PALAEOZOIC CORAL FAUNAS FROM VENEZUELA, II. DEVONIAN AND CARBONIFEROUS CORALS FROM THE SIERRA DE PERIJÁ

BY

COLIN T. SCRUTTON
Department of Geology
The University
Newcastle upon Tyne

Pp. 221–281; 10 *Plates;* 12 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 23 No. 4
LONDON : 1973

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 23, *No.* 4 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation

Bull. Br. Mus. nat. Hist. (Geol.)

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 31 *May*, 1973 *Price* £4·35

PALAEOZOIC CORAL FAUNAS FROM VENEZUELA, II. DEVONIAN AND CARBONIFEROUS CORALS FROM THE SIERRA DE PERIJÁ

By C. T. SCRUTTON

CONTENTS

SYNOPSIS

Rugose and tabulate corals of Middle Devonian, and Lower Pennsylvanian age are described from localities in the northern part of the Sierra de Perijá, western Venezuela. The Palaeozoic stratigraphy of the area is briefly reviewed and the ages and relationships of the coral faunas are discussed. The new taxa *Bowenelasma typa* gen. et sp. nov., *B. breviseptata* sp. nov., *Amplexizaphrentis sutherlandi* sp. nov., *Briantelasma oliveri* sp. nov. and *Heliophyllum wellsi* sp. nov., as well as species of *Stereolasma*, ?*Stewartophyllum*, *Syringaxon*, *Heterophrentis* (*H.*), *Cylindrophyllum*, *Durhamina*, *Plasmophyllum* and *Favosites* are described.

I. INTRODUCTION

This is the second of two papers describing rugose and tabulate corals from the Palaeozoic rocks of the Venezuelan Andes. The first paper (Scrutton 1971) dealt with Silurian and Permo-Carboniferous corals from the Mérida Andes. This paper describes material of Devonian and Carboniferous ages from localities in the northern Sierra de Perijá (see Fig. 1), some 300 km to the north-west and close to the Venezuelan-Colombian border.

The bulk of the material was collected during 1959 by Dr J. M. Bowen (then Compañia Shell de Venezuela) but the opportunity is taken here to revise in addition the small samples of corals collected by C. W. Yeakel, P. W. McFarland and R. A. Liddle in 1924 (described by Weisbord 1926) and by R. A. Liddle in 1942 (described by Wells 1943) which came from the same or nearby sections. The richest fauna is one of upper Onesquethaw age (considered equivalent to the early Middle Devonian) in terms of the eastern North American stages (see Oliver 1968, fig 1), represented by 14 of Bowen's samples and including most if not all of the older collections. A further three of Bowen's samples are also Devonian in age. The Devonian corals, which show very strong affinities with coral faunas of the same age in eastern North America, include sixteen species belonging to eleven genera; one genus and four species are new. Three of Bowen's samples contain corals which, with some supporting evidence, indicate probable Carboniferous ages. Three species, two of them new, belonging to two genera are involved. The material is housed in the Department of Palaeontology, British Museum (Natural History).

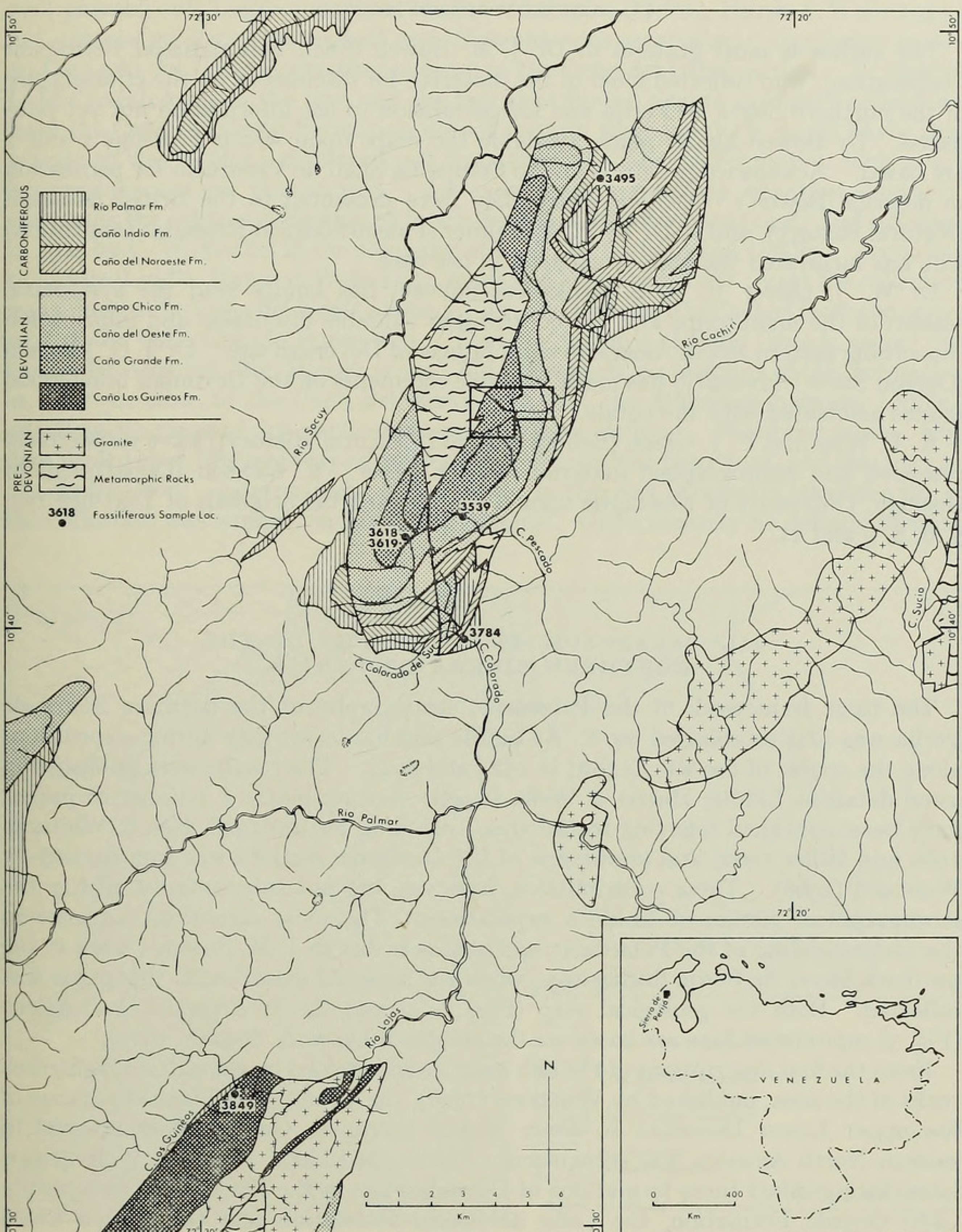


FIG. 1. Geological map of the northern Sierra de Perijá showing sample locations (for further information see Appendix). The area covered in detail in Fig. 2 is outlined. Based on maps supplied by J. M. Bowen.

II. ACKNOWLEDGEMENTS

The author is most grateful to Dr J. M. Bowen (Shell International Petroleum Corporation), who collected most of the material, for discussions on the stratigraphy of the northern Sierra de Perijá and for permission to use information not yet published. Dr Bowen kindly made available the maps upon which Text-figs 1 and 2 are based. Acknowledgement is due to Compañia Shell de Venezuela for permission to describe Bowen's collection which they have presented to the British Museum (Natural History), and to Dr K. V. W. Palmer (Paleontological Research Institution) who has facilitated the loan of material in her care.

Dr W. J. Oliver Jr. (U.S. Geological Survey) has kindly read the systematic section of the manuscript and has contributed valuable discussion and information concerning eastern North American coral faunas of Devonian age. Dr J. G. Johnson (Oregon State University) has made valuable comments on the Devonian brachiopod faunas associated with the corals.

R. F. Wise and P. J. Green (British Museum (Natural History)) have respectively prepared and photographed material for this paper. E. Lawson (Department of Geology, University of Newcastle upon Tyne) drafted the originals of Text-figs 1–3, 5, 6, 8, 9 and 11.

III. PALAEOZOIC STRATIGRAPHY OF THE NORTHERN SIERRA DE PERIJÁ

The basic framework of the Palaeozoic stratigraphy of the northern Sierra de Perijá was first established by R. A. Liddle and his co-workers during expeditions along the course of the Río Cachirí in 1924 and 1942. The results were published in some detail in Liddle, Harris & Wells (1943). Subsequently a number of papers have been published referring to the area (including Sutton 1946, Hea & Whitman 1960 and Miller 1962) and knowledge of the Devonian sections was summarised by Weisbord (1968). These contributions, however, did not substantially modify the stratigraphical results of Liddle's expeditions. The most significant advance in the understanding of the Palaeozoic successions is due to J. M. Bowen's work in the northern Sierra de Perijá during 1959 when the material described in this paper was collected. Both the geological map (Figs 1, 2) and the stratigraphic successions (Fig. 3) reproduced here are based on the results of his work (Bowen 1972).

From the first descriptions of the rich macrofauna yielded by the oldest fossiliferous rocks of the area, published by Weisbord (1926), the strong resemblance to faunas of the upper Lower Devonian to lower Middle Devonian Onesquethaw interval in eastern North America was recognized. Liddle, in Liddle, Harris & Wells (1943) later distinguished three formations of Devonian age in the Río Cachirí section, the Caño Grande Formation, the Caño del Oeste Formation and the Campo Chico Formation in order of decreasing age, grouped together as the Río Cachirí Series (Cachirí Group of Sutton 1946 : 1634). The rich invertebrate fauna was confined to the Caño Grande Formation and Liddle described both the other formations as unfossiliferous (Liddle, Harris & Wells 1943 : 286, 289), although as Weisbord (1968 :

221) pointed out, Liddle records in his list of samples (Liddle, Harris & Wells 1943 : 313, sample 37) *Heliophyllum halli* and '*Heterophrentis venezuelense*' apparently *in situ* on the Caño del Oeste Formation outcrop in the Caño del Oeste section. In view of Liddle's statement in the text and the fact that Bowen's more extensive collections from the Caño del Oeste Formation do not contain these corals, it seems likely that sample 37 was in fact a displaced raft from the Caño Grande Formation such as are known to occur on this section. An even more anomalous situation, however, surrounds the original collection of fossils described by Weisbord (1926) and collected in 1924 by C. W. Yeakel in the company of P. W. McFarland and Liddle. According to Liddle (Liddle, Harris & Wells 1943, map) and Weisbord (1968 : 217) the collection was taken in the Caño del Norte about 4·5 km north of the Río Cachirí from the upper part of the Caño Grande Formation. That the fauna is of Caño Grande aspect can hardly be doubted, but Bowen (1972; Fig. 4) records no outcrop of this formation in, or even close to the Caño del Norte. In fact the difference between Liddle's and Bowen's maps of this particular section is most striking. Weisbord (1926 : 223) does record that 'the majority of our fossils were collected from float' and this may be the explanation. Alternatively, it is possible, in this sort of country, that the site of the collection was wrongly located (*fide* Bowen). Unfortunately no definite solution

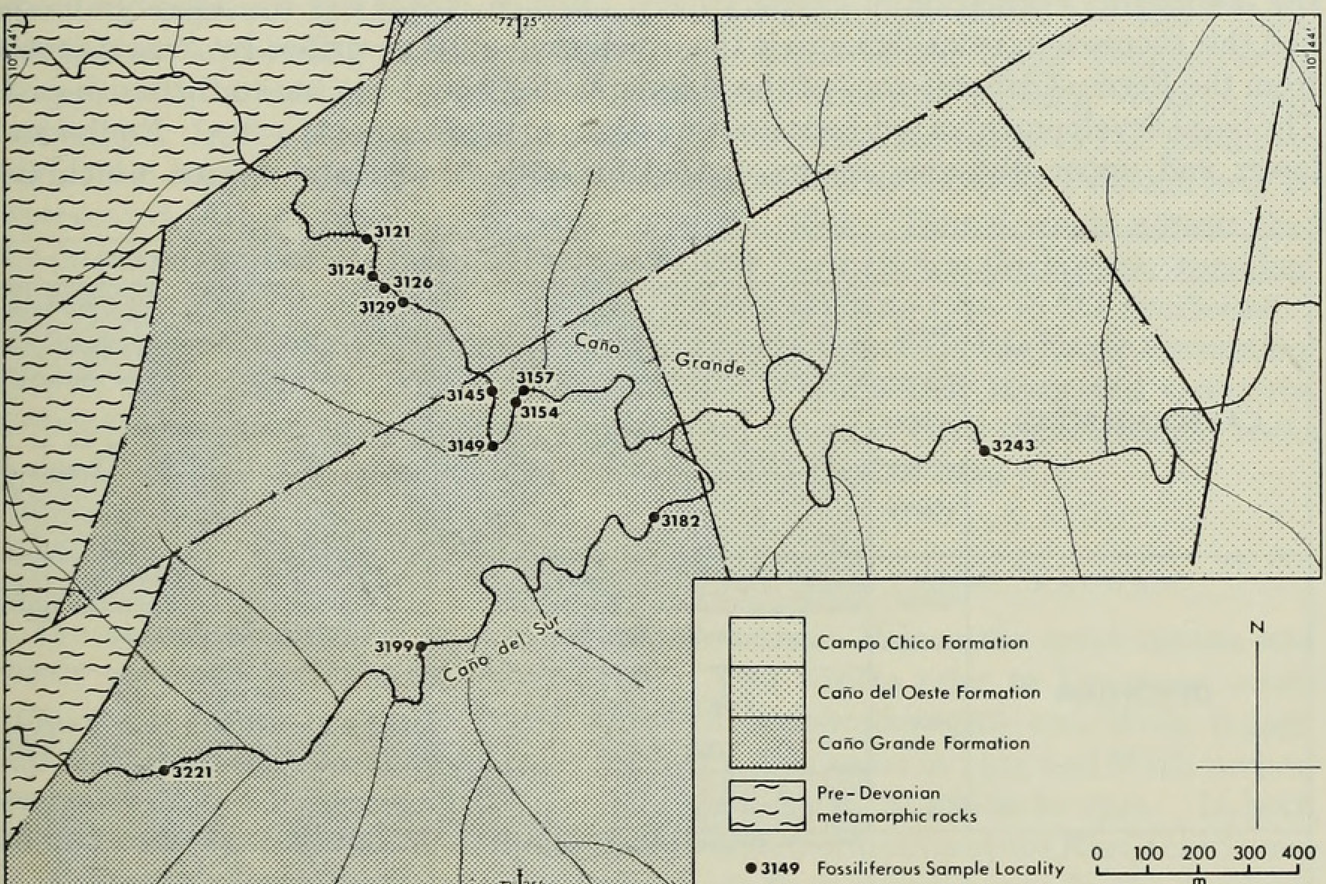


FIG. 2. Geological map of the upper reaches of the Río Cachirí, Sierra de Perijá showing sample locations (for further information see Appendix). The area covered here is indicated in Fig. 1. Based on maps supplied by J. M. Bowen.

to this problem seems possible at the moment and in this paper Yeakel's collection is considered as most likely to have originated from a displaced raft or possibly faulted slice of Caño Grande Formation in the Caño del Norte.

Bowen (1972) has recognized a fourth division of the Devonian Río Cachirí Group in the Sierra de Perijá. This, the Caño Los Guineos Formation of the Río Lajas area, he considers to be lower in the sequence than the Caño Grande Formation although the two formations do not crop out in the same sections. They have a very similar macrofauna and both formations are dated as Lower Devonian (Emsian, equivalent to the middle Onesquethaw) mainly on the basis of brachiopods although an early Middle Devonian age (upper Onesquethaw) is considered more likely here (see p. 230–31). Bowen has also collected a fossil suite dominated by brachiopods from the Caño del Oeste Formation, previously not satisfactorily dated, from which he deduces a lower Middle Devonian age. Finally, the highest, Campo Chico Formation has yielded palynomorphs indicating a Middle to Upper Devonian (probably Frasnian) age (Bowen 1972). The Devonian corals, discussed in detail in the following sections, come mainly from the Caño Grande Formation, for which they suggest an upper Onesquethaw age.

Liddle (Liddle, Harris & Wells 1943 : 290) assigned all the Permo-Carboniferous 'red-bed' sequence and overlying crinoidal limestones in the Río Cachirí section to the Palmarito Formation of Christ (1927). Bowen (1972) has considerably modified this succession, recognizing in it the lithological units described by Arnold (1966) from the Permo-Carboniferous of the Mérida Andes, about 300 km to the south-east. The basal development of red-beds Bowen assigns to the Sabaneta Group. Equivalent lower and upper divisions are recognized by both Arnold and Bowen which the

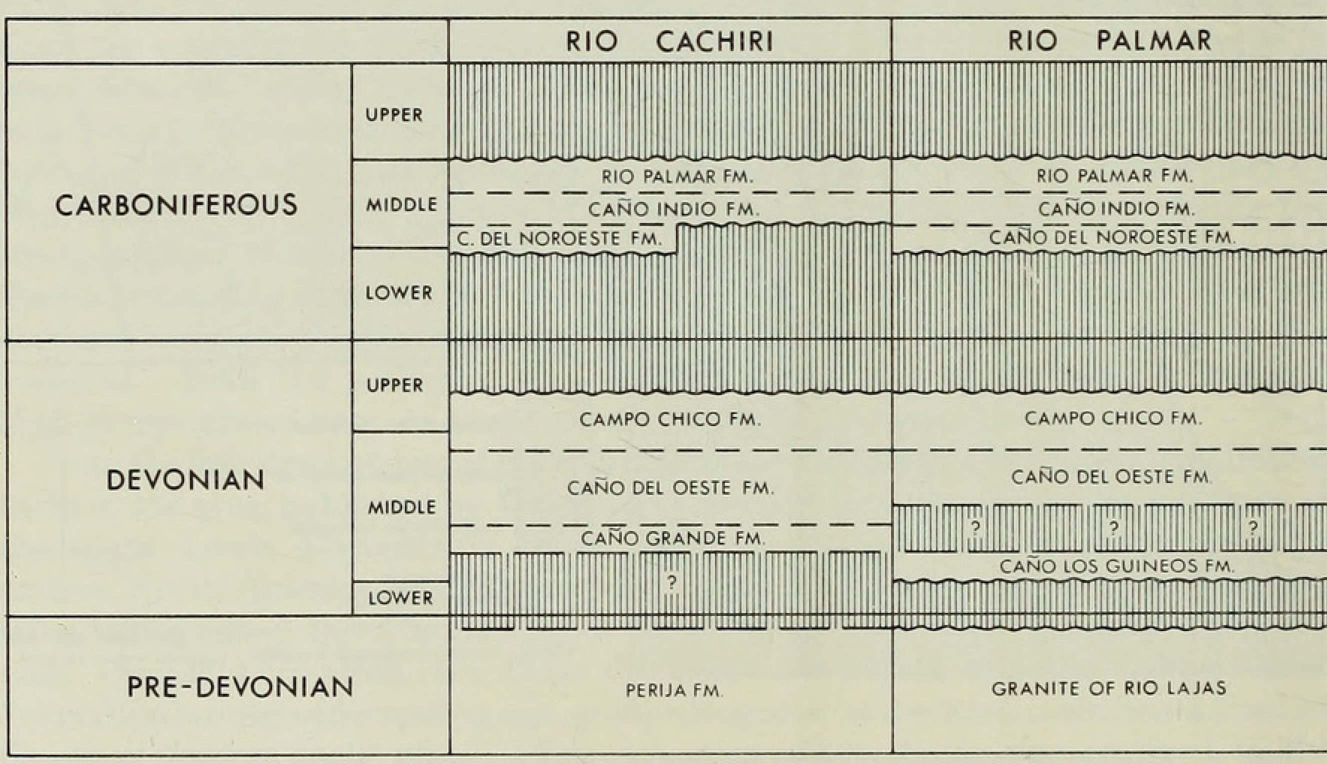


FIG. 3. Devonian and Carboniferous successions in the northern Sierra de Perijá (after Bowen 1972). For comments see text.

latter erects as new formations. The Caño del Noroeste Formation below (equivalent to Arnold's lower clastic member) contains a fauna of fusulinids, brachiopods and palynomorphs indicating a lower Middle Carboniferous Namurian to Lower Westphalian age (Lower Pennsylvanian) according to Bowen (1972) whilst the Caño Indio Formation above is unfossiliferous. The age of the Caño Indio Formation is fixed as low in the Pennsylvanian, however, by the dating of the overlying Río Palmar Formation. This contrasts with the as yet poorly dated Sabaneta Group (Sabaneta Formation of Arnold 1966) of the Mérida Andes, the type area, where fossiliferous marine horizons are not known. Here, Arnold (1966 : 2371–2372) records a possible Permian age for the higher parts of the Sabaneta Group on the evidence of spores.

The Río Palmar Formation is a thick carbonate sequence conformably succeeding the Sabaneta Group. It is dated late Middle Carboniferous (late Lr. Pennsylvanian) on the basis of fusulinids and palynomorphs (Bowen 1972) and is the only level in the Permo-Carboniferous from which corals are described in this paper. This new formation is not represented in the Mérida Andes (Bowen 1972) where Arnold (1966 : 2373, 2377) records the Sabaneta Group grading upwards through a transitional zone into the Palmarito Formation. In the northern Sierra de Perijá, the typical facies of the Palmarito Formation, which is absent from the Río Cachirí area but crops out further south, comes in unconformably above the Río Palmar Formation. According to Bowen (1972), the whole of the Upper Pennsylvanian is apparently missing here, with the Palmarito Formation yielding Wolfcampian fusulinids. In the Mérida Andes, however, the rich marine fauna of the Palmarito Formation suggests that the late Pennsylvanian as well as the early Permian may be represented (Arnold 1966 : 2378; Scrutton 1971 : 189). Thus it would appear that the distinctive carbonate facies of the Río Palmar Formation is the lateral equivalent of rocks of upper Sabaneta or, less likely, lower Palmarito type to the south-east.

Between the Palmarito Formation and the Lower Cretaceous Río Negro Formation, Bowen (1972) has described a succession of pyroclastics, lavas and terrestrial sediments of ?Permian to Jurassic age. As no material from these younger rocks is described in this paper, they are not considered further here.

IV. AGES AND RELATIONSHIPS OF THE CORAL FAUNAS

The extent of previous work on South American Palaeozoic coral faunas was briefly reviewed by Scrutton (1971 : 190). Two papers refer to Devonian corals from the northern Sierra de Perijá, those of Weisbord (1926) and Wells (1943). Weisbord described the material collected by C. W. Yeakel in 1924 and Wells revised the corals on the basis of further collections made by R. A. Liddle in 1942. In both collections, the corals were all from the Caño Grande Formation of the Río Cachirí area. J. M. Bowen's much more extensive collections from a wider area in the northern Sierra de Perijá have more than doubled the species list for the Caño Grande Formation as well as yielding small coral faunas from three further horizons. The compositions of the faunas are listed in Table 1 and are discussed below in ascending stratigraphical order.

Table I

Composition of coral faunas from the Río Cachirí Group (Devonian) and Río Palmar Formation (Carboniferous) of the Sierra de Perijá.

Species	Río Cachirí Group			Río Palmar Fm.
	Caño Los Guineos Fm.	Caño Grande Fm.	Caño del Oeste Fm.	
Stereolasma sp.	×			
Syringaxon sp.	×			
Heliophyllum halli	×	×		
H. wellsi		×		
Heterophrentis (*H.*) *simplex*	×	×		
H. (*H.*) *venezuelensis*		×		
Plasmophyllum secundum americanum		×		
P. sp.		×		
Acinophyllum vermetum		×		
Briantelasma oliveri		×		
Bowenelasma typa		×		
B. breviseptata		×		
Favosites venezuelensis		×		
F. arbuscula		×		
Cylindrophyllum elongatum		—— ?	——	
?*Stewartophyllum* sp.			×	
Hadrophyllum sp.			×	
Amplexizaphrentis sutherlandi				×
?*Durhamina* sp.				×
Durhamina sp. nov.				?

(a) *Río Cachirí Group*

(i) *Caño Los Guineos Formation.* A small fauna of four different corals only is available from this formation. Its composition suggests affinities with Middle Devonian coral faunas of eastern North America where *Heliophyllum halli* Edwards & Haime in particular is characteristic of the Onondaga Limestone and Hamilton Group of New York and their equivalents elsewhere. *Stereolasma* appears to have a similar, though less well documented range and *Heterophrentis* (*H.*) *simplex* (Hall) has been recorded so far only from horizons of Hamilton age in New York and the Ohio Valley (see Oliver 1968, fig. 1 for a correlation chart of the eastern North America Devonian).

Bowen (1972) lists other fossils, principally brachiopods, from the Caño Los Guineos Formation which he takes to indicate an upper Lower Devonian (Emsian) age. There is some doubt, however, as to the reliability of this brachiopod fauna in distinguishing between a late Lower and an early Middle Devonian age (J. G. Johnson, pers. comm.). This matter is discussed more fully in the following section on the Caño Grande Formation which has yielded similar but richer coral-brachiopod faunas. In view of the ambiguity of the brachiopod evidence, the affinities of the coral fauna suggest that an upper Onesquethaw age (early Middle Devonian) is more likely than a late Lower Devonian age for this formation.

(ii) *Caño Grande Formation.* The principal Onondaga—Hamilton species present in this much richer coral fauna are *Heliophyllum halli, Heterophrentis* (*H.*) *simplex, Plasmophyllum secundum americanum* (Edwards & Haime) and *Favosites arbuscula* Hall. In addition, *Acinophyllum vermetum* (Weisbord)[1] is considered to agree in all its essential characteristics with *A. stramineum* (Billings) from the lower part of the Onondaga Limestone of Ontario (Oliver, in preparation) and *Cylindrophyllum elongatum* Simpson, which comes either from the Caño Grande Formation or the overlying Caño del Oeste Formation, is also found at the same horizon in New York. This evidence would clearly suggest an upper Onesquethaw (lower Middle Devonian) age for the Caño Grande coral fauna. Also present, however, is a new species of *Briantelasma.* This genus has previously been recorded from rocks of Silurian (?Wenlock) and Lower Devonian (Helderberg) age in eastern North America (Oliver 1960a, b, 1963) and is the only element in the coral fauna not previously recorded from the Middle Devonian. The new genus *Bowenelasma* provides no direct evidence but its general characteristics relate it more to *Briantelasma* and Silurian streptelasmatids rather than to typical Middle Devonian members of the family. It should be stressed, however, that there is no sign of typical eastern North American middle Onesquethaw corals in the Venezuelan fauna.

Bowen (1972) lists a brachiopod fauna from the Caño Grande Formation, very similar to that in the Caño Los Guineos Formation, which he takes to indicate a late Lower Devonian age. He infers that this is supported by palynomorphs. As previously noted (p. 230), however, Dr J. G. Johnson (pers. comm.) doubts that confidence can be placed in the brachiopod fauna at the moment to distinguish between a middle and an upper Onesquethaw age (that is, late Lower Devonian and early Middle Devonian as currently understood in North America). In particular, Johnson notes that *Eodevonaria* has been collected from rocks of upper Onesquethaw age, and he regards the upper limits of the range of *Leptocoelia* to be uncertain. Both genera have been taken to indicate a Lower Devonian horizon. He also draws attention to the occurrence of *Tropidoleptus* (Morales 1965) and common *Pentagonia* and *Spinulicosta,* all more suggestive of an upper Onesquethaw than a Lower Devonian age, in the Floresta fauna of Colombia, with which the Venezuelan faunas have much in common. Johnson thinks it likely that these South American occurrences represent an overlap of late Lower and early Middle Devonian forms. Dr L. Nijssen (pers. comm.), who made the palynological determinations, also has reservations about distinguishing between an Emsian and an early Eifelian age on the basis of the flora.

Although much revision of the North American coral faunas is necessary, Oliver (1968 : 741) clearly indicates that an important break in the sequence of coral assemblages there occurs between the middle and upper Onesquethaw. In this light, the strong affinities of the coral fauna with faunas of upper Onesquethaw age in eastern North America suggests that the Caño Grande Formation should be dated upper Onesquethaw (early Middle Devonian) rather than middle Onesquethaw at the present time.

---

[1] As Dr W. J. Oliver Jr. has a review of this species in preparation it is not described in the systematic section of this paper.

The affinities between the Venezuelan and eastern North American coral faunas indicates that the two areas must have formed part of the same province in early Middle Devonian time. The presence of *Bowenelasma* and some species endemic to Venezuela suggests that north–south migration may have been partially restricted in some way, although these corals may be recorded from eastern North America in the future.

(iii) *Caño del Oeste Formation.* This formation appears to be poor in corals although it has provided a fairly varied fauna of brachiopods and molluscs which are listed by Bowen (1972). One specimen each of ?*Stewartophyllum* sp. and *Hadrophyllum* sp. indicate a tentative Middle Devonian age, whilst the brachiopods have been more precisely dated as early Middle Devonian.

Although the specimen of *Cylindrophyllum elongatum*, which comes from a slipped block, is listed by Bowen (1972) with the Caño del Oeste fauna, Bowen has informed the writer that the block compared lithologically with the Caño Grande Formation outcropping further up the Caño Pescado and may well have come from that formation. If the block did originate from the Caño del Oeste Formation, however, then it would be from near the base, whereas the rest of the fauna, providing evidence for the age, derives from the very top of the formation.

(b) *Río Palmar Formation*

This formation has also yielded two corals among a rather limited invertebrate fauna. *Amplexizaphrentis sutherlandi* sp. nov. and ?*Durhamina* sp. indicate a general Carboniferous age and compare most closely with North American cordilleran species. The other faunal elements provide more precise information and indicate a late Lower Pennsylvanian age.

Durhamina sp. nov. is known only from a loose block whose stratigraphic relationships are obscure. Of the known stratigraphy, it is most likely to have come from the Río Palmar Formation which is where Bowen (1972) lists it as 'durhaminido gen. and sp. nov.'. Possible Mississippian brachiopods were reported from the same block, however, and it may represent an horizon as yet not recognized *in situ* in the stratigraphic sequence.

V. SYSTEMATIC DESCRIPTIONS

The terminology used in the following descriptions is that proposed by Smith (1945 : 4–9) and Moore, Hill & Wells (1956) unless otherwise indicated.

All the material collected by Bowen is now housed in the Department of Palaeontology, British Museum (Natural History). The registered numbers for these specimens are prefixed R and in each case the number of the sample in which the specimen was collected is given in parentheses after the registered number. The locations of Bowen's samples are plotted on Text-figs 1 and 2 and full details are given in the Appendix.

