Remarks on lithostrotionid phylogeny in western North America and western Europe

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Abstract: Faunal exchange between Tournaisian-Visean corals of western North America and Europe was limited by paleoenvironmental factors and by the great distance between those faunas, which were separated by the land-mass of Euramerica. Morphological comparison indicates that there is no direct relationship between species groups traditionally assigned to *Siphonodendron* in those areas. The immature morphology and stratigraphic distribution of the genus *Dorlodotia* suggest that it is the common ancestor for *Siphonodendron* in Europe and for *Siphonodendron*-like species in western North America. An unnamed, Ivorian species of *Dorlodotia* from western Canada initiated the phylogenetic succession, which led to the North American *Siphonodendron*-like lineage in the latest Tournaisian and subsequently to the European *Siphonodendron* lineage in the early Visean.

Key words: Lithostrotioninae, phylogeny, Tournaisian, Visean, Canada, Europe

Contents

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1. INTRODUCTION

In her remarkably comprehensive treatment of the Rugosa in the Treatise on Invertebrate Paleontology, HILL (1981) recognized six subfamilies within the family Lithostrotionidae D'ORBIGNY, 1852, based on general morphological similarities within several groups of genera. A partial re-evaluation of this family was provided by the ideas of SANDO (1983) and the preliminary considerations of POTY (1975a, 1984, 1993) and NUDDS (1993), which are devoted mostly to its European representatives. In the present paper we have restricted ourselves to the Lithostrotioninae, with special attention to its earliest known representatives.

North American lithostrotionid species have been described in several papers (e.g. SIMPSON, 1900; KELLY, 1942; EASTON, 1957; NELSON, 1961; BAMBER, 1966; SANDO & BAMBER, 1985). Thus, the abundance of fasciculate forms currently assigned to *Siphonodendron* McCoY, 1849, and the early occurrence of *"Diphyphyllum" mutabile* KELLY, 1942 are well established. An even lower Tournaisian occurrence of *Dorlodotia* SALÉE, 1920 was reported by SANDO & BAMBER (1985, p. 50), but that specimen was not described. It was studied for the present paper and appears to be the earliest known lithostrotionid in the world. In this paper we describe the septal microstructure and blastogeny of *"D." mutabile* and compare its blastogeny with that in the Tournaisian specimen of *Dorlodotia* mentioned above. We have placed the names *Diphyphyllum* and *Siphonodendron* in quotation marks when referring to western North American species. *"Diphyphyllum" mutabile* from that area has an inconsistent columella and offsets laterally, thus differing from the type species in these diagnostic characters. We consider it to be congeneric with younger species assigned to *"Siphonodendron"*, but we have provisionally followed KELLY's (1942) generic assignment, pending more thorough study. *"Siphonodendron"* from western North America differs morphologically and phylogenetically from the European type species, as will be explained below.

2. DISTRIBUTION OF LITHOSTROTIONID CORALS IN SOUTHWESTERN CRATONAL CANADA AND EUROPE

In the Rocky Mountains and Foothills of southwestern Alberta and southeastern British Columbia, species of the fasciculate lithostrotionid genera *"Siphonodendron"*, *Dorlodotia* and *Schoenophyllum* SIMPSON, 1900 occur at several levels in Upper Tournaisian and Viséan shelf carbonates of the Rundle Assemblage, deposited along the northeastern margin of Prophet Trough (Fig. 1). These corals form part of a widespread, western North American rugose coral succession, divided into eleven biostratigraphic zones and subzones by SANDO & BAMBER (1985).

The oldest known lithostrotionid specimen belongs to an undescribed, Ivorian (early Late Tournaisian) species of *Dorlodotia*. It was collected from the lower part of the Shunda Formation, approximately in the middle of Coral Zone II$_B$ [Fig. 2; SANDO & BAMBER, 1985, p. 50, Geological Survey of Canada (GSC) locality C-22] and is succeeded by several other unnamed species of the genus, ranging as high as late middle Visean in age (Fig. 2). *"Siphonodendron"*, which first appears at a level slightly higher in the Upper Tournaisian than the lowest occurrence of *Dorlodotia*, is represented by a number of distinctive species, beginning in the upper part of Coral Zone II$_B$ with *"D". mutabile*

and the longer ranging *"Siphonodendron" sinuousum* (KELLY, 1942). It should be noted that the age (mid-Tournaisian) and distribution of *"D". mutabile* given by SANDO & BAMBER (1985, Figs. 5–7) are incorrect. They were based on inaccurate correlations which have since been modified as shown in Fig. 2. The position of the Tournaisian-Visean boundary shown in Fig. 2 coincides with that shown by DEVUYST et al. (2003), utilizing the stratigraphic distribution of morphotypes in *Eoparastaffella*.
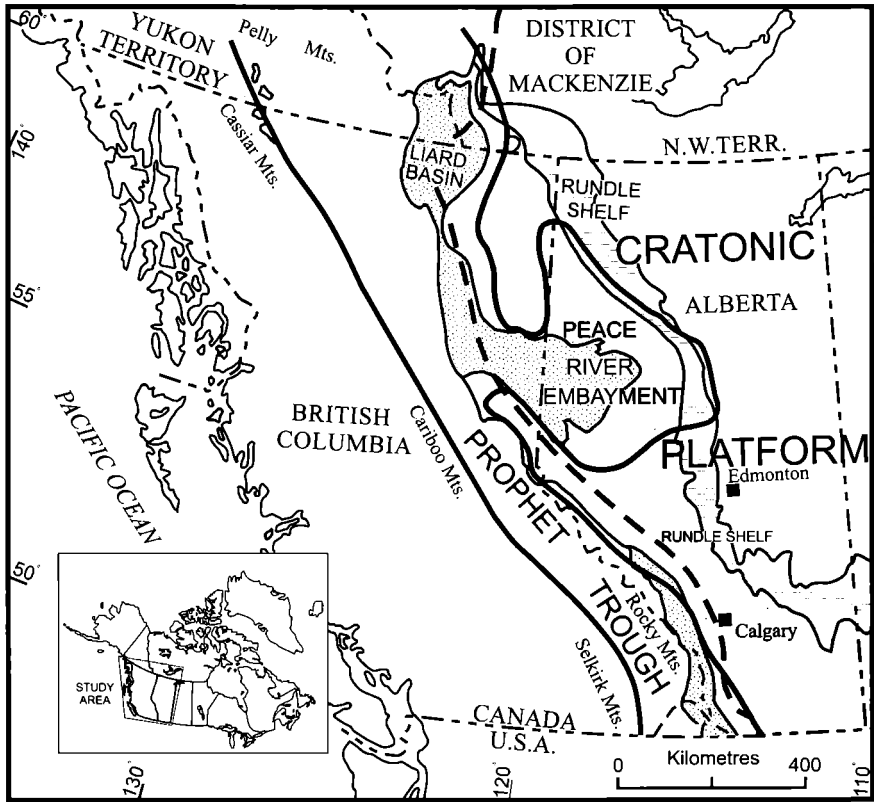
LEGEND

