

REVISION OF THE ORDER STROMATOPORIDA

by COLIN W. STEARN

ABSTRACT. The genus *Stromatopora* has been widely misinterpreted as characterized by vertical structural elements, but the type species, *Stromatopora concentrica*, has a structure, here called cassiculate, dominated by oblique elements like a chainlink fence. Only twenty-six species of the several hundred attributed to *Stromatopora* conform to a redefinition of the genus presented here. Cellular microstructure is distinct from microreticulate microstructure. As presently defined the Order Stromatoporida is polyphyletic. Genera that have cellular microstructure are placed in the redefined Order Stromatoporida and evolved from unknown ancestors in Llandovery time. Genera that have microreticulate microstructure are separated as the Order Syringostromatida (emended), that evolved from densastromatid ancestors about the same time. In a major episode of adaptive radiation starting in the Pridoli and culminating in Emsian time the ancestral syringostromatid, *Parallelostroma*, gave rise to *Coenostroma*, *Habrostroma*, *Syringostroma*, *Columnostroma* and *Parallelopora*. In late Early to Middle Devonian time *Stromatopora* radiated into *Lineastroma*, *Arctostroma*, *Pseudotruperostroma*, *Glyptostromoides* and *Taleastroma*. The position of *Ferestromatopora* is problematic. *Syringostromella* coexisted with *Stromatopora* in Middle and Late Silurian time and gave rise to *Salairella* in late Early Devonian time. Concise definitions of all these genera are formulated, problems of distinguishing them are discussed, and representative species are listed.

THE genus *Stromatopora* Goldfuss, 1826, was originally described on the basis of external form and a crude vertical polished section of the type species by monotypy, *Stromatopora concentrica* Goldfuss, 1826. Before the internal structure of stromatoporoids was investigated using thin sections, the genus was used for nearly all stromatoporoids and for other laminated, cabbage-like structures, such as stromatolites.

In the first comprehensive review of stromatoporoids using their internal structure, H. Alleyne Nicholson (1886a) illustrated a specimen which according to him was 'absolutely identical with the original example of the species' from the Middle Devonian of the type locality, Gerolstein, Germany. Although the captions indicate that this specimen was shown only in external view and in tangential thin section (pl. 11, figs 15–16), labels on the thin sections indicate that the vertical section (pl. 11, fig. 18) is from the same specimen although it was identified as from another specimen (see Appendix for discussion of this plate). Nicholson's thin sections are difficult to match with the drawings.

Nicholson's vertical section (1886a, pl. 11, fig. 18; see Pl. 1, fig. 1) shows a skeleton dominated by vertical structural elements separated by dissepiments. Nicholson's concept of the genus in vertical section was used by palaeontologists for the next sixty-six years, during which sixty-nine species were established.

The type specimen of *Stromatopora concentrica* is in the Institut für Paläontologie, Bonn. The hand specimen illustrated by Goldfuss (1826) has been cut into a large vertical thin section and a small tangential thin section (both labelled 80) apparently at Nicholson's (1888a, p. 81) request, and three thin sections, one large (Pl. 1, fig. 3; Pl. 2, fig. 1) and one small vertical and a tangential apparently cut for Lecompte in about 1950. Lecompte (1952, pl. 53, fig. 1) illustrated the large vertical cut for Nicholson at low magnification, and Mistiaen (1985) illustrated the large vertical section cut for Lecompte. Lecompte (1952) also published illustrations of well-preserved specimens from the Devonian of Belgium that he believed better illustrated the structure of the type specimen (Pl. 2, fig. 2). These illustrations show that the type specimen is poorly preserved, latilaminar, and has a network structure like that of a chainlink fence with relatively insignificant continuous vertical structural elements. Neither the type nor the Belgian specimens assigned to *S. concentrica* by

Lecompte (Pl. 2, fig. 2) resemble Nicholson's (1886a) illustrations on which the widely accepted concept of *Stromatopora* had been based, and Lecompte (1952, p. 274) suggested that Nicholson's specimens were not conspecific with the type. Photographs of the Belgian specimens were also used by Lecompte (1956, fig. 91, 2) to illustrate the characteristics of *Stromatopora concentrica* in the *Treatise on Invertebrate Paleontology*. St. Jean (1957, p. 838) regarded these photographs as not representative of *Stromatopora concentrica* (whose type he incorrectly stated was illustrated by Nicholson 1886a, pl. 11, figs 16, 18), identifying them as *Ferestromatopora tyrganensis* Yavorsky, 1955. Galloway (1957, p. 447) endorsed this interpretation. Since then most stromatoporoid workers have continued to use Nicholson's concept of *Stromatopora* (see references under *Stromatopora* below), but described species under this generic umbrella that have included a wide range of internal morphologies. Up to 1990, two hundred and eight species have been first described as belonging to this genus, and many more have been referred to it subsequent to first description. V. I. Yavorsky alone (in many papers published between 1929 and 1956) has been responsible for describing fifty-four species of *Stromatopora*.

Mori (1970, p. 121) examined the sections of Goldfuss's types and agreed with Lecompte's (1952) interpretation.

Mistiaen (1985) re-examined Lecompte's and Goldfuss's specimens and reaffirmed Lecompte's view that *Stromatopora* is a genus with suppressed vertical elements and a tangled structure (*enchevêtrée*). Stearn (1990) suggested that a revision of the genus was long overdue as it had become useless as a taxon. This revision of *Stromatopora* and its relatives placed by Stearn (1980) in the Order Stromatoporida is attempted in this paper.

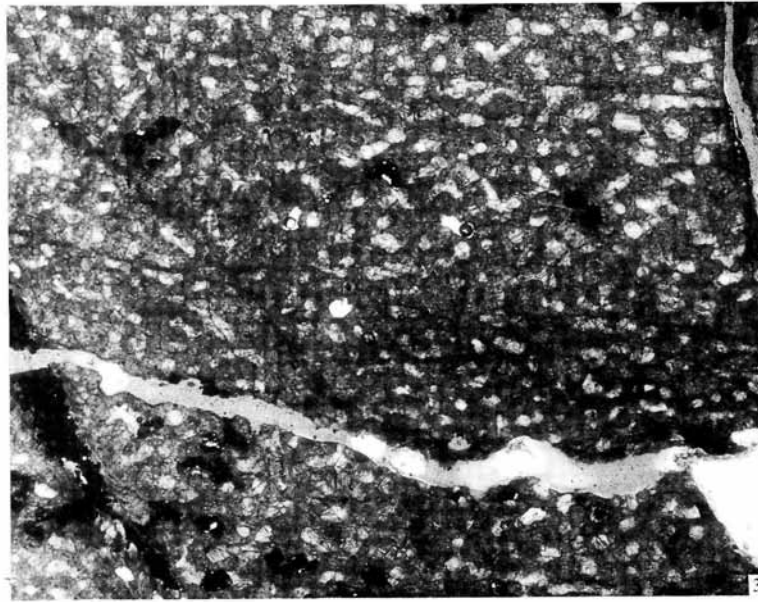
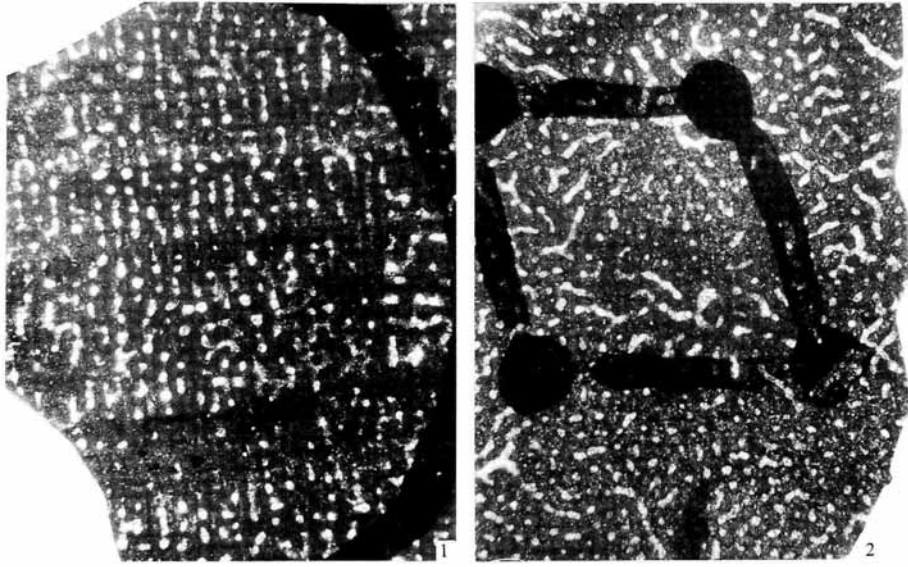
Many new genera have been proposed by authors in an effort to split useful taxa from the equivocally defined genus, *Stromatopora*. In this paper the diagnoses of these genera are reviewed and an attempt is made on the basis of a literature survey to divide species that have been assigned to *Stromatopora* in the broad sense between these new genera. Only those that closely resemble the type species as redescribed by Lecompte (1952) and Mistiaen (1985) are retained in *Stromatopora*. In this revision only twenty-six species are recognized as valid; *Stromatopora* and another eleven are doubtfully assigned to it. The genera previously placed by Stearn (1980) in the order Stromatoporida are divided between the redefined orders Stromatoporida and Syringostromatida, for which new concise definitions have been formulated. Lists of representative species of each genus are given in the text or, where extensive, deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14042 (24 pages). The species have been revised on the basis of a survey of the literature and the writer's examination of all major stromatoporoid collections in museums outside the former Soviet Union and China.

STRUCTURAL ELEMENTS

Typical stromatoporids and syringostromatids have coenosteles (wall-like structures) as vertical elements, but some have pillars (post-like structures) or megapillars (complex vertical thickenings of the skeleton in mamelon columns). Coenosteles in tangential section are one, or commonly a combination of, the following: (1) separate, irregular, vermiform; (2) an open labyrinthine network enclosing galleries of labyrinthine outline; and (3) a closed network enclosing subcircular galleries. Tangential sections of the coenosteles are rarely diagnostic of genera (with exceptions, such as *Salirella*), as most show a wide range of forms including all three of the above conditions within a single thin section.

EXPLANATION OF PLATE I

Figs 1–3. *Stromatopora concentrica*. 1, vertical section; 2, tangential section illustrating Nicholson's concept of the species and genus; Sections 1a and 1 (Nicholson collection, P5869, Natural History Museum, London), $\times 10$. 3, Goldfuss's (1836) type specimen, number 80, Institut für Paläontologie, Bonn, vertical section cut for Lecompte, No. Lecompte 32.2, $\times 10$.



STEARN, *Stomatopora*

Pillars are characteristic of certain genera such as *Columnostroma* and *Coenostroma* and commonly occur combined with coenosteles. The distinction between them is arbitrary.

In vertical section coenosteles are vertically elongate elements, irregular in form, joining and splitting. In species grouped in the same genus, large differences in the vertical extent of the coenosteles have been accepted by many workers. Stearn (1980) used the vertical persistence of coenosteles to separate the families Stromatoporoidae and Syringostromellidae.

Horizontal structural elements in the Stromatoporida are of three types: (1) horizontal coenostroms; (2) oblique coenostroms; and (3) microlaminae. The first are generally thick, horizontally continuous and are well-illustrated by *Parallelostroma* and *Lineastroma*. Thick laterally persistent coenostroms may enclose thin, dense microlaminae, as in *Parallelostroma*, or microlaminae may exist independently. In genera with structures dominated by coenosteles, coenostroms may be suppressed entirely and replaced by dissepiments or they may form short connections between two coenosteles.

