Revised classification and terminology of Palaeozoic stromatoporoids

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Stearn, C.W., Webby, B.D., Nestor, H., & Stock, C.W. 1999. Revised classification and terminology of Palaeozoic stromatoporoids. — *Acta Palaeontologica Polonica* **44**, 1, 1–70.

Palaeozoic stromatoporoids comprise an extinct class of non-spiculate poriferans that are represented as fossils by their basal carbonate skeleton. A revised terminology for the description of these fossils is presented. Seven orders (Labechiida, Clathrodictyida, Actinostromatida, Stromatoporellida, Stromatoporida, Syringostromatida, Amphiporida) are recognized. The following is recorded for each genus: (1) type species, catalogue number and depository of the primary holotype; (2) synonyms and their type species; (3) diagnosis; (4) stratigraphic range; (5) estimate of the number of species assigned to the genus; (6) stratigraphic and geographic distribution of the genus. Problems in the definition and recognition of the genus are briefly discussed in annotations. One hundred and nine genera are considered valid, or doubtfully valid. Fifty three genera are placed in synonymy. An additional 14 genera are considered to be of uncertain placement in the classification.

Key words: Stromatoporoids, Porifera, taxonomy, morphologic terminology, Palaeozoic, distribution.

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Introduction

> *'The propriety of... keeping the Stromatoporoids as a separate group is the more evident when it is remembered that our knowledge of these singular organisms is necessarily derived from an examination of their hard parts alone.'* (Nicholson, 1886b: pp. 71–72)

In common with a number of reef-building lower to middle Palaeozoic organisms, the stromatoporoids are characterized by large simple, calcified, skeletons of laminar, domical, bulbous, or (less commonly) branching or columnar form. They differ from cnidarians and bryozoans that also contributed to these reefs in lacking receptacles (tubes and cups) to contain individuals of a colony. Internally they exhibit skeletal elements more or less parallel and perpendicular to the growth surface which define a continuous network of repeating pattern. Superficially and internally they have distinctive aquiferous canal systems of radial form, each converging on a centre. These features are closely comparable to living coralline sponges in which radial canals are manifestations of a filter-feeding system that drains water from choanocyte chambers and disposes of it in a jet away from the organism.

No trace of spicules has been found preserved in the calcareous skeletons of early and middle Palaeozoic stromatoporoids, and in this they differ from the convergently similar late Palaeozoic and Mesozoic sponges that have been called stromatoporoids, in some of which spicules have been found. However, this does not imply that they are not sponges, as not all living or fossil sponges, including several genera of living coralline sponges, preserve spicules in their skeletons. The Cambrian archaeocyaths and early Palaeozoic representatives of the sphinctozoan sponges also lack any trace of spicules. The spiculate late Palaeozoic and Mesozoic stromatoporomorphs have now been classified within the classes Demospongia and Calcarea. In this paper the term stromatoporoid and the Class Stromatoporoidea are restricted to the group of coralline sponges without spicules of Ordovician to Devonian age.

This paper is not concerned primarily with the affinity of this extinct group to living organisms. In the last 130 years that their internal structure has been studied, the stromatoporoids have been assigned to six or seven groups of the lower invertebrates (briefly reviewed in Stearn 1982, 1983). During this time most of the discussion has been on whether they are more closely allied to the Porifera or Cnidaria. The relatively recent suggestion that stromatoporoid skeletons were formed by cyanobacteria (Kaźmierczak 1976, 1981) has been specifically challenged by Riding & Kershaw (1977). We acknowledge that some intergrowths of stromatoporoids and cyanobacteria did occur, but, like the example described and illustrated by Webby (1991: pp. 198–200), the morphologies of the stromatoporoid can be distinguished readily from associated, close-spaced, micritic layers of the cyanobacterium. The stromatoporoid is associated with, not formed by the cyanobacterium. We consider that the evidence from comparative anatomy and functional morphology that the stromatoporoids belong to the Porifera is convincing. Recent contributions from palaeontologists and zoologists that support this view include the following: Hartman & Goreau (1970), Stearn (1975), Vacelet (1985), Boyajian & Labarbera (1987), Reitner (1987), Wood (1990), and Stearn & Pickett (1994).

Currently there are two approaches to the study of the Stromatoporoidea (*sensu* Nicholson & Murie 1878). The first is to regard the group as having taxonomic unity and to assign members to a separate class divided into seven orders within the Porifera. This approach is used in this paper.

Those who propose the second approach argue against the taxonomic usefulness of the group. They claim the stromatoporoid-type skeleton is a convergent feature, that the group is polyphyletic, and that it merely represents a stromatoporoid grade of organization characterized by modules that comprise superficial aquiferous systems and heavily calcified basal skeletons. These skeletons are developed in various lineages of sponges in response to the need for stability on firm substrates in reef environments. The following history of 'stromatoporoid-grade sponges' was noted by Wood (1991: p. 119):

1. They first appeared briefly in the early Cambrian (archaeocyaths);
2. They appear again in the Middle Ordovician and became abundant and widespread through Silurian and Devonian time (Palaeozoic stromatoporoids);
3. They were common in Jurassic and Cretaceous reefal successions (Mesozoic stromatoporomorphs).

This succession is composed of three taxonomically distinct groups. The first two are aspiculate, but spicules have been found in the third. Those that favour this second approach believe that the Palaeozoic stromatoporoids belong to various classes of the living sponges that are classified on the basis of their spicules, but the stromatoporoids can not be classified because they do not have spicules. In addition, because the basal skeleton is 'easily' developed (it is facultative), its features are useless for establishing phylogeny and a classification that should reflect phylogenetic relationships.

The use of names, such as stromatoporoid, that have established taxonomic significance to distinguish grades is inappropriate and confusing, mixing grade and clade terminology. The stromatoporoid grade does not include all Palaeozoic stromatoporoids or Mesozoic stromatoporomorphs as the columnar and branching growth forms are excluded.

The present state of knowledge allows the Palaeozoic stromatoporoids to be regarded as a class of the Porifera with close relationships to other fossil poriferans secreting continuous calcareous skeletons, such as the Archaeocyathida, Chaetetida, and Sphinctozoa. In the absence of other criteria, the classification and history of the class can be based on only the interpretation of their basal calcareous skeleton. Without the evidence of spicules in this class, its phylogenetic relationship to modern sponges secreting siliceous spicules remains obscure, but the similarity of its members in growth form, structural elements, and aquiferous systems to living coralline sponges (sclerosponges) is striking.

Many Palaeozoic stromatoporoid fossils are poorly preserved and microstructural details may be lost in the diagenetic conversion of their high-magnesium calcite and aragonite skeletal material to low-magnesium calcite of the preserved specimens. However, many specimens, particularly those infiltrated by bitumen from petroleum-bearing reefs, show exquisite detail and contrast. No record of soft tissue has ever been found, yet we now have an understanding of the nature and methods of secretion of the skeleton by analogy with those of the living coralline sponges documented by Hartman & Goreau (1970) and Vacelet (1985). Over the last few decades, new faunas have been documented and older taxonomic descriptions have been revised to form a reliable database. The temporal and spatial distributions of Palaeozoic stromatoporoids are now better known, allowing the global patterns of biostratigraphy and paleobiogeography to emerge.

Institutional abbreviations: AMNH – American Museum of Natural History, New York; BM(NH) – Natural History Museum, London; CIGMR – Chengdu Institute of Geology and Mineral Resources, Chengdu; CNIGR – CNIGR Museum, St. Petersburg; CSGM – Central Siberian Geological Museum, Novosibirsk; DPI – Geological Museum, Donetsk Polytechnic Institute, Donetsk, Ukraine; FMNH – Field Museum of Natural History, Chicago (formerly Walker Museum); GFCL – Faculté Libre des Sciences, Université de Lille, Lille; GMU – Geological Museum of Uzbekistan (Geologicheskii Musei Uzbekistana), Tashkent; GSC – Geological Survey of Canada, Type collection, Ottawa; IGPS – Institute of Geology and Paleontology, Tôhoku University; IGTTU – Institute of Geology, Tallinn Technical University (Tallinna Tehnikauliko Geologoogia Instituut), Tallinn; IPB – Institut für Paläontologie, University of Bonn, Bonn; IRScNB a – Institut Royal Sciences Naturelles, Belgique, Brussels (Lecompte Collection); MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MLP – Institute für Paläontologie, University Erlangen at present, to be transferred to Universidad National de la Plata, Argentina; MMF – Geology and Mineralogy Museum, Sydney; NIGP – Nanjing Institute of Geology and Paleontology, 'Academia Sinica'; PIN – Paleontological Museum, Russian Academy of Science, Moscow; PMO – Paleontological Museum, Oslo; ROM – Royal Ontario Museum, Toronto; SMF – Senckenberg Museum, Frankfurt; SMNH – Naturhistorisk Riksmuseet, Stockholm; SOAN – Institute of Geology and Geophysics, Novosibirsk, Russian Academy of Science, Siberian Branch; SSGC – South-Siberian Geological Committee, Novokuznetsk; SUP – University of Sydney Paleontological collections (in the current transfer of types to the Australian Museum, SUP numbering is being retained, though linked to new AMF numbers to ensure continuity of easy access); UGM – Urals Geological Museum, Ekaterinburg; UMMP – Paleontology Museum, University of Michigan, Ann Arbor; UNC – University of North Carolina, Department of Geology, Chapel Hill; UQF – University of Queensland, Geological Museum, Brisbane; USNM – National Museum of Natural History (U.S. National Museum), Washington.

Terminology

One aspect of our current work preparing the contribution on Palaeozoic stromatoporoids for the revised calcified sponge volume of the *Treatise on Invertebrate Paleontology* has been the establishment of a standardized glossary of terminology. Stearn and Webby initially (in the late 1980s) prepared a draft glossary for the Stromatoporoidea, and this was circulated to other *Treatise* participants for their suggestions and amendment prior to adoption. Additionally, one group of stromatoporoids (the Labechiida) was chosen in a pilot study to develop and test early versions of the new, comprehensive, *Treatise*-based, user-friendly, relational database named *PaleoBank*. This required the preparation of a further list of stromatoporoid morphological terms for incorporation in the data-capture software of *PaleoBank*, specifically added to the menu-driven screens so that all relevant morphological information on stromatoporoid taxa can be entered into the database. The outline of the stromatoporoid terminology presented herein is derived from both current *Treatise* and *PaleoBank* usages.

The glossary is an attempt to provide a concise, simple, comprehensive, and standardized morphological framework for use in describing the Class Stromatoporoidea, the first in English since the late 1950s (Galloway 1957: pp. 350–360). Other glossaries have been proposed by Bogoyavlenskaya (1968, 1973a, 1984), Khalfina (1972), and Bol'shakova (1973).

It has been customary practice of stromatoporoid specialists, since Rosen in the 1860s and Nicholson in the 1870s, to use carefully oriented thin sections as the primary means of studying stromatoporoid skeletons. In order to elucidate the three-dimensional form of skeletons of laminar, domical, and bulbous shape, two sections are cut, one (traditionally called a vertical section) perpendicular to the growth surface, and the other (traditionally called a tangential section) parallel to it. For the study of skeletons of columnar and dendroid shapes, three sections are required, one (longitudinal section) parallel to the long axis of the column or branch, the second (transverse section) perpendicular to the long axis, and the third (tangential section) parallel to the long axis but slightly within the outer margin of the column or branch. Gross morphology, polished slabs, and broken surfaces of the collected specimens, and obliquely oriented thin sections, provide important supplementary data for fully characterizing these fossils.

Because the growth direction of the skeleton is directed radially in parts of domical, columnar and bulbous skeletons, the common use of the terms vertical and horizontal to refer to the orientation of structural elements is misleading. Growth can be thought of as taking place longitudinally, as the organism extends outward from the growth surface; and tangentially, as it extends laterally parallel to the growth surface. The terms longitudinal and tangential are appropriate for referring, not only to orientations within the skeleton, but also to the thin sections that are used to study them. Consequently, these terms will be used in this paper, but the term vertical, equivalent to longitudinal, is well entrenched in stromatoporoid literature.

Morphological terminology

Morphological terms are arranged alphabetically for easy reference. The skeletal features of stromatoporoids can be classified into those that are: (1) related to skeletal form and structure (skeleton), (2) parallel to growth surfaces (tangential), (3) normal to growth surfaces (longitudinal), (4) related to the aquiferous filtration system (aquiferous), (5) related to microstructure (microstructure). The group of terms to which each of the following terms refers is indicated in parentheses after the term, unless it is obvious.

Amalgamate structure (skeleton) — the three-dimensional network in which discrete, persistent tangential structural elements are poorly defined (Fig. 1B).

Astrorhiza (aquiferous) — a set of radiating branching grooves, ridges, or openings to the interior that join to form a stellate system on the terminal growth surface; the structures are commonly associated with mamelons (Figs 1B, 4A, 5F).

Astrorhizal canal (aquiferous) — part of a stellate, radiating or branching, walled or unwalled canal system within the skeleton (both longitudinally and tangentially oriented). These canals may be partitioned by tabulae or dissepiments (Fig. 1B).

Axial canal (aquiferous) — a longitudinally oriented median structure of the astrorhizal system in domical, laminar, bulbous and irregular skeletons that may be analogous to the axial canal in some columnar to dendroid stromatoporoids. It may be tabulated (Fig. 2B).

Cassiculate structure (skeleton) is formed by oblique skeletal elements joined to enclose diamond-shaped galleries in a network like that of a chain-link fence (Figs 1B, 7A).

Cellular (microstructure) — speckled skeletal material filled with closely spaced, irregularly distributed, subspherical, clear areas (cellules) that appear to have been voids in the structural element (Figs 2C, 7A).

Coenostele (longitudinal) — a wall-like part of the amalgamate net, either meandriform or fused to form a closed continuous network in tangential section (in orders Stromatoporida and Syringostromatida) (Figs 1B, 2B).

Coenostrome — a tangential part of the amalgamate net that parallels the growth surface in the orders Stromatoporida and Syringostromatida (Figs 1B, 2B).

Coenotube (longitudinal) — an elongate space within the skeleton aligned normal to the growth surface, meandriform or irregular in tangential section, bounded by amalgamate net of coenosteles and coenostromes, internally divided by dissepiments (in orders Stromatoporida and Syringostromatida) (pseudozooidal tube of

Galloway 1957). **Autotube** is a similar elongate space, circular to subcircular in tangential section (Fig. 1B).

Colliculus (tangential) — a rod that joins other such rods to form a net parallel to the growth surface in the order Actinostromatida, hence the laminae in this group are composed of colliculi (Figs 2A, 5B, D).

Column — a longitudinal skeletal structure (of macrostructural level) in which the arrangement of the skeletal elements differs from that of the intercolumn areas. The difference is commonly in the concentration and width of astrorhizae, pillars, or other longitudinal structures (Figs 2B, 5A).

Compact (microstructure) — specks in structural elements are distributed evenly so that the elements have no regular internal microstructure (Fig. 2C).

Crenulation (longitudinal) — a small upwardly inflected extension of a cyst plate or lamina (Fig. 1A).

Cyst plate (tangential) — an upwardly and outwardly convex (in a few taxa concave or flat) skeletal plate parallel to the growth surface in the order Labechiida. A **cyst** is the space inclosed by the cyst plate (Figs 1A, 3C, E).

Denticle (longitudinal) — a short, solid, skeletal rod raised above the surface of cyst plates, or extending from the flanks of some pillars in the order Labechiida (incorporates villi of Galloway 1957) (Fig. 1A).

Dissepiment (tangential) — an upwardly convex or inclined plate occupying inter-laminar space; this term is also applied to partitions in coenotubes and astrorhizal canals (Fig. 1B).

Epitheca (tangential) — a thin layer of fine structure directly above the basal growth surface (Fig. 1C).

Fibrous (microstructure) — specks and crystal boundaries in the structural elements are aligned. In laminae this alignment is transverse; in pillars it may curve upward and outward from the axis in a water-jet or feather structure (Fig. 2C).

Gallery (skeleton) — the three-dimensional interlaminar space between adjacent pillars and may be bounded by other structural elements (e.g., dissepiments). The term is not usually used in the Labechiida (Fig. 1C).

Growth form (skeleton) may be laminar, domical, bulbous, irregular, columnar, or dendroid. Laminar, domical, irregular and bulbous forms may interfinger at their outer edges with the surrounding sediment.

Growth surface (tangential) — any level in the skeleton where addition to the surface is contemporaneous; **basal** and **terminal** refer to the first and last surfaces of skeletal growth (Fig. 1A).

Lamina (= lamella of Lecompte 1956, plural **laminae**) — a tangentially extensive skeletal plate or net parallel to the growth surface; it may be single-layered or tripartite – i.e., with a less opaque central zone, a line of cellules in the central zone (ordinicellular) or an opaque central microlamina, or it may be composed of multiple microlaminae (Figs 1C, 2A, 6C).

Latilamina (plural **latilaminae**) — a tangentially continuous set of layers of skeletal material bounded above and below by phase changes or growth interruption surfaces (Figs 1C, 2A).

Mamelon (longitudinal) — an updomed area of skeletal material on the terminal growth surface (Fig. 2B).

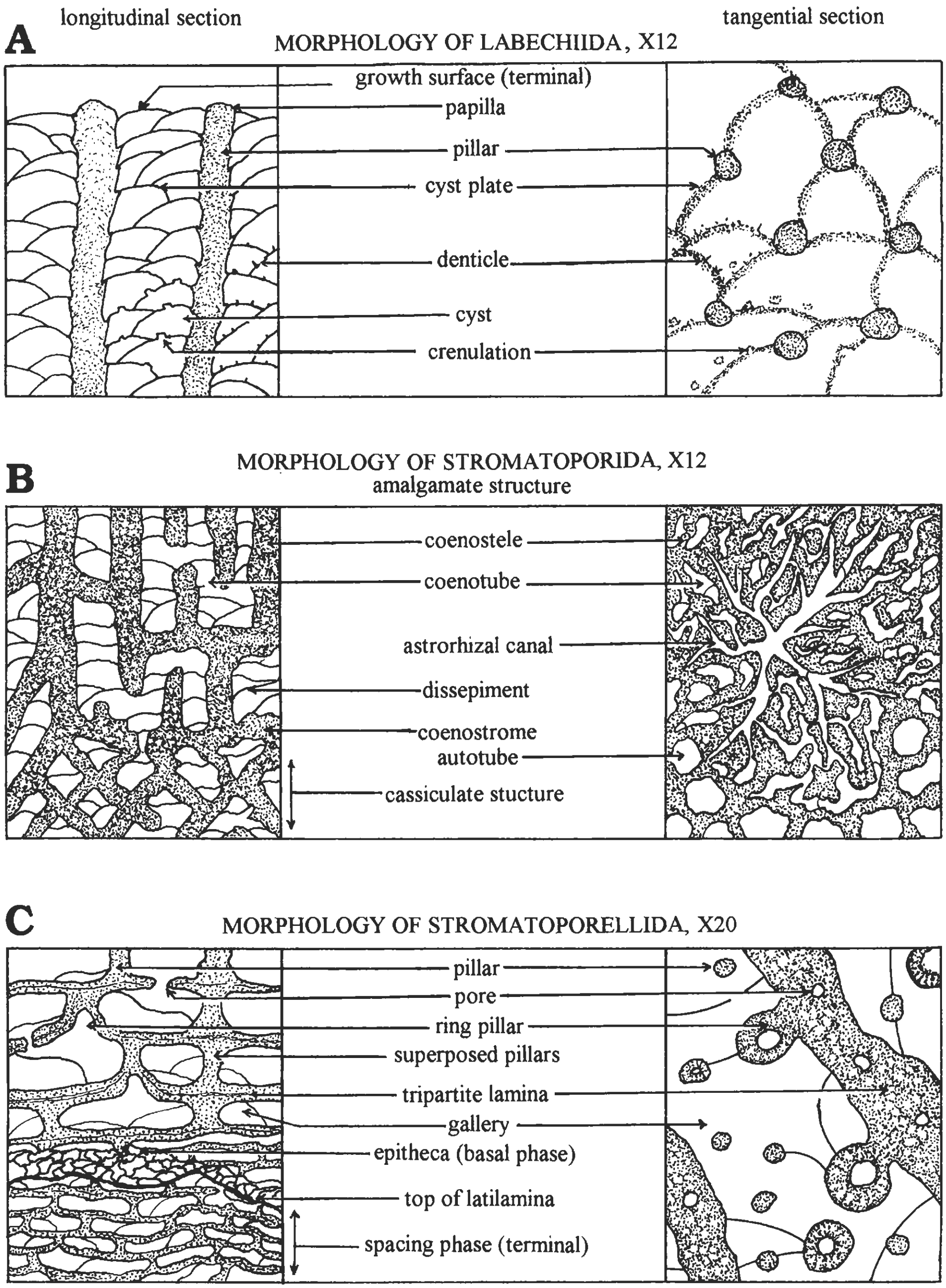


Fig. 1. Morphological terms applied to stromatoporoids. Features are illustrated diagrammatically and the drawings are not based on any particular genus.

Mamelon column (longitudinal) — a structure composed of upwardly inflected laminae, cyst plates, or coenostromes formed by superposition of mamelons (Fig. 2B).

Megapillar (longitudinal) — a rodlike structure of a larger order of magnitude than a pillar with compact microstructure. Megapillars can be distinguished in taxa having two sizes of pillars, such as *Bifariostroma, Oslodictyon, Yabeodictyon*, and *Actinodoctyon* (Figs 2A, 4C).

Melanospheric (microstructure) — specks in structural elements are concentrated in closely spaced, irregularly distributed, subspherical, opaque areas separated by clear areas (Fig. 2C).

Microcolliculus (tangential) — a rod that forms a network joining micropillars within microreticulate microstructure (Figs 2C, 5A, B, H).

Microlamina (tangential) — a thin, compact, laterally persistent plate that may be part of a lamina, or a single element parallel to the growth surface, or it may consist of microcolliculi (Fig. 2B).

Micropillar (longitudinal) — a very fine rodlike structure within microreticulate microstructure.

Microreticulate (microstructure) — structural elements composed of micropillars and microlaminae (composed of microcolliculi) giving a three-dimensional, rectilinear network of fine posts and beams. May be divided into:

- **Acosmoreticulate** — orientation of micropillars and microcolliculae is without order (Fig. 2C).
- **Clinoreticulate** — micropillars curve upward and outward from pillar axes (Fig. 2C).
- **Orthoreticulate** — micropillars are normal to laminae/coenostromes and the microlaminae are parallel to the laminae (Figs 2C, 8F).

Ordinicellular (microstructure) — axial planes of laminae are marked by a layer of subspherical clear areas (cellules) giving laminae a three-layered, or tripartite, appearance in longitudinal section. Where divisions between these cellules is missing, the semicontinuous, clear, middle layer accentuates this tripartite appearance. In some tripartite laminae the central layer may be more opaque than those above and below (Figs 1C, 2C).

Papilla (longitudinal) — a raised rounded extension of a pillar on the terminal growth surface (Figs 1A, 2A).

Paralamina — a planar, tangential skeletal plate that traverses, single-layer, chevron-shaped laminae of a few genera of the order Clathrodictyida (Nestor 1966: fig. 5).

Phase (skeleton) — a part of the skeleton characterized by a change of growth structure either longitudinally (successive) or tangentially (contemporary). May be divided into:

- **Basal phase** (tangential) — distinguished by structures different from those of the mature skeleton formed in the initial growth of skeletal material across a surface of the sediment or hard substrate or resumption of growth at the base of a latilamina (Fig. 1C).
- **Contemporary phase** (longitudinal) — a unit of skeletal growth of characteristic structure that displaces others tangentially reflecting different structures formed contemporaneously along the growth surface (e.g., areas exhibiting structures unique to those formed by the superposition of mamelons) (Fig. 2B).
- **Spacing phase** (tangential) — distinguished by changes in the spacing of laminae, cysts, or coenostromes (Fig. 1C).
- **Successive phase** (tangential) — a unit of growth distinguished and bounded by longitudinal changes in structure within the skeleton; the phase may be terminal, basal, or spacing (Fig. 1C).
- **Terminal phase** (tangential) — the last units of skeletal growth that preserve a change in structure (Fig. 1C).

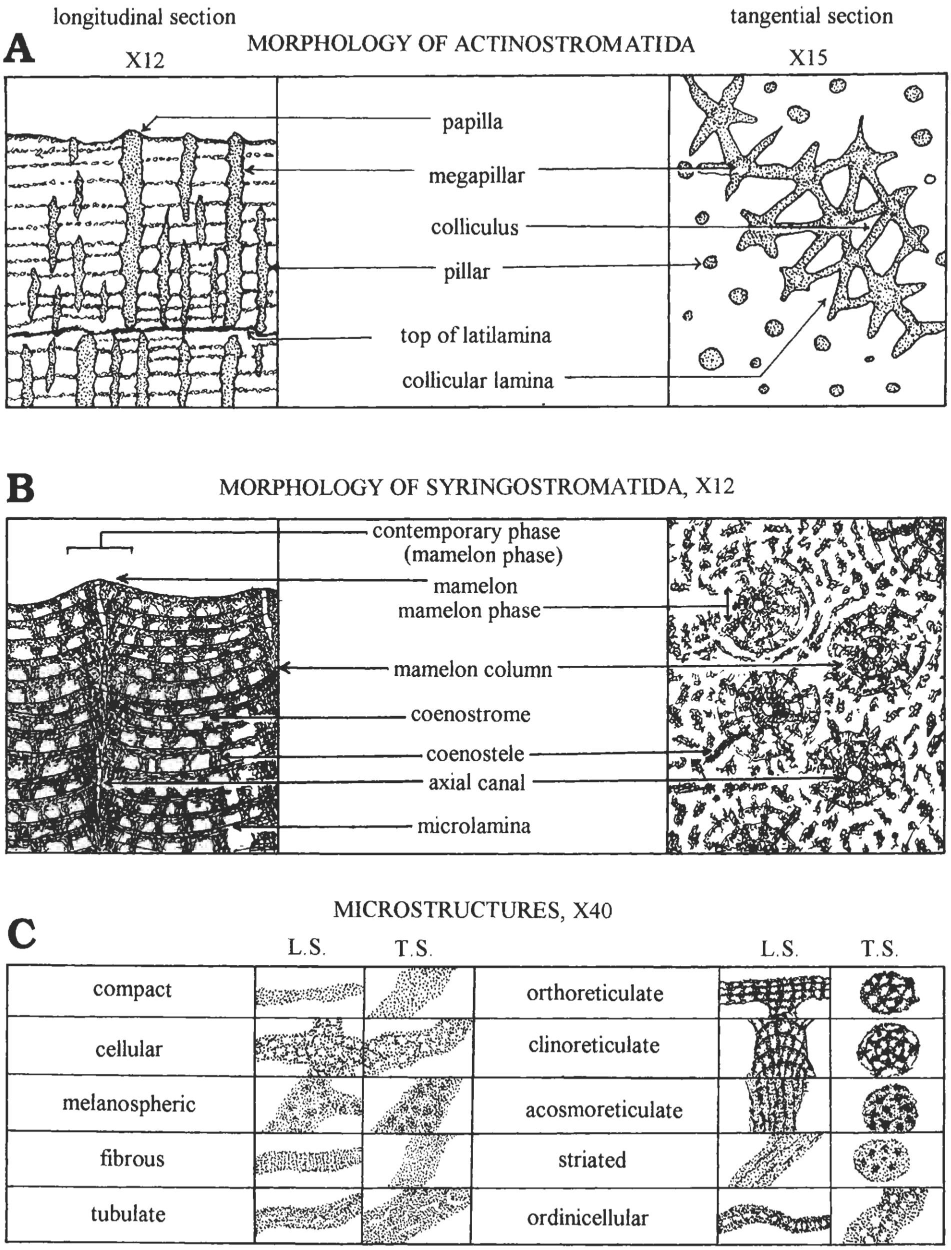


Fig. 2. Morphological terms applied to stromatoporoids. Features are illustrated diagramatically and the drawings are not based on any particular genus

Pillar — a longitudinal skeletal rod (rarely a plate); may be long, columnar, continuous through laminae and interlaminar spaces, or may be confined to an interlaminar space, upwardly conical, spool-shaped, grading into upwardly or downwardly inflected laminae. Pillars of the order Labechiida may be circular, irregular, meandriform or bladed (with or without flanges) in tangential section. Ring pillars are hollow cones formed by the upward inflection of laminae. A series of short, superposed interlaminar pillars (in families Trupetostromatidae, Gerronostromatidae), may be difficult to distinguish from long, continuous pillars unless the traces of the laminae cross them (Figs 1A–C, 2A).

