LABECHIIDA: SYSTEMATIC DESCRIPTIONS

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Order LABECHIIDA Kühn, 1927

[nom. correct. BOGOYAVLENSKAYA, 1969b, p. 16, pro order Labechioidea KUHN, 1927, p. 547] [=Lophiostromatida NESTOR, 1978, p. 18; =Lophiostromatida STEARN, 1980, p. 888; =Protolabechiida BOGOYAVLENSKAYA, 2001a, p. 46, parim; =Cystostromatida BOGOYAVLENSKAYA in BOGOYAVLENSKAYA KYAK & YELKIN, 2011, p. 18; =Aulaceratida BOGOYAVLENSKAYA in BOGOYAVLENSKAYA ENSKAYA & YELKIN, 2011, p. 19; =Stromatoceriidae BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & YELKIN, 2011, p. 19; =Tuvaechiida BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & YELKIN, 2011, p. 19]

Stromatoporoids with cysts usually defined by long, low to upwardly convex, blisterlike plates, and intersected by continuous, upwardly inflected pillars with rounded, irregular or flanged cross sections, and/or denticles confined to tops of cyst plates; in a few latilaminate forms, skeletal layers become much thickened; mamelons and mamelon columns may occur; astrorhizae rarely well developed; microstructure usually compact and imperforate. [The ordinal conception of the Labechiida was drastically restricted by BOGOYAVLENSKAYA (in BOGOYAVLENSKAYA & YELKIN, 2011, p. 19), in her major revision of the classification of Paleozoic and Mesozoic stromatoporoids, to just one family: the Labechiidae. This radical change in the scope and importance of the order greatly limits its usefulness as a major group. It fragments what had previously been regarded an almost natural grouping of taxa and is difficult to justify. The proposal should be abandoned in favor of the subdivisions used, more or less continuously, since the 1980s (see Classification of the Paleozoic Stromatoporoidea, p. 699-705). These earlier schemes included first the recognition of five labechiid families by BOGOYAVLENSKAYA (1984), then four family subdivisions were employed by NESTOR (1994), and more recently, six family subdivisons by WEBBY (in STEARN & others, 1999). Here, with a little additional fine tuning, this older, more traditional approach is followed, with the subdivion of the order into seven separate families (see also discussion on p.

582)]. Middle Ordovician (Darriwilian)– Upper Devonian, ?Triassic.

INTRODUCTION TO ORDER LABECHIIDA GENERAL RELATIONSHIPS

The order Labechiida is regarded as having sufficiently common morphological features to warrant assignment within the class Stromatoporoidea (WEBBY, 1979a, 1993), rather than being separated from so-called more advanced stromatoporoid orders because of their characteristic cyst plates and limited preservation of astrorhizae (HEINRICH, 1914b; KÜHN, 1927, 1939b; TRIPP, 1929). STEARN (1982a) also favored the view that the stromatoporoids were essentially a unified, homogeneous group because a good level of morphological continuity existed between labechiids and other Paleozoic stromatoporoids. However, opinions remain divided about the role and/or significance that particular ancestral labechiid genera played in the derivation of new stromatoporoid groups like the Clathrodictyida and Actinostromatida (WEBBY, 1993, 1994). Also, there appears to be little evidence that close links existed between Ordovician-Devonian stromatoporoids and a number of examples of early Cambrian stromatoporoid-like structures. Fuller discussions of these matters are presented elsewhere (see p. 575-592).

A separation of the Labechiida into two very unequally sized orders, the Labechiida and Lophiostromatida, was adopted for a time (NESTOR, 1978; STEARN, 1980), but not all workers accepted this subdivision, given the very small size of the latter group (based largely on the type species *Lophiostroma schmidtii*). A relatively large morphological gap appears to separate the two groups, but it is preferable here to maintain the separation of the two groups only up to the family level. Further studies of the lophiostromatids are needed to resolve their taxonomic relationships.

The order Protolabechiida BOGOYAVLEN-SKAYA, 2001a, represents a heterogeneous grouping of three families, two of which belong to the order Labechiida: Stratodictyidae, previously merged as part of family Labechiidae (WEBBY in STEARN & others, 1999, p. 13), and the family Lophiostromatidae, as well as the Pulchrilaminidae, now included in the independent order Pulchrilaminida (see description on p. 837-844). None of these family groups is closely related to one another, nor, as the name implies, are any of BOGOYAVLENSKAYA's (2001a) protolabechiids close to roots of either the Labechiida (see p. 582-589) or the Pulchrilaminida (see p. 837-838).

BOGOYAVLENSKAYA's (2001a, p. 46) diagnosis of the order Protolabechiida (translation courtesy of Heldur NESTOR) is as follows: "Structure, zonal laminate. Horizontal elements represented by stratocysts [=long, low cysts herein] in some cases inflecting into mamelons [=mamelon columns herein]. Vertical elementsdenticles, sometimes sporadic. Astrorhizae may be diagnosed." The problem with this definition is that comparatively few of these morphological features are common to the three groups. For example, taking the characteristic longitudinal structural elements of each family group, as follows: (1) representatives of family Labechiidae (including the stratodictyid-like forms) have pillars that are continuous across cyst plates and occasionally emerge on upper surfaces as papillae (shortened denticle-like elements are rarely developed); (2) members of the Lophiostromatidae commonly feature thickened skeletal layers that updome into pillarlike upgrowths and papillae on upper surfaces (denticles usually lacking); and (3) in family Pulchrilaminidae, the longitudinally directed structures are long, slender, spinose rods that may appear to be loosely aggregated and may extend upward well above their prominent latilaminae (denticles, mamelons, and astrorhizae apparently not formed). In consequence, none of these family groupings can be satisfactorily accommodated within order Protolabechiida BOGOYAVLENSKAYA, 2001a; see BOGOYAVLENSKAYA and YELKIN (2006, p. 186; 2011, p. 16, 18); and hence use of this particular ordinal grouping should be abandoned.

IMPLICATIONS OF DIFFERENT PRESERVATIONAL FEATURES

The poor preservation of many early (Ordovician-early Silurian) labechiids may be attributed to their skeletons of cysts and pillars (or denticles) being composed of relatively high volumes of void space and the instability of aragonite that they probably secreted, making them rather more susceptible to alteration by diagenesis than many other, skeletally more dense stromatoporoid groups (STEARN, 1972; MALLAMO & STEARN, 1991; MISTIAEN, 1994; TOBIN & WALKER, 1998). It is generally agreed that solid dark pillars may be formed as primary structures in both Labechia and Stromatocerium. But two different explanations have been offered to explain the other types of so-called pillars found in Stromatocerium and related forms; that is, the structures that have been commonly termed hollow [but they are filled with sparry calcite] (or tubelike) pillars and wall-less rods.

First, KAPP and STEARN (1975, p. 167, see especially fig. 3) noted that, in addition to the presence of solid dark pillars, sometimes a pillar may develop as a tubelike hollow wall (or plate) with a lightcolored, spar-filled center by secondary dissolution of the center of a once-solid pillar (or by a process of eruption of superposed denticles), or sometimes the entire pillarlike structure (including the tube wall) may become replaced as a wallless rod or plate. The selective process of subaerial leaching of skeletal material seems the best way to explain this differential type of transformation of pillars, with both hollow and solid often being preserved in the same skeleton (WEBBY, 1979a, p. 96), like the partial dissolution of septal structures and tabulae with sparry calcite infilling of molds recognized in the well-known Ordovician genus *Tetradium* (now interpreted as a florideophyte alga [replacement name *Prismostylus* OKULITCH, 1935a] by STEELE-PETROVICH, 2011, p. 802), also thought to represent original aragonite frameworks (SEMENIUK, 1971; WEBBY, 1990).

Second, NESTOR (1964a, 1976), in a very different interpretation, again based on structures found in Stromatocerium, argued that secondary diagenetic processes were not capable of selectively destroying the centers of the pillarlike elements. NESTOR (1964a, p. 17, see especially fig. 2b-d) preferred to interpret the tubelike, so-called pillars as primary structures, suggesting a threestage process of development of upwardly inflected, superposed, conical updomes of cyst plates into short, superposed tubes, then these in turn became united into longer, open, tube-walled structures that intersected successive cyst plates. Other workers (e.g., Kaźmierczak, 1971; Khromykh, 1999b) have adopted views similar to those of NESTOR, namely that the longitudinal structural elements are primary hollow tubes or plates.

NESTOR (1964a, p. 17, fig. 3) also regarded the tube-walled, so-called pillars as transforming originally into rather complicated shapes: in outline these were rounded, angular, elongate, meandriform, and flanged. In 1976, NESTOR further noted some individual skeletons of Stromatocerium that exhibited all three different kinds of longitudinal structural elements (tube-walled, wall-less rods, and solid). He referred to the primary cavities in the centers of the tube walls as being the best passageways for movement of solutions, and suggested that, in life, they may have been occupied by soft tissue (NESTOR, COPPER, & STOCK, 2010, p. 58).

NESTOR, COPPER, and STOCK (2010, p. 57-60) have also applied the term pore tubes from archaeocyath sponge nomenclature of DEBRENNE, ZHURAVLEV, and KRUSE (p. 887) to the tubelike longitudinal elements of labechiids. However, the archaeocyath structures are confined in rows of small, fine, obliquely to sigmoidally shaped slots within inner walls, whereas the so-called pore tubes of labechiids represent longitudinally oriented tubes that are localized, apparently randomly, within the body of a skeleton; hence, this latter type of structure bears little resemblance to an archaeocyath pore tube. Consequently, use of pore tubes as a term in labechiids should be abandoned (see p. 411).

Currently there are two ways of approaching the study of Ordovician-early Silurian Labechiida. The first treats many of the differences in skeletal structures (especially pillars) as substantially being the result of secondary alteration; consequently the taxonomic differences between groups of taxa included in the family Labechiidae and the family Stromatoceriidae may not be that significant. The second approach argues that virtually all differences in appearance of hollow, so-called pillars, including the range of shapes that these structures depict in tangential section, are taxonomically important. The later (post-middle Silurian) labechiids, most notably the Late Devonian (late Famennian) forms, exhibit solid pillars with little evidence of diagenetic or other effects, perhaps because they developed calcitic skeletons originally. Consequently, taxonomic study of these forms is rather more straightforward, and certainly less controversial.

Family ROSENELLIDAE Yavorsky in Khalfina & Yavorsky, 1973

[Rosenellidae YAVORSKY in KHALFINA & YAVORSKY, 1973, p. 32] [=Cystostromatidae KHROMYKH, 1974a, p. 28, partim]

Simple, small to large, highly arched, upward to flattened cyst plates; longitudinal elements limited to denticles or crenulations. *Middle Ordovician (Darriwilian)–Upper Devonian.*

KHROMYKH (1999b) has maintained the separation of the Rosenellidae YAVORSKY in KHALFINA & YAVORSKY, 1973, and Cystostromatidae KHROMYKH, 1974a, despite the fact that his diagnoses of the respective families are virtually identical. For the Rosenellidae (1999b, p. 226), the key features are: "moderately convex cyst plates," "denticles or short, extremely scarce superposed pillars," and microstructure "compact." For the Cystostromatidae (1999b, p. 223) the characters are: "cyst plates of various convexity," vertical elements "either absent or include denticles, sometimes short pillars," and microstructure "compact fibrous." Both families are tied to their respective type genera Rosenella and Cystostroma, but the two genera are related to each other, exhibiting similar diagnostic features at the family level; consequently the two families are combined, and the original family name Rosenellidae YAVORSKY in KHALFINA & YAVORSKY, 1973, is retained on grounds of priority. KHROMYKH (1974b, 1996, 1999b) assigned these families to the order Clathrodictyida, characterized by simple cysts, whereas typical clathrodictyids are composed of single-layered, continuous laminae that may be downwardly inflected into short pillars (see STEARN, 1980; NESTOR, 1994, 1997; STEARN & others, 1999; and see p. 755). No other stromatoporoid worker has followed KHROMYKH's approach.

BOGOYAVLENSKAYA (in BOGOYAVLENSKAYA, VASSILYUK, & GLEBOV, 1990), and BOGOYAV-LENSKAYA (in BOGOYAVLENSKAYA & LOBANOV, 1990), added further nomenclatural confusion when she proposed new families with the same names (Rosenellidae and Cystostromatidae), and subsequent misspellings of Rosenellidae (see BOGOYAVLENSKAYA, 2001a, p. 48; BOGOYAVLENSKAYA & YELKIN, 2006, p. 189; BOGOYAVLENSKAYA & YELKIN, 2011, p. 18). Key features of her diagnoses of the two families are similar. In BOGOYAVLENSKAYA (2001a, p. 48), these conceptions of her new families were proposed as emendments to the original definition of the family Rosenellidae YAVORSKY in KHALFINA & YAVORSKY, 1973, and to KHROMYKH's family Cystostromatidae, respectively. However, it seems that all the groupings and revised groupings of these closely related taxa should be rejected in favor of the original YAVORSKY in KHALFINA and YAVORSKY (1973) classification of the Rosenellidae, where he first recognized the importance of grouping simple cystose genera like *Rosenella*, *Cystostroma*, and *Rosenellinella* into one family. The group is united by its primitive features and seems to have a position near the root of the stromatoporoids.

Rosenella NICHOLSON, 1886a, p. 84 [*R. macrocystis NICHOLSON, 1886a, p. 84, pl. 7, 12-13; OD; NICH-OLSON, 1886c, p. 20, pl. 1,8; NICHOLSON, 1886a, included a description of the genus and figures and the name of the species, without description (the type species is illustrated in both papers). The figures are not photos but lithographs prepared on stone, based on NICHOLSON's accurate original drawings. The figures of R. macrocystis in NICHOLSON (1886a) included longitudinal and tangential views of the type, and the figure in NICHOLSON (1886c) included another longitudinal section from a slightly different aspect]. Skeleton commonly composed of large-sized, overlapping, gently convex-upward cyst plates; in a few places alternating with flatter, thickened bands; with or without denticles. Middle Ordovician (Darriwilian)-Upper Devonian: China (Anhui, Shandong), Malaysia, Darriwilian; Australia (New South Wales, Tasmania), China, Mongolia, Russia (Gornaya Shoriya), USA (New York), Sandbian-Katian; China (Guizhou), Estonia, lower Silurian; Australia (New South Wales), Canada (Ontario), Sweden (Gotland), Russia (Tuva), Wenlock; Ukraine (Podolia), upper Silurian; Australia (northern Queensland), Lower Devonian-Middle Devonian (lower Eifelian); China (Sichuan), Russia (Urals, Kuznetsk Basin, Vaigach Island, Pay Khoy), Ukraine (Donets Basin), Vietnam, Upper Devonian.-FIG. 387, 1a-c. *R. macrocystis, Wenlock limestone, Visby, Gotland (specimen collected by G. J. Hinde; precise locality and stratigraphic level unknown); holotype, NHM P.5490, Nicholson's slides no. 280, 280a-d; a, longitudinal section of slide 280 showing long, low cyst plates with small denticles on their tops, especially thicker cyst plates, $\times 5$; b, tangential section of slide 280d showing tiny, darkcolored, solid, dot-shaped denticles (best seen in lighter-colored areas where spar-filled gallery spaces are preserved); whereas a few denticles preserved as darker rings with lighter centers (near center of figure) and, in darkest areas (lower part of figure), equivalent, dot-shaped, lighter colored, replacement structures (voids or hollow denticles) are represented within an intersected, thick, cyst plate, ×10; c, tangential section of slide 280a shows many finely preserved, darker, dot-shaped denticles, ×10



FIG. 387. Rosenellidae (p. 712–719).



FIG. 388. Rosenellidae (p. 714).

(Webby, 2012c; photos of Nicholson's slides 280, 280a-280d, rephotographed by Webby in 1989).

Cystostroma GALLOWAY & ST. JEAN in GALLOWAY, 1957, p. 421 [*C. vermontense GALLOWAY & ST. JEAN in GALLOWAY, 1957, p. 421, pl. 31, 1, pl. 32,1; OD; GALLOWAY & ST. JEAN, 1961, p. 12, pl. 1,1a-c, non fig. 2 (illustrations of the types in GALLOWAY & ST. JEAN in GALLOWAY, 1957, are drawings, whereas GALLOWAY & ST. JEAN, 1961, includes photos of the types)]. Skeleton has moderately convex-upward cyst plates of comparatively small size, forming an imbricated pattern, with or without denticles. [STEARN (1980) and WEBBY (1993) considered Bullulodictyon YAVORSKY, 1967, to be a junior synonym of Cystostroma, given particularly the vesicular nature of horizontal elements resembling rows of cyst plates, but NESTOR (in STEARN & others, 1999, p. 24; and see p. 755) transferred the taxon to Clathrodictyida after reexamination of type material revealing paths of numerous astrorhizae largely simulating the vesicular structure.] Middle Ordovician (Darriwilian)-Upper Devonian: USA (Vermont), Darriwilian; Australia (New South Wales, Tasmania), Canada (Ontario), Central Asia, China (Xinjiang), Estonia, Russia (Urals, Siberian platform, Tuva), USA (Tennessee, Kentucky), Sandbian-Katian; Russia (Urals), lower Silurian; Australia (northern Queensland),

Russia (northeastern Siberia), Emsian; China (Sichuan), Russia (Urals, ?North Caucasus), ?Uzbekistan, Upper Devonian.---FIG. 388a-c. *C. vermontense, middle Chazy Group, Darriwilian, Isle La Motte, Vermont; holotype, YPM.450460, including slides 300-17, 300-18, 300-25 (note, photos of slides were retouched by original authors), $\times 10$; *a*, longitudinal section of slide 300-17 showing latilaminae with imbricated cyst plates separated by dark bands of sedimentary rock; b, longitudinal section of slide 300-18 exhibiting rather varied range of sizes and shapes of moderately convex, imbricated cyst plates; c, tangential section of slide 300-25 showing wide range of sizes of approximately rounded, obliquely intersected cyst plates; two factors are responsible for variations: overall size and relative heights of tangential cuts across individual cysts (Galloway & St. Jean, 1961, pl. 1,1a-1c).-FIG. 388d. C. simplex GALLOWAY & ST. JEAN in GALLOWAY (1957, p. 421), Carter Limestone, Upper Ordovician, Mill Creek, south of Nashville, Tennessee; holotype, YPM.222148, including slide 299-60, ×10; longitudinal section showing highly convex cysts and scattered, well-defined, sharply pointed, denticles on tops of cyst plates, formerly differentiated as villi by GALLOWAY (1957, p. 359), see p. 416 (retouched photo, Galloway & St. Jean, 1961, pl. 1,3a).

