THE HYSTERO-ONTOGENY OF *LONSDALEIA* McCOY AND *THYSANOPHYLLUM ORIENTALE* THOMSON

by R. K. JULL

ABSTRACT. Increase in thirteen specimens of *Lonsdaleia* and two of *Thysanophyllum orientale* from Great Britain was studied by means of closely spaced acetate peel sections. With the exception of one example of intermural increase, only lateral increase was observed. *Lonsdaleia* is characterized during early development by having a long cardinal septum, the axial end of which forms the median lamella of the axial structure. Septal insertion is at first of the zaphrentid mode but subsequently becomes variable, depending on the development of minor septa. Most daughter corallites are radially orientated to the parent, but some are tangential. Interseptal dissepiments are typically formed first, followed by their modification to lonsdaleoid dissepiments.

Development in *Thysanophyllum orientale*, type species of *Thysanophyllum*, resembles that in *Lonsdaleia* in the nature of the cardinal septum and dissepimental development. These characters, together with the presence in a few adult corallites of *T. orientale* of a weakly developed axial structure suggest that *Thysanophyllum* is related to the Lonsdaleiidae rather than the Lithostrotionidae as has been suggested by some workers.

SOME of the taxonomic problems resulting from the morphologic variation of rugose corals have not been satisfactorily solved by the standard technique of examining adult characters alone. Such difficulties exist as regards the family affinities of *Thysanophyllum* Nicholson and Thomson, a widely distributed genus of Carboniferous and Permian age which lacks an axial structure and has short septa and lonsdaleoid dissepiments (Pl. 102, figs. 5*a–b*). Some workers (Lecompte 1952, Hill 1956, Fedorowski 1965) regard this genus as being a diphymorphic lonsdaleoid and thus place it with the Lonsdaleiidae. Others, however (Minato 1955, Easton 1960, Fontaine 1961, Soshkina and Dobrolyubova 1962), assign it to the Lithostrotionidae partly since corallites of *Lithostrotion* Fleming may lack an axial structure and possess lonsdaleoid dissepiments, thus closely resembling the characters of *Thysanophyllum*.

A solution to this problem is attempted here by a study of closely spaced acetate peel sections of the characters of increase in thirteen specimens of *Lonsdaleia* and two of *Thysanophyllum orientale*, type species of *Thysanophyllum*. These specimens, which are listed in text-fig. 1, are all from Viséan beds in Great Britain. From a comparison of the hystero-ontogeny of *Thysanophyllum orientale* with that in *Lithostrotion* (see Jull 1965) and *Lonsdaleia*, typical genera respectively of the Lithostrotionidae and Lonsdaleiidae, it is concluded that *Thysanophyllum* is probably related to the Lonsdaleiidae.

Observations of hystero-corallite development range from the start of increase up to the late neanic stage and sometimes the ephebic stage. Crushing in three coralla has destroyed the early stages of development in some or all of the corallites studied.

The terminology applied by Jull (1965) to increase in *Lithostrotion* is used herein. Abbreviations associated with catalogue numbers are as follows: BM—British Museum (Natural History), London; RSM—Royal Scottish Museum, Edinburgh; UQ—Department of Geology and Mineralogy, University of Queensland, Brisbane.

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Name	*Number*	*Locality*	*Zonal age*	*Corallites studied*	*Remarks*
Lonsdaleia duplicata duplicata (Martin)	BM R1366	Corwen, North Wales	D_2–D_3	4	
	RSM 1878.11.267	Hafod, near Corwen, North Wales	D_2–D_3	3	early stages crushed
L. floriformis floriformis (Martin)	UQ F11035	Wrekin, Shropshire	D_2	1	diphymorphic corallites
	UQ F2961	Pen-y-ghent, Yorkshire	D_2–D_3	3	
	RSM 1966.6.1	Coldstone Quarries, Greenhow, Pately Bridge, Yorkshire	D_2	8	
	BM R17160	Coalbrookdale, Shropshire	D_2	5	
	BM R24850	Longstone Edge, north of Bakewell, Derbyshire	D_2	2	diphymorphic corallites
L. floriformis crassiconus McCoy	UQ F5683	Clifton, near Bristol	D_2	8	
	RSM 1966.6.2	Gathorn Plain, Orton, Westmorland	D_2	14	
	BM R16995	Avon Gorge, Bristol	D_2	17	topotype
	BM R16997	Avon Gorge, Bristol	D_2	13	topotype
L. floriformis near *laticlavia* Smith	BM R36865	Oswestry, Shropshire	D_2–D_3	3	
L. caledonia Smith	RSM 1966.6.3	Coalburn, Lesmahagow, Lanarkshire, Scotland	D_2	3	early stages crushed
Thysanophyllum orientale Thomson	UQ F46767	Aberlady Bay, East Lothian, Scotland	Coral Zone 3	6	topotype
	RSM 1966.6.4	West Kirkton Quarry, Bathgate, West Lothian, Scotland	Coral Zone 3	7	early stages crushed in 3

