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PART E, REVISED, VOLUME 4, CHAPTER 16B: LABECHIIDA

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Order LABECHIIDA Kühn, 1927

[*nom. correct.* BOGOYAVLENSKAYA, 1969, p. 16, *pro* order Labechioidea KÜHN, 1927, p. 547] [=Lophiostromatida NESTOR, 1978, p. 18; =Lophiostromatida STEARN, 1980, p. 888; =Protolabechiida BOGOYAVLENSKAYA, 2001, p. 46, *partim*; =Cystostromatida BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & YELKIN, 2011, p. 18; =Aulaceratida BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & 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, blister-like 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 latilaminar forms, skeletal layers become much thickened; mamelons and mamelon columns may occur; astrophorae 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. The justification for this change is not entirely clear, and so the proposal should be abandoned, given the extent to which it will fragment what had previously been an almost natural grouping, retained with only small changes more or less continuously since the 1980s (STEARNS, 2010). Earlier, five families were recognized by BOGOYAVLENSKAYA (1984), four subdivisions by NESTOR (1994), and six families by WEBBY (in STEARN & others, 1999). Consequently, BOGOYAVLENSKAYA's proposal is rejected herein in favor of the more traditional approach of the order as being comprised of seven families (see also discussion in WEBBY, 2012b, p. 8)].

Middle Ordovician (Darriwilian)–Silurian (Aeronian), ?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 astrophorae (HEINRICH, 1914; KÜHN, 1927, 1939b; TRIPP, 1929). STEARN (1982) 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 WEBBY, 2012b, p. 1–8).

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 BOGOYAVLENSKAYA, 2001, 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 in WEBBY, 2012a, p. 1). None of these family groups is closely related to one another, nor, as the name implies, are any of BOGOYAVLENSKAYA'S (2001) protolabechiids close to roots of either the Labechiida (see WEBBY, 2012b, p. 7–8) or the Pulchrilaminida (see WEBBY, 2012a, p. 1–2).

BOGOYAVLENSKAYA'S (2001, 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 elements—denticles, 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, 2001; 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 (STEARNS, 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 light-colored, 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 wall-less 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, 1935] by STEELE-PETROVICH, 2011, p. 802), also thought to represent original aragonite frameworks (SEMENIUK, 1971; WEBBY, 1990).

Second, NESTOR (1964, 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 (1964, p. 17, see especially fig. 2b–d) preferred to interpret the tubelike, so-called pillars as primary structures, suggesting a three-stage 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., KAŻMIERCZAK, 1971; KHROMYKH, 1999b) have adopted views similar to those of NESTOR, namely that the longitudinal structural elements are primary hollow tubes or plates.

NESTOR (1964, 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 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 (2012, p. 43) 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.

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 Stromatoceridae 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 ROSELLIDAE Yavorsky in Khalфина & Yavorsky, 1973

[Rosnellidae 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; NESTOR, 2011, p. 1). No other stromatoporoid worker has followed KHROMYKH’s approach.

BOGOYAVLENSKAYA (in BOGOYAVLENSKAYA, VASSILYUK, & GLEBOV, 1990), and BOGOYAVLENSKAYA (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, 2001, 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 (2001, 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.

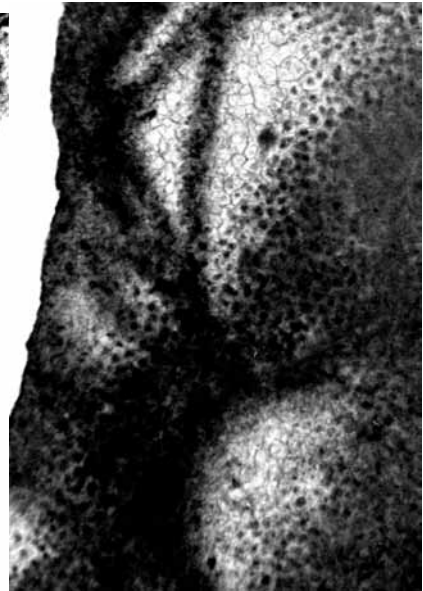
Rosenella NICHOLSON, 1886a, p. 84 [**R. macrocystis* NICHOLSON, 1886a, p. 84, pl. 7, 12–13; OD; NICHOLSON, 1886b, p. 20, pl. 1, 8; NICHOLSON, 1886a, included a description of the genus and figures and the name of the species, without description (the type species is illustrated in both papers). The figures 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 (1886b) 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 (Tiva), *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. 1, 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, dark-colored, 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, $\times 10$; c, tangential section of slide 280a shows many



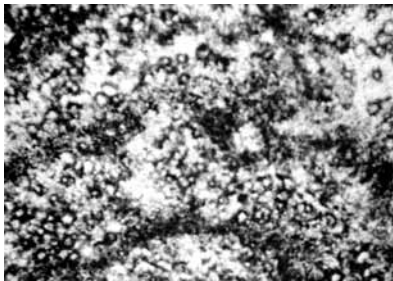
1a



1b



1c



2a



2b

FIG. 1. Rosenellidae (p. 4-11).

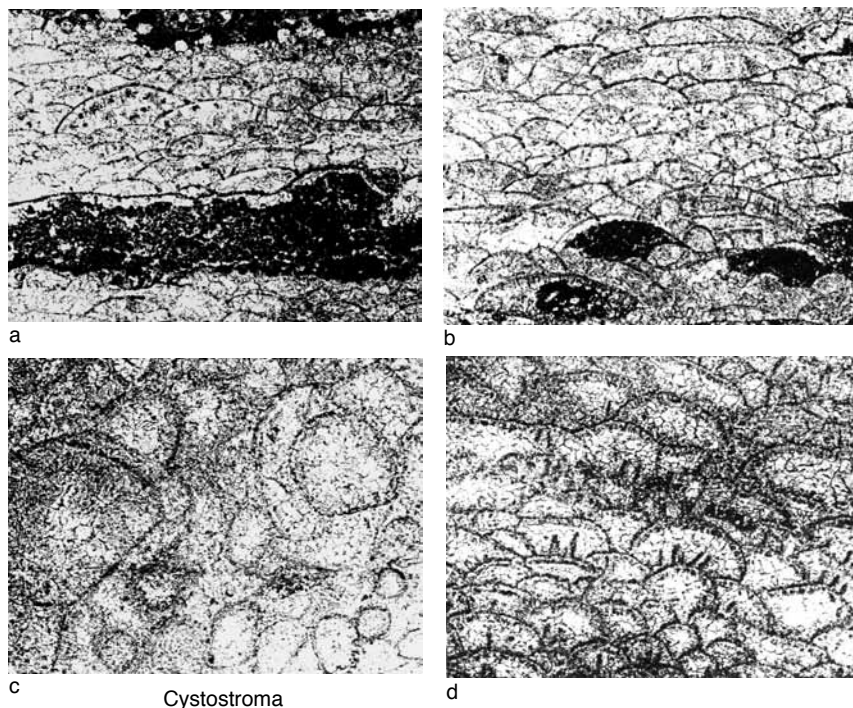


FIG. 2. Rosenellidae (p. 6–7).

finely preserved, darker, dot-shaped denticles, $\times 10$ (new; 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, *I*, pl. 32, *I*; 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 NESTOR, 2011, p. 1) transferred the taxon to Clathrodictyida after reexamination of type material revealing paths of numerous astrophorizae 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. 2*a–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. 2*d*. *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, $\times 10$; 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 WEBBY (2010, p. 19) (retouched photo, Galloway & St. Jean, 1961, pl. 1, 3*a*).

Forolinia NESTOR, 1964, p. 31 [**Rosenella pachyphylla* NICHOLSON, 1886b, 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. 1, 1*b*) with the *Forolinia* type species (Fig. 3*b*). 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. 2*a*–*f*, 4*c*–*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. 12 herein.)] *Lower Silurian*: China (Guizhou), Estonia.—FIG. 3*a*–*c*. **F. pachyphylla* (NICHOLSON), Llandovery, Adavere stage, Pääri outcrop (20th century Kattentack fossil locality), Estonia; holotype, NHM P5629 (Nicholson's slides 283, 283*a*–*e*; note that sections 283 and 283*a* 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 283*b* 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, $\times 7.5$; *c*, longitudinal section of slide 283*a* shows part of skeleton with latilaminar 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,

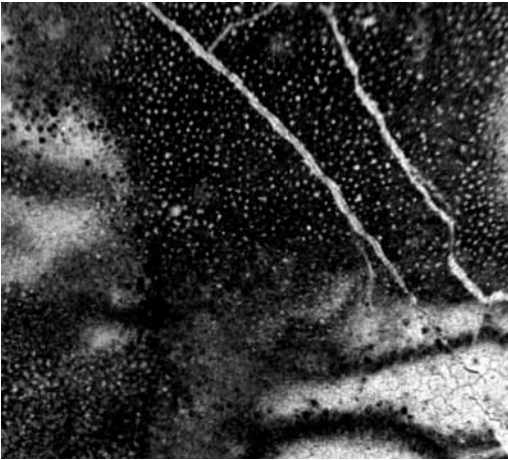
and lenses filled with dark sedimentary material, $\times 5$ (new; Nicholson's slides 283, 283*a*–*b*, rephotographed by Webby in 1989).

Priscastroma KHROMYKH, 1999a, p. 801 [178] [**P. gemina* KHROMYKH, 1999a, p. 801, fig. 1*a*–*b*, 2*a*–*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 astrophorae 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. 41–45 herein). However, it bears little resemblance to other early lophiostromatids like *Lophiostroma shantungensis* YABE & SUGIYAMA, 1930 (see OZAKI, 1938), from a similar Middle Ordovician (Darriwilian) stratigraphic horizon in Shandong Province, northern China, which characteristically exhibits much thickened skeletons and long pillarlike columns.] *Middle Ordovician (Darriwilian)*: Siberian platform, Russia.—FIG. 4*a*–*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. 2*a*, 2*d*); *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, $\times 8$ (Khromykh, 1999a, fig. 2*c*); *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 undomed cyst plates, $\times 20$; *e*, $\times 15$ (Khromykh, 1999a, fig. 1*a*–*b*).

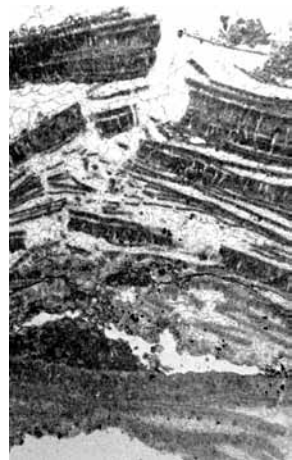
Pseudostylodictyon OZAKI, 1938, p. 208 [**P. poshannense* OZAKI, 1938, p. 208, pl. 24, 2; M; holotype, pl. 25, 1*a*–*e*] [= *Parksodictyon* BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & LOBANOV, 1990, p. 85 (type, *Pseudostylodictyon?* KAYI GALLOWAY & ST. JEAN in GALLOWAY, 1957, p. 425, OD)]. Skeleton with cyst 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.



a



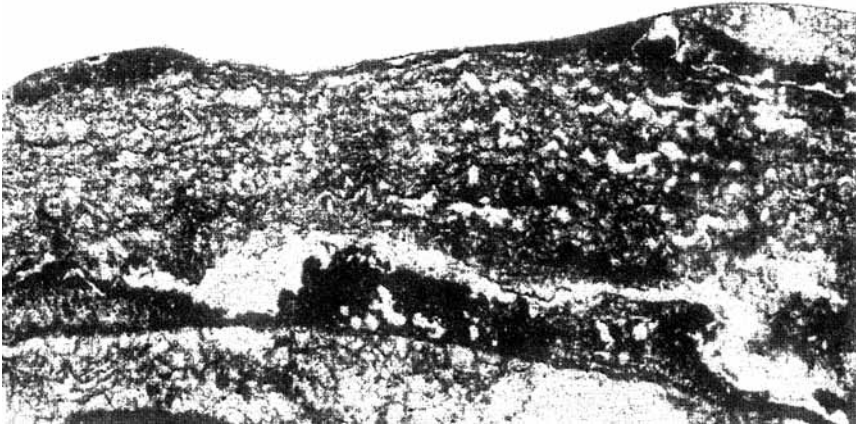
b



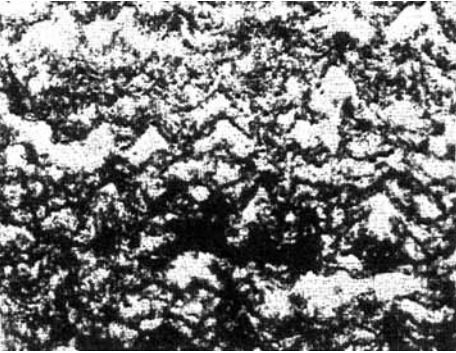
c

Forolnia

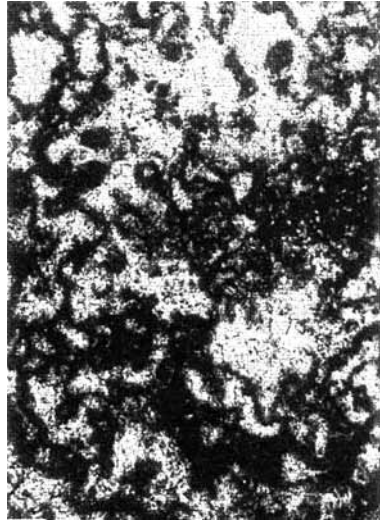
FIG. 3. Rosenellidae (p. 7).



a



b



c



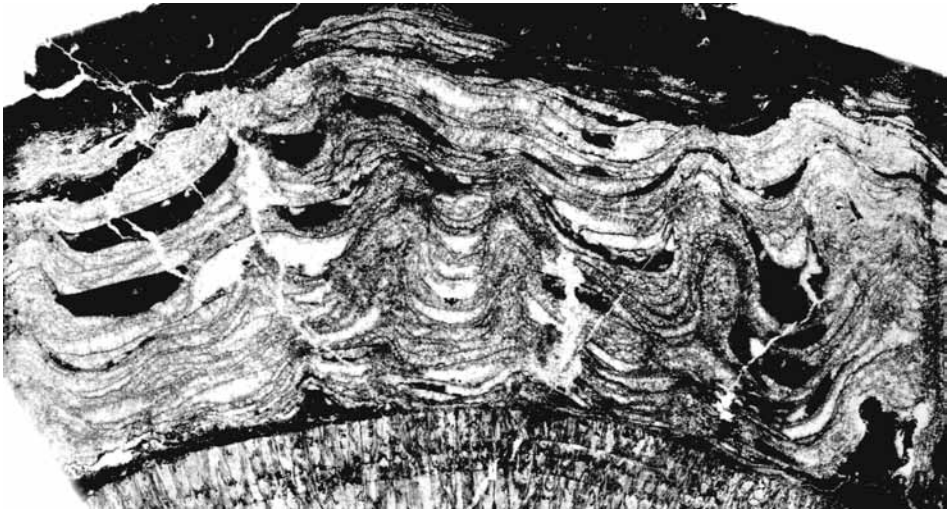
d

Priscastroma



e

FIG. 4. Rosenellidae (p. 7).



a



b



c



d

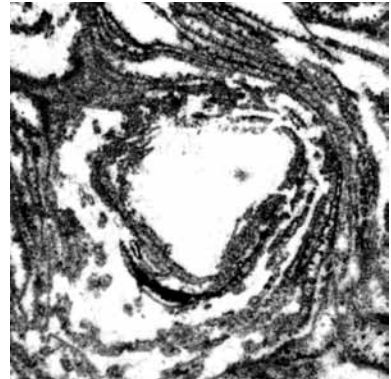


g



e

Pseudostylodictyon



f

FIG. 5. Rosenellidae (p. 7-11).

