculatus*, Pl. 6, fig. 5; Fig. 41a; *P. petrovi*, Kachanov, 1971, p. 75). They are present in most species from Ellesmere Island, but are particulary well developed in those with thicker axial structures, such as *P. crassicolumnus* sp. nov. and *P. multilamellatus* sp. nov. In general, corallites exhibit only one lateral lamella at any level in transverse section, but in the new species *P. crassicolumnus*, *P. multilamellatus* and *P. baculatus* up to three (rarely four) are locally present (Figs. 21e[1], 30a, 35, 41a). They are gently curved to sinuous, vary considerably in thickness, are vertically discontinuous, and their length in transverse section is commonly less than, but may greatly exceed that of, the median lamella. In *P. baculatus* sp. nov., the lateral lamellae are strongly thickened to form vertically discontinuous rods that have an oval to circular cross-section and are separated from the cardinal septum over considerable vertical distances.

Lateral lamellae may bear septal lamellae and also may be locally connected by them to the median lamella. The thickness of lateral lamellae is normally less than, but may be equal to that of, the median lamella. Although they normally lie approximately parallel to the median lamella, they locally curve around it and partly enclose it. They also may lie at high angles (up to 90°) to the median lamella and rarely are positioned beyond its cardinal or counter edges, across the counter-cardinal plane (Fig. 23). The formation of a series of lateral lamellae by adaxial elongation and thickening of the cardinal septum is illustrated in Figure 21, from serial transverse peels through the growth stages of a single corallite from the holotype (GSC 109646) of *Petalaxis multilamellatus* sp. nov. During the early growth stages of this corallite (Fig. 21a-n), the extended, thickened axial margin of the cardinal septum forms only the median lamella. In the late neanic stage the cardinal septum becomes sharply deflected from the counter-cardinal plane adjacent to the median lamella. While remaining laterally attached to the latter, the cardinal septum then extends adaxially and to the right, thus forming the first lateral lamella (Fig. 21o-q). Subsequently, the cardinal septum retreats from both the lateral lamella and the median lamella, then lengthens adaxially to form a second lateral lamella near the first one (Fig. 21r-u). As this occurs, the first lateral lamella becomes shorter in transverse section (Fig. 21u, v) and terminates distally, leaving only the median lamella and the second lateral lamella (Fig. 21x). Curvature, abaxial withdrawal and subsequent adaxial elongation of the cardinal septum is then repeated to form a third lateral lamella on the other (left) side of the median lamella (Fig. 21x-c[1]). During formation of the third lateral lamella, the cardinal septum rejoins the median lamella and again withdraws from it. This growth stage is immediately followed by development of a new offset in the right counter quadrant (Fig. 21c[1], d[1]) and another in the left counter quadrant (Fig. 21e[1]). During budding, the cardinal septum again extends into the axial area to form a fourth lateral lamella to the right of the second lateral lamella. The latter then terminates distally. A similar pattern of development is shown by the axial structures of other corallites in this specimen, but there is considerable variation in the number, orientation and positioning of lateral lamellae.

In species having fewer lateral lamellae than *P. multilamellatus* sp. nov. (e.g., *Petalaxis ellesmerensis* sp. nov., *P. thorsteinssoni* sp. nov.), the cardinal septum is commonly detached from the median lamella over short vertical intervals. Within these intervals, the cardinal septum is deflected from the counter-cardinal plane and commonly extends into the axial area. Lateral lamellae formed by thickening of the cardinal septum in such species normally extend only a short distance along the corallite.

In many species of *Petalaxis* there are widely spaced, short, vertical intervals containing a few axial tabellae along the median lamella. These may coincide with intervals in which tabulae are upwardly deflected at the median lamella (e.g., *P. baculatus* sp. nov., Pl. 6, fig. 8), thus approaching the structure of periaxial cones, as in *Cystolonsdaleia* (see below). In contrast to *Cystolonsdaleia*, however, the upwardly deflected parts of tabulae in *Petalaxis* extend only a short distance vertically and do not separate the axial parts of subsequently formed tabulae from the median lamella. The impression of periaxial cones in *Petalaxis* may also be given by other vertical elements in the axial structure, such as slightly lengthened axial tabellae or the intercepts of discontinuous septal lamellae or lateral lamellae (e.g., *P. donbassicus*, Pl. 2, fig. 3; *P. multilamellatus* sp. nov., Pl. 4, figs. 4, 7).

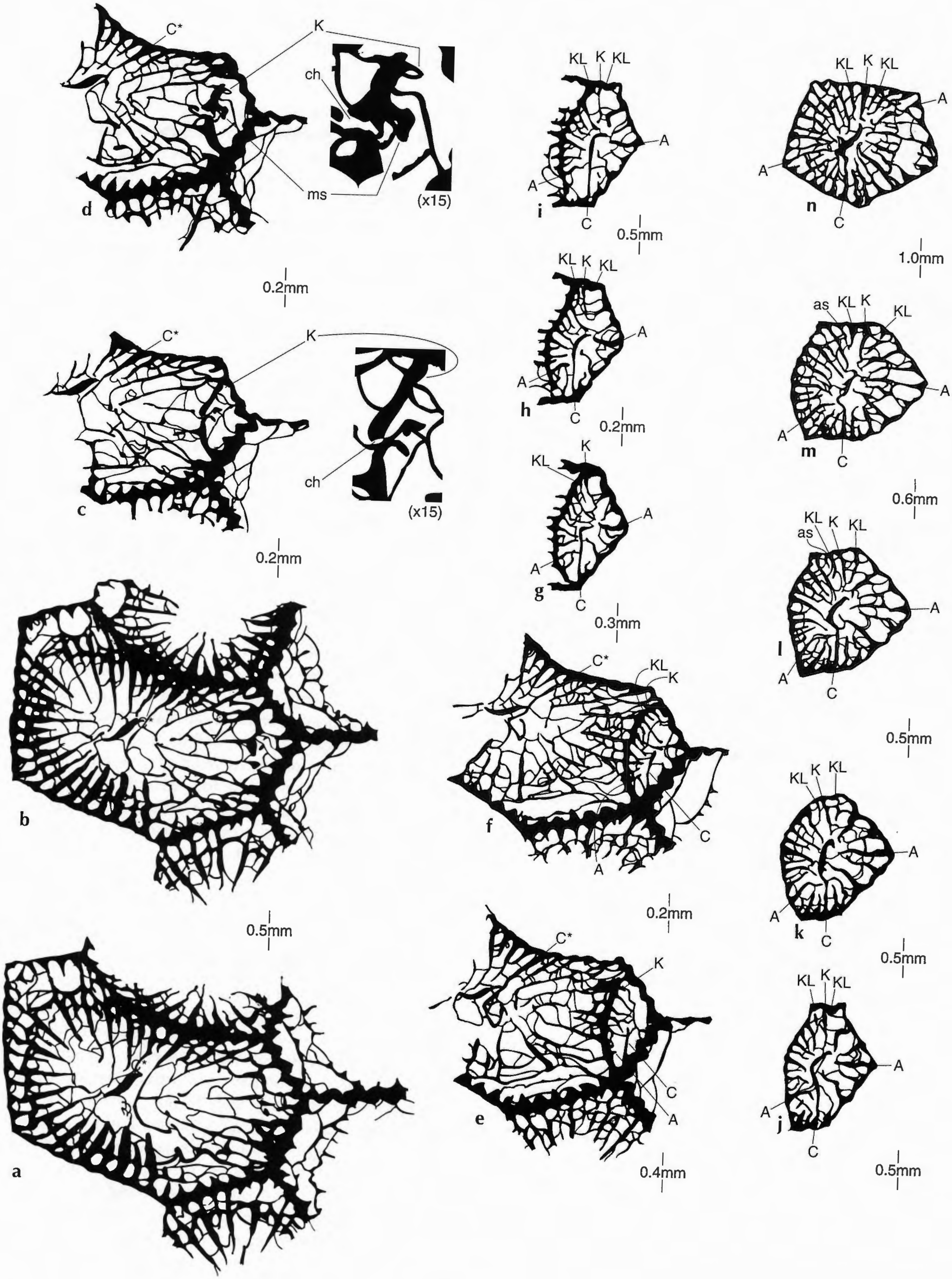
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Figure 21a-n.

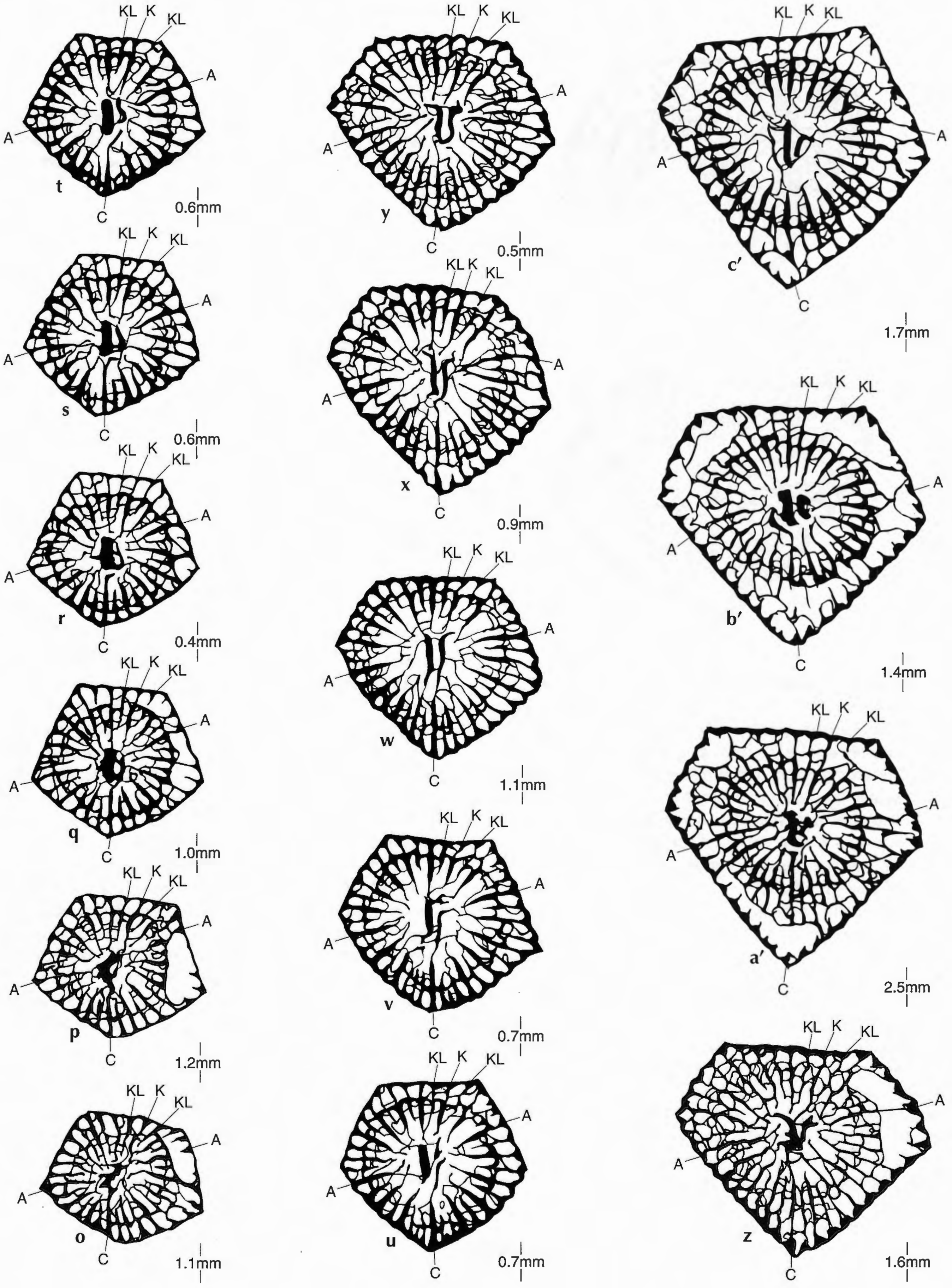
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Figure 21o-z.

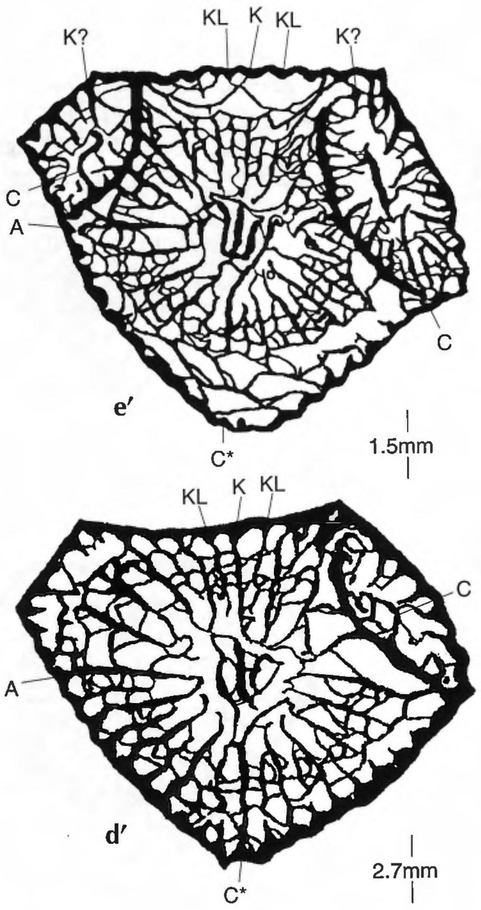

Figure 21. Petalaxis multilamellatus *sp. nov., holotype GSC 109646, drawings of serial transverse acetate peels through hysterobrephic* ***(a-d)*** *to mature* (**c**^{1}-**e**^{1}) *growth stages of offset, showing insertion of septa and formation of median lamella, septal lamellae and a series of lateral lamellae on thickened axial margin of cardinal septum; counter septum - K, alar septa - A, counter lateral septa - KL, cardinal septum of offset - C, cardinal septum of parent corallite - C*, major septum - ms, abberrant? septum - as, x6, parts of c and d enlarged (x15) to show channel - ch.*

Tabularium. *Petalaxis* has a biform tabularium (Hill, 1981, p. F25) – a morphological feature rarely reported in colonial rugosans (Weyer, 1972). In *Petalaxis*, tabellae in positions I and II of Sutherland (1965) occupy alternate interseptal loculi in the outermost tabularium. Those in position I are moderately to steeply declined adaxially and could be mistaken for clinotabellae. Those in position II are normally subhorizontal or abaxially declined, but a few are gently declined adaxially, particularly in species with strongly depressed tabulae. The alternate occurrence in the outermost tabularium of these two, differently oriented groups of tabellae is best shown by oblique longitudinal sections intersecting several interseptal loculi (e.g., Pl. 1, figs. 5, 11; Figs. 24b-d, 26b; Pl. 4, fig. 11; Fig. 35b). Biform morphology has been observed in the tabularia of all species found on Ellesmere Island and in Russian specimens of the type species, *P. mcoyanus*. In the Russian specimens studied by us (e.g., Pl. 1, fig. 10; GSC loc. C-222965), tabellae and peripheral parts of complete tabulae in position I are moderately to steeply declined adaxially. Those in position II are generally subhorizontal or abaxially declined, but some may also be gently declined adaxially (Fig. 24b, d). Similar biform morphology was illustrated in a longitudinal section of a topotype of *P. mcoyanus* by Sutherland (*ibid.*, Pl. 1, fig. 6). On the left side of the tabularium in this figure, adaxially declined tabellae (position I) are visible on the exposed surface of a minor septum, which extends through the lower two thirds of the section. In the adjacent interseptal loculus, shown in the upper one third of the section, most of the tabellae are subhorizontal or slightly declined toward the dissepimentarium (position II). Biform tabularia can also be seen in published illustrations of appropriately oriented longitudinal sections of other species [e.g., *P. belinskiensis* Fomichev, *P. hangzhouensis* Yamagiwa, Wang and Maeda, *P. nandanensis* Wang, *P. orboensis* (de Groot), *P. sexangulata* (de Groot)].

In the remaining, more axial parts of the tabularium, the tabulae are normally concave to subplanar and are less commonly slightly convex upward. In general, they are subhorizontal or depressed adaxially, but may also be slightly elevated toward the axial structure. The predominance of near horizontal tabulae has been widely used as a diagnostic feature for defining *Petalaxis* (Fomichev, 1953, p. 449; Kozyreva, 1974, p. 25; Hill, 1981, p. F401; Sando, 1983, p. 24; Wang, 1989, p. 535). However, the orientation of the tabulae varies greatly within the genus, which includes species with strongly depressed tabulae, others in which steeply elevated tabulae occur locally in individual corallites, and a broad range of intermediate forms. Species with tabulae steeply declined toward the axial structure include *P. cantabricus* (de Groot), *P. parapertuensis* (de Groot), *P. occidentalis* (Merriam), and *P. thorsteinssoni* sp. nov. (Pl. 5, figs. 11-13). In his review of the type species, Sutherland (1977, p. 187, Pl. 1, fig. 6) noted the local presence of tabulae that are quite steeply elevated toward the axial structure. This is also shown by the Russian specimens of *P. mcoyanus* from Leninskye Gorki, illustrated here (Pl. 1, figs. 7, 8, 10). Moderately to steeply elevated tabulae are also locally present in *P. mohikanus* (Fomichev, 1953, p. 459, Pl. 32, figs. 1b, 2b) and in several of the species from Ellesmere Island (e.g., *P. ellesmerensis* sp. nov., Pl. 3, figs. 8-10, 12, 13; *P. crassicolumnus* sp. nov., Pl. 2, figs. 9, 12).

In addition to the variation in orientation discussed above, the tabulae in *Petalaxis* also show a great range in their structural make-up. They may be almost entirely complete and possess few tabellae [e.g., *P. beauchampi* sp. nov. (Pl. 5, figs. 1-4), *P. exilis* Kozyreva, *P. persubtilis* Kozyreva, *P. simplex* (Hayasaka)] or they may be more complex, comprising numerous tabellae of varied shape and size [e.g., *P. mcoyanus* (Milne Edwards and Haime) (type species) (Pl. 1, figs. 7, 8, 10), *P. radians* (de Groot), *P. ellesmerensis* sp. nov., *P. multilamellatus* sp. nov. (Pl. 4, figs. 4-6)]. The complex tabularium in *P. crassicolumnus* sp. nov. (Pl. 2, figs. 9, 12; Pl. 3, figs. 2, 4, 5; Fig. 30b) is dominated by incomplete, vesicular tabulae made up of peripheral and periaxial series of fairly large, convex, concave and undulose tabellae.

From the present study and from a review of previously described species (see above), it appears that the orientation, shape and construction of the tabulae are useful criteria for defining species within *Petalaxis*, but because of the great variability exibited by these features, they must be used with caution as independant means for distinguishing the genus from closely related genera. A more dependable generic indicator may be the biform morphology outlined above.

Dissepimentarium. Transeptal dissepiments are strongly developed in *Petalaxis*. In most species, the outer dissepimentarium contains numerous transeptal dissepiments of the first order (Poty, 1981, Figs. 3, 4; Rodriguez, 1984, Figs. 28, 29), which interrupt both major and minor septa. Smaller, second-order, transeptal dissepiments (*ibid.*), which interrupt only the minor septa, are relatively rare and are confined almost entirely to the inner part of the dissepimentarium. They are developed to a minor extent in all of the species from Ellesmere Island, except those with very short minor septa (e.g., *P. parvus*) or poorly developed transeptal dissepiments (*P.* sp.). The abundance of transeptal dissepiments, in comparison to regular dissepiments, has been used to distinguish groups of species within the genus. De Groot (1963, p. 86-93) proposed a new subgenus under the preoccupied name *Hillia* for six species with a narrow dissepimentarium occupied almost entirely by regular dissepiments. She noted that the few transeptal dissepiments in these species occur mainly in corners of the corallites just below offsets (*ibid.*, p. 87). Sando (1983, p. 25) assigned these species to his *Petalaxis wagneri* species group and used the width of the dissepimentarium to distinguish the *P. flexuosus* group from the *P. vesiculosus* group.

The dissepiments in *Petalaxis* vary greatly in shape, size, orientation and number. In some species, they are almost all small and convex, forming a narrow outer ring consisting of one or two locally discontinuous rows [e.g., *P.* sp. cf. *P. elyensis*, Pl. 7, figs. 3-12, Fig. 45c; *P. sexangulata* (de Groot)]; in others, there is a wide dissepimentarium containing numerous rows of small, medium and large dissepiments, which may be convex or elongate and flattened [e.g., *P. crassicolumnus* sp. nov., *P. thorsteinssoni* sp. nov., *P. vesiculosus* (Dobrolyubova)]. A wide range of intermediate types occurs, and a few species are characterized by large, inflated dissepiments occurring in one or two rows [e.g., *P. simplex* (Hayasaka), *P. tchucoticus* (Onoprienko), *P. beauchampi* sp. nov.]. In transverse section, the dissepiments in *Petalaxis* are generally smooth and adaxially convex, but may also be angular or irregular in outline. Short series of small, inosculating dissepiments occur locally in the inner dissepimentarium. As a general rule, the dissepiments are moderately to steeply declined adaxially, and commonly are very steeply declined to vertical along the inner margin of the dissepimentarium.

Blastogeny. The following observations on the early growth stages of *Petalaxis* were made from series of closely spaced acetate peels through the new species *P. crassicolumnus*, *P. ellesmerensis, P. multilamellatus*, and *P. thorsteinssoni*. Supplementary information was obtained from transverse thin sections of all Ellesmere species used for this study. The terminology used follows that of Fedorowski and Jull (1976) and Fedorowski (1978).

New corallites develop in the outer dissepimentaria of parent corallites, commonly in the corners or along very short sides. They normally occur singly, but two or more may develop together in a single parent corallite. In our collections, no instance of budding has been observed in which two or more offsets originate from the parent at exactly the same level. Locally, clusters of several offsets are formed by budding in adjacent corallites (Pl. 3, fig. 3; Pl. 4, fig. 3). Clusters of young corallites also form during colony rejuvenation. Offsets may form in any quadrant of the parent corallite and the region of increase may include the peripheral margins of protosepta. The counter-cardinal planes of offsets are normally oriented tangentially with respect to the axes of parent corallites, but radial and near-radial orientation also occurs. During early development, the orientation of offsets commonly changes slightly because of accelerated insertion of septa in one or more quadrants.

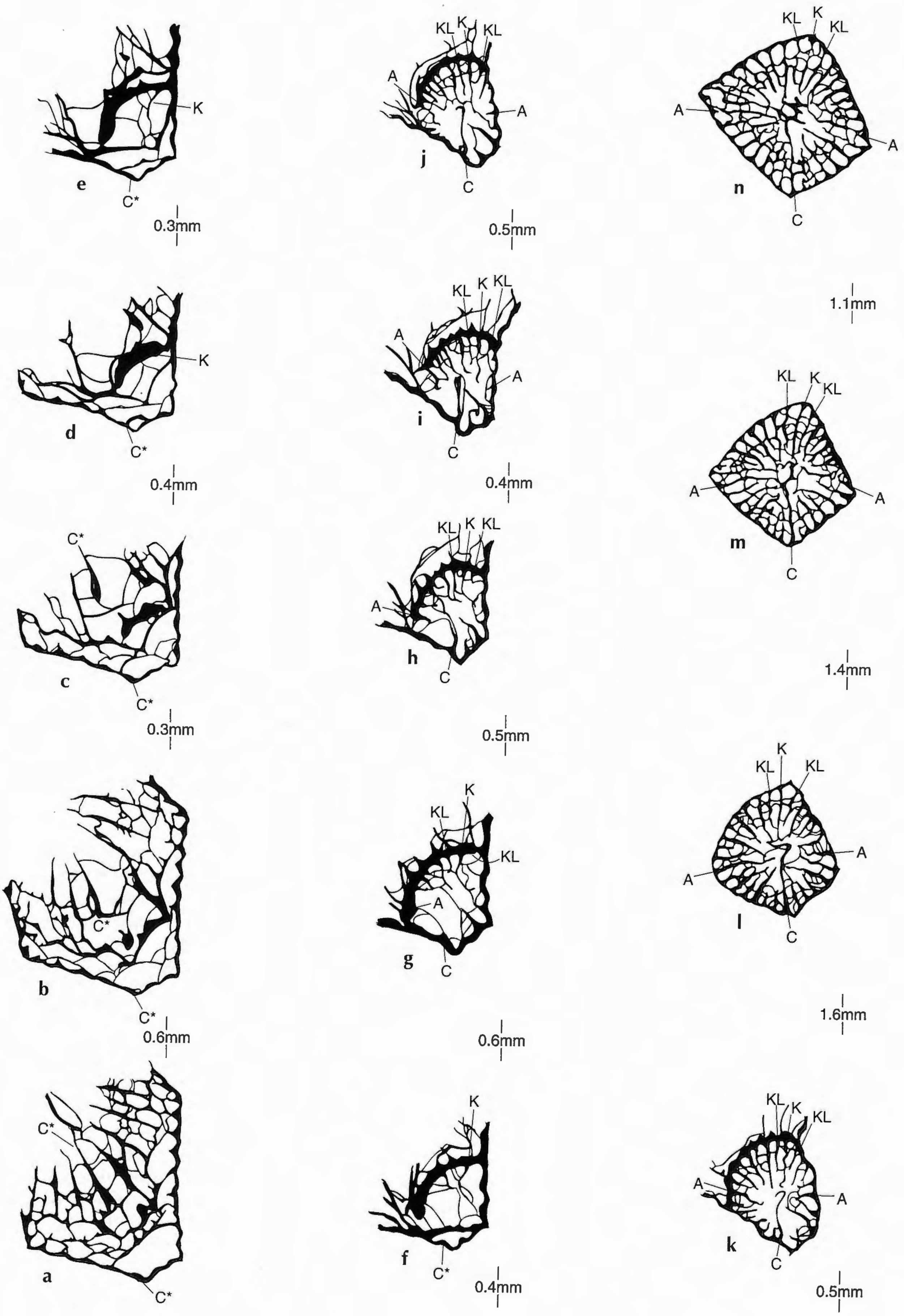
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***Figure 22. Petalaxis multilamellatus** sp. nov., holotype GSC 109646, drawings of serial transverse acetate peels through hysterobrephic (**a-f**) to late neanic (**m, n**) growth stages of offset, showing insertion of septa and formation of median lamella, septal lamellae and the first lateral lamellae on thickened axial margin of cardinal septum; counter septum - K, alar septa - A, counter lateral septa - KL, cardinal septum of offset - C, cardinal septum of parent corallite - C*, x6.*

The information on developmental stages given below was derived mainly from serial peel sections through one corallite of the holotype of *P. multilamellatus* sp. nov. (GSC 109646), beginning with its hysterobrephic stage and progressing through maturity and the development of two offsets (Fig. 21a-z; a^1-e^1).

Hysterobrephic stage (Fig. 21a-e). The vertical interval occupied by this stage is approximately 1.6 mm. Budding begins with the thickening of parent major and minor septa in the left cardinal quadrant, accompanied by dissociation of these septa into peripheral (septal bases on parent wall), medial (septal swellings and pinnacles), and axial parts (Fig. 21a). Sclerenchymal deposits on the dissepiments of the parent, in combination with septal swellings and pinnacles, form the beginning of the new wall of the offset. At this level, wide channels connect the offset with the parent and the new wall is attached to the parent wall along one margin only. At a slightly higher level, the new wall becomes more complete as the channels narrow. The axial parts of the parent septa become thin and curved or sinuous and the dissociated bases of these septa remain strongly developed on the inherited wall of the offset. The offset is floored by newly formed tabellae and the incomplete new wall develops a median dark line (Fig. 21b). In the latter part of this stage the new wall is joined to septal bases on the parent wall, but this junction is vertically discontinuous along one margin. One channel of varying width remains in approximately the middle of the new wall (Fig. 21c, d). Several septal pinnacles and a few tabulae are present within the offset, and the new wall bears one new septal base - the rudimentary counter septum (K). Some thin, irregularly curved axial segments of parent major septa are attached to the parent side of the new wall, but no parent minor septa are present in this region. In the upper part of the hysterobrephic stage (Fig. 21d), the counter septum has lengthened slightly and two new major septa are present within the offset on the new wall. One of these is quite thick and appears to be attached to a septal pinnacle. Major and minor septal bases, inherited from the parent corallite, are strongly expressed on the inherited wall. Channels remain open at this level. In his analysis of the blastogeny of *Heritschioides*, Fedorowski (1978, p. 184) showed that the tabular bodies appearing within channels were secreted later in the hystero-ontogeny. Thus, communication between the gastrovascular cavities of the parent and the offset polyp occurred at this stage of growth.

The interval between the peels shown in Figure 21d and e is too large to show the details of septal insertion at this level. At this stage of development in a second corallite from the same corallum (Fig. 22f-h), however, the cardinal and alar septa are developed after insertion of several major and minor septa on the new wall and the lengthening of several septal bases to form new septa on the inherited wall. In the highest peel prepared within the hysterobrephic stage (Fig. 21e), the new wall is attached at one margin to the parent wall. The opposite side of the new wall remains incomplete, leaving an open channel, which is bridged during completion of the wall through the vertical interval between Figure 21e and f (beginning of hysteroneanic stage). The counter septum is short and several major septa (including the left alar septum) have been inserted on the new wall, thus producing early acceleration of septal insertion in the left counter quadrant. The cardinal septum (C) has been inserted as a new septum on the inherited wall adjacent to its earliest junction with the new wall (Fig. 21e). Along with three of the new major septa, the cardinal septum extends into the axial area. In the parent corallite, several short major and minor septa of normal thickness and shape are attached to the outside of the new wall.

Hysteroneanic stage (begins after appearance of earliest metasepta; Fig. 21f-n). The vertical interval occupied by this stage is approximately 4.3 mm. At the beginning of this stage (Fig. 21f), the left counter lateral septum (KL) and a series of minor septa have been inserted on the new wall in the left counter quadrant. The left alar septum has lengthened and thickened and the right alar septum has developed from an inherited septal base. The cardinal septum is slightly inflated axially to form the median lamella of the axial structure (see previous discussion for development of axial structure). Through the next 0.5 mm (Fig. 21g, h), septal insertion begins adjacent to the cardinal septum, first in the left cardinal quadrant, then in the right. Insertion continues in the left counter quadrant, with new major and minor septa appearing alternately on the counter side of the alar septum. (Septal insertion does not begin in the right counter quadrant until the late neanic stage - Fig. 21u). A few regular dissepiments are present. These increase

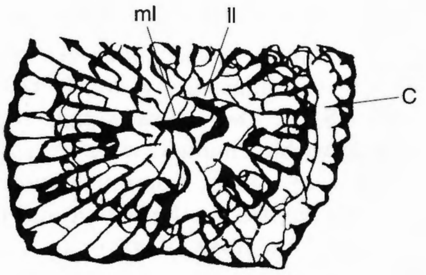


***Figure 23. Petalaxis multilamellatus** sp. nov., holotype GSC 109646. Drawing of transverse thin section of mature corallite (x6) showing cardinal septum (C) attached to curved lateral lamella (ll) lying across counter-cardinal plane and partly enclosing median lamella (ml) (see Pl. 4, fig. 3, top left), x6.*

in abundance as the corallite grows. Through the next 1.2 mm (Fig. 21i, j), the right counter lateral septum begins to develop on the inherited wall and septal insertion continues in both cardinal quadrants adjacent to the cardinal septum. In the right counter quadrant, two septa develop from inherited major and minor septal bases. At the top of this interval, the first transeptal dissepiments develop, interrupting the left counter lateral septum and the septa of the left cardinal quadrant (Fig. 21e-j).

Over much of the remainder of the hysteroneanic stage, alternate insertion of major and minor septa occurs adjacent to the cardinal and alar septa in all quadrants except the right counter quadrant. This, combined with earlier septal insertion, produces marked acceleration in the left counter quadrant, leading to a righthand shift in the location of the counter and counter lateral septa (Fig. 21m-p). Within the axial structure, the first septal lamellae appear (Fig. 21k). This stage of development ends with insertion of a series of minor septa in the right cardinal quadrant, causing expansion of the right cardinal quadrant and a rapid shift in the position of the right alar septum over a vertical distance of 1 mm (Fig. 21m, n). In addition, a single, ?aberrant septum (as) is inserted on the alar side of the left counter lateral septum. This new septum terminates within 2 mm distally (Fig. 21l-n). Strong development of transeptal dissepiments begins late in this stage and continues throughout succeeding stages.

Late neanic stage (begins when offset possesses all or nearly all characters of mature stage, but has smaller diameter and fewer septa; Fig. 21o-b^1). The vertical interval occupied by this stage is approximately 13.2 mm. It begins with the development of lateral lamellae and additional septal lamellae in the axial structure, thus completing introduction of structures found in mature corallites. Approximately 4.5 mm above the base of this stage, septal insertion in the right counter quadrant begins for the first time, with development of two minor septa (Fig. 21u). The existing major septa in this quadrant originated as septal bases inherited from the parent. Subsequent insertion in this quadrant results in migration of the counter and counter lateral septa to a position more in line with the cardinal septum. For the remainder of this stage, septal insertion continues adjacent to alar and cardinal septa in all quadrants, and transeptal dissepiments increase in abundance. Several septa in the right counter quadrant remain short prior to formation of a new offset in the mature stage (Fig. 21u-b^1).

Mature stage (Fig. 21c^1-e^1). The full septal count is reached at the beginning of this stage (Fig. 21c^1), accompanied by sclerenchymal thickening of septa and dissepiments in the region of increase, as a new offset begins to form within the right counter quadrant. After initiation of the first offset, a second offset begins to develop in the left counter quadrant. As the offsets develop, lateral lamellae continue to be introduced into the axial structure of the mature corallite (Fig. 21d^1, e^1), in the manner described previously. The pattern of early development of the two new offsets is similar to that in their parent corallite, described above (Fig. 21e-j), except for the positions at which the cardinal and counter septa are inserted. In the offsets, the cardinal septum forms on the new wall and the counter septum appears to form on the inherited wall (Fig. 21d^1, e^1) – the reverse of their relative positions in the parent corallite.

The degree to which the sequence of development described above is representative for the genus *Petalaxis* has not been thoroughly investigated. The general pattern of initiation of budding, insertion of major and minor septa, and development of the different elements of the axial structure appears to be fairly consistent in *P. multilamellatus* sp. nov. and other species in our collection but, as discussed below, other features of blastogeny are less consistent.

There is considerable variation in the position in which the cardinal and counter septa are introduced. The cardinal septum may develop from either the new wall or the inherited wall. In corallites in which the early position of the counter septum could be determined, it originates on the wall opposite that initially bearing the cardinal septum. As noted above, the positions of these septa with respect to new and inherited corallite walls show inconsistency between a corallite and its offsets in GSC 109646, the holotype of *P. multilamellatus* sp. nov. (Fig. 21e, f, d^1, e^1). There is also inconsistency in the method of emplacement of the cardinal septum in different corallites of this specimen. In the corallite described in detail above, the cardinal septum originates as a newly inserted septum on the inherited wall (Fig. 21e). In another budding corallite of the same corallum, however, the cardinal septum of the offset arises from the dissociated base of the parent cardinal septum, which lies in the region of increase (Fig. 22f-i). Details of the origin of the counter and cardinal septa have not been investigated further.

The level at which transeptal dissepiments first develop varies greatly. They may first appear very early in the hysterobrephic stage or at succeeding levels into the hysteroneanic stage. In many corallites, transeptal dissepiments are inherited from the parent corallite and continue to develop through all growth stages of the offset.

Formation of the new wall is consistently preceded by local thickening of the dissepiments of the parent with sclerenchymal deposits. A variable number of channels remain open between the parent and the offset in the hysterobrephic stage. Bridging of channels in the middle part of the new wall commonly occurs before final attachment of the new wall to inherited septal bases on the parent wall. Initial attachment normally takes place at only one margin of the new wall, leaving a channel open at the other margin until final attachment to the parent wall occurs. In some offsets, however, neither margin is initally attached to the parent. The shape of the new wall and the timing of its attachment to the parent wall depend on the degree to which transeptal dissepiments are developed in the hysterobrephic stage. In offsets initially lacking transeptal dissepiments, the wall is moderately to strongly curved from its initiation and joins the parent wall relatively early. In those possessing numerous inherited or newly formed transeptal dissepiments where the new wall is first formed, the latter is straight or only slightly curved. It remains so over a significant vertical distance before becoming more stongly curved and joining the parent wall, thus prolonging the direct connection between the parent and offset. In species characterized by weak development of transeptal dissepiments at all stages of development (e.g., *P.* sp. cf. *P. elyensis* and *P.* sp.), the new wall is highly curved and attached to the parent along both margins very early in its development.

Age and distribution. Petalaxis ranges in age from Early Carboniferous (late Viséan) to Early Permian (Asselian or ?Sakmarian). It has been found in North Africa, Spain, Ukraine, Russia, Spitsbergen, Canada, U.S.A., Japan, China and Mongolia.

One of the earliest reviews of the distribution of *Petalaxis* was given by Kozyreva (1974, p. 24), who assigned species to the genus from the Lower Carboniferous of North America, the Bashkirian of Ukraine and Japan, the Moscovian of Russia and Ukraine, and the mid-Carboniferous of North Africa and Spain. Sutherland (1977, p. 188) gave a mid-Carboniferous (Bashkirian and Moscovian) range for the genus in most areas, but noted the possibility that it may range from the upper part of the Lower Carboniferous to the Lower Permian. This expanded range was confirmed by Sando (1983), who re-assigned several western North American Lower Carboniferous and Permian species to *Petalaxis*, and by Wilson (1982, 1985), who described six Lower Permian species from California. A Bashkirian age was assigned to species from the Kitakami Mountains of Japan (Kato et al., 1979, 1989), and more recently the genus was reported from Bashkirian deposits of the Bechar Basin in North Africa (Semenoff-Tian-Chansky, 1985).

In China, as in other areas, *Petalaxis* occurs widely in Bashkirian and Moscovian strata (Luo et al., 1989b, p. 275, 283-287, Tables 44, 52). It has also been reported under the names *Hillia* and *Grootia* from rocks of Kasimovian or Gzhelian age (*Triticites* zone) of eastern Inner Mongolia and the eastern Tibet–western Sichuan area (Guo, 1983; Luo et al., 1989b, p. 286, Table 5). Recently, several species were described from the Lower Permian (Asselian?) of Guangxi Province (Ding and Xu, 1993).

In her recently presented paper on the zonation and distribution of Bashkirian to Gzhelian rugose corals in western Russia, Kossovaya (in press) showed *Petalaxis* first appearing in abundance and becoming widespread in the latter part of the Early Bashkirian (Askynbashskian substage), decreasing abruptly in diversity in earliest Moscovian (Vereian) time, subsequently becoming more diverse during the remainder of the Moscovian, and disappearing from the area during latest Moscovian (late Myachkovian) time. A newly discovered, upper Moscovian fauna from the Isfjorden area, central Spitsbergen (Somerville, 1995, 1997; pers. comm., 1995), contains several species of *Petalaxis* in common with coeval faunas from western Russia. *Petalaxis thorsteinssoni* sp. nov., which occurs in the upper Moscovian of Ellesmere Island, is also represented in the Isfjorden fauna (see section on occurrence and age of *P. thorsteinssoni* sp. nov.).

On Ellesmere Island, *Petalaxis* is most abundant in the Moscovian, but a few specimens have been collected from younger, Kasimovian to ?lowest Gzhelian strata as well (Fig. 3). These younger specimens, and those reported by Guo (1983) and Luo et al. (1989b) from western China and Mongolia, are the only post-Moscovian Carboniferous representatives of the genus known to the authors.

Several of the morphological characters in *Petalaxis* show a fairly consistent pattern of change through time. The *Petalaxis simplex* group of Sando (1983, p. 25), which consists of species characterized by complete tabulae and simple axial structures, is restricted to the Lower Carboniferous (Viséan and Serpukhovian). Kozyreva (1974, p. 26; see also Sutherland, 1977, p. 187) described a change from simple, complete tabulae in the Bashkirian species of Ukraine to incomplete, complex tabulae in those from Moscovian rocks of the Donets Basin in Ukraine and the Moscow Basin of Russia. Kozyreva (1974, p. 26) and Sutherland (1977, p. 187, 188) have also drawn attention to the change from wide dissepimentaria and numerous, large transeptal dissepiments in Bashkirian species to smaller transeptal dissepiments in Moscovian species. There are exceptions to this pattern of morphological development, however. Large dissepiments and simply constructed tabulae also occur in several species younger than Bashkirian, including *P. petrovi* (Kachanov) from the Moscovian of the Ural Mountains and the Ellesmere Island species *P. beauchampi* sp. nov. (early to mid-Moscovian) and *P. baculatus* sp. nov. (Kasimovian). Furthermore, the morphology of dissepiments and tabulae may be strongly affected by changes in the strength of accompanying axial structures, regardless of stratigraphic level. Variable species that normally have numerous dissepiments and complex, elevated tabulae may locally develop large dissepiments and relatively simple, sub-horizontal or depressed tabulae where their axial structures are weakly developed or discontinuous. This may affect entire colonies or only a few corallites locally.

Axial structures in *Petalaxis* show an overall increase in complexity over the interval from Viséan to approximately the middle of the Moscovian, followed by simplification through loss or reduction of axial elements in the remainder of the Carboniferous and the Lower Permian. Most Viséan to Bashkirian species have only a median lamella attached to the cardinal septum, but septal lamellae are weakly expressed in some (e.g., *P. immanis* Kozyreva, 1974, Pl. 2, figs. 4a, b, 5a). Septal lamellae are commonly well developed in younger Carboniferous species, and are accompanied by lateral lamellae and axial tabellae in many Moscovian species. This increase in axial elements is best expressed in the mid-Moscovian (Kashirian-Podolskian) species of Ellesmere Island, such as *P. crassicolumnus* sp. nov. and *P. multilamellatus* sp. nov., and in the similar, middle or upper Moscovian species, *P. yosti* Stevens, recently described from eastern California, U.S.A. (Stevens, 1995). Lower and middle Moscovian faunas also contain species [e.g., *P. orboensis* (de Groot), *P. beauchampi* sp. nov.] with relatively simple axial structures, similar to those of Bashkirian age. With some exceptions, such as *P. mcoyanus* (Milne Edwards and Haime) and *P. baculatus* sp. nov., species of latest Moscovian (Myachkovian) and Kasimovian or Gzhelian age have few septal lamellae and may lack lateral lamellae or axial tabellae [*P.* sp. cf. *P. elyensis* (Wilson and Langenheim), *P. parvus* sp. nov.; see Guo, 1983]. The Permian species described from California and Nevada in the western U.S.A. (Wilson and Langenheim, 1962; Wilson, 1982) resemble upper Moscovian and younger Carboniferous forms in the relative simplicity of their axial structures, which consist of a variably inflated median lamella that bears septal lamellae in some species.

Description of species

Petalaxis mcoyanus (Milne Edwards and Haime), 1851

Plate 1, figures 1-10; Figures 16, 24, 25

Stylaxis M'Coyana Milne Edwards and Haime, 1851, p. 453, Pl. 12, figs. 5, 5a.

Petalaxis M'Coyana Milne Edwards and Haime, 1852, p. 205; Milne Edwards, 1860, p. 440, 441.

Lithostrotion Portlockii Milne Edwards and Haime. Eichwald, 1861, p. 149, 150.

Lithostrotion Mac-Coyanum Milne Edwards and Haime. Eichwald, 1861, p. 150.

?*Lithostrotion flexuosum* Trautschold, 1879, p. 37, Pl. 5, figs. 7a, b.

Petalaxis Mc'Coyana Milne Edwards and Haime. Roemer, 1883, p. 387, 388.

Lithostrotionella flexuosa (Trautschold). Dobrolyubova, 1935a, p. 11, Pl. 3, figs. 1, 2; 1935b, p. 18, 19, Pl. 3, figs. 1, 2; ?Heritsch, 1939, p. 30, Pl. 13, fig. 5; Pl. 19, fig. 5; ?Heritsch, 1940, p. 72-74, Pl. 2, figs. 1, 2; ?Gorsky, 1978, p. 152, Pl. 20, fig. 7.

?*Lithostrotion* [*Lithostrotionella*] *flexuosum* Trautschold. Bassler, 1950, p. 235.

Lithostrotion maccoyanum (Edwards and Haime). Bassler, 1950, p. 222.

non *Petalaxis maccoyana* Milne Edwards and Haime var. *belinskiensis* Fomichev, 1953, p. 457, Pl. 31, figs. 3a, b.

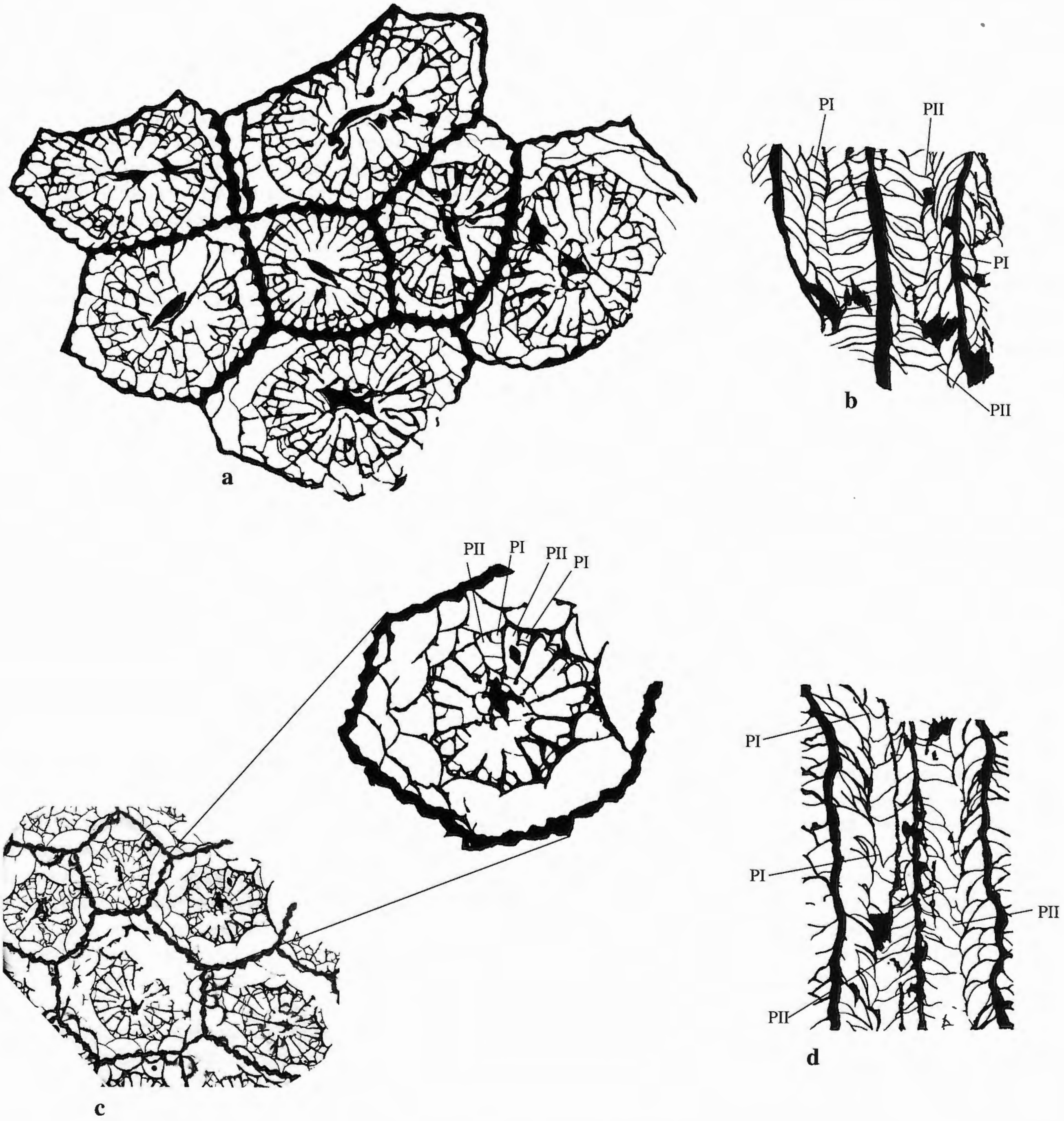


Figure 24. ***Petalaxis mcoyanus*** *(Milne Edwards and Haime), hypotypes GSC 109631 (figs. a, b), GSC 109633 (figs. c, d);* ***a****, drawing of transverse thin section (see Pl. 1, fig. 4), note short septal lamellae and lateral lamella (corallite at lower left), x5;* ***b, d****, drawings of longitudinal thin sections (see Pl. 1, figs. 5, 10), note biform morphology of tabularium (tabellae or peripheral parts of tabulae in position I - PI, those in position II - PII), x5;* ***c****, photograph of transverse thin section (x3) with drawing (x6) of corallite showing intercepts of biform tabularium (tabellae or peripheral parts of tabulae in position I - PI, those in position II - PII).*

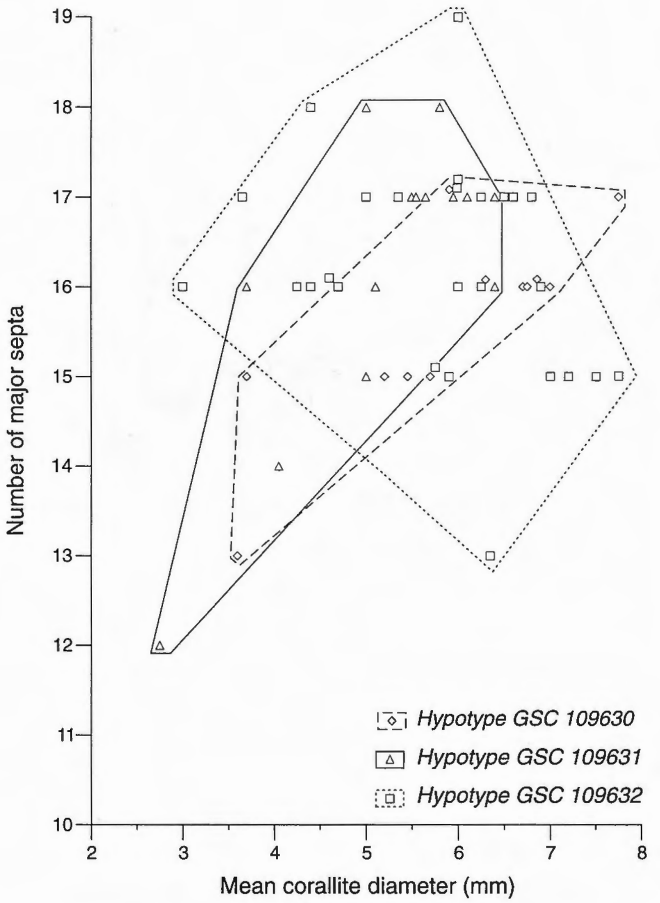


Figure 25. *Relationship between mean corallite diameter and number of major septa in* ***Petalaxis mcoyanus*** *(Milne Edwards and Haime).*

non *Petalaxis maccoyana* Milne Edwards and Haime var. *multiseptata* Fomichev, 1953, Pl. 31, fig. 4.
Lithostrotionella maccoyana (Edwards and Haime). de Groot, 1963 (part), p. 82, 83, Pl. 16, figs. 1a, b; ?Fan, 1978, p. 182, Pl. 67, figs. 6b, c; non Xu, 1977, 202, Pl. 76, figs. 3a, b.
non *Lithostrotionella maccoyana* f. *major* de Groot, 1963, p. 83, 84, Pl. 16, figs. 2a, b.
Petalaxis mccoyana (Milne Edwards and Haime). Fedorowski and Gorianov, 1973, p. 58, Pl. 12, figs. 4a, b, Textfigs. 20a, b.
Petalaxis mccoyana (Milne Edwards and Haime). Sutherland, 1977, p. 185-187, Pl. 1, figs. 1-7.
Petalaxis grootae Sando, 1983, p. 30.
Petalaxis maccoyanus Milne Edwards and Haime. Sando, 1983, p. 34.
Petalaxis flexuosus (Trautschold). Sando, 1983, p. 27.
?*Petalaxis regularis* (Fan). Yu Xue-guang, 1989, p. 367, Pl. 4, fig. 2a-c.