TEXT-FIG. 1. Specimens of *Lonsdaleia* McCoy and *Thysanophyllum orientale* Thomson studied by means of closely spaced acetate peel sections.

INCREASE IN *LONSDALEIA*

Studies of increase in Lower Carboniferous representatives of *Lonsdaleia* have been made by thin section examination of British material by Smith (1916) and on material from the Russian Platform by Dobrolyubova (1958). Fedorowski (1965) described development in two Lower Permian species of *Lonsdaleia* from Hornsund, Vestspitsbergen, using serial acetate peel sections. These studies include a large number of species but there are nevertheless significant aspects of the hystero-ontogeny requiring clarification. These are mainly: (1) the orientation of the axial plane of the daughter corallite with respect to the axis of the parent; (2) the manner of development of lonsdaleoid dissepiments; (3) the pattern of septal insertion; and (4) the nature of the wall dividing the daughter from the parent corallite. These characters, together with present and past knowledge of other characters, are dealt with in turn in the following discussion. Species are discussed collectively since there generally seems to be little fundamental difference between their hystero-ontogenies. As text-fig. 1 indicates, most of the observations are made on *L. floriformis floriformis* and *L. floriformis crassiconus*. Complete details of increase were obtained from only one specimen each of *L. floriformis* near *laticlavia* and *L. duplicata duplicata*, and the early characters of development are unknown in *L. caledonia*.