Oblique coenostroms have been characterized as chevron-shaped or tangled elements united in a network. No term presently exists for the three-dimensional network formed by these oblique elements, which in vertical section is comparable to that of a chainlink fence whose 'wire' encloses diamond-shaped voids, or to that of a trellis. The term 'cassicate' (Latin, *cassicula* = a small net) is proposed in this paper (Pl. 2, fig. 2) for this type of network. The adjective can be used to describe the network as a whole, or the coenostroms that form it. Such a network is particularly characteristic of genera such as *Ferestromatopora* and *Arctostroma* and, to a lesser extent, of *Stromatopora*.

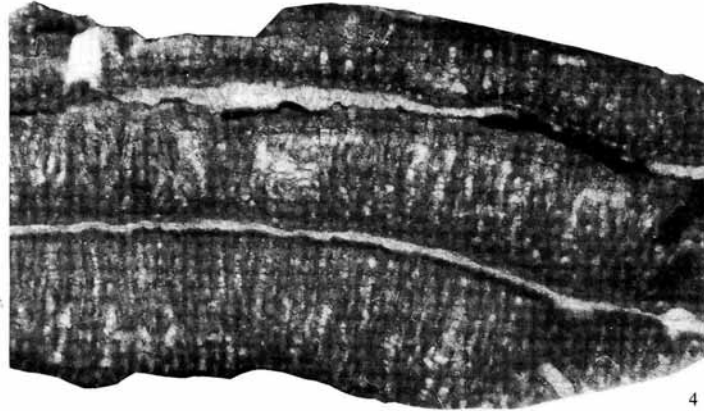
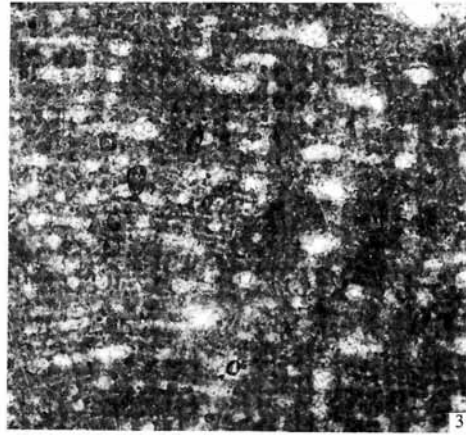
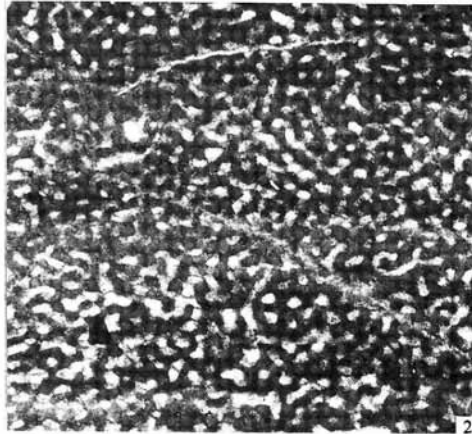
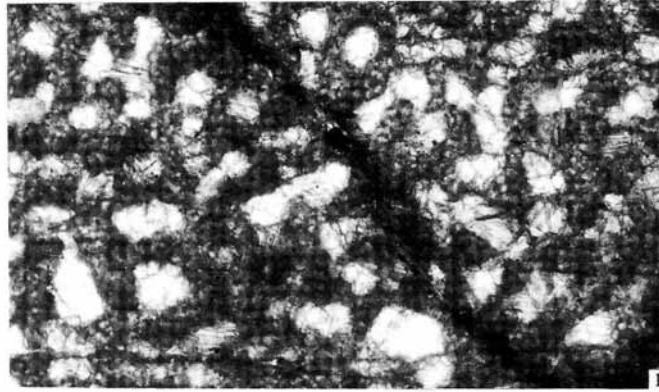
The structures in vertical section of genera can be represented as fields distributed in two-dimensional space between three end-members (Text-fig. 1). The end-members represent genera dominated by: (1) long vertical elements (coenosteles or pillars); (2) persistent coenostroms; or (3) a cassicate network. To carry the fence analogy further, these would be equivalent, in vertical section, to (1) picket; (2) rail or corral; and (3) chainlink fences, respectively. Near the three end-members are the fields of *Salirella*, *Lineastroma* and *Arctostroma*, respectively. The field of the genus *Stromatopora* in this morphological plane is near the centre but displaced toward the cassicate end-member. Genera characterized by a grid of subequal coenostroms and vertical elements, such as *Coenostroma*, plot between poles 1 and 2. Those with strong coenosteles traversing a cassicate network, for example *Glyptostromoides*, fall between poles 1 and 3.

If an axis along which pillars grade into coenosteles is added, the triangular morphological plane becomes a tetrahedron (Text-fig. 2). The pillar-dominant end-member is close to the field of *Columnostroma*. The field of *Taleastroma* separates from that of *Glyptostromoides* along the pillar-cassicate axis. The imperfect integration of coenosteles into a network in *Syringostromella* places its field along the network-pillar axis. The fields of *Coenostroma* and *Pseudotrumpetostroma* separate along the network-coenostrom axis.

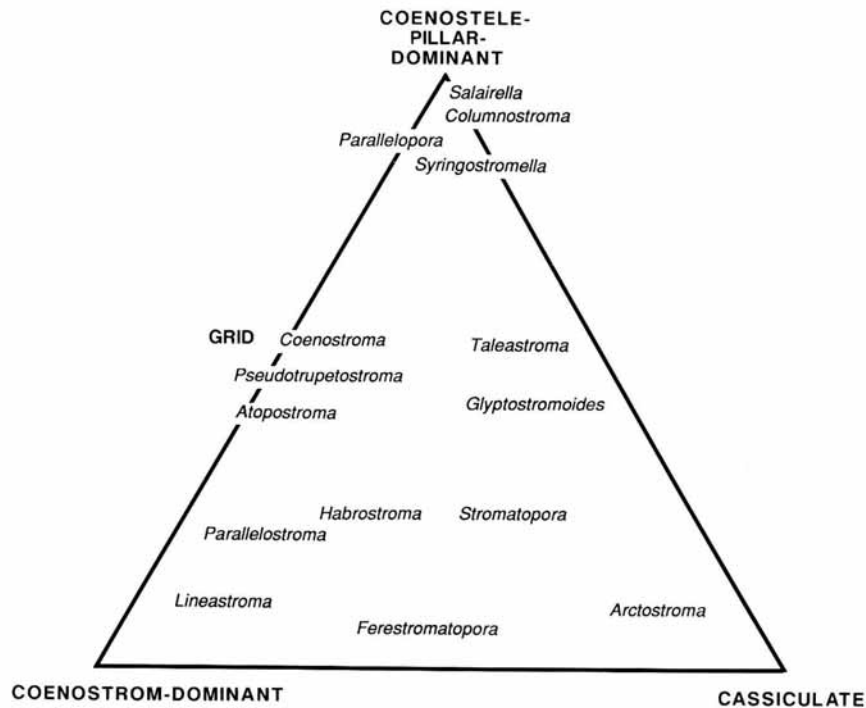
These diagrams are an aid to visualizing morphological variation among the genera but do not include genera distinguished by features not easily plotted as end-members (e.g. megapillars). They do not imply close phylogenetic relationships between adjacent genera.

EXPLANATION OF PLATE 2

- Figs 1–2. *Stromatopora concentrica*. 1. type specimen, number 80, Institut für Paläontologie, Bonn; vertical section cut for Lecompte, enlarged to show the cellular microstructure of a well-preserved part of the section, $\times 25$. 2. vertical section of specimen from the Ardennes to illustrate Lecompte's concept of the genus; number 6224a, Institut Royal des Sciences Naturelles de Belgique, Brussels (Lecompte's pl. 53, fig. 2), $\times 10$.
 Fig. 3. *Coenostroma monticuliferum*. Vertical section to show microstructure of the type specimen, number 32409a University of Michigan; Galloway and Ehlers' (1960) thin section WI-1, $\times 25$.
 Fig. 4. *Pachystroma antiquum*. Vertical section of type specimen; Nicholson collection number 290a (P6003, Natural History Museum, London), $\times 10$.



STEARN, *Stromatopora*, *Coenostroma*, *Pachystroma*



TEXT-FIG. 1. Genera of the Stromatoporida and Syringostromatida plotted on a two-dimensional field with cassiculate, vertical-dominant, and horizontal-dominant elements as end-members. Genera with vertical and horizontal elements of equal prominence intersecting at right angles plot at the GRID position.

MICROSTRUCTURE

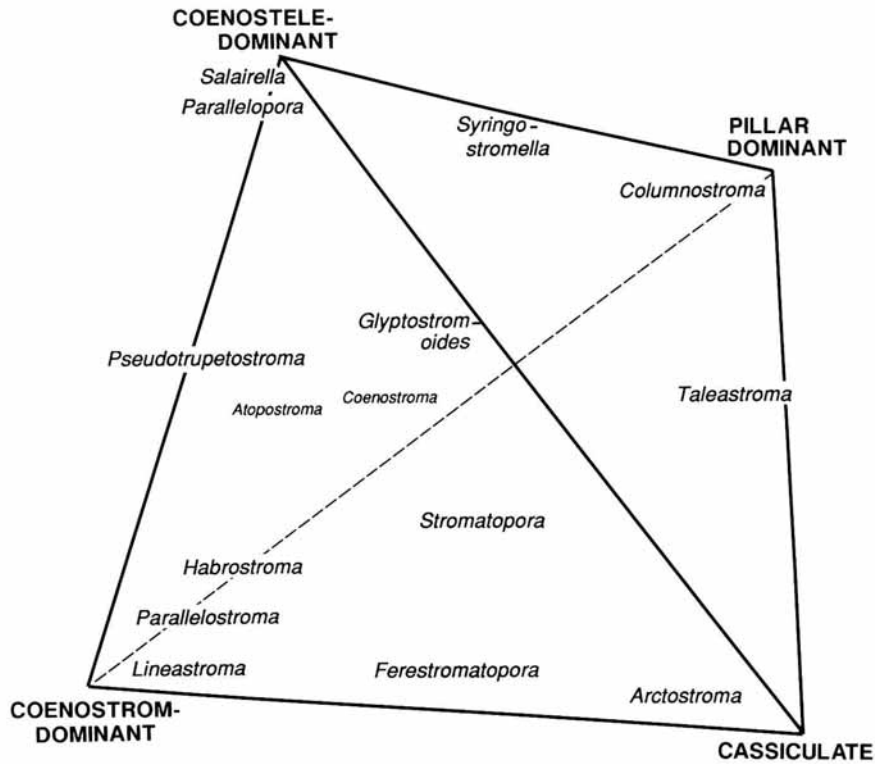
Cellular microstructure

The microstructure of the type specimen of *Stromatopora concentrica* (Pl. 2, fig. 1) is locally coarsely cellular, that is, crowded with randomly arranged, subcircular parts that are less opaque than surrounding parts in both tangential and vertical section. These lighter parts have been interpreted by most workers as the remnants of subspherical voids (cellules), or of originally spherulitic texture.

In many genera of Stromatoporida this cellular microstructure is evident, but its expression is affected by diagenesis. In many specimens the microstructure can appropriately be described as consisting of dark (in transmitted light), subspherical masses in a lighter ground, a microstructure referred to as melanospheric. The origin and diagenesis of these microstructures have been discussed elsewhere (Stearn 1966a, 1977, 1980, 1989; St. Jean 1967; Wendt 1984; Stearn and Mah 1987). Melanospheric and cellular microstructure are not confined to the genera discussed here but are found in other orders and particularly in the Stromatoporellida.

