SYSTEMATIC DESCRIPTIONS FOR THE SUBORDER PTILODICTYINA

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Suborder PTILODICTYINA Astrova & Morozova, 1956

[*nom. correct.* herein, *pro* Ptilodictyoidea ASTROVA & MOROZOVA, 1956, p. 663, suborder]

Zoaria are erect and characterized by bifoliate growth habit. Autozooecia usually are in linear ranges and offset in adjacent ranges, forming rhombic pattern. Basal attachments of zoaria are either skeletally continuous or, rarely, flexibly jointed. Zoaria expand from basal attachments, generally bifurcating in mesothecal plane. Mesothecae are usually planar, having a median granular zone and laminated layers; the median granular zone may contain median rods. Mesothecae are partitioned to form basal autozooecial walls.

Autozooecia consist of compound walls and generally include two distinct growth zones, endozones and exozones. In endozones, most autozooecial walls have distally elongated, subrectangular to subrhomboid shapes in cross section at junction with the mesothecae, but may be subelliptical to subcircular in cross section. Autozooecial boundaries in endozones are thin, rarely discontinuous, granular zones. In exozones, autozooecia generally form angles between 40 and 90 degrees with the mesothecae and are subelliptical, subcircular, subrectangular, or hexagonal in cross section. Autozooecia are contiguous or may be separated by polymorphic zooecia or extrazooecial skeleton.

Autozooecial wall laminae are either broadly U-shaped and form broadly serrated autozooecial boundaries or broadly to narrowly V-shaped and form narrowly serrated autozooecial boundaries. Autozooecial living chambers extend either from mesothecae or from skeletal diaphragms forming basal walls (mostly in exozones) to autozooecial apertures. In endozones, autozooecial living chambers are generally subrectangular to subelliptical in cross section; in exozones, living chambers are subtubular and may contain abandoned chambers proximal to living chambers. Autozooecial chambers may contain various lateral structures; inferior and superior hemisepta, rarely mural spines, are characteristic of some taxa. Such lateral structures are lacking in many taxa.

Polymorphism is expressed by modified zooecia in zoarial margins, zoarial basal attachments, and monticular zooecia. In exozones, exilazooecia are common, small polymorphs having few or no diaphragms; mesozooecia having numerous diaphragms are rare. Monticules consisting of polymorphic zooecia and extrazooecial stereom in various combinations are common.

Extrazooecial skeletal deposits of laminated stereom or laminated stereom and vesicles form connective skeleton between zooecia, margins of zoaria, and basal zoarial attachments. Vesicular extrazooecial skeleton is generally present in inner exozones. Pustules and mural styles are common in zooecial walls and extrazooecial stereom. Acanthostyles are rare. *Ord.-Carb.*

Family PTILODICTYIDAE Zittel, 1880

[*nom. correct.* BASSLER, 1953, p. G136, *pro* Ptilodictyonidae ZITTEL, 1880, p. 603] [=Clathroporidae SIMPSON, 1897, p. 543; Ptilodictyinae ZITTEL (*nom. transl.* ASTROVA, 1965, p. 251); Phaenoporinae ASTROVA, 1965, p. 254]

Zoaria unbranched and commonly lanceolate, or explanate and cribrate, or branched; commonly tapering proximally. Mesothecae straight to sinuous, rarely zigzag in transverse section. Median granular zones extend discontinuously through most of mesothecae, terminate near thickened mesothecal margins. In endozones, autozooecia in straight to curving ranges, aligned on opposite sides of mesothecae, subrectangular in cross section parallel to mesotheca, contiguous, with generally straight transverse walls, continuous longitudinal walls. Boundaries become broadly serrated, or laminae from adjacent autozooecia merge so that boundaries are not visible at base of exozone. In exozones, autozooecia form angles with mesotheca ranging from 50° to 80°; in straight to curving ranges; subrectangular, elliptical, or subhexagonal in cross section; generally contiguous laterally, and contiguous or separated transversely within ranges by exilazooecia. Longitudinal walls continuous, extending into ridges at zoarial surfaces. Wall laminae broadly curved and U-shaped. Boundaries broadly serrated or not visible. Pustules rare to common and scattered throughout exozonal walls. Living chambers subrectangular in cross section in endozones; elliptical, subelliptical, or subcircular in cross section in exozones. Basal diaphragms rare. Chamber lining and superior and inferior hemisepta common. Mural spines and cysts generally rare and scattered in zoaria. Cystiphragms present in one genus. Polymorphs marginal, monticular, and basal; exilazooecia abundant to rare or lacking; mesozooecia in one genus. Monticules rare to common in most genera, lacking in some; distributed irregularly; consisting in varying combinations of exilazooecia, larger or smaller zooecia, and extrazooecial stereom. Extrazooecial deposits laminated and irregularly delineated; sparse in zoarial midregions and distally. *M.Ord.-L.Dev.*

Ptilodictya LONSDALE in MURCHISON, 1839, p. 676 [**Flustra lanceolata* GOLDFUSS, 1829, p. 104; OD; glacial drift, "encrinite limestone," ?U. Sil., Groningen, Ger.] [=*Heterodictya* NICHOLSON, 1875, p. 33, L. Dev., Ont., Can.]. Zoarium lanceolate with tapering proximal segment. Mesothecae straight, rarely zigzag locally. In endozones, autozooecia in straight ranges, subrectangular to subhexagonal in cross section. In exozones, autozooecia in straight ranges, arranged in rhombic to reticulate pattern in adjacent ranges; contiguous; commonly subrectangular in cross section, few irregularly polygonal in lateral regions. Autozooecial boundaries generally not visible; pustules rare. Living chambers elliptical to subrectangular in cross section; lining common in endozones, discontinuous or lacking in exozones. Superior hemisepta few, blunt, short, thick; inferior hemisepta few, thin, short. Both hemisepta scattered in a zoarium. Spines curved proximally; cysts rare at mesotheca. Exilazooecia few, generally lacking. Monticules irregularly distributed, flat to raised, indistinct; consisting of slightly larger, possible autozooecia. [Two syntypes of *P. lanceolata* are at the Geologisch-Paläontologisches Institut, Bonn, Germany, and are poorly preserved (Ross, 1960a, p. 440). The specimen figured by GOLDFUSS is lost and its original locality is unknown. Ross (1960a, p. 440) redescribed and subjectively defined *P. lanceolata* on the basis of material from the Wenlock Limestone (Silurian) of Dudley, England; from calcareous clay, lower Ludlovian Series (Silurian) at Mulde, near Klinteham, Gotland, Sweden; and from the upper Llandoverian Series at Roneham, Gotland. According to Ross (1960a, p. 444), LONSDALE described *Ptilodictya* and its type species, *P. lanceolata*, on the basis of material from the Wenlock Limestone, Malvern Hills, England.] *U.Ord.-L.Dev.*, USSR, Swed., Eng., N.Am., India.——FIG. 240, *1a–h*. **P. lanceolata* (GOLDFUSS), Wenlock Ls., U. Sil., Dudley, Eng.; *a*, mesotheca, straight longitudinal walls, slightly flexed transverse walls; transv. sec., USNM 137913, ×30; *b*, autozooecia in distinct linear ranges, reticulate in lateral regions, smaller living chambers in mid zoarium; external view, USNM 137913, ×4; *c*, indistinctly subhexagonal autozooecia in endozone, indistinct brown bodies near mesotheca; deep tang. sec., USNM 137913, ×30; *d*, elliptical to subrectangular living chambers between structurally continuous longitudinal walls, autozooecial boundaries not visible; tang. sec., USNM 137913, ×30; *e*, mesotheca, shape of living chambers parallel to growth direction; oblique long. sec., USNM 137913, ×30; *f*, broadly curved laminae of mesotheca in zoarial margin, reduced endozone in zoarial margin; transv. sec., USNM 137912, ×30; *g*, median granular zone along middle of mesotheca, U-shaped laminae in transverse walls, discontinuous lining, recurved mural spine in living chamber; long. sec., USNM 137911, ×50; *h*, granular zone in mesotheca, broadly curved laminae in longitudinal walls, zooecial boundaries indistinct, zooecial lining in endozone and exozone; transv. sec., USNM 137911, ×100.

Clathropora HALL in SILLIMAN, SILLIMAN, & DANA, 1851, p. 400 [**C. frondosa* HALL, 1852, p. 159; SD ULRICH, 1890, p. 392; Rochester Sh., M. Sil., Lockport, N.Y., USA]. Zoarium branched or unbranched and cribrate with tapering, connecting segments. Fenestrules ovate to subcircular, varying in size in cribrate zoaria, generally aligned in growth direction; marginal zooecia in indistinct ranges. Mesothecae slightly sinuous in longitudinal section. In endozones, autozooecia

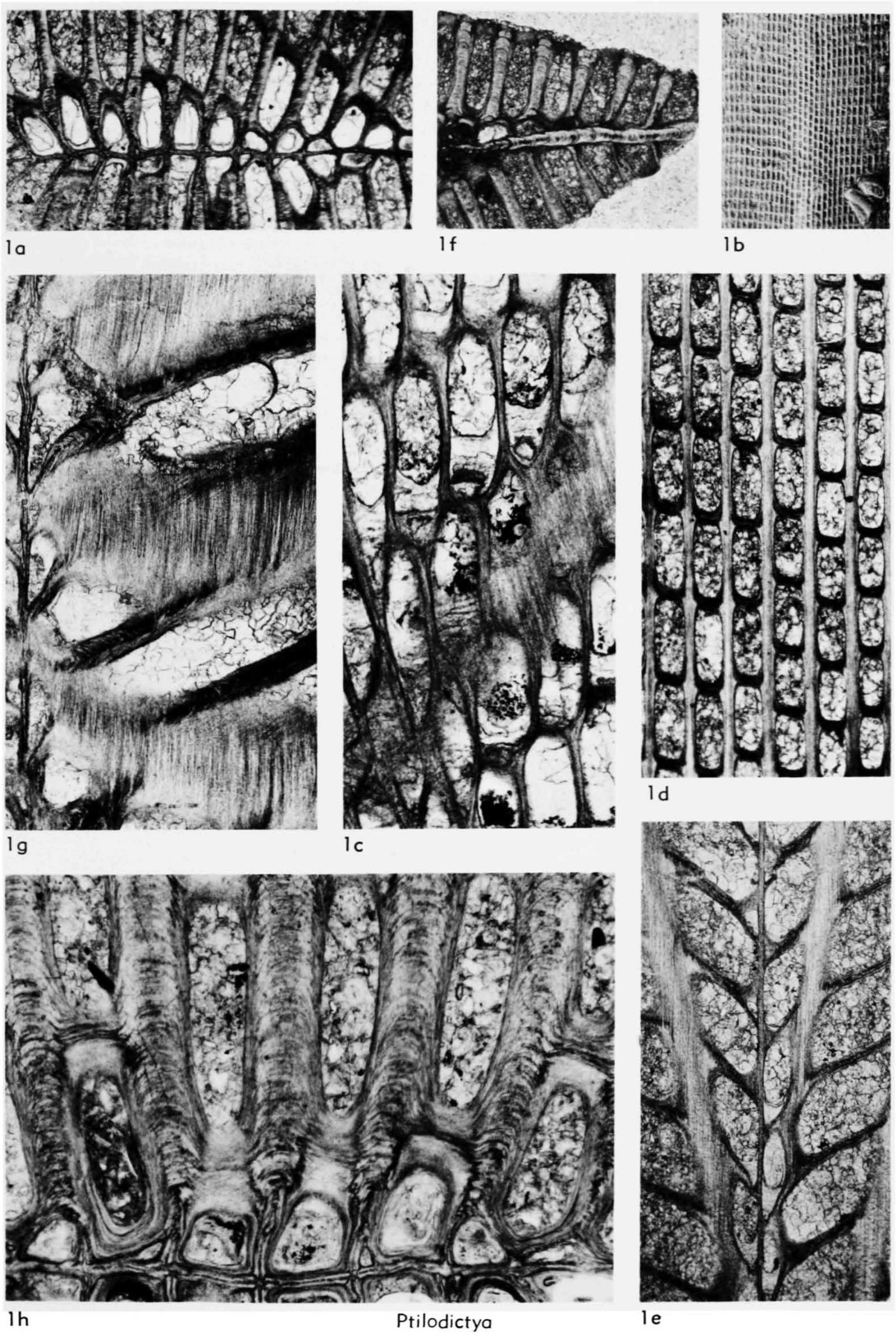


FIG. 240. Ptilodictyidae (p. 490).

in straight or curving ranges. In exozones, autozooecia subhexagonal in cross section, contiguous, in straight ranges in midregions between fenestrules, in curving ranges near fenestrules and margins. Autozooecial boundaries broadly serrated, rarely with pustules. Living chambers broadly elliptical in cross section, generally with distinct lining in cribrate zoaria. Superior hemisepta common, short, blunt or irregularly shaped, regularly arranged. Inferior hemisepta lacking. Exilazooecia rare to lacking in midregions, scattered at bifurcations; singly or in scattered groups near fenestrules and zoarial margins. Extrazooecial stereom rarely fills fenestrules in proximal regions, commonly forming annular ridge around distal parts of connecting segments. Monticules not observed. *U.Ord.-L.Dev.,* Eu. (Est., France), USA.——Fig. 241,*1a–d.* **C. frondosa,* lectotype, AMNH 1734/2; *a,* arrangement of autozooecial ranges, shape of fenestrules; external view, ×5; *b,* alignment of autozooecia across mesotheca; transv. sec., ×30; *c,* subhexagonal autozooecia in endo-exozone, sinuous longitudinal walls, exilazooecia near fenestrule (lower right); tang. sec., ×30; *d,* sinuous mesotheca, thick lining on distal sides of zooecial walls; long. sec., ×50.

Ensiphragma Astrova in Astrova & Yaroshinskaya, 1968, p. 61 [**E. mirabilis*; OD; Kireyev stratum, L. Dev., Solov'ikha River basin, Altai Mts., USSR]. Zoarium unbranched. Mesotheca straight. Autozooecia in straight ranges throughout ontogeny. In exozones, autozooecia subrectangular in cross section, contiguous laterally, partly separated within ranges by mesozooecia. Autozooecial boundaries not visible; pustules indistinct, scattered in exozonal walls. Living chambers elliptical in cross section, variable in length; lining thin, locally discontinuous. Superior hemisepta common, blunt, thick, straight; inferior hemisepta common, thin, straight, projecting from mesothecae or distal walls. Cystiphragms regularly arranged, generally open with irregularly curved proximal tips. Basal diaphragms thin, slightly curved, relatively uniform in spacing. Mesozooecia common, subcircular in cross section, regularly arranged in pairs between successive autozooecia in midregions; abundant along zoarial margins. Mesozooecial diaphragms closely spaced; chamber linings thin, discontinuous. Monticules absent. *L.Dev.,* USSR (Altai Mts.).——Fig. 241,*2a–d.* **E. mirabilis*; *a,* alignment of autozooecia across mesotheca; transv. sec., holotype, PIN 2218/508, ×40; *b,* continuous laminae of longitudinal walls (left), basal diaphragms, abandoned chambers, open cystiphragms, mesozooecia between autozooecia; long. sec., holotype, ×40; *c,* autozooecial lining along walls, open cystiphragms in autozooecial chambers, diaphragms in mesozooecia, hemisepta (chamber in endozone, middle right); long. sec., paratype, PIN 2218/514, ×100; *d,* straight autozooecial ranges, mesozooecia between successive autozooecia; tang. sec., paratype, PIN 2218/510, ×30 (photographs courtesy G. G. Astrova).

Ensipora Astrova, 1965, p. 263 [**Escharopora tenuis* Hall, 1874, p. 99; OD; low. Helderberg Gr., L. Dev., Clarksville, N.Y., USA]. Zoarium unbranched and lanceolate. Mesothecae generally straight. Autozooecia in straight ranges throughout ontogeny; subrectangular in cross section of exozone, generally contiguous, with relatively thin walls. Living chambers elliptical in cross section, relatively large. Superior hemisepta thin, long, straight, regularly arranged. Inferior hemisepta shorter, extending from distal walls. Exilazooecia and monticules probably absent. [The concept of *Ensipora,* to which numerous species have been assigned (Astrova, 1965; Astrova in Astrova & Yaroshinskaya, 1968), is unclear because the type material of *E. tenuis* is poorly preserved. Hall did not designate a holotype and primary types cannot be related to subsequently figured specimens (Hall, 1883a, pl. 13, fig. 14, pl. 17, fig. 7–13; Hall, 1887, pl. 13, fig. 14, pl. 17, fig. 7–12, pl. 23A, fig. 15). The budding pattern, cross-sectional shape of autozooecia, straight longitudinal walls in zoaria, and hemisepta in exozones resemble ptilodictyids; however, microstructure of laminae and presence of exilazooecia cannot be verified in primary material.] *M.Ord.-L.Dev.,* USSR, ?Baltic region, ?Eng., N. Am.——Fig. 242,*1a–e.* **E. tenuis* (Hall); *a,* shape, alignment of autozooecia across mesotheca; transv. sec., lectotype, AMNH 2309/2310, ×50; *b,* arrangement of autozooecial ranges along middle and margins of zoarium; external view, lectotype, ×5; *c,* shape of living chambers; tang. sec., lectotype, ×50; *d,* hemisepta; long. sec., lectotype, ×50; *e,* zoarium with distal, tapered connecting segment and partly closed (?encrusted) basal zooecia in narrow ranges; external view, paralectotype, NYSM 893, from New Scotland Ls., N.Y., ×5.

Insignia Astrova, 1965, p. 271 [**Phaenopora insignis* Nekhoroshev, 1961, p. 89; OD; Nishnyaya Chunka River, U. Ord., Sib., USSR]. Zoarium branched or unbranched and subcylindrical to irregularly explanate, relatively large and variable in thickness. Unbranched zoaria subcylindrical with conical, proximal tips. Branched zoaria with approximately parallel branches and tapering proximal segments. Zoarial midregions slightly raised, subcylindrical in transverse section, tapering to flattened lateral regions. Mesothecae slightly sinuous in longitudinal section. In endozone, autozooecia in straight and variably curving ranges. In exozones, autozooecia ontogenetically subrectangular to subelliptical in cross section; in straight ranges for varying distances in zoarial midre-

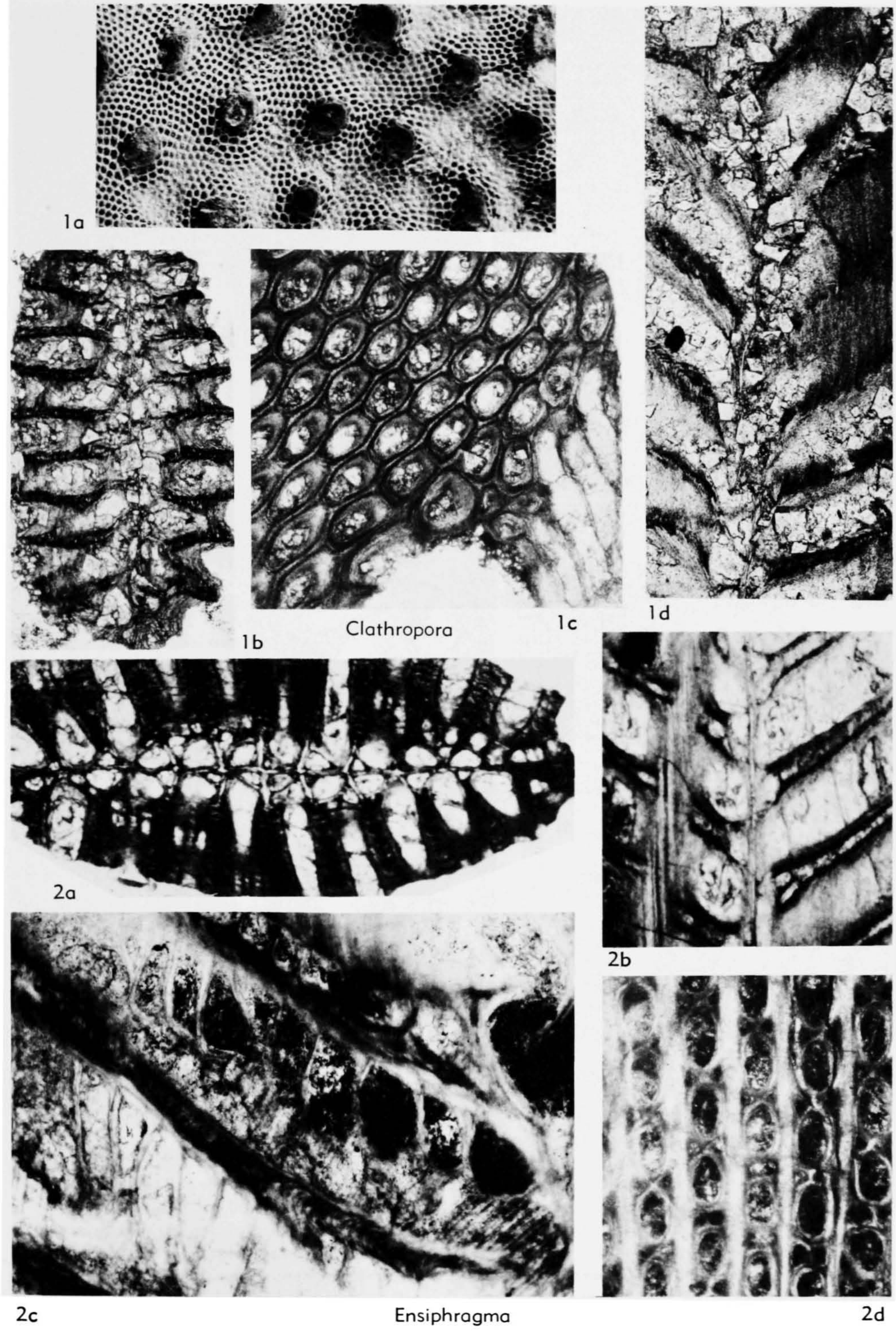


FIG. 241. Ptilodictyidae (p. 490–492).

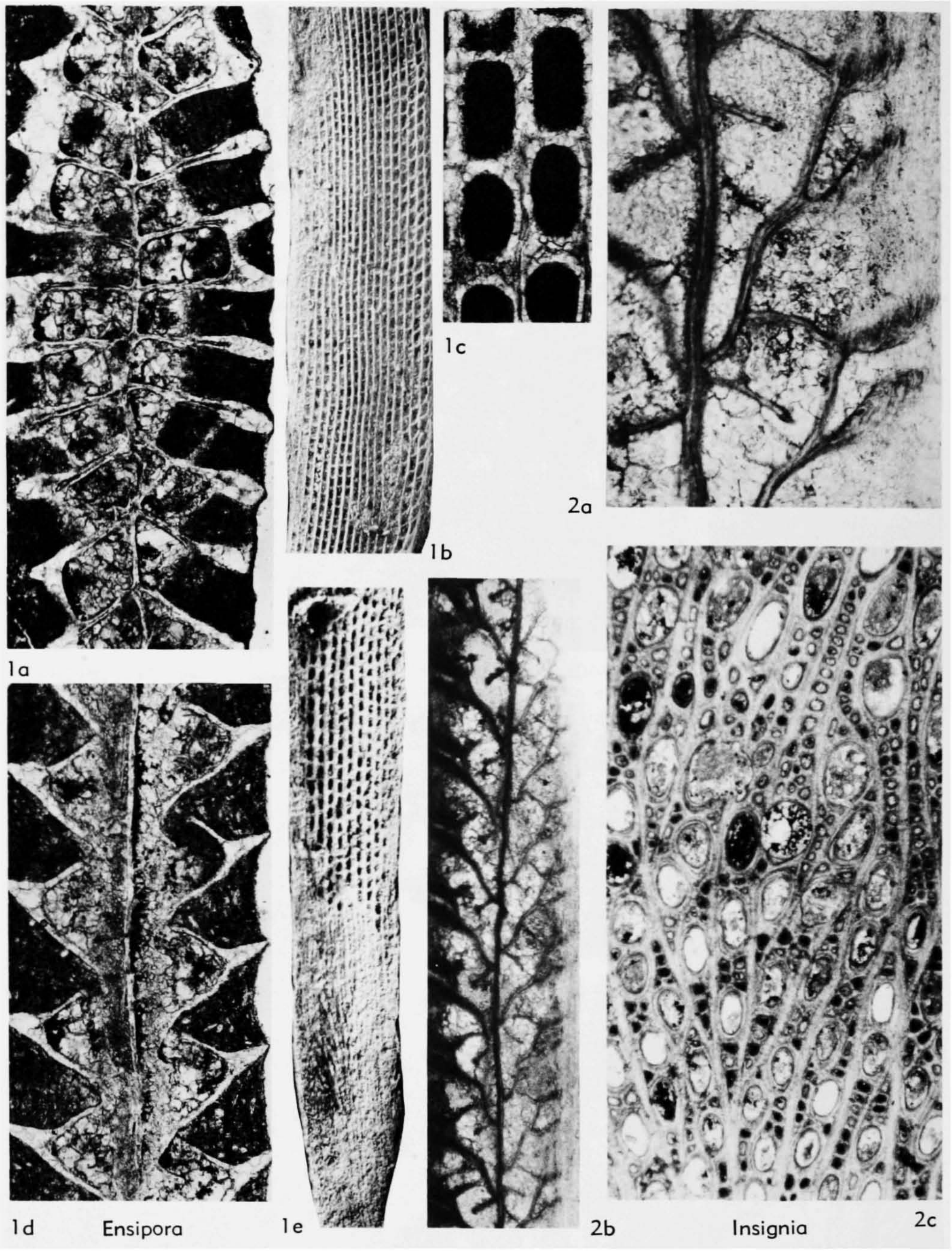


FIG. 242. Ptilodictyidae (p. 492).

gions; in irregularly curving, converging, or bifurcating ranges in greater part of zoarium. Autozooecia contiguous or separated laterally and within ranges by exilazooecia, commonly replaced by groups of exilazooecia at irregular intervals. Autozooecial boundaries generally not visible; pustules scattered in exozonal walls. Living chambers broadly elliptical to subcircular in cross section, lining thick to lacking. Superior and inferior hemisepta common, long, straight, relatively thick, and regularly arranged. Inferior hemisepta projecting from mesothecae or distal walls; superior hemiseptum locally a basal diaphragm in some species. Exilazooecia abundant,

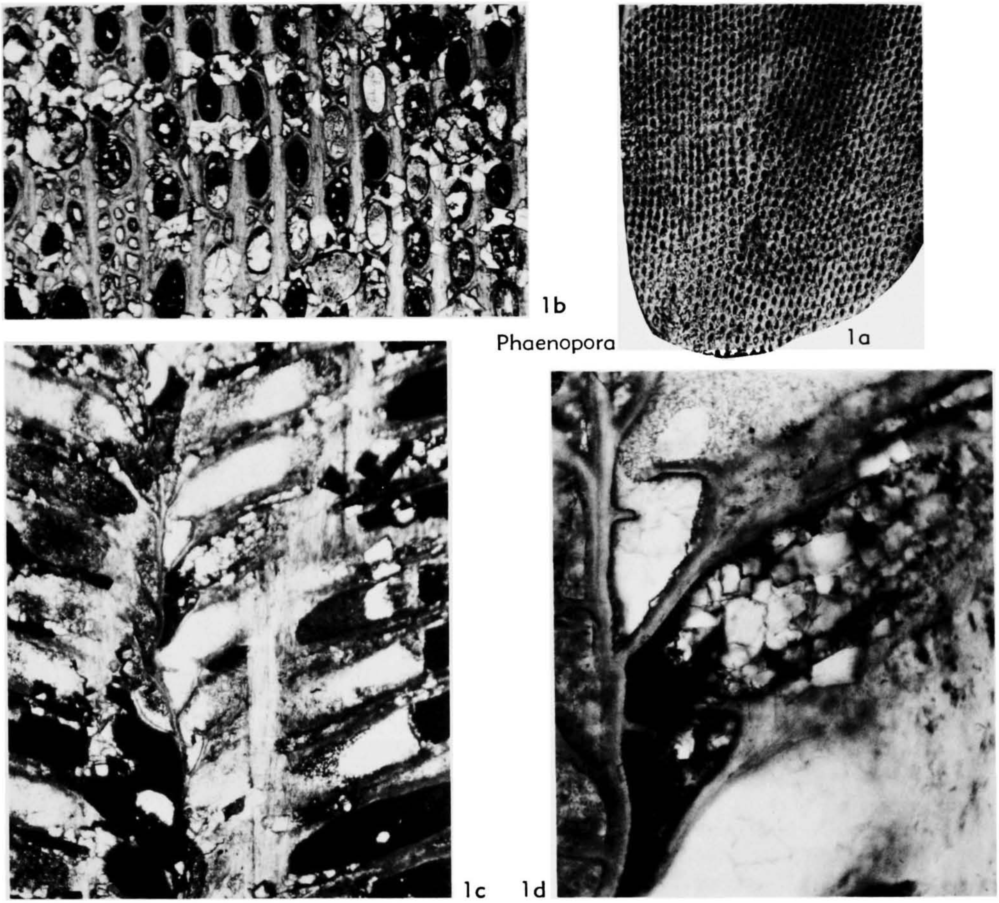


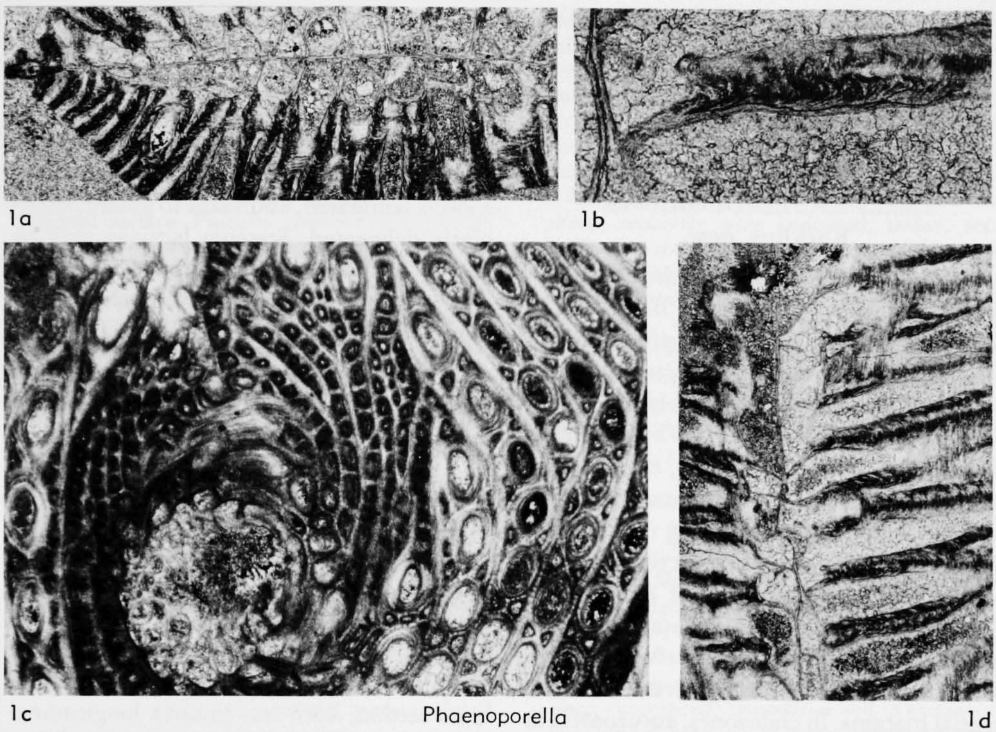
FIG. 243. Ptilodictyidae (p. 495).

irregularly subcircular or varying in cross section; slightly variable in size, commonly with narrower chambers in outer exozones; generally arranged in irregular groups, rarely in pairs between successive autozooecia, or in one or two relatively straight rows of variable length in areas of replaced autozooecia. Monticules common, consisting of several exilazooecia and scattered zooecia in varying combinations; pustules common in walls. [*Insignia* is closely related to *Phaenopora* but differs from it in having a modified autozooecial budding pattern, in abundance and distribution of exilazooecia, in having massive zoaria, and in having unbranched zoaria of variable growth habits that probably result from the irregular autozooecial budding pattern. According to ASTROVA (1965, p. 271), variations in growth habits in *Insignia* do not seem to have been controlled by changes in depositional environments.] *M.Ord.-U.Ord.*, USSR (Sib.).——FIG. 242,*2a–c*. **I. insignis* (NEKHOROSHEV), Podkamennaya Tunguska River, Sib.; *a,* mesotheca with discontinuous median granular zone, abandoned chambers with superior hemisepta as basal diaphragms and inferior hemisepta in endozone, exilazooecial chambers at base of exozone; long. sec., PIN 1242/81, ×100; *b,* living chambers with alternating hemisepta, curved transverse walls in endozone; long. sec., PIN 1242/81, ×30; *c,* irregularly aligned ranges, monticule with larger zooecium, (upper left); tang. sec., PIN 1242/87, ×30.

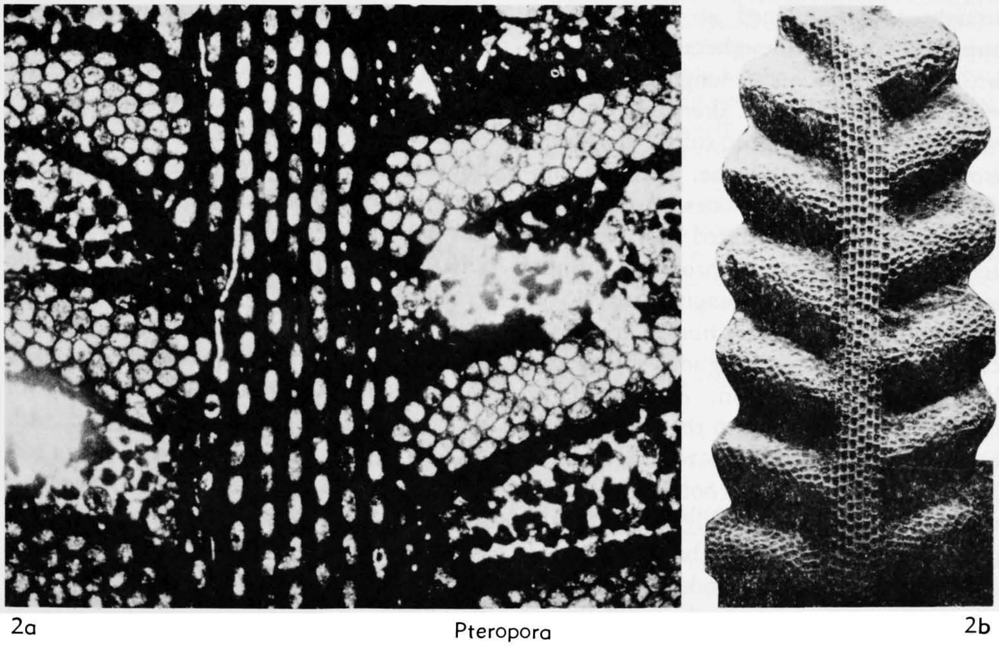
Phaenopora HALL, in SILLIMAN, SILLIMAN, & DANA, 1851, p. 399 [**P. explanata* HALL, 1852, p. 46; SD ULRICH, 1890, p. 392; ?Cataract F., L. Sil., Flamborough Head, Ont., Can.]. Zoarium branched or unbranched and explanate. Mesothecae sinuous in longitudinal section. Autozooecia in straight ranges throughout ontogeny. In exozones, autozooecia subrectangular in cross section, generally contiguous laterally, partially separated within ranges by exilazooecia; may be replaced by exilazooecia. Autozooecial boundaries generally not visible; pustules indistinct, scattered in zoaria. Living chambers elliptical in cross section, generally without lining. Superior and inferior hemisepta common, regularly arranged. Superior hemisepta curved proximally, relatively long and thick; inferior hemisepta extending from mesotheca, relatively thick, variable in length. Exilazooecia common, irregularly triangular to subcircular or elongate longitudinally in cross section; regularly arranged in pairs or may be in short rows between successive autozooecia; singly or in short rows in areas of bifurcation and margins, and in areas of replaced autozooecia. Monticules common in some zoaria, raised, consisting of exilazooecia and sparse zooecia. [Internal structure in type specimens of *P. explanata* is poorly preserved (Ross, 1960c, p. 1072; 1961a, p. 332); however, it is reasonable to assume that the internal structure in *P. explanata* was closely similar to that in *P. constellata* HALL and to that in the other ptilodictyid genera.] *M.Ord.-U.Sil.,* USSR, N.Am., Eng., Swed.——FIG. 243,*1a*. **P. explanata,* lectotype, AMNH 1490; alignment of autozooecial ranges; external view, ×5.——FIG. 243,*1b–d*. *P. constellata* HALL, ?Cataract F., Ont.; *b,* straight autozooecial ranges, structurally continuous longitudinal walls, pairs of exilazooecia between successive autozooecia, and exilazooecia in groups between longitudinal walls; tang. sec., USNM 242618, ×30; *c,d,* shape of living chambers, exilazooecia and sinuous mesotheca, superior and inferior hemisepta projecting into living chambers in endozone; long. sec., USNM 242617, ×30, 100.

Phaenoporella NEKHOROSHEV, 1956a, p. 48 [**Phaenopora transenna* SCHOENMANN, 1927, p. 788; OD; M. Ord. (Mangaze.), Podkamennaya Tunguska River, Sib., USSR]. Zoarium cribrate, commonly fan shaped. Fenestrules ovate to subcircular, variable in size, irregularly arranged or in indistinct rhombic pattern, rarely delineated transversely by relatively straight cross segments of zooecia; in proximal regions, may be closed by extrazooecial stereom, exilazooecia, or both. Autozooecial ranges generally curve around fenestrules. Low expansions at right angles to zoarial surface may result in irregular, three-dimensional, cribrate growth. Mesotheca irregularly sinuous in longitudinal section. Autozooecia in straight to curving ranges throughout ontogeny. In exozones, autozooecia subelliptical to irregularly subelliptical in cross section, generally contiguous laterally across pronounced longitudinal walls, partially separated within ranges, and probably replaced locally by exilazooecia. Autozooecia aligned irregularly in cross segments between fenestrules. Autozooecial boundaries broadly serrated or not visible; pustules common, irregularly arranged in exozonal walls. Living chambers elliptical to irregularly subcircular in cross section; lining common, variable in thickness. Superior and inferior hemisepta common, somewhat irregularly arranged. Superior hemisepta generally short, blunt; inferior hemisepta long, straight, and may curve proximally from mesothecae or distal walls. Exilazooecia common to abundant, irregularly triangular to elongate subcircular or variable in cross section, commonly with narrower chambers in outer exozones, rarely with lining; generally in pairs, rarely in groups of three or more between successive autozooecia; in groups in scattered areas of replaced autozooecia, and in groups or curving rows in fenestrule margins. Monticules absent. *M.Ord.-L.Sil.,* USSR (Tuva).——FIG. 244,*1a–d*. *P. transenna mesofenestralia,* paratype, USNM 171741; *a,* autozooecia aligned across mesotheca, endozone narrows toward margins, broadly curved laminae in walls in exozone; transv. sec., ×30; *b,* mesotheca with median granular zone, distinct lining along distal wall, blunt superior hemiseptum; long. sec., ×100; *c,* exilazooecia in ranges in margin surrounding fenestrule, curving autozooecial ranges in midregion; tang. sec., ×30; *d,* sinuous mesotheca, hemisepta, exilazooecia with wide chambers at base of exozone; long. sec., ×30.

Pteropora EICHWALD, 1860, p. 395 [**P. pennula*; OD; Pirgu and Porkuni horizons at Haapsalu and Seli-Metskula respectively, U. Ord., Est., USSR]. Zoarium unbranched; consisting of straight midsegments and lateral ribs diverging obliquely from midsegments at regular intervals. Mesothecae straight in midsegments, probably merging with extrazooecial stereom between lateral ribs. In exozones, autozooecia in straight ranges in midsegment, subrectangular in cross section, contiguous laterally, partially separated within ranges by exilazooecia. In lateral ribs, autozooecia irregularly rhombic to subcircular in cross section, arranged in rhombic pattern, generally contiguous without continuous longitudinal walls. Autozooecial boundaries not visible; pustules probably absent. Living chambers elliptical in cross section in midsegment, irregularly polygonal to subcircular in cross section in lateral ribs. Chamber lateral structures probably absent. Exilazooecia common to abundant, subcircular in cross section, variable in size; arranged singly, in pairs, or in short rows between successive autozooecia in midregions; scattered to lacking in lateral ribs. Exilazooecial and extrazooecial stereom common to abundant between ribs. [*Pteropora* is characterized by a ribbed growth habit, which is unusual among ptilodictyines. It is included in the Ptilodictyidae because of the linear arrangement and shape of autozooecia in the zoarial midsegment. In the lateral ribs, autozooecia are in a rhombic pattern instead of linear ranges and are indistinctly polygonal in cross section. This autozooecial arrangement and shape is somewhat similar to that near the margins in generalized ptilodictyids; however, structural relationship between the mesotheca and autozooecia, or mar-



Phaenoporella



Pteropora

FIG. 244. Ptilodictyidae (p. 496).

ginal zooecia, in areas between the midsegment and the ribs is not determinable from available illustrations. This diagnosis is summarized from MÄNNIL (1958, p. 344), because type material was not available.] *U.Ord.,* USSR (Est.).——FIG. 244,*2a,b*. **P. pennula*; *a,* autozooecia in linear ranges between structurally continuous longitudinal walls in midsegment, exilazooecia in midsegment and ribs; tang. sec., ×20; *b,* ribbed zoarium, arrangement of autozooecia in midsegment and ribs, extrazooecial stereom between diverging ribs, external view, ×5 (Männil, 1958).

Family ESCHAROPORIDAE
Karklins, new

Zoaria branched or unbranched and lanceolate, explanate, or cribrate. Basal attachments continuous with erect parts of zoaria in some genera; with tapering proximal connecting segments, which probably articulated with encrusting zoarial bases, in other genera. Mesothecae straight to sinuous, rarely zigzag in transverse section. Mesothecae in zoarial margins thickened, consisting of broadly curved laminae in transverse section, forming serrated zones along middle of zoarial margins beyond median granular zones. Median granular zones discontinuous through most of mesothecae, terminating near thickened zoarial margins. In endozones, autozooecia in straight ranges, aligned or alternating on opposite sides of mesothecae, contiguous, with sinuous continuous longitudinal walls, expanded and narrowed alternately in adjacent ranges, rectangular to subrhomboidal in cross section at mesothecae, generally subelliptical in later endozones. Autozooecial boundaries broadly serrated in later endozones. In exozones, autozooecia forming angles with mesothecae ranging from 45° to 90°, subpolygonal and elliptical to subcircular in cross section, contiguous or separated by extrazooecial stereom. Autozooecia in rhombic arrangement such that lateral walls restricted to individual autozooecia and longitudinal walls and ranges not formed. Autozooecial wall laminae broadly curved and U-shaped; zooecial boundaries broadly serrated. Pustules common to abundant throughout exozonal walls and stereom. Living chambers subrectangular to subelliptical in cross section of endozones, subelliptical to subcircular in cross section of exozones. Basal diaphragms rare to common in some genera, absent in others. Chamber lining absent to common. Superior hemisepta common in most genera; inferior hemisepta and mural spines absent to common in some genera, lacking in others. Exilazooecia few to absent. Monticules consisting of polymorphs and extrazooecial stereom in varying combinations. Extrazooecial stereom between autozooecia laminated, abundant to absent, irregularly delineated. Stereom laminae may be slightly sinuous, locally crinkled, generally parallel to zoarial surface, commonly forming striae at zoarial surfaces. *M.Ord.-L.Sil.*

Distinguishing features of the Escharoporidae are the mode of arrangement and cross-sectional shape of autozooecia parallel to mesothecae in endozones and exozones, skeletal microstructure in exozones, and distribution and relative sparsity of exilazooecia in the erect parts of zoaria. Arrangement of autozooecia in the Escharoporidae is similar to that in the Intraporidae and Stictoporellidae; however, in those families, autozooecia in endozones are generally subrectangular in cross section, with less sinuous longitudinal walls, and autozooecia in exozones are polygonal to subcircular in cross section. Compound autozooecial walls in exozones of the Escharoporidae have U-shaped laminae like those in the Ptilodictyidae and Intraporidae, but differ in having well-defined boundaries between autozooecia (Fig. 245,*1f*), numerous pustules throughout exozones (Fig. 246,*1c*), and crinkled laminae in parts of the exozonal skeleton (Fig. 246,*1a*; 247,*1a*). Ptilodictyids also differ in having autozooecia in distinct linear ranges throughout zoarial midregions. Stictoporellids differ from escharoporids in having autozooecia with broadly V-shaped laminae and narrowly serrated autozooecial boundaries in exozones. The Escharoporidae, Ptilodictyidae, and Stictoporellidae all have exilazooecia; however, in the Escharoporidae they are sparse or may be absent. Where present, the exilazooecia are mostly along zoarial margins and in proximal zoarial parts, but generally are uncommon in zoarial midregions.

Escharopora Hall, 1847, p. 72 [**E. recta*; OD; Trenton Gr., M. Ord., Trenton, Middleville, N.Y., USA]. Zoarium generally unbranched and lanceolate, rarely branched; connecting segments with tapered proximal tips, probably articulating with encrusting bases. Mesothecae straight to sinuous; autozooecial ranges aligned or alternating across mesotheca. In exozones, autozooecia form angles between 50° and 80° with mesothecae, subelliptical in cross section. Autozooecial wall and stereom laminae form sinuous striae at zoarial surface. Pustules common along autozooecial boundaries, striae scattered in exozonal walls and stereom. Living chambers subelliptical in cross section. Superior hemisepta common, generally blunt and short, rarely thin and long, curving proximally, usually scattered in zoaria, but may be regularly arranged. Mural spines absent to common, irregularly shaped, scattered in zoaria; may be regularly arranged. Exilazooecia few, subelliptical to subcircular in cross section, commonly closed at zoarial surfaces by thickened walls, sparse in zoarial margins and in proximal zoarial parts, generally absent in zoarial midregions. Monticules absent to common, flat to slightly raised, irregularly shaped or may form annular ridges at regular intervals across zoaria. *M.Ord.-U.Ord.,* N.Am., USSR(Eu.), Greenland, Burma.——FIG. 245,*1a–f.* **E. recta*; *a,* laminae on opposite sides of mesotheca intertongue along broadly serrated zone in zoarial margin, closed and open zooecia without endozone in margin; transv. sec., lectotype, AMNH 668/1, ×30; *b,* autozooecia with thickened walls, elongated and closed exilazooecia, extrazooecial stereom in proximal part of zoarium; tang. sec., lectotype, ×50; *c,* autozooecia in distinct rhombic pattern; external view, lectotype, ×5; *d,* subelliptical autozooecia in inner exozone; tang. sec., lectotype, ×30; *e,* slightly sinuous mesotheca with median granular zone, blunt hemisepta (fragment crushed); long. sec., lectotype, ×30; *f,* microstructure of serrated autozooecial boundaries in exozone; transv. sec., paralectotype, NYSM 654, ×100.

Championodictya Ross, 1964a, p. 18 [**C. pleasantensis*; OD; up. "Denmark?" F., low. "Cobourg?" F., ?U. Ord., Pleasant Lake, N.Y., USA]. Zoarium branched or unbranched and explanate. Mesothecae straight, locally crenulated in longitudinal section. Autozooecial ranges aligned across mesotheca. Endozones relatively wide. In exozones, autozooecia generally at right angles with mesothecae, locally sloping proximally, irregularly subpolygonal in cross section. Pustules abundant in exozonal walls, locally aligned in series at right angles to zoarial surface. Living chambers subelliptical to subcircular in cross section. Basal diaphragms common, scattered in zoaria; relatively thick, irregularly curved, incomplete locally. Lining common locally, variable in thickness. Superior hemisepta common, regularly arranged, relatively thick, irregularly shaped; locally with thin, proximally curved terminal edges. Spines common, blunt, relatively thick, scattered in zoaria. Exilazooecia absent to few, subelliptical to polygonal in cross section, scattered in outer exozone, commonly closed by thickened walls. Monticules absent to rare, indistinct. *?M.Ord., U.Ord.,* N.Am.——FIG. 245,*2