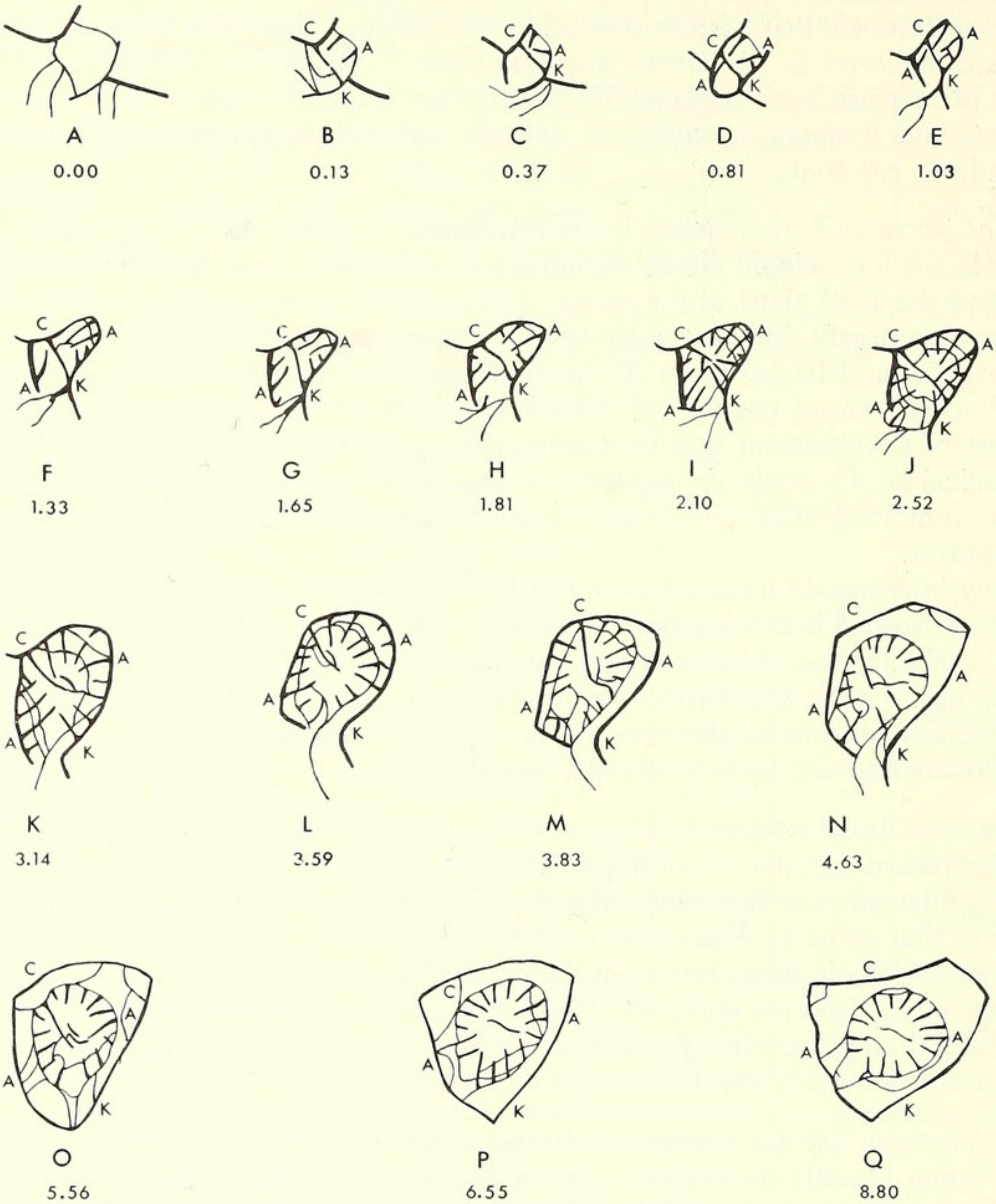
Mode of increase. This is almost invariably lateral in nature with the daughter corallite arising in the lonsdaleoid dissepimentarium of the parent in no preferred position with respect to the axial plane of the parent. Commonly as many as five daughter corallites may develop nearly simultaneously from the same parent (Pl. 102, fig. 2), especially in the proximal and lateral parts of the corallum. The rate of corallite development in cerioid species varies greatly but usually about 20–30 mm. of growth occurs between the start of development and the achievement of the ephebic stage. Development in the fasciculate *L. duplicata duplicata* is considerably slower, extending over some 40 mm. or more of distal growth with about 35 mm. of this occurring during late neanic development.

Rarely intermural increase (*sensu* Jull 1965, p. 206) also occurs whereby a youthful corallite is formed between adjacent corallites and lacks a single (obvious) parent. One example of this type of increase was observed in *L. floriformis floriformis* (text-fig. 2; Pl. 102, figs. 4 *a*, *b*), and Dobrolyubova (1958, p. 79–81, pl. 9, fig. 1; text-figs. 14–16) described and illustrated this type of increase in *L. rossica rossica* Stuckenberg from Lower Namurian C_1^{2st} beds on the Russian Platform.

Dividing wall. In all examples of increase observed, the wall which divides the daughter from the parent corallite is similar to the wall bounding adult corallites. It is formed either by thickening at the peripheral ends of parent septa (Pl. 100, figs. 2 *b–f*), a character similar to that noted by Fedorowski (1965, p. 121), or by apparent modification of one or more lonsdaleoid dissepiments of the parent (corallite D3, Pl. 101, figs. 1 *a–c*). When corallites of *L. duplicata duplicata* (text-fig. 4, *1 a–j*) become discontiguous, this wall is split rather than progressively disappearing as does the partition which divides daughter from parent in most fasciculate species of *Lithostrotion*.

Septal insertion. In the specimens studied, septa are inserted independently of the parent septa. Usually the cardinal septum is the first to appear and the other primary septa, the counter septum and two alar septa, may not all be present when metasepta first start to appear, especially if the dividing wall is late in forming. Insertion is of a zaphrentid nature in all quadrants (Pl. 100, figs. 2 *f–j*) and this may either continue up to the ephebic stage or minor septa may appear during development and insertion alters in all quadrants to the cyathaxonid mode (Pl. 100, figs. 2 *k–m*). The development of minor septa is discussed below.