Microreticulate microstructure

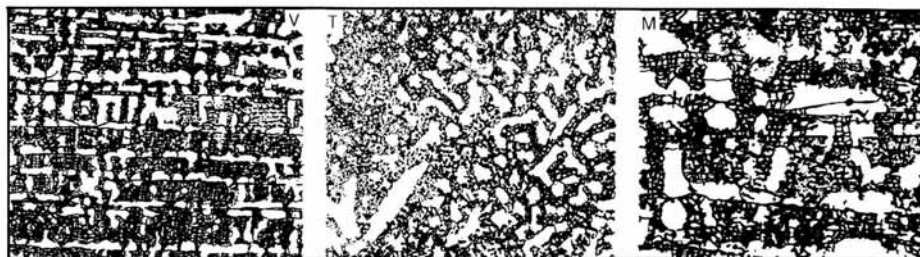
Not all stromatoporoid palaeontologists recognize that cellular microstructure is an expression of random voids in the skeletal material. A second concept of the origin and evolution of the



TEXT-FIG. 2. Genera of the Stromatoporida and Syringostromatida plotted on a three-dimensional solid (tetrahedron) with coenostrom-dominant, coenostele-dominant, pillar-dominant and cassiculate end-members. Genera in small type (*Coenostroma*, *Atopostroma*) are located on the back surface of the tetrahedron.

microstructure of the Stromatoporida emphasizes the origin of the more opaque skeletal material rather than that of the spaces that separate it. Parks (1909) appears to have originated the idea that the microstructure of *Stromatopora* and its relatives is defined by a fine, rectilinear, three-dimensional framework of posts and connecting beams (now called micropillars and microcolliculi) enclosing equidimensional voids (microgalleries). Parks (1936, p. 9) later explained this viewpoint of the microstructure of *Stromatopora* as 'reticulate' and as 'nothing more than the gross fibre of *Actinostroma* greatly reduced'. Unfortunately, he did not live to work out these ideas in a classification, but the idea that the skeletal material of *Stromatopora* and its allies evolved from 'very fine *Actinostroma*-like forms' (now called densastromatids) by the opening of cavities that became galleries is clearly stated in his work.

The 'reticulate' microstructure of Parks is now referred to as microreticulate, and some palaeontologists regard cellular microstructure as originating in microreticulate skeletal material. Stock (1989) extended the idea of the origin of stromatoporid microstructure from micropillars and microcolliculi to explain cellular microstructure through the breakdown of the regularity of the microreticulum. He called such cellular microstructures 'akosmoreticulate' but the suffix -reticulate seems inappropriate for a microstructure that is not a regular framework. The concept has also been discussed by Kazmierczak (1971) and Nestor (1974).



TEXT-FIG. 3. Structure of *Parallelostroma* in vertical (V) and tangential (T) sections, $\times 10$, and microstructure in vertical section (M), $\times 20$ (based on photographs of Rosen's type specimen of *P. typica*, number Co009, Estonian Academy of Science, Tallinn).

The microreticulate microstructure of genera such as *Parallelostroma* can be attributed to the alignment of cells in vertical and horizontal rows reducing the more opaque skeletal material to a rectilinear network or to a scaffold of minute posts and beams (Text-fig. 3). The preservation of most specimens does not allow an easy choice between these two models. However, in species in which the microreticulate microstructure is well-preserved, the microcolliculi (beam-like elements) tend in tangential section to protrude from the margins of structural elements, giving them poorly defined borders and margins with only partly enclosed cavities of the microgalleries. Cellular species are distinct in the smoother, more discrete borders of the structural elements and the cellules do not appear to open into galleries as do microgalleries. This evidence indicates that cellular skeletal material is not merely a variant of microreticulate but a distinct microstructural type.

Nestor (1974) called 'orthoreticulate' the microreticulate microstructure in which darker skeletal material forms a rectilinear framework; it is best shown in his genus *Parallelostroma*. He called stromatoporoids in which the micropillars diverge upward 'clinoreticulate'.

In advanced syringostromatids the increase in size of the microgalleries reduces the tissue between them to a fine, tenuous, lacy network.

Microstructure evolution

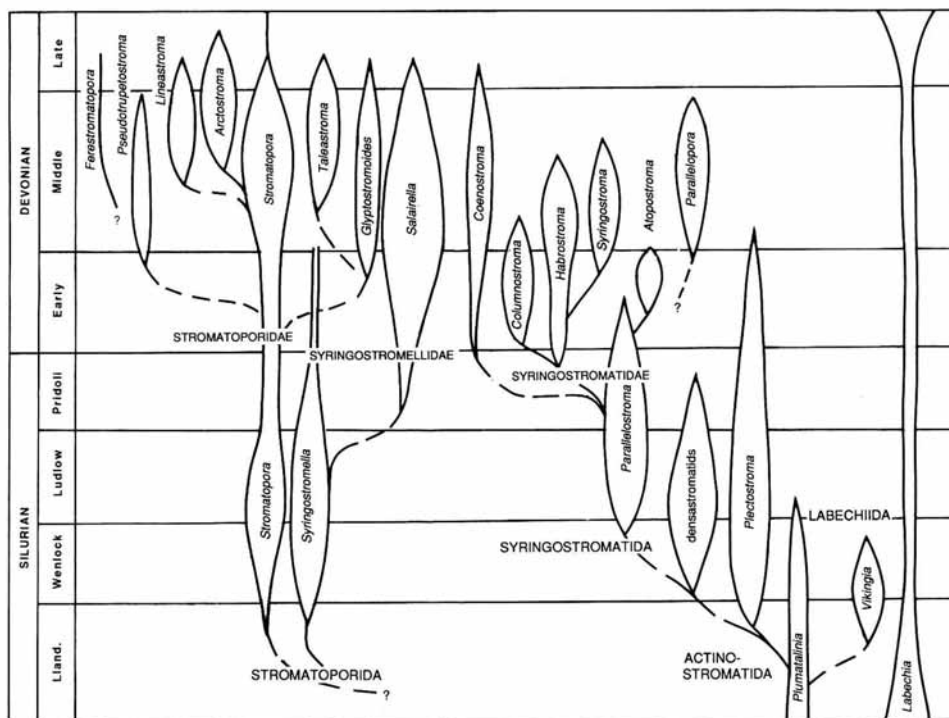
The following discussion is based on the premise that cellular and microreticulate microstructure are fundamentally different in origin. Orthoreticulate microstructure seems likely to have evolved from the densastromatids, through forms such as *Actinostromella*, and Nestor (1974) and Stock (1983) have traced phylogenies based on this premise. The tendency of the orthoreticulate laminae to break up into microlaminae in diagenesis is further proof that this microstructure is formed by a fine reticulum of posts and beams. Cellular microstructure is unlikely to have formed by the modification of this reticulum. Genera such as *Syringostromella* and *Stromatopora* have cellular microstructure fully developed by the late Llandovery before the densastromatids appear in the early Wenlock, and *Actinostromella* and *Parallelostroma* appear in late Wenlock time. Mori (1968, 1970) and Nestor (1982, 1990) documented the faunal succession in the Wenlock and Ludlow of the Baltic area; Llandovery faunas are less well known but have been described by Parks (1909), Nestor (1966), Bolton and Copeland (1972), and Bolton (1991). Nestor (1974) suggested the derivation of the cellular *Stromatopora* lineage from stromatoporoids of compact microstructure because there are only labechiids and clathrodictyids of compact skeletal material in early Llandovery rocks, but the ancestors of the lineage are still unclear. He also suggested an origin of the clinoreticulate group from labechiids like *Plumatalinia* (late Ordovician to mid-Silurian) and *Vikingia* (mid-Silurian) through actinostromatid genera such as *Pseudolabechia*.

If genera with cellular microstructure are not closely related to those of clinoreticulate and orthoreticulate microstructure, then the Order Stromatoporida as defined by Stearn (1980) is

polyphyletic and contains at least two branches in Llandovery time. The microreticulate branch may include an early divergence of clinoreticulate from orthoreticulate genera as Stock (1989) believed, or genera with these two microstructures may have evolved independently as suggested by Nestor (1974).

PHYLOGENY

Text-figure 4 is an attempt to arrange the stromatoporida genera in a phylogeny. Clearly the Stromatoporida had two periods of adaptive radiation: late Early Silurian and late Early Devonian times. These correspond to similar increases in diversity in other stromatoporoid orders and to episodes when seas were transgressing widely over continental platforms. Decreases in diversity took place at times of regression of the epeiric seas at the end of the Silurian and Devonian.



TEXT-FIG. 4. Phylogeny of the Stromatoporida and Syringostromatida (the range of *Lineastroma* is shown in the Devonian only, as the stratigraphical placement of the type species in the Silurian is uncertain).

Microstructure analysis suggests that the Order Stromatoporida is polyphyletic despite the similarity of the mid-Devonian members of the two lineages. The *Stromatopora* lineage was derived from unknown ancestors, either the clathrodictyids or labechiids, in early Llandovery time, and early on split into genera with dominantly vertical elements (*Syringostromella*) and those with cassiculate structure (*Stromatopora*). The second radiation of the *Stromatopora* group gave rise to

such genera as *Arctostroma* and *Glyptostromoides*. The position of *Ferestromatopora* is problematic. *Syringostromella* survived into the Devonian and appears to have given rise to *Salairella*.

The Actinostromatida appear to have evolved from labechiid ancestors in late Llandovery time through transitional genera such as *Plumatalinia*. The rootstock of the Actinostromatidae, represented by *Plectostroma*, and of the Densastromatidae separated shortly afterwards. In Wenlock time *Parallelostroma* had evolved from densastromatid stock by the opening of dominantly horizontal galleries. The diversification of this lineage took place in Emsian time with the evolution of forms with dominant pillars of clinoreticulate microstructure such as *Syringostroma* and *Columnostroma*. *Atopostroma* arose from *Parallelostroma* in Early Devonian time by the superposition and thinning of the pillars, but apparently did not survive into the Eifelian. The possibility that clinoreticulate forms arose independently of *Parallelostroma* from advanced labechiids, like *Pseudolabechia*, suggested by Nestor (1974) cannot be discounted. The relationships between *Habrostroma*, *Coenostroma* and *Syringostroma* must be close, but their relationship to *Columnostroma* and *Parallelopora*, and of these two to each other, are less certain.

CLASSIFICATION

The stromatoporids have been separated from other stromatoporoid orders by a combination of: (1) thick cellular or microreticulate skeletal material; and (2) vertical elements that are coenosteles. Nearly all members have coenosteles but a few genera have pillars in combination with coenosteles, and *Columnostroma* has only pillars joined in an incipient network. Both cellular microstructure and coenosteles appear in other orders and neither is diagnostic of the stromatoporids.

The genera of the Order Stromatoporida have been considered to be divided into three families, the Stromatoporidae, Syringostromellidae and Syringostromatidae (Stearn 1980) on the basis of the form of the structural elements. Because these genera did not have an immediate common ancestor, the Order Stromatoporida as recognized in Stearn's (1980) classification is polyphyletic and should be divided into two orders. The name Stromatoporida is retained and redefined for the branch including cellular genera; the branch including microreticulate genera is redefined as the order Syringostromatida. The Stromatoporida are divided into the redefined families Stromatoporidae and Syringostromellidae on the basis of the dominance of cassiculate-laminate structures in the former and of coenosteles in the latter. The only family recognized in the Syringostromatida is the redefined Syringostromatidae.

SYSTEMATIC PALAEONTOLOGY

Phylum PORIFERA Grant, 1836

Class STROMATOPOROIDEA Nicholson and Murie, 1878

Order STROMATOPORIDA Stearn, 1980 (emended)

Diagnosis. Stromatoporoids with cellular microstructure and structure dominated by coenosteles and coenostroms forming amalgamate networks.