Diagnosis (*emended*). *Petalaxis* having 14-19 (commonly 15-17) long major septa at mean diameter 4-8 mm; minor septa extend adaxially from dissepimentarium one quarter to two thirds of tabularium radius; axial structure consists of thickened median lamella, short, discontinuous septal lamellae, one, rarely two lateral lamellae, and rare axial tabellae; tabulae commonly incomplete, concave, subhorizontal, periaxial tabellae may be convex and moderately to strongly elevated adaxially, 5-12 (commonly 9 or 10) tabulae in 5 mm, tabularium to corallite diameter ratio 0.65-0.73; transeptal dissepimentarium continuous, dissepiments of medium size.

Description. Mean diameter of mature corallites 4-7.75 (commonly 4.5-7) mm (Fig. 25). Septa slightly to strongly sinuous in transverse section, thin, extend to corallite wall as septal crests. Major septa number 14-19 (commonly 15-17) (Fig. 25); arranged almost radially, some curve toward cardinal septum, axial margins of some strongly curved in transverse section; major septa long, vary in length vertically, many reach or closely approach axial structure, maximum abaxial withdrawal approximately one third of tabularium radius. Minor septa well developed, variable in length, extend adaxially from dissepimentarium approximately one quarter to one half (rarely two thirds) of tabularium radius.

Axial structure continuous, straight to sinuous in longitudinal section; median lamella moderately to strongly thickened, straight to gently curved in transverse section, discontinuously connected with axial edge of cardinal septum, rarely connected with counter septum; septal lamellae vertically discontinuous, short and planar to highly curved in transverse section, present in all specimens, locally numerous, discontinuously connected with major septa; lateral lamellae vertically discontinuous, thin and curved, rarely more than one developed in a few corallites at any level in a colony; axial tabellae rare.

Tabulae commonly incomplete, locally complete; subhorizontal to moderately elevated adaxially, locally depressed adaxially; commonly concave, but many approximately planar to slightly convex; incomplete tabulae consist of planar, curved, or undulose tabellae, many of which are convex, others concave; most tabulae join median lamella at angles near 90°, some slightly depressed, others slightly elevated (locally in one specimen tabulae sharply elevated at median lamella); biform morphology well developed (Pl. 1, fig. 5), tabellae in position I slightly to strongly elevated at dissepimentarium, those in position II join it at angles near 90° or slope downward toward it; some complete, concave tabulae slope downward from dissepimentarium to median lamella; 9-11 (commonly 9 or 10) tabulae in 5 mm corallite length; ratio of tabularium diameter to corallite diameter 0.65-0.73.

Dissepimentarium well developed, continuous, varies in width approximately from one quarter to one third corallite radius; dissepiments in one or two (rarely three) rows, mainly transeptal, regular dissepiments rare; dissepiments slightly flattened to globose in longitudinal section, many transeptal dissepiments have irregular outline in transverse section; both regular and transeptal dissepiments moderately to steeply declined adaxially, many nearly vertical adjacent to tabularium; usually 7-9, rarely as few as five transeptal dissepiments in 5 mm corallite length.

In immature growth stages (mean diameter of smallest corallite studied, 2.25 mm), wall separating young corallite from parent rarely completely developed at mean corallite diameters below 3.5 mm; septa curved or sinuous, several in each corallite closely approach the axis, cardinal septum long, forms part of axial structure, counter septum commonly shorter than adjacent major septa; relationship between number of major septa and mean corallite diameter shown in Figure 25; minor septa first present, but incompletely developed at mean corallite diameter of 2.25 mm, well developed in most corallites at mean diameters of 3.5 mm and greater; axial structure present in smallest corallites studied (mean diameter 2.25 mm), consists of thin to moderately thickened lamella or lens-shaped rod formed by thickening of axial edge of cardinal septum, septal lamellae absent or weakly developed at mean corallite diameters below 4.3 mm, lateral lamellae rarely occur below mean diameter of 4.5 mm; regular dissepiments present at all immature levels studied; transeptal dissepiments weakly developed at mean corallite diameters below 3.5 mm, numerous and strongly developed at larger diameters. Tabulae subhorizontal or adaxially depressed, planar to gently curved at corallite diameter below 3 mm.

Discussion. The most consistent, characteristic features of *P. mcoyanus* are its small corallite diameter, correspondingly small number of septa, subhorizontal to slightly inclined, incomplete tabulae, and well developed transeptal dissepiments. Topotypes of *P. mcoyanus* were described and illustrated by Fedorowski and Gorianov (1973) and by Sutherland (1977). The occurrence and historical significance of the species was discussed in detail by Sando (1983). Two specimens from near the type locality in Russia are illustrated here for comparison (Pl. 1, figs. 6-10; Fig. 24).

Petalaxis grootae breviseptum Wang is similar to *P. mcoyanus* in corallite diameter and number of septa, but has more complete tabulae and longer major septa (Wang, 1989, p. 538, 544, Pl. 5, fig. 7). The specimen referred to *Lithostrotionella maccoyana* by Xu (1977, p. 202, Pl. 76, fig. 3a, b) has more septa and more steeply inclined tabulae than *P. mcoyanus*. In the corals referred to *Lithostrotion flexuosum* by Trautschold (1879) and *Lithostrotionella flexuosa* by Heritsch (1939, 1940) and Gorsky (1978) the structure in longitudinal section is unknown, incompletely described, or not illustrated. These are, therefore, questionably included in *Petalaxis mcoyanus* by us. The specimen referred to *Lithostrotionella maccoyana* by Xu (1977, p. 202, Pl. 76, fig. 3a, b) has more septa and more steeply inclined tabulae than *P. mcoyanus* and is here excluded from that species. The differences between *P. mcoyanus* and *P. donbassicus* (Fomichev) are discussed below, in the discussion of the latter species.

In published descriptions of other specimens assigned by the present authors to this species, details of the axial structures were not always given, but from accompanying illustrations (e.g., Dobrolyubova, 1935a, b, Pl. 3, fig. 1; de Groot, 1963, Pl. 16, fig. 1) they appear to contain some or all of the skeletal elements found in the Canadian material and show a similar range of variation.

Sutherland (1977) described and illustrated topotypes of *P. mcoyanus* having skeletal features closely resembling those in the Canadian specimens. These features include irregularly developed axial tabellae, comparable vertical and lateral variation in the components of the axial structures, and the slope, shape and biform morphology of the tabulae (see previous discussion).

In *P. mcoyanus* from Ellesmere Island, the minor septa are longer than in most illustrated specimens of the species, but are comparable in length to those shown by Fedorowski and Gorianov (1973, p. 58, Fig. 20; Pl. 12, fig. 4a) for a Myatchkovian specimen from the type area for the species in Russia. Skeletal elements of the axial structures in the Ellesmere Island specimens show considerable variation in the nature and degree of their development along individual corallites and between different corallites in the same corallum. The development of septal lamellae is similar to that in other described specimens of the species, but our specimens have much more strongly developed lateral lamellae.

Material. Hypotypes GSC 109630, 109631, small fragments of colonies of unknown size from GSC loc. C- 193105; Hypotype, GSC 109632, 109633, collected by M. Kato, 1975, from GSC loc. C-222965; additional material: a single, unfigured specimen from GSC loc. C-193105.

Occurrence and age. Three specimens of *Petalaxis mcoyanus* from Ellesmere Island were collected from rubble near outcrop, 387 m above the base of the Canyon Fiord Formation in the Greely Fiord section (GSC loc. C-193105, section 10, Fig. 1). The age of these specimens is early Moscovian (Kashirian), based on associated fusulinaceans (Appendix 1, Fig. 8, Table 3). Hypotype GSC 109632, a specimen from a limestone quarry near Leninskie Gorki, approximately 35 km south of Moscow, Russia, is from the lower part of the Myatchkovo "horizon" in the Novlinskaya Formation (uppermost Moscovian - GSC loc. C-222965). Matrix attached to another specimen (GSC 109633) from the same stratigraphic level at that locality contains the Myatchkovian fusulinaceans *Fusulina cylindrica* Fischer emend. Moeller and *Fusulinella* ex. gr. *bocki* Moeller.

Petalaxis mcoyanus appears to be restricted to rocks of middle to late Moscovian age. Several reported occurrences of the species are in upper Moscovian (Myatchkovian) strata [Dobrolyubova, 1935b, p. 3 - *Lithostrotionella flexuosa* (Trd.); Fedorowski and Gorianov, 1973, p. 59; Sutherland, 1977; Sando, 1983, p. 34). The specimens described by de Groot (1963) from Palencia, Spain were collected from the lower to middle Podolskian Vanes Formation and the lower to middle Myatchkovian Cotarraso Formation (de Groot, *ibid.*, p. 83; S. Rodriguez, pers. comm., 1994).

Petalaxis donbassicus (Fomichev), 1939

Plate 1, figures 11-13, Plate 2, figures 1-5;
Figures 26, 27

Lithostrotionella donbassica Fomichev, 1939, p. 60, Pl. 9, figs. 4a, b.

Lithostrotion (*Lithostrotionella*) *donbassica* (Fomichev). Bassler, 1950, p. 222.

?*Petalaxis maccoyana* Milne Edwards and Haime forma *orlovkensis* Fomichev, 1953, p. 457.

Petalaxis maccoyana Milne Edwards and Haime. Fomichev, 1953 (part), p. 453, Pl. 31, figs. 1a, b, v, g, 2a, b, v, g.

non *Petalaxis maccoyana* Milne Edwards and Haime var. *belinskiensis* Fomichev, 1953, p. 457, Pl. 31, fig. 3a, b.

?*Petalaxis maccoyana* Milne Edwards and Haime var. *multiseptata* Fomichev, 1953, p. 458, Pl. 31, fig. 4.

Petalaxis fomichevi Sando, 1983, p. 30 (objective synonym).

Petalaxis donbassicus (Fomichev). Sando, 1983, p. 27, 28.

Hillia wagneri de Groot. Rodriguez, 1984, p. 358, Figs. 193, 194.

?*Lithostrotionella* (*Hillia*) *wagneri* de Groot, 1963, p. 88 (part), Pl. 18, fig. 2.

Diagnosis (*emended*). *Petalaxis* having 13-23 (commonly 14-19) long major septa at mean diameter 3.5-7.5 (commonly 4-7) mm; minor septa extend adaxially from dissepimentarium one third to one half of tabularium radius; axial structure strong, vertically continuous, with thick median lamella, short septal lamellae, one or two lateral lamellae and rare axial tabellae; tabulae commonly complete, concave, subhorizontal to slightly depressed, 9-16 (commonly 12-14) in 5 mm; tabularium to corallite diameter ratio 0.61–0.82; transeptal dissepimentarium locally discontinuous, dissepiments of medium size.

Description. Corallite walls moderately thick. Mean diameter of mature corallites 3.5-7.5 mm (commonly 4-7) mm (Fig. 27). Septa straight to slightly sinuous in transverse section, generally thin, but moderately thickened locally in some specimens, continuous in tabularium, represented in part by septal crests in dissepimentarium, commonly extending uninterrupted to wall. Major septa number 15-23 (commonly 16-19) (Fig. 27); arranged almost radially, some curve slightly toward counter-cardinal plane, axial margins of some strongly curved in transverse section; major septa long, many reach or closely approach axial structure, maximum abaxial withdrawal commonly less than one quarter of tabularium radius. Minor septa well developed, variable in length, commonly extend adaxially one third to one half of tabularium radius.

Axial structure vertically continuous, commonly moderately to strongly thickened in transverse section, gently curved to slightly sinuous in longitudinal section; median lamella strongly thickened, forms thick lens in parts of most specimens, varies in thickness vertically, locally only moderately thick, straight to gently curved or (rarely) sinuous in transverse section, connection with cardinal septum locally discontinuous where lateral lamellae developed, commonly closely approached by counter septum; septal lamellae vertically discontinuous, occur on median lamella and lateral lamellae, numerous in some specimens, rare in others, generally short and curved or straight in transverse section, discontinuously connected with major septa; lateral lamellae present in all specimens studied, vertically discontinuous, generally only one, rarely two per corallite, developed as curved, thickened, axial extension of cardinal septum; axial tabellae rare, locally attached to median lamellae of some specimens, either singly or (rarely) in series of two or three.

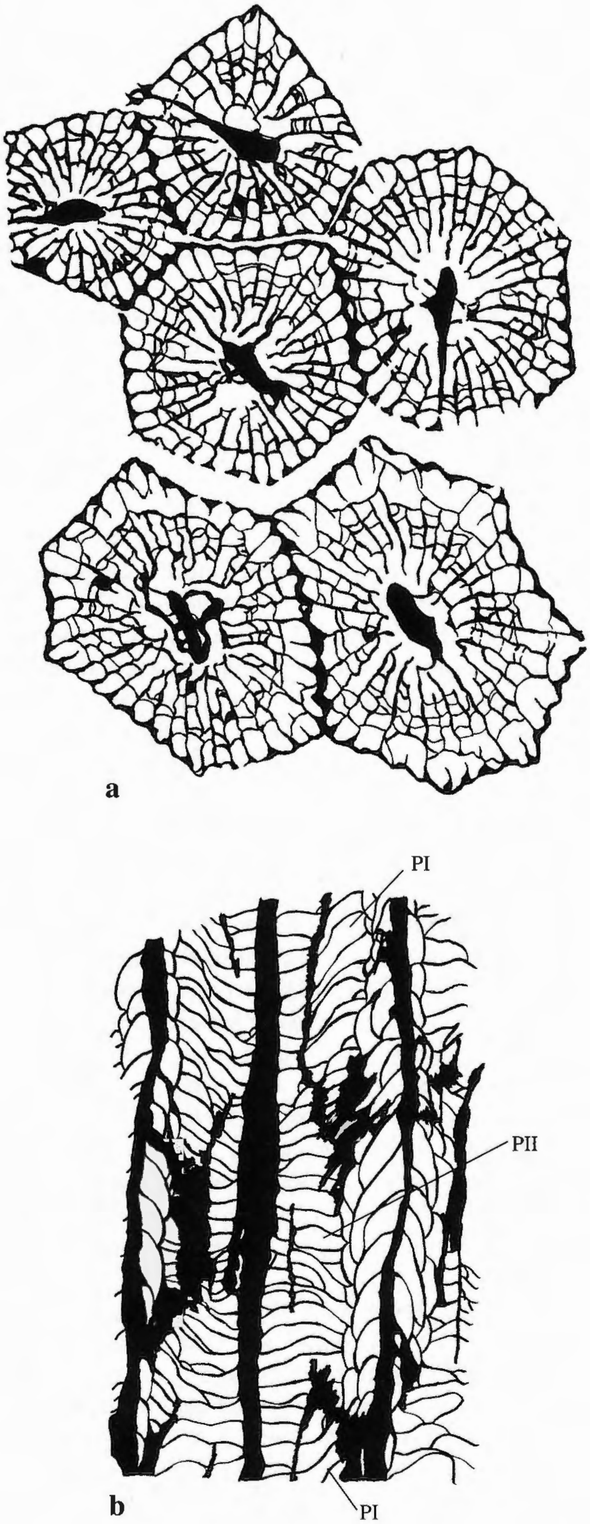


Figure 26. ***Petalaxis donbassicus*** *(Fomichev), hypotype GSC 109634, x5;* ***a****, drawing of transverse thin section (see Pl. 1, fig. 13), showing lens-shaped median lamellae and short lateral lamellae;* ***b****, drawing of longitudinal thin section, showing subhorizontal, closely spaced tabulae and biform morphology of tabularium (tabellae in position I - PI, tabellae or perpheral parts of complete tabulae in position II - PII) (see Pl. 1, fig. 11).*

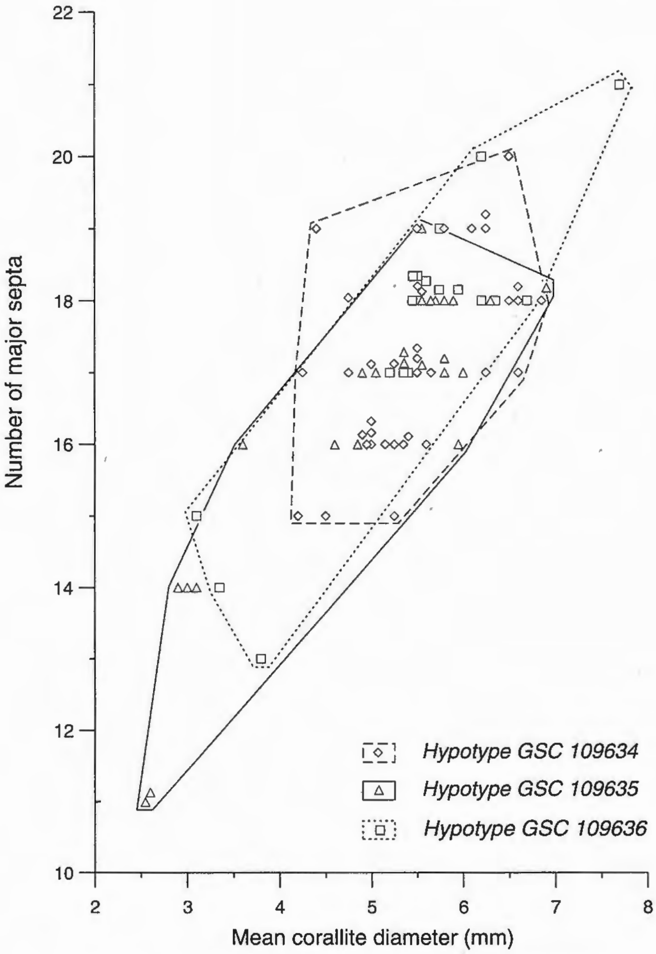


Figure 27. *Relationship between mean corallite diameter and number of major septa in* ***Petalaxis donbassicus*** *(Fomichev).*

Tabulae commonly complete, but incomplete tabulae present in all specimens studied; axially depressed, subhorizontal, or slightly elevated adaxially; generally concave, locally slightly convex; incomplete tabulae consist of large, strongly concave to strongly convex tabellae; tabulae join median lamella at angles near 90° or may be slightly elevated, rarely sharply elevated, to extend a short distance along median lamella; some complete tabulae slope downward from dissepimentarium to median lamella; biform morphology strongly developed, tabellae in position I generally convex and steeply declined adaxially, those in position II subhorizontal or declined toward dissepimentarium, less commonly slightly declined adaxially; tabulae closely spaced, 9-16 (commonly 12-14) in 5 mm corallite length; ratio of tabularium diameter to corallite diameter 0.61-0.82, most commonly 0.68-0.75.

Dissepimentarium well developed, rarely discontinuous vertically in some specimens, varies in width from two thirds to four fifths of corallite radius; dissepiments in one or two (rarely three) rows, mainly transeptal, regular dissepiments locally present, particularly adjacent to tabularium; dissepiments slightly flattened to globose in longitudinal section; both regular and transeptal dissepiments moderately to steeply declined adaxially; 5-9 dissepiments in 5 mm corallite length.

In immature growth stages (mean diameter of smallest corallite studied, 2.15 mm), wall separating young corallite from parent rarely completely developed at mean corallite diameters below 2.9 mm; septa curved or sinuous, several majors in each corallite reach or closely approach axis, cardinal septum long, forms part of axial structure, locally withdrawn from axial area, counter septum variable in length, may be shorter than adjacent major septa; relationship between number of major septa and mean corallite diameter shown in Figure 27; minor septa incompletely developed at mean corallite diameters of 2.15-2.7 mm, completely developed at diameters of 2.8 mm and greater; axial structure not developed below mean corallite diameters of 2.5 mm, consists at greater diameters of thin to moderately thickened lamella formed by thickening of axial edge of cardinal septum, septal lamellae rarely developed below mean corallite diameter of 3 mm, lateral lamellae absent below diameters of 4 mm; regular dissepiments not observed at mean corallite diameters below 2.5 mm, transeptal dissepiments rarely present at mean diameters below 3 mm, weakly developed at mean diameters of 3 and 3.7 mm, numerous and strongly developed at larger diameters.

Discussion. *Petalaxis donbassicus* is characterized by its unusually closely spaced, generally concave tabulae and by the moderately to strongly thickened, lens-shaped median lamella in its axial structure. Two thin sections from the holotype (by monotypy) of the species, from Limestone L_5 of the Donets Basin in Ukraine, were illustrated by Fomichev (1939, p. 60, Pl. 9, figs. 4a, b). These thin sections were re-illustrated by Fomichev (1953, Pl. 31, figs. 1a, g, specimen 57) and assigned, along with numerous other specimens from the area, to *Petalaxis mcoyanus* (Milne Edwards and Haime). Fomichev (*ibid.*, p. 453, 454) described the axial structure in his material as a compact, tabular to lenticular columella of variable thickness. This led Sando (1983, p. 30) to assign Fomichev's material to a new species, *P. fomichevi* Sando, characterized by the simplicity of its axial structure. At increased magnification, however, the illustrations published by Fomichev (1939, Pl. 9, figs. 4a, b; 1953, Pl. 31, figs. 1, 2) show axial structures possessing variably developed septal lamellae and rare axial tabellae, as in the Canadian specimens described above. Lateral lamellae cannot be definitely identified from Fomichev's illustrations, but other aspects of the skeletal structure in the specimens from Ellesmere Island match those of the Donets Basin material.

Petalaxis donbassicus is similar to *P. mcoyanus*, but has more major septa (commonly up to 19) at comparable corallite diameters, more strongly thickened, lens-shaped median lamellae, more closely spaced (commonly 12-14 in 5 mm), and generally concave tabulae. Also, the ring of transeptal dissepiments in *P. donbassicus* is commonly interrupted by locally developed regular dissepiments in transverse section. *Petalaxis donbassicus* resembles *P. belinskiensis* Fomichev (Sando, 1983, p. 29), but the latter is distinguished by its wide dissepimentarium.

A specimen from GSC loc. C-10814, tentatively included in *P. donbassicus*, has relatively few transeptal dissepiments and up to 23 major septa in a few corallites. Also tentatively included in the species is *P. mcoyanus* forma *orlovkensis* Fomichev, which was not illustrated. It has corallite diameters slightly larger than normal for *P. donbassicus* and is thickened by stereoplasm on the inner ends of the septa and along the inner border of the dissepimentarium (Fomichev, 1953, p. 457). The specimen illustrated by de Groot (1963, Pl. 18, fig. 2) as *P. wagneri* (de Groot) may belong in *P. donbassicus*, but the mean corallite diameter of this coral appears to be slightly smaller than is normal for the latter species. No longitudinal section was provided by de Groot, so the nature of the tabulae cannot be determined without restudying her specimen. The other specimens of *P. wagneri* illustrated by de Groot (*ibid.*, Pl. 18, figs. 1, 3) appear to be distinct from *P. donbassicus*. Compared to that species, they have fewer septa and smaller corallite diameters, shorter minor septa, a narrower dissepimentarium and weaker axial structures in part, apparently lacking septal lamellae.

Material. Hypotypes: GSC 109634, from GSC loc. 58924; GSC 109635 and 109636, from GSC loc. C-193105. Additional material: single specimens from GSC locs. 60190, C-10814?, C-10815, C-31226; two specimens from GSC loc. C-193087. All specimens incomplete colonies.

Occurrence and age. Petalaxis donbassicus was collected from the middle part of the Canyon Fiord Formation in the Greely Fiord section (GSC loc. C-193105; section 10, Figs. 1, 8) and from the lower Hare Fiord Formation, immediately above the reefs of the "Tellevak limestone" in the northeast Blue Mountains section (GSC locs. C-10814 and C-10815; section 6, Figs. 1, 6) and at localities 7 and 8 (GSC locs. 58924, 60190, Fig. 1). It also occurs in the lower part of the Nansen Formation at the Otto Fiord section (GSC loc. C-31226, section 3, Figs. 1, 4) and in the lowest limestone unit of the Belcher Channel Formation in the Agassiz Ice Cap section (GSC loc. C-193087, section 11, Figs. 1, 9). The species is late Bashkirian to Podolskian (mid-Moscovian) in age. In the northeast Blue Mountains and Greely Fiord sections (Figs. 6, 8) it occurs with Kashirian fusulinaceans. In the Agassiz Ice Cap section (Fig. 9) it occurs above Bashkirian (Atokan) ammonoids (GSC loc. 52445; Nassichuk, 1975, p. 49) and is overlain by upper Moscovian (Podolskian or Myachkovian) fusulinaceans. At all three localities from which it is known in the Blue Mountains (section 6, localities 7, 8; GSC locs. 58924, 60190, C-10814, C-10815), *Petalaxis donbassicus* was collected immediately above the "Tellevak" reef buildups, which contain Atokan (Bashkirian) ammonoids (Nassichuk, 1975, p. 44-46; 1984, p. 160; pers. comm., 1993). Those from GSC locs. C-10814 and C-10815 (northeast Blue Mountains section) occur with early Moscovian (Kashirian) fusulinaceans. Podolskian fusulinaceans occur below this species (GSC loc. C-31217) in the Otto Fiord section (Fig. 4, Table 3).

In the Donets Basin of Ukraine (Fomichev, 1939, p. 60; 1953, p. 456) *P. donbassicus* (= *P. maccoyana* Mn. Edw. et H. of Fomichev, 1953; = *P. fomichevi* Sando, 1983) ranges from limestone K_8 to limestone M_2 and is most abundant in limestone L_5. The K_8–M_2 interval was assigned a Kashirian age by Solov'eva (1986, p. 16, Table 2) in a summary paper on the biostratigraphy of Moscovian fusulinaceans. The specimen described by Rodriguez (1984, p. 358) as *Hillia wagneri* de Groot and assigned herein to *P. donbassicus* comes from the upper Bashkirian Valdeteja Formation of eastern Asturias, Spain.

Petalaxis sp.

Plate 2, figures 6-8; Figures 28, 29

Description. Corallite walls strongly thickened where joined by septa. Mean diameter of mature corallites 3-6 (commonly 4.5-5.5 mm) (Fig. 29). Septa straight to slightly sinuous in transverse section, thin near axial edges, become slightly thicker abaxially, strongly thickened at corallite walls. Major septa number 15-17 (rarely 18) (Fig. 29); arranged almost radially, some curve toward counter septum, axial margins of some strongly curved in transverse section; major septa long, closely approach, but rarely reach, axial structure, normally withdrawn from axial structure one fifth to one third tabularium radius; reach corallite walls with only minor interruption in dissepimentarium at all levels cut by transverse thin sections. Minor septa well developed, almost entirely continuous in dissepimentarium at all levels studied, variable in length, usually less than one half of length of major septa and extend only short distance into tabularium.

Axial structure continuous, slightly curved and of variable thickness in longitudinal section; median lamella moderately to strongly thickened in most corallites, rarely thin and tabular, varies in thickness vertically, usually straight, rarely slightly curved in transverse section, connection with axial edge of cardinal septum vertically discontinuous, rarely connected with counter septum; septal lamellae vertically discontinuous, short, thick, straight or curved, one or more observed in most corallites, discontinuous connections with major septa rarely expressed in transverse section; lateral lamellae weakly developed, vertically discontinuous, in any transverse section a few corallites have only one developed as thickened, curved extension of cardinal septum, a second lateral lamella seen in only one corallite; isolated, widely spaced, steeply to moderately sloping periaxial tabellae attached to the median lamella, clearly defined axial tabellae not seen.

Tabulae usually incomplete, locally complete, subhorizontal to adaxially elevated, rarely adaxially depressed; strongly concave, rarely approximately planar or slightly convex; incomplete tabulae consist of a few curved or undulose, convex to concave tabellae;

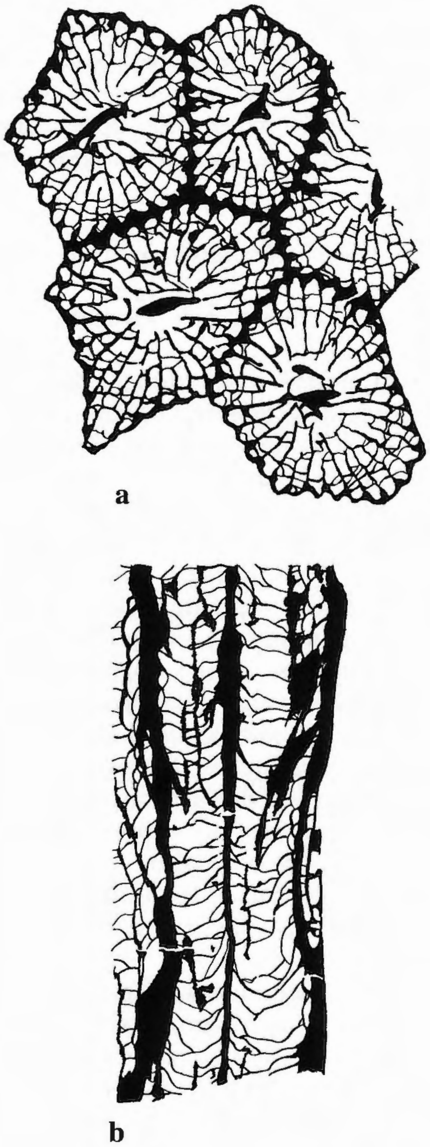


Figure 28. ***Petalaxis*** *sp., hypotype GSC 109637, x5;* ***a****, drawing of transverse thin section (see Pl. 2, fig. 6), showing thick corallite walls, lateral and septal lamellae and rare transeptal dissepiments in corners of corallites;* ***b****, drawing of longitudinal thin section, showing concave tabulae and biform morphology of tabularium (see Pl. 2, fig. 8).*

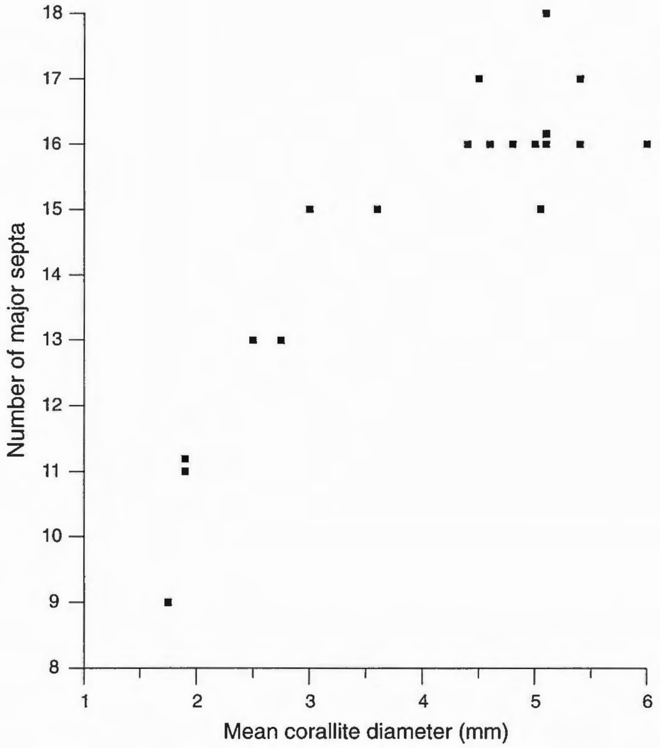


Figure 29. Relationship between mean corallite diameter and number of major septa in ***Petalaxis*** *sp. (hypotype GSC 109637).*

tabulae moderately to steeply elevated at median lamella, rarely slope upward adaxially across entire tabularium; biform morphology well expressed, tabellae in position I moderately to strongly convex and steeply declined adaxially, those in position II generally subhorizontal or slightly declined adaxially, less commonly slightly declined toward dissepimentarium; 10-12 tabulae in 5 mm; ratio of tabularium diameter to corallite diameter 0.69-0.85, most commonly 0.73-0.82.

Dissepimentarium locally discontinuous, width usually one fifth to one quarter of corallite radius, boundary with tabularium generally distinct, marked by slight stereoplasmic thickening of septa and dissepiments; dissepiments in one or two (rarely three) rows, locally absent, almost entirely regular, transeptal dissepiments seen only in corners of corallites in transverse section, may be represented by large dissepiments shown in longitudinal section (Pl. 2, fig. 7); in longitudinal section, smaller dissepiments generally strongly convex, most larger dissepiments elongate and slightly flattened; most dissepiments steeply declined adaxially, many vertical adjacent to tabularium; usually 9-11 dissepiments in 5 mm of corallite length.

In immature growth stages, wall separating young corallite from parent is complete at mean corallite diameter of 1.38 mm (smallest corallite studied); septa curved or sinuous, at mean diameters below 2.5 mm several major septa in each corallite closely approach axis and some extend beyond it; at greater diameters, cardinal septum long, extended to form part of axial structure, counter septum commonly shorter than adjacent major septa; relationship between number of major septa and mean corallite diameter shown in Figure 29; minor septa first present, but incompletely developed, at mean corallite diameter of 1.75 mm, well developed at mean corallite diameters of 2.4 mm and greater; axial structure first developed at mean corallite diameter of 2.5 mm, consists of thin to moderately thickened lamella or lens-shaped rod formed by thickening of axial edge of cardinal septum, septal lamellae absent below mean corallite diameter of 3.5 mm, lateral lamellae not observed below mean corallite diameter of 4.25 mm; in longitudinal section of immature corallite with diameters of 2-2.5 mm and showing no dissepiments, tabulae mainly complete, slightly curved to undulose, subhorizontal to slightly elevated adaxially, subplanar to slightly concave, some slightly elevated at corallite wall; dissepimentarium consists of regular dissepiments, weakly developed at corallite diameters below 3.25 mm, wider but locally discontinuous at larger diameters.

Discussion. In corallite diameter, number of septa and nature of tabulae and axial structure, the specimen described above resembles *Petalaxis santaemariae* (de Groot), from the Bashkirian Santa Maria Limestone of northern Palencia, Spain (de Groot, 1963, p. 109). The Ellesmere Island specimen, however, has longer minor septa and thinner, more denticulate corallite walls than *P. santaemariae*. The Spanish specimen also possesses transeptal dissepiments near the periphery of the corallum (de Groot, 1963, p. 91). No well defined transeptal dissepiments were seen in our specimen, but the full range of variation in its dissepimentarium cannot be determined from the small corallum fragment available for study.

The Canadian specimen is similar to *P. intermedius* (de Groot), but the latter has numerous transeptal dissepiments and its tabulae are not strongly elevated near the dissepimentarium (de Groot, 1963, p. 90, Pl. 20, figs. 2a, b, 3).

Material. Hypotype GSC 109637, small fragment of colony from GSC loc. C-10813.

Occurrence and age. The described specimen was collected from the lower Hare Fiord Formation, 6.5 m above the top of the "Tellevak" reef limestone, in the northeast Blue Mountains section (GSC loc. C-10813, locality 6, Figs. 1, 6). It is Kashirian (early Moscovian) in age, based on associated fusulinaceans (Appendix 1) and its stratigraphic position above Atokan (Bashkirian) ammonoids in the "Tellevak" limestone (Nassichuk, 1975, p. 45; 1984, p. 160; pers. comm., 1993).

Petalaxis crassicolumnus sp. nov.

Plate 2, figures 9-12; Plate 3, figures 1-5;
Figures 17, 30, 31, 32

Etymology. Combination of Latin adjective *crassus*, meaning thick, and Latin noun *columna*, meaning pillar.

Diagnosis. Petalaxis having 18-27 (commonly 19-24) long major septa at mean diameter 6-13 (commonly 7-11) mm; septa weakly naotic; minor septa extend adaxially from dissepimentarium one half to three quarters of tabularium radius; axial structure strong, continuous, with thick median lamella, rare to numerous septal lamellae, 1-4 lateral lamellae, and few axial tabellae; tabulae highly variable, vesicular, usually incomplete, convex in some corallites, 9-14 tabulae in 5 mm, tabularium to corallite diameter ratio 0.60-0.80; transeptal dissepimentarium continuous, dissepiments small.

Description. Corallite walls strongly thickened where joined by septal crests. Mean diameter of mature corallites 6-13 mm (commonly 7-11) mm (Fig. 31). Septa gently curved to slightly sinuous in transverse section, wedge-shaped, moderately to strongly thickened in outer tabularium, become thinner adaxially and toward corallite wall, represented in dissepimentarium by septal crests, irregular protuberances or series of small, convex plates (Fig. 32a) on surfaces of dissepiments, septal crests thickened where attached to corallite wall; in coralla with strongly thickened septa, septal crests locally become highly sinuous or split into several connected plates, thus becoming weakly naotic in outermost dissepimentarium (Figs. 32b, c). Major septa number 19-24, ranging to 18 and 27 (Fig. 31); arranged almost radially, axial margins of some are strongly curved toward counter-cardinal plane in transverse section; major septa long, closely approach or (rarely) join axial structure. Minor septa well developed, long, variable in length, extend adaxially from dissepimentarium approximately one half to three quarters of tabularium radius.

Axial structure strongly developed, thick, continuous, straight to slightly sinuous in longitudinal section; median lamella moderately to strongly thickened in most specimens, very strongly thickened

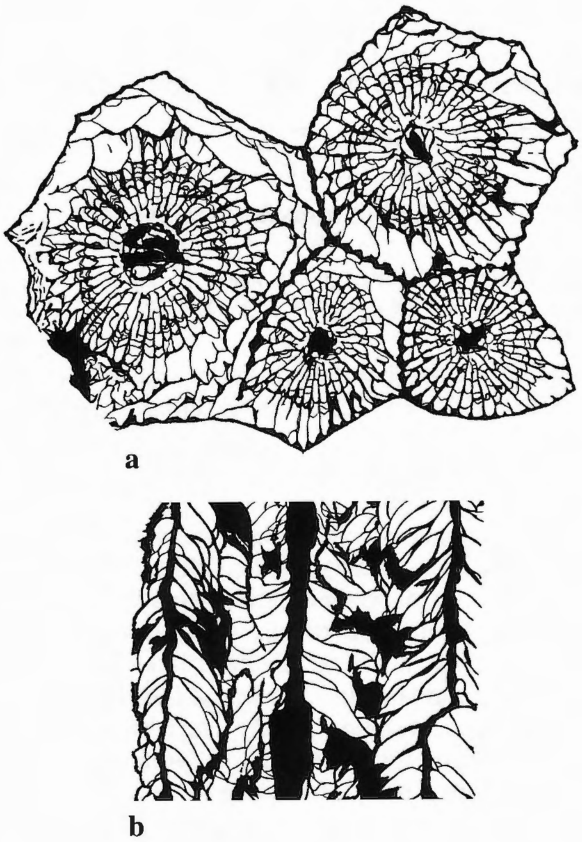


Figure 30. ***Petalaxis crassicolumnus*** *sp. nov., holotype GSC 109638;* ***a****, drawing of transverse thin section (see Pl. 2, fig. 10), showing thick axial structure with septal and lateral lamellae and weakly naotic septa, x3;* ***b****, drawing of longitudinal thin section, showing axially elevated, vesicular tabulae (see Pl. 2, fig. 9), x4.*

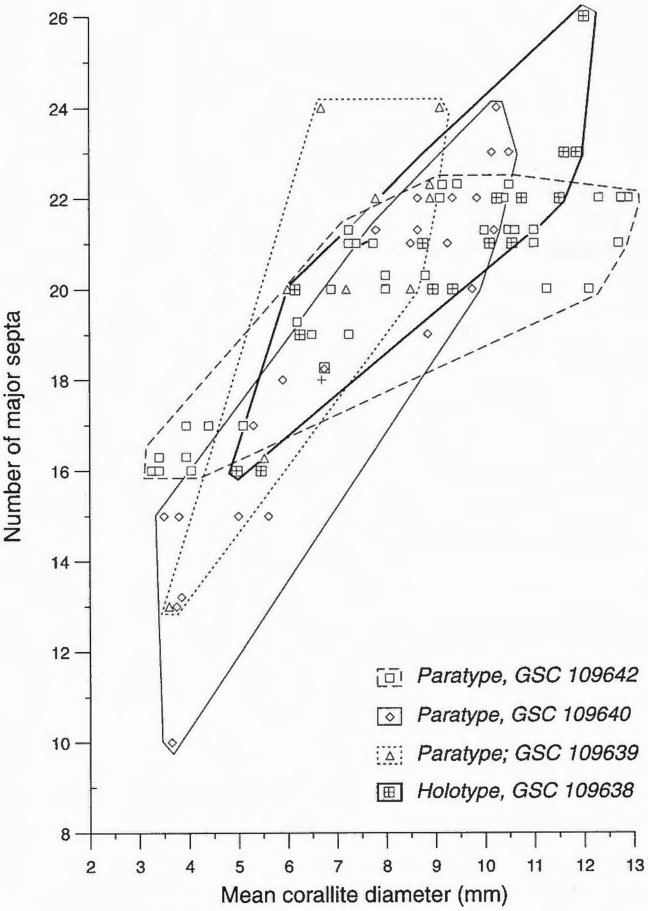


Figure 31. Relationship between mean corallite diameter and number of major septa in ***Petalaxis crassicolumnus*** *sp. nov.*

to form a thick lens in others, in transverse section straight to slightly curved, rarely sinuous, connection with axial margin of cardinal septum vertically discontinuous, rarely joined to counter septum; septal lamellae variably developed, vertically discontinuous, developed mainly on median lamella, but also on lateral lamellae, discontinuously connected with major septa, rare in most coralla with thinner, lens-shaped axial structures, numerous and well developed in others of this type, generally thick, curved or sinuous and fairly numerous in coralla with thicker, roughly circular axial structures; lateral lamellae present in all specimens, vertically discontinuous, variable in number and degree of development, at least one discontinuously developed as thickened, curved axial extension of cardinal septum in all specimens, up to three additional, thick, curved lamellae developed in corallites of specimens with thicker, circular axial structures; axial tabellae rare, most numerous in corallites with thickest axial structures, usually isolated, rarely two or three in vertical series, fairly large, very steeply sloping to vertical, attached to median lamella, bases rest on median lamella or, rarely, on underlying axial or periaxial tabellae, upper surfaces of some coated with stereoplasm.

Tabularium highly variable, vesicular; tabulae mainly incomplete, locally complete; adaxially elevated or depressed, less commonly subhorizontal; concave to strongly convex; incomplete tabulae consist of fairly large, convex, concave and undulose tabellae; series of periaxial tabellae axially elevated to subhorizontal, convex to doubly curved, locally highly convex, rarely strongly elevated to extend vertically along median lamella for short distance, locally occupy more than half of tabularium; narrower, peripheral series shows biform morphology, generally concave, but many are convex or undulose, those in position I moderately to steeply declined adaxially, those in position II subhorizontal to gently declined toward dissepi-

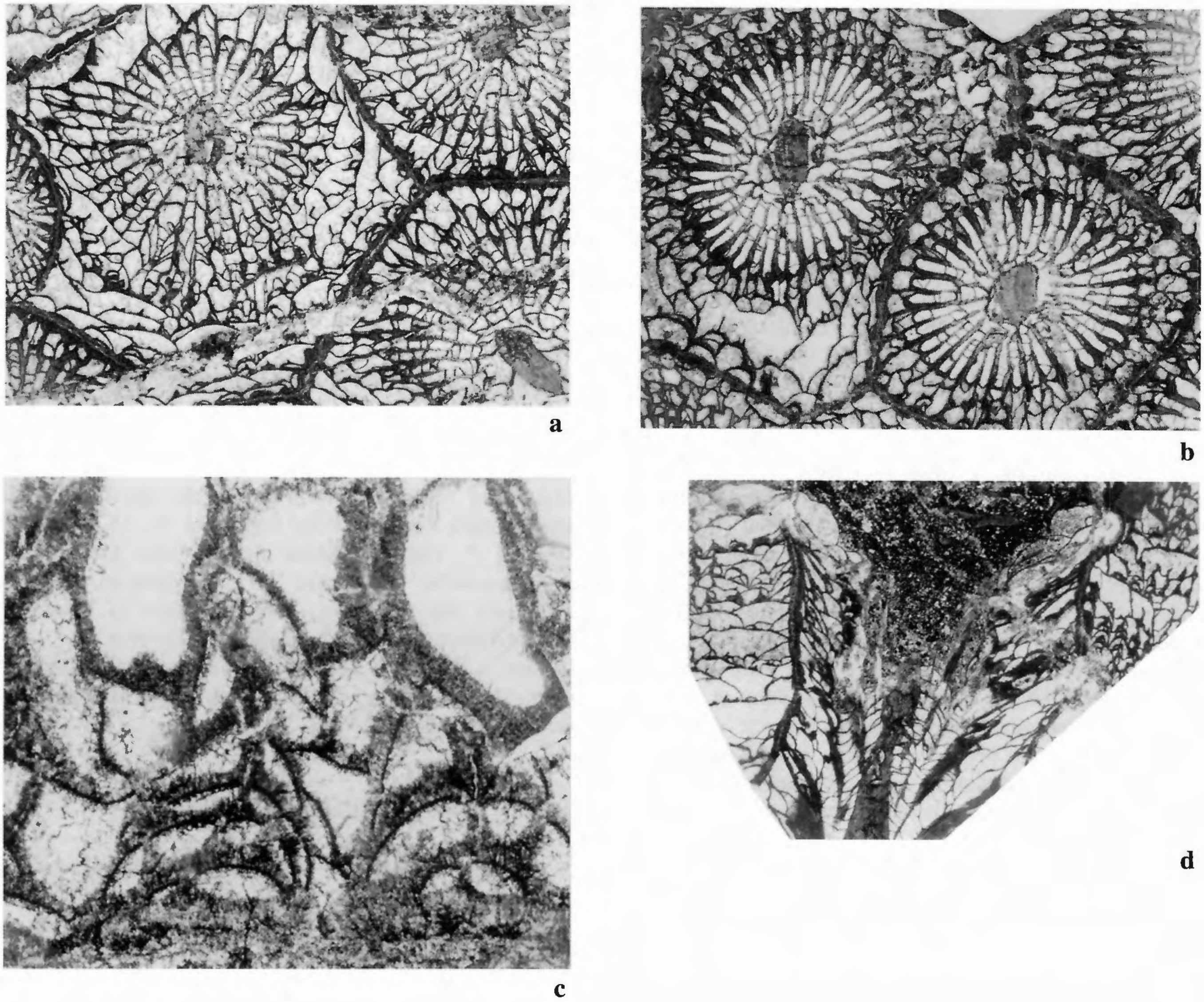


Figure 32. ***Petalaxis crassicolumnus*** *sp. nov., paratype GSC 109641, thin sections of mature corallites;* ***a****, transverse section showing trabeculae in dissepimentarium forming septal crests and irregular papillae, x5;* ***b****, transverse section showing thick, weakly naotic septa, x5;* ***c****, enlargement from central part of Figure 32b, showing peripheral parts of trabecular, naotic septa, x50;* ***d****, slightly oblique longitudinal section showing short vertical series of dissepiments with discontinuous peripheral parts of weakly naotic septa, x4.*

mentarium; complete tabulae curved or undulose, many elevated from dissepimentarium to axial structure, others concave and elevated toward axis and dissepimentarium, and some adaxially depressed; 9-14 (commonly 11 or 12) tabulae in 5 mm; ratio of tabularium diameter to corallite diameter 0.60-0.80, most commonly 0.65-0.73.

Dissepimentarium well developed, continuous, varies in width approximately from one fifth to two fifths of corallite radius, boundary with tabularium distinct; number of rows of dissepiments variable, usually three or four, locally five or more where regular dissepiments developed; most dissepiments transeptal, but regular dissepiments locally numerous, especially adjacent to tabularium; larger dissepiments generally elongate and slightly flattened, less commonly globose in longitudinal section, smaller dissepiments commonly globose to subspherical; all dissepiments moderately to steeply declined adaxially, many nearly vertical adjacent to tabularium; six or seven (rarely five or eight) dissepiments in 5 mm corallite length.