[The type species of *Parksodictyon* BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & LOBANOV, 1990 (*Pseudostylodictyon kaji* GALLOWAY & ST. JEAN in 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 Silurian*.—FIG. 5a–d. **P. poshanense*, Darriwilian, 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 latilaminar 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, $\times 2.5$ (new, 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, $\times 5$ (new, 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, $\times 8$ (Ozaki, 1938, pl. 25, 1d–1e).—FIG. 5e–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, $\times 10$ (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 light-colored 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 (1971, p. 37), they may prove on further study to represent a single taxon.] *lower Silurian*—*middle Silurian*: Russia (Tuva).—FIG. 1, 2a–b. **R. venusta*; Wenlock, Elegend River; a, specimen CNIGR 7351/556, tangential section showing numerous, small, rounded, spar-filled blebs, $\times 10$; b, holotype, CNIGR 7351/555, longitudinal section showing main features of cyst plates and crenulations, $\times 10$ (Yavorsky, 1967, pl. 3, 3–4).

Family LABECHIIDAE Nicholson, 1879

[*nom. correct.* NICHOLSON, 1886a, p. 74, ex Labechiidae NICHOLSON, 1879, p. 28] [=Stratodictyidae BOGOYAVLENSKAYA, 1977, 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, 1886b). 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 BOGOYAVLENSKAYA's (1984) family Tuvaechiidae is also a junior synonym of family Labechiidae NICHOLSON, 1879.

BOGOYAVLENSKAYA's (1977) 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 WEBBY, 2010, p. 18). 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*, *Pseudostylo-dictyon*), stromatocerids (*Stromatocerium*), and stylostromatids (*Pachystylostroma*, *Stylostroma*). Therefore, the Stratodictyidae also cannot be maintained as a separated valid group on the basis of stratocysts. BOGOYAVLENSKAYA's (2001; 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 2001 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. 15 herein).

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 & 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, 1886b, 1889, 1891) 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, low-convexity 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; finer-textured *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. 6a–b.**L. conferta* (Lonsdale), Wenlock Limestone, Dudley, England, $\times 5$, 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, dome-like, growth-banded bryozoan colony, near bottom center of field of view (new; Nicholson's thin section 264g, rephotographed by Webby in 1989);

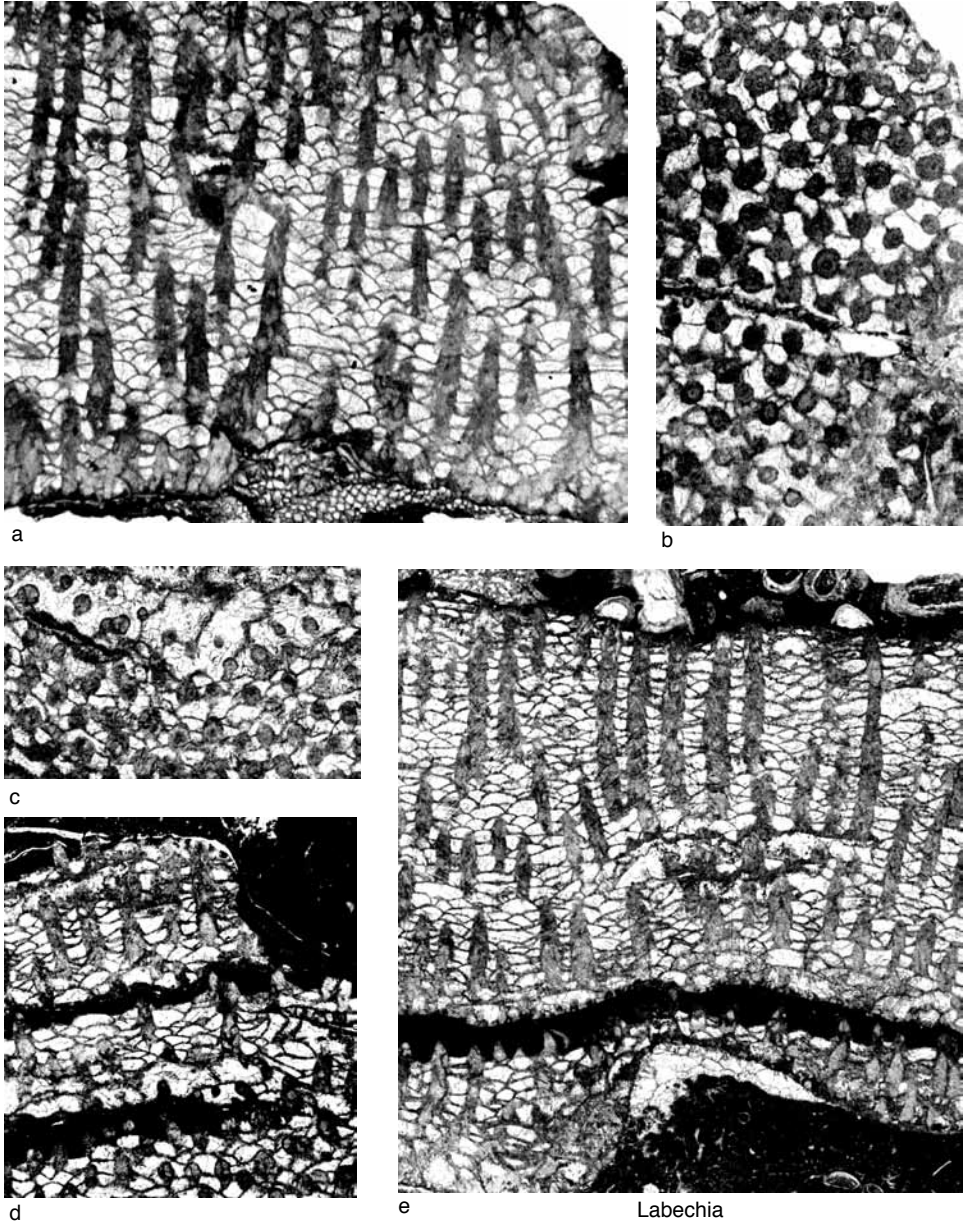


FIG. 6. Labechiidae (p. 12-14).

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 (new; part of NICHOLSON's thin section 264, rephotographed by Webby in 1989).—FIG. 6*c-e*. *L. conferta* (LONSDALE), prob-

ably from same Dudley locality and stratigraphic level; specimen AMF.134351, originally presented by T. W. Edgeworth David to Sydney University, $\times 5$ (Webby, new); *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

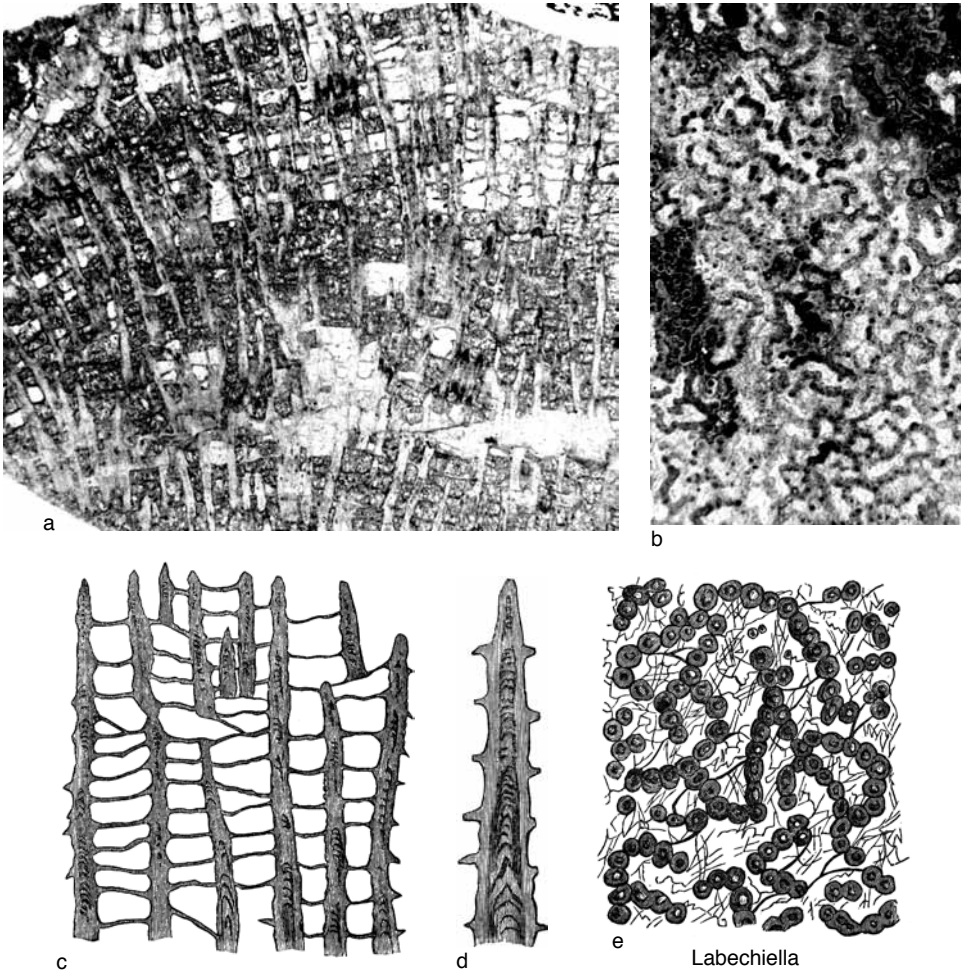


FIG. 7. Labechiidae (p. 14–15).

latilaminae; *e*, longitudinal section showing initial latilaminar 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 papillae occur at tops of both latilaminae (papillae on terminal surface of this specimen are illustrated in WEBBY & KERSHAW, 2011, fig. 44.1) (Webby, new).

Labechiella YABE & SUGIYAMA, 1930, p. 54 [**Labechia serotina* NICHOLSON, 1886b, 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* BOGOYAVLENSKAYA, 1971, p. 34 (type, *Labechia regularis* YABE & SUGIYAMA, 1930, p. 56, OD)]. Skeleton of longitu-

dinally 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, SUGIYAMA (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* (SUGIYAMA, 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 Devonian*.—FIG. 7a–e. **L. serotina* (NICHOLSON), Middle Devonian limestone, Teignmouth, near Torquay, England; holotype, NHM R5988 (NICHOLSON'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, $\times 5$ (new; Nicholson section 268a, rephotographed by Webby in 1989); b, tangential section showing rounded, interlinked pillars in slightly sinuous, incomplete, chainlike rows, $\times 5$ (new; 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, $\times 12$ (Nicholson, 1891, p. 162, fig. 19B); d, enlarged longitudinal section showing a

single upwardly tapering pillar, with detail of axial cone-in-cone banding, $\times 25$ (Nicholson, 1891, 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, $\times 12$ (Nicholson, 1891, 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. 8a–d. **S. ozakii*, lower part of Fossil Hill Limestone, lower Eastonian, Licking Hole Creek area, central New South Wales; a–b, holotype, AMF99377 (AMFT.15020, 15021), longitudinal and tangential sections showing part of latilaminar skeleton with rows of long low cyst plates and scattered short pillars, in tangential section, represented by fine, rounded, dark dots, $\times 10$ (Webby, 1969, pl. 119, 4–5); c, paratype, AMF99382 (AMFT.15023), tangential section showing pillars mainly as rounded black dots, and a few light-colored (spar-filled) astrorhizal tracts, $\times 10$ (Webby, 1969, pl. 120, 2); d, topotype IG TUT 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, $\times 25$ (new; preparation and photography courtesy of Heldur Nestor).—FIG. 8e. *S. colummare* WEBBY, Fossil Hill Limestone near west Boonderoo shearing shed, central New South Wales; holotype, AMF99378, exhibiting a fine-textured latilaminar 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, $\times 5$ (Webby, 1969, pl. 118, 4).