The sources of other material described below are indicated by the following abbreviations: PRI—Paleontological Research Institution, Ithaca, N.Y.; NYSM—New York State Museum, Albany, N.Y.

Order RUGOSA Edwards & Haime 1850
Suborder STREPTELASMATINA Wedekind 1927
Superfamily **CYATHAXONIICAE** Edwards & Haime 1850
Family **LINDSTROEMIIDAE** Počta 1902

1971 Lindstroemiidae; Scrutton: 192, *cum syn.*

Discussion. The family concept was reviewed by Scrutton (1971 : 192).

Genus ***STEREOLASMA*** Simpson 1900

1900 *Stereolasma* Simpson: 205.
1941 *Stereolasma* Busch: 395.
1949 *Stereoelasma* Stumm: 7.
1962 *Stereolasma* Stumm: 234.
1965 *Stereolasma* Stumm: 14.

Diagnosis. Small ceratoid to trochoid corals. Major septa fuse in the axis to form, with or without additional sclerenchyme, a prominent axial pillar. Minor septa short, usually contratingent. Peripheral stereozone narrow. Cardinal fossula narrow, poorly developed. Tabulae complete or incomplete, strongly arched with a flat or slightly depressed axial area. No dissepiments.

Type species (by original designation). *Streptelasma rectum* Hall 1876, pl. 19, figs 1–13 in part ?=*Strombodes*? *rectus* Hall 1843 : 210, text-fig. 87, 5 on p. 209, and no. 48, fig. 5 on p. 44 of tables. Middle Devonian, Hamilton Group; western New York State, U.S.A.

Discussion. Reference should be made to Stumm (1949 : 7) and Stumm & Watkins (1961 : 445) for comments on and a redescription of *Stereolasma rectum.*

Stereolasma sp.
(Pl. 1, figs 6, 7)

Material. R45129 (3849). Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian (upper Onesquethaw).

Description. Small ceratoid coral, incomplete.

In the late neanic stage the mean diameter is 11 mm with 25 major septa. The lumen is completely infilled by laterally contiguous wedge-shaped major septa merging in the axial area with a core of sclerenchyme 3 mm in diameter. This core may be formed by irregularly intertwined septal ends but the structure is not clear. There are signs of rudimentary minor septa as wedges about 1 mm long between the major septa.

In the ephebic stage (Pl. 1, fig. 6) there are 25 major septa at a mean diameter of 14·5 mm. The major septa, except the cardinal septum, are 0·6–0·75 mm thick where they are very slightly waisted one-third of the way along their length from the periphery. The cardinal septum is notably thinner at 0·4 mm. The septa are thickest about two-thirds of their length to the axis where they become laterally contiguous. From this point they taper smoothly into the axis in a slight counter clockwise vortex maintaining contact with their neighbours. The septa are longest in the alar area where they all but meet in the axis. The counter and cardinal septa are shorter, however, each reaching only three-quarters of the radius, leaving a narrow axial gap about 4·5 mm long and 0·5 mm wide in the otherwise solid oval core of fused septal ends, 7 mm × 6 mm in size. The peripheral ends of the septa alternate with contratingent minor septa in a peripheral stereozone 1–1·2 mm thick. The minor septa generally appear as short thorny projections from the stereozone mainly in the counter quadrants where they are more free standing. The minor septa flanking the counter septum are 2 mm long and they decrease in size round towards the cardinal septum near which they are 1·5 mm long. The minor septa contratingent on the major septa immediately flanking the cardinal septum, however, are again 2 mm long. Septal microstructure consists of an irregular structureless core embedded in calcite showing growth lamellae running at a very low angle to the septal faces axially and inward towards the core.

In the longitudinal section (Pl. 1, fig. 7), cut between the two sections described above, the lumen is infilled with septal material except for two small peripheral areas. The septal material shows bowl-shaped laminations, notched in the axis, which are interpreted as growth-lines. In the smaller of the two voids, part of a tabula can be seen curving upward and axially from the peripheral stereozone. There are no dissepiments.

The specimen contains circular borings, 0·8–1·1 mm in diameter, of unknown origin.

Discussion. This specimen appears to compare most closely in size and structure with the type species of *Stereolasma*, *S. rectum* (Hall) from the Middle Devonian Hamilton Group of eastern North America as illustrated by Simpson (1900, figs 16–18) and Stumm & Watkins (1961, pl. 58, figs 1–16). *S. rectum*, however, has much thinner skeletal elements and less well developed minor septa except for the counter-lateral minor septa which are strongly accelerated. The Venezuelan specimen may belong to a new species but further material is required to confirm this.

Genus ***STEWARTOPHYLLUM*** Busch 1941

1941 *Stewartophyllum* Busch: 393.
1949 *Stewartophyllum* Stumm: 9.
?1965 *Stewartophyllum* Federowski: 344.

Type species (by original designation). *Amplexus intermittens* Hall 1876; pl. 32, figs 8–15. Middle Devonian, Hamilton Group; Moscow, N.Y., U.S.A.

DIAGNOSIS. Small subcylindrical to trochoid corals. Major septa dilated and extending to axis where they fuse in neanic stage, withdrawn from axis in ephebic stage. Cardinal fossula present. Minor septa very short or absent. Tabulae complete and incomplete, flat axially, variably orientated peripherally. No dissepiments (based on Stumm 1949 : 9 and Stumm & Watkins 1961 : 447).

DISCUSSION. The type specimens of *S. intermittens* (Hall) have been redescribed by Stumm and Watkins (1961 : 447) who showed that three other species described by Busch should also be referred to Hall's species. The diagnosis for the genus given above takes account of this redescription.

?*Stewartophyllum* sp.

(Pl. 1, figs 4, 5)

MATERIAL. R45110 (3243). Caño Grande; Caño del Oeste Fm., early Middle Devonian.

DESCRIPTION. Small curved trochoid coral, about 25 mm high and 20 mm in maximum diameter.

In the late neanic-early ephebic stage, the lumen is almost entirely infilled. The septa occur in a single series up to 1·25 mm thick at the periphery and wedge-shaped, reaching between three and four-fifths of the way to the axis. They are arranged in an irregularly pinnate pattern and are mostly laterally contiguous with scattered very narrow gaps in the peripheral area between some septa. The axial ends of the septa merge into solid sclerenchyme completely infilling the axis, in which no structural details can be seen. The septal structure compares with that described as pseudotrabecular by Kato (1963, text-fig. 9e).

In higher sections a subtriangular cardinal fossula containing a short, thin cardinal septum, 4 mm long, is present on the convex side of the coral. There are slightly larger gaps between the septa and signs of tabulae can occasionally be seen. The axis of the coral is filled by a subcircular core of sclerenchyme 7 mm in diameter. As the subcalicular level is approached, the subtriangular cardinal fossula increases in size at the expense of the cardinal half of the core. The pinnate septal symmetry is also more regularly developed immediately below the calice. The diameter here is 16 mm with about 40 septa.

No longitudinal section is available.

DISCUSSION. This single specimen is tentatively assigned to *Stewartophyllum*. It appears to have considerable structural similarity with *S. intermittens* (Hall) from the Middle Devonian Hamilton Group of eastern North America (see Stumm & Watkins 1961, pl. 58, figs 17–28, 37–39) although it is clearly not conspecific. Apart from the much higher septal number in the Venezuelan specimen, the large axial core of sclerenchyme makes even a congeneric assignment open to question. More material is required to assess the variability and significance of the axial core.

Genus *SYRINGAXON* Lindström 1882

1970 *Syringaxon* Sutherland: 1125.
1971 *Syringaxon* Scrutton: 194, *cum syn.*

DISCUSSION. See Scrutton (1971 : 194) for a diagnosis and full discussion of the status of this genus.

Syringaxon sp.
(Pl. 1, figs 1–3)

MATERIAL. R45130 (3849). Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian (upper Onesquethaw).

DESCRIPTION. Small conico-cylindrical coral with moderately developed septal grooves.

Coral circular in cross-section with a variably corrugated epitheca and a peripheral stereozone about 0·6 mm thick. In the mature stages the major septa are 0·13–0·2 mm thick midway along their length where they are very slightly waisted; the cardinal septum is the thinnest. They reach approximately seven-eighths of the radius towards the axis. The axial ends of the major septa are rhopaloid causing them to be laterally contiguous and to form, with a small amount of additional sclerenchyme, an aulos 2–2·5 mm in external diameter. In a subcalicular section (Pl. 1, fig. 1), the internal dimensions of the aulos are 1·2 × 0·9 mm. In a section approximately 1·5 mm below this (Pl. 1, fig. 2), the aulos is solidly infilled, possibly by sclerenchyme coating a tabula as the longitudinal section shows the aulos to be open for at least another 2·5 mm below the level of this section. The minor septa are approximately half the radius in length except for the counter-lateral minor septa which are equal in length to the counter septum. They are closely contratingent so that the lumen between a major septum and its contratingent minor may be closed at sub-calicular levels.

The longitudinal section is two-thirds infilled by septal material due to its being cut slightly off-centre. There is a very narrow open core in the distal part of the aulos containing irregularly spaced flat tabulae averaging 0·25 mm apart. In the interseptal loculi one tabula can be clearly seen, flat near the peripheral stereozone, and curving upwards towards the aulos. There are faint indications of what may be further tabulae but none can be positively identified as such.

The subcalicular section is about 6·8 mm mean diameter with 20 major septa and the section 1·5 mm below is 6·4 mm in mean diameter with 18 major septa.

DISCUSSION. This single specimen, although slightly larger in size at the same septal number, is quite similar to *S. arnoldi* Scrutton (1971 : 196) from rocks of Ludlovian age in the Mérida Andes of Venezuela. Further material is necessary, however, to determine the status of the Devonian specimen.

S. rudis (Girty 1897 : 299, pl. 2, figs 7, 8), from the Lower Devonian of North America, is in need of redescription and cannot be compared with the present material.

Family *HADROPHYLLIDAE* Nicholson 1889

1937 Palaeocyclidae Bassler: 189, *pars*.
1949 Hadrophyllidae Stumm: 4.
1955 Porpitidae Jeffords: 12, *pars*.
1956 Hadrophyllidae Hill: 262.
1961 Hadrophyllidae Fontaine: 69.
1969 Hadrophyllidae Sutherland & Haugh: 27.

TYPE GENUS. *Hadrophyllum* Edwards & Haime 1850 : 67.

DIAGNOSIS. Small, simple, discoid, patellate, button shaped or depressed turbinate corals. Major septa usually arranged in quadrants and cardinal and alar fossulae often strongly developed. Minor septa short and contratingent. Horizontal partitions (?tabulae) developed in some genera.

DISCUSSION. A brief resumé of the classification of this group of corals is given by Sutherland & Haugh (1969 : 28). For the moment, Hill's (1956 : 262) interpretation of the Hadrophyllidae is accepted and attention is drawn to the presence of what are probably tabulae in the specimen described below as *Hadrophyllum* sp. and in *Gymnophyllum wardi* Howell (see Sutherland & Haugh 1969 : 35).

Genus *HADROPHYLLUM* Edwards & Haime 1850

1850 *Hadrophyllum* Edwards & Haime: 67.
1851 *Hadrophyllum* Edwards & Haime: 357.
1937 *Hadrophyllum* Bassler: 197.
1952 *Hadrophyllum* Le Maitre: 41.
1955 *Hadrophyllum* Jeffords: 8.
1961 *Hadrophyllum* Fontaine: 69, *cum syn.*

DIAGNOSIS. Discoid to broadly trochoid. Cardinal septum in oval fossula; other cardinal quadrant septa pinnate and sub-parallel, counter quadrant septa more or less radially arranged with a long counter septum. Minor septa short. Horizontal partitions (?tabulae) may be developed.

TYPE SPECIES (by original designation). *Hadrophyllum orbignyi* Edwards & Haime 1851 : 357, pl. 6, figs 4, 4a. Devonian; Charleston Landing, Indiana and Clark County above Louisville, Kentucky, U.S.A.

DISCUSSION. The status of this genus has been discussed by Jeffords (1955 : 8). An amended diagnosis is given here to cover the occurrence of tabula-like structures in the specimen of *Hadrophyllum* described below.

Hadrophyllum sp.

(Pl. 1, fig. 8, Text-fig. 4)

MATERIAL. R49275 (3243). Caño Grande; Caño del Oeste Fm., early Middle Devonian.

Description. Small, broadly trochoid coral with smooth, slightly worn exterior. Calice not seen.

A single section at the ephebic stage shows the lumen largely infilled by thick septa arranged with striking pinnate symmetry. The septa are mostly between 1 and 1·4 mm in thickness peripherally. The counter and alar septa are longest, all three meeting in the axis. In the counter quadrants, the counter-lateral and next four metasepta are roughly equal in length and about three-quarters the length of the counter septum. The fifth and subsequent metasepta in the counter quadrants become progressively shorter and more wedge-shaped against the alar septa. On the cardinal side of the alar septa the first two metasepta are equal in length to the alar septa and the subsequent metasepta become progressively shorter and more wedge-shaped round towards the cardinal septum. The wall of the cardinal fossula appears to be the result of sclerenchyme coating the successive ends of the metasepta in the cardinal quadrants and is not formed by extra long metasepta flanking the short, 3·5 mm long, cardinal septum. Very narrow gaps, about 0·1 mm wide, separate the major septa in the peripheral area of the corallum. In several places the gaps are crossed by narrow bars that are probably tabulae. There are short triangular minor septa, about 1 mm long, inserted between nearly all the major septa. The septal formula is *C6A8K7A8C* at a mean diameter of 13 mm.

No longitudinal section is available.

Discussion. The general characters of this coral agree with those of the genus *Hadrophyllum* although it cannot be readily assigned to any described species. Comparison is made difficult as virtually no other species of *Hadrophyllum* has been

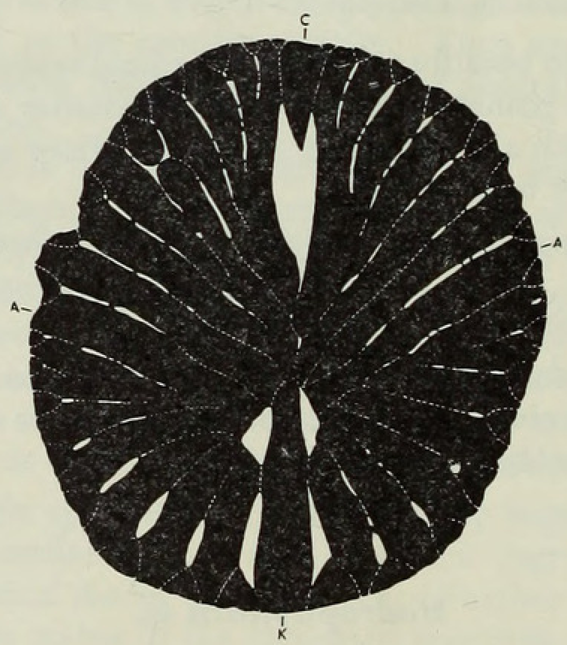


Fig 4. Septal arrangement in *Hadrophyllum* sp. (R49275). ×5.
C = cardinal septum; K = counter septum; A = alar septa.

studied with, or illustrated by, thin sections. The appearance of interseptal structures like tabulae in cross-section has never previously been recorded in a species of *Hadrophyllum* but this may also be due to a lack of thin section study. For example, rare tabulae have recently been recorded in thin sections of another member of the Hadrophyllidae, *Gymnophyllum wardi* Howell, by Sutherland and Haugh (1969 : 35).

Family **HAPSIPHYLLIDAE** Grabau 1928

1956 *Hapsiphyllidae* Hill: 267.
1964 *Hapsiphyllidae* Rowett & Sutherland: 46.

Genus ***AMPLEXIZAPHRENTIS*** Vaughan 1906

1906 *Amplexizaphrentis* Vaughan: 315.
1958 *Amplexizaphrentis* Sutherland: 44.
1962 *Amplexizaphrentis* Armstrong: 30.
1962 *Enniskillenia* Kabakovitch *in* Soshkina & Kabakovitch: 323.
1964 *Amplexizaphrentis* Rowett & Sutherland: 47.

DIAGNOSIS. Small, solitary, trochoid to ceratoid corals in which major septa may or may not unite around a conspicuous cardinal fossula. Septa commonly withdraw from axis in late stages of growth. Alar pseudofossulae usually well developed in early stages, but may become inconspicuous in ephebic stage. Tabulae usually complete, arched or flattened axially except where abruptly depressed in the fossula. No dissepiments. (After Rowett & Sutherland 1964 : 47).

TYPE SPECIES (see Opinion 854, I.C.Z.N. 1968). *Zaphrentis curvulena* Thomson 1881 : 223, 236. Lower Limestone Group, Lower Carboniferous; Brockley, near Lesmahagow, Lanarkshire, Scotland.

DISCUSSION. The status of the genus *Amplexizaphrentis* has been discussed by Sutherland (1958 : 44 *et seq.*) and his conclusions are accepted here. More recently a case to stabilize the generic name and type species was submitted to the I.C.Z.N. by Shrestha (1966), supported by Mitchell (1966) and approved by the Commission in Opinion 854. This effectively answered the comments on the validity of *Amplexizaphrentis* expressed by de Groot (1963 : 39).

According to Rowett & Sutherland (1964 : 51) *Barytichisma* (Moore & Jeffords 1945 : 131) is distinguished from *Amplexizaphrentis* 'primarily on the basis of the unusually wide peripheral stereozone'. They also note in the diagnosis for that genus that the septa are amplexoid and reach the axis immediately above the tabulae only. Weyer (1965 : 450) also laid emphasis on amplexoid septa in *Barytichisma* in maintaining the genus distinct from *Amplexizaphrentis.* If this distinction is accepted, the species described below seems to fall more naturally into *Amplexizaphrentis* than *Barytichisma* despite a tendency to amplexoid septa at all stages of growth. Certainly *A. sutherlandi* sp. nov. does not develop an unusually wide peripheral stereozone.

Amplexizaphrentis sutherlandi sp. nov.

(Pl. 1, figs 9–13, Text-fig. 5)

Derivation of name. After Dr P. K. Sutherland (University of Oklahoma).

Diagnosis. Curved ceratoid *Amplexizaphrentis* with cardinal fossula on concave side of corallum. Major septa thick, tending to amplexoid throughout ontogeny; 34 present in ephebic stage of holotype at 14 mm diameter. Minor septa rudimentary. Tabulae wide, flat with downturned edges, inclined strongly from the counter to cardinal side.

Holotype. R45127 (3784). Caño Colorado; Río Palmar Formation, Lr. Pennsylvanian.

Paratypes. R49291 (3784; ?distal end of holotype), R49292 (3784). Same locality and horizon as holotype.

Description. Curved ceratoid corals up to 60–70 mm long and about 25 mm maximum diameter (estimated because of crushing of the calice). The cardinal fossula is on the concave side of the corallum. Septal grooves weak or absent on a slightly rugate epitheca.

In the early neanic stage (Pl. 1, fig. 10) the septa are short and variably developed with a wide, open lumen. On the cardinal side a tabula is cut, on the upper surface of which the cardinal septum and several metasepta in the left cardinal quadrant are well developed. They are approximately 1·3 mm long and 0·5 mm wide at their bases, the cardinal septum being fractionally longer than the others. No septa can be distinguished in the zone where the tabula is in the plane of section and immediately below the tabula, in the alar areas, the septa are very short and thorn-like. In the counter area the counter septum is short and thin, about 1·3 mm long and 0·1 mm wide expanding to 0·5 mm wide where it merges into the thin peripheral stereozone. The flanking septa are similar in shape but become progressively shorter, from a maximum of 0·8 mm long, towards the alar areas. The mean diameter is 7 mm; 19 septa can be counted but there are probably 22 or 24 present at this level.

In a later neanic section (Pl. 1, fig. 11), approximately 2 mm higher than the first, the septa in the cardinal quadrants are much more strongly developed. The alar septa appear to meet across the axis of the corallum in a continuous band 0·5–0·8 mm thick and the metasepta in the cardinal quadrants are arranged in strongly pinnate groups. The ends of successive metasepta outline a large suboval cardinal fossula bisected by a long waisted cardinal septum extending to the axis. The metasepta in the cardinal quadrants are 0·4–0·6 mm thick peripherally and taper towards the axis. Where tabulae are sectioned, they and the adjacent septa are thickened by about 0·2 mm towards the periphery. In the counter quadrants, the septa are thin short spines as in the previous section. Measurements are difficult as the peripheral stereozone has been removed around much of these quadrants. The mean diameter is 7·5 mm and the septal formula is *C6A4K4A6C*.

In an ephebic stage section (Pl. 1, fig. 9) 14 mm higher (measured centre to centre) than the previous section, the counter quadrants are fully developed. The counter septum 1 mm thick, is thicker than all other septa, which range between 0·5–0·7 mm thick, and reaches into the axial area to meet other septal material. The flanking septa are long and pinnately arranged with their axial ends fused and coated with sclerenchyme to form strong walls parallel to the alar septa and suggesting very weak alar fossulae. The arrangement of the septa in the cardinal quadrants is similar to that described in the previous section except that the alar septa are now of similar aspect to the cardinal metasepta and meet in the axis with an angle of about 120°. The cardinal fossula is more pear shaped and the cardinal septum has shortened to 3–4 mm long (its axial end is damaged). Most of the major septa taper towards the axis but some are slightly rhopaloid and may have very thin needle-like axial extensions from the club-shaped thickening. The peripheral stereozone is 1 mm thick where it is undamaged and slight kinks in it on either side of the counter septum suggest the presence of rudimentary minor septa. The mean diameter is 14 mm and the septal formula is *C6A9K9A6C*.

A section in the ephebic stage of another specimen (R49292) shows all the septa withdrawn from the axis except the metasepta flanking the cardinal septum. These with a considerable thickening of sclerenchyme, outline an oval cardinal fossula bisected by a thin cardinal septum. The diameter is 15 mm with an estimated 38 septa (*C18K?18C*).

In longitudinal section the tabulae are largely complete with few subsidiary plates and a rather irregular spacing. They slope strongly downwards from the counter to the cardinal side with a flat or slightly undulating surface and down-turned peripheral margins. Successive complete tabulae may be as much as 3–4 mm

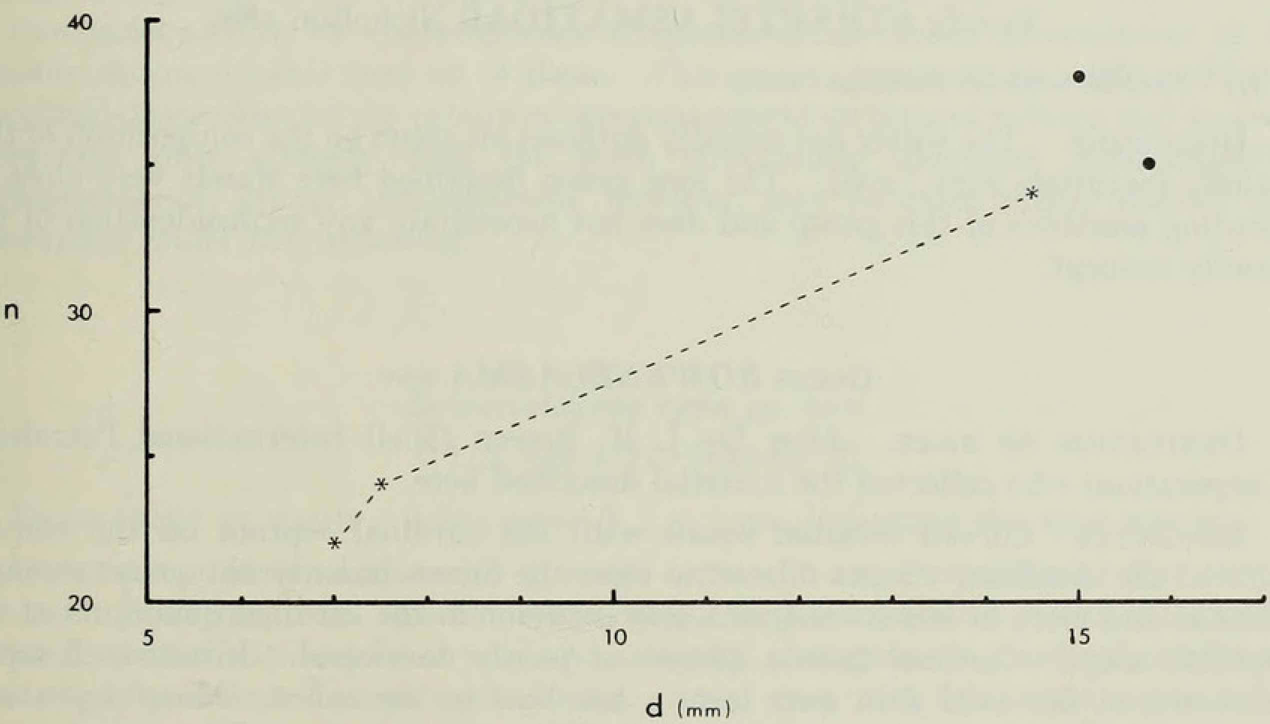


FIG. 5. Number of major septa plotted against diameter for specimens of *Amplexi-zaphrentis sutherlandi*. The dashed line joins asterisks representing different sections of the holotype.

apart during the late neanic-early epebic stages but become much closer-spaced, less than 1 mm at the subcalicular level. The tabulae are extensively crested with septal material in the peripheral areas. This material shows fibres directed axially and upwards at varying angles and growth lines steeply dipping at the periphery, curving round to the horizontal in the axial area. The tabulae in the axial area are coated with sclerenchyme showing a zigzag fibre pattern. Although in some places this appears to be an alteration phenomenon based on the calcite cleavage pattern, in others it appears to be original and could reflect lateral movements in the basal ectoderm of the polyp during calcification (see also Sutherland 1958 : 49). There are no dissepiments.

Discussion. This species seems to compare quite closely with *Amplexizaphrentis cassa* Sutherland (1958 : 54, pl. 8, figs 1–5, pl. 10, figs 1–4) from the middle Mississippian Kindle Formation of the Tetsa River area, and particularly closely with *A.* sp. B (Sutherland 1958 : 57, pl. 11, figs 1–5) from the Prophet Formation (?early Mississippian) of the Prophet-Muskwa Rivers area, both British Columbia. *A. sutherlandi* is distinguished by the thickness of its septa, its large size and a slightly higher septal ratio than *A. cassa.* In these features, however, it approaches very closely to *A.* sp. B of Sutherland although the cardinal fossula in the latter may be larger in proportion. The age of the Río Palmar Formation appears to be lower Pennsylvanian and thus *A. sutherlandi* is somewhat younger than either of the Canadian species.

Superfamily **ZAPHRENTICAE** Edwards & Haime 1850
Family **STREPTELASMATIDAE** Nicholson 1889

1971 *Streptelasmatidae* Scrutton: 206.

Discussion. The writer has recently outlined his views on the composition of this family (Scrutton 1971 : 206). The new genus described here stands very close to existing members of this group and does not necessitate any reconsideration of the family concept.

Genus ***BOWENELASMA*** nov.

Derivation of name. After Dr J. M. Bowen (Shell International Petroleum Corporation) who collected the material described here.

Diagnosis. Curved ceratoid corals with the cardinal septum on the convex side of the corallum. Septa dilated to close the lumen in early ontogeny; strongly dilated and more or less coated with sclerenchyme in the cardinal quadrants at the ephebic stage. Cardinal fossula narrow or poorly developed. Intertwined septal elements in the axial area may form a low boss in the calice. Minor septa well developed. Tabulae steeply sloping axially and upwards at the periphery, undulating or highly domed in the axial area. No dissepiments.

Type species. *Bowenelasma typa* sp. nov.

DISCUSSION. *Bowenelasma* is recorded so far only from the early Middle Devonian of Venezuela. The genus is distinguished first and foremost by the strong, consistent dilatation and thickening of the cardinal quadrant septa in the later, but subcalicular, ontogenic stages. This feature appears occasionally in other streptelasmatid corals and it is also characteristic of the genus *Pseudophaulactis* Zaprudskaya in Ivanovskii (1963 : 32, pl. 6, fig. 2) from the Llandovery of the Siberian Platform. *Bowenelasma* and *Pseudophaulactis* are very similar in appearance, the latter differing only in the very attenuate nature of the septa in the counter quadrants and the general lack of twisted septal ends in the axial area (see Ivanovskii 1965, pls 5, 6 and 7, fig. 1). It should also be noted, however, that the two genera are widely separated stratigraphically and geographically.

Species of other streptelasmatid genera occasionally show significantly prolonged dilatation and thickening in the cardinal quadrants during ontogeny as a specific character or a subspecific variant. They include *Kiaerophyllum semilunatum* Scheffen (1933 : 21, pl. 2, figs 4–6) from the Upper Ordovician of the Oslo region which is considered a variant of *Grewingkia buceros* according to Neuman (1969 : 36), *Grewingkia europaeum hosholmensis* Kaljo (1961 : 58, pl. 3) from the Upper Ordovician of Estonia and the specimen identified as *Dalmanophyllum dalmani* by Ivanovskii (1963 : 36, pl. 7, fig. 4) (= *Ditoecholasma dalmani* in Ivanovskii 1965, pl. 1, fig. 6) from the Llandovery of the Siberian Platform. All these are considerably older than the new Devonian genus. *Bowenelasma* is clearly not congeneric with *Grewingkia*, which is principally distinguished by its wide spongy axial structure (Neuman 1969 : 35). *Bowenelasma* also lacks the distinctive blade-like columella so prominent in illustrations of the type species of *Dalmanophyllum* (Edwards & Haime's 1851, pl. 1, fig. 6; Minato 1961, pl. 11, figs 16, 3c, 5b).

Comparison with its contemporary streptelasmatids shows *Bowenlasma* to be readily distinguishable from all of them. This genus appears to be a late and little modified descendant of the primitive streptelasmatid structural pattern and as such contrasts quite strongly with the more structurally divergent *Heterophrentis*/*Siphonophrentis* group. *Briantelasma*, however, may be more closely related (see discussion under *Briantelasma*).

Bowenelasma typa sp. nov.

(Pl. 2, figs 1–11, Text-fig. 6)

DERIVATION OF NAME. From *typus* (L.) = type, indicating the type species.

DIAGNOSIS. *Bowenelasma* with 45 major septa at a mean subcalicular diameter of 27 mm (holotype). In ephebic stage, major septa four-fifths radius in length, dilated, coated with sclerenchyme and laterally contiguous in cardinal quadrants and slightly deflected counter-clockwise. Axial area with few septal ends intertwined to form low calicular boss. Minor septa up to one-quarter radius in length. Cardinal septum short in narrow fossula. Tabulae simple, convex, steeply sloping upwards and axially at periphery, obscured in axis but apparently gently undulating.