In immature growth stages (mean diameter of smallest corallite studied, 2.75 mm), wall separating young corallite from parent rarely completely developed at mean corallite diameters below 4 mm, incomplete walls curved; septa curved or sinuous, thin in most specimens; in corallites with mean diameter of 2.75-3.5 mm, several major septa in each corallite closely approach axis, cardinal septum variable in length, commonly reaches axis, counter septum usually shorter than adjacent major septa; in most corallites with mean diameter larger than 3.5 mm, long cardinal septum is thickened to form axial structure; relationship between number of major septa and mean corallite diameter shown in Figure 31; minor septa first present, but incompletely developed at mean diameter of 2.75 mm, well developed at mean diameters of 3.5 mm and greater; axial structure lens-shaped or tabular, simple, formed from thickened axial margin of cardinal septum in most immature corallites with mean diameter greater than 3.5 mm, septal lamellae absent at mean corallite diameters below 4.2 mm, lateral lamellae rare, not present below mean corallite diameter of 4.5 mm; tabulae depressed adaxially, incomplete, tabellae near dissepimentarium weakly to moderately convex, periaxial tabellae strongly concave; regular dissepiments present, but rare at mean corallite diameters below 4.5 mm, fairly abundant at higher diameters, transeptal dissepiments absent at mean corallite diameters below 3.25 mm, weakly developed between mean diameters of 3.25 mm and 5 mm, numerous and strongly developed at large diameters.

Discussion. The thick axial structure of *P. crassicolumnus* contains all structural elements typical for the genus *Petalaxis*, but the degree of development of these elements and the overall size and shape of the axial structures vary greatly between specimens assigned to the species (Pl. 2, figs. 10, 11; Pl. 3, fig. 3). Common to all of these specimens, however, is the highly variable, vesicular tabularium described above, with convex to concave, mainly incomplete tabulae. This feature, combined with an unusual axial structure, and numerous, long, weakly naotic, wedge-shaped septa distinguish *P. crassicolumnus* from all other species of *Petalaxis*. Rarely, periaxial tabellae extend a short distance up the median lamella to form structures resembling the periaxial cones found in *Cystolonsdaleia*.

Material. Holotype, GSC 109638 (five pieces cut from incomplete colony, one transverse and two longitudinal thin sections, two transverse acetate peels), from GSC loc. C-179729. Paratypes: GSC 109639, from GSC loc. C- 179729; GSC 109640, from GSC loc. C-179727; GSC 109641, from GSC loc. C-11403; GSC 109642, from GSC loc. C-11403. Additional material: single specimens from GSC locs. C-10813 (identification uncertain), C-11402, C-179723, C-179724, and C-193107; two specimens from GSC locs. C-179722, C-179731 and C-193105; three specimens from GSC loc. C-11403; four specimens from GSC loc. C-179729. Several colonies almost complete.

Occurrence and age. Petalaxis crassicolumnus was collected from the lower and middle Canyon Fiord Formation of the Greely Fiord, northeast Trold Fiord, east Blind Fiord (A), and south Trold Fiord sections (GSC locs. C-11402, C-11403, C-193105, C-193107, C-179722, C-179723, C-179724, C-179727, C-179729, C-179731, sections 10, 12, 14, 15, Figs. 1, 8, 10, 12, 13) and was tentatively identified from the lower Hare Fiord Formation of the northeast Blue Mountains section (GSC loc. C-10813, locality 6, Figs. 1, 6). Fusulinaceans indicate a Kashirian age for these corals in the northeast Blue Mountains, Greely Fiord, and east Blind Fiord (A) sections. In the northeast and south Trold Fiord sections (localities 12, 15, Figs. 1, 10, 13) *P. crassicolumnus* occurs with Moscovian fusulinaceans, but these do not include species diagnostic for precise age determination to substage level (Appendix 1). The lowest occurrence of the species in the south Trold Fiord section lies within an interval containing fusulinaceans of Kashirian to Podolskian age (Fig. 13).

Petalaxis ellesmerensis sp. nov.

Plate 3, figures 6-13; Plate 4, figures 1, 2;
Figures 33, 34

?*Lithostrotionella* aff. *stylaxis* Trautschold. Dobrolyubova, 1936b, p. 127, Figs. 55, 56.

Etymology. Adjective coined from Ellesmere Island and suffix *ensis.*

Diagnosis. Petalaxis having 15-23 (commonly 16-21) long major septa at mean diameter 4.2-11.75 (commonly 5-9.5) mm; minor septa extend adaxially from dissepimentarium one third to two thirds tabularium radius; axial structure typically vertically continuous with comparatively thin median lamella, generally few, short septal lamellae, one or two lateral lamellae and widely spaced axial tabellae; tabulae generally incomplete, commonly slightly to moderately elevated adaxially, rarely subhorizontal or steeply elevated, normally slightly to moderately concave, 9-13 in 5 mm; tabularium to corallite diameter ratio 0.64-0.78; transeptal dissepimentarium continuous, dissepiments small to medium size.

Description. Mean diameter of mature corallites variable, from 4.2 to 11.75 mm (commonly 5-9.5 mm)

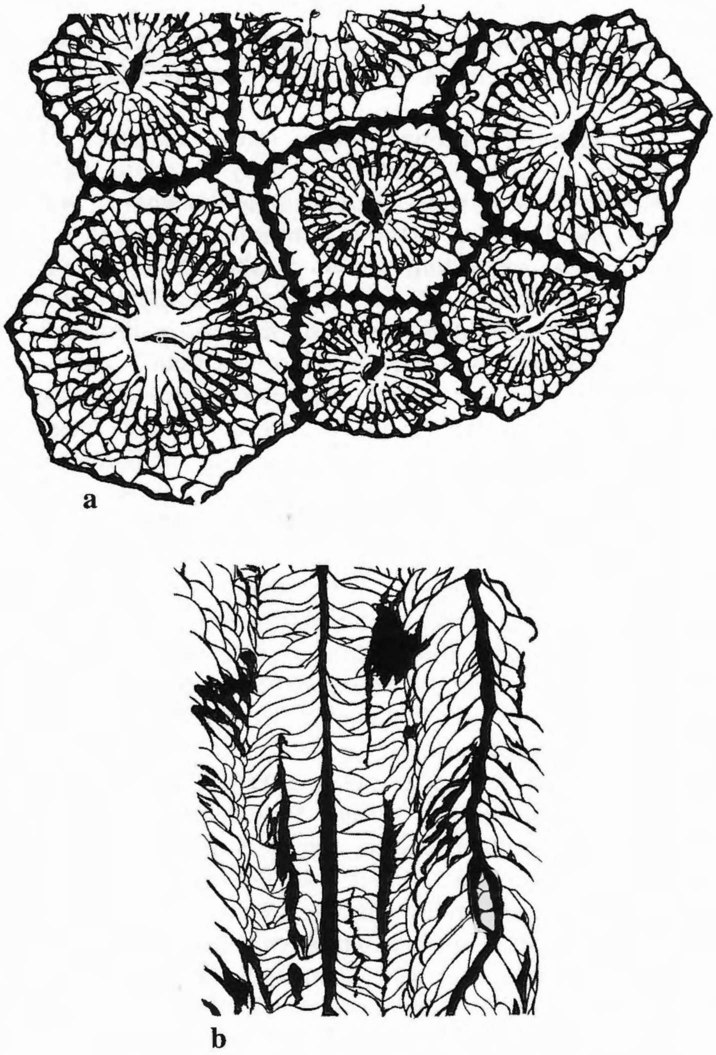


Figure 33. ***Petalaxis ellesmerensis*** *sp. nov., holotype GSC 109643, x4;* ***a****, drawing of transverse thin section (see Pl. 3, fig. 6), showing slightly thickened median lamellae, weakly developed lateral lamellae and short septal lamellae;* ***b****, drawing of longitudinal thin section, showing incomplete, moderately elevated tabulae (see Pl. 3, fig. 8).*

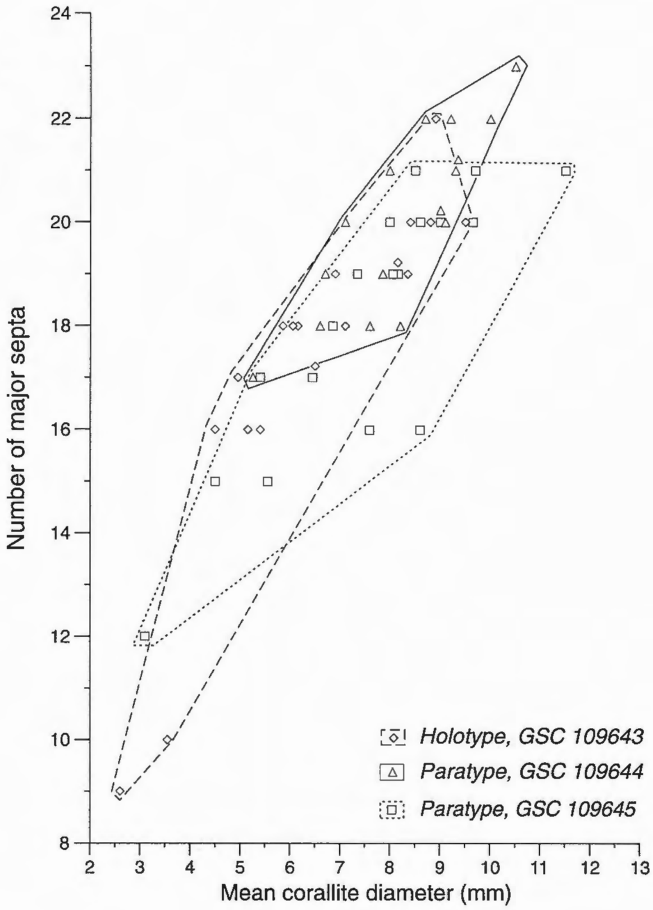


Figure 34. Relationship between mean corallite diameter and number of major septa in ***Petalaxis ellesmerensis*** *sp. nov.*

(Fig. 34). Septa gently curved to sinuous in transverse section, thin to moderately thick, thickest in outer tabularium, cardinal septum slightly thicker than adjacent major septa in many specimens, septa extend to corallite walls as septal crests. Major septa number 16-21 (rarely 15, or up to 23) (Fig. 34); generally radially arranged, but those in counter quadrants rarely curve toward counter septum, axial parts of many slightly curved or sharply deflected laterally; major septa long, rarely reach axial structure, vary in length vertically, maximum withdrawal from axial structure rarely exceeds one third tabularium radius. Minor septa well developed, variable in length, extend adaxially from dissepimentarium approximately one third to one half (rarely two thirds) of tabularium radius.

Axial structure variable, generally continuous vertically, locally discontinuous in early growth stages, rarely discontinuous at maturity, straight or gently curved to sinuous in longitudinal section; median lamella varies vertically in thickness and shape, slightly to moderately thickened, tabular to lens-shaped, rarely forms thick lens, straight or slightly curved where strongly thickened, curved to highly sinuous and (rarely) sharply curved in transverse section where only slightly thickened, discontinuously connected to axial margin of cardinal septum, rarely attached to one or two major septa, commonly extends well past axis and closely approaches but does not reach counter septum, rarely absent from axial area at maturity because of abaxial withdrawal or strong lateral curvature of cardinal septum; septal lamellae present in all specimens, formed on median lamella, less commonly on lateral lamellae, locally absent in some coralla, usually one or two (rarely more than five) present, vertically discontinuous, commonly very short and straight, rarely long and curved in transverse section, moderately to strongly thickened; lateral lamellae well developed in most coralla, rare in some, normally only one, rarely two, developed in some corallites at any level sectioned, vertically discontinuous, normally thinner than median lamella, gently to strongly curved in transverse section, rarely sinuous, may be longer than median lamella and curve around it, locally joined to median lamella by one edge or by septal lamellae, formed by axial thickening of cardinal septum or (rarely) another major septum, may be deflected from axial area where cardinal septum strongly curved, rarely joined by one or two major septa; axial tabellae rare, slightly to moderately convex, occur as widely spaced, isolated plates attached to median lamella, rarely form series of two or three.

Tabulae generally incomplete, some complete tabulae in all corallites, commonly slightly to moderately concave, less commonly slightly convex or subplanar, incomplete tabulae consist of several curved or undulose, concave to strongly convex tabellae; most tabulae slightly to moderately elevated adaxially but some tabulae in many corallites steeply elevated, approximately horizontal, or slightly depressed, most complete tabulae and periaxial tabellae moderately to steeply elevated to join axial structure, some join it at approximately 90°; biform morphology well expressed, tabellae in position I concave to strongly convex, moderately to steeply declined adaxially, those in position II slightly concave to convex or undulose, generally declined gently toward dissepimentarium, less commonly subhorizontal; 9-13 (commonly 11 or 12) tabulae in 5 mm of corallite length; ratio of tabularium diameter to corallite diameter 0.64-0.78, most commonly 0.67-0.75, rarely ranges as low as 0.54 and as high as 0.84.

Dissepimentarium well developed, vertically continuous, width commonly one quarter to one third of corallite radius; boundary with tabularium generally distinct, marked by slight stereoplasmic thickening of dissepiments in most specimens; dissepiments in two to four (most commonly two or three) rows, rarely one or five rows present, most dissepiments transeptal, regular dissepiments present adjacent to tabularium in all specimens; in longitudinal section large dissepiments range from elongate and slightly convex or irregular to strongly convex, smaller dissepiments are strongly convex to globose; dissepiments moderately to steeply declined adaxially, becoming near vertical at tabularium boundary; five to eleven (commonly seven to nine) dissepiments in 5 mm of corallite length.

In immature growth stages (mean diameter of smallest corallite studied, 2.25 mm), corallite walls strongly curved below mean corallite diameter of 4.6 mm, slightly curved between diameters of 4.6 and 6.2 mm, those separating young corallite from parent incomplete in most offsets with mean diameters below 3.8 mm; septa straight to slightly sinuous, major septa generally short at mean diameters less than 3.1 mm, with one or two reaching axial area, generally long with several reaching axial area at greater mean diameters, cardinal septum elongate at all diameters studied, rarely slightly thickened to form axial structure at mean diameters as low as 3.25 mm, most commonly thickened at diameters greater than 4 mm, counter septum slightly to significantly shorter than adjacent major septa; relationship between number of major septa and mean corallite diameter shown in Figure 34; minor septa incompletely developed between mean diameters of 2.25 (smallest diameter studied) and 3.5 mm, well developed at greater diameters; axial structure developed at mean corallite diameter of 3.25 mm and greater, formed from axially thickened margin of cardinal septum, median lamella present at diameters as low as 2.6 mm, but thin; septal lamellae absent at mean corallite diameters below 2.6 mm, very rarely developed between diameters of 2.6 and 4.1 mm, well developed at greater diameters; lateral lamellae rarely developed in some specimens at mean corallite diameter between 4.4 and 5 mm, well developed at greater diameters; transeptal and regular dissepiments present at smallest mean corallite diameter studied (2.25 mm).

Discussion. Petalaxis ellesmerensis sp. nov. is characterized by its adaxially elevated, generally incomplete tabulae and by the nature of its variable axial structure. Within individual colonies, the latter ranges from a thin to moderately thick, sinuous to straight median lamella to a more complex structure consisting of a median lamella, several vertically discontinuous septal lamellae, and one or (rarely) two thin, lateral lamellae.

In comparison to *P. crassicolumnus* sp. nov., *P. ellesmerensis* has fewer septa, a slightly smaller mean corallite diameter, a narrower axial column containing fewer lateral lamallae, and it lacks naotic septa. In a specimen from GSC loc. C-179723, tentatively assigned to this species, the tabulae are subhorizontal to concave as in *P. multilamellatus* sp. nov. and *P. mcoyanus*. All other features of this specimen are normal for *P. ellesmerensis*.

Lithostrotionella aff. *stylaxis* (Trautschold) of Dobrolyubova (1936b, p.127), based on a single Moscovian(?) specimen from the northern Ural Mountains, may be conspecific with *P. ellesmerensis.* The nature of the axial structure in the Russian specimen is unclear, however, and its septal number is slightly lower than in most Canadian specimens assigned to the species.

The elevated tabulae in *P. ellesmerensis* sp. nov. resemble those of *P. mohikanus* (Fomichev) from the upper Moscovian of the Donets Basin, but the latter has fewer septa at corresponding corallite diameters, fewer septal lamellae (Fomichev, 1953, p. 460, 461, Pl. 32, figs. 1a, 2a), and apparently lacks lateral lamellae. *Petalaxis orboensis* (de Groot), from the upper Moscovian of Spain (de Groot, 1963, p. 85, 110) has adaxially elevated, incomplete tabulae and approximately the same number of septa as *P. ellesmerensis* sp. nov., but has a very thin axial structure with neither lateral lamellae nor well developed septal lamellae. In its corallite diameter and in the number and character of its septa, *P. ellesmerensis* sp. nov. is similar to *P. major* Sando [= *Petalaxis major* (de Groot) of Sando, 1983, p. 29], but the tabulae in the Canadian species are generally adaxially elevated, whereas those in *P. major* are subhorizontal to adaxially depressed. Also, the axial structure of *P. ellesmerensis* sp. nov. has only one or two short, fairly straight septal lamellae and consistently has lateral lamellae. In contrast, the axial structure of *P. major* has numerous long, sinuous septal lamellae and shows no lateral lamellae in the illustrated longitudinal section of the holotype (de Groot, 1963, Pl. 16, fig. 2b). *Petalaxis planitabulatus* (Yan), from the upper Moscovian of China, appears similar in some respects to *P. ellesmerensis* sp. nov., but the tabulae of *P. planitabulatus* do not appear to be as strongly elevated adaxially as those of the Ellesmere Island species. Closer comparison of the two species cannot be made because no details of the axial structure were described or clearly illustrated for the Chinese coral (Yan, 1981, p. 68, Pl. 1, figs. 1a, b).

Material. Holotype, GSC 109643, (14 pieces cut from incomplete colony, two transverse and two longitudinal thin sections, 59 transverse acetate peels) from GSC loc. C-179729. Paratypes: GSC 109644, from GSC loc. C-179729; GSC 109645, from GSC loc. C-11403. Additional material: single specimens from GSC locs. C-31217, C-179723, C-179726, and C-179731; two specimens from each of GSC locs. C-2082, C-179724, and C-179732; three specimens from C-11403; four specimens from C-179721; eight specimens from GSC loc. C-179729; nine specimens from GSC loc. C-179722.

Occurrence and age. Petalaxis ellesmerensis sp. nov. was collected from the lower part of the Canyon Fiord Formation at locality 1 and in the northeast Trold Fiord, east Blind Fiord (A), and south Trold Fiord sections (GSC locs. C-2082, C-11403, C-179721 to C-179724, C-179726, C-179729, C-179732, sections 12, 14, 15, Figs. 1, 10, 12, 13), and from the lower part of the Nansen Formation in the Otto Fiord section (GSC loc. C-31217, locality 3, Figs. 1, 4). The species was not dated by other fossil groups at locality 1, but at all other collecting sites it is associated with Moscovian fusulinaceans. These indicate a more precise, Kashirian (early Moscovian) age for the corals collected 150 m above the base of the Canyon Fiord Formation in the east Blind Fiord (A) section (GSC loc. C-11403, Appendix 1). In the Otto Fiord section, the species is associated with Podolskian fusulinaceans (GSC loc. C-31217). *Lithostrotionella* aff. *stylaxis* (Trautschold) of Dobrolyubova (1936b, p. 127), a specimen from the northern Ural Mountains that may be conspecific with *P. ellesmerensis* sp. nov., was assigned a tentative mid-Carboniferous (Myatchkovian?) age by that author (*ibid.*, p. 81).

Petalaxis multilamellatus sp. nov.

Plate 4, figures 3-11; Figures 16c-n,
p-s, 21-23, 35, 36

Etymology. Combination of Latin adjective *multus*, meaning much, and Latin noun *lamella*, meaning small plate, with suffix *atus*.

Diagnosis. Petalaxis having 16-23 (commonly 17-21) long major septa at mean diameter of 4-9 (commonly 5.5-8.5) mm; minor septa extend adaxially from dissepimentarium one quarter to two thirds of tabularium radius; axial structure vertically continuous with thickened median lamella, short to long, locally numerous septal lamellae, usually two or three lateral lamellae and widely spaced axial tabellae; tabulae generally incomplete, commonly concave and adaxially depressed or horizontal, 9-13 in 5 mm; tabularium to corallite diameter ratio 0.62-0.78; transeptal dissepimentarium continuous, dissepiments generally small.

Description. Mean diameter of mature corallites 4.1-8.9 (commonly 5.4-8.5) mm (Fig. 36). Septa gently curved to slightly sinuous in transverse section, thin to moderately thick, thickest in outer tabularium, cardinal septum slightly thicker than adjacent major septa at many levels in all specimens, septa extend to corallite walls as septal crests. Major septa number 16-21 (commonly 17-21), rarely up to 23 (Fig. 36);

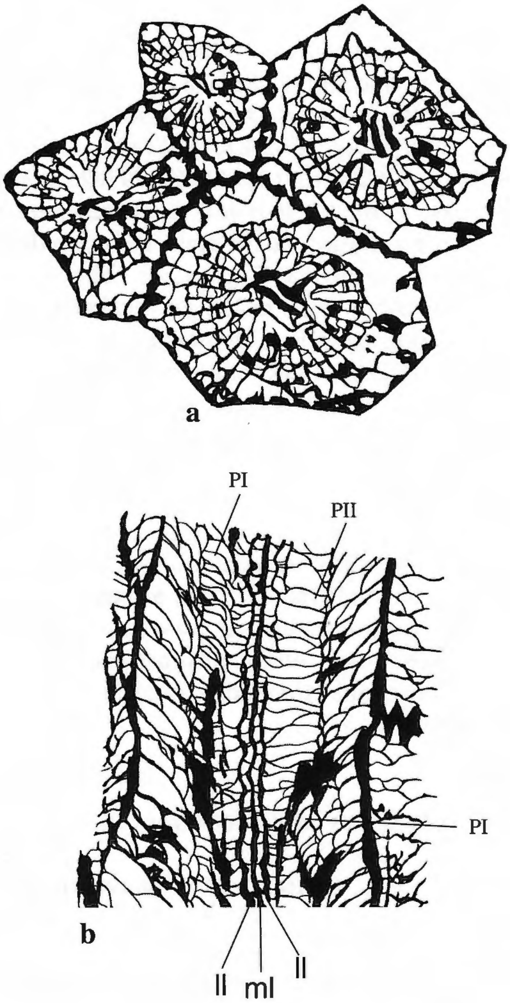


***Figure 35. Petalaxis multilamellatus** sp. nov., paratype GSC 109648, x4; **a**, drawing of transverse thin section (see Pl. 4, fig. 10), showing numerous lateral lamellae in axial structures; **b**, drawing of longitudinal thin section, showing median lamella (ml), lateral lamellae (ll) and incomplete, generally concave tabulae (see Pl. 4, fig. 11); biform morphology of tabularium well expressed (tabellae in position I - PI, tabellae or peripheral parts of complete tabulae in position II - PII).*

generally radially arranged, axial parts of many slightly curved or sharply deflected laterally; long, closely approach and rarely reach axial structure, vary in length vertically, maximum withdrawal from axial structure rarely exceeds one quarter of tabularium radius. Minor septa well developed, variable in length, extend adaxially from dissepimentarium approximately one quarter to one half (rarely two thirds) of tabularium radius.

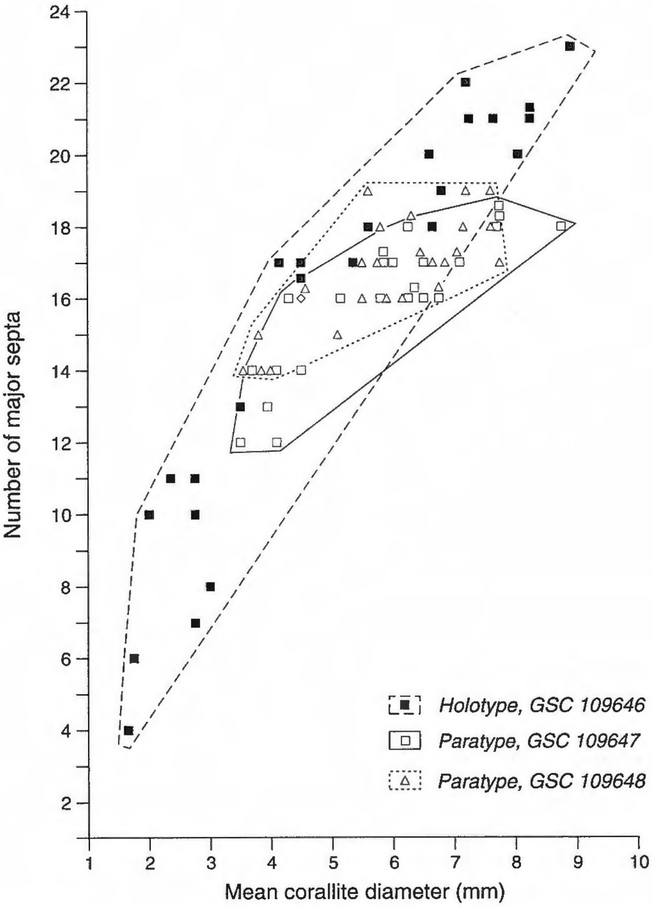


***Figure 36.** Relationship between mean corallite diameter and number of major septa in **Petalaxis multilamellatus** sp. nov.*

Axial structure vertically continuous, slightly curved to sinuous in longitudinal section; median lamella variable in thickness and shape, moderately to strongly thickened, tabular to lens-shaped, slightly to strongly curved or sinuous, discontinuously connected to axial margin of cardinal septum, not connected with counter septum; septal lamellae present in all specimens, formed on median and lateral lamellae, locally numerous and strongly developed, vertically discontinuous, very short to long and curved, moderately to strongly thickened; lateral lamellae well developed, numerous, vertically discontinuous, commonly two, locally three present in many corallites at any level sectioned, commonly thinner than median lamella, gently to strongly curved or sinuous and irregular in transverse section, short or long in transverse section, may be longer than median lamella and curve around it, locally joined to median lamella by one edge or by septal lamellae, discontinuously connected to straight or highly curved inner margin of cardinal septum, locally joined by one or two major septa; axial tabellae commonly occur as widely spaced, isolated plates, locally up to three or four in series, mainly attached to median lamella, rarely to septal lamellae or lateral lamellae.

Tabulae generally incomplete, some complete tabulae in all corallites, slightly to strongly concave, less commonly subplanar to slightly convex, incomplete tabulae consist of several curved or undulose, concave to strongly convex tabellae; most tabulae adaxially depressed or approximately horizontal, some elevated adaxially in most corallites, many periaxial tabellae moderately to steeply elevated to join axial structure, some join it at angles near 90°; biform morphology well developed in all specimens, tabellae in position I steeply declined adaxially, moderately to strongly convex or globose, those in position II slightly concave, undulose or slightly convex, generally subhorizontal to slightly declined adaxially, rarely declined toward dissepimentarium; 9-13 (commonly 10-12) tabulae in 5 mm corallite length; ratio of tabularium diameter to corallite diameter 0.62-0.78, most commonly 0.64-0.75, rarely ranges as low as 0.56 and as high as 0.81.

Dissepimentarium well developed, vertically continuous, width variable, commonly one quarter to one third of corallite radius; boundary with tabularium generally distinct, marked by slight stereoplasmic thickening of dissepiments in some specimens; dissepiments in one to three (most commonly one or two) rows, rarely up to four or five where small dissepiments are numerous; most dissepiments transeptal, but regular dissepiments locally abundant, particularly near margin of tabularium; in longitudinal section large dissepiments range from elongate and slightly convex or irregular to strongly convex, rarely globose, smaller dissepiments strongly convex or globose, rarely moderately convex or slightly flattened; dissepiments moderately to steeply declined adaxially, becoming almost vertical at tabularium boundary; 5-12 (commonly six or seven) dissepiments in 5 mm of corallite length.

Details of the earliest growth stages of this species are given in the section dealing with the morphology (blastogeny) of *Petalaxis*. Corallite walls curved below mean corallite diameter of 5 mm, those separating young corallite from parent incomplete in most corallites with mean corallite diameters below 3.7 mm; septa slightly curved to slightly sinuous, major septa generally short at mean diameter less than 3 mm, except for one or two that approach axis, generally long with several approaching axis at greater mean diameters, cardinal septum slightly thickened to form axial structure at mean diameters greater than 2.75 mm, counter septum slightly shorter than adjacent major septa; relationship between number of major septa and mean corallite diameter shown in Figure 36; minor septa absent at mean diameters below 2.75 mm, incompletely developed between diameters of 2.75 mm and 3.25 mm, and well developed at larger diameters; axial structure well developed at mean diameters of 3.25 mm and greater, formed from axially thickened margin of long cardinal septum; septal lamellae absent below mean corallite diameter of 3.5 mm, rare and short between mean diameters of 3.5 mm and 4.25 mm, and well developed at greater diameters; lateral lamellae first developed but rare at mean diameter of 4 mm, well developed at mean diameters of 5 mm and greater; tabulae concave, similar to those in mature stages; transeptal and regular dissepiments present at all corallite diameters studied.

Discussion. *Petalaxis multilamellatus* sp. nov. is one of the most distinctive species of *Petalaxis*. It is distinguished from all other species of the genus by the numerous lateral and septal lamellae in its strongly developed axial structure, combined with its concave to subhorizontal tabulae. It resembles *P. mcoyanus* (Milne Edwards and Haime) in the structure of its tabulae, but the latter species has fewer steeply declined peripheral tabellae, fewer septa at corresponding corallite diameters, and fewer lamellae in its axial structure. *Petalaxis major* Sando [= *Petalaxis major* (de Groot) of Sando, 1983, p. 29] has concave tabulae, strongly developed septal lamellae and numerous septa, as in *P. multilamellatus*, but lacks the strongly developed lateral lamellae of the latter (de Groot, 1963, Pl. 16, fig. 2a). The development of lateral lamellae in the axial structure of *P. yosti* Stevens, from the Moscovian of California, is similar to that in *P. multilamellatus* sp. nov. In comparison to *P. yosti*, however, the tabulae in *P. multilamellatus* sp. nov. are subhorizontal rather than axially elevated, and the Canadian species has more strongly developed transeptal dissepiments, a wider dissepimentarium and longer minor septa. The remarkable development of lateral lamellae and strongly depressed, concave tabulae in *P. multilamellatus* sp. nov. clearly separate it from *P. ellesmerensis* sp. nov., with which it is associated at GSC loc. C-179722.

Material. Holotype, GSC 109646 (10 pieces cut from incomplete colony, two transverse thin sections, one longitudinal thin section cut through two corallites, 89 transverse acetate peels); paratypes, GSC 109647 and GSC 109648; all from GSC loc. C-179722. Additional material: two specimens from GSC loc. C-179721; five specimens from GSC loc. C-179722.

Occurrence and age. *Petalaxis multilamellatus* sp. nov. was found only in the northeast Trold Fiord section (GSC locs. C-179721, C-179722, locality 12, Figs. 1, 10), where it occurs 94-97 m above the base of the Canyon Fiord Formation in association with *P. crassicolumnus* sp. nov., *P. ellesmerensis* sp. nov. and Moscovian fusulinaceans (Table 3, Appendix 1). *Petalaxis multilamellatus* sp. nov. is probably Kashirian in age, based on its occurrence with *P. crassicolumnus* sp. nov., which is found elsewhere with Kashirian foraminifers.

Petalaxis beauchampi sp. nov.

Plate 4, figure 12; Plate 5, figures 1-9;
Figures 37, 38

Etymology. In honour of Dr. B. Beauchamp, who provided essential field support and stratigraphic data for this study.

Diagnosis. *Petalaxis* having 14-22 (commonly 18-21) long major septa at mean diameter 5-11 (commonly 5.5-6.5 mm); minor septa extend adaxially from dissepimentarium one tenth to one half of tabularium radius; axial structure weak, locally discontinuous, consists of thin median lamella, one vertically discontinuous lateral lamella and rare axial tabellae; tabulae mainly complete, concave, generally subhorizontal, 9-12 in 5 mm; tabularium to corallite diameter ratio 0.54–0.80; transeptal dissepimentarium continuous, dissepiments generally large.

Description (based on holotype GSC 109649 and paratype, GSC 109650). Mean diameter of mature corallites 5-6.8 (commonly 5.5-6.5 mm) (Fig. 38). Septa curved and sinuous in transverse section, thin, wedge-shaped, slighty thickened in outer tabularium and dissepimentarium, becoming very thin adaxially, extend to corallite walls as septal crests, cardinal septum slightly thicker than adjacent major septa, counter septum generally short, but locally reaches axial area. Major septa number 17-22 (commonly 18-21) (Fig. 38); irregularly arranged in roughly radial pattern, with axial margins locally curved toward counter-cardinal plane, septal pattern altered by strong curvature of axial part of cardinal septum in many corallites; major septa long, closely approach corallite axis, rarely join axial structure, vary in length vertically. Minor septa well developed, variable in length, extend adaxially from dissepimentarium approximately one tenth to one half (commonly one quarter to one half) of tabularium radius.

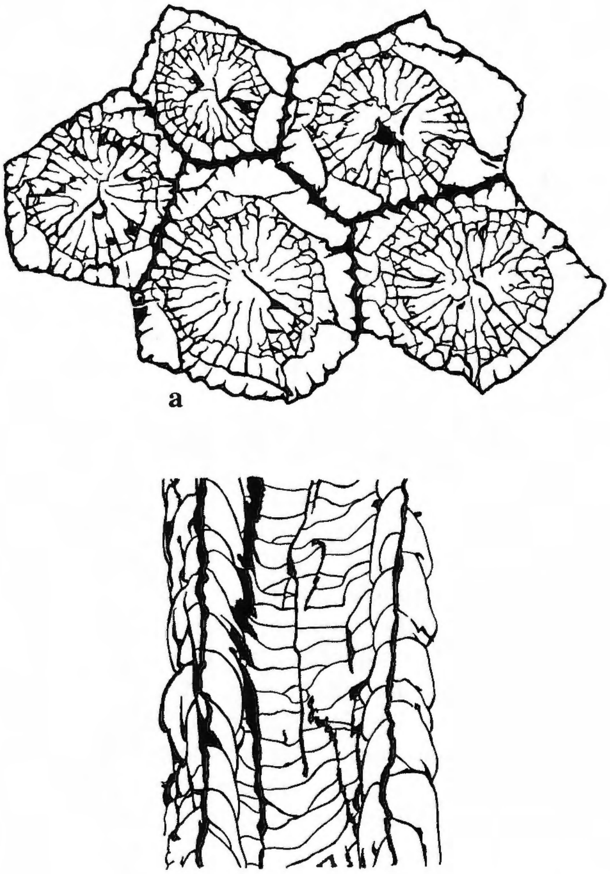


Figure 37. Petalaxis beauchampi *sp. nov., holotype GSC 109649, x5;* ***a****, drawing of transverse thin section (see Pl. 5, fig. 5), showing large dissepiments and weakly expressed axial structure formed by slight thickening of cardinal septum;* ***b****, drawing of longitudinal thin section, showing thin median lamella and concave, axially depressed tabulae (see Pl. 5, fig. 3).*

Axial structure weakly developed, locally discontinuous, consists of median lamella and poorly expressed, vertically discontinuous lateral lamella; thin median lamella gently to strongly curved or sinuous in transverse and longitudinal section, formed by slight axial thickening of cardinal septum, to which it is consistently connected, commonly deflected from corallite axis by curvature of cardinal septum, not joined to counter septum, rarely joined by other long major septa; septal lamellae not developed; axial structure locally absent where both cardinal and counter septa are short, leaving open axial area bordered by other long major septa; axial tabellae not observed.

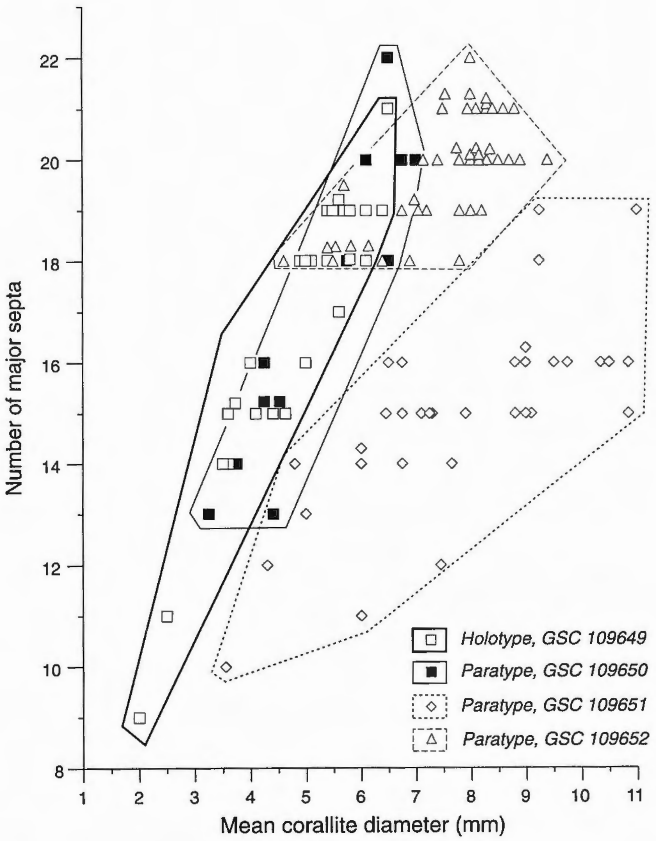


Figure 38. *Relationship between mean corallite diameter and number of major septa in* ***Petalaxis beauchampi*** *sp. nov.*

Tabulae mainly complete, concave, gently curved to undulose, generally subhorizontal to adaxially depressed, locally elevated toward median lamella where the latter is strongly developed, moderately to strongly elevated at dissepimentarium, strongly concave where axial structure absent; incomplete tabulae consist of only one or two large tabellae; biform morphology weakly expressed, tabellae and peripheral parts of complete tabulae in position I moderately to gently declined adaxially, generally subplanar or slightly concave, those in position II generally subhorizontal or slightly declined toward dissepimentarium, rarely slightly declined adaxially; 9-13 (commonly 9-12) tabulae in 5 mm of corallite length; ratio of tabularium diameter to corallite diameter 0.54-0.80, most commonly 0.63-0.75.

Dissepimentarium well developed, continuous, varies in width approximately from one fifth to one half of corallite radius, boundary with tabularium distinct; dissepiments large, in one (rarely two) rows, almost entirely transeptal, regular dissepiments locally developed adjacent to tabularium; dissepiments strongly convex to globose, rarely elongate and flattened, steeply declined adaxially; 4-6 dissepiments in 5 mm corallite length.

In immature growth stages, wall separating young corallite from parent incomplete at mean corallite diameters lower than 3.4 mm; septa curved or sinuous, pattern similar to that in mature stages, cardinal septum reaches axis to form slightly thickened median lamella, counter septum usually shorter than adjacent major septa but rarely extends to axis to form lateral lamella; relationship between number of major septa and mean corallite diameter shown in Figure 38; minor septa first present, but incompletely developed at mean corallite diameter of 2.5 mm, generally well developed at mean diameters of 4 mm and greater; axial structure not developed at mean corallite diameter of 2 mm (smallest corallite studied), poorly developed from slightly thickened cardinal septum at mean diameter of 3 mm, consists of median lamella and (rarely) lateral lamella at higher diameters; transeptal dissepiments well developed at mean corallite diameters of 3.2 mm and greater, rare regular dissepiments present at smaller diameters.

Discussion. There is little information on the intraspecific variation within *P. beauchampi*, because of the limited number of specimens available for study. A Myachkovian specimen (GSC 109651, Pl. 5, figs. 6-9) from GSC loc. C-10884 has a greater mean corallite diameter (6-11 mm, Fig. 38), fewer septa (14-16, rarely up to 19) and more numerous, slightly smaller dissepiments than the holotype and paratype, described above. Many of the major septa closely approach or reach the corallite axis in GSC 109651 and, where the cardinal septum is abaxially withdrawn, one or more may extend beyond the axis. Also, this specimen possesses rare axial tabellae and has locally developed incomplete tabulae, consisting of a few large, convex or undulose tabellae. In the remaining specimen in our collection (GSC 109652), collected from talus (GSC loc. C-193107) stratigraphically above Kashirian foraminifers, the number of major septa is approximately equal to that in the holotype and paratype from GSC loc. C-179732, but the mean corallite diameter reaches a maximum of 9.4 mm (Fig. 38) and the median lamella of the axial structure is slightly thicker.

Petalaxis beauchampi sp. nov. resembles *P. thorsteinssoni* sp. nov. in the length and shape of its thin septa, the width of its dissepimentarium, and the overall axial depression of its tabulae. *Petalaxis thorsteinssoni*, however, has more septa (up to 27), a greater mean corallite diameter (commonly up to 18 mm), more strongly concave tabulae, and in most specimens, a thicker median lamella bearing rare septal lamellae in its axial column.

The weakly developed axial structure, concave, almost complete tabulae, and single row of highly convex transeptal dissepiments typical for *P. beauchampi* sp. nov. also occur in several other species of *Petalaxis*, such as *P. sexangulus* (de Groot, 1963), *P. simplex* (Hayasaka, 1936; see Sando, 1983), *P. tolmachevi* (Rukhin, 1938), *P. taishakuensis* (Yokoyama, 1957), *P. tchucoticus* (Onoprienko, 1976), and *P. mirus* Kosyreva (1974). *Petalaxis beauchampi* sp. nov. is distinguished from these and other similar species, however, by its generally greater number of septa in mature corallites and by the presence of lateral lamellae in its axial structure. In addition, comparisons with the Canadian species show that: *P. sexangulus* has a thicker wall, shorter minor septa, and less inflated dissepiments; the minor septa in *P. mirus*, *P. simplex*, *P. tchucoticus* and *P. tolmachevi* are much shorter; and the corallite diameter in *P. taishakuensis* is much smaller.

Material. Holotype GSC 109649 (12 pieces cut from incomplete colony, two transverse and four longitudinal thin sections, six transverse and two longitudinal acetate peels), incomplete colony from GSC loc. C-179732. Paratypes: GSC 109650, from GSC loc. C-179732; GSC 109651, almost complete colony from GSC loc. C-10884; GSC 109652, incomplete colony (unfigured) from GSC loc. C-193107.

Occurrence and age. Petalaxis beauchampi sp. nov. appears to range from Kashirian or Podolskian to Myachkovian in age. It was collected with Moscovian fusulinaceans 299.5 m above the base of the Canyon Fiord Formation in the south Trold Fiord section section (GSC loc. C-179732, locality 15, Figs. 1, 13, Appendix 1). Fusulinaceans of Kashirian or Podolskian age occur 39.5 m lower in this section (GSC loc. C-188666). In the Greely Fiord section, a specimen (paratype, GSC 109652) was collected from talus (GSC loc. C-193107, locality 10, Figs. 1, 8) stratigraphically above Kashirian fusulinaceans (Appendix 1, GSC locs. C-193105, C-193106), in the middle of the Canyon Fiord Formation. Paratype, GSC 109651 was collected from the Canyon Fiord Formation, 172 m above the base of the middle limestone member in the east Blind Fiord (B) section (GSC loc. C-10884, section 13, Figs. 1, 11). This specimen is associated with upper Moscovian (Myachkovian) fusulinaceans (Appendix 1, GSC loc. C-27968), and is overlain by Kasimovian ammonoids (GSC loc. C-10885, 23 m higher in the section (Table 3).

Petalaxis thorsteinssoni sp. nov.

Plate 5, figures 10-14; Plate 6, figures 1-4;
Figures 18-20, 39, 40

Petalaxis sp. C, Somerville, 1997, Pl. 1, figs. 1, 2

Etymology. In honour of Dr. R. Thorsteinsson, who collected the holotype.

Diagnosis. Petalaxis having 17-27 (commonly 18-24) long major septa at mean diameter 6 to 18.5 (commonly 8-16) mm; minor septa extend adaxially from dissepimentarium one third (rarely two thirds) of tabularium radius; axial structure rarely vertically discontinuous, consists of median lamella, few short, vertically discontinuous septal lamellae, one discontinuous lateral lamella and few axial tabellae; tabulae mainly complete, deeply concave, 6-10 (commonly 7 or 8) in 5 mm, tabularium to corallite diameter ratio 0.43-0.74; transeptal dissepimentarium continuous, wide, dissepiments medium-sized to large.

Description. Mean diameter of mature corallites highly variable, ranges from 6 to 18.5 (commonly 8-16 mm) (Fig. 40). Septa slightly to strongly sinuous in transverse sections of most specimens, rarely straight or gently curved, generally thin, slightly thickened in outer tabularium; cardinal septum slightly thicker than adjacent major septa in all specimens, varies in thickness vertically; septa extend to corallite walls as septal crests. Major septa number 17-27 (commonly 18-24) (Fig. 40); generally radially arranged, but show variable bilateral symmetry with respect to counter-cardinal plane, those in counter quadrants commonly curve toward counter septum, axial parts of many highly sinuous and sharply deflected laterally; major septa long, closely approach and rarely reach axial structure, vary in length vertically, maximum withdrawal from axial structure rarely exceeds one third of tabularium radius. Minor septa well developed, variable in length, extend adaxially approximately one third to one half (rarely two thirds) of tabularium radius.

Axial structure continuous in most specimens, rarely discontinuous vertically, curved to sinuous in longitudinal section; median lamella highly variable in thickness and shape, moderately to strongly thickened in most specimens, thin and tabular in others, straight or curved in most in transverse section, highly curved or sinuous in some specimens, commonly extends well beyond corallite axis across inner one third of tabularium, connection with axial margin of cardinal septum discontinuous, commonly joined by one or two other major septa, connection with major septa

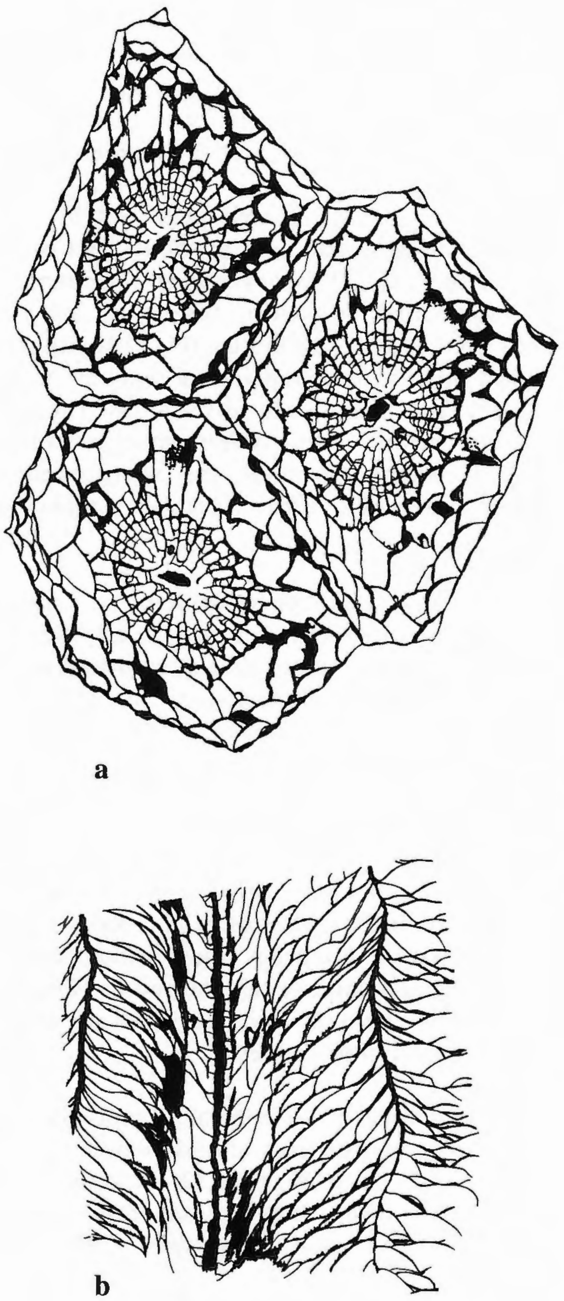


***Figure 39. Petalaxis thorsteinssoni** sp. nov., holotype GSC 109653, x3; **a**, drawing of transverse thin section (see Pl. 5, fig. 10), showing lens-shaped median lamella, slightly thickened cardinal septum and wide dissepimentarium; **b**, drawing of longitudinal thin section, showing incomplete, strongly concave tabulae (see Pl. 5, fig. 13).*

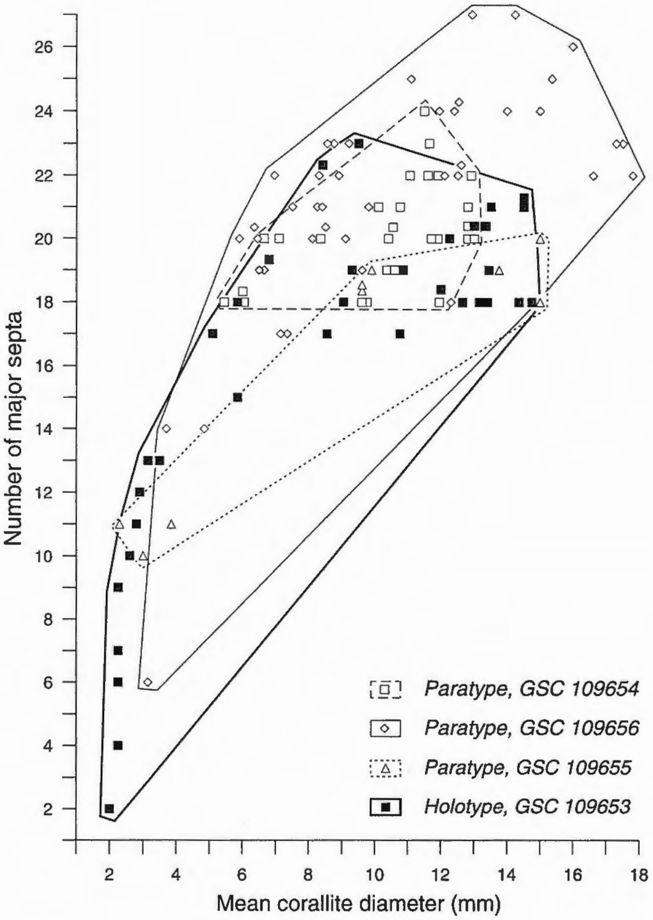


***Figure 40.** Relationship between mean corallite diameter and number of major septa in **Petalaxis thorsteinssoni** sp. nov.*

vertically discontinuous; few short, irregularly shaped, vertically discontinuous septal lamellae present in all specimens, weakly developed in most specimens; lateral lamellae weakly developed in most specimens, vertically discontinuous, curved or sinuous in transverse section, only one present in axial structures of a few corallites in all sections studied, formed by thickening of curved axial margin of cardinal septum; axial structure locally absent and, where cardinal septum is abaxially withdrawn, axial area occupied by several other long major septa; axial tabellae generally rare, commonly occur as isolated, curved, steeply inclined to vertical plates attached to median lamella, but locally may form series of up to eight tabellae in some specimens.