- Forolinia NESTOR, 1964a, p. 31 [*Rosenella pachyphylla NICHOLSON, 1886c, p. 21, pl. 1,6, 7; OD]. Skeleton formed of large, gently arched to flattened cyst plates, in places resembling laminae; some thickened to form palisade bands (like superposed cyst plates) that may be perforated by short, longitudinally oriented, cylindrical voids, possibly representing leached-out small pillars and/or superposed denticles; tops of some cyst plates exhibit small, dark, rounded denticles, and a few unthickened cyst plates may show a three-layered microstructure of transversely fibrous layers above and below dense median layer. [This genus bears close similarities to Rosenella, especially to the type species, R. macrocystis. Compare the respective tangential sections of the Rosenella type species (Fig. 387,1b) with the Forolinia type species (Fig. 389b). The main basis for distinguishing between the two taxa is that Forolinia develops much thicker palisade bands containing perforated, slenderly cylindrical, spar-filled voids (or hollow pillars); these latter are considered to be diagenetically altered replacement structures like those developed in a number of early labechiid genera, as outlined above. At least one of the species included recently in genus Forolinia-described as F. lenticularis NESTOR, COPPER, & STOCK (2010, p. 59, pl. 2a-f, 4c-d)-should be included in the genus Labechia. In particular, this species is closely related to representatives of the Labechia prima species group (see p. 720).] lower Silurian: China (Guizhou), Estonia.-FIG. 389a-c. *F. pachyphylla (NICHOLSON), Llandovery, Adavere stage, Päri outcrop (20th century Kattentack fossil locality), Estonia; holotype, NHM P.5629 (Nicholson's slides 283, 283a-e; note that sections 283 and 283a have been partially damaged); a, longitudinal section of slide 283, showing latilaminae consisting of much thickened, flattened to gently curved, palisade bands that alternate with layers composed of large to small, flattened to gently convex, spar-filled cysts; one very large, lens-shaped fill of sedimentary material that probably represents a growth interruption; and palisade bands showing lighter colored, longitudinally oriented, cylindrical voids, with tops of individual palisade bands exhibiting solid, rounded, denticles, $\times 7.5$; b, tangential section of slide 283b showing a large, speckled area of numerous small, light-colored dots on a dark background of an intersected palisade band; these dot-shaped, replacement structures (voids) represent superposed, hollow denticles (or pillars) below upper surfaces (i.e., within thickened palisade bands), whereas the tiny, rounded, dark denticles scattered in lighter, spar-filled, gallery spaces are dark-colored solid structures that have evidently not been replaced on upper surfaces of cyst plates, ×7.5; c, longitudinal section of slide 283a shows part of skeleton with latilaminate alternations between thickened palisade bands, and long-low, very slightly convex, cyst plates, as well as zones with large, light-colored, calcite-spar-filled voids, and lenses filled with dark sedimentary material, ×5 (Webby, 2012c; Nicholson's slides 283, 283a-b, rephotographed by Webby in 1989).
- Priscastroma Кнкомукн, 1999а, р. 801 [178] [*P. gemina KHROMYKH, 1999a, p. 801, fig. 1a-b, 2a-e; M]. Skeleton of irregularly wavy to flattened walls, though in places enclose discrete, chevron-shaped cyst plates; in tangential sections where intersected, these may appear as ring structures; also in a few places, short, dark, solid, cone-shaped elements of finely reticulate (possibly secondary) skeletal material partially filling cyst spaces; in other areas, successive, undulating walls only make contacts at irregular intervals, leaving laterally extensive, calcite-spar-filled gallery spaces with few partitions; walls may have a fibrous microstructure; no pillars, denticles, or astrorhizae recorded. [This simple genus bears only a few diagnostic features: for example, the chevron-shaped cyst plates within individual latilaminae resemble patterns in rosenellid labechiids. Other characters such as the small (possibly secondary) columnlike thickenings and the fibrous microstructure may support KHROMYKH's view (1999a) that the genus was a member of the Lophiostromatidae (see p. 749-753). However, it bears little resemblance to other early lophiostromatids like Lophiostroma shangtungensis YABE & SUGIYAMA, 1930 (see OZAKI, 1938), from a similar Middle Ordovician (Darriwilian) stratigraphic horizon in Shandong Province, northern China, which chararacteristically exhibits much thickened skeletons and long pillarlike columns.] Middle Ordovician (Darriwilian): Siberian platform, Russia.-FIG. 390a-e. *P. gemina, upper Kochakan Formation, Muktei horizon, right bank of Moiero River, 1 km upstream from the mouth of Bugarikta River tributary, central Siberia, holotype, CSGM, T-781/7 (no. 367/1); a-b, views of longitudinal section, a, $\times 4$; b, $\times 8$ (Khromykh, 1999a, fig. 2a, 2d); c, paratype CSGM, T-781/7-1 (no. 367/2), tangential section showing a few ring structures intersected near apices of chevron-shaped cyst plates, ×8 (Khromykĥ, 1999a, fig. 2c); d-e, sketches of longitudinal sections of holotype (no. 367/1) and paratype (no. 367/2), respectively, showing irregular distribution of fine serrations on upper and lower surfaces of walls; d, a few small patches of darker, finely reticulate secondary material in localized places beneath updomed cyst plates, ×20; e, ×15 (Khromykh, 1999a, fig. 1a-b).
- Pseudostylodictyon OZAKI, 1938, p. 208 [*P. poshanense OZAKI, 1938, p. 208, pl. 24,2; M; holotype, pl. 25, 1a-e] [=Parksodictyon BOGOYAVLENSKAYA in Bogoyavlenskaya & Lobanov, 1990, p. 85 (type, Pseudostylodictyon? kayi GALLOWAY & ST. JEAN in GALLOWAY, 1957, p. 425, OD)]. Skeleton with cyst plates, commonly long-low (resembling laminae) in specimens lacking mamelon columns and 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 in interspaces. [The type species of Parksodictyon BOGOYAVLEN-SKAYA in BOGOYAVLENSKAYA & LOBANOV, 1990 (Pseudostylodictyon kayi GALLOWAY & ST. JEAN in



Forolinia

FIG. 389. Rosenellidae (p. 715).



FIG. 390. Rosenellidae (p. 715).



FIG. 391. Rosenellidae (p. 715–719).

GALLOWAY, 1957), is a junior subjective synonym of Pseudostylodictyon lamottense (SEELY, 1904), according to KAPP and STEARN (1975, p. 171). Most of the morphological features of the two species are the same, and both come from similar stratigraphic levels in the Chazy Group and localities on the Isle La Motte, Vermont (United States). Moreover, the characteristic presence or absence of mamelon columns is not regarded as a basis for generic subdivision. Accordingly, it is inappropriate to retain Parksodictyon as a separate genus.] Middle Ordovician (Darriwilian)-upper Silurian: China (Shandong), USA (Vermont, New York), Darriwilian; Australia (New South Wales, Tasmania), ?Kazakhstan, Russia (Chukotsk Peninsula, Urals), USA (Texas), Sandbian-Katian; Norway, lower Silurian; Sweden (Gotland), middle Silurian; Australia (New South Wales), China (Inner Mongolia), middle Silurian-upper Silu--FIG. 391a-d. *P. poshanense, Darriwilian, rian.– Majiagou Group, north of Woyu, Boshan County, Shandong Province; holotype, NIGP no. 121556a; a, longitudinal section of holotype showing overall skeleton of type species in overgrowth relationship with possible lichenariid coral; skeleton shows superposed latilaminate growth best in interspaces between well-developed, variably spaced, mamelon columns, where dark sedimentary rock infills (originally inclusions of mud) intervene successively; cyst plates of variable size and shape, with cyst plates updomed over mamelon columns and broadly flattened to sagging across interspaces, ×2.5 (Webby, 2012c; photos of OZAKI's type thin section in Nanjing collection; see also OZAKI, 1938, pl. 25,1b); b, enlarged view of right side of holotype showing mamelon column with associated denticles, and also a vague impression of one or two, more continuous, upwardly and outwardly radiating, pillarlike structures, ×5 (Webby, 2012c; photos of OZAKI's type thin section in Nanjing collection; see also OZAKI, 1938, pl. 25,1b); c-d, longitudinal and tangential sketches based on type material showing mamelon columns with weakly developed pattern of concentrically arranged cyst plates, outwardly radiating structures, mainly denticles and a few incomplete pillars, ×8 (Ozaki, 1938, pl. 25, 1d-1e). FIG. 391e-g. P. lamottense (SEELY), lower Crown Point Formation, Chazy Group, Darriwilian, Isle La Motte, Vermont; e, specimen RM 14.000 (slide RM 14.000a) from Fisk quarry (Isle La Motte), longitudinal section showing cyst plates that are upwardly inflected adjacent to mamelon column and flattened to slightly concave across interspaces, $\times 10$; f, specimen RM 14.021 (slide RM 14.021b) from Fisk quarry, Isle La Motte, longitudinal section across a mamelon column, some cyst plates that simulate laminae, and denticles; g, specimen RM 14.001 (slide RM 14.001a) from Goodsell quarry, Isle La Motte, longitudinal section showing rows of hollow denticles on upper surfaces of slightly wavy, long, low, cyst plates, ×10 (KAPP & STEARN, 1975, pl. 1,1–3).

Rosenellinella YAVORSKY, 1967, p. 16 [*R. venusta; OD]. Skeleton of long, low cyst plates that typically form in gently wavy to flattened rows; some (including type species) exhibit numerous crenulations represented by calcite spar-filled blebs at tops of cyst plates (only rarely seen to involve upward flexure of cyst plate itself); in tangential sections these small structures appear as rings with lightcolored centers; others show thickened rows of cyst plates with palisade banding, and their upper surfaces have small, solid, dark denticles. [All four recorded species of Rosenellinella have been described from one region in Tuva, southern Russia, based on few specimens, and through a limited stratigraphic interval; consequently, as noted by BOGOYAVLENSKAYA (1971b, p. 37), they may prove on further study to represent a single taxon.] lower Silurian-middle Silurian: Russia (Tuva).-—Fig. 387,2a-b. *R. venusta; Wenlock, Elegest River; a, specimen CNIGR 7351/556, tangential section showing numerous, small, rounded, spar-filled blebs, ×10; b, holotype, CNIGR 7351/555, longitudinal section showing main features of cyst plates and crenulations, ×10 (Yavorsky, 1967, pl. 3,3-4).

Family LABECHIIDAE Nicholson, 1879

[nom. correct. NICHOLSON, 1886a, p. 74, ex Labechidae NICHOLSON, 1879b, p. 28] [=Stratodictyidae BOGOYAVLENSKAYA, 1977a, p. 6; =Tuvaechiidae BOGOYAVLENSKAYA, 1984, p. 6]

Simple, upwardly convex to flattened cyst plates of variable size and rounded pillars exhibiting a range of morphologies, from somewhat sporadically developed small pillars and denticles to, more commonly, more continuous, large, solid pillars, and occasionally where closely spaced, forming chainlike rows. *Middle Ordovician (Darriwilian)–Upper Devonian.*

The group unites genera that characteristically exhibit solid, rounded, large or small pillars. Other features are not taxonomically diagnostic; for example, whether the pillars as seen in tangential sections are separated or occasionally develop in chainlike rows, or whether the cyst plates form imbricated, vesicle-shaped cysts or are more flattened. The genus Tuvaechia (based on type species Labechia regularis YABE & SUGIYAMA, 1930) is regarded as a junior synonym of Labechiella (based on type species Labechia serotina NICHOLSON, 1886c). The only taxonomically significant difference is at the species level (e.g., between the two type species, one with separated pillars and the other showing chainlike rows). Consequently, not only is the genus *Tuvaechia* a junior synonym of *Labechiella*, but BOGOYAVLEN-SKAYA's (1984) family Tuvaechiidae is also a junior synonym of family Labechiidae NICHOLSON, 1879b.

BOGOYAVLENSKAYA's (1977a) family Stratodictyidae, with Stratodictyon WEBBY, 1969, as type genus, is based mainly on the presence of the distinctive long, low cyst rows (what she has called stratocysts; see p. 414). However, similar, elongate, long, low cyst plates are recorded by her in a number of other genera (BOGOYAVLENSKAYA, 1984, p. 11) that belong to other families, recorded here in the rosenellids (Rosenella, Pseudostylodictyon), stromatocerids (Stromatocerium), and stylostromatids (Pachystylostroma, Stylostroma). Therefore, the Stratodictyidae also cannot be maintained as a separated valid group on the basis of stratocysts. BOGOYAV-LENSKAYA's (2001a; and see BOGOYAVLENSKAYA & YELKIN, 2011, p. 18) incorporation of the Stratodictyidae in her order Protolabechiida seems to add further confusion to current taxonomic nomenclature, given that the relevant part of her 2001a diagnosis of that new order states (p. 46): "Vertical elements-denticles, sometimes sporadic," when Stratodictyon, the type genus of Stratodictyidae, exhibits characteristic small pillars (see p. 723).

Labechia Edwards & Haime, 1851, p. 155, 279 [*Monticularia conferta LONSDALE, 1839, p. 688, pl. 16,5,5a; M; only external surfaces of one (or possibly two) of LONSDALE's syntypes from Benthall Edge and/or Gleedon Hill were illustrated initially, and that material is presumed lost; then EDWARDS and HAIME (1855, p. 269, pl. 62,6,6a-c) figured external surfaces of a topotype from Benthall Edge (specimen placed in MNHM, Paris); later, SMITH (1932, pl. 1,1-2) chose a specimen from Wenlock Limestone, Benthall Edge as the neotype (BGS no. 28183, Nottingham), because it had been presented originally by R. I. MURCHISON to the Geological Society of London, and SMITH thought it might have represented one of LONSDALE's syntypes; however SMITH's neotype has remained unsectioned and unstudied. hence it is probably invalidly designated; NICHOLSON (1886a, 1886c, 1889, 1891a) was the first to study thin sections based on specimens from Dudley, Benthall, and Ironbridge, including the Dudley specimen NHM P.5984, with nine thin sections (no.

264, 264a-h) apparently cut from it, but that specimen is missing]. 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 may show upwardly converging cone-in-cone banding in longitudinal section (concentric rings in tangential section). [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 Labechia prima species group to those with long and stout, rounded pillars of the L. conferta species group (WEBBY, 1979a, p. 90). Representatives of the L. prima group commonly show aligned rows of small to moderately sized, lowconvexity cyst plates that, in places, alternate with irregularly laterally continuous bands of spar with loss of original structural elements, perhaps because they were originally poorly calcified bands; finertextured Stratodictyon WEBBY, 1969, exhibits similar patterns of aligned rows of low-convexity cyst plates. Members of the L. conferta group, on the other hand, have interspaces between pillars filled by a meshwork of cysts that are characteristically coarser, more vesicular and more imbricated.] Middle Ordovician (Darriwilian)-Upper Devonian (Famennian): Canada (Quebec), China (Shandong), ?Korea, USA (New York, Vermont), Darriwilian; Australia (Tasmania), Canada (Ontario, Akpatok Island, Newfoundland), China (Xinjiang), Mongolia, Norway, Kazakhstan, Russia (Urals, Gornaya Shoriya, Tuva), Scotland, USA (Alabama, Tennessee, Virginia, Kentucky, Indiana, Ohio, Michigan), Sandbian-Katian; China (Guizhou), Estonia, Russia (Siberian platform, Tuva), lower Silurian; Central Asia, England, Sweden (Gotland), Russia (Russian and Siberian platforms, Urals, Kolyma, Tuva), Ukraine (Podolia), USA (Indiana), middle Silurian; Russia (Siberian platform, Urals, Altai Mountains), Sweden (Gotland), upper Silurian; Canada (Ellesmere Island), China (Sichuan, Guizhou, Hunan), Russia (Kolyma), Lower Devonian; Canada (Alberta), Russia (Russian platform, Novaya Zemlya, Vaigach Island, Urals, northern Caucasus), Ukraine (Donets basin), Frasnian-Famennian.—FIG. 392a-b.*L. conferta (Lonsdale), Wenlock Limestone, Dudley, England, ×5, NHM P.5984, Nicholson's thin sections no. 264, 264g; a, longitudinal section showing solid, vertically aligned pillars with thickening close to skeletal base and in places a cone-in-cone appearance, as well as well-imbricated series of upwardly convex cyst plates; note also thin film of dark matter (possibly originally sediment) and a small, domelike, growth-banded bryozoan colony, near bottom center of field of view (Webby, 2012c; Nicholson's thin section 264g, rephotographed by Webby in 1989); b, tangential section (part of NICHOLSON thin section no. 264) showing round pillars, some with lighter- or darker-colored centers where apices of compositionally distinct cone-in-cone layers are intersected, and cyst plates are represented by offsets between pillars (Webby, 2012c; part of NICHOLSON's



FIG. 392. Labechiidae (p. 720-722).

thin section 264, rephotographed by Webby in 1989).——FIG. 392*c*–*e. L. conferta* (LONSDALE), probably from same Dudley locality and stratigraphic level; specimen AMF.134351, originally presented by T. W. Edgeworth David to Sydney University, ×5 (Webby, 2012c); *c*, tangential section showing rounded pillars with a wide range of diameters; *d*, longitudinal section showing successive latilaminae and pillars extending as papillae into darker sedimentary material above successive tops of latilaminae; *e*, longitudinal section showing initial latilaminate growth over an uneven (possibly unconsolidated) substrate, and a small cavity (now represented as a calcite-spar-filled space) at the base that possibly formed when the initial growth spread (and uparched) over the substrate; note well-developed



FIG. 393. Labechiidae (p. 722-723).

papillae occur at tops of both latilaminae (papillae on terminal surface of this specimen are illustrated in Fig. 316.1) (Webby, 2012c).

Labechiella YABE & SUGIYAMA, 1930, p. 54 [*Labechia serotina NICHOLSON, 1886c, p. 15, pl. 2,3,4; OD] [=?Columna IVANOV in IVANOV & MYAKOVA, 1955, p. 13 (type, C. sokolovi, OD), non PERRY, 1811 (mollusk), nec SIGNORET, 1877 (hemichordate), nec COOPER, 1892 (mollusk); =Tuvaechia BOGOY-AVLENSKAYA, 1971b, p. 34 (type, Labechia regularis YABE & SUGIYAMA, 1930, p. 56, OD)]. Skeleton of longitudinally aligned, continuous pillars, in places closely spaced even in contact, and acutely branching; pillars in transverse section have rounded outline and, where in contact, form incomplete, chainlike 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. [YABE and SUGIYAMA (1930, p. 54) introduced Labechiella as a subgenus of Labechia but misinterpreted the flattened cyst plates of L. serotina as being bars and recognized L. regularis YABE & SUGIYAMA, 1930, p. 56, Ordovician, Liaoning Province, China, as an independent species. Then, nine years later, SUGI-YAMA (1939, p. 443-444) used the same binominal, Labechiella regularis, duplicating the name based on different material from the Silurian of Japan. This action ignored common practices adopted under the International Code of Zoological Nomenclature and caused some confusion (GALLOWAY, 1957; FLÜGEL & Flügel-Kahler, 1968; Webby, 1979a; Mori, 1994). Apparently realizing the error, SUGIYAMA (1940, p. 111-112) substituted the name Labechiellata (printed on an errata slip in SUGIYAMA, 1940, no pagination), which avoided his genus Labechiella SUGIYAMA, 1939, p. 443 (type, Labechiella regularis SUGIYAMA, 1939, p. 444) becoming a junior homonym of Labechiella YABE & SUGIYAMA, 1930 (MORI, 1994, p. 677). However, given the presence of flat-lying cyst plates in SUGIYAMA's Japanese species (a key feature of genus Labechiella YABE & SUGIYAMA, 1930), it was evident that Labechiellata SUGIYAMA, 1940, was also a junior synonym of Labechiella YABE & SUGIYAMA, 1930 (WEBBY in STEARN & others, 1999, p. 14). Furthermore, given broad acceptance of the genus-level status of Labechiella YABE & SUGIYAMA, 1930 (GALLOWAY, 1957; FLÜGEL & Flügel-Kahler, 1968; Webby, 1979a), it was apparent that SUGIYAMA's (1939) L. regularis being a junior homonym of the well-established L. regularis (YABE & SUGIYAMA, 1930) required an alternative name; consequently Labechiella sugiyami WEBBY (1979a, p. 92) was proposed. Reinterpretation of the type material of L. sugiyami by MORI (1994) has since revealed that SUGIYAMA's holotype is part of rugose coral Mazaphyllum CROOK, 1955. With name reversions, the SUGIYAMA taxon becomes the cystiphyllid rugosan Labechiellata regularis (SUGI-YAMA, 1939). Labechiellata SUGIYAMA, 1940, is therefore excluded from the Stromatoporoidea]. Middle Ordovician (Darriwilian)-Upper Devonian: China (Anhui, Liaoning, Shandong), Korea, Malaysia, Darriwilian; Australia (New South Wales, Tasmania), China (Xinjiang), Kazakhstan, Mongolia, Russia (?Altai Mountains, Chukotsk Peninsula, Siberian platform, eastern Siberia, Tuva), USA (Alabama), Sandbian-Katian; Russia (Urals), upper Silurian; Australia (Queensland), Lower Devonian; England, Russia (Urals, ?Altai Mountains, ?Salair), Middle Devonian; China (Sichuan, Hunan), Upper Devo--FIG. 393a-e. *L. serotina (NICHOLSON), nian.-Middle Devonian limestone, Teignmouth, near Torquay, England; holotype, NHM P.5988 (NICH-OLSON's thin sections no. 268, 268a-d); a, longitudinal section (thin section 268a) showing long, continuous, moderate- to large-sized, subparallel pillars, with, in places, acutely shaped branching and closely spaced pillars where chainlike rows have been intersected obliquely; cyst plates mainly thin, flattened to slightly inclined at rather irregular, relatively widely spaced intervals, ×5 (Webby, 2012c; Nicholson section 268a, rephotographed by Webby in 1989); b, tangential section showing rounded, interlinked pillars in slightly sinuous, incomplete, chainlike rows, ×5 (Webby, 2012c; Nicholson's section 268c, rephotographed by Webby in 1989); c, sketch of longitudinal section showing large, regular boxwork of columnar-shaped pillars and platelike cyst plates, and in places, upwardly converging, conelike banding along pillar axes, referred to as axial canals, ×12 (Nicholson, 1891a, p. 162, fig. 19B); d, enlarged longitudinal section showing a single upwardly tapering pillar, with detail of axial cone-in-cone banding, ×25 (Nicholson, 1891a, fig. 19C); e, sketch of tangential section showing pillars arranged in sinuous, mainly incomplete, chainlike rows, and darker and lighter centers of the rounded pillars, ×12 (Nicholson, 1891a, fig. 19A).