Family STROMATOCERIIDAE Bogoyavlenskaya, 1969

[Stromatoceriidae BOGOYAVLENSKAYA, 1969, 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

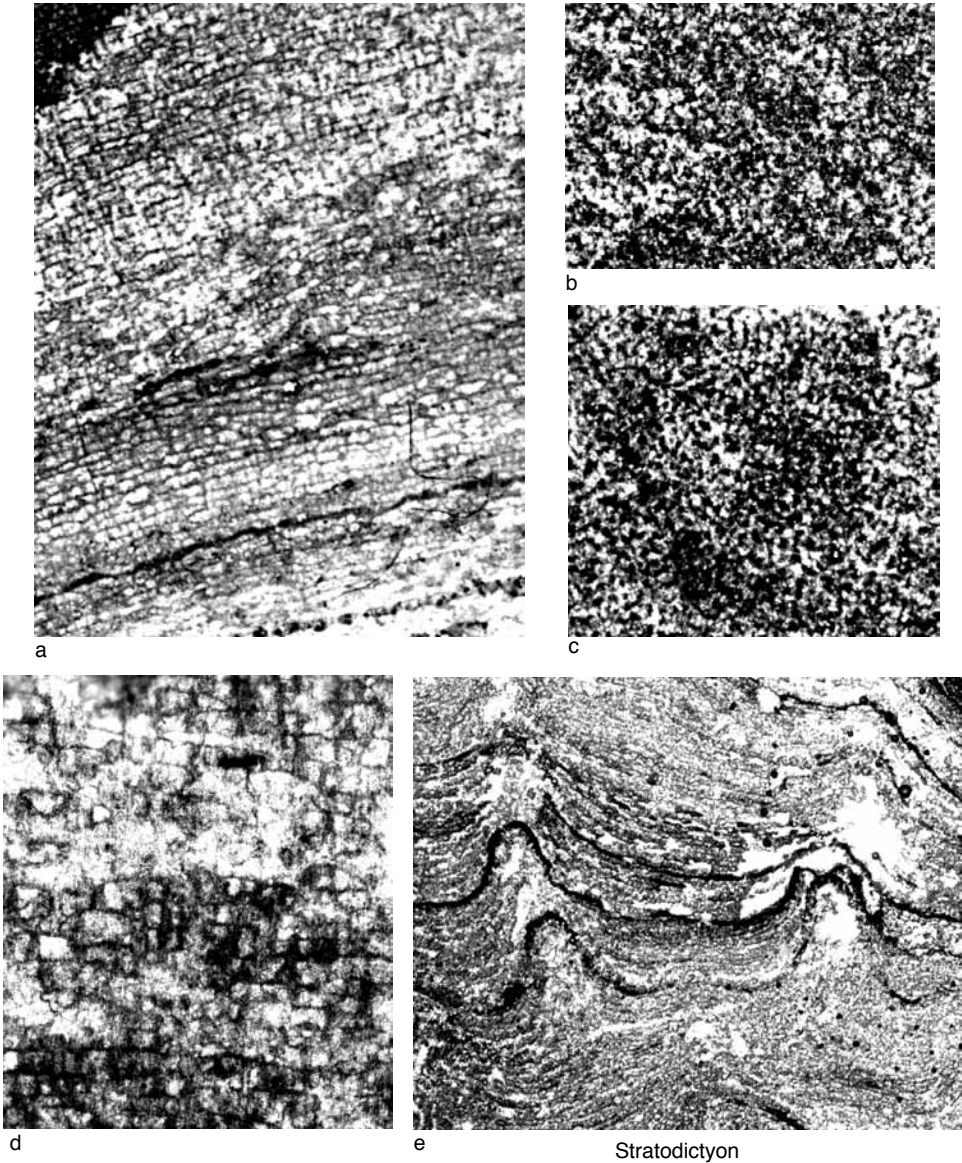


FIG. 8. Labechiidae (p. 15).

moderately convex and concave cyst plates; usually flattened to concave across narrower interspaces but may be convex upward in near proximity to mamelon 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* KHROMYKH, 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 are 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, 1979c, 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, 1977), 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, ?Michigan).—FIG. 9*a–d*. **S. rugosum*, Upper Ordovician 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*, ×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]. Coarse-textured 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. 10*a–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, speckled 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, 1979b, p. 208 [**R. tenue* WEBBY, 1979b, 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. 11*a–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

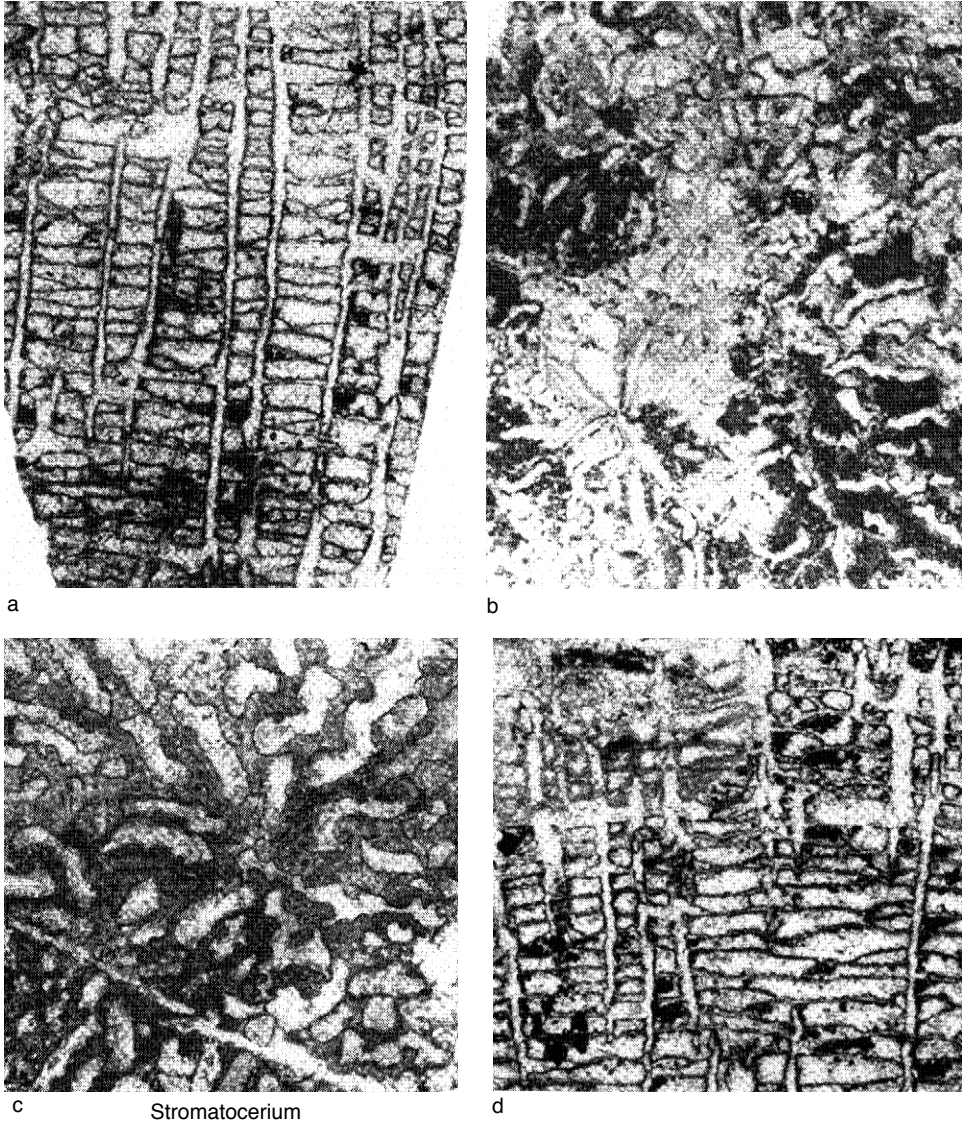
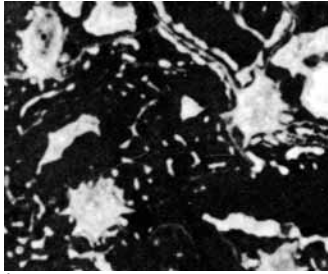


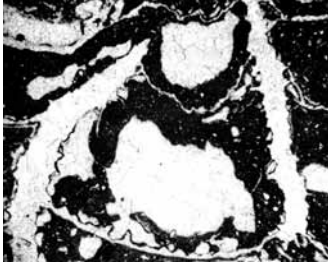
FIG. 9. Stromatoceriidae (p. 17).

one or more cyst plates are involved across wider spaces; in a few places denticles occur on upper cyst plates, $\times 5$ (Webby, 1979b, 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, 1979b, 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,

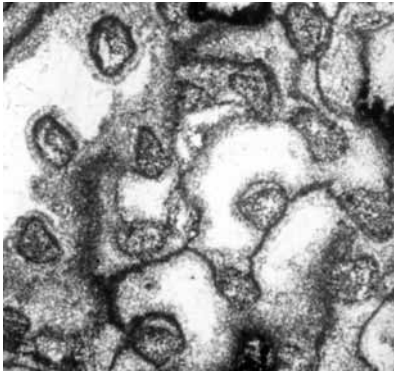
polygonal spaces, $\times 5$ (Webby, 1979b, fig. 5C); *d*, longitudinal section showing vanelike, vertical pillars (some parts of plates being intersected at right angles, others obliquely or near parallel to individual plates, and in these latter areas, traces of tiny, parallel spines may be seen inclined 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, $\times 10$ (Webby, 1979b, fig. 5E).



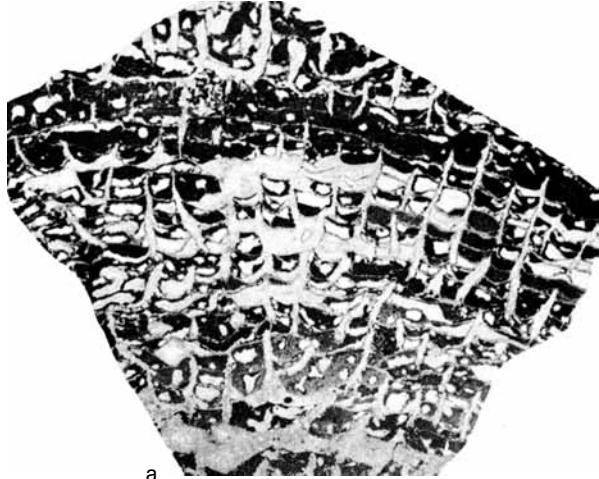
b



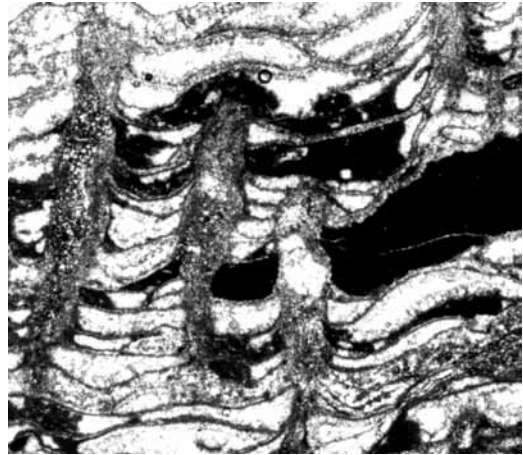
c



d



a

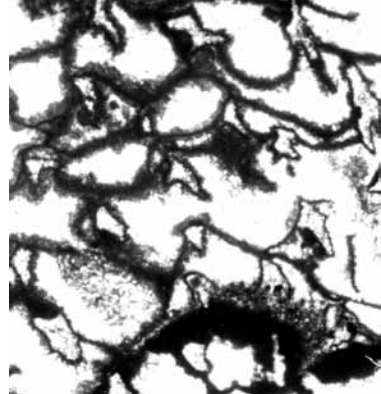


e



f

Cystistroma



g

FIG. 10. Stromatoceriidae (p. 17).

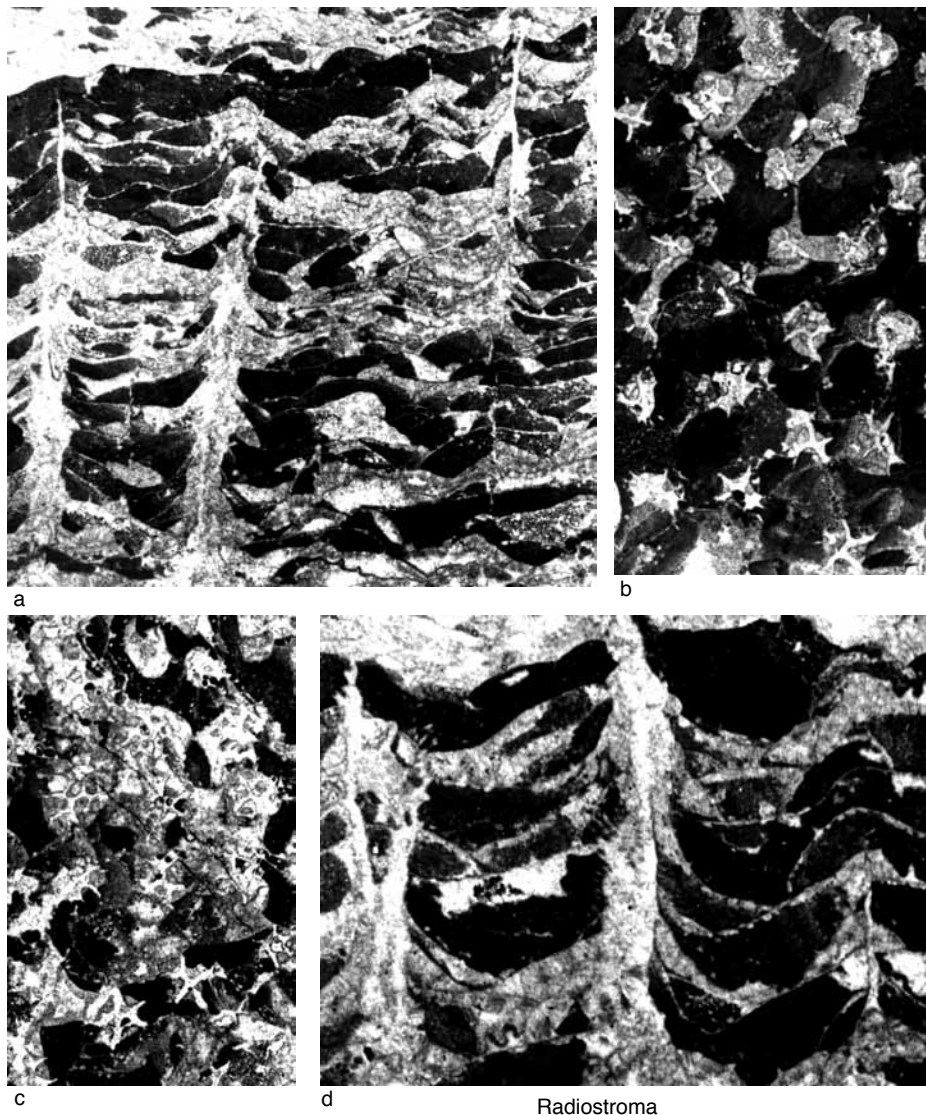


FIG. 11. Stromatoceriidae (p. 17–18).