Pore (tangential) — an opening of rounded section through a lamina (foramen of Galloway 1957 is a large pore) (Fig. 1C).

Skeletal structure (skeleton) — frameworks (laminae, pillars and other elements) of the basal calcareous skeleton. The frameworks are dominated by grid-like combinations of **structural elements** that characterize the main orders of the class Stromatoporoidea: (a) Domes (**cyst plates**) and pillars in the order Labechiida (Fig. 1A); (b) Floors (**laminae**) and **pillars** in the order Clathrodictyida and the order Stromatoporellida (Fig. 1C); (c) Beams (**colliculi**) and pillars in the order Actinostromatida (Fig. 2A), and (d) an **amalgamate structure** composed of floors (**coenostromes**) and walls (**coenosteles**) in the order Stromatoporida (Fig. 1B).

Skeleton — all the hard parts secreted by the living organism in order to maintain itself above the substrate and avoid mantling sediment and/or overgrowth by competitors.

Speck (microstructure) — an equidimensional opaque body in stromatoporoid tissue a few micrometers across that is the smallest unit of microstructure seen in the light microscope.

Striated (microstructure) — specks are concentrated in short, rod-like bodies; a microstructure apparently unique to the genus *Stachyodes* (Fig. 2C).

Subcolumn (longitudinal) is a columnar structure of subcircular cross-section which consists of micropillars and microcolliculi arranged in an acosmoreticulate or clinoreticulate pattern (Nestor 1966: figs 17, 18).

Tubulate (microstructure) — clear, vermiform areas extend irregularly through speckled skeletal material, best shown in the genus *Clathrocoilona* (Fig. 2C).

Stratigraphic terms

The methods of expressing stratigraphic distribution of genera have been chosen by the individual authors and dictated by the precision of occurrences recorded in the original species descriptions. Generally for the Devonian the following stages have been recognized: Lochkovian, Pragian, Emsian (Lower Devonian); Eifelian, Givetian (Middle Devonian); Frasnian, Famennian (Upper Devonian). For a few genera of the typical 'Strunian' fauna at the end of the Devonian the designation Upper Famennian is used. In the Silurian the four series names Llandovery (Lower Silurian), Wenlock (Middle Silurian), Ludow, and Pridoli (Upper Silurian) have been used. The stage name Telychian is used to emphasize that the genus was part of a widespread radiation of the stromatoporoids in this late Llandovery time.

Only limited formalized global nomenclature currently exists for the Ordovician. The International Union of Geological Sciences Subcommission on Ordovician Stratigraphy has recommended series subdivisions of Lower, Middle and Upper, each further divided into two stages. Currently the two divisions of the Lower Ordovician may for convenience be referred to informally using British terminology as 'Tremadoc' and 'post-Tremadoc' (the latter equivalent to British lower Arenig). The two divisions of the Middle Ordovician may be referred to as pre-Darriwilian (= British middle Arenig or the correlative North American lower Whiterockian) and the formally defined Darriwilian (= British latest Arenig and Llanvirn, or North American middle Whiterockian, inclusive of lower Chazyan); and of the Upper Ordovician defined by the base of the *Nemagraptus gracilis* graptolite zone as British 'Caradoc' and 'Ashgill' (Webby 1998).

Consequently, the Ordovician faunal succession commences with the 'post-Tremadoc' occurrences of *Pulchrilamina* in North America, then the more diverse Darriwilian assemblages of the Labechiida of north China (Dong 1982), followed by the 'early Caradoc' (mid-upper Chazyan) associations of North America and eastern Australia (Kapp & Stearn 1975; Webby 1991). Faunas of the Clathrodictyida appear in the succeeding 'middle-late Caradoc' interval (Webby 1994).

Within the stratigraphic intervals, the geographic distribution is listed alphabetically by country.

Classification

The most important early classification of stromatoporoids is that of Nicholson (1886b). His, and other early classifications, have been adequately reviewed by Lecompte (1956) in his contribution on stromatoporoids published in the first edition of the Coelenterate volume of the *Treatise on Invertebrate Paleontology*. Since then there has been rapid progress and a number of alternative classifications proposed. These have been reviewed briefly by Stearn (1980). A new framework for classifying Palaeozoic stromatoporoids giving primary focus to the grouping of genera that share common morphological features was adopted by Stearn (1980, 1983). The present classification is an update of this work contributed by the team responsible for preparing most parts of the contribution on Palaeozoic stromatoporoids for the revised calcified sponge volume of the *Treatise on Invertebrate Paleontology* (Stearn, Webby, Nestor, Stock).

Although all authors have commented on all sections of this summary, primary responsibility for preparation of the descriptions of the orders is as follows: Labechiida – Webby; Clathrodictyida – Nestor; Actinostromatida – Stock; Stromatoporida, Stromatoporellida, Syringostromatida, Amphiporida – Stearn.

Phylum Porifera Grant, 1836

Class Stromatoporoidea Nicholson & Murie, 1878

= Stromatoporata Stearn, 1972.

Diagnosis. — Extinct invertebrate organisms of poriferan affinities with non-spiculate, calcareous, basal skeletons of laminar, domical, bulbous, branching to columnar form; internally composed of regular, continuous network of growth parallel and normal to growth skeletal elements, either interconnected laminae, or cyst plates, and pillars; or an amalgamated network in which growth normal, growth parallel, and oblique elements are poorly differentiated; skeletons may be interrupted by a system of astrorhizae, canal-like voids that branch between structural elements and converge toward centres on growth surfaces.

Range. — Lower Ordovician to uppermost Devonian.

Order Labechiida Kühn, 1927

nom. correct. Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969b), *pro* Labechioidea Kühn, 1927, *nom. imperf.*

Diagnosis. — Stromatoporoids with discrete, upwardly convex, blister-like cyst plates, intersected by continuous, upwardly inflected pillars, having rounded, irregular or flanged cross sections, and/or denticles confined to the top of cyst plates; mamelons may occur; astrorhizae rarely preserved; microstructure compact, imperforate.

Comment. — The Labechiida are presently regarded as having sufficiently common morphological features to warrant that they be retained in the Class Stromatoporoidea (Webby 1979a, 1993), rather than being separated from the 'more advanced' stromatoporoid orders because of their characteristic vesicular cystlike structure and rare preservation of astrorhizae (Heinrich 1914; Tripp 1929; Kühn

1927, 1939). Stearn (1982) noted the good level of morphological continuity between the Labechiida and other Paleozoic stromatoporoids, and the belief that an essentially unified, homogeneous, group is represented. However, major differences of opinion exist when it comes to interpreting the role and significance of particular 'ancestral' genera of the Labechiida in deriving the new stromatoporoid groups, such as the Clathrodictyida and Actinostromatida (Webby 1993, 1994).

Family Rosenellidae Yavorsky, 1973

See Khalfina & Yavorsky 1973.

= Cystostromatidae Khromych, 1974 *partim.* = Rosenellidae Bogoyavlenskaya, 1990 in Bogoyavlenskaya *et al.* 1990.

Diagnosis. — Simple, small to large cyst plates, highly arched upward and flattened; intersecting longitudinal elements limited to denticles or crenulations.

Genus *Rosenella* Nicholson, 1886

See Nicholson 1886b: p. 84.

Type species: *R. macrocystis* Nicholson, 1886 (Nicholson 1886b: p. 84, pl. 7: 12–13; see also Nicholson 1886c: p. 20, pl. 1: 8); BM(NH) P5490 (Nicholson No. 280).

= *Rosenellinella* Yavorsky, 1967 (Yavorsky 1967b: p. 16); type species: *R. venusta* Yavorsky, 1967 (Yavorsky 1967b: p. 16).

Diagnosis. — Skeleton commonly composed of large sized, overlapping, convex upward cyst plates; in a few places alternating with flatter, more thickened bands; with or without denticles, or crenulations in place of denticles, reflecting upward, bubble-like inflections of cyst plates.

Range. — Middle Ordovician to Upper Devonian (about 25 species).

Distribution. — Middle Ordovician (Darriwilian) – China (Anhui, Shantung), Malaysia; Upper Ordovician (Caradoc–Ashgill) – Australia (New South Wales, Tasmania), China, Mongolia, Russia (Siberia – Gornaya Shoriya), U.S.A. (New York); Lower Silurian – China (Guizhou), Estonia, Russia (Tuva); Middle Silurian (Wenlock) – Australia (New South Wales), Canada (Ontario), Sweden (Gotland), Russia (Tuva); Upper Silurian – Ukraine (Podolia); Lower Devonian – Australia (N. Queensland); Upper Devonian – China (Sichuan), Russia (Urals, Kuznetsk Basin, Vaigach Island, Pay Khoy), Ukraine (Donetsk Basin), Vietnam.

Genus *Cystostroma* Galloway & St. Jean, 1957

See Galloway 1957: p. 421.

Type species: *C. vermontense* Galloway & St. Jean, 1957 in Galloway 1957: p. 421, pl. 31: 1, pl. 32: 1; UNC thin sections 300. 15-18, 25-27.

= *Cyclostroma* Bogoyavlenskaya, 1987 (Bogoyavlenskaya 1987: p. 99), *nom. null.*

Diagnosis. — Skeleton composed of imbricated pattern of convex-upward cyst plates of comparatively small size and moderate convexity, with or without denticles.

Range. — Upper Ordovician (Caradoc) to Upper Devonian (about 20 species).

Distribution. — Upper Ordovician – Australia (New South Wales, Tasmania), Canada (Ontario), Central Asia, China (Xinjiang), Estonia, Russia (Urals, Siberian Platform, Tuva), U.S.A. (Vermont, Tennessee, Kentucky); Lower Silurian – Russia (Urals); Lower Devonian – Australia (N. Queensland), Russia (NE. Siberia); Upper Devonian – China (Sichuan), Russia (Urals, ?N. Caucasus).

Comment. — The genus *Bullulodictyon* Yavorsky, 1967 (see Yavorsky 1967a), previously regarded by Stearn (1980) and Webby (1993) as a junior synonym of *Cystostroma*, is reinterpreted elsewhere in this paper by Nestor as a valid genus of the Clathrodictyida.

Genus ?*Forolinia* Nestor, 1964

See Nestor 1964: p. 31.

Type species: *Rosenella pachyphylla* Nicholson, 1886 (Nicholson 1886a: p. 21, pl. 1: 6, 7); BM(NH) P5629 (Nicholson No. 283).

Diagnosis. — Skeleton formed of large, gently arched to flattened cyst plates, in places simulating laminae; perforated by short, cylindrical voids (vertical 'canals') possibly representing leached out small pillars and/or denticles; in places cyst plates exhibit three-layered microstructure of transversely fibrous layers above and below dense median layer.

Range. — Lower Silurian (4 species).

Distribution. — China (Guizhou), Estonia.

Comment. — Webby regards this genus as a diagenetically altered *Labechia* (see also Kapp & Stearn 1975: p. 168), whereas Nestor considers it to be a valid genus allied to *Rosenella*.

Genus *Pseudostylodictyon* Ozaki, 1938

See Ozaki 1938: p. 208.

Type species: *P. poshanense* Ozaki, 1938 (Ozaki 1938: p. 208, pl. 24: 2; pl. 25: 1a–e); NIGP 121556a–b.

= ?*Plumatalinia* Nestor, 1960 (Nestor 1960: p. 225); type species: *P. ferax* Nestor, 1960 (Nestor 1960: p. 226). = *Parksodictyon* Bogoyavlenskaya, 1990 in Bogoyavlenskaya & Lobanov 1990: p. 85; type species: *Pseudostylodictyon kayi* Galloway & St. Jean, 1957 in Galloway 1957: p. 425.

Diagnosis. — Skeleton with cyst plates commonly long and low (resembling laminae) in those lacking mamelon columns; in others (including type species) upwardly inflected into mamelon columns; denticles (less commonly crenulations) locally prominent on upper surfaces of cyst plates, and may be present in mamelon columns as well as interspaces (Fig. 3B).

Range. — Middle Ordovician (Darriwilian) to Upper Silurian (about 12 species).

Distribution. — Middle Ordovician – China (Shandong); Upper Ordovician – Australia (New South Wales, Tasmania), Estonia, ?Kazakhstan, Russia (Chukotsk Peninsula, Urals), U.S.A. (Vermont, New York, Texas); Lower Silurian – Norway; Middle Silurian – Sweden (Gotland); Middle and Upper Silurian – Australia (New South Wales), China (Inner Mongolia).

Comment. — Nestor (1960) interpreted the fine subrecticulate skeletal material occupying the mamelon columns of *Plumatalinia* as the main basis for distinguishing the genus from *Pseudostylodictyon*. However, Webby (1979a, 1994) raised doubts about this type of subreticulate texture having a primary origin; he continues to believe that the original cyst plates of *P. ferax* have been secondarily, diagenetically altered. Careful reevaluation of *Plumatalinia* is required because this monotypic genus has now been singled out by some authors as the key transitional form in direct line to the order Actinostromatida (Bogoyavlenskaya 1969a; Stearn 1993; Stock 1994; this paper: pp. 36–37).

Family Labechiidae Nicholson, 1879

nom. correct. Nicholson 1886b: p. 74, *pro* Labechidae Nicholson, 1879 (Nicholson 1879: p. 330).

= Stratodictyidae Bogoyavlenskaya, 1977 *partim.* = Tuvaechiidae Bogoyavlenskaya, 1984.

Diagnosis. — Simple, upwardly convex to flattened cyst plates of variable size, and pillars exhibiting a range of morphologies – from somewhat sporadically developed small pillars and denticles, to more commonly, continuous, large pillars with rounded to slightly irregular outlines, rarely, where closely spaced, forming chain-like rows.

Genus *Labechia* Milne-Edwards & Haime, 1851

See Milne-Edwards & Haime 1851: p. 155.

Type species: *Monticularia conferta* Lonsdale, 1839 in Murchison 1839: p. 688, pl. 16: 5, 5a; holotype presumably lost, topotype BM(NH) P5984 (Nicholson No. 264).

Diagnosis. — Skeleton composed of long, stout, rounded pillars to more sporadically developed, less continuous, small pillars, and an intricate mesh of cyst plates with moderately upward convexity; pillars may terminate as papillae on upper surface and show upwardly converging cone-in-cone banding with lighter axial canals in longitudinal section (Fig. 3C, D).

Range. — Middle Ordovician (Darriwilian) to Upper Devonian (Famennian) (about 55 species).

Distribution. — Middle Ordovician – China (Shandong), ?Korea; Upper Ordovician – Australia (Tasmania), Canada (Quebec, Ontario, Akpatok Island), China (Xinjiang), Mongolia, Norway, Kazakhstan, Russia (Urals, Gornaya Shoriya, Tuva), Scotland, U.S.A. (Alabama, New York, Vermont, Tennessee, Virginia, Kentucky, Indiana, Ohio, Michigan); Lower Silurian – China (Guizhou), Estonia, Russia (Siberian Platform, Tuva); Middle Silurian – Central Asia, England, Sweden (Gotland), Russia (Russian and Siberian Platforms, Urals, Kolyma, Tuva), Ukraine (Podolia), U.S.A. (Indiana); Upper Silurian – Russia (Siberian Platform, Urals, Altai mountains), Sweden (Gotland); Lower Devonian – Canada (Ellesmere Island), China (Sichuan, Guizhou, Hunan), Russia (Kolyma); Upper Devonian – Canada (Alberta), Russia (Russian Platform, Novaya Zemlya, Vaigach Island, Urals, N. Caucasus), Ukraine (Donetsk Basin).

Comment. — The genus includes a wide range of longitudinal structural elements, from those with a patchy development of small short pillars that are grouped in the *L. prima* species group (with resemblances to *Stratodictyon* Webby, 1969) to those with long and stout, rounded pillars assigned to the *L. conferta* species group (Webby 1979a).

Genus *Labechiella* Yabe & Sugiyama, 1930

See Yabe & Sugiyama 1930: p. 54.

Type species: *Labechia serotina* Nicholson, 1886 (Nicholson 1886c: p. 15, pl. 2: 3, 4); BM(NH) P5988 (Nicholson No. 268).

= *Tuvaechia* Bogoyavlenskaya, 1971 (Bogoyavlenskaya 1971b: p. 34); type species: *Labechia regularis* Yabe & Sugiyama, 1930 (Yabe & Sugiyama 1930: p. 56).

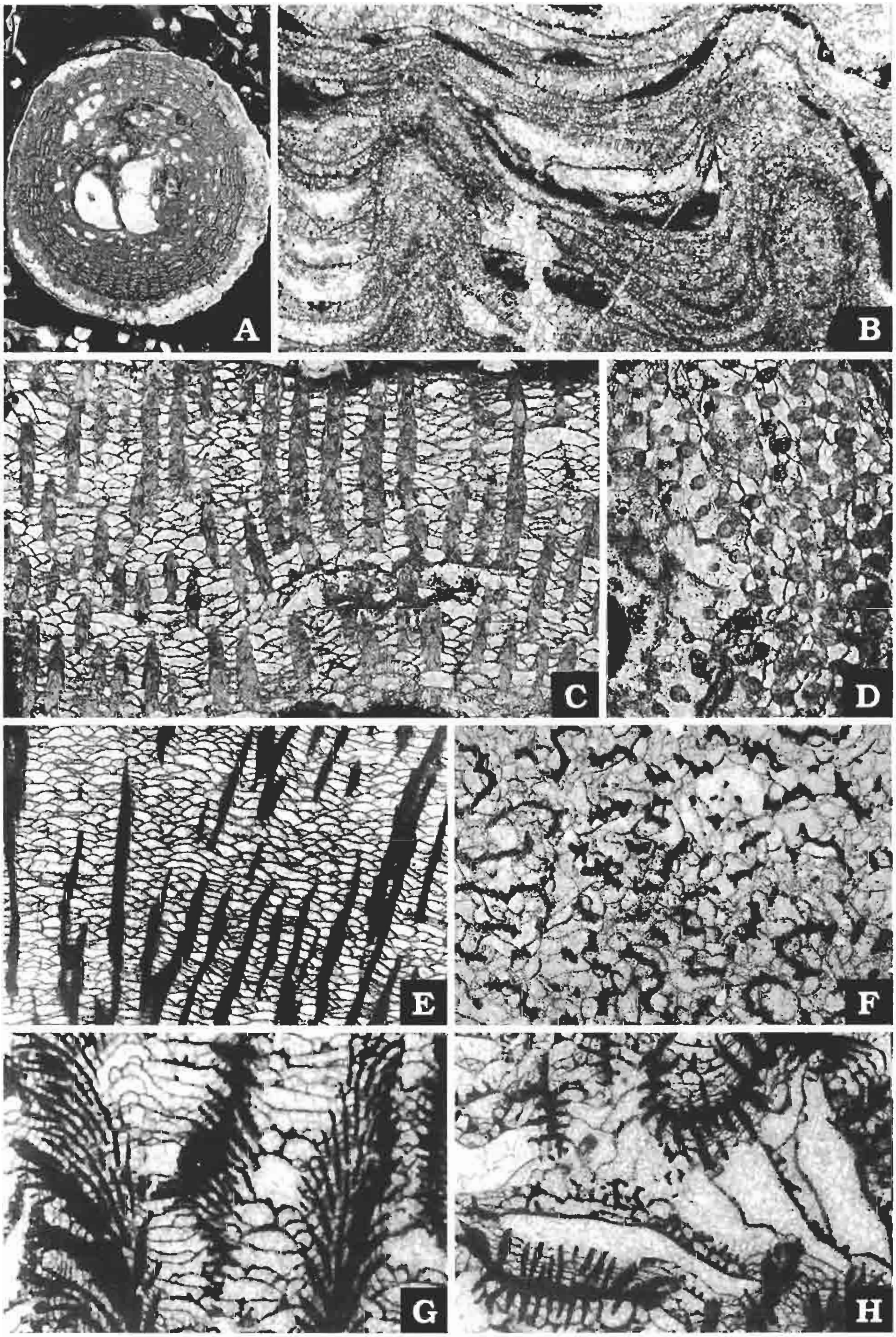
Diagnosis. — Skeleton of stout, erect, continuous pillars, in places closely spaced even in contact, and branching; in tangential section pillars have rounded outline and, where in contact, form incomplete chain-like rows (approximating a vermicular appearance); in longitudinal section may show upwardly converging cone-in-cone banding with lighter axial canals; cyst plates flattened, rarely vesicular.

Range. — Middle Ordovician (Darriwilian) to Upper Devonian (Famennian) (about 15 species).

Distribution. — Middle Ordovician – China (Anhui, Liaoning, Shandong), Korea, Malaysia; Upper Ordovician – Australia (New South Wales, Tasmania), China (Xinjiang), Kazakhstan, Mongolia, Russia (?Altai mountains, Chukotsk Peninsula, Siberian Platform, E. Siberia, Tuva), U.S.A. (Alabama); Upper Silurian – Russia (Urals); Lower Devonian – Australia (Queensland); Middle Devonian – England, Russia (Urals, ?Altai mountains, ?Salair); Upper Devonian – China (Sichuan, Hunan).

Comment. — The name *Labechiellata* Sugiyama, 1940 (see Sugiyama 1940: p. 112) was substituted for the junior synonym *Labechiella* Sugiyama, 1939 (Sugiyama 1939: p. 443; type species: *Labechiella regularis* Sugiyama, 1939; Sugiyama 1939: p. 444) after Sugiyama realized his error in using a preoccupied name (Webby 1979a). Broadening of the generic conception of *Labechiella* Yabe & Sugiyama, 1930, led to renaming of Sugiyama's (1939) *L. regularis* as *Labechiella sugiyami* Webby, 1979 (see Webby 1979a). Reinterpretation of the type material of *L. sugiyami* by Mori (1994)

Fig. 3. **A**. Aulaceratidae: *Alleynodictyon nicholsoni* Webby, 1971; transverse section of holotype SUP 34170, × 4. Note the columnar form and the radiating septalike, bladed pillars. **B.** Rosenellidae: *Pseudostylodictyon poshanense* Ozaki, 1938; longitudinal section of holotype NIGP 121556 (slide 121556a), × 5. Note that a few denticles are visible on the upper surface of cyst plates in the mamelon columns. **C, D.** Labechiidae: *Labechia conferta* (Lonsdale, 1839), longitudinal and tangential sections, SUP 285, × 5. Note the laminar skeleton (sediment above and below), with erect, stout, rounded pillars embedded in a meshwork of imbricated cyst plates. **E, F.** Stromatoceriidae: *Platiferostroma hybridum* (Dong, 1964), × 5; **E** – longitudinal section of holotype NIGP Kw044-3 (slide 14170); **F** – tangential section of paratype NIGP Kw044-2 (slide 14170). Note the long erect and branching pillars that in tangential section are meandriform with flange-like offsets forming incomplete polygonal networks. **G, H.** Stylostromatidae: *Pennastroma yangi* Dong, 1964, longitudinal and oblique sections of holotype NIGP Kw 047-2 (**G** – slide 14160; **H** – slide 14161), × 5. Note the composite pillars with upwardly and outwardly flaring branches in longitudinal section, and the pinnate arrangement of these pillars in oblique section, with branches to either side of central bladelike or vanelike plate.


A
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revealed that it is part of the rugose coral *Mazaphyllum* Crook, 1955. With name reversions this becomes the cystiphyllid rugosan *Labechiellata regularis* (Sugiyama, 1939). Consequently *Labechiellata* Sugiyama, 1940, is now excluded from the Labechiidae.

Genus *Stratodictyon* Webby, 1969

See Webby 1969: p. 647.

Type species: *S. ozakii* Webby, 1969 (Webby 1969: p. 647, pl. 119: 4, 5; pl. 120: 1, 2; pl. 124: 1); SUP 26252, to be transferred to Australian Museum (AMF), Sydney.

Diagnosis. — Skeleton latilaminate, weakly undulating to mammillate, with tangential more conspicuous than longitudinal elements; cyst plates comparatively small, of low convexity, and may be imbricated with irregular distribution, or form regular rows; small to moderate sized, rounded, short pillars, and/or denticles, only locally developed.

Range. — Upper Ordovician (Caradoc–Ashgill) (5 species).

Distribution. — Australia (New South Wales, Tasmania), Russia (Tuva, NE. Russia); U.S.A. (Alabama, New York).

Family Stromatoceriidae Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969b.

= Platiferostromatidae Khalfina & Yavorsky, 1973.

Diagnosis. — Coarse-textured Labechiida with skeletal mesh of large, erect, postlike to complexly flanged pillars and cyst plates ranging in size and shape from extensive, low convexity, simulating laminae, to small, imbricated and moderately convex; pillars may have irregularly rounded to elongate, serrated, meandriform, or star-shaped outlines, or even in extremes, may exhibit partially closed polygonal meshworks; denticles may be present on tops of cyst plates and outer walls of the pillars; astrorhizae may also occur.

Genus *Stromatocerium* Hall, 1847

See Hall 1847: p. 48.

Type species: *S. rugosum* Hall, 1847 (Hall 1847: pl. 12: 2); AMNH 590/5A-H.

= ?*Columna* Ivanov, 1955 in Ivanov & Myagkova 1955: p. 13; type species: *C. sokolovi* Ivanov, 1955 in Ivanov & Myagkova 1955: p. 13.

Diagnosis. — Pillars large, continuous, with interiors preserved as sparry calcite infills (rarely solid); angular, meandriform to star-shaped outlines in tangential section; in places, short, denticle-like flanges occur on outer walls of pillars; cyst plates large, of low convexity; in places radially arranged pillars but not apparently incorporated into mamelon columns.

Range. — Upper Ordovician (Caradoc) (3 species).

Distribution. — Canada (Ontario), Russia (Urals, Chukotsk Peninsula), U.S.A. (New York).

Comment. —Nestor (1979) recognized three separate species-groups each based on well known species: *S. rugosum* Hall, 1847; *S. canadense* Nicholson & Murie, 1878; and *S. michiganense* Parks, 1910. A modified version of that scheme, upgraded to generic rank, is here proposed. Elements of the *S. rugosum* group (including *S. rugosum*, and ?*S. tumidum* Wilson, 1948) are retained in the genus *Stromatocerium* because they are characterized by having pillars with vermicular to irregular, radiating outlines; also pillars are rarely denticulate, and not apparently associated with mamelon columns.

The representatives of the *S. canadense* group, including *S. canadense, S. leipersense* Galloway & Ehlers, 1961 in Galloway & St. Jean 1961, *S. sakuense* Nestor, 1964, ?*S. definitum* (Ivanov, 1955 in Ivanov & Myagkova 1955), and ?*S. amsterdamense* Galloway & St. Jean, 1961, based on the common occurrences of pillars with angular to vermicular, serrated (flanged) outlines and the development of denticles on tops of cyst plates, are here included in the genus *Cystistroma* Etheridge, 1895.

Elements of the *S. michiganense* group (including *S. michiganense, S. platypilae* Galloway, 1961 in Galloway & St. Jean (1961), *S. granulosum* (James, 1871), *S. pergratum* Nestor, 1976 = *S. moierense* Bogoyavlenskaya, 1977 (Bogoyavlenskaya 1977c), given the presence of pillars made up of partially closed polygonal meshworks, are here grouped in Hung's (in press) new genus based on *S. kueichowense* Dong, 1964.

A fourth grouping includes members like *S. australe* Parks, 1910, with vane-like, upwardly flaring, pillars that are closely associated with mamelon columns, as in *Radiostroma* Webby, 1979 (see Webby 1979b). *S. australe* is here assigned to *Radiostroma*.

Genus *Cystistroma* Etheridge, 1895

See Etheridge 1895: p. 134.

Type species: *Labechia* (?)*(Cystistroma) donnellii* Etheridge, 1895 (Etheridge 1895: p. 134, pl. 14: 1–6; pl. 15: 1–2; pl. 16: 1–3); lectotype MMF F907 (Pickett 1970: p. 89).