Stratodictyon WEBBY, 1969, p. 647 [*S. ozakii; OD]. Skeleton of flattened, undulating to mamelonate latilaminae, with dominantly fine-textured internal features; tangential skeletal elements uniformly more conspicuous than longitudinal structures; cyst plates commonly thin, closely and regularly spaced in rows that enclose long, low cysts, or very sporadically, rows may be more imbricated with irregular distribution; small- to moderate-sized, short pillars, and/or their shorter counterparts (denticles), have patchy distribution in longitudinal section but apparently more evenly spread, preserved as rounded, dark dots in tangential section; also rather inconspicuous astrorhizae may occur. Upper Ordovician (Sandbian-Katian): Australia (New South Wales, Tasmania), Russia (Tuva, northeastern Russia), USA (Alabama, New York) .----- FIG. 394a-d. *S. ozakii, lower part of Fossil Hill Limestone, lower Eastonian, Licking Hole Creek area, central New South Wales; a-b, holotype, AMF.99377 (AMFT.15020, 15021), longitudinal and tangential sections showing part of latilaminate skeleton with rows of long, low cyst plates and scattered short pillars, in tangential section, represented by fine, rounded, dark dots, ×10 (Webby, 1969, pl. 119,4–5); c, paratype, AMF.99382 (AMFT.15023), tangential section showing pillars mainly as rounded black dots, and a few light-colored (spar-filled) astrorhizal tracts, ×10 (Webby, 1969, pl. 120,2); d, topotype IGTUT 477, enlarged view of longitudinal section showing cysts arranged in rows bounded by rather thin, laterally continuous, lamina-like cyst plates, but in a few places these elements are downwardly inflected to close off cystlike (lenticular) spaces, and short, dark pillars of variable lengths and thicknesses are represented, as well as small areas where skeletal structures are barely recognizable because of spar replacement, ×25 (Webby, 2012c; preparation and photography courtesy of Heldur Nestor).-—Fig. 394e. S. columnare WEBBY, Fossil Hill Limestone near west Boonderoo shearing shed, central New South Wales; holotype, AMF.99378, exhibiting a fine-textured latilaminate skeleton very similar to that of S. ozakii but additionally producing moderately large, vertically persistent mamelon columns that also include areas of spar replacement toward their axes, ×5 (Webby, 1969, pl. 118,4).

Family STROMATOCERIIDAE Bogoyavlenskaya, 1969

[Stromatoceriidae BOGOYAVLENSKAYA, 1969b, p. 16] [=Cystostromatidae KHROMYKH, 1974a, p. 28, *partim*]

Coarse-textured labechiids with skeletal mesh of large, erect, post- to platelike pillars, cyst plates of large to moderate sizes, and shapes that vary from flattened or low convexity elements simulating laminae to both moderately convex and concave cyst plates; usually flattened to concave across narrower interspaces but may be convex upward in near proximity to mamelon



FIG. 394. Labechiidae (p. 723).

columns or across wider interspaces; in tangential outline, pillars may be irregularly rounded to elongate, serrated, meandriform or star shaped, or may even develop partially closed polygonal meshworks; intersections between rows of cyst plates and pillars may vary from approximately right-angle relationships to inclined at angles of at least 45° to alignment of erect pillar centers; denticles may be present on tops of cyst plates and locally on outer walls of pillars; astrorhizae not positively confirmed. *Upper Ordovician* (Sandbian–Katian).

Stromatocerium HALL, 1847, p. 48 [**S. rugosum* HALL, 1847, pl. 12,2; M] [?=*Nestoridictyon* KHRO-MYKH, 2001, p. 348 (type, *N. webbyi*, OD)]. Pillars large, continuous, with interiors preserved as sparry calcite infills (rarely solid); angular-oval to meandriform with lateral offsets to star-shaped (rarely regularly rounded) 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. [The genus includes a comparatively wide range of forms with rather different longitudinal structural elements, recognized presently as belonging to three species groups: (1) S. rugosum group (including type species), which is characterized by having pillars that in tangential section show vermicular to irregularly radiating outlines, rarely exhibit denticles, and apparently not associated with mamelon columns (GALLOWAY & ST. JEAN, 1955); (2) S. bigsbyi group, based on S. bigsbyi WEBBY, 1979b, p. 248, characterized by pillars that in tangential section are oval to angular (rarely more complex), they lack denticles (were it not for the predominant sparry calcite pillar infills, such a form might be more appropriately assigned to Labechiella); and (3) S. michiganense group (including S. michiganense, S. platypilae GALLOWAY in GALLOWAY & ST. JEAN, 1961, and S. pergratum NESTOR, 1976; =S. moierense BOGOYAVLENSKAYA, 1977a), which exhibits pillars with meandriform, platelike offsets that in places become partially closed polygonal meshworks.] Upper Ordovician (Sandbian-Katian): Australia (Tasmania), Canada (Manitoba, Ontario, Quebec), China (Xinjiang, Qinghai) ?Mongolia, Russia (Taimyr Peninsula, Urals, Chukotsk Peninsula, Siberian platform, Tuva), USA (New York, Ohio, Kentucky, ?Mich--FIG. 395a-d. *S. rugosum, Upper Ordoigan).vician Black River Group, Watertown, New York, holotype, AMNH 590/5A, B, C, E; a, longitudinal section (thin section 590/5A) showing a coarse, gridlike pattern of laterally continuous, flattened to gently undulating cyst plates, and moderately large, subparallel, calcite-spar-filled pillars usually growing apart, but in a few places they become more closely associated with lateral flanges or offsets, seemingly interconnecting them together in composite structures; b, tangential section (thin section 590/5C) showing varied slender, composite pillar outlines, from elongate to vermicular (with or without flanges), even sometimes radiating outward from a center; c, tangential section (thin section 590/5E) through another radial center with thicker, elongate to vermicular patterns; d, longitudinal section (thin section 590/5B) showing similar features to those exhibited in view a, $\times 10$ (Galloway & St. Jean, 1955, fig. 2,3,5,6).

Cystistroma ETHERIDGE, 1895, p. 134 [*Labechia(?) (Cystistroma) donnellii ETHERIDGE 1895, p. 134, pl. 14, 1-6; pl. 15, 1-2; pl. 16, 1-3; M]. Coarsetextured skeletal mesh of large pillars and cyst plates; pillars, long, stout, may radiate upward and outward but rarely branch; in tangential section including oval, irregular, elongated, and,

in places where tiny, outwardly directed, spinelike denticles are intersected, show serrated outlines; pillar interiors commonly preserved as sparry calcite infills; a few denticles also occur on tops of large, undulating to sagging cyst plates; away from intersecting pillars, cyst plates may be more gently convex. Upper Ordovician (upper Sandbian-Katian): Australia (New South Wales), Canada (Ontario, Quebec), Estonia, Russia (?Urals, Siberian platform), USA (New York, Kentucky, Michigan).---FIG. 396a-g. *C. donnellii, lower part of Fossil Hill Limestone, lower Eastonian, Fossil Hill, near Belubula River, Boonderoo property, central New South Wales, Australia; a-c, lectotype, MMF907, 14517; a, longitudinal section showing general appearance of skeletal meshwork with large, spar-filled pillars and flattened to gently concavely shaped cyst plates, ×2 (Pickett, 1970, pl. 1,1); b, tangential section showing spinelike denticles on outer walls of spar-filled pillars; tiny spar-filled dots and rods in central dark area of sedimentary matrix are difficult to interpret but are unlikely to represent denticles associated with an obliquely intersected cyst plate, ×10 (Pickett, 1970, pl. 2,1); c, longitudinal section that shows scattered, spar-filled denticles on both the outer surfaces of large pillars and the upper surface of a cyst plate, ×10 (Pickett, 1970, pl. 2,2); d-e, topotype, AMF.98995 (variant A), tangential and longitudinal sections showing large pillars with oval outlines in tangential section and cyst plates that mainly drape across interspaces between adjacent pillars; localized areas of the pillars and cyst plates of this better preserved specimen exhibit brown, compact, specked material, ×5 (Webby, 1969, pl. 122,7, pl. 123,1); f-g, topotype, AMF.99005 (variant B), longitudinal and tangential sections showing pillars with more angular to bladelike outlines in tangential section and more complete alternation of skeletal elements, especially the pillars, replaced by calcite spar, ×5 (Webby, 1969, pl. 123,2-3).

Radiostroma WEBBY, 1979c, p. 208 [*R. tenue WEBBY, 1979c, p. 210, fig. 5B-E; M]. Pillars long, slender, erect, vanelike, commonly fused at centers of closely associated, narrow, mamelon columns; in tangential section, pillars commonly stellate shaped, but in a few places more complex, partially closed, polygonal meshworks occur; denticles randomly developed on tops of cyst plates, and in places denticle-like spines may be present on free outer edges of bladelike pillars; cyst plates extend as thin, commonly undulate to concave-upward elements between pillars. Upper Ordovician (Katian): Norway.—FIG. 397a-d. *R. tenue, Mjøsa Limestone, north of Bergvika, Lake Mjøsa; holotype, PMO 97113; a, longitudinal section showing pillars with long, slender, vertical vanelike plates (looking spinelike where a plate is intersected at right angles), and cyst plates that typically drape successively off pillars, either sagging across narrower interspaces or undulating where one or more cyst plates are involved across



С

Stromatocerium

FIG. 395. Stromatoceriidae (p. 724-725).

wider spaces; in a few places denticles occur on upper cyst plates, ×5 (Webby, 1979c, fig. 5B); b, tangential section showing pillars are formed of four or five short, radiating, vanelike plates that may be fused near axis to give a stellate outline (Webby, 1979c, fig. 5D); c, tangential section showing complex pillars with their outwardly radiating, vanelike plates, but also in places, one or two concentrically arranged, closely spaced cyst plates intersect these vanelike plates, producing centers with fine meshworks of tiny, complete and incomplete, polygonal spaces, ×5 (Webby,

1979c, fig. 5C); d, longitudinal section showing vanelike, vertical pillars (some parts of plates being intersected at right angles, others obliquely or near parallel to individual plates, and in these latter areas, traces of tiny, parallel spines may be seen inclined upward and outward away from the pillar centers to about 25 degrees; also in places, well-defined, spar-filled denticles are exhibited on tops of cyst plates, and the spar-replaced cyst plates also seem to have been disrupted (perhaps even perforated) in places, ×10 (Webby, 1979c, fig. 5E).



FIG. 396. Stromatoceriidae (p. 725).



FIG. 397. Stromatoceriidae (p. 725-726).

Family PLATIFEROSTROMATIDAE Khalfina & Yavorsky, 1973

[Platiferostromatidae KHALFINA & YAVORSKY, 1973, p. 32]

Pillars long, solid, erect and branching, platelike elements, with tangential sections that show a variety of outlines from rounded, angular, triangular, starshaped, meandriform, and anastomosing to zigzagged shapes, even locally, incomplete polygonal networks; cyst plates also exhibit a range of form from long, low, extended elements, simulating laminae, to more numerous, variably sized, blisterlike, imbricated cyst plates, with minimal upflexing of cyst rows adjacent to pillars; astrorhizal centers and pathways may be present, but their taxonomic significance remains uncertain. *Silurian (Llandovery)–Upper Devonian (Famennian).*

- Platiferostroma KHALFINA & YAVORSKY, 1973, p. 32 [*Stromatocerium hybridum Dong, 1964, p. 284 [294], pl. 2,3-8; OD; some discrepancies exist between catalogue numbers marked on thin sections of types of P. hybridum housed in Nanjing collections, and published registration numbers cited in descriptions and captions of plates published by DONG (1964); a few details are noted below]. Pillars long, continuous, intermittently branched, platelike, elements that may be moderately widely spaced and/or of varying thickness, dependent on orientation of pillarlike plates where intersected in longitudinal section, and proximity to a branch; in tangential section outlines are mainly irregularly elongate to meandriform, though a few, small, rounded or more complexly flanged offsets, even incompletely fused polygonal meshworks, may also be shown; cyst plates are thin and enclose numerous, variably sized (mainly small), convex-upward, imbricated cysts across interspaces between pillars, with rows not noticeably upflexed adjacent to pillars. Upper Devonian (Famennian): Australia (Bonaparte basin), China (Guangxi, Guizhou, Sichuan, Hunan), Vietnam, Russia (Northern Caucasus, Novaya Zemlya), Ukraine (Donets basin), Uzbekistan.-FIG. 398, 1a-d. *P. hybridium (DONG), lower part of Shizixu Formation, between Huangjin and Muliu, Luocheng County, Guangxi Province, ×5; a, holotype, NIGP Kw044-3 (14167), longitudinal section showing pillars of variable thickness, and in places, forklike branches and small- to moderate-sized, upwardly convex cyst plates (this specimen is recorded as a paratype; Dong, 1964, pl. 2,5); b, paratype, NIGP Kw044-2 (14170), tangential section showing darkcolored, irregular, elongate, flanged, meandering, sinuous, and rarely small-rounded outlines of pillars and patchy development of finer, obliquely intersected cyst plates (this specimen is recorded as part of the holotype; Dong, 1964, pl. 2,4; 2001, pl. 19,2); c, doubtful holotype, NIGP Kw044-3 (14168), oblique section showing mainly elongate to irregularly meandering pillars and cyst plates (Webby, 2012c; courtesy of Dong De-yuan); d, paratype, NIGP Kw044-2 (14169), longitudinal section showing long pillars that are thickened and branched in places, and vaguely aligned, imbricated rows of small, upwardly convex cyst plates (this figure was recorded as part of holotype; Dong, 1964, pl. 2,3; 2001, pl. 19,1).
- Cystocerium NESTOR, 1976, p. 41 [*C. sincerum NESTOR, 1976, p. 42; OD]. Pillars long, stout, sporadically branching, platelike structures; in tangential section showing rounded, angular, oblong, and vermicular shapes; walls of long, low cyst plates, thin and simulate laminae; astrorhizae represented by stellate pattern of radiating, wall-less pathways. [Cystocerium exhibits some similarities to Parastylostroma BOGOYAVLENSKAYA, 1982a, but it has a much denser concentration of branching, pillarlike elements than is characteristic of Parastylostroma.] Silurian (Wenlock): Russia (Siberian platform).—FIG. 399a-b. *C. sincerum,

Moiero River section, Siberian Platform, holotype, IGTUT 166-29 (Co3217); a, longitudinal section showing latilaminate skeleton, prominent solid pillars that frequently branch and rapidly thicken from slender initial offshoots, and rather thin, long, low cyst plates; b, tangential section exhibiting highly variable shapes and sizes of pillar outlines within skeleton, from small-rounded to larger-triangular to irregular-oblong and vermicular, and a few, well-defined, calcite-spar-filled, wallless, astrorhizal pathways, ×10 (Nestor, 1976, pl. 9,1a-b).—FIG. 399c-d. C. stellatum NESTOR, Wenlock, Moiero River section (different locality and slightly higher stratigraphic level), Siberian Platform, holotype, IGTUT, 166-30 (Co3216); c, tangential section exhibiting wall-less pathways radiating and branching from astrorhizal centers and pillars with regularly rounded to subangular outlines; d, longitudinal section showing more regularly aligned pillars with fewer branches and more narrowly spaced long, low cyst plates, ×10 (Nestor, 1976, p. 43, pl. 9,2a-b).

- Parastylostroma BOGOYAVLENSKAYA, 1982a, p. 36 [*Stromatocerium irregularis VASSILYUK, 1966, p. 44; OD]. Pillars are long, solid, rod- to platelike, longitudinal elements, and in places, branched; in tangential sections, outlines of pillars may be rounded, elongate, or meandering with short, lateral offsets; rare denticles occurring on tops of cyst plates; in most places, cyst plates are thin, flattened (long, low), or more gently convex to wavy; cyst plates usually maintain a relatively flattened to slightly sagging disposition between pillars; no astrorhizae seen. [The relationships between Parastylostroma and Vietnamostroma are discussed herein (see p. 732)]. Upper Devonian (Famennian): Russia (Northern Caucasus, Novaya Zemlya), Ukraine (Donets basin), Uzbekistan.-—Fig. 400, 1a-b. *P. irregularis (VASSILYUK), Famennian sequence, Porfirtovaya ravine, near Novotroitskoye village, Donbass, Ukraine, holotype, DPI 12/130, longitudinal and tangential sections, ×5 (Vassilyuk, 1966, pl. 32,8a-b).
- Pleostylostroma WANG, 1982, p. 24 [*Labechia shiniulanense WANG, 1978a, p. 14, pl. 2, 1a-b; OD]. Pillars are long, erect, moderately closely spaced, platelike elements that are of variable thickness dependent on orientation of longitudinal section and incidence of branches; in tangential section, pillars exhibit irregularly rounded to elongated, or triangular to starlike shapes; cyst plates vary from small and incomplete to larger and complete cystlike elements across pillar interspaces; cyst plates have variable convexity and in many places show overlapping relationships but are not regularly imbricated; cyst plates usually thin; cyst rows extending without conspicuous sagging or updoming between pillars; in tangential section, cyst plates show approximately rounded outlines; no denticles or astrorhizae. [This genus exhibits a superficial resemblance to stromatocerid genus Radiostroma WEBBY, 1979c, but it has thicker, solid, platelike pillars rather than the thin, bladed,



FIG. 398. Platiferostromatidae (p. 729-732).



FIG. 399. Platiferostromatidae (p. 729).

or flanged pillars of *Radiostroma*; and smaller, nondenticulate, cystose elements that are not markedly inflected upwardly against adjacent pillars, in contrast to the cysts of *Radiostroma* that are larger, denticulate, and become steeply inclined close to adjacent pillars.] *lower Silurian (Llandovery):* China (Sichuan).——FIG. 401*a*–*d.* **P. shiniulanesse* (WANG), Shiniulan Formation, Shiniulan, Guanyinqiao, Qijiang County, holotype, CIGMR, Gsf 105-5 (Ss1001); *a*, longitudinal section showing long, slender pillars, thickened only in a few places, in proximity to a branch, and with moderately upflexed, blisterlike, imbricated cyst plates of variable size; *b*, tangential section exhibiting solid pillars with round, elongate to subtriangular outlines, and thin cyst plates that enclose irregularly rounded, spar-filled spaces; *c*, tangential section showing solid pillars with elongated to subtriangular and

subrounded outlines, in part aligned radially, and small, subrounded cyst plates in interspaces; d, longitudinal section exhibiting thicker pillars, where platelike or branching forms are intersected obliquely, and cyst plates upwardly arch and are of markedly different sizes, ×5 (Wang, 1982, pl. 1,3-6).——FIG. 401e-f. P. coalitum WANG, 1982, Shiniulan Formation, Shimenkair, Qijiang County; holotype, CIGMR, Sf1-3 (Ss1069); e, longitudinal section showing thinner, erect, platelike pillars and very thin, gently convex, cyst plates; f, tangential section showing that pillars may sometimes develop more complex polygonal to starlike outlines representing outwardly flanged, platelike pillars, ×5 (Webby, 2012c, courtesy of Wang Shu Bei; see also WANG, 1982, pl.1,7-8).

?Stromatodictyon KHALFINA, 1972, p. 148 [*S. repentinium KHALFINA, 1972, p. 152, pl. C-12, fig. 4-5, M]. Skeleton with broad, continuous, longitudinally branched, irregular to bladelike or flanged pillars (with somewhat ragged margins) that are intersected by banded, laminar (or latilaminar) elements composed of an alternating lower part, with a laterally somewhat discontinuous, comparatively finer, denser meshwork of cystose layers and/ or microlaminae and short micropillars or denticles, and with an upper part of large, spar-filled chambers that are bounded by large, flattened to sagging cyst plates. In tangential section, coarser, interconnected, open and closed meshworks are represented that comprise darker, irregularly rounded to bladed or flangelike pillars and lighter areas with irregularly branching to sinuous sparfilled canals, including astrorhizal structures, as well as some irregular to more rounded spar-filled cystlike cavities. [The genus was incompletely described, and no holotype specimen number was printed in the original publication, but the genus does seem to be a distinctive labechiid, here tentatively included in the family Platiferostromatidae. Previously the genus was referred to the order Actinostromatida (included in the subfamily Plumataliniinae BOGOYAVLENSKAYA, 1969b, family Pseudolabechiidae BOGOYAVLENSKAYA, 1969b) by STOCK (in STEARN & others, 1999, p. 37), but since excluded (see Actinostromatida, p. 769-779). Stromatodictyon has slight resemblances to Cystocerium NESTOR, 1976, with its well-developed, dense, branching pillars, but these pillars are more distinctively flanged, micropillars and denticles may be associated at the margins of the pillars, and a much finer development of cystose elements occurs within laminar layers of the skeleton. Stromatodictyon may also be compared to another genus, Tarphystroma NESTOR, COPPER, & STOCK (2010, p. 62), which these authors tentatively included in the Lophiostromatidae (the genus is similarly treated herein as a questionable member of the family Lophiostromatidae; see p. 753); however, compared to Stromatodictyon, with its characteristically branching, flanged pillars and traces of marginal micropillars and denticles, Tarphystroma has markedly different, comparatively short, stout, longitudinally oriented, cone-in-cone type, bundled upgrowths.] *Silurian (upper Llandovery–lower Wenlock)*: Russia (Siberian Platform).——FIG. 398,2*a–b.* **S. repentinium*, Moiero River section; holotype may exist in CSGM but has not been found, presumed lost; *fide*, V. G. Kromykh, personal communication, November 2011); *a*, longitudinal section of holotype, ×10 (Khalfina, 1972, pl. 12,4); *b*, tangential section of holotype, ×5 (Khalfina, 1972, pl. 12,5).