Holotype. R45094 (3149). Caño Grande; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

Paratypes. R45075, R45077 (both 3121), R45100 (3157); same locality and horizon as holotype. R45121 (3618); Caño Colorado; same horizon as holotype.

Other material. R45082, R49247–9, R49251 (all 3121), R49263 (3157); same locality and horizon as holotype. R45118 (3618), Caño Colorado; R45279 (3323), loose boulder on Caño del Oeste; both same horizon as holotype.

Description. Curved ceratoid corals up to about 90 mm long and 27 mm mean diameter at the subcalicular level. The cardinal septum is located on the convex side of the corallum. The epitheca is lightly rugate with weak septal grooves.

In the neanic stage (Pl. 2, fig. 4), the lumen is almost completely infilled by thick, irregularly pinnate septa. The major septa are between 0·6–0·7 mm thick near the periphery and taper towards the axis, contiguous with their neighbours over most of their length. Major septa in the counter and alar sectors, 3·0–3·5 mm long, reach into the axial area where they fuse and almost completely fill the lumen. The other septa wedge against these. The cardinal septum is about 1·3 mm long. Minor septa are present as very short wedges 0·7–1·0 mm long, nearly always with very small openings in the lumen beyond their axial ends. The counter septum is flanked by extra long (1·7 mm) minor septa. There are also small openings in the lumen periaxially, beyond the axial end of the cardinal septum and on the counter side of one of the alar septa. The septal formula is $C3A5K5A4C$ at a mean diameter of 7 mm.

Sections in the late neanic stage of the holotype (R45094c–d, Pl. 2, fig. 2) show major septa of very variable length twisted in a wide counter-clockwise axial vortex. Most of the major septa are 0·3–0·4 mm wide and half the radius in length. Only a few irregular septal ends cross the axial area where there may also be a few isolated spots of septal tissue. The cardinal septum is short and heavily invested with sclerenchyme. Some of the other septa in the cardinal quadrants also appear to be thickened but there is no marked contrast with the septa in the counter quadrants at this level. Minor septa cannot be easily distinguished in the wider parts of the very irregularly developed peripheral stereozone. Some of them appear to reach 2·5 mm in length and the stereozone may be up to 4 mm wide. There are 38 septa at a mean diameter of 17 mm.

In the ephebic stage (Pl. 2, fig. 1) there is a strong contrast between cardinal and counter quadrants. In both the major septa extend four-fifths of the distance to the axis and are twisted in a weak counter-clockwise vortex. Those in the cardinal quadrants however are between 1·1–1·4 mm thick and laterally contiguous for most of their length, whilst those in the counter quadrants are only 0·25–0·35 mm across and more or less parallel sided. The cardinal septum, also contiguous with its neighbours, is 5·5 mm long and situated in a weak narrow fossula closed on the axial side by a tabula and converging septa. The axial area of the coral, about a fifth of the diameter across, is traversed by two or three septal strands and traces of tabulae. There may also be a few isolated spots of septal tissue. In R45077b there is evidence that this structure in the axial area may produce a low boss in the floor of the calice. Minor septa are also well developed, as wedges of variable size up to 1·5 mm across at the base and 3·5 mm long in the cardinal quadrants and as thin spines projecting up to 2 mm beyond the peripheral stereozone in the counter quadrants. The minor septa flanking the counter septum are markedly longer than their neighbours but measurement is difficult as this part of the coral is nearly always crushed. The peripheral stereozone in the counter quadrants is quite thin, only about 1 mm thick. In the holotype, the septal formula is *C*10*A*13*K*10*A*8*C* at a mean diameter of 27 mm.

At subcalicular levels, the septa in the cardinal quadrants thin and separate from their neighbours first on the axial side of the minor septa. The cardinal septum thins most rapidly leaving a narrow, parallel sided fossula which it bisects. It maintains a length of about half the radius whilst the septa in the cardinal quadrants are still somewhat thicker than those in the counter quadrants but at slightly higher levels it rapidly withdraws to about a fifth of the radius in length. In a paratype, R45121a (Pl. 2, fig. 10), the minor septa flanking the counter septum are about 5·5 mm long at this level and the septal formula is *C*10*A*12*K*12*A*9*C* at a mean diameter of 28 mm.

The longitudinal section is dominated by septal traces and the shape of the tabulae is difficult to see. At both walls there are thick solid septal deposits, rather irregularly developed but much more pronounced on the cardinal side. In the axial area individual septal traces form a complex and irregular pattern breaking up and obscuring the tabulae. The tabulae can be clearly seen in the peripheral areas, slightly convex, moderately spaced and sloping axially and upward at 5–20° to the wall. In the axial area, the tabulae appear to be gently undulating and in one case (Pl. 2, fig. 6) sloping distinctly downward from the cardinal to the counter side. The angle of slope is difficult to assess but appears to be as much as 45° in some cases.

Measurements on the holotype and paratypes are plotted in Text-fig. 6.

Discussion. The only species so far assigned to *Bowenelasma* are the two species from the Sierra de Perijá described here. The type species, *B. typa*, which is the more abundant by a factor of three in Bowen's collection, is compared with *B. breviseptata* under the discussion of the latter species.

Bowenelasma breviseptata sp. nov.

(Pl. 3, figs 1–7; Text-fig. 6)

Derivation of name. From *brevis* (L) = short + septum, in reference to the characteristically short major septa.

Diagnosis. *Bowenelasma* with 43 major septa at a mean subcalicular diameter of 33 mm (holotype). In ephebic stage, major septa half radius in length, cardinal quadrants heavily coated with sclerenchyme peripherally. Cardinal septum very slightly longer than adjacent metasepta; no fossula developed. Wide axial area partially filled by thickened and twisted septal ends. Minor septa up to one-third radius in length. Tabulae simple, convex, steeply sloping upwards and axially at the periphery, domed in the axis or obscured by septal traces.

Holotype. R45123 (3619). Caño Colorado; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

Paratype. R45125 (3619). Same locality and horizon as holotype.

Other material. R45105 (3199), Caño del Sur; ? R49256 (3154), Caño Grande; both same horizon as holotype.

Description. Large curved ceratoid corals with the cardinal septum located in the convex side of the corallum. Estimated original length of holotype 80–90 mm. The epitheca has weak septal grooves and is gently rugate.

The late neanic stages (Pl. 3, fig. 3) are largely infilled by major septa up to 1·7 mm thick and laterally contiguous along most of their length. The major septa are two-thirds the radius in length leaving a wide axial zone mostly infilled by loosely and irregularly twisted septal elements. The cardinal septum is only just over one-third the radius in length with a gap in the lumen beyond its axial end: the other protosepta cannot be distinguished. The minor septa are well developed wedges up to 5 mm long and 1 mm or a little more across the base.

In the ephebic stage (Pl. 3, fig. 1) septal thickening is confined to the cardinal quadrants. The septa are about half the radius in length with a slight anticlockwise displacement. In the cardinal quadrants the peripheral half to three-quarters of the septa are thickened to about 2 mm across bringing adjacent septa into contact.

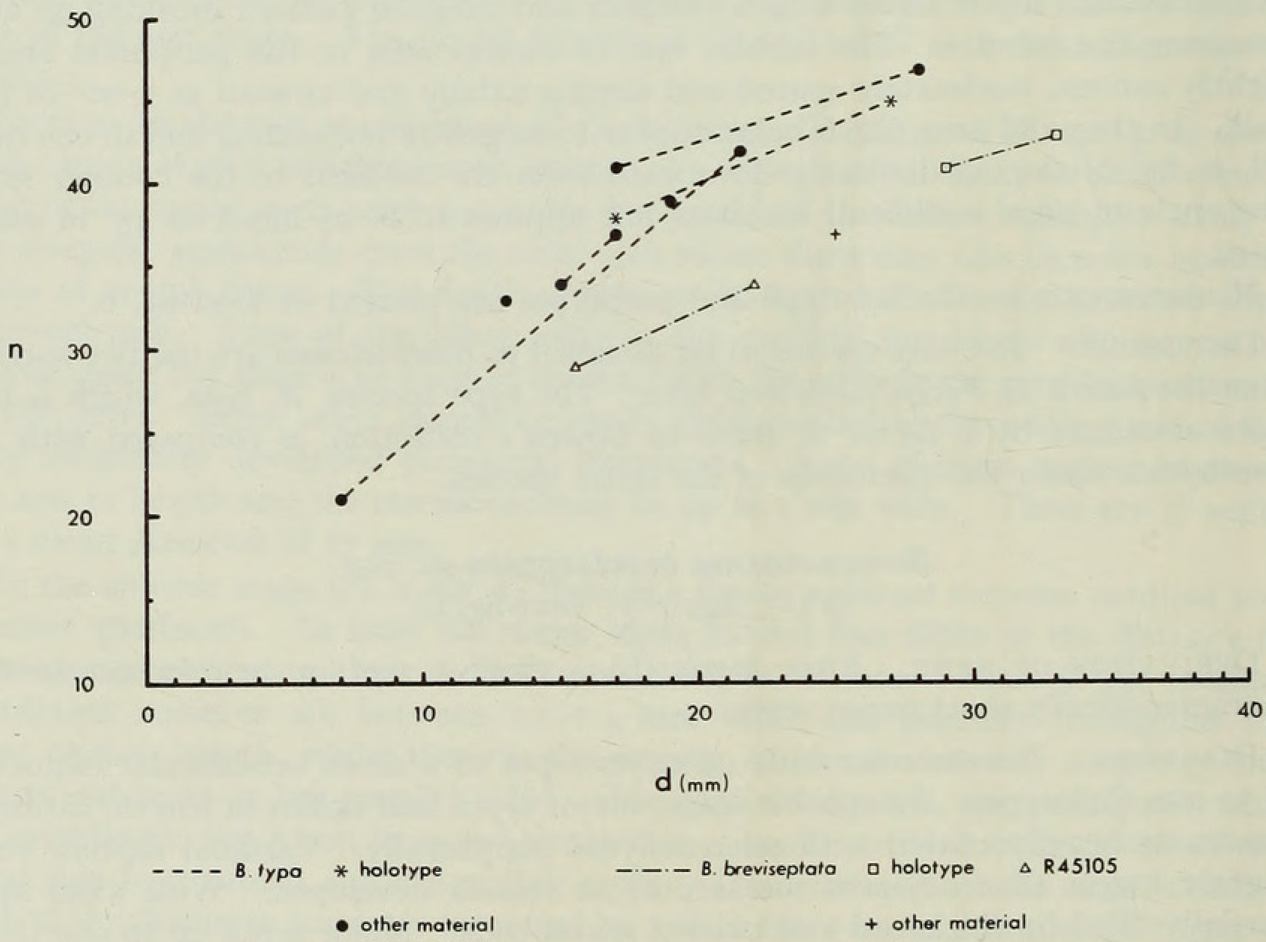


Fig. 6. Number of major septa plotted against diameter for specimens of *Bowenelasma typa* and *B. breviseptata*.

Otherwise the septa are between 0·6 and 0·7 mm across and parallel sided in both quadrants. The cardinal septum is slightly longer than adjacent metasepta with the peripheral dilatation imperfect; there is no cardinal fossula. In the axial half of the diameter, septal elements are loosely and irregularly twisted together and thickened in part. This structure forms a low boss in the floor of the calice. The minor septa are very long, and regularly developed reaching 5 mm or a third of the radius in length. Unfortunately those flanking the counter septum cannot be seen in the holotype due to crushing in this area. The minor septa are wedge-shaped in the cardinal quadrants and parallel sided to gently tapering, 0·5–1·0 mm across in the counter quadrants. The peripheral stereozone in the counter quadrants appears to be thin but is everywhere worn and cannot be measured.

R45105 (Pl. 3, figs 5–7) differs somewhat from the other specimens through its septa being generally less thickened. The section of the neanic stage available (Pl. 3, fig. 5) shows no lateral contiguity between septa. In the ephebic stage the septa are only slightly thicker in the cardinal quadrants than the counter quadrants, although the cardinal septum itself is notably thick at 1·2 mm across. The minor septa are up to 4·4 mm or two-fifths the radius in length and slightly variable in development. The septal formula is $C6A9K9A5C$ at a diameter of 22 mm.

The longitudinal section of the holotype (Pl. 3, fig. 4) is dominated by septal traces and the peripheral stereozone. The latter is particularly thick on the cardinal side. Traces of tabulae can be seen in the peripheral areas, sloping steeply axially and upwards but they cannot be identified in the axial area among the irregular vertical sections of septal elements. In R45105d (Pl. 3, fig. 7), however, the structure is very clear. The tabulae consist of large curved plates, convex upwards and outwards. They form a high axial dome and are almost vertical peripherally where they form a narrow trough against the peripheral stereozone. They are irregularly spaced between 1 and 2·5 mm vertically.

Measurements are plotted in Text-fig. 6.

Discussion. At present it is not certain how much weight should be given to the differences between R45105 and the holotype. R45105 is considered conspecific with *Bowenelasma breviseptata* here although with more material and a better understanding of the variation it may prove to be subspecifically or even specifically distinct.

B. breviseptata is distinguished from *B. typa* principally through the much shorter major septa in the mature stages and the lower septal number at comparable diameters. *B. breviseptata* also has more strongly developed minor septa and lacks any clear sign of a cardinal fossula.

Genus ***BRIANTELASMA*** Oliver 1960

1960a *Briantelasma* Oliver: 89.
1960b *Briantelasma* Oliver: 6.
1963 *Briantelasma* Oliver: 26.

Diagnosis. Trochoid to cylindrical corals with subpinnately arranged major septa extending half way or more to the axis. Lumen partly or completely infilled by laterally contiguous septa and axial sclerenchyme especially in early growth stages. Cardinal fossula present. Minor septa usually well developed. Tabulae strongly domed with axial depression, complete and closely spaced. (Based on Oliver 1960b : 6.)

Type species (by original designation). *Briantelasma americanum* Oliver 1960 : 89, pl. 14, figs 1–4. Reef facies of Coeymans Limestone, Helderbergian, Lower Devonian; Madison and Oneida Counties, New York.

Discussion. The writer follows Oliver (1960b : 6) in regarding *Briantelasma* as a member of the Streptelasmatidae in which the structural elements are completely invested in sclerenchyme during almost the full ontogeny. The ancestors of *Briantelasma* could well belong to the same lineage that evolved *Bowenelasma* as there are similarities in the basic structural patterns of the two genera. They differ principally, and very obviously, in the manner and extent of the development of sclerenchyme and also in the detailed appearance of the tabularium and the peripheral stereozone. There is no doubt that they represent distinct and divergent genera over their presently known range.

Briantelasma oliveri sp. nov

(Pl. 4, figs 1–7; Text-figs 7, 8)

Derivation of name. After Dr W. A. Oliver, Jr. (United States Geological Survey).

Diagnosis. Ceratoid to trochoid *Briantelasma* of variable size up to 39 mm diameter with 60 major septa in the holotype. Lumen completely infilled by septa and sclerenchyme to immediately sub-calicular levels. Major septa withdraw from axis to approximately half radius in length in ephebic stage. Axis plugged by structureless to vermiform loops of sclerenchyme which persists as low boss in calice. Minor septa up to one-quarter radius in length. Tabulae present in floor of calice; not distinguished in sclerenchyme.

Holotype. R45090 (3129). Caño Grande; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

Paratypes. R45091 (3129); same locality and horizon as holotype. R45119 (3618); Caño Colorado, same horizon as holotype.

Other material. ? R45099 (3157); same locality and horizon as holotype. ? R49290 (3618); Caño Colorado, same horizon as holotype. ? PRI 24426 (= 24433); ? loose block in Caño del Oeste, same horizon as holotype. ? PRI 24429 (= 24430A); same locality and horizon as holotype. ? PRI 24430B; ? locality of holotype or PRI 24426, same horizon as holotype.

Description. Ceratoid to trochoid, straight to slightly horn shaped corals up to 40 mm diameter at the base of the calice and an estimated 100 mm long. The holotype, which is the longest specimen, is incomplete and has a crushed calice. The cardinal septum is on the convex side in curved coralla. Epitheca moderately rugate and bearing weak septal grooves.

In the neanic section R45091a (Pl. 4, fig. 5) the lumen is completely or almost completely infilled by laterally contiguous septa and axial sclerenchyme. The major septa vary between half and the full radius in length and their axial ends merge into the sclerenchyme almost completely infilling the axis. They are between 0·6 and 0·7 mm in width and contiguous with their neighbours except for occasional narrow gaps between one-quarter and one-third the radius from the periphery, probably on the axial side of wedge-shaped minor septa. These minor septa are extremely difficult to distinguish but appear to be present only in the counter quadrants. There is a slight pinnate septal symmetry but again difficult to distinguish mainly due to the character of the preservation. The septal formula is *C6A8K9A6C* at a mean diameter of 10 mm.

In the ephebic stage (Pl. 4, figs 3, 6), the laterally contiguous major septa are very evenly developed 0·5 to 0·6 of the radius in length. With the exception of a few specific major septa, they all have open axial ends merging with a solid axial core of sclerenchyme which is either more or less structureless or contains a large scale vermiform pattern (R45119a, b). The septal pattern in the holotype is illustrated in Text-fig. 7. The counter septum, which is fractionally wider and longer than the average, 1·5 mm × 11 mm in the holotype, is characteristically flanked by counter-lateral septa slightly shorter than the average and with closed axial ends. Some septa in the alar areas, particularly new metasepta appearing immediately on the counter side of the alar septa are also less than average length and have closed axial ends. The cardinal septum, which is difficult to distinguish, appears to be about average length and is flanked by shorter metasepta with the next adjacent meta-septa curved slightly towards the cardinal septum at their axial ends. Minor septa are well developed wedges up to a maximum of one-quarter the radius in length.

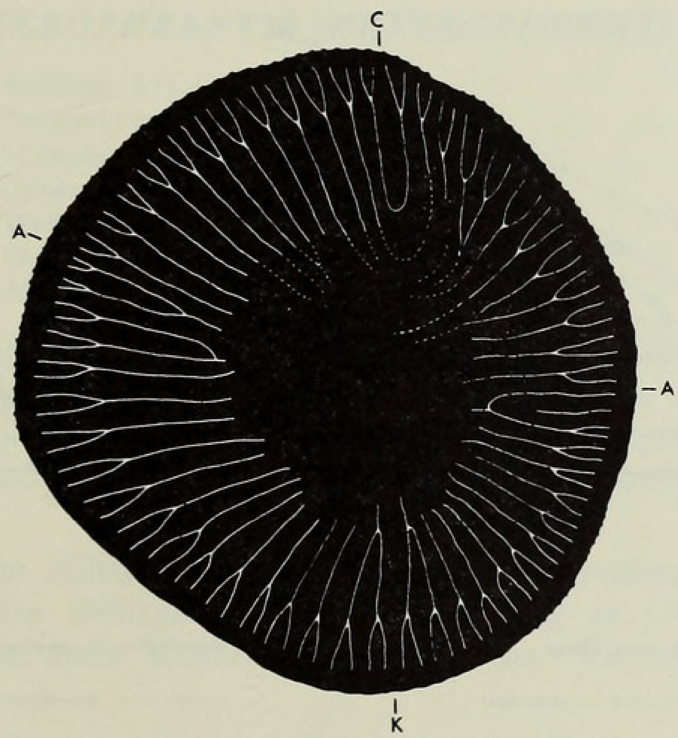


FIG. 7. Septal arrangement in *Briantelasma oliveri* (R45090a). ×2.
C = cardinal septum; K = counter septum; A = alar septa.

The lumen is totally infilled. The septal formula is *C*10*A*13*K*15*A*10*C* at a mean diameter of 23 mm in R45091b

Close to the base of the calice (Pl. 4, fig. 1) an opening first appears on the axial side of the cardinal septum which shortens rapidly at this level. A narrow elongate or sub-oval fossula is formed. Subsequently gaps appear between the major septa on the axial side of the minor septa and rapidly enlarge. The septa appear to thin almost simultaneously in all quadrants; contrasted thickening in various quadrants at this level is due to sections slightly angled to the growth lines. As the major septa withdraw to the periphery, with gently tapered axial ends, the axial plug of sclerenchyme is isolated briefly as a low mound in the calice base. At this level in the holotype, there is a peripheral stereozone 4 mm wide at a mean diameter of 39 mm. The stereozone thins in the walls of the calice and the minor septa project from it, thin and narrowly attenuate.

In longitudinal sections (Pl. 4, fig. 4), there is evidence of some gaps in between the septa and sclerenchyme at the neanic stage and in the cardinal area at later stages. Two such gaps in the cardinal area occur in the longitudinal section of the holotype (R45090e) and show signs of tabulae trough shaped against the peripheral stereozone and capped by flat subsidiary tabulae. The septa and sclerenchyme show a strongly developed grain shallowy arched across the axis and sharply down turned towards the peripheral trough-shaped tabulae. This may reflect the shape of

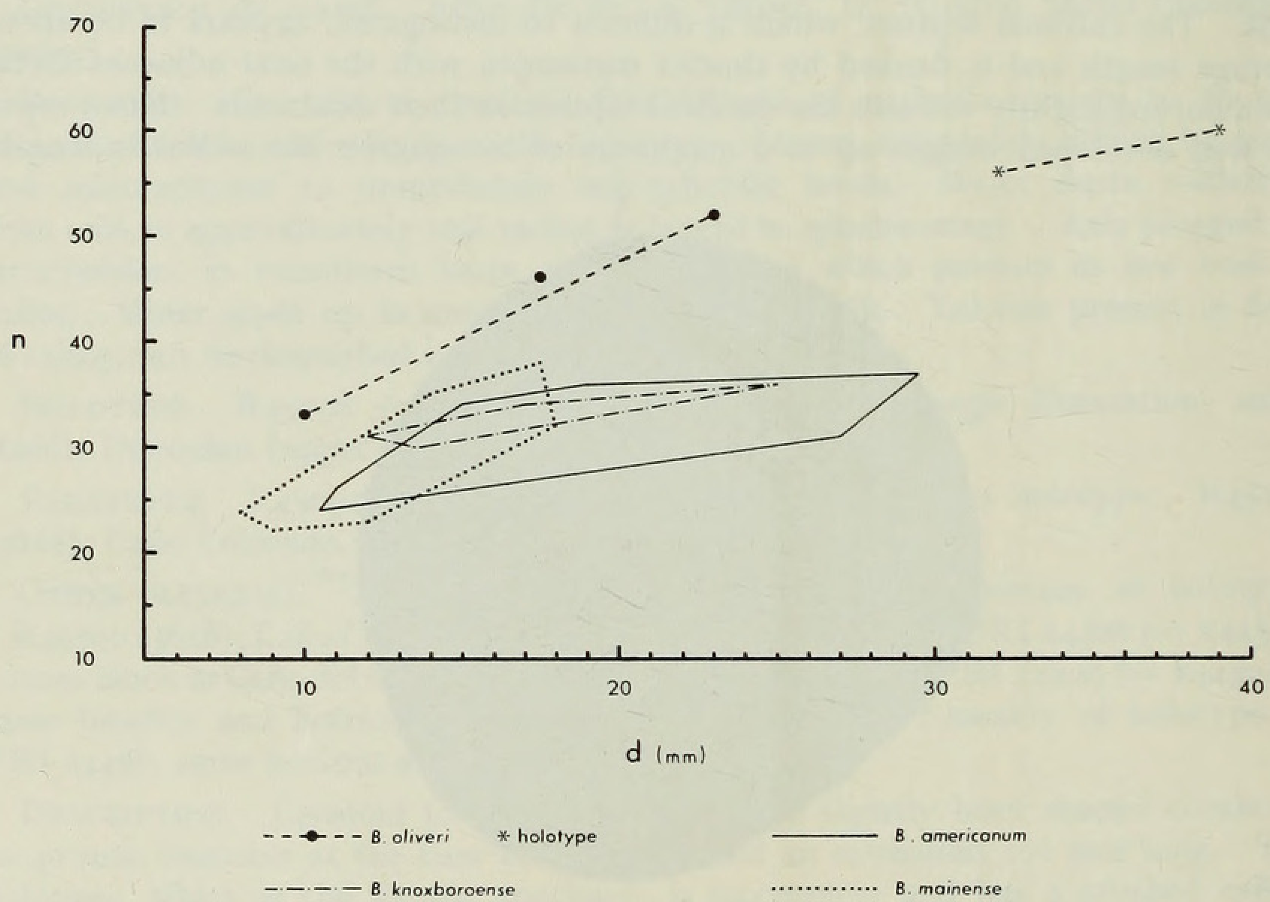


FIG. 8. Number of major septa plotted against diameter for specimens of *Briantelasma oliveri*. The polygons outline the **n**/**d** variation fields for other species of *Briantelasma*.

tabulae suppressed, or obscured in the sclerenchyme. Unfortunately no longitudinal section is available through the base of the calice, where tabulae are known to be developed, to support this.

Measurements on the holotype and paratypes are plotted in Text-fig. 8. There is a considerable variation in size, basal calice diameters ranging from 15·5 mm to 39 mm.

DISCUSSION. Previous records of *Briantelasma* come from Silurian (? Wenlock) and Lower Devonian (Helderberg) rocks in eastern North America. *Briantelasma oliveri*, from the early Middle Devonian of the Sierra de Perijá, thus considerably extends the known range of the genus. The new species can be distinguished from all earlier described species of *Briantelasma* through the major septa withdrawing from the axis in the ephebic stage. Also, over the ontogenetic range available, *B. oliveri* lies wholly outside the fields of variation in septal number with diameter shown by the other species (see Text-fig. 8). It has higher septal ratios at corresponding diameters and reaches a higher maximum diameter than the North American species.

Genus ***HETEROPHRENTIS*** Billings 1875

DISCUSSION. Oliver (1958 : 817, 825) suggested that *Compressiphyllum* Stumm (1949 : 13), which differs from *Heterophrentis s.s.* only through a pronounced compression of the corallum at right angles to the counter-cardinal plane, was best considered as a subgenus of *Heterophrentis*.

Subgenus ***HETEROPHRENTIS (HETEROPHRENTIS)*** Billings 1875

1875 *Heterophrentis* Billings: 235.
1938 *Heterophrentis* Stewart: 20.
1949 *Heterophrentis* Stumm: 11.
1958 *Heterophrentis* (*Heterophrentis*) Oliver: 825.
?1964 *Heterophrentis* Webby: 7.
1965 *Heterophrentis* Stumm: 18.
1968 *Heterophrentis* Altevogt: 762.

DIAGNOSIS. Ceratoid to trochoid corals, circular in cross-section. Septa thin throughout ontogeny; major reach more or less to axis, minor up to one-third radius in ephebic stage; peripheral stereozone variable in thickness. Cardinal fossula prominent. Tabulae complete or incomplete, flat axially, arched peripherally. No dissepiments.

TYPE SPECIES (see Miller 1889 : 193). *Zaphrentis spatiosa* Billings 1858 : 178 = *Zaphrentis prolifica* Billings 1858 : 176 (according to O'Connell 1914 : 183). Onondaga Limestone, early Middle Devonian; Rama's Farm, near Port Colborne, Ontario, Canada.

DISCUSSION. Numerous species of *Heterophrentis* (*H.*) have been described and the scope of the subgenus is reasonably well defined despite the fact that, according to Sutherland (1958 : 45), the original specimens of neither *Z. spatiosa,* nor *Z. prolifica* have been sectioned. The traditional interpretation of the subgenus is followed here and would surely need to be stabilised even if *Z. spatiosa* proved not to have the characters attributed to *Heterophrentis* (*H.*).

Heterophrentis (*H.*) is common in the Lower and Middle Devonian of eastern North America. The subgenus has also been recorded in the Middle Devonian of Spain and north-west Africa and is confirmed here in the early Middle Devonian of Venezuela.

Heterophrentis (Heterophrentis) venezuelensis (Weisbord 1926)

(Pl. 5, figs 1, 2)

1926 *Cyathophyllum venezuelense* Weisbord: 4 *pars.*, pl. 1, fig. 5 only.
1943 *Heterophrentis venezuelensis* (Weisbord) Wells: 97 *pars.*, pl. 10, fig. 7 only.

Diagnosis. *Heterophrentis* (*H.*) with major septa two-thirds radius in ephebic stage, tapering axially; about 64 at 33 mm mean diameter in lectotype. Wide axial area occupied by tabulae only. Minor septa confined to peripheral stereozone one-quarter radius in width. Cardinal fossula present but weak. Tabulae mainly complete, gently undulating to depressed axially, sharply downturned peripherally, very close spaced beneath calice floor.

Lectotype (here chosen). PRI 21594 (= PRI 24421, same specimen). Loose block (?) in Caño del Norte; Caño Grande Fm., early Middle Devonian (upper Onesquethaw).

Description. The lectotype is an incomplete curved conical coral 80 mm high between a diameter of 23 mm and the top of the calice. The epitheca is lightly rugate. The counter-cardinal plane is at right angles to the plane of curvature.

In the ephebic stage, 10 to 15 mm below the base of the calice, the major septa are regularly developed, 9–10 mm or two-thirds the radius in length. They are between 1 and 1·3 mm thick at the edge of the peripheral stereozone and taper gently towards the axis. Their arrangement is more or less radial except near the cardinal septum which is flanked on either side by three or four shorter metasepta and fronted axially by the concave side of a tabula. The cardinal septum itself cannot be easily distinguished but may be slightly longer than the flanking metasepta. The axial area of the corallum contains sections of tabulae but no septal material. The peripheral stereozone is between 3·5 and 4 mm wide which is also the length of the wedge shaped minor septa. There are at least 60 and an estimated 64 major septa at a mean diameter of about 33 mm and thus a septal ratio of about 1·94.

In longitudinal section, the tabulae are mainly complete and spaced about 1 mm or slightly less apart at the subcalicular level. Towards the proximal end, the spacing becomes wider and less regular. The tabulae are gently undulating or very slightly depressed across the axial area and are sharply downturned peripherally.

They appear to be inclined downwards from the convex to the concave side of the corallum. Subsidiary tabulae occur mainly on the periphery of the wide axial plateau formed by the complete tabulae. Evidence from the cross-section suggests that the tabulae are depressed in the cardinal fossula. Many tabulae have signs of septa strongly developed on their upper surfaces and some tabulae are thickly coated with septal deposits. The closer spaced tabulae in the 6–7 mm below the calice floor, however, are not affected in this way.