Diagnosis. — Coarse-textured skeletal mesh of large pillars and cyst plates; pillars, long, stout, may radiate upwards and outwards but rarely branch; in tangential section include oval, irregular, elongated and, where intersecting, tiny outwardly directed, spinelike denticles, serrated outlines; pillar interiors commonly preserved as sparry calcite infills; a few denticles also occur at tops of large, undulating, to upwardly convex cyst plates.

Range. — Upper Ordovician (Caradoc–Ashgill) (about 6 species).

Distribution. — Australia (New South Wales), Canada (Ontario, Quebec), Estonia, Russia (?Urals, Siberian Platform), U.S.A. (New York, Kentucky, Michigan).

Genus *Cystocerium* Nestor, 1976

See Nestor 1976: p. 41.

Type species: *C. sincerum* Nestor, 1976 (Nestor 1976: p. 41, pl. 9: 1); IGTTU Co3217.

Diagnosis. — Pillars long, stout, sporadically branching; in tangential section rounded to angular and vermicular; cyst plates thin, long, low, giving laterally extensive appearance simulating laminae; astrorhizae represented by stellate pattern of radiating wall-less canals.

Range. — Wenlock (2 species).

Distribution. — Russia (Siberian Platform).

Genus *Platiferostroma* Khalfina & Yavorsky, 1973

See Khalfina & Yavorsky 1973: p. 32.

Type species: *Stromatocerium hybridum* Dong, 1964 (Dong 1964: p. 294, pl. 2: 3–8); NIGP Kw044-3 (14167). Note that the catalogue numbers attached to Dong's thin sections in the Nanjing collection are not the same as those cited in the caption of his illustration (Dong 1964: pl. 2: 3–8). In study of the thin sections of the types in 1993 Webby found the holotype labelled as NIGP Kw044-3 (thin section 14167, see Dong 1964: pl. 2: 5) and the two paratypes as NIGP Kw044-1 (thin sections 14171, see Dong 1964: pl. 2: 7, 8) and NIGP Kw044-2 (thin section 14170, see Dong 1964: pl. 2: 4).

Diagnosis. — Pillars stout, widely spaced, continuous, and in places, branching; in tangential section commonly rounded to irregularly elongate to meandriform in outline; rarely with more complexly flanged offsets, or incompletely fused polygonal meshworks; numerous small, moderately uparched, thin-walled cyst plates occupy interspaces between pillars; not markedly upflexed against pillars (Fig. 3E, F).

Range. — Upper Devonian (Famennian) (about 9 species).

Distribution. — Australia (Bonaparte Basin), China (Guangxi, Guizhou, Sichuan, Hunan), Russia (Novaya Zemlya), Vietnam.

Comment. — Nestor (1976) singled out this genus, given the modification of its pillars to complicated polygonal networks, as probably belonging to the Chaetetida (see West & Clark 1983). Bogoyavlenskaya (1973b) has expressed similar sentiments in relation to other Stromatoceriidae including Hung's new genus (see below). This seems most unlikely, given that such patterns are represented in at least three different genera of Stromatoceriidae (*Platiferostroma, Radiostroma*, and new genus (Hung in press).

Genus *Pleostylostroma* Wang, 1982

See Wang 1982: p. 24.

Type species: *Labechia shiniulanense* Wang, 1978 (Wang 1978a: p. 14, pl. 2: 1); CIGMR Ss1001.

Diagnosis. — Pillars long, erect, moderately closely spaced and rarely branched; in tangential section with varied, irregularly rounded to angularly triangular and star-shaped outlines; cyst plates uniformly distributed across interspaces between pillars, upwardly convex, overlapping, of variable size; not conspicuously aligned in rows or updomed adjacent to pillars; no denticles.

Range. — Lower Silurian (Llandovery) (5 species).

Distribution. — China (Sichuan).

Genus *Parastylostroma* Bogoyavlenskaya, 1982

See Bogoyavlenskaya 1982: p. 36.

Type species: *Stromatocerium irregularis* Vassiljuk, 1966 (Vassiljuk 1966: p. 44, pl. 32: 8a–b); DPI 12/230.

Diagnosis. — Pillars large, stout, moderately persistent and sporadically branching, but in a few places, short and limited to denticle-like upgrowths at the tops of cyst plates; in tangential section rounded to irregular, locally meandriform in outline; cyst plates thin, gently arched to flattened, forming rows with some lateral continuity.

Range. — Upper Devonian (5 species).

Distribution. — Russia (N. Caucasus, Novaya Zemlya), Ukraine (Donetsk Basin), Uzbekistan.

Comment. — This genus bear similarities to *Cystocerium* Nestor, but may have areas of skeleton with less persistent and less concentrated development of stout pillars and it lacks any trace of the distinctive astrorhizae seen in the latter.

Genus *Radiostroma* Webby, 1979

See Webby 1979b: p. 208.

Type species: *R. tenue* Webby, 1979 (Webby 1979b: p. 210, fig. 5B–E); PMO 97113.

Diagnosis. — Pillars long, slender, erect, vanelike; in cross section commonly star-shaped in outline but in a few places form a more complex polygonal meshwork; denticles randomly developed on cyst plate tops; cyst plates large, thin, commonly undulate to concave-upward between pillars.

Range. — Upper Ordovician (Caradoc) (2 species).

Distribution. — Norway, Russia (Siberian Platform), U.S.A. (Tennessee).

New Genus Hung, in press

Type species: *Stromatocerium kueichowense* Dong, 1964 (Dong 1964: p. 295, pl. 3: 7, 8; pl. 4: 1, 2); NIGP Gy311-1 (thin sections No. 14156-57).

Diagnosis. — Pillars complexly flanged to vane-like and erect, forming partially closed polygonal meshworks, or a more meandriform outline; cyst plates thin, long, low, simulating laminae.

Range. — ?Lower Cambrian, Upper Ordovician and Upper Devonian (about 10 species).

Distribution. — ?Lower Cambrian – Russia (Kuznetskii-Alatau); Upper Ordovician – ?Mongolia, Russia (Siberian Platform), U.S.A. (Ohio, Kentucky, ?Michigan); Famennian – China (Guizhou, Sichuan), Vietnam.

Comment. — Khalfina (in Khalfina & Yavorsky 1974) figured two *Stromatocerium*-like species supposedly from the top of Lower Cambrian but the occurrences remain problematical, since the species look remarkably like some Upper Devonian representatives of this genus. The material requires proper description with full assessment of relationships.

Family Stylostromatidae Webby, 1993

Diagnosis. — Strongly mammillate with longitudinal elements ranging from discrete, simple, rounded, outwardly radiating, branching pillars in mamelon columns to flanged, vane-like or pinnately arranged, composite pillars; cyst plates range widely in size and shape, commonly low convexity to flattened, and upwardly convex adjacent to mamelon columns (and composite pillars); denticles commonly formed at the top of cyst plates and locally superposed to form short pillars; markedly latilaminate skeletons may exhibit successive phases of thickened skeletal material.

Genus *Stylostroma* Gorsky, 1938

See Gorsky 1938: p. 15.

Type species: *S. crassum* Gorsky, 1938 (Gorsky 1938: p. 15, pl. 2: 1–9; pl. 3: 1–7); CNIGR 5767/6.
= *Mamelolabechia* Khromych, 1977 (Khromych 1977: p. 44); type species: *Pseudolabechia tuberculata* Yavorsky, 1955 (Yavorsky 1955: p. 66).

Diagnosis. — Skeleton mammillate with pillars commonly restricted to mamelon columns, as simple, postlike, and upwardly and outwardly radiating, branching elements; also denticles or, less commonly, short, unbranched, superposed pillars between columns; cyst plates commonly of small to moderate size and low convexity; in places may simulate laminae.

Range. — Upper Ordovician (Caradoc) to Upper Devonian (Famennian) (about 30 species).

Distribution. — Upper Ordovician – Australia (Tasmania), China (Xinjiang), Norway; Lower Silurian – China (Guizhou); Middle Silurian – Russia (Siberian Platform); Lower Devonian – Australia (N. Queensland); Upper Devonian – Canada (Alberta), China (Sichuan, Guizhou, Guangxi, ?Hunan), Kazakhstan, Russia (N. Caucasus, Novaya Zemlya, Urals, NE. Siberia), Ukraine (Donetsk Basin).

Genus *Pachystylostroma* Nestor, 1964

See Nestor 1964: p. 23.

Type species: *Stromatopora ungerni* Rosen, 1867 (Rosen 1867: p. 75, pl. 9: 5, 6); lectotype (Nestor 1962: p. 7) IGTTU Co3011.

Diagnosis. — Skeleton moderately to strongly mammillate; structural elements dominated by cyst plates of variable size, characteristically in alternation with thicker, laminae-like layers; mamelon columns of some species have simple upwardly and outwardly branching pillars, and/or axial thickening of skeletal elements; denticles commonly developed on tops of cyst plates and laminae-like layers and in places locally superposed to form short pillars, especially in less strongly mammillate forms.

Range. — Upper Ordovician (Caradoc–Ashgill) to Upper Devonian (about 20 species).

Distribution. — Upper Ordovician (Caradoc to Ashgill) – Australia (Tasmania), Canada (Ontario), U.S.A. (Alabama, Vermont, New York); Upper Ordovician (Ashgill) to Lower Silurian – Estonia; Lower Silurian (Telychian) – U.S.A. (Iowa); Middle Silurian – Russia (Siberian Platform), Sweden (Gotland); Upper Devonian – China (Sichuan), Russia (Novaya Zemlya, Vaigach Island, Urals).

Comment. — Nestor (1964) recognized three species groups: (1) *P. ungerni* group for those with strongly compacted mamelon columns; (2) *P. contractum* group for those with weakly developed mamelon columns; and (3) *P. estoniense* group for those with well developed, slender mamelon columns incorporating clearly differentiated branching pillars. The distinction between species of *Pachystylostroma*, especially members of the *P. estoniense* group, and representatives of *Stylostroma* is difficult, but best made on the basis of the presence or absence of the thickened laminae-like layers.

Genus *Pennastroma* Dong, 1964

See Dong 1964: p. 296.

Type species: *P. yangi* Dong, 1964 (Dong 1964: p. 296, pl. 4: 3–5); NIGP Kw047-2 (14160-14162).
= *Eopennastroma* Wang, 1978 (Wang 1978c: p. 104); type species: *E. sinense* Wang, 1978 (Wang 1978c: p. 104).

Diagnosis. — Long, slender, vanelike composite pillars, commonly developing pinnately arranged, branching, flangelike offsets representing short pillars and/or denticles; cyst plates small, closely spaced and upwardly arched in columns associated with these composite pillars; larger, weakly convex to flattened or concave upward cyst plates cross intervening spaces though, in some places, in alternation with rows of smaller cyst plates, and a few denticles developed at top of cyst plates, even superposed to form short pillars (Fig. 3G, H).

Range. — Upper Devonian (Famennian) (9 species).
Distribution. — Australia (Bonaparte Basin), China (Guangxi, Guizhou, Hunan).

Genus *Spinostroma* Wang, 1978

See Wang 1978b: p. 131.

Type species: *S. diversum* Wang, 1978 (Wang 1978b: p. 131, pl. 41: 2, 3); CIGMR Ss2025.

= *Sichuanostroma* Wang, 1978 (Wang 1978b: p. 133); type species: *S. robustum* Wang, 1978 (Wang 1978b: p. 133, pl. 42: 3).

Diagnosis. — Pillars long, moderately thickened, composite, vane-like plates, upwardly and outwardly branching; in transverse section commonly outlined as irregularly rounded straight or curved, branching bars, rimmed by small, bluntly pointed, spine-like denticles; large flattened to concave-upward cyst plates across pillar interspaces, with small inclined to upwardly convex elements close to pillars; denticles sporadically developed on tops of cyst plates.
Range. — Upper Devonian (Famennian) (7 species).
Distribution. — China (Sichuan), Russia (Novaya Zemlya).

Family Aulaceratidae Kühn, 1927

= Beatricidae Raymond, 1931. = Beatriceidae Ulrich, 1915 (in Bassler 1915); the later name has priority but Kühn's name, based on the senior generic synonym, was introduced prior to 1961 (see Ride *et al.* 1985, International Zoological Code, Article 40), and has won general acceptance. Consequently this name is to be maintained.

Diagnosis. — Branched dendroid to unbranched, columnar skeletons, with differentiated axial and lateral zones; axial columns of large stacked or overlapping cyst plates, in a few places denticulate; lateral zones with rows of small imbricated cyst plates, and sporadically distributed short pillars or denticles; pillars commonly simple, rounded, but in one genus have a composite, fused, outwardly radiating, vane-like form.

Genus *Aulacera* Plummer, 1843

See Plummer 1843: p. 293, fig. 1.

Type species: *A. plummeri* Galloway & St. Jean, 1957 in Galloway 1957: p. 422 (by monotypy), pl. 37a–c; UNC sections 285-35, 299-35, 300-9.

= *Beatricea* Billings, 1857 (Billings 1857: p. 344); type species: *B. nodulosa* Billings, 1857 (see Miller 1889: p. 155).

Diagnosis. — Large, unbranched, columnar skeleton, differentiated into axial column and lateral zone; axial column comprised of a single series of large stacked cyst plates; lateral zone has multiple rows of smaller, imbricated cyst plates, and sporadic development of short, rounded pillars.
Range. — Upper Ordovician (Caradoc–Ashgill) (about 20 species).
Distribution. — Australia (Tasmania), Canada (Anticosti Island, Akpatok Island, Hudson Bay, Ontario, Manitoba, British Columbia), Russia (Siberian Platform, Novaya Zemlya), U.S.A. (Indiana, Kentucky, Ohio).

Genus *Alleynodictyon* Webby, 1971

See Webby 1971: p. 10.

Type species: *A. nicholsoni* Webby, 1971 (Webby 1971: p. 11, pl. 5: 1–8; text-fig. 1); SUP 34170.

Diagnosis. — Slender, branching, columnar skeleton with outwardly radiating, vane-like, composite pillars in outer margin of axial column and lateral zone; axial column exhibits large, upwardly convex cyst plates with a few scattered denticles on upper surface; rows of small, long, low, cyst plates occupy lateral zone, being flattened to concave outward between radiating pillars and gently convex outward in areas lacking pillars (Fig. 3A).
Range. — Upper Ordovician (Caradoc) (2 species).
Distribution. — Australia (New South Wales, Tasmania).

Genus *Cryptophragmus* Raymond, 1914

See Raymond 1914: p. 8.

Type species: *C. antiquatus* Raymond, 1914 (Raymond 1914: p. 8, pls 1–4); GSC 5390.

Diagnosis. — Unbranched cylindrical skeleton composed of narrow axial column with large stacked axial cyst plates and a few small cyst plates at margins, and an outer, sheath-like lateral zone exhibiting regular skeletal meshwork of small pillars intersected by laterally persistent, thin, undulating to flattened cyst plates (resembling laminae).

Range. — Upper Ordovician (Caradoc) (2 species).

Distribution. — Canada (Ontario, Quebec), ?Russia (Siberian Platform), U.S.A. (New York, Pennsylvania, Virginia, Tennessee, Alabama, Indiana).

Genus *Ludictyon* Ozaki, 1938

See Ozaki 1938: p. 219.

Type species: *L. vesiculatum* Ozaki, 1938 (Ozaki 1938: p. 219, pl. 33: 3a–c; pl. 34: 3); NIGP 121555a-b (thin sections).

Diagnosis. — Skeleton unbranched and broadly cylindrical with poorly defined axial and lateral zones; no clearly differentiated axial column; commonly, large stacked to overlapping cyst plates of axial zone alternate successively with rows of small, long, low imbricated cyst plates; denticles may occur on upper surfaces of larger, axial cyst plates and also on smaller cyst plates laterally.

Range. — Middle Ordovician (Darriwilian) to Lower Silurian (3 species).

Distribution. — Middle Ordovician – China (Shandong, Anhui); Upper Ordovician – ?Mongolia; Lower Silurian – China (Guizhou).

Genus *Pararosenella* Vassiljuk & Bogoyavlenskaya, 1990

See Bogoyavlenskaya *et al.* 1990: p. 75.

Type species: *Rosenella lissitzini* forma *cylindrica* Vassiljuk, 1966 (Vassiljuk 1966: p. 46, pl. 32: 1–7); DPI 12/141.

Diagnosis. — Dichotomously branching columnar skeleton with single row of large doughnut-shaped axial cyst plates of high convexity; denticles limited to tops of some axial cyst plates; lateral zone very incomplete, composed of very few small cyst plates filling spaces at margins between bulbous axial cyst plates, and angles of dichotomous branches.

Range. — Upper Devonian (Famennian) (2 species).

Distribution. — Russia (N. Caucasus), Ukraine (Donetsk Basin).

Genus *Sinodictyon* Yabe & Sugiyama, 1930

See Yabe & Sugiyama 1930: p. 52.

Type species: *S. columnare* Yabe & Sugiyama, 1930 (Yabe & Sugiyama 1930: p. 52, pl. 18: 7–10; pl. 19: 2–5; pl. 20: 1–4); IGPS 37674-75, 37678.

Diagnosis. — Skeleton branching to cylindrical with large, denticled cyst plates axially, and rows of smaller, long, low cyst plates with denticles and short, rounded pillars laterally.

Range. — Middle Ordovician (Darriwilian) (2 species).

Distribution. — China (Shandong, Liaoning).

Genus *Thamnobeatricia* Raymond, 1931

See Raymond 1931: p. 180.

Type species: *T. parallela* Raymond, 1931 (Raymond 1931: p. 180, pl. 2: 4–9); MCZ 9302.

= *Cladophragmus* Raymond, 1931 (Raymond 1931: p. 182); type species: *Cladophragmus bifurcatus* Raymond, 1931 (Raymond 1931: p. 182, pl. 3: 1–4). = *Rosenellina* Radugin, 1936 (Radugin 1936: p. 92); type species: *R. wellenformis* Radugin, 1936 (Radugin 1936: pl. 2: 8, 9, 11).

Diagnosis. — Branching cylindrical skeleton with axial column composed of large, variably sized cyst plates, commonly but not always spanning axial column, and very narrow lateral zone of small cyst plates; pillars mentioned as occurring in lateral zone but this needs confirmation; denticles may occur on upper surface of cyst plates.

Range. — Middle Ordovician (Darriwilian) to Lower Silurian (12 species).

Distribution. — Middle Ordovician – China (Anhui); Upper Ordovician – Australia (Tasmania), Canada (Ontario), Russia (Siberian Platform), U.S.A. (Alabama, Pennsylvania, Tennessee, Kentucky); Ordovician – Russia (Gornaya Shoria).

Family Lophiostromatidae Nestor, 1966

Diagnosis. — Encrusting laminar, latilaminate, composed of much thickened, tangential skeletal layers almost completely filling interskeletal space, sharply undulate skeletal layers form pillarlike upgrowths appearing as papillae on upper surface; discrete longitudinal and tangential elements rare.

Comment. — Only two genera, *Lophiostroma* and *Dermatostroma* are regarded as valid. *Solidostroma* Khromych, 1974, from the Lower Devonian of NE. Siberia was originally described as a member of the Lophiostromatidae but currently has uncertain status, doubtfully included as a junior synonym of *Euryamphipora* Klovan, 1966 (see below).

Genus *Lophiostroma* Nicholson, 1891

See Nicholson 1891b: p. 160.

Type species: *Labechia*? *schmidtii* Nicholson, 1886 (Nicholson 1886c: p. 16, pl. 2: 6–8); BM(NH) P5606 (Nicholson No. 279).

= *Chalazodes* Parks, 1908 (Parks 1908: p. 33); type species: *C. granulatum* Parks, 1908 (Parks 1908: p. 36).

Diagnosis. — Skeleton commonly latilaminate and laminar, consists of, dominantly, much thickened, sheet-like layers, sharply and regularly undulating into columnar, pillar-like upgrowths giving a kind of cone-in-cone structure; these upgrowths expressed as papillae on upper surfaces; the sheet-like layers almost entirely occupy the interiors, and do not represent true laminae, only rarely discernible cyst plates preserved.

Range. — Middle Ordovician (Darriwilian) to Silurian, ?Upper Devonian, ?Triassic (about 10 species).

Distribution. — Middle Ordovician – China (Shandong); Upper Ordovician – Mongolia, Russia (Siberian Platform); Middle to Upper Silurian – Canada (Ontario, Quebec), England, Sweden (Gotland), Estonia, Turkey, U.S.A. (Michigan, Kentucky), Ukraine (Podolia); ?Upper Devonian – Russia (Kuznetsk Basin); ?Triassic – Tajikistan (SE. Pamirs).

Genus *Dermatostroma* Parks, 1910

See Parks 1910: p. 29.

Type species: *Stromatopora papillata* James, 1878 (James 1878: p. 2; see also Parks 1910: p. 30, pl. 23: 8–10); FMNH 160.

Diagnosis. — Skeleton encrusting and laminar; at most only exhibits a few rows of irregular, undulating to even, long, low cyst plates (some simulating laminae), and intersected by short, solid pillars, rounded to polygonal in tangential section; tops of pillars preserved as papillae.

Range. — Upper Ordovician (6 species).

Distribution. — Canada (Ontario), U.S.A. (Ohio, Kentucky, Indiana, Tennessee, Iowa).

Comment. — This problematical genus needs further revision. Some of the species originally included by Parks (1910), but not including the type species, have a skeleton consisting of layers of vertically oriented prismatic crystalline material. Dixon *et al.* (1986) have demonstrated that these are heliolitine corals. Others, previously inferred to be independent species overgrowing parts of the skeletons of *Aulacera* (see descriptions in Galloway & St. Jean 1961: pp. 74–78), should be excluded because they probably represent the outer part of the Aulaceratidae skeletons (the 'outer lamellar layer' of Cameron and Copper 1994: p. 17; see also discussion by Nestor 1976: p. 35). The regular laminae and aligned denticles ('pseudopillars') of *Dermatostroma concentricum* Galloway & Ehlers, 1961 in Galloway & St. Jean 1961 (see their pl. 11: 4a–c) are remarkably similar to the structures figured by Cameron & Copper (1994: fig. 2b, d) as the 'outer lamellar layer' of a new, as yet unnamed genus of the Aulaceratidae from Anticosti Island.

?Family Pulchrilaminidae Webby, 1993

Diagnosis. —Large, laminar, domical, strongly latilaminate skeleton; internally the undulating rows of fine, long, low cyst plates with erect, spinelike pillars, or intermingling wispy, threadlike, elements, are only locally preserved.

Comment. — This small group of large, calcified, frame-building organisms occupies an important place in Lower–Middle Ordovician reefs but their affinities remain to be fully evaluated. They may be related to cyanobacterial constructions (stromatolites) or to the Labechiidae, or to both. First, the long, spine-like pillars of *Pulchrilamina* have a tendency to protrude farther upward into overlying sediment and there are fewer traces of associated, well developed, intersecting cyst plates to provide structural support than in typical members of the Labechiida. Secondly, the thread-like elements of *Zondarella* are not characteristic of stromatoporoid fabrics, but resemble some thrombolitic textures and, therefore, may be of cyanobacterial (or ?algal) origin (see Webby 1991: fig. 10a–c). Also Narbonne and Arbuckle (1989) have compared diagenetically altered latilaminate structures from Lower Cambrian reef mounds with *Pulchrilamina*.

As previously noted (Webby 1993: p. 61), it is difficult to establish whether *Pulchrilamina* is, despite its minor differences, ancestral to later Labechiida, or represents another convergently similar group.

Genus *Pulchrilamina* Toomey & Ham, 1967

See Toomey & Ham 1967: p. 983.

Type species: *P. spinosa* Toomey & Ham, 1967 (Toomey & Ham 1967: p. 983, pl. 128: 1–4); 3 paratypes figured; holotype (a thin section) USNM 155300 remains unfigured.

Diagnosis. — Large, strongly latilaminate, laminar to domical skeleton; internally may exhibit rows of undulating, thin, long, low cyst plates as well as randomly spaced vertical to near vertical, long and slender, spine-like pillars; these latter characteristically protrude through the tops of latilaminae into overlying sediment; a few may be tilted out of an orderly, more-or-less parallel alignment.

Range. — Lower Ordovician (post-Tremadoc) (1 species).

Distribution. — U.S.A. (Texas, Oklahoma).

Genus *Zondarella* Keller & Flügel, 1996

See Keller & Flügel 1996: p. 188.

Type species: *Z. communis* Keller & Flügel, 1996 (Keller & Flügel 1996: p. 188, pl. 47: 1, 7, 9; pl. 48: 1–3); MLP – number to be determined when the type specimen, informally numbered RA641, is transfered from Erlangen University (Keller personal communication 1998).

Diagnosis. — Like *Pulchrilamina*, but exhibits randomly spaced and variably continuous, intermingling, thread-like structural elements, rather than spine-like pillars.

Range. — Middle Ordovician (pre-Darriwilian) (1 species).

Distribution. — Argentina (pre-Cordillera), Canada (Newfoundland).

Order Clathrodictyida Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969b.

= Gerronostromatida Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969b).

Diagnosis. —Structure sublaminate to laminate, composed of single-layer continuous laminae and short or superposed pillars; microstructure compact; interspaces are galleries.

Comment. — Clathrodictyids were separated from actinostromatids by Kühn (1939) as an independent taxonomic unit of family rank. Bogoyavlenskaya (1969a) elevated the group to ordinal rank defining them as stromatoporoids with inflected laminae. The stromatoporoids with well-differentiated planar laminae and rod-shaped pillars were distinguished by her as the separate order Gerronostromatida but are here reclassified as a family within the Clathrodictyida.

Family Clathrodictyidae Kühn, 1939

nom. correct. Lecompte, 1956, *pro* Clathrodictyonidae Kühn, 1939.

= ?Coenellostromatidae Bogoyavlenskaya, 1977 (Bogoyavlenskaya 1977a).

Diagnosis. — Structure sublaminate, laminae inflected, bending down into merged short pillars; galleries open, lenticular in longitudinal section.

Genus *Clathrodictyon* Nicholson & Murie, 1878

See Nicholson & Murie 1878: p. 220.

Type species: *C. vesiculosum* Nicholson & Murie, 1878 (Nicholson & Murie 1878: p. 220, pl. 2: 1–13); BM(NH) P5495 (Nicholson No. 216).

Diagnosis. — Skeleton domical to laminar, laminae irregularly wrinkled, pillars short, commonly oblique or Y-shaped, rodlike at base, galleries lenticular or irregular, astrorhizae common (Fig. 4A, B).

Range. — Upper Ordovician (Caradoc–Ashgill) to Givetian (about 50 species).

Distribution. — Upper Ordovician – Australia (New South Wales, Tasmania), Canada (Anticosti), China (Inner Mongolia, Guangxi, Shaanxi, Zhejiang), Estonia, Norway; Silurian – cosmopolitan at lower paleolatitudes (N. America, Europe, Asia, Australia); Lower Devonian (Emsian) – Canada (Arctic); Middle Devonian – China (Yunnan), England, Russia (Urals, NE. Siberia), U.S.A. (Ohio).

Genus *Bullulodictyon* Yavorsky, 1967

See Yavorsky 1967a: p. 17.

Type species: *B. patokense* Yavorsky, 1967 (Yavorsky 1967a: p. 17, pl. 3: 5–7, text-fig. 1); CNIGR 7351/557.

Diagnosis. — Skeleton laminar, laminae moderately inflected, zonally indefinite, pillars weakly differentiated, galleries lenticular, of different sizes, astrorhizae large, common.

Range. — Upper Devonian (1 species).

Distribution. — Russia (Pechora Basin).

Comment. — The genus *Bullulodictyon* has been transferred from the order Labechiida to the order Clathrodictyida as the re-examination of the type specimen of the typical species of the genus revealed that its sublaminar structure resembles that of *Clathrodictyon* while only its zonally developed numerous astrorhizae simulate the vesicular structure characteristic of the Labechiida.

Genus ?*Coenellostroma* Bogoyavelenskaya, 1977

See Bogoyavelenskaya 1977a: p. 14.

Type species: *C. kaljanum* Bogoyavlenskaya, 1977 (Bogoyavlenskaya 1977a: p. 15, pl. 4: 1a, b); UGM 1089/40a.

Diagnosis. — Skeleton domical; laminae wrinkled, inflexional, bending into Y-shaped pillars which merge into coenostele-like chains or walls, bounding meandroid galleries or chambers subhexagonal in tangential section, arcade-like in longitudinal section; astrorhizae large, common.