In contrast to septal formation in Lower Carboniferous forms, Fedorowski (1965, p. 121) noted that the earliest septa in daughter corallites of the two Lower Permian species that he studied are formed from the detached ends of parent septa. In both species parent septa extend to the wall in the zone of increase preceding the appearance of the daughter corallite whereas in the Lower Carboniferous forms, this zone of increase is usually free of parent septa.



TEXT-FIG. 2. Intermural increase in *Lonsdaleia floriformis floriformis* (Martin), UQ F11035. Numbers below figures are cumulative distances of distal growth in mm. Thick lines are intercorallite walls and septa; thin lines are dissepiments and tabulae. In A, the youthful corallite is formed in lonsdaleoid dissepiments and is only separated from adult corallites lying to the upper-right and lower-left by lonsdaleoid dissepiments. Neither of these adult corallites could be established as the parent. The union of axial septa in C–H is uncommon in *Lonsdaleia*. Developmental stages, of which the late neanic is the last illustrated (Q), merge into one another. ×4.

Axial septa and axial structure. During early development, the cardinal septum is almost invariably the longest septum and the counter and alar septa are typically indistinguishable from metasepta. The median lamella of the axial structure is formed from the axial end of the cardinal septum, and during the progressive appearance of tabellae and other lamellae in the axial structure, the cardinal septum may or may not remain attached to the median lamella. During the ephebic stage and later part of the late neanic stage the two are usually detached.

Dobrolyubova (1958, p. 27) did not trace septal insertion in the species which she examined but suggested that the longer septum was the cardinal septum. Smith (1916, pp. 230, 232), on the other hand, considered the longer septum to be the counter septum but he likewise did not trace septal insertion. In some of the youthful corallites which he illustrated (ibid., pl. 17, figs. 5–23), insertion appears to be taking place beside this septum, indicating that it is perhaps the cardinal septum. De Groot (1963, p. 80) remarked that an elongate cardinal septum is characteristic of lonsdaleoid genera, but Fedorowski (1965) did not note any long septum during development in his lonsdaleoid species.

Name	*Number*	*Radial*	*Tan-gential*	*Indeter.*	*Total*
L. duplicata duplicata (Martin)	BM R1366	2	1(?)	1	4
	RSM 1878.11.267	—	—	3	3
L. floriformis floriformis (Martin)	UQ F2961	3	—	—	3
	RSM 1966.6.1	6	1	1	8
	BM R17160	1	2	2	5
	BM R24850	2	—	—	2
L. floriformis crassiconus McCoy	UQ F5683	7	1	—	8
	RSM 1966.6.2	10	3	1	14
	BM R16995	14	1	2	17
	BM R16997	11	—	2	13
L. floriformis near *laticlavia* Smith	BM R36865	1	1	1	3
L. caledonia Smith	RSM 1966.6.3	—	—	3	3

TEXT-FIG. 3. The number of corallites with radial and tangential orientation in the specimens studied. Orientation is based on the position of the axial plane of the daughter corallite with respect to the axis of the parent. Indeterminate corallites are those in which the early stages are not preserved, usually through crushing, or the position of the axial plane could not be definitely established.

Orientation of the daughter corallite. Text-fig. 3 shows that the majority of corallites studied are radially orientated with the cardinal septum positioned on the outer side, furthest from the axis of the parent. Most of these corallites are orientated at less than 30° from a true radial orientation (Pl. 100; corallites D2 and D3, Pl. 101), a few are up to 45° away from this position (corallite D1, Pl. 101) and those that are tangentially orientated lie at from 60° to 90° away from a radial position (Pl. 102, figs. 1*a–c*; text-fig. 4, 2*a–e*). Preference to radial orientation is exemplified by those specimens in which up to five daughter corallites, all radially orientated, are ranged simultaneously around the periphery of the parent (Pl. 102, fig. 2). With one exception in which two corallites develop together, all tangentially orientated daughter corallites observed arise singly.

In many of Dobrolyubova's (1958) illustrations, the axial plane of the daughter corallite appears to be radial to the parent, but in *L. arctica* Gorsky (ibid., text-fig. 3), *L. subtilis* Dobrolyubova (ibid., text-fig. 19) and *L. floriformis floriformis* (ibid., text-fig. 12) radial orientation appears to be lacking. Possibly this may be due to the axial plane of the daughter corallite rotating during development, as I have observed in the Viséan *Aphrophyllum hallense* Smith, but this effect has not been observed in the specimens of *Lonsdaleia* here studied.