DISCUSSION. The syntypes of *Cyathophyllum venezuelense* Weisbord and the additional specimens assigned to the species by Wells when he redescribed it as *Heterophrentis venezuelensis* have been re-examined with the aid of a number of new slices from which acetate peels have been prepared. No less than five species and four genera are thought to be represented. Only two of the original syntypes are species of *Heterophrentis* and these are not conspecific. One, PRI 21594 (= PRI 24421), has been selected as the lectotype and only known example of *H.* (*H.*) *venezuelensis* and is the specimen described above. The other, PRI 21593, is a specimen of *H.* (*H.*) *simplex* (Hall) and is described below. The only additional material of either species among Bowen's collection is a single specimen assigned to *H.* (*H.*) *simplex*. Of the other syntypes PRI 21592 (Weisbord 1926, pl. 1, fig. 1) is probably *Bowenelasma typa*, and PRI 21791 (Weisbord 1926, pl. 1, fig. 4) is *Heliophyllum halli*. Of the additional material studied by Wells, PRI 24426 (two thin sections cut from PRI 24433 and figured by Wells 1943, pl. 10, figs 8, 9), PRI 24429 (cut from PRI 24430A) and PRI 24430B are all questionably assigned to *Briantelasma oliveri*. Wells (1943 : 98) did observe that *Heterophrentis venezuelensis* as then understood would probably prove, with the study of additional material, to contain more than one species.

Heterophrentis (*H.*) *venezuelensis* is difficult to compare with the many species of *Heterophrentis* (*H.*) named from the Devonian of North America as very few comprehensive illustrations and descriptions for these species exist. Furthermore, the Venezuelan species is represented only by the lectotype so that its range of variation is unknown. As far as can be determined at the moment, the major septa are comparatively short in *H.* (*H.*) *venezuelensis*, with a weak cardinal fossula and minor septa confined to a well developed peripheral stereozone. This appears to distinguish the species, at least from *H.* (*H.*) *prolifica* (Billings) and *H.* (*H.*) *spissa* (Hall), the two species with which Wells (1943 : 98) chiefly compared *H.* (*H.*) *venezuelensis*. Stumm (1965 : 20) considered *H.* (*H.*) *spissa* conspecific with *H.* (*H.*) *inflata* (Hall) which he suggested in turn might be a junior synonym of *H.* (*H.*) *prolifica*. All these 'species' appear to be characteristic of the early Middle Devonian in eastern North America. *H.* (*H.*) *venezuelensis* certainly appears to differ markedly from the holotype of *H.* (*H.*) *inflata* illustrated by Stumm (1965, pl. 4, figs 11, 12). As noted above the writer believes that *H.* (*H.*) *simplex*, a third species compared with *H.* (*H.*) *venezuelensis* by Wells (1943 : 98), is actually represented by a single specimen among the syntypes. This specimen and the holotype of *H.* (*H.*) *simplex* are figured here (Pl. 5, figs 3–5) and described below. They can be seen to contrast strongly with the lectotype of *H.* (*H.*) *venezuelensis*.

Heterophrentis (Heterophrentis) simplex (Hall) 1843
(Pl. 5, figs 3–5; Text-fig. 9)

1843 *Strombodes simplex* Hall: 210, text-fig. 87, 6 on p. 209, no. 48, fig. 6 on p. 44 of tables.
1876 *Zaphrentis simplex* (Hall) Hall *pars*, pl. 21, figs 5, 8–10 (*non* figs 6, 7, 11).
1926 *Cyathophyllum venezuelense* Weisbord: 4 *pars*, pl. 1, figs 2, 3 only.
?1938 *Heterophrentis simplex* (Hall) Stewart: 23, pl. 2, figs 5–7.
1965 *Heterophrentis simplex* (Hall); Stumm: 21, ?*pars*, pl. 11, fig. 19, pl. 14, figs 5, 6.
?1968 *Heterophrentis simplex* (Hall); Stumm: 38, pl. 1, figs 6, 7.

DIAGNOSIS. Ceratoid *Heterophrentis* (*H.*). Major septa three-quarters radius in ephebic stage, thin and tapering axially with a very slight counter-clockwise deflection in axis. Cardinal septum short in suboval fossula. Minor septa one quarter radius in length, confined to or more commonly projecting from variably developed peripheral stereozone.

HOLOTYPE. NYSM 360. Middle Devonian, Hamilton Group; Moscow, New York.

OTHER MATERIAL. PRI 21593. Loose block (?) in Caño del Norte; Caño Grande Fm., early Middle Devonian (upper Onesquethaw). R49293 (3849). Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian (upper Onesquethaw).

DISTRIBUTION. Middle Devonian, Hamilton Group of New York, U.S.A. and equivalent horizons elsewhere in eastern North America; early Middle Devonian of Sierra de Perijá, Venezuela.

DESCRIPTION. The Venezuelan specimens are slightly curved incomplete ceratoid corals lacking the proximal end.

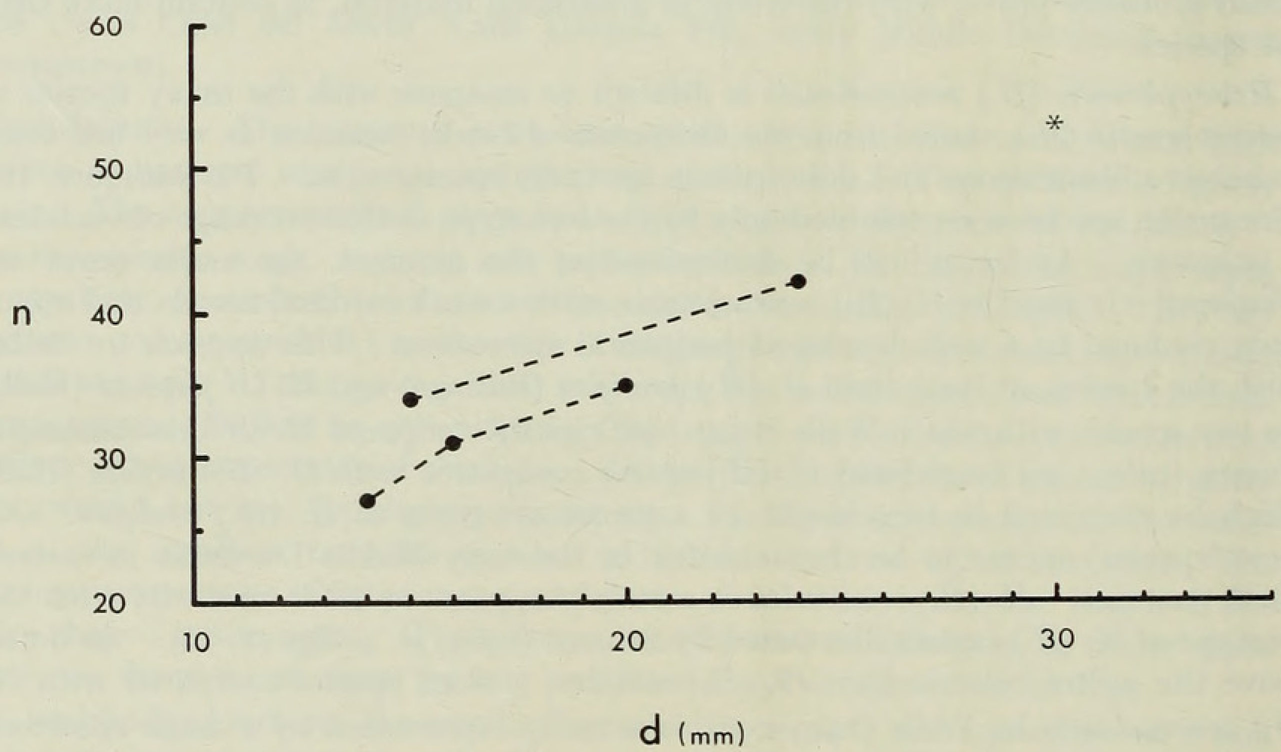


FIG. 9. Number of major septa plotted against diameter for specimens of *Heterophrentis* (*H.*) *simplex*. The holotype is indicated by an asterisk. The dashed lines join points representing different sections of the same specimen.

In the neanic stage of PRI 21593 (Pl. 5, fig. 4), the lumen is partially infilled by major septa between 0·8 and 1·0 mm thick, parallel sided and with blunt axial ends. These septa are mostly laterally contiguous along the axial third of their length where they are involved in a weak counter-clockwise vortex. A small area in the axis is free of septal material. The cardinal septum is short, 3·5 mm or half the radius in length, and flanked by short curved metasepta concave towards the cardinal septum. Towards the periphery the major septa are separated by narrow, parallel sided, ovoid or gradually widening wedge-shaped gaps terminated by the peripheral stereozone. The stereozone is rather variably developed up to 1·25 mm thick and contains traces of rudimentary wedge-shaped minor septa. The septal formula is *C7A8K8A7C* at a diameter of 15 mm.

In the ephebic stage of PRI 21593 (Pl. 5, fig. 5), the major septa are very slim and taper gently from the peripheral stereozone where they are about 0·4 mm thick to within a quarter of the radius or slightly less of the axis. There is a weak counter clockwise vortex. A few isolated bars of septal material may occur in the axis. In the cardinal quadrants, three or four metasepta flanking the cardinal septum curve to meet each other, or join sections of tabulae, across the axial end of the cardinal septum, delimiting a strong suboval fossula. The fossula is bisected by the cardinal septum, 4·5–5 mm or two-fifths the radius in length. The peripheral stereozone is variably developed from 3·3 mm thick where the minor septa are completely confined to the stereozone, to 1 mm thick from which the minor septa may project up to a further 2 mm towards the axis. There are 42 major septa at a diameter of 24 mm, a septal ratio of 1·75. Measurements are plotted in Text-fig. 9.

No longitudinal section is available.

Discussion. The Venezuelan specimens are considered conspecific with the holotype of *H.* (*H.*) *simplex* which is figured here on Pl. 5, fig. 3. The polished ephebic section of Hall's specimen is slightly larger—30 mm diameter with 53 major septa—but in other features the specimens are almost identical.

H. (*H.*) *simplex* has slimmer, longer major septa and a much more distinct cardinal fossula than *H.* (*H.*) *venezuelensis*. Furthermore, the septal ratio in this the smaller species (1·77 at 30 mm in the holotype) is lower than that in *H.* (*H.*) *venezuelensis* (1·94 at 33 mm in the lectotype).

Family **CYATHOPHYLLIDAE** Dana 1846

1963 Cyathophyllidae Birenheide: 367.
1966 Cyathophyllidae Pedder: 182, *pars*.
1969 Phillipsastraeidae Jell: 62, *pars*.

Discussion. Following his valuable revision of the Cyathophyllidae, Birenheide (1963 : 368) commented on the structural similarities between this family and the Disphyllidae, and Pedder (1966 : 182) later united the two groups of corals as subfamilies within the Cyathophyllidae. Jell (1969; see particularly pp. 64, 69), who on the other hand united the disphyllids with the phillipsastreids in the Phillipsastraeidae, has also discussed this relationship. Although disputing Pedder's classification, he did point out the close similarities of the Billingsastraeinae, a new subfamily of his Phillipsastraeidae, to the cyathophyllids.

The writer is of the opinion that *Billingsastraea* (as widely interpreted) and *Cylindrophyllum* belong together with *Heliophyllum* in the same suprageneric group. This is essentially the Billingsastraeinae of Jell (1969 : 68) with the addition of *Heliophyllum*. Birenheide (1963 : 368) included *Heliophyllum* in his undivided Cyathophyllidae but the *Heliophyllum—Billingsastraea* group, although considered here to be more closely related to the cyathophyllids than the disphyllids, deserves to be distinguished from the former on the basis of septal characteristics (see Text-fig. 11). It is therefore proposed that the Billingsastraeinae and the Cyathophyllinae be considered subfamilies of the Cyathophyllidae.

The Phillipsastraeidae is interpreted in the sense of Scrutton (1968) (= Phillipsastraeinae of Jell 1969 : 65) but admitting the Marisastrinae (*sensu* Jell 1969 : 66) if the presence of rhipidacanths can be confirmed in *Marisastrum sedgwicki*. The Disphyllidae (= Disphyllinae of Jell 1969 : 68 and ? Paradisphyllinae Jell 1969 : 67) is also accorded full family status. Perhaps the affinities of the three families Cyathophyllidae, Disphyllidae and Phillipsastraeidae would be best recognized at the superfamily level.

Subfamily **BILLINGSASTRAEINAE** Jell 1969

Genus ***HELIOPHYLLUM*** Hall 1846

1846 *Heliophyllum* Hall *in* Dana: 356.
1938 *Heliophyllum* Stewart: 35.
1938 *Heliophyllum* Fenton & Fenton: 209.
1945 *Heliophyllum* Smith: 25.
1947 *Heliophyllum* Le Maitre: 30.
1949 *Heliophyllum* Stumm: 21, *pars*.
non 1949 *Heliophyllum* Soshkina: 88.
1962 *Heliophyllum* Stumm & Tyler: 267.
1963 *Heliophyllum* Birenheide: 404.

Diagnosis. Solitary or colonial rugose corals with long slender major and minor septa bearing well developed yard-arm carinae in the dissepimentarium. Septa dilated to fill the lumen in early ontogeny; dilatation may persist in tabularium of cardinal quadrants in ephebic stage. Cardinal fossula long, narrow and weak. Dissepimentarium of several rows of small globose dissepiments, horizontal or reflexed peripherally, steeply sloping downwards axially. Tabulae complete or incomplete, usually low domes but may be flat or slightly sagging.

Type species (by monotypy). *Strombodes helianthoides*? Hall (*non* Phillips, *nec* Goldfuss) 1843 : 209, fig. 87, 3 on p. 209, fig. 48, 3 on p. 44 of tables = *Heliophyllum halli* Edwards & Haime 1850 : 69. York, Livingstone Co., N.Y., U.S.A.; Ludlowville Fm., Middle Devonian (Hamilton Group) (Wells 1937 : 9).

Discussion. Birenheide (1963) in a revision of cyathophyllids from the German Devonian has confirmed the views of Wang (1948 : 11) and others that *Keriophyllum* Wedekind is not congeneric with *Heliophyllum*. He (1963 : 392) assigned the type species of *Keriophyllum* to *Cyathophyllum* (*Peripaedium*) *turbinatum*, type species of *Peripaedium* Ehrenberg. Birenheide (1963 : 405) did regard *Keriophyllum dahlemense* Haller (1936 : 615, pl. 33, figs 1–2, pl. 34, fig. 1), however, as a valid species of *Heliophyllum*.

Heliophyllum is particularly common in the Middle Devonian of eastern North America but it has also been recorded from Europe, Asia, North Africa and South America. Some of these records may be species of *Cyathophyllum* but the acceptance of *K. dahlemense* as a species of *Heliophyllum* and the confirmation of records of *H. halli* from Spain (Altevogt 1968 : 764), North Africa (Le Maitre 1947 : 31) and Afghanistan (Brice 1971 : 263) supports this distribution in part. It is doubtful, however, if true *Heliophyllum* occurs in Australia.

Heliophyllum halli Edwards & Haime 1850

(Pl. 5, figs 6–8; Pl. 6, figs 1–6; Text-figs 10, 11)

1850 *Heliophyllum halli* Edwards & Haime: 69.
1926 *Cyathophyllum venezuelense* Weisbord: 224 (4), *pars.*, pl. 35 (1), fig. 4 only. (PRI 21791).
1937 *Heliophyllum halli* Edwards & Haime; Wells: 9, pl. 1, figs 1–15.
1943 *Heliophyllum halli* Edwards & Haime; Wells: 363 (95), pl. 36 (10), figs 1–2.
1947 *Heliophyllum halli* Edwards & Haime; Le Maitre: 31, pl. 1, figs 1–7, pl. 2, figs 1–6, pl. 3, fig. 1.
1965 *Heliophyllum halli* Edwards & Haime; Stumm: 36, pl. 32, figs 5, 6, 20–23.
1968 *Heliophyllum halli* Edwards & Haime; Altevogt: 764, pl. 2, figs 5a, b, c.
?1969 *Heliophyllum halli* Edwards & Haime; Kaplan: 28, pl. 3, fig. 1.
1970 *Heliophyllum halli* Edwards & Haime; Brice: 263, pl. 18, fig. 6.

Diagnosis. Usually curved, ceratoid to turbinate solitary corals but capable of considerable shape variation and rare increase. Major septa long, uniformly attenuate in dissepimentarium but may be thickened in tabularium of cardinal quadrants. Cardinal septum slightly shorter than other metasepta in long narrow fossula, other metasepta usually arranged with bilateral symmetry about counter-cardinal plane. Minor septa one-third to one-half radius in length. Septa in dissepimentarium with well developed yard-arm carinae. Dissepiments small, globose, horizontal or inclined towards epitheca peripherally, steeply sloping towards the axis. Tabulae wide low-domed complete plates with subsidiary domed plates in axis and small, inclined subsidiary plates periaxially.

Material. R45076, R45078, R45080–1, R45084–6, R49250, R49252, R49296 (3121); R45087 (3124); R45092–3, R49253 (3145); R49254 (3149); R45096–7, R49255, R49258, R49260 (3154); R49262 (3157); all Caño Grande; Caño Grande Formation. R45104, R49268–9 (3199); R45107–9, R49274 (3221); all Caño del Sur; Caño Grande Formation. R45120, R45122, R49286, R49288–9 (3618); R45124

(3619); all Caño Colorado; Caño Grande Formation. R45111–5, R49277–8, R49281, R49284 (3323); all from loose boulder in Caño del Oeste; Caño Grande Formation. R45128, R49294–5 (3849); all Caño Los Guineos; Caño Los Guineos Formation. All early Middle Devonian (upper Onesquethaw).

Distribution. Widespread in Middle Devonian of eastern North America and also present in the Middle Devonian of North Africa, Spain, Afghanistan and Venezuela. Records of this species from other areas doubtful.

Description. Curved conical trochoid to turbinate corals attaining a maximum mean diameter of 38 mm and a height of about 50 mm. Corallum shape not greatly variable. Epitheca with very weak septal grooves and gently rugate. The cardinal fossula is invariably located on the convex side of the corallum.

In neanic sections, the lumen is almost entirely closed by thickened septa. In R45104c (Pl. 6, fig. 2), the major septa, 0·8–1·1 mm thick extend almost to the axis where their ends are coated with sclerenchyme which fills the axial area. Along their length they are laterally contiguous in parts and separated elsewhere by a narrow sub-parallel sided gap between 0·05 mm and 0·2 mm wide crossed at intervals by the traces of tabulae. There is a distinct bilateral symmetry, the cardinal septum being longer than all the other septa and flanked by pinnate groups of metasepta. Minor septa appear mostly as short wedges up to 2·8 mm long and 0·7 mm wide between the peripheral ends of the major septa forming a solid septal stereozone around the cardinal quadrants. In the counter qudrants, however, there is a very narrow unthickened zone around the periphery, about half as wide as the length of the minor septa, in which major and minor septa alike are 0·2–0·3 mm wide. Signs of carinae are seen only rarely as incipient structures within the thickened peripheral parts of some septa. R45104c is 14·5 mm in mean diameter with 35 major septa.

In higher sections (R45108a, R45111c), the unthickened peripheral zone in the counter quadrants grows in width and gradually extends circumferentially across the alar areas towards the cardinal septum. Yard-arm carinae appear, one or two per septum, on the peripheral unthickened parts of the septa. In the axis, where there may be a weak counter-clockwise vortex, the core of sclerenchyme disappears in most cases and the ends of the septa, usually just short of the centre, may be gently tapered in an axial zone about 0·2 of the diameter across. The cardinal septum shortens and the arrangement of the flanking metasepta defines a long narrow cardinal fossula, well developed in some sections but hardly distinguishable in others.

Septal thickening is developed on the crests of the innermost series of dissepiments and the tabulae. It begins to diminish first in the counter quadrants and often disappears here completely by the late neanic—early ephebic stage. The boundary between the unthickened and thickened portions of the septa remains sharp until all trace of thickening disappears. The cardinal quadrants, however, are usually heavily thickened into and throughout much of the ephebic stage, often with the septa laterally contiguous except in the long narrow cardinal fossula. The outer edge of the thickened zone moves inwards towards and usually across the dis-sepimentarium/tabularium boundary, and the zone itself may be as small as half the diameter in width in some ephebic sections. On the cardinal septum and one or two flanking metasepta, however, the thickening starts very much closer to the periphery and serves to emphasise the cardinal fossula.

In ephebic sections the epitheca is about 0·25 mm thick and the peripheral parts of the septa about 0·1 mm across. The major septa, with the exception of the cardinal septum and a few flanking metasepta, all reach the axial area usually with tapered ends bilaterally arranged about the counter-cardinal axis. Nearly always the major septa are slightly thickened in the inner part of the tabularium. Sections such as R49278a (Pl. 6, fig. 5) with no notable septal thickening at all are rare. One specimen R45115a–b (Pl. 5, fig. 6) shows an irregular network of septal material in an axial area about a fifth the diameter across. Minor septa range from a third to just over half the radius in length and those flanking the counter septum may be slightly longer than their neighbours. Yard-arm carinae are developed on major and minor septa in the dissepimentarium, rarely with a strong contrast between counter (better developed) and cardinal quadrants. Variation from specimen to specimen is notable with individual carinae between 0·4 and 0·65 mm in average width, 0·6 to 1·2 mm in average spacing and between means of 3 to 6 per septum. The intensity of carination tends to increase with increasing size and septal number and with decreasing septal thickening. The appearance of the cardinal fossula is also variable with the cardinal septum ranging between extremes of a quarter to two-thirds of the radius in length in a narrow, parallel sided fossula closed axially by the incurving ends of the adjacent metasepta. Dissepiments are intercepted on average 0·5 mm apart, usually uniserial between adjacent septa. Up to three rows closest to the epitheca are concave abaxially, the rest concave adaxially. They may in some cases loop between carinae rather than from septum to septum. Traces of tabulae are wider spaced and more diffuse.

In longitudinal section, the lower parts and much of the peripheral areas particularly on the cardinal side are infilled by sclerenchyme. The dissepimentarium is composed of small globose dissepiments up to 1·2 mm high but normally fairly evenly developed around 0·75 mm high. The width of the dissepimentarium increases towards the calice and contains up to six rows of dissepiments. They are horizontal to slightly reflexed peripherally and steeply sloping downwards axially. The dissepimentarium is notably modified in the cardinal fossula (Pl. 6, fig. 6) where the peripheral two or three rows of normal globose dissepiments are followed axially after a sharp break by large axially and downward sloping vesicles. The tabulae are complete and incomplete. The complete series are broad low domes 1–2 mm apart. The incomplete tabulae are mainly subsidiary broad low domes across the axial four-fifths of the tabularium diameter with a few small flanking vesicles. The sclerenchyme coating the septa is commonly seen cresting the tabulae as well. Traces of carinae are confined to the dissepimentarium. Close to the epitheca they slope inwards and upwards at no more than 10° to the wall, but towards the axis they curve over to an angle of about 45° and occasionally as low as 30° to the horizontal.

Septal microstructure is only clear in parts, where uniserial monacanthine trabeculae can be seen. The cross-bar carinae which cut, and definitely precede the septa in formation have the same general appearance as septal tissue but no details of their trabecular structure can be determined.

Measurements of septal number against diameter are plotted in Text-fig. 10.

Discussion. Although the Venezuelan specimens have a considerably smaller range of adult diameters than topotypic *Heliophyllum halli* (see Text-fig. 10) there appears to be no structural distinction of note between the two groups of specimens. Size and size linked factors such as septal number and intensity of carination, and possibly also the more prevalent septal thickening in the Venezuelan sample are probably all of ecological rather than genetic importance. Furthermore, although the legendary variability of *H. halli* in external form is well documented (Wells 1937), variation in internal structure is not so well known neither for this species nor for the host of other North American 'species' of *Heliophyllum* (see for example Stumm (1965 : 35–38)). For these reasons it seems preferable not to distinguish the Venezuelan material in any way from *H. halli*.

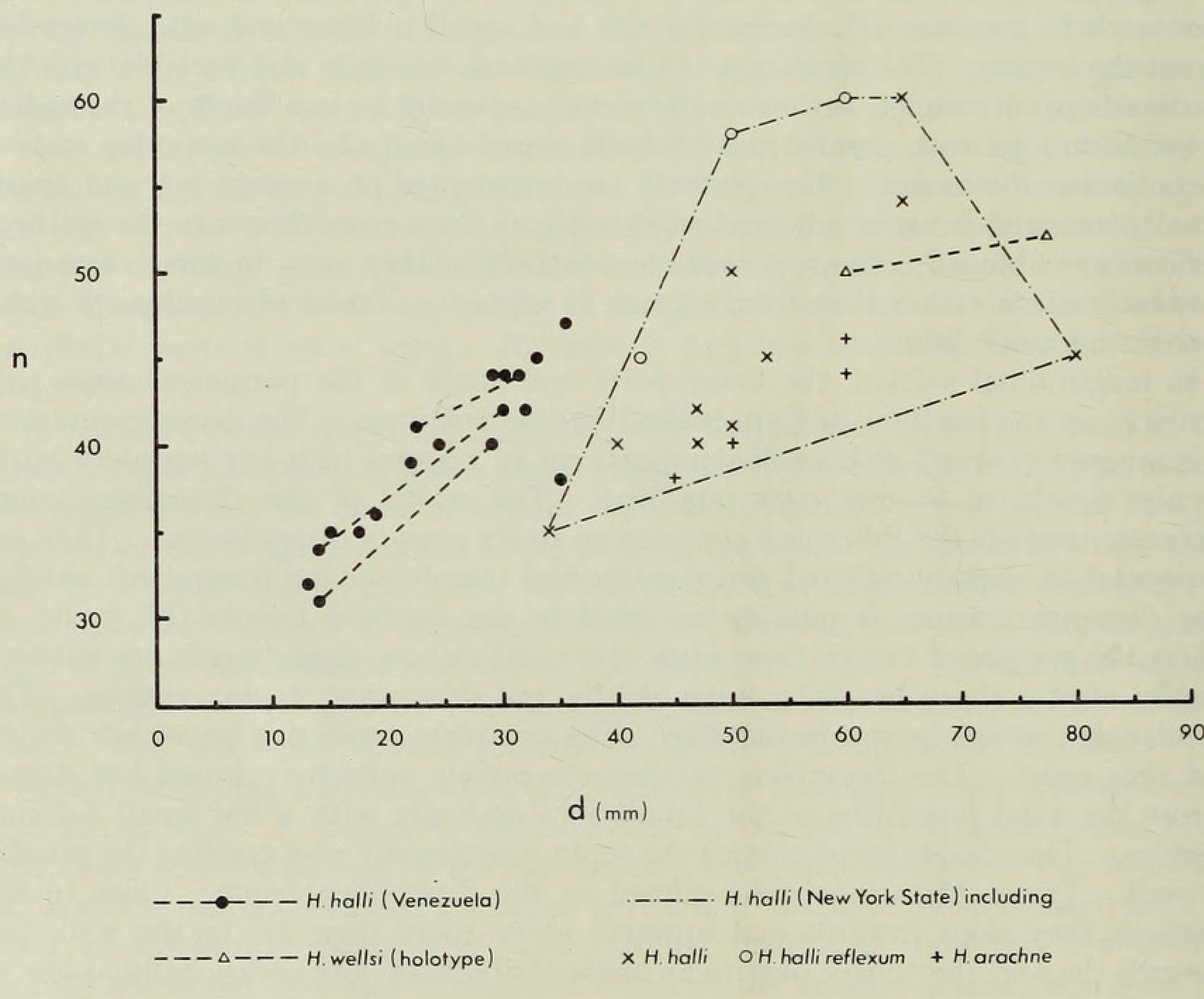


Fig. 10. Number of major septa plotted against diameter for specimens of *Heliophyllum halli* from Venezuela and New York State, and for specimens of *H. wellsi*.

Heliophyllum wellsi sp. nov.

(Pl. 6, figs 7, 8; Pl. 7, figs 1, 2; Text-figs 10, 11)

Derivation of name. After Professor J. W. Wells (Cornell University, Ithaca, N.Y., U.S.A.).

Diagnosis. Large solitary *Heliophyllum* with dissepimentarium one-half to three-fifths the radius. Attenuate major and minor septa densely carinate in dissepimentarium. Carinae yard-arm, sometimes with branching ends; they may form reticulate network with septa close to the epitheca. Axial core of reticulate septal lamellae about one-fifth the diameter across. Dissepiments small, globose, numerous; tabulae incomplete, tabularium horizontal or slightly domed.

Holotype. R45088 (3126). Caño Grande; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

Paratype. R45089 (3126). Same locality and horizon as holotype.

Description. The specimens are large conico-cylindrical fragments of the mature stages of two coralla. The epitheca is moderately rugate.

In cross-section the epitheca is 0·2 mm thick and only slightly penetrated by the expanded and shallowly convex ends of the septa. The septa are extremely thin across the broad dissepimentarium, measuring 0·05–0·10 mm across; the peripheral expansion is variable but not more than 0·30 mm across and less than 1 mm long. There is no sign of a cardinal fossula. In the dissepimentarium, the septa bear abundant yard-arm carinae, averaging 22–24 per septum, spaced 0·7 mm apart and reaching 2 mm in length near the periphery. The carinae towards the inner dissepimentarium are shorter and closer spaced normal cross-bars but many of those in the outer dissepimentarium have bifurcating or geniculate ends. In some instances septa and carinae may form an intricate reticulate network just inside the epitheca. The minor septa are about as long as the dissepimentarium is wide, that is half to three-fifths the radius. A slight but well defined septal thickening to 0·3–0·4 mm in width takes place at the dissepimentarium-tabularium boundary, gently tapering towards the axis over some 5–7 mm. Incipient carinae can be clearly seen embedded in these thickened parts of the major septa in higher ephebic sections. The axial ends of the major septa terminate against an axial area 10–20 mm across containing a dense and rather irregular reticulate network of septal material which is occasionally weakly carinate. The details of this axial structure show considerable variation in the sections available.

In longitudinal section the dissepimentarium is composed of numerous small globose dissepiments on average 0·7 mm high, horizontally arranged near the periphery and curving over to slope steeply downward towards the axis. The tabulae are incomplete longer, flatter, vesicular plates arranged horizontally or slightly domed across the axis. In the axial three-fifths of the tabularium diameter, the tabulae are disrupted by numerous, vertical and sub-parallel, wavy septal lamellae. The dissepimentarium is crossed by the traces of carinae, very regularly spaced 0·5–0·6 mm apart normal to their length. The carinae are inclined 25–30° to the epitheca at the periphery, curving over gently through 40° to lie approximately

40° to the horizontal at the inner edge of the dissepimentarium. They may just penetrate the tabularium, bending sharply upwards through about 20° as they do so.