Vietnamostroma NGUYEN HUU HUNG & MISTIAEN, 1998, p. 63 [* V. vietnamense Nguyen Huu Hung & MISTIAEN, 1998, p. 64, pl. 5, 1a-e; OD]. Pillars long, complex, platelike to flanged and, in places, multibranched; tangential sections show meandering to anastomosing outlines with zigzag offsets; these latter commonly developing areas with open, incompletely partitioned, polygonal meshworks, even becoming partially closed meshes in a few forms; cyst plates thin, long, low, simulating laminae; astrorhizae may be present. [This genus, like Parastylostroma BOGOYAVLENSKAYA, 1982a, exhibits long, low, rather flattened, cyst plates but differs in having pillars that are longitudinally more complexly flanged and multibranched, and in showing in outlines that they are more meandriform to anastomose, or incompletely partitioned meshworks. The pillars of a few Late Devonian species such as V. kueichowense (DONG, 1964), V. kwangsiense (DONG, 1964), and V. chaetetiporoides WANG (1988) even exhibit patchy clustering of completely closed polygonal outlines, resembling meshworks seen in some Ordovician stromatocerids, e.g., members of the Stromatocerium michiganense species group (see especially S. michiganense PARKS in GALLOWAY & ST. JEAN, 1961, p. 64, pl. 9,3b). BOGOYAVLENSKAYA (1973b, p. 22) and NESTOR (1976, p. 25) have suggested that Late Devonian species exhibiting these features were more likely to be chaetetids, but these views are rejected in favor of maintaining their relationships within labechiids, and herein, members of family Platiferostromatidae.] Upper Devonian (Famennian): China (Guizhou, Sichuan), Vietnam.-FIG. 400, 2a-b. *V. vietnamense, upper part of the Cù Bai Formation,1 km northeast of Phong Nha Cave, Phong Nha area, Quang province, Vietnam; holotype, FN.743/2, RIGMR; a, longitudinal section showing long, slender, erect, manybranched, platelike pillars, as well as rows of long, low cyst plates, ×10; b, tangential section exhibiting incomplete meshworks of irregular to sinuous, platelike pillars with numerous, short, lateral, zigzagged offsets, obliquely intersected cyst plates, and patterns of broadly ramifying and branching astrorhizal pathways, ×10 (Webby, 2012c, courtesy of Nguyen Huu Hung & Bruno Mistiaen).-—Fig. 400,2c-d. V. kueichowense (DONG, 1964), p. 286 [295], pl. 3,7-8, pl. 4,1-2, lower part of Gelaohe Formation, Famennian, between Wuliqiao and Biaoli, Dushan County, Guizhou Province, holotype, NIGP, Gy311-1 (14156-14157); c, tangential section showing variety of anastomosing, meandering, partially and completely fused meshworks of



FIG. 400. Platiferostromatidae (p. 729-734).



FIG. 401. Platiferostromatidae (p. 729-732).

platelike, zigzag-shaped pillars across broad centers, identified by the near-parallel, curved lines of cyst plates, $\times 5$; *d*, longitudinal section showing flanged or platelike pillars that produce offsetting branches as they radiate upward and outward from weakly developed centers, defined by weakly updomed, closely spaced, long, low cyst rows, $\times 5$ (Dong, 2001, pl. 19,3–4).

Family STYLOSTROMATIDAE Webby, 1993

[Stylostromatidae WEBBY, 1993, p. 58]

Strongly mamelonate with longitudinal elements ranging from discrete, simple, rounded, outwardly radiating branched pillars to more platelike, flanged or pinnately arranged, composite pillars in mamelon columns; cyst plates range widely in size and shape, commonly low convexity to flattened, and upwardly arching into closely spaced rows across mamelon columns (and composite pillars); denticles commonly formed on tops of cyst plates and locally superposed to form short pillars; markedly latilaminate skeletons may exhibit successive phases of thickened skeletal material. *Middle Ordovician (Darriwilian)–Upper Devonian* (*Famennian*).

Stylostroma GORSKY, 1938, p. 15 [*S. crassum; OD] [=Mamelolabechia KHROMYKH, 1977, p. 44 (type, Pseudolabechia tuberculata YAVORSKY, 1955, p. 66-67, OD)]. Skeleton mamelonate with pillars commonly restricted to mamelon columns, as simple, postlike, and upwardly and outwardly radiating, branching elements; pillars may be clustered in multibranched arrays, developing stellate or other less regular patterns tangentially, or may be more loosely interconnected where branching is more open and at less frequent intervals; denticles, or less commonly, short, unbranched, superposed pillars may occupy interspaces between columns; cyst plates commonly of small to moderate size and low convexity in regular cyst rows, but sometimes more cystose and imbricated patterns occur, especially across interspaces. [The type species of Stylostroma (S. crassum) is characterized by having upwardly and outwardly radiating pillars that branch repeatedly within broad mamelon columns, giving an approximately stellate appearance of platelike forms where pillar branches remain fused toward the axis, but the pillars have a postlike form where unbranched, especially away from centers. S. tuberculata (YAVORSKY) is at the other end of the range of morphological forms assigned to this genus. It shows more open and much less frequent branching in mamelon columns, and these pillars mainly exhibit postlike structures. A complete gradation of morphological forms exists between end members, here referred to as the S.crassum and S. tuberculata species groups. No clear-cut, age-related subdivision exists between the two morphological types: the simpler, mainly postlike S. tuberculata morphologies are not restricted to the Ordovician-Silurian record, nor are the more complexly fused S. crassum-type morphologies limited to the Late Devonian. Consequently, it remains preferable not to divide the genus into two, as favored by KHROMYKH (1977), with Mamelolabechia reserved for the Ordovician-Silurian species, and Stylostroma for the Late Devonian species. Additionally, a number of Chinese Ordovician species of Stylostroma have been retained in Pseudolabechia YABE & SUGIYAMA, 1930, by DONG and WANG (1984), and DONG (2001), but

should be excluded from that genus, as the type species is an actinostromatid (see MORI, 1968, 1970; STOCK in STEARN & others, 1999; and see p. 771-776). Apart from some differences in preservation of the early forms, all the species of Stylostroma exhibit mamelon columns and pillars that branch and splay upward and outward from their centers, and cyst rows that range from long, low to imbricated, blisterlike profiles.] Upper Ordovician (Sandbian)-Upper Devonian: Australia (Tasmania), China (Xinjiang), Norway, Sandbian-Katian; China (Guizhou), lower Silurian; Russia (Siberian platform), middle Silurian; Australia (northern Queensland), Lower Devonian; Canada (Alberta), China (Sichuan, Guizhou, Guangxi, ?Hunan), Kazakhstan, Russia (northern Caucasus, Novaya Zemlya, Urals, northeastern Siberia), Ukraine (Donets basin), Upper Devonian .--Fig. 402*a-i*. *S. crassum, southern shore of Melkaya Bay (loc. 401), Samolet Peninsula, probably upper Famennian, Novaya Zemlya, Russia; holotype, CNIGR, 5767/6; a-c, slide 5767/6b, low to high magnification longitudinal sections; a, $\times 2$; b, $\times 5$; c, ×10; *d-e*, slide 5767/6c, longitudinal sections, ×5; f-h, slide 5767/6a, low to high magnification sections; f, ×2; g, ×5; h, ×10; i, topotype, tangential section, ×5; this latter specimen was termed an autotopotype by GORSKY (1938), probably to signify its special significance as collected from the type locality by the original author of the species (Gorsky, 1938, p. 15, pl. 2,2-7, pl. 3,2).

Eopennastroma WANG, 1978c, p. 104 [*E. sinense; OD]. Skeleton usually exhibits moderately upraised, relatively narrow (mamelon-like) columns and broad intercolumnar spaces; pillars centered in columns and comprising relatively long, slender, platelike axial structure with associated open branches or weakly bundled elements; shorter lateral offsets occurring in places off main axial plates; abundant, small, closely spaced, imbricated cyst plates usually dominate columnar areas, but in a few places they extend outward in rows across intercolumnar spaces, alternating with large, nearly complete cyst plates with gently convex to flattened, or concave-shaped profiles; denticles occur sporadically on tops of cyst plates; becoming short pillars in places where associated with rows of small cyst plates; in oblique-tangential section, pillars appear dominantly as elongated to curved plates with short lateral offsets. [Platelike pillars in Eopennastroma are markedly less densely clustered than in Pennastroma. The holotype of Eopennastroma is not illustrated in a section that is precisely oriented tangentially. However, WANG (1978c, p. 105) designated two other species, E. guizhouense WANG, 1978c, and E. multicystosum WANG, 1978c, from the same locality and horizon as the type species that do exhibit pillar shapes set within columns and completely encircled by outwardly directed cyst plates, demonstrating that they are well-oriented tangential sections. The pillar shapes in E. guizhouense include one example that has four unequal branches (with lateral offsets) diverging



FIG. 402. Stylostromatidae (p. 735).



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FIG. 403. Stylostromatidae (p. 735-738).

from a center to one side of a column (WANG, 1978c, pl. 27,4b), and in *E. multicystosum*, several examples of gently arcuate, slender, single, stipelike structures with spiny lateral offsets occur (WANG, 1978c, pl. 28,1b). It seems therefore that *Eopennastroma* has a pillar outline that is more bar shaped than outwardly radiating (stellate) from centers of the columns.] *Upper Devonian (Famennian):* China (Guangxi, Guizhou).——FIG. 403,1*a*–*b.* **E. sinense*, lower part of Gelaohe Formation, Pinglang, Duyun, Guizhou Province, holotype, CIGMR, no. GS–70, 71, longitudinal and partially tangential to oblique sections, ×5 (Webby, 2012c, courtesy of Wang Shu Bei; see also WANG, 1978c, pl. 27,3*a*–*b*).

- Pachystylostroma NESTOR, 1964a, p. 23 [*Stromatopora ungerni Rosen, 1867, p. 75, pl. 9; OD]. Skeleton usually moderately to strongly mamelonate; cysts of variable size; cyst plates alternating between thicker, gently wavy laminae; mamelon columns sometimes lacking; where present have simple, upwardly and outwardly branching pillars, and in some cases axial thickening of skeletal elements; denticles commonly developed on upper surfaces of thickened laminae, less common on tops of individual cyst plates; locally, successive, close-spaced laminae may appear palisade-like where intersected by short, superposed pillars. [The main feature of this genus that allows it to be distinguished from Stylostroma is the presence of thickened, wavy laminae. NESTOR (1964a) recognized the following three species groups: (1) P. ungerni species group that exhibits strongly compacted mamelon columns; (2) P. contractum species group that has weakly developed mamelon columns; and (3) P. estoniense species group that shows well-developed, slender mamelon columns incorporating well-differentiated branching pillars.] Middle Ordovician (Darriwilian)–Upper Devonian: USA (Vermont, New York), Darriwilian; Australia (Tasmania), Canada (Ontario), Norway, Estonia, Russia (Altai-Sayan, Tuva), USA (Alabama), Sandbian-Hirnantian; Estonia, Ireland, Llandovery; Russia (Siberian platform), Sweden (Gotland), Wenlock; Estonia, Ludlow-Pridoli; China (Sichuan), Russia (Novaya Zemlya, Vaigach Island, Urals), Upper Devonian.—FIG. 404a-c. *P. ungerni (ROSEN), Hilliste Formation, Suuremõisa, Hiiumaa Island, Estonia; a-b, lectotype, IGTUT 112-2 (Co3011), longitudinal and tangential sections, ×5 (Nestor, 1962, pl. 2,1-2; 1964a, pl. 4,4-5); c, paralectotype, IGTUT 112-2 (Co3012), longitudinal section, note uneven base of skeleton in part overgrowing fragment of halysitid coral and large area of calcite spar fill, ×5 (Webby, 2012c, courtesy of Heldur Nestor).
- Pennastroma DONG, 1964, p. 296 [**P. yangi*; OD]. Pinnately arranged, composite, platelike pillars developing within rather narrowly centralized, upwardly arching (possibly mamelon) columns as upwardly and outwardly splayed elements on either side of a more continuous, centralized, platelike structure, or grading into areas where central plate has mainly lateral, yard-arm-type offsets,

best represented in obliquely oriented sections; in other areas these composite pillars may either branch, maintain their rather sinuous courses, or develop breaks in upward continuity; broad, intercolumnar spaces composed dominantly of large, complete to near complete, weakly convex to flattened, or concave cyst plates; in places these may alternate with one or more rows of small, imbricated cyst plates that seldom extend entirely across an intercolumnar space; successive rows of tiny, imbricated cyst plates are most commonly intermeshed with pillar offsets within uparching columns; denticles (and short pillars) of intercolumnar spaces are usually confined to tops of more complete cyst plates. [This genus differs from Stylostroma in displaying more concentrated, centralized, columnar areas with innumerable well-developed lateral (yard arm) offsets from its platelike pillars. However, MISTIAEN, HOU, and WU (1997) questioned the validity of the genus Pennastroma based on a study of material from Famennian deposits in the Etaoucun section of the Guilin region, Guangxi province. They identified their species as belonging to Stylostroma, claiming that features-in longitudinal sections, pectinate and penniform aspects of the pillars, and in tangential sections, the V-shaped outlines of pillars-were not diagnostic, therefore arguing that DONG's (1964) original genus Pennastroma was a junior synonym of Stylostroma GORSKY, 1938. But MISTIAEN, HOU, and WU (1997) did not study (or revise) the original type material of Pennastroma (P. yangi) housed in Nanjing, nor use comparative material from the original type locality (Luocheng area, Guangxi province), nor attempt to compare their species with species of Stylostroma (more than 10 species) already described from the Famennian of southern China (DONG, 1964; WANG, 1978b, 1978c, 1988). The case for relegating Pennastroma to junior synonomy within Stylostroma is, therefore, not based on comparisons between the same or similar type material and should be rejected. It remains, however, a matter of concern that so few, well-oriented, tangential sections have been used to describe Pennastroma and related taxa, preventing their three-dimensional form from being fully evaluated. Upper Devonian (Famennian): Australia (Bonaparte basin), China (Guangxi, Guizhou, Hunan), ?Uzbekistan.-FIG. 403,2a-d. *P. yangi, lower part of Shizixu Formation, between Huangjin and Muliu, Luocheng district, northern part of Guangxi Province, holotype, NIGP, Kw047-2 (14160-14162); a, longitudinal section, thin section no. 14162, $\times 2$; b, obliquely oriented section, thin section no. 14161, ×3.5; c, enlarged longitudinal section, thin section no. 14162, $\times 2$; d, longitudinal section, thin section no. 14160, ×3.5 (Webby, 2012c, courtesy of Dong De Yuan; see also DONG, 1964, pl. 4,3-5).

Spinostroma WANG, 1978b, p. 131 [*S. diversum; OD] [=Sichuanostroma WANG, 1978b, p. 133 (type, S. robustum WANG, 1978b, p. 133, pl. 42,3, OD)]. Pillars large, erect, rather compact, solid, rodlike to



FIG. 404. Stylostromatidae (p. 738).

narrowly elongated, platelike structural elements, and may be irregularly thickened along margins where associated lateral offsets occur; these latter may be directed outward and upward in places, having a spinose appearance; where main pillars become more thickened and rounded, lateral offsets may become obscured; in tangential section, pillar outlines vary from subrounded to angular or more elongated and irregular, with associated, short, zigzagged lateral offsets; cyst plates are large, thin, sagging to flattened, and complete or incomplete across pillar interspaces, but near the pillars, much smaller cysts become clustered and inclined; a few thicker cyst plates may also occur across interspaces, and tops of these are more likely to show denticles than elsewhere. [The genus *Sichuanostroma* WANG, 1978b, is a junior synonym of *Spinostroma*, only differing in the presence of more dilated, pillarlike elements. On the other hand, *Spinostroma* is distinguished from *Pennastroma* by having a more thickened, rodlike or platelike (narrowly elongated) pillar structure that largely masks the lateral offsets except at their spinose tips, in contrast to *Pennastroma*, which has conspicuous, upwardly and outwardly splayed elements (lateral offsets) on either side of a widely elongated, platelike, pillar structure.] *Upper Devonian (Famennian):* China (Sichuan), Russia (Novaya Zemlya).——Fic. 405*a*–*d.* **S. diversum*, lower part of Changtanzi



FIG. 405. Stylostromatidae (p. 738-740).

Formation, Shawozi, Ganxi, Sichuan Province; holotype, CIGMR, no. Ss2025; *a–b*, longitudinal and tangential sections, ×2; *c–d*, detailed tangential and longitudinal sections, ×5 (Webby, 2012c, courtesy of Wang Shu Bei; see also WANG, 1978b, pl. 41,2*a–b*).

Family AULACERATIDAE Kühn, 1927

[Aulaceratidae KOHN, 1927, p. 548] [=Beatriceidae ULRICH in BASSLER, 1915 (rarely used family-group name and not replaced prior to 1961, so has not been adopted; Art. 40, ICZN, 1985, p. 81); =Beatricidae RAYMOND, 1931b, p. 178; =Aulaceridae BOGOYAVLENSKAVA, 1969b, p. 16, nom. null.]

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 represented by composite, fused, outwardly radiating, platelike elements. *Middle Ordovician (Darriwilian)–Upper Devonian (Famennian).*

Aulacera Plummer, 1843, p. 293, fig. 1 [**A. plummeri* Galloway & St. Jean in Galloway, 1957, p. 422; SD GALLOWAY & ST. JEAN in GALLOWAY, 1957, p. 422] [=Beatricea BILLINGS, 1857, p. 344 (type, B. nodulosa, SD MILLER, 1889, p. 155)]. 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. Middle Ordovician (Darriwilian)–Upper Ôrdovician (Hirnantian): China (Anhui), Darriwilian; Australia (Tasmania, ?New South Wales), Canada (Anticosti Island, Akpatok Island, Hudson Bay, Ontario, Manitoba, British Columbia), Russia (Siberian Platform, Novaya Zemlya), USA (Indiana, Kentucky, Ohio), Sandbian-Hirnantian.-FIG. 406a-h. *A. plummeri GALLOWAY & ST. JEAN, Saluda Formation, Elkhorn Creek, 6.4 km south of Richmond, Indiana; a-c, holotype, YPM.222149, including slides 285-46, 299-35, 299-36, 300-9; a, external view exhibiting upward enlargement and gently raised spiraling ridges, ×0.38 (Galloway & St. Jean in Galloway, 1957, pl. 37, 1a); b, longitudinal section showing axial column and lateral zones with latilaminae and calcite-filled lacunae, ×1 (Galloway & St. Jean in Galloway, 1957, pl. 37, 1b); c, longitudinal section of slide 300-9 showing lateral zone, ×15 (Galloway & St. Jean in Galloway, 1957, pl. 37,1c); d-g, topotype (and hypotype), YPM.222147, including slides 282-58, 299-40; *d*-*e*, sketches of transverse and longitudinal sections of topotype, ×2 (Galloway & St. Jean in Galloway, 1957, pl. 32,3); f-g, ×10; f, transverse section of slide 299-40 showing cyst plates of lateral zone with small pillars restricted to outer part (Galloway & St. Jean 1961, pl. 3,1a); g, longitudinal section of slide 282-58 showing rows of cyst plates and, additionally, in the outer part of lateral zones, upwardly and outwardly inclined pillars (Galloway & St. Jean, 1961, pl. 3,1b); h, sketch of PLUMMER's (1843) originally named genus Aulacera, Richmond Group of Indiana, magnification approximate, at least ×0.25 (Schuchert, 1919, fig. 1).

Alleynodictyon WEBBY, 1971, p. 10 [*A. nicholsoni WEBBY, 1971, p. 11; OD]. Slender, branching, columnar skeleton with outwardly radiating, platelike pillars in outer margin of axial column and lateral zone; axial column exhibiting large, upwardly convex cyst plates with a few scattered denticles on upper surfaces; rows of small, long, low cyst plates occupy lateral zone, being flattened to concave outwardly between radiating pillars and gently convex outwardly in areas lacking pillars. Upper Ordovician (Katian): Australia (New South Wales, Tasmania).-–Fig. 407a-e. *A. nicholsoni; a-c, Daylesford Limestone, lower Bowan Park Group, Paling Yards Creek, 7 km southeast of Cudal, New South Wales, holotype, AMF.98943, transverse, centered-longitudinal and offset-longitudinal sections; d-e, silicified specimens, middle Regan's Creek Limestone, southeast of Cargo; d, paratype, AMF.98941, interior view of outer part of axial column showing some intersections between large, uparching cyst plates and inner ends of vertical, platelike pillars; *e*, paratype, AMF.98946, top view showing broadly uparched cyst plates of axial column and more densely fused lateral zone of platelike pillars and small cyst plates, ×4 (Webby, 1971, pl. 5, *1–5*).