Tabulae mainly complete, locally incomplete, strongly concave, consist of few large, curved or undulose, concave or slightly convex tabellae; all tabulae slope moderately to steeply downward from dissepimentarium toward axis, periaxial tabellae in most become approximately horizontal or are elevated to join axial structure, but others remain axially depressed; biform morphology weakly expressed, tabellae or peripheral parts of complete tabulae in position I steeply declined adaxially, slightly concave to moderately convex, those in position II generally subhorizontal to slightly declined adaxially, slightly concave to slightly convex; 6-10 (commonly 7 or 8) tabulae in 5 mm of corallite length; ratio of tabularium diameter to corallite diameter 0.43-0.74, most commonly 0.50-0.65.

Dissepimentarium well developed, vertically continuous, wide, usual width approximately one third to one half of corallite radius, boundary with tabularium generally distinct; dissepiments in one to seven (most commonly two to five) rows, number of rows varies greatly with size of dissepiments and number of regular dissepiments present, most dissepiments transeptal, but regular dissepiments locally form one or two discontinuous rows adjacent to tabularium and a few occur in middle and outer dissepimentarium; in longitudinal section, large dissepiments range from elongate and slightly convex or irregular to strongly convex or globose, smaller dissepiments generally moderately to strongly convex, locally elongate and slightly convex; dissepiments moderately to steeply declined adaxially, locally almost horizontal near corallite wall in a few specimens, commonly one or more rows of vertical or very steeply declined dissepiments adjacent to tabularium; four to eight (commonly five or six) dissepiments in 5 mm corallite length.

In immature growth stages (mean diameter of smallest corallite studied, 2 mm), corallite walls curved, those separating young corallite from parent incomplete at mean corallite diameters below 3 mm; septa curved or sinuous, major septa usually short, rarely approach axial area, very short where transeptal dissepiments well developed, cardinal septum long, rarely thickened to form axial structure at mean corallite diameters below 5 mm, counter septum commonly shorter than adjacent major septa; relationship between number of major septa and mean corallite diameter shown in Figure 40; minor septa first present, but incompletely developed at mean diameter of 3 mm, well developed at mean diameters of 5 mm and greater; axial structure well developed at mean corallite diameters of 5 mm and greater, formed from axially thickened margin of long cardinal septum; septal lamellae rare, short, first developed at mean corallite diameter of 5 mm; lateral lamellae rare, first developed a mean corallite diameter of 7 mm; tabulae subplanar, slightly elevated adaxially in earliest stages (Pl. 5, fig. 12) becoming concave distally, similar to those in mature stages; regular dissepiments present at lowest mean corallite diameter studied (2.2 mm); transeptal dissepiments absent at mean diameters below 3 mm, well developed at larger diameters.

Septal microstructure is well preserved in several specimens of this species (see previous discussion in section on morphology of *Petalaxis*). The septa are finely monacanthine, with numerous adaxially elevated, gently curved trabeculae (Fig. 19a, b), which are aligned with the median planes of septa in the outer tabularium but commonly diverge in the inner tabularium. Within the dissepimentarium and on septally thickened parts of the wall, randomly distributed trabeculae form irregular papillae and crests (Fig. 20).

Discussion. Petalaxis thorsteinssoni sp. nov. is characterized by its strongly concave, axially depressed tabulae, unusually wide dissepimentarium and numerous septa, a combination of features distinguishing it from all other species of *Petalaxis*. Similar tabulae occur in several other species, such as *P. perapertuensis* (de Groot), *P. cantabricus* (de Groot), *P. sinensis* Wang, and *P. occidentalis* (Merriam) but none of these has a wide dissepimentarium. A wide dissepimentarium, similar to that in *P. thorsteinssoni* sp. nov., occurs in *P. vesiculosus* (Dobrolyubova) and *P. lisitschanskensis* Fomichev, but neither of these species has strongly concave tabulae and *P. vesiculosus* has fewer septa than *P. thorsteinssoni* sp. nov. at corresponding corallite diameters.

Material. Holotype, GSC 109653, from GSC loc. C-147456; 15 pieces cut from almost complete colony, approximately 25 cm x 26 cm x 12 cm (height), four transverse and seven longitudinal thin sections, 62 transverse acetate peels. Paratypes: GSC 109654, from GSC loc. C-1877; GSC 109655, from GSC loc. C-10881; GSC 109656, from GSC loc. C-10861. Additional material: single specimens from GSC locs. 58967, C-1877, C-193094, C-193095.

Occurrence and age. Petalaxis thorsteinssoni sp. nov. was collected from the lower part of the Canyon Fiord Formation of the East Blind Fiord (B) and Bjorne Peninsula sections (GSC locs. C-10881, C-147456, sections 13, 17, Figs. 1, 11, 15), the lower part of the Nansen Formation at locality 4 (GSC loc. C-1877, Fig. 1), and the lower part of the Hare Fiord Formation of the Van Hauen Pass section (GSC loc. C-10861, section 5, Figs. 1, 5). It was also found in talus from the lower Belcher Channel Formation at the Agassiz Ice Cap section (GSC locs. C-193094, C-193095). The species appears to be late Moscovian

(Podolskian to Myachkovian) in age, but its upper age limit has not been definitely determined. It occurs with upper Moscovian fusulinaceans (Appendix 1) in the east Blind Fiord (B) section (GSC loc. C-27962, C-10881 - Podolskian) and the Agassiz Ice Cap section (GSC loc. C-193095 - late Moscovian), and overlies Myachkovian fusulinaceans in the Bjorne Peninsula section (GSC loc. 57728, Appendix 1). The specimens from locality 4 have not been dated by other fossil groups. In the Van Hauen Pass section (type section of the Hare Fiord Formation, locality 5, Figs. 1, 5) a specimen of *P. thorsteinssoni* sp. nov. occurs as a clast in a debris flow bed, 81 m above the base of the formation (GSC loc. C-10861). This bed contains fusulinaceans of late Moscovian (Podolskian or Myachkovian) age (Appendix 1) and is overlain by fusulinaceans of Gzhelian age (GSC loc. 47866).

Corals belonging to *P. thorsteinssoni* sp. nov. have recently been discovered by I.D. Somerville (pers. comm., 1995; 1997) in the upper Moscovian of the Isfjorden area, central Spitsbergen. A Myachkovian age is suggested by other species of *Petalaxis* found at this locality (Somerville, 1997). To avoid early publication of our new species name, Dr. Somerville has kindly referred to his specimens by the provisional name *Petalaxis* C (*ibid.*, see Pl. 1, figs. 1, 2).

Petalaxis baculatus sp. nov.

Plate 6, figures 5-10; Figures 16o, 41, 42

Etymology. Combination of Latin noun *baculus*, meaning rod, with suffix *atus*.

Diagnosis. *Petalaxis*, partly subcerioid, with 14-24 (commonly 15-22) short major septa at mean diameter 5.5-11.75 (commonly 6-10) mm; minor septa as ridges on dissepiments or corallite walls; axial structure locally discontinuous, consists of rod-shaped, commonly isolated median lamella, one to two lateral lamellae and rare axial tabellae; tabulae incomplete in part, with large tabellae, subhorizontal to elevated adaxially, commonly concave, 6-10 (commonly 7 or 8) in 5 mm, tabularium to corallite diameter ratio 0.61-0.82; transeptal dissepimentarium continuous, dissepiments large, convex to slightly flattened.

Description. Corallum cerioid, locally subcerioid near its outer margins, walls strongly curved in early growth stages, generally thin, but thickened where joined by septal crests; mean diameter of mature corallites 5.5-11.75 (commonly 6-10) mm (Fig. 42). Septa straight to slightly curved in transverse section, rarely slightly sinuous; thin, wedge-shaped, thickest at outer margin of tabularium, become thinner adaxially, reach corallite walls as low septal crests. Major septa number 14-24 (commonly 15-22) (Fig. 42); arranged almost radially, some curve slightly toward counter-cardinal plane, cardinal septum consistently thicker than other major septa; most major septa extend adaxially two fifths to one half of tabularium radius from inner margin of dissepimentarium, vary slightly in length vertically, rarely one or two reach axial structure. Minor septa very weakly developed, represented by septal crests in dissepimentarium and ridges on corallite walls, rarely extend very short distance into tabularium.

Axial structure varies in thickness vertically, locally discontinuous, slightly curved to sinuous in longitudinal section; in immature corallites, axial structure formed by elongate, slightly thickened margin of cardinal septum, lateral lamellae or rods rare; in mature corallites, median lamella thickened to form rod with lens-shaped or circular outline in transverse section, connection with cardinal septum vertically discontinuous, median lamella commonly isolated in axial area, rarely joined or closely approached by axially thickened cardinal septum or another long major septum; no septal lamellae present; lateral lamellae rare in early growth stages, one or two present at various levels in most mature corallites, usually well separated from median lamella, rarely in contact with it; commonly thickened to form rods with lens-shaped or circular cross-section, usually isolated from septa in transverse section, rarely connected to axial margin of curved, elongate cardinal septum; at some levels axial structure not developed and cardinal septum strongly curved laterally or abaxially withdrawn to leave axial area open; axial tabellae rare, commonly isolated, rarely more than two or three in continuous vertical series.

Tabulae complete and incomplete, subhorizontal to slightly elevated adaxially, rarely adaxially depressed; commonly concave, rarely almost planar; most incomplete tabulae consist of several large, curved, undulose, or slightly concave tabellae, many of which are convex; most tabulae slightly to strongly elevated at axial structure, few join it at angles near 90°; some complete tabulae slope gently downward from dissepimentarium to axial structure; biform morphology weakly expressed because minor septa very short, tabellae in position I generally slightly concave, gently to moderately declined adaxially, those in position II subhorizontal to gently declined toward dissepimentarium; 6-10 (commonly 7 or 8) tabulae in 5 mm; ratio of tabularium diameter to corallite diameter 0.61-0.82, most commonly 0.67-0.75.

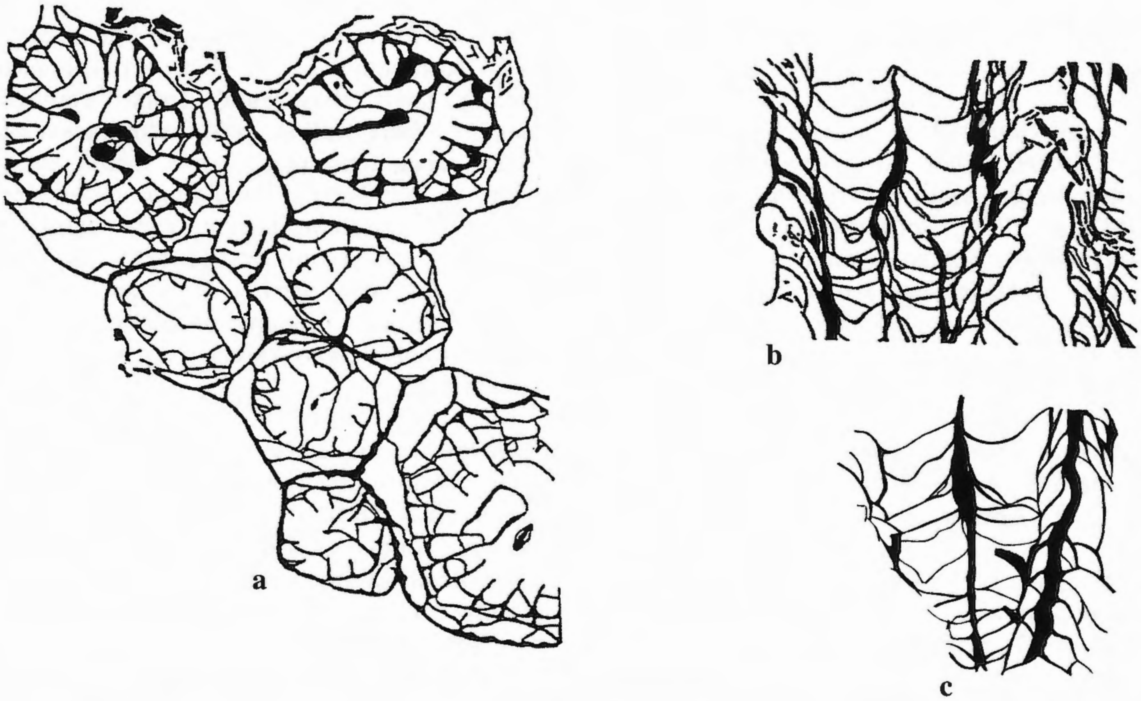


***Figure 41. Petalaxis baculatus** sp. nov., holotype GSC 109657; **a**, digital image of transverse thin section (see Pl. 6, fig. 5), showing locally thickened median lamella, thick, rod-shaped lateral lamellae (in upper left corallite) and weakly developed minor septa expressed as ribs on walls and rare septal crests, x4; **b**, digital image of longitudinal thin section, showing axially elevated tabulae, axial tabellae and variable thickness of median lamella (see Pl. 6, fig. 8), x4; **c**, drawing of longitudinal thin section, showing axially depressed tabulae in early growth stage, x5.*

Dissepimentarium well developed, continuous in mature stages, rarely absent in parts of immature corallites, varies in width approximately from one fifth to two fifths of corallite radius, boundary with tabularium distinct, commonly marked by stereoplasmic thickening of dissepiments; dissepiments in one or two (rarely three) rows, large, almost entirely transeptal, strongly convex to slightly flattened and elongate in longitudinal section, many have irregular outline in transverse section and may extend for a considerable distance along circumference of corallite; most are steeply declined adaxially, some nearly vertical adjacent to tabularium; three to five dissepiments in 5 mm of corallite length.

In immature growth stages, wall separating young corallite from parent complete at and above mean corallite diameter of 3.1 mm (smallest corallite studied); corallites circular to oval in transverse section, particularly in subcerioid zones near margins of corallum; septa straight or curved, major septa other than the cardinal are short, commonly extending less than one third of the distance from dissepimentarium to axis, cardinal septum long, axially thickened to form part of axial structure, counter septum commonly shorter than adjacent major septa, rarely adaxially extended and thickened to form lateral lamella or rod; relationship between mean corallite diameter and number of major septa shown in Figure 42; minor septa incompletely developed, first expressed as low ridges on corallite walls at mean corallite diameter of 3.5 mm, consistently developed at mean corallite diameter greater than 4.5 mm; axial structure formed by elongate, axially thickened cardinal septum at smallest corallite diameter studied (mean diameter 3.1 mm); lateral lamellae or rods rarely occur below mean diameter of 5 mm; axial structure rarely discontinuous; dissepimentarium incompletely developed around periphery of corallites, transeptal dissepiments present at all corallite diameters observed.

Discussion. Petalaxis baculatus sp. nov. is distinguished by the presence of rod-shaped median and lateral lamellae in its axial structure, by its short major septa, and by its weakly developed minor septa. It resembles the Moscovian species *Petalaxis petrovi* (Kachanov), from the west slope of the central Ural Mountains, in its growth form (partly subcerioid), the nature of its axial structure, tabularium, and dissepimentarium, and the weak development of its minor septa. Kachanov (1971, p. 75, Pl. 4, figs. 1a, b) described and illustrated small lateral projections (i.e.,

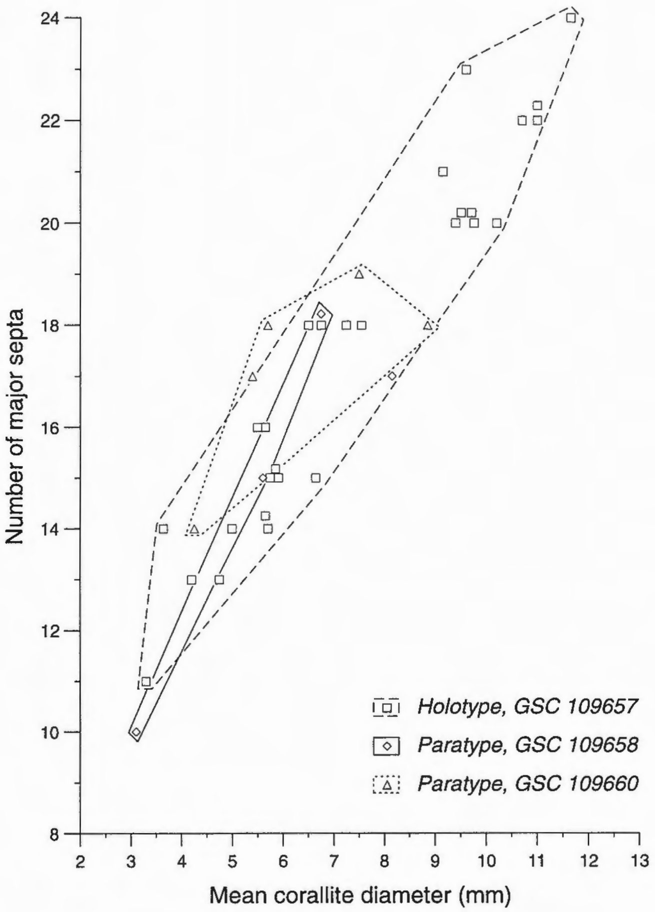


Figure 42. *Relationship between mean corallite diameter and number of major septa in* ***Petalaxis baculatus*** *sp. nov.*

septal lamellae) on the median lamellae of his species. He also noted that the columella splits to give the impression of two columellae, thus indicating the presence of lateral lamellae or rods like those in the axial structures of *P. baculatus* sp. nov. In comparison to Kachanov's species, however, *P. baculatus* sp. nov. has a greater range in corallite diameter and septal number, completely lacks septal lamellae, and has many more lateral lamellae or rods.

Material. Holotype, GSC 109657 [11 pieces cut from an almost complete colony, approximately 8.5 cm x 10 cm x 6.5 cm (height), four transverse and four longitudinal thin sections, one transverse and one longitudinal acetate peel]. Paratypes: GSC 109658, 109659, 109660 (all are small, incomplete colonies). All specimens from GSC loc. C-10891.

Occurrence and age. The described specimens were collected from the upper Canyon Fiord Formation in the east Blind Fiord (B) section (GSC loc. C-10891, locality 13, Fig. 1), 59.5 m above the top of the upper clastic member. The age of the collection is Kasimovian, based on ages from associated foraminifers and ammonoids (Fig. 11, Appendix 2, Table 2; see section on biostratigraphy for discussion of age relationships).

Petalaxis parvus sp. nov.

Plate 6, figures 11-17; Plate 7, figures 1, 2;
Figures 43, 44

Etymology. Latin adjective *parvus*, meaning small.

Diagnosis. Petalaxis having 14-18 short major septa at mean diameter 3.4-7.2 (commonly 4.5-6.5 mm); minor septa mainly as ridges on corallite walls; axial structure consists of thick median lamella and rare septal and lateral lamellae; tabulae mostly complete, horizontal to adaxially elevated, mainly concave, 5 to 8 (commonly 7) in 5 mm; tabularium to corallite diameter ratio 0.64-0.89 (commonly 0.66-0.77); transeptal dissepimentarium locally incomplete, dissepiments medium-sized to large, in one or two rows.

Description. Corallum small, maximum diameter of largest specimen (holotype) 4.5 cm, height 3 cm, corallite walls thick, strongly denticulate where joined by thick bases of septa; mean diameter of mature corallites 3.4-7.2 mm (commonly 4-6.5 mm) (Fig. 44). Septa commonly slightly curved in transverse section, rarely sinuous, thin, reach corallite walls as septal crests. Major septa number 14-18 (rarely 13) (Fig. 44); arranged almost radially, some curve toward counter-cardinal plane; cardinal septum thick, reaches axial structure, counter septum commonly slightly shorter than adjacent major septa, rarely extended adaxially; most other major septa extend adaxially one third to one half of tabularium radius from inner margin of dissepimentarium, vary in length vertically, rarely approach or reach axial structure. Minor septa very weakly developed, represented by ridges on corallite walls and rarely observed as low septal crests in dissepimentarium.

Axial structure continuous in all specimens, straight to slightly curved in longitudinal section; consists of thick lamella or lens-shaped rod formed from swollen axial margin of thick, elongate cardinal septum, shows strong vertical variation in thickness and shape (compare figures 1 and 2 in Plate 7), connection with cardinal septum vertically discontinuous, not connected with counter septum; septal lamellae rare, thick, vertically discontinuous; lateral lamellae rare,

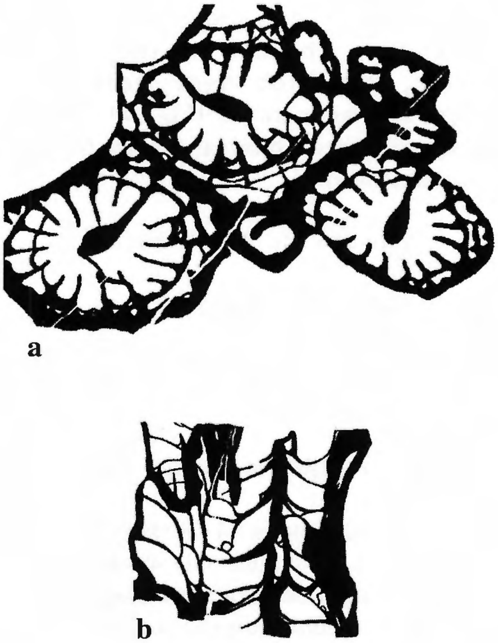


Figure 43. ***Petalaxis parvus*** *sp. nov., holotype GSC 109661;* ***a****, digital image of transverse thin section (see Pl. 6, fig. 14), showing thick cardinal septum, lens-shaped median lamella, weakly developed minor septa and narrow dissepimentarium, x5;* ***b****, digital image of longitudinal thin section, showing axially elevated tabulae and discontinuity of dissepimentarium (see Pl. 6, fig. 12), x4.*

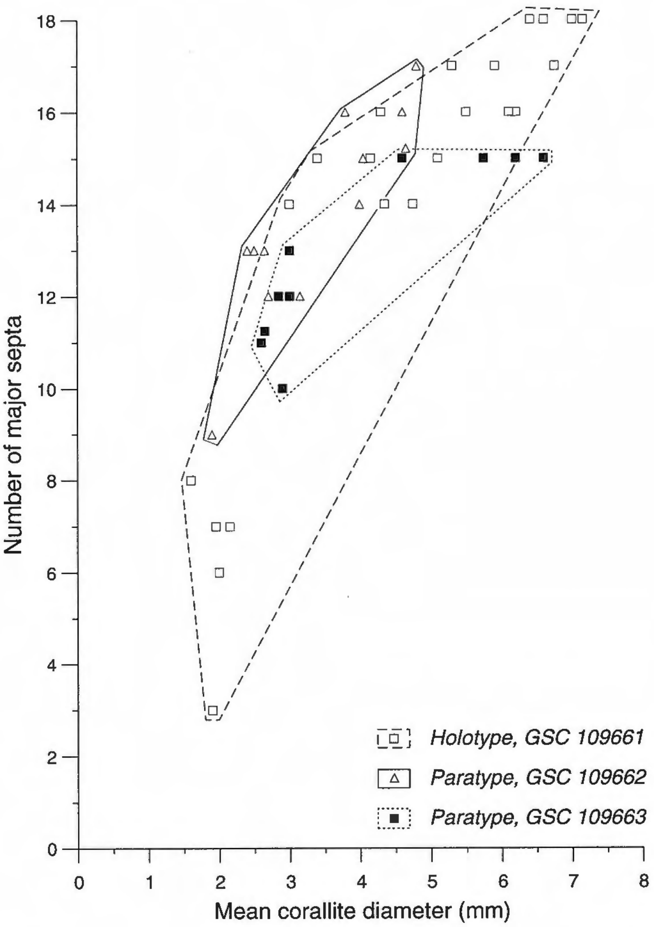


Figure 44. Relationship between mean corallite diameter and number of major septa in ***Petalaxis parvus*** *sp. nov.*

occur as axial thickening of curved cardinal septum or are isolated from septa in axial area; axial tabellae not found.

Tabulae mainly complete; approximately horizontal to adaxially elevated, rarely depressed adaxially; commonly concave, but some planar to slightly convex; incomplete tabulae consist of few convex or planar (rarely concave) tabellae; many tabulae slightly to strongly elevated to join axial structure, others join it at angles near 90°; biform morphology very weakly expressed because minor septa very short, peripheral parts of tabulae in position I slightly to moderately depressed adaxially, those in position II gently depressed at dissepimentarium; five to eight (commonly seven) tabulae in 5 mm; ratio of tabularium diameter to corallite diameter 0.64-0.89, most commonly 0.66-0.77.

Dissepimentarium well developed, continuous in most corallites in mature stages, commonly absent from parts of immature corallites, varies in width approximately from one tenth to one third of corallite radius, boundary with tabularium distinct, commonly marked by stereoplasmic thickening of dissepiments; dissepiments in one or two (rarely three) rows, mainly transeptal, regular dissepiments present adjacent to tabularium; dissepiments strongly convex to slightly flattened and elongate in longitudinal section, many have irregular outline in transverse section; most are steeply declined adaxially, some nearly vertical adjacent to tabularium; four or five (rarely three) dissepiments in 5 mm corallite length.

In immature growth stages, wall separating young corallite from parent complete at and above mean corallite diameter of 1.5 mm (smallest corallite studied), walls commonly strongly curved at mean corallite diameters of up to 4 mm; septa curved to slightly sinuous, commonly curve toward counter-cardinal plane, length varies, approximately one third to two thirds of corallite radius; cardinal septum long, axially thickened to form axial structure, counter septum rarely shorter than adjacent major septa;

relationship between mean corallite diameter and number of major septa shown in Figure 44; minor septa incompletely developed, first expressed as low ridges on corallite walls at mean corallite diameter of 2.6 mm, consistently developed at mean corallite diameter of 4.5 mm and greater; axial structure present in smallest corallite studied (mean diameter 1.5 mm), formed by thickened axial edge of adaxially extended cardinal septum, no septal lamellae or lateral lamellae observed; dissepimentarium consists of rare, locally developed regular dissepiments below mean corallite diameter of 3.5 mm, transeptal dissepiments developed at diameters above 3.5 mm.

Discussion. Petalaxis parvus sp. nov. is distinguished from most other species of the genus by its small corallite diameter, low septal number, very weakly developed minor septa, and thick, relatively simple axial structure. It closely resembles *P. exiguus* Sando, from the Permian McCloud Limestone of California (Sando, 1983, p. 28), but the cardinal septum in that species is not strongly thickened and the transverse thin section from its holotype shows well developed septal lamellae in the axial structure. *Petalaxis elyensis* (Wilson and Langenheim) and *P. brokawi* (Wilson and Langenheim), from the Lower Permian (Wolfcampian) of Nevada, are similar to *P. parvus*, but both have longer minor septa and a stronger development of septal lamellae in their axial structures (Wilson and Langenheim, 1962, p. 512, 513, Pl. 88, figs. 4, 5, 7). *Petalaxis parvus* sp. nov. is similar in corallite diameter, septal number, and development of minor septa to *P. kitikamiensis* (Minato), from the Upper Carboniferous of Japan (Minato, 1955; Kato et al., 1979), but the nature of the axial structure and tabulae in the Japanese species has not been illustrated or described in detail. The Canadian species has more septa, shorter minor septa and more complete and widely spaced tabulae than *P. stylaxis* (Trautschold), reported from the upper Moscovian (Myatchkovian) of the Moscow Basin by Dobrolyubova (1935a, p. 3, 16).

Material. Holotype GSC 109661 [five pieces cut from complete colony, approximately 4 cm x 3 cm x 3 cm (height), three transverse and three longitudinal thin sections, two transverse acetate peels]. Paratypes: GSC 109662 and GSC 109663. Additional material: two undescribed specimens. All small, complete colonies from GSC loc. C-179734.

Occurrence and age. Petalaxis parvus sp. nov. is known from only a single limestone bed, 4 m above the lowest exposure of the Nansen Formation, 793 m below the top of the formation in the west Blind Fiord section (GSC loc. C-179734, locality 16, Figs. 1, 14). Biostratigraphic information from associated foraminifers (Appendix 1) and conodonts indicates a Kasimovian [possibly early(?) Kasimovian] age for this species. Age relationships in the lower part of the Nansen Formation at this locality are discussed in the section on biostratigraphy.

Petalaxis sp. cf. *P. elyensis*
(Wilson and Langenheim), 1962

Plate 7, figures 3-12; Figures 45, 46

Description (Hypotype GSC 109664). Corallite walls strongly thickened where joined by septa to give denticulate appearance, thinner where transeptal dissepiments developed. Mean diameter of mature corallites 2.35-4.9 (commonly 3.5-4.5 mm) (Fig. 46). Septa thick, wedge-shaped, thinner where transeptal dissepiments developed, curved or sinuous in transverse section, almost continuously joined to corallite wall in some parts of corallum (Pl. 7, fig. 3), commonly interrupted by transeptal dissepiments elsewhere (Pl. 7, fig. 4); cardinal septum locally slightly thicker than major septa near corallite wall, continuous with median lamella; counter septum commonly shorter than adjacent major septa. Major septa number 12-16 (commonly 13 or 14) (Fig. 46); radially arranged, axial margins rarely strongly curved in transverse section; major septa moderately long, vary in length vertically, generally extend one half to two thirds of distance from corallite wall to axis, do not reach axial structure, but some may appear to do so where joined to axial structure by tabula intercept in transverse section. Minor septa consistently developed, but very short, generally forming low ridges on corallite wall.

Axial structure continuous, straight to slightly sinuous in longitudinal section, varies in thickness vertically; median lamella moderately to strongly thickened, thinner where transeptal dissepiments developed and in immature corallites, straight to gently or (rarely) strongly curved in transverse section, continuously connected with axial edge of cardinal septum, not connected to counter septum, except rarely in early growth stages; septal lamellae vertically discontinuous, not connected with major septa, form low, broad ridges on median lamella, rarely more elongate in transverse section, commonly only one or two present, locally up to five; lateral lamellae very rare, only one observed in very few corallites; axial tabellae absent.

Tabulae commonly complete, but incomplete tabulae present in all corallites studied; adaxially depressed to subhorizontal, less commonly adaxially

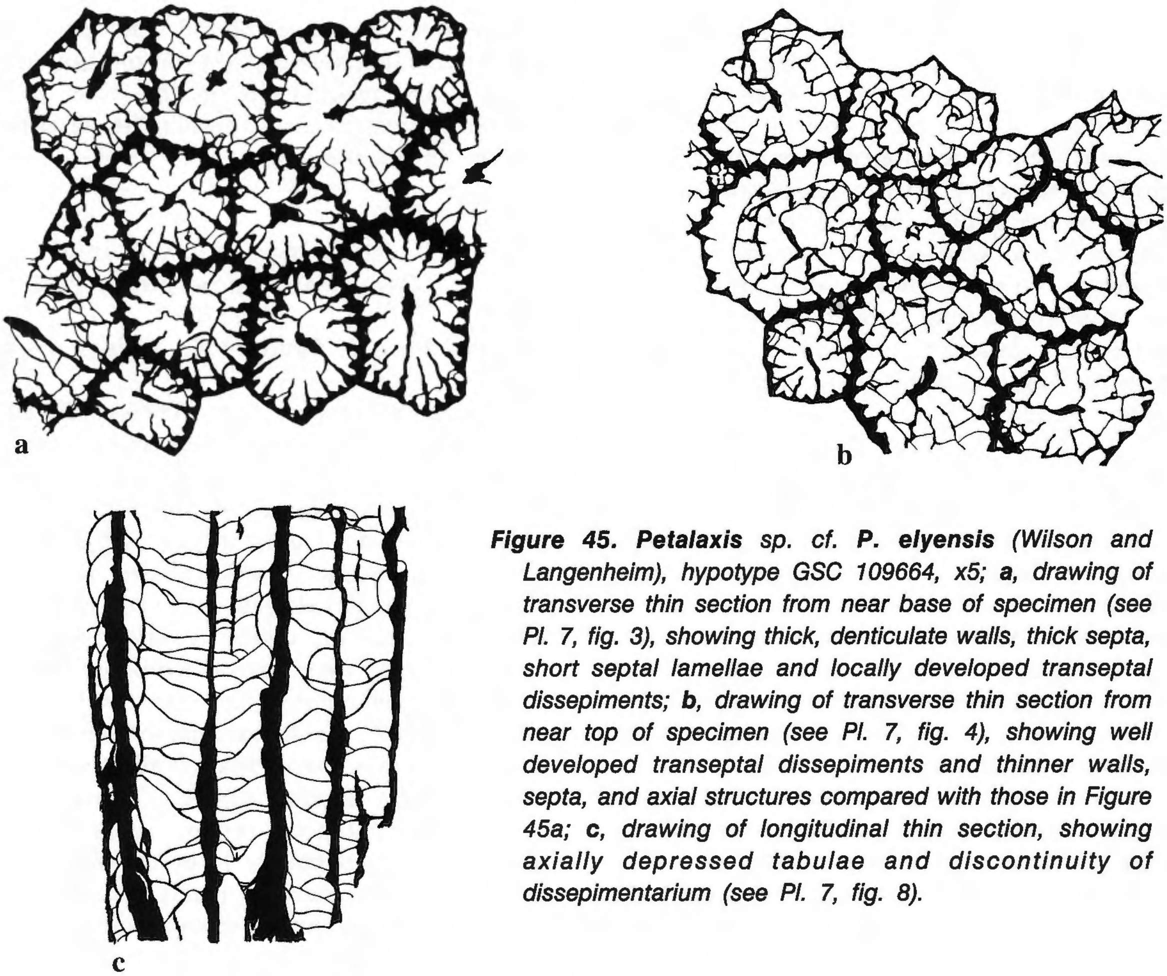


Figure 45. ***Petalaxis*** *sp. cf.* ***P. elyensis*** *(Wilson and Langenheim), hypotype GSC 109664, x5;* ***a****, drawing of transverse thin section from near base of specimen (see Pl. 7, fig. 3), showing thick, denticulate walls, thick septa, short septal lamellae and locally developed transeptal dissepiments;* ***b****, drawing of transverse thin section from near top of specimen (see Pl. 7, fig. 4), showing well developed transeptal dissepiments and thinner walls, septa, and axial structures compared with those in Figure 45a;* ***c****, drawing of longitudinal thin section, showing axially depressed tabulae and discontinuity of dissepimentarium (see Pl. 7, fig. 8).*

elevated; concave or approximately planar, less commonly slightly to strongly convex; incomplete tabulae consist of a few large, curved or (rarely) planar tabellae, most of which are convex, some strongly so; many tabulae join the axial structure at angles near 90°, others are slightly depressed at the axis, and a few are axially elevated; in all corallites studied, several complete tabulae slope downward from dissepimentarium to median lamella; biform morphology weakly expressed, peripheral parts of tabulae in position I moderately to strongly depressed adaxially, those in position II gently depressed adaxially, join dissepimentarium at angles near 90° or (rarely) are depressed toward it; 7-9 (rarely 11) tabulae in 5 mm of corallite length; where dissipementarium is developed, ratio of tabularium diameter to corallite diameter is 0.66-0.88 (commonly 0.72-0.78).

Dissepimentarium narrow, vertically discontinuous locally, varies in width approximately from one fifth to one third of corallite radius, boundary with tabularium generally distinct; dissepiments in one discontinuous row, occur as isolated, short series or are absent over considerable intervals in some corallites (Pl. 7, figs. 7, 8), mainly regular in some parts of corallum (Pl. 7, fig. 3), numerous transeptal dissepiments locally developed elsewhere (Pl. 7, fig. 4); dissepiments generally strongly inflated to globose in longitudinal section, some slightly flattened and elongate; all dissepiments steeply declined adaxially, many nearly vertical; where dissepiments form continuous series, five or six occur in 5 mm of corallite length.

In immature growth stages, wall separating young corallite from parent rarely incomplete at mean diameter of 1.25 mm (smallest corallite studied), complete at greater diameters; septa gently curved to sinuous, major septa other than cardinal septum withdrawn from axial area, cardinal septum long, forms part of axial structure, counter septum varies in length, may join axial structure; relationship between number of major septa and mean corallite diameter shown in Figure 46; minor septa first present, but incompletely developed as low ridges on wall at mean corallite diameter of 1.6 mm, completely developed, but very short at mean diameters of 2.5 mm and

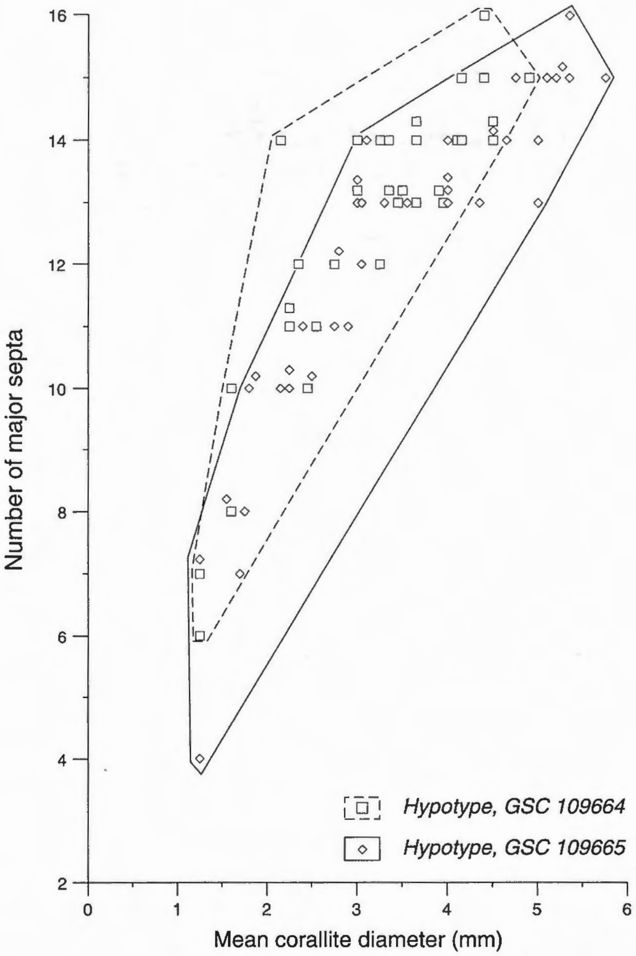


Figure 46. *Relationship between mean corallite diameter and number of major septa in* ***Petalaxis*** *sp. cf.* ***P. elyensis*** *(Wilson and Langenheim).*

greater; axial structure present in smallest corallite studied (mean diameter 1.25 mm), consists of slightly to strongly thickened lamella formed by thickened axial edge of cardinal septum, may extend well beyond corallite axis to join counter septum in earliest growth stages, septal lamellae absent or weakly developed at mean corallite diameters below 2.5 mm, lateral lamellae not developed in immature corallites; regular dissepiments rare.

Discussion. The above description is based on GSC hypotype 109664. Another specimen (GSC hypotype 109665), collected from the same locality (GSC loc. 60192; Pl. 7, figs. 9-12), has slightly larger corallite diameters than GSC hypotype 109664 (Fig. 46) and a well developed, almost continuous dissepimentarium with numerous regular and transeptal dissepiments and a width of one quarter to one third of the corallite radius. Where transeptal dissepiments are most numerous, the corallite walls and the median lamellae are relatively thin, the septa are thin and sinuous, the connection between the cardinal septum and the median lamella is vertically discontinuous and the axial structure is locally discontinuous (Pl. 7, fig. 11). Where regular dissepiments are more numerous, the thickness of these skeletal elements is greater, as in GSC hypotype 109664.

GSC hypotype 109664 resembles *P. elyensis* (Wilson and Langenheim), from the Lower Permian of Nevada, in its axial structure and in the nature of its septa and dissepimentarium. The Canadian specimen has more strongly concave tabulae and, in part, thinner walls than *P. elyensis.* Wilson and Langenheim (1962, p. 512) reported contratingent minor septa in the holotype of their species. From their transverse section (*ibid.*, Pl. 36, fig. 4), however, it appears that their specimen has normal minor septa that do not join the majors, but are connected to them by intercepts of small plates, possibly representing peripheral tabellae in a biform tabularium. Biform morphology is further suggested by the variation in slope of the peripheral parts of the tabulae in the corallite shown in longitudinal section on the right side of their Figure 6. The presence of numerous transeptal dissepiments in parts of both Ellesmere Island specimens suggests that variation in the dissepimentarium of the Canadian species may be similar to that in *P. elyensis* (*ibid.*, p. 511, 512, Pl. 88, figs. 4, 5).

Petalaxis sp. cf. *P. elyensis* is distinguished by its concave tabulae and numerous septal lamellae from *P. parvus* sp. nov. and *P. stylaxis* (Trautschold). It also has fewer transeptal dissepiments than either of these species, and its median lamella is less inflated than that in *P. parvus* sp. nov.

Material. Hypotypes, GSC 109664 and 109665, small fragments of colonies from GSC loc. 60192.

Occurrence and age. Petalaxis sp. cf. *P. elyensis* was found only in the southwest Blue Mountains (C) section (GSC loc. 60192, locality 9, Figs. 1, 7), where it occurs as clasts in a debris flow bed within the Hare Fiord Formation, approximately 173 m above the top of the "Tellevak" limestone in association with *C.* sp. aff. *C. carteri.* Kasimovian or lowest Gzhelian foraminifers are present in the matrix of the debris flow bed (Table 3, Appendices 1, 2). *Petalaxis* sp. cf. *P. elyensis* may be the same age as the foraminifers, or it may predate them, if derived from older strata during the debris flow. It has not been found in older strata. *Petalaxis elyensis* was reported by Wilson and Langenheim, 1962, p. 512) from the Lower Permian (Wolfcampian) of Nevada, U.S.A.

Genus *Cystolonsdaleia* Fomichev, 1953

Petalaxis (*Cystolonsdaleia*) Fomichev, 1953, p. 464-469; Soshkina et al., 1962, p. 339; Cotton, 1973, p. 64; Sutherland, 1977, p. 187; Cotton, 1984, p. 53.

Cystolonsdaleia Fomichev. Wu and Zhao, 1974, p. 271; Yu Xue-guang, 1976, p. 227(?); Kozyreva, 1978, p. 80; Hill, 1981, p. F401-403; Sando, 1983, p. 24, 36; Guo, 1983, p. 227(?); Rodriguez, 1984, p. 342-348; Yu Xue-guang, 1984, p. 106; Yu and Wang, 1987, p. 84; Huang Zhu-xi, 1988, p. 32(?), 33(?); Wu and Zhao, 1989, p. 131(?); Luo et al., 1989a, p. 121; Wu and Lin, 1992, p. 107(?).

Petalaxis Milne Edwards and Haime. Stuckenberg, 1888, p. 22(?); Sando, 1982, p. 239 (part); 1983, p. 35, 36 (part); Stevens and Rycerski, 1989, p. 178, 179; Luo and Xu, 1990, p. 680(?).

Acrocyathus (d'Orbigny). Sando, 1982, p. 238 (part); 1983, p. 21-23 (part), Pl. 17, figs. 3, 4; Sando and Bamber, 1985, p. 16 (part), Pl. 1, figs. 10, 11; Wang and Yu, 1986, p. 660, 661; (?)Zheng Chun-zi, 1986, p. 33, 34; Wang Zhi-gen, 1989, p. 531-533 (part), Pl. 1, figs. 2, (?)3a, b, 4a, b, 5a-c, Pl. 2, figs. (?)1a-c, 4a, b; Yu, 1989, p. 363(?); Wu and Zhao, 1989, p. 119-124; Luo et al., 1989a, p. 120; Luo and Qi, 1990, p. 703, 704, Pl. 4, figs. 1(?), 3(?), 4(?), 5.

Lithostrotion Fleming. Shimer, 1926, p. 27, 28 (part), Pl. 5, figs. 3, 4, 5; Bassler, 1950, p. 234.

Lithostrotionella Yabe and Hayasaka. Chi, 1931, p. 28(?); Hayasaka, 1936, p. 65, 66 (part); Kelly, 1942, p. 352 (part), Pl. 50, figs. 1, 2, 5, 6, 8; Parks, 1951, p. 180; Nelson, 1960, p. 114, 115 (part), Pl. 21, figs. 9-15, Pl. 22, figs. 1-3, p. 117-120 (part), Pl. 22, figs. 4-6, Pl. 23, figs. 3, 6-10; 1961, Pl. 14, figs. 3-5, Pl. 16, figs. 8, 9, Pl. 17, figs. 3-6, Pl. 18, figs. 4, 5; Pl. 26, figs. 1-4; Armstrong, 1962, p. 39, 40 (part), Pl. 3, figs. 13-15; Yu et al., 1962, p. 24(?); de Groot, 1963, p. 82 (part), Pl. 15, figs. 2a-d; Nations, 1963, p. 1257, Pl. 176, figs. 1, 2; Bamber, 1966, p. 19-23 (part); Armstrong, 1970, p. 31, 32 (part), Pl. 9, figs. 1-3, p. 35-37 (part), Pl. 12, figs. 8-11; Bamber and Copeland, 1970, Pl. 12, figs. 18a, b; Wang et al., 1978, p. 134(?) (part), Pl. 41, fig. 5(?); p. 135(?) (part), Pl. 41, fig. 2(?); Yu et al., 1978, p. 38-40; Wu et al., 1982, p. 123(?) (part), Pl. 4, fig. 9(?). Guo, 1983, Pl. 1, fig. 3(?); (?)Zheng and Cai, 1983, p. 152 (part).

Lithostrotion (*Lithostrotionella*) Merriam, 1942, p. 378; Bassler, 1950, p. 220, 221 (part).

Lonsdaleia McCoy. Dobrolyubova, 1935a, p. 12(?); 1935b, p. 29-32(?); Bassler, 1950, p. 222 (part); Crickmay, 1955, 1961, p. 13, 14; de Groot, 1963, p. 79; (?)Zheng and Cai, 1983, p. 201 (part); Wu and Zhao, 1989, p. 146(?) (part).

Lonsdaleia (*Actinocyathus*) Sando, 1982, p. 239; 1983, p. 37.

(?)*Protolonsdaleia* Lissitzin. Vasilyuk, 1960, p. 107.

Actinocyathus d'Orbigny. Minato and Kato, 1974, p. 70, 71 (part); Sando and Bamber, 1985, p. 16; Huang Zhu-xi, 1988, p. 31(?); Wang Zhi-gen, 1989, p. 533, 534; Luo and Qi, 1990, Pl. 4, fig. 6(?).

Kleopatrina (*Porfirievella*) Wilson, 1982, p. 63 (part), Figs. 37c-e.

Type species. *Petalaxis* (*Cystolonsdaleia*) *lutugini* Fomichev, 1953, p. 464, Limestone L_5, Upper Carboniferous, Moscovian (Kashirian), Donets Basin, Ukraine.

Diagnosis (*emended*). Cerioid; corallite walls fibrous, fibronormal or four-layered, commonly thickened where joined by septa. Septa of two orders, finely trabecular, thickened at corallite wall, usually discontinuous in dissepimentarium. Major septa commonly long and slightly sinuous. Minor septa usually well developed, but may be weakly developed as septal crests and ridges on corallite walls. Axial structure joined to cardinal septum; vertically continuous; ranges from simple axial plate to complex axial column consisting of median lamella, septal lamellae, discontinuous series of axial tabellae and periaxial cones, and lateral lamellae. Tabularium biform; tabulae subhorizontal to adaxially elevated; generally concave; some deflected distally to form periaxial cones in axial column. Dissepiments ordinarily transeptal. Increase lateral.

Taxa assigned to genus

Stuckenberg, 1888: *Petalaxis portlocki* E. H.(?).

Shimer, 1926: *Lithostrotion pennsylvanicum*.

Chi, 1931: *Lithostrotionella tingi*(?).

Dobrolyubova, 1935a: *Lonsdaleia ivanovi* Dobr.(?), *L. portlocki* (Stuck.)(?).

Dobrolyubova, 1935b: *Lonsdaleia ivanovi* Dobr.(?), *L. portlocki* (Stuck.)(?).

Hayasaka, 1936: *Lithostrotionella girtyi*.

Kelly, 1942: *Lithostrotionella pennsylvanica* (Shimer).

Merriam, 1942: *Lithostrotion* (*Lithostrotionella*) *berthiaumi*.

Parks, 1951: *Lithostrotionella* sp.

Fomichev, 1953: *Cystolonsdaleia lutugini*, *C. portlocki* (Dobrol.)(?).

Crickmay, 1955, 1961: *Lonsdaleia pennsylvanica* (Shimer), *Lonsdaleia shimeri*.

Nelson, 1960: *Lithostrotionella americana* Hayasaka(?), *L. pennsylvanica* (Shimer), *L. shimeri* (Crickmay), *L. stelcki*.

Vasilyuk, 1960: *Protolonsdaleia mariupoliensis* Liss.(?).

Nelson, 1961: *Lithostrotionella americana* Hayasaka(?), *L. pennsylvanica* (Shimer), *L. shimeri* (Crickmay), *L. stelcki.*

Armstrong, 1962: *Lithostrotionella shimeri* (Crickmay).

Yu et al, 1962: *Lithostrotionella tingi* Chi.

de Groot, 1963: *Lithostrotionella celadensis*, *Lonsdaleia portlocki* (Stuckenberg) *densiconus.*

Nations, 1963: *Lithostrotionella shimeri* (Crickmay).

Bamber, 1966: *Lithostrotionella pennsylvanica* (Shimer).

Bamber and Copeland, 1970: *Lithostrotionella pennsylvanica* (Shimer).

Armstrong, 1970: *Lithostrotionella pennsylvanica* (Shimer), *L. peratrovichensis.*

Wu and Zhao, 1974: *Cystolonsdaleia sinensis.*

Yu Xue-guang, 1976: *Cystolonsdaleia wenhuashanensis*(?).