– – – – EASTERN LIMIT OF DISTURBED BELT

───── LIMITS OF PROPHET TROUGH
AND PEACE RIVER EMBAYMENT

☐ BANFF ASSEMBLAGE

☐ RUNDLE ASSEMBLAGE

▦ MATTSON ASSEMBLAGE

Fig. 1: Principal tectonic elements and Lower Carboniferous stratigraphic depositional units in western Canada (after RICHARDS et al., 1994).
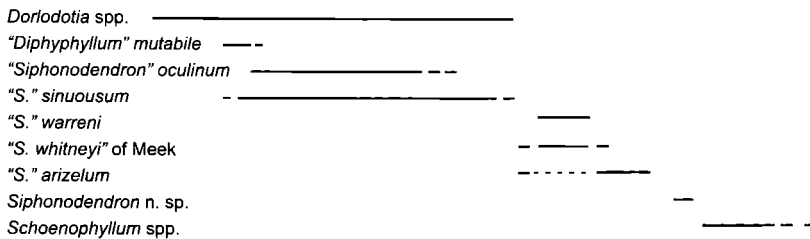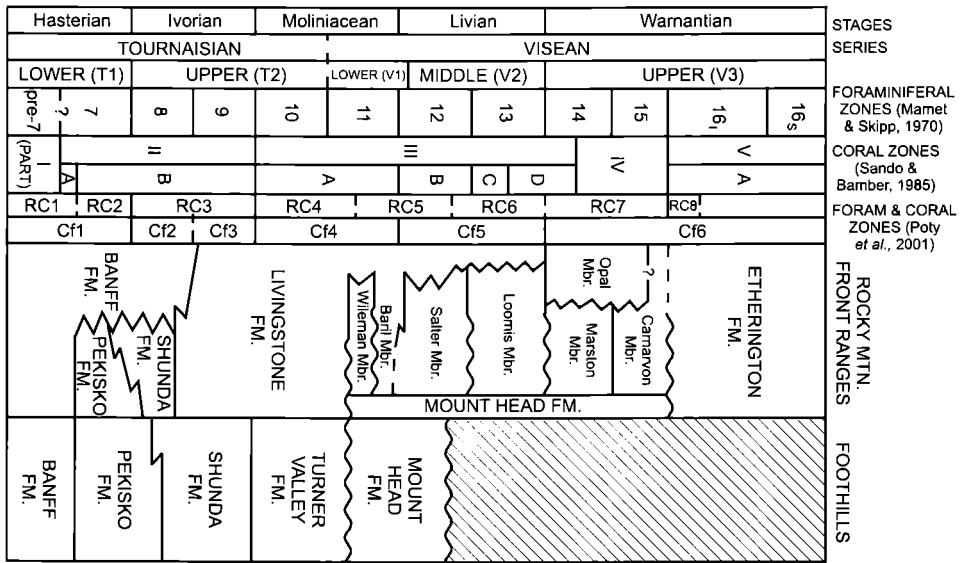
STAGES	Hasterian	Ivorian	Moliniacean	Livian	Warnantian
SERIES	TOURNAISIAN		VISEAN		
	LOWER (T1)	UPPER (T2)	LOWER (V1) · MIDDLE (V2)	UPPER (V3)	

FORAMINIFERAL ZONES (Mamet & Skipp, 1970): pre-7 | ? | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16i | 16s

CORAL ZONES (Sando & Bamber, 1985): I (PART) / A | II / B | III / A · B · C · D | IV | V / A

FORAM & CORAL ZONES (Poty et al., 2001): RC1 | RC2 | RC3 | RC4 | RC5 | RC6 | RC7 | RC8 ; Cf1 | Cf2 | Cf3 | Cf4 | Cf5 | Cf6

ROCKY MTN. FRONT RANGES: BANFF FM. — PEKISKO FM. — SHUNDA FM. — LIVINGSTONE FM. — Wileman Mbr. / Baril Mbr. / Salter Mbr. / Loomis Mbr. — Opal Mbr. / Marston Mbr. / ? / Carnarvon Mbr. (MOUNT HEAD FM.) — ETHERINGTON FM.

FOOTHILLS: BANFF FM. — PEKISKO FM. — SHUNDA FM. — TURNER VALLEY FM. — MOUNT HEAD FM.

Dorlodotia spp. ——————————
"Diphyphyllum" mutabile ——-
"Siphonodendron" oculinum ———————— — —
"S." sinuousum - —————————— --
"S." warreni ———
"S. whitneyi" of Meek - ——— -
"S." arizelum - - - - - - ———
Siphonodendron n. sp. —
Schoenophyllum spp. ——— — —

Fig. 2:   Age and distribution of Lithostrotioninae in cratonal western Canada.

3. STATUS OF KNOWLEDGE OF THE LITHOSTROTIONINAE

Such features as the blastogeny and septal microstructure have been studied in detail in only a few species of the genera included by HILL (1981) in the Lithostrotioninae. Existing knowledge of the remaining genera is restricted to the main characteristics of their macro-morphology.

The nature of the septal microstructure in *Dorlodotia* is uncertain. POTY (1975b, p. 96) suggested fibrous tissue with lamellar coating. An adequately enlarged photo is needed to determine whether such microstructure is fibro-normal or finely trabecular. Unfortunately, that feature was not illustrated by POTY (1975b). Also, the Canadian specimen investigated by us is partly silicified, partly re-crystallized and does not provide information on septal microstructure. Diffuso-trabecular septal microstructure was established by KATO (1963) for several Visean species of *Siphonodendron* from western Europe, along with trabecular microstructure in coeval *Lithostrotion* from the same area. SEMENOFF-TIAN-CHANSKY (1984) found the microstructure of *Siphonodendron* to be trabec-

ular and the same position was adopted by SORAUF (1996). We can now confirm the presence of trabecular microstructure for *"Diphyphyllum" mutabile* (Pl. 2, Fig. 1). Thus, we provisionally accept trabecular microstructure as a characteristic for the subfamily, although we were not able to confirm this either in the North American or European representatives of *Dorlodotia*.

Information on the blastogeny of the Lithostrotioninae is limited to only three published papers (JULL, 1965; POTY, 1975a; KHOA, 1977), but is adequate for general comparison with western North American species. For this paper, we have made a detailed blastogenetic analysis of *"D." mutabile* (Pl. 1), supplemented by a preliminary study of several younger species of western North American *"Siphonodendron"* for comparison with both *"D." mutabile* and western European siphonodendrons.

POTY (1975b) investigated the blastogeny in a single colony of *Dorlodotia briarti*, the type species for the genus. His observations were supplemented in a later paper (POTY, 1993) as well as by NUDDS (1993). In the present paper we briefly describe the main characteristics of the blastogeny in the oldest known representative of the genus. The importance of the role of *Dorlodotia* in the phylogeny of the Lithostrotioninae has been generally underestimated, except by NUDDS (1993), who proposed it as the ancestor for the European representatives of *Siphonodendron*. Our new findings confirm the phylogenetic value of this genus as an ancestor to both North American and European taxa, as discussed below.

The type specimen of *Schoenophyllum aggregatum* SIMPSON, 1900 was revised by EASTON (1957), who included it in *Siphonodendron* and applied the new name *genevievensis* because *aggregatum* is preoccupied by *Siphonodendron aggregatum* MCCOY, 1849. SANDO & BAMBER (1985, p. 27) diagnosed this genus as having slender connecting tubules and a solid, compressed, styliform columella, formed by prolongation of the counter septum. They accepted *Schoenophyllum* as a distinct genus and consequently placed *S. genevievensis* EASTON, 1957 in synonymy with *Schoenophyllum aggregatum*. We accept their decision despite the lack of information on the septal microstructure and blastogeny of that species.

The family status of the genus *Orionastraea* SMITH, 1917 has been in doubt since HUDSON (1929) considered the British species of that genus to be polyphyletic. The blastogeny, microstructure of septa, and the formation and reduction of the columella in most species of that "genus" remain unknown. Reduction of intercorallite walls is, in fact, the only character uniting those obviously different taxa. Thus, we restrict the genus to its type species *Orionastraea phillipsi* (MCCOY), which is obviously different from all contemporaneous western European lithostrotionid genera.

From the remaining genera included in the Lithostrotioninae by HILL (1981), we omit *Akiyosiphyllum* YABE & SUGIYAMA, 1942 as being too poorly documented for discussion. Also, specimens from the Lower Carboniferous of SE Australia, included by earlier authors in *Siphonodendron*, were excluded from this discussion. They were shown by FEDOROWSKI (1981) and WEBB (1990, 2000) to be unrelated to the family Lithostrotionidae.