Diameter and septal number in the holotype are plotted on Text-fig. 10. The paratype, of comparable size, is too crushed to measure accurately.

The fine structure of the epitheca, dissepiments and tabulae can be clearly seen to be fibronormal. The septa appear to be composed of unitrabecular monacanths and the fine structure of the carinae is of septal type but is otherwise obscure.

DISCUSSION. *Heliophyllum wellsi* is distinguished in general by its large size, the intensity of the septal carination and the apparent lack of a cardinal fossula. The most striking feature of the new species, is however, the axial core of reticulate septal lamellae which appears to be unique to *H. wellsi* among species of *Heliophyllum*.

Genus ***CYLINDROPHYLLUM*** Simpson 1900

1938 *Cylindrophyllum* Stewart: 43.
1949 *Cylindrophyllum* Stumm: 33.
1949 *Cylindrophyllum* Ehlers & Stumm: 23.

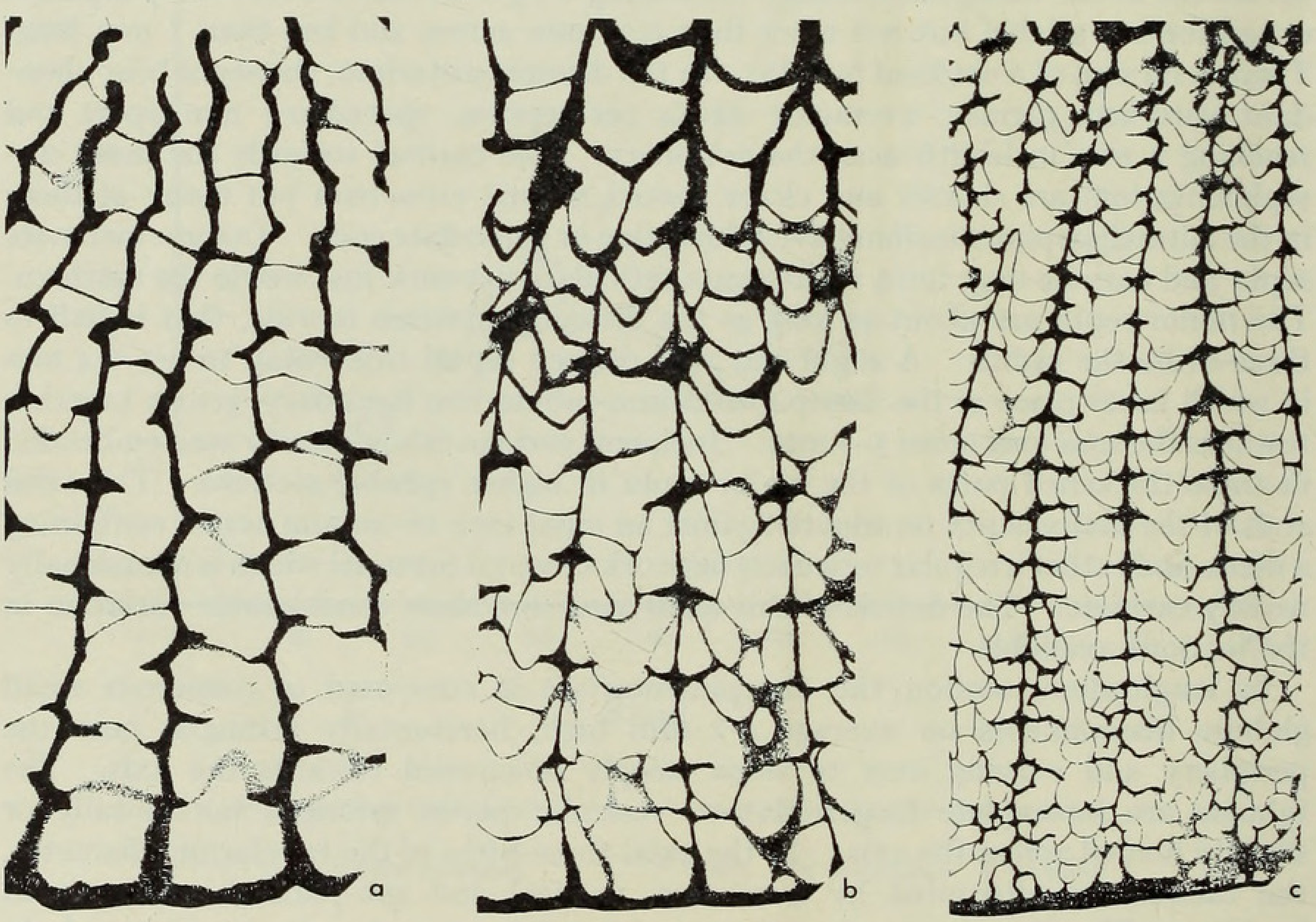


FIG. 11. Comparative septal carination in (a) *Cylindrophyllum elongatum* (R45116a) ×25, (b) *Heliophyllum halli* (R45115a) ×10, and (c) *Heliophyllum wellsi* (R45088a) ×6.

DIAGNOSIS. Dendroid or phaceloid rugose corals. Corallites with attenuate major and minor septa and radial symmetry. Septa with variably developed yard-arm carinae in dissepimentarium, the major septa irregular in course with occasional lateral projections in tabularium and frequently withdrawn from axis. Dissepiments small, globose, usually sloping steeply downwards towards the axis. Tabulae mainly incomplete; tabularium surface usually bowl-shaped, occasionally flat or more rarely arched.

TYPE SPECIES (by original designation). *Cylindrophyllum elongatum* Simpson 1900 : 217, text-fig. 42. Onondaga Limestone (Edgecliff Member), early Middle Devonian; Clarksville, Albany Co., N.Y., U.S.A.

DISCUSSION. *Cylindrophyllum* has been commonly placed in the Disphyllidae but the septal characteristics in particular suggest that the genus is more likely to be related to the *Heliophyllum-Billingsastraea* group (see discussion of the Cyathophyllidae).

Cylindrophyllum elongatum Simpson 1900

(Pl. 7, figs 3–6; Text-fig. 11)

1900 *Cylindrophyllum elongatum* Simpson: 217, fig. 42.

DIAGNOSIS. Phaceloid *Cylindrophyllum* with corallites up to about 20 mm diameter. Major and minor septa almost equal in length, more or less confined to dissepimentarium. Septa straight or zigzagged, carinae usually well developed but may be variable to almost absent in some corallites. Dissepiments small, globose, up to four rows deep, strongly sloping axially and downwards. Tabulae complete or incomplete; tabularium surface flat or bowl-shaped, rarely arched.

MATERIAL. R45116 (3539). Slipped block in Caño Pescado; Caño Grande Formation or lower part of Caño del Oeste Formation, early Middle Devonian (upper Onesquethaw).

DISTRIBUTION. Onondaga Limestone; New York, U.S.A. Caño Grande Fm. or lower Caño del Oeste Fm. Sierra de Perijá, Venezuela. Both early Middle Devonian.

DESCRIPTION. The specimen is a portion, 120 mm × 100 mm × 70 mm, of a phaceloid colony in which most of the corallites are partially crushed. There are no signs of connecting processes between corallites in this colony.

In cross-section the corallites were nearly all originally circular with a regularly developed fibronormal epitheca 0·1 mm thick. In a few cases, adjacent corallites grow with short lengths of their epithecae cemented back to back. Major and minor septa are uniformly attenuate, 0·03 mm thick on average, except in the peripheral 1 mm or less in which they gradually thicken towards the epitheca. The septa have very bluntly wedge-shaped peripheral ends reaching 0·25 mm in thickness which may penetrate up to half the thickness of the epitheca. Major and minor septa appear to be formed of unitrabecular monacanthine trabeculae and are differentiated by no more than 0·3 to 0·4 mm in length. They reach between a half and two-thirds the radius to the axis, the minor septa ending at the tabularium/dissepimentarium boundary, the major septa just penetrating the tabularium. The septa may be straight or zigzagged. A few corallites have scattered carinae on one or two septa only but most corallites have moderately developed carinae on all or nearly all septa. The carinae appear to be of the yard-arm type as developed in *Heliophyllum* but many are geniculate with a central portion displacing the septum obliquely and only the extremities orientated normal to the septal face, thus giving the appearance of alternate carinae on zig-zag septa. Dissepiments usually appear as a single series between septa of straight to slightly curved bars 0·3–0·5 mm apart. There is a wide axial area between a third and a half the radius across free of septa and crossed only by curved sections of tabulae. No signs of the type of increase were observed. Because of the crushing, accurate measurements were possible on only a few corallites. The largest individual was 10·5 mm in diameter with 29 major septa.

In longitudinal section the dissepiments are small, globose and regularly developed 0·4–0·6 mm high. The dissepimentarium is usually four rows, or sometimes possibly five rows of dissepiments deep. The surface slopes axially and downwards at 45°–55° to the horizontal. The carinae crossing the dissepimentarium may be almost parallel to the epitheca at the periphery but incline more and more towards the axis when traced towards the inner edge of the dissepimentarium where they are 45°–50° to the horizontal. The tabulae are complete and incomplete, arranged horizontally or with a slight axial depression. The complete tabulae are either slightly arched or more usually slightly sagging and are supplemented or partially replaced by large vesicular plates.

Discussion. This specimen appears to be conspecific with photographs of the holotype and other specimens from the Edgecliff member of the Onondaga Limestone of New York kindly provided by Dr W. A. Oliver, Jr. (U.S. Geological Survey). The only points of difference appear to be a tendency for the New York material to have a higher percentage of complete tabulae and to reach a larger corallite diameter.

The diagnosis for the species given here has been constructed with the aid of these photographs.

Family **DURHAMINIDAE** Minato & Kato 1965b

1965b Durhaminidae Minato & Kato: 28.
1967 Durhaminidae Stephens: 426.
1967 Durhaminidae Federowski: 25.

Diagnosis. Solitary, fasciculate, cerioid or plocoid rugose corals. Axial structure with median counter-cardinal plate in early ontogeny, poorly developed or lost in ephebic stage and replaced by few irregularly arranged septal ends or septal lamellae. Minor septa variably developed and scattered third order septa may occur. Septa usually thin, sinuous or zigzagged in dissepimentarium, slightly dilated in tabularium. Lonsdaleoid dissepiments may be variably developed, the others concentric or herringbone: all dip steeply axially and downwards. Tabulae mainly incomplete, peripherally flat or trough-shaped, axially flat-topped or arched domes. Clinotabellae usually present. Axial tabellae may or may not be clearly differentiated.

TYPE GENUS. *Durhamina* Wilson & Langenheim 1962 : 504.

DISCUSSION. The specimen described below as *Durhamina* sp. nov. definitely possesses poorly developed sporadic third order septa and an examination of Easton's (1960, text-fig. 18) illustration of the holotype of *Lonsdaleia cordillerensis* (lower right quadrant of largest corallite) shows them to be present to a similar extent in the type species of *Durhamina* itself. This serves to underline the extremely close relationship between the Durhaminidae and Waagenophyllidae and is of particular interest in view of Minato & Kato's (1965a : 13) observations on tertiary and higher orders of septa in the Waagenophyllidae. The diagnosis given above is emended accordingly.

Members of the Durhaminidae occur in the Middle Carboniferous to Middle Permian rocks of Eurasia, western North America and South America.

Genus *DURHAMINA* Wilson & Langenheim 1962

1962 *Durhamina* Wilson & Langenheim: 504.
1965b *Durhamina* Minato & Kato: 34.

DIAGNOSIS. Fasciculate Durhaminidae with weakly constructed axial structure and scattered, weakly developed third order septa. Lonsdaleoid dissepiments sporadically developed.

TYPE SPECIES (by original designation). *Lonsdaleia cordillerensis* Easton 1960 : 580, Text-figs 17, 18. Lr. Permian; nr. Ruth, eastern Nevada, and other localities in eastern Nevada and southern California, U.S.A.

DISCUSSION. Wilson & Langenheim (1962 : 504) provided a very full comparison of *Durhamina* with similar genera, supplemented by Minato & Kato (1965b : 34). It is only necessary here to draw attention to the scattered third order septa (see discussion of family) not hitherto recorded in the genus.

?*Durhamina* sp.

(Pl. 7, figs 7, 8)

MATERIAL. R49285 (3495). Caño del Norte; Río Palmar Formation, Lr. Pennsylvanian.

DESCRIPTION. Solitary cylindrical fragment 9 mm maximum diameter.

In cross-section the epitheca is thin and smooth. The major septa are between a half and the full radius in length and are very slightly thicker in the tabularium than dissepimentarium. The longer septa meet in the axial area, the shorter septa have free tapered ends. Minor septa are fairly evenly developed, up to a third the radius in length. Dissepiments are concentric between them and their flanking majors but weakly herringbone beyond their axial ends when they are particularly short. There are no lonsdaleoid dissepiments. There are 21 major septa at a diameter of 7·5 mm.

In longitudinal section the dissepimentarium is narrow, a quarter the radius in width, and composed of steeply inclined vesicles averaging 1 mm long and 0·25–0·3 mm high. The tabulae are complete and incomplete but mostly the latter. The complete tabulae are flat or gently sagging across the axis and downturned peripherally. The incomplete tabulae are undulating plates, inclined gently axially and upwards to meet the vertical trace of a septum in the axis. There are scattered clinotabellae.

Discussion. This fragment can be closely matched with corallites from species of *Durhamina* in which the axial structure is weak, and is therefore assumed to be part of a corallite detached from a fasciculate coral colony. In view of the limitations of the single specimen, however, the identification must be treated with reserve.

Durhamina sp. nov.

(Pl. 8, figs 1–10; Text-fig. 12)

Material. R49276 (3270). From a boulder in the Caño Grande; horizon uncertain, ? Río Palmar Fm., Lr. Pennsylvanian, but see p. 232.

Description. The specimen is a large fragment, some 150 × 150 × 100 mm before cutting, of a phaceloid or in parts cerioid colony set in a tough fine-grained reddish-brown calcareous matrix. No external details of the corallites can be observed.

In cross-section, the corallites are circular when free and uncrushed. There are areas in the colony where groups of three to eight corallites become laterally contiguous and assume a cerioid habit. Young hysterocorallites have slim major septa, three-fifths to the full radius in length from corallite to corallite but of fairly uniform length within a single corallite. In the smallest corallite (Pl. 8, fig. 5), 4 mm in diameter, the major septa are about 0·07 mm thick near the periphery, tapering towards but not reaching the axis. The counter septum, however, crosses the axial area with a slim blade-like expansion centred on the axis, 0·8 mm long and 0·12 mm thick, which imparts a strong bilateral symmetry to the corallite. In slightly larger corallites (Pl. 8, figs 6, 7) with longer major septa, several of them meet in the axis often deflecting the end of the counter septum or obscuring its identification and the bilateral symmetry is weakened or lost. The peripheral ends of the septa are often, but not in all corallites, interrupted by a single series of lonsdaleoid dissepiments. When the septa are not interrupted they are usually somewhat irregular in course and thickness at the periphery. The dissepiments are very variable in appearance. Among the lonsdaleoid series and the inner two or three series of similar sized normal dissepiments are scattered very much smaller and more highly globose dissepiments. The dissepiments are irregularly arranged in a single series or weakly herringbone between adjacent major septa. Minor septa are absent or sporadically developed as short spines on the dissepiments.

In mature corallites, most major septa extend from the epitheca to the axis with occasional interruptions along their length. The epitheca is a very smoothly and regularly developed fibronormal wall 0·12 mm thick. It shows no signs of septal grooves. The septa which have slightly expanded, flat to shallowly convex or wedge shaped peripheral ends show little or no penetration of the inner face of the epitheca. The major septa are slim and are usually irregularly zigzagged or sinuous in the dissepimentarium due to dissepimental interference. They are not frequently interrupted, however, and there is no well defined series of lonsdaleoid dissepiments. Most septa show a slight and often sharp dilatation at the inner edge of the dissepimentarium associated with a slight thickening of the innermost series of dissepiments. Major septa are between 0·1 and 0·2 mm thick at this point from which they taper smoothly towards the axis. In any one corallite about half the major septa will meet in the axis usually resting against an irregular median plate formed by the extended end of what is assumed to be the counter septum. These septa may be slightly thickened in the immediate axial area. The rest of the major septa taper to a point just short of the axis. A few of the septa may be interrupted periaxially thus lending definition to the axial structure but no additional septal lamellae are involved. Also, tabulae are intercepted more frequently in the axial area. Minor septa are extremely irregularly developed. In some corallites they extend to or just across the dissepimentarium/tabularium boundary, or very rarely up to half way across the tabularium to the axis. They are very thin and zigzagged in the dissepimentarium or may be frequently interrupted. At the other extreme the minor septa may be no more than scattered spines on the crests of a few dissepiments. The dissepimentarium is between 0·3–0·4 of the radius in width and disordered in appearance. An irregular herringbone pattern is developed either between major septa when the minor septa are weak, or between major and minor septa when the minor septa are strong. In the latter case, scattered third order septa are developed as very short pegs on the epitheca and as short spines cresting dissepiments (Pl. 8, fig. 2). Septal structure, although clearly trabecular, cannot be distinguished in detail and the style of increase cannot be determined in cross-section.

In longitudinal section the dissepiments are mixed larger, less inflated, rather elongate vesicles and smaller, more globose vesicles. The longer vesicles may reach up to 3–4 mm long and 1 mm high normal to the dissepimental surface, whilst the smaller average about 0·75 mm long and 0·4 mm high. The dissepiments slope steeply and fairly uniformly axially and downwards at about 50° to the horizontal. The tabularium is wide, between 0·6 and 0·7 of the diameter and consists of complete and incomplete plates. Complete tabulae are rare, fairly wide flat-topped domes with the peripheral extremities sigmoidally curved downwards and meeting the dissepimental wall horizontally. The incomplete tabulae are axially dome-shaped and periaxially trough-shaped plates with occasional clinotabellae, combined to give a broad axial plateau to the tabularium surface, which may be gently domed or depressed across the axis. There is no sign of any great modification of the tabulae in the axial area corresponding to the weak axial structure in cross-section. In longitudinal section, increase appears to be peripheral non-parricidal or lateral.

Measurements of corallite diameter and septal number are plotted in Text-fig. 12. Corallites reach a maximum of 18 mm diameter but data are restricted by the partial crushing of many corallites.

Discussion. *Durhamina* sp. nov. compares most closely with *D. cordillerensis* (Easton) from the Lr. Permian of Nevada and California although it can be distinguished from that species on a number of points. The most striking is the more regular development and greater simplicity of the axial structure in the Venezuelan species. In *D. cordillerensis* the axial structure is of quite variable density and may rarely be absent. When it is well developed, however, the septal lamellae involved are clearly distinguished from the major septa, in contrast to the very primitive arrangement in *Durhamina* sp. nov. The latter also has a more strongly developed dissepimentarium than *D. cordillerensis* and indeed most other species of *Durhamina*. Finally the Venezuelan species has larger corallites than the North American species. Mature corallites are about 14 mm mean diameter with 22–25 major septa, reaching a maximum of 18 mm diameter in *D.* sp. nov., compared to mean diameter about 8–9 mm with 22 to 28 major septa (Easton 1960 : 580) or 20–22 major septa (Wilson & Langenheim 1962 : 506) and maximum diameter about 15 mm in *D. cordillerensis*.

The Venezuelan species has not been formally named here as it is represented by only a single specimen from a loose block of uncertain stratigraphic position.

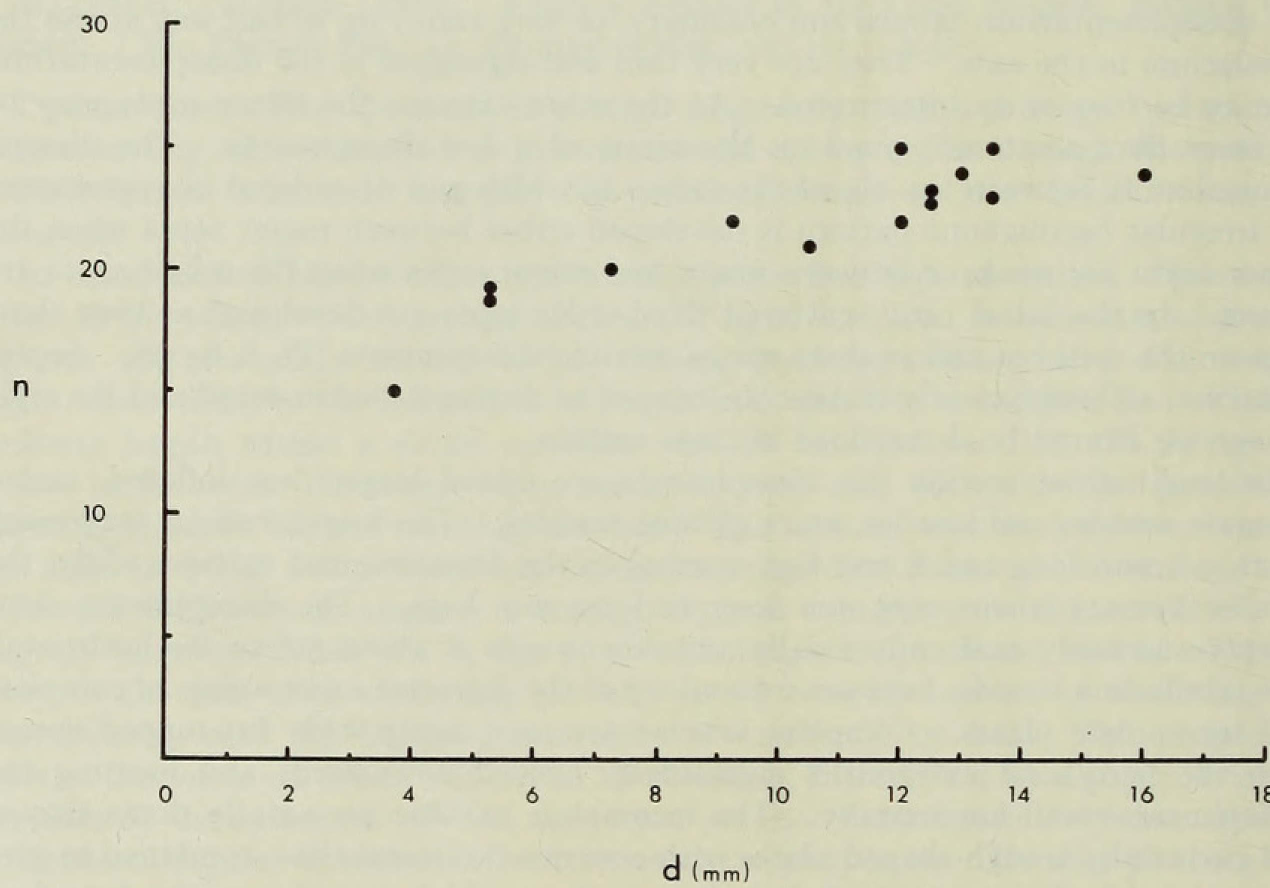


Fig. 12. Number of major septa plotted against diameter for corallites in one colony of *Durhamina* sp. nov.

Suborder CYSTIPHYLLINA Nicholson 1889
Family **CYSTIPHYLLIDAE** Edwards & Haime 1850
Subfamily **PLASMOPHYLLINAE** Dybowski 1873

1964 Plasmophyllinae; Birenheide : 15.

Genus ***PLASMOPHYLLUM*** Dybowski 1873

1873 *Plasmophyllum* Dybowski : 340
1964 *Plasmophyllum* (*Plasmophyllum*); Birenheide: 16 *cum syn.*

DIAGNOSIS. Solitary or weakly colonial corals in which the lumen is filled by vesicular tissue which may or may not be thickened with sclerenchyme. Septa are absent or represented by short irregularly developed spines. The vesicles in general increase in size towards the axis and are arranged with a shallow bowl-shaped to inverted sub-conical surface. Thickening when present is based on this surface and may extend from epitheca to axis or be confined to a single concentric zone.

TYPE SPECIES (by subsequent designation of Schlüter 1885 : 10). *Cyathophyllum limbatum* Quenstedt 1879 : 465, pl. 158, fig. 37 (*non* fig. 38) = *Cyathophyllum goldfussi* Edwards & Haime 1851 (*non* Castelnau 1843). Gerolstein, Eifel, Germany; Ahrdorf-Schichten, Middle Devonian (Eifelian).

DISCUSSION. Birenheide (1964) has provided a most valuable review of the Devonian cystimorph group of corals, placing them all, with a few exceptions, in the subgenera *Plasmophyllum* (*Plasmophyllum*) and *Plasmophyllum* (*Mesophyllum*). The writer feels, however, that these two groups deserve full generic status based on the distinction in septal development between them and that their close relationship is best indicated at the subfamily level.

Plasmophyllum secundum americanum (Edwards & Haime) 1851
(Pl. 9, figs 1–4)

1851 *Cystiphyllum americanum* Edwards & Haime: 464, pl. 13, figs 4, 4a.
1964 *Plasmophyllum* (*Plasmophyllum*) *secundum americanum* (Edwards & Haime) Birenheide: 23, pl. 24, fig. 117 (*cum syn.*).

DIAGNOSIS. Trochoid or turbinate tending to subcylindrical *Plasmophyllum* with vesicles clearly separable into two concentric zones. Vesicles of the inner zone slightly larger than in the outer zone and increasing in size towards the axis in both zones. Short blunt septal spines developed, particularly in the inner half of the outer zone. Usually sclerenchyme is heaviest in a broad concentric band or bands coating or completely obscuring the vesicles in the outer part of the inner zone.

MATERIAL. R45098 (3157). Caño Grande; Caño Grande Formation, early Middle Devonian (Upper Onesquethaw). R45106, R49270, R49272 (3221). Caño del Sur; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

Distribution. Widespread in rocks of Middle Devonian age in North America. Caño Grande Fm., early Middle Devonian; Sierra de Perijá, Venezuela. Also present in the Middle Devonian of Spain, U.S.S.R., south-east Asia and Australia according to Birenheide (1964 : 24, synonymy).

Description. Turbinate corals up to 40 mm diameter and 70 mm height. Calice a shallow bowl with a strongly everted rim. Epitheca moderately rugate.

In cross-section, the epitheca is fibronormal and of somewhat variable thickness, 0·1–0·3 mm thick in the small part preserved. The lumen is entirely filled by vesicular tissue, fine in an outer zone one-third the radius across in smaller sections to one-half the radius in the largest subcalicular section, and coarser in the axial zone. In the peripheral area the vesicles are highly globose and often circular or subcircular in cross-section, but somewhat variable in shape and generally ranging in diameter from 0·5 to 2 mm. They may be thin walled or lightly coated with fibronormal material locally extended into short, blunt septal spines up to 1 mm long and 0·5 mm across at the base (Pl. 9, fig. 3). The coating has a general concentric disposition in the corallum but does not form obvious zones. Towards the axis the vesicles become less and less globose and the circular sections disappear. In the general region of the boundary between the zones of large and small vesicles the thickening abruptly increases. It may form a single broad somewhat ill defined concentric band extending well into the zone of larger vesicles and ringing a relatively narrow axial zone of lighter thickening about one-fifth the diameter across. In other sections this may grade into a series of relatively narrow concentric bands of thickening in the zone of larger vesicles. The thickening partly obscures the septal spines which are coarser here and are developed to within a short distance of the axis. Often isolated spots of sectioned septal spines occur in the immediately periaxial area. The larger vesicles average about 2 mm across periaxially and increase in size towards the axis.

In longitudinal section, the relative width of the zone of smaller dissepiments and the degree of eversion of its upper surface is seen to increase with increasing size. The vesicles gradually increase in size towards the axis and the septal spines are best developed just outside the zone of larger vesicles and heavy thickening. The spines may reach 1·7 mm in length. Their microstructure is not perfectly clear but they appear to consist of localized broad fans in the fibronormal material. At the inner edge of the zone of smaller vesicles the surface slope is about 50° to the horizontal. The larger vesicles are much thickened and may be completely obscured in a dense mass of sclerenchyme. Towards the edge of the zone the thickening can be seen as separate cones on the surface of the vesicles but the cones tend to merge in the axial area. The vesicles in the axial area do not exceed 3·5 mm across their bases, and are arranged with a shallow bowl-shaped surface across the axis.

Discussion. Birenheide (1964 : 23), in his comprehensive revision of the Devonian cystimorphs, made *Cystiphyllum americanum* a subspecies of the Middle Devonian species *Plasmophyllum secundum*. In particular he noted that larger examples of *P. secundum americanum* could scarcely be distinguished from the West European subspecies *P. secundum conistructum* Quenstedt. To judge from Birenheide's figures, however, and from a general comparison of American and German material, there would appear to be several points of difference. *Plasmophyllum secundum americanum* has much more regularly developed vesicles, both in size and shape, particularly in the peripheral areas of the corallum. Furthermore, the development of short blunt wedge-shaped septal spines, most conspicuous in the inner part of the zone of smaller vesicles, is a characteristic feature of *P. secundum americanum* but does not appear to be present in *P. secundum conistructum*. On the other hand, typical *P. secundum americanum*, for example R45098 figured here (Pl. 9, figs 1–4), compares remarkably well with Wedekind & Vollbrecht's (1931, pl. 17, figs 1–2) illustrations of *Paralytophyllum crassum* (Wedekind) from the Givetian of Germany. In particular, the development of septal spines and the size are more or less identical, as is the calice shape, although this appears to be more variable in *P. secundum americanum* as a whole. Birenheide (1964 : 28) listed *Paralytophyllum crassum* in his synonymy for *P. secundum pseudoseptatum* (Schulz). The fact remains that but for the geographical isolation, any sort of distinction between the American material and European *P. secundum* would be difficult to maintain. Birenheide's synonymy for *P. secundum americanum* is accepted uncritically.

Plasmophyllum sp.

(Pl. 9, figs 5–7)

1943 *Zonophyllum* sp. Wells: 98, pl. 10, figs 5, 6.

MATERIAL. R45095, R49259 (3154), PRI 24425 (PRI 24427 cut from same specimen). Caño Grande; Caño Grande Fm., early Middle Devonian (upper Onesquethaw).

DESCRIPTION. Small subcylindrical fragments 12–16 mm in diameter. The corallum may be strongly constricted at intervals as a result of rejuvenation.

In cross-section the vesicles appear rather flattened sub-semicircular and variable in size from about 0·5 mm to 5 mm across their bases. The epitheca and two or three concentric internal surfaces are heavily thickened with fibronormal sclerenchyme. The external wall thus varies between 0·6 and 1·5 mm in thickness. When it is thinner, short blunt septal spines can be distinguished extending inwards about 1 mm from the periphery and approximately 0·6 mm apart. Thickening of the wall tends to obscure these spines completely. Similar septal spines may or may not occur associated with inner zones of thickening. The vesicles show a general increase in size towards the axis but the gradation, although irregular, is more or less continuous and inner and outer size zones cannot be distinguished.