Radial orientation of the daughter to parent corallite is certainly the most common condition in *Lonsdaleia* but non-radial orientation is too common to be an abnormal occurrence. Perhaps orientation of the daughter to parent corallite is a factor of individual variation, with radial orientation being the most common tendency.

Dissepiments. The first one or two rows of dissepiments in the daughter corallite are typically formed first as interseptal dissepiments when ten or more major septa have been inserted. These are subsequently altered to lonsdaleoid dissepiments by the withdrawal of septa from the wall. In a few cases, however, lonsdaleoid dissepiments of the parent corallite are incorporated as such into the morphology of the daughter (text-fig. 4, *1 a–j*).

Minor septa. Minor septa in *Lonsdaleia* are variably developed in different specimens. In some examples of increase, especially those in which major septa are mainly confined

EXPLANATION OF PLATE 100

Numbers below Figs. 2 *a–m* are cumulative distances of distal growth in mm. C = cardinal septum; K = counter septum; A = alar septum.

Figs. 1, 2. *Lonsdaleia floriformis floriformis* (Martin). 1, UQ F2961, transverse section of normal and diphymorphic corallites, ×1. 2 *a–m*, lateral increase in the same specimen; *a–f*, hystero-brephic stage; *g–l*, early neanic stage, showing the appearance of the counter septum in *g* and of minor septa in *k*; *m*, late neanic stage, also showing another youthful corallite with a long cardinal septum on the right, ×4.

EXPLANATION OF PLATE 101

Numbers below figures are cumulative distances of distal growth in mm. D = daughter corallite; P = parent corallite; C = cardinal septum; K = counter septum.

Figs. 1 *a–h*. *Lonsdaleia floriformis crassiconus* McCoy, UQ F5683. Lateral increase in three corallites, with daughter corallites D1, D2, and D3 arising from parent corallites P1, P2, and P3 respectively. Note that the axial plane of D3 is nearly radially disposed with respect to the axis of its parent, while in D1 and D2, it is approximately 20 to 30 degrees away from a radial disposition. Minor septa in D3 appear in *f–h*, and interseptal dissepiments are formed in *d*, followed by their alteration to lonsdaleoid dissepiments in *e–g*, ×4.

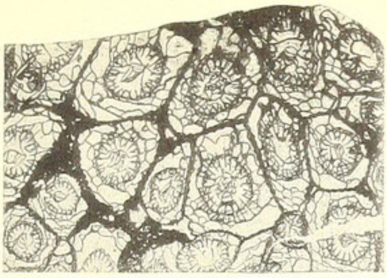
EXPLANATION OF PLATE 102

Numbers below Figs. 1 *a–c* are cumulative distances of distal growth in mm. D = daughter corallite; P = parent corallite; C = cardinal septum; K = counter septum.

Figs. 1–3. *Lonsdaleia floriformis crassiconus* McCoy. 1 *a–c*, UQ F5683, laterally arising corallite with its axial plane orientated tangential to the axis of the parent; *a*, *b*, early neanic stage; *c*, late neanic stage, ×4. 2, BM R16997, five radially orientated daughter corallites arising from the same parent, ×4. 3, transverse view of the same specimen as in Figs. 1 *a–c*, ×1.

Figs. 4 *a*, *b*. *Lonsdaleia floriformis floriformis* (Martin). UQ F11035, transverse and longitudinal sections of diphymorphic corallites, ×1.

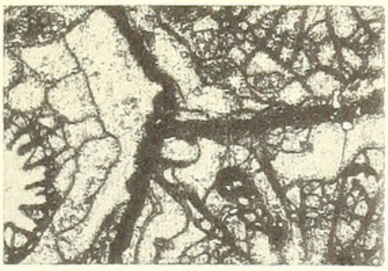
Figs. 5 *a*, *b*. *Thysanophyllum orientale* Thomson. Topotype, UQ F46767, transverse and longitudinal sections, ×1.