Wang et al., 1978: *Lithostrotionella baijinensis* (Wang)(?), *L. changshunensis* (Wang)(?)

Kozyreva, 1978: *Cystolonsdaleia vassiljukae.*

Yu et al., 1978: *Lithostrotionella crassus*, *L. pennsylvanica* (Shimer), *L. shimeri* (Crickmay).

Hill, 1981: *Cystolonsdaleia lutugini.*

Wilson, 1982: *Kleopatrina* (*Porfirievella*) *zulloi.*

Wu et al., 1982: *Lithostrotionella jomdaensis* Wu(?).

Sando, 1983: *Petalaxis celadensis* (de Groot), *P. dobrolyubovae*(?), *P. donetsensis*, *P. ivanovi* (Dobrolyubova) (?), *Acrocyathus girtyi* (Hayasaka), *A. pennsylvanicus* (Shimer), *Lonsdaleia* (*Actinocyathus*) *berthiaumi* (Merriam), *L.* (*A.*) *peratrovitchensis* (Armstrong).

Guo, 1983: *Cystolonsdaleia hormos*(?), *C. obesa*(?), *Lithostrotionella ivanovi* (Dobrolyubova)(?).

Zheng and Cai, 1983: *Lithostrotionella pennsylvanium* (Shimer)(?), *L. shimeri* (Crickmay)(?), *Lonsdaleia simplex* Yu et al.(?).

Rodriguez, 1984: *Cystolonsdaleia portlocki* (Stuckenberg).

Yu, Xue-guang, 1984: *Cystolonsdaleia incerta*, *Acrocyathus intermedius*(?), *A. xinjiangensis* Wang and Yu(?).

Sando and Bamber, 1985: *Acrocyathus girtyi* (Hayasaka), *A. pennsylvanica* (Shimer), *A.*(?) *shimeri* (Crickmay), *Actinocyathus stelcki* (Nelson).

Wang and Yu, 1986: *Acrocyathus xinjiangensis.*

Zheng, 1986: *Acrocyathus solidum*(?), *A. kweichowense*(?), *A. orientalis*(?).

Yu and Wang, 1987: *Cystolonsdaleia incerta.*

Huang Zhu-xi, 1988: *Cystolonsdaleia jilinensis*(?), *C. panshienensis*(?), *C. tenuis*(?), *Actinocyathus elegantus*(?).

Stevens and Rycerski, 1989: *Petalaxis guaspariniae*, *P. neriae.*

Wu and Zhao, 1989: *Cystolonsdaleia major*(?), *Acrocyathus changshunensis*, *A. longiseptatus*, *A. major*, *A. sinensis*, *A. variabilis*(?), *A. zhanyiensis*, *Lonsdaleia* sp.(?).

Wang, 1989: *Acrocyathus grechovkae* (Degtjarev)(?), *A. pennsylvanica* (Shimer), *A. tingi* (Chi), *A. tingi proliferus*, *A. yohi*(?), *Actinocyathus densiconus* (de Groot), *A. lutugini* (Fomichev).

Luo and Qi, 1990: *Acrocyathus* sp.(?), *A. baijinensis* (Wang)(?), *A. sinensis*, *A. tingi* (Chi)(?), *Actinocyathus similus* (Dobrolyubova) (?).

Luo and Xu, 1990: *Cystolonsdaleia vesiculosa* (?).

Wu and Lin, 1992: *Cystolonsdaleia hongliangouensis*(?).

Discussion. *Cystolonsdaleia* was proposed as a subgenus of *Petalaxis* by Fomichev (1953, p. 464), for cerioid corals having transeptal dissepiments, concave, generally incomplete tabulae, and axial structures more complex than those of *Petalaxis* and resembling those in "primitive *Lonsdaleia*". He described the axial structure in *Cystolonsdaleia* as a well developed median lamella bearing radial lamellae and vesicular tissue on its lateral surfaces, and indicated that in some transitional forms the axial vesicular tissue is weakly developed or locally absent. In his description of the type species, *C. lutugini*, Fomichev (*ibid.*, p. 465, 466) stated that the axial vesicles are, in part, flattened and elongated along the median lamella, and that they may be rare and isolated in more simply constructed parts of the axial structure. Emended diagnoses were given for *Cystolonsdaleia* by Hill (1981, p. F401–F403) and Rodriguez (1984, p. 342). Hill (*ibid.*), who re-illustrated the holotype of *C. lutugini*, referred to the axial structure as a narrow axial column with a thickened medial plate, short, thickened radial lamellae and widely spaced, steeply inclined axial tabellae.

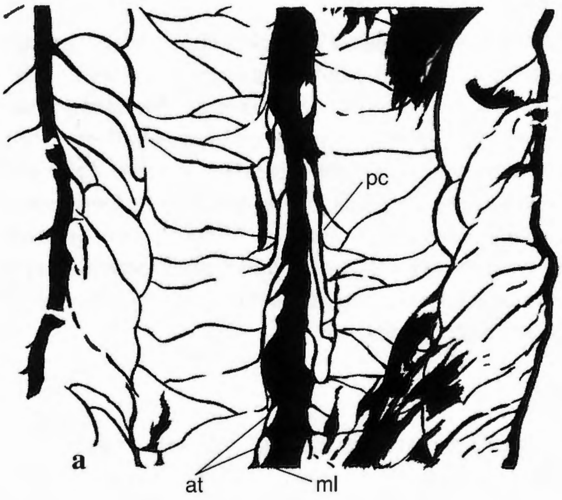
The longitudinal section illustrated by Fomichev (1953, Pl. 33, fig. 2) and Hill (1981, p. F402, fig. 263.1b) shows biform morphology in the tabularium of the holotype. This is best expressed on the right side of this section, where the intercept of a septum separates steeply declined, convex tabellae in the upper part of the section from concave, subhorizontal to moderately declined tabellae in the lower part.

The morphology of *Cystolonsdaleia* from Ellesmere Island corresponds to that described for the type species in most respects, including growth form, presence of transeptal dissepiments, nature of the tabularium and major septa, and the presence of an axial column comprising a thickened median lamella, septal lamellae, and discontinuous series of axial tabellae. In addition, the axial parts of some tabulae in the Ellesmere species are steeply elevated near the median lamella and extend distally along the axial column to form irregular, incomplete conical structures that partly enclose other structural elements of the column. These vertical extensions of tabulae are herein termed *periaxial cones* (Figs. 47, 48b, 54b, 56b; Pl. 7, figs. 14, 15; Pl. 8, figs. 2-5, 7-9, 11). They may develop on only one side, or simultaneously on both sides of the counter-cardinal plane and may also incorporate vertically elongated axial tabellae. Commonly, the subhorizontal or slightly elevated parts of one or more subsequently formed tabulae terminate adaxially against a periaxial cone. Lateral lamellae, similar to those found in *Petalaxis* but less numerous, are also present in all of the Canadian species described below. They do not appear in the transverse section of several corallites from the holotype of *C. lutugini*, illustrated by Fomichev (1953, Pl. 33, fig. 2a). In the longitudinal illustrations of this specimen (Fomichev, 1953, Pl. 33, fig. 2b; Hill, 1981, p. F402, fig. 263.1b) there appear to be several examples of periaxial cones, represented by steeply elevated axial parts of tabulae and vertically extended axial tabellae. Other tabulae terminate adaxially against them, as in the Ellesmere specimens. These structures, combined with axial tabellae, were referred to by Fomichev (1953, p. 464) as axial vesicular tissue and were not described by him in detail. The type specimen is not available to the authors for study, and therefore the degree to which periaxial cones are developed in its axial column could not be investigated. A specimen of *C. lutugini* from the Donets Basin was obtained for study from Dr. N. P. Vasilyuk through the kind cooperation of Dr. T.I. Nemirovskaya. It is from Limestone L_5 (lower Moscovian, Kashirian), on the right bank of the Lugan River, at Golubovka (formerly Kirovsk) Village in the Luganskaya region, Ukraine (GSC loc. C-147802). The axial columns of this specimen (hypotype GSC 109666) have periaxial cones, vertically discontinuous series of axial tabellae, lateral lamellae and a variable number of septal lamellae attached to the median lamellae (Pl. 9, figs. 16-19; Fig. 48b). Its tabularium shows biform morphology similar to that in Fomichev's holotype (Pl. 9, fig. 16). Other features of GSC 109666 are also similar to those of the holotype, including the concave, incomplete tabulae, the wide, variable dissepimentarium, the long major septa, the short minor septa, and the ratio between the mean diameter of mature corallites (12.5-15.5 mm) and the number of major septa (20-24). The single specimen available is insufficient material for a detailed redescription of *C. lutugini*.

In her description of *C. vassiljukae* from the Bashkirian of Ukraine, Kozyreva (1978, p. 80) stated that the axial tabellae have the form of dissepiments lengthened along the median lamella. She further stated (*ibid.*) that the "cone in cone" structure typical for Lower Carboniferous *Lonsdaleia*, in which the upper margins of axial tabellae join the median lamella and the lower margins rest on underlying axial tabellae, was not observed in her new species. Her illustration of a longitudinal section from the holotype of *C. vassiljukae* (*ibid.*, Pl. 2, fig. 3d, corallite at upper right) shows the vertically elongated, axial part of a tabula forming a periaxial cone. These structures have also been described but not named in corals from several areas. De Groot (1963, p. 79), in her description of *C. densiconus* (de Groot) from the upper Moscovian of Palencia, Spain, stated that the tabellae in its axial structure are locally replaced by "steeply conical inner ends of tabulae". Armstrong (1970, p. 36) described tabulae that are sharply reflexed upward near the median lamella and extend parallel to it for some distance in the axial column of *C. peratrovichensis* (Armstrong), from the upper Viséan of southeastern Alaska. Similar axially steepened, vertically elongated tabulae were described by Bamber (1966, p. 20, 21) in the lectotype of *C. pennsylvanica* (Shimer), from the upper Viséan of southwestern Alberta, Canada.

Cystolonsdaleia neriae and *C. guasperiniae*, from Lower Permian (Asselian?) limestone of the Stikine assemblage of northwestern British Columbia, were assigned to the genus *Petalaxis* by Stevens and Rycerski (1989, p. 178, 179). Both species are here included in *Cystolonsdaleia* because they possess periaxial cones typical of that genus. These structures are evident in an illustrated longitudinal section of *C. neriae* (*ibid.*, fig. 13-2), and they are present in new longitudinal sections prepared from the holotype of *C. guasperiniae* for the present study.

Many of the species from China and North America that are here included in the genus *Cystolonsdaleia* were previously assigned to *Acrocyathus*, *Lithostrotionella* or *Actinocyathus*. Periaxial cones appear to be present in the published illustrations of all of the re-assigned Chinese species listed in the synonymy above. *Lithostrotionella tingi* Chi (1931, p. 28) has elevated tabulae and its axial structure shows steeply elevated tabular plates similar to those in *Cystolonsdaleia*. This species was assigned to *Acrocyathus* d'Orbigny by Wang (1989, p. 532), but is tentatively re-assigned to *Cystolonsdaleia* by the authors. The nature of the axial structure is not clear from the illustrations given by Chi (*ibid.*, Pl. 4, figs. 6a, b).



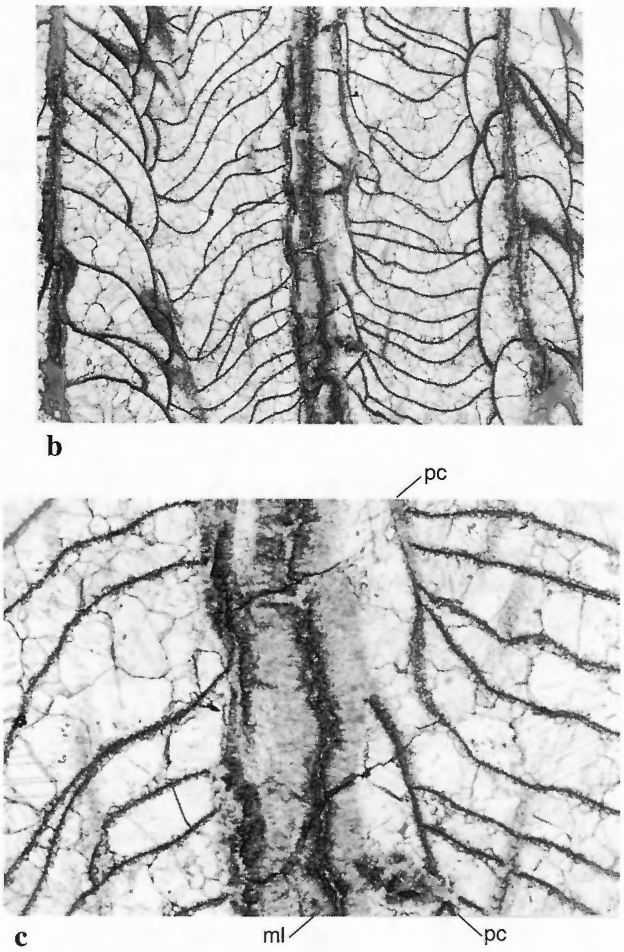


Figure 47. Longitudinal sections of axial column in ***Cystolonsdaleia****; a,* ***Cystolonsdaleia*** *sp., hypotype GSC 109667, drawing of longitudinal thin section of mature corallite (see Pl. 7, fig. 15), showing periaxial cones (pc) and axial tabellae (at) attached to median lamella (ml), x10;* ***b, C. arctica****, paratype GSC 109669, longitudinal thin section (see Pl. 8, fig. 11) showing periaxial cones on right side of axial column, in part separated from median lamella by intercepts of lateral or septal lamellae, x10;* ***c****, enlargement of lower part of Figure 47b, showing junction between periaxial cone and fibrolamellar tissue of median lamella, x30.*

Some of the Lower Carboniferous (Viséan) North American species, formerly included in *Lithostrotion*, *Lithostrotionella* and *Lonsdaleia* (see generic synonymy, above) are now referred to *Acrocyathus* by several authors (Easton, 1973; Sando, 1983; Sando and Bamber, 1985). A review of these species, however, has shown that periaxial cones are present in all cerioid forms from the Western Interior Province, but are absent from all species occurring to the east, in the mid-continent area of the U.S.A. The western North American species that we have assigned to *Cystolonsdaleia* include *C. girtyi* (Hayasaka), *C. pennsylvanica* (Shimer) and *C. shimeri* (Crickmay). Three other western North American species - *C. berthiaumi* (Merriam), *C. peratrovichensis* (Armstrong) and *C. stelcki* (Nelson) - have previously been referred to *Actinocyathus* (Sando, 1983, p. 37; Sando and Bamber, 1985, p. 16), but all have well developed periaxial cones, and therefore belong to the genus *Cystolonsdaleia*.

In our discussion of the genus *Petalaxis*, we noted that *Cystolonsdaleia* and *Petalaxis* have several morphological features in common with *Lithostrotionella* Yabe and Hayasaka, as exemplified by published illustrations of an obliquely oriented thin section from the lectotype of the type species, *L. unica* Yabe and Hayasaka (Minato and Kato, 1974, p. 72, 73; Hill, 1981, p. F403, Fig. 264.1). Transeptal dissepiments and axially elevated tabulae are well expressed, and the corallite in the upper left corner of the illustration (*ibid.*) shows a biform tabularium and vertical elements in its axial structure representing either septal lamellae or lateral lamellae adjacent to the median lamella. It also shows a possible periaxial cone to the right of the median lamella, which suggests a close relationship between this specimen and those assigned by us to *Cystolonsdaleia*. The existence of periaxial cones in *L. unica* cannot be confirmed from the published illustrations (*ibid.*), however, and there is no clear indication of axial tabellae, which are characteristic for *Cystolonsdaleia*. Without new information on the axial structure of *L. unica*, based on additional specimens from its type locality, the relationship between *Lithostrotionella* and *Cystolonsdaleia* will remain unresolved.

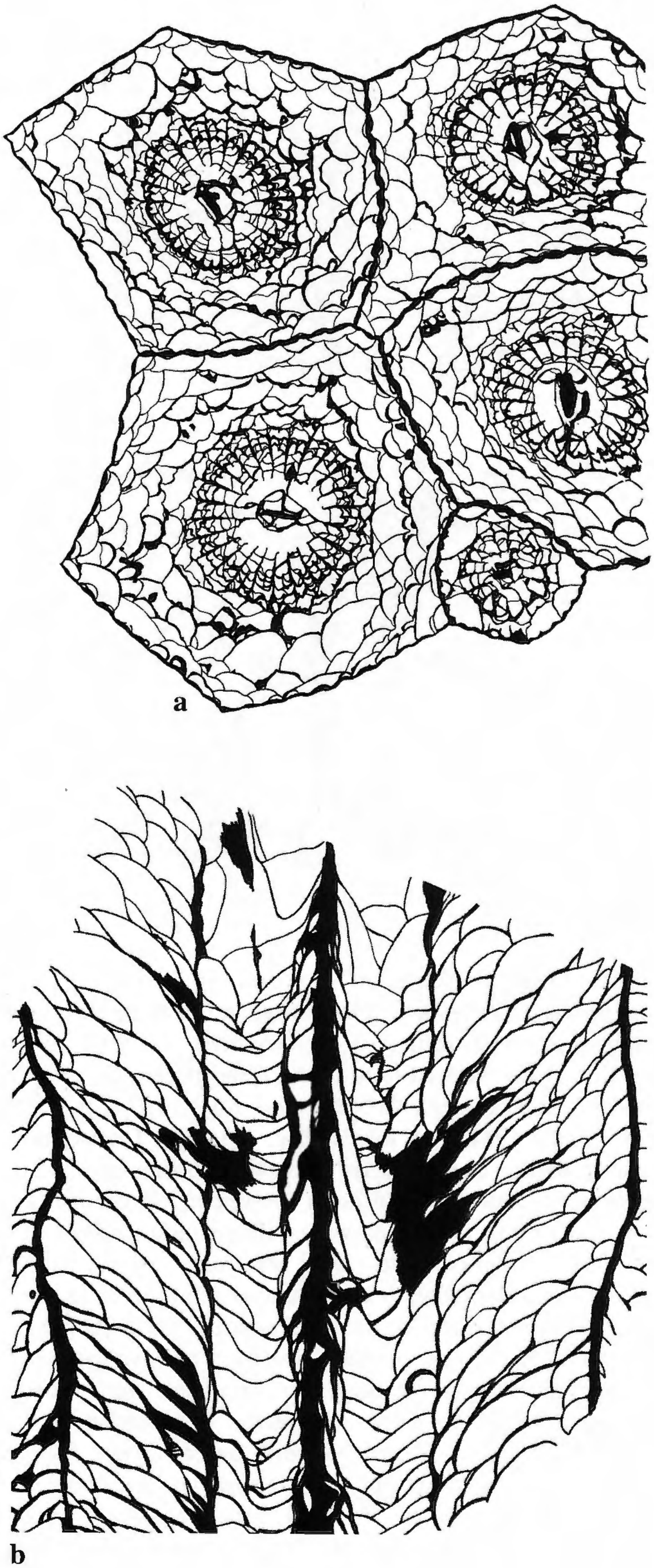


***Figure 48. Cystolonsdaleia lutugini** Fomichev, hypotype GSC 109666, from Luganskaya region, Ukraine, GSC loc. C-147802; **a**, drawing of transverse thin section (see Pl. 9, fig. 15), showing wide dissepimentarium, short minor septa, lateral lamellae (corallite at lower right) and numerous septal lamellae, x3; **b**, drawing of longitudinal thin section (see Pl. 9, fig. 19), showing two periaxial cones on right side of axial column, short series of axial tabellae and lateral or septal lamella crossing tabulae to left of median lamella, x6.*

Morphology. *Cystolonsdaleia* closely resembles *Petalaxis* in the morphology of all of its skeletal structures except the axial structure, which is a poorly defined axial column characterized by the presence of periaxial cones, discontinuous series of axial tabellae, few lateral lamellae, and the consistent occurrence of septal lamellae (see below). Its biform tabularium and periaxial cones also distinguish *Cystolonsdaleia* from other similar cerioid corals having complex axial structures and transeptal dissepiments (e.g., *Actinocyathus* d'Orbigny, *Porfirievella* Minato and Kato). *Cystolonsdaleia* ranges in age from Viséan to Early Permian (Asselian) and is represented by numerous species, many of which are incompletely described and illustrated. Those from the Serpukhovian and Bashkirian of western North America are mainly undescribed. Therefore, no comprehensive morphological treatment of the genus was attempted for this paper. The following descriptions of its structural elements and the emended diagnosis given above are based mainly on species from Ellesmere Island (Table 5). Additional information was derived from published descriptions and illustrations of the holotype of *C. lutugini* Fomichev and from the specimen of that species from Ukraine (GSC 109666; Pl. 9, figs. 15-19; Fig. 48), sent to the authors by N.P. Vasilyuk.

Wall structure. All specimens available for this study have been recrystallized, but local preservation of the original structure permits several observations to be made. In transverse section, the wall has a denticulate or beaded appearance, caused by local thickening from addition of attached septal tissue. Depending on the distribution of septal tissue, the wall may be planar (Fig. 49a) to highly sinuous (Fig. 49b), as described above for *Petalaxis*. Septal thickening of the wall is strongest in those species in which transeptal dissepiments are weakly developed (e.g., *C. carteri* sp. nov., Pl. 9, figs. 1, 4, 8).

Under the light microscope, it appears that the corallite walls in *Cystolonsdaleia* generally have septal microstructure, similar to that seen in the early stages of wall development in *Petalaxis* (see above). The four-layered wall, typical of mature corallites in *Petalaxis*, appears to be less commonly developed in *Cystolonsdaleia*. Wall development was studied in a series of sixteen thin sections cut at intervals of 0.3-0.4 mm through several corallites of *Cystolonsdaleia* sp. aff. *C. carteri* (GSC hypotype 109675). Full reconstruction and satisfactory photographic documentation of the growth of the wall was limited by diagenetic alteration of the specimen. Also, comparison of our specimen with others was prevented by lack of detailed information on the wall structure in the type species and other species of *Cystolonsdaleia*. Therefore, the data presented below may not be typical for the entire genus.

In all corallites that were serially sectioned, there is a close relationship between the septa of offsetting corallites and the dividing wall; the latter appears at an early stage of development. The offset begins with the appearance of outgrowths, having trabecular microstructure, on the lateral surfaces of several septa of the parent corallite. These outgrowths form the foundations of the new, dividing wall (Fig. 50a, left centre). Initially isolated outgrowths soon coalesce to form connections between adjacent septa (Fig. 50a, right centre).

Following the above stage, a segment of the dividing wall is formed by growth of calcite crystals concentrated in the central part of the zone common to the parent and offset. The new wall bears a few new septa on the side of the parent, but none on the side of the offset (Fig. 50b). A dark, medial zone of undetermined microstructure is present in the wall, which appears to have a slightly recrystallized, fibronormal microstructure. At this early stage, the margins of the new wall are not connected to either the septa or the wall of the parent corallite, but in a section 0.3-0.4 mm higher in the series, both margins have joined parent septa (Fig. 50c). At this higher level, the medial dark line has moved toward the periphery of the dividing wall adjacent to the parent, where secondary sheets of fibrous calcite have almost totally disappeared. They are well developed on the opposite side of the wall, however, where the first septum (s.o.) of the offset has appeared (Fig. 50c). From the sequence of structural changes illustrated in Figures 50b and c, it is evident that major and minor septa are inserted alternately and that, following its insertion, a minor septum moves away from the preceding major septum during growth of the dividing wall. Further development of the dividing wall is marked first by the insertion of new

Table 5

Characteristic features of species of *Cystolonsdaleia* from Ellesmere Island. DT/DC, ratio of tabularium diameter to corallite diameter (most commonly occurring values for number of septa, mean corallite diameter and DT/DC given in brackets.)

Species	Mean Corallite Diameter (mm)	Number of Major Septa	Septa	Axial Structure	Median Lamellae	Septal Lamellae	Lateral Lamellae	Periaxal Cones	Axial Tabellae	Tabulae	Dissepimentarium	DT/DC
Cystolonsdaleia arctica sp. nov.	4.5-7.25 (5.5-7)	17-22 (19-22)	Thin; majors long; minors long, variable	Continuous; thickness variable	Commonly thick, curved or sinuous	Numerous, variable in shape and length	1, rarely 2	Locally well, developed, long	Locally numerous, up to 6 in series	Mainly complete, concave, slightly to moderately elevated adaxially, tabellae in 2 series, 11-15 in 5 mm	Continuous, transeptal; dissepiments small to large, flattened to convex, steeply declined, in 1-3 rows	0.6-0.83 (0.67-0.75)
C. carteri sp. nov.	3.2-5.4 (3-5)	12-18 (13-17)	Thin, locally thickened; majors long; minors variable in length	Continuous; thickness variable; forms solid rod locally	Thick, locally thin, curved or sinuous	Numerous, straight to sinuous, generally short and thick	1, consistently developed	Locally well developed to rare, short to long	Locally numerous, up to 4 in series	Generally complete, concave and depressed adaxially; 8-14 in 5 mm	Discontinuous, narrow, transeptal dissepiments rare to locally numerous; dissepiments generally small, convex to flattened, steeply declined, in 1 to 5 rows	0.6-0.86 (0.67-0.75)
C. sp. aff. *C. carteri*	3.5-5.5 (3-5.5)	12-18 (13-17)	Thin, wedge-shaped; majors long; minors variable in length	Continuous; thickness variable	Variably thickened, straight to sinuous	Locally numerous; short and thick	1, rarely 2	Weakly developed, short	Relatively rare, isolate or in short series of up to 3	Generally complete, concave to planar, slightly elevated adaxially; 10-14 in 5 mm	Discontinuous, narrow; transeptal dissepiments locally developed, dissepiments generally small, convex, steeply declined, in 1 to 3 rows	0.62-0.79 (0.7-0.76)
C. sp.	4.75-8.2 (6-8)	14-18 (17-18)	Wedge-shaped, straight to sinuous; majors long; minors long	Continuous; thickness variable, locally forms solid rod	Normally thick, straight or curved	Locally numerous, short and thick to long and thin	Rare	Numerous, long	Weakly developed, up to 4 in series	Generally complete and concave, axially depressed to elevated; 8-11 in 5 mm	Continuous, transeptal, dissepiments mainly large, strongly convex to elongate and flattened, moderately to steeply declined, in 1-3 rows	0.60-0.77 (0.67-0.69)

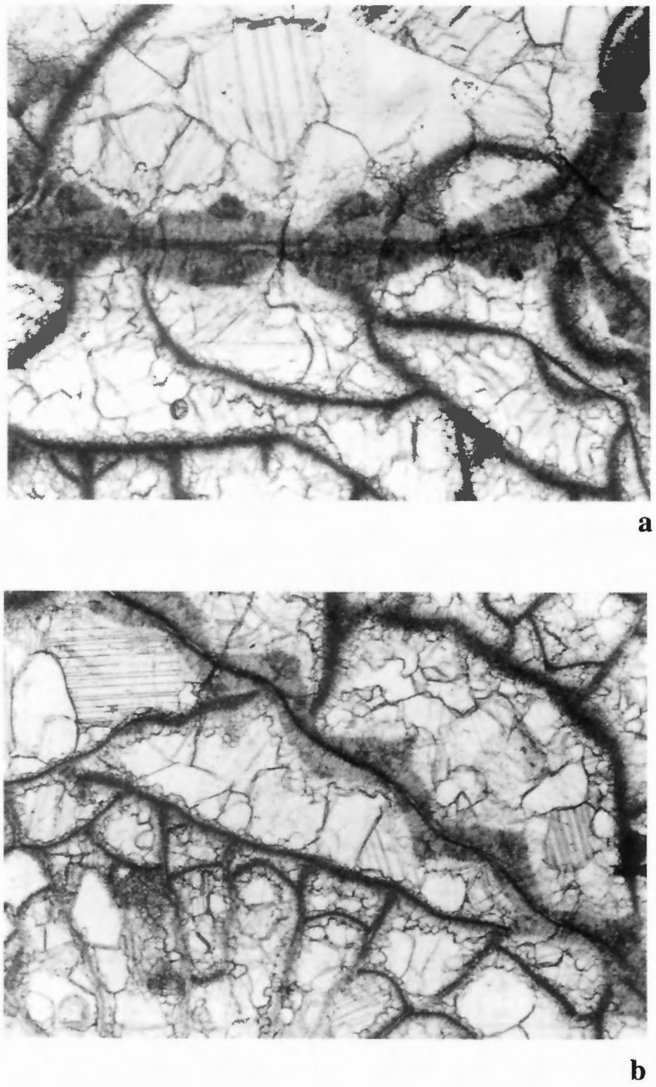


*Figure 49. Denticulate corallite wall of **Cystolonsdaleia arctica** sp. nov. with apparent four-layered structure; **a**, paratype GSC 109669, transverse thin section of approximately planar wall bearing peripheral parts of opposing septa from adjacent corallites, x30; **b**, holotype GSC 109668, transverse thin section of sinuous wall, thickened by peripheral parts of offset septa from adjacent corallites, x30.*

septa that extend into the offset (Figs. 50d, e). The insertion pattern of these septa has not been established, but the cardinal septum, from which the columella developed, appeared on the new dividing wall. Segments of this wall appear to consist of four layers (Fig. 50d, left), but the apparent separation of the median dark layer into two parts may also be the result of diagenetic alteration. Individual septa of the parent corallite may deeply penetrate the tabularium of the offset (Fig. 50d, e, left) to form part of its septal apparatus.

Consolidation of the dividing wall may involve the entire area common to the parent and offset polyps (Fig. 50f). In such instances, interseptal segments of the wall ("dark lines") form a chain extending along the bases of the parent septa. These "dark lines" are undoubtedly septal in microstructure, although it has not been established whether they consist of closely packed, small trabeculae or are fibronormal. As in other sectioned corallites from this specimen, there are no septa on the offset side of the dividing wall at this growth stage.

Although the dividing wall consistently becomes attached to either a septum or the foundation of septum in the parent corallite, the mode of attachment may vary considerably. This may be true even for the two margins of the same dividing wall. For instance, in one of the corallites observed (Fig. 50g), the right margin of the partly developed dividing wall is attached along its planar, lateral surface to the base of a septum (SB). A major and a minor septum of the parent corallite have already been inserted along this attachment zone. The opposite (left) margin of the dividing wall curves sharply toward a minor septum (Mi) of the parent corallite, and is connected to it by a skeletal body (B) consisting of randomly oriented calcite crystals. This structure is thought to have been formed in an elongate invagination of the basal disc, within which the septal microstructure of the dividing wall will continue to develop. At the same (left) margin (Fig. 50g), a major septum (MS) on the opposite (parent) side of the wall appears to have originated as a lateral outgrowth from a major septum attached to the wall of the parent. This curved outgrowth will become attached to the new dividing wall, whereas the main, peripheral part of the septum will remain attached to the old, parent wall. Thus, one major septum of the parent will divide to form two septa. Evidence for the beginning of this division is provided by the presence of a secondary sheet of calcite fibres that covers the peripheral part of the newly formed septum and is continuous with the adjacent part of the dividing wall. We have included this detailed discussion to stress the high degree of morphological variation possible in these rugose corals during the formation of offsets and the creation of the new septal apparatus of both the parent and the offset.

In most corallites studied, the margin of the dividing wall grew toward the septum to which it is attached (i.e., opposite to the direction of growth of the septum; Fig. 50h). Less commonly, the wall grew in the same direction as the septum (Fig. 50i). We interpret these two modes of growth as representing two successive steps in the development of the dividing wall. In the first instance (Fig. 50h) the epidermal folds that

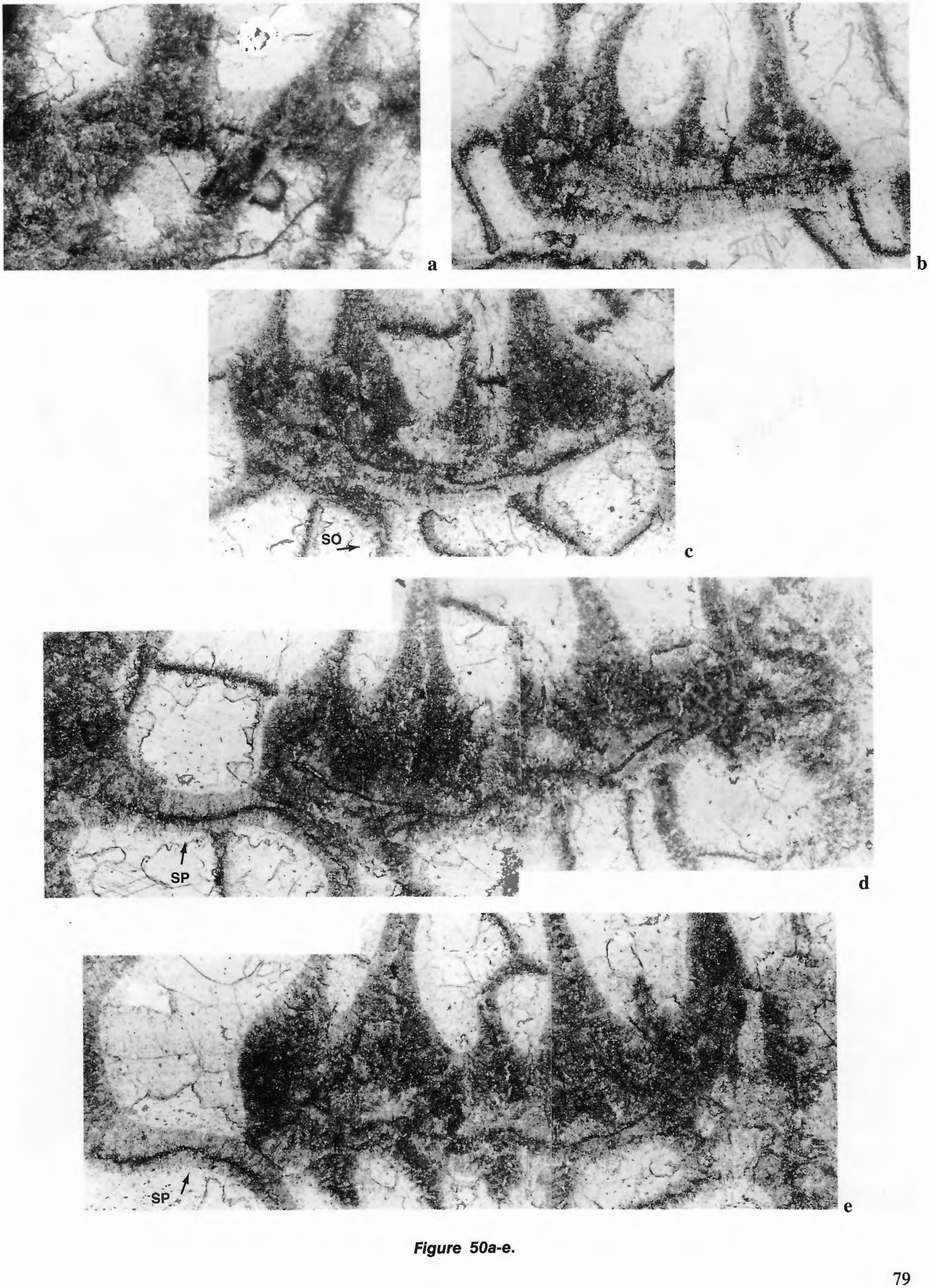


Figure 50a-e.

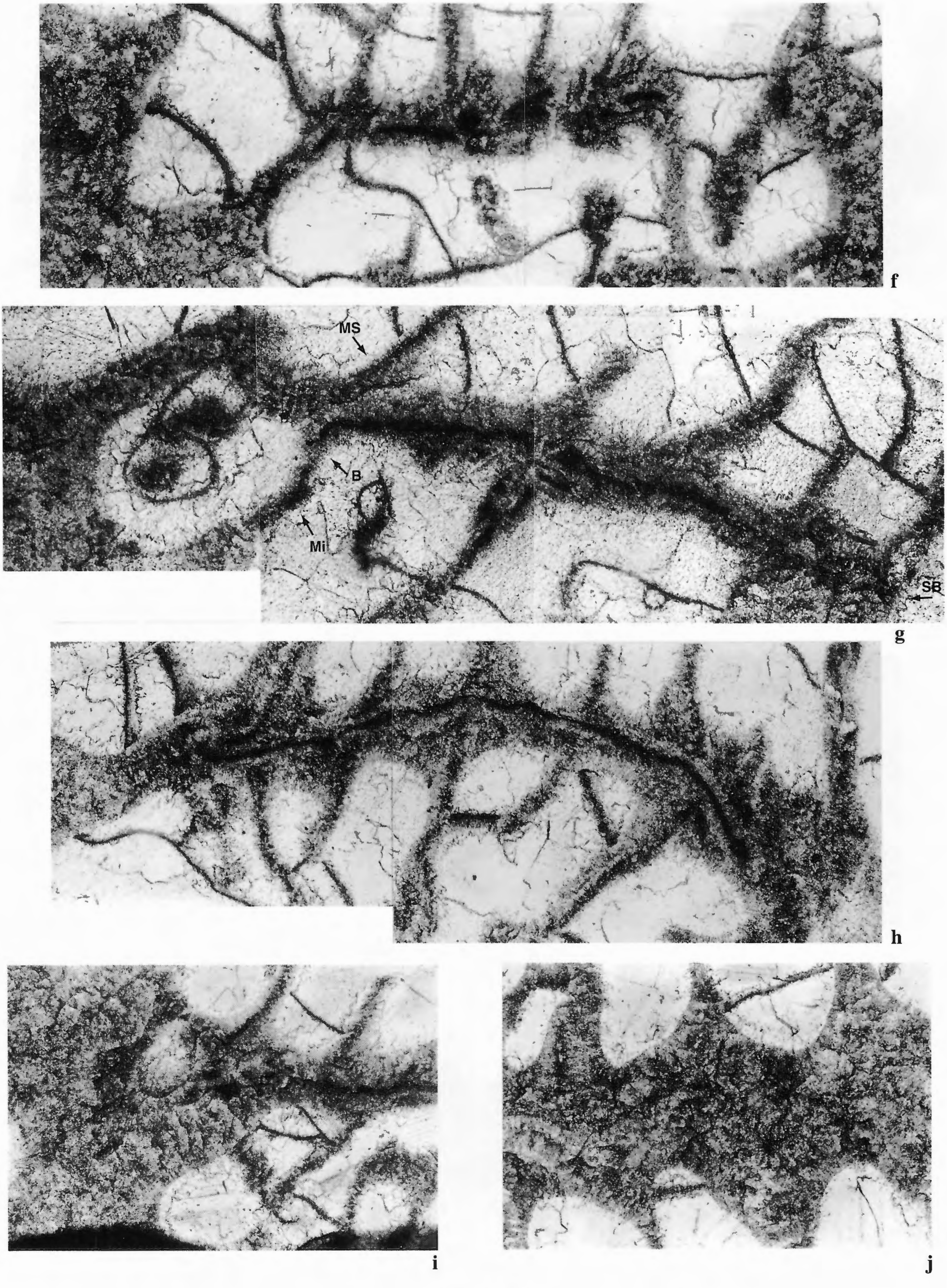


Figure 50f-j.

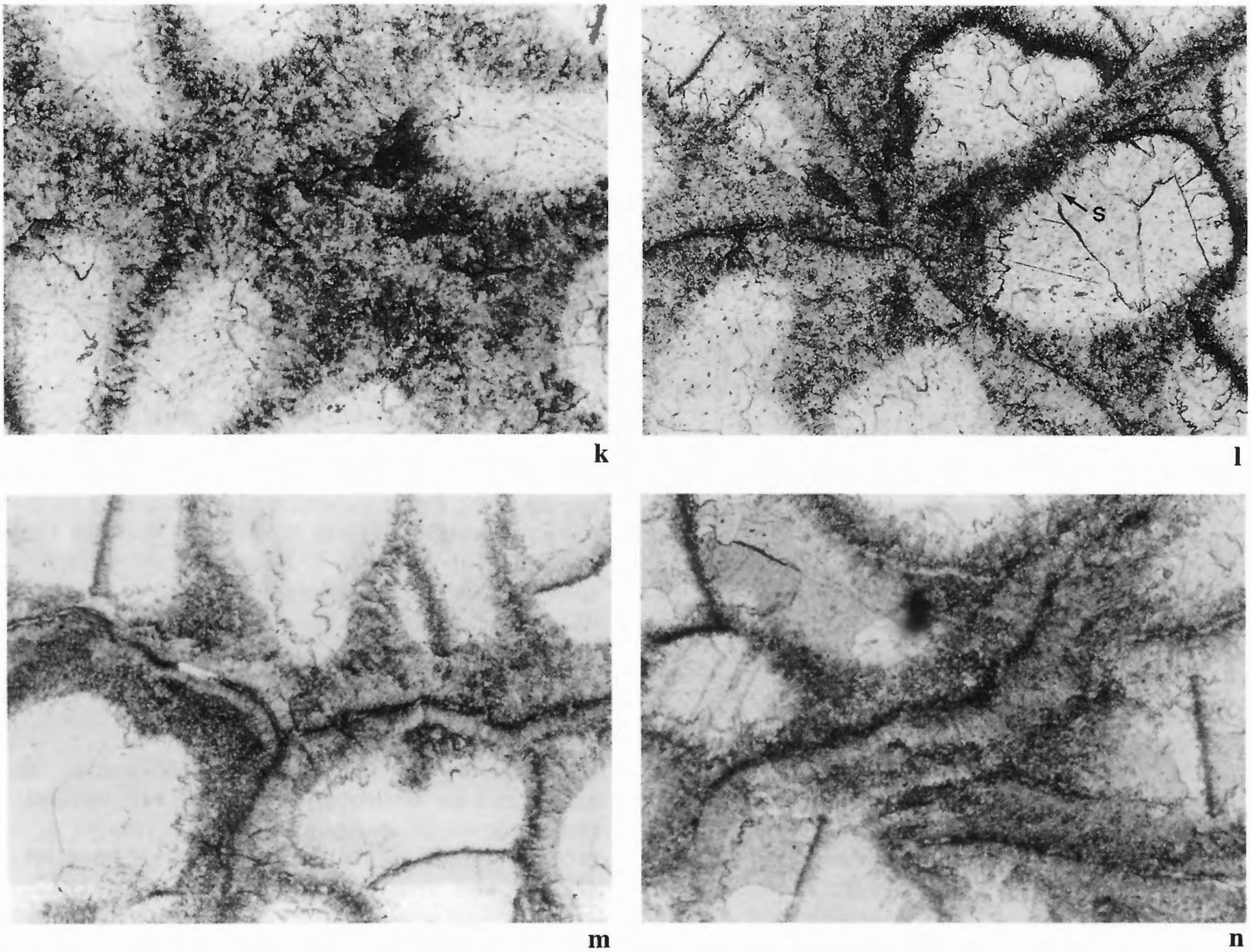


Figure 50. Wall development in ***Cystolonsdaleia*** *sp. aff.* ***C. carteri*** *(hypotype GSC 109675), x70;* ***a****, earliest stage of development of dividing wall, formed by lateral outgrowths from septa;* ***b****, earliest consolidated part of dividing wall, located in middle of parent/offset common area; septa developed only on parent side of wall;* ***c****, further development of dividing wall shown in b, first septum (SO) inserted on offset side of wall;* ***d****,* ***e****, both margins of dividing wall attached to parent septa, parent septum (SP) at left has penetrated tabularium of offset to become part of offset septal apparatus;* ***f****, early growth stage of dividing wall showing chain of wall segments at bases of parent septa; septa of offset not yet developed;* ***g****, different attachment modes of dividing wall – to septal base (SB) at right, and to axial margin of minor septum (Mi) through intermediate skeletal body (B) at left; also shows division of parent septum (left) into two parts – peripheral part remains attached to parent wall, axial part has grown laterally to form major septum (MS) on new wall;* ***h****, dividing wall with growth direction at both margins opposite to that of secondary septal sheets to which wall is attached;* ***i****, growth direction of dividing wall continuous with that of septum to which it is attached (middle of photo);* ***j****, septal microstructure of wall separating two mature corallites;* ***k****, junction of walls with septal microstructure (left centre), separating three adjacent, mature corallites;* ***l****, junction of three mature corallite walls with either fibronormal or four-layered structure; septum (S) attached at junction;* ***m****, junction of three mature corallite walls – wall at left appears to be four-layered, wall at right appears to be mainly fibronormal and wall in lower part of photo appears to be at least partly septal in microstructure;* ***n****, walls of two adjacent corallites with only their secondary, fibrous layers in contact and their median, dark layers completely isolated.*

secreted the wall margin and the septum remained isolated from each other, whereas in the second (Fig. 50i), they united to form a single fold in which the dividing wall, which has septal microstructure, was secreted. In most of the corallites sectioned, this appears to be the last step in the development of the dividing wall, judging by the fact that the mature wall generally shows fairly obvious septal microstructure (Figs. 50j, k). Other corallites, however, show the possible development of a four-layered wall (Figs. 50l, m; also see Figs. 50a, b), but we cannot be certain whether this is original microstructure or the product of diagenesis. We tentatively conclude that *Cystolonsdaleia* sp. aff. *C. carteri* sp. nov. has four-layered walls, as well as those with the more commonly occurring septal microstructure. The predominance of septal microstructure in the walls would indicate a high degree of integration of the polyps in this species, with only local separation of neighboring individuals in those parts of the colony with four-layered walls.

In rare instances, two complete, external walls of adjacent corallites, both apparently with four layers, may be in contact laterally (Fig. 50n). Such a structural arrangement indicates that the adjacent polyps were fully integrated during the formation of these walls. If this were so, however, one would expect fibronormal, rather than four-layered wall structure. Therefore, it is possible that at least some of the corallite walls in this specimen originally had fibronormal microstructure, but have been diagenetically altered to an apparent four-layered structure.

Septa. *Cystolonsdaleia* has two orders of wedge-shaped septa that generally are thickest in the outer dissepimentarium and become thinner adaxially and toward the periphery. All septa are thickened where they join the wall. In species with few transeptal dissepiments, the septa are generally thickest at the corallite wall and become thinner adaxially. Transeptal dissepiments interrupt the septa to some extent in all species studied. The major septa may be straight, curved or sinuous. They range from thin to thick and their axial margins are commonly curved or sharply deflected laterally. They are generally long, vary in length vertically, and may closely approach the axial column, but rarely join it. The cardinal septum, which was identified, as in *Petalaxis*, by the pattern of septal insertion (see discussion of blastogeny, below), is commonly slightly thicker than adjacent major septa (Pl. 8, figs. 1, 6, 10). It is thickened along its axial margin to form the median lamella and becomes detached from the latter at one or more levels to form vertically discontinuous lateral lamellae (Fig. 52a-g). The counter septum varies in length vertically. Its length equals or is slightly less than that of adjacent major septa and it may closely approach or reach the axial column at some levels.

In the Ellesmere Island species, the minor septa are well developed and variable in length, with the longest occurring in species having numerous transeptal dissepiments. *Cystolonsdaleia lutugini* Fomichev has short, weakly developed minor septa almost entirely confined to the dissepimentarium (Pl. 9, fig. 15; Fomichev, 1953, p. 465, Pl. 33, fig. 2a).

Septal microstructure is poorly preserved in the species from Ellesmere Island and in GSC 109666 from Golubovka, Ukraine. In transverse section, the septa appear to be finely trabecular, but no details of the trabecular structure can be determined. With the kind permission of Professor S. Rodriguez, well preserved specimens of *Cystolonsdaleia* described by him (Rodriguez, 1984) from the Cantabrian Mountains of Spain were re-examined for the present study. As mentioned previously, they show fine trabeculae, similar to those in *Petalaxis*.

Axial structure. In the Ellesmere Island species, the axial structure is strongly developed and vertically continuous in all specimens studied. It consists of a median lamella, septal and lateral lamellae, discontinuous series of axial tabellae, and periaxial cones (defined above), all of which combine to form an axial column (Hill, 1981, p. F401) of variable width and complexity. In some specimens, the axial column may be thickened by stereoplasm to form a broad lens in transverse section, in which the structural details are partly obscured (Pl. 9, fig. 4). Of the elements in the axial column, only the median lamella occurs consistently at all levels in all corallites. Both the septal lamellae and the lateral lamellae are vertically discontinuous and the number of the former varies considerably along any corallite (Fig. 51a-c; maximum of 12 observed). Generally only one (rarely two) lateral lamellae are developed at any level in a corallite. Axial tabellae form short, vertically discontinuous series or occur as isolated plates attached to the median lamella (Figs. 54b, 56b). Periaxial cones commonly occur singly, but may form vertical series not normally containing more than three cones (Fig. 47, Pl. 7, fig. 14; Pl. 8, fig. 11). They appear to have random vertical distribution and are separated by series of axial tabellae or intervals with simple structure, lacking tabellae (Pl. 8, figs. 2, 4; Pl. 9, fig. 5). As a result of such interrupted and variable development of its components, the axial column shows marked variation over short vertical intervals (Fig. 51a-c). In some specimens, relatively simple axial structures may predominate, leading to their possible confusion with

Petalaxis, which they closely resemble in transverse section. As outlined above, *Cystolonsdaleia* and *Petalaxis* are distinguished only by the details of their axial structures - the former genus being characterized by the presence of periaxial cones, discontinuous series of axial tabellae, and a stronger, more consistent development of septal lamellae. Furthermore, periaxial cones are not evident in all longitudinal sections of *Cystolonsdaleia*. At all levels, they are absent in some corallites, and where they are developed, they may be easily detected only in well orientated longitudinal thin sections or acetate peels from surfaces cut parallel to the axis, through the central part of the axial column, and approximately perpendicular to the counter-cardinal plane. In off-centre or oblique sections and in those orientated closer to the counter-cardinal plane, periaxial cones are less obvious and may appear as nondescript vesicular tissue or be mistaken for normal axial tabellae. This emphasizes the importance, in studies of *Cystolonsdaleia* and genera of similar morphology, of preparing accurately and consistently orientated longitudinal thin sections or acetate peels in numbers (preferably three or more) sufficient to confidently establish the presence or absence of periaxial cones. As noted above, the median and lateral lamellae are formed as thickened, adaxial extensions of the cardinal septum. The formation of lateral lamellae, as shown by a series of acetate peels through a corallite from *Cystolonsdaleia* sp. aff. *C. carteri* (GSC 109675; Fig. 52a-g), is similar to that observed in *Petalaxis*. After formation of the median lamella, the cardinal septum withdraws from it, then extends adaxially and thickens to form a lateral lamella adjacent to the median lamella (Fig. 52e). The cardinal septum then withdraws from the lateral lamella, which terminates distally (Fig. 52g). No peels could be obtained from higher levels in this corallite. In several other corallites intersected by the same series of peels, the formation of a lateral lamella is followed by abaxial withdrawal of the cardinal septum, which then extends adaxially to the other side of the median lamella, where it thickens to form another lateral lamella. The total number of lateral lamellae and their positions relative to the median lamella have not been further investigated. Each lateral lamella persists through only a short distance vertically, commonly terminating before the succeeding one is developed. Thus, in a transverse section, rarely more than one lateral lamella is evident in any corallite. Lateral lamellae in *Cystolonsdaleia* have many of the same features as those in *Petalaxis*. As in that genus, they are gently curved to sinuous, vary considerably in thickness, and their length in transverse section is commonly less than, but may be equal to or greater than that of the median lamella. Septal lamellae locally connect the median lamella with lateral lamellae and also occur separately on the latter.