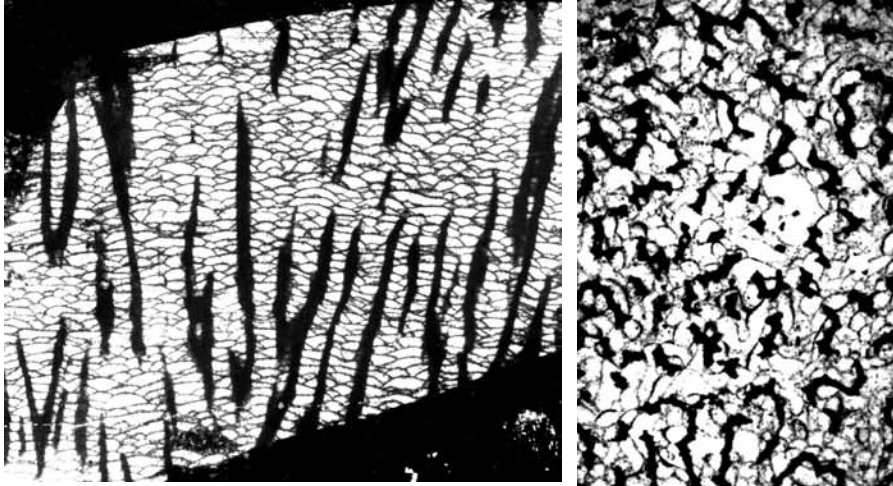
Family **PLATIFEROSTROMATIDAE**
Khalфина & Yavorsky, 1973

[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, star-shaped, 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 [**Stromatocarium 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. 12, 1a–d. **P. hybridum* (DONG), lower part of Shizixu Formation, between Huangjin and Muliu, Luocheng County, Guangxi Province, X5; a, holotype, NIPG 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, NIPG Kw044-2 (14170), tangential section showing dark-colored, 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, NIPG Kw044-3 (14168), oblique section showing mainly elongate to irregularly meandering pillars and cyst plates (new; courtesy of Dong De-yuan); d, paratype, NIPG 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).
- Cystocarium** 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. [*Cystocarium* exhibits some similarities to *Parastylostroma* BOGOYAVLENSKAYA, 1982, but it has a much denser concentration of branching, pillarlike elements than is characteristic of *Parastylostroma*.] *Slurian (Wenlock)*: Russia (Siberian platform).—FIG. 13a–b. **C. sincerum*, Moiero River section, Siberian Platform, holotype, IG TUT 166-29 (Co3217); a, longitudinal section showing latilaminar 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, wall-less, astrorhizal pathways, X10 (Nestor, 1976, pl. 9, 1a–b).—FIG. 13c–d. *C. stellatum* NESTOR, Wenlock, Moiero River section (different locality and slightly higher stratigraphic level), Siberian Platform, holotype, IG TUT, 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, X10 (Nestor, 1976, p. 43, pl. 9, 2a–b).
- Parastylostroma** BOGOYAVLENSKAYA, 1982, p. 36 [**Stromatocarium 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, p. 24]. *Upper Devonian (Famennian)*: Russia (Northern Caucasus, Novaya Zemlya), Ukraine (Donets basin), Uzbekistan.—FIG. 14, 1a–b. **P. irregularis* (VASSILYUK), Famennian sequence, Porfirtovaya ravine, near Novotroitskoye village, Donbass, Ukraine, holotype, DPI 12/130, longitudinal and tangential sections, X5 (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, 1979b, but it has thicker, solid, platelike pillars rather than the thin, bladed, or flanged pillars of *Radiostroma*; and smaller,

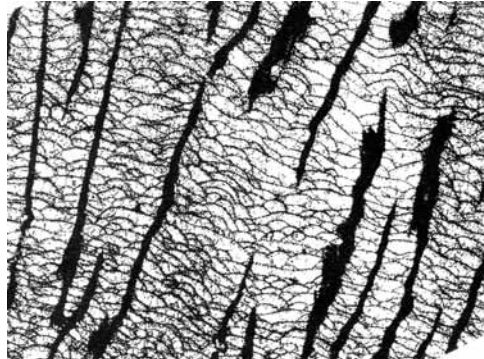


1a

1b



1c

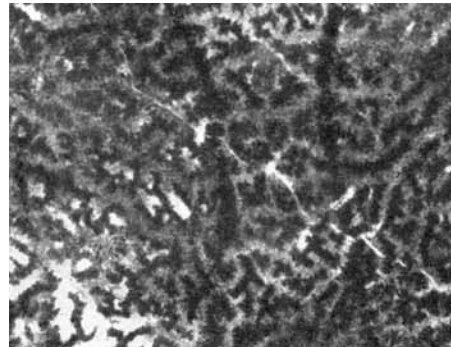


1d

Platiferostroma



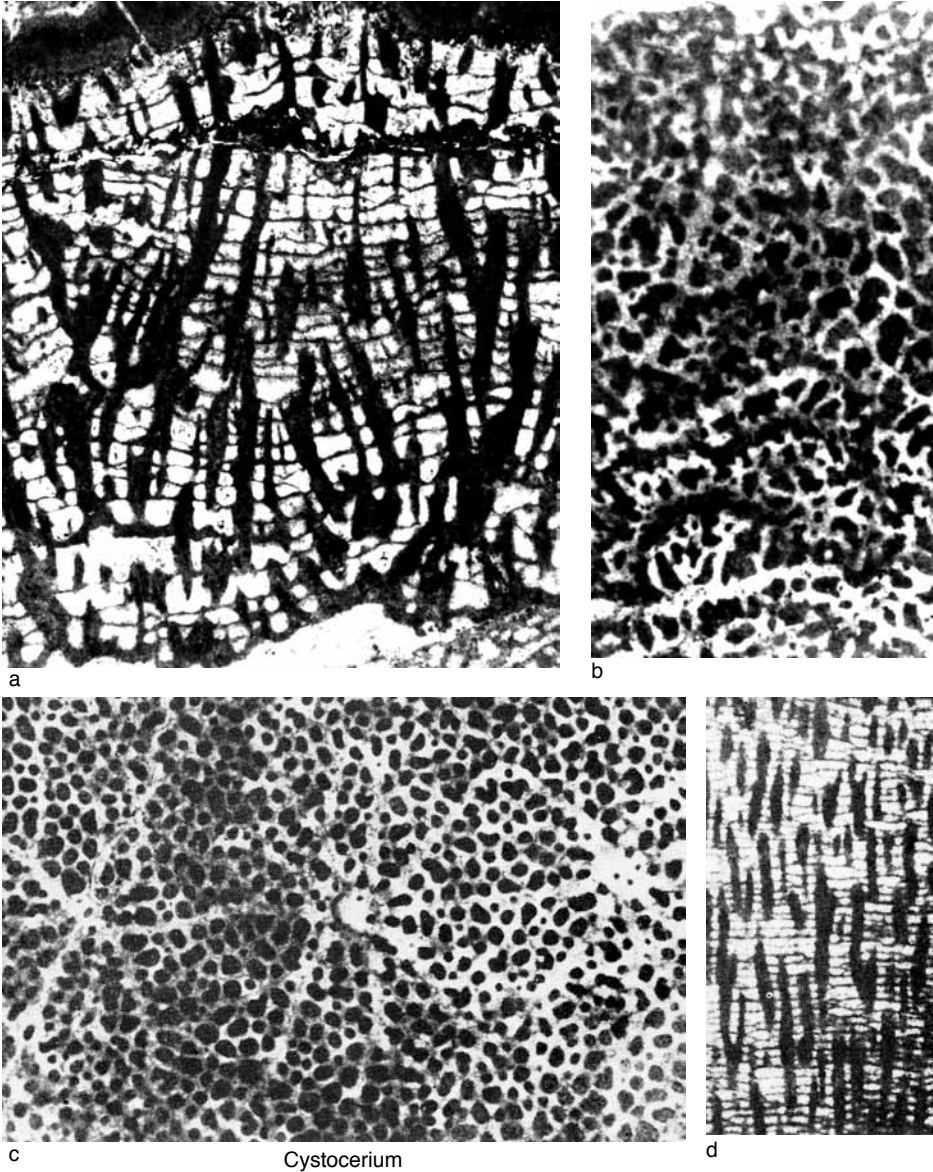
2a



2b

Stromatodictyon

FIG. 12. Platiferostromatidae (p. 21–24).



Cystocerium

FIG. 13. Platiferostromatidae (p. 21).

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. 15*a-d*. **P. shiniulanense* (WANG), Shiniulan Formation, Shiniulan, Guanyinqiao, Qijiang County, holotype, CIGMR, Gsf 105-5 (Ss1001); *a*, longitudinal section showing

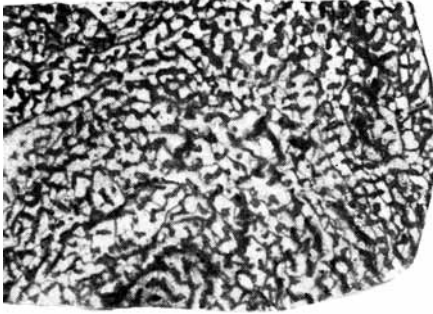
long, slender pillars, thickened only in a few places, in proximity to a branch, and with moderately upflexed, blisterlike, imbricated cyst plates of variable size; *b*, tangential section exhibiting solid pillars with round, elongate to subtriangular outlines, and thin cyst plates that enclose irregularly 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, $\times 5$ (Wang, 1982, pl. 1,3–6).—FIG. 15*e–f*. *P. coalitum* WANG, 1982, Shiniulan Formation, Shimenkair, Qijiang County; holotype, CIGMR, Sf1-3 (Ss1069); *e*, longitudinal section showing thinner, erect, plate-like 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, $\times 5$ (new, courtesy of Wang Shu Bei; see also WANG, 1982, pl.1,7–8).

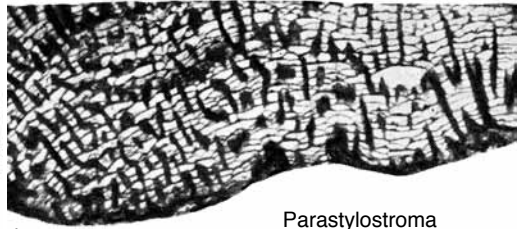
?**Stromatodictyon** KHALFINA, 1972, p. 148 [**S. repentinum* KHALFINA, 1972, p. 152, pl. C-12, fig. 4-5, M]. Skeleton with broad, continuous, longitudinally branched, irregular to bladelike or flanged pillars (with somewhat ragged margins) that are intersected by banded, laminar (or latilaminar) elements 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 spar-filled canals, including astrophthal 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, 1969, family Pseudolabechiidae BOGOYAVLENSKAYA, 1969) by STOCK (in STEARN & others, 1999, p. 37), but since excluded (see STOCK, 2012). *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. 45 herein); 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. 12,2*a–b*. **S. repentinum*, Moiero River section; holotype may exist in CSGM but has not been found, presumed lost; *vide*, V. G. Kromykh, personal communication, November 2011); *a*, longitudinal section of holotype, $\times 10$ (Khalfina, 1972, pl. 12,4); *b*, tangential section of holotype, $\times 5$ (Khalfina, 1972, pl. 12,5).

Vietnamostroma NGUYEN HUU HUNG & MISTIAEN, 1998, p. 63 [**V. vietnamense* NGUYEN HUU HUNG & MISTIAEN, 1998, p. 64, pl. 5,1*a–e*; OD]. Pillars long, complex, platelike to flanged and, in places, multibranching; 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; astrophthal may be present. [This genus, like *Parastylstroma* BOGOYAVLENSKAYA, 1982, exhibits long-low, rather flattened, cyst plates but differs in having pillars that are longitudinally more complexly flanged and multibranching, 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. kweichowense* (DONG, 1964), *V. kwangsiense* (DONG, 1964), and *V. chaetiporooides* WANG (1988) even exhibit patchy clustering of completely closed polygonal outlines, resembling meshworks seen in some Ordovician stromatocercids, e.g., members of the *Stromatocerium michiganense* species group (see especially *S. michiganense* PARKS in GALLOWAY & ST. JEAN, 1961, p. 64, pl. 9,3*b*). BOGOYAVLENSKAYA (1973, p. 22) and NESTOR (1976, p. 25) have suggested that Late Devonian species exhibiting these features were more likely to be chaetecids, 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. 14,2*a–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, many-branched, plate-like pillars, as well as rows of long-low cyst plates, $\times 10$; *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 astrophthal pathways, $\times 10$ (new, courtesy of Nguyen Huu Hung & Mistiaen).—FIG. 14,2*c–d*. *V. kweichowense* (DONG, 1964), p. 286 [295], pl. 3,7–8, pl. 4,1–2, lower part of Gelaohe Formation, Famennian, between Wuliqiao and Biaoqi, Dushan County, Guizhou Province, holotype, NIPG, Gy311-1 (14156-14157); *c*, tangential section showing variety of anastomosing, meandering, partially and completely fused meshworks of platelike,



1a

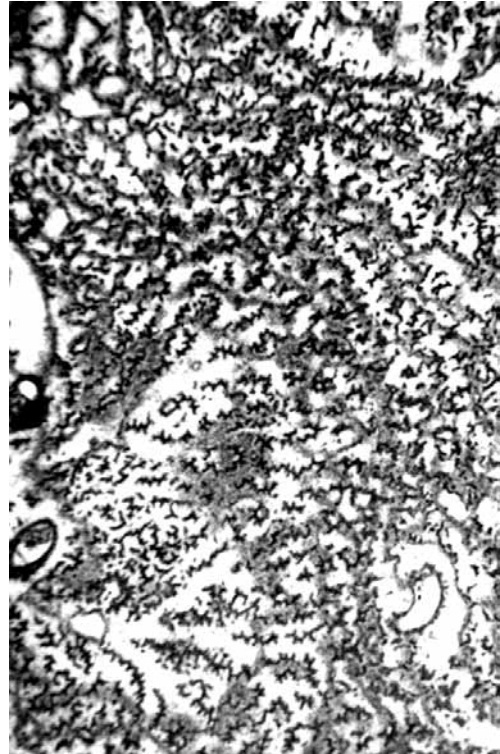


1b

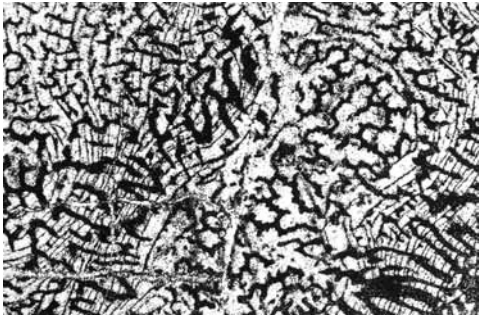
Parastylostroma



2a

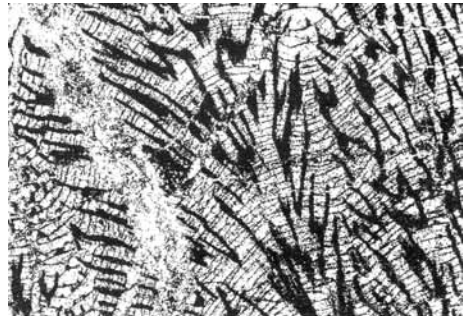


2b



2c

Vietnamostroma



2d

FIG. 14. Platiferostromatidae (p. 21–26).