- Cryptophragmus RAYMOND, 1914, p. 8 [*C. antiquatus; OD]. 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, sheathlike lateral zone exhibiting regular skeletal meshwork of small pillars intersected by laterally persistent, thin, undulating-to-flattened cyst plates (resembling laminae). Upper Ordovician (Sandbian-Katian): Canada (Ontario, Quebec), Russia (?Siberian platform), USA (New York, Pennsylvania, Virginia, Tennessee, Alabama, Indiana).-FIG. 408a-h. *C. antiquatus, upper Pamelia Limestone, near hilltop beyond quarry on continuation of Broad Street, Aylmer, Quebec (holotype), and Carden township, Ontario (paratypes); a, holotype, GSC 5390, lateral view of unsectioned specimen, ×1 (Raymond, 1914, pl. 1,1); b, paratype, GSC 4329e, offset-longitudinal section of lateral zone showing numerous, tiny, dotlike, spar-replaced pillars, ×3 (Raymond, 1914, pl. 3,4); c, paratype, GSC 4329c, and a fragment that was cut from GSC 4329c, now catalogued as YPM.222170, including slide 308-31 (this slide, however, is missing and presumed lost), transverse section showing sparreplaced pillars and cyst plates, ×10 (Galloway & St. Jean, 1961, pl. 2,3c); d, paratype, GSC 4329h, tangential section showing alternation between latilaminae and a mud-rock sheath, and spar-filled pillars, the outermost surface of which are markedly papillate, ×3 (Raymond, 1914, pl. 4,2); e-f, paratypes, GSC 4329a-b, longitudinal and transverse sections of best-preserved and most complete specimens, ×4 (Raymond, 1914, pl. II, 1-2; see also Fig. 296.1-296.2); g, paratype, GSC 4329i, slightly oblique transverse section showing papillae surmounting spar-replaced pillars, ×3 (Raymond, 1914, pl. IV, 1); h, paratype, GSC 4329, lateral view of uncut specimen exhibiting bulblike enlargement toward apical end, ×0.6 (Raymond, 1914, pl. I,2).
- Ludictyon OZAKI, 1938, p. 219 [*L. vesiculatum OZAKI, 1938, p. 219, pl. 33, 3a-c, pl. 34, 3; OD; NIGP, holotype, thin sections no.121555a-b]. 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. Middle Ordovician (Darriwilian)-lower Silurian: China (Shandong, Anhui), Darriwilian; ?Mongolia, Upper Ordovician; China (Guizhou), lower Silurian. — FIG. 409a-c. *L. vesiculatum, Majiagou Group, west of Beizhuang, Zhangqiu county, Shandong Province, holotype, NIGP, slides 121555a-b; a, longitudinal section



FIG. 406. Aulaceratidae (p. 740-741).

(121555a), $\times 2$; *b*, partially transverse to oblique section (121555b), $\times 5$; *c*, enlarged part of longitudinal section (121555a) depicting a few poorly defined denticles on tops of cyst plates, $\times 5$ (Webby, 2012c, photos of OZAKI's type thin sections in Nanjing collection; see also OZAKI, 1938, pl. 33,3*b*-*c*).

Pararosenella VASSILYUK & BOGOYAVLENSKAYA in BOGOYAVLENSKAYA, VASSILYUK, & GLEBOV, 1990, p. 75 [*Rosenella lissitzini forma cylindrica VASSILYUK, 1966, p. 46, pl. 32,1–7; OD; Donets Polytechnical Institute (DPI), Ukraine, no. 12/141]. Dichotomously branching, columnar skeleton with single row of large doughnut-shaped axial cyst plates of



FIG. 407. Aulaceratidae (p. 741).



FIG. 408. Aulaceratidae (p. 741).


Ludictyon

FIG. 409. Aulaceratidae (p. 741-742).

high convexity; branches are usually dichotomous but may be rarely as lateral offsets; 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. *Upper Devonian (Famennian):* Russia (northern Caucasus), Ukraine (Donets basin).——FIG. 410, *Ia-h. *P. cylindrica* (VASSILYUK), Famennian sequence, Porfirtovaya ravine, near Novotroitskoye village, Donbass, Ukraine; a-c, holotype, DPI, 12/141; a-b, transverse sections showing parts of skeleton with dichotomous branching and very large axial cyst plates, thickened outer wall with tiny lateral cyst plates in places; c, transverse section of top of one axial cyst plate showing presence of denticles (Vassilyuk, 1966, pl. 32,2a,b,v); d-h, other figured material from type locality as basis for subspecies, not specifically designated by author but probably has status as paratypes; d-e,



2a

Quasiaulacera

FIG. 410. Aulaceratidae (p. 742-749).



FIG. 411. Aulaceratidae (p. 748–749).



FIG. 412. Aulaceratidae (p. 749).

longitudinal and transverse sections of specimen showing bulbous shape of axial cyst plates, a few localized, very small, lateral cyst plates associated with outer wall; f, transverse-oblique section of another specimen showing comparatively large denticles; g-h, approximately longitudinally and transversely oriented sections of a third specimen; and see other examples of dichotomous and lateral branching of P. cylindrica (see Fig. 299.4–299.5), ×5 (Vassilyuk, 1966, pl. 32, fig. 1a–b, 3a–b, 4–7).

Quasiaulacera COPPER, STOCK, & JIN, 2013, p. 670 [*Q. occidua COPPER, STOCK, & JIN, 2013, p. 671; OD]. Large to very large, columnar, nonbranching skeleton, and longitudinally fluted externally. Skeleton of three layers: axial column with large cyst plates occupying about 30%–50% of skeleton, surrounded by envelope of small cyst plates, ultimately covered by outer layer of multiple, thin, concentric laminae, penetrated by thick, radiating, superposed pillars. Axial cyst plates occur in a single, stacked row. *Upper Ordovician (Hirnantian):* Canada (Anticosti Island).——FIG. 410,2*a*–*b*. * Q. occidua, upper Lousy Cove Member, 5–8 m below Laframboise Member, Ellis Bay Formation, type locality A972, tidal flat outcrops adjacent to Laframboise Creek, ~300 m NNW of Pointe Laframboise, western Anticosti Island, holotype, GSC 129346, transverse (*a*) and tangential (*b*) sections, ×5 (scale bar, 1 mm) (Copper, Stock, & Jin, 2013, fig. 6.2, 7.2).——FIG. 411,2*a*–*b.* **Q. occidua; 2a*, holotype, GSC 129346, transverse section from NNW of Pointe Laframboise, western Anticosti Island, type locality A972, $\times 2.5$ (scale bar, 2 mm) (Copper, Stock, & Jin, 2013, fig. 6.3); 2*b*, juvenile specimen, GSC 129722, longitudinal section showing large axial cyst plates, from upper Lousy Cove Member, Ellis Bay Formation (locality A1163), eastern Anticosti Island, Quebec, Canada, $\times 2.5$ (scale bar, 2 mm) (new, courtesy of Paul Copper, Carl Stock, and Jisua Jin).

- Sinodictyon YABE & SUGIYAMA, 1930, p. 52 [*S. columnare; OD]. Skeleton branching (fasciculate) to cylindrical with large cyst plates with denticles axially, and rows of smaller, long, low cyst plates with denticles and short, rounded pillars laterally. [In their original description of S. columnare, YABE and SUGIYAMA (1930) allocated the same registration number to more than one specimen. Here, where such specimens are reillustrated, an additional lower case letter is added to that number to avoid any confusion. All these specimens are presumed to be syntypes. Also, note that most of YABE and SUGI-YAMA's illustrations have been crudely overdrawn in black ink over photos to emphasize the skeletal structures. Middle Ordovician (Darriwilian): China (Shandong, Liaoning).-FIG. 411, Ia-e. *S. columnare, Majiagou Group, slopes of hill near Chenxing wharf, Wuhuzui, Fuxian County, Liaoning Province; a, syntype, IGPS 37676a, lateral view of a broadly fasiculate skeleton, ×0.6 (Yabe & Sugiyama, 1930, pl. 19,5); b, syntype, IGPS, 37676b, longitudinal section, ×5 (Yabe & Sugiyama, 1930, pl. 19,3); c, syntype, IGPS 37678, transverse section, ×5 (Yabe & Sugiyama, 1930, pl. 18,10); d, syntype, IGPS 37676c, obliquely cut section, ×5 (Yabe & Sugiyama, 1930, pl. 19,4); e, specimen from Chien-shih-hui-yao-tzu locality, western coast of Liaoning Bay, Jinxian County (about 25 km south of Yabe and Sugiyama's 1930 type locality); sketch of transverse section showing differentiation of cyst plates, particularly rows of smaller cyst plates in lateral zone, a few with associated short pillars, ×8 (Ozaki, 1938, p. 219, pl. 34,2; specimen not traced, possibly in NIGP).
- Thamnobeatricea RAYMOND, 1931b, p. 180 [*T. parallela; OD] [=Cladophragmus RAYMOND, 1931b, p. 182 (type, C. bifurcatus RAYMOND, 1931b, p. 182, pl. 3,1-4, OD); =Rosenellina RADUGIN, 1936, p. 92 (type, *R. wellenformis* RADUGIN, 1936, pl. 2,8,9,11, OD)]. Unbranched or branched 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; lateral offsets or dichotomous branches may occur; pillars mentioned as occurring in lateral zone but needs confirmation; denticles may occur on upper surfaces of cyst plates. Middle Ordovician (Darriwilian)-Upper Ordovician (Katian): China (Anhui), Darriwilian; Australia (Tasmania), Canada (Ontario), Russia (Siberian platform, Gornaya Shoria), USA (Alabama, Pennsylvania, Tennessee, Kentucky), Sandbian-Katian.-FIG. 412a-d. *T. parallela, middle of Stones River Group, Sandbian-Katian, large quarry north of Bellefonte-Miles Gap road, west of Bellefonte, Pennsylvania; a-b,

holotype, MCZ 9302; *a*, lateral view showing a number of lateral offsets, ×0.3 (Raymond, 1931b, pl. 2, 9); *b*, longitudinal section of part of one of branches showing large axial column and very narrow lateral zone, ×2.67 (Raymond, 1931b, pl. 2, 4); *c*, paratype, MCZ 9304, showing ornamentation of fine longitudinal ridges, ×1.33 (Raymond, 1931b, pl. 2, 5); *d*, specimen MCZ, thin section no. 127, showing large axial cyst and very small lateral cyst plates (at right) associated with base of lateral offset [RAYMOND's other paratypes are listed as MCZ 9303, 9305 (see his pl. 2, *6*–7)], ×3.5 (Raymond, 1931b, pl. 2,*8*).

Family LOPHIOSTROMATIDAE Nestor, 1966

[Lophiostromatidae NESTOR, 1966a, p. 58]

Encrusting laminar, latilaminate, composed of much thickened, tangential skeletal layers almost completely filling interskeletal space, sharply undulated skeletal layers forming pillarlike upgrowths appearing as papillae on upper surface; discrete longitudinal and tangential elements rare. [Only two genera, Lophiostroma and Dermatostroma, are regarded as valid, and one other, the genus Tarphystroma, is tentatively included in the family. Solidostroma KHROMYKH, 1974a, from the Lower Devonian of northeastern 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 p. 826). Priscastroma KHROMYKH, 1999a, from the Middle Ordovician of the Siberian Platform, was considered to be an early representative of the group (KHROMYKH, 1999b, p. 223), but it is not a typical member of the family given its very thin, long-low to irregularly undulating to zigzag-shaped elements, resembling cyst plates, with these mainly separated by an abundance of unfilled interskeletal spaces; consequently this genus is here transferred to family Rosenellidae (see p. 715). Taymyrostroma Кнкомукн, 2001, from the Upper Ordovician, Taimyr Peninsula, has also been assigned to the lophiostromatids (Кнкомукн, 2001, p. 347), but this genus remains inadequately described and illustrated; here it is regarded as convergent toward younger (Siluro-



Lophiostroma

FIG. 413. Lophiostromatidae (p. 750-752).

Devonian) clathrodictyid genera, such as Intexodictyides and Atelodictyon and is best grouped elsewhere (see p. 829–836) within the stromatoporoid order and family uncertain.] Middle Ordovician (Darriwilian)– Upper Devonian (Frasnian), ?Triassic.

Lophiostroma NICHOLSON, 1891a, p. 160 [*Labechia? schmidtii NICHOLSON, 1886c, p. 16, pl. 2,6–8; OD] [=Chalazodes PARKS, 1908, p. 33 (type, C. granulatum PARKS, 1908, p. 36, OD)]. Skeleton commonly latilaminate and laminar, consists of, dominantly, much thickened, superposed, sheetlike layers, sharply and regularly undulating into columnar, pillarlike upgrowths, giving a kind of cone-in-cone structure; these upgrowths expressed as papillae on upper surfaces; sheetlike layers almost entirely occupy interiors and do not represent true laminae, only rarely discernible cysts preserved; compact microstructure has a transverse fibrosity within sheetlike layers. [NICHOLSON's original spelling of the species name with its double "ii" termination is retained, in accordance with ICZN Art. 33.4 (1999) rather than schmidti (see GALLOWAY, 1957, p. 439; NESTOR, 1966a, p. 60; FLÜGEL & Flügel-Kahler, 1968, p. 381; Mori, 1970, p. 141), which is deemed to be an incorrect subsequent spelling. A number of Upper Paleozoic-Triassic stromatoporoid-like forms have been described as species of Lophiostroma, but their affinities remain in doubt. Stearn and Stock (see p. 310) recognized two of them as "calcareous crusts" coming from the Carboniferous and Permian of Japan (YABE & SUGIYAMA, 1931b; SUGIYAMA, 1939) but excluded them completely from a close association with the genus, even suggesting one was a brachiopod, based on a restudy by MORI (1980). A third species from the Triassic of the southeastern Pamirs was described by BOIKO (1970a) as Lophiostroma boletiformis. It



FIG. 414. Lophiostromatidae (p. 752-753).

was based on a single specimen with clearly discernable zigzagged upper and lower boundaries of the sheetlike latilaminae and longitudinally oriented, dark, columnar to cone-shaped upgrowths that align and may be superposed across the upwardly bent parts of the latilaminar boundaries, but other parts of the skeleton are composed of spar-filled calcite that is nondiagnostic, making it difficult to confirm this early Mesozoic species unquestionably as a member of the genus.] *Middle Ordovician* (*Darriwilian*)–Upper Devonian (Frasnian), ?Triassic: China (Shandong), Darriwilian; Mongolia, Russia (Siberian platform), Upper Ordovician; Canada (Ontario, Quebec), England, Sweden (Gotland), Estonia, Turkey, USA (Michigan, Kentucky), Ukraine (Podolia), middle Silurian-upper Silurian; Russia (Kuznetsk basin), Frasnian; Tadjikistan (southeastern Pamirs), ?Triassic.—FIG. 413a-f. *L. schmidtii (NICHOLSON), Paadla stage, Ludlow, Pilguse (=Hoheneichen) locality, 33 km west of Kuressaare, Saaremaa, Estonia; a-b, holotype, NHM, P5606, longitudinal and tangential sections, ×7.5 (Webby, 2012c; Nicholson's slides 279a, 279, rephotographed by Webby in 1989); c, topotype,





FIG. 415. Lophiostromatidae (p. 753).

IGTUT 114-49 (Co3178), showing papillae representing tops of pillarlike upgrowths, ×2 (Nestor, 1966a, p. 60, pl. 23,3); d, specimen SMNH, B10-X (GIK-195), Ludlow Hamra Formation of loc. 150 (south of Burgsvik) Gotland, showing papillose upper surface, with addition of an encrusting auloporoid coral, ×2 (Mori, 1970, p. 28, pl. 19,2); e-f, specimen IGTUT 114-48 (Co3177), from another Paadla age locality at Riiumägi, Saaremaa, longitudinal and tangential sections showing better preserved details of internal features of skeleton than in designated holotype, ×10 (Webby 2012c, photos courtesy of Heldur Nestor; see also NESTOR, 1966a, p. 60, pl. 23, 1-2).

Dermatostroma PARKS, 1910, p. 29 [*Stromatopora papillata JAMES, 1878, p. 2; OD]. 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. [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, BOLTON, and COPPER (1986) have demonstrated that these are heliolitine corals. Others, previously inferred to be independent species, overgrow parts of skeletons of Aulacera (see descriptions in GALLOWAY & ST. JEAN, 1961, p. 74-78) and should be excluded because they probably represent outer parts of aulaceratid skeletons ("outer lamellar layer," CAMERON & COPPER, 1994, p. 17; see also discussion by NESTOR, 1976, p. 35). The regular laminae and aligned denticles (so-called pseudopillars) of Dermatostroma concentricum GALLOWAY & EHLERS in GALLOWAY & ST. JEAN (1961, pl. 11,4a-c) are remarkably similar to structures termed the outer lamellar layer of the new aulaceratid genus Quasiaulacera COPPER, STOCK, & JIN, 2013 from Anticosti Island (see p. 748-749, Fig. 410,2a-b, 411,2a-b; and also CAMERON & COPPER, 1994, p. 17, fig. 2b, 2d). The authentic, coarse-textured forms like type species D. papillatum and species D. scabrum usually develop only as very thin encrusting sheets and in this respect bear close resemblances to thinner latilaminar growths of stromatocerids like Stromatocerium bigbysi WEBBY (1979b, p. 248, fig. 5A-B).] Upper Ordovician (?Sandbian, Katian): Canada (Ontario), USA (Ohio, Kentucky, Indiana, Tennessee, Iowa).-FIG. 414a-c. *D. papillatum (JAMES), Maysvillian, middle Katian, Cincinnati, Ohio, holotype, FMNH (formerly Walker Museum, no. 160); a, external surface of brachiopod shell (?Hebertella) partially encrusted by sheetlike skeleton, ×1; b, more magnified view showing finely papillate surface of skeleton, ×1.7; c, sketch of part transversely and part obliquely cut section of skeleton, intersecting a few rounded tips of papillae (top right), and pillarlike extensions within encrusting skeleton and small area of apparent radial ribbing of brachiopod shell (bottom center), ×10 (Parks, 1910, p. 30, pl. 23,8-10).—FIG. 414d-i. D.

scabrum (James, 1879); d-f, Richmondian, upper Katian, Kentucky end of bridge, Madison, Indiana, hypotype YPM.222150 (including slide 299-50); d, brachiopod shell (?Hebertella) partially encrusted by sheetlike skeleton, ×1 (Galloway & St. Jean, 1961, pl. 13,1); e-f, sketches of longitudinal and tangential sections of skeleton encrusting brachiopod shell with pillars and showing a polygonal shape near base of skeleton, ×10 (Galloway, 1957, pl. 33,2; originally labeled D. papillatum but later transferred to D. scabrum, see GALLOWAY & ST. JEAN, 1961, p. 70); g. Katian, Warren County, southwestern Ohio, specimen (USNM 40080) showing sheetlike skeleton with small mamelons and smaller papillae encrusting part of bivalve shell (Byssonychia), ×1.7 (Parks, 1910, pl. 24,3); h-i, middle Katian, Leipers Formation, Mt. Parnassus, Columbia, Tennessee, hypotype divided into two: MUO spec. 821 (not studied, possibly lost), and a small fragment of the hypotype studied and labeled YPM.450501, with addition of slide 302-10; this latter shows rounded outlines of pillars in tangential section and encrusting skeletal growth over bryozoan colony (Escharopora), cyst plates simulating laminae that define a broadly raised mamelon column, and short pillars in longitudinal section, ×10 (Galloway & St. Jean, 1961, pl. 10,2a-b).