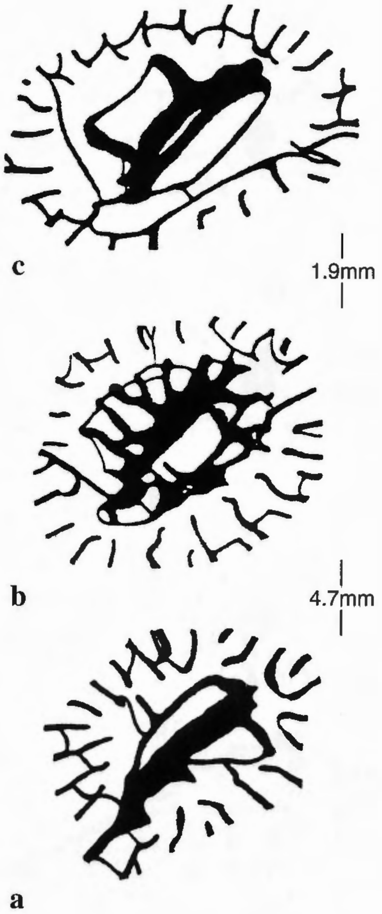


***Figure 51. Cystolonsdaleia arctica** sp. nov., paratype GSC 109669; digital images of serial transverse acetate peels through axial column, over vertical distance of 6.6 mm, showing variation in number of septal lamellae attached to median lamella and periaxial cones or axial tabellae, viewed from top of corallite, x15; middle peel (**b**) shows marked increase in number and length of septal lamellae, compared to peels at bottom (**a**) and top (**c**) of series.*

The thickness of the lateral lamellae is normally less than, but may be equal to, that of the median lamella. Although they are normally approximately parallel to the median lamella, they also may lie at high angles (up to 90°) to it and rarely are positioned beyond its cardinal or counter edges, across the counter-cardinal plane.

Tabularium. *Cystolonsdaleia* has a biform tabularium similar to that in *Petalaxis*. It was illustrated in the type species, as discussed above, has been observed in all species from Ellesmere Island (e.g., Pl. 8, figs. 4, 5, Pl. 9, figs. 6, 12, 14, Fig. 60C) and can be seen in published illustrations of many published species [e.g., *C. shimeri* (Crickmay) (see Nelson, 1960, Pl. 21,

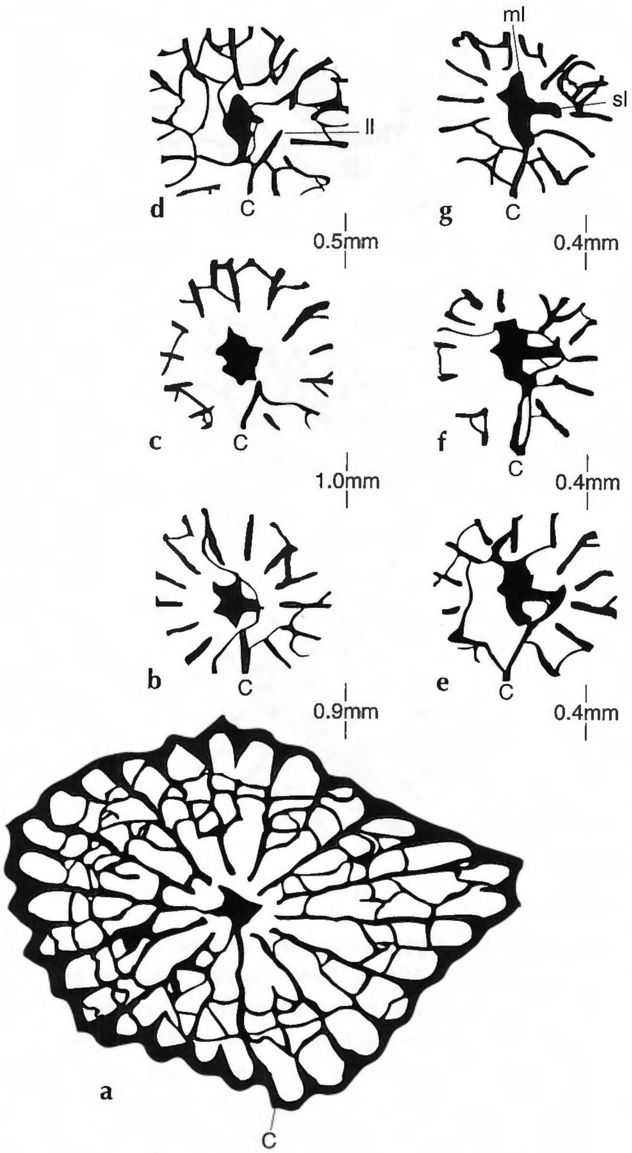


***Figure 52. Cystolonsdaleia** sp. aff. **C. carteri**, hypotype GSC 109675, x10; digital images of serial peels through axial zone of mature corallite, showing formation of vertically discontinuous lateral lamella (ll) by adaxial extension and thickening of cardinal septum (C); **a** - base of series, **g** - top of series; note variation in number and length of septal lamellae (sl) on median lamella (ml).*

figs. 13, 14), *C. densiconus* (de Groot), *C. guaspariniae* (Stevens and Rycerski), and *C. wenhuashanensis* Yu].

Tabulae of two types are present in *Cystolonsdaleia*. Those of the first type extend adaxially from the dissepimentarium to reach the axial area, where they join the median lamella at various angles or are deflected distally to form periaxial cones. Those of the second type, which are emplaced immediately following the formation of a periaxial cone, extend from the dissepimentarium to the outer margin of the axial column, but terminate adaxially against a periaxial cone or an axial tabella and do not reach the median lamella (Fig. 47, Pl. 7, fig. 14; Pl. 8, figs. 3, 5, 11). These abbreviated tabulae may occur singly or in groups, depending on the distal extent of the periaxial cone to which they are attached.

The overall shape and orientation of the tabulae are quite variable in the species from Ellesmere Island. In most specimens they are mainly complete, but in *Cystolonsdaleia* sp. (Pl. 7, figs. 13-15) incomplete tabulae predominate. The tabulae in all four species described below are mainly concave and are elevated in the outer tabularium to join the dissepimentarium. *Cystolonsdaleia arctica* has adaxially elevated tabulae, whereas those in the other three species are generally adaxially depressed to subhorizontal.

Dissepimentarium. *Cystolonsdaleia* closely resembles *Petalaxis* in the structure of its dissepimentarium. The two genera show a similar range of variation in the shape, size, orientation and number of dissepiments and in the width of the dissepimentarium. Transeptal dissepiments are strongly developed in all species here included in *Cystolonsdaleia* (see generic synonymy), with the exception of the two species of Kasimovian or earliest Gzhelian age (*C. carteri* and *C.* sp. aff. *C. carteri*), described below. The dissepimentaria of those two species consist mainly of regular dissepiments, but transeptal dissepiments are locally well developed (Pl. 9, figs. 4, 10; Fig. 60b). The two Moscovian species from Ellesmere Island (*C. arctica* and *C.* sp.) show the strong predominance of transeptal dissepiments typical for the genus.

Blastogeny. The following observations on the early growth stages of *Cystolonsdaleia* were made from a series of closely spaced acetate peels (Fig. 53a-m), a series of closely spaced thin sections, and one transverse thin section through several immature corallites of a specimen of *C.* sp. aff. *C. carteri* (GSC hypotype 109675). In our collection, no other specimen showing the earliest growth stages of the genus is sufficiently well preserved for preparation of serial acetate peels. Supplementary information was obtained from transverse thin sections of the other species from Ellesmere Island. The terminology used follows that of Fedorowski and Jull (1976) and Fedorowski (1978).

As in *Petalaxis*, new corallites develop in the outer dissepimentaria of parent corallites, commonly in the corners or along very short sides. Clusters of several offsets formed by budding in adjacent corallites are common in GSC 109675 (*C.* sp. aff. *C. carteri*, Pl. 9, fig. 10). Offsets may form in any quadrant of the parent corallite and the region of increase may include the peripheral margins of protosepta. In all offsets in which the early growth stages were observed, the counter-cardinal planes are orientated tangentially with respect to the axes of parent corallites.

The information on developmental stages given below was derived mainly from serial peel sections of one corallite in GSC hypotype 109675, through its hysterobrephic and hysteroneanic growth stages (Fig. 53).

Hysterobrephic stage (Fig. 53b-d). The vertical interval occupied by this stage is approximately 1 mm (initiation of budding between Fig. 53a and b). Budding begins with thickening of major and minor septa in the left cardinal quadrant to form an incomplete new wall adjacent to the cardinal septum of the parent (Fig. 53b). The septa are not interrupted at this level. At a slightly higher level (Fig. 53c), the new wall is extended by further lateral thickening of the septa, but only one margin is attached to a septal base on the parent wall. Septa inherited from the parent are strongly developed along the inherited wall and several extend across the offset. The latter is floored by dissepiments of the parent. In the latter part of this stage (Fig. 53d), the new wall develops a median dark line and is permanently joined at both margins to septal bases on the parent wall. In other corallites of this specimen, investigated with serial thin sections, the wall remains detached until a later stage of development, as outlined below. A septal pinnacle (P) is evident near the new wall, the inherited septa have begun to withdraw toward the old wall, and the new wall bears one new septal base near the parent cardinal septum — the rudimentary right alar septum (A). Adjacent to the alar septum, there is a slight swelling marking the beginning of the cardinal septum (C) on the old wall. Insertion of two new major septa in the right counter quadrant is indicated by slight protuberances on the new wall.

Hysteroneanic stage (Fig. 53e-m). The vertical interval occupied by this stage is at least 5.4 mm. In the lowest peel prepared within it (Fig. 53e), the cardinal septum of the offset (C) has developed, two new septa are well expressed on the new wall, and septal pinnacles are present. At a slightly higher level (Fig. 53f), the cardinal septum has lengthened and all inherited septa have withdrawn toward the old wall. One of the inherited septa forms the left alar septum (A). Three major septa are present on the new wall, and the axial area shows intercepts of tabulae. In the succeeding peel (Fig. 53g), from 0.6 mm higher in the offset, the counter septum (K) and two counter lateral septa (KL) have appeared, two septa have been inserted in the right cardinal and one in the left counter quadrant, and minor septa are present in the right counter quadrant. Through the succeeding 1 mm of this stage (Fig. 53h), the cardinal and counter septa lengthen and thicken, minor septa are inserted in the right cardinal quadrant, and a transeptal dissepiment develops in the left counter quadrant. This is followed (Fig. 53i-m) by further lengthening of the cardinal septum into the axial area, where its axial margin is thickened to form the median lamella of the axial structure. This is accompanied by development of vertically discontinuous septal lamellae on both sides of the median lamella. Also, insertion of major and minor septa continues in the right cardinal and counter quadrants, thus producing early acceleration of septal insertion along the new wall. The counter lateral septa (KL) are considerably lengthened through this interval. Septal insertion in the left cardinal quadrant begins late in this stage (Fig. 53j), accompanied by further insertion of septa in the right counter quadrant (Fig. 53m). Later growth stages of this corallite were not included in the peel series.

The degree to which the sequence of development described above is representative of the genus *Cystolonsdaleia* could not be determined, because only one specimen was investigated in detail. Within this specimen (GSC 109675), there is consistency in several features of early development. Initiation of the new walls of all offsets investigated is accomplished by lateral thickening of parent septa, following the same general pattern as that described above (Fig. 53b-d). Inherited septa extend across the new offsets during their early development, before withdrawing toward the inherited wall. Subsequent insertion of major septa and minor septa begins along the new wall and is consistently accelerated in the quadrants adjacent to it.

Less consistency is shown in this specimen, however, by other features of its blastogeny, which resembles that of *Petalaxis* in this respect. In most offsets, the cardinal septum is inserted on the inherited wall, but it may also originate on the new wall. The counter septum appears to originate on the wall opposite that initially bearing the cardinal septum. Initial attachment of the new wall to the parent normally takes place at only one margin, leaving a channel open at the other margin until final attachment to the parent wall occurs. In several corallites, studied by means of closely spaced serial thin sections, the wall, after its four-layered structure is developed, remains detached at both margins, leaving two long-lasting channels between parent and offset. These sections also showed that, during its growth toward the wall of the parent

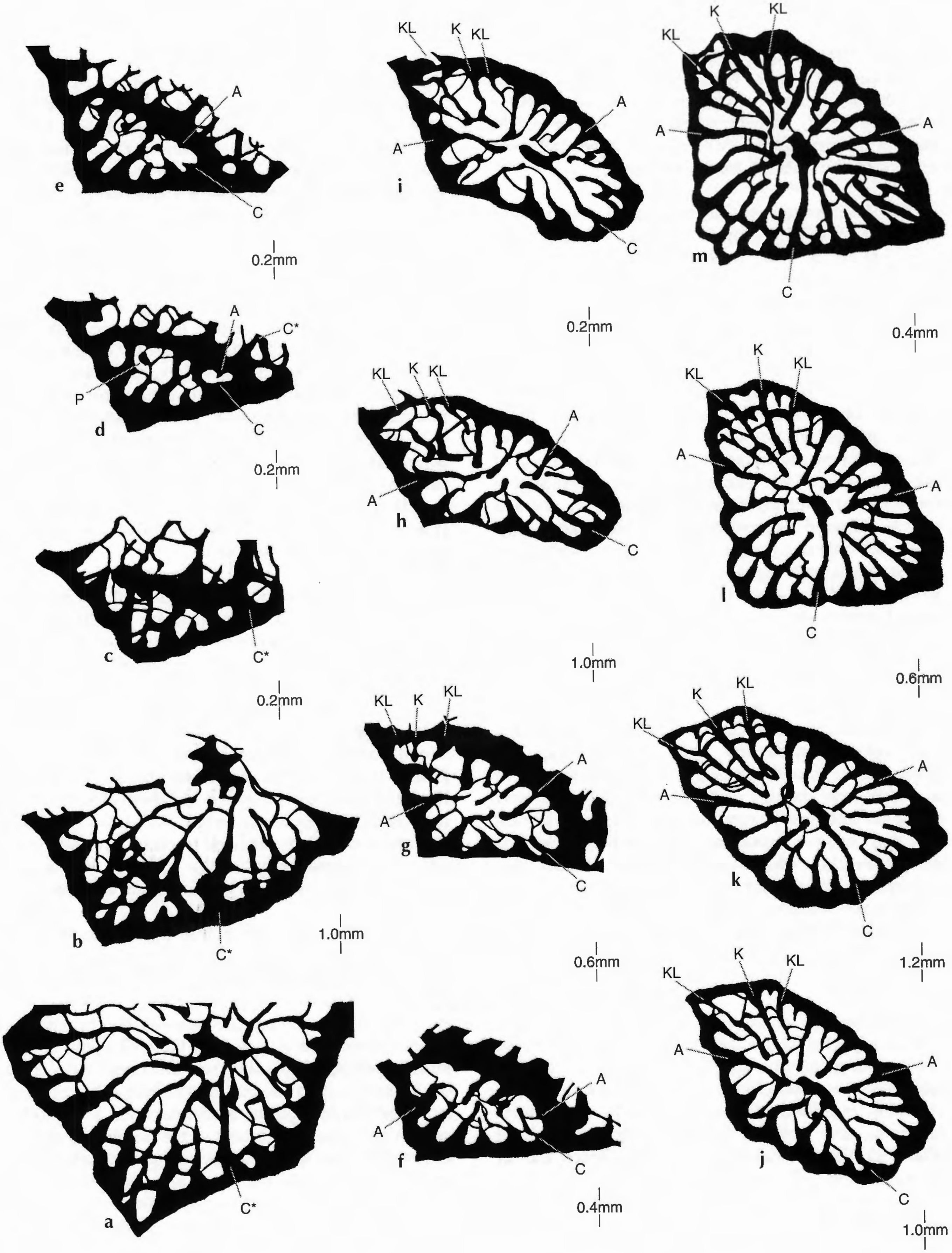

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***Figure 53. Cystolonsdaleia** sp. aff. **C. carteri**, hypotype GSC 109675, x15, drawings of serial transverse acetate peels through hysterobrephic (**a-d**) and hysteroneanic (**e-m**) growth stages of offset, showing insertion of septa and formation of median lamella and short septal lamellae on thickened axial margin of cardinal septum; cardinal septum of parent corallite - C*, cardinal septum of offset - C, alar septa - A, counter septum - K, counter lateral septa - KL, pinnacle - P.*

corallite, the new wall commonly joins the inner part of a parent septum, rather than a septal base on the parent wall. As in *Petalaxis*, the shape of the new wall and the timing of its attachment to the parent wall depend on the degree to which transeptal dissepiments are developed in the hysterobrephic stage. In offsets initially lacking transeptal dissepiments, the wall is moderately to strongly curved from its beginning and joins the parent wall relatively early. In those possessing transeptal dissepiments where the new wall is first formed, the latter is straight or only slightly curved and remains so over a significant vertical distance, before becoming more stongly curved and joining the parent wall.

As a result of local acceleration in the insertion of septa, the pattern of septal increase in early growth stages does not follow the classical rugosan pattern, but is very irregular in individual quadrants. This deviation is also caused, in part, by the fact that septa inherited from the parent corallite initially cross the entire lumen of the offset and subsequently withdraw abaxially to form opposing major septa.

Septal lamellae are present, but vertically discontinuous in the axial column from the hysteroneanic stage to maturity. From limited observation, it appears that development of lateral lamellae first takes place in the late neanic stage.

Transeptal dissepiments rarely appear in offsets during the hysterobrephic and hysteroneanic stages in GSC 109675. At succeeding levels, however, they form discontinuous vertical series in many corallites. They occur in a similar manner in *C. carteri* sp. nov., but are less numerous. Transeptal dissepiments are strongly developed in the hysteroneanic, late neanic and mature growth stages of all corallites studied in *Cystolonsdaleia arctica* sp. nov. and in the late neanic and mature stages of *C.* sp. Earlier growth stages were not observed in these species.

Age and distribution. *Cystolonsdaleia* ranges in age from middle Viséan to Early Permian (Asselian). It has been found in Spain, Ukraine, Russia, Canada, U.S.A., China and Mongolia.

The earliest, firmly dated occurrence of the genus is in middle Viséan strata of the Mount Head Formation in the southern Rocky Mountains of Canada. *Cystolonsdaleia* is widespread in the upper Viséan and Serpukhovian of the Western Interior Coral Province of Canada and the U.S.A., where it has been referred to several other colonial genera (see discussion above). It was reported by Armstrong (1970, p. 35) from the upper Viséan of southeastern Alaska [*C. peratrovichensis* (Armstrong)] and is abundant in Geological Survey of Canada collections from Sepukhovian and Lower Permian (Asselian) strata in the Stikine assemblage of northwestern British Columbia. *Cystolonsdaleia neriae* and *C. guaspariniae* were described from the latter area as Lower Permian representatives of *Petalaxis* by Stevens and Rycerski (1989). More recent stratigraphic and micropaleontological evidence from new collections in the area confirms an Early Permian (Asselian?) age for these species. *C. zulloi* (Wilson) was described as a Lower Permian representative of *Kleopatrina* (*Porfirievella*) by Wilson (1982) from the McCloud Limestone of northern California, U.S.A. The only known representatives of *Cystolonsdaleia* from arctic North America are the Moscovian and Kasimovian or earliest Gzhelian species described below.

Cystolonsdaleia was originally described from Moscovian strata in the Donets Basin of Ukraine (Fomichev, 1953). It has since been described in that area from Bashkirian strata in the subsurface of the Voronezh anticline (Kozyreva, 1978). Moscovian species occur in Spain (de Groot, 1963, *C. celadensis*, *C. densiconus*; Rodriguez, 1984, *C. lutugini*, *C. portlocki*) and are probably present in the Moscow Basin of Russia (Dobrolyubova, 1935a, b, *C.*(?) *ivanovi*, *C.*(?) *portlocki*).

The genus is widely distributed in China, where it occurs mainly in the Bashkirian and Moscovian (Luo et al., 1989b). It also has been reported from younger Carboniferous strata (Kasimovian or Gzhelian - *Triticites* zone) in eastern Inner Mongolia and the eastern Tibet-western Sichuan area (Guo, 1983, p. 221, Table 1; Luo et al., 1989b, p. 286, Tables 44, 52).

Description of species

Cystolonsdaleia sp.

Plate 7, figures 13-15; Figures 47, 54, 55

Description. Walls generally thin, moderately thickened where joined by septa to give denticulate appearance. Mean diameter of mature corallites 4.75-8.2 (commonly 6-8 mm) (Fig. 55). Septa straight, gently curved or slightly sinuous in transverse section, vertically discontinuous in dissepimentarium, extend to walls as septal crests, wedge-shaped in transverse section, thin in axial area and thickened in outer tabularium and adjacent to walls, commonly slightly thickened along axial margins. Major septa number 14-18 (commonly 17 or 18) in mature corallites (Fig. 55); radially arranged, axial margins commonly curved or sharply deflected laterally in transverse section; cardinal septum locally slightly thicker than other major septa, connection with median lamella of axial structure almost continuous, broken only where rare lateral lamellae formed; counter septum approximately equal in length to major septa, but varies in length vertically and may closely approach axial column; other major septa long, vary slightly in length vertically, closely approach axial column but do not join it; minor septa well developed, long, variable in length, commonly more than three quarters the length of major septa.

Axial column vertically continuous, straight to gently curved in longitudinal section, varies in thickness vertically, locally thickened by stereoplasm to form solid rod in which lamellae and tabellae are not evident; median lamella moderately to strongly thickened, less commonly thin and tabular, straight or curved, rarely sinuous in transverse section, commonly slightly sinuous in longitudinal section, connection with cardinal septum rarely interrupted, commonly closely approached, but not joined by counter septum; septal lamellae discontinuous vertically, strongly developed on median lamellae, rarely on axial tabellae or periaxial cones, commonly five to nine developed but may be very few or none at different levels, vary in length vertically, range from short and thick to moderately long and thin in transverse section, closely approached by major septa, not joined to them, rarely split abaxially into two joined plates; lateral lamellae rare, formed as thickened extension of cardinal septum; axial tabellae poorly developed, commonly isolated, but locally form vertical series of two or three (rarely four), slightly to moderately convex, vertically elongate, rest on underlying axial tabellae or periaxial cones; periaxial cones numerous in all corallites studied in longitudinal section, extend along axial column past series of up to five succeeding tabulae.

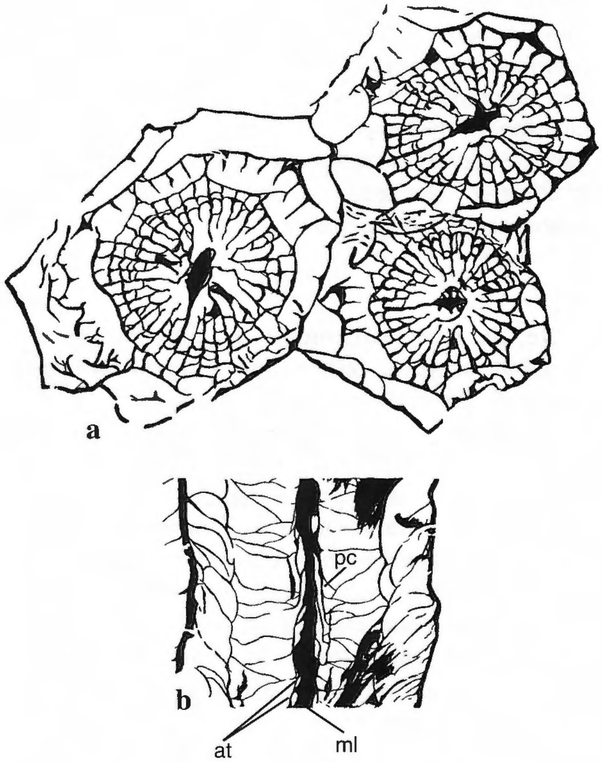

***Figure 54. Cystolonsdaleia** sp., hypotype GSC 109667, x5; **a**, drawing of transverse thin section, showing long septa, slightly thickened cardinal septum attached to variable axial column and well developed transeptal dissepiments; **b**, drawing of longitudinal thin section of mature corallite, showing subhorizontal tabulae, with periaxial cones (pc) and axial tabellae (at) attached to median lamella (ml) (see Pl. 7, fig. 15; Fig. 47).*

Tabulae generally incomplete, but complete tabulae present in all corallites studied; subhorizontal or adaxially depressed, locally adaxially elevated; curved or undulose, generally concave, locally convex in outer tabularium; incomplete tabulae consist of few (commonly two) curved or undulose tabellae; periaxial parts of many tabulae rise steeply to form periaxial cones in axial column, other tabulae are slightly elevated to join axial column and some join it at angles near 90°; biform morphology well developed, tabellae in position I convex and steeply declined adaxially, those in position II subhorizontal or gently declined adaxially, less commonly slightly depressed toward dissepimentarium; 8-11 tabulae in 5 mm of corallite length; ratio of tabularium diameter to corallite diameter 0.60-0.77, most commonly 0.67-0.69.

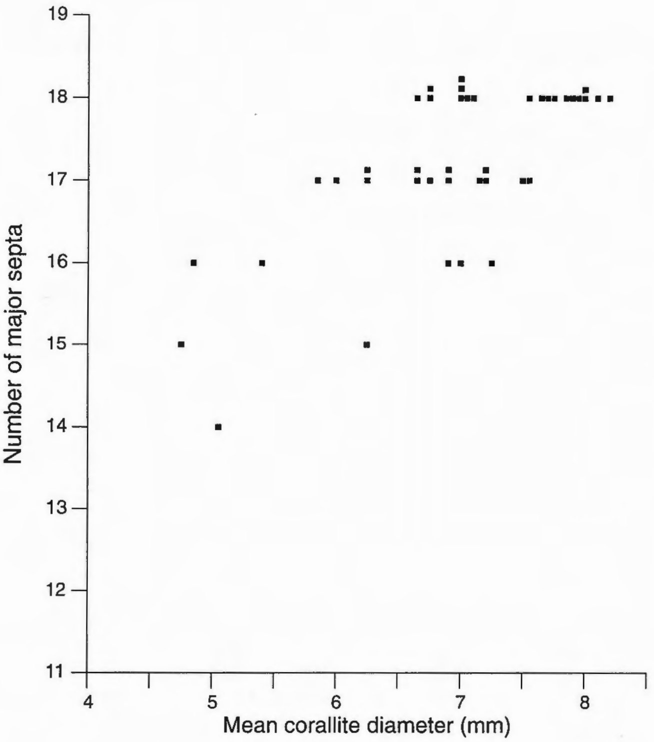

Figure 55. *Relationship between mean corallite diameter and number of major septa in* ***Cystolonsdaleia*** *sp. (hypotype GSC 109667).*

Dissepimentarium well developed, continuous, varies in width from approximately one quarter to two fifths of corallite radius, boundary with tabularium distinct, marked by slight stereoplasmic thickening of dissepiments; dissepiments in one or two (rarely three) rows, moderately to steeply declined adaxially, mainly transeptal, regular dissepiments rare; transeptal dissepiments large, strongly convex to elongate and flattened, six or seven (rarely eight) in 5 mm of corallite length.

No immature corallites were found in several transverse sections through the small fragment described.

Discussion. The above description is based on a small, poorly preserved fragment of a cerioid colony with no early growth stages preserved. Thin sections are difficult to obtain from this specimen, because it is recrystallized, partly replaced by quartz, partly crushed and highly porous. As a result, they show apparent discontinuity in structures (e.g., corallite walls and tabulae; Pl. 7, figs. 13, 15), caused by poor preservation and damage during laboratory preparation. No serial peels could be made because of the poor preservation.

Our specimen resembles *C. densiconus* (de Groot) (see also, Sando, 1983, p. 36) in corallite diameter and number of septa, but has larger transeptal dissepiments, shorter minor septa and less strongly elevated tabulae than the Spanish species. De Groot (1963, p. 79) noted steeply conical periaxial parts of tabulae (i.e., periaxial cones) locally replacing axial tabellae in the axial column of her specimen. From her illustration (*ibid.*, Pl. 15, fig. 1b), the construction of the axial column appears comparable to that in the Canadian specimen.

The septal number, corallite diameter, axial column and dissepimentarium of *C.* sp. are similar to those of *C. tingi prolifera* (Wang), from the lower Moscovian of Guangxi, China (Wang, 1989, p. 532), but the tabulae in the latter are steeply elevated adaxially, whereas those in the Ellesmere specimen are generally subhorizontal or adaxially depressed.

Material. Hypotype GSC 109667, small fragment of colony from GSC loc. C-69857.

Occurrence and age. The single studied specimen of *Cystolonsdaleia* sp. was collected by U. Mayr from the lower or middle part of the Canyon Fiord Formation (GSC loc. C-69857, Table 2) near Henrietta Nesmith Glacier (locality 2, Fig. 1, Table 1). It occurs within a mid-Moscovian stratigraphic interval dated by fusulinacean foraminifers as Kashirian or Podolskian (GSC locs. C-69854 and C-69858; Mayr, 1992, p. 111; internal GSC Report Misc. 1-CAR 1978).

Cystolonsdaleia arctica sp. nov.

Plate 8, figures 1-11; Figures 49, 51, 56, 57

Etymology. For the occurrence of this species in Arctic Canada.

Diagnosis. Cystolonsdaleia having 17-22 (commonly 19-22) long major septa at mean diameter 4.5-7.25 (commonly 5.5-7) mm; minor septa long, commonly extend adaxially from dissepimentarium more than three quarters of tabularium radius; axial column strong, vertically continuous, with thick median lamella, numerous septal lamellae, one or two lateral lamellae and locally numerous axial tabellae; tabulae generally complete, subhorizontal to moderately elevated adaxially, 11-15 (commonly 12-14) in 5 mm; tabularium to corallite diameter ratio 0.6-0.83; transeptal dissepimentarium continuous, dissepiments of moderate size.

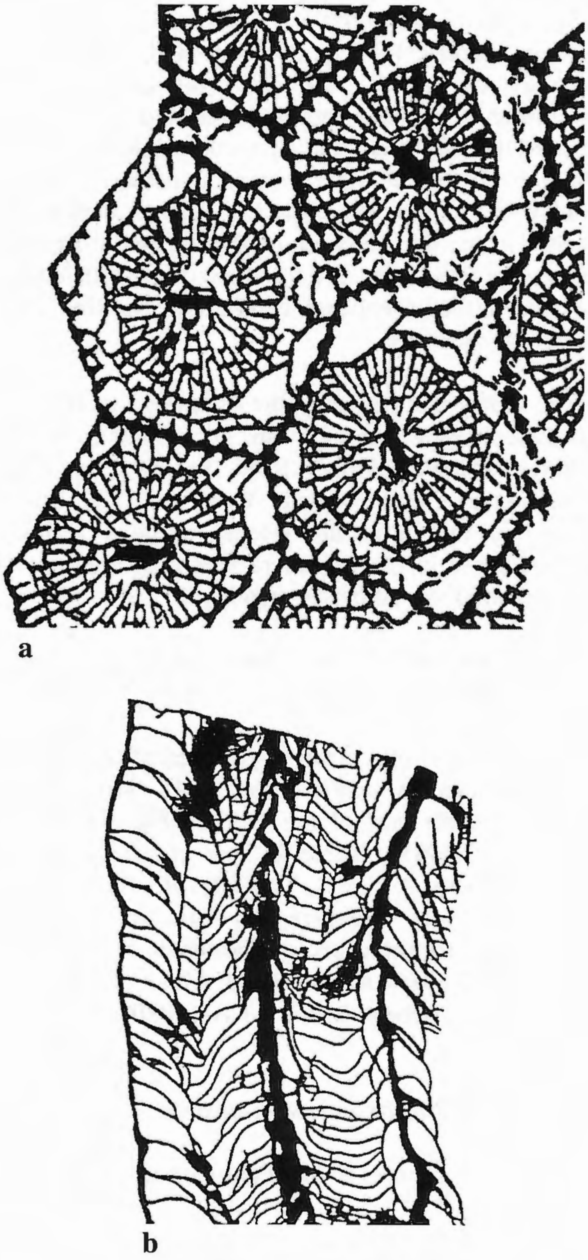

Figure 56. ***Cystolonsdaleia arctica*** *sp. nov., paratype GSC 109669, x6;* ***a****, digital image of transverse thin section (see Pl. 8, fig. 10), showing long septa, locally thickened cardinal septum attached to variable axial column, and well developed transeptal dissepiments;* ***b****, drawing of longitudinal thin section of mature corallite, showing periaxial cones (right side of axial column, lower half of figure), well developed axial tabellae and numerous, adaxially elevated tabulae (see Pl. 8, fig. 11; Fig. 47b, c).*

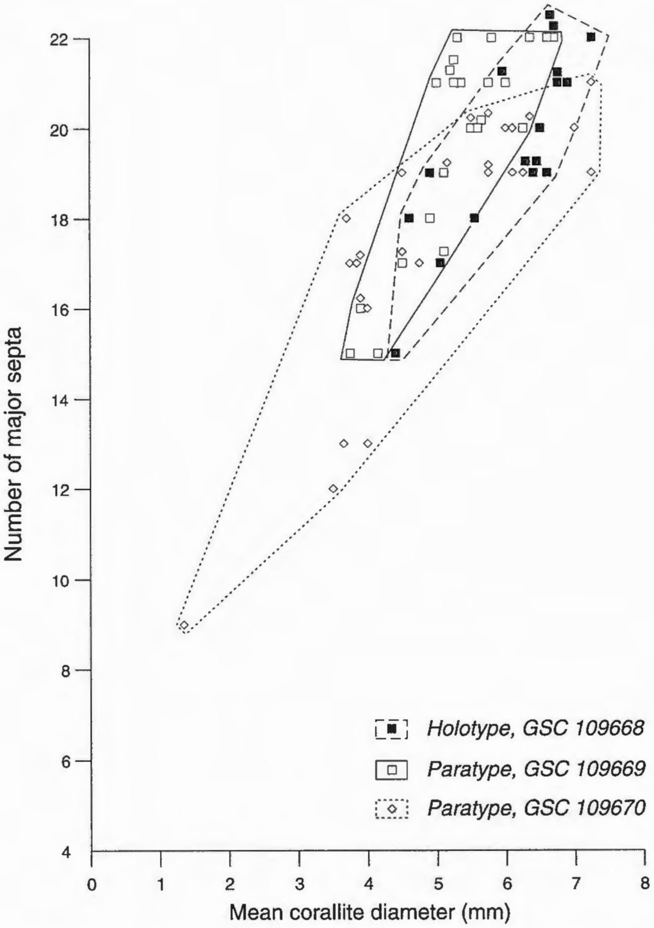

Figure 57. Relationship between mean corallite diameter and number of major septa in ***Cystolonsdaleia arctica*** *sp. nov.*

Description. Walls moderately thickened where joined by septa to give denticulate appearance, thinner locally, where transeptal dissepiments interrupt septa. Mean diameter of mature corallites 4.5-7.25 (commonly 5.5-7) mm (Fig. 57). Septa straight, gently curved, or slightly sinuous in transverse section, vertically discontinuous in dissepimentarium, extend to walls as septal crests, generally thin, except where they thicken to join corallite walls, commonly slightly thickened along axial margins. Major septa number 17-22 (commonly 19-22) in mature corallites (Fig. 57); generally radially arranged, several curve toward counter-cardinal plane in most corallites, axial margins commonly strongly curved or sharply deflected laterally in transverse section. Cardinal septum locally slightly thicker than other major septa, connection with median lamella of axial column generally continuous vertically, but locally interrupted over short intervals; counter septum approximately equal in length to adjacent major septa, but varies in length vertically and may join or closely approach axial column; other major septa long, vary slightly in length vertically, closely approach axial column but rarely join it; minor septa well developed, long, variable in length, commonly more than three quarters the length of major septa.

Axial column vertically continuous in all corallites studied, gently curved to sinuous in longitudinal section, varies in thickness vertically; median lamella moderately to strongly thickened, less commonly thin and tabular, curved or sinuous (rarely straight) in transverse section, commonly sinuous in longitudinal section, connection with cardinal septum locally interrupted, commonly closely approached but very rarely joined by counter septum; septal lamellae vertically discontinuous (Fig. 51), strongly developed on median lamella and less commonly on rare lateral lamellae and periaxial cones or axial tabellae, commonly 4-8 developed, locally more numerous (up to 12) but may be very few or none at different levels, vary in length vertically, range in shape from short and thick to long and thin in transverse section, curved to sinuous (rarely straight) in both transverse and longitudinal section, closely approached by major septa, not joined to them, commonly split abaxially into two joined plates; lateral lamellae locally well developed, vertically discontinuous, generally one (rarely two) developed at one level in any corallite, most commonly developed in marginal part of axial column as curved, thickened extension of cardinal septum; axial tabellae locally well developed, form vertical series of up to six tabellae, commonly elongate, narrow, moderately convex, most rest on underlying axial and periaxial tabellae, some on axial parts of tabulae, and others are entirely attached to median lamella; periaxial cones well developed locally in all specimens, extend along axial column past series of up to seven succeeding tabulae.

Tabulae generally complete, but incomplete tabulae locally numerous; closely spaced, slightly to moderately elevated adaxially, locally subhorizontal or adaxially depressed; curved or undulose, generally slightly to moderately concave, locally convex near axial column in all corallites studied; incomplete tabulae consist of few (commonly two) curved or undulose tabellae, forming two poorly defined series – an inner, generally convex, periaxial series and an outer series that is concave, planar or slightly convex; periaxial parts of almost all tabulae slightly to strongly elevated to join axial column, very few join it at angles near 90°; biform morphology well developed, tabellae in position I convex to slightly concave, moderately declined adaxially, those in position II generally concave, declined toward dissepimentarium, many turn up slightly to join it; 11-15 (commonly 12-14) tabulae in 5 mm of corallite length; ratio of tabularium diameter to corallite diameter 0.6-0.83, most commonly 0.67-0.75.

Dissepimentarium well developed, continuous, varies in width from approximately one fifth to one third of corallite radius, boundary with tabularium distinct; dissepiments in one or two (rarely three) rows, mainly transeptal, but regular dissepiments consistently present; large dissepiments elongate and flattened to highly convex, smaller dissepiments moderately to strongly convex, occur mainly adjacent to tabularium; all dissepiments steeply declined adaxially; large dissepiments number five or six in 5 mm of corallite length.

In immature growth stages (mean diameter of smallest corallite studied, 1.4 mm; Fig. 57), wall separating young corallite from parent incomplete at mean corallite diameter of 3.5 mm and less; sections of only a few immature corallites available for study; in corallite with mean diameter of 1.4 mm, four short, curved major septa present on incomplete new wall, which is detached from parent wall along one margin, five septal bases from detached parent septa present on inherited wall, no axial column developed, minor septa absent, and neither cardinal nor counter septum can be identified; at mean corallite diameters of 3.25 mm to 3.5 mm, septa curved or slightly sinuous, several major septa closely approach axial area, cardinal septum long, axial margin slightly thickened to form median lamella, counter septum slightly shorter than adjacent major septa, minor septa completely developed, laterally extended transeptal dissepiments well developed along inherited wall, regular dissepiments present along new wall; septal lamellae well developed in axial column at mean corallite diameters of 3.9 and greater; lateral lamellae not observed at mean diameters below 4 mm; transeptal dissepiments well developed at mean corallite diameters of 3.25 mm and greater.

Discussion. *Cystolonsdaleia arctica* is distinguished by its adaxially elevated, closely spaced tabulae, its relatively high number of septa and the strong development of septal lamellae and periaxial cones in the axial column. Its axial column, tabulae and dissepimentarium resemble those of *C. tingi prolifera* (Wang), from the lower Moscovian of Guangxi, China, but the latter has fewer septa at corresponding corallite diameters (Wang, 1989, p. 532). In its corallite diameter, septal number and dissepimentarium, *C. longiseptata* Wu and Zhao, from the lower Moscovian part of the Weining Formation, China, is similar to *C.*

arctica but the Chinese species has less strongly elevated tabulae. The features of its axial column in longitudinal section are not sufficiently well illustrated for close comparison (Wu and Zhao, 1989, p. 121, 122, fig. 4). The middle or upper Moscovian species *C. incerta* Yu and Wang, from Guizhou Province, China (Yu and Wang, 1987, p. 84), resembles *C. arctica* in its septal number and corallite diameter and by the nature of the axial column, but has less strongly elevated tabulae and a wider dissepimentarium.

Material. Holotype GSC 109668 (10 pieces from incomplete colony, one transverse and five longitudinal thin sections, seven transverse and five longitudinal acetate peels). Paratypes: GSC 109669 and GSC 109670. All incomplete colonies from GSC loc. C-193090. Additional material: one incomplete, partly crushed colony from GSC loc. C-193091.

Occurrence and age. Cystolonsdaleia arctica was found only in the Agassiz Ice Cap section [GSC locs. C-193090 (rubble near outcrop), C-193091, locality 11, Figs. 1, 9], where it was collected 28.2-33.2 m above the base of the Belcher Channel Formation. It is associated with upper Moscovian (Podolskian or Myachkovian) foraminifers (Table 3, Appendix 1), and occurs 26.5 m above *Petalaxis donbassicus* (Fomichev) of Kashirian to Podolskian age (see discussion of occurrence and age for that species).

Cystolonsdaleia carteri sp. nov.

Plate 9, figures 1-9; Figures 58, 59

Etymology. In honour of Dr. G.F. Bonham-Carter, who collected all of the specimens included in the species.

Diagnosis. Cystolonsdaleia having 12-18 (commonly 13-17) long major septa at mean diameter 3.2-5.4 (commonly 3-5) mm; minor septa extend from corallite wall one sixth to one half of corallite radius; axial column strong, continuous, with thick median lamella, numerous septal lamellae, few lateral lamellae, and discontinuous series of axial tabellae and periaxial cones; tabulae mostly complete, commonly adaxially depressed, generally strongly concave, 8-14 (commonly 10-12) in 5 mm; tabularium to corallite diameter ratio commonly 0.6-0.86; dissepimentarium discontinuous, narrow, dissepiments mainly regular, small; corallite wall thick.

Description. Corallite walls strongly thickened where joined by septa to give denticulate appearance, thinner locally, where transeptal dissepiments interrupt septa. Mean diameter of mature corallites 3.2-5.4 (commonly 3-5) mm (Fig. 59). Septa straight, gently curved, or slightly sinuous in transverse section, generally vertically continuous in dissepimentarium, but locally interrupted by transeptal dissepiments, strongly thickened at corallite walls and in outer tabularium adjacent to transeptal dissepiments, otherwise generally thin to moderately thickened in tabularium, locally slightly thickened along axial margins. Major septa number 12-18 (commonly 13-17) in mature corallites (Fig. 59); generally radially arranged, commonly

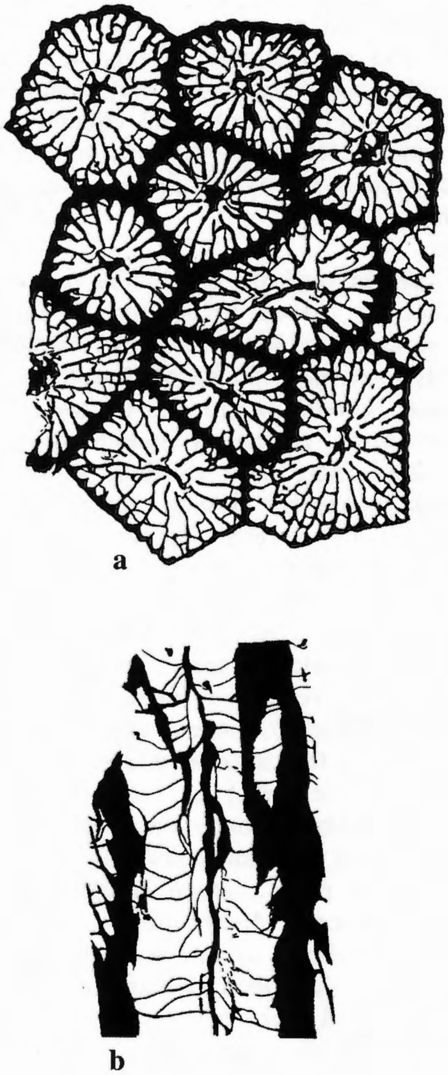

Figure 58. Cystolonsdaleia carteri *sp. nov., holotype GSC 109671, x5;* ***a****, drawing of transverse thin section (see Pl. 9, fig. 1), showing thick, denticulate walls, variable axial column and weakly developed transeptal dissepiments;* ***b****, drawing of longitudinal thin section of mature corallite, showing subhorizontal tabulae, weakly developed periaxial cones and discontinuity of dissepimentarium (see Pl. 9, fig. 3).*

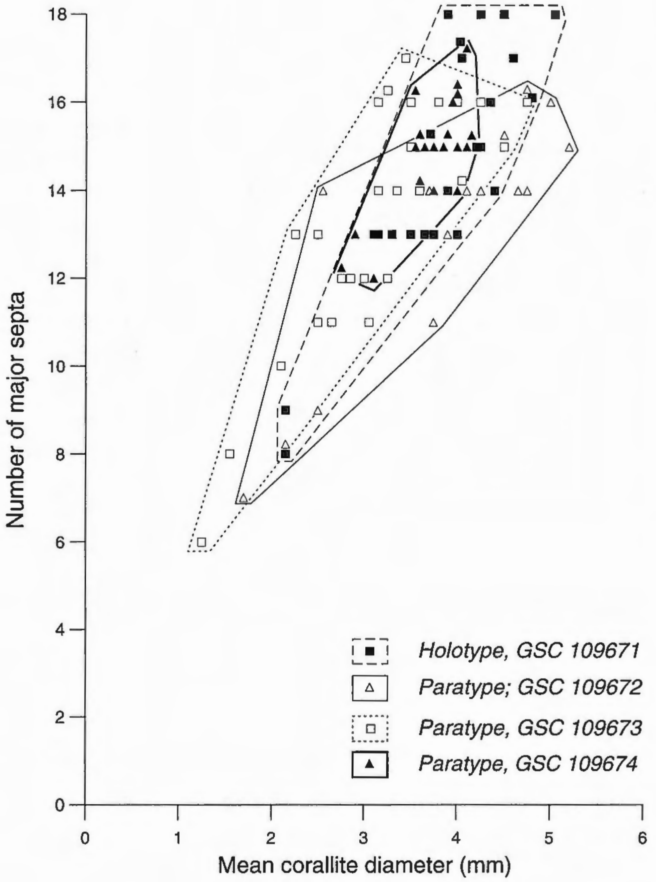

Figure 59. *Relationship between mean corallite diameter and number of major septa in **Cystolonsdaleia carteri** sp. nov.*

several curve toward counter-cardinal plane, axial margins rarely strongly curved in transverse section. Cardinal septum locally slightly thicker than other major septa, connection with median lamella locally discontinuous; counter septum commonly slightly shorter than adjacent major septa but varies in length vertically and may closely approach or reach axial column; other major septa long, vary slightly in length vertically, may closely approach axial column and rarely one or two join it; minor septa well developed, variable in length, extend adaxially from wall approximately one sixth to one half of corallite radius.

Axial structure continuous in all corallites studied, straight to slightly curved or sinuous in longitudinal section, varies in thickness vertically; infilled and thickened by stereoplasm in some specimens to form a thick rod of roughly circular or lens-shaped cross-section in which median and septal lamellae are difficult to distinguish; median lamella generally moderately to strongly thickened, locally thin and tabular, curved to sinuous in transverse section, commonly sinuous in longitudinal section, connection with cardinal septum locally interrupted, rarely closely approached but not joined by counter septum; septal lamellae vertically discontinuous, strongly developed on median lamella, rarely present on lateral lamellae, locally numerous (up to eight), curved, straight, or sinuous in transverse section, generally short and thick, rarely long and thin, closely approached locally by major septa, rarely joined to them; lateral lamellae locally well developed, vertically discontinuous, only one present at any level in a corallite, most commonly developed in marginal part of axial column as curved, thickened extension of cardinal septum; axial tabellae locally well developed in most specimens, rare in others, form vertically discontinuous series of up to four tabellae, commonly elongate and moderately convex, rest on underlying axial tabellae or (rarely) on axial parts of tabulae, less commonly entirely attached to median lamella; periaxial cones well developed locally in several specimens, weakly developed in others, extend along axial column past series of three to four, rarely up to six, succeeding tabulae.