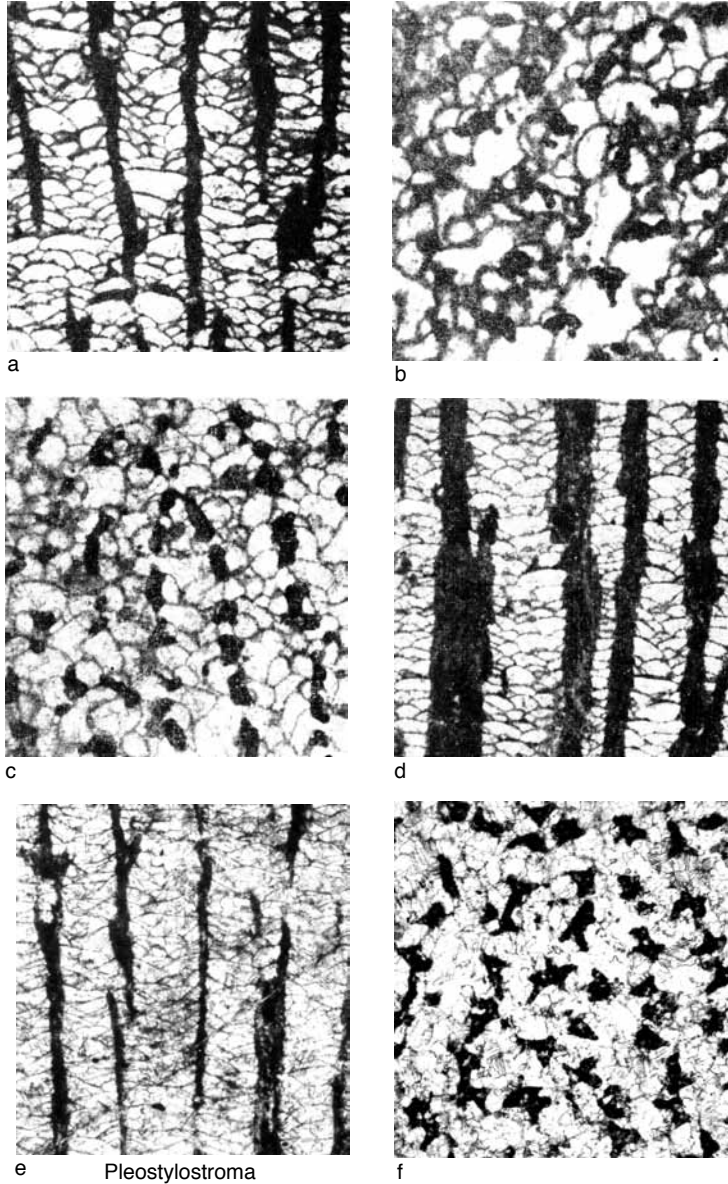


FIG. 15. Platiferostromatidae (p. 21–24).

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 latilaminar 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 multibranching 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; STOCK, 2012, p. 3). 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, *Mamelian–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. 16*a–i*. **S. crassum*, southern shore of Melkaya Bay (loc. 401), Samolet Peninsula, probably upper Famennian, Novaya Zemlya, Russia; holotype, CNIGR, 576716; *a–c*, slide 576716b, low to high magnification longitudinal sections; *a*, $\times 2$; *b*, $\times 5$; *c*, $\times 10$; *d–e*, slide 576716c, longitudinal sections, $\times 5$; *f–h*, slide 576716a, low to high magnification sections; *f*, $\times 2$; *g*, $\times 5$; *h*, $\times 10$; *i*, topotype, tangential section, $\times 5$; 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

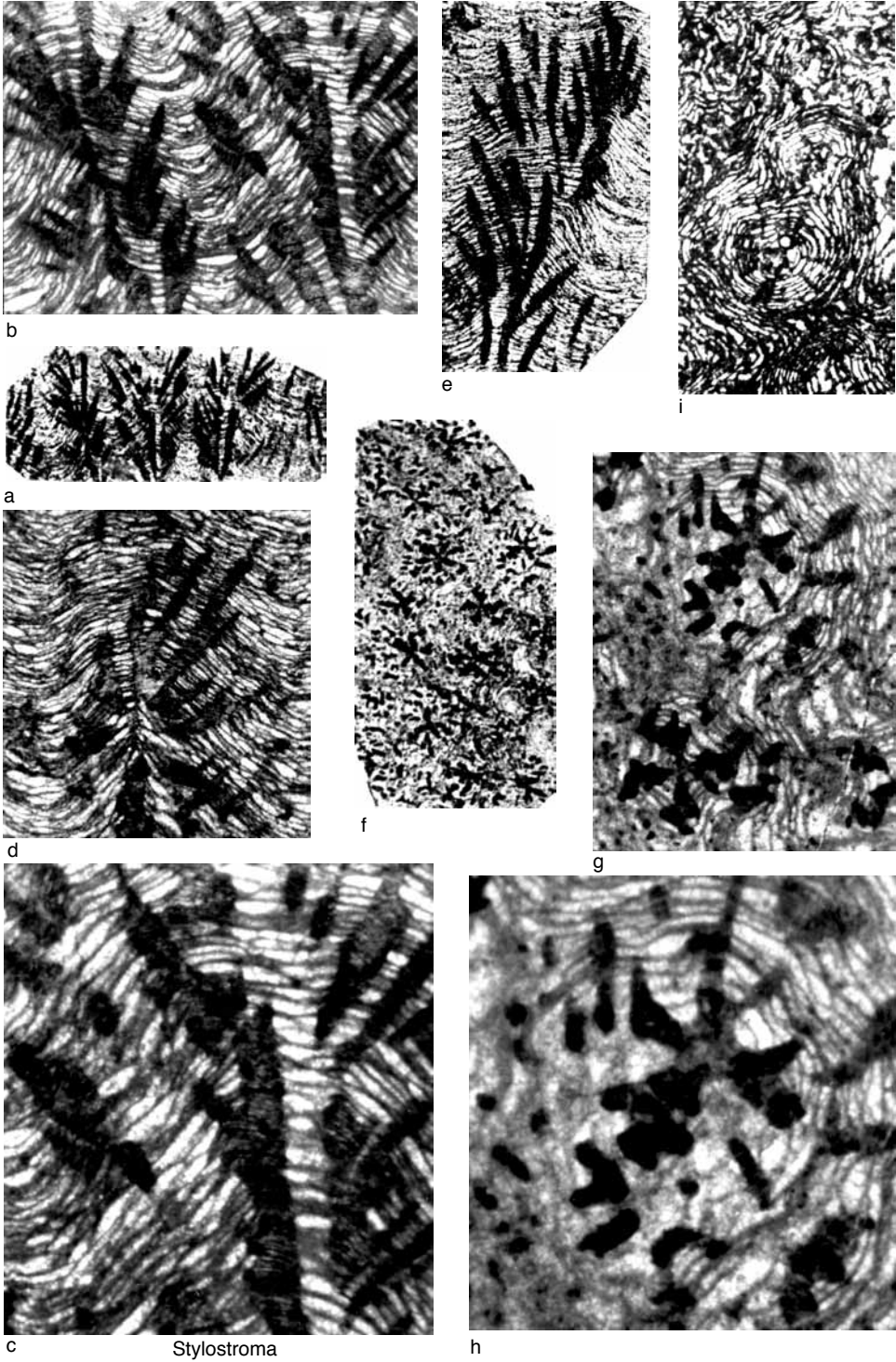
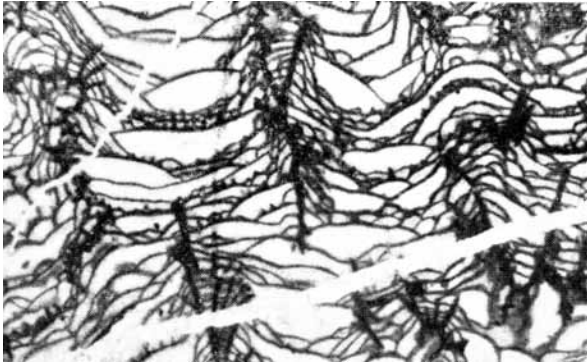
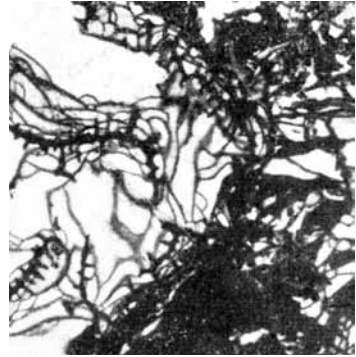


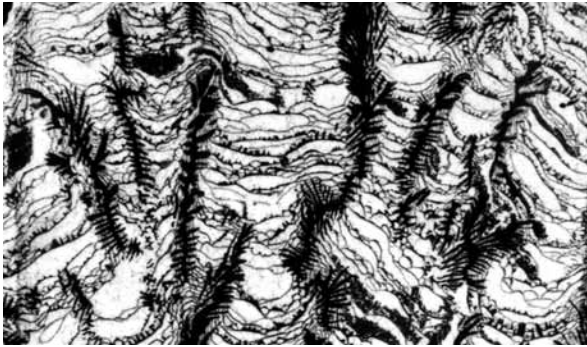
FIG. 16. Stylostromatidae (p. 27).



1a Eopennastroma



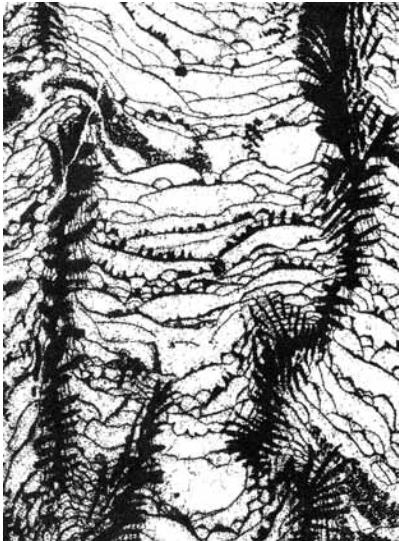
1b



2a Pennastroma



2b



2c



2d

FIG. 17. Stylostromatidae (p. 27–30).

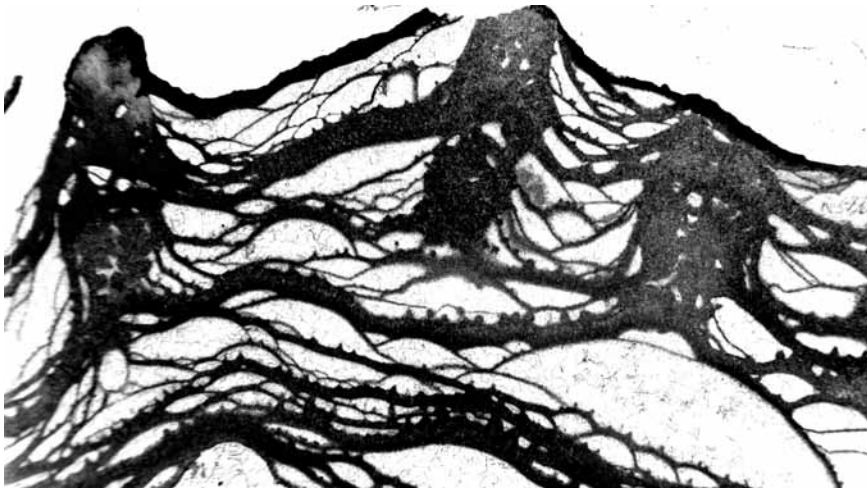
from a center to one side of a column (WANG, 1978c, pl. 27, 4b), and in *E. multicystosum*, several examples of gently arcuate, slender, single, stipelike structures with spiny lateral offsets occur (WANG, 1978c, pl. 28, 1b). It seems therefore that *Eopennastroma* has a pillar outline that is more bar shaped than outwardly radiating (stellate) from centers of the columns.] *Upper Devonian (Famennian)*: China (Guangxi, Guizhou).—FIG. 17, 1a–b. **E. sinense*, lower part of Gelaohu Formation, Pinglang, Duyun, Guizhou Province, holotype, CIGMR, no. GS-70, 71, longitudinal and partially tangential to oblique sections, $\times 5$ (new, courtesy of Wang Shu Bei; see also WANG, 1978c, pl. 27, 3a–b).

Pachystylostroma NESTOR, 1964, 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 (1964) 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. 18a–c. **P. ungerni* (ROSEN), Hilliste Formation, Suuremõisa, Hiiumaa Island, Estonia; a–b, lectotype, IG TUT 112-2 (Co3011), longitudinal and tangential sections, $\times 5$ (Nestor, 1962, pl. 2, 1–2; 1964, pl. 4, 4–5); c, paralectotype, IG TUT 112-2 (Co3012), longitudinal section, note uneven base of skeleton in part overgrowing fragment of halysitid coral and large area of calcite spar fill, $\times 5$ (new, courtesy of Helder 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, plate-like 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 cysts 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 synonymy 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. 17, 2a–d. **P. yangi*, lower part of Shizixu Formation, between Huangjin and Muliu, Luocheng district, northern part of Guangxi Province, holotype, NIPG, Kw047-2 (14160-14162); a, longitudinal section, thin section no. 14162, $\times 2$; b, obliquely oriented section, thin section no. 14161, $\times 3.5$; c, enlarged longitudinal section, thin section no. 14162, $\times 2$; d, longitudinal section, thin section no. 14160, $\times 3.5$ (new, 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 narrowly elongated, platelike structural elements,



a



b

Pachystylostroma



c

FIG. 18. Stylostromatidae (p. 30).