?Tarphystroma NESTOR, COPPER, & STOCK, 2010, p. 62 [*T. tuberosum NESTOR, COPPER, & STOCK, 2010, p. 62, pl. 5a-5b, 6a-f; fig. 3c, 9a-b; M]. Low domical skeleton with comparatively closely spaced, variably thickened, planar to undulating composite skeletal layers that resemble composite laminae or latilaminae, with associated upwardly extending, stout, relatively short longitudinal elements with the appearance of columnar to slightly cone-in-cone-type upgrowths; these latter may be superposed across up to three or four successive latilaminae but more commonly appear as shorter upgrowths that may, at certain levels, only extend partially or entirely through one latilamina, and tops may form tubercles. Each latilamina may be differentiated into two parts, comprising a lower, mainly laterally continuous, variably thickened, dark skeletal layer, but in a few places, successive microlaminae are preserved with a vague microreticulation over short distances laterally; and in upper part, a series of spar-filled gallery spaces occur between intervening columnar upgrowths and are bounded above and below by medium-to-large, concave-to-flattened cyst plates; and in a few places, additional cyst plates may subdivide individual spar-filled gallery spaces. In tangential section, rounded to irregular, closespaced upgrowths coalesce together to form large, rounded to variably shaped, mamelon-like bundles or clusters, up to 5 mm in diameter; also extensive lighter interspaces occur around lateral margins of mamelon-like bundles, and within these areas, there are spar-filled radial to vermiform-shaped astrorhizal canals and other irregular spar-filled cavities. In many places, skeletal structures are rather dense and poorly defined, but in localized areas of latilaminae, longitudinal elements may show flocculent to finely microreticulated microstructures. [The genus is based on limited material, with only the holotype being illustrated. Consequently, NESTOR, COPPER, and STOCK (2010, p. 62) have had difficulty placing the genus within existing families, suggesting tentatively that it be included in the family Lophiostromatidae, because, like Lophiostroma NICHOLSON, 1891a, it has a "comparatively dense general architecture" and a vaguely similar pattern of cone-in-cone-type, columnar, longitudinal elements arising above undulating skeletal layers (NESTOR, COPPER, & STOCK, 2010, p. 62). However, Tarphystroma shows a markedly more complicated skeletal pattern, as seen in tangential section, with mamelon-like bundles or clusters of upgrowths, as well as astrorhizae. Another genus, Stromatodictyon KHALFINA, 1972 (see p. 732), though it remains poorly known, exhibits distinctive, long, branching, bladed to flanged pillars, which contrast markedly with the comparatively short, columnar, knoblike, cone-in-cone type of longitudinal elements seen in Tarphystroma.] Silurian (middle Llandovery): Canada (Anticosti Island).-FIG. 415a-b. *T. tuberosum, holotype GSC127868; longitudinal and tangential sections, ×10 (Nestor, Copper, & Stock, 2010, p. 116, pl. 5a-b).

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- Paleontological Research Institution, Ithaca, New York, Paula M. Mikkelsen, Editor and Director of Publications: *Aulacera*, Fig. 406*a–g; Cystostroma*, Fig. 388*a–d; Dermatostroma*, Fig. 414*d*,*f*,*h*,*i*.
- American Museum of Natural History Library, Mary DeJong, Reference Librarian; and approval of coauthor J. J. St. Jean, Jr., Chapel Hill, North Carolina: *Stromatocerium*, Fig. 395*a*–*d*.
- Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, Catherine Weisel, Museum Projects Coordinator: *Thamnobeatricea*, Fig. 412*a*–*d*.
- Norwegian Journal of Geology, Geological Survey of Norway, Trondheim, Per Terje Osmundsen, Editor: *Radiostroma*, Fig. 397*a*-*d*.
- Estonian Academy Publishers, Tallinn, Estonia, Ülo Niine, Director, and author Heldur Nestor: *Cystocerium*, Fig. 399*a*–*d*.
- Stockholm Contributions in Geology, Stockholm, Sweden, Jan Backman, Editor: *Lophiostroma*, Fig. 413*d*.
- Nanjing Institute of Geology & Palaeontology, Chinese Academy of Sciences, Nanjing, China, Yang Qun, Deputy Director of Academic Affairs; as well as help of author Dong De Yuan and Chen Xu: *Pseudostylodictyon*, Fig. 391*a–b; Platiferostroma*, Fig. 398, *1a–d; Pennastroma*, Fig. 403, *2a–d; Ludictyon*, Fig. 409*a–c*. Photographs of Dong's and Ozaki's thin sections of types were provided during a visit in 1993, and some were used here instead of earlier printed figures.

- Chengdu Institute of Geology & Mineral Resources, Wang Shu Bei, author, Chengdu, China: *Pleostylostroma*, Fig. 401*a-f; Eopennastroma*, Fig. 403,1*a-b; Spinostroma*, Fig. 405*a-d*. A few new photographs of Wang's thin sections of types were also supplied in Nanjing and used here instead of older printed figures.
- Scientific Reports of Tohoku University, Institute of Geology & Paleontology, Sendai, Japan, K. Osuki, Director; also Kei Mori and J. Nemoto: *Sinodictyon*, Fig. 411, *1a–d*.
- Pleiades Publishing Inc., Moscow, Russia, Doklady Earth Sciences, vol. 365, no.
 2, author V. G. Khromykh, 1999, New genus of the earliest stromatoporoids, p. 178–180, fig. 1a–b, 2a,c,d; and with approval of author, V. G. Khromykh, Institute of Petroleum Geology & Geophysics Siberian Branch, Russian Academy of Science, Novosibirsk: Priscastroma, Fig. 390a–e.
- New South Wales Department of Primary Industries: Geological Survey of New South Wales, Bruce Ward, Manager of Publishing Communications; and author John Pickett: *Cystistroma*, Fig. 396*a*–*c*.

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CLATHRODICTYIDA: SYSTEMATIC DESCRIPTIONS

Heldur Nestor

Order CLATHRODICTYIDA Bogoyavlenskaya, 1969

[Clathrodictyida Bogoyavlenskaya, 1969b, p. 17; *emend.*, Nestor in Stearn & others, 1999, p. 23] [=Gerronostromatida Bogoyavlenskaya, 1969b, p. 19]

Skeleton consists of continuous, singlelayer, inflected to planar laminae and short to superposed pillars; microstructure compact; interspaces are galleries. [Clathrodictyids were separated from actinostromatids by KÜHN (1939a) as an independent family. BOGOYAVLENSKAYA (1969b) elevated the group to the ordinal rank, defining it as being represented by stromatoporoids with inflected laminae and poorly differentiated pillars. The stromatoporoids with welldifferentiated planar laminae and rod-shaped pillars were distinguished by her as the separate order Gerronostromatida. NESTOR in STEARN and others (1999) reclassified gerronostromatids as a family within the order Clathrodictyida.] Upper Ordovician (Katian)–Carboniferous (Serpukhovian).

Family CLATHRODICTYIDAE Kühn, 1939

[nom. correct. LECOMPTE, 1956, p. 128, pro Clathrodictyonidae KUHN, 1939a, p. 340; emend., BOGOYAVLENSKAYA, 1969b, p. 17] [=Coenellostromatidae BOGOYAVLENSKAYA, 1977c, p. 14]

Skeletal elements weakly differentiated; laminae irregularly inflected, bending down into short pillars; galleries open, lenticular or irregular in longitudinal section. [BOGOY-AVLENSKAYA (1969b) restricted the scope of Clathrodictyidae to the forms having inflected laminae. Later, BOGOYAVLENSKAYA (1977c) established a new family Coenellostromatidae, merged with Clathrodictyidae by NESTOR in STEARN and others (1999).] *Upper Ordovician (Katian)–Carboniferous* (Mississippian, Serpukhovian).

Clathrodictyon NICHOLSON & MURIE, 1878, p. 220 [**C. vesiculosum*; OD; holotype NHM P5495]. Growth form domical to laminar; laminae irregularly wrinkled; pillars short, in many cases oblique or funnel shaped, rodlike at base; galleries lenticular or irregular in longitudinal section; astrorhizae common. Upper Ordovician (Katian)-Middle Devonian: Australia (New South Wales, Tasmania), Canada (Anticosti), China (Inner Mongolia, Guangxi, Shaanxi, Zhejiang), Estonia, Norway, Katian-Hirnantian; Canada (Anticosti, Arctic islands, Hudson Bay, eastern Quebec), central Asia (Tien Shan), China (Quizhou), Estonia, Greenland, Norway, Russia (Altai, Arctic islands, Siberian Platform, Tuva, western Urals), Ukraine (Podolia), United States (Missouri, Ohio), Llandovery; Canada (Arctic islands, Hudson Bay, Manitoba, Ontario, eastern Quebec), central Asia (Tien Shan), England, Estonia, Greenland, Norway, Russia (Altai, Pechora Basin, northeastern Siberia, Siberian Platform, Tuva), Sweden (Gotland), United States (Kentucky), Wenlock; Australia (New South Wales), Canada (Ontario), central Asia (Tien Shan), Estonia, Iran, Russia (Altai, Arctic islands, Pechora Basin, Siberian Platform, western Urals), Sweden (Gotland), Ukraine (Podolia), Ludlow; Canada (Arctic islands), Emsian; China (Yunnan), England, Russia (Urals, northeastern Siberia), United States (Ohio), Middle -FIG. 416, 1a-b. *C. vesiculosum, Devonian.-Clinton, Llandovery, Yellow Springs, Ohio, United States, holotype NHM P5495; longitudinal and tangential sections, ×10 (Nestor, 2011).

- Bullulodictyon YAVORSKY, 1967, p. 17 [*B. patokense; OD; holotype CNIGR 7351/557]. Growth form laminar; laminae moderately inflected, zonally indefinite; pillars very weakly differentiated; galleries lenticular, of different sizes; astrorhizae large, frequent. Upper Devonian (Frasnian): Russia (Pechora Basin).——FIG. 416,2a-b. *B. patokense, River Bol'shoi Potok, holotype CNIGR 7351/557; longitudinal and tangential sections, ×10 (YAVORSKY, 1967, pl. 3,5,7).
- Coenellostroma BOGOYAVLENSKAYA, 1977c, p. 14 [*C. kaljanum BOGOYAVLENSKAYA, 1977c, p. 15; OD; holotype UGM 1089a]. Growth form domical; laminae wrinkled, inflected downward into funnel-shaped pillars; galleries arch shaped in longitudinal, meandroid or subhexagonal in tangential section; astrorhizae large, superposed, frequent. Lower Devonian–Middle Devonian: Russia (Eastern Urals).—FIG. 416,3a–b. *C. kaljanum, Karpinskiĭ Horizon, Middle Devonian, Kal'ia village, Severoural'skiĭ District, holotype, UGM 1089a; longitudinal and tangential sections, ×10 (Nestor, 2011).
- Kyklopora BOGOYAVLENSKAYA, 1982a, p. 37 [*K. kalmiusensis; OD; holotype UGM 15/57/103]. Growth form laminar; laminae abruptly wrinkled;



FIG. 416. Clathrodictyidae (p. 755–757).



FIG. 417. Clathrodictyidae (p. 757-758).

pillars very weakly differentiated; galleries irregular; astrorhizae obscure. *Carboniferous (Mississippian, Serpukhovian):* Russia (Donetsk Basin).——FIG. 416,4*a*–*b.* **K. kalmiusensis*, Kal'mius River at Zhelvakovaia, holotype, UGM 15/57/103; longitudinal and tangential sections, ×10 (Nestor, 2011).

Labechiina KHALFINA, 1961b, p. 55 [*L. cylindrica KHALFINA, 1961b, p. 56, holotype, CSGM 401/50; OD]. Growth form columnar, without axial canal; laminae moderately wrinkled, thin, bending downward into short pillars; long, stout megapillars well developed, densely spaced. Silurian–Lower Devonian: Canada (Mackenzie District), Silurian; Russia (Salair), *Lower Devonian.*—FIG. 417, *1a–b.* **L. cylindrica*, Sukhaia Suite, Lochkovian, Aleksandrovka, Salair, holotype CSGM 401/50; transverse and tangential sections, ×10 (Nestor, 2011, courtesy of V. G. Khromykh).

Oslodictyon MORI, 1978, p. 134 [*O. henningsmoeni MORI, 1978, p. 135, holotype, PMO 45420; OD] [=Distylostroma KOSAREVA in BOGOYAVLENSKAYA & KHROMYKH, 1985, p. 75 (type, D. crassum, nom. nud.)]. Growth form domical to laminar; laminae moderately wrinkled, bending downward into short pillars; long, stout megapillars are present; astrorhizae obscure. Silurian (Llandovery)- Middle Devonian: Canada (Anticosti), Estonia, Norway, Llandovery; Urals, Silurian; Canada (Arctic islands), Russia (northeastern Siberia), Lower Devonian; Russia (Salair), Middle Devonian.—FIG. 417,2a-b. *O. henningsmoeni, Rytteråker Formation (7b), Llandovery, Vesleøya, Ringerike, Norway, holotype PMO 45420; longitudinal and tangential sections, ×10 (Mori, 1978, fig. 9A–B).

Stelodictyon BOGOYAVLENSKAYA, 1969b, p. 17 [*S. iniquum; OD; holotype UGM 990/61a]. Growth form domical or laminar; laminae microundulate at junctions of funnel-shaped pillars, may be penetrated by pores; galleries arch shaped in longitudinal section, open in tangential section; astrorhizae rare, irregular. Upper Ordovician (Hirnantian)-Lower Devonian (Lochkovian): Estonia, Hirnantian; Canada (Manitoba, Ontario), England, Russia (western Urals, Siberian Platform), Sweden (Gotland), Ukraine (Podolia), Wenlock; Russia (Urals), Ludlow; United States (New York), Lochkovian.—FIG. 417, 3a-b. *S. iniquum, Isovskaia Suite, Ludlow, Is River, Isovskoĭ District, Middle Urals, holotype UGM 990/61a; longitudinal and tangential sections, ×10 (Nestor, 2011).

Family ACTINODICTYIDAE Khalfina & Yavorsky, 1973

[Actinodictyidae KHALFINA & YAVORSKY, 1973, p. 26; emend., NESTOR in STEARN & others, 1999, p. 25] [=Ecclimadictyidae STEARN, 1980, p. 890; =Plexodictyidae BOGOYAVLENSKAYA, 1981, p. 30]

Skeletal elements very weakly differentiated; laminae crumpled (zigzag), forming cassiculate network; pillars indistinct or oblique; galleries labyrinthine, subangular in longitudinal section; megapillars and paralaminae may be present. [KHALFINA and YAVORSKY (1973) restricted the family Actinostromatidae to the genera having long megapillars, in addition to crumpled laminae. BOGOYAVLENSKAYA (1981) erected a new family Plexodictyidae, based on the presence of crumpled laminae and paralaminae. STEARN (1980) treated the presence of megapillars and paralaminae as genus-level characters and combined all genera with crumpled laminae, including Actinodictyon and *Plexodictyon*, into the newly erected family Ecclimadictyidae, which by priority became a junior synonym of Actinodictyidae (NESTOR in STEARN & others, 1999).] Upper Ordovician (Katian)–Lower Devonian (Emsian).

Actinodictyon PARKS, 1909, p. 30 [*A. canadense PARKS, 1909, p. 32; SD BASSLER, 1915, p. 15, holotype GSC 9123]. Growth form columnar; laminae irregularly crumpled, fused with dissepiments, intersected by scattered, crooked megapillars; galleries very irregular, labyrinthine; astrorhizae obscure. *Silurian:* Russia (Pechora Basin); Canada (Hudson Bay), *Llandovery;* Australia (New South Wales), *Ludlow.*—FIG. 418, *Ia–b. *A. canadense*, lower Silurian, Southampton Island, Hudson Bay, holotype GSC 9123; transverse and tangential sections, ×10 (Nestor, 2011).

- Camptodictyon NESTOR, COPPER, & STOCK, 2010, p. 83-84 [*C. penefastigiatum NESTOR, COPPER, & STOCK, 2010, p. 84-85; OD; holotype, GSC 128021]. Growth form laminar to domical; laminae chevronlike folded to smoothly microundulating; pillars imperfect, oblique inflexions of laminae, partly superposed, forming longer zigzag-shaped pseudopillars; galleries labyrinthine, round, oval or meandriform in longitudinal section, often superposed forming subvertical rows, separated from each other by zigzag pseudopillars; astrorhizae inconspicious. Upper Ordovician (Katian)-lower Silurian (Telychian): Russia (Gornaia Shoriia, Altai), Australia (New South Wales), Katian; Canada (Anticosti and Baffin islands), Estonia, Llandovery.—___FIG. 419,3a-b. *C. penefastigiatum, Goéland Member, Jupiter Formation, Aeronian, Gull Cape, Anticosti, holotype GSC 128021; transverse and tangential sections, ×10 (Nestor, Copper, & Stock, 2010, pl. 21c-d).
- Desmidodictyon NESTOR, COPPER, & STOCK, 2010, p. 85–86 [*D. exoticum NESTOR, COPPER, & STOCK, 2010, p. 86–87; OD; holotype, GSC 129268]. Growth form fasciculate or digitate; subcylindrical stems lacking axial canal, but possessing a broad axial zone with irregularly twisted rodlike pillars and collicul; very narrow, reduced peripheral zone consists of small number of minutely crumpled laminae. Silurian (Llandovery): Canada (Anticosti Island), Rhuddanian.——FiG. 419,4a-b.
 *D.exoticum, Merrimack Formation, Rhuddanian, Jupiter River at 24 mile bridge, Anticosti, holotype, GSC 129268; transverse and tangential sections, ×10 (Nestor, Copper, & Stock, 2010, pl. 22a–b).
- Ecclimadictyon NESTOR, 1964a, p. 60 [*Clathrodictyon fastigiatum NICHOLSON, 1887, p. 8; OD; holotype NHM P5773]. Growth form laminar to domical; laminae crumpled, forming cassiculate network; pillars oblique or indistinct; galleries labyrinthine, subangular in longitudinal section; astrorhizae fasciculate, irregular. Upper Ordovician (Katian)-Silurian: Australia (New South Wales, Tasmania), China (Quinghai, Xinjiang, Zhejiang), Estonia, Kazakhstan, Russia (Urals, Altai, Gornaia Shoria), Katian-Hirnantian; Canada (Anticosti, Arctic islands, eastern Quebec), central Asia (Tien Shan), China (Guizhou, Hubei, Sichuan), Estonia, Greenland, Iran, Norway, Russia (Arctic islands), United States (Iowa, Michigan, Missouri, Ohio, Oklahoma), Llandovery; Australia (New South Wales), Canada (eastern Quebec, Ontario), central Asia (Tien Shan), England, Estonia, Norway, Russia (Altai, Arctic islands, Siberian Platform, Urals), Sweden (Gotland), Ukraine (Podolia),



FIG. 418. Actinodictyidae (p. 758–761).



FIG. 419. Actinodictyidae (p. 758–761).

United States (Michigan), *Wenlock*; Canada (eastern Quebec, Ontario), China (Inner Mongolia), Norway, Russia (Arctic islands, Urals), Sweden (Gotland), *Ludlow*; Russia (Urals), *Pridoli*; Russia (Pechora Basin, northeastern Siberia, Tuva), *Silurian.*——FIG. 418,2*a–b.* **E. fastigiatum* (NICH-OLSON), Much Wenlock Limestone Formation, Wenlock, Ironbridge, Shropshire, holotype NHM P5773; longitudinal and tangential sections, ×10 (Nestor, 2011).

- Labyrinthodictyon NESTOR, COPPER, & STOCK, 2010, p. 74-75 [*L. angulosum; OD; holotype, GSC 127961]. Growth form laminar to domical; skeleton consists of planar paralaminae and irregular interlaminar meshwork, formed by tangled , oblique and tortuous, randomly oriented plate- or rodlike skeletal elements; astrorhizae unknown. [NESTOR, COPPER, and STOCK (2010) erroneously placed the description of this genus under the heading of the family Clathrodictyidae.] Upper Ordovician: Canada (Anticosti Island), Hirnantian; Australia (New South Wales), Katian.--Fig. 418,4a-b. *L. angulosum, Prinsta Member, Ellis Bay Formation, Hirnantian, Table Head, Anticosti, holotype, GSC 127961; transverse and tangential sections, ×10 (Nestor, Copper, & Stock, 2010, pl. 16a-b).
- Neobeatricea RUKHIN, 1938, p. 95 [*Beatricea tenuitextilis YAVORSKY, 1929, p. 92; OD; holotype CNIGR 2595/20]. Growth form columnar, without axial canal; laminae irregularly crumpled, intertwined with flat dissepiments; short pillars indistinguishable, megapillars absent; astrorhizae rare, with short unbranched canals. *Silurian*: Russia (Siberian Platform, Urals), *Wenlock;* Canada (Quebec), *Ludlow;* Russia (northeastern Siberia, Novaya Zemlya, Pechora Basin), *Silurian.*—FiG. 418,*3a–b.* *N. tenuitextilis (YAVORSKY), Silurian, Rusanov valley, Novaya Zemlya, northern island, holotype CNIGR 2595/20; longitudinal and tangential sections, ×10 (Nestor, 2011).
- Plexodictyon NESTOR, 1966a, p. 20 [*P. katriense NESTOR, 1966a, p. 21; OD; holotype IGTUT 114-18 (Co 3132)]. Growth form laminar or domical; laminae crumpled, forming regular cassiculate network traversed by planar paralaminae; astrorhizae rare, tubular. [A few superficially similar species from the Upper Ordovician and Llandovery (Silurian) may represent another genus.] ? Upper Ordovician, Silurian (?Llandovery, Ludlow-Pridoli): Australia (New South Wales, Queensland), ? Upper Ordovician; China (Guizhou, Hubei), ?Llandovery; Australia (New South Wales, Queensland), Canada (Arctic islands), central Asia (Tien Shan), China (Inner Mongolia), Estonia, Sweden (Gotland, Scania), Russia (Arctic islands, northeastern Siberia, Pechora Basin, Urals), Ukraine (Podolia), United States (Michigan, Virginia), Ludlow-Pridoli.—FIG. 419,1a-b. *P. katriense, Paadla Stage, Ludlow, Katri, Saaremaa Island, Estonia, holotype IGTUT 114-18 (Co 3132); longitudinal and tangential sections, ×10 (Nestor, 2011).
- Yabeodictyon MORI, 1968, p. 67 [* Y. balticum MORI, 1968, p. 68; OD; holotype SMNH Cn 68177 (GIK-35)] [=Neoclathrodictyon LESSOVAJA, 1971,

p. 116 (type, N. flexibilis, OD)]. Growth form domical or laminar; laminae crumpled, intersected by long megapillars; galleries labyrinthine; astrorhizae common, small. [NESTOR (1976, p. 59) treated Neoclathrodictyon as a junior synonym of Yabeodictyon.] Silurian (Llandovery)-Lower Devonian (Emsian): Canada (Arctic islands, eastern Quebec), Russia (Siberian Platform), Sweden (Gotland), Wenlock; Canada (Arctic islands), central Asia (Tien Shan), Russia (Urals, ?Salair), Ludlow-Pridoli; Canada (Hudson Bay), Russia (Pechora Basin), Silurian; central Asia (Tien Shan), -FIG. 419,2a-b. *Y. balticum, Slite Emsian.— Beds, Wenlock, Slite, Gotland, holotype SMNH Cn 68177 (GIK-35); longitudinal and tangential sections, $\times 10$ (Nestor, 2011).