Comment. — Coenostele-like longitudinal elements joined into chains suggest a placement of the genus in the Atelodictyidae but lack of planar laminae favours placement in the Clathrodictyidae.

Range. — Lower to Middle Devonian (3 species).

Distribution. — Russia (E. Urals).

Genus ?*Kyklopora* Bogoyavlenskaya, 1982

See Bogoyavlenskaya 1982: p. 10.

Type species: *K. kalmiusensis* Bogoyavlenskaya, 1982 (Bogoyavlenskaya 1982: p.37, pl. 4: 3); UGM 15/57/103.

Diagnosis. — Skeleton laminar; laminae abruptly wrinkled, pillars weakly differentiated; galleries irregular; astrorhizae obscure.

Range. — Upper Famennian (1 species).
Distribution. — Russia (Donetsk Basin).

Genus *Labechiina* Khalfina, 1961

See Khalfina 1961: p. 55.

Type species: *L. cylindrica* Khalfina, 1961 (Khalfina 1961: p. 55, pl. S–7: 3; pl. S–8: 1); CSGM 401/50.

Diagnosis. — Skeleton columnar, cylinders locally coalescent, without axial canal, laminae moderately wrinkled, thin, bending into merged short pillars, megapillars well-developed.

Range. — ?Upper Ordovician to Lower Devonian (3 species).

Distribution. — ?Upper Ordovician – Russia (NE. Siberia); Middle Silurian – Canada (Mackenzie Distr.); Lower Devonian – Russia (Salair).

Genus *Oslodictyon* Mori, 1978

See Mori 1978: p. 13.

Type species: *O. henningsmoeni* Mori, 1978 (Mori 1978: p. 135, fig. 9A, B); PMO 45420.

= *Distylostroma* Kosareva, 1985 in Bogoyavlenskaya & Khromych 1985: p. 75; type species: *D. crassum* Kosareva, 1985 in Bogoyavlenskaya & Khromych 1985.

Diagnosis. — Skeleton domical to laminar, laminae moderately wrinkled, bending into merged short pillars, long megapillars present, astrorhizae obscure.

Range. — Llandovery to ?Middle Devonian (7 species).

Distribution. — Llandovery – Estonia, Norway; Upper Silurian – Russia (Urals); Lower Devonian – Canada (Arctic), Russia (NE. Siberia); ?Middle Devonian – Russia (Salair).

Genus *Stelodictyon* Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969b: p. 17.

Type species: *S.iniquum* Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969b: p. 17, pl. 3: 1a, b); UGM, 990/61a.

Diagnosis. — Skeleton domical to laminar, laminae microundulate at junctions of funnel-shaped pillars, penetrated by pores; galleries arcade-like; astrorhizae rare, tubular.

Range. — Upper Ordovician (Ashgill) to Lochkovian (11 species).

Distribution. — Upper Ordovician – Estonia; Middle Silurian (Wenlock) – Canada (Manitoba, Ontario), England, Sweden (Gotland), Russia (W. Urals, Siberian Platform), Ukraine (Podolia); Upper Silurian – Russia (E. Urals); Lochkovian – U.S.A. (New York).

Comment. — Stearn (1980) classified *Stelodictyon* and *Coenellostroma* together in the Actinostromatida and placed them close to *Atelodictyon*. Later, Stearn (1991) related them to *Aculatostroma*. Here these genera are treated as members of the family Clathrodictyidae because their pillars (*Stelodictyon*) or coenosteles (*Coenellostroma*) are formed by downturnings of inflected laminae.

Family Actinodictyidae Khalfina & Yavorsky, 1973

= Ecclimadictyidae Stearn, 1980. = Plexodictyidae Bogoyavlenskaya, 1981.

Diagnosis. — Structure sublaminate; laminae crumpled (zigzag) forming cassiculate meshwork, pillars oblique or indistinguishable; galleries labyrinthine in tangential section, oval in longitudinal section.

Comment. — The Clathrodictyidae encompass the forms with irregularly inflected laminae; the Ecclimadictyidae those with crumpled (zigzag) laminae. However, Stearn (1980) included the genus *Actinodictyon* in his newly erected family Ecclimadictyidae. Consequently the family name Actinodictyidae Khalfina & Yavorsky, 1973, has priority.

Genus *Actinodictyon* Parks, 1909

See Parks 1909: p. 30.

Type species: *A. canadense* Parks, 1909 (Parks 1909: p. 32, pl. 20: 1, 2); GSC 9123; selected by Bassler 1915: p. 16.

Diagnosis. — Skeleton cylindrical, laminae irregularly crumpled, fused with dissepiments, pierced by scattered crooked megapillars; astrorhizae obscure (Fig. 4C, D).
Range. — Lower to Upper Silurian (4 species).
Distribution. — Llandovery – Canada (N. Hudson Bay); Silurian (undivided) – Russia (Pechora basin); Upper Silurian (Ludlow) – Australia (New South Wales).

Genus *Ecclimadictyon* Nestor, 1964

See Nestor 1964: p. 60.
Type species: *Clathrodictyon fastigiatum* Nicholson, 1886 (Nicholson 1886b: p. 43, fig. 3: p. 78, fig. 12; see also Nicholson 1887: p. 8, pl. 2: 3, 4); BM(NH) P5773.
Diagnosis. — Skeleton laminar to domical; laminae crumpled, zigzag, forming cassiculate network, pillars oblique or indistinguishable.
Range. — Upper Ordovician (Caradoc–Ashgill) to Upper Silurian (Pridoli) (34 species).
Distribution. — Upper Ordovician – Australia (New South Wales, Tasmania), China (Qinghai, Xinjiang, Zhejiang), Estonia, Kazakhstan, Russia (W. Urals, Altai, Gornaya Shoria); Lower and Middle Silurian – cosmopolitan at lower paleolatitudes (N. America, Europe, Siberia, China, Central Asia, Iran, Australia); Upper Silurian – China (Guizhou, Hubei, Sichuan, Inner Mongolia), Sweden (Gotland), Russia (E. Urals, Arctic islands), U.S.A. (midcontinent).

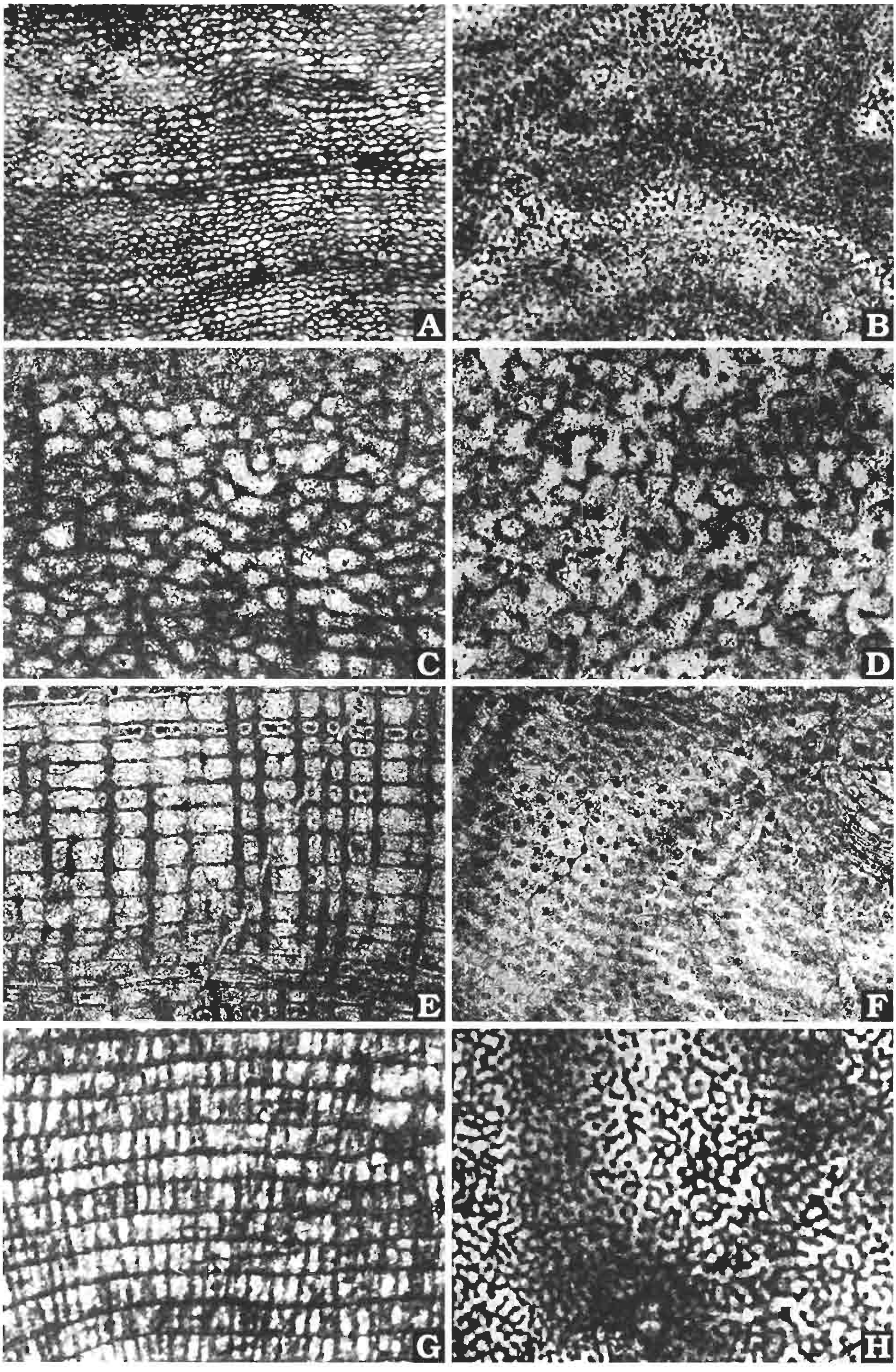
Genus *Neobeatricea* Rukhin, 1938

See Rukhin 1938: p. 95.
Type species: *Beatricea tenuitextilis* Yavorsky, 1929 (Yavorsky 1929: p. 92, pl. 11: 10; pl. 12: 4–10); CNIGR 2595/76.
Diagnosis. — Skeleton columnar, cylinders partly coalescent, without axial canal, laminae crumpled (zigzag), pillars indistinguishable, astrorhizae rare with short unbranched canals.
Range. — Wenlock to Ludlow (8 species).
Distribution. — Wenlock – Russia (Urals, Siberian Platform); Ludlow – Canada (Quebec); Silurian (undifferentiated) – Russia (Pechora Basin, Novaya Zemlya, NE. Siberia).

Genus *Plexodictyon* Nestor, 1966

See Nestor 1966: p. 20.
Type species: *P. katriense* Nestor, 1966 (Nestor 1966: p. 21, pl. 7: 2–5); IGTTU Co3132.
Diagnosis. — Skeleton laminar or domical, laminae crumpled, forming cassiculate network, intertwined with planar paralaminae, astrorhizae rare, tubular.
Range. — ?Upper Ordovician to ?Lower Silurian, Upper Silurian (Ludlow–Pridoli, 31 species).
Distribution. — ?Upper Ordovician – Australia (N. Queensland, New South Wales); ?Lower Silurian – China (Guizhou, Hubei); Upper Silurian – Australia (New South Wales, Queensland), Canada (Arctic islands), Central Asia (Tien Shan), China (Inner Mongolia), Estonia, Sweden (Scania, Gotland), U.S.A. (Michigan, Virginia), Russia (Arctic islands, Pechora basin, Urals, NE. Siberia), Ukraine (Podolia).
Comment. — Typical representatives of *Plexodictyon* are restricted to the Upper Silurian (Ludlow, Pridoli). Earlier representatives may belong to a new genus.

Fig. 4. **A, B**. Clathrodictyidae: *Clathrodictyon vesiculosum* Nicholson & Murie, 1878, longitudinal and tangential sections of holotype BM(NH) P5495 (216a, 216), × 10. Note irregularly wrinkled laminae inflected into merged short pillars; tiny, superposed astrorhizae visible with difficulty in places. **C, D**. Actinodictyidae: *Actinodictyon canadense* Parks, 1909, longitudinal and tangential sections of holotype GSC 9123 (432, 433), × 10. Note irregularly crumpled laminae pierced by scattered crooked megapillars and rare dissepiments. **E, F**. Gerronostromatidae: *Gerronostroma elegans* Yavorsky, 1931, longitudinal and tangential sections of holotype CNIGR 338/3 (a, c), × 10. Note single-layered, continuous, planar laminae and rodlike, long pillars. **G, H**. Atelodictyidae: *Atelodictyon fallax* Lecompte, 1951, longitudinal and tangential sections of the holotype IRScNB a 7411(c, d), × 10. Note continuous planar laminae and branched, bladelike pillars, joined into chains in tangential section.


A
B
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Genus *Yabeodictyon* Mori, 1968

See Mori 1968: p. 67.

Type species: *Y. balticum* Mori, 1968 (Mori 1968: p. 68, pl. 18: 1, 2); SMNH GIK-35.

= *Neoclathrodictyon* Lessovaja, 1971 (Lessovaja 1971: p. 116); type species: *N. flexibilis* Lessovaja, 1971 (Lessovaja 1971: p. 117).

Diagnosis. — Skeleton domical or laminar, laminae crumpled (zigzag), pierced by long megapillars, astrorhizae small, common.

Range. — Wenlock to Emsian (11 species).

Distribution. — Wenlock – Canada (Arctic, Quebec), Sweden (Gotland), Russia (Siberian Platform); Upper Silurian – Canada (Arctic islands), Central Asia (Tien Shan), Russia (W. Urals, ?Salair); Silurian – Canada (Hudson Bay), Russia (Pechora Basin); Emsian – Central Asia (Tien Shan).

Family Gerronostromatidae Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969b.

= Clathrostromatidae Khalfina & Yavorsky, 1971.

Diagnosis. — Structure laminate with well differentiated skeletal elements, laminae planar, pillars simple, rodlike, short or superposed, galleries rectangular in longitudinal section, astrorhizae rare.

Genus *Gerronostroma* Yavorsky, 1931

See Yavorsky 1931: p. 1392.

Type species: *G. elegans* Yavorsky, 1931 (Yavorsky 1931: p. 1393, pl. 1: 12; pl. 2: 3–6); CNIGR 3338/3, selected by Galloway 1957: p. 438.

= *Clathrostroma* Yavorsky, 1960 (Yavorsky 1960: p. 132); type species: *C. stolbergenense* Yavorsky, 1960 (Yavorsky 1960: p. 132).

Diagnosis. — Skeleton domical or bulbous; laminae planar, continuous; pillars rodlike, mostly long or superposed; astrorhizae rare, fasciculate (Fig. 4E, F).

Range. — Upper Llandovery (Telychian) to Upper Famennian (40 species).

Distribution. — Llandovery – Canada (Arctic islands); Upper Silurian – Canada (E. Quebec), Russia (Pechora Basin, Urals); Lower Devonian – Canada (Arctic islands), Central Asia (Tien Shan); Russia (Urals, Kuznetsk Basin, Kolyma); Middle Devonian – Afghanistan, Australia (Victoria, N. Queensland), Central Asia (Tien Shan), Russia (Pechora Basin, Urals, Kuznetsk Basin, Kolyma), U.S.A. (Indiana, Ohio); Upper Devonian – Canada (Alberta), Germany, Russia (Russian Platform, Kuznetsk Basin; Upper Famennian – Russia (S. Urals).

Comment. — The family Gerronostromatidae unites stromatoporoids with both short and long superposed pillars. Yavorsky (1960) erected a new genus *Clathrostroma* having partly short and partly long pillars. However, many species traditionally included in *Gerronostroma* (e.g., *G. concentricum* Yavorsky, 1931) have short pillars as well as long superposed ones. Therefore this character has no generic value.

Genus *Gerronodictyon* Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969b: p. 20.

Type species: *G. incisum* Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969b: p. 20, pl. 3: 2; pl. 4: 1); UGM 990/189a.

Diagnosis. — Skeleton domical or irregular, laminae discontinuous, pillars rodlike, long, superposed, astrorhizae rare, fasciculate.

Range. — Wenlock (1 species).

Distribution. — Russia (E. Urals).

Genus *Petridiostroma* Stearn, 1992

See Stearn 1992: p. 531.

pro *Petrostroma* Stearn, 1991 (Stearn 1991: p. 617), non *Petrostroma* Döderlein, 1892.

Type species: *Simplexodictyon simplex* Nestor, 1966 (Nestor 1966: p. 25, pl. 8: 3–6); IGTTU Co3134.
= *Faciledictyon* Lessovaja, 1991 (Lessovaja 1991: p. 28); type species: *Simplexodictyon torosum* Lessovaja, 1972 (Lessovaja 1972: p. 49).

Diagnosis. — Skeleton laminar to domical; laminae planar, continuous; pillars short, rodlike to spool-shaped; galleries arcadelike in longitudinal section; astrorhizae obscure.

Range. — Upper Llandovery (Telychian) to Givetian (about 40 species).

Distribution. — Llandovery – Estonia, Norway, Sweden (Gotland); Wenlock – Central Asia (Tien Shan), Estonia, Russia (Urals), Sweden (Gotland), U.S.A. (midcontinent); Silurian – Russia (Pechora Basin, NE. Asia); Lower Devonian – Australia (Victoria), Canada (Arctic islands), Central Asia (Tien Shan), Czech Republic (Bohemia), Russia (Urals, Salair, NE. Asia), U.S.A. (New York); Middle Devonian – Central Asia (Tien Shan), Germany, Russia (Pechora Basin, Urals, Kuznetsk Basin, NE. Siberia), U.S.A. (midcontinent).

Comment. — Stearn (1991) introduced a new name, *Petrostroma* (later renamed *Petridiostroma* as the former name was preoccupied) for a group of species usually identified as *Simplexodictyon*. The type species of *Simplexodictyon* (*S. podolicum* Yavorsky, 1929) has tripartite, divided laminae and therefore *Simplexodictyon* belongs in the order Stromatoporellida.

Family Atelodictyidae Khalfina, 1968

See Khalfina 1968b.

= Aculatostromatidae Khalfina & Yavorsky, 1971.

Diagnosis. — Structure laminate with well differentiated structural elements; laminae planar, pillars or coenosteles, irregularly branching or bladed, joined into chains or walls; galleries labyrinthine in tangential section, subrectangular in longitudinal section; astrorhizae rare.

Comment. — Genera of the Clathrodictyida with planar laminae and complicated interlaminar (pillar) structure have usually been classified in the family Tienodictyidae. Nestor (1974) demonstrated that this subdivision united taxa of different origins. The genus *Atelodictyon*, for a long time considered a genus of the Actinostromatida due to a misinterpretation of the interlaminar structure in tangential section, has now been transferred to the Clathrodictyida (Stearn, 1991). The family Atelodictyidae is here accepted and unites genera such as *Intexodictyon, Cubodictyon,* and *Coenostelodictyon* that have laterally branching or blade-shaped pillars (or coenosteles), forming in tangential section angular chainlike or netlike structures similar to the 'hexactinellid' network of the collicate laminae of genera of the Actinostromatida. Transfer of these genera to the Atelodictyidae results in reduction in the heterogeneity of the family Tienodictyidae; only taxa with upwardly bifurcating or oblique pillars and numerous dissepiments forming a tangled network in tangential section are retained in the latter family.

Genus *Atelodictyon* Lecompte, 1951

See Lecompte 1951: p. 124.

Type species: *A. fallax* Lecompte, 1951 (Lecompte 1951: p. 125, pl. 15: 1, 2); IRScNB a 7411.
= *Aculatostroma* Khalfina, 1968 (Khalfina 1968b: p. 62); type species: *Syringostroma verrucosum* Khalfina, 1961 (Khalfina 1961: p. 342).

Diagnosis. — Skeleton tabular or domical; laminae thin, planar, continuous; pillars (or coenosteles) bladelike or irregularly branched, joined in chains, short to superposed, galleries labyrinthine in tangential section, subrectangular in longitudinal section; astrorhizae rare (Fig. 4G, H).

Range. — Lochkovian to Upper Famennian (about 40 species).

Distribution. — Lower Devonian – Australia (N. Queensland), Central Asia (Tien Shan), Russia (Kuznetsk Basin, NE. Siberia); Middle Devonian – Afghanistan, Austria, Belgium, China (Guizhou), France, Poland, Russia (Urals, Kuznetsk Basin, NE. Siberia), U.S.A. (Indiana); Upper Devonian – Canada (Alberta), Czech Republic (Moravia), Poland, Russia (Russian Platform, Kuznetsk Basin, NE. Siberia), U.S.A. (Iowa); Upper Famennian – Belgium, Germany, Kazakhstan.

Comment. — The genus *Aculatostroma* is considered synonymous with *Atelodictyon* because the photographs of the type species (*Syringostroma verrucosum* Khalfina, 1961, see Khalfina 1961: pl. D-13: 3a–b) show clearly that the so-called hexactinellid network was developed in the interlaminar space, just as in *Atelodictyon*, and not on the level of the laminae as in *Actinostroma*.

Genus *Coenostelodictyon* Yavorsky, 1971

See Khalfina & Yavorsky 1971: p. 118.

Type species: *Clathrodictyon krekovi* Yavorsky, 1955 (Yavorsky 1955: p. 50, pl. 19: 5, 6; CNIGR 7351/62.

Diagnosis. — Skeleton laminar; laminae planar, thin; pillars bladelike, circular in tangential section at base, isolated or joined in chains at top; galleries subrectangular in longitudinal section.

Range. — Lower to Middle Devonian (2 species).

Distribution. — Lower Devonian – Russia (Kuznetsk Basin); Middle Devonian – China (Yunnan).

Genus ?*Cubodictyon* Yang & Dong, 1979

See Yang & Dong 1979: p. 46.

Type species: *C. sinense* Yang & Dong, 1979 (Yang & Dong 1979: p. 46, pl. 20: 5, 6); NIGP Bd644-4 (32959, 32960).

Diagnosis. — Skeleton domical or irregular; laminae wrinkled on a small scale; vertical elements with bounding chambers subhexagonal in tangential section, astrorhizae unknown.

Range. — Eifelian (1 species).

Distribution. — China (Guangxi).

Comment. — The presence of chamber-like structures shows that the relationship of the genus with stromatoporoids is problematic.

Genus *Intexodictyon* Yavorsky, 1963

See Yavorsky 1963: p. 34.

Type species: *I. perplexum* Yavorsky, 1963 (Yavorsky 1963: p. 36, pl. 6: 6, 7; pl. 8: 1–4); CNIGR 7351/469, lectotype chosen by Nestor 1964: p. 72.

Diagnosis. — Skeleton domical; laminae thin, planar, continuous; pillars thin, irregularly branching, forming a fine tangled network in interlaminar space; additional laminae locally developed in interlaminar space or below the primary laminae.

Range. — Llandovery to Emsian (12 species).

Distribution. — Llandovery – Canada (Arctic islands), Estonia; Upper Silurian – Central Asia (Tien Shan), Russia (Pechora Basin, NE. Siberia); Silurian undifferentiated – Russia (Pechora Basin, Tuva); Lower Devonian – Russia (Kuznetsk Basin), China (Inner Mongolia).

Family Tienodictyidae Bogoyavlenskaya, 1965

See Bogoyavlenskaya 1965a.

= Dualestromatidae Khalfina & Yavorsky, 1973.

Diagnosis. — Structure laminate; laminae distinct, planar; pillars branching or oblique, forming vermiform or tangled network beneath overlying lamina; dissepiments common; galleries irregular.

Genus *Tienodictyon* Yabe & Sugiyama, 1941

See Yabe & Sugiyama 1941: p. 139.

Type species: *T. zonatum* Yabe & Sugiyama, 1941 (Yabe & Sugiyama 1941: p. 139, figs 1–6); IGPS 65229.

Diagnosis. — Skeleton domical, laminae planar; interlaminar space divided into two zones by additional laminae formed by processes of pillars; pillars in lower zone meandroid, in upper zone circular, in tangential section; galleries irregular; dissepiments abundant in upper zone; astrorhizae indistinct.

Range. — Lower Devonian to Frasnian (11 species).

Distribution. — Lower Devonian – Australia (N. Queensland), Russia (NE. Siberia); Middle Devonian – Australia (N. Queensland), Canada (Northwest Territories), China (Yunnan), Russia (E. Urals, Kuznetsk Basin, Salair); Upper Devonian – Czech Republic (Moravia).
Comment. — This genus and *Hammatostroma* have been considered congeneric but the species commonly included in the latter form a definite grouping mainly restricted to the Frasnian. *Hammatostroma* has discontinuous, crumpled secondary laminae in the middle of interlaminar spaces but *Tienodictyon* has more planar secondary laminae and different pillar structure on each side of these laminae.

Genus *Anostylostroma* Parks, 1936

See Parks 1936: p. 44.
Type species: *A. hamiltonense* Parks, 1936 (Parks 1936: p. 46, pl. 8: 1, 3, 4; ROM 16536 (2098, 2099), revised by Stearn 1991: p. 612.
Diagnosis. — Skeleton laminar to domical; laminae thin, planar, penetrated by scattered pores; pillars thick, expanding and branching at tops, vermiform in tangential section; galleries irregular; dissepiments common; astrorhizae rare, small.
Range. — Eifelian to upper Famennian (17 species).
Distribution. — Middle Devonian – Canada (Arctic islands), China (Guangxi), Russia (E. Urals, Kuznetsk Basin), U.S.A. (Indiana, Missouri); Upper Devonian – Kazakhstan, Russia (Pechora Basin); upper Famennian – China (Guangxi), France, Germany (Aachen), Russia (Pechora Basin).

Genus *Belemnostroma* Stearn, 1990

See Stearn 1990: p. 504.
Type species: *B. hastatum* Stearn, 1990 (Stearn 1990: p. 505, figs 5.7, 5.8, 8.3; GSC 95772.
Diagnosis. — Skeleton laminar to domical; laminae planar, inflected upward at megapillars; short pillars expanding and branching at top; rodlike megapillars of diffuse tissue; astrorhizae inconspicuous.
Range. — Lochkovian (1 species).
Distribution. — Canada (Arctic islands).

Genus *Hammatostroma* Stearn, 1961

See Stearn 1961: p. 939.
Type species: *Hammatostroma albertense* Stearn, 1961 (Stearn 1961: p. 940, pl. 106: 2, 4, text-fig. 3); GSC 15318.
Diagnosis. — Skeleton domical to laminar, laminae planar, transversely fibrous; interlaminar spaces occupied by tangled, irregular structure forming crumpled discontinuous additional laminae in their middle part; galleries irregular; astrorhizae obscure.
Range. — Givetian to Frasnian (10 species).
Distribution. — Givetian – China (Guangxi); Frasnian – Canada (Alberta, Saskatchewan), China (Guangxi), Czech Republic (Moravia), Poland, Russia (Arctic islands, Timan, Urals), U.S.A. (Iowa, SW. states).

Genus *Nexililamina* Mallett, 1971

See Mallett 1971: p. 241.
Type species: *N. dipcreekensis* Mallett, 1971 (Mallett 1971: p. 241, pl. 14: 5–8, not 4); UQF 47608, revised by Webby & Zhen 1997: p. 35.
Diagnosis. — Skeleton laminar to domical; laminae regular, continuous, with few pores; dissepiments scattered; pillars of two types – long, superposed, spool-shaped (megapillars), and simple, short, rodlike and upwardly forking, in tangential section rounded to irregular, not ringlike to vermicular as in *Schistodictyon*; apparently lacking astrorhizae.
Range. — Emsian to Eifelian (1 species).
Distribution. — Australia (N. Queensland).

Genus *Pseudoactinodictyon* Flügel, 1958

See Flügel 1958a: p. 137.

Type species: *P. juxi* Flügel, 1958 (Flügel 1958a: p. 137, pl. 1: a–d); SMF XXV-1184.

= *Dualestroma* Khalfina, 1961 (Khalfina 1961: p. 332); type species: *Stromatoporella dualis* Khalfina, 1961 (Khalfina 1961: p. 332). = *Intexodictyonella* Yavorsky, 1969 (Yavorsky 1969: p. 102); type species: *Stromatoporella undata* Yavorsky, 1950 (Yavorsky 1950: p. 258).