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, pillar-like 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).—FIG. 19a–d. **S. diversum*, lower part of Changtanzi

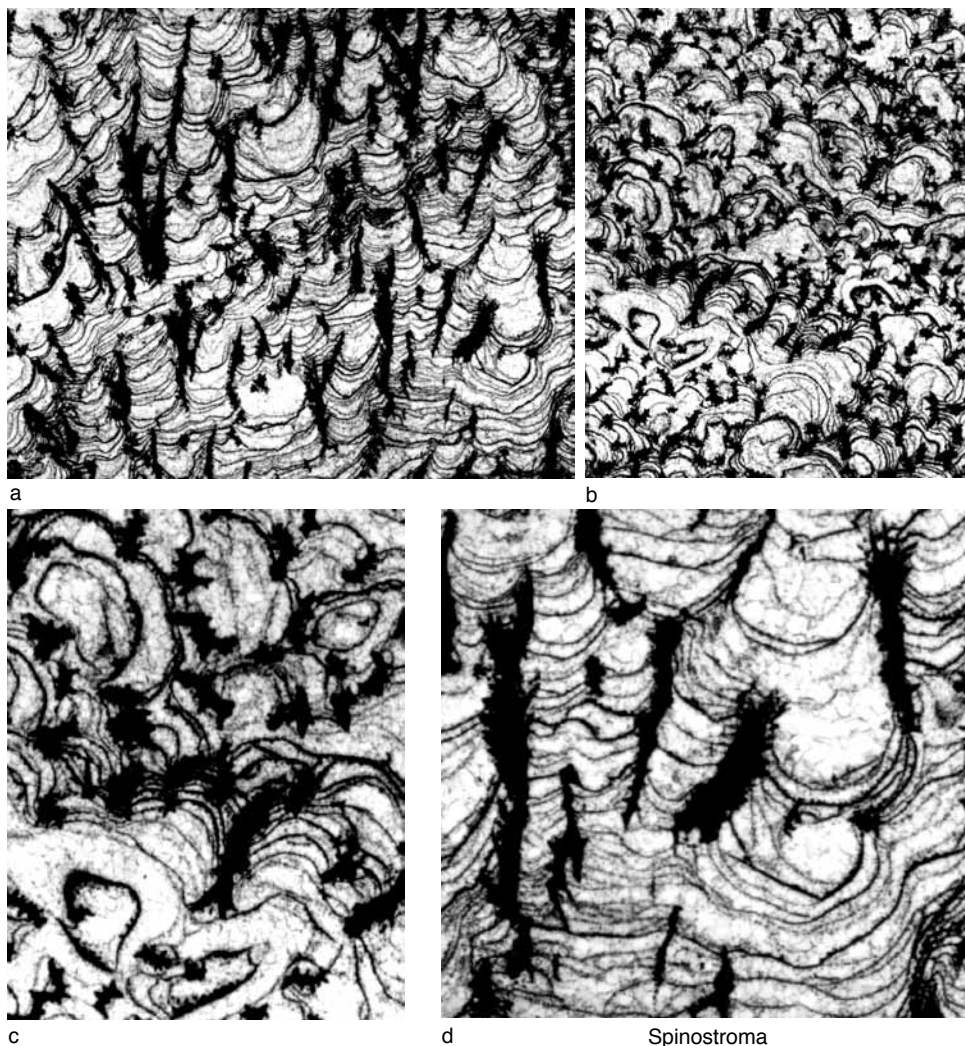


FIG. 19. Stylostromatidae (p. 30–32).

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

Family AULACERATIDAE Kühn, 1927

[Aulaceratidae KÜHN, 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); =Beatriceidae RAYMOND, 1931, p. 178; =Aulacerae BOGOYAVLENSKAYA, 1969, p. 16, *nom. null.*]

Branched dendroid to unbranched, columnar skeletons, with differentiated

axial and lateral zones; axial columns of large, stacked or overlapping cysts, 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 Ordovician (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. 20*a–b*. **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, $\times 0.38$ (Galloway & St. Jean in Galloway, 1957, pl. 37,1*a*); *b*, longitudinal section showing axial column and lateral zones with latilaminae and calcite-filled lacunae, $\times 1$ (Galloway & St. Jean in Galloway, 1957, pl. 37,1*b*); *c*, longitudinal section of slide 300-9 showing lateral zone, $\times 15$ (Galloway & St. Jean in Galloway, 1957, pl. 37,1*c*); *d–g*, topotype (and hypotype), YPM.222147, including slides 282-58, 299-40; *d–e*, sketches of transverse and longitudinal sections of topotype, $\times 2$ (Galloway & St. Jean in Galloway, 1957, pl. 32,3); *f–g*, $\times 10$; *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. 3,1*a*); *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. 3,1*b*); *b*, sketch of PLUMMER'S (1843) originally named genus *Aulacera*, Richmond Group of Indiana, magnification approximate, at least $\times 0.25$ (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. 21*a–e*. **A. nicholsoni*; *a–c*, Daylesford Limestone, lower Bowman 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, $\times 4$ (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 cysts 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. 22*a–b*. **C. antiquatus*, upper Pamela 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, $\times 1$ (Raymond, 1914, pl. 1,1); *b*, paratype, GSC 4329c, offset-longitudinal section of lateral zone showing numerous, tiny, dotlike, spar-replaced pillars, $\times 3$ (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 spar-replaced pillars and cyst plates, $\times 10$ (Galloway & St. Jean, 1961, pl. 2,3*c*); *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, $\times 3$ (Raymond, 1914, pl. 4,2); *e–f*, paratypes, GSC 4329a–b, longitudinal and transverse sections of best-preserved and most complete specimens, $\times 4$ (Raymond, 1914, pl. 11,1–2; see also WEBBY & KERSHAW, 2011, fig. 24.1–24.2); *g*, paratype, GSC 4329i, slightly oblique transverse section showing papillae surmounting spar-replaced pillars, $\times 3$ (Raymond, 1914, pl. 1V,1); *h*, paratype, GSC 4329, lateral view of uncut specimen exhibiting bulblike enlargement toward apical end, $\times 0.6$ (Raymond, 1914, pl. 1,2).
- Ludictyon** OZAKI, 1938, p. 219 [**L. vesiculatum* OZAKI, 1938, p. 219, pl. 33,3*a–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 cysts and also on smaller cyst plates laterally. *Middle Ordovician (Darriwilian)*–*lower Silurian*: China (Shandong, Anhui), *Darriwilian*; ?Mongolia, *Upper Ordovician*; China (Guizhou), *lower Silurian*.—FIG. 23*a–c*. **L. vesiculatum*, Majiagou Group, west of Beizhuang, Zhangqiu county, Shandong Province, holotype, NIPG, slides 121555a–b; *a*, longitudinal

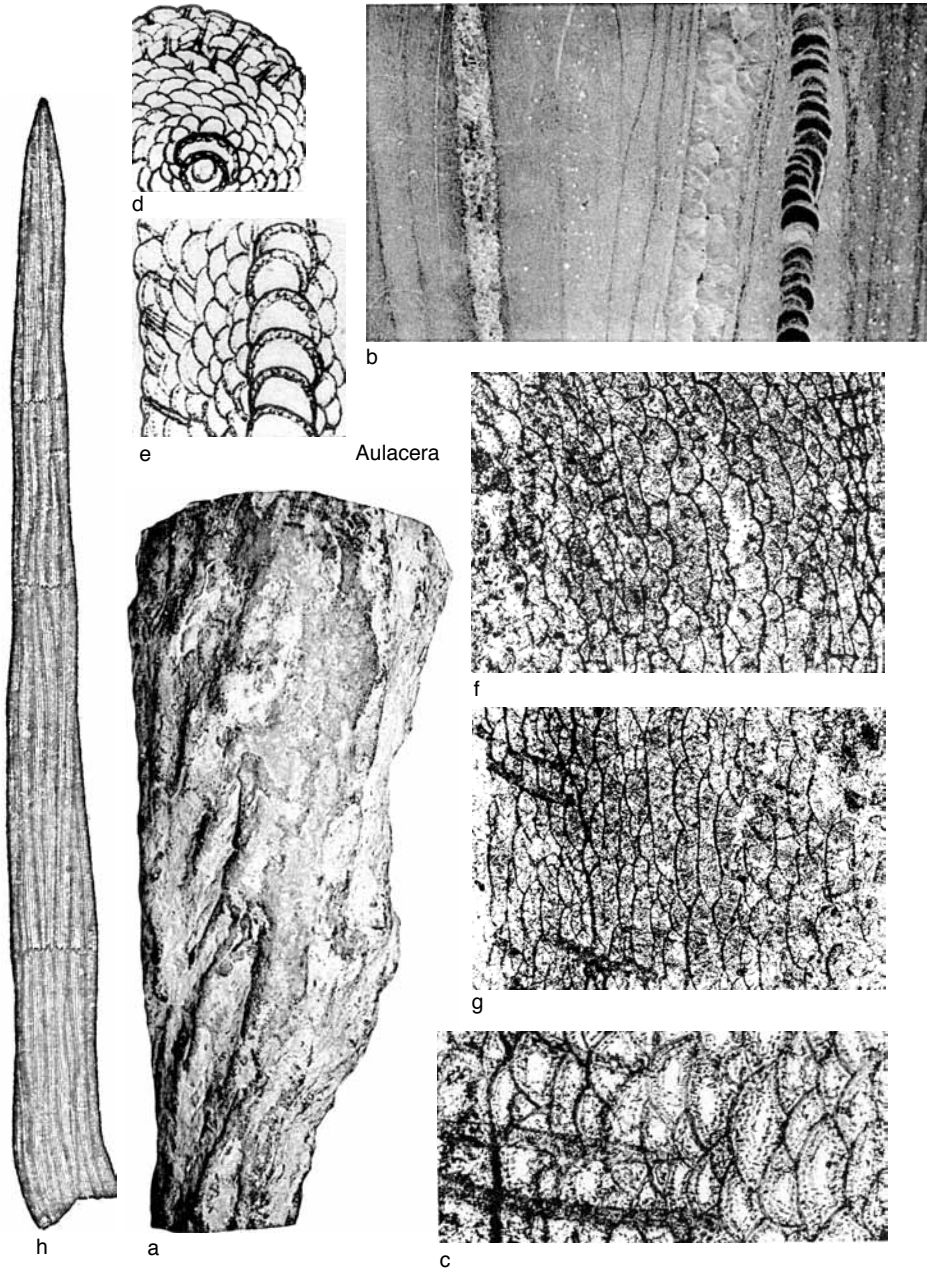


FIG. 20. Aulaceratidae (p. 32–33).

section (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, $\times 5$ (new, 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; Donetsk Polytechnical Institute (DPI), Ukraine, no. 12/141]. Dichotomously branching, columnar skeleton with single row of large doughnut-shaped axial cysts

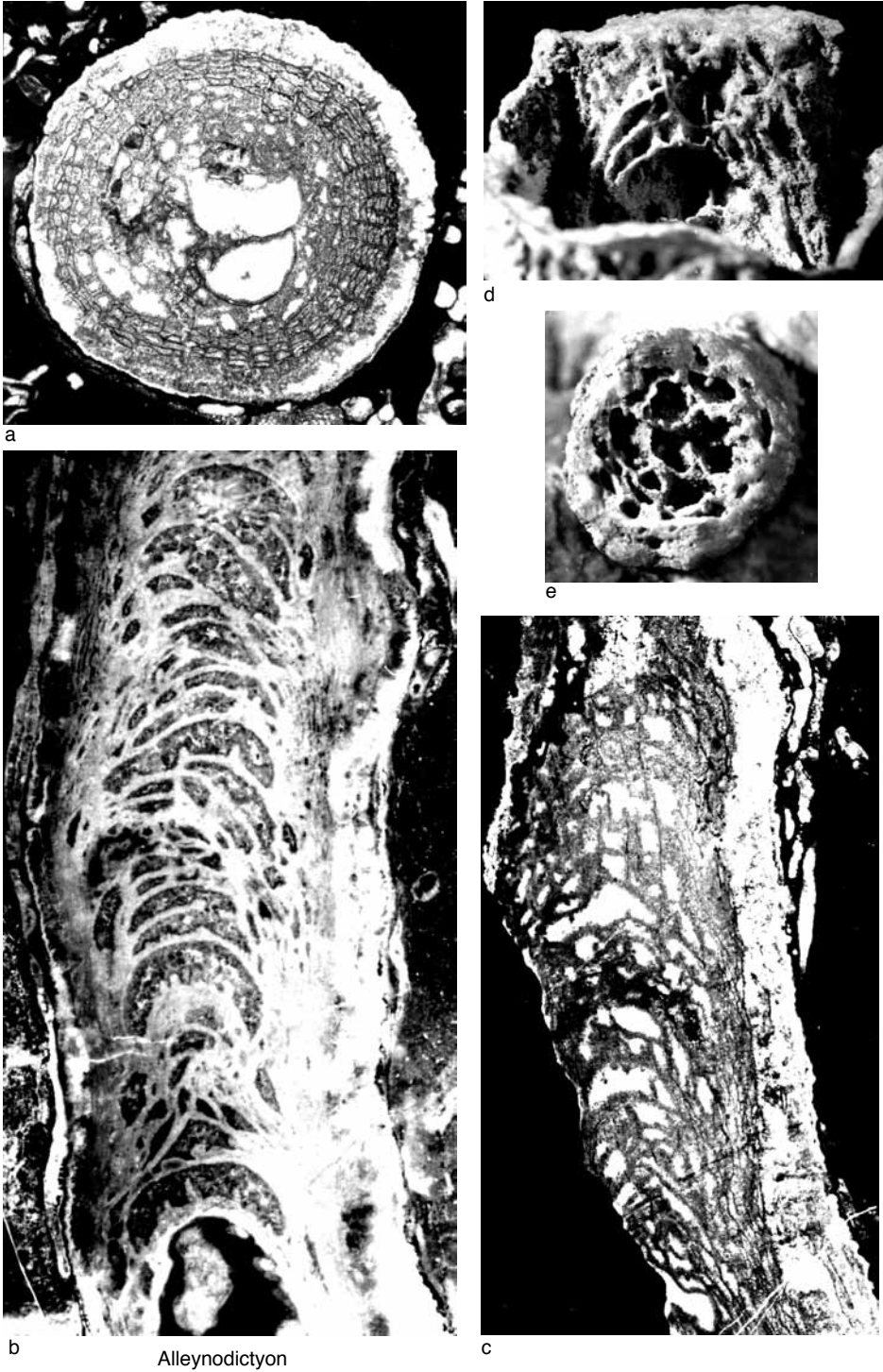
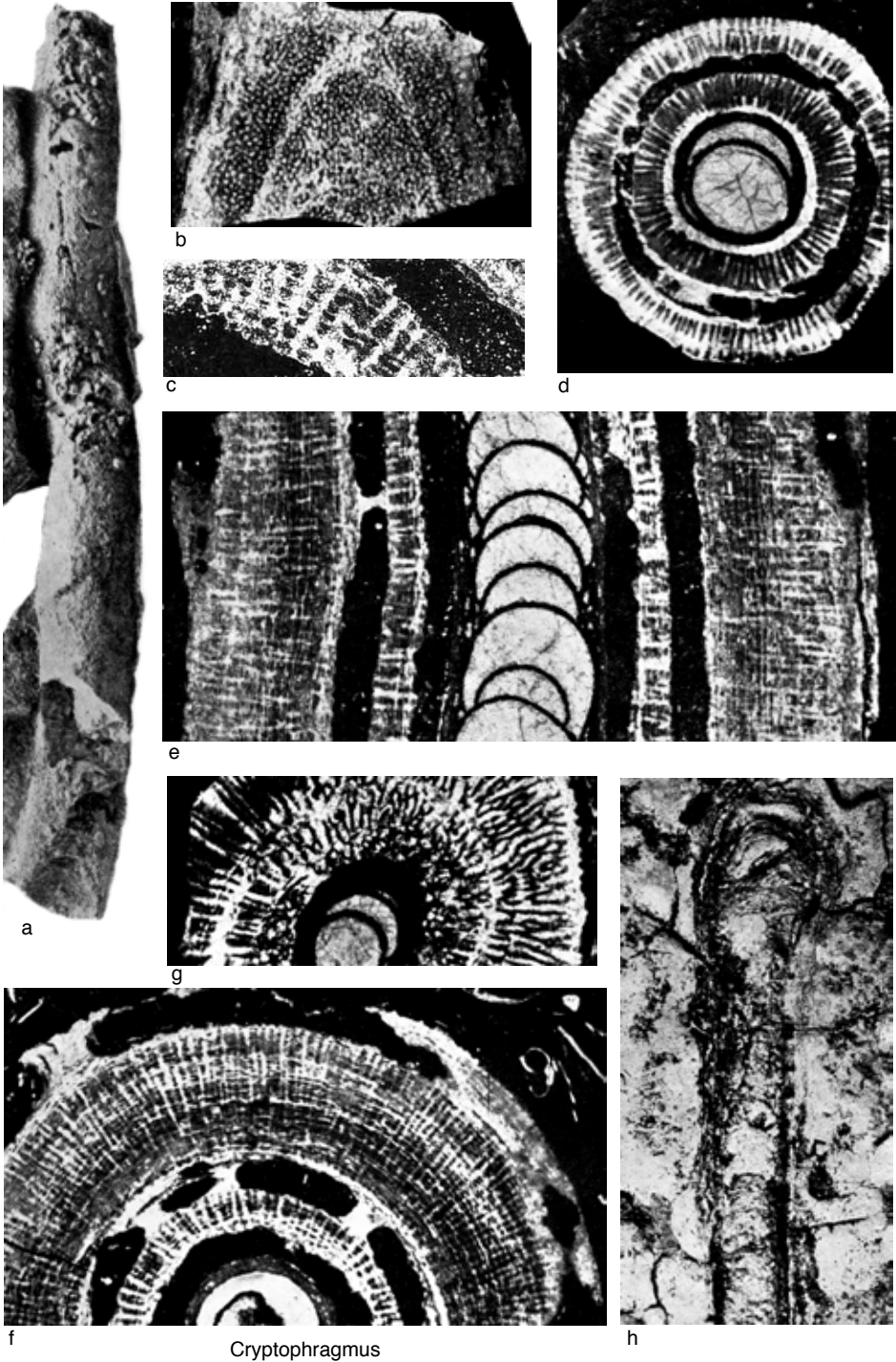