In longitudinal section, the vesicles slope axially and downwards at the periphery and flatten out across the axis giving a bowl-shaped calice. The upper surface of the vesicles is frequently thickened. At intervals up the length of the corallite the lumen is entirely filled by sclerenchyme, more heavily deposited at the periphery so that vesicular tissue is seen only infrequently to reach the epitheca unobscured.

Discussion. Wells (1943 : 98) originally described some of this material as *Zonophyllum* sp. Following Birenheide's (1964) revision of the cystimorphs, the Venezuelan material clearly belongs to the group of *Zonophyllum* he regards as congeneric with *Plasmophyllum*.

Wells (*op. cit.*) noted that the Venezuelan material was similar in structure to *Cystiphyllum conifollis* Hall (1876, pl. 30, figs 3–9) as redescribed by Fenton & Fenton (1938 : 232, fig. 20, pl. 23, figs 9, 10, pl. 24, figs 4–7). Unfortunately the Fentons did not section and figure Hall's type material, all of which looks from Hall's figures to be too highly cystose to be closely related to the Venezuelan species. On the other hand, one specimen figured by Fenton & Fenton (1938, pl. 24, figs 5–7) from the Hamilton Group (Moscow Fm.) of Leicester, N.Y. as '*Cystiphyllum*' *conifollis* looks extremely similar to the Venezuelan specimens and may indeed be conspecific with them. It seems best therefore neither to use the name *conifollis* nor to erect a new species until Hall's original material has been redescribed.

Order TABULATA Edwards & Haime 1850
Suborder FAVOSITINA Sokolov 1962
Family **FAVOSITIDAE** Dana 1846
Genus ***FAVOSITES*** Lamarck 1816

1816 *Favosites* Lamarck: 204.
1851 *Emmonsia* Edwards & Haime: 152, 245.
1939 *Favosites* Lecompte: 80, *cum syn.*
1953 *Favosites* Ross: 48, *cum syn.*
1960 *Favosites* Philip: 196.
1965 *Favosites* Stumm: 60.
1965 *Emmonsia* Stumm: 65.

Diagnosis. Massive, ramose, foliaceous or encrusting cerioid corals. Corallites generally contiguous, polygonal, of similar diameter throughout their length. Corallite walls unthickened internally, but may be variably dilated in a thin peripheral zone. Mural pores confined to corallite wall faces, usually one or two but may be three to a face, arranged in vertical series. Septa present in some species, may be variably developed usually as spines in vertical rows but also as septal striae. Squamulae also present in some species, with or without septal spines, and also may be variable in development. Tabulae usually complete and horizontal, frequently suspended in squamulate forms.

Type species (see Edwards & Haime 1850 : 60). *F. gothlandicus* Lamarck 1816 : 205 = *Specimen . . . corallinum Gothlandicum* Linnaeus 1745 : 39, fig. 27 and 1749 : 106, pl. 4, fig. 27.

Discussion. Considerable discussion of the genus *Favosites* has been published. It is sufficient here to state that the writer accepts Philip's (1960 : 190) opinion on the status of squamulae in *Favosites* and also considers that *Thamnopora* should be maintained as a distinct genus.

Favosites venezuelensis (Weisbord) 1926
(Pl. 10, figs 1, 2)

1926 *Pleurodictyum venezuelense* Weisbord: 6, pl. 1, figs 8, 9.
1943 *Thamnopora venezuelensis* (Weisbord) Wells: 99, pl. 10, fig. 10.

DIAGNOSIS. *Favosites*, apparently nodular in form, with monomorphic corallites, up to 2 mm diameter, having walls unthickened within the colony. Corallite walls heavily thickened in a subcalicular zone 5–7 mm deep so as to completely close the lumen in most cases. Squamulae present, particularly well developed in thickened zone. Mural pores uniserial, sporadically biserial, 0·3 mm diameter. Tabulae complete, horizontal, 7 in 5 mm.

HOLOTYPE. PRI 21597 (PRI 24428 same specimen). Loose block (?) in Caño del Norte; Caño Grande Fm., early Middle Devonian (upper Onesquethaw).

MATERIAL. R45079 (3121). Caño Grande; same horizon as holotype. R45101 (3182). Caño del Sur; same horizon as holotype.

DESCRIPTION. Nodular colonies; R45101 is partly crushed, 85 mm long and about 50 mm maximum diameter.

Internally, the corallites are polygonal in cross-section, 3 to 4 sided in immature stages and mainly 6 to 7 sided when mature. They range up to almost 2 mm diameter when measured between the axial plates of opposite walls but mature corallites average about 1·4 mm diameter. The corallite walls are thin with the axial plate about 0·01–0·02 mm thick coated on either side by fibronormal tissue 0·02 to 0·04 mm thick in mid-wall positions. The fibronormal tissue thickens slightly into the corners of the corallites which are slightly rounded. Mural pores appear sporadically in mid-wall or slightly offset positions. No definite indications of septal spines or squamulae are seen in cross-sections through the centre of the colony.

Tangential sections close to the colony surface show variable degrees of thickening of the corallite walls (Pl. 10, fig. 2). Thickening first builds up in the angles of the corallite walls so that the lumen becomes increasingly rounded. At the same level increasing signs of squamulae appear, of variable size with truncate or bluntly tapering ends. There are also very rare indications of what may be septal spines. Towards the colony surface, wall thickening may build up to almost or completely close the corallites. The mural pores however appear to be least affected by this excess thickening and even maintain close to their usual diameter when the corallites they connect are apparently closed. At the colony surface, the thickening rapidly diminishes leaving calices rounded and separated by walls about 0·3 mm thick at their midpoints.

In longitudinal section the tabulae are complete, flat or slightly arched or sagging, and fairly wide spaced 7 in 5 mm. They either cross from wall to wall or link facing squamulae. The squamulae are flat to very faintly trough-shaped plates directed horizontally in most cases. They are up to 0·8 mm long, 0·5 mm wide and become more strongly developed as wall thickening begins to build up where they average 0·6 mm apart vertically. Corallites are normal to the colony surface for about 10 mm or rather more of their length and the corallite walls start to thicken quite rapidly about 5–7 mm from the surface. Associated with the thickening, both squamulae and tabulae become more numerous, the former also becoming increasingly thickened. Mural pores are sectioned more frequently due to the thicker walls. They are large and circular about 0·3 mm diameter and usually 1 mm apart in single vertical rows. Most corallite walls show occasional doubling up of the pores with variable horizontal spacing. Many pores appear to be capped by squamulae but the relationship is apparently not invariable. In longitudinal section, the calices appear to be bowl or funnel shaped and 1 to 2 mm deep for the most part but there is considerable variability. Most but not all of them are floored by a zone where the infilling of the corallites is more or less complete.

Discussion. This description is based mainly on the new material collected by Bowen, particularly R45101, and considerably supplements the previous descriptions. In particular, the well developed squamulae in this species have not been recorded before.

The species should clearly be placed in *Favosites* as that genus is now understood. The character of the wall thickening in *F. venezuelensis* although apparently unique in its development is comparable with that seen in many other species of *Favosites* (for example see Ross 1953, pl. 21, fig. 6; Philip 1960, pl. 24, fig. 4), and is essentially a mature surface feature of the colony. In *Thamnopora* the corallites are more or less rounded throughout the colony.

F. venezuelensis shows some similarities with *Emmonsia radiciformis* (Stewart 1938 : 69, pl. 16, figs 8–10, *non* Rominger 1876 : 34, pl. 12) and to a lesser extent with *Emmonsia carmani* Stewart (1938 : 67, pl. 15, figs 1–3). Both these species from the Middle Devonian of Ohio, however, appear to be more intensely squamulate and lack the strong thickening of the distal corallite walls.

Favosites arbuscula Hall 1876

(Pl. 10, figs 3–6)

1876 *Favosites arbuscula* Hall, pl. 36, figs 1–9.
1953 *Favosites* (*Emmonsia*) *arbuscula* (Hall); Ross: 54, pl. 14, figs 2–9.
1965 *Emmonsia arbuscula* (Hall); Stumm: 65, pl. 64, fig. 13.

Diagnosis. Ramose *Favosites* with branches averaging 14 mm diameter. Corallites oblique or perpendicular to surface, 1·2 to 1·8 mm mean mature diameter. Walls 0·1 mm thick with little or no thickening at aperture. Mural pores 0·2 mm diameter, uniserial. Squamulae abundant, sometimes concentrated in distinct zones. Tabulae thin, often suspended from squamulae, 1–1·5 mm apart.

Material. R45102–3, R49264–5 (3182). Caño del Sur; Caño Grande Formation, early Middle Devonian (upper Onesquethaw).

Distribution. Middle Devonian (Hamilton Group and equivalent units) of eastern North America. Caño Grande Fm. (early Middle Devonian) of the Sierra de Perijá, Venezuela.

DESCRIPTION. Colonies ramose with branches averaging 14 mm diameter, close packed or diverging. Largest fragment 80 mm long branching twice in planes at right angles to each other.

In cross-section the corallites are three or four sided when immature, six or seven sided when mature. There is a tendency for mature and immature corallites to be arranged in a regular pattern. Mature corallite diameters reach 1·8 mm and average about 1·5 mm. Their walls are thin, the axial plate about 0·02 mm thick flanked on either side by fibronormal tissue 0·04 mm thick. There is only slight rounding of corallite angles internally. Mural pores are infrequently sectioned, always close to the mid-wall position and signs of septal spines or squamulae are extremely rare.

At the colony surface, corallite walls are slightly thickened up to about 0·25 mm from side to side and often irregularly scalloped or provided with very short stubby spines. The corallites are nearly all polygonal with rounded corners and are only rarely subcircular. Mural pores are sectioned more frequently and occasional signs of squamulae are seen.

In longitudinal section, the corallites diverge at a low angle to the axis of the branch and curve over to open at the surface somewhat obliquely. Internally corallite walls show slight irregular thickening and thinning with a more marked but only slightly thicker zone within 1 to 1·5 mm of the branch surface. Mural pores are infrequently sectioned up to 0·2 mm diameter and of indeterminate vertical spacing. Squamulae are present as generally unthickened plates of flat to shallow trough-shaped section, horizontally or slightly upwardly directed and about 0·5 mm long. They are concentrated about 0·25 mm vertically apart in distinct zones 1 to 2 mm deep and with a vertical frequency of 4 to 5 mm. The tabulae are complete, unthickened, flat to gently undulating and mostly wide spaced 1 to 1·5 mm but sometimes up to 4 mm apart. They are often suspended from the squamulae.

DISCUSSION. The Venezuelan material appears to agree in most respects with *Favosites arbuscula* Hall as redescribed by Ross (1953 : 54). Whether or not *Favosites digitata* Rominger (1876 : 39, pl. 15) is conspecific with and therefore a senior synonym of *F. arbuscula* cannot be determined in the absence of a modern description and illustration of Rominger's species. For the present it seems preferable to accept the well described *F. arbuscula*.

The Venezuelan material possesses a combination of characters within the range of *F. arbuscula* but not matched exactly in any of Ross' (1953 : 55) subspecies. No new subspecies designation is felt to be justified, however, and the material is referred to *F. arbuscula sensu lato*.

VI. REFERENCES

ALTEVOGT, G. 1968. Devonian tetracorals from Spain and their relation to North American species. *In* OSWALD, D. H. (Ed.) *International Symposium on the Devonian System*, Vol. **2** : 755–769, 2 pls. Calgary.

ARMSTRONG, A. K. 1962. Stratigraphy and palaeontology of the Mississippian System in southwestern New Mexico and adjacent southeastern Arizona. *Mem. Inst. Min. Technol. New Mex.*, Socorro, **8** : i–vi, 1–99, pls 1–12.

ARNOLD, H. C. 1966. Upper Palaeozoic Sabaneta-Palmarito sequence of Mérida Andes, Venezuela. *Bull. Am. Ass. Petrol. Geol.*, Tulsa, **50** : 2366–2387.

BASSLER, R. S. 1937. The Paleozoic rugose coral family Palaeocyclidae. *J. Paleont.*, Tulsa, **11** : 189–201.

BILLINGS, E. 1858. Report for the year 1857 of E. Billings, Esq., Palaeontologist, addressed to Sir W. E. Logan, F.R.S., Director of the Geological Survey of Canada. *Geol. Surv. Canada, Report of Progress for the year* 1857 : 147–192.

—— 1875. On some new or little known fossils from the Silurian and Devonian rocks of Ontario. *Can. Nat.*, Montreal, N.S., **7**, 4 : 230–240.

BIRENHEIDE, R. 1963. *Cyathophyllum-* und *Dohmophyllum-* Arten (Rugosa) aus dem Mitteldevon der Eifel. *Senckenburg. leth.*, Frankfurt a.M., **44** : 363–458, pls 46–62.

—— 1964. Die 'Cystimorpha' (Rugosa) aus dem Eifeler Devon. *Abh. Senckenb. naturforsch. Ges.*, Frankfurt a.m., **507** : 1–120, 28 pls.

BOWEN, J. M. 1972. Estratigrafía del Precretáceo en la parte norte de la Sierra de Perijá. *Boln Geol. Dir. Geol. Publ. Espec.*, Caracas, **5** : 729–761.

BRICE, D. 1971. Étude paléontologique et stratigraphique du Dévonien de l'Afghanistan. Contribution à la connaissance des brachiopodes et des polypiers rugueux. *Notes Mém. Moyen-Orient*, Paris, **11** : i–viii + 1–364, pls 1–20.

BUSCH, D. A. 1941. An ontogenetic study of some rugose corals from the Hamilton of western New York. *J. Paleont.*, Tulsa, **15**, 4 : 392–411, 73 text-figs.

CHRIST, P. 1927. La coupe géologique le long du chemin de Mucuchachí a Santa Bárbara dans le Andes Vénézueliennes. *Eclog. geol. Helv.*, Lausanne, **20**, 4 : 769–792.

DANA, J. D. 1846. Genera of fossil corals of the family Cyathophyllidae. *Am. J. Sci.* Arts., New Haven, (2), **1** : 178–189, text-figs 1–5.

DE GROOT, G. E. 1963. Rugose corals from the Carboniferous of Northern Palencia (Spain). *Doctor. Thesis Wis. Naturk. Rijksuniv. Leiden*, **1963** : 1–123, pls 1–26.

DYBOWSKI, W. N. 1873–4. *Monographie der Zoantharia sclerodermata rugosa aus der Silurformation Estlands, Nord-Livlands und der Insel Gotland . . .*, pp. 257–532, pls 1–5, Dorpat.

EASTON, W. H. 1960. Permian corals from Nevada and California. *J. Paleont.*, Tulsa, **34**, 3 : 570–583, 18 text-figs.

EDWARDS, H. M. & HAIME, J. 1850. A Monograph of the British Fossil Corals, Part 1. Introduction, etc.: i–lxxxv + 1–71, pls 1–11. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1851. Monographie des Polypiers fossiles des Terrains palaeozoïques. *Arch. Mus. natn. Hist. nat.* Paris, **5** : 1–501, pls. 1–20.

EHLERS, G. M. & STUMM, E. C. 1949. Corals of the Devonian Traverse Group of Michigan. Part II, *Cylindrophyllum, Depasophyllum, Disphyllum, Eridophyllum* and *Synaptophyllum*. *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **8**, 3 : 21–41, 8 pls.

FEDOROWSKI, J. 1965. Lindstroemiidae and Amplexocariniidae (Tetracoralla) from the Middle Devonian of Skały, Holy Cross Mountains, Poland. *Acta palaeont. pol.*, Warszawa, **10** : 335–363, pls 1–6.

—— 1967. The Lower Permian Tetracoralla and Tabulata from Treskelodden, Vestspitsbergen. *Norsk Polarinstitutt Skrifter*, Oslo, **142** : 1–44, 7 pls.

FENTON, C. L. & FENTON, M. A. 1938. *Heliophyllum* and '*Cystiphyllum*' corals of Hall's 'Illustrations of Devonian corals'. *Ann. Carneg. Mus.*, Pittsburgh, **27** : 207–250, pls 1–24.

FONTAINE, H. 1961. Les Madréporaires paléozoïques du Viêt-Nam, du Laos et du Cambodge. *Archs géol. Viêt-Nam*, Saigon, **5** : 1–276. Atlas, pls 1–35.

GIRTY, G. H. 1897. A revision of the sponges and coelenterates of the Lower Helderberg Group of New York. *New York State Mus., Ann. Rept*, Albany, **48**, 2 : 259–322.

HALL, J. 1843. *Geology of New York, pt.* 4, *comprising the survey of the Fourth geological district*, pp. i–xxviii + 1–683, tables pp. 1–68, pls 1–19, Albany, N.Y.

—— 1876. *Illustrations of Devonian fossils; corals of the upper Helderberg and Hamilton groups*, pp. 1–7, pls 1–39. Albany N.Y.

HALLER, W. 1936. Einige biostratigraphische Untersuchungen in der Rohrer Mulde unter besonderer Berücksichtigung der Keriophyllen. *Jb. preuß. geol. Landesanstalt*, Berlin, **56** : 590–632, pls 32–43.

HEA, J. P. & WHITMAN, A. B. 1960. Estratigrafía y petrología de los sedimentos precretácios de la parte norte-central de la Sierra de Perijá, Estado Zulia, Venezuela. *Boln Geol. Dir. Geol. Publ. Espec.*, Caracas **3,** 1 : 351–376.

HILL, D. 1956. *Rugosa. In* MOORE, R. C. (Ed.) *Treatise on Invertebrate Paleontology*, **F** : 233–324, text-figs 165–219. Lawrence, Kansas.

IVANOVSKII, A. B. 1963. *Rugozy ordovika i Silura Sibirskoi Platformy*, pp. 1–160, 33 pls. Nauka, Moskva. (In Russian).

—— 1965. *Drevneishie rugozy*, pp. 1–152, 39 pls. Nauka, Moskva. (In Russian).

JEFFORDS, R. M. 1955. Septal arrangement and ontogeny of some porpitid corals. *Palaeont. Contr. Univ. Kans.*, Lawrence, Coelent. Art 2 : 1–16.

JELL, J. S. 1969. Septal microstructure and classification of the Phillipsastraeidae. *In* CAMPBELL, K. S. W. (Ed.) *Stratigraphy and Palaeontology : Essays in honour of Dorothy Hill:* 50–73, pls 7, 8. Canberra.

KALJO, D. L. 1961. Dopolneniya k izucheniyu streptelazmid ordovika Estonii. *Geoloogia Inst. Uurim.*, Tallinn, **6** : 51–67, pls 1–4.

KAPLAN, A. A. 1969. Chetyrekhluchevye korally zhivetskikh otlozhenii beyanaula, chingiza i predchingizya. *Izv.vyssh.ucheb.Zaved.geol.raz.* Moscow, **12,** 1 : 19–29, 4 pls. (In Russian.)

KATO, M. 1963. Fine skeletal structures in Rugosa. *J. Fac. Sci. Hokkaido Univ.* (4, geol. min.) **11** : 571–630, 3 pls.

LAMARCK, J. B. P. DE 1816. *Histoire naturelle des animaux sans vertèbres*, **2** : 1–568. Paris.

LECOMPTE, M. 1939. Les tabulés du Dévonien moyen et supérieur du bord sud du bassin de Dinant. *Mém. Mus. r. Hist. nat. Belg.*, Bruxelles, **90** : 1–229, pls 1–23.

LE MAITRE, D. 1947. Le récif coralligène de Ouihalane. *Notes Mém. Serv. Mines Carte géol. Maroc*, **67** : 1–112, pls 1–24.

—— 1952. La faune du Dévonien Inférieur et Moyen de la Saoura et des abords de l'Erg el Djemel (Sud-Oranais). *Matér. Carte géol. Algér.*, Alger, 1. Paléont., **12** : 1–171, 22 pls.

LIDDLE, R. A., HARRIS, G. D., & WELLS, J. W. 1943. The Rio Cachirí section in the Sierra de Perijá, Venezuela. *Bull. Am. Paleont.*, Ithaca, **27** : 269–368 (1–100), pls 27–36 (1–10).

LINNAEUS, C. 1745. *Dissertatio, Corallia Baltica adumbrans, Quam . . . submittit Henricus Fougt*, pp. viii + 1–40, 1 pl. Upsala.

—— 1749. Corallia Baltica . . . proposita ab Henrico Fougt. *Amoen. Acad. Stockholm & Leipzig*, **4** : 74–106, pl. 4.

MILLER, J. B. 1962. Tectonic trends in Sierra de Perijá and adjacent parts of Venezuela and Columbia. *Bull. Am. Assoc. Petrol. Geol.*, Tulsa **46** : 1565–1595, 15 figs.

MILLER, S. A. 1889–1897. *North American geology and palaeontology . . . 3rd Edition*, pp. 1–664 (1889). *First Appendix*, pp. 665–718 (1892). *Second Appendix*, pp. 719–793 (1897). Cincinnati.

MINATO, M. 1961. Ontogenetic study of some Silurian corals of Gotland. *Stockh. Contr. Geol.*, **8,** 4 : 37–100, pls 1–22.

MINATO, M. & KATO, M. 1965a. Waagenophyllidae. *J. Fac. Sci. Hokkaido Univ.* (4, geol. min.), **12,** 3–4 : 1–241, 20 pls.

—— 1965b. Durhaminidae (Tetracoral). *J. Fac. Sci. Hokkaido Univ.* (4, geol. min.), **13,** 1 : 11–86, 5 pls.

MITCHELL, M. 1966. Comment on the proposed designation of a type-species for *Amplexizaphrentis* Vaughan, 1906 (Anthozoa). Z.N. (S.) 1669. *Bull. zool. Nomencl.* London, **23,** 2–3 : 82–83.

MOORE, R. C., HILL, D. & WELLS, J. W. 1956. *Glossary of morphological terms applied to corals. In* MOORE, R. C. (Ed.) *Treatise on Invertebrate Paleontology*, **F** : 245–251. Lawrence, Kansas.

MOORE, R. C. & JEFFORDS, R. M. 1945. Description of Lower Pennsylvanian corals from Texas and adjacent areas. *Publs. Bur. econ. Geol. Univ. Tex.* Austin, **4401** : 77–208, 214 figs.

MORALES, P. A. 1965. A contribution to the knowledge of the Devonian faunas of Colombia. *Boln Geol. Fac. Petròl. Univ. ind. Santander* **19** : 51–111, 9 pls.

NEUMAN, B. 1969. Upper Ordovician streptelasmatid corals from Scandinavia. *Bull. geol. Instn Univ. Uppsala*, N.S. **1**, 1 : 1–73, 59 figs.

O'CONNELL, M. 1914. Revision of the genus *Zaphrentis*. *Ann. N.Y. Acad. Sci.*, **23** : 177–192.

OLIVER, W. A., Jr. 1958. Significance of external form in some Onondagan rugose corals. *J. Paleont.*, Tulsa, **32**, 5 : 815–837, pls 104–106.

—— 1960a. Rugose corals from reef limestones in the Lower Devonian of New York. *J. Paleont.*, Tulsa, **34**, 1 : 59–100, pls 13–19.

—— 1960b. Devonian rugose corals from northern Maine. *Bull. U.S. Geol. Surv.*, Washington, **1111A** : 1–23, pls 1–5.

—— 1963. A new *Kodonophyllum* and associated rugose corals from the Lake Matapedia area, Quebec. *Prof. Pap. U.S. geol. Surv.*, Washington, **430-C** : 21–31, pls 9–14.

—— 1968. Succession of rugose coral faunas in the Lower and Middle Devonian of eastern North America. *In* OSWALD, D. H. (Ed.) *International Symposium on the Devonian System*, Vol. **2** : 733–744. Calgary.

OPINION 854. 1968. *Amplexizaphrentis* Vaughan, 1906 (Anthozoa) : designation of a type-species under the plenary powers. *Bull. zool. Nomencl.* London, **25**, 2–3 : 82–83.

PEDDER, A. E. H. 1966. The Devonian tetracoral *Haplothecia* and new Australian phacellophyllids. *Proc. Linn. Soc., N.S.W.*, Sydney, **90** : 181–189, pl. 6.

PHILIP, G. M. 1960. The Middle Palaeozoic squamulate favositids of Victoria. *Palaeontology*, London, **3** : 186–207, pls 30–34.

QUENSTEDT, F. A. VON. 1878–81. *Petrefactenkunde Deutschlands*, **6.** *Die Rohren- und Sternkorallen.*, pp. 1–144 (1878); 145–624 (1879); 625–912 (1880); 913–1094 (1881); and Atlas. Leipzig.

ROMINGER, C. 1876. Palaeontology. Fossil Corals. *Geol. Surv. Michigan*, Lansing, **3**, 2 : 1–161, 55 pls.

ROSS, M. H. 1953. The Favositidae of the Hamilton Group (Middle Devonian of New York). *Bull. Buffalo Soc. nat. Sci.*, **21** : 37–89, pls 12–27.

ROWETT, C. L. & SUTHERLAND, P. K. 1964. Wapanucka Rugose Corals. *Bull. Okla geol. Surv.* Norman, **104** : 1–124, pls 1–9.

SCHEFFEN, W. 1933. Die Zoantharia Rugosa des Silurs auf Ringerike im Oslogebiet. *Skr. norske Vidensk-Akad. mat.-nat. Kl.*, Oslo, **1932**, 5 : 1–64, 11 pls.

SCHLÜTER, C. 1885. Ueber neue Korallen aus dem mitteldevon der Eifel. *Sber. niederrhein. Ges. Nat. u. Heilk.*, Bonn, **1885** : 6–13.

SCRUTTON, C. T. 1968. Colonial Phillipsastraeidae from the Devonian of south-east Devon, England. *Bull. Br. Mus. nat. Hist.* (Geol.), **15**, 5 : 181–281, 18 pls.

—— 1971. Palaeozoic coral faunas from Venezuela, I. Silurian and Permo-Carboniferous corals from the Mérida Andes. *Bull. Br. Mus. nat. Hist.*, (Geol.), **20**, 5 : 183–227, 5 pls.

SHRESTHA, C. L. 1966. *Amplexizaphrentis* Vaughan, 1906 (Anthozoa): proposed designation of a type-species under the plenary powers. Z.N. (S.) 1669. *Bull. zool. Nomencl.* London, **22**, 5–6 : 348–350.

SIMPSON, G. B. 1900. Preliminary descriptions of new genera of Paleozoic rugose corals. *Bull. N.Y. St. Mus.* Albany, **8**, 39 : 199–222.

SMITH, S. 1945. Upper Devonian corals of the Mackenzie River region, Canada. *Spec. Pap. geol. Soc. Am.*, New York, **59** : viii + 1–126, pls 1–35.

SOSHKINA, E. D. 1949. Devonskie korally Rugosa Urala. *Trudy paleont. Inst.*, Leningrad, **15** : 1–160, pls 1–58. (In Russian.)

SOSHKINA, E. D. & KABAKOVICH, N. V. 1962. Podotryad Streptelasmatina. *In* ORLOV, U. A. (Ed.) *Osnovy paleontologii*, 2. *Gubki, Arkheotsiaty, Kishechnopolostnye, Chervi*: 317–324. Moscow. (In Russian.)

STEPHENS, C. H. 1967. Leonardian (Permian) compound corals of Nevada. *J. Paleont.*, Tulsa, **41**, 2 : 423–431, pls 52–54.

STEWART, G. A. 1938. Middle Devonian corals of Ohio. *Sp. Pap. Geol. Soc. Am.*, New York, **8** : vii + 1–120, 20 pls.

STUMM, E. C. 1949. Revision of the families and genera of the Devonian Tetracorals. *Mem. geol. Soc. Am.*, New York, **40** : viii + 1–92, pls 1–25.

—— 1962. Corals of the Traverse Group of Michigan. Part VIII, *Stereolasma* and *Heterophrentis*. *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **17**, 10 : 233–240, 2 pls.

—— 1965. Silurian and Devonian corals of the Falls of the Ohio. *Mem. geol. Soc. Am.*, New York, **93** : x + 1–184, 80 pls. (Dated 1964 but published January 1965, *vide* Dr W. A. Oliver, Jr.).

—— 1968. The corals of the Middle Devonian Tenmile Creek Dolomite of northwestern Ohio. *Contr. Mus. Paleont. Univ. Mich.* Ann Arbor, **22**, 3 : 37–44, 3 pls.

STUMM, E. C. & TYLER, J. H. 1962. Corals of the Traverse Group of Michigan. Part IX, *Heliophyllum*. *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **17**, 12 : 265–276, 3 pls.

STUMM, E. C. & WATKINS, J. L. 1961. The metriophylloid coral genera *Stereolasma*, *Amplexiphyllum* and *Stewartophyllum* from the Devonian Hamilton Group of New York. *J. Paleont.*, Tulsa, **35**, 3 : 445–447, pl. 58.

SUTHERLAND, P. K. 1958. Carboniferous stratigraphy and rugose coral faunas of Northeastern British Columbia. *Mem. Geol. Surv. Can.*, Ottawa, **295**, 1–177, pls 1–33.

—— 1970. A redescription of the Silurian rugose coral *Syringaxon siluriense* (McCoy). *J. Paleont.*, Tulsa **44**, 6 : 1125–1128, pl. 152.

SUTHERLAND, P. K. & HAUGH, B. N. 1969. The discoid rugose coral *Gymnophyllum*: growth form and morphology. *In* CAMPBELL, K. S. W. (Ed.) *Stratigraphy and Palaeontology: Essays in honour of Dorothy Hill*: 27–42, pls 3, 4. Canberra.

SUTTON, F. A. 1946. Geology of Maricaibo Basin, Venezuela. *Bull. Am. Ass. Petrol. Geol.*, Tulsa, **30** : 1621–1741, pls 1–9.

THOMPSON, J. 1881. On the genus *Alveolites*, *Amplexus*, and *Zaphrentis*, from the Carboniferous System of Scotland. *Proc. R. phil. Soc. Glasg.*, **13** : 194–237, 4 pls.

VAUGHAN, A. 1906. An account of the faunal succession and correlation. *In* MATLEY, C. A. & VAUGHAN, A. The Carboniferous rocks at Rush (County Dublin). *Q. Jl geol. Soc. Lond.*, **71** : 1–52.

WANG, H. C. 1948. The Middle Devonian rugose corals of eastern Yunnan. *Contr. Geol. Inst., Nat. Univ. Peking*, **33** : 1–45, 5 pls.