Diagnosis. — Skeleton laminar to domical; laminae planar, thin; pillars short, partly superposed, locally crooked, expanding at tops; wide interlaminar spaces filled with abundant dissepiments; astrorhizae present.

Range. — Emsian to Frasnian (23 species).

Distribution. — Lower Devonian – Australia (Victoria), ?U.S.A. (Michigan); Middle Devonian – Australia (N. Queensland), Canada (Alberta, N. Ontario), China (Yunnan), Czech Republic (Moravia), England, France, Poland, Russia (S. Urals, Kuznetsk Basin); U.S.A. (Ohio); Upper Devonian – Belgium, Canada (Alberta, Arctic islands), China (Guangxi), Germany, Russia (Russian Platform).

Comment. — Reexamination of the original collections has confirmed the need to expand the scope of this genus and to assign it to the Tienodictyidae. It is characterized by numerous dissepiments in the comparatively wide interlaminar spaces. The type species of *Dualestroma* and *Intexodictyonella* are here assigned to the genus *Pseudoactinodictyon*.

Genus *Schistodictyon* Lessovaja, 1970

See Lessovaja & Zakharova 1970: p. 47.

Type species: *S. posterium* Lessovaja, 1970 in Lessovaja & Zakharova 1970: p. 49, pl. 5: 2a, b; GMU 240/2 – 9/74.

Diagnosis. — Skeleton domical; laminae thin, planar; pillars funnel-shaped, branching in longitudinal section once or twice before reaching overlying lamina; galleries irregular to vermicular, ring-like in tangential section; astrorhizae rare.

Range. — Ludlow to Frasnian (24 species).

Distribution. — Ludlow – Australia (New South Wales, N. Queensland), Pridoli – Central Asia (Tien Shan); Lower Devonian – Australia (New South Wales, N. Queensland), Russia (Kuznetsk Basin); Middle Devonian – Belgium, Canada (Ontario), U.S.A. (Missouri, Michigan, Ohio), Russia (S. Urals, Kuznetsk Basin); Upper Devonian – Canada (Arctic islands), Russia (Kuznetsk Basin), Turkey.

Order Actinostromatida Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969b.

Diagnosis. — Skeletons internally composed of a network of long pillars and colliculi that form a hexactinellid pattern in tangential sections of most genera; astrorhizae present in some; microstructure compact, or microreticulate.

Family Actinostromatidae Nicholson, 1886

See Nicholson 1886b.

Diagnosis. — Skeleton consists of parallel pillars that are usually more prominent than colliculi; thickness and spacing of pillars varies among and within genera; astrorhizae in a few examples; microstructure compact.

Genus *Actinostroma* Nicholson, 1886

See Nicholson 1886b: p. 75.

Type species: *A. clathratum* Nicholson, 1886 (Nicholson 1886a: p. 226; pl. 6: 1–3); lectotype (Schouppé 1954: p. 431) BM(NH) P5774.

= *Rosenia* Waagen & Wentzel, 1887 (Waagen & Wentzel 1887: p. 943); type species: *Stromatopora astroites* Rosen *sensu* Bargatzky, 1881 (Bargatzky 1881a: p. 284). = *Bullatella* Bogoyavlenskaya, 1977 (Bogoyavlenskaya 1977b: p. 13); type species: *B. crassa* Bogoyavlenskaya, 1977 (Bogoyavlenskaya 1977b: p. 14). = *Auroriina* Bogoyavlenskaya, 1977 (Bogoyavlenskaya 1977b: p. 16); type species: *A. primigenia* Bogoyavlenskaya, 1977 (Bogoyavlenskaya 1977b: p. 17).

Diagnosis. — All pillars thick and of similar length and width; colliculi laterally persistent and aligned as seen in longitudinal section (Fig. 5E, F).

Range. — Lochkovian to Frasnian (about 86 species).

Distribution. — Lower Devonian – Russia (Kuznetsk Basin); Lochkovian – Russia (E. Urals); Pragian – Australia (New South Wales, Queensland); Emsian – Australia (New South Wales, Queensland), Austria, Mongolia, Russia (NE. Siberia), Spain; Middle Devonian – China (Hunan, NE. China), Italy, Russia (Pechora Basin, Salair, Siberia, Urals), Vietnam; Eifelian – Australia (Queensland), Austria, Belgium, China (Guangxi, Xinjiang), Germany, Mongolia, Russia (Altai, Kuznetsk Basin, Siberia), Slovenia, Spain, Uzbekistan; Givetian – Afghanistan, Australia (Queensland), Austria, Belgium, Canada (Manitoba, Northwest Territories), China (Guangxi, Guizhou, Hunan, Sichuan, Xizang, Yunnan), Czech Republic, France, Germany, Poland, Russia (Kuznetsk Basin, Omolon Massif, Pechora Basin, Salair, Siberia, NE. Siberia, Urals), Thailand, U.S.A. (Indiana), Uzbekistan, Vietnam; Upper Devonian – Russia (Pechora Basin, Russian Platform), Turkey; Frasnian – Australia (Western Australia), Belgium, Canada (Alberta, Manitoba, Northwest Territories, Saskatchewan), China (Guangxi, Sichuan, Yunnan), Czech Republic, France, Germany, Mexico (Sonora), Poland, Russia (Kuznetsk Basin, NE. Siberia. Russian Platform, St. Petersburg, Timan), U.S.A. (Alaska, Iowa, Montana, Nevada), Vietnam.

Comment. — The few Silurian (Ludlow) forms assigned to *Actinostroma* in recent years (e.g., Mori 1970; Savelle 1979) contain both aligned and unaligned colliculi; these forms are here considered *Plectostroma*. Also within *Actinostroma* there are two groups of species that are atypical. First group has unusual complexly arranged colliculi and typically short pillars; possible type species: *Actinostroma verrucosum* (Goldfuss, 1826). Second group has mostly short pillars, although some long pillars may be present, and simple colliculi; possible type species: *Actinostroma stellulatum* Nicholson, 1886 (see Nicholson 1886a).

Genus *Bicolumnostratum* Stock, 1998

See Stock & Burry-Stock 1998: p. 191.

Type species: *Actinodictyon mica* Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969a: p. 20); UGM 26-M/67.

Diagnosis. — Pillars of two types, some long, continuous, and thick, others short and narrow; colliculi not aligned.

Range. — Ludlow to Pridoli (1 species).

Distribution. — Ludlow – Ukraine (Podolia); Pridoli – U.S.A. (New York).

Genus *Bifariostroma* Khalfina, 1968

See Khalfina 1968a: p. 149.

Type species: *Actinostroma bifarium* Nicholson, 1886 (Nicholson 1886a: p. 231, pl. 4: 4, 5); lectotype (chosen by Flügel 1958b: p. 134) BM(NH) P5639.

Diagnosis. — Pillars of two types, some long, continuous and thick (megapillars), others short and thin; colliculi aligned.

Range. — Emsian to Frasnian (8 species).

Distribution. — Emsian – Austria, Spain; Middle Devonian – Italy; Eifelian – Belgium. Spain, Uzbekistan; Givetian – Belgium, China (Guangxi, Sichuan), Czech Republic, France, Poland; Frasnian – Afghanistan, Belgium, Czech Republic, Poland, Russia (Timan).

Genus ?*Crumplestroma* Khalfina, 1972

See Khalfina 1972: p. 148.

Type species: *C. lacerilaminatum* Khalfina, 1972 (Khalfina 1972: p. 148, pl. C-2: 1–2); CSGM, number unknown.

Diagnosis. — Structure of long conspicuous pillars, steplike offsets of colliculi interrupted by paralaminae.

Range. — Ludlow (1 species).
Distribution. — Russia (Altai).
Comment. — The genus is inadequately described in a plate caption. The original illustration does not allow a clear determination of the nature of the paralaminae; they may be original skeletal structures or the product of diagenesis. If the latter, *Crumplestroma* is a junior synonym of *Plectostroma*.

Genus *Plectostroma* Nestor, 1964

See Nestor 1964: p. 78.
Type species: *Actinostroma intertextum* Nicholson, 1886 (Nicholson 1886a: p. 233, pl. 8: 3–6); BM(NH) P5620.
Diagnosis. — Pillars long, continuous, colliculi not aligned (Fig. 5C, D).
Range. — Llandovery to Frasnian (about 48 species).
Distribution. — Silurian – Russia (Altai, Salair); Llandovery – Estonia, Russia (Tuva, Urals), Sweden? (Gotland), U.S.A. (Michigan), Uzbekistan; Middle Silurian – China; Wenlock – Canada (Northwest Territories), Estonia, Mongolia, Norway, Russia (Kuznetsk Basin, Urals), Sweden (Gotland), United Kingdom; Upper Silurian – China, Russia (Kuznetsk Basin, Pechora Basin, Urals); Ludlow – Canada (Quebec), Estonia, Mongolia, Russia (Altai, Novaya Zemlya), Sweden (Gotland, Scania), Ukraine (Podolia); Pridoli – Canada (Quebec), Estonia, Mongolia, Ukraine (Podolia); Lower Devonian – Russia (NE. Siberia), Uzbekistan; Lochkovian – Uzbekistan; Pragian – Australia (Victoria); Middle Devonian – Russia (Salair); Emsian – Canada (Arctic islands); Eifelian – China (Guangxi), Russia (Altai), Uzbekistan; Givetian – China (Guangxi), France; Frasnian – Vietnam.

Family Pseudolabechiidae Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969a.
= Plumataliniidae Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969b).
Diagnosis. — Skeleton contains pillars and colliculi, or micropillars and microcolliculi, in columns or subcolumns, respectively; colliculi and microcolliculi restricted to columns and subcolumns, intercolumnar spaces contain flat cyst plates or dissepiments, and may also contain a few pillars, or micropillars; astrorhizae absent.

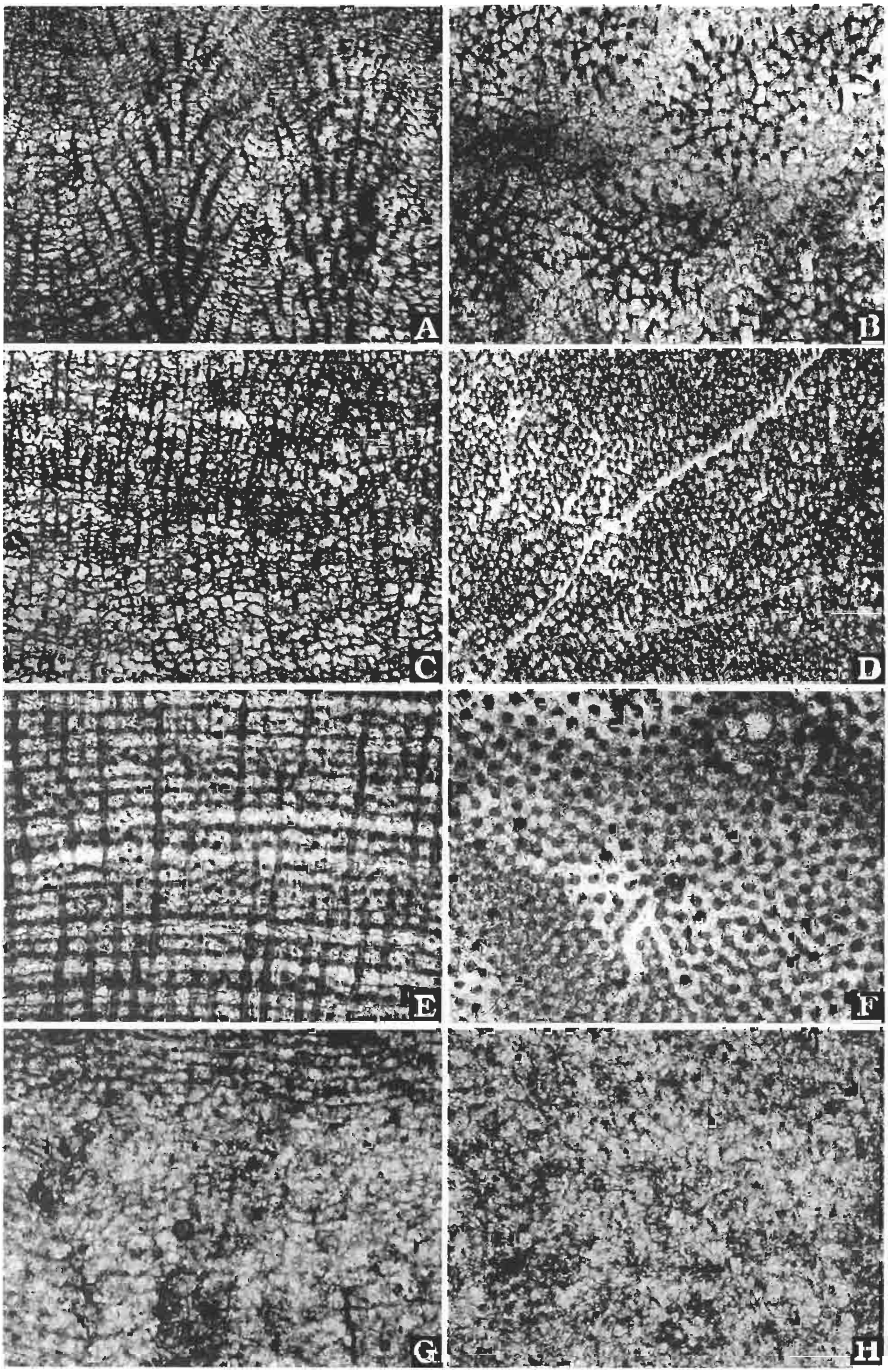
Subfamily Pseudolabechiinae Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969a.
nom. transl. Stock herein *ex* Pseudolabechiidae Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969a).
Diagnosis. — Pillars or micropillars arranged in an upwardly divergent pattern, forming columns or subcolumns; dissepiments developed in intercolumnar space.

Genus *Pseudolabechia* Yabe & Sugiyama, 1930

See Yabe & Sugiyama 1930: p. 59.
Type species: *P. granulata* Yabe & Sugiyama, 1930 (Yabe & Sugiyama 1930: p. 59, pl. 22: 5–12); IGPS RN720.

Fig. 5. **A, B.** Pseudolabechiidae: *Pseudolabechia granulata* Yabe & Sugiyama, 1930, longitudinal and tangential sections of topotype USNM 458898, × 10. Note the columns formed of bundles of upwardly divergent, cylindrical pillars that are connected by colliculi. **C–F.** Actinostromatidae: **C, D.** *Plectostroma intertextum* (Nicholson, 1886), longitudinal and tangential sections of holotype BM(NH) P5620, × 10. Note the non-alignment of colliculi; a poorly developed astrorhiza is present on the left side of the tangential section. **E, F.** *Actinostroma clathratum* Nicholson, 1886, longitudinal and tangential sections of the holotype BM(NH) P5774. Note the long cylindrical pillars and alignment of colliculi; a poorly developed astrorhiza is present towards the lower left of center of the tangential section. **G, H.** Densastromatidae: *Densastroma astroites* (Rosen, 1867), longitudinal and tangential sections of topotype USNM 492564, × 50. Note the alignment of microcolliculi, especially near the top of the longitudinal section.


A
B
C
D
E
F
G
H

Diagnosis. — Longitudinal skeletal elements pillars, horizontal elements in columns colliculi (Fig. 5A, B).

Range. — Wenlock to Ludlow (about 6 species).

Distribution. — Wenlock – Russia (Urals); Ludlow – Estonia, Russia (Novaya Zemlya), Sweden (Gotland).

Genus *Desmostroma* Bol'shakova, 1969

See Bol'shakova 1969: p. 29.

Type species: *D. columnatum* Bol'shakova, 1969 (Bol'shakova 1969: p. 30, pl. 5: 1a–b); PIN 2336/629.

= *Hexastylostroma* Dong, 1984 (Dong 1984: p. 71); type species: *H. neimongolense*, Dong, 1984 (Dong 1984: p. 71).

Diagnosis. — Clinoreticulate subcolumns constitute more than half the volume of the skeleton and are connected in some places by colliculi and in other places by coenostromes.

Range. — Llandovery to Pridoli (about 14 species).

Distribution. — Llandovery – Sweden (Gotland), U.S.A. (Iowa); Wenlock – Central Asia (Tien Shan), Mongolia, Sweden (Gotland), Ukraine (Podolia), U.S.A. (Kentucky); Upper Silurian – China (Inner Mongolia); Ludlow – Australia (New South Wales), Sweden (Gotland), Ukraine (Podolia); Pridoli – Russia (Urals).

Genus *Pachystroma* Nicholson & Murie, 1878

See Nicholson & Murie 1878: p. 223.

Type species: *P. antiqua* Nicholson & Murie, 1878 (Nicholson & Murie 1878: p. 224, pl. 4: 2–5); BM(NH) P6003.

Diagnosis. — Clinoreticulate subcolumns constitute about half the volume of the specimen, and are connected to some degree by coenostromes; longitudinal skeletal elements micropillars.

Range. — Llandovery to Wenlock (about 5 species).

Distribution. — Llandovery – Canada (Ontario), Estonia, U.S.A. (Michigan); Wenlock – Canada (Ontario, Quebec).

Genus *Vikingia* Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969a: p. 19.

Type species: *Actinodictyon*? *vikingi* Nestor, 1966 (Nestor 1966: p. 62, pl. 24: 1, 2); IGTTU Co3146.

Diagnosis. — Clinoreticulate subcolumns constitute less than half the volume of the skeleton; intercolumnar structures dissepiments.

Range. — Llandovery to Wenlock (about 4 species).

Distribution. — Llandovery – Ukraine (Podolia)?; Wenlock – Estonia, Russia (Siberian Platform), Sweden (Gotland), Ukraine (Podolia), U.S.A. (Alaska).

Subfamily Plumataliniinae Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969b.

nom. transl. Stock herein *ex* Plumataliniidae Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969b).

Diagnosis. — Skeleton consists of cyst plates and acosmoreticulate columns formed by randomly arranged micropillars and microcolliculi.

Genus *Plumatalinia* Nestor, 1960

See Nestor 1960: p. 225.

Type species: *P. ferax* Nestor, 1960 (Nestor 1960: p. 226, pl. 1: 1, 2; pl. 2: 1, 2); IGTTU Co3001.

Diagnosis. — Cyst plates flat; columns contain randomly arranged micropillars and microcolliculi forming an acosmoreticulate pattern.

Range. — Ashgill (2 species).

Distribution. — Estonia.
Comment. — *Plumatalinia* was formerly included in the order Labechiida due to its well developed cyst plates; however, the presence of microreticulation places it in the Actinostromatida. Webby (see above) believes this genus is based on diagenetically altered specimens. Well preserved specimens from Estonia that show a resemblance to Silurian *Desmostroma* give credibility to this genus.

Genus *Stromatodictyon* Khalfina, 1972

See Khalfina 1972: p. 148.
Type species: *S. repentinum* Khalfina, 1972 (Khalfina 1972: p. 152, pl. C-12: 4–5); CSGM, number unknown.
Diagnosis. — Columns have an irregular cross-section characterized by radial flanges. Cyst plates thickened.
Range. — Llandovery to Wenlock (1 species).
Distribution. — Russia (Siberian Platform).
Comment. — This genus is inadequately described in a plate caption and poorly illustrated. Thickening of cyst plates is reminiscent of similar thickening in Silurian species of *Pachystylostroma*.

Family Actinostromellidae Nestor, 1966

= Pichiostromatidae Bogoyavlenskaya, 1981.
Diagnosis. — Skeleton a microreticulate mass that is pierced by elongate, longitudinal spaces (autotubes or slits); astrorhizae not confirmed.

Genus *Actinostromella* Boehnke, 1915

See Boehnke 1915: p. 162.
Type species: *A. tubulata* Boehnke, 1915 (Boehnke 1915: p. 163, text-figs 6, 7); holotype presumably lost (see below).
Diagnosis. — Micropillars long, connected by microcolliculi that are not aligned; longitudinal spaces autotubes.
Range. — Wenlock to Lochkovian (about 8 species).
Distrubution. — Wenlock – Sweden (Gotland); Upper Silurian – China (Inner Mongolia); Ludlow – Australia (New South Wales), Ukraine (Podolia); Pridoli – Canada (Quebec), Estonia, U.S.A. (New York); Lochkovian – China (Inner Mongolia).
Comment. — Boehnke was killed in the First World War (1914) and did not complete his work. His collections and the holotype were almost certainly lost when Koenigsberg (now Kaliningrad) was destroyed at the end of the Second World War. Selection of a new type species of the genus is now appropriate.

Genus *Pichiostroma* Bogoyavlenskaya, 1972

See Bogoyavlenskaya 1972a: p. 29.
Type species: *P. pichiense* Bogoyavlenskaya, 1972 (Bogoyavlenskaya 1972a: p. 29, pl. 5: 1); UGM 2808/3.
Diagnosis. — Skeleton a microreticulate mass pierced by vertical slits.
Range. — ?Wenlock to Ludlow (2 species).
Distribution. — Wenlock – ?U.S.A. (Kentucky); Ludlow – Russia (Tuva), Ukraine (Podolia).
Comment. — Nestor treats this genus as a synonym of *Araneosustroma* Lessovaja.

Family Densastromatidae Bogoyavlenskaya, 1974

Diagnosis. — Skeleton a microreticulate mass uninterrupted by galleries, coenotubes or autotubes; astrorhizae in many taxa.

Genus *Densastroma* Flügel, 1959

See Flügel 1959: p. 196.

Type species: *Stromatopora astroites* Rosen, 1867 (Rosen 1867: p. 62, pl. 2: 6, 7); lectotype IGTTU Co3181, selected by Nestor 1970: p. 259.

= *Pycnodictyon* Mori, 1970 (Mori 1970: p. 103); type species: *P. densum* Mori, 1970 (Mori 1970: p. 104).

Diagnosis. — Microcolliculi aligned as to give the impression of microlaminae; micropillars short to moderately long; result in an orthoreticular pattern; astrorhizae present in many species (Fig. 5G, H).

Range. — Llandovery to Pridoli (about 12 species).

Distribution. — Llandovery – Sweden (Gotland), U.S.A. (Iowa); Wenlock – Canada (Quebec), Estonia, Sweden (Gotland), Ukraine (Podolia), U.S.A. (Kentucky); Upper Silurian – China (Inner Mongolia); Ludlow – Australia (New South Wales), Canada (Quebec), Estonia, Russia (Siberian Platform, Urals), Sweden (Gotland), Ukraine (Podolia); Pridoli – Canada (Quebec), Estonia, Russia (Urals), Ukraine (Podolia).

Comment. — Flügel (1959) first designated the material illustrated by Rosen (1867) as lectotype, but this was invalid because Rosen originally figured two different specimens and Flügel failed to distinguish between them. In an attempt to validate the species, Nestor (1962) chose as 'holotype' what was then thought to be the only surviving type specimen, Rosen's unfigured syntype (IGTTU Co3010), but this was an incorrect designation. Then, later, other type specimens, including the originally figured Rosen syntypes, were rediscovered, so Nestor (1970) was able to validly establish Rosen's (1867: pl. 2: 6) figured specimen, IGTTU Co3181, as lectotype.

Genus *Acosmostroma* Stock, 1998

See Stock & Burry-Stock 1998: p. 195.

Type species: *A. ataxium* Stock, 1998 in Stock & Burry-Stock 1998: p. 195; USNM 248115.

Diagnosis. — Skeleton an acosmoreticulate mass, micropillars are added in parts of the skeleton of some species, astrorhizae may be present.

Range. — Pridoli (3 species).

Distribution. — U.S.A. (New York, Tennessee, Virginia).

Genus *Araneosustroma* Lessovaja, 1970

See Lessovaja 1970: p. 80.

Type species: *A. fistulosum* Lessovaja, 1970 (Lessovaja 1970: p. 81, pl. 2: 2); GMU 9994-6/149.

= *Petschorostroma* Bogoyavlenskaya, 1983 (Bogoyavlenskaya 1983: p. 84); type species: *P. kozhimense* Bogoyavlenskaya, 1983 (Bogoyavlenskaya 1983: p. 84).

Diagnosis. — Microcolliculi aligned at some levels, not aligned at other levels, parallel micropillars clustered into indistinct subcolumns, giving the impression of closely packed microreticulate pillars; astrorhizae present.

Range. — Wenlock to Lochkovian (about 3 species).

Distribution. — Wenlock – Estonia, Russia (Novaya Zemlya), Sweden (Gotland), Ukraine (Podolia); Ludlow – Estonia, Russia (Novaya Zemlya, Urals), Sweden (Gotland), Ukraine (Podolia); Pridoli – Ukraine (Podolia); Lochkovian – Uzbekistan.

Order Stromatoporellida Stearn, 1980

Diagnosis. — Stromatoporoids with extensive, thick, prominent laminae marked by an axial zone or zones (light or dark, ordinicellular, cellular, or tubulate); and short, generally simple pillars confined to an interlaminar space.

Comment. — Stearn & Pickett (1994) inferred that the stromatoporoids of this order secreted their skeletons within soft tissue as modules composed of upper and lower laminae surrounding a gallery and the pillars traversing it. As the animal grew, these modules were then attached to each other in a variety of ways: fused without trace (compact laminae), fused with a suture showing (tripartite), connected with small bridges defining cellules (ordinicellular), connected by multiple lines of cellules (cellular), and connected only locally (as in *Simplexodictyon*).

Family Stromatoporellidae Lecompte, 1951

= Simplexodictyidae Lessovaja, 1972. = Stictostromatidae Khalfina & Yavorsky, 1973. = Diplostromatidae Stearn, 1980. = Clathrocoilonidae Bogoyavlenskaya, 1984.

Diagnosis. — Genera of the Stromatoporellida with short pillars, not superposed from one interlaminar space to another.

Genus *Stromatoporella* Nicholson, 1886

See Nicholson 1886b: p. 92.

Type species: *Stromatopora. granulata* Nicholson, 1873 (Nicholson 1873: pl. 4: 3, 3a; Nicholson & Murie 1878: pl. 1: 11–13; Nicholson 1886a: pl. 1:4, 5, 14, 15, pl. 4: 6, pl. 7: 5, 6); neotype BM(NH) P6021 (Nicholson No. 329) (ICZN 1215, Melville 1982).

= ?*Cancellatodictyon* Khalfina & Yavorsky, 1971; type species: *Stromatoporella granulata* sensu Yavorsky 1951: p. 14, pl. 6: 1–2. = *Pseudostictostroma* Flerova, 1969 (Flerova 1969: p. 26); type species: *P. mitriformis* Flerova, 1969 (Flerova 1969: p. 26). = *Pseudostromatoporella* Kaźmierczak, 1971 (Kaźmierczak 1971: p. 76); type species: *Stictostroma huronense* Parks, 1936 (Parks 1936: p. 83). = *Stictostromella* Galloway & St. Jean, 1956 in Fritz & Waines 1956: p. 92, withdrawn p. 126.

Diagnosis. — Extensive, thick laminae and short pillars confined to an interlaminar space, not superposed, many formed by upward inflection of laminae into cones (ring pillars), others simple spool-shaped posts; microstructure of laminae ordinicellular but appearing in various states of preservation as transversely porous, tripartite, cellular, tubulate, or fibrous. Pillars cellular to fibrous (Fig. 6A, B).

Range. — Pragian to Givetian, ?Frasnian (56 species).

Distribution. — Pragian – Australia (Victoria); Emsian – Afghanistan, Australia (Queensland), Canada (Arctic islands, Ontario), Russia (Salair); U.S.A. (Michigan); Eifelian – Belgium (Ardennes), Canada (Ontario, Manitoba, Arctic islands), China (Sichuan), Germany (Eifel), Russia (Altai mountains, Salair, Kuznetsk Basin), U.S.A. (Indiana, Missouri, Kentucky); Givetian – England (Devon), Germany (Eifel), Russia (W. Urals, Kuznetsk Basin), U.S.A. (Missouri, Indiana, Kentucky); ?Frasnian – Belgium.