From the considerations listed above, we conclude that the content of the subfamily Lithostrotioninae should be reduced to the genera *Dorlodotia*, *Lithostrotion*, *Orionastraea s.s.*, *Schoenophyllum*, *Siphonodendron* and an unnamed genus that includes most western North American *"Siphonodendron"* species.

4. THE OLDEST KNOWN LITHOSTROTIONINAE

The early late Tournaisian specimen of *Dorlodotia* from Canada [hypotype, GSC 123636] is the oldest member of the subfamily presently known. It is not completely described here, but in order to establish its generic identity, its diagnostic morphological characters are illustrated (Pl. 2, Fig. 7, Pl. 3, Figs. 2–6) and described below, with comparisons to *Dorlodotia briarti*, the European type species, and *"Cyathophyllum" pseudovermiculare* McCoy, which was transferred by Poty (1993) to *Dorlodotia*.

1. The early growth is acolumellate with major septa in the form of short, continuous plates attached to the atavotheca and neotheca [Pl. 3, Figs. 2 (upper), 3, 6]. In some corallites, the major septa remain continuous at least into the stage of development in which a columella and continuous minor septa appear (Pl. 2, Fig. 7). In other corallites, lonsdaleoid dissepiments develop earlier (Pl. 3, Figs. 5, 6, upper left). This morphological variability matches that in comparable stages of development in some specimens of *D. briarti* (Poty, 1975b, 1993, Fig. 11.1; Nudds, 1993, Figs. 1.5, 1.6). The number of septa (n) and the minimum diameter in millimeters (d) in representative corallites of *Dorlodotia* sp. is as follows: 19:6.5 (immature), 22:9.0 (offsetting), 22:8.5, 22:9.0, 22:10.5.

2. The dissepiments are exclusively interseptal when they first appear. They are absent from some loculi in early stages, including those in which the corallite diameter exceeds 5 mm and a columella is developed (Pl. 2, Fig. 7). Similar morphology was illustrated by Poty (1975, Fig. 3A-D). In some corallites of the Canadian specimen, most of the dissepiments are interseptal up to the level at which they began to offset.

3. In corallites where lonsdaleoid dissepiments have been observed, they first interrupt the minor septa and subsequently interrupt the major septa as well. The peripheral parts of both major and minor septa almost always persist as short plates attached to the external wall. No presepiments were developed in this specimen.

4. We were unable to establish the mode of formation of the columella. In the single specimen available, it lies in the cardinal-counter plane and appears to be an independent structure formed on the surface of a tabula. It was not formed as an axial extension of a major septum, although the cardinal or counter septum is slightly elongated toward it locally. Thus, we presume the columella lies in the cardinal-counter plane, as in the overwhelming majority of the Rugosa. Also, the columella is a discontinuous structure absent at some levels in mature corallites (Pl. 3, Fig. 6, right). In younger North American and European species, the counter and/or cardinal septum is discontinuously connected to the columella. Elongation of a major septum, probably the cardinal, commonly occurs in *"Cyathophyllum" pseudovermiculare*, which lacks a true columella. This species, recently considered to be latest Tournaisian in age (Professor Edouard Poty, e-mail transmission, August 19th, 2004), requires a thorough re-study before it will be useful for phylogeny.

5. In longitudinal sections in which the columella is continuous over a significant interval (Pl. 3, Fig. 4), the tabulae are steeply elevated near the columella and are strongly depressed peripherally. Many of them become horizontal or rarely slightly concave adjacent to the dissepimentarium, but others terminate peripherally on the shoulders of underlying tabulae. Where the columella is absent, the axial parts of the tabulae are flat, horizontal or slightly convex.

Dorlodotia sp., the oldest lithostrotionid known, is followed in western Canada by the next youngest representative of the Lithostrotioninae, *"Diphyphyllum" mutabile* KELLY, 1942, of latest Tournaisian age (Fig. 2). As in Canada, *Dorlodotia* has been proposed by NUDDS (1993) as the oldest lithostrotionid genus in Europe. According to that author, its first appearance in that area is doubtfully in the uppermost Tournaisian or Lower Viséan; as noted above, Professor E. Poty has confirmed the first alternative for Belgium. *Dorlodotia* was included by POTY (1993) in the family Lonsdaleidae. Thus, his opinion about the ancestry of the Lithostrotionidae must be different from ours. We do not accept his opinion, because it is supported solely by the development of lonsdaleoid dissepiments, whereas all remaining characters point toward the Lithostrotionidae, as documented in the present paper.

5. MAIN MORPHOLOGICAL CHARACTERISTICS OF *"DIPHYPHYLLUM" MUTABILE*

The holotype of this species (Pl. 2, Figs. 1–6, 8–12, Pl. 3, Fig. 1) is distinguished by a discontinuous, isolated, lens-shaped columella, a narrow, discontinuous dissepimentarium, tabulae which are sub-horizontal to slightly elevated axially and sharply depressed peripherally, short major septa, minor septa reaching or slightly exceeding one-half the length of the major septa, and 21–24 major septa at corallite diameters of 4.5–6.0 mm. In several other specimens, the dissepimentarium is wider and more consistently developed than in the holotype.

Blastogeny
     The blastogeny began without any peripheral protrusion of the parent corallite (Pl. 1, Figs. 1–4). In the offsetting sector of the parent corallite, the dissepiments disappeared and the minor septa became shortened to form thickened plates on the external wall (Pl. 1, Figs. 1–4). The major septa became strongly thickened at the former border of the dissepimentarium and were continuous when thickening began, but their peripheral parts soon separated from the thickened segments. The process of thickening and division was sequential, involving one septum after another. In some instances the inner margins of minor septa became thickened (Pl. 1, Fig. 2) or thickened bodies developed, corresponding to but not connected to minor septa. These bodies were free or were attached to thickened parts of major septa (Pl. 1, Figs. 1–4). All major and minor septa of the parent remain attached to the atavotheca of the offset, forming its atavosepta, whereas almost all septa of the offset at its neotheca are neosepta. Only one of them, located in the middle, may have been inserted by division of a parent septum (Pl. 1, Fig. 5, middle) and should be considered as the only atavoseptum developed at the neotheca. None of the atavosepta or neosepta is elongated so as to suggest a leading role in the development of the columella.
     During most of its early growth (i.e., until the dividing wall was formed; Pl. 1, Figs. 3–7), the offset was strongly elongated and protruded only slightly, because as many as five major septa were involved in the blastogeny. The dividing wall was either preceded by a discontinuous partition (Pl. 1, Figs. 5, 6) or the wall fragments were composed of four crystalline layers from the beginning. Neither this nor the position of the protosepta can be established from the material studied. The columella is absent from

this early growth stage as confirmed by longitudinal sections (Pl. 2, Figs. 4, 10). All atavosepta remained attached to the atavotheca in their original positions and were transferred directly into the major and minor septa of the offset. Neosepta were probably inserted in sequence.

Summary of early blastogeny

Absence of the columella through more than 6–8 mm of early growth following completion of the dividing wall was observed in the offsets of the holotype (Pl. 2, Figs. 4, 10, GSC 9642). The columella may be totally undeveloped if the young corallite died in early ontogeny (Pl. 2, Fig. 4). Thus, delay in the appearance of the columella should be considered as typical for the species. The same is true for the insertion of atavosepta and neosepta in the holotype, which occurs in a manner identical to that described above (Pl. 2, Fig. 2). The following features, all observed both in the specimen investigated in detail (hypotype, GSC 123635) and in offsets of the holotype, should also be considered typical for the species: sequential division of the major septa into parent and offset septa; a slight peripheral protrusion of the offsets in the initial stage of their formation; and the lack of elongation of a single major septum or two opposing major septa very early in the blastogeny, suggesting potential for the development of a columella.