1

2a
0.00

2b
0.60

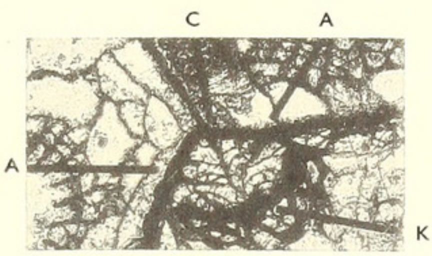


2c
1.40

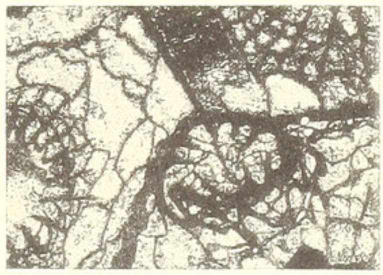
2d
1.64

2e
1.88

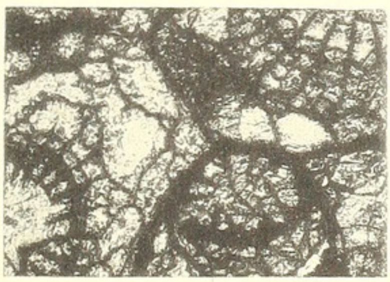
2f
2.14



2g
2.44

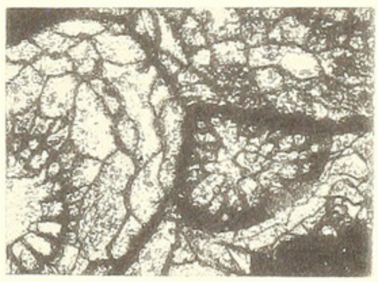


2h
2.58

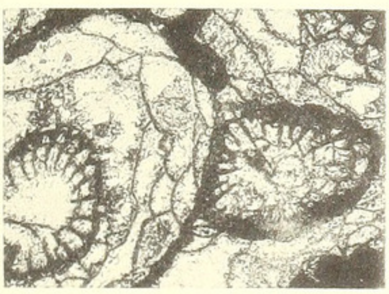


2i
2.74

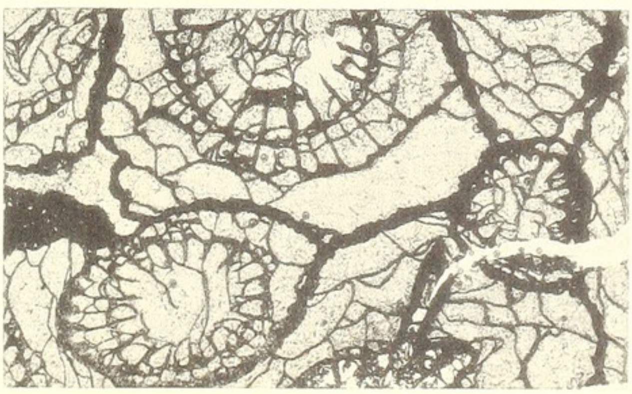
2j
2.94



2k
3.26



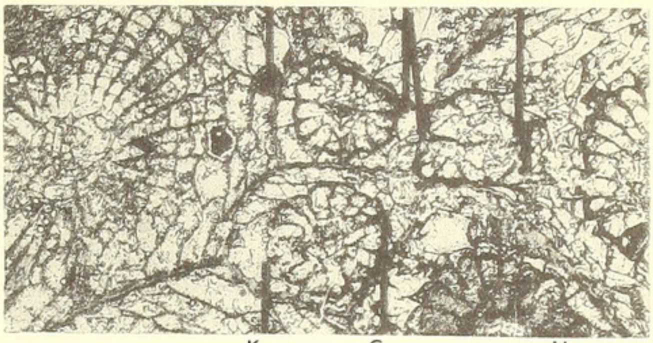
2l
3.58



2m

JULL, Hystero-ontogeny of *Lonsdaleia*

1a
0.00



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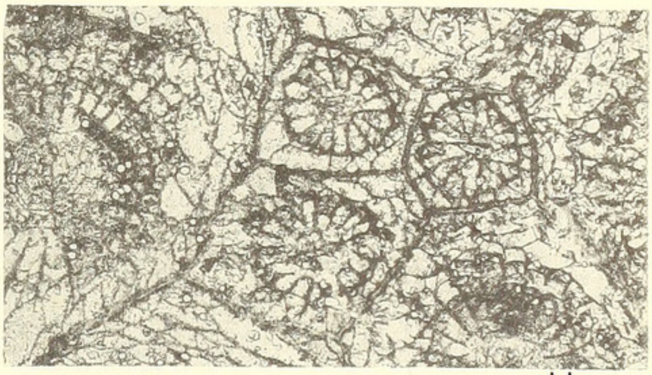
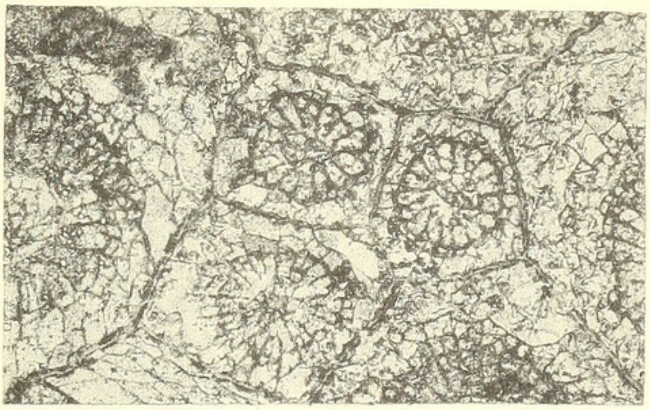
0.84