Comment. — *Stromatoporella* is defined on the basis of its ring pillars, persistent laminae, non-superposition of pillars and one or a combination of: transversely fibrous, ordinicellular, cellular, tubulate, tripartite, or transversely porous microstructures. Although many of these structures appear to be derived diagenetically from ordinicellular skeletal material, some variation in the original material secreted seems necessary to account for the wide range of microstructures. Controversy concerning the genus has generally focussed on the correlation, or lack of it, between the ring pillars and the microstructure. Several genera have been separated from *Stromatoporella* because they had the microstructure, ordinicellular, cellular, or tubulate, but no ring pillars (in part *Stictostroma*) or had the ring pillars but compact microstructure (*Pseudostictostroma, Pseudostromatoporella*). Summaries of these controversies and attempts to resolve the different concepts of the genera can be found in the work of St. Jean (1962, 1977), Stearn (1966), Kaźmierczak (1971), and Mistiaen (1985).

Genus *Clathrocoilona* Yavorsky, 1931

See Yavorsky 1931: p. 1394.

Type species: *C. abeona* Yavorsky, 1931 (Yavorsky 1931: pl. 2: 2, 2a); CNIGR 3338/8a, b (Kosareva 1976).

Diagnosis. — Laminae extensive, thick (of thickness comparable to the gallery height), of tripartite, ordinicellular, microreticulate, or tubulate microstructure. Pillars postlike, commonly spool-shaped, confined to an interlaminar space, not superposed, compact or obscurely cellular. Commonly irregular, encrusting in growth with algal interlayers.

Range. — ?Emsian, Eifelian to Frasnian (39 species).

Distribution. — ?Emsian – Austria (Carnic Alps), Canada (Arctic islands), Russia (NE. Siberia, Salair); Eifelian – Belgium (Ardennes), Canada (Arctic islands, Manitoba), Central Asia (Altai), Germany (Eifel), Russia (NE. Siberia, Salair); Givetian – Belgium (Ardennes), Canada (N. Alberta, Manitoba), Czech Republic (Moravia), U.S.A. (Indiana, Michigan); Middle Devonian – China

(Guangxi, Sichuan), Czech Republic (Moravia), Germany (Eifel), Russia (Kuznetsk Basin, NE. Siberia, Salair); Frasnian – Australia (Canning Basin). Belgium (Ardennes), Canada (Alberta, Manitoba), Czech Republic (Moravia), France (Boulonnais), Russia (Russian Platform, Kuznetsk Basin), U.S.A. (Iowa).

Comment. — The laminae of most species of *Clathrocoilona* are tripartite or stranded, showing central less opaque zones. In tangential section the thick skeletal material commonly appears to be tubulate (Kosareva 1976, 'felted'). Some specimens preserve ordinicellular microstructure, and locally several ranges of cellules in the thick skeletal material may give the appearance of microreticulation (Kosareva 1976). See also *Synthetostroma* (Trupetostromatidae).

Genus *Dendrostroma* Lecompte, 1952

See Lecompte 1952: pp. 320–321.

Type species: *Idiostroma oculatum* Nicholson, 1886 (Nicholson 1886b: p. 101, figs 14–15); BM(NH) P6073 (Nicholson No. 403).

Diagnosis. — Dendroid skeleton with axial tube; laminae distinct, thick, extensive, compact to fibrous commonly, obscurely tripartite with axial light or dark zone; pillars postlike, confined to interlaminar spaces, not superposed, compact to fibrous.

Range. — ?Pragian, Givetian, Frasnian, ?U. Famennian (about 15 species).

Distribution. — ?Pragian – Australia (Victoria); Givetian – Canada (Manitoba), Czech Republic, Germany (Eifel), Russia (NE. Siberia), U.S.A. (Michigan); Middle Devonian – Germany (Eifel), India (Himalaya), Russia (Urals), Vietnam; Frasnian – Australia (Canning Basin, Carnarvon Basin), Russia (Kuznetsk Basin), Czech Republic; ?U. Famennian – Kazakhstan.

Genus *Simplexodictyon* Bogoyavlenskaya, 1965

See Bogoyavlenskaya 1965b: p. 110.

Type species: *Clathrodictyon regulare* var. nov., Yavorsky, 1929 (Yavorsky 1929: p. 83, 103, pl. 4: 5, 6). = *C. regulare podolicum* Yavorsky, 1955. = *Simplexodictyon podolica* (Yavorsky, 1955) (Bogoyavlenskaya 1965b); CNIGR 2595/30(6).

= *Diplostroma* Nestor, 1966 (Nestor 1966: pp. 27–28); type species: *Clathrodictyon pseudobilaminatum* Khalfina, 1961 (Khalfina 1961: p, 47). = *Nuratadictyon* Lessovaja, 1972 (Lessovaja 1972: p. 48); type species: *N. duplexolaminum* Lessovaja, 1972 (Lessovaja 1972: p. 48).

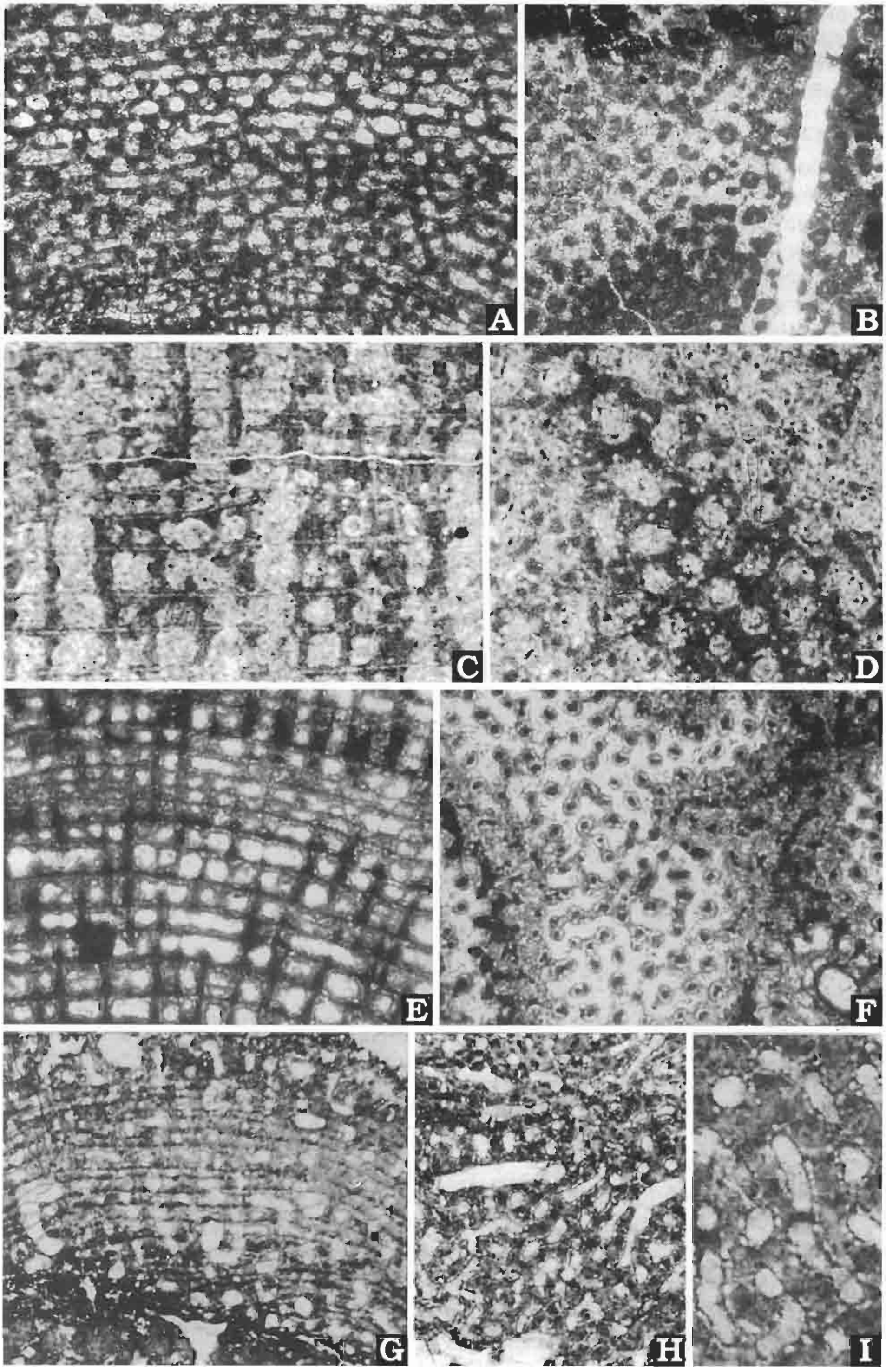
Diagnosis. — Laminae extensive, composed of two compact layers separated by: (1) spar cement, (2) sediment, (3) epibionts, or (4) a line of cellules, or fused into a single layer (may be all in same specimen). Pillars compact, simple, postlike, commonly incomplete or oblique.

Range. — Wenlock–Ludlow, Emsian–Eifelian (7 species).

Distribution. — Wenlock – Estonia (Saaremaa), Russia (Moiero Range, Siberian Platform), U.S.A. (Kentucky); Ludlow – Australia (Queensland), Central Asia (Tien Shan), Estonia, Russia (Salair, Altai), Ukraine (Podolia); Emsian – Australia (Victoria, N. Queensland); Eifelian – Canada (Arctic islands, Yukon).

Comment. — Although some authors have attributed the varietal name *podolicum* to Yavorsky (1929) it was not proposed until 1955 (Yavorsky 1955: p. 43).

Fig. 6. **A**, **B**. Stromatoporellidae: *Stromatoporella granulata* Nicholson, 1886, longitudinal and tangential sections of holotype BM(NH) P6021 (329a and 329), × 10. Note the expression of the ring pillars in both sections. **C**, **D**. Trupetostromatidae: *Trupetostroma warreni* Parks, 1936, longitudinal and tangential sections of the holotype ROM 2608D (section 1885a), × 10. Note the central clear layer of the tripartite laminae and the superposed pillars of vacuolate microstructure. **E**, **F**. Trupetostromatidae: *Hermatostroma schlueteri* Nicholson, 1886, longitudinal and tangential sections of holotype BM(NH) P5527 (386a, 386f), × 10. Note the opaque central layers of the tripartite laminae and the peripheral membranes. **G–I**. Trupetostromatidae: *Hermatoporella maillieuxi* (Lecompte, 1952), holotype IRScNB a 5760; **G**, **H** – longitudinal and tangential section, × 10; **I** – tangential section, × 25. Note the peripheral vacuoles on some of the coenosteles.


A
B
C
D
E
F
G
H
I

In *Simplexodictyon* the fusion of the upper and lower bounding layers of the modules into a lamina is variable. Locally they may seem to make a single layer, as in *Clathrodictyon*, locally they are incompletely fused, as in *Stictostroma*; and locally they are completely separate and sediment and epibionts may occupy the gap.

Genus *Stictostroma* Parks, 1936

See Parks 1936: p. 78.

Type species: *S. gorriense* Stearn, 1995 (Stearn 1995a); ICZN Opinion 1843 (1996) Case 2109; see also Stearn (1995b: figs 1.6, 1.7, 2.5, 2.6) and Fagerstrom (1977, 1982); ROM 9360.

Diagnosis. — Laminae thick, extensive, ordinicellular in microstructure but commonly appearing transversely porous, tripartite, fibrous, rarely tubulate; pillars confined to an interlaminar space, not systematically superposed, post-like, only rarely ring pillars, cellular where best preserved, commonly fibrous.

Range. — Emsian to Frasnian (about 40 species).

Distribution. — Emsian – Australia (Victoria), Canada (Arctic islands, Ontario, Yukon); Eifelian – Belgium (Ardennes), Canada (Northwest Territories, Manitoba, Ontario), Russia (NE. Siberia, Kuznetsk Basin, Salair), U.S.A. (Michigan, Ohio); Givetian – Afghanistan, Belgium (Ardennes), Canada (Ontario), Germany (Sauerland), Russia (Kuznetsk Basin, NE. Siberia, Urals), U.S.A. (Missouri); Middle Devonian – Canada (British Columbia, N. Ontario), China (Guangxi), Russia (Kuznetsk Basin, NE. Siberia, Urals), U.S.A. (Missouri); Frasnian – Australia (Canning Basin), Belgium (Ardennes), Canada (Alberta, Northwest Territories), Russia (Kuznetsk Basin), U.S.A. (Iowa).

Comment. — *Stictostroma* has many of the characteristics of *Petridiostroma*, persistent laminae and postlike pillars that are not superposed, but the latter has laminae of compact microstructure. *Clathrocoilona* has laminae thicker than gallery height and more complex microstructure.

Genus *Styloporella* Khalfina, 1956

See Khalfina 1956: p. 61 (proposed as subgenus of *Stromatoporella*, elevated to full generic rank by Khalfina 1961: p. 338).

Type species: *Stromatoporella (Styloporella) grata* Khalfina, 1956 (Khalfina 1956: p. 61, pl. 1: 6; pl. 2: 1, 2); SOAN 402/67b.

Diagnosis. — Like *Stromatoporella* but with structural elements thickened into astrorhizal columns with prominent axial canal where laminae inflect upward.

Range. — Frasnian (3 species).

Distribution. — Russia (Kuznetsk Basin, E. Siberia).

Genus *Syringodictyon* St. Jean, 1986

See St. Jean 1986: p. 1050.

Type species: *Stromatopora tuberculata* Nicholson, 1873 (Nicholson 1873: pp. 92–93, pl. 4: 2); BMM(NH) P5627 (Nicholson No. 332).

Diagnosis. — Laminae extensive, thick, inflected upward in invaginating cones into vertically extensive columns with narrow lumens. Pillars formed by superposition of upward inflections of laminae, other pillars scarce.

Range. — Lower Eifelian (1 species).

Distribution. — Canada (Ontario).

Comment. — The difference between *Syringodictyon* St. Jean, 1986 and *Tubuliporella* Khalfina, 1968 (see Khalfina 1968a) is in the size and nature of the vertical tubes formed by the upwardly inflected laminae – small and formed of invaginating cones in the former, and large and continuous in the latter – and in the absence of ring pillars between the columns of the former.

Genus *Tubuliporella* Khalfina, 1968

See Khalfina 1968a: p. 150.

Type species: *T. lecomptei* Khalfina, 1968 (Khalfina 1968a: pl. 1: 5; pl. 2: 2; spelled *lecompti* and *lecomti* in original publication); CSGM 409/3a-b.

Diagnosis. — Like *Stromatoporella* but some ring pillars superposed forming vertical open channels crossed by thin dissepiments.

Range. — Lower Devonian to Eifelian (7 species).

Distribution. — Lower Devonian – Russia (Altai); Pragian – Australia (Victoria); Eifelian – Russia (Kuznetsk Basin, Altai, Salair).

Family Trupetostromatidae Germovsek, 1954

nom. correct. Stearn herein, *pro* Trupetostromidae Germovsek, 1954.

= Synthetostromatidae Khromych, 1969. = Hermatostromatidae Nestor, 1964. = Imponodictyidae Khalfina & Yavorsky, 1971.

Diagnosis. — Stromatoporellida with superposed postlike pillars and tripartite or ordinicellular laminae forming a grid in longitudinal section.

Comment. — Genera placed on the basis of macrostructure in the Trupetostromatidae do not have diagnostic microstructures. Many of the genera include some species that have compact-vacuolate microstructure and some that are cellular. This problem might be resolved by recognizing separate genera for each microstructural variant, but this would result in several more genera being recognized and problems in placing species whose microstructure, for any of several reasons, was obscure.

Genus *Trupetostroma* Parks, 1936

See Parks 1936: p. 55.

Type species: *T. warreni* Parks, 1936 (Parks 1936: p. 55, pl. 10: 1, 2); ROM 12197 (specimen DU677 at the University of Alberta referred to by Parks as the type is lost.

= *Flexiostroma* Khalfina, 1961 (Khalfina 1961: p. 345); type species: *Flexiostroma flexuosum* Khalfina, 1961 (Khalfina 1961: p. 346, see also Stock 1982: p. 666). = ?*Imponodictyon* Khalfina & Yavorsky, 1971 (Khalfina & Yavorsky 1971: p. 119); type species: *Stromatoporella loutouguini* var. *postera* Khalfina, 1956 (Khalfina 1956: p. 60).

Diagnosis. — Laminae extensive, thick, typically ordinicellular but commonly showing a central clear zone or opaque axis, pierced by large foramina joining galleries above and below. Pillars short, expanded above and below at laminae, systematically superposed across successive laminae forming a grid with the laminae; microstructure vacuolate, cellular, compact (Fig. 6C, D).

Range. — ?Emsian, Eifelian to Frasnian, ?Famennian (about 50 species).

Distribution. — ?Emsian – Canada (Arctic islands); Eifelian – Canada (Manitoba), China (Guangxi), Morocco, Russia (NE. Siberia), U.S.A. (Indiana); Givetian – Belgium (Ardennes), Canada (Alberta, British Columbia, Manitoba, Northwest Territories), Germany (Rhineland), Russia (Urals, Salair, Kuznetsk Basin), Vietnam; Middle Devonian – ?Australia (Queensland), China (Guangxi, Guizhou, Yunnan), Poland (Holy Cross Mountains), Russia (Salair, S. Urals, Kuznetsk Basin), U.S.A. (Missouri); Frasnian – Australia (Canning Basin), Belgium (Ardennes), Canada (Alberta, Northwest Territories, Saskatchewan), Czech Republic (Moravia), Russia (Russian Platform, W. Pechora Basin, S. Urals), U.S.A. (Iowa), Vietnam; ?Famennian – China (Guangxi), Kazakhstan.

Comment. — *Flexiostroma* Khalfina has no unique characters or combination of characters that would separate it from *Trupetostroma*. The typical species is a *Trupetostroma* with mamelon columns, a feature common in other species assigned to this genus and one not generally regarded as diagnostic at the generic level. Stock (1982) has discussed the synonymy.

Genus *Hermatostroma* Nicholson, 1886

See Nicholson 1886b: p. 105.

Type species: *H. schlueteri* Nicholson, 1886 (Nicholson 1886b: p. 215, pl. 3: 1, 2; pl. 28: 12. 13; text-figs 1, 16, 29, 30, 31, 32); BM(NH) P5527 (Nicholson No. 386).

= *Argostroma* Yang & Dong, 1979 (Yang & Dong 1979: p. 45; type species *A. typicum* Yang & Dong, 1979 (Yang & Dong 1979: p. 45, see Mistiaen 1985: pp. 189–190).

Diagnosis. — Laminae extensive, prominent, tripartite with central dark or light zone and more opaque lateral zones, penetrated by large foramina between pillars, pillars spool-shaped, confined to interlaminar spaces, regularly superposed in longitudinal section, subcircular in tangential section, surrounded by peripheral cyst plates or bordered by peripheral vacuoles. Microstructure compact, vacuolate, cellular (Fig. 6E, F).

Range. — Eifelian to Frasnian (about 20 species).

Distribution. — Eifelian – Australia (Queensland), Russia (Kuznetsk Basin); Givetian – Australia (Canning Basin), Belgium (Ardennes), China (Guizhou, Yunnan), France (Boulonnais, Ancenis), Poland (Holy Cross Mountains), Thailand; Middle Devonian – England (Devon), Germany (Eifel), China (Guangxi, Sichuan, Yunnan), U.S.A. (Missouri); Frasnian – Australia (Canning Basin), Belgium (Ardennes), Canada (Alberta, Manitoba, Saskatchewan), China (Sichuan, Yunnan), Czech Republic (Moravia), Germany, Poland (Holy Cross Mountains), Russia (NE. Siberia), U.S.A. (Iowa).

Comment. — *Argostroma* Yang & Dong, 1979 (Yang & Dong 1979, see also Dong & Wang 1982: pl. 6: 7) has pillars and laminae forming a grid both with opaque, compact borders and translucent median axial zones that are confluent at the pillar-lamina junctions. Mistiaen (1985: pp. 189–190) has argued convincingly that the type species of the genus is based on a diagenetic phase of a species of *Hermatostroma*. *Trupetostroma* grades into *Hermatostroma* through forms with lines of vacuoles along the pillar edges.

Genus *Hermatoporella* Khromych, 1969

See Khromych 1969: p. 34.

Type species: *Trupetostroma maillieuxi* Lecompte, 1952 (Lecompte 1952: pp. 237–239, pl. 43: 2, 3); IRScNB a 5760.

Diagnosis. — Irregular grid formed by coenosteles and microlaminae; microlaminae intersecting coenosteles, locally replaced by aligned dissepiments; coenosteles superposed systematically, with peripheral vacuoles in parts of type, in tangential section, forming a labyrinthine network, rarely cut as isolated subcircular masses; microstructure compact, vacuolate, or cellular (Fig. 6G–I).

Range. — ?Eifelian, Givetian to Frasnian (about 20 species).

Distribution. — ?Eifelian – Morocco; Givetian – Belgium (Ardennes), Canada (Northwest Territories), China (Guangxi, Yunnan), Russia (NE. Siberia, S. Urals); Givetian–Frasnian – Belgium, Vietnam; Middle Devonian (undifferentiated) – China (Guizhou), Russia (Salair); Frasnian – Australia (Canning Basin), China (Yunnan), Canada (Alberta, Northwest Territories, Rocky Mountains, Saskatchewan), Czech Republic (Moravia), Russia (S. Urals), U.S.A. (Iowa).

Genus *Hermatostromella* Khalfina, 1961

See Khalfina 1961: p. 52.

Type species: *Hermatostromella parasitica* Khalfina, 1961 (Khalfina 1961: p. 52, pl. S-5: 1; pl. S-6: 1); CSGM 401/33.

= *Amnestostroma* Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969b: p. 99); type species: *Syringostroma federovi* Yavorsky, 1929 (Yavorsky 1929: p. 109). = *Gerronostromina* Khalfina & Yavorsky, 1971 (Khalfina & Yavorsky 1971: p. 119); type species: *Gerronostroma kitatense* Yavorsky, 1961 (Yavorsky 1961: p. 12).

Diagnosis. — Laminae and pillars subequal in thickness forming a grid; laminae extensive, locally with axial dark or light zone, or ordinicellular; pillars postlike, locally appearing continuous, locally superposed and interrupted by a lighter central zone in laminae, mostly discrete and subcircular in tangential section; microstructure compact, vacuolate, rarely cellular.

Range. — Pridoli to Emsian (12 species).

Distribution. — Pridoli – Russia (E. Siberia, Urals); Lochkovian – Canada (Arctic islands), Central Asia (Tien Shan), Russia (Salair, Urals); Pragian – Australia (Victoria); Emsian – Australia (New

South Wales); Lower Devonian – Russia (E. Siberia, Altai Sayan), Central Asia (Tien Shan); ?Givetian – Australia (Queensland).

Comment. — The most extensive discussion of the genus is that of Khromych (1974) who emphasizes as diagnostic characters the equal thickness of pillars and laminae, the light or dark central line in the laminae, the superposed pillars and cellular microstructure.

Amnestostroma Bogoyavlenskaya was established for species with extensive or interrupted laminae, vertical elements that are long, and coenosteles breaking up into isolated pillars. The type species holotype shows the following features diagnostic at the generic level: (1) extensive laminae and pillars forming a grid; (2) tripartite to ordinicellular laminae, evident in photographs of the type, despite the assertion of Khalfina & Yavorsky (1971) that they are single layers; (3) discrete postlike pillars systematically superposed; (4) vaguely flocculent to cellular microstructure; (5) pillars that may be joined to adjacent pillars in tangential section; (6) laminae with irregular foramina, like those of *Trupetostroma*.

In some ways *Amnestostroma* is intermediate between *Hermatostromella* and *Trupetostroma* and this is how it has been used by Stearn (1983), Webby & Zhen (1993), and Webby *et al.* (1993). Stearn (1990) says distinctive features are sporadic development of tripartite laminae and lack of distinctly vacuolate microstructure in the pillars. However, because the features of the type listed above are basically those of *Hermatostromella*, it is therefore placed as a junior synonym of that genus.

The diagnosis of *Gerronostrómina* does not clarify how the genus can be separated from such related genera as *Amnestostroma* and *Hermatostromella*.

Genus *Synthetostroma* Lecompte, 1951

See Lecompte 1951: p. 193.

Type species: *S. actinostromoides* Lecompte, 1951 (Lecompte 1951: p. 194, pl. 20: 3, 4); IRScNB a 7296Gi.

Diagnosis. — Laminae extensive, continuous, composed of multiple microlaminae or imbricating dissepiments giving a tangled appearance, commonly with a central lighter zone or zones. Pillars postlike, confined to interlaminar spaces but systematically superposed. Microstructure compact.

Range. — Givetian to Frasnian (2 species).

Distribution – Givetian – Belgium, Frasnian – Czech Republic

Comment. — Many paleontologists have placed this genus in synonymy with *Clathrocoilona* (Nestor 1966; Kaźmierczak 1971; Kosareva 1976), however, the holotype clearly has well-superposed pillars interrupted by laminae of stranded appearance, locally tripartite, and many dissepiments. The type species of *Clathrocoilona* has very little superposition. Many species assigned to *Synthetostroma* should be removed to other genera.

Family Idiostromatidae Nicholson, 1886

See Nicholson 1886b.

nom. correct. Galloway, 1957, *pro* Idiostromidae Nicholson, 1886, see Nicholson 1886b.

Diagnosis. — As for genus.

Comment. — The family name Idiostromatidae Nicholson, 1886, see Nicholson 1886b (as Idiostromidae) originally included genera (*Idiostroma, Amphipora, Stachyodes, Hermatostroma*) that are here considered to belong to 3 different orders. The family name came to be used for any dendroid genus although the original description noted that growth form was not a diagnostic feature.

Genus *Idiostroma* Winchell, 1867

See Winchell 1867: p. 99.

Type species: *Stromatopora caespitosa* Winchell, 1866 (Winchell 1866: p. 91); lectotype (Galloway & Ehlers 1960: p. 63, pl. 4: 1a–e) UMMP 32401A (slides W2-17, 18).

Diagnosis. — Growth form dendroid with axial tabulated canal and in some species subsidiary canals. Axial zone of amalgamate structure in cross-section, passing outward into peripheral zone of well-defined continuous or superposed coenosteles, intervening coenotubes crossed by dissepiments, and concentric laminae. Laminae variably expressed by alignment of opaque dissepiments to form microlaminae, by well defined opaque microlaminae passing through coenosteles, and/or by tripartite laminae with central light zone. Laminae form parabolas parallel to successive growth surfaces in longitudinal section. Microstructure coarsely and irregularly vacuolate (Fig. 8A).

Range. — Eifelian to Frasnian, ?Famennian (about 12 species).

Distribution. — Eifelian – Germany (Sauerland); Givetian – Belgium (Ardennes), China (Guizhou, Hunan, S. Tien Shan, Guangxi), Spain (Cantabria), U.S.A. (Michigan, Iowa); Middle Devonian – China (Sichuan, Xizang), Germany (Eifel), Russia (Urals), Uzbekistan; Frasnian – Australia (Canning Basin, Carnarvon Basin), Belgium (Ardennes), Canada (Alberta), China (Sichuan), Czech Republic (Moravia); Upper Devonian – Uzbekistan; ?Famennian. — Russia (Pechora basin).

Comment. — The lectotype and paralectotypes of *I. caespitosum* show a wide range of expression of the laminae from obscure to well-defined tripartite. Striated microstructure is suggested in parts of the holotype which are poorly preserved. Vacuolate tissue, tripartite laminae, and the tendency for the domination of concentric laminae over coenosteles are distinguishing features of the holotype of *Idiostroma*. The tripartite laminae and resemblance of several species of the genus to *Trupetostroma* in their vacuolate tissue place this genus in the Stromatoporellida. As a model of the internal features of *Idiostroma*, Nicholson (1886b) arbitrarily used *I. roemeri* Nicholson, 1886 from Germany because the internal structures of the type species, *I. caespitosum*, had not been adequately described by Winchell. The type species was not critically examined until 1960 by Galloway and Ehlers. Paleontologists generally followed this definition of *Idiostroma* as having well-defined coenosteles, spooled in longitudinal section, superposed and crossed by tripartite laminae consisting of a central microlamina and less opaque outer layers. *Idiostroma* differs from *Stachyodes* in the prominence and continuity of laminae, their tripartite nature, and the vacuolate microstructure of the coenosteles.

Order Stromatoporida Stearn, 1980

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

Family Stromatoporidae Winchell, 1867

= Angulatostromatidae Khalfina, 1968, see Khalfina 1968a.

Diagnosis. — Genera of the Stromatoporida dominated by coenostromes, laminae and/or cassiculate structures.