Formation of the columella in "D." mutabile

A septal origin cannot be established for the median plate in "D." mutabile, although it is apparently located in the cardinal-counter plane of symmetry as indicated by the rarely observed elongation of one or two opposing major septa (possibly protosepta) at maturity (see above). As descibed below, it appears to have been derived from the tabulae, as in Cyathaxonia. Thus, we have applied the term "columella", although we are aware of the rather distant analogy between the axial structure in the latter genus and in the North American "siphonodendrons".

The insertion of the columella in "D." mutabile was independent or semi-independent of the major septa. As outlined above, its appearance was preceded in offsets by a comparatively long-lasting acolumellate growth period. Derivation of the columella from the counter septum, considered typical for European siphonodendrons, is unlikely. It may only be stated that one major septum in "D." mutabile, located in the symmetry plane of the columella, tends to temporarily lengthen toward it during maturity. This may be either the cardinal or the counter septum. Our blastogenetic study did not indicate which of these septa was involved, because all major septa in the early growth stages of offsets are equal in length (Pl. 1, Figs. 9–11).

Since the columella has septal microstructure, its insertion in an ectodermal fold is the only possible interpretation. Thus, we conclude that it was inserted in the axial segments of a chain of elongated folds formed by the basal ectoderm on the calice floors, i.e. on the tabulae. Peripheral segments of those folds probably produced the protosepta, although the latter are not distinguished by length in early blastogeny. Basal insertion of septa was demonstrated by FEDOROWSKI (1997) in etched corallites. The relationship between the columella and the tabulae and the absence of any connection between the columella and the septa are best demonstrated by series of transverse peels, of which two well separated examples are illustrated (Pl. 2, Figs. 8, 9).

Observations from transverse acetate peels and longitudinal serial thin sections confirmed that the tabulae and columella are directly attached and that no such close re-

lationship exists between the columella and the major septum (cardinal or counter?) located in its plane of symmetry. In some instances one of the margins of the columella is thin and attenuated and probably points toward the major septum most closely related to it. Also, an incompletely notched outline, very rarely observed in transverse sections of the columella (Pl. 2, Fig. 12), may indicate the incorporation of septal lamellae within it. It is worth noting that the incorporation of septal lamellae within a complex median lamella commonly occurs in European lithostrotionids. The development of this feature is commonly random, however – i.e., it may occur in some corallites within a colony, but be absent from others, or it may be present in some colonies and absent from others having otherwise similar morphology. This problem has never been studied in adequate detail. The same is true for the European species *Dorlodotia briarti*, some corallites of which may show 1 or 2 incorporated septal lamellae (Poty, 1975b, Pl. 2, Figs. 3, 6) whereas most possess simple columellae. Complexity of the columella has not been observed in the oldest, Canadian representative of *Dorlodotia*. Thus, the microarchitecture of the columella has not yet been proven to have constant taxonomic value. We note this phenomenon, which is very rare in *"D." mutabile*, as a matter for consideration in future investigations of the relationships between true European *Siphonodendron* and its North American analogue.

The continuous growth of the columella in *"D." mutabile* illustrated by Bamber (1966, Pl. 1, Figs. 1a-e; also see Pl. 2, Fig. 11 in the present paper) does not contradict the interpretation that the columella was mainly or entirely isolated from the major septa. His illustrations indicate only that the upward growth of the columella was comparatively persistent in some corallites.

To investigate the relationship of the tabulae to individual segments of a strongly discontinuous columella and the mechanism by which such isolated segments were inserted, we studied serial transverse and longitudinal thin sections from the holotype (Pl. 2, Figs. 5, 6) and serial peels through a single corallite from the hypotype (GSC 123635; Pl. 2, Figs. 8, 9). The tabulae, which were inserted by horizontal surfaces of the basal disc of the polyp, curve upward toward the columella segment from both sides, illustrating the formation of an ectodermal pocket in which the columella segment was secreted, in the manner characteristic for septa.

In conclusion: The insertion of the columella in *"Diphyphyllum" mutabile* was independent of the major septa but was closely associated with the tabulae. It may have appeared several times during the growth of individual corallites and was inserted under intermittently occurring, more or less persistant upwards folds in the basal disc of the polyp.

6. COMPARISON OF BLASTOGENY IN EUROPEAN SIPHONODENDRONS AND NORTH AMERICAN *SIPHONODENDRON*-LIKE TAXA

Three models of earliest hystero-ontogenetic growth stages can be distinguished in European siphonodendrons:
1. The offset did not inherit septa from the parent and is aseptate during earliest growth (Jull, 1965, Figs. 1:1c-e, 4:2; Khoa, 1977, Figs. 6, 7, 23, 25). This model has so far been established only in *Siphonodendron junceum* (Fleming, 1828).

2. The offset inherited peripheral segments of the parent's septa but is acolumellate at the very beginning This is the most common model, probably already existing in *S. ondulosum* and investigated in *S.* cf. *martini* (JULL, 1965, Figs. 5, 11), *S. "fraiponti"* (POTY, 1975a, Fig. 2) and *S. rossicum rossicum, S. rossicum strzelcense* and *S. affine* (KHOA, 1977, Figs. 9, 12, 17, respectively).

3. The offset inherited all peripheral segments of the parent's septa and parts of their inner segments at the neotheca. In such offsets, the protosepta were united at the very beginning to form a columella. This was established in *S. rossicum rossicum* and *S. volkovae* (KHOA, 1977, Figs. 10, 15). An earliest growth stage with long septa and a columella, probably derived from one or two major septa in *S.* cf. *martini* (KHOA, 1977, Fig. 16), is a variant of this model.

Stratigraphic and morphological criteria may be applied only to explain the unique character of the first model and the differences between that model and the other two. All species that produced aseptal offsets are relatively young (late Visean/Serpukhovian) and either lack dissepiments or have incomplete dissepimentaria. All are characterized by strongly protruded earliest growth stages (JULL, 1965, Figs. 1, 4:2; KHOA (1977, Figs. 6, 7, 23, 25).

The presence of very simple morphology is the only reason we can propose for those species having earliest blastogenetic growth stages of the first type listed above. Assignment of such species to a genus other than *Siphonodendron* (e.g., *Kwangsiphyllum* GRABAU, 1931) is another alternative. Unfortunately, the exact status of the latter genus is uncertain. Thus, we leave this question open.

Variation in models 2 and 3 is comparatively great. Some characters are strikingly similar to the early blastogeny of *"D." mutabile*, whereas there are obvious differences in others. For instance *Lithostrotion (Siphonodendron) affine* (FLEMING) of KHOA (1977, Fig. 17) shows strong thickening of the middle parts of septa in the offsetting area and sequential division of those septa into the parental septa and atavosepta of the offset. Also, peripheral protrusions of the offsets are very inconspicuous in the beginning and an acolumellate early growth stage is obvious, but independent insertion of the columella is not evident.

JULL (1965, Fig. 5) observed similar thickening and sequential division of parental septa and an acolumellate earliest growth stage, but he did not report or illustrate isolation of the columella from the major septa. The offset illustrated by POTY (1975a, Fig. 2) shows an early protrusion, an acolumellate early growth stage, the appearance of the columella with no connection to septa and a connection between the columella and either the cardinal or the counter septum after further growth. A dissepimentarium having at least a moderate width is a character common to all instances discussed above.

KHOA (1977, Figs. 10, 15) provided the best documentation of early protrusion by offsets combined with sequential division of septa in the parent corallite and their inheritance by an offset at both the atavotheca and the neotheca. These offsets show a connection between the columella and two oppositing major septa very early in the blastogeny; i.e., they lack an acolumellate growth stage. The dissepimentarium is incomplete in both species illustrated by KHOA, but it may locally incorporate two rows of globose dissepiments.

In all adequately investigated colonies displaying blastogeny corresponding to models 2 and 3, the connection between the columella and the major septa is inconsistant.

During the growth of a given corallite, the columella may be connected to a single major septum or two opposing major septa, or it may be temporarily isolated from all major septa. Such a relationship contrasts with that described above for *"D." mutabile*. In other North American "siphonodendrons", according to our preliminary observations, the cardinal septum remains short and only the counter septum may by intermittently elongated to meet the columella at maturity.