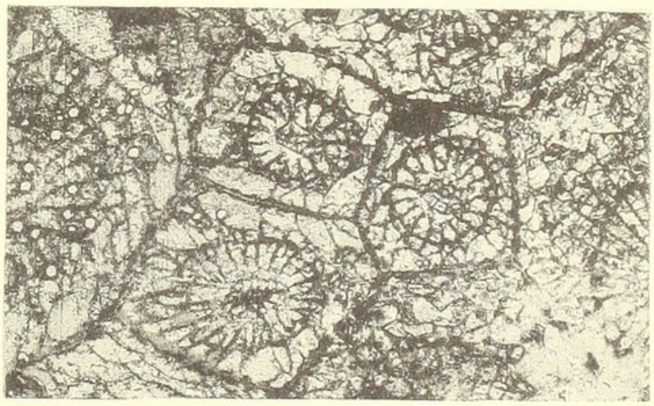
1c
1.20



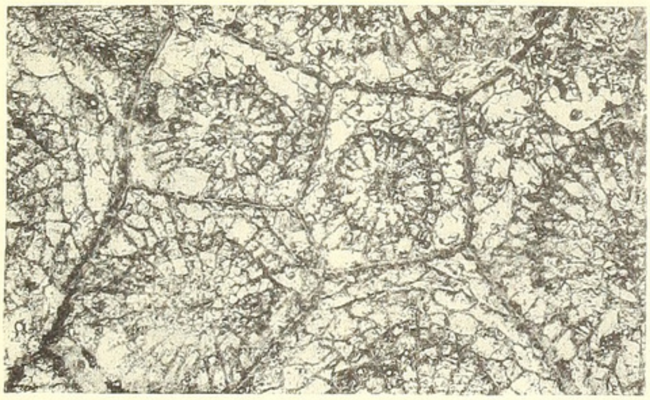
1d
1.98



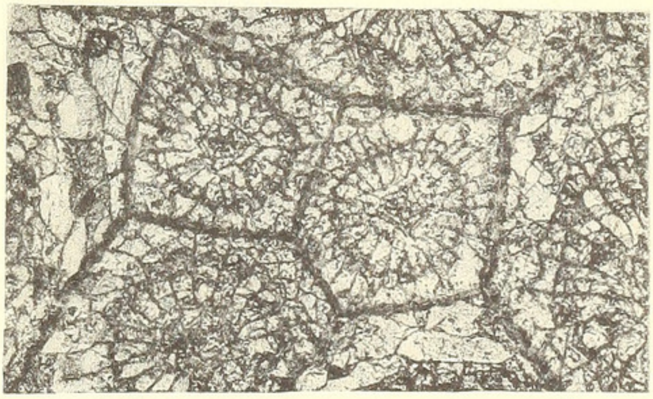
1e
2.60



1f
3.34

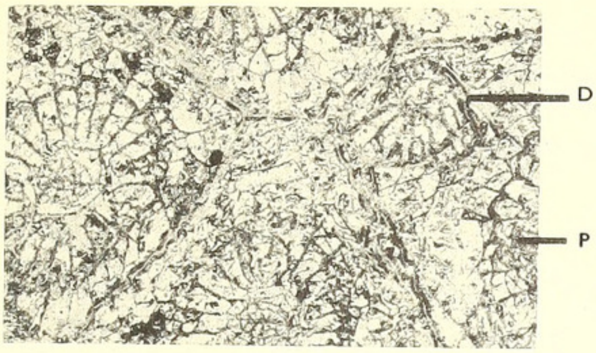


1g
5.44

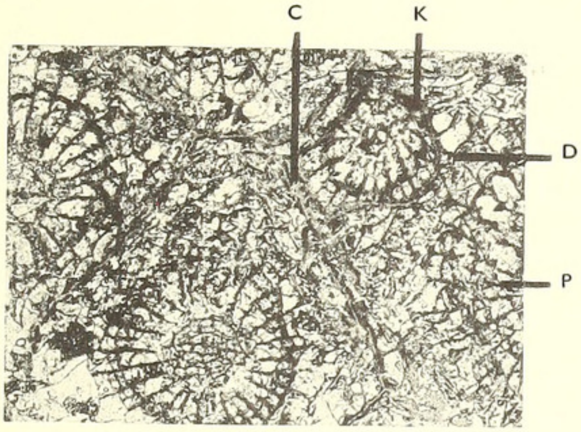