Genus *Stromatopora* Goldfuss, 1826

See Goldfuss 1826: p. 21.

Type species: *S. concentrica* Goldfuss, 1826 (Goldfuss 1826: p. 22, pl. 8: 5a–c); IPB 80.

= *Angulatostroma* Khalfina, 1968 (Khalfina 1968a: p. 152); type species: *Stromatopora angulata* Yavorsky, 1947 (Yavorsky 1947: p. 10).

Diagnosis. — Skeleton of cellular, cassiculate, oblique coenostromes and scattered dissepiments; in some successive phases including short coenosteles; structural elements in tangential section cut as labyrinthine network or discrete vermiform elements (Fig. 7A).

Range. — ?Telychian, Middle Silurian to Famennian (about 35 species).

Distribution. — ?Telychian – Canada (Arctic islands); Middle Silurian – Central Asia (Turan lowland), Russia (Novaya Zemlya), Ukraine (Podolia); Ludlow–Pridoli – Czech Republic, Estonia, Russia (Vajgach Island, Siberian platform), U.S.A. (New York); Lower Devonian – Australia (Victoria, New South Wales), Canada (Arctic islands); Middle Devonian – Belgium, China (Sichuan, Guangxi), Russia (Salair, Pechora Basin); Eifelian – Morocco, Russia (Kuznetsk Basin); Givetian – Canada (Northwest Territories), U.S.A. (Missouri); Frasnian – Belgium, Canada (Alberta), Poland, NW. Russia (Timan); Famennian – Belgium, Canada (Alberta), Russia (Novaya Zemlya).

Comment. — Problems concerning the definition and type species of *Stromatopora* were fully explored by Stearn (1993).

Genus *Climacostroma* Yang & Dong, 1979

See Yang & Dong 1979: p. 72.

Type species: *C. guangxiense* Yang & Dong, 1979 (Yang & Dong 1979: p. 72, pl. 39: 7, 8); NIGP 33129, 33130.

= in part *Lineastroma* Khalfina & Yavorsky of Stearn (1993).

Diagnosis. — Structure dominated by thick, discontinuous coenostromes associated with microlaminae. Coenosteles short, confined to intercoenostrome space, not superposed, forming a closed network in tangential section. Microstructure cellular.

Range. — Middle Devonian (about 10 species).

Distribution. — Middle Devonian – China (Guangxi, Sichuan), Russia (S. Urals); Eifelian – Russia (Kuznetsk Basin); Givetian – Australia (Canning Basin), Belgium (Ardennes), Canada (Northwest Territories), Poland (Holy Cross Mountains).

Genus *Glyptostromoides* Stearn, 1983

See Stearn 1983b: p. 553.

Type species: *Glyptostroma simplex* Yang & Dong, 1979 (Yang & Dong 1979: p. 66, pl. 35: 5, 6); NIGP 33083, 33084.

= *Glyptostroma* Yang & Dong, 1979 (Yang & Dong 1979: p. 65); type species: *Stromatopora beuthii* Yavorsky, 1955 (Yavorsky 1955: p. 106); not *S. beuthii* Bargatzky, 1881 (Bargatzky 1881a).

Diagnosis. — Structure cassiculate in longitudinal section, formed by network of oblique structural elements penetrated by thick, cellular, long coenosteles joined into a labyrinthine network in tangential section (Fig. 7G, H).

Range. — Emsian to Givetian (6 species).

Distribution. — Emsian – Canada (Arctic islands); Emsian/Eifelian – Spain (Cantabria); Middle Devonian – China (Guangxi), Russia (Kuznetsk Basin, Salair); Givetian – Canada (British Columbia), China (Guangxi), Russia (Kuznetsk Basin).

Genus *Lineastroma* Khalfina & Yavorsky, 1973

See Khalfina & Yavorsky 1973: p. 31.

Type species: *Stromatopora vorkutensis* Yavorsky, 1961 (Yavorsky 1961: p. 39, pl. 23: 1–3); CNIGR, 7354/420. = *Stromatopora sibirica* Riabinin, 1928 (Riabinin 1928: p. 1046). = *S. elegestica* Riabinin, 1937 (Riabinin 1937: p. 16, see Nestor 1976: p. 78).

Diagnosis. — Prominent, extensive but interrupted coenostromes and short, mostly vertical but locally oblique, coenosteles largely confined to an intercoenostrome interval, only locally superposed or more continuous longitudinally; in tangential section isolated dots or irregular vermicular masses, rarely joined. Microstructure finely and inconspicuously cellular.

Range. — Middle Silurian (3 species).

Distribution. — Russia (Siberian Platform, Pre Urals, Tuva), Ukraine (Podolia).

Comment. — Stearn (1993) had difficulty accounting for the peculiar range of *Lineastroma* as he included forms with both postlike pillars and coenosteles in the genus. This resulted in the range of the genus being split between the type species (*L. vorkutense*) in Middle Silurian rocks and the other species in Middle Devonian rocks. If the species that have coenosteles forming a closed network in tangential section are transferred to *Climacostroma*, the stratigraphic distribution makes better sense. Fagerstrom (1982) has compared *Climacostroma* to *Habrostroma*. The latter has a microstructure of 'lacy' structural elements and microlaminae that place it closer to *Syringostroma* and in the family Coenostromatidae.

Genus *Neosyringostroma* Kaźmierczak, 1971

See Kaźmierczak 1971: p. 117.

Type species: *Hermatostroma logansportense* Galloway & St. Jean, 1957 (Galloway & St. Jean 1957: p. 219, pl. 21: 2); UNC 278-18, 19; 279-23, Cat. 5339.

Diagnosis. — Long pillars of cellular/melanospheric microstructure pass through an amalgamate structure of impersistent coenostromes and cassiculate structural elements, commonly chevron-shaped in longitudinal section. In tangential section the pillars are circular structures within amalgamate structural elements.

Range. — ?Emsian, Middle Devonian (about 5 species).

Distribution. — ?Emsian – Afghanistan; Emsian/Eifelian – Spain (Cantabria); Eifelian – Belgium (Ardennes), Russia (Kuznetsk Basin); Middle Devonian – China (Guangxi. Guizhou); Givetian – Afghanistan, Canada (British Columbia, Manitoba), Poland, U.S.A. (Indiana).

Genus *Pseudotrupetostroma* Khalfina & Yavorsky, 1971

See Khalfina & Yavorsky 1971: p. 120.

Type species: *Stromatopora pellucida artyschensis* Yavorsky, 1955 (Yavorsky 1955: p. 100, pl. 52: 1, 2); CNIGR 7351/132; elevated to species rank by Khalfina & Yavorsky 1971.

Diagnosis. — Coenosteles/pillars confined to interlaminar space, commonly well superposed, very coarsely cellular. Tangential elements fine microlaminae coated with coarsely cellular tissue like that of the pillars. In tangential section longitudinal elements cut as a closed network or as vermiform isolated masses.

Range. — ?Pragian, Emsian to Givetian (12 species).

Distribution. — ?Pragian – Australia (Victoria); Emsian – Australia (New South Wales, Victoria); Eifelian – Canada (Arctic islands), Russia (SW. Kuznetsk Basin, E. Urals); Givetian – Canada (British Columbia, Northwest Territories), China (Gueizhou), Russia (SW. Kuznetsk Basin, Salair).

Comment. — *Pseudotrupetostroma* has recently been recognized in many places in the world on the basis of its very coarse cellular microstructure and superposed pillars. The voids in the structural elements are large enough to be classified as vacuoles and in this resemble the vacuoles in the pillars of *Trupetostroma*. A case might be made for including the genus in the Stromatoporellida. However, the microlaminae, cellular tissue, and coenosteles favor placement of the genus in the Stromatoporida.

Genus *Taleastroma* Galloway, 1957

See Galloway 1957: p. 448.

Type species: *Stromatopora cumingsi* Galloway & St. Jean, 1957 (Galloway & St. Jean 1957: p. 182, pl. 15: 4); UNC 304-47.

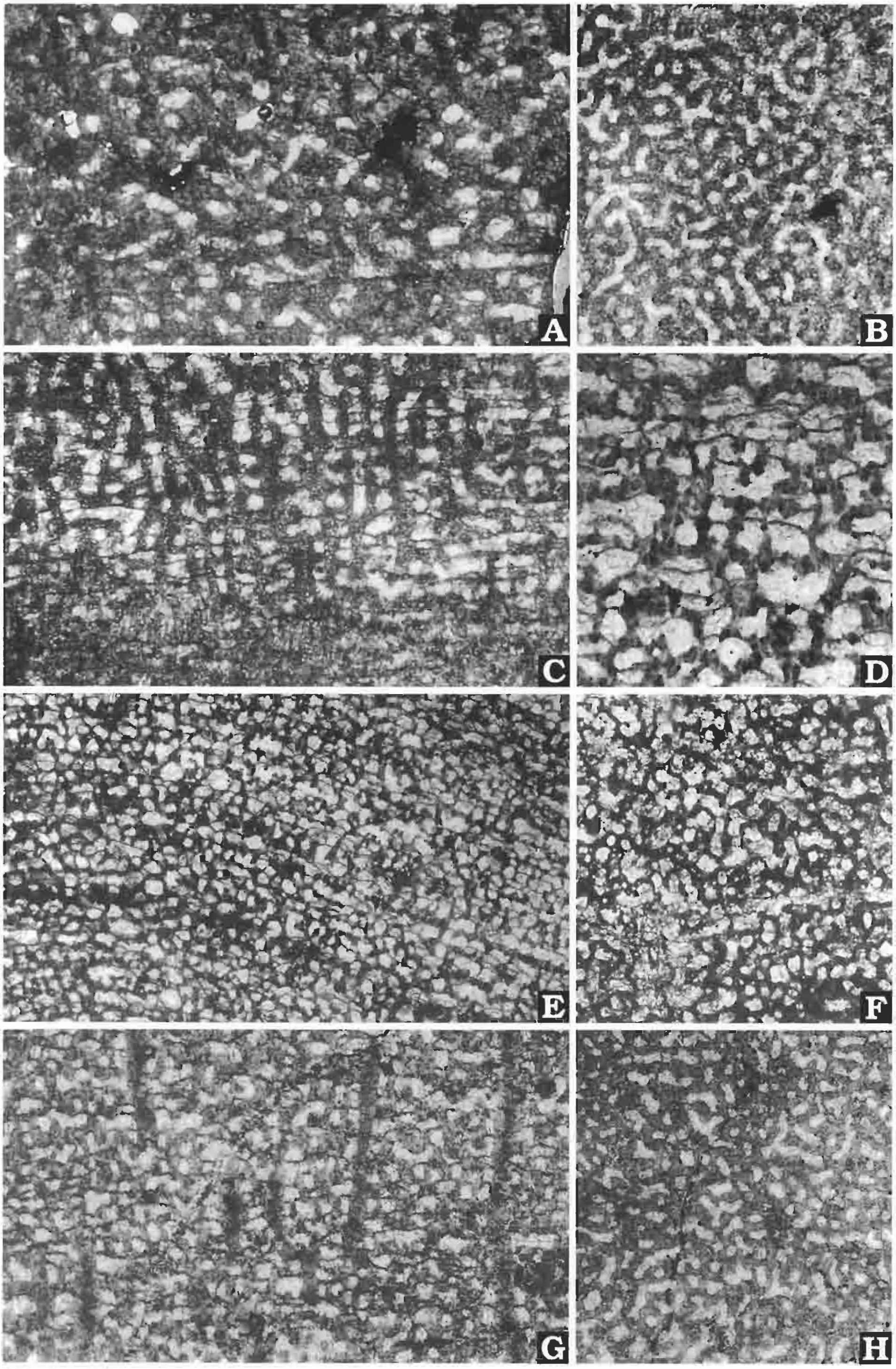
Diagnosis. — Structure amalgamate with small round galleries, dominated by thick coenostromes commonly showing microlaminae and traces of microreticulation, pillars penetrate structure, of melanospheric microstructure, commonly with clear axes, probably originally cellular. Round ends of pillars cut tangentially within the amalgamate, melanospheric structural elements.

Range. — Middle Devonian (about 4 species).

Distribution. — Belgium (Ardennes), U.S.A. (Indiana).

Comment. — Stearn (1993) placed *Neosyringostroma* in synonymy with *Taleastroma* on the basis that the type species of the former is *Taleastroma logansportense*. However, the type of *Taleastroma* (*T. cumingsi*) has well-developed coenostromes. *Taleastroma* is close to *Coenostroma* but has postlike pillars that are somewhat clear in their axes but not to the extent illustrated in the retouched photographs of Galloway & St. Jean (1957). In *Neosyringostroma* the cellular pillars pass through →

Fig. 7. **A.** Stromatoporidae: *Stromatopora concentrica* Goldfuss, 1926, longitudinal section of holotype cut for Lecompte, IPB 80, × 10. Note oblique structural elements and cellular microstructure. **B, C.** Syringostromellidae: *Syringostromella borealis* (Nicholson, 1891), tangential and longitudinal sections of the holotype BM(NH) P5894, × 10. **D–F.** Ferestromatoporidae: *Arctostroma contexta* (Stearn, 1963), holotype GSC 16,856. **D.** longitudinal section, × 25 to show the melanospheric microstructure; **E, F.** longitudinal and tangential sections, × 10. **G, H.** *Glyptostromoides simplex* (Yang & Dong, 1979), longitudinal and tangential sections of a hypotype GSC 108,894, × 10. Note the cellular pillars traversing a cassiculate network in longitudinal section.


A
B
C
D
E
F
G
H

a dominantly cassiculate structure with no peristent coenostromes. The lighter axes of the pillars in *Taleastroma* may prove to be merely a diagenetic effect.

Family Ferestromatoporidae Khromych, 1969

Diagnosis. — Stromatoporids of melanospheric to obscurely cellular microstructure composed of oblique structural elements forming a closely spaced cassiculate network.

Comment. — The microstructure commonly appears to be finely melanospheric or compact and vacuolate. The uncertainty about the microstructure is reflected in the original description of Yavorsky (1955) and in the discussion in Flügel & Flügel-Kahler (1968: p. 544). *Ferestromatopora* has been compared with *Plexodictyon* by Nestor (in Stearn 1993) because both have paralaminae running through a cassiculate structure.

Genus *Ferestromatopora* Yavorsky, 1955

See Yavorsky 1955: p. 109.

Type species: *F. krupennikovi* Yavorsky, 1955 (Yavorsky 1955: p. 109, pl. 58: 1–5); CNIGR 7351/165.

Diagnosis. — Structural elements largely oblique forming cassiculate network traversed by thin, continuous paralaminae, forming a labyrinthine network in tangential section. Coenosteles absent. Microstructure obscurely cellular, commonly melanospheric.

Range. — ?Emsian, Givetian–Frasnian (5 species).

Distribution. — Emsian – ?Canada (Arctic islands); Middle Devonian – China (Guangxi, Sichuan); Givetian – Germany (Rhineland), Poland (Holy Cross Mountains), Russia (Kuznetsk Basin, Salair), U.S.A. (Missouri); Frasnian – Canada (Alberta), Germany (Rhineland), Poland (Holy Cross Mountains), Russia (E. Siberia).

Genus *Arctostroma* Yavorsky, 1967

See Yavorsky 1967a: p. 30.

Type species: *Arctostroma ignotum* Yavorsky, 1967 (Yavorsky 1967a: p. 30, pl. 12: 4, 5, 6); CNIGR number unknown. = *Ferestromatopora contexta* Stearn, 1963 (Stearn 1963: p. 666, pl. 88: 3–5); GSC 16,856. = *Stromatopora mikkwaensis* Stearn, 1966 (Stearn 1966: p. 55; Stearn 1980).

Diagnosis. — Oblique structural elements form a continuous cassiculate network in longitudinal section enclosing galleries arched at the top; neither coenosteles nor coenostromes prominent; structural elements cut as a labyrinthine network in tangential section; microstructure cellular, commonly altered to melanospheric with vertical alignment of melanospheres (Fig. 7D–F).

Range. — Givetian to Frasnian (about 2 species).

Distribution. — Givetian – Belgium (Ardennes); Frasnian – Australia (Canning Basin), Belgium (Ardennes), Canada (Alberta, Manitoba, Saskatcehwan), China (Guangxi), Germany (Rhineland), Russia (Pechora Basin).

Family Syringostromellidae Stearn, 1980

Diagnosis. — Stromatoporids with structure dominated by coenosteles and dissepiments.

Genus *Syringostromella* Nestor, 1966

See Nestor 1966: p. 47.

Type species: *Stromatopora borealis* Nicholson, 1891 (Nicholson 1891a: p. 315, pl. 9: 7, 8); BM(NH) P5894 (Nicholson No. 38).

= *Yavorskiina* Khalfina, 1968 (Khalfina 1968a: p. 148), *nom. nud.*

Diagnosis. — Coenosteles long, continuous, joining and dividing in longitudinal section; coenostromes rudimentary or absent; dissepiments common. In tangential section coenosteles vermiform or a loose labyrinthine network. Microstructure cellular, some species may appear microreticulate (Fig. 7B, C).

Range. — Lower Silurian (Telchyian) to Lower Devonian, ?Eifelian (about 25 species).

Distribution. — Telychian – Canada (Hudson Bay lowland), Norway (Oslo region); Wenlock – Canada (E. Quebec), England (Shropshire), Japan, Russia (Siberian Platform, Tuva), Sweden (Gotland), Ukraine (Podolia); Ludlow–Pridoli – Canada (Arctic islands), China (Inner Mongolia), Estonia, Russia (Siberian Platform, E.Urals), Central Asia (Tien Shan), U.S.A. (New York); Lower Devonian – Australia (Victoria), Canada (Arctic islands), Russia (Salair); ?Eifelian – Russia (E. Siberia).

Genus *Salairella* Khalfina, 1961

See Khalfina 1961: p. 230.

Type species: *S. multicea* Khalfina, 1961 (Khalfina 1961: p. 331, pl. D-5: 3); CSGM 402/37.

= *Lecomptella* Khalfina, 1972 (Khalfina 1972: p. 151); type species: *Stromatopora racemifera* Khalfina, 1961 (Khalfina 1961: p. 327). = ?*Tubuliporellina* Kosareva, 1985 in Bogoyavlenskaya & Khromych 1985: p. 93; type species: *T. crispa* Kosareva, 1985 in Bogoyavlenskaya & Khromych 1985: p. 93, pl. 14: 2.

Diagnosis. — Coenosteles long, joining and dividing in longitudinal section, coenostromes rudimentary to absent, dissepiments common in autotubes between coenosteles. In tangential section most coenosteles joined in a closed network enclosing autotubes; microstructure finely cellular.

Range. — Pragian to Frasnian (about 25 species).

Distribution. — Pragian – Australia (Victoria); Emsian – Australia (New South Wales), Canada (Arctic islands), Russia (Salair, Omulev dist.); Pragian/Emsian – Russia (E. Urals); Eifelian – Canada (Arctic islands), China (Guangxi, Sichuan), Central Asia (Tien Shan), Russia (Altai, Salair, Kuznetsk Basin); Givetian – Belgium (Ardennes), Russia (Kuznetsk Basin), U.S.A. (Missouri); Frasnian – Belgium (Ardennes), Canada (Alberta, Manitoba), Russia (Russian Platform).

Comment. — Although the genus *Tubuliporellina* was attributed by Bogoyavlenskaya & Khromych (1985) to Kosareva (1968), a generic analysis was not published until that in Bogoyavlenskaya & Khromych in 1985 and the proposed type species was only illustrated at that time but not described.

Genus ?*Zeravshanella* Lessovaja, 1986

See Lessovaja 1986: p. 36.

Type species: *Z. cavernosa* Lessovaja, 1986 (Lessovaja 1986: p. 36, pl. 3: 2); GMU 270/7a-33/412.

Diagnosis. — Coenosteles highly irregular in outline in both longitudinal and tangential sections, tangential elements are dissepiments.

Range. — Lower Devonian (1 species).

Distribution. — Central Asia (Tien Shan).

Comment. — Nestor believes that further study may show this genus to be a diagenetically altered *Syringostromella* Nestor.

Order Syringostromatida Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969b.

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

Comment. — Although the Syringostromatida and Stromatoporida are separated at the ordinal level by their microstructure, the grouping of genera is based on additional features that are interpreted as suggestive of their phylogenetic position. Stearn (1993) suggested that the two orders arose in Llandovery time from different stocks; the Stromatoporida from the Clathrodictyida and the Syringostromatida from the Actinostromatida. Some genera of the Stromatoporida show traces of microreticulation as the cellules are aligned longitudinally but the general aspect of the microstructure is predominantly randomly cellular.

Family Syringostromatidae Lecompte, 1952

nom. correct. (Bogoyavlenskaya 1969b), *pro* Syringostromidae Lecompte, 1952.

Diagnosis. — Syringostromatida of laminar, bulbous, and domical growth form with structure dominated by longitudinal structural elements (coenosteles and pillars) of clinoreticulate microstructure.

Comment. — *Vikingia* Bogoyavlenskaya, 1969 (see Bogoyavlenskaya 1969a), is a possible ancestor of this group and might be placed within it.

Genus *Syringostroma* Nicholson, 1875

See Nicholson 1875: p. 251.

Type species: *Syringostroma densa* Nicholson, 1875 (Nicholson 1875: p. 251, pl. 24: 2; subsequently designated by Nicholson 1886a: p. 98); BM(NH) P5598 (Nicholson No. 311).

= *Stylodictyon* Nicholson & Murie, 1878 (Nicholson & Murie 1878: pp. 221–222); type species: *Syringostroma columnaris* Nicholson, 1875 (Nicholson 1875: p. 263).

Diagnosis. — Coenosteles short, irregular, coarsely cellular, without precise boundaries, irregular in shape in tangential section; subcolumns long, continuous, clinoreticulate, round in tangential section; coenostromes persistent, thick, cellular, containing one or more microlaminae; dissepiments rare (Fig. 8C, D).

Range. — Lochkovian to lower Givetian, ?upper Givetian (about 25 species).

Distribution. — Lochkovian – Canada (Arctic islands); Emsian/Eifelian – Canada (SW. Ontario, Hudson Bay lowland), U.S.A. (Missouri, Michigan, Ohio, Indiana); lower Givetian – U.S.A. (Ohio); ?upper Givetian – U.S.A (Indiana).

Comment. — A great majority of the species that have been included in the genus do not have the subcolumns that are characteristic of the type of the genus. These have been reassigned to other genera by Galloway & St. Jean (1957), Flügel & Flügel-Kahler (1968), Fagerstrom (1982), and Stearn (1993).

Genus *Atopostroma* Yang & Dong, 1979

See Yang & Dong 1979: p. 74.

Type species: *A. tuntouense* Yang & Dong, 1979 (Yang & Dong 1979: p. 74, pl. 41: 7, 8); NIGP Bd343-9.

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

Range. — Lower Devonian, ?Eifelian, ?Givetian (about 5 species).

Distribution. — Lochkovian – Canada (Arctic islands), U.S.A (New York); Emsian – Australia (New South Wales, Victoria), Canada (Arctic islands), China (Sichuan); Lower Devonian – China (Guangxi); ?Eifelian – Russia (Kuznetsk Basin), ?Givetian – Afghanistan.

Comment. — The range of *Atopostroma* appears to be from Lochkovian to Emsian. The recognition of *A. flexuosum* (Yavorsky, 1955) extends its range into the Eifelian according to Webby *et al.* (1993). The recognition of *Atopostroma* sp. by Mistiaen (1985) in the Givetian of Afghanistan also appears to extend the range far beyond the occurrences in other parts of the world.

Genus *Columnostroma* Bogoyavlenskaya, 1972

See Bogoyavlenskaya 1972a: p. 33.

Type species: *Coenostroma ristigouchense* Spencer, 1884 (Spencer 1884: p. 599, pl. 6: 12, 12a); repository of specimen unknown, type slide BM(NH) P5591 (Nicholson No. 309) illustrated by Nicholson (1886b: pl. 11: 11, 12) and Stearn (1993: text-fig. 6c–d); topotype illustrated by Fagerstrom (1982: pl. 3: 7, 8).

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

Range. — Lochkovian to Givetian (about 8 species).

Distribution. — Lochkovian – Canada (New Brunswick); Pragian – Australia (Victoria); Lower Devonian – Russia (N. Urals, E. slope Urals); Eifelian – Canada (Ontario, Hudson Bay), U.S.A. (Indiana, Ohio); Givetian – ?England (Devon), Russia (N. Urals, E. slope Urals, Kuznetsk Basin).

Genus *Parallelopora* Bargatzky, 1881

See Bargatzky 1881a: p. 63 (p. 292).

Type species: *P. ostiolata* Bargatzky, 1881 (Bargatzky 1881a: p. 64); IPB 571b, illustrated by Nicholson 1886b: pl. 2: 6, 7; slides of type BM(NH) P5936 (Nicholson No. 125); see also Lecompte 1952: pl. 51: 3a–c.

Diagnosis. — Coenosteles long, continuous, branching and joining in longitudinal section, in tangential section mostly joined into closed network enclosing autotubes; coenostromes suppressed or absent; dissepiments abundant. Microstructure of coenosteles coarsely microreticulate (orthoreticulate), apparently formed of closely spaced, opaque micropillars and more widely spaced, short microlaminae.

Range. — Emsian to Givetian (about 15 species).

Distribution. — Emsian – Australia (Victoria); Emsian/Eifelian – Canada (Arctic islands), U.S.A. (Indiana, Ohio); Eifelian – Morocco; Givetian – Belgium (Ardennes), Canada (Manitoba), Germany (Eifel, Rhineland), Poland (Holy Cross Mountains), Russia (Kuznetsk Basin, S. Urals); Middle Devonian – China (Guangxi, Sichuan).

Family Coenostromatidae Waagen & Wentzel, 1887

= Parallelostromatidae Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969b).

Diagnosis. — Syringostromatids of laminar, bulbous and domical growth forms with structure dominated by coenostromes and microlaminae; microstructure orthoreticulate.

Genus *Coenostroma* Winchell, 1867

See Winchell 1867: p. 99.

Type species *Stromatopora monticulifera* Winchell, 1866 (Winchell 1866: p. 91), designated by Miller 1889, described by Galloway & Ehlers (1960: p. 51, pl. 1: 1a–d, 2); lectotype UMMP 32409A.

= ?*Parallelostromella* Kosareva, 1968 in Ivaniya & Kosareva (1968: p. 80); type species: *P. collina* Kosareva, 1968 (Kosareva 1968: pp. 80–81), *nom. nud.*

Diagnosis. — Persistent, thick coenostromes, superposed coenosteles, and pillars forming an imperfect grid in longitudinal section; galleries small, irregular; microstructure of structural elements obscurely microreticulate, locally with microlaminae in coenostromes. In tangential section structural elements form an irregular network or, in some species, longitudinal elements appear as dots (i.e., they are pillars) (Fig. 8H, I).

Range. — ?Upper Silurian, Devonian (Lochkovian–Givetian, ?Famennian) (about 15 species).

Distribution. — ?Upper Silurian – Russia (Kuznetsk Basin, Urals), U.S.A. (New York); Lochkovian – U.S.A. (New York); Emsian – Australia (Victoria); Middle Devonian – China (Guangxi), Germany (Eifel); Eifelian – Canada (Ontario), Russia (Kuznetsk Basin, NE. Siberia, Salair); Givetian – Canada (Manitoba), Czech Republic, Poland, Russia (Kuznetsk Basin), U.S.A. (Michigan); ?Famennian – Australia (Canning Basin), Russia (Arctic islands).

Comment. — *Parallelostromella* Kosareva appears to be similar to *Coenostroma* but, because it was published without a diagnosis, it is an invalid genus under ICZN Article 13.

Genus *Habrostroma* Fagerstrom, 1982

See Fagerstrom 1982: p. 11.

Type species: *Stromatopora proxilaminata* Fagerstrom, 1961 (Fagerstrom 1961: p. 8, pl. 1: 4–6); UMMP 36177.

Diagnosis. — Coenosteles short, irregular, largely confined between coenostromes, forming an irregular network of cellular skeletal tissue with diffuse boundaries in tangential section; coenostromes prominent, of similar cellular to microreticulate tissue containing one or more microlaminae.

Range. — Pridoli to Lower Givetian, ?Frasnian (about 20 species).