7. DISCUSSION

The stratigraphic position of individual taxa, combined with their paleogeographic distribution, should be a starting point for any considerations concerning their phylogeny. A brief survey of the published occurrences of potential Lithostrotioninae in the world produced no representatives of definite Tournaisian age, other than those in western North America and those newly re-established by Professor E. Poty in western Europe (see above). DOBROLYUBOVA & KABAKOVICH (1966, Pl. 31, Fig. 1) described two species of partly acolumellate, *Siphonodendron*-like corals from the Kuznets Basin, but these originated from the Podyakovsky Horizon and are evidently of early Visean age. It cannot be determined if these Kuznets Basin corals are related to European or North American corals presently assigned to *Siphonodendron*. Also, we know of no Asiatic lithostrotionids that are older than Visean. Thus, the western North American specimens from the Upper Tournaisian are the oldest known, fully documented Lithostrotioninae.

In Late Tournaisian and Visean time, the western and central European marine shelves were located in the pre-Variscan basin on the opposite side of Euramerica from those in western Canada (Fig. 3). In addition to the great distance between these two areas, the northern and southern marine connections were dominated by siliciclastic deposits shed from the Ellesmerian, Appalachian and Variscan orogens (ZIEGLER, 1988, Fig. 7). Resulting conditions in these areas were unfavourable for colonization by rugose corals, thus constituting a barrier to migration for a vast majority of them and leading to obvious differences between the western North American and European coral faunas. The taxonomic relationship and morphological and blastogenetic similarities and differences between European and North American lithostrotionids cannot be meaningfully discussed without reference to this palaeogeographic context.

The suspected lineage of European species (POTY, 1984, 1993) leads toward simplification. *S. ondulosum* POTY, 1981, the oldest (late Moliniacian-early Livian, V2a- V2b) species of western Europe, is characterized by large corallite diameters, long septa, a wide dissepimentarium, an almost continuous columella aligned with the cardinal and counter septa and commonly united with one or both of them, and a fairly well developed cardinal fossula. These features also characterize the slightly younger but long-ranging species *S. martini* and *S. sociale*, with the exception that the columella is less continuous in the latter (POTY, 1981, 1984, 1993). POTY (1993, p. 145) considered the long-lasting European *S. sociale* (upper Molinacian-upper Warnantian), with large corallites and a wide dissepimentarium, to have arisen from *S. ondulosum* through the process of hypermorphosis. We have not discussed this subject further, because *S. sociale* is not on the main phylogenetic line of western European siphonodendrons, established by that author and provisionally accepted by us in the present paper. Younger Euro-
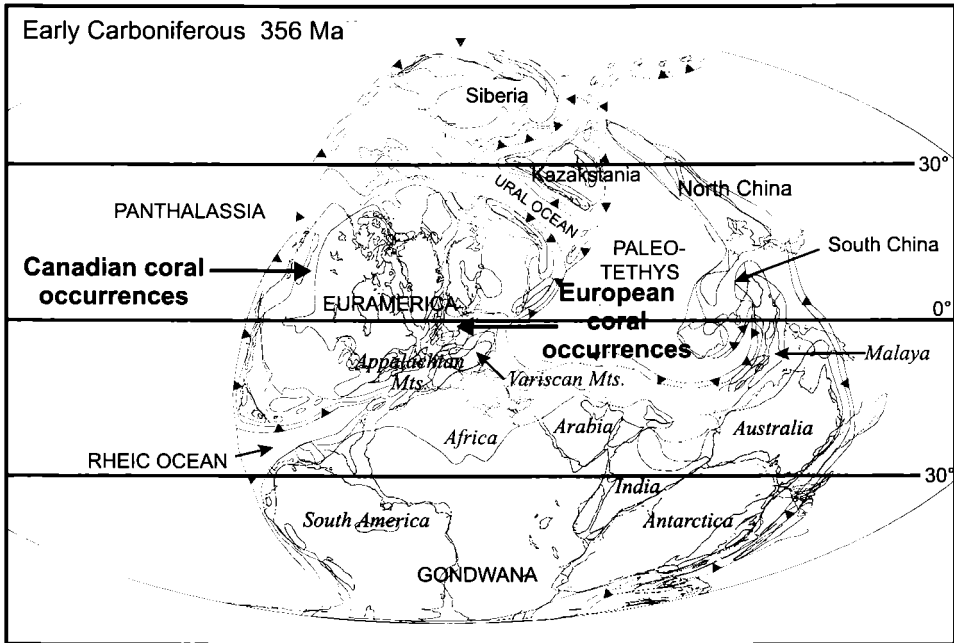
Fig. 3: Paleogeographic map, Early Carboniferous, 350 Ma, after C. R. SCOTESE (2002, supplemented).

pean siphonodendrons of the main phylogenetic line show septal shortening, especially in the major septa, and narrowing of the dissepimentarium. The blastogeny corresponding to model 2 (see above) in European siphonodendrons, although closest to that seen in North American species, is comparable to but probably not related to that in *"Diphyphyllum" mutabile*. We consider this morphological similarity to be coincidental because of differences noted above. The other alternative, i.e. derivation of European siphonodendrons directly from north American "siphonodendrons", rather than from European species of *Dorlodotia*, is less likely. Model 2 appeared in *Siphonodendron* after *Dorlodotia* appeared in Europe. Thus, the appearance of its bearers in western Europe, independent of *Dorlodotia* requires: (a) a separate migration of *Siphonodendron*-like corals, concurrent modification of their morphology from simple to complex, and phylogenetic development leading again toward simplification. Such an evolutionary return to an abandoned morphology seems highly improbable to us; (b) formation of a blind phylogenetic line by western European *Dorlodotia*. The second alternative cannot be totally rejected, but existing data point strongly toward the alternative provisionally proposed in this paper – i.e., an independent derivation of northern American "siphonodendrons" and western European siphonodendrons from *Dorlodotia*.

In contrast to the European lineage, that in western North America comprises a group of late Tournaisian to middle Viséan *"Siphonodendron"* species with narrow dissepimentaria, relatively smaller corallite diameters, fewer septa, and a discontinuous columella. In younger species, of middle and early late Visean age, the dissepimentarium

generally widens, the corallite and septal number increase, and the columella becomes continuous, indicating a morphological trend opposite to that in Europe.

Despite the opposing trends in Europe and western North America, some similarities are evident in the septal microstructure and general morphology of the species in these two areas. These include the radial arrangement of septa, the presence of a columella, the morphology of the tabularium, and exclusively interseptal dissepiments in all but *S. ondulosum* in Belgium and *"Koninckophyllum" arizelum* CRICKMAY, 1955 in Canada, which have rare lonsdaleoid dissepiments. All of these characters in common indicate a taxonomic relationship between the North American and European species only at the subfamily level. Thus, direct derivation of the morphologically complex, oldest European siphonodendrons from North American *Siphonodendron*-like ancestors is unlikely. This consideration led us to search for a common ancestor for these two faunal groups and for an appropriate phylogenetic concept.

NUDDS (1993) introduced the concept of paedomorphic evolution of *Siphonodendron* from *Dorlodotia*. We consider his idea worthwhile with respect to the relationship between these two genera and we have applied it to the earlier lithostrotionids from western North America. As described above, the main features of the morphology of the early growth stages in the western Canadian *Dorlodotia* sp. are indistinguishable from that in both the early and mature stages of *"Diphyphyllum" mutabile*. In both species, the early growth stage is acolumellate, no cardinal fossula develops, and the columella is commonly interrupted, with no direct connection to any of the major septa but some relationship to the counter or cardinal septum. The microstructure of the columella, always simple in North American *Dorlodotia* and in the early blastogeny of European *Dorlodotia* and in both European *Siphonodendron* and its North American counterpart, provides additional evidence for the derivation of both of the latter taxa from *Dorlodotia*. Complexity in the structure of the columella, common in European siphonodendrons and rare in North American taxa (Pl. 2, Fig. 10), is interpreted by us as an independent development in two phylogenetic lines. The rare appearance of that character in European *Dorlodotia* and its absence from the oldest Canadian representative of that genus (see above) support such a position.