Family GERRONOSTROMATIDAE Bogoyavlenskaya, 1969

[Gerronostromatidae BOGOYAVLENSKAYA, 1969b, p. 19; *emend.*, NESTOR in Stearn & others, 1999, p. 28] [=Clathrostromatidae Khalfina & Yavorsky, 1971, p. 118]

Skeletal elements very well differentiated; laminae continuous, planar (straight); pillars simple, rodlike, short or long (superposed); galleries open, subrectangular in longitudinal section; astrorhizae rare, irregular. [BOGOYAVLENSKAYA (1969b) originally incorporated stromatoporoids with single-layer and tripartite laminae both in the present family. STEARN (in STEARN & others, 1999) removed those with tripartite laminae into the family Stromatoporellidae and thus restricted the scope of Gerronostromatidae. KHALFINA and YAVORSKY (1971) established a new family Clathrostromatidae, which differs from Gerronostromatidae by the presence of short pillars in addition to the long ones. This feature is not considered to be diagnostic of the family level by other investigators.] Silurian (Llandovery)-Upper Devonian (upper Famennian).

Gerronostromaria NESTOR, 2011, p. 6, nom. nov. pro Gerronostroma YAVORSKY, 1931, p. 1392, nom. nud. [*Gerronostroma elegans YAVORSKY, 1931, p. 1393; OD; holotype CNIGR 3338/3] [=Clathrostroma YAVORSKY, 1960, p. 132 (type, C. stolbergense, OD)]. Growth form domical or bulbous; laminae planar, continuous; pillars rodlike, mostly long or superposed; galleries rectangular in longitudinal section; astrorhizae rare, fasciculate. [YAVORSKY (1931) established a new genus Gerronostroma without designation of the type species, and therefore, according to the IZCN Code (1999), Article 13.3, its name is invalid and requires replacement. YAVORSKY



FIG. 420. Gerronostromatidae (p. 761-763).

(1960) established the new genus *Clathrostroma*, differing from *Gerronostroma* by the presence of both short and long (superposed) pillars. The presence of partly short and partly long pillars is not considered here to be a generic character.] *Silurian (Llandovery)–Upper Devonian (upper Famennian)*: Canada (Arctic islands), *Llandovery;* Canada (Quebec), Russia (Pechora Basin, Urals), *Ludlow–Pridoli;* Canada (Arctic islands), central Asia (Tien Shan), Russia (Kuznetsk Basin, northeastern Siberia, Urals), *Lower Devonian*; Afghanistan, Australia (Queensland, Victoria), central Asia (Tien Shan), Russia (Kuznetsk Basin, northeastern Siberia, Pechora Basin, Urals), United States (Indiana, Ohio), *Middle Devonian*; Canada (Alberta), Germany, Russia (Kuznetsk Basin, Russian Platform), *Upper Devonian*; Germany, Russia (southern Urals), *upper Famennian.*— FIG. 420, *Ia-b.* **G. elegans* (YAVORSKY), Middle Devonian, Bachat village, Kuznetsk Basin, holotype CNIGR 3338/3; longitudinal and tangential sections, ×10 (Nestor, 2011).

- Gerronodictyon BOGOYAVLENSKAYA, 1969b, p. 20 [*G. incisum; OD; holotype UGM 990/189a]. Growth form domical or irregular; laminae thick, discontinuous; pillars rodlike, mostly superposed, unequally situated; astrorhizae rare, fasciculate. Silurian (Wenlock): Russia (Urals).——FIG. 420,2a-b. *G. incisum, Pavdinsk Horizon, Wenlock, Is River, Isovskoi District, Middle Urals, holotype UGM 990/189a; longitudinal and tangential sections, ×10 (Nestor, 2011).
- Petridiostroma STEARN, 1992, p. 531, nom. nov. pro Petrostroma STEARN, 1991, p. 617, non DÖDERLEIN, 1892 [*Simplexodictyon simplex NESTOR, 1966a, p. 25; OD; holotype IGTUT 114-20 (Co3134)] [=Faciledictyon LESSOVAJA, 1991, p. 28 (type, Simplexodictyon torosum Lessovaja, 1972, p. 49, OD)]. Growth form laminar to domical; laminae planar, continuous; pillars short, rodlike to spool shaped; galleries open, rectangular, oval to archshaped in longitudinal section; astrorhizae rare, inconspicuous. [STEARN (1991) and LESSOVAJA (1991) in the same year published the morphologically identical genera Petrostroma and Faciledictyon. The former name has priority, as it was published in July, while the latter appeared in November.] Silurian (Telychian)-Middle Devonian: Estonia, Norway, Sweden (Gotland), Canada (Anticosti), Telychian; central Asia (Tien Shan), Estonia, Russia (Urals), Sweden (Gotland), United States (Kentucky), Wenlock; Russia (Pechora Basin, northeastern Siberia), Silurian; Australia (Victoria), Canada (Arctic islands), central Asia (Tien Shan), Czech Republic (Bohemia), Russia (northeastern Siberia, Salair, Urals), United States (New York), Lower Devonian; Canada (Ontario), central Asia (Tien Shan), Germany, Russia (Kuznetsk Basin, northeastern Siberia, Pechora Basin, Urals), United States (Ohio), Middle Devonian.-FIG. 420, 3a-b. *P. simplex (NESTOR), Jaani Stage, Wenlock, Liiva, Saaremaa Island, Estonia, holotype IGTUT 114-20 (Co3134); longitudinal and tangential sections, ×10 (Nestor, 2011).

Family TIENODICTYIDAE Bogoyavlenskaya, 1965

[Tienodictyidae BOGOYAVLENSKAYA, 1965c, p. 37, emend., STEARN, 1980,
 p. 890; NESTOR, 1997, p. 327; NESTOR in STEARN & others, 1999, p.
 30; NESTOR, 2011, p. 10] [=Dualestromatidae KHALFINA & YAVORSKY,
 1973, p. 27]

Skeletal elements well differentiated; laminae continuous, planar; branching or oblique longitudinal skeletal elements, together with dissepiments, form tangled network in interlaminar space; galleries irregular, astrorhizae weakly developed. *Silurian (Llandovery)–Upper Devonian (Frasnian).*

Tienodictyon YABE & SUGIYAMA, 1941b, p. 139 [**T. zonatum;* OD; holotype TUM 65229]. Growth

form domical, structure laminate; laminae planar; interlaminar space divided into two zones, longitudinal skeletal elements in lower zone very irregular, connected with processes into tangled network, in upper zone, isolated pillars occur, circular in cross section; galleries irregular; dissepiments abundant in upper zone; astrorhizae indistinct. Lower Devonian-Upper Devonian (Frasnian): Australia (northern Queensland), Russia (northeastern Siberia), Lower Devonian; Australia (northern Queensland), Canada (Northwest Territories), China (Yunnan), Russia (eastern Urals, Kuznetsk Basin, Salair), Middle Devonian; Czech Republic (Moravia), Frasnian.-FIG. 421, 1a-b. *T. zonatum, Middle Devonian, Nanshan, Paichiaying, eastern Yunnan, China, holotype TUM 65229; oblique longitudinal and tangential sections, ×10 (Nestor, 2011).

- Hammatostroma STEARN, 1961, p. 939 [*H. albertense STEARN, 1961, p. 940; OD; holotype GSC 15318]. Growth form domical to laminar; laminae planar or irregularly wavy, transversely fibrous; interlaminar spaces occupied by tangled, irregular structure, forming discontinuous, crumpled additional laminae in the middle part; galleries irregular; astrorhizae inconspicuous. Lower Devonian-Upper Devonian (Frasnian): Austria (Carnic Alps), Lower Devonian; China (Guangxi), Givetian; Canada (Alberta, Saskatchewan), China (Guangxi), Czech Republic (Moravia), Poland, Russia (Arctic islands, Timan, Urals), United States (Iowa), Frasnian.-FIG. 421,2a-b. *H. albertense, Cairn Formation, Frasnian, Isaac Creek, Rocky Mountains, Alberta, holotype GSC 15318; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of T. E. Bolton).
- Intexodictyides NESTOR, 2011, p. 8, nom. nov. pro Intexodictyon YAVORSKY, 1963, p. 34, nom. nud. [*Intexodictyon perplexum YAVORSKY, 1963, p. 36; OD; lectotype CNIGR 7351/469]. Growth form domical; laminae thin, planar; longitudinal skeletal elements (pillars) thin, irregularly branching, forming a fine tangled network in interlaminar space; additional inflected lamina locally developed in interlaminar space or below the planar lamina. [YAVORSKY (1963) erected the new genus Intexodictyon without designation of the type species, and therefore, according to the IZCN Code (1999), Article 13.3, its name is invalid and requires replacement.] Silurian (Llandovery)-Lower Devonian: Canada (Arctic islands, eastern Quebec), China (Quizhou), Estonia, United States (northern Michigan), Llandovery; Russia (northeastern Siberia, Pechora Basin, Tuva), Silurian; China (Inner Mongolia), Russia (Kuznetsk Basin), Lower Devonian.——FIG. 421, 3a-b. *I. perplexum (YAVORSKY), upper Silurian, R. Iblagas, Magadan, northeastern Siberia; lectotype CNIGR 7351/469; longitudinal and tangential sections, ×16 (Nestor, 2011).
- Pseudoactinodictyon FLügel, 1958, p. 137 [*P. juxi; OD; holotype SMF XXV-1184] [=Dualestroma KHALFINA, 1968b, p. 61 (type, Stromatoporella



FIG. 421. Tienodictyidae (p. 763–766).



FIG. 422. Anostylostromatidae (p. 766).

dualis KHALFINA, 1961d, p. 332, OD); =Intexodictyonella YAVORSKY, 1969b, p. 102 (type, Stromatoporella undata YAVORSKY, 1950, p. 258, OD)]. Growth form laminar to domical; laminae planar; pillars short, partly superposed, locally crooked or oblique, expanding at tops; wide interlaminar spaces filled with abundant convex dissepiments; astrorhizae irregular. [FLÜGEL (1958) originally published negative prints of Pseudoactinodictyon with low magnification that complicated identification of the genus. Therefore, the species Stromatoporella dualis KHALFINA, 1961d, and Stromatoporella undata YAVORSKY, 1950, were distinguished as new genera Dualestroma and Intexodictyonella, respectively]. Lower Devonian (Pragian)-Upper Devonian (Frasnian): Australia (Victoria), United States (?Michigan), Pragian; Australia (northern Queensland), Canada (Alberta, Ontario), China (Yunnan), Czech Republic (Moravia), England, France (Boulonnais), Germany (Sauerland), Poland, Russia (Kuznetsk Basin, southern Urals), United States (Ohio), Middle Devonian; Belgium, Canada (Alberta, Arctic islands), China (Guangxi), Germany (Sauerland), Russia (Russian Platform), Frasnian.—FIG. 421,4a-b. *P. juxi, holotype SMF XXV-1184, "Massenkalk," Givetian, Delsten-Milchenbach, Sauerland, Germany; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of E. Schindler).

Family ANOSTYLOSTROMATIDAE Nestor, 2011

[Anostylostromatidae NESTOR, 2011, p. 10] [type genus, Anostylostroma PARKS, 1936, p. 44]

Skeletal elements well differentiated; laminae continuous, planar; pillars expanding and branching at tops. [The genera included herein in the family Anostylostromatidae were formerly included in the family Tienodictyidae (STEARN & others, 1999).] *Silurian (Ludlow)–Upper Devonian* (upper Famennian).

Anostylostroma PARKS, 1936, p. 44 [*A. hamiltonense PARKS, 1936, p. 46; OD; emend., STEARN, 1991, p. 612, holotype ROM 16536 (2240)]. Growth form laminar to domical; laminae thin, planar, penetrated by scattered pores; pillars thick, expanding and branching at tops, oblong to vermiform in tangential section; galleries irregular; dissepiments common; astrorhizae rare, small. Middle Devonian-Upper Devonian (upper Famennian): Canada (Arctic islands), China (Guangxi), Russia (eastern Urals, Kuznetsk Basin), United States (Indiana, Missouri), Middle Devonian; Kazakhstan, Russia (Pechora Basin), Frasnian; China (Guangxi), France, Germany (Aachen), Russia (Pechora Basin), upper Famennian.—Fig. 422, 1a-b. *A. hamiltonense, Long Lake, Alpena, Michigan, Hamilton Formation, holotype ROM 16536 (2240); longitudinal and tangential sections, ×10 (Nestor, 2011).

- Belemnostroma STEARN, 1990, p. 504 [*B. hastatum STEARN, 1990, p. 505; OD; holotype GSC 95772]. Growth form laminar to domical; laminae planar, inflected upward at megapillars; ordinary, short pillars expanding and branching at top; thicker megapillars, circular in cross section, penetrate through several laminae; astrorhizae inconspicuous. Lower Devonian (Lochkovian): Canada (Arctic Islands).——FIG. 422,2a-b. *B. hastatum, Loc. B24A near Polar Bear Pass, Bathurst Island, Stuart Bay Formation, holotype GSC 95772; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of C. W. Stearn).
- Nexililamina MALLETT, 1971, p. 241 [*N. dipcreekensis; OD; emend., WEBBY & ZHEN, 1997, p. 35, holotype UQF 47608]. Growth form laminar to domical; laminae planar with few pores; pillars of two types: superposed, long, spool-shaped (megapillars) and simple, short, rodlike, expanding and branching at top, rounded to angular in cross section; dissepiments scattered; astrorhizae apparently lacking. Lower Devonian (Emsian)–Middle Devonian (Eifelian): Australia (northern Queensland).—FIG. 422,3a–b. *N. dipcreekensis, Martins Well, Broken River, Dip Creek Limestone, holotype, UQF 47608; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of B. D. Webby).
- Schistodictyon Lessovaja in Lessovaja & Zakharova, 1970, p. 47 [*S. posterium; OD; holotype GMU 240/2-9/74]. Growth form domical; laminae thin, planar; pillars upward forking or funnel shaped, branching in longitudinal section once or twice before reaching overlying lamina, pillars vermicular, irregular to circular in cross section; galleries irregular; astrorhizae rare. Silurian (Ludlow)-Upper Devonian (Frasnian): Australia (New South Wales, northern Queensland), central Asia (Tien Shan), Ludlow-Pridoli; Australia (New South Wales, northern Queensland), Russia (Kuznetsk Basin), Lower Devonian; Belgium, Canada (Ontario), United States (Michigan, Missouri, Ohio), Russia (southern Urals, Kuznetsk Basin), Middle Devonian; Canada (Arctic islands), Russia (Kuznetsk Basin), Turkey, Frasnian.——FIG. 422, 4a-b. *S. posterium, Isfara River, Tien Shan, Isfarinsk Horizon, Pridoli, holotype GMU 240/2-9/74; longitudinal and tangential sections, ×10 (Nestor, 2011).

Family ATELODICTYIDAE Khalfina, 1968

[Atelodictyidae Khalfina, 1968a, p. 148; *emend.*, STEARN & others, 1999, p. 29] [=Aculatostromatidae Khalfina & YAVORSKY, 1973, p. 27]

Skeletal elements well differentiated; laminae continuous, planar; pillars blade shaped, laterally joined in chains or walls; galleries labyrinthine in tangential section,



FIG. 423. Atelodictyidae (p. 767-768).

subrectangular in longitudinal section; astrorhizae rare. [STEARN (1991) transferred the genus *Atelodictyon* from Actinostromatida to Clathrodictyida, as it has continuous and not colliculate laminae. The so-called hexactinellid structure occurs in the interlaminar space of *Atelodictyon* and not at the level of lamina, as in actinostromatids. The representatives of the family Aculatostromatidae KHALFINA & YAVORSKY, 1973, have quite analogous interlaminar structure and continuous laminae. Therefore, the latter family is synonymous with Atelodictyidae.] *Lower Devonian–Upper Devonian (upper Famennian)*.

Atelodictyon LECOMPTE, 1951 in 1951–1952, p. 124 [**A. fallax* LECOMPTE, 1951 in 1951–1952, p. 125; OD; holotype IRScNB 7411] [=*Aculatostroma* KHALFINA, 1968b, p. 62 (type, Syringostroma verrucosum KHALFINA, 1961d, p. 342, OD)]. Growth form laminar or domical; laminae continuous, planar, thin; pillars bladelike, laterally joined in chains, short to superposed; galleries labyrinthine in tangential section, rectangular in longitudinal section; astrorhizae rare. [The original figures of Syringostroma verrucosum (KHALFINA, 1961d, pl. D13, 3a-b, designated as the type species of the genus Aculatostroma KHALFINA, 1968b, clearly demonstrate that it has continuous laminae and so-called hexactinellid structure in the interlaminar space. Therefore, Aculatostroma is treated as a junior synonym of Atelodictyon.] Lower Devonian-Upper Devonian (upper Famennian): Australia (northern Queensland, Victoria), central Asia (Tien Shan), Russia (Kuznetsk Basin, northeastern Siberia), Lower Devonian; Afghanistan, Austria, Belgium, China (Quizhou), France (Boulonnais), Poland, Russia (Kuznetsk Basin, northeastern Siberia, Urals), United States (Indiana), Middle Devonian; Canada (Alberta), Czech Republic (Moravia), Poland, Russia (Kuznetsk Basin, northeastern Siberia, Russian Platform), United States (Iowa), Upper Devonian; Belgium, Germany, Kazakhstan, upper Famennian. FIG. 423, 1a-b. *A. fallax, Couvinian, Eifelian, Dinant Basin, Belgium, holotype IRScNB 7411; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of C. W. Stearn).

- Coenostelodictyon YAVORSKY in KHALFINA & YAVORSKY, 1971, p. 118 [*Clathrodictyon krekovi YAVORSKY, 1955, p. 50; OD; holotype CNIGR 7351/62]. Growth form laminar; laminae thin, planar, slightly inflected at the junctions with pillars; pillars bladelike, circular at base, mainly isolated but laterally joined in chains at top; galleries open in tangential section, subrectangular in longitudinal section; astrorhizae unknown. Lower Devonian (Pragian)–Middle Devonian (Eifelian): Russia (Kuznetsk Basin), Pragian; China (Yunnan), Eifelian.—FIG. 423,2a-b. *C. krekovi (YAVORSKY), Krekov Horizon, Pragian, River Chernovoĭ Bachat, Kuznetsk Basin, holotype CNIGR 7351/62; longitudinal and tangential sections, $\times 20$ (Nestor, 2011).
- ?Cubodictyon YANG & DONG, 1979, p. 45 [88] [*C. sinense; OD; holotype NIGP Bd 644-4]. Growth form domical or irregular; laminae thin, continuous, wrinkled on a small scale; longitudinal elements, walls of subhexagonal chambers; astrorhizae unknown. [The presence of chamberlike structures in interlaminar spaces shows that the relationship of the genus with stromatoporoids is problematic.] Middle Devonian (Eifelian): China (Guangxi).—FIG. 423,3a-b. *C. sinense, Beiliu Formation, holotype NIGP Bd 644-4; longitudinal and tangential sections, ×10 (Yang & Dong, 1979, pl. 20,5-6).

ACTINOSTROMATIDA: SYSTEMATIC DESCRIPTIONS

CARL W. STOCK

Order ACTINOSTROMATIDA Bogoyavlenskaya, 1969

[Actinostromatida BOGOYAVLENSKAYA, 1969b, p. 18]

Skeleton network of pillars or micropillars, and horizontal colliculi or microcolliculi that form hexactinellid pattern in tangential sections of most genera; microstructure compact to microreticulate. Upper Ordovician (Katian)-Upper Devonian (Frasnian).

Family ACTINOSTROMATIDAE Nicholson, 1886

[nom. correct. LECOMPTE, 1956, p. 127, pro Actinostromidae NICHOLSON, 1886a, p. 75]

Skeleton consists of well developed, parallel pillars, usually more prominent than colliculi; microstructure compact. *lower Silurian (Llandovery)–Upper Devonian (Frasnian)*.

Actinostroma NICHOLSON, 1886a, p. 75 [*A. clathratum NICHOLSON, 1886b, p. 226; OD] [=Rosenia WAAGEN & WENTZEL, 1887, p. 943 (type, Stromatopora astroites ROSEN sensu BARGATZKY, 1881a, p. 284); =Bullatella BOGOYAVLENSKAYA, 1977b, p. 13 (type, B. crassa BOGOYAVLENSKAYA, 1977b, p. 14, OD); =Auroriina BOGOYAVLENSKAYA, 1977b, p. 16 (type, A. primigenia BOGOYAVLENSKAYA, 1977b, p. 17, OD)]. Pillars thick, usually long, continuous; colliculi horizontally aligned. [NICH-OLSON (1886a, 1886b) published the type species before he published the initial description of the genus. STOCK in STEARN and others (1999) noted that there are two groups of species within Actinostroma that are atypical. One group has complexly arranged colliculi and mostly short pillars, as in A. verrucosum (GOLDFUSS, 1826). The other group has simple colliculi and mostly short pillars, as in A. stellulatum NICHOLSON, 1886b.] Lower Devonian (Lochkovian)-Upper Devonian (Frasnian): Russia (Kuznetsk Basin), Uzbekistan, Lower Devonian; Canada (Arctic islands), Russia (eastern Urals), Lochkovian; Australia (New South Wales, Queensland), Czech Republic, Pragian; Australia (New South Wales, Queensland), Austria, Czech Republic, Mongolia, Russia (northeastern Siberia, UlakhanSis Range), Spain, Emsian; China (Hunan, northeastern China), Italy, Russia (Pechora Basin, Salair, Siberia, Urals), Vietnam, Middle Devonian: Australia (Queensland), Austria, Belgium, China (Guangxi, Xinjiang), Czech Republic, Germany, Mongolia, Russia (Altai, Kuznetsk Basin, Siberia), Slovenia, Spain, Uzbekistan, Eifelian; 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, Ulakhan-Sis Range, Urals), Thailand, United States (Indiana), Uzbekistan, Vietnam, Givetian; Russia (Pechora Basin, Russian Platform), Turkey, Upper Devonian; Australia (Western Australia), Belgium, Canada (Alberta, Manitoba, Northwest Territories, Saskatchewan), China (Guangxi, Sichuan, Yunnan), Czech Republic, France, Germany, Iran, Mexico (Sonora), Poland, Russia (Kuznetsk Basin, northeastern Siberia, Russian Platform, St. Petersburg, Timan), United States (Alaska, Iowa, Montana, Nevada, Utah), Uzbekistan, Vietnam Frasnian -----FIG. 424a-d. *A. clathratum NICH-OLSON; a-b, lectotype, Givetian, Gerolstein, Eifel, Germany, NHM P5774; a, longitudinal section, showing long pillars and horizontally aligned colliculi; isolated dots, as in center of figure, represent cross sections of colliculi; b, tangential section, showing pillar cross sections as isolated dots, and dark bands with poorly preserved colliculi and pillars forming hexactinellid network, $\times 10$; *c*–*d*, hypotype, Mason City Member, Shell Rock Formation, Frasnian, Nora Springs, Iowa, USNM 307172; c, longitudinal section; d, tangential section, better preserved than view b; hexactinellid network best displayed in lower half of figure, ×10 (Stock, 2012).

Bicolumnostratum STOCK in STOCK & BURRY-STOCK, 1998, p. 191 [*Actinodictyon mica BOGOY-AVLENSKAYA, 1969a, p. 20; OD; holotype, BOGOY-ALENSKAYA, 1969a, p. 20, pl. 4,2a-b, UGM 26-M 113 67, Ekaterinburg, Sverdlovsk]. Pillars mix of two types, some long, continuous and thick, others short and thin; colliculi not horizontally aligned. upper Silurian (Ludlow-Pridoli): Ukraine (Podolia), Ludlow; United States (New York), Pridoli.—FIG. 425a-d. *B. micum (BOGOYAV-LENSKAYA); a-b, holotype, Sokol Beds, Malinovtsy Horizon, Ludlow, Podolia, Ukraine, UGM 26-M 113 67; a, longitudinal section; b, tangential section, × 30 (Bogoyavlenskaya, 1969a); c-d,



FIG. 424. Actinostromatidae (p. 769).

hypotype, Cobleskill Member, Rondout Formation, Pridoli, Cobleskill, New York, USNM 492553; c, longitudinal section, black dots represent air bubbles in thin section mounting medium; d, tangential section, black dots represent cross sections of well developed pillars, from which extend colliculi, ×30 (Stock, 2012).

Bifariostroma KHALFINA, 1968a, p. 149 [*Actinostroma bifarium NICHOLSON, 1886b, p. 231; OD]. Pillars mix of two types, some long, continuous, and thick, others short and thin; colliculi horizontally aligned. Lower Devonian (Emsian)-Upper Devonian (Frasnian): Austria, Spain, Emsian; Italy, Middle Devonian; Belgium, Spain, Uzbekistan, Eifelian; Belgium, China (Guangxi, Sichuan), Czech Republic, France, Poland, Germany, *Givetian*; Afghanistan, Belgium, Czech Republic, Poland, Russia (Timan), *Frasnian.*— FIG. 426, *Ia–b.* **B. bifarium* (NICHOLSON); lectotype, Givetian, Büchel bei Bensberg, Paffrath-Mulde, Germany, NHM P5639; *a*, longitudinal section, Nicholson slide 165c, apparent cellules in pillars and some colliculi represent diagenetic alteration of original compact microstructure; *b*, tangential section, Nicholson slide 165b; hexactinellid pattern best developed in center to lower center of figure, ×10 (Stock, 2012).

Crumplestroma KHALFINA, 1972, p. 148 [*C. lacerilaminatum; OD]. Skeleton consists of long pillars and steplike offsets of colliculi interrupted by paralaminae, thicker than colliculi. upper Silurian (Ludlow): Russia (Altai).——FIG. 426,2a-b. *C.



FIG. 425. Actinostromatidae (p. 769-770).

lacerilaminatum; holotype, photomicrographs, CSGM no. unknown; *a*, longitudinal section showing crumpled paralaminae between which pillars and colliculi developed; *b*, tangential section, poorly developed hexactinellid pattern in upper half of figure, $\times 10$ (Khalfina, 1972, pl. C-II, *I*-2).

Plectostroma NESTOR, 1964a, p. 78 [*Actinostroma intertextum NICHOLSON, 1886b, p. 233; OD]. Pillars long, continuous; colliculi not horizontally aligned, in many cases not perfectly horizontal. lower Silurian (Llandovery)-Upper Devonian (Frasnian): Russia (Altai, Salair), Silurian; Estonia, Russia (Siberian Platform, Tuva, Urals), Sweden (Gotland), Uzbekistan, Llandovery; China, middle Silurian; Canada (Northwest Territories), Estonia, Mongolia, Norway, Russia (Kuznetsk Basin, Urals), Sweden (Gotland), United Kingdom, Wenlock; China, Russia (Kuznetsk Basin, Pechora Basin, Urals), upper Silurian; Canada (Quebec), Estonia, Mongolia, Russia (Altai, Novaya Zemlya), Sweden (Gotland, Scania), Ukraine (Podolia), Ludlow; Canada (Quebec), Estonia, Mongolia, Ukraine (Podolia), Pridoli; Russia (northeastern Siberia), Uzbekistan, Lower Devonian; Canada (Arctic islands), Uzbekistan, Lochkovian; Australia (Victoria), Pragian; Canada (Arctic islands, Northwest Territories), Czech Republic, Spain, Emsian; Russia (Salair), Middle Devonian; Canada (Arctic islands, Northwest Territories), China (Guangxi), Czech Republic, Russia (Altai), Uzbekistan, Eifelian; China (Guangxi), Czech Republic, France, Givetian; Vietnam, Frasnian.-FIG. 426,3a-b. *P. intertextum (NICHOLSON); holotype, Wenlock, Ironbridge, England, NHM P5620; a, longitudinal section, Nicholson slide 188b, latilaminar phases with short pillars low in figure and long pillars high in figure; b, tangential section, Nicholson slide 188, showing well developed hexactinellid pattern, ×10 (Stock, 2012).

Family PSEUDOLABECHIIDAE Bogoyavlenskaya, 1969

[Pseudolabechiidae BOGOYAVLESKAYA, 1969a, p. 17]

Skeleton contains pillars and colliculi, or micropillars and microcolliculi, clustered



FIG. 426. Actinostromatidae (p. 770–771).



FIG. 427. Pseudolabechiidae (p. 774–776).



FIG. 428. Pseudolabechiidae (p. 775).

in columns or subcolumns respectively; pillars or micropillars diverge upward; areas between columns or subcolumns contain microlaminae and may contain few pillars; colliculi or microcolliculi occur in only columns or subcolumns; microstructure compact or microreticulate. *lower Silurian (Llandovery)-upper Silurian (Pridoli).*

- Pseudolabechia YABE & SUGIYAMA, 1930, p. 59 [*P. granulata; OD]. Vertical skeletal elements with pillars diverging upward in columns, horizontal elements with colliculi in columns; microstructure compact. middle Silurian (Wenlock)-upper Silurian (Ludlow): Russia (Urals), Ukraine (Podolia), Wenlock; Estonia, Russia (Novaya Zemlya), Sweden (Gotland), Ludlow.——FIG. 427,1a-b. *P. granulata; holotype, Hemse Beds, Ludlow, Gotland, Sweden, TUM 720, photomicrographs; a, longitudinal section; b, tangential section, ×10 (Yabe & Sugiyama, 1930, pl. XXII,11-12).
- Desmostroma BOL'SHAKOVA, 1969, p. 28 [*D. columnatum Bol'sHAKOVA, 1969, p. 30; OD] [=Hexastylostroma DONG, 1984, p. 71 (type, H. neimongolense, OD)]. Clinoreticular subcolumns constitute more than half volume of skeleton; intercolumnar structures acosmoreticular. [Desmostroma was first published as a new genus in 1969 (p. 30, pl. 5, 1ab), with type species D. columnatum, holotype PIN 2336/629. However, BOL'SHAKOVA (1973, p. 82) again published Desmostroma as a new genus, with type species D. columnum, labeled as a so-called holotype, PIN 2336/628; however the illustrated "holotype" was cited as PIN 2336/628 in the text but PIN 2336/548 is listed in the figure caption of plate 12, fig. 2a-b (on p. 111). Notably, a copy of BOL'SHAKOVA (1973) that was presented to B. D. Webby about 1993 included a handwritten amendment of the specimen number in her text on p. 83, with the 628 part of the number crossed out and replaced by 548, so it was consistent with the original number in her figure caption. However this designation of D. columnum as the type species of Desmostroma does not represent a valid type fixation.] lower Silurian (Llandovery)-upper Silurian (Pridoli): Sweden (Gotland), United States (Iowa), Llandovery; Kirghizstan (Tien Shan), Mongolia, Sweden (Gotland), Ukraine (Podolia), United States (Kentucky), Wenlock; China (Inner Mongolia), upper Silurian; Australia (New South Wales), China (Inner Mongolia), Sweden (Gotland), Ukraine (Podolia), Ludlow; Russia (Urals), Ukraine (Podolia), Pridoli.-FIG. 427,2a-b. *D. columnatum; holotype, Mukshinsky Horizon, Wenlock, Podolia, Ukraine, PIN 2336/629; a, longitudinal section; b, tangential section, $\times 30$ (Stock, 2012, photos courtesy of Heldur Nestor).



FIG. 429. Plumataliniidae (p. 776).

Pachystroma NICHOLSON & MURIE, 1878, p. 223 [*P. antiqua; OD]. Skeleton latilaminate, irregular; clinoreticular subcolumns consist of fused micropillars and constitute about half volume of skeleton; microlaminae occur in intersubcolumnar space; thickened acosmoreticular structure developed at base of latilaminae. lower Silurian (Llandovery)-middle Silurian (Wenlock): Canada (Ontario), Estonia, United States (Michigan), Llandovery; Canada (Ontario, Quebec), United States (Kentucky), Wenlock.—FIG. 428a-c. *P. antiquum; holotype, Niagara Limestone, Wenlock, Thorold, Ontario, Canada, NHM P6003; *a*, longitudinal section, note conspicuous latilamination; *b*, tangential section, $\times 10$; *c*, longitudinal section, $\times 30$ (Stock, 2012).

Vikingia BOGOYAVLENSKAYA 1969a, p. 19 [*Actinodictyon? vikingi NESTOR, 1966a, p. 62; OD]. Longitudinal skeletal elements composed of clinoreticular subcolumns with distinct to fused micropillars and microcolliculi, and constitute less than half volume of skeleton; intersubcolumnar structures cyst plates. *lower*



FIG. 430. Actinostromellidae (p. 776-777).



FIG. 431. Actinostromellidae (p. 776–777).

Silurian (Llandovery)-upper Silurian (Pridoli): Russia (Siberian Platform), Ukraine (Podolia), United States (Iowa), Llandovery; Estonia, Russia (Novaya Zemlya, Siberian Platform), Sweden (Gotland), Ukraine (Podolia), United States (Alaska), Wenlock; Ukraine (Podolia), Pridoli.—FIG. 427,3a-b. *V. vikingi (NESTOR); holotype, Jaagarahu Stage, Wenlock, Estonia, IGTUT 114-51 (Co3146); a, longitudinal section; b, tangential section, ×30 (Stock, 2012, courtesy of Heldur Nestor).

Family PLUMATALINIIDAE Bogoyavlenskaya, 1969

[Plumataliniidae BOGOYAVLENSKAYA, 1969b, p. 17]

Skeleton contains micropillars and microcolliculi, clustered in subcolumns; areas between subcolumns contain cyst plates or microlaminae; microstructure of subcolumns acosmoreticular. Upper Ordovician (Katian).

Plumatalinia NESTOR, 1960, p. 225 [*P. ferax NESTOR, 1960, p. 226; OD]. Skeleton of acosmoreticular subcolumns, and cyst plates or microlaminae. Upper Ordovician (Katian): Estonia.—FIG. 429a-b. *P. ferax; holotype, Pirgu Stage, late Katian, IGTUT 111-1 (Co3001); a, longitudinal section, ×10; b, longitudinal section, enlargement of upper right portion of view a, ×25 (Stock, 2012, courtesy of Heldur Nestor).

Family ACTINOSTROMELLIDAE Nestor, 1966

[Actinostromellidae NESTOR, 1966a, p. 50] [=Pichiostromatidae BOGOYAVLENSKAYA, 1981, p. 31]

Skeleton a microreticulate mass pierced by elongate, vertical spaces. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian)*.

Actinostromella BOEHNKE, 1915, p. 162 [*A. tubulata BOEHNKE, 1915, p. 163; OD]. Micropillars long, connected by microcolliculi that may or may not align horizontally; longitudinal spaces autotubes. [The holotype, and only known specimen of A. tubulata BOEHNKE, 1915, is from Silurian glacial erratics in eastern Prussia (=Kaliningrad District). All type material was lost during the Second World War. Subsequent authors did not report A. tubulata from other localities, so no potential neotype specimens are available. Silurian-age glacial erratics in northern Poland, Germany, and Kaliningrad District, Russia most likely originated in Sweden (Gotland), Estonia, or the floor of the Baltic Sea. Therefore, A. vaiverensis NESTOR, 1966a, from western Estonia (Saarema) is used here as the



FIG. 432. Actinostromellidae (p. 777).

reference species.] middle Silurian (Wenlock)-Lower Devonian (Lochkovian): Sweden (Gotland), Wenlock; Australia (New South Wales), China (Inner Mongolia), Sweden (Gotland), Ukraine (Podolia), Ludlow; Canada (Quebec), Estonia, United States (Alabama, New York), Pridoli; China (Inner Mongolia), Lochkovian.-FIG. 430a-b. *A. tubulata; holotype, glacial erratic, Kaliningrad District, Russia, specimen no. unknown, micrographs, lower case a on photos indicates what BOEHNKE (1915) called zooidal tubes (=autotubes); a, longitudinal section; note some colliculi are horizontally aligned, but others are not; b, tangential section, magnification unknown, reproduced here at same size as original publication (Boehnke, 1915, fig. 6-7).-FIG. 431a-c. A. vaiverensis NESTOR; holotype, Kaugatuma stage, Pridoli, Saarema, Estonia, IGTUT 114-42 (Co3159); a, longitudinal section, note change in density of macrostructures associated with base of a latilamina about two-fifths above base of photomicrograph; b, tangential section, ×10; c, longitudinal section, note horizontal alignment of microcolliculi, ×20 (Stock, 2012, courtesy of Heldur Nestor).

Pichiostroma BOGOYAVLENSKAYA, 1972a, p. 28 [*P. pichiense; OD]. Skeleton microreticulate, pierced by vertical slitlike spaces. middle Silurian (Wenlock)-upper Silurian (Ludlow): United States (?Kentucky), Wenlock; Russia (Tuva), Ukraine (Podolia), Ludlow.—FIG. 432a-b. *P. pichiense; holotype, Ludlow, Tuva, Russia, UGM 2808/3, a, longitudinal section; b, tangential section, ramifications of extensive astrorhizae may be responsible for slitlike spaces noted in longitudinal section, ×10 (Stock, 2012, courtesy of Heldur Nestor).

Family DENSASTROMATIDAE Bogoyavlenskaya, 1974

[Densastromatidae BOGOYAVLENSKAYA, 1974, p. 22]

Skeleton microreticulate, uninterrupted by accessory spaces. *lower Silurian (Llandovery)–Lower Devonian (Lochkovian).*

- Densastroma Flügel, 1959, p. 196 [*Stromatopora astroites ROSEN, 1867, p. 62; OD] [=Pycnodictyon MORI, 1970, p. 103 (type, P. densum, OD)]. Microcolliculi horizontally aligned, giving impression of microlaminae; micropillars short; forming orthoreticular pattern. lower Silurian (Llandovery)-upper Silurian (Pridoli): Sweden (Gotland), United States (Iowa), Llandovery; Canada (Quebec), Estonia, Sweden (Gotland), Ukraine (Podolia), United States (Kentucky), Wenlock; China (Inner Mongolia), upper Silurian; Australia (New South Wales), Canada (Quebec), Estonia, Russia (Siberian Platform, Urals), Sweden (Gotland), Ukraine (Podolia), Uzbekistan, Ludlow; Canada (Quebec), Estonia, Russia (Urals), Ukraine (Podolia), Pridoli. FIG. 433, 1a-b. *D. astroites (ROSEN); lectotype, Ludlow, Saarema, Estonia, IGTUT 115-1 (Co3181); a, longitudinal section; b, tangential section, ×30 (Stock, 2012, courtesy of Heldur Nestor).
- Acosmostroma STOCK in STOCK & BURRY-STOCK, 1998, p. 195 [*A. ataxium; OD]. Skeleton acosmoreticular, to which micropillars added in some species. upper Silurian (Pridoli): United States (New York, Tennessee, Virginia).— FIG. 433,2a-b. *A. ataxium; holotype, Glasco Member, Rondout Formation, Alligerville, New



FIG. 433. Densastromatidae (p. 777–779).

York, USNM 248115; *a*, longitudinal section; *b*, tangential section, ×30 (Stock, 2012).

Araneosustroma LESSOVAYA, 1970, p. 80 [*A. fistulosum LESSOVAYA, 1970, p. 81; OD] [=Petschorostroma BOGOVAVLENSKAYA, 1983, p. 84 (type, *P. kozhmiense*, OD)]. Microreticulate structure orthoreticular to acosmoreticular, in some species combined with microlaminae; microcolliculi horizontally aligned at some levels, not aligned at other levels; in some species, micropillars clustered into indistinct, narrow subcolumns, giving impression of closely packed microreticulate pillars. middle Silurian (Wenlock)-Lower Devonian (Lochkovian): Estonia, Russia (Novaya Zemlya), Sweden (Gotland), Ukraine (Podolia), Wenlock; Estonia, Russia (Novaya Zemlya, Urals), Sweden (Gotland), Ukraine (Podolia), Ludlow; Ukraine (Podolia), Pridoli; Uzbekistan, Lochkovian.—FIG. 433,3a-b. *A. fistulosum; holotype, Bursykhirman Horizon, Lochkovian, Uzbekistan, GMU 9994-6/149; a, Iongitudinal section; b, tangential section, ×20 (Stock, 2012, courtesy of Heldur Nestor).