Distribution. — Pridoli – U.S.A (New York, Virginia); Lochkovian – Canada (Arctic islands), U.S.A. (New York, Virginia); Pragian – Australia (Victoria); Emsian–Eifelian – Australia (New South Wales), Belgium (Ardennes), Canada (SW. Ontario, Arctic islands), Russia (Kuznetsk Basin, Russian Platform, Urals), U.S.A. (Missouri, Ohio, Indiana); Givetian – Belgium (Ardennes), U.S.A. (Indiana); Middle Devonian – China (Sichuan,Guangxi); ?Frasnian – Belgium (Ardennes), Russia (Russian Platform).

Comment. — The limits of the genus *Habrostroma* have not been easy to define. At the beginnings of its range at the Silurian–Devonian boundary it is easily confused with *Parallelostroma* and several authors have discussed this transition (Fagerstrom 1982; Stock & Holmes 1986; Stock 1989; Stearn 1990). At the end of its range are several species described by Lecompte (1951, 1952) from Belgian Frasnian rocks which might find a place in the genus or in similar genera such as *Climacostroma*. Until further work on these equivocal species is done, it seems best to give an upper end to the range of *Habrostroma* in the lower Givetian. The genus was most widespread and diverse in the Emsian–Eifelian interval. As the dating of some of the beds at this boundary is a matter of discussion, the occurrences in these stages have been combined.

Genus *Parallelostroma* Nestor, 1966

See Nestor 1966: p. 52.

Type species: *Stromatopora typica* Rosen, 1867; see Rosen 1867: p. 58, pl. 1: 1–3; pl. 2: 1; IGTTU Co3009.

Diagnosis. — Coenostromes thick, composed of orthoreticulate tissue enclosing multiple microlaminae and micropillars, at base short coenotubes separate coenosteles of same microstructure; coenosteles largely confined to intercoenostrome space, some superposed, form labyrinthine or closed network in tangential section (Fig. 8E–G).

Range. — Wenlock to Pragian, ?Middle Devonian (about 25 species).

Distribution. — Wenlock – Russia (Pechora Basin), Ukraine (Podolia), Ludlow–Pridoli – Canada (Quebec), China (Inner Mongolia), Estonia, Ukraine (Podolia), U.S.A (New York, Alabama), Russia (E. Urals), Sweden (Gotland); Lochkovian – Russia (E. and W. Urals), U.S.A (New York); Lower Devonian – China (Sichuan), Russia (E.Urals), Ukraine (Podolia); ?Middle Devonian – China (Guangxi), Russia (W. Urals, Arctic islands).

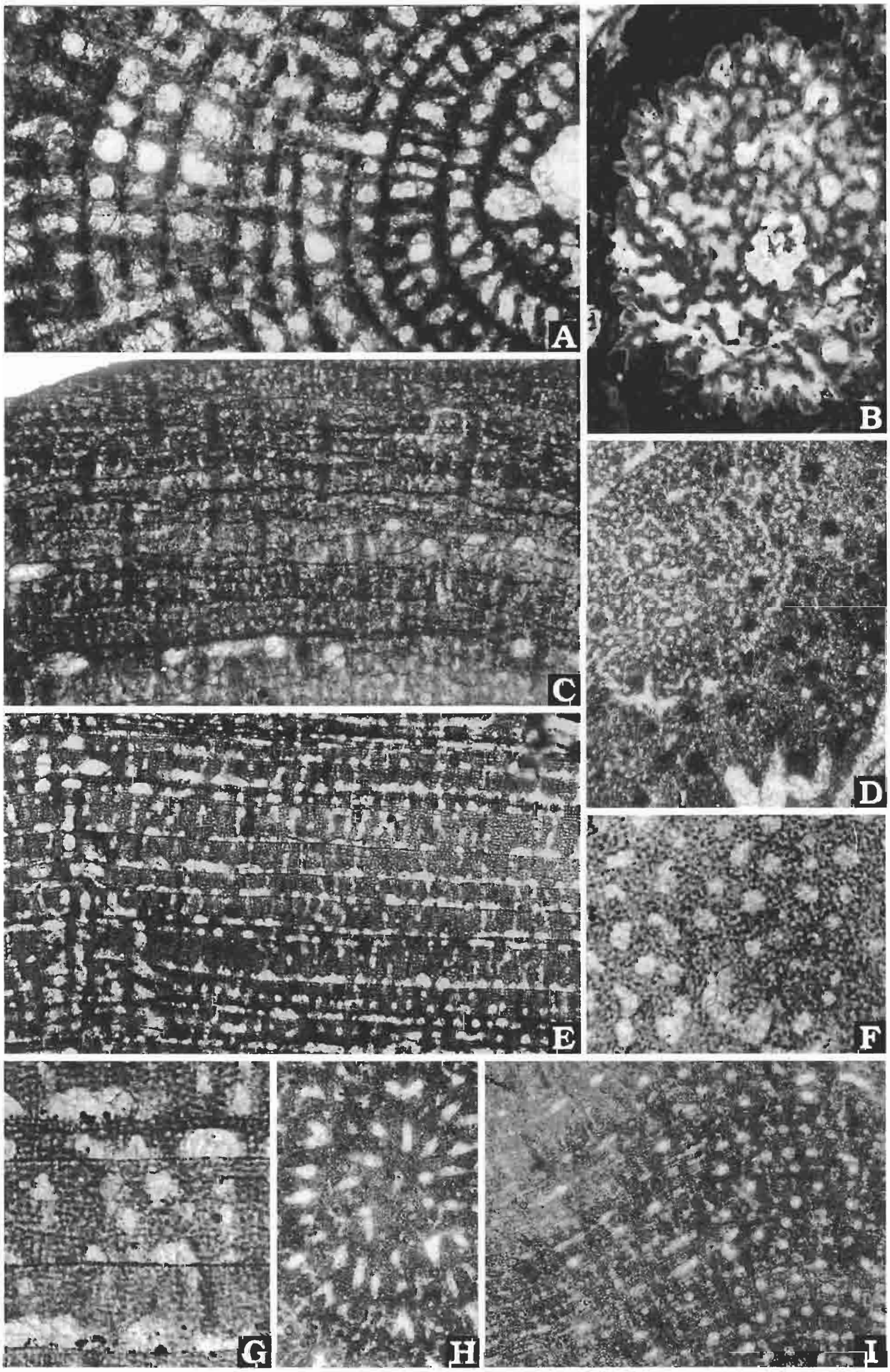
Comment. — The extension of *Parallelostroma* into Middle Devonian time suggested by Bol'shakova (1973) requires further biostratigraphic documentation. Extensive Emsian faunas recently described from Australia and Canada do not contain this genus and suggest that its range extended to only Pragian time.

Family Stachyoditidae Khromych, 1967

nom. correct. Khromych 1969 *pro* Stachyodidae Khromych, 1967.

Diagnosis. — Syringostromatida of dendroid growth form with a structure dominated by coenostele-like elements, microlaminae, and coenotubes.

Fig. 8. **A**. Idiostromatidae: *Idiostroma roemeri* Nicholson, 1886, holotype BM(NH) P6070, (406c), × 10. Cross section of part of a stem. Note superposed pillars and tripartite laminae. **B**. Amphiporidae: *Amphipora ramosa* (Phillips, 1841), neotype BM(NH) PO 308, × 10. Cross section of a stem. **C**, **D**. Syringostromatidae: *Syringostroma densum* Nicholson, 1875, longitudinal and tangential sections of holotype BM(NH) P5598 (311a, 311g), × 10. Note the megapillars in both sections. Preservation is not good in this holotype. **E–G**. Coenostromatidae: *Parallelostroma typicum* (Rosen, 1867), holotype IGTTU Co 3009. **E** – longitudinal section, × 10; **F**, **G** – tangential and longitudinal sections, × 25, showing the microreticulate (orthoreticulate) microstructure. **H**, **I**. Coenostromatidae: *Coenostroma monticuliferum* (Winchell, 1866), tangential and longitudinal sections of holotype UMMP 32,409A, × 10. Note the strongly developed coenostromes and coenosteles forming a grid. Preservation of microreticulate microstructure is poor in the holotype.


A
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Genus *Stachyodes* Bargatzky, 1881

See Bargatzky 1881b: p. 688.

Type species: *Stachyodes ramosa* Bargatzky, 1881 (Bargatzky 1881b: p. 691); type specimen 'in collection of Herrn Schlüter', apparently lost, synonymized by Nicholson (1886b: p. 107) with *Stromatopora verticillata* M'Coy, 1850 (M'Coy 1850: p. 377); type specimen at Cambridge University apparently lost (Wood 1995 personal communication).

= *Sphaerostroma* Gürich, 1896 (Gürich 1896: p. 127); type species: *Sphaerostroma exiguum* Gürich, 1896 (Gürich 1896: p. 128); type specimen repository not designated. = *Stachyodella* Delage & Hérouard, 1901 (Delage & Hérouard 1901: p. 162; see Mistiaen 1985: p. 192). = *Keega* Wray, 1967 (Wray 1967: p. 18); type species: *Keega australe* Wray, 1967 (Wray 1967: p. 18; see Riding 1974a: p. 572). not *Stachyodes* Wright & Studer, 1889 (Wright & Studer, 1889, v. 31: p. 54); type species: *Stachyodes regularis* Wright & Studer, 1889 (Wright & Studer 1889: p. 55; an alcyonarian according to Mistiaen 1985: p. 192).

Diagnosis. — Growth form commonly dendroid, rarely laminar or combination of laminar growing into erect branches; with axial canal, or canals crossed by tabulae. Smaller canals and coenotubes/autotubes radiating upward and outward to periphery in dendroid forms. Structure defined by canals and coenotubes/autotubes cut in axial parts of cross-sections of branches as round and irregular voids and at periphery as irregular radial canals opening at the margin (covered with a rarely preserved enveloping membrane). Peripheral coenotubes separating irregular, radial coenostele-like structural elements. Structure traversed by dark microlaminae parallel to successive growth surfaces, forming concentric rings in the peripheral zone of cross-sections only, and parabolas in longitudinal sections. Structural elements thick, microreticulate in well preserved specimens, more commonly appearing striated, with vacuoles in some species, commonly recrystallized to diagenetic fibrous microstructures.

Range. — Eifelian to Frasnian (about 45 species).

Distribution. — ?Lochkovian – Australia (New South Wales); Eifelian – Central Asia (Tien Shan), Germany (Sauerland), Russia (Kuznetsk Basin); Givetian – Australia (Canning Basin, Queensland), Belgium (Ardennes), Canada (British Columbia, Manitoba), China (Guangxi, Guizhou), Czech Republic (Moravia), Germany (Sauerland, Eifel), Russia (Kuznetsk Basin), Thailand, U.S.A. (Missouri), Uzbekistan; Middle Devonian (undifferentiated) – Australia (Queensland), Central Asia (Kara-Kalpak), China (Guangxi, Sichuan), England (Devon), Germany (Waldgrimes, Eifel, Schladetal), Russia (Pechora Basin, Urals); Frasnian – Afghanistan, Australia (Canning Basin, Carnarvon Basin), Belgium (Ardennes), Canada (Alberta, Saskatchewan), Central Asia (Tien Shan, Zeravshan Ridge), China (Guangxi, Yunnan, Guizhou), France (north), Germany (Rhineland), Poland (Holy Cross Mountains), Russia (NE. Siberia, Pechora Basin, Timan), U.S.A. (Missouri, Iowa).

Comment. — *Stachyodes* is placed in the Syringostromatida because its microstructure is microreticulate, although usually preserved as striated. The type specimens of both possible type species (*S. ramosa* Bargatzky and *S.verticillata* M'Coy) are lost. They have been searched for at Cambridge, Belfast, Dublin and Bonn. In the absence of a type of either species, taxonomists have accepted Nicholson's contention that they are synonymous and recognized the genus on the basis of his illustrations and description. *Idiostroma* was distinguished from *Stachyodes* by Nicholson (1886b) using *Idiostroma roemeri* as a model before the true nature of the type species (*I. caespitosum*), that has many characteristics of *Stachyodes,* was known from thin sections. The concepts of these two genera adopted by Nicholson are followed.

Order Amphiporida Rukhin, 1938

nom. transl. Webby *et al.*, 1993 *ex* Amphiporidae Rukhin, 1938.

Diagnosis. — Stromatoporoids of dominantly dendroid form composed of compact to fibrous, single layer skeletal elements, commonly arranged in irregular, amalgamate networks but also in pillars radiating upwards and outwards from the growth axis; with or without axial canals, obscure laminae, and peripheral membranes enclosing the whole skeleton.

Family Amphiporidae Rukhin, 1938

Diagnosis. — As for order.

Genus *Amphipora* Schulz, 1883

See Schulz 1883: p. 245.

Type species: *Caunopora ramosa* Phillips, 1841 (Phillips 1841: p. 19, pl. 8: 22a, b, c); types lost, neotype BM(NH) PO 308 sections A1 to A6 established by Stearn (1997).

= *Haraamphipora* Rukhin, 1938 (Rukhin 1938: p. 93); type species: *H. pachyroides* Rukhin, 1938 (Rukhin 1938: p. 93). = *Paramphipora* Yavorsky, 1955 (Yavorsky 1955: p. 56); type species: *P. mirabilis* Yavorsky, 1955 (Yavorsky 1955: p. 56). = *Vicinustachyodes* Yavorsky, 1961; type species: *V. mirabilis* Yavorsky, 1961 (Yavorsky 1961: p. 56). = *Vicinostachyodes* Yavorsky, 1967. = *Stellopora* Bogoyavlenskaya, 1972 (Bogoyavlenskaya 1972b: p. 56; see Webby *et al.* 1993: p. 174–176 for discussion of date); type species: *Amphipora intexta* Yavorsky, 1957 (Yavorsky 1957: p. 62). = *Taeniostroma* Dong & Wang, 1982 (Dong & Wang 1982: p. 29); type species: *T. yunnanense* Dong & Wang, 1982 (Dong & Wang 1982: p. 29). = *Columndictyon* Dong & Wang, 1982 (Dong & Wang 1982: p. 29); type species: *C. regulare* Dong & Wang, 1982 (Dong & Wang 1982: p. 30). = *Tianshanostroma* Dong & Wang, 1984 (Dong & Wang 1984: p. 269); type species: *T. xinjiangense* Dong & Wang, 1984 (Dong & Wang 1984: pp. 269–270). = *Qinghaipora* Dong, 1991 (Dong 1991: p. 75); type species *Q. gracilenta* Dong, 1991 (Dong 1991: p. 75).

Diagnosis. — Skeleton dendroid, branching dichotomously, with axial canal locally absent, locally with well defined wall, locally poorly defined, opening into the interskeletal network of voids and irregular canals by pores. Skeletal network formed by pillars radiating upward and outward obliquely from the axis, and short elements extending from and joining them to form an irregular structure that may, in cross sections, define open or closed spaces. Peripheral vesicles sporadically developed in most species, bounded by an imperforate calcareous membrane supported beyond the skeletal network by extensions of the skeletal elements. Microstructure compact, fibrous (Fig. 8B).

Range. — ?Middle Silurian, Upper Silurian to Upper Devonian (about 20 species).

Distribution. — ?Middle Silurian – Russia (L. Khaendo); Ludlow – Estonia, Russia (Urals, Kuznetsk Basin, central Siberia, Timan), Sweden (Gotland), Central Asia (Tien Shan); Lower Devonian – Australia (Victoria), Canada (Arctic islands), China (Xinjiang), Russia (central and east Siberia, Salair, Kuznetsk Basin), Central Asia (Tien Shan), U.S.A. (Alaska); Middle Devonian – cosmopolitan at lower paleolatitudes; Frasnian – cosmopolitan at lower paleolatitudes; Famennian – China (Guangxi), Russia (Pechora Basin).

Comment. — Stearn (1997) has discussed the neotype of *A. ramosa* and the variations in the neotype suite that justify the placing in synonymy of the genera listed above. About 175 species have been described but in the light of the extensive variation found in suites of specimens, are in need of extensive revision. The plethora of Middle and Upper Devonian species makes listing of their distribution in this summary impractical.

Genus *Clathrodictyella* Bogoyavlenskaya, 1965

See Bogoyavlenskaya 1965a: p. 42.

Type species: *Amphipora turkestanica* Lessovaja, 1962 (Lessovaja 1962: p. 117, pl. 7: 2); GMU 46/489.

Diagnosis. — Like *Amphipora* in axial canal and peripheral vesicles but in axial section structural elements are gently arched, crumpled laminae or cyst plates arranged in parabolic series transverse to the axial canal.

Range. — Ludlow (7 species).

Distribution. — Russia (E. Urals), Uzbekistan (Tien Shan).

Genus *Euryamphipora* Klovan, 1966

See Klovan 1966: p. 14.

Type species: *E. platyformis* Klovan, 1966 (Klovan 1966: p. 15, pl. 3: 4a, 4b; pl. 4: 1–7); GSC 19834.

= ?*Solidostroma* Khromych, 1974 (Khromych 1974: p. 30); type species: *S. congesta* Khromych, 1974 (Khromych 1974: p. 30).

Diagnosis. — Growth form tabular, platelike, amalgamate in longitudinal sections, with marginal vesicles; may have long pillars evident in tangential sections.

Range. — Frasnian (about 3 species).

Distribution. — Afghanistan, Australia (W. Australia), Canada (Alberta, Saskatchewan).

Comment. — Cockbain (1984) reconstructed the skeleton as a vertical plate but Mistiaen (1985) described the genus as growing as a horizontal plate.

Genus *Novitella* Bogoyavlenskaya, 1984

See Bogoyavlenskaya & Dan'shina 1984: p. 22.

Type species: *Paramphipora tschussovensis* Yavorsky, 1955 (Yavorsky 1955: p. 159, pl. 86: 8, 9; pl. 87: 3–5; pl. 88: 1–4); CNIGR 7351/136.

Diagnosis. — Like *Amphipora* but with prominent gently arched laminae in sections cutting the axial canal longitudinally.

Range. — Frasnian (about 6 species).

Distribution. — Russia, Tsaritsin (now Volgograd) region, E. and W. Urals.

Genus *Vacuustroma* Hung & Mistiaen, 1997

See Hung & Mistiaen 1997: pp. 193–195.

Type species: *V. michelini* Hung & Mistiaen, 1997 (Hung & Mistiaen 1997: pp. 195–199, figs 4a–c, 7-1 to 7-7, 8-10); GFCL 149. = *Amphipora* sp. in Mistiaen 1988: p. 187, fig. 16, pl. 23: 5–8.

Diagnosis. — Structure like that of *Amphipora* but with structural elements of vacuolate microstructure.

Range. — Emsian to Frasnian (about 4 species).

Distribution. — Emsian – Vietnam; Givetian – Vietnam, China (Xizang); Frasnian – France (Boulonnais).

Order and Family Uncertain

Genus *Clavidictyon* Sugiyama, 1939

See Sugiyama 1939: p. 441.

Type species: *C. columnare* Sugiyama, 1939 (Sugiyama 1939: p. 441, pl. 25: 6–8); IGPS 60,813.

Diagnosis. — Columnar, without axial canal, amalgamate in axial zone but with well-defined laminae and short pillars confined to an interlaminar space in peripheral zone.

Range. — Middle Silurian to Upper Devonian (about 5 species).

Distribution. — Middle Silurian – Japan; Middle Devonian – U.S.A. (Michigan); Upper Devonian (Famennian) – China (Guangxi).

Comment. — Stearn suggests that the well-defined single-layer laminae and short pillars in the periphery resemble those of the Clathrodictyida and the genus could be placed in that order. Nestor prefers to assign it to the Amphiporida.

Genus *Eostachyodes* Dong & Wang, 1982

See Dong & Wang 1982: pp. 28 and 33.

Type species: *E. compacta* Dong & Wang, 1982 (Dong & Wang 1982: p. 28, pl. 17: 7, 8); NIGP 61351-61352.

Diagnosis. — Columnar growth form, without axial canal, structural elements in axial zone completely amalgamate, peripheral zone with coenostele-like elements; microstructure fibrous or melanospheric.

Range. — Middle Devonian (1 species).

Distribution. — China (Yunnan).

Comment. — Dong (1988) placed this genus in the Stachyoditidae. Further study is needed.

Genus *Lamellistroma* Bogoyavlenskaya, 1977

See Bogoyavlenskaya 1977b: p. 17.

Type species: *L. lamelliferum* Bogoyavlenskaya, 1977 (Bogoyavlenskaya 1977b: p. 18, pl. 1: 3a–b).

Range. — Lochkovian to Eifelian (3 species).

Distribution. — Lochkovian – Russia (E. Urals); Pragian/Emsian – Russia (eastern trans-Urals); Eifelian – Russia (E. Urals).

Comment. — Bogoyavlenskaya placed this genus in the family Densastromatidae but it appears to lack the basic characteristics of the family – a microreticulate mass interrupted by accessory openings. Stearn (1980) placed it in synonymy with *Actinostroma*. In the opinion of other coauthors it may be synonymous with *Coenostroma*, *Gerronostroma*, or *Densastroma*.

Genus *Paschkoviella* Kosareva, 1979

See Kosareva 1979: p. 43.

Type species: *P. aequicrassa* Kosareva, 1979 (Kosareva 1979: p. 43, pl. 3: 1, 2, 6).

Comment. — Opinions of the coauthors differ greatly on its classification.

Genus *Perplexostroma* Bogoyavlenskaya, 1981

See Bogoyavlenskaya 1981: p. 32.

Type species: *Stromatopora dzvenigorodensis* Riabinin, 1953 (Riabinin 1953: p. 51, pl. 23: 2, pl. 24: 1).

Range. — Pridoli (1 species).

Distribution. — Ukraine (Podolia).

Comment. — Bogoyavlenskaya (1981) pointed out a possible close relationship of this genus to *Vikingia*, probably due to the presence of clinoreticulate pillars or narrow columns in both genera. Stearn (1993) suggested it may be a synonym of *Stromatopora*.

Genus *Praeidiostroma* Bogoyavlenskaya, 1971

See Bogoyavlenskaya 1971a: p. 108.

Type species: *P. praecox* Bogoyavlenskaya, 1971 (Bogoyavlenskaya 1971a: p. 108, pl. 29: 5–7, pl. 30: 1).

Comment. — The type species appears to be a dendroid form of *Gerronostroma* with an axial canal.

Genus *Pseudoactinostroma* Lessovaja, 1970

See Lessovaja 1970: p. 81.

Type species: *P. hamidulense* Lessovaja, 1970 (Lessovaja 1970: p. 82, pl. 3: 3, pl. 4: 1).

Comment. — Stearn (1980) agreed that the genus combined features of *Actinostroma* and *Intexodictyon*, and placed it in the Actinostromatida.

Genus *Pseudostromatopora* Dong, 1991

See Dong 1991: p. 70.

Type species: *P. yushuensis* Dong, 1991 (Dong 1991: p. 71, pl. 4: 3a–b).

Comment. — The genus is a homonym of *Pseudostromatopora* Simionescu, 1927, a bryozoan.

Phylum, Class and Order Uncertain

Probably not Stromatoporoidea.

Family Khasaktiidae Sayutina, 1980

Diagnosis. — Small, thin, crust-like, laminar or branching; composed dominantly of fine, irregularly wavy, cystose elements with crenulations or denticles on upper surfaces; in a few places superposed to form mamelon-like or pillar-like upgrowths; branching forms differentiated into axial column with large, stacked cyst plates and lateral zone with fine, undulating to globose cyst plates; in places inflected into small, columnar outgrowths, possibly having mamelon affinities.

Comment. — Sayutina (1980) noted that at least two members of the family (*Vittia* and *Khasaktia*) have close morphological affinities to representatives of the Rosenellidae, Labechiidae and Lophiostromatidae. However, Zhuravlev *et al.* (1993) have since argued that, given their distinctive layered skeleton and microstructure, the family Khasaktiidae should be regarded as a 'corallomorph' group. In consequence, the group is currently thought to have no direct phylogenetic links with the Labechiida. Nestor regards *Khasaktia* and *Vittia* as fragments of holdfasts of archaeocyathans.

Genus *Khasaktia* Sayutina, 1980

See Sayutina 1980: p. 22.

Type species: *K. vesicularis* Sayutina, 1980 (Sayutina 1980: p. 22, pl. 3: 4–6; pl. 4: 7); PIN 3900/5.

Diagnosis. — Skeleton laminar, composed of a variety of large undulating, laterally extensive, to small, globose, upwardly convex cyst plates; laterally continuous cyst plates commonly upflexed into small, regular, cone-shaped, superposed mamelon columns (may be vertical or inclined); all cyst-like elements exhibit crenulations (no denticles).

Range. — Lower Cambrian (3 species).

Distribution. — Russia (Siberian Platform), Mongolia (Khasakt-Khayrkhan Range).

Genus *Edelsteinia* Vologdin, 1940

See Vologdin 1940: p. 18.

Type species: *E. mongolica* Vologdin, 1940 (Vologdin 1940: p. 18: 7); neotype PIN 3175 (holotype lost).

Diagnosis. — Skeleton branching, dendroid, with rounded axial canal, and layered lateral zone of fine undulating and globose cyst plates crossed by rod– or column-like elements; these latter radiate out from axial canal and project as papillae on outer surface (probably not true pillars).

Range. — Lower Cambrian (2 species).

Distribution. — Mongolia (Khasakt-Khayrkhan Range), Russia (Altai-Sayan mountains, Gornaya Shoriya, Tuva).

Genus *Drosdovia* Sayutina, 1980

See Sayutina 1980: p. 27.

Type species: *D. aenigmatica* Sayutina, 1980 (Sayutina 1980: p. 27, pl. 3: 7); PIN 3302/107.

Diagnosis. — Skeleton branching, dendroid, with a few connecting processes; axial column, comprising single row of stacked, large, upwardly convex cyst plates with denticles on upper surfaces; lateral zone of fine, dense, undulose, elements like cyst plates, and these upflexed in a series of small outwardly tapering, mamelon-like columns (doubtfully true pillars); skeletal elements perforate (?possibly suggests archaeocyath affinity).

Range. — Lower Cambrian (1 species).

Distribution. — Mongolia (Khasakt-Khayrkhan Range).

Genus *Rackovskia* Vologdin, 1940

See Vologdin 1940: p. 21.

Type species: *R. mongolica* Vologdin, 1940 (Vologdin 1940: p. 21, figs g, h, i); neotype PIN 3302/111 (holotype lost).

Diagnosis. — Skeleton small, branching, cylindrical to chain-like, with stellate-shaped axial canal; lateral zone with dense (?finely cystose) skeletal material, lacking outwardly radiating columnar elements.

Range. — Lower Cambrian (1 species).

Distribution. — Mongolia (Khasakt-Khayrkhan Range).

Genus *Vittia* Sayutina, 1980

See Sayutina 1980: p. 21.

Type species: *V. vallaris* Sayutina, 1980 (Sayutina 1980: p. 21, pl. 3: 1); PIN 3900/1.

Diagnosis. — Skeleton encrusting, laminar, composed of a few thin, undulating layers (?long, low cyst plates), and scattered denticles in places superposed to form small pillars.
Range. — Lower Cambrian (2 species).
Distrbution. — Russia (Siberian Platform), Mongolia (Khasakt-Khayrkhan Range).

Family uncertain

Genus *Shirdagopora* Lessovaja, 1986

See Lessovaja 1986: p. 36.
Type species: *S. bullata* Lessovaja, 1986 (Lessovaja 1986: p. 37, fig. 1d, e); GMU 38/412.
Columnar with large axial canal crossed by cyst plates, open structure of indistinct pillars joined by bridges and dissepiments, with large marginal vesicles.
Range. — Lower Devonian (1 species).
Distribution. — Uzbekistan (Zeravshan Range).
Comment. — The type species may be a cystiphyllid coral.

Genus *Trigonostroma* Bogoyavlenskaya, 1969

See Bogoyavlenskaya 1969b: pp. 18–19.
Type species: *T. abruptum* Bogoyavlenskaya, 1969 (Bogoyavlenskaya 1969b: p. 19, pl. 3: 3).
Comment. — The type species resembles a heliolitid coral. Correspondence between Stearn and Owen Dixon (personal communication 1997) indicates that Dixon does not regard this genus as having features that would justify placing it in the heliolitids.

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