The dissepimentarium is absent from the earliest stages of all three taxa. In subsequent early stages of most corallites of *Dorlotodia* sp. and all corallites of *"Diphyphyllum" mutabile* it is narrow and interseptal. In *"D." mutabile* and its probable immediate descendants (Fig. 2, *"Siphonodendron"*) the dissepimentarium maintains these characteristics into maturity (Pl. 2, Fig. 3, Pl. 3, Fig. 1). In some corallites of *Dorlodotia* sp., lonsdaleoid dissepiments are still absent (Pl. 2, Fig. 7) until comparatively late in the ontogeny. Such corallites are indistinguishable from corallites of comparable ontogenetic development in *"D." mutabile* (compare with Pl. 2, Fig. 3). This morphological similarity and the relative stratigraphic positions of these two species suggest the probable derivation of *"D."mutabile* from *Dorlodotia* sp. Intermediate forms have not been discovered to date.

The derivation of *Siphonodendron* from *Dorlodotia* in Europe was suggested by NUDDS (1993). It seems indisputable for Belgian and British coral specialists that the earliest appearances of *Dorlodotia* preceded that of *Siphonodendron* both in Belgium and Britain. The first occurrence of the genus in Belgium was suggested by POTY et al. (2001) as Foraminiferal Subzone Cf4γ – i.e., still within the upper Molinacian (former

upper Lower Visean V1b Subzone). The level of this occurrence has since been indicated by Professor E. Poty (e-mail transmission of 19th August, 2004) as the uppermost Tournaisian RC4β1 Coral Subzone or Cf4α1 Foraminiferal Subzone in Belgium. He also postulated an occurrence of that genus at the same level in the Cracov area in Poland, but the illustration kindly provided by him was identified by us as a probable solitary *Corphalia* POTY, 1981 rather than a colonial *Dorlodotia*. Nevertheless, the Belgian occurrence may be either older than or coeval with that in Britain and only slightly younger than the North American occurrence. Whatever the true stratigraphic relationships may be, both the British and Belgian occurrences of *Dorlodotia* are older than any species of European *Siphonodendron*.

In addition to documenting the appearance of *Dorlodotia* in Europe prior to the oldest *Siphonodendron*, it is necessary to establish the paleobiological basis for a phylogenetic relationship between these two taxa. The paper by POTY (1975b) is the only detailed study of blastogeny in *Dorlodotia* known to us. A single offset illustrated in that paper left some doubt concerning the origin of the dissepiments and columella. In his helpful comments on the manuscript of our paper, Professor E. Poty pointed out that, on the basis of numerous offsets, the columella is clearly related to the cardinal and counter plane and in some corallites it is connected only with the counter septum. We accept his remarks, which are substantiantiated, in part, by his published illustrations (POTY, 1993, Fig. 11) of both *D. briarti* and *"Cyathophyllum" pseudovermiculare* Mc-Coy, 1855, transferred by POTY (1993) to *Dorlodotia*. We wish to point out an immature corallite (POTY, 1993, Fig. 11.1, lower right) showing a relationship between the columella and a tabula almost exactly matching that illustrated by us (Pl. 2, Fig. 9) for *"D."* *mutabile* to demonstrate the tabular origin of its columella. Thus, it appears that this feature may also occur in European *Dorlodotia*. The appearance of interseptal dissepiments prior to lonsdaleoid dissepiments is based herein mainly on random illustrations by POTY (1975b, 1993) and NUDDS (1993), rather than on a serial peels, thin sections or drawings.

The microstructure of the septa briefly described by POTY (1975b, p. 96) as "tissu fibreux" and not illustrated by him with a photo (see section 3), cannot be considered as truly known. Also, details of the blastogeny in the oldest European *Siphonodendron*, *S. ondulosum* POTY, 1981 are unknown. On the basis of random transverse sections (POTY, 1981, Pl. 8; POTY, 1993, Fig. 7. 1, 2) we may only suspect the occurrence of an acolumellate early stage. The columella drawn by POTY (1981, Fig. 17) may rather be the intercept of a tabula (compare with Pl. 8, Fig. 1b, upper right, in the same paper). Thus, the extent to which the early morphology of *D. briarti* resembles that of *S. ondulosum* remains uncertain, as does the ontogenetic sequence in the appearance, morphology and relationships of the taxonomically most important characters of both species, such as the columella, dissepiments and the microstructure of septa.

Despite the lack of complete data, the derivation of European *Siphonodendron* from *Dorlodotia* is supported by the following: 1. Consistent lateral offsetting in both taxa. 2. Delay in the development of the columella, documented in *D. briarti* and young specimens of *S. ondulosum* illustrated by POTY (1981, 1993) in random transverse sections; thus, our model 2 probably applies to both taxa. 3. Delay in the formation of lonsdaleoid dissepiments until development of the columella in some corallites of *D. briarti*, as reconstructed by POTY (1975b, Fig. 4); such corallites resemble immature

PHYLOGENY

North America | Western Europe

STAGES — SERIES — FORAMINIFERAL ZONES (Mamet & Skipp, 1970) — CORAL ZONES (Sando & Bamber, 1985) — FORAM & CORAL ZONES (Poty et al., 2001)
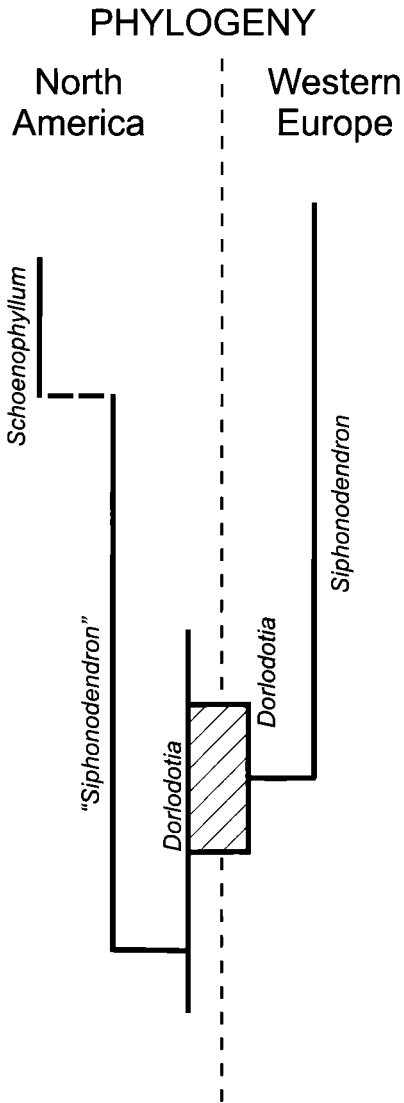
STAGES	SERIES	FORAMINIFERAL ZONES (Mamet & Skipp, 1970)	CORAL ZONES (Sando & Bamber, 1985)	FORAM & CORAL ZONES (Poty et al., 2001)	
LOWER NAMURIAN	SERPUKHOVIAN	19	VI	Not Zoned	Not Zoned
		18			
		17	B		
Warnantian	UPPER (V3)	16_s	V		
			A		
		16_l		RC8	Cf6
		15	IV	RC7	
		14			
Livian	MIDDLE (V2)	13	D / C	RC6	Cf5
		12	B	RC5	
Moliniacean	LOWER (V1)	11	III	RC4	Cf4
		10	A		
Ivorian	UPPER (T2)	9		RC3	Cf3
		8	II B	RC2	Cf2
Hasterian	LOWER (T1)	7	A	RC1	Cf1
		?			
		pre-7	I (PART)		

(VISEAN — TOURNAISIAN)

Schoenophyllum

"Siphonodendron" — Siphonodendron

Dorlodotia

Fig. 4: Phylogeny of early Lithostrotioninae in western North America and Europe. Lined quadrangle in the middle shows time of the occurrence of *Dorlodotia* in both areas.