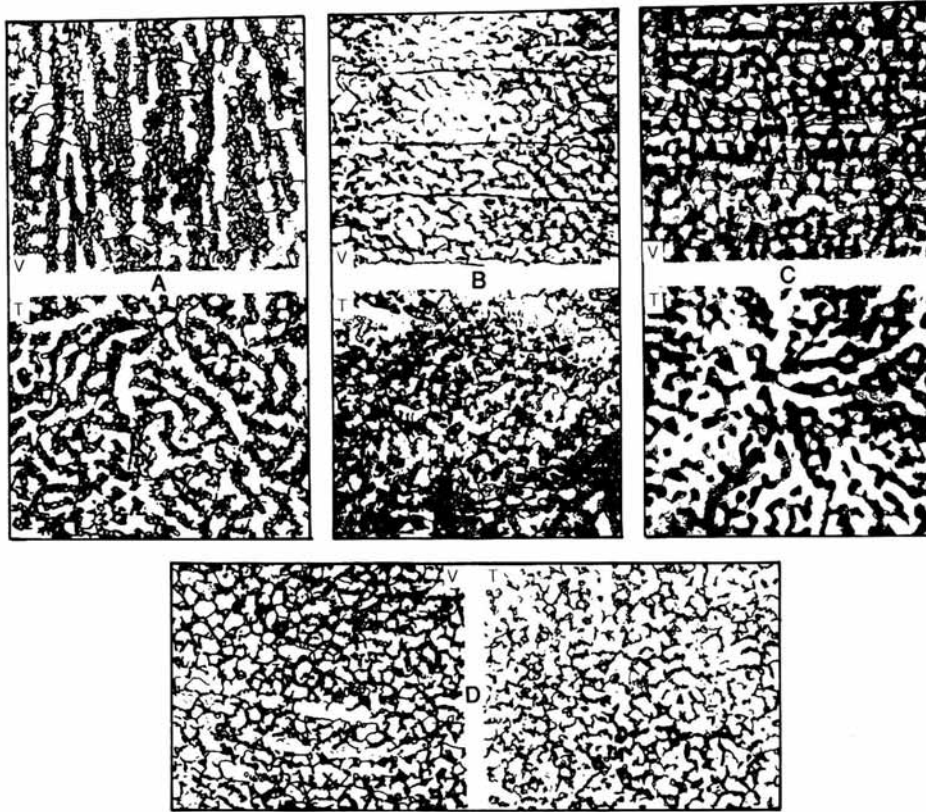
Family STROMATOPORIDAE Winchell, 1867 (emended)

Diagnosis. Stromatoporids dominated by coenostroms, laminae, and cassiculate structures.

Genus STROMATOPORA Goldfuss, 1826

Plate 1, figs 1-3; Plate 2, figs 1-2

[= *Stromatopora* Goldfuss, 1826, p. 21 (see Flügel and Flügel-Kahler (1968) for pre-1968 synonymy); Sleumer 1969, p. 46; Mori 1970, p. 121; Kazmierczak 1971, p. 88; Stock 1979, p. 336, 1984, p. 778; Mistiaen 1980, p. 208, 1985, p. 134; Bogoyavlenskaya and Khromych 1985, p. 84; Stearn 1990, p. 506. ? *Perplexostroma*



TEXT-FIG. 5. Sketches of Stromatoporida in vertical (V) and tangential (T) section, $\times 10$. Microstructure somewhat stylized. A, *Syringostromella* (based on *S. borealis* in Mori 1970). B, *Ferestromatopora* (based on *F. kruppenikovi* in Yavorsky 1955). C, *Lineastroma* (based on *Stromatopora vorkutensis* in Yavorsky 1961. The original photograph is interpreted as inverted). D, *Arctostroma* (based on *Stromatopora contexta* in Stearn 1966b).

Bogoyavlenskaya 1981, p. 32; Bogoyavlenskaya and Khromych 1985, p. 84. *Ferestromatopora* Yavorsky; Galloway 1957, p. 446; Stearn 1966a, p. 111. *non Stromatopora* Goldfuss, Nicholson 1886a, p. 23; Galloway 1957, pp. 447; St. Jean 1957, p. 838; Zukalova 1971, p. 60.]

Type species. *Stromatopora concentrica* Goldfuss, 1826, p. 22, pl. 8, fig. 5a-c.

Diagnosis. Skeleton composed largely of cellular, cassiculate, oblique coenostoms and scattered dissepiments; in some successive phases in latilaminae containing short coenosteles; structural elements in tangential section labyrinthine network or discrete vermiform elements.

Discussion. Confusion concerning the internal structure of this genus has been reviewed in the introduction to this paper. Recognition of the dominantly cassiculate structure of the genus leaves twenty-six species definitely assigned to *Stromatopora*, and a further eight species placed in it

provisionally. The list of these species has been deposited with the British Library as Supplementary Publication No. SUP 14042.

Stromatopora is close to *Arctostroma* Yavorsky, 1967 (see below) but does not have the prominently arched galleries of this genus, the tendency for the melanospheres to be aligned vertically, and the finer and more regular cassiculate network. Although these features might seem to have taxonomic value below the generic level, the species grouped below under *Arctostroma* do constitute a taxon readily separable from *Stromatopora*.

Perplexostroma Bogoyavlenskaya, 1981, based on *Stromatopora dzvenigorodensis* Riabinin, 1953, is monotypic. Riabinin's illustrations of the type species show prominent discrete pillars and large astrorhizal systems of the hidden type (Nestor 1966, p. 37). Bogoyavlenskaya's (1981) illustrations show a structure like that of *Arctostroma* with no discrete pillars or coenosteles and small simple astrorhizae. Khromych (1982) retained the species in *Stromatopora*. The diagnosis in Bogoyavlenskaya and Khromych (1985) is too brief to distinguish the genus from others.

Stromatopora is rare in the late Llandovery and Wenlock, increases in diversity during the Late Silurian and Early Devonian, and reaches its acme in Middle Devonian time. It is less abundant and diverse in Frasnian and rare in Famennian time.

Genus FERESTROMATOPORA Yavorsky, 1955

Text-fig. 5B

Type species. *Ferestromatopora krupennikovi* Yavorsky, 1955, subsequently designated by Galloway (1957, p. 446).

Discussions of the genus. Yavorsky 1955, p. 109; St. Jean 1957, p. 838; Galloway 1957, p. 446; Stearn 1963, p. 665, 1966a, p. 111, 1966b, p. 57, 1980, p. 898, 1990, p. 506; Flügel and Flügel-Kahler 1968, p. 544; Sleumer 1969, p. 45; Mori 1968, p. 85; Kazmierczak 1971, p. 52; Khromych 1974, p. 52, 1976, p. 63; Bogoyavlenskaya and Khromych 1985, p. 76.

Diagnosis. Skeleton composed of elements that are largely oblique in vertical section and form a cassiculate network in which neither coenostroms nor coenosteles are easily distinguished. The network is traversed by thin, continuous, compact, widely spaced paralaminae. In tangential section the structural elements join in a labyrinthine network. Dissepiments are common but coenotubes are absent. The microstructure is obscurely cellular or, more commonly, melanospheric.

Discussion. Yavorsky's original definition stressed the net-like nature of the skeleton, its latilamination, the short vertical elements (columns), oblique horizontal elements (leaning on columns), and similarity of the galleries to those of *Clathrodictyon confertum* Nicholson, 1889. In his description of the type species the fibre is described as porous in contrast to the compact tissue of *C. confertum*. The microstructure of Nicholson's species is, unfortunately, obscure, for his specimens from Devon are completely recrystallized.

Flügel and Flügel-Kahler (1968, p. 544) discussed the microstructure of *Ferestromatopora* and recorded that Yavorsky indicated in a personal communication that the microstructure should be considered to be compact and the genus placed in synonymy with *Intexodictyon* Yavorsky, 1963. If the microstructure is compact, then *Ferestromatopora* is closer to *Plexodictyon* Nestor, 1966 than to *Intexodictyon* as pointed out by Nestor (personal communication).

The confusion between *Ferestromatopora* and *Stromatopora* begun by St. Jean's (1957, p. 838) and Galloway's (1957) assertions that the specimens used by Lecompte (1952, pl. 53, fig. 2, 1956, fig. 91) to illustrate *Stromatopora concentrica* Goldfuss is a *Ferestromatopora* is reviewed in the introduction to this paper. Sleumer (1969) considered *Ferestromatopora* to be an ecophenotypic variant of *Stromatopora*.

Since the genus was established, at least twenty species of *Ferestromatopora* have been proposed, but few of them closely resemble the typical species in its cassiculate structure and paralaminae.

Nearly all these species can be reassigned to genera such as *Lineastroma*, *Habrostroma*, *Parallelostroma*, *Clathrocoilona* and *Stromatopora*, in the revised sense, and these assignments are listed under the appropriate genera in this paper. As here reinterpreted, the following species (in addition to the type species) can be assigned to *Ferestromatopora*: *Ferestromatopora tyrganensis* Yavorsky, 1955; *Ferestromatopora formosa* Yang and Dong, 1979; *Ferestromatopora talovensis* Yavorsky, 1955 (established as a variety of *F. krupennikovi* but given species status here). Investigation of the type material of this last taxon may show that it is better placed in *Habrostroma* Fagerstrom, 1982. *Clathrodictyon confertum* Nicholson, 1889 may also prove to be a *Ferestromatopora* when topotype material of better preservation is collected to supplement the type specimen, which is very poorly preserved. Unfortunately the type locality, the Pit Park quarry near Dartington, Devon, UK, has been filled in. The stratigraphical range of *Ferestromatopora* as here restricted appears to be Givetian to Frasnian.

Genus LINEASTROMA Khalina and Yavorsky, 1973

Text-fig. 5c

[= *Lineastroma* Khalina and Yavorsky, 1973, p. 31 (p. 150 of translation); Stearn 1980, p. 818; Bogoyavlenskaya and Khromych 1985, p. 80; Dong 1988, p. 35. In part, *Stromatopora* Goldfuss; Yavorsky 1951, p. 11, 1955, p. 81, 1961, p. 44; Yang and Dong 1979, p. 48. *Stromatopora* ? Yang and Dong 1979, p. 52. In part, *Parallelostroma* Nestor; Bol'shakova 1973, p. 86. In part, *Climacostroma* Yang and Dong 1979, p. 72. In part, *Ferestromatopora* Yavorsky; Wang 1978, p. 30; Yang and Dong 1979, p. 898.]

Type species. *Stromatopora vorkutensis* Yavorsky, 1961, p. 39, pl. 23, figs 1–3.

Diagnosis. Skeleton composed of prominent but interrupted coenostroms and short largely vertical, but locally oblique, coenosteles largely confined to an interval between coenostroms and only locally superposed or more continuous vertically. Dissepiments scattered. Microlaminae missing or inconspicuous. Coenosteles in tangential section isolated irregular masses or more or less joined in a labyrinthine pattern. Microstructure finely and inconspicuously cellular.

Discussion. Only a single species, the type, has been ascribed to this genus, but a group of species that are poorly accommodated in *Stromatopora*, *Parallelostroma* and *Ferestromatopora* can be grouped conveniently in *Lineastroma*. These are stromatoporoids whose skeletal structure is dominated by coenostroms but are not conspicuously microreticulate, or characterized by microlaminae like *Habrostroma* Fagerstrom, 1982, and *Parallelostroma* Nestor, 1966, or by oblique structural elements like *Arctostroma* Yavorsky, 1967, and *Ferestromatopora* Yavorsky, 1955. By this diagnosis, *Lineastroma* is a convenient receptacle for species that do not have the unique features of other coenostrom-dominated stromatoporoids. Future workers may find criteria by which to further clarify the relationships of species included here in *Lineastroma*.