WEBBY, B. D. 1964. Devonian corals and brachiopods from the Brendon Hills, West Somerset. *Palaeontology*, London, **7**, 1 : 1–22, pl. 1.

WEDEKIND, R. & VOLLBRECHT, E. 1931. Die Lytophyllidae des mittleren Mitteldevon der Eifel. *Palaeontographica*, Stuttgart, **75** : 81–110, pls 15–46.

WEISBORD, N. E. 1926. Venezuelan Devonian Fossils. *Bull. Am. Paleont.*, Ithaca, **11** : 221–256 (1–36), pls 35–41 (1–7).

—— 1968. The Devonian System in Western Venezuela. *In* OSWALD, D. H. (Ed.) *International Symposium on the Devonian System*, Vol. **2** : 215–226, 2 figs. Calgary.

WELLS, J. W. 1937. Individual variation in the rugose coral species *Heliophyllum halli* E. & H. *Palaeontogr. Am.*, Ithaca, **2**, 6 : 1–22, pl. 1.

—— 1943. Anthozoa. *In* LIDDLE, R. A., HARRIS, G. D. & WELLS, J. W. The Rio Cachirí section in the Sierra de Perijá, Venezuela. *Bull. Am. Paleont.*, Ithaca, **27** : 363–368 (95–100), pl. 36 (10).

WEYER, D. 1965. Uber *Amplexus zaphrentiformis* White 1876 (Pterocorallia; Oberkarbon, Pennsylvanian). *Geologie*, Berlin, **14** : 449–463, 2 pls.

WILSON, E. C. & LANGENHEIM, R. L., Jr. 1962. Rugose and tabulate corals from Permian rocks in the Ely Quadrangle, White Pine County, Nevada. *J. Paleont.*, Tulsa, **36**, 3 : 495–520, pl. 86–89.

VII. APPENDIX—COMPOSITION AND LOCATION OF SAMPLES

The most accurate system for the location of samples available is by means of the Maracaibo Cathedral co-ordinates employed by Compañia Shell de Venezuela on their 1 : 10,000 topographic maps. The co-ordinates are in km. All the localities are in the northern part of the Sierra de Perijá, Zulia State, Venezuela and the locations of *in situ* samples are plotted in Text-figs 1 and 2.

Caño Los Guineos Formation

Caño Los Guineos section:

3849	*Heliophyllum halli*	S 11·32	W 97·58
	Heterophrentis (*H.*) *simplex*		
	Stereolasma sp.		
	Syringaxon sp.		

Caño Grande Formation

Caño Grande section:

3121	*Bowenelasma typa*	N 10·11	W 89·36
	Favosites venezuelensis		
	Heliophyllum halli		
3124	*Heliophyllum halli*	N 10·04	W 89·34
3126	*Heliophyllum wellsi*	N 10·02	W 89·32
3129	*Briantelasma oliveri*	N 9·99	W 89·28
3145	*Heliophyllum halli*	N 9·81	W 89·11
3149	*Bowenelasma typa*	N 9·70	W 89·10
	Heliophyllum halli		
3154	? *Bowenelasma breviseptata*	N 9·79	W 86·06
	Heliophyllum halli		
	Plasmophyllum sp.		
3157	*Bowenelasma typa*	N 9·81	W 89·04
	? *Briantelasma oliveri*		
	Heliophyllum halli		
	Plasmophyllum secundum americanum		

Caño del Sur section:

3182	*Favosites arbuscula*	N 9·56	W 88·78
	F. venezuelensis		
3199	*Bowenelasma breviseptata*	N 9·29	W 89·25
	Heliophyllum halli		
3221	*Briantelasma* sp.	N 9·05	W 89·79
	Heliophyllum halli		
	Plasmophyllum secundum americanum		

	Caño del Oeste section (boulder):		
3323	*Bowenelasma typa*	N 12·83	W 87·79
	Briantelasma sp.		
	Heliophyllum halli		
	Caño Colorado section:		
3618	*Bowenelasma typa*	N 6·01	W 91·98
	Briantelasma oliveri		
	Heliophyllum halli		
3619	*Bowenelasma breviseptata*	N 6·01	W 91·98
	Heliophyllum halli		

Caño Grande Fm. or lower Caño de Oeste Fm.

	Caño Pescado section (slipped block):		
3539	*Cylindrophyllum elongatum*	N 6·32	W 89·83

Caño del Oeste Formation

	Caño Grande section:		
3243	*Hadrophyllum* sp.	N 9·69	W 88·11
	? *Stewartophyllum* sp.		

Río Palmar Formation

	Caño del Norte section:		
3495	? *Durhamina* sp.	N 16·97	W 85·97
	Caño Colorado section:		
3784	*Amplexizaphrentis sutherlandi*	N 3·11	W 90·47

? Río Palmar Formation

	Caño Grande section (boulder):		
3270	*Durhamina* sp. nov.	N 10·51	W 86·68

Dr Colin T. Scrutton,
Department of Geology
The University
Newcastle upon Tyne.
NE1 7RU.

PLATE 1

Syringaxon sp.

FIGS 1, 2. Cross-sections (slides). R45130b, a. ×6.
FIG. 3. Longitudinal section (slide). R45130k. ×6.
Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian.

?*Stewartophyllum* sp.

FIGS 4, 5. Cross-sections (slides). R45110b, a. ×2·5.
Caño Grande; Caño del Oeste Fm., early Middle Devonian.

Stereolasma sp.

FIG. 6. Cross-section (slide). R45129a. ×3.
FIG. 7. Longitudinal section in counter-cardinal plane; C on left (slide). R45129g. × 3.
Caño Los Guineos; Caño Los Guineos Fm., early Middle Devonian.

Hadrophyllum sp.

FIG. 8. Cross-section (polished surface). R49275. ×2·5.
Caño Grande; Caño del Oeste Fm., early Middle Devonian.

Amplexizaphrentis sutherlandi sp. nov.

FIG. 9. Cross-section (peel), early ephebic stage. R45127b (taken from holotype). ×3.
FIG. 10. Cross-section (slide), early neanic stage 16 mm below R45127b. R45127a (cut from holotype). ×3.
FIG. 11. Cross-section (peel), neanic stage 14 mm below R45127b. R45127d (taken from holotype). ×3.
FIG. 12. Longitudinal section in counter-cardinal plane; C on right (slide). R45127e (cut from holotype). ×3.
FIG. 13. Longitudinal section in counter-cardinal plane; C on left (slide). R49291b. ×2.
Both Caño Colorado; Río Palmar Fm., Lr. Pennslyvanian.

All cross-sections orientated with the cardinal septum at top centre.

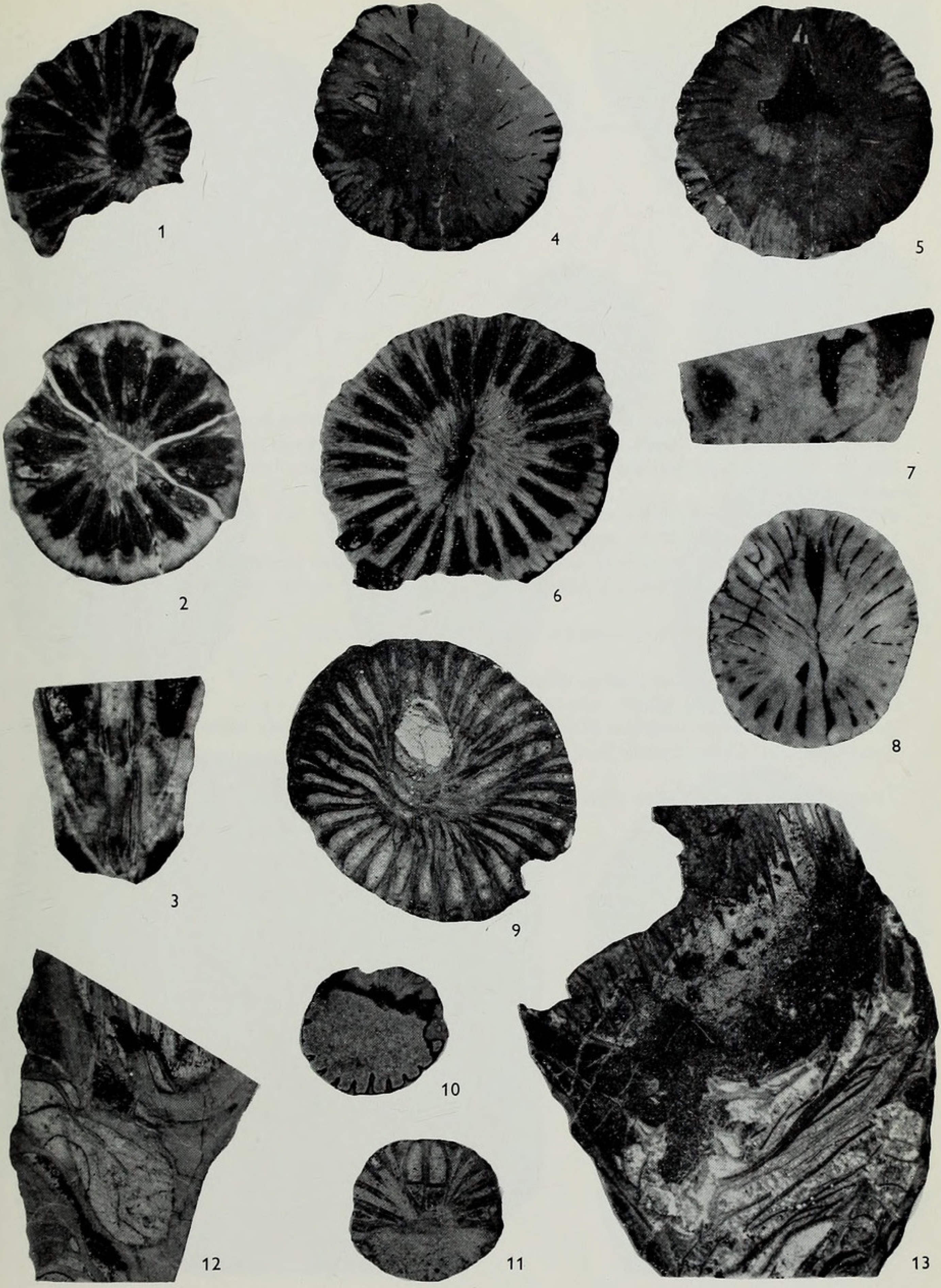

1
4
5
2
6
7
8
3
9
12
10
11
13

PLATE 2

Bowenelasma typa gen. et sp. nov.

FIG. 1. Cross-section (slide), ephebic stage. R45094b (cut from holotype). ×2.
FIG. 2. Cross-section (peel), neanic stage. R45094d (taken from holotype). ×2.
FIG. 3. Longitudinal section in counter-cardinal plane; C on left (slide). R45094e (cut from holotype). ×2.
FIG. 4. Cross-section (slide), early neanic stage. R45100b. ×4.
FIG. 5. Cross-section (slide), ephebic stage. R45100a. ×2.
FIG. 6. Longitudinal section in counter-cardinal plane; C on left (slide). R45100c. ×2.
FIG. 7. Cross-section (slide), ephebic stage, to illustrate septal structure. R45094b (cut from holotype). ×6.
Both Caño Grande; Caño Grande Fm., early Middle Devonian.

FIGS 8, 9. Cross-sections (peels), neanic stage. R45121f, e. ×2.
FIG. 10. Cross-section (slide), sub-calicular level. R45121a. ×2.
FIG. 11. Longitudinal section in counter-cardinal plane; C on left (slide). R45121h. ×2.
Caño Colorado; Caño Grande Fm., early Middle Devonian.

All cross-sections orientated with the cardinal septum at top centre.

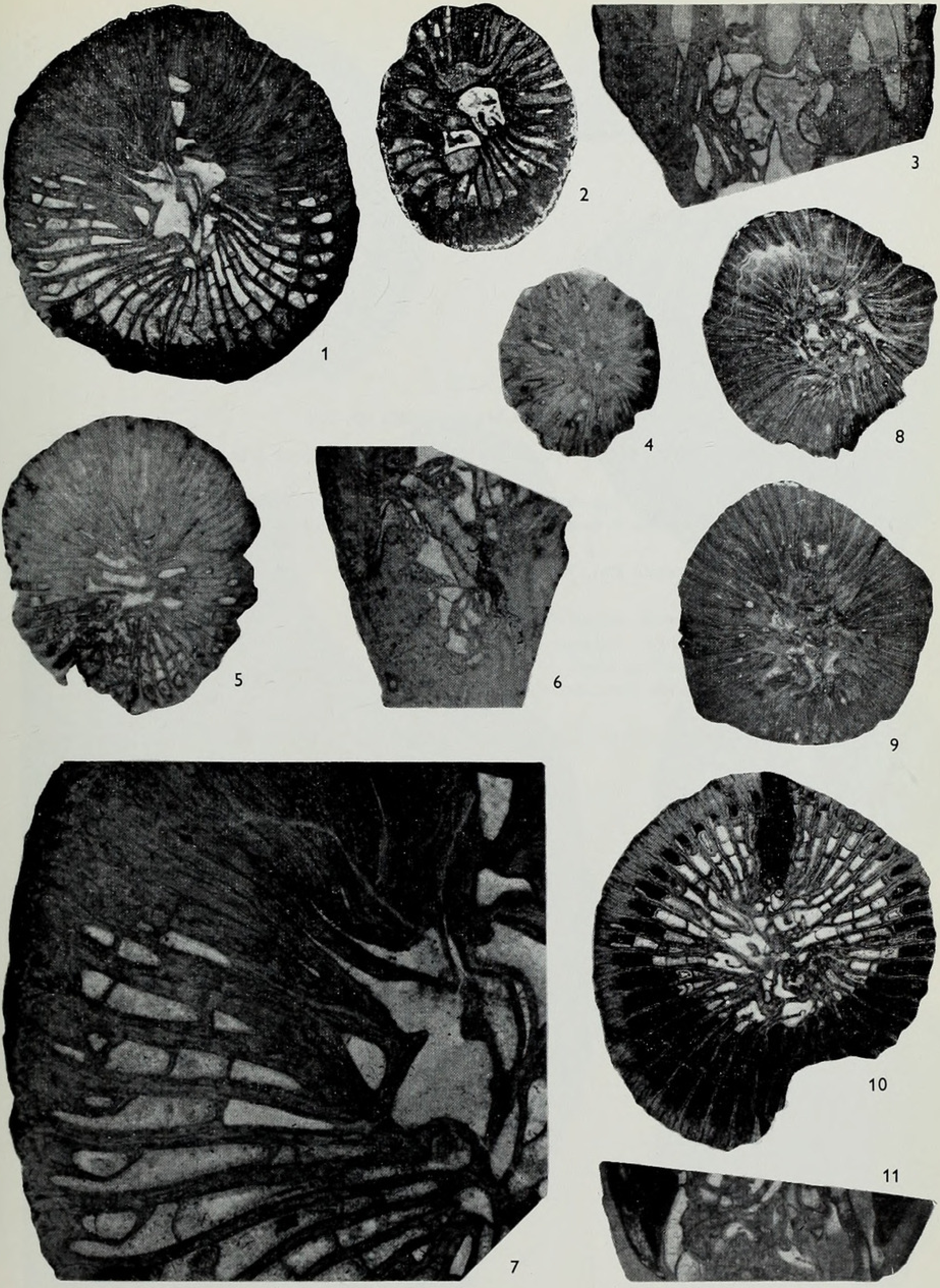

1
2
3
4
5
6
7
8
9
10
11

PLATE 3

Bowenelasma breviseptata sp. nov.

FIGS 1, 2. Cross-section (slide), ephebic stage. R45123a (cut from holotype). Fig. 1 ×2; fig. 2, ×6.

FIG. 3. Cross-section (slide), neanic stage. R45123b (cut from holotype). ×2.

FIG. 4. Longitudinal section in counter-cardinal plane; C on left (slide). R45123d (cut from holotype). ×2.

Caño Colorado; Caño Grande Fm., early Middle Devonian.

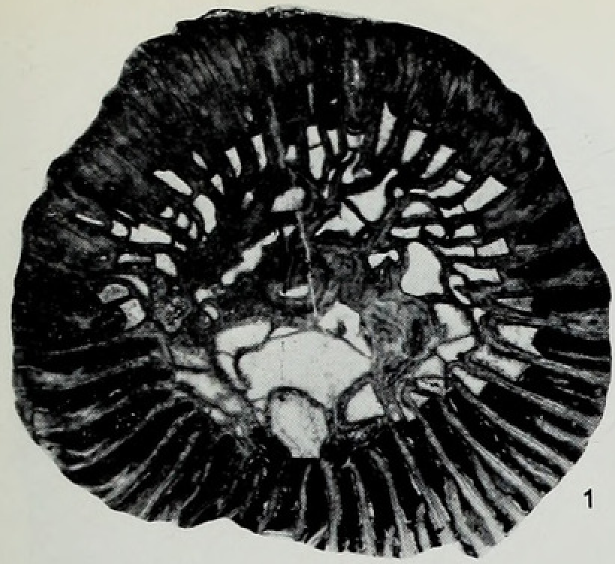
FIG. 5. Cross-section (peel), neanic stage. R45105c. ×2.

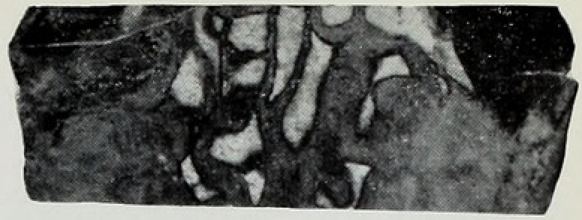
FIG. 6. Cross-section (slide), ephebic stage. R45105b. ×2.

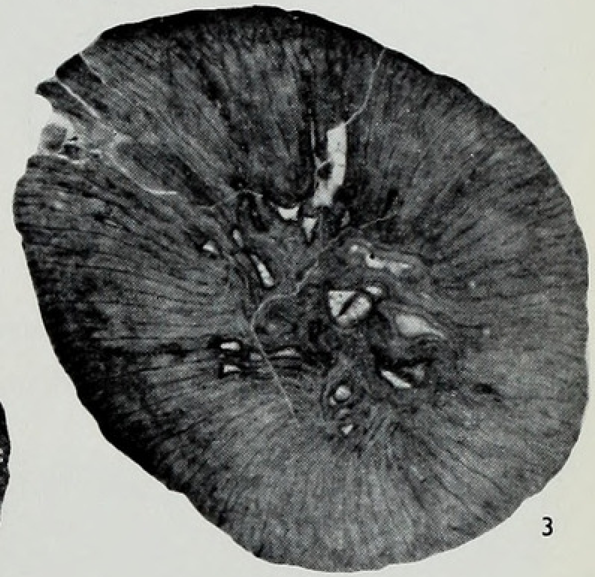
FIG. 7. Longitudinal section (slide). R45105d. ×2.

Caño del Sur; Caño Grande Fm., early Middle Devonian.

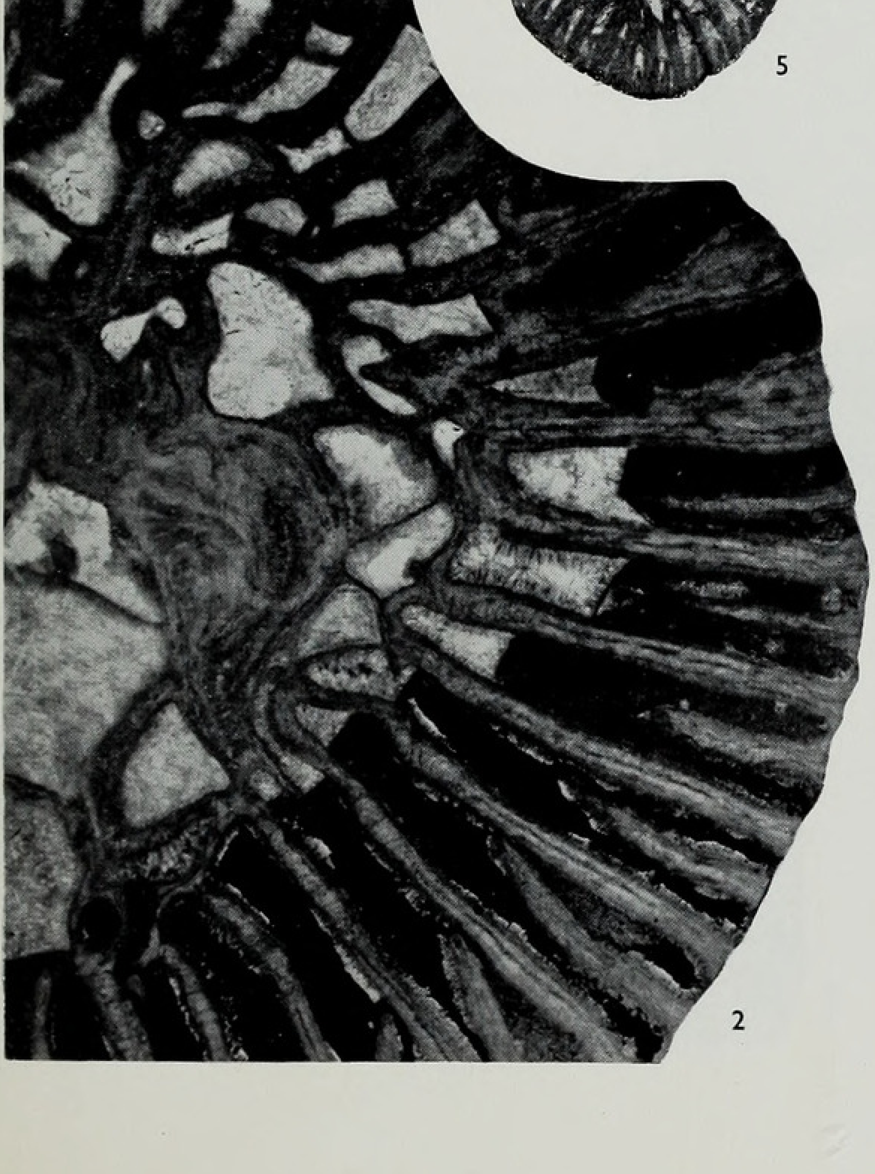
All cross-sections orientated with the cardinal septum at top centre.

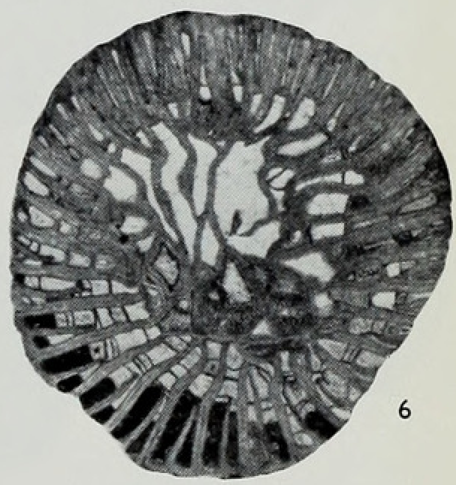

1


4


3


5


2


6

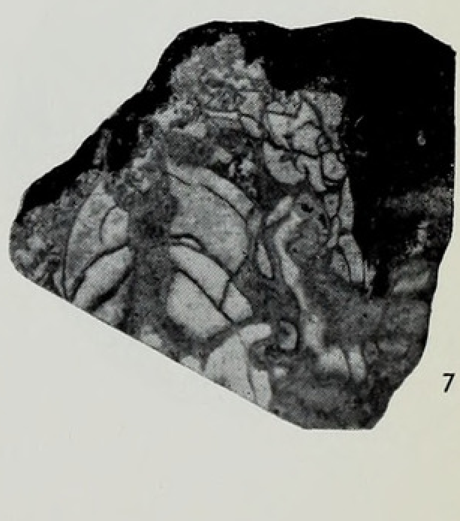

7

PLATE 4

Briantelasma oliveri sp. nov.

FIGS 1, 2. Cross-section (slide), sub-calicular. R45090b (cut from holotype). Fig. 1, ×2; fig. 2, ×4.

FIG. 3. Cross-section (slide), ephebic stage. R45090a (cut from holotype). ×2.

FIG. 4. Longitudinal section (slide) in counter-cardinal plane; C on right. R45090e (cut from holotype). ×2.

FIG. 5. Cross-section (slide), neanic stage. R45091a. ×3.

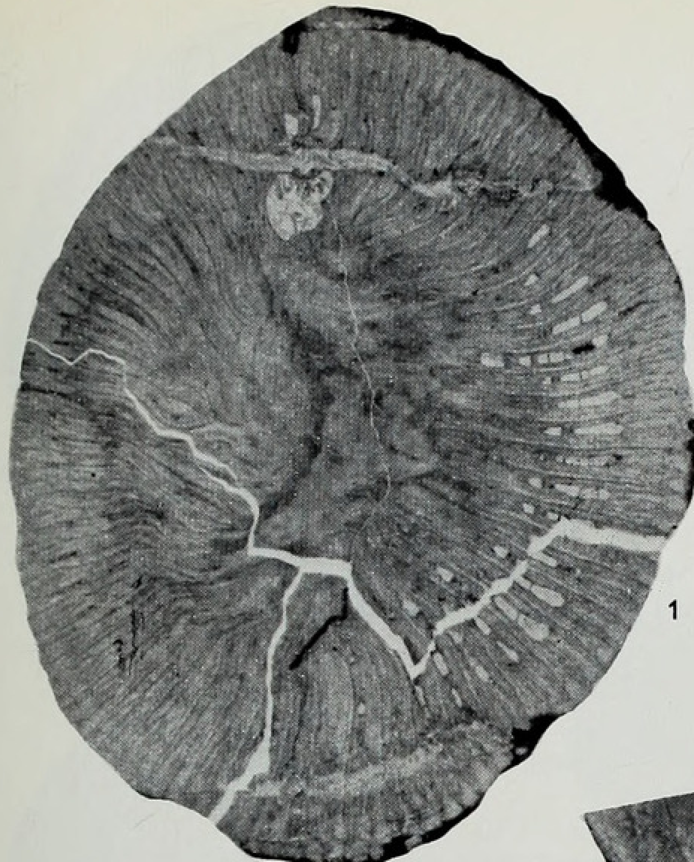
FIG. 6. Cross-section (slide), ephebic stage. R45091b. ×2.

Both Caño Grande; Caño Grande Fm., early Middle Devonian.

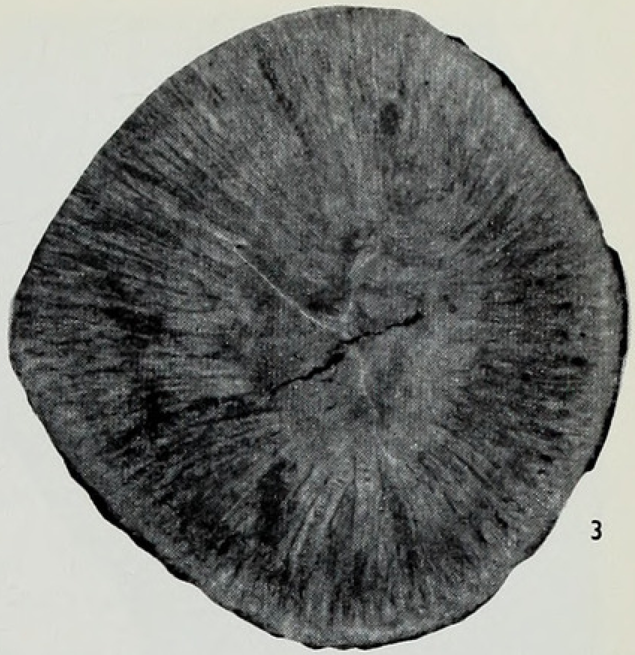
FIG. 7. Cross-section (slide), sub-calicular. R49290a. ×2.

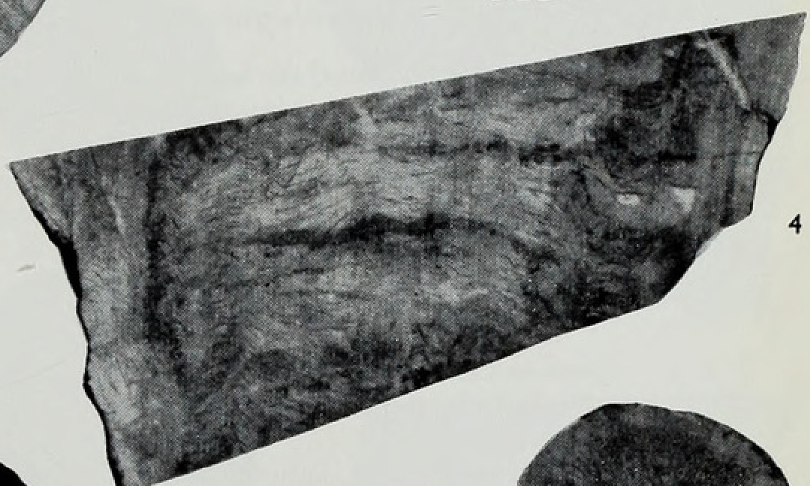
Caño Colorado; Caño Grande Fm., early Middle Devonian.

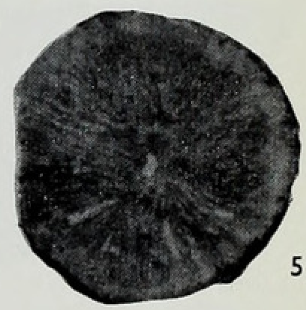
All cross-sections orientated with the cardinal septum at top centre.

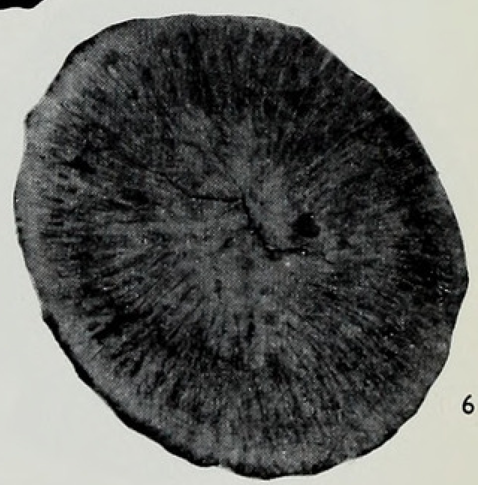

1


2


3


4


5


6


7

PLATE 5

Heterophrentis (H.) venezuelensis (Weisbord)

FIG. 1. Cross-section (peel), ephebic stage. PRI 21594/PRI 24421 (taken from lectotype). ×2.
FIG. 2. Longitudinal section (peel). PRI 24421 (taken from lectotype). ×1·5.
?Loose boulder in Caño del Norte; Caño Grande Fm., early Middle Devonian.