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corallites of *S. ondulosum* and other siphonodendrons that offset according to model 2 and suggest the probability of neoteny; corallites developing a lonsdaleoid dissepimentarium earlier in the hystero-ontogeny (POTY, 1975b, Fig. 3N-S) suggest continuation of the main *Dorlodotia* line. 4. Microarchitecture of the columella, which is invariably simple at the beginning of its development in both North American and European *Dorlodotia* and in their potential descendents, probably including *S. ondulosum*, as indicated by random transverse sections of young corallites (POTY, 1981, 1993); the orientation of the columella in the cardinal/counter plane is less important because almost all columellate Rugosa developed columellae in that position. 5. Such characters as the occurrence in mature corallites of *S. ondulosum* of lonsdaleoid dissepiments, which may be rudiments from *Dorlodotia*; the morphology of the tabularium in all three of the genera in question (*Dorlodotia*, *Siphonodendron* and "*Siphonodendron*" – tent-shaped where columella present, generally flat axially or trapezoid where it is absent); these are additional features indicating derivation from *Dorlodotia* of the stratigraphically oldest European *Siphonodendron* (*S. ondulosum*), although forms intermediate between these two taxa are presently unknown. Also, as noted above, older *Siphonodendron*-like corals occur in the Kuznets Basin (DOBROLYUBOVA & KABAKOVICH, 1966), so *S. ondulosum* is not necessarily the ancestral species of *Siphonodendron*.

From the above considerations, we suggest the probable phylogenetic scheme shown in Fig. 4 for the early Lithostrotioninae in western North America and Europe. The genus *Dorlodotia* is consistently present and is represented by several species in both areas, with the Canadian *Dorlodotia* sp. being the oldest. The ancestor from which this species was derived is unknown, as are the roots of the Lithostrotionidae. The earliest appearance of *Dorlodotia* in North America and the isolation of individual coral-bearing areas during the Famennian and Early Tournaisian, documented by faunal endemism in most areas of the World, point toward the southern and western North American shelves as areas in which the Lithostrotionidae may have originated. Unfortunately, none of the taxa described from those areas fulfills the requirements for ancestry of that family.

In the late Tournaisian, *Dorlodotia* sp. gave rise to "*Siphonodendron*" in North America, beginning with "*Diphyphyllum*" *mutabile*, followed by the succession of species shown in text-figure 2. The route by which the earliest European *Dorlodotia* migrated from North American has not been established, but the similarity in the morphology and blastogeny of species from both areas indicate that they belong to the same genus. As discussed above, *Dorlodotia* appeared in Europe in the latest Tournaisian and subsequently gave rise to the earliest *Siphonodendron*. We suggest, therefore, that European *Siphonodendron* and western North American "*Siphonodendron*" appeared independently at different times and that these two lineages are related through *Dorlodotia*, their common ancestor, but were not derived one from the other. Western North American and European species cannot, therefore, be included in the same genus. We postpone the formal establishment of a new generic name for the western North American "*Siphonodendron*" and "*Diphyphyllum*" until we have completed a general revision of the lithostrotionids in that area.

the early phylogeny of the Lithostrotionidae. Although we did not agree with all of his suggestions, they were all used to improve our paper. We also wish to express our appreciation for excellent technical support from: Marta Bartkowiak MSc. and Greg Martin (preparation of thin sections and acetate peels); Kazimierz Frys MSc. and Bryan Rutley (photography); and Denise Then and Glen Edwards (digital preparation of text-figures and plates).

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Plate 1

Figs. 1–11: Serial acetate peels showing blastogeny of *"Diphyphyllum" mutabile* Kelly, 1942; distance (mm) between peels indicated by values in lower left corners, hypotype, GSC 123635; x 10.

1

0.4 | 5

0.1 | 2

0.4 | 6

0.3 | 3

0.8 | 7

0.2 | 4

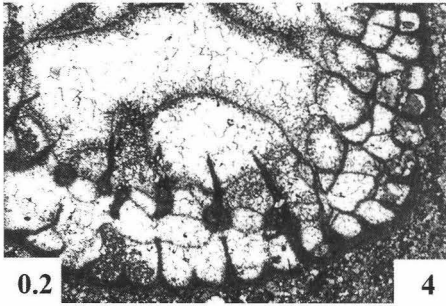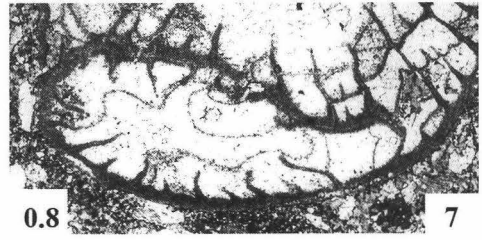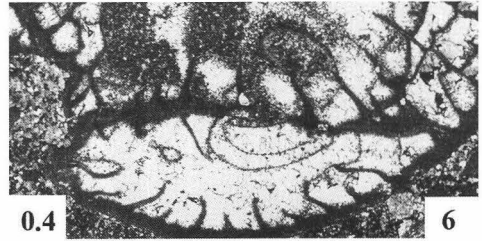0.6 | 8

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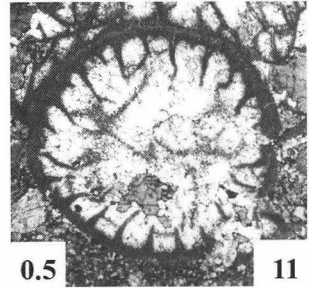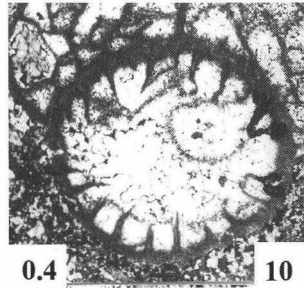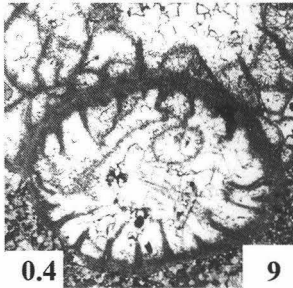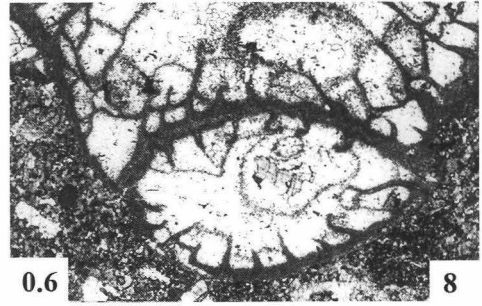
Plate 2

Figs. 1–6 : Thin sections of *"Diphyphyllum" mutabile* Kelly, 1942; holotype, GSC 9642.

Fig. 1: Septal microstructure; x 100.

Fig. 2: Early growth stage; x 12.

Fig. 3: Mature growth stage; x 6, enlarged from Pl. 3, Fig. 1.

Fig. 4: Longitudinal section of acolumellate immature corallite; x 8

Figs. 5, 6: Mature corallites showing relationship between tabulae and discontinuous columella in longitudinal sections; x 6.

Fig. 7: Transverse thin section of immature corallite from *Dorlodotia* sp., hypotype GSC 123636; x 5, enlarged from Pl. 3, Fig. 6, lower left; note lack of lonsdaleoid dissepiments, compare with figure 3.

Figs. 8–12: Thin sections and acetate peels of *"Diphyphyllum" mutabile* Kelly, 1942.

Figs. 8, 9: Acetate peels, mature corallites showing relationship between tabulae and columella, hypotype GSC 123635, from GSC locality C-413008; x 12.

Figs. 10–12: Thin sections of holotype, GSC 9642

Fig. 10: Longitudinal section showing immature, acolumellate offsets; x 5.

Fig. 11: Longitudinal section showing continuous columella; x 5.

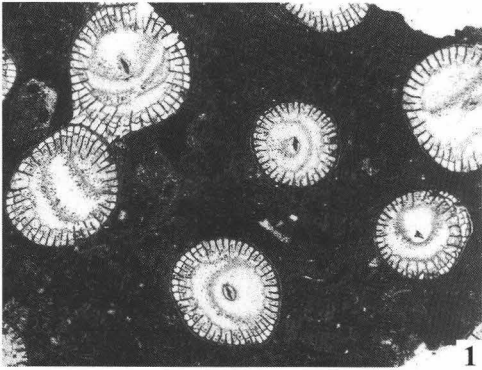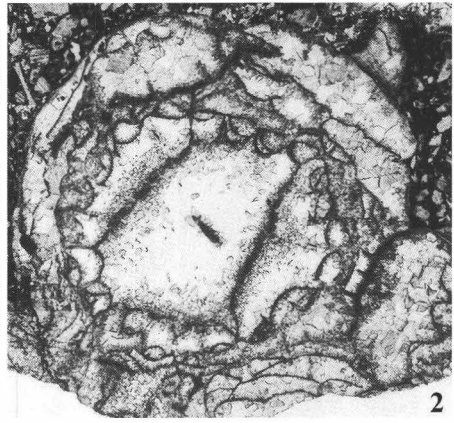Fig. 12: Mature corallite showing columella with incompletely notched outline; x 18.
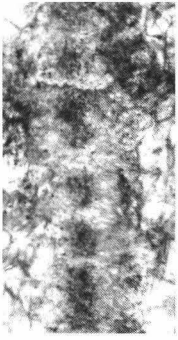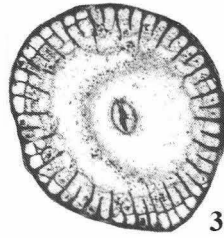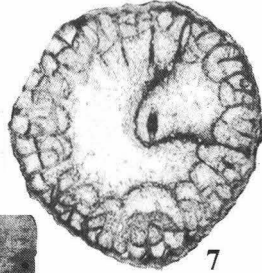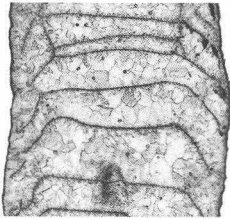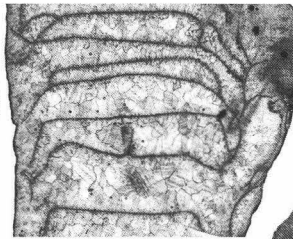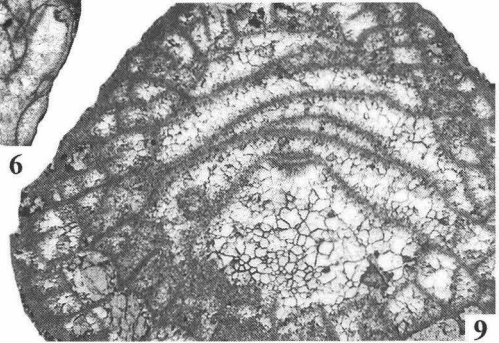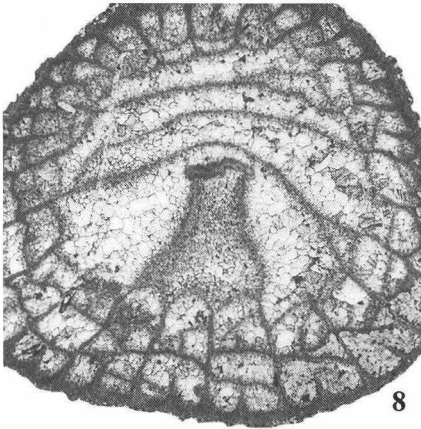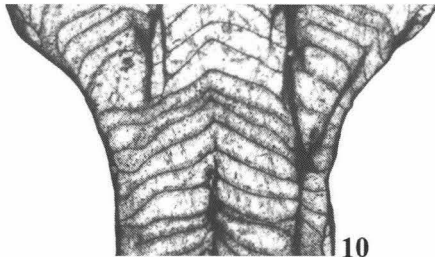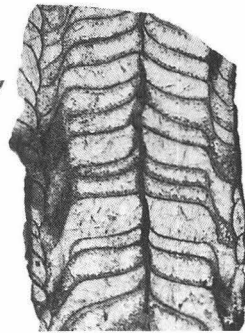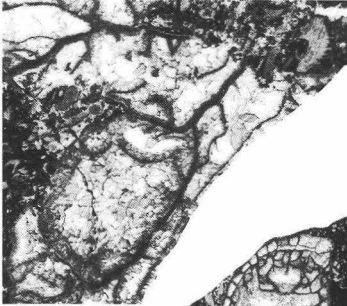
Plate 3

Fig. 1:   Transverse thin section of holotype of *"D."* *mutabile* (GSC 9642), showing inconsistent development of columella, x3.

Figs. 2–6: Thin sections of *Dorlodotia* sp., hypotype GSC 123636, from GSC locality C-22.

Figs. 2, 3: Transverse thin sections showing various development of offsets; x 6, enlarged from figure 6.

Fig. 4:   Longitudinal section of mature corallite showing well developed columella and axially elevated, peripherally depressed tabulae; x 3.

Figs. 5, 6: Two successive transverse sections; thin section for figure 5 cut approximately 3 mm above that for figure 6; x 3. Note the following: a) lonsdaleoid dissepiments absent from immature corallite at left side of Fig. 6 (see enlargement, Pl. 2, Fig. 7), but well developed at maturity (Fig. 5); offset from this corallite shows early development of londaleoid dissepiments (Fig. 5); b) lower middle corallite; very simple offset (Fig. 6, see enlargement, Fig. 2) develops into regular young corallite with almost all dissepiments interseptal (Fig. 5); c) acolumellate mature corallite (lower right) with two simple offsets (see enlargement, Fig. 3) showing early appearance of lonsdaleoid dissepiments (Fig. 5), offsets remain acolumellate; d) very late appearance of columella, demonstrated by young corallite (Figs. 5, 6, upper left).
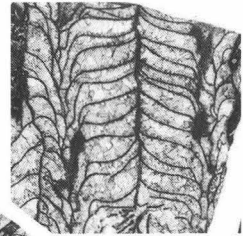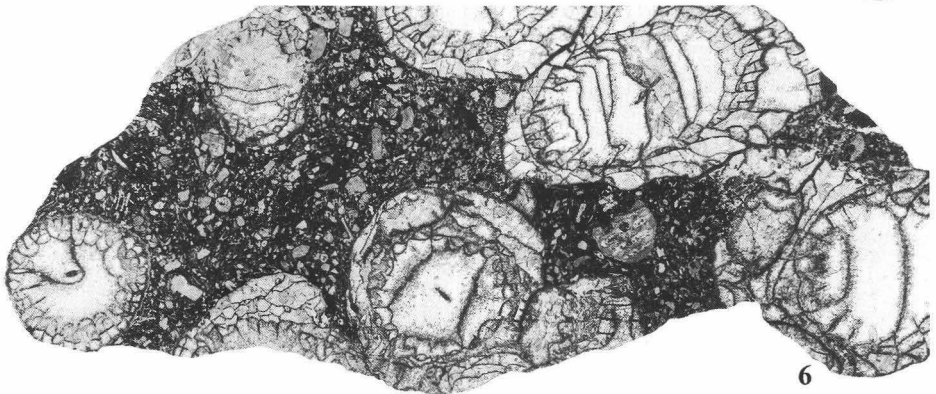
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