Tabulae generally complete, but incomplete tabulae common; generally depressed adaxially, less commonly subhorizontal and rarely slightly elevated adaxially; commonly moderately to strongly concave, locally subplanar to moderately convex (mainly near dissepimentarium); incomplete tabulae consist of few curved or undulose tabellae, many of which are concave, others convex or approximately planar; periaxial parts of most tabulae slightly to strongly elevated to join axial column, some join at angles near 90°, and others (rare) depressed; rarely, in mature stages, tabulae strongly elevated toward axis and have numerous convex periaxial tabellae; biform morphology well expressed, tabellae and peripheral parts of complete tabulae in position I generally slightly convex, moderately to strongly declined adaxially, those in position II subplanar to slightly concave, generally slightly elevated toward dissepimentarium, rarely slightly declined toward it; many complete, concave tabulae slope gently downward from dissepimentarium to median lamella; 8-14 (commonly 10-12) tabulae in 5 mm of corallite length; ratio of tabularium diameter to corallite diameter 0.60-0.86, most commonly 0.67-0.75.

Dissepimentarium discontinuous, locally absent over considerable vertical distance, varies in width, where present, from one sixth to two fifths of corallite radius, boundary with tabularium distinct and locally marked by slight stereoplasmic thickening of dissepiments; dissepiments normally in one or two discontinuous rows, up to five rows locally developed, mainly regular, transeptal dissepiments locally present in all specimens, well developed in only two of the six specimens in our collection; regular dissepiments moderately convex to flattened and elongate, transeptal dissepiments larger, elongate and flattened; all dissepiments steeply adaxially declined to vertical, five to seven occur in 5 mm of corallite length.

In immature growth stages (mean diameter of smallest corallite studied, 1.3 mm), wall separating young corallite from parent commonly incompletely developed at mean corallite diameters below 2.5 mm; septa straight or curved, several major septa in each corallite closely approach or reach axial area, cardinal septum long, forms part of axial structure, counter septum commonly slightly shorter than adjacent major septa; relationship between number of major septa and mean corallite diameter shown in Figure 59; minor septa incompletely developed or absent at mean corallite diameters below 2 mm, generally well developed at mean diameters of 2.6 mm or greater; axial structure present in smallest corallites studied, consists of thin to irregularly thickened, straight or curved lamella formed by axial margin of cardinal septum, septal lamellae absent or poorly developed at mean diameters below 2.6 mm, well developed at higher mean diameters, lateral lamellae not observed below mean diameter of 3.75 mm; regular dissepiments absent at mean corallite diameters below 2 mm, poorly developed at mean diameters between 2 and 2.75 mm, present in discontinuous series at larger diameters, transeptal dissepiments not observed at mean diameters below 2.75 mm.

Discussion. *Cystolonsdaleia carteri* sp. nov. is distinguished by its thick, denticulate corallite walls, small corallite diameter, axially depressed tabulae, and by the weak development of its transeptal dissepiments. It resembles *C.*? *ivanovi* (Dobrolyubova) in the nature of its corallite walls and dissepimentarium, and the strong development of septal lamellae, but has more strongly concave tabulae, a greater number of septa and smaller corallite diameters than the Russian species. In the transverse section of *C.*? *ivanovi* illustrated by Dobrolyubova (1935a, Figs. 3, 5, Pl. 11, fig. 1; 1935b, Pl. 11, fig. 1), some of the axial structures appear to have lateral lamellae similar to those in the specimen from Ellesmere Island. There is uncertainty as to the exact nature of the axial and periaxial tabellae in the specimen described by Dobrolyubova, and the presence of periaxial cones cannot be established in her species. Therefore, it has not been been definitely assigned to *Cystolonsdaleia* by the authors.

Material. Holotype GSC 109671 (four pieces cut from incomplete colony, one transverse and two longitudinal thin sections, one transverse acetate peel). Paratypes: GSC 109672, GSC 109673, and GSC 109674. All fragments of small colonies from GSC loc. 60193. Additional material: two specimens from GSC loc. 60193.

Occurrence and age. *Cystolonsdaleia carteri* was found only in the southwest Blue Mountains (C) section (GSC loc. 60193, locality 9, Figs. 1, 7), where it occurs as clasts in a debris flow bed within the Hare Fiord Formation, 174 m above the top of the "Tellevak" limestone. Kasimovian or lowest Gzhelian foraminifers are present in the matrix of the debris flow bed (Table 3, Appendix 1). The corals may be the same age as the foraminifers or may predate them, if derived from older strata during the debris flow. *Cystolonsdaleia carteri* has not been found in older strata.

Cystolonsdaleia sp. aff. *C. carteri*

Plate 9, figures 10-14, Figures 50a-n,
52, 53, 60, 61

Description and discussion. *Cystolonsdaleia* sp. aff. *C. carteri*, represented by a single specimen from GSC loc. 60192, closely resembles *C. carteri* sp. nov. in the nature of its corallite walls, septa, and corallite diameters (Fig. 61), but is distinguished from that species by several features of the axial column, tabulae and dissepimentarium. The axial tabellae in *C.* sp. aff. *C. carteri* are less numerous than in *C. carteri*, commonly occurring as isolated plates and locally forming vertical series of only two (rarely three) tabellae. *Cystolonsdaleia* sp. aff. *C. carteri* also has relatively few, weakly developed periaxial cones, which extend along the axial column past only one or two succeeding tabulae (Fig. 60c, d). In comparison to *C. carteri*, its tabulae are more commonly adaxially elevated, the tabellae in position II are more commonly depressed at the dissepimentarium and the latter is better developed with fewer vertical discontinuities. The blastogeny and the development of the axial column in *C.* sp. aff. *C. carteri* are discussed in detail above, in the section dealing with the morphology of *Cystolonsdaleia*.

Cystolonsdaleia sp. aff. *C. carteri* is similar to *C*(?) *ivanovi* (Dobrolyubova) in the nature of its corallite

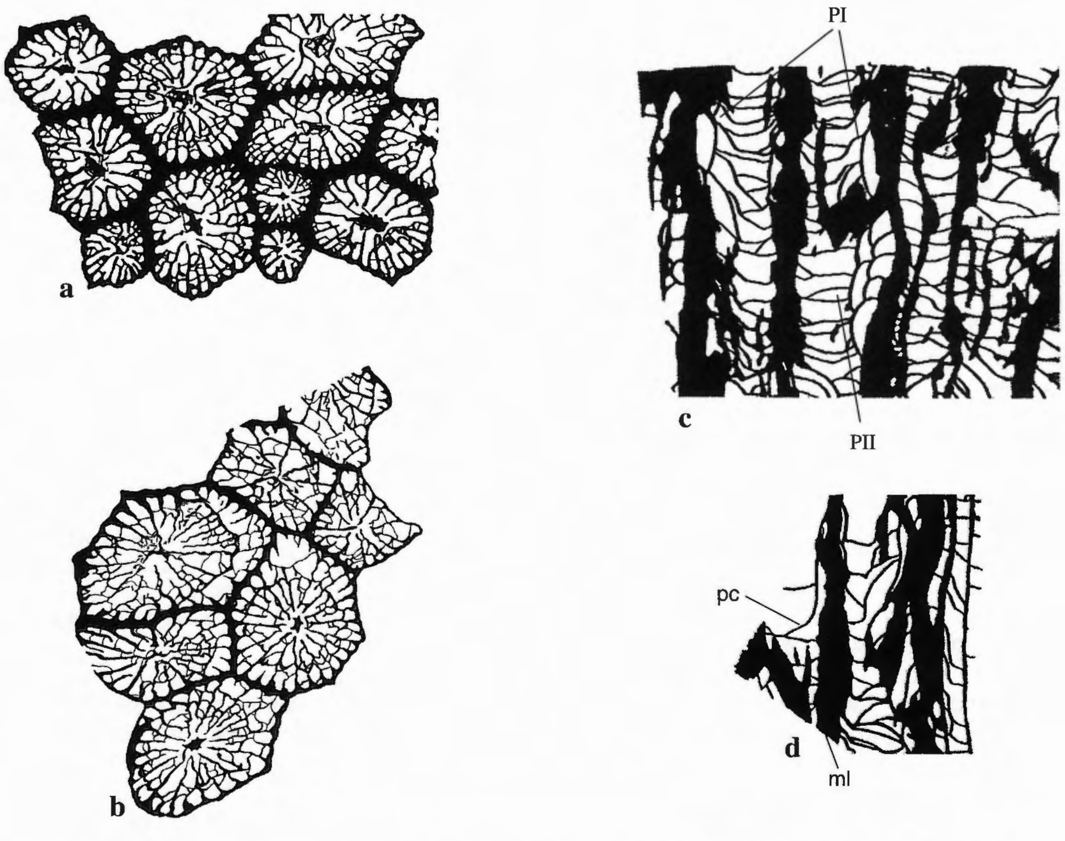

Figure 60. ***Cystolonsdaleia*** *sp. aff.* ***C. carteri****, hypotype GSC 109675;* ***a****, digital image of transverse thin section (see Pl. 9, fig. 10), showing thick, denticulate walls, variable axial structure and general lack of transeptal dissepiments, x4;* ***b****, drawing from same transverse thin section as in Figure 60a, showing local development of transeptal dissepiments, x4;* ***c****,* ***d****, digital images of longitudinal thin sections through mature corallites, showing rare periaxial cones (pc) and axial tabellae attached to median lamella (ml), and discontinuous dissepimentarium (see Pl. 9, figs. 11, 12), x6; biform morphology of tabularium well expressed on right side of left corallite in Figure 60c (tabellae in position I - PI, tabellae in position II - PII).*

walls, the strong development of septal lamellae, and the shape of the tabulae, but has a more continuous dissepimentarium, a slightly greater number of septa and smaller corallite diameters than the Russian species.

Material. Hypotype GSC 109675, incomplete colony from GSC loc. 60192, collected by G.F. Bonham-Carter.

Occurrence and age. Cystolonsdaleia sp. aff. *C. carteri* was found only in the southwest Blue Mountains (C) section (GSC loc. 60192, locality 9, Figs. 1, 7), where it occurs as a clast in a debris flow bed within the Hare Fiord Formation, 173 m above the top of the "Tellevak" limestone in association with *Petalaxis* sp. cf. *P. elyensis*. Kasimovian or lowest Gzhelian foraminifers are present in the matrix of the debris flow bed (Table 3, Appendices 1, 2). The corals may be the same age as the foraminifers or may predate them, if derived from older strata during the debris flow. *Cystolonsdaleia* sp. aff. *C. carteri* has not been found in older strata.

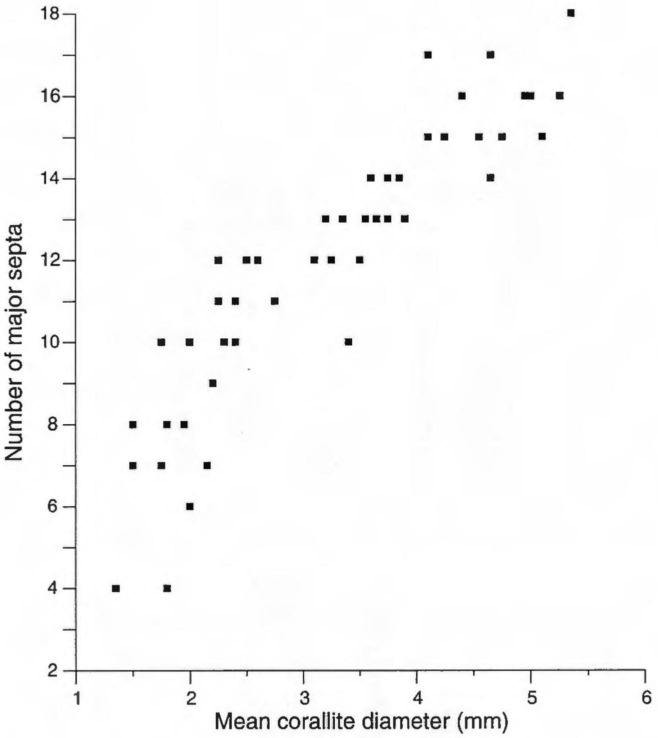

Figure 61. Relationship between mean corallite diameter and number of major septa in ***Cystolonsdaleia*** *sp. aff.* ***C. carteri*** *(hypotype GSC 109675).*

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APPENDICES

Identifications of foraminifers associated with Upper Carboniferous corals from the study area, by L. Rui (fusulinaceans) and S. Pinard (small foraminifers). See Figure 1 for section locations. See Locality Register (Table 2) and Figures 4-15 for stratigraphic position of GSC localities listed below.

APPENDIX 1

Identifications of fusulinaceans by L. Rui

Otto Fiord section (locality 3)

GSC loc. C-31216
Neostaffella sp. indet.
Beedeina sp. indet.
Age: mid-Carboniferous (Moscovian)

GSC loc. C-31217
Fusulinella subelliptica Rui, Ross, and Nassichuk
Beedeina ex. gr. *B. arizonensis* (Ross and Sabins)
Pseudoendothyra ellesmerensis Rui, Ross, and Nassichuk
Age: late Moscovian (Podolskian)

GSC loc. C-31218
Fusulinella sp. indet.
Beedeina sp. indet.
Staffella sp. indet.
Age: mid-Carboniferous (Moscovian)

GSC loc. C-31219
Fusulinella sp. indet.
Beedeina sp. indet.
Neostaffella sp. indet.
Age: mid-Carboniferous (Moscovian)

GSC loc. C-31223
Ozawainella sp.
Staffella sp.
Age: mid-Carboniferous (Moscovian)

GSC loc. C-31227
Wedekindellina sp.
Staffella sp.
Age: late Moscovian (Podolskian or Myachkovian)

Van Hauen Pass section (locality 5)

GSC loc. C-10861
Neostaffella sp. indet.
Age: late? Moscovian (?Podolskian or Myachkovian)

GSC loc. C-10866
Schwagerina sp. indet.
Age: Early Permian (Asselian)

GSC loc. 47866
Triticites spp.
Thompsonella? spp.
Pseudofusulinella spp.
Age: Late Carboniferous (Gzhelian)

Northeast Blue Mountains section (locality 6)

GSC loc. C-10813
Profusulinella ex. gr. *P. copiosa* Thompson
P. prisca timanica Kireeva
P. skelnevatica Putrja
P. sp. indet.
Profusulinella? ex. gr. *P. plummeri* Skinner and Wilde
Pseudostaffella sp. indet.
Ozawainella sp. indet.

GSC loc. C-10815
Profusulinella? sp. indet.

Age of GSC locs. C-10813, C-10815: early Moscovian (Kashirian)

Southwest Blue Mountains (C) section (locality 9)

GSC loc. 60192
Pseudofusulinella ex. gr. *P. antiqua* Skinner and Wilde
P. ex. gr. *P. fusiformis* Skinner and Wilde

GSC loc. 60193
Pseudofusulinella sp. indet.

GSC loc. C-99027
Pseudofusulinella ex. gr. *P. prima* Skinner and Wilde

GSC loc. C-99028
Pseudofusulinella sp. indet.

Age of GSC locs. 60192, 60193, C-99027, C-99028: Kasimovian or Gzhelian

GSC loc. C-99035
Pseudofusulina ex. gr. *P. plana* Skinner and Wilde
P. spp.
Schwagerina sp. indet.
Pseudofusulinella sp. indet.

GSC loc. C-99052
Schwagerina schencki Skinner and Wilde

Age of GSC locs. C-99035, C-99052: Early Permian (Asselian)

GSC loc. C-99432
Fusulinella sp. indet.

Wedekindellina sp. indet.
Neostaffella sp. indet.

GSC loc. C-99436
Wedekindellina ex. gr. *W. pulchra* Rui, Ross, and Nassichuk

Age of GSC locs. C-99432, C-99436: late Moscovian (Podolskian or Myachkovian)

Greely Fiord section (locality 10)

GSC loc. C-193096
Eofusulina trianguliformis Putrja
Profusuinella ex. gr. *P. prisca sphaeroidea* Rauser
Pseudostaffella ex. gr. *P. subquadrata* Grozdilova and Lebedeva
Age: early Moscovian (Vereian)

GSC loc. C-193097
Profusulinella sp. indet.
Pseudostaffella sp. indet.
Pseudoendothyra sp. indet.

GSC loc. C-193100
Profusulinella ex. gr. *P. prisca* (Deprat)
Eofusulina sp. indet.
Pseudoendothyra sp. indet.

Age of GSC locs. C-193097, C-193100: early Moscovian (Vereian or Kashirian)

GSC loc. C-193105
Profusulinella ovata Rauser

GSC loc. C-193106
Fusulinella sp. indet.

Age of GSC locs. C193105, C193106: early Moscovian (Kashirian)

Agassiz Ice Cap section (locality 11)

GSC loc. C-193088
Pseudoendothyra struvei (Moeller)
Staffella ex. gr. *S. moelleri* Ozawa

GSC loc. C-193091
Schubertella sp. indet.

GSC loc. C-193095
Beedeina ex. gr. *B. paradistenta* Safonova

Age of GSC locs. C-193088, C-193091, C-193095: late Moscovian (Podolskian or Myachkovian)

Northeast Trold Fiord section (locality 12)

GSC loc. C-179719
?*Profusulinella* sp. indet.

GSC loc. C-179721
Staffella ex. gr. *S. pseudosphaeroides* (Dutkevich)
Pseudoendothyra sp. indet.

GSC loc. C-179722
Staffella sp. indet.
Pseudoendothyra sp. indet.
?*Profusulinella* sp. indet.

GSC loc. C-179723
Pseudoendothyra sp. indet.

GSC loc. C-179724
Schubertella obscura Lee and Chen
Pseudostaffella sp. indet.
?*Fusulinella* sp. indet.

GSC loc. C-179728
Staffella ex. gr. *S. pseudosphaeroides* (Dutkevich)
Pseudoendothyra sp. indet.

Age of GSC locs. C-179719, C-179721 to C-179724, C-179728: Moscovian

East Blind Fiord (B) section (locality 13)

GSC loc. C-10872
?*Schubertella* sp. indet.

GSC loc. C-10873
Neostaffella subquadrata vozhgalica Safonova

GSC loc. C-10877
Fusiella ex. gr. *F. typica* Lee and Chen
Neostaffella sp. indet.

GSC loc. C-27950
Pseudoendothyra sp. indet.

Age of GSC locs. C-10872, C-10873, C-10877, C-27950: Moscovian (Vereian to Podolskian)

GSC loc. C-10881
Fusulinella ex. gr. *F. devexa* Thompson
F. ex. gr. *subpulchra submesopachis* Putrja
Wedekindellina sp. indet.

GSC loc. C-27962
Wedekindellina cabezasensis Ross and Sabins
W. spp.

GSC loc. C-27964
Wedekindellina cabezasensis Ross and Sabins
Neostaffella sp. indet.

Age of GSC locs. C-10881, C-27962, C-27964: late Moscovian (Podolskian)

GSC loc. C-27968
Fusulinella ex. gr. *F. eopulchra* Rauser
Age: Late Moscovian (Myachkovian)

GSC loc. C-10886
Pseudofusulinella spp. indet.

GSC loc. C-10888
Pseudofusulinella pulchra (Rauser and Beljaev)

GSC loc. C-10891
?*Schubertella* sp. indet.

GSC loc. C-10892
Pseudofusulinella pulchra (Rauser and Beljaev)

GSC loc. C-27977
Pseudofusulinella? sp. indet.

GSC loc. C-27978
Pseudofusulinella? sp. indet.

GSC loc. C-27982
Pseudofusulinella sp. indet.

GSC loc. C-27984
Pseudofusulinella pulchra (Rauser and Beljaev)

GSC loc. C-27985
Pseudoendothyra? sp. indet.

GSC loc. C-27988
Pseudofusulinella sp. indet.

GSC loc. C-27997
Pseudofusulinella ex. gr. *usvae* (Dutkevich)
P. ex. gr. *pulchra* (Rauser and Beljaev)

Age of GSC locs. C-10886, C-10888, C-10891, C-10892, C-27977, C-27978, C-27982, C-27984, C-27985, C-27988, C-27997: Kasimovian or Gzhelian

GSC loc. C-10893
Oketaella spp. indet.
Age: Kasimovian to Asselian

East Blind Fiord (A) section (locality 14)

GSC loc. C-28059
Eofusulina triangula (Rauser and Beljaev)

GSC loc. C-28063
Profusulinella ex. gr. *P. priscoidea* Rauser

GSC loc. C-28064
Profusulinella ex. gr. *P. priscoidea* Rauser

GSC loc. C-28065
Profusulinella priscoidea Rauser
Eofusulina sp. indet.

GSC loc. C-28066
Profusulinella ex. gr. *P. priscoidea* Rauser

GSC loc. C-28067
Profusulinella sp. indet.
Schubertella sp. indet.

Age of GSC locs. C-28059, C-28063 to C-28067: early Moscovian (Vereian or Kashirian)

GSC loc. C-11402
Profusulinella sp. indet.
Fusulinella sp. indet.
Pseudostaffella sp. indet.

GSC loc. C-11403
Profusulinella sp. indet.
Staffella ex. gr. *S. powwowensis* Thompson
S. spp. indet.
Pseudostaffella sp. indet.
Schubertella gracilis Rauser
S. spp. indet.

Age of GSC locs. C-11402, C-11403: early Moscovian (Kashirian)

South Trold Fiord section (locality 15)

GSC loc. C-179729
Fusulinella sp. indet.
Pseudostaffella sp. indet.
Eostaffella ex. gr. *E. ampla* (Thompson)

GSC loc. C-179731
Schubertella gracilis Rauser
Staffella sp. indet.
Pseudoendothyra ex. gr. *P. holmensis* (Ross and Dunbar)

GSC loc. C-179732
Staffella ex. gr. *S. pseudosphaeroides* (Dutkevich)
Pseudoendothyra ex. gr. *P. holmensis* (Ross and Dunbar)

Age of GSC locs. C-179729, C-179731, C-179732: Moscovian

GSC loc. C-188642
Pseudostaffella sp. cf. *P. subquadrata vozhgalica* Safonova
Ozawainella sp. indet.

GSC loc. C-188644
Ozawainella sp. ex. gr. *O. tingi* Lee

GSC loc. C-188645
Pseudostaffella sp. indet.

GSC loc. C-188646
Pseudostaffella? sp. indet.
Profusulinella sp. indet.

GSC loc. C-188649
Profusulinella sp. indet.

GSC loc. C-188650
Profusulinella sp. ex. gr. *P. ovata* Putrja

Age of GSC locs. C-188642, C-188644 to C-188656, C-188649, C-188650: early Moscovian (Vereian or Kashirian)

GSC loc. C-188651
Profusulinella? sp. indet.

GSC loc. C-188652
Profusulinella? sp. indet.

Age of GSC locs. C-188651 and C-188652: early to mid-Moscovian

GSC loc. C-188653
Pseudostaffella sp. cf. *P. umbilicata* Putrja and Leontovich
Age: mid-Moscovian (Kashirian or Podolskian)

GSC loc. C-188654
Profusulinella sp. cf. *P. postaljutovica* (Safonova)
Age: early Moscovian (Kashirian)

GSC loc. C-188655
Fusulinella sp. indet.

GSC loc. C-188656
Profusulinella sp. indet.
Schubertella sp. indet.
Pseudoendothyra sp. indet.

C-188658
Profusulinella? sp. indet.
Fusulinella? sp. indet.

Age of GSC locs. C-188655, C-188656 and C-188658: early to mid-Moscovian

GSC loc. C-188660
Eofusulina sp. indet.
Pseudoendothyra sp. indet.

GSC loc. C-188661
Eofusulina sp. nov.
Pseudostaffella sp. indet.

Age of GSC locs. C-188660, C-188661: early to mid-Moscovian (Vereian to Podolskian). *Eofusulina* is common in the Vereian and Kashirian, and rare in the Podolskian.

GSC loc. C-188662
Fusulinella? sp. indet.
Schubertella sp. indet.

GSC loc. C-188663
Profusulinella sp. indet.
Pseudostaffella sp. indet.

GSC loc. C-188664
Fusulinella? sp. indet.

GSC loc. C-188665
Pseudoendothyra sp. indet.
Schubertella sp. indet.
Fusulinella sp. indet.

GSC loc. C-188666
Beedeina sp. indet.
Schubertella sp. indet.

Age of GSC locs. C-188662 to C-188666: mid-Moscovian (Kashirian or Podolskian)

West Blind Fiord section (locality 16)

GSC loc. C-179734
Pseudofusulinella sp. ex. gr. *P. praeantiqua* Wilde
P. pulchra (Rauser and Beljaev)
P. usvae (Dutkevich)
Age: Kasimovian

Bjorne Peninsula section (locality 17)

GSC loc. 57728
Fusulina ex. gr. *F. cylindrica* Fischer emend. Moeller
Fusulinella alta Verville, Thompson, and Lokke
Age: late Moscovian (Myachkovian)

APPENDIX 2

Identifications of small foraminifers by S. Pinard

Southwest Blue Mountains (C) section (locality 9)

GSC loc. 60192
- apterrinellids, indet.
- *Bradyina* sp.
- *Climacammina* sp.
- *Earlandia* of the group *E. minima* (Birina)
- *Endothyra* sp.
- Lasiodiscidae?, indet.
- *Globivalvulina* sp.
- palaeotextulariid, indet.
- *Polytaxis*? sp.
- *Protonodosaria praecursor* (Rauser-Chernoussova)
- *Syzrania bella* Reitlinger
- *Syzranella* sp. nov.
- *Tetrataxis* sp.
- Age: Kasimovian to Early Permian (Sakmarian)

GSC loc. C-99027
- ?*Asselodiscus primitivus* Mamet and Pinard or *Pseudovidalina*? sp. (oblique section)
- *Climacammina*? sp. or *Deckerella*? sp. (oblique section)
- *Globivalvulina pergrata* Konovalova
- *G.* of the group *G. bulloides* (Brady)
- *Hemigordius schlumbergeri* (Howchin)
- palaeotextulariid indet.
- *Syzrania* sp.
- *Tetrataxis* sp.
- *Tuberitina* sp.
- Age: Kasimovian to earliest Gzhelian

GSC loc. C-99028
- apterrinellids indet.
- *Climacammina* sp.
- *Deckerella* sp.
- *Globivalvulina pergrata* Konovalova
- *G.* sp. indet.
- palaeotextulariid indet.
- *Pseudobradyina* sp.
- *Pseudovidalina* sp. nov.
- ?*Syzrania* sp. nov.
- Age: Gzhelian

GSC loc. C-99035
- *Climacammina* sp.
- *Deckerella* sp.
- *Globivalvulina* sp.
- *Tetrataxis* sp.
- Age: Late Carboniferous or Permian

GSC loc. C-99432
- *Bradyina* spp.
- *Climacammina grandis*? Reitlinger
- *C.* sp. indet.
- palaeotextulariid indet.
- *Tetrataxis* sp.
- *Tuberitina* sp.
- Age: Moscovian

East Blind Fiord (B) section (locality 13)

GSC loc. C-10891
- apterrinellids
- *Asselodiscus primitivus* Mamet and Pinard
- *Globivalvulina granulosa* Reitlinger
- *G.* sp. indet.
- ?*Hemigordius schlumbergeri* (Howchin)
- ?*Neohemigordius megasphaericus* (Gerke)
- palaeotextulariid indet.
- ?*Protonodosaria praecursor* (Rauser-Chernoussova)
- *Syzrania bella* Reitlinger
- *S.* sp. nov.
- Age: Kasimovian?

Plate 1

(Figures x3, unless stated otherwise)

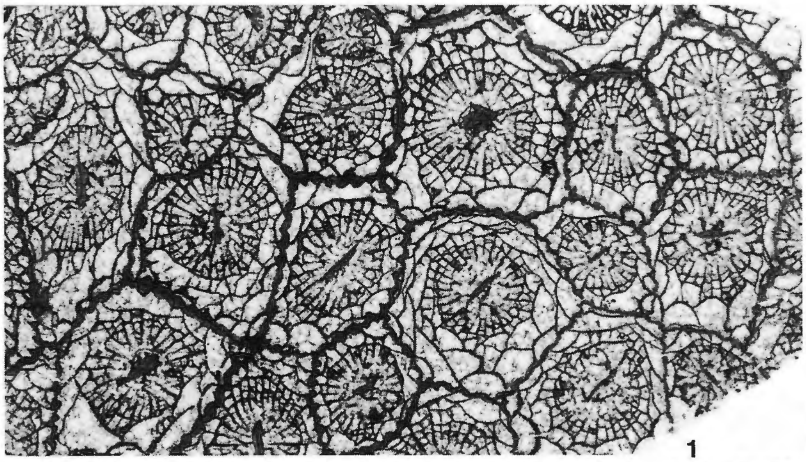
Figures 1-10. *Petalaxis mcoyanus* (Milne Edwards and Haime, 1851).

1-3. Hypotype GSC 109630, from GSC loc. C-193105; early Moscovian (Kashirian). 1, transverse thin section, showing septal lamellae and rare lateral lamellae. 2, 3, longitudinal thin sections showing subhorizontal to adaxially elevated tabulae.

4, 5. Hypotype GSC 109631, from GSC loc. C-193105; early Moscovian (Kashirian). 4, transverse thin section, partly silicified, note lateral lamella in mature corallite near lower margin of figure. 5, longitudinal thin section showing axially elevated tabulae and biform morphology of tabularium; section off centre in upper part of corallite on right.

6-10. Hypotypes GSC 109632 (figs. 6-8), 109633 (figs. 9, 10), from near type locality for species, Leninskie Gorki, south of Moscow, Russia, GSC loc. C-222965; late Moscovian (Myachkovian); specimens lack matrix, internal structure of several illustrated corallites partly destroyed. 6, 9, transverse thin sections showing numerous septal lamellae and weakly developed lateral lamellae. 7, 8, 10, longitudinal thin sections showing subhorizontal to axially elevated tabulae with rare axial tabellae; figure 10 shows biform morphology on left side of tabularium, x5; section slightly off centre in middle of figure 7 and in central corallite of figure 8.

Figures 11-13. *Petalaxis donbassicus* (Fomichev, 1953), hypotype GSC 109634, from GSC loc. 58924; Moscovian, probably Kashirian. 11, 12, longitudinal thin sections, showing closely spaced, generally concave tabulae with strongly developed biform morphology. 13, transverse thin section, showing thick, lens-shaped median lamellae and locally developed, short septal lamellae.



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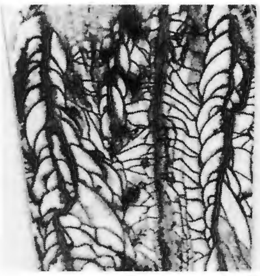

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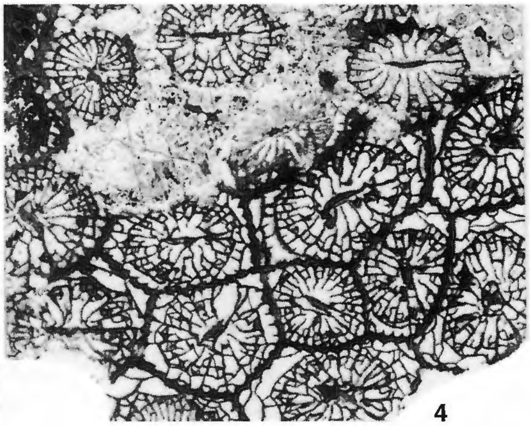

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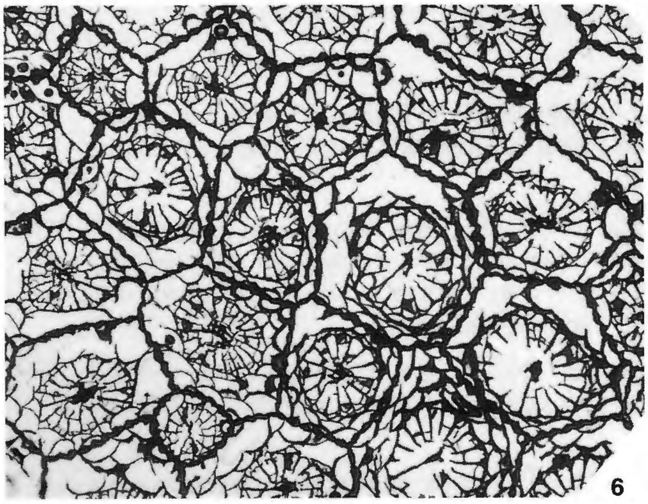

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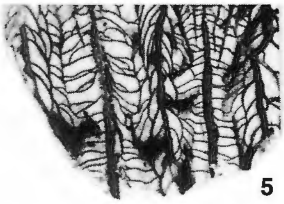

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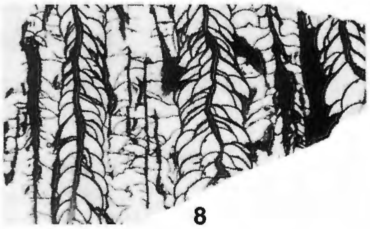

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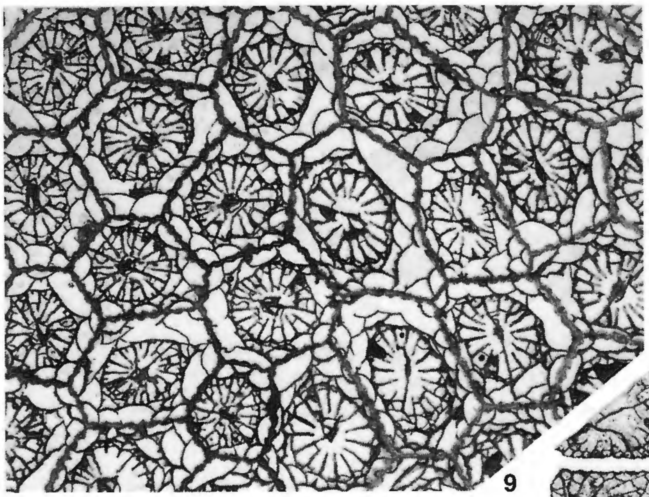

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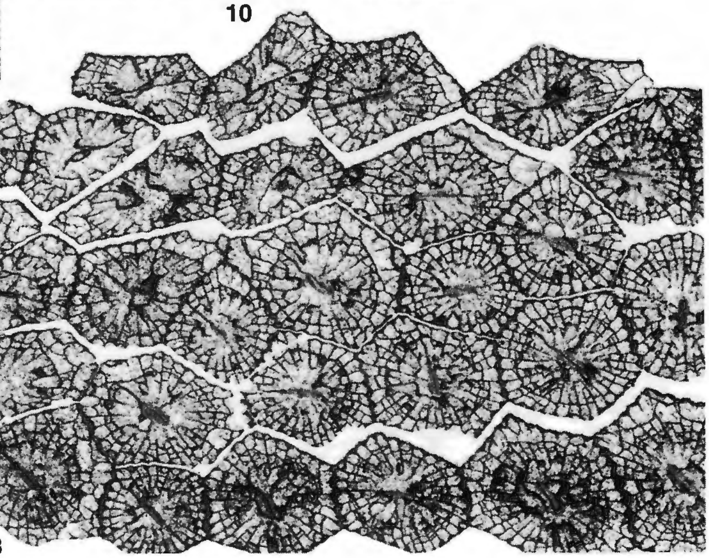

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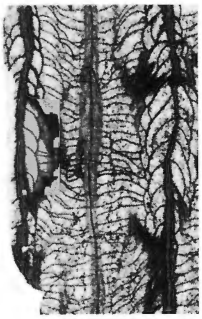

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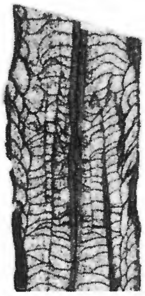

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Plate 2

(Figures x3, unless stated otherwise)

Figures 1-5. *Petalaxis donbassicus* (Fomichev, 1953), showing thick, lens-shaped median lamellae, locally well developed septal lamellae, rare lateral lamellae, and closely spaced, concave tabulae.

1-3. Hypotype GSC 109635, from GSC loc. C-193105; early Moscovian (Kashirian). 1, transverse thin section; internal structure of small corallite in lower left destroyed by recrystallization. 2, 3, longitudinal thin sections; section in figure 3 oblique to counter-cardinal plane, biform morphology shown on left side.

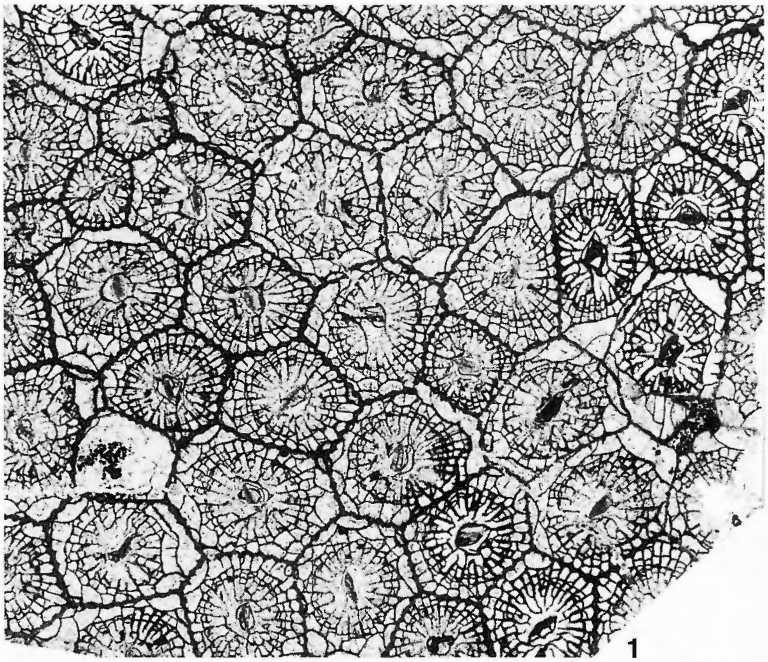
4, 5. Hypotype GSC 109636, from GSC loc. C-193105; early Moscovian (Kashirian). 4, transverse thin section. 5, longitudinal thin section with upper part showing lateral lamella to left of median lamella.

Figures 6-8. *Petalaxis* sp., hypotype GSC 109637, from GSC loc. C-10813; early Moscovian (Kashirian). 6, transverse thin section, showing thick corallite walls, long septa, and rarity of transeptal dissepiments. 7, 8, longitudinal thin sections, showing concave tabulae and biform morphology; upper half of figure 7 has inflated ?transeptal dissepiments.

Figures 9-12. *Petalaxis crassicolumnus* sp. nov., showing highly vesicular, adaxially elevated tabulae and thick axial columns with numerous septal and lateral lamellae.

9, 10. Holotype GSC 109638, from GSC loc. C-179729; Moscovian, probably Kashirian or Podolskian. 9, longitudinal thin section showing axial tabellae at top, x4. 10, transverse thin section showing well expressed lateral lamellae in large, mature corallites in upper part of figure, x2.

11, 12. Paratype GSC 109639, from GSC loc. C-179729; Moscovian, probably Kashirian or Podolskian. 11, transverse thin section showing immature growth stages of several corallites, x2. 12, longitudinal thin section with biform morphology shown on right side of tabularium, x4.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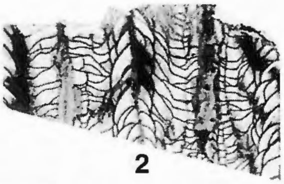
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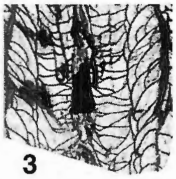
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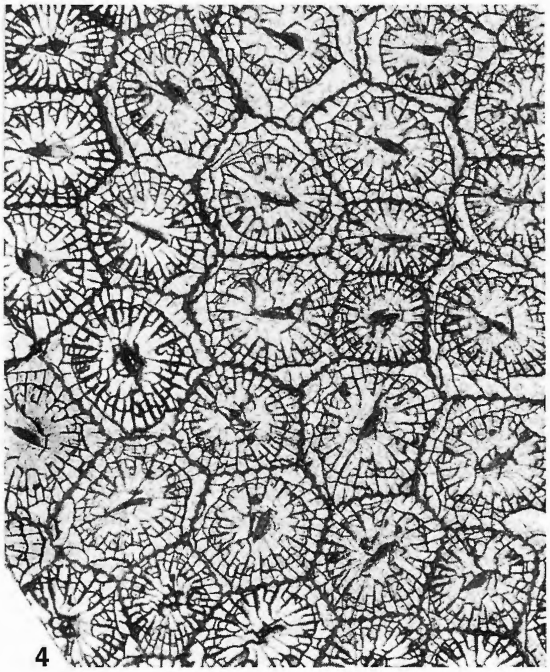
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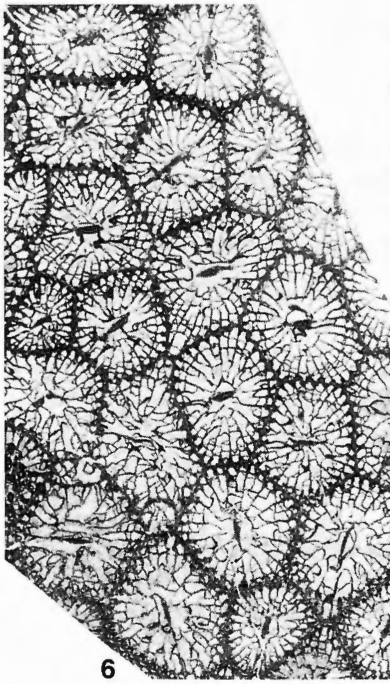
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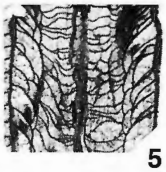
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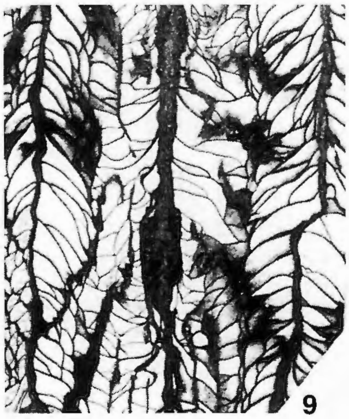
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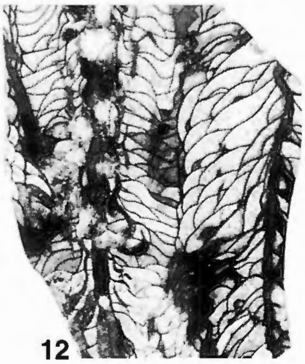
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Plate 3

(Figures x2 unless stated otherwise)

Figures 1-5. *Petalaxis crassicolumnus* sp. nov., showing highly vesicular, subhorizontal to adaxially elevated tabulae and thick axial columns with numerous septal and lateral lamellae.

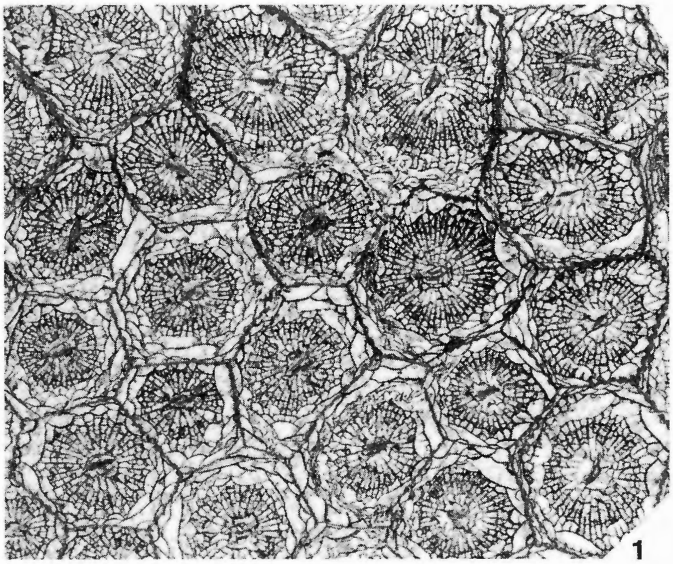
1, 2. Paratype GSC 109640, from GSC loc. C-179727; Moscovian, probably Kashirian or Podolskian. 1, transverse thin section. 2, longitudinal thin section showing several axial tabellae, x4.

3-5. Paratype, GSC 109642, from GSC loc. C-11403; early Moscovian (Kashirian). 3, transverse thin section showing relatively thin axial structures and immature growth stages of numerous corallites. 4, longitudinal thin section showing axially depressed tabulae in early growth stage, x3. 5, longitudinal thin section showing subhorizontal and depressed tabulae.

Figures 6-13. *Petalaxis ellesmerensis* sp. nov., showing narrow, variable axial structures and generally incomplete, axially elevated tabulae.

6-9. Holotype GSC 109643, from GSC loc. C-179729; Moscovian, probably Kashirian or Podolskian. 6, 7, transverse thin sections, central parts of tabularia replaced by coarsely crystalline calcite in three coralla in figure 7. 8, 9, longitudinal thin sections, showing tabulae moderately elevated toward median lamella; cause unknown for deformity in upper left part of tabularium of corallite in figure 9.

10-13. Paratype GSC 109645, from GSC loc. C-11403; early Moscovian (Kashirian). 10, 12, 13, longitudinal thin sections showing moderate to steep adaxial elevation of tabulae; figures 12 and 13, x3; note lateral lamella at top of corallite in figure 12. 11, transverse thin section, lateral lamellae in several corallites (e.g., bottom centre).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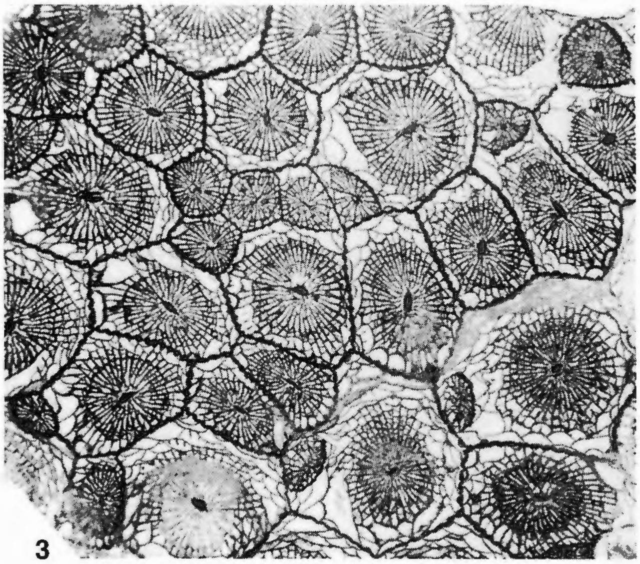
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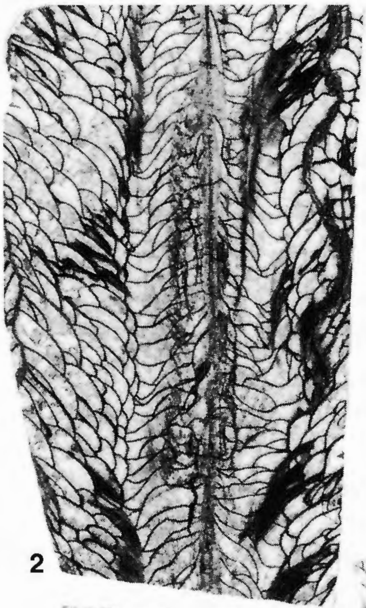
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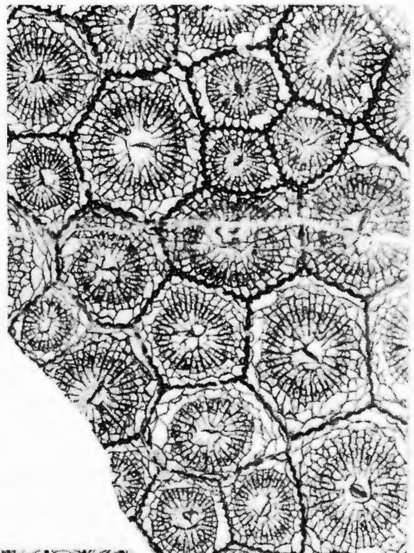
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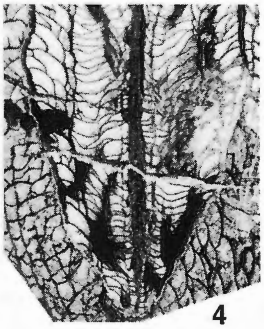
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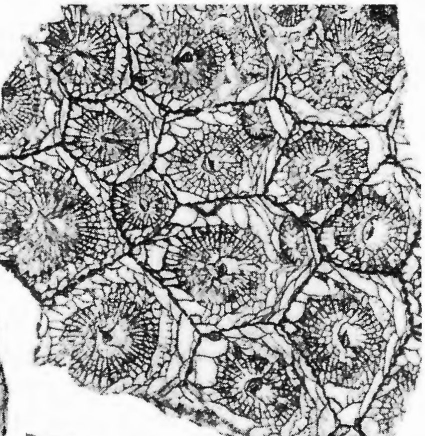
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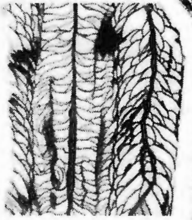
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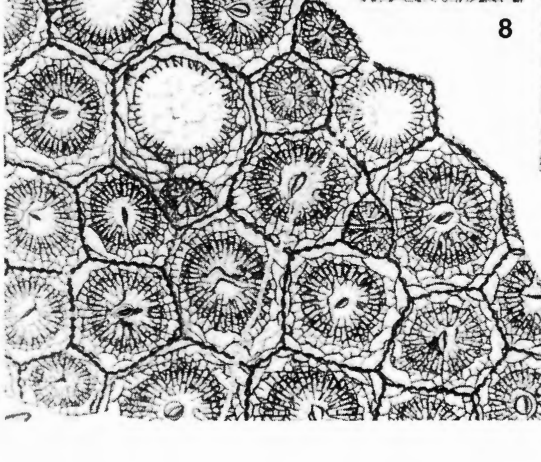
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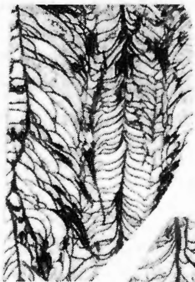
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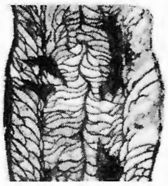
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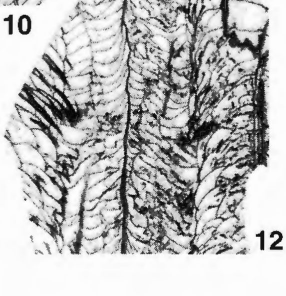
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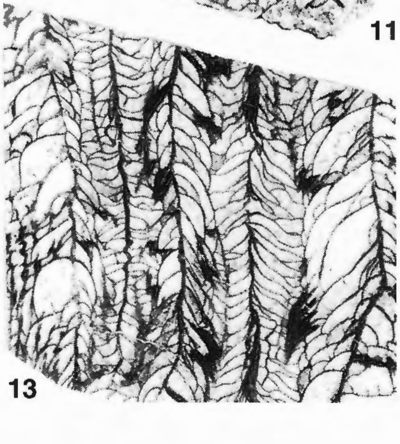
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Plate 4

(Figures x2 unless stated otherwise)

Figures 1, 2. *Petalaxis ellesmerensis* sp. nov., paratype GSC 109644, from GSC loc. C-179729; Moscovian, probably Kashirian or Podolskian. 1, transverse thin section. 2, longitudinal thin section showing subhorizontal to moderately elevated tabulae and vertical variation in thickness and shape of median lamella; note biform morphology of tabularium; section slightly off centre where arcuate septal intercepts appear in tabularium, a short distance above base of figure, exaggerating decreased thickness of median lamella over that interval.