FIG. 21. Aulaceratidae (p. 33).



Cryptophragmus

FIG. 22. Aulaceratidae (p. 33).

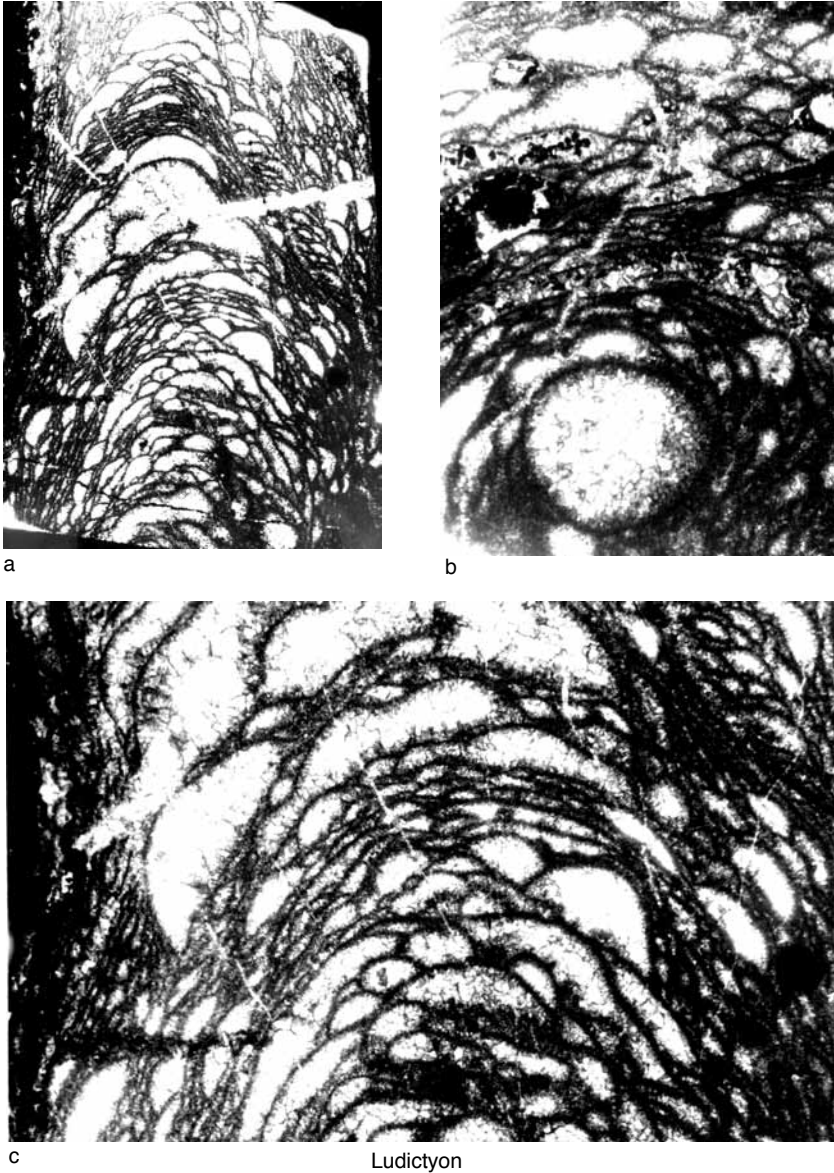


FIG. 23. Aulaceratidae (p. 33–34).

of high convexity; branches are usually dichotomous but may be rarely as lateral offsets; denticles limited to tops of some axial cysts; lateral zone very incomplete, composed of very few small cyst plates filling spaces at margins between bulbous axial cysts and angles of dichotomous branches. *Upper Devonian (Famennian)*: Russia (northern Caucasus), Ukraine (Donets basin).—FIG. 24*a–b*. **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 cysts, thickened outer wall with tiny lateral cysts in places; *c*, transverse section of top of one axial cyst showing presence of denticles (Vassilyuk, 1966, pl. 32, 2*a, b, v*); *d–b*, other figured material from type locality as basis for subspecies, not specifically designated by author but probably has status as paratypes; *d–e*, longitudinal and transverse sections

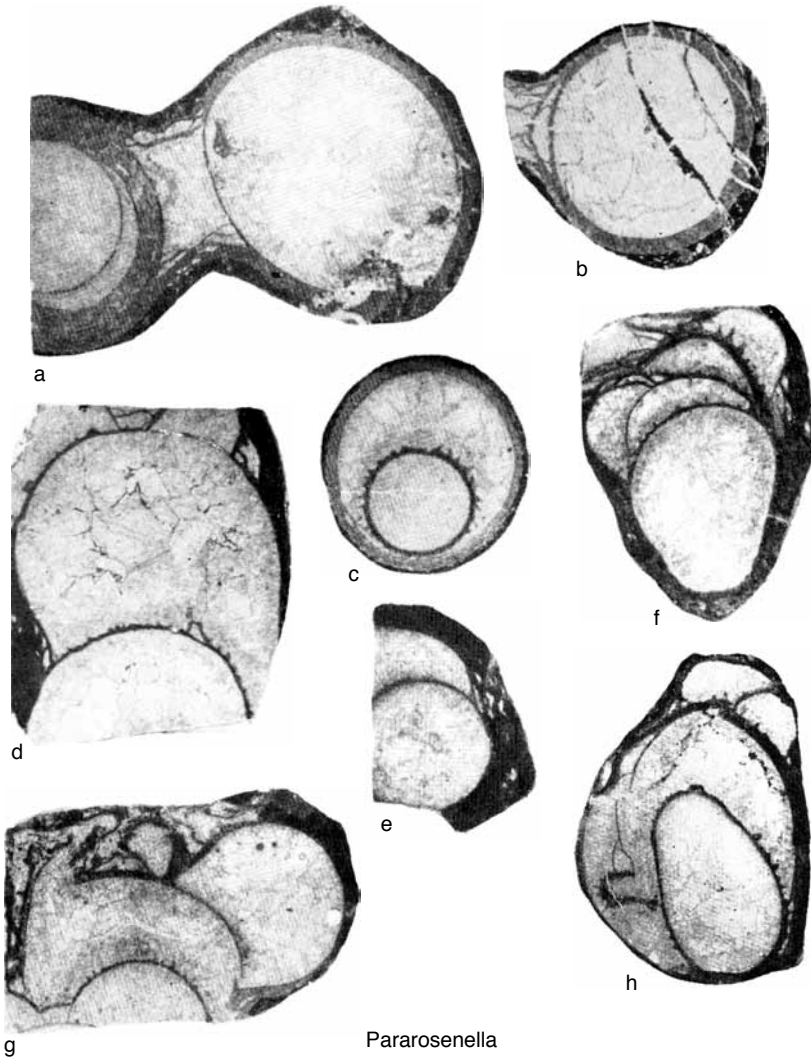


FIG. 24. Aulaceratidae (p. 34–38).

of specimen showing bulbous shape of axial cysts, a few localized, very small, lateral cysts 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* in WEBBY and KERSHAW (2011, fig. 27, 4–5), $\times 5$ (Vassilyuk, 1966, pl. 32, fig. 1a–b, 3a–b, 4–7).

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 SUGIYAMA's illustrations have been crudely overdrawn in black ink over photos to emphasize the skeletal structures. *Middle Ordovician (Darrwilian)*: China (Shandong, Liaoning).—FIG. 25*a–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 fasciculate skeleton, $\times 0.6$ (Yabe & Sugiyama, 1930,

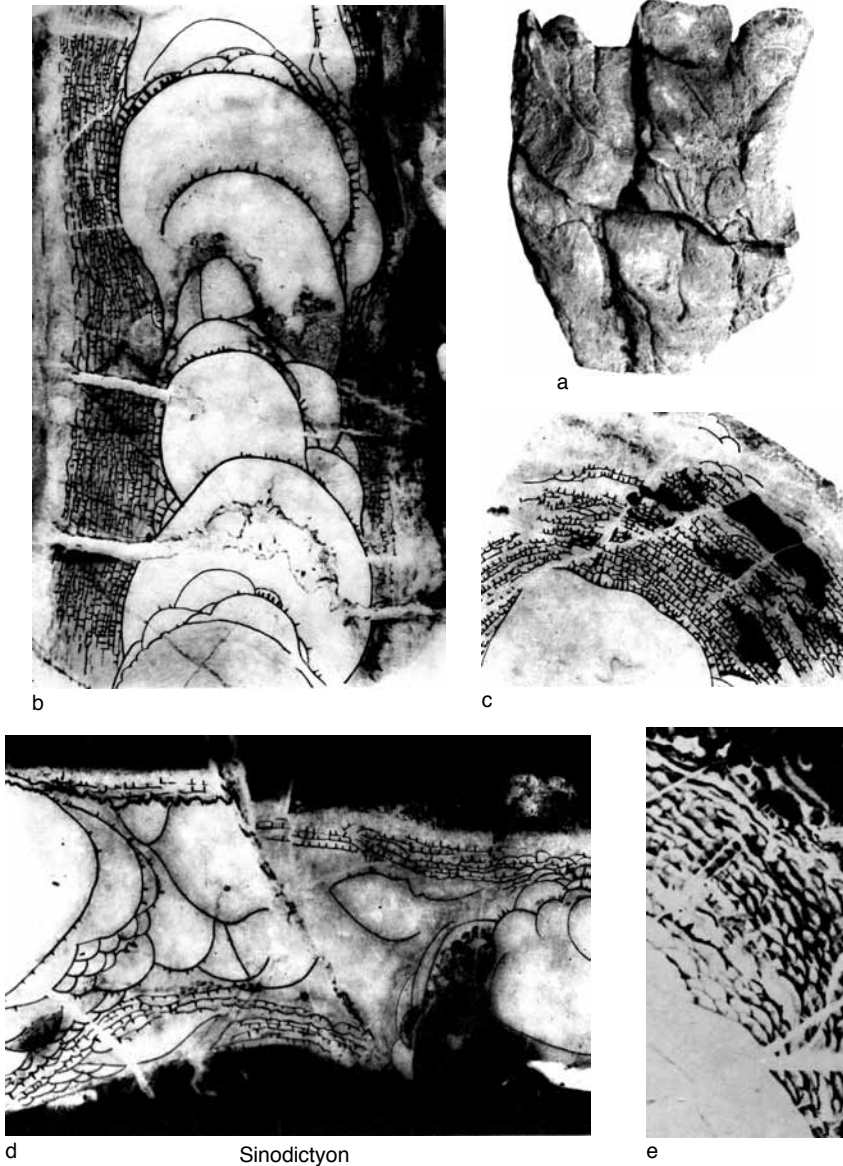


FIG. 25. Aulaceratidae (p. 38–39).

pl. 19,5); *b*, syntype, IGPS, 37676b, longitudinal section, $\times 5$ (Yabe & Sugiyama, 1930, pl. 19,3); *c*, syntype, IGPS 37678, transverse section, $\times 5$ (Yabe & Sugiyama, 1930, pl. 18,10); *d*, syntype, IGPS 37676c, obliquely cut section, $\times 5$ (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 cysts,

particularly rows of smaller cysts in lateral zone, a few with associated short pillars, $\times 8$ (Ozaki, 1938, p. 219, pl. 34,2; specimen not traced, possibly in NIGP).