1h
7.44

JULL, Hystero-ontogeny of *Lonsdaleia*

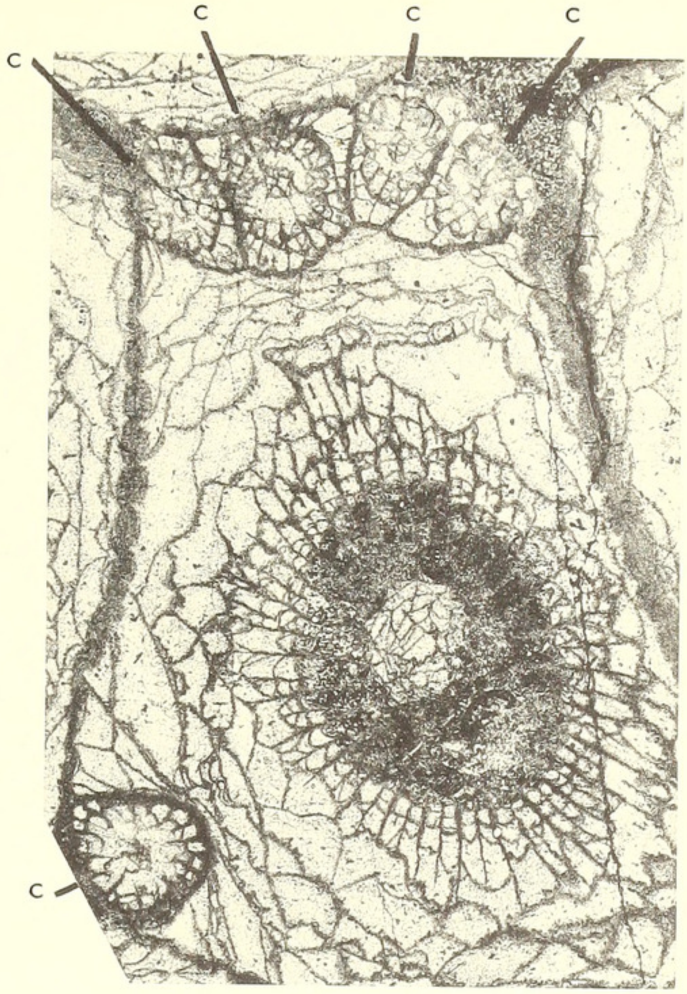


1a
0.00



1b
0.64

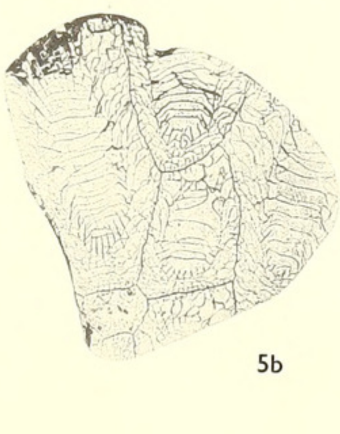
1c
4.40



2

3

5a



5b

4a

4b

JULL, Hystero-ontogeny of *Lonsdaleia* and *Thysanophyllum*