Heterophrentis (H.) simplex (Hall)

FIG. 3. Cross-section (polished surface), ephebic stage. NYSM 360 (holotype). ×1·5.
Moscow, New York; Middle Devonian (Hamilton Group).

FIG. 4. Cross-section (polished surface), neanic stage. PRI 21593. ×1·5.
FIG. 5. Cross-section (polished surface), ephebic stage. PRI 21593. ×1·5.
?Loose boulder in Caño del Norte; Caño Grande Fm., early Middle Devonian.

Heliophyllum halli Edwards & Haime

FIG. 6. Cross-section (slide), ephebic stage. R45115a. ×2.
Loose boulder in Caño del Oeste; Caño Grande Fm., early Middle Devonian.

FIG. 7. Cross-section (slide), ephebic stage. R49289a. ×2.
FIG. 8. Longitudinal section in counter-cardinal plane; C on right (slide). R49289b. ×2.
Caño Colorado; Caño Grande Fm., early Middle Devonian.

All cross-sections orientated with the cardinal septum at top centre.

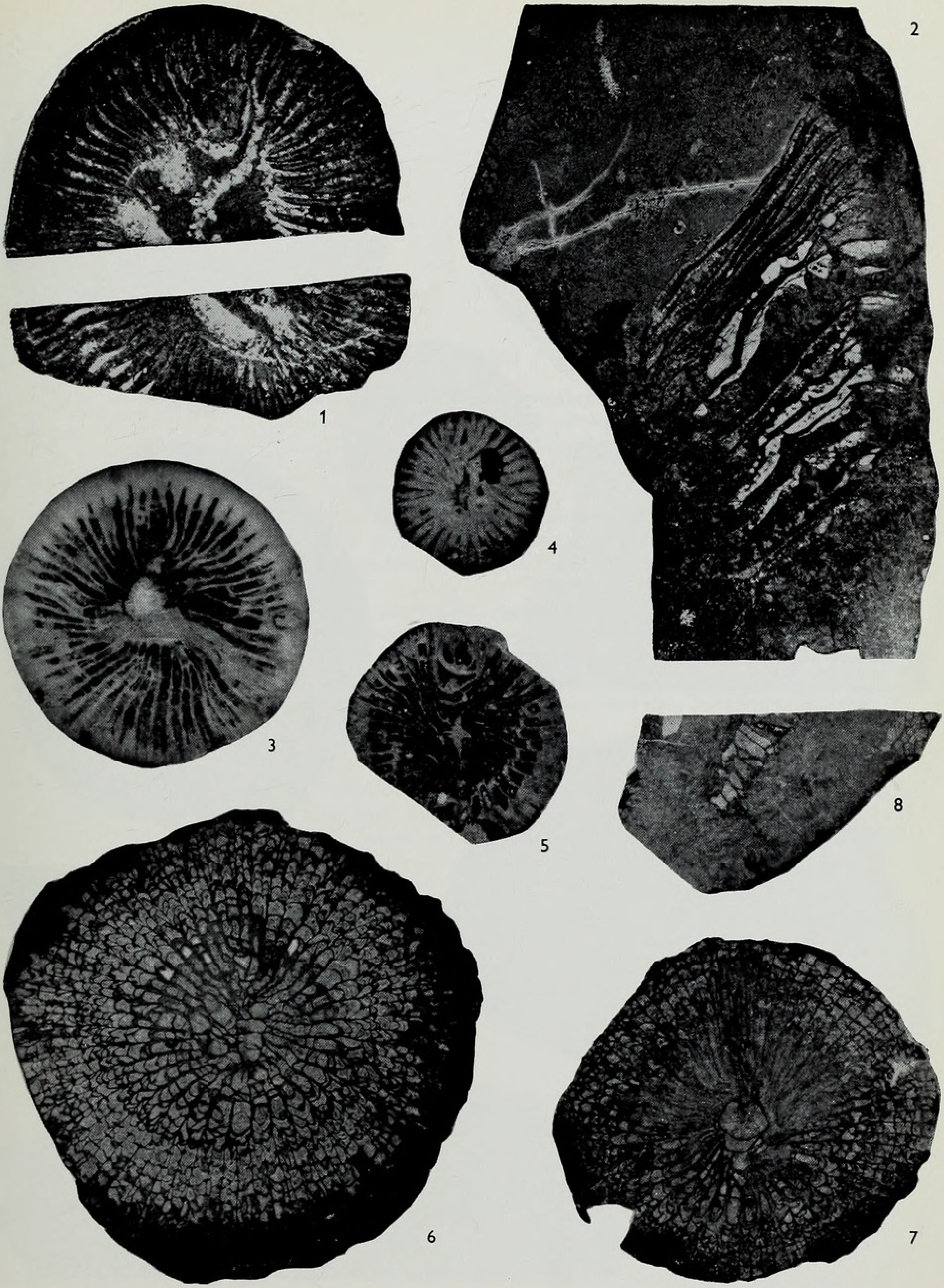

1
2
3
4
5
6
7
8

PLATE 6

Heliophyllum halli Edwards & Haime

FIG. 1. Cross-section (slide), ephebic stage. R45104a. ×2.
FIG. 2. Cross-section (slide), neanic stage. R45104c. ×2.
Caño del Sur; Caño Grande Fm., early Middle Devonian.

FIG. 3. Cross-section (slide), ephebic stage. R45092b. ×2.
FIG. 4. Longitudinal section in counter-cardinal plane; C on left (slide). R45092c. ×2
Caño Grande; Caño Grande Fm., early Middle Devonian.

FIG. 5. Cross-section (slide), ephebic stage. R49278a. ×2.
FIG. 6. Longitudinal section in counter-cardinal plane; C on left (slide). R49278d. ×2.
Loose boulder in Caño del Oeste; Caño Grande Fm., early Middle Devonian.

All sections orientated with the cardinal septum at top centre.

Heliophyllum wellsi sp. nov.

FIG. 7. Cross-section (slide), ephebic stage. R45088b (cut from holotype). ×1.
FIG. 8. Longitudinal section (slide). R45088e (cut from holotype). ×1·5.
Caño Grande; Caño Grande Fm., early Middle Devonian.

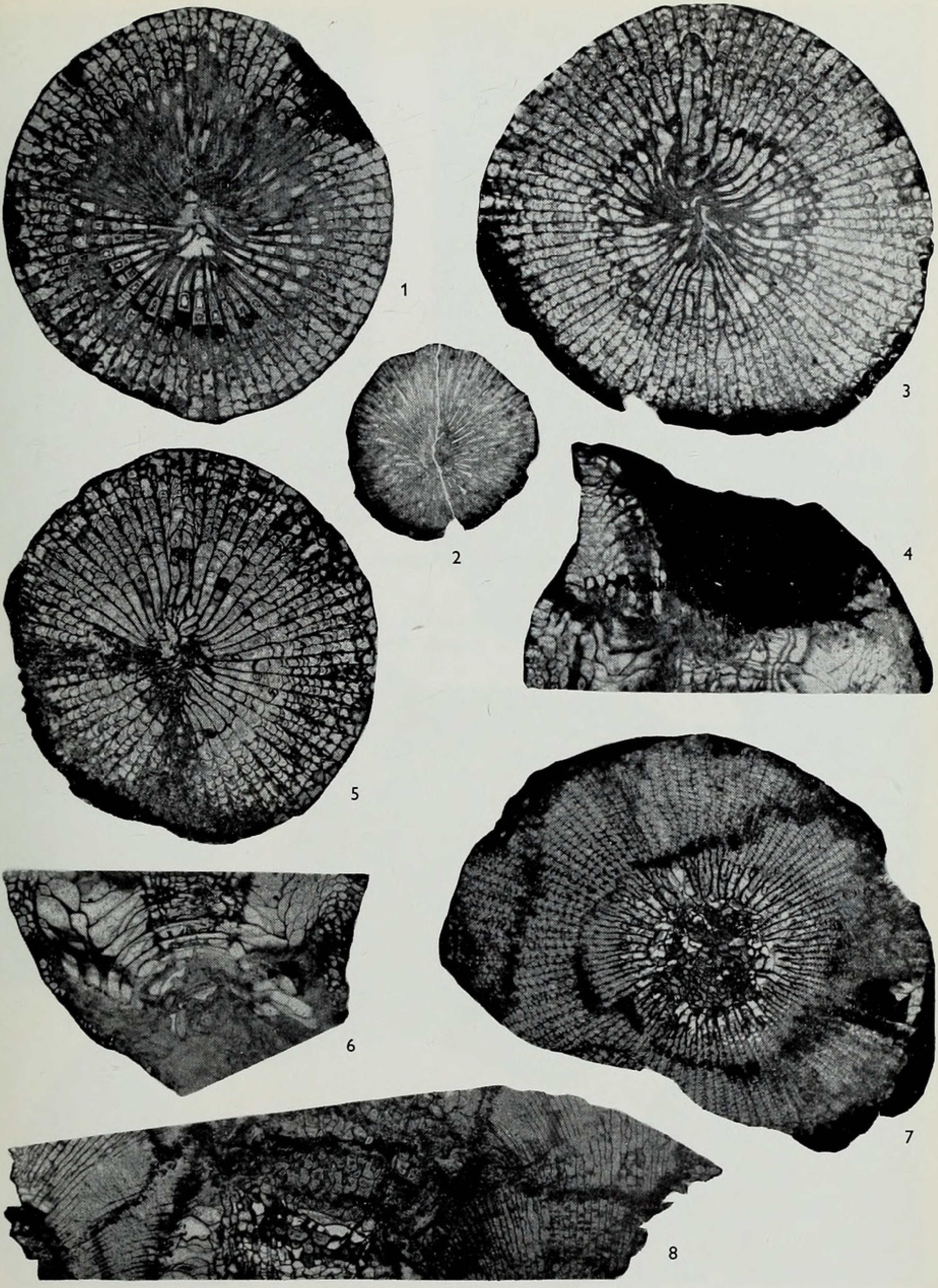

1
2
3
4
5
6
7
8

PLATE 7

Heliophyllum wellsi sp. nov.

FIGS 1, 2. Cross-sections (slides), illustrating character of axial structure in ephebic stage. R45088a, b (both cut from holotype). ×2.
Caño Grande; Caño Grande Fm., early Middle Devonian.

Cylindrophyllum elongatum Simpson

FIG. 3. Cross-section (slide). R45116a. ×2·5.
FIGS 4–6. Longitudinal sections (slides). R45116h, j, g. ×2·5.
Loose block in Caño Pescado; either Caño Grande Fm. or low in Caño del Oeste Fm., early Middle Devonian.

?***Durhamina*** sp.

FIG. 7. Cross-section (slide). R49285a. ×4.
FIG. 8. Longitudinal section (slide). R49285b. ×4.
Caño del Norte; Río Palmar Fm., Lr. Pennsylvanian.

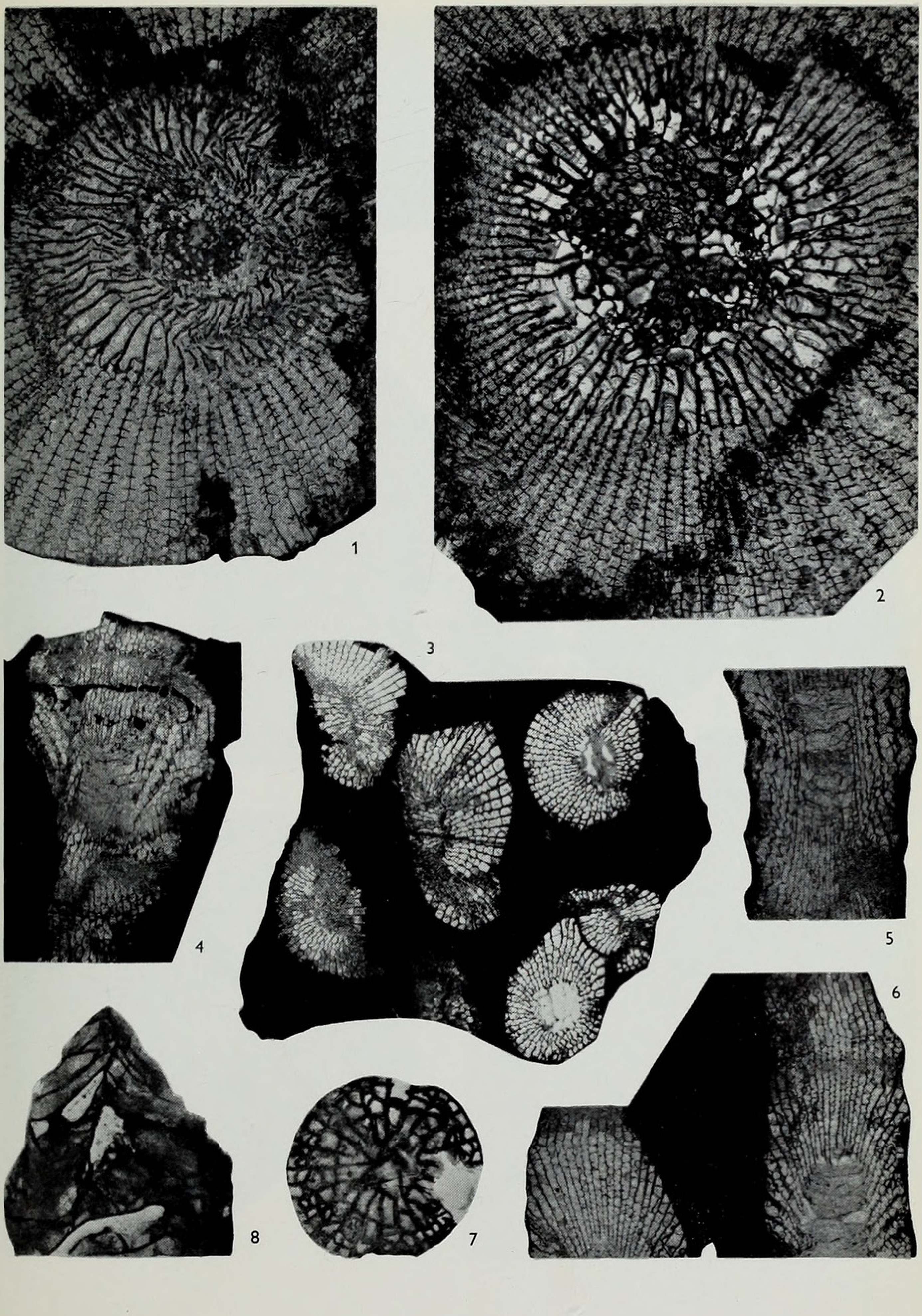

1
2
3
4
5
6
7
8

PLATE 8

Durhamina sp. nov.

FIG. 1. Cross-section (slide) of corallite arrangement in colony. R49276b. ×1.

FIG. 2. Cross-section (slide) of corallite with third order septa. R49276b. ×6.

FIGS 3–4. Cross-sections (slides) showing variation in appearance of mature corallites. R49276c, a. ×2.

FIGS 5–7. Cross-sections (slide) of immature corallites. R49276a. ×4.

FIGS 8–10. Longitudinal sections (slides), fig. 8 showing increase. R49276h, i, j. ×2.

Loose block in Caño Grande; Carboniferous, (?Río Palmar Fm., Lr. Pennsylvanian).

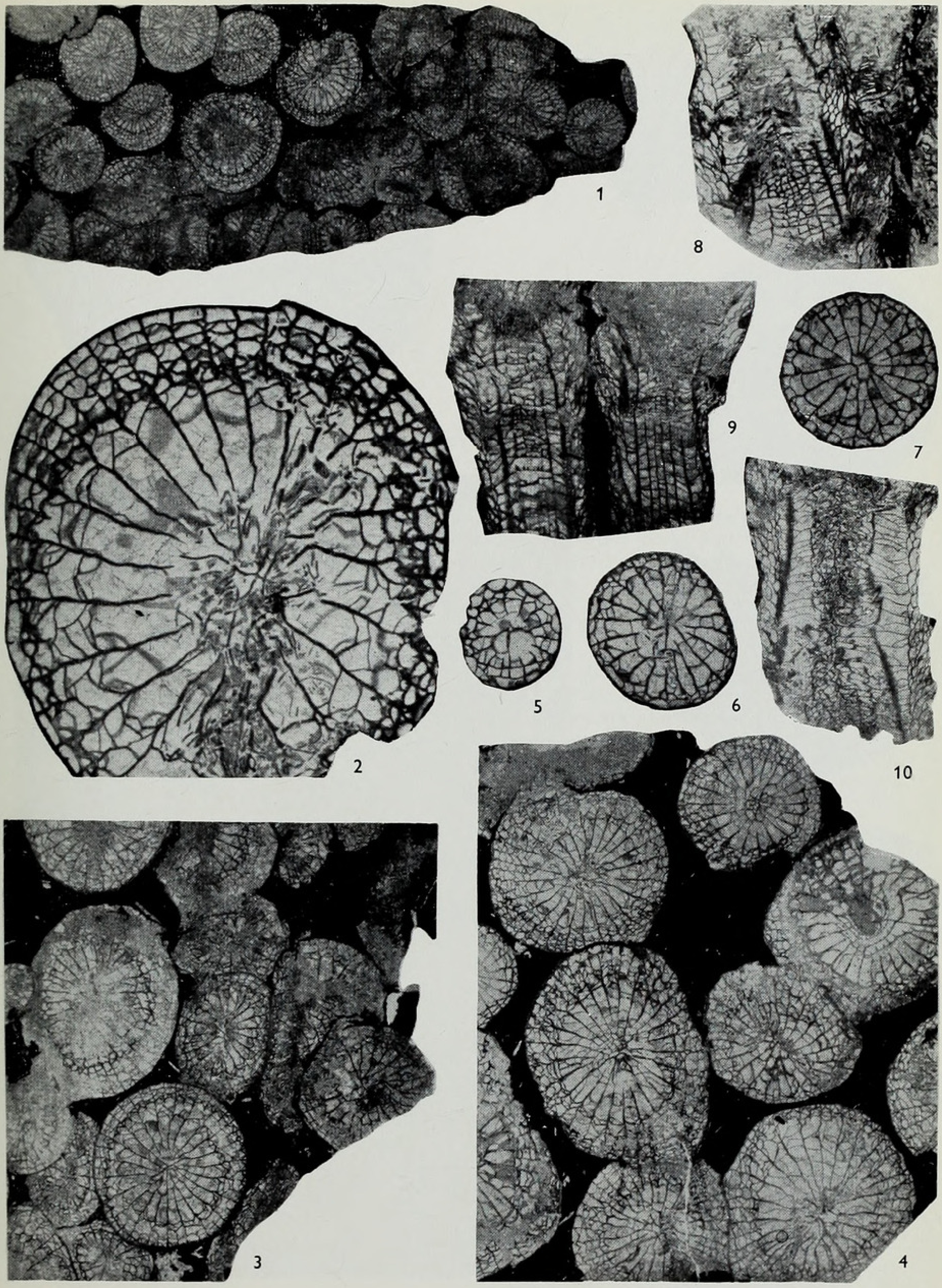

1
8
9
7
2
5
6
10
3
4

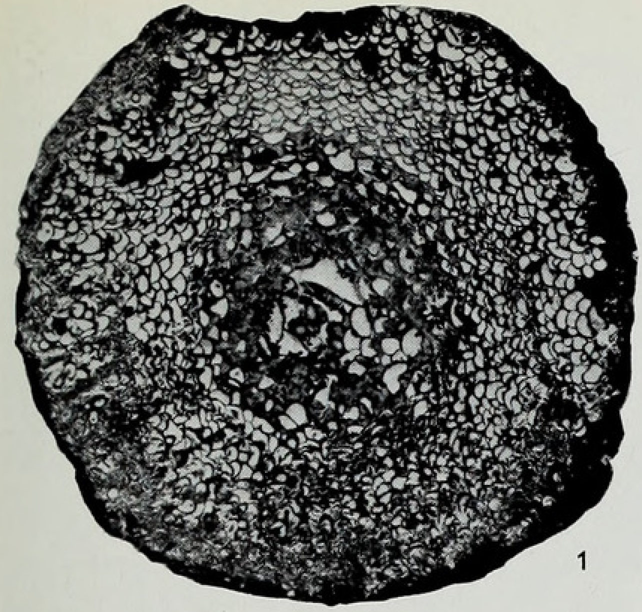
PLATE 9

Plasmophyllum secundum americanum (Edwards & Haime)

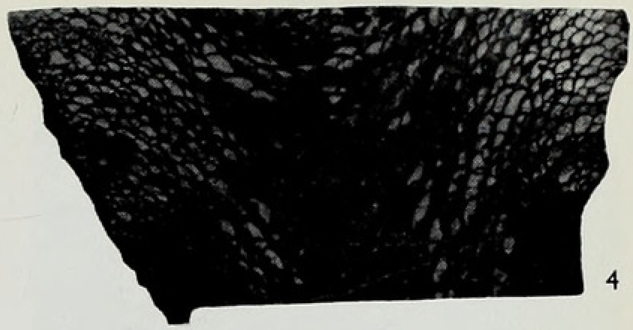
FIG. 1, 2. Cross-sections (slides). R45098b, c. ×1·5.
FIG. 3. Cross-section (slide) showing form and arrangement of septal spines. R45098b. ×6.
FIG. 4. Longitudinal section (slide). R45098d. ×1·5.
Caño Grande; Caño Grande Fm., early Middle Devonian.

Plasmophyllum sp.

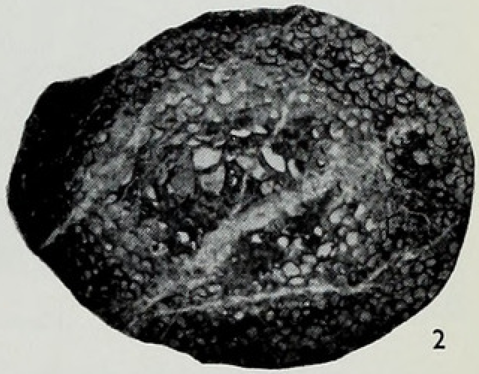
FIGS 5–6. Cross-sections (slides). R45095a, b. ×3.
FIG. 7. Longitudinal section (slide). R45095c. ×3.
Caño Grande; Caño Grande Fm., early Middle Devonian.



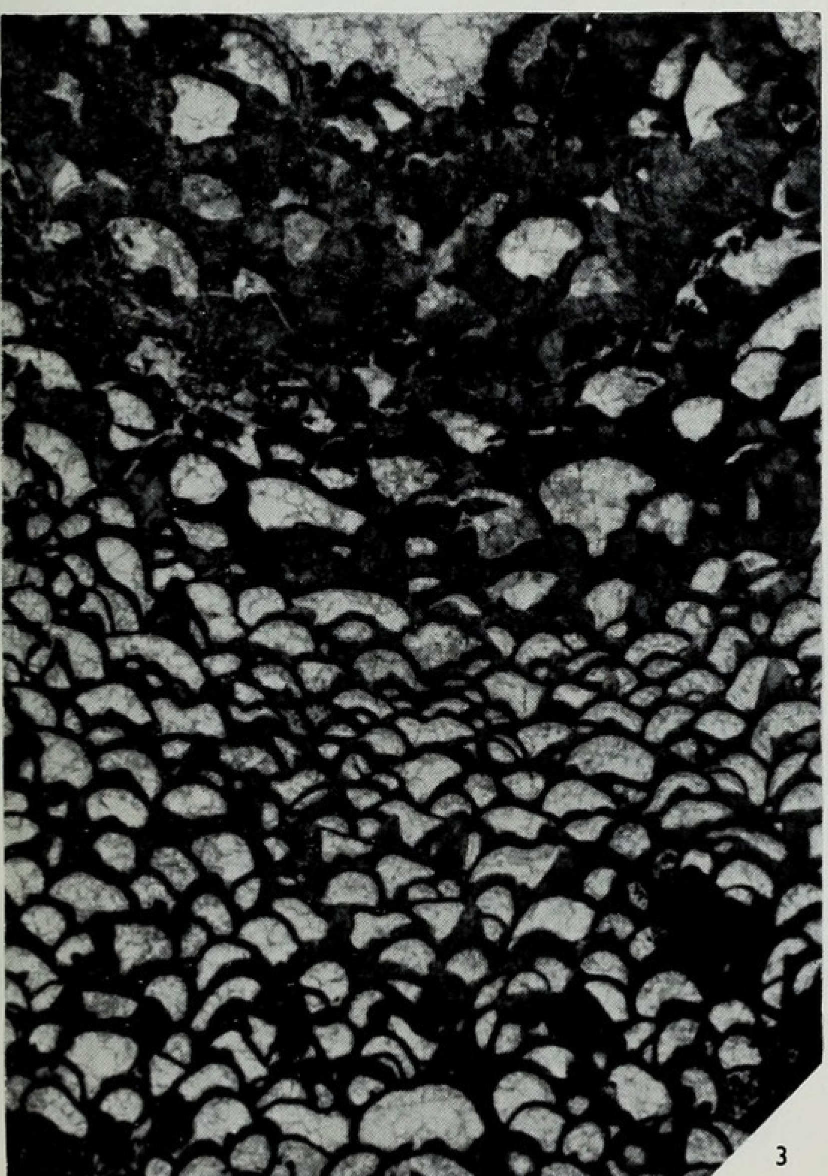
1



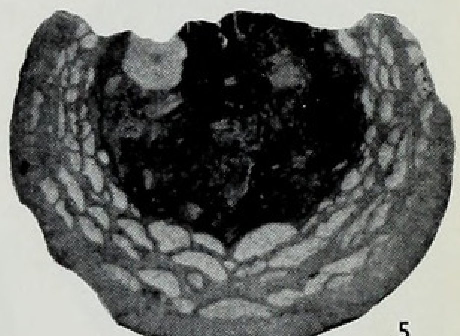
4



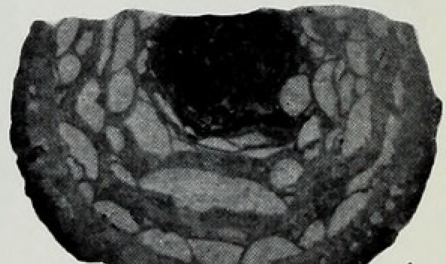
2



3



5



6

7

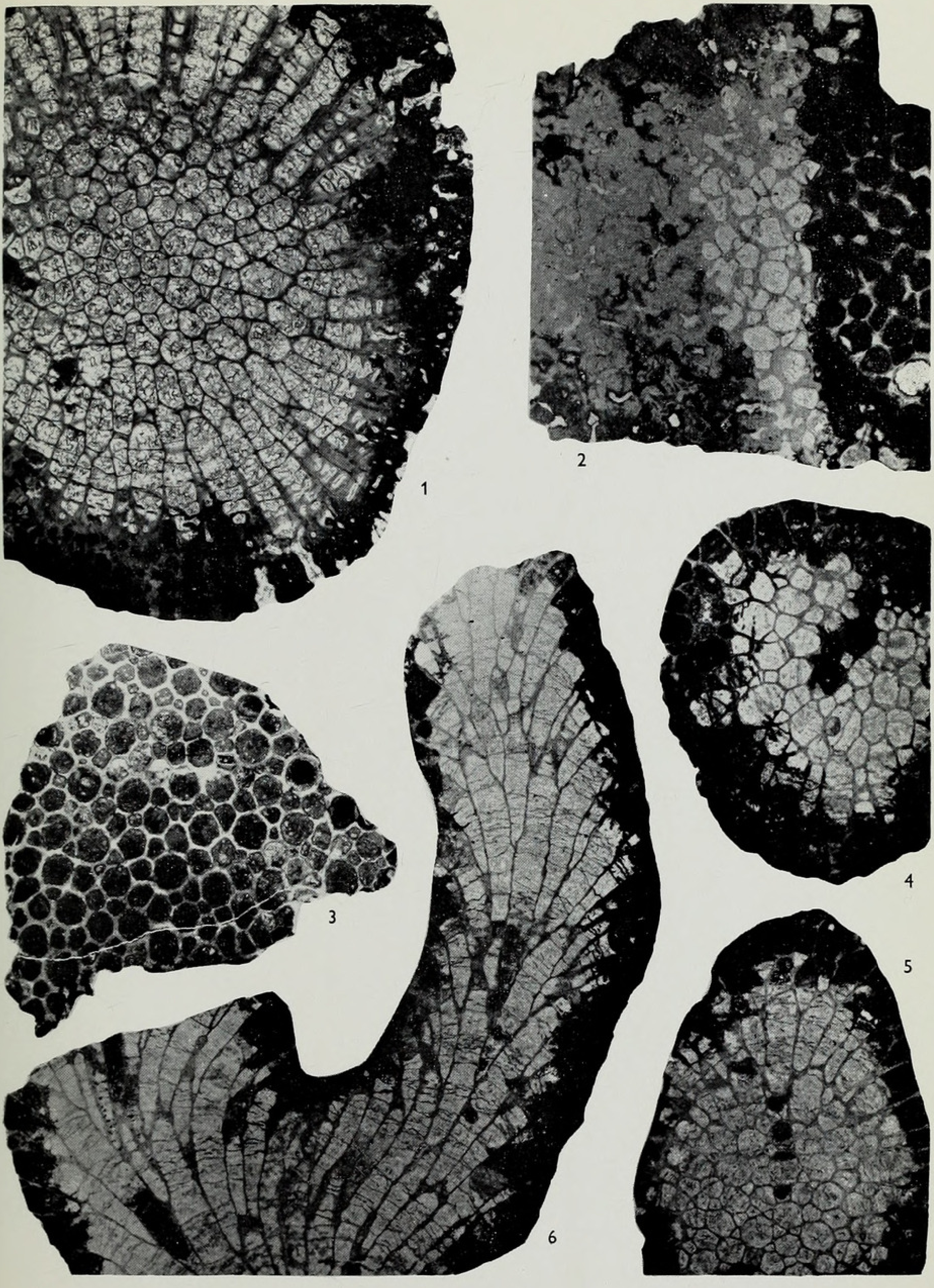
PLATE 10

Favosites venezuelensis (Weisbord)

FIG. 1. Cross and longitudinal sections (slide). R45101b. ×3.
FIG. 2. Tangential section (slide). R45101a. ×3.
Caño del Sur; Caño Grande Fm., early Middle Devonian.

Favosites arbuscula Hall

FIG. 3. Tangential section (slide). R45103a. ×3.
FIGS 4–5. Cross-sections (slides). R49264a, R45103b. ×3.
FIG. 6. Longitudinal section (slide). R49264b. ×3.
Caño del Sur; Caño Grande Fm., early Middle Devonian.


1
2
3
4
5
6