Thamnobeatricea RAYMOND, 1931, p. 180 [*T. parallela*: OD] [= *Cladophragmus* RAYMOND, 1931, p. 182 (type, *C. bifurcatus* RAYMOND, 1931, 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



Thamnobeatricea

FIG. 26. Aulaceratidae (p. 39–40).

with axial column composed of large, variably sized cysts, 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. 26a–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, $\times 0.3$ (Raymond, 1931, pl. 2,9); b, longitudinal section of part of one of branches showing large axial column and very narrow lateral zone, $\times 2.67$ (Raymond, 1931, pl. 2,4); c, paratype, MCZ 9304, showing ornamentation of fine longitudinal ridges, $\times 1.33$ (Raymond, 1931, 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)], $\times 3.5$ (Raymond, 1931, pl. 2,8).

Family LOPHIOSTROMATIDAE

Nestor, 1966

[Lophiostromatidae NESTOR, 1966, p. 58]

Encrusting laminar, latilaminar, 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 (STEARNS, 2011, p. 46). *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. *Taymyrostroma* KHROMYKH, 2001, from the Upper Ordovician, Taimyr Peninsula, has also been assigned to the lophiostromatids (KHROMYKH, 2001, p. 347), but this genus remains inadequately described and illustrated; here it is regarded as convergent toward younger (Siluro-Devonian) clathrodictyid genera, such as *Intexodictyides* and *Atelodictyon* and is best grouped elsewhere; see STEARNS (2011, p. 56) within the stromatoporoid order and family uncertain.] *Middle Ordovician (Darriwilian)–Silurian (Aeronian)*, ?*Triassic*.

Lophiostroma NICHOLSON, 1891, p. 160 [**Labechia schmidtii* NICHOLSON, 1886b, p. 16, pl. 2, 6–8; OD] [= *Chalazodes* PARKS, 1908, p. 33 (type, *C. granulatum* PARKS, 1908, p. 36, OD)]. Skeleton commonly latilaminar 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, 1966, 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. STEARNS and STOCK (2010, p. 4), recognized two of them as "calcareous crusts" coming from the Carboniferous and Permian of Japan (YABE & SUGIYAMA, 1931; 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 (1970) as *Lophiostroma boletiformis*. It was based on a single specimen with clearly discernible zigzagged upper and lower boundaries of the sheetlike latilaminar 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. 27a–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, $\times 7.5$ (new; Nicholson's slides 279a, 279, rephotographed by Webby in 1989); c, topotype, IG TUT 114-49 (Co3178), showing papillae representing tops of pillarlike upgrowths, $\times 2$ (Nestor, 1966, 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, $\times 2$ (Mori, 1970, p. 28, pl. 19.2); e–f, specimen IG TUT 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, $\times 10$ (new, photos

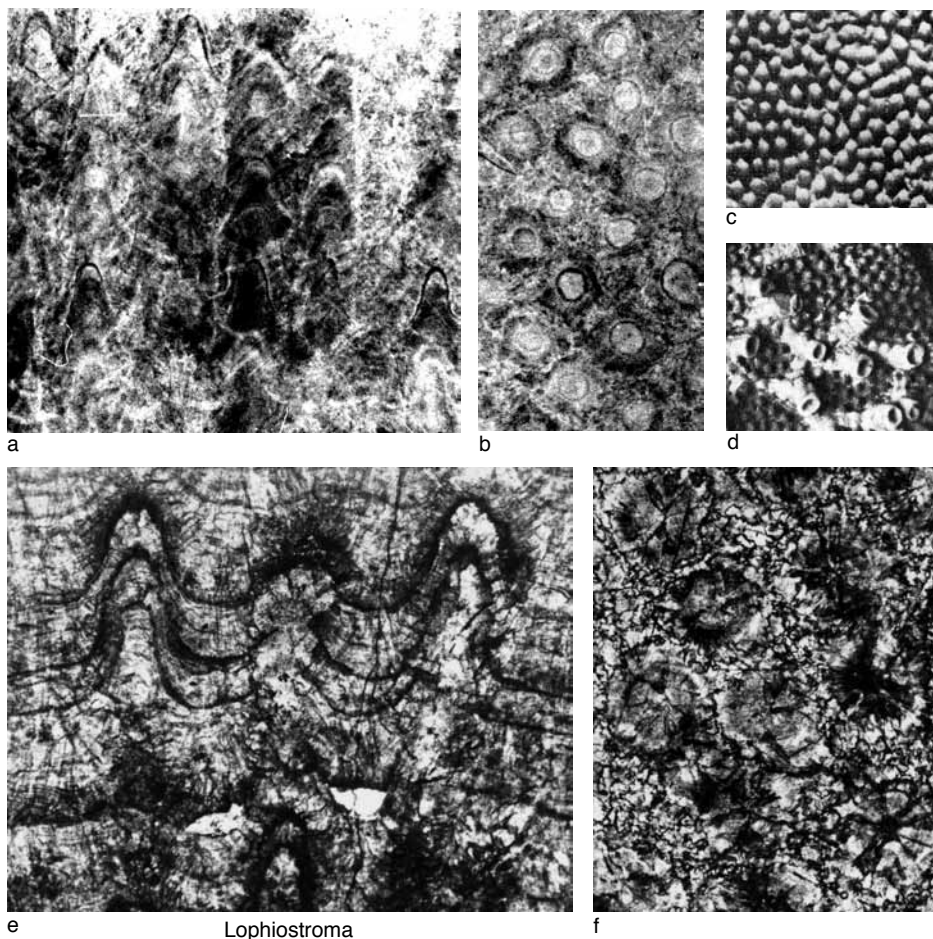


FIG. 27. Lophiostromatidae (p. 41–42).

courtesy of Helder Nestor; see also NESTOR, 1966, 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, as yet unnamed, aulaceratid genus from Anticosti Island (see 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 bigbyi* WEBBY (1979c, p. 248, fig. 5A–B).] *Upper Ordovician* (?Sandbian, Katian): Canada (Ontario), USA (Ohio, Kentucky, Indiana, Tennessee, Iowa).—FIG. 28a–c. **D. papillatum*

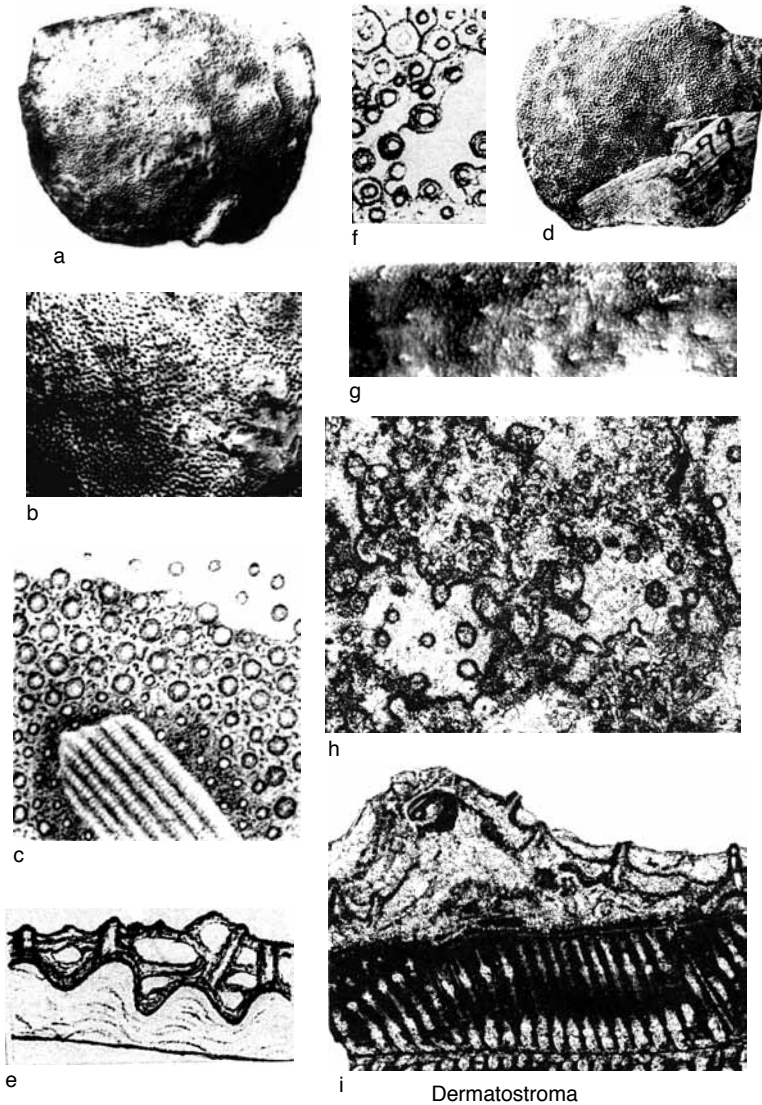
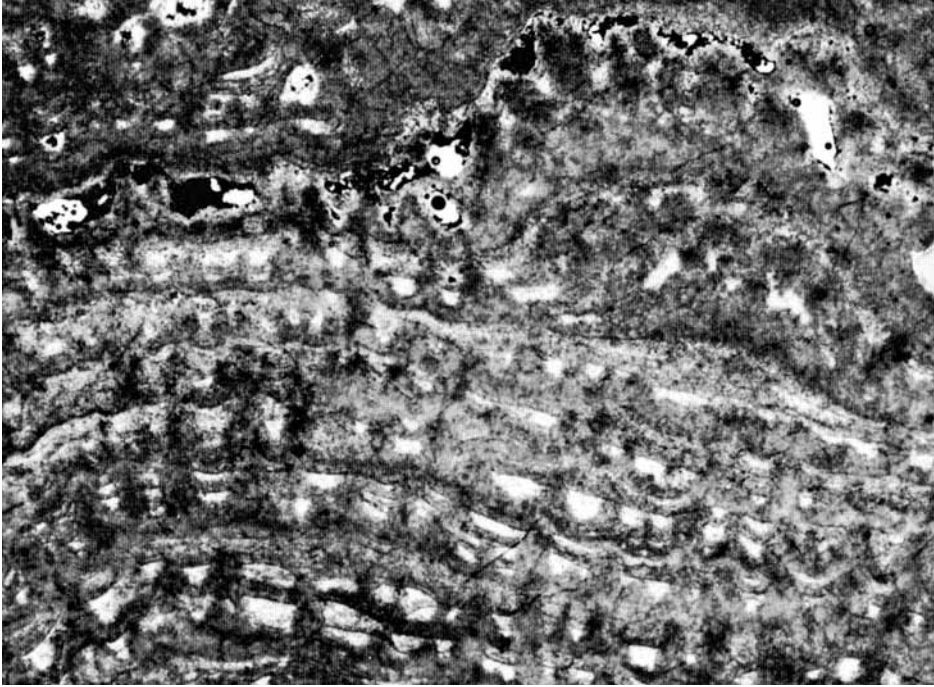


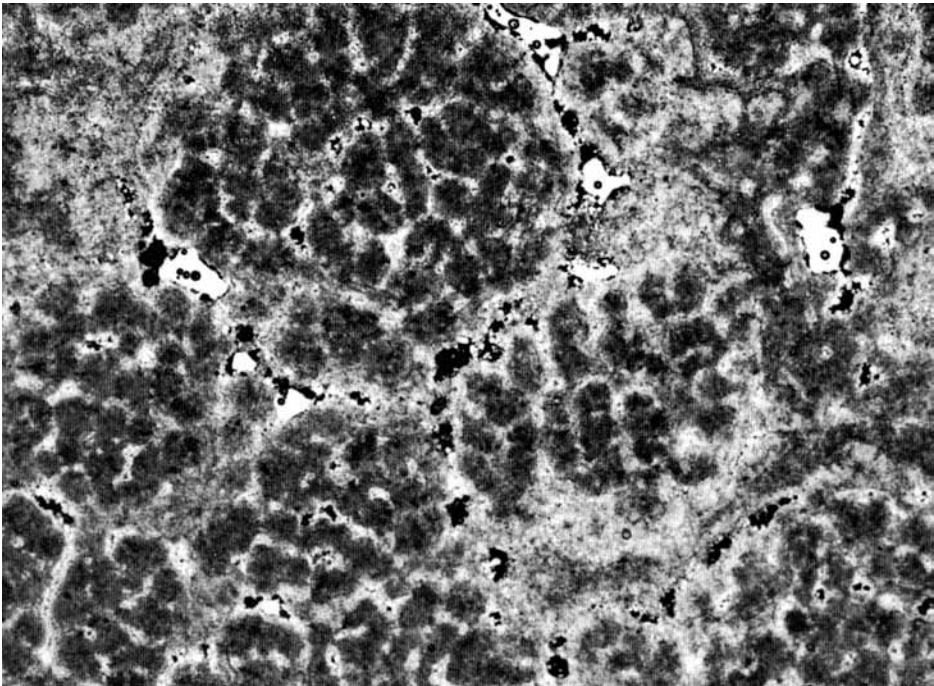
FIG. 28. Lophiostromatidae (p. 42-45).

(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, $\times 1$; *b*, more magnified view showing finely papillate surface of skeleton, $\times 1.7$; *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), $\times 10$ (Parks, 1910,

p. 30, pl. 23,8-10).—FIG. 28*d-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, $\times 1$ (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, $\times 10$ (Galloway, 1957, pl. 33,2; originally labeled *D. papillatum* but later transferred



a



b

Tarphystroma

FIG. 29. Lophiostromatidae (p. 45).

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*), $\times 1.7$ (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, $\times 10$ (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, close-spaced 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, 1891, 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. 22 herein), 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. 29a-b. **T. tuberosum*, holotype GSC127868; longitudinal and tangential sections, $\times 10$ (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. 20a–g; *Cystostroma*, Fig. 2a–d; *Dermatostroma*, Fig. 28d,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. 9a–d.

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, Catherine Weisel, Museum Projects Coordinator: *Thamnobeatricea*, Fig. 26a–d.

Norwegian Journal of Geology, Geological Survey of Norway, Trondheim, Per Terje Osmundsen, Editor: *Radiostroma*, Fig. 11a–d.

Estonian Academy Publishers, Tallinn, Estonia, Ülo Niine, Director, and author Heldur Nestor: *Cystocerium*, Fig. 13a–d.

Stockholm Contributions in Geology, Stockholm, Sweden, Jan Backman, Editor: *Lophiostroma*, Fig. 27d.

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. 5a–b; *Platiferostroma*, Fig. 12, 1a–d; *Pennastroma*, Fig. 17, 2a–d; *Ludictyon*, Fig. 23a–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. 15a–f; *Eopennastroma*, Fig. 17, 1a–b; *Spinostroma*, Fig. 19a–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. 25a–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. 4a–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. 10a–c.

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