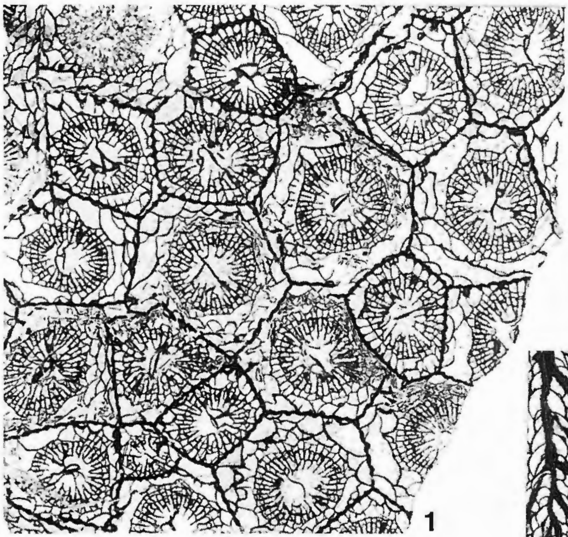
Figures 3-11. *Petalaxis multilamellatus* sp. nov.; Moscovian, probably Kashirian or Podolskian; showing long septa, concave tabulae, biform tabularium, and numerous septal and lateral lamellae.

3-5. Holotype GSC 109646, from GSC loc. C-179722. 3, transverse thin section. 4, 5, longitudinal thin sections, showing discontinuous lateral lamellae, x3; section slightly off centre in lower part of corallite in figure 5.

6-9. Paratype GSC 109647, from GSC loc. C-179722. 6, 7, longitudinal thin sections; section slightly off centre in upper part of corallite in figure 7 (x3). 8, 9, transverse thin sections; axial structures show variation in development of septal lamellae and lateral lamellae.

10, 11. Paratype GSC 109648, from GSC loc. C-179722. 10, transverse thin section showing two or three lateral lamellae in many corallites. 11, longitudinal thin section showing continuous median lamella and several discontinuous lateral lamellae, x3.

Figure 12. *Petalaxis beauchampi* sp. nov., paratype GSC 109650, from GSC loc. C-179732; Moscovian, probably Kashirian or Podolskian; transverse thin section, showing typical long, thin septa and weakly developed axial structure, specimen partly crushed, x3.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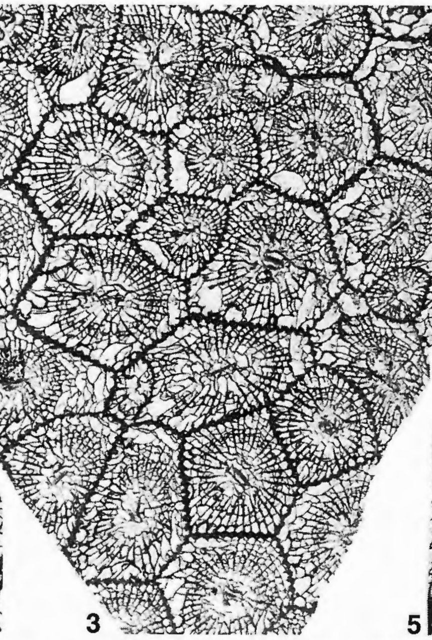
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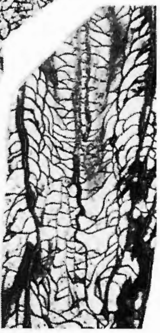
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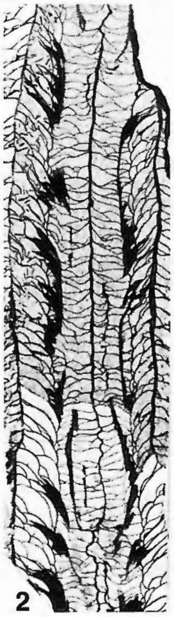
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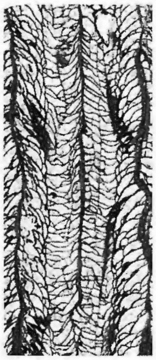
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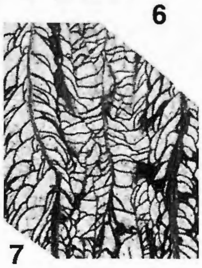
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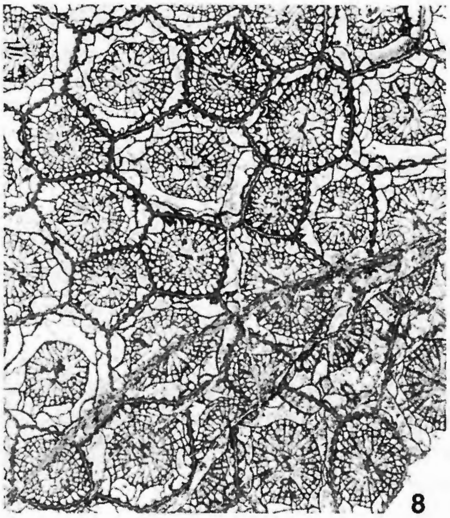
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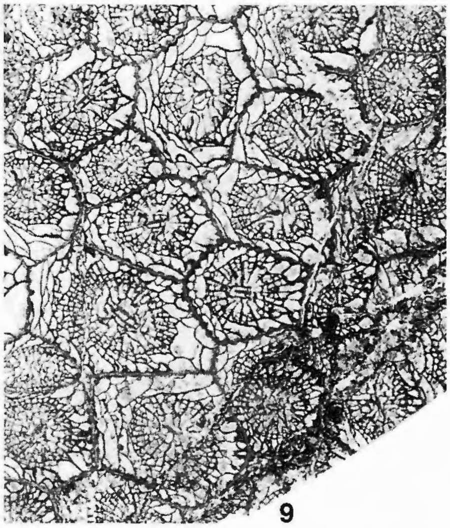
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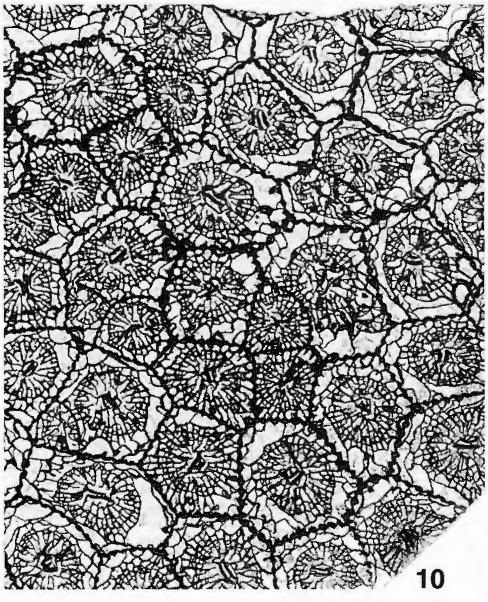
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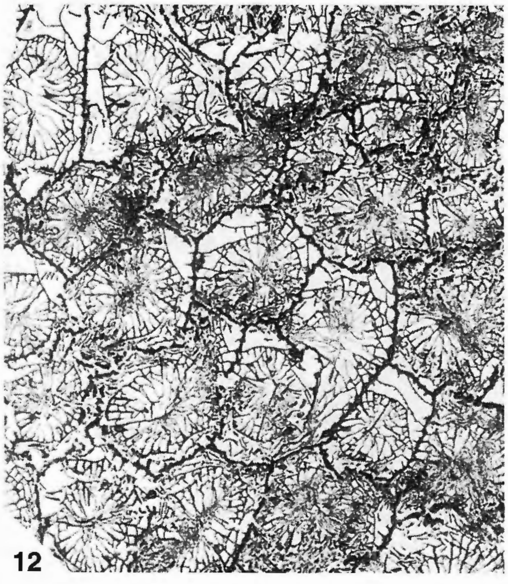
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Plate 5

(Figures x2 unless stated otherwise)

Figures 1-9. *Petalaxis beauchampi* sp. nov.; specimens in figures 1-5 from GSC loc. C-179732, Moscovian, probably Kashirian or Podolskian; specimen in figures 6-9 from GSC loc. C-10884, late Moscovian (Myachkovian); showing long, thin septa, weakly developed, locally discontinuous axial structure, concave, generally complete tabulae, and medium to large, inflated dissepiments.

1. Paratype GSC 109650, longitudinal thin section showing concave tabulae slightly elevated to join median lamella, x4.

2-5. Holotype GSC 109649. 2-4, longitudinal thin sections showing concave tabulae and intercepts of axial margins of long major septa; note biform morphology, weakly expressed in tabularium, x3. 5, transverse thin section showing thin median lamella, locally withdrawn or deflected from axial area, x3.

6-9. Paratype GSC 109651, from GSC loc. C-10884. 6, transverse thin section showing long, sinuous septa occupying axial areas of corallites where cardinal septum withdrawn. 7-9, longitudinal thin sections, showing closely spaced tabulae, sinuous median lamellae, and intercepts of long major septa.

Figures 10-14. *Petalaxis thorsteinssoni* sp. nov., showing variable thickness of axial structure, long septa, wide dissepimentarium, and concave tabulae.

10-13. Holotype GSC 109653, from GSC loc. C-147456; probably late Moscovian (Myachkovian); 10, transverse thin section, note slight thickening of cardinal septum. 11-13, longitudinal thin sections; section off centre in lower part of both corallites illustrated in figure 11, x3; early growth stage shown in figure 12 (x4); figure 13, x3.

14. Paratype GSC 109655, from GSC loc. C-10881, late Moscovian (Podolskian), transverse thin section.


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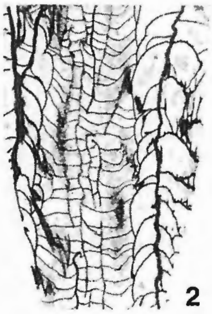
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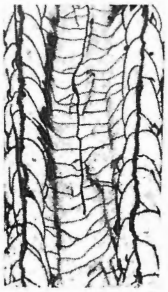
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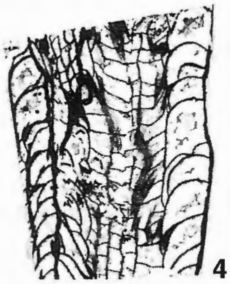
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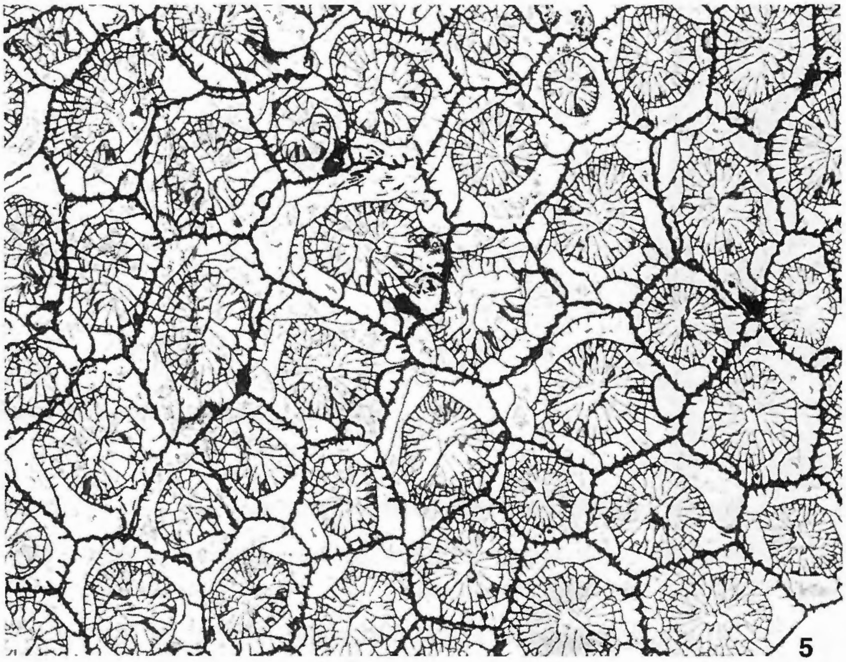
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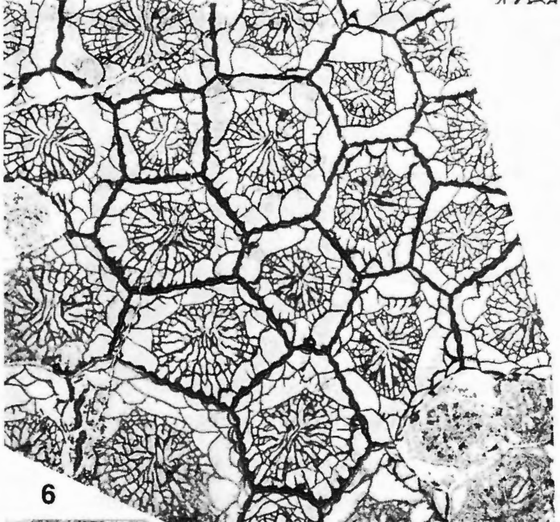
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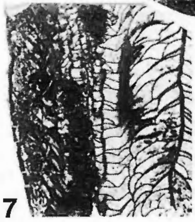
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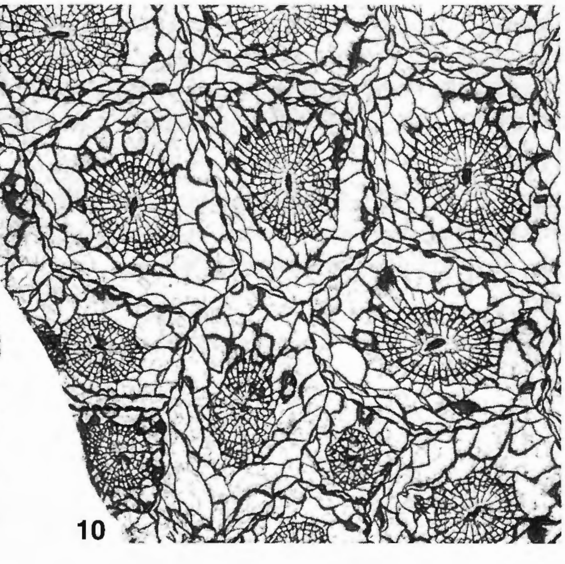
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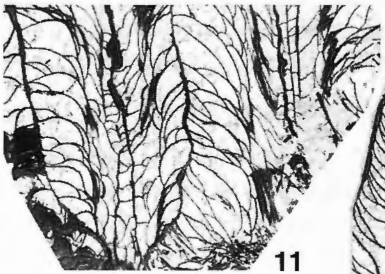
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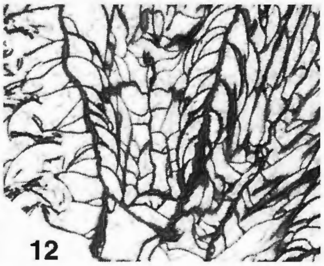
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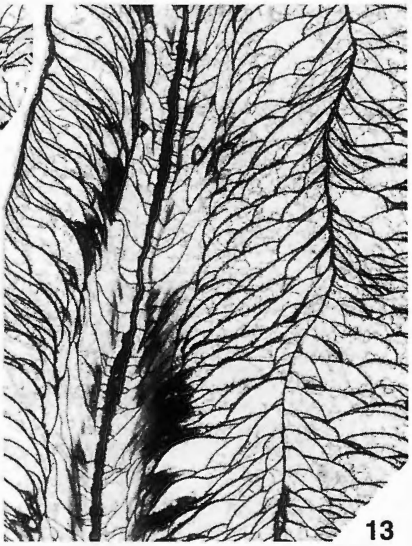
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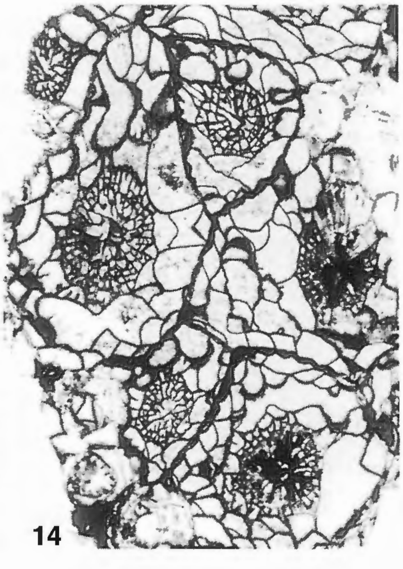
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Plate 6

(Figures x2 unless stated otherwise)

Figures 1-4. *Petalaxis thorsteinssoni*, sp. nov.

1. Paratype GSC 109655, from GSC loc. C-10881, late Moscovian (Podolskian), longitudinal thin section, x3.

2-4. Paratype GSC 109654, from GSC loc. C-1877; probably late Moscovian. 2, transverse thin section; several corallites show slightly thickened cardinal septum continuous with long, thin median lamella. 3, 4, longitudinal thin sections, showing thin, sinuous median lamella and intercepts of long major septa; figure 3 shows biform morphology in tabularium.

Figures 5-10. *Petalaxis baculatus* sp. nov., from GSC loc. C-10891; Kasimovian.

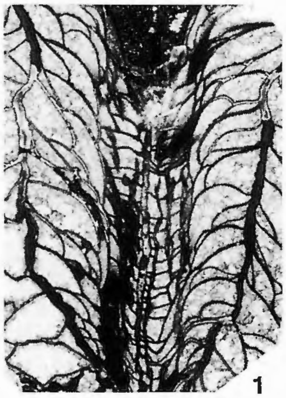
5-8. Holotype GSC 109657. 5, 7, transverse thin sections showing local subcerioid growth habit, very weak development of minor septa, and lens-shaped to circular, rod-like median and lateral lamellae; figure 5, x3. 6, 8, longitudinal thin sections showing generally concave tabulae with rare axial tabellae; curvature of continuous median lamellae locally causes apparent discontinuity in axial structures of all corallites illustrated; section through corallite on right side of figure 8 is oblique to counter-cardinal plane.

9, 10. Paratype GSC 109660. 9, longitudinal thin section showing subhorizontal tabulae and discontinuous dissepimentarium in early growth stages. 10, transverse thin section.

Figures 11-17. *Petalaxis parvus* sp. nov., from GSC loc. C-179734, Kasimovian (possibly early Kasimovian), showing thick cardinal septum, moderately to strongly thickened median lamella, very short minor septa, rare lateral lamellae, generally complete, subhorizontal to adaxially elevated tabulae, and narrow, locally discontinuous dissepimentarium.

11-14. Holotype GSC 109661. 11, longitudinal thin section of five corallites, section off centre and oblique to counter-cardinal plane in middle corallite and two corallites on left, x3. 12, longitudinal thin section showing lateral lamella to right of median lamella in lower part and adaxially elevated tabulae. 13, longitudinal thin section, off centre at base. 14, transverse thin section, x3.

15-17. Paratype GSC 109663, x3. 15, 16, longitudinal thin sections; section in figure 16 oblique to counter-cardinal plane and slightly off centre in lower part. 17, transverse thin section showing immature growth stages in several corallites.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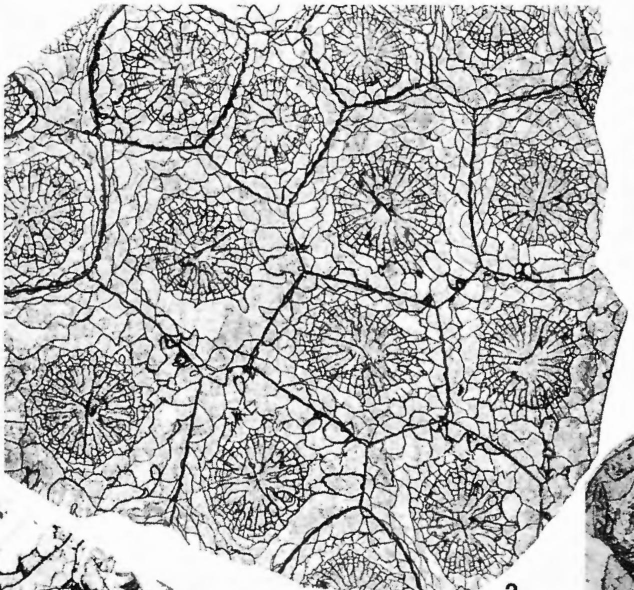
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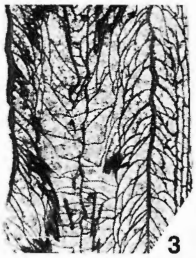
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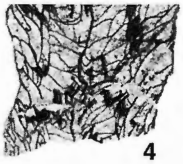
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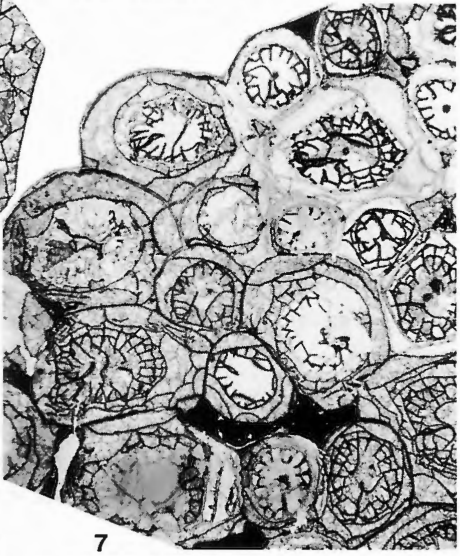
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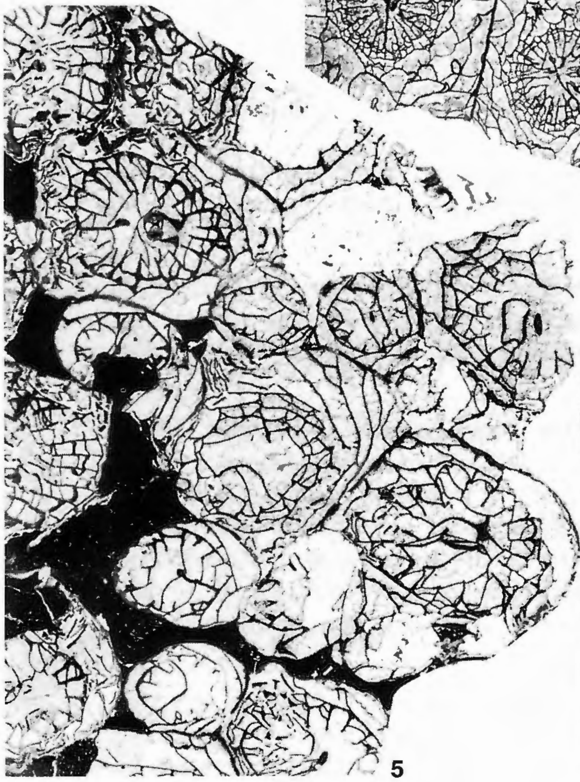
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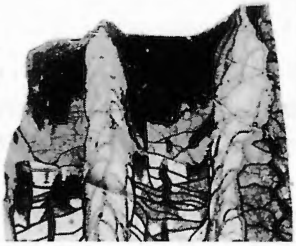
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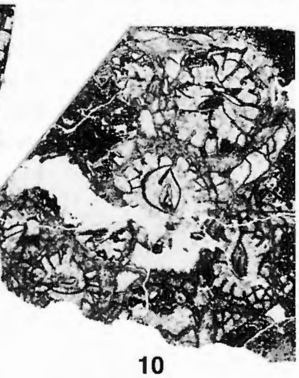
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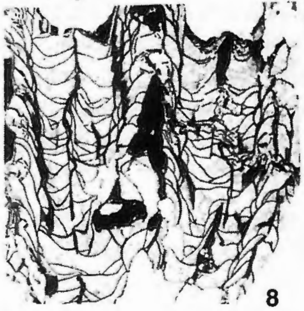
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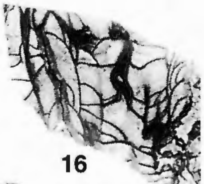
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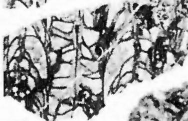
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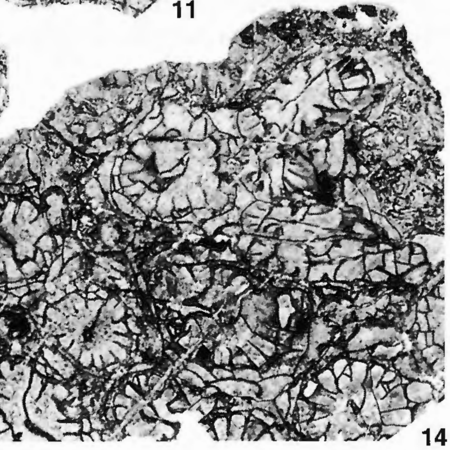
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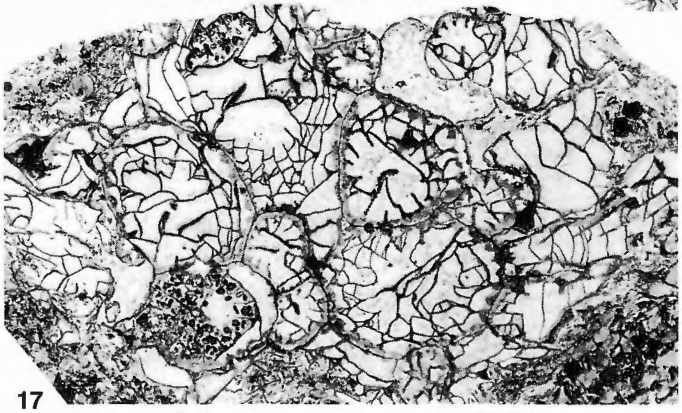
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Plate 7

(Figures x3 unless stated otherwise)

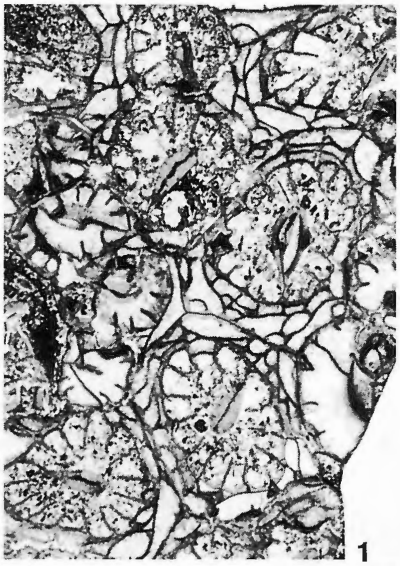
Figures 1, 2. *Petalaxis parvus* sp. nov., paratype GSC 109662, from GSC loc. C-179734, Kasimovian, serial transverse thin sections showing vertical changes in thickness and shape of median lamella, x5; figure 1 from approximately 2.5 mm above figure 2.

Figures 3-12. *Petalaxis* sp. cf. *P. elyensis* (Wilson and Langenheim, 1962), from GSC loc. 60192, Kasimovian or earliest Gzhelian; showing variably thickened corallite wall, generally well developed axial structure, narrow dissepimentarium and subhorizontal to axially depressed tabulae.

3-8. Hypotype GSC 109664. 3, transverse thin section from near base of specimen, showing thick, denticulate corallite walls, thick septa, local development of transeptal dissepiments in several corallites and lens-shaped axial structure with short septal lamellae. 4. transverse thin section from near top of specimen (approximately 1.7 cm. above that in figure 3), showing thinner corallite walls and septa, more numerous transeptal dissepiments and thinner axial structures. 5-8, longitudinal thin sections showing discontinuous, single row of dissepiments and variation in shape and orientation of tabulae; note biform morphology shown on left side of tabularum in figure 7.

9-12. Hypotype GSC 109665. 9, 10, longitudinal thin sections showing narrow, but continuous dissepimentarium and tabulae similar to those in GSC 109664 (figs. 5-8). 11, 12, transverse thin sections showing numerous transeptal dissepiments, relatively thin septa and reduction and local discontinuity of axial structure.

Figures 13-15. *Cystolonsdaleia* sp., hypotype GSC 109667, from GSC loc. C-69857, mid-Moscovian, Kashirian or Podolskian; 13, transverse thin section showing long septa, wide dissepimentarium consisting mainly of large, transeptal dissepiments, and oval axial column with numerous septal lamellae. 14, 15, longitudinal thin sections, showing thick axial column with numerous, elongate periaxial cones and predominantly subhorizontal to axially depressed tabulae, x4.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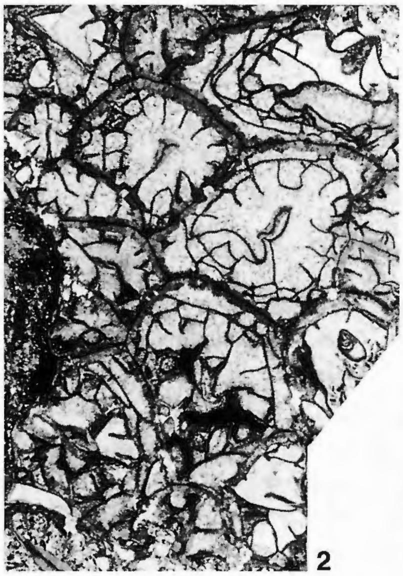
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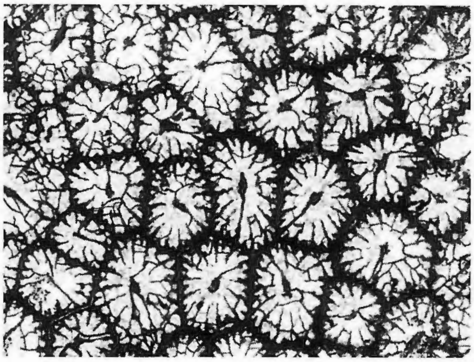
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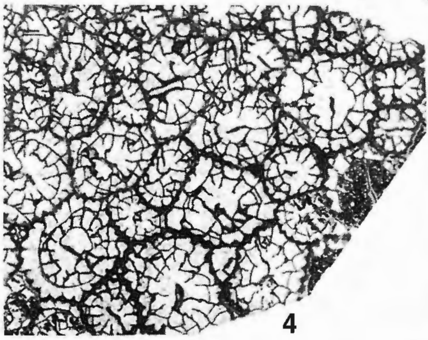
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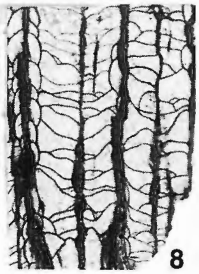
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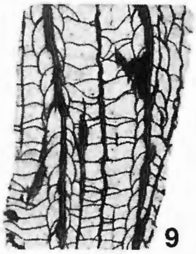
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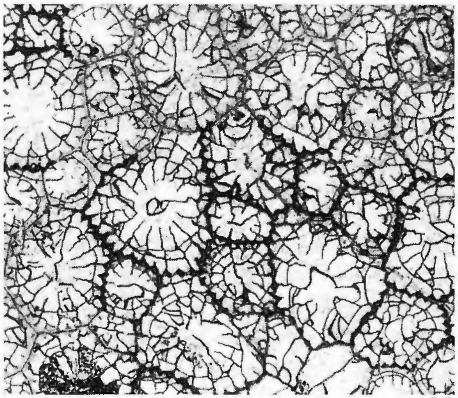
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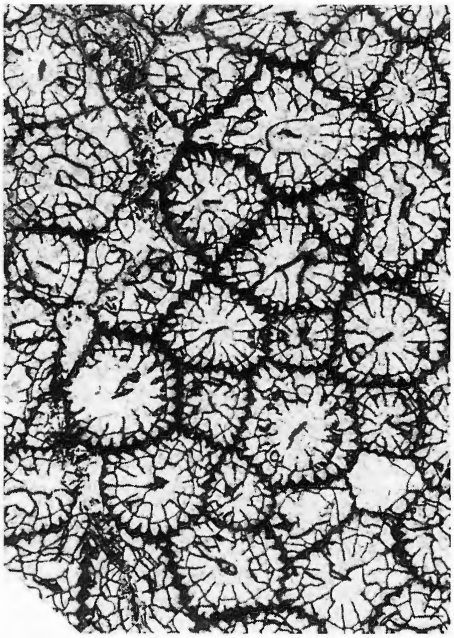
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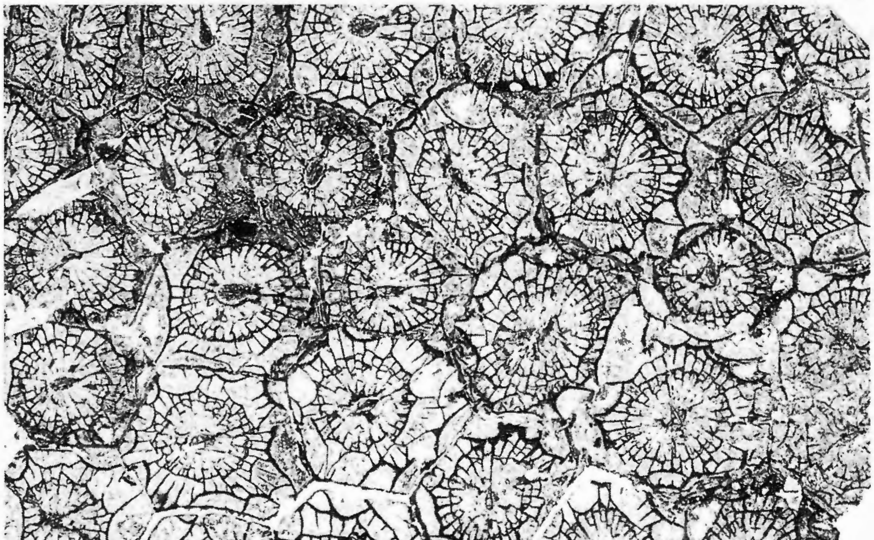
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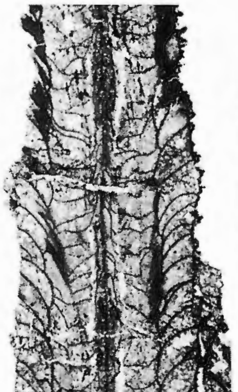
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15

Plate 8

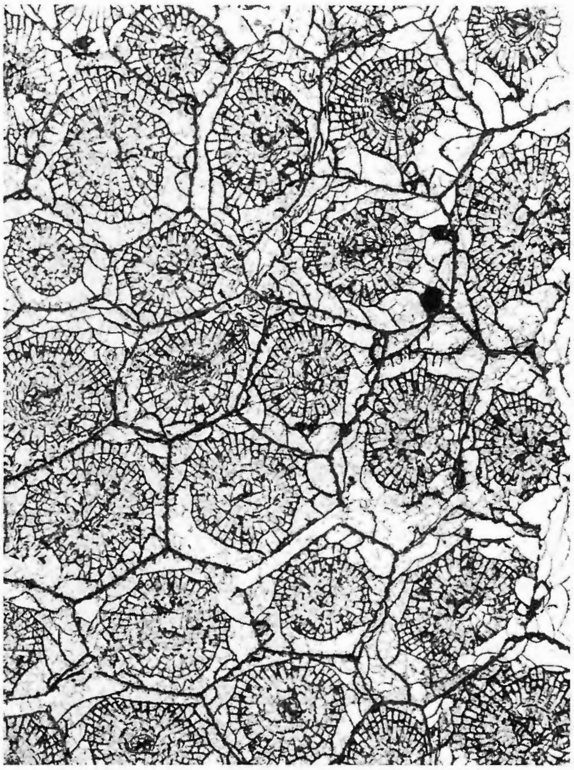
(All figures x3)

Figures 1-11. *Cystolonsdaleia arctica*, sp. nov., from GSC loc. C-193090, late Moscovian, Podolskian or Myachkovian; showing long septa, continuous axial column, abundant transeptal dissepiments and closely spaced, generally concave and adaxially elevated tabulae.

1-5. Holotype GSC 109668. 1, transverse thin section showing numerous septal lamellae in wide axial column. 2-5, longitudinal thin sections showing variation in number and distribution of periaxial cones and axial tabellae in axial column; biform morphology of tabularium shown in several places (e.g., upper parts of figures 4 and 5); middle part of section slightly off centre in figure 3.

6-9. Paratype, GSC 109670. 6, transverse thin section showing variation between corallites in thickness of median lamella and number of attached septal lamellae. 7-9, longitudinal thin sections showing well developed periaxial cones and short series of axial tabellae; figures 7 and 8 from adjoining parts of single corallite, note variation in shape and orientation of tabulae resulting from biform morphology.

10, 11. Paratype GSC 109669. 10, transverse thin section. 11, longitudinal thin section showing long series of periaxial cones, succeeded by short series of axial tabellae.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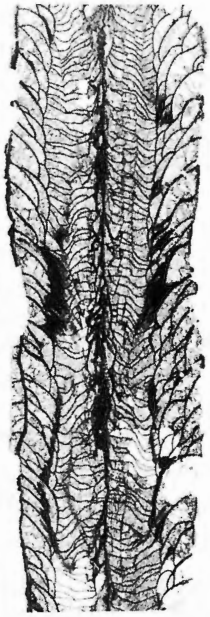
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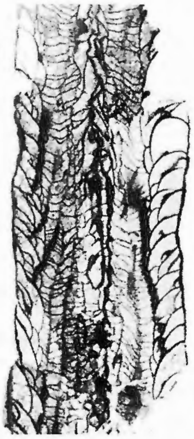
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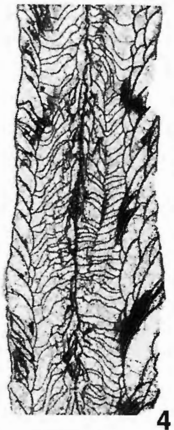
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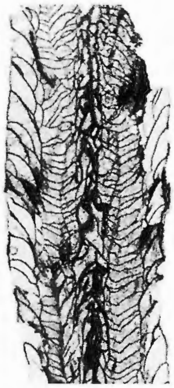
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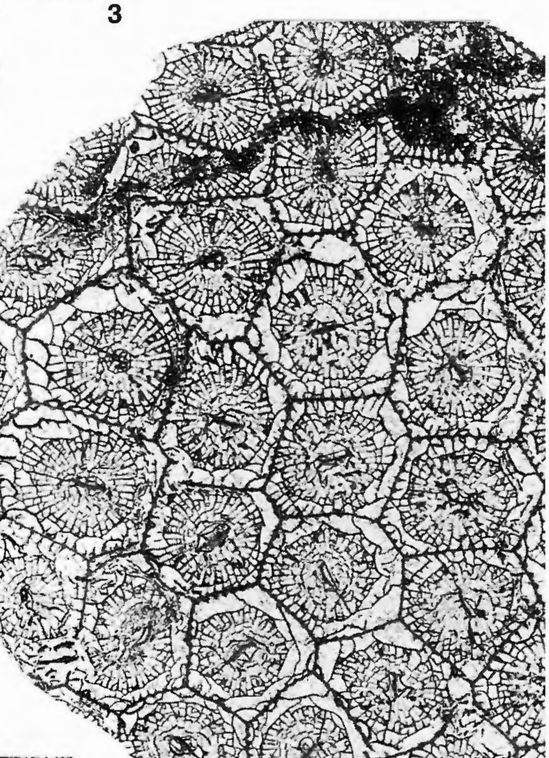
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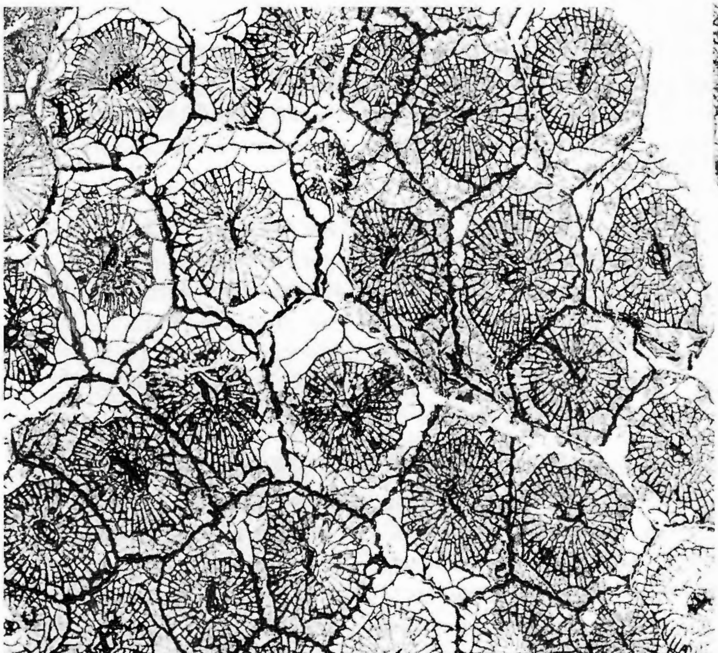
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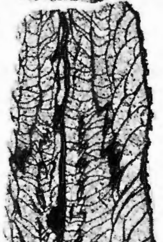
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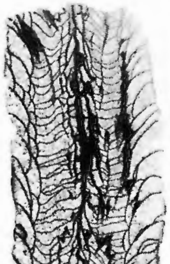
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11

Plate 9

(Figures x3 unless stated otherwise)

Figures 1-9. *Cystolonsdaleia carteri* sp. nov., from GSC loc. 60193, Kasimovian or earliest Gzhelian; showing small corallite diameter, thick corallite walls, long septa, discontinuous dissepimentarium, weak development of transeptal dissepiments, variable axial column and strongly concave tabulae.

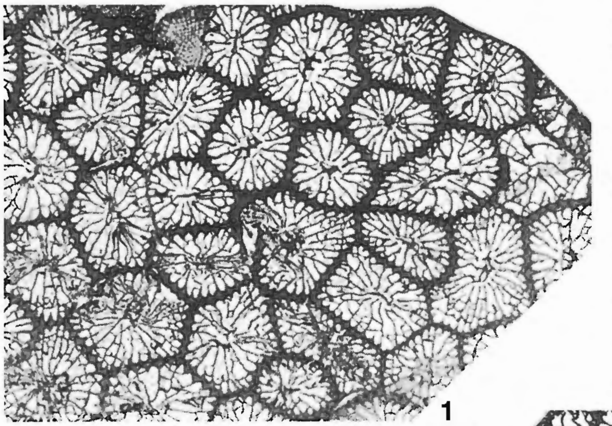
1-3. Holotype GSC 109671. 1, transverse thin section showing relatively narrow axial structure and few corallites with transeptal dissepiments. 2, 3, longitudinal thin sections showing discontinuous dissepimentarium and several periaxial cones.

4-6. Paratype GSC 109672. 4, transverse thin section showing lens-shaped axial column thickened by stereoplasm, and locally well developed transeptal dissepiments, x5. 5, 6, longitudinal thin sections showing several discontinuous rows of dissepiments and predominance of axially depressed tabulae; vertically extended periaxial cones present in lower part of figure 5.

7-9. Paratype GSC 109674. 7, 9, longitudinal thin sections showing axially depressed tabulae, biform morphology and discontinuous dissepimentarium. 8, transverse thin section showing very few transeptal dissepiments in corners of corallites and relatively wide axial structure with strongly developed septal lamellae; corallite at lower right almost entirely replaced by crystalline calcite.

Figures 10-14. *Cystolonsdaleia* sp. aff. *C. carteri*, hypotype GSC 109675, from GSC loc. 60192, Kasimovian or early Gzhelian. 10, transverse thin section showing variation in thickness of corallite walls and in width of axial structure, long septa and local development of transeptal dissepiments. 11-14, longitudinal thin sections showing discontinuous dissepimentarium, concave tabulae and weak development of short septal cones; left half of figure 11 is part of incompletely preserved tabularium; biform morphology of tabularium shown in figures 12-14; sections mainly off centre in corallites on right side of figures 12 and 13.

Figures 15-19. *Cystolonsdaleia lutugini* Fomichev, 1953, hypotype GSC 109666, from GSC loc. C-147802, Limestone L_5 (lower Moscovian, Kashirian), right bank of Lugan River, at Golubovka (formerly Kirovsk) Village in Luganskaya region. 15, transverse thin section showing wide dissepimentarium with well developed transeptal dissepiments, short minor septa and strong axial column with variable number of septal lamellae and lateral lamellae (e.g., large corallite in lower right of figure), x2. 16-19, longitudinal thin sections showing concave tabulae, periaxial cones (e.g., right side of axial structure in figure 19) and vertically discontinuous series of axial tabellae; biform morphology evident on left side of tabularium in figure 16.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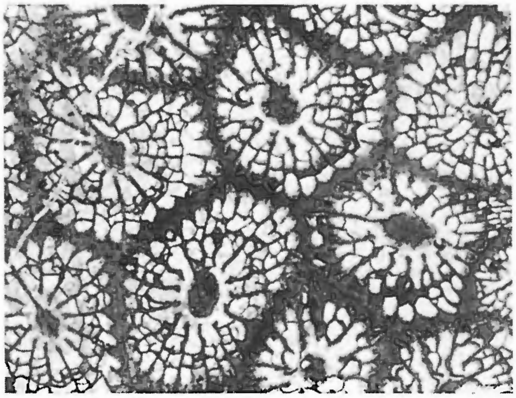
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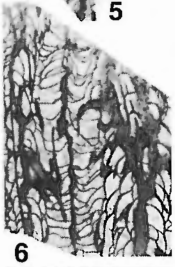
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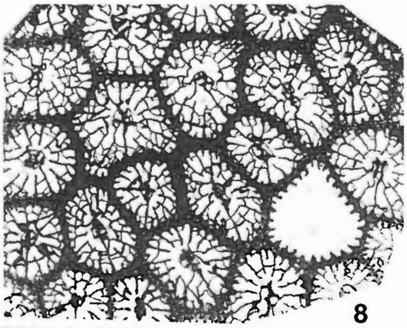
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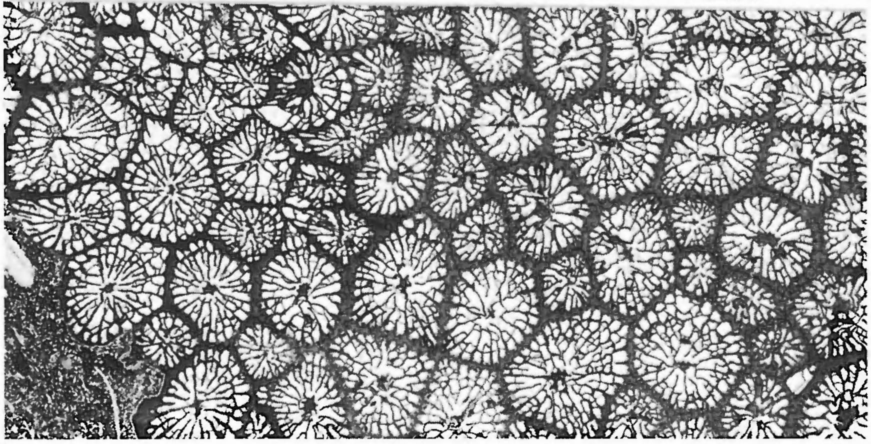
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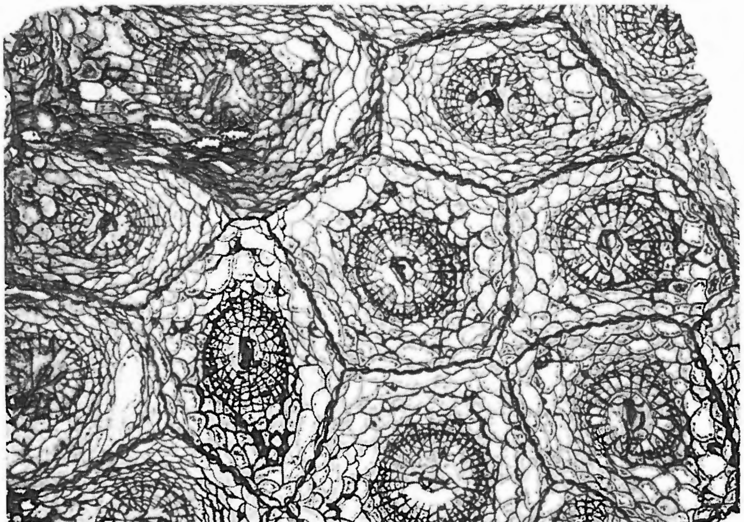
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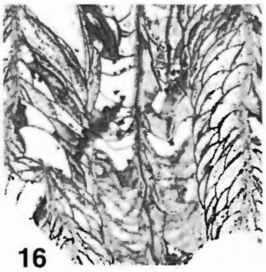
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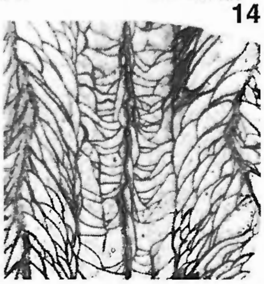
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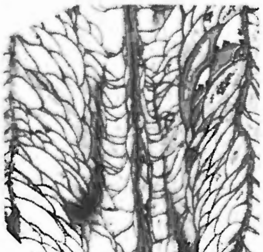
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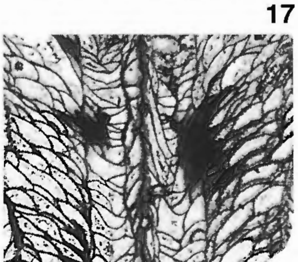
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