In typical *Parallelostroma* the coenostroms are sharply bounded above by a microlamina and the microstructure is microreticulate, commonly breaking down in diagenesis into a set of closely spaced microlaminae. In *Habrostroma* the tissue has a diffuse, lacy appearance typical of the advanced syringostromatids.

Climacostroma Yang and Dong, 1979, is based on the type species *C. guangxiense* Yang and Dong, 1979. The distinctive features ascribed to the genus are largely microstructural and include microlaminae and pillars with small vertical tubules and vertical rods. These features are not clearly shown in the illustrations of *C. guangxiense*, which has the structure of *Lineastroma* and is considered here to belong in this genus. The other two species placed by Yang and Dong (1979) in *Climacostroma* show vertically aligned melanospheres and arched galleries that characterize species of *Arctostroma* and are now assigned to that genus. Fagerstrom (1982) has discussed the relationship of *Climacostroma* to *Habrostroma*.

In addition to the type species, the following species are assigned here to *Lineastroma*: *Stromatopora fortuita* Yavorsky, 1955 (referred to ?*Parallelostroma* by Bol'shakova 1973);

Stromatopora pulchra Yavorsky, 1955; *Stromatopora schelmonensis* Yavorsky, 1955 (referred to *Trupetostroma* by Yavorsky 1963 and to *Stromatopora* by Stearn 1966a); *Stromatopora karaensis* Yavorsky, 1961; *Ferestromatopora jacquesensis* Galloway, 1960; *Stromatopora? mammillaris* Yang and Dong, 1979; *Ferestromatopora compacta* Yang and Dong, 1979; *Climacostroma guangxiense* Yang and Dong, 1979.

Species that can probably be placed in *Lineastroma* but require further investigation include: *Stromatopora obrutchevi* Yavorsky, 1955 (referred by Bol'shakova 1973 to *Parallelostroma*); *Stromatopora czekanowskii* Yavorsky, 1955; *Stromatopora vlychensis* Riabinin, 1939; *Stromatopora sokolensis* Yavorsky, 1951; *Syringostroma minutitextum* Lecompte, 1951 (referred doubtfully to *Habrostroma* by Fagerstrom 1982); *Stromatopora praelonga* Bogoyavlenskaya, 1977; *Ferestromatopora tuqiaoziensis* Wang, 1978; *Stromatopora interrupta* Yang and Dong, 1979.

Species of *Lineastroma* have stratigraphical ranges within Silurian (stage unspecified for the type species by Yavorsky 1961) to Frasnian strata. All species definitely assigned to the genus, other than the type, are from the Eifelian to Frasnian interval.

Genus ARCTOSTROMA Yavorsky, 1967

Text-fig. 5D

[= *Arctostroma* Yavorsky, 1967, p. 30; Bogoyavlenskaya and Khromych 1985, p. 69; Dong 1988, p. 35. *Angulatostroma* Khalina, 1968a, p. 152; Bogoyavlenskaya and Khromych 1985, p. 68; Dong 1988, p. 35. In part, *Ferestromatopora* Yavorsky; Stearn 1963, p. 665, 1980, p. 898; Wang 1978, p. 30.]

Type species. *Ferestromatopora contexta* Stearn, 1963, p. 666, pl. 88, figs 3–5. [= *Arctostroma ignotum* Yavorsky, 1967; *Stromatopora mikkwaensis* Stearn, 1966b (Stearn and Shah 1990)].

Diagnosis. Skeleton composed of oblique structural elements forming a continuous cassiculate network in vertical section, enclosing galleries that are arched at the top. Neither coenosteles nor coenostroms prominent; structural elements and galleries typically labyrinthine in tangential section; microstructure coarsely cellular, commonly melanospheric, commonly with vertical alignment of melanospheres.

Discussion. Stearn (1980) placed *Arctostroma ignotum* Yavorsky, 1967 in synonymy with *Ferestromatopora contexta* Stearn, 1963, and concluded that *Arctostroma* should be considered a synonym of *Ferestromatopora*. However, the type species, *A. ignotum*, and other species considered to belong to the genus, do not have paralaminae that are characteristic of *Ferestromatopora*, and the two genera are now considered to be separate. The nominal type species should be *F. contexta*, as this name has precedence. Apart from the paralaminae, the skeletal structure of *Ferestromatopora* and *Arctostroma* are similar.

Angulatostroma Khalina, 1968a, based on *Stromatopora angulata* Yavorsky, 1947, was described as having short laminae bent into chevron form, like those of *Ecclimadictyon* Nestor, 1964, but composed of porous tissue (Khalina 1968a). Stearn (1980) suggested that the genus was synonymous with both *Ferestromatopora* and *Arctostroma*, but synonymy with the former now seems unlikely. The only species, other than two *nomina nuda* and the type species, ascribed to *Angulatostroma* by Khalina (1968a) was *Stromatopora compacta* Yavorsky, 1955.

Species, other than the type which are included in this review in *Arctostroma* are: *Stromatopora angulata* Yavorsky, 1947; *Stromatopora compacta* Yavorsky, 1955; *Climacostroma microlaminata* Yang and Dong, 1979; *Climacostroma facetum* Yang and Dong, 1979; *Trupetostroma kennisoni* Birkhead, 1967; *Ferestromatopora fistulosum* Wang, 1978; *Stromatopora longitubulata* Riabinin, 1941; *Stromatopora maculata* Lecompte, 1952.

These species are recorded from Middle and Upper Devonian rocks, and the genus appears to be particularly characteristic of the Givetian–Frasnian interval. It has been described from Russia, western Canada, China and Australia.

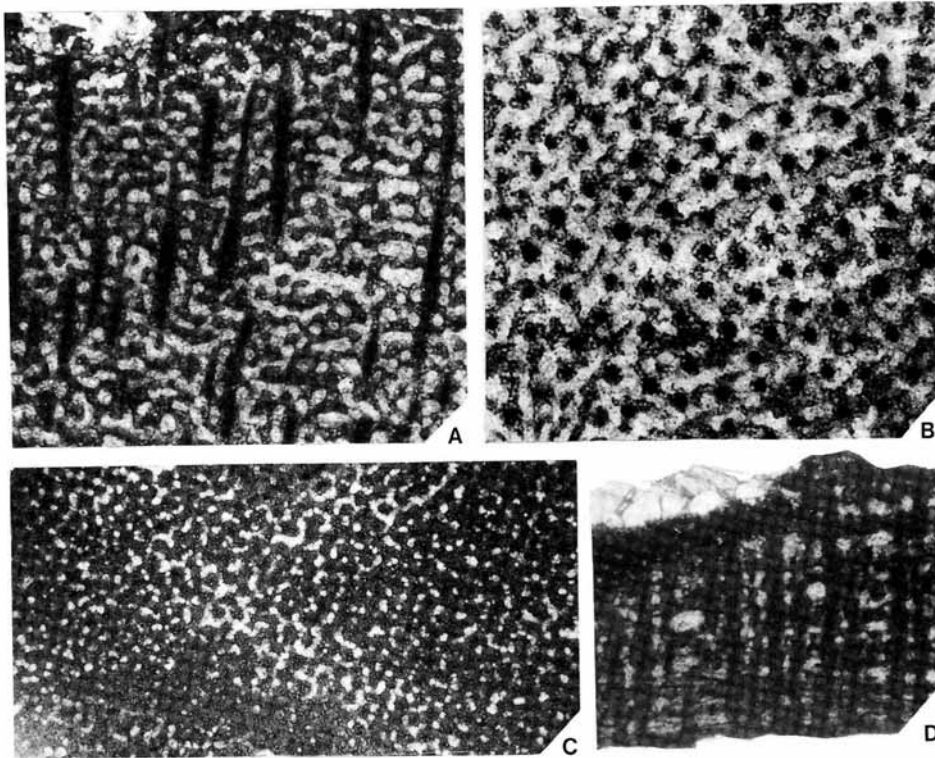
Genus TALEASTROMA Galloway, 1957

Text-figs 6A-B, 7A

[= *Taleastroma* Galloway, 1957, p. 448; Stearn 1966a, p. 112; Flügel and Flügel-Kahler 1968, p. 578; Stearn 1980, p. 898; Bogoyavlenskaya and Khromych 1985, p. 91; Mistiaen 1985, p. 148. In part, *Neosyringostroma* Kazmierczak, 1971, p. 117. In part, *Glyptostroma* Yang and Dong, 1979, p. 65.]

Type species. *Stromatopora cummingsi* Galloway and St. Jean, 1957, p. 182, pl. 15, fig. 4a-b.

Diagnosis. Horizontal structure an irregular cassiculate network of cellular elements like that of *Stromatopora* penetrated by thick, persistent, columnar pillars that in well-preserved specimens are compact in axial regions and cellular or melanospheric peripherally. Pillars circular or annular, prominent and distinct in tangential section.



TEXT-FIG. 6. A-B *Taleastroma logansportense*. Vertical (A) and tangential (B) sections; Slave Point Limestone, N.E. British Columbia; Geological Survey of Canada, plesiotype 102,372, $\times 10$. C-D, *Columnostroma ristigouchense*. Vertical (C) and tangential (D) sections of Spencer's type in the Nicholson collection 309 (P5591, Natural History Museum, London), $\times 10$. The vertical section is too thick to show the microstructure clearly and only the thinner part is illustrated.

Discussion. Questions about the validity of this genus have centred on the microstructure of the pillars, which Galloway (1957) originally characterized as peripherally maculate and axially compact. Most later workers have ascribed the more opaque outlines of the typical species to diagenesis, yet this feature is consistently present in the group of species usually united under the generic name *Talestroma*. The origin of the microstructure characteristic of the pillars is obscure, but they appear to be axially compact, possibly trabecular, and certainly different from the other structural elements. This microstructure is clearly shown by specimens from the Slave Point Limestone at Evie Lake, British Columbia (Text-fig. 6A–B).

Talestroma is close to *Glyptostromoides*, but the long pillars that cross the cassiculate network are conspicuously round in cross-section, commonly dark with melanospheres on their edges giving them an annular appearance, and may have a dark axial spot. In *Glyptostromoides* the vertical elements are submerged in the labyrinthine network of tangential sections and their configuration in cross-section is uncertain.

Neosyringostroma Kazmierczak, 1971, is based on the type species *Hermatostroma logansportense* Galloway and St. Jean, 1957. Stearn (1980) placed this genus in the Ecclimadictyidae, but Mistiaen (1985) considered it a synonym of *Talestroma* and this placement is endorsed here. Mistiaen (1985) discussed at length the relationship between *Talestroma*, *Glyptostromoides* and *Neosyringostroma*, and placed the last two in synonymy. He showed that the species assigned by Kazmierczak (1971) to his genus cannot be recognized as forming a valid generic grouping. I have examined the types of the several species of *Syringostroma* of Fritz and Waines (1956) that Kazmierczak placed in *Neosyringostroma*. They are all poorly preserved specimens of a single species of *Syringostroma* and should not be referred to either *Talestroma* or *Neosyringostroma*.

Representative species of *Talestroma* (in addition to the type species) include the following: *Stromatopora boiarschinovi* Yavorsky, 1961; *Hermatostroma logansportense* Galloway and St. Jean, 1957; *Stromatopora magnimamillata* Galloway and St. Jean, 1957; *Stromatopora pachytextum* Lecompte, 1952; *Stromatopora sinopachytextum* Yang and Dong, 1963; *Glyptostroma sinense* Yang and Dong, 1979; *Glyptostroma yangdongi* Mistiaen, 1985 (new name for *G. pachytextum* Yang and Dong, 1979).

The assignment of several other species to *Talestroma* is of doubtful validity. The generic assignment of *T. vitreum* Galloway, 1960, and *T. lenzi* Galloway, 1960, needs to be re-examined; they appear to be poorly preserved species of *Trupetostroma*. Both *T. steleforme* Stearn, 1975 and *T. condensum* Zukalova, 1971 are poorly preserved and do not have the cassiculate network of this genus.

All the species that can be assigned to *Talestroma* with confidence occur in Middle Devonian rocks.

Genus GLYPTOSTROMOIDES Stearn, 1983

Text-fig. 7B

[= *Glyptostromoides* Stearn, 1983, p. 553. In part, *Glyptostroma* Yang and Dong, 1979, p. 65; Stearn 1980, p. 553; Bogoyavlenskaya and Khromych 1985, p. 77. In part, *Talestroma* Galloway; Mistiaen 1985, p. 148.]

Type species. *Glyptostroma simplex* Yang and Dong, 1979, p. 66, pl. 35, figs 5–6.

Diagnosis. Horizontal structure a cassiculate network of cellular elements like that of *Stromatopora* penetrated by thick, cellular, persistent coenosteles joined into a labyrinthine network in tangential section.

Discussion. Stearn (1980, 1983) and Mistiaen (1985) have reviewed the unfortunate choice of '*Stromatopora beuthii*' of Yavorsky, 1955, as the type species of *Glyptostroma*, the change of the typical species to *Glyptostroma simplex* and the generic name to *Glyptostromoides*. The differences between *Glyptostromoides* and *Talestroma* are discussed under the latter genus.

In addition to the type species, the following are representative of the genus: '*Stromatopora beuthii*' Yavorsky, 1955 (not Bargatzky, 1881); *Glyptostroma liujingensis* Yang and Dong, 1979; *Glyptostroma oblique* Yang and Dong, 1979; *Stromatopora pseudotyrganicum* Khalfina, 1960; *Stromatopora tyrganica* Yavorsky, 1947.

All these species are found in rocks of Early or Middle Devonian age.

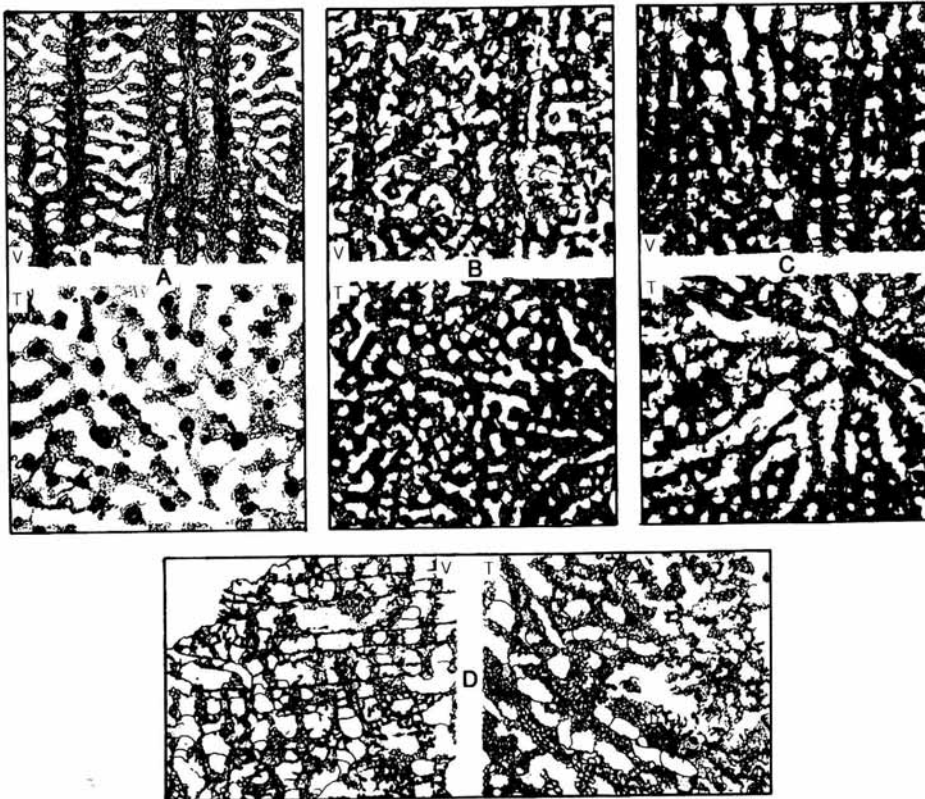
Genus PSEUDOTRUPETOSTROMA Khalfina and Yavorsky, 1971

Text-fig. 7D

[= *Pseudotruperetostroma* Khalfina and Yavorsky, 1971, p. 120; Bogoyavlenskaya and Khromych 1985, p. 86; Dong 1988, p. 35.]

Type species. *Stromatopora pellucida* var. *artyschtensis* Yavorsky, 1955, p. 100, pl. 52, figs 1-2.

Diagnosis. Coenosteles short, interlaminar, commonly superposed in vertical section, in tangential



TEXT-FIG. 7. Sketches of Stromatoporida in vertical (V) and tangential (T) section. A, *Taleastroma* (based on *T. logansportense* in Kazmierczak 1971). B, *Glyptostromoides* (based on *G. simplex* in Yang and Dong 1979). C, *Salirella* (based on *Stromatopora nices* in Yavorsky 1955). D, *Pseudotruperetostroma* (based on *P. artyschtense* in Yavorsky 1955). All figures $\times 10$.

section forming a closed network, vermicular or rarely isolated, coarsely cellular; horizontal elements fine microlaminae, locally coated with cellular tissue.

Discussion. Because the original diagnosis of Khalfina and Yavorsky (1971) is brief, a discussion of the genus is absent from the proposal, and the illustrations of the tangential section of the type species are obscure, this genus has been little used and is difficult to characterize. The original diagnosis, translated from Russian, is 'vertical plates and pillars most often combined, sporadically not combined; laminae irregular type with dark median line'. This diagnosis was repeated by Bogoyavlenskaya and Khromych (1985).

Pseudotruperetostroma is close to *Atopostroma* Yang and Dong, 1979, but in the latter the pillars are round in cross-section and finely clinoreticulate. It differs from *Truperetostroma* Parks, 1936 in its coarsely cellular tissue throughout the coenosteles and their union into a network in tangential section. This genus could be accommodated in either the Stromatoporidae or the Hermatostromatidae.

The following species closely resemble the type species and can be assigned to the genus: *Truperetostroma cincinnatum* Khalfina, 1960; *Stromatopora flexuosa* Yavorsky, 1955; *Parallelopora jucunda* Khalfina, 1953; *Syringostroma tschichatchevi* Yavorsky, 1931; *Truperetostroma virgulatum* Khalfina, 1960. The following species may belong in this genus but their placement deserves further study: ?*Parallelopora crassa* Yavorsky, 1963; *Truperetostroma lecomptei* Stearn, 1961; *Stromatopora pellucida* Yavorsky, 1955; ?*Parallelopora yangmeishanensis* Yang and Dong, 1963.

Pseudotruperetostroma is restricted to Middle Devonian strata.

Family SYRINGOSTROMELLIDAE Stearn, 1980 (emended)

Diagnosis. Stromatoporids with structure dominated by coenosteles.

Genus SYRINGOSTROMELLA Nestor, 1966

Text-fig. 5A

[= *Syringostromella* Nestor, 1966, p. 47; Mori 1968, p. 87, 88; Bogoyavlenskaya 1973, p. 53; Bol'shakova 1973, p. 96; Khromych 1974, p. 56, 1976, p. 102; Stearn 1980, p. 898; Bogoyavlenskaya and Khromych 1985, p. 91. *Yavorskiina* Khalfina, 1968a, p. 148 (*nomen nudum*); Nestor 1976; pp. 71, 90; Stearn 1980, p. 898; Bogoyavlenskaya and Khromych 1985, p. 94; Dong 1988, p. 36. ? *Pachystroma* Nicholson and Murie, 1878, pp. 214, 223; Nicholson 1886a, p. 91; Flügel and Flügel-Kahler 1968, p. 555.]

Type series. *Stromatopora borealis* Nicholson, 1891a, p. 175; 1891b, p. 315, pl. 9, figs 7-8.

Diagnosis. Coenosteles long, continuous, joining and dividing in vertical section; coenostroms rudimentary or absent; dissepiments common. In tangential section coenosteles vermiform or a loose labyrinthine network. Microstructure cellular.

Discussion. *Syringostromella* differs from *Parallelopora* Bargatzky in the fine cellular microstructure of its coenosteles and the lack of rectilinear micropillars within them. It differs from both *Parallelopora* and *Salairella* in the labyrinthine form of both the coenosteles, and the galleries between them, in tangential section. In *Salairella* the galleries are small, mostly circular in cross-section. *Syringostromella* is one of the most abundant and diverse of the Stromatoporida. It originated in Wenlock time and persisted into the beginning of the Middle Devonian when it was largely displaced by *Salairella*. Nestor (1974) suggested that it could have arisen from *Labechia*, but its cellular microstructure indicates that derivation from *Stromatopora* in late Llandovery time is more probable.

Yavorskiina Khalfina (1968a) was proposed in a parenthesis without an adequate definition to distinguish it from other genera and is therefore invalid according to Article 13a of the *International Code of Zoological Nomenclature* (1985). However, Nestor (1976), while recognizing that the

proposal was invalid, used the genus and remarked on the clinoreticulate microstructure of the coenosteles and its relationship in this to *Vikingia*. There is little in the diagnosis of Bogoyavlenskaya and Khromych (1985) or in the original description of the type species *Stromatopora membroosa* Yavorsky, 1957, to justify distinguishing this taxon from *Syringostromella*.

Pachystroma Nicholson and Murie, 1878, is characterized by prominent latilaminae commonly separated by thin sediment layers and a structure dominated by coarsely cellular coenosteles and dissepiments (Pl. 2, fig. 4). The type species is *Pachystroma antiquum* Nicholson and Murie, 1878. Nicholson (1886a, p. 91) placed the genus in synonymy with *Stromatopora* soon after it was proposed, and since then few authors have used it. However, Nicholson (1891b, p. 311) recognized that *P. antiquum* strongly resembles *Syringostroma* in the prominence of the vertical structures and differs from *Stromatopora*, in which such elements are suppressed. *Pachystroma antiquum* is unlike *Stromatopora* in vertical section and resembles *Syringostromella*. It differs in its extreme latilamination and the round shape of many of the coenosteles (or pillars) in tangential section. Unfortunately, Nicholson's type tangential section is very thick and does not show the form of the pillars/coenosteles clearly. Other specimens of *P. antiquum* are poorly preserved (Parks 1908). Either *Pachystroma* is a valid taxon separate from *Stromatopora* and *Syringostromella*, or the latter is its junior synonym. This problem needs further consideration and resectioning of the type specimen.

A survey of species of *Syringostromella* in the literature has shown that twenty-five can be positively assigned to this genus and another eleven probably belong in it but require further investigation. The Supplementary Publication No. SUP 14042 deposited in the British Library lists species that have the structure and microstructure typical of the genus.

Genus SALAIRELLA Khalina, 1980

Text-fig. 7c

[= *Salairella* Khalina, 1960, p. 330; Flügel and Flügel-Kahler 1968, p. 563; Stearn 1983, p. 555; Bogoyavlenskaya and Khromych 1985, p. 87. ?*Lecomptella* Khalina, 1972, p. 151.]

Type species. Salairella multicea Khalina, 1960, p. 331, pl. D5, fig. 3.

Diagnosis. Coenosteles long, continuous, joining and dividing in vertical section; in tangential section most are joined in a closed network enclosing coenotubes which are round in cross-section; coenostroms rudimentary or absent; dissepiments common. Microstructure finely cellular.

Discussion. *Salairella* is similar to *Syringostromella*, particularly in vertical section. It differs in the tangential section of the coenosteles. In *Salairella* they typically enclose round coenotubes but in *Syringostromella* these tubes are vermiform and open into each other forming a labyrinth. It also resembles *Parallelopora* Bargatzky, 1881, but does not have the coarse reticulate microstructure of this genus. *Salairella* first appeared in the Early Devonian, thrived in Middle Devonian time and at least two species survived into early Late Devonian time.

Lecomptella has been used only by Khalina for the type species *Stromatopora racemifera* Khalina, 1960. In this species coenostroms are more prominent and continuous than in typical *Salairella*, and this feature may justify retaining the taxon despite the close resemblance to *Salairella*.

Species considered representative of the genus *Salairella*, and those provisionally assigned to it are listed in Supplementary Publication No. SUP 14042 deposited in the British Library.

Order SYRINGOSTROMATIDA Bogoyavlenskaya, 1969 (emended)

Diagnosis. Stromatoporoids of microreticulate microstructure and skeleton composed of discrete structural elements including commonly dominant coenostroms and microlaminae, coenosteles and pillars.

Discussion. Justification for the establishment of this new order has been given in the section on classification. The syringostromatids evolved from the family Densastromatidae of the order Actinostromatida by the introduction in the microreticulum of galleries which divided it into structural elements such as coenostroms and coenosteles. Not all microreticulate stromatoporoids belong to this order; only those in which discrete structural elements can be distinguished. The transition to syringostromid structure can be recognized in such advanced densastromatids as *Actinostromella*.

Family SYRINGOSTROMATIDAE Lecompte, 1951
Genus PARALLELOSTROMA Nestor, 1966

Text-fig. 3

[= *Parallelostroma* Nestor, 1966, p. 52; Mori 1970, p. 132; Bol'shakova 1973, p. 86; Nestor 1976, p. 69; Stock 1979, p. 342, 1988, p. 10; Guo 1980, p. 103; Dong 1984, p. 66; Stock and Holmes 1986, p. 562; Stearn 1990, p. 505.]

Type species. *Stromatopora typica* Rosen, 1867, p. 58, pl. 1, figs 1-3; pl. 2, fig. 1.

Diagnosis. Coenostroms thick, composed of orthoreticulate tissue enclosing multiple microlaminae and micropillars, at base separated by short coenotubes into coenosteles of same microstructure; coenosteles largely confined to intercoenostrom space, some superposed, labyrinthine or a closed network in tangential section.

Discussion. Nestor (1986) related this genus to the densastromatids and particularly to *Actinostromella* Boehnke. Mori (1970) placed the genus in the Stromatoporidae and decreased the emphasis on the microreticulation as a generic character. Bol'shakova (1973) listed many species ranging from Early Silurian to Middle Devonian that she assigned to *Parallelostroma*. Fagerstrom (1982) and Stock and Holmes (1986) discussed the relationship between *Parallelostroma* and *Habrostroma*. Stock (1989) reinforced previous conclusions about the origin of *Parallelostroma* from the densastromatids. *Habrostroma* is distinguished from *Parallelostroma* by the irregularity of its microreticulation, giving the tissue a diffuse, lacy appearance, but is similar in its structural elements. Some species with long coenosteles, such as *Stromatopora constellata* Hall, 1852, have been placed in *Parallelostroma* on the basis that *P. typica*, the type species, shows some superposed coenosteles, but these are not typical of the genus. Species considered by the writer to be representative of the genus *Parallelostroma* are listed in Supplementary Publication No. SUP 14042, deposited in the British Library.

Stratigraphical and microstructural evidence suggests that this genus is the rootstock of the Syringostromatida and arose from densastromatid ancestors in Wenlock time. Its acme was in Ludlow time and in Přídolí to Early Devonian time it gave rise to the more advanced members of the family such as *Habrostroma*, *Syringostroma*, *Atopostroma* and *Coenostroma*.

Genus ATOPOSTROMA Yang and Dong, 1979

[= *Atopostroma* Yang and Dong, 1979, p. 74; Stearn, 1980, pp. 889, 895; Stearn, 1983, p. 548.]

Type species. *Atopostroma tuntouense* Yang and Dong, 1979.

Diagnosis. Laminae regular, persistent, formed of a single microlamina with skeletal material from pillars spread irregularly below; pillars confined to interlaminar spaces, typically superposed through many interlaminar spaces, narrow, subcircular in cross-section at base, spreading upward on to bottom of microlaminae forming an irregular network, composed of orthoreticulate to clinoreticulate skeletal material.

Discussion. Owing to its resemblance to *Gerronostroma* this genus was placed in the Clathrodictyidae by Stearn (1980). Further examination has shown that the microstructure is microreticulate and much like that of *Parallelostroma*. Transitional forms between *Atopostroma* and *Parallelostroma* occur in the Martin Well Limestone of Pragian age in Queensland, Australia. *Atopostroma* differs from *Parallelostroma* in the consistent superposition of the pillar/coenosteles and the opening out of galleries by thinning of the vertical elements in *Atopostroma*. The genus is here transferred to the Syringostromatida.

In the grid formed by pillars and laminae and the microreticulate skeletal material, *Atopostroma* resembles *Coenostroma*. It differs in the upward spreading of the pillars as a network on to the laminae. Apart from the network evident in tangential sections formed by the pillars below the laminae, the microreticulate skeletal material, and the upward-spreading (rather than spooled) shape of the pillars, *Atopostroma* resembles *Gerronostroma*.

The genus evolved from *Parallelostroma* early in Devonian time and became common in Emsian time in China, Australia and arctic Canada. In these areas it is a distinctive element of Early Devonian faunas.

Genus COENOSTROMA Winchell, 1867

Plate 2, fig. 3; Text-fig. 8A

[= *Coenostroma* Winchell, 1867, p. 99; Nicholson 1886b, p. 11; Miller 1889, p. 157; Flügel and Flügel-Kahler 1968, p. 539. *Coenostoma* Winchell; Spencer 1884; p. 598 (*lapsus calami*)].

Type species. *Stromatopora monticulifera* Winchell, 1866, p. 91 (subsequently designated by Miller 1889, p. 157).

Diagnosis. Persistent, thick coenostroms, coenosteles and pillars forming an imperfect grid in vertical section; galleries small, irregular; microstructure of structural elements obscurely microreticulate, locally with microlaminae. In tangential section coenosteles an irregular network or, in some species, circular.

Discussion. Nicholson (1886b) placed Winchell's genus in synonymy with *Stromatopora* because it was defined only on the basis of external characteristics, and he did not investigate the internal structure of the type species. Miller (1889) distinguished it from *Stromatopora* on the number of astrorhizal tubes in the mamelon columns. Subsequently the name *Coenostroma* has only been used as a subgenus of *Stromatopora* by Grabau and Shimer (1909). Galloway and Ehlers (1960) described Winchell's specimens of the type species and continued to place the species in *Stromatopora*. My re-examination of these type specimens confirms what is evident from Galloway and Ehlers' illustrations: the internal structure is not close to that of *Stromatopora concentrica* Goldfuss and represents a structure that can be recognized in other species of stromatoporoids. Although the genus was established before internal structures were investigated by thin section, it is valid, as is the genus *Stromatopora* or as brachiopod genera described before serial sections were used.

The preservation of Winchell's suite of type specimens of *S. monticulifera* is not good, and in the lectotype (University of Michigan, 32409A, Galloway and Ehlers 1960, pl. 1, fig. 1b) the microstructure shows vague clusters of specks but is not clearly melanospheric. In places the lectotype shows traces of microreticulation (Pl. 2, fig. 3). Away from the mamelons the upper part of the laminae seems to be a darker microlamina like those typical of *Parallelostroma* Nestor. In the vertical section of the paralectotype (University of Michigan 32409B, section WI-1) microlaminae in the laminae are prominent. Galloway and Ehlers (1960) described as *Parallelopora winchelli* specimens from Winchell's type suite of *S. monticulifera* with well-preserved 'maculae' arranged in vertical rows in the pillars. The similarity in structure, external appearance and occurrence leaves little doubt that these specimens are *Coenostroma monticuliferum* with better preserved micro-

reticulate microstructure. The prominent thick coenostroms in the specimens they called *P. winchelli* preclude their assignment to *Parallelopora*.

The similarity of *Coenostroma monticuliferum* to species of *Habrostroma* Fagerstrom, 1982, is striking. This is particularly true of *Habrostroma* species with prominent pillars, such as *H. beachvillense* Fagerstrom, 1982, which should be transferred to *Coenostroma*. *Habrostroma* should be restricted to species like the type species that do not have prominent pillars/coenosteles. *Coenostroma* differs from *Syringostroma* Nicholson, 1875, in its lack of diffuse megapillars associated with mamelon columns, but some species that have been referred to *Syringostroma* should be transferred to *Coenostroma* (see below). *Parallelostromella* Kosareva, 1968, may be a junior synonym of *Coenostroma* but is not valid as it was published without diagnosis (*International Code of Zoological Nomenclature* 1985, Article 13).

Representative species of *Coenostroma* (in addition to the type species) are listed in Supplementary Publication No. SUP 14042 deposited at the British Library. I have examined type specimens of *Coenostroma botryoideum* (Spencer, 1884), and *Coenostroma galtense* Dawson, 1879; both are dolomitized and indeterminate at the generic level.

Most of the species of *Coenostroma* come from Middle Devonian strata, but the range of the genus spans the Devonian and possibly the older Přídolí (Stock, personal communication, 1991).

Genus HABROSTROMA Fagerstrom, 1982

Text-fig. 8B

[= *Habrostroma* Fagerstrom, 1982, p. 11; Dong 1984, p. 189; Stock and Holmes 1986, p. 562; Stearn 1990, p. 508].

Type species. *Stromatopora proxilaminata* Fagerstrom, 1961, p. 8, pl. 1, figs 4–6.

Diagnosis. Coenosteles short, irregular, largely confined between coenostroms, forming a diffuse irregular network in tangential section, of irregularly cellular tissue with diffuse boundaries; coenostroms prominent, of similar cellular tissue, containing one or more microlaminae. Structural elements may appear microreticulate in well-preserved specimens.

Discussion. Fagerstrom (1982) discussed the relationship of this genus to similar genera at length. Stock and Holmes (1986) suggested that it cannot be separated from *Parallelostroma* although Stock (1989) later used the genus. Stearn (1990) suggested that species assigned to *Habrostroma* by Fagerstrom that have persistent coenosteles should be referred to genera such as *Salairella* and *Columnostroma*. The similarity of *Habrostroma* and *Climacostroma* Yang and Dong, 1979 has been noted by Fagerstrom (1982). Differences between their microstructures must be investigated by comparison of the type specimens (see *Lineastroma* above).

Habrostroma has been recognized in rocks as old as Přídolí (Stock 1989), and ranges as high as Frasnian strata but is most diverse in the Eifelian.

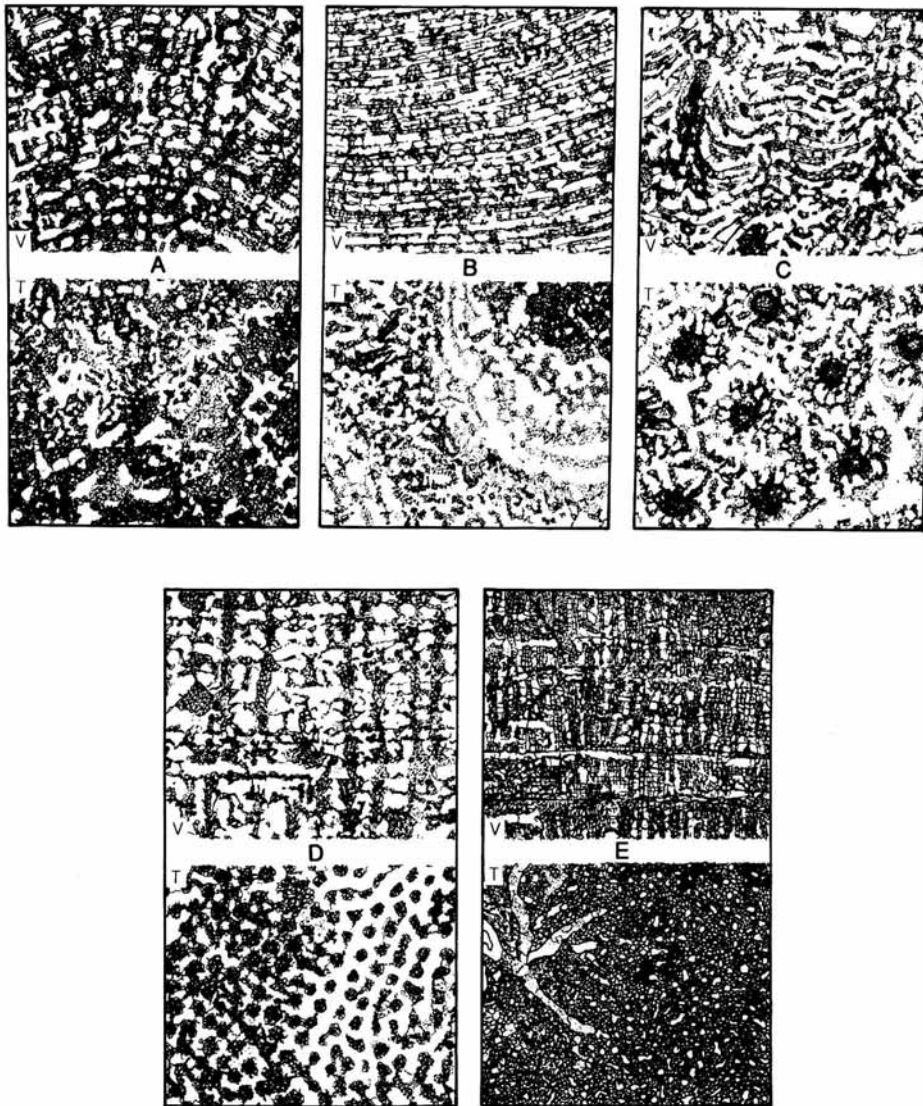
Species that are considered representative of this genus are listed in Supplementary Publication No. SUP 14042 deposited in the British Library.

Genus SYRINGOSTROMA Nicholson, 1875

Text-fig. 8C

[= *Syringostroma* Nicholson. Fagerstrom (1982) has provided a complete synonymy. Discussion since 1982 has been provided by Bjerstedt and Feldmann 1985, p. 1049; Stearn and Shah 1990, p. 507. *Stylodictyon* Nicholson and Murie, 1878, p. 221.]

Type species. *Syringostroma densa* Nicholson, 1875, p. 251 (subsequently designated by Nicholson 1886a, p. 98).



TEXT-FIG. 8. Sketches of Syringostromatida in vertical (V) and tangential (T) section. A, *Coenostroma* (based on photographs of the type specimen of *C. monticuliferum*). B, *Habrostroma* (based on *H. proxilaminatum* in Fagerstrom 1982). C, *Syringostroma* (based on *S. scherzeri* in Fagerstrom 1982). D, *Columnnostroma* (based on illustrations of Parks's topotype of *Coenostroma ristigouchense* in Fagerstrom 1982). E, *Parallelopora* (based on Bargatzky's type of *P. ostiolata* illustrated by Lecompte 1952). All figures $\times 10$.

Diagnosis. Coenosteles short, irregular, coarsely cellular, without precise boundaries, irregular in tangential section; megapillars long, continuous, clinoreticulate, round in tangential section; coenostroms persistent, thick, cellular, containing one or more microlaminae; dissepiments rare.

Discussion. Fagerstrom (1982) discussed the relationship between *Syringostroma*, *Habrostroma*, *Parallelopora* and *Stylodictyon*. The characteristic features that distinguish *Syringostroma* are the clinoreticulate megapillars, the diffuse nature of the tissue of the structural elements and the prominent microlaminae. In the light of Fagerstrom's (1982) extensive review of the species assigned to this genus, no attempt is made to reassign the many species that have been incorrectly attributed to this genus.

The genus evolved from *Parallelostroma* in the mid-Early Devonian (Pragian) and reached its acme during the Eifelian. The genus did not survive into the Givetian.

Genus COLUMNOSTROMA Bogoyavlenskaya, 1972

Text-figs 6C-D, 8D

[= *Columnostroma* Bogoyavlenskaya, 1972, p. 33; Stearn 1980, p. 899; Bogoyavlenskaya and Khromych 1985, p. 74.]

Type species. *Coenostroma ristigouchense* Spencer, 1884, p. 599, pl. 6, figs 12, 12a (*Coenostroma* is consistently misspelled *Coenostoma* in this paper).

Diagnosis. Pillars long, continuous, rarely joining or dividing, clinoreticulate, round in tangential section and joined by radial processes; coenostroms thick, only locally laterally persistent, interrupted by foramina; dissepiments common crossing coenotubes between pillars.

Discussion. Nicholson's (1886a, 1891b) illustrations of the type do not show the thick coenostroms that are present in parts of the slides in his collection (P5591, Natural History Museum, London, marked as from Spencer's original) (Text-fig. 6C-D). Fagerstrom (1982) illustrated Parks's (1909) topotype. The microstructure is not well preserved in the type specimen and Nicholson's sections are thick, but the pillars appear to be clinoreticulate and the coenostroms are vaguely orthoreticulate. Stearn (1966a) suggested it was better assigned to *Parallelopora*, but the tangential aspect of round pillars is distinctive and the microreticulate microstructure is not as coarse as that of typical *Parallelopora*. Fagerstrom (1982) retained Nicholson's (1891b) assignment of the species to *Syringostroma*. Features that distinguish *Columnostroma* appear to be the dominant, discrete, clinoreticulate pillars joined in tangential section, but not into a continuous network, and lack of the smaller secondary pillars and microlaminae typical of *Syringostroma*. It closely resembles *Coenostroma* but can be distinguished by the dominantly vertical structure of the clinoreticulate tissue and the lesser importance of the coenostroms. The 'arms' joining the pillars in tangential section appear near the laminae to be of microreticulate skeletal material and between the laminae to be dissepiments.

Only Bogoyavlenskaya (1972, 1977) has assigned species to the genus. The following are considered sufficiently similar to the type to justify assigning them to *Columnostroma*: *Actinostroma fenestratum* Nicholson, 1889; *Stromatopora gallowayi* Fritz and Waines, 1956; *Columnostroma grandisculum* Bogoyavlenskaya, 1977; *Syringostroma parallelum* Parks, 1908; *Actinostroma parksi* Fritz and Waines, 1956; *Parallelopora pulchra* Galloway and St. Jean, 1957; *Parallelopora snoufferensis* Galloway and St. Jean, 1957.

The type species comes from rocks of Early Devonian (?Gedinnian) age near Dalhousie, New Brunswick, Canada. The genus is most diverse in Eifelian rocks and there is no evidence that it extends above this stage.

Genus PARALLELOPORA Bargatzky, 1881

Text-fig. 8E

[= *Parallelopora* Bargatzky, 1881, p. 63 (see Flügel and Flügel-Kahler for pre-1968 synonymy); Flügel and Flügel-Kahler 1968, p. 556; Mori 1970, p. 130; Zúkalova 1971, p. 68; Kazmierczak 1971, p. 119.]

Type species. Parallelopora ostiolata Bargatzky, 1881, p. 64 (subsequently designated by Nicholson 1886a, p. 193).

Diagnosis. Coenosteles long, continuous, branching and joining in vertical section, in tangential section mostly joined in a closed network enclosing round coenotubes; coenostroms suppressed or absent, dissepiments abundant. Microstructure of coenosteles coarsely microreticulate, apparently formed of closely spaced opaque micropillars and more widely spaced short microlaminae.

Discussion. *Parallelopora* has been used as a repository for many species with prominent coenosteles and indifferent preservation. Most of the species tentatively assigned to the genus in Flügel and Flügel-Kahler (1968) should be referred to genera such as *Syringostromella* and *Salairella*. *Parallelopora* is distinguished from *Salairella* by the coarse microreticulate microstructure of the coenosteles. The microgalleries between the micropillars are large enough to be confused with galleries in the typical species. From *Columnostroma* it is distinguished by this microstructure and the fact that the coenosteles in tangential section join into a closed network enclosing coenotubes rather than being discrete.

As defined above, *Parallelopora* is restricted to Eifelian and Givetian rocks.

A review of the literature suggests that only the species listed in Supplementary Publication No. SUP 14042 deposited at the British Library have the features (above) which closely relate them to the type species.

Acknowledgments. I am grateful to the officers of various museums for giving me access to type specimens on which this study is based including: the Natural History Museum, London; Institut Royal des Sciences Naturelles de Belgique, Brussels; Institut für Paläontologie, Bonn; Forschungsstelle für Korallen Paläozoologie, Münster; Institut Geologii, Tallinn; Naturhistoriska Riksmuseet, Stockholm; Royal Ontario Museum, Toronto. Heldur Nestor kindly made available new photographs of types from the former Soviet Union. I thank Carl Stock and Barry Webby for helpful comments on the manuscript. My research is supported by the Natural Sciences and Engineering Research Council of Canada.

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Typescript received 13 November 1991
 Revised typescript received 10 March 1992

APPENDIX

Nicholson's thin sections of *Stromatopora concentrica* in the Natural History Museum, London, are difficult to match with the drawings and the captions of his illustrations as the captions do not correspond with the notations on the thin sections. In plate 11 Nicholson (1886a) illustrated a whole specimen (fig. 15), two tangential sections (figs 16–17) and a vertical section (fig. 18). The vertical section and one of the tangentials (pl. 11, fig. 17) are identified in the caption as coming from a specimen in the Caunopora-state, one different from that of figures 15 and 16, which was identified as 'absolutely identical with the original example of the species' (Nicholson 1886a, pl. 11). (The term 'Caunopora-state' was used by early workers to indicate specimens intergrown with syringoporoid corals.) The relevant thin sections in the collection are labelled as from specimens 1 and 3. Only specimen 3 is in the 'Caunopora-state'. Labels on the thin sections indicate that figures 16 and 18 come from sections 1 and 1a, and figure 17 comes from 3a. The three thin sections cannot be matched precisely with the drawings in Nicholson's plate 11; however, the tangential section of figure 17 is in the 'Caunopora-state' and is likely to come from specimen 3, as the section label indicates. The label on thin section 1a and the fact that the drawing of the vertical section of figure 18 does not show the 'Caunopora-state' both indicate that the caption for figure 18 is incorrect, and both figures 18 and 16 are from the specimen Nicholson regarded as 'identical' with the type, that is specimen 1 (P5869). The thin sections 1 and 1a which I conclude are the basis of figures 16 and 18 respectively are illustrated above in Plate 1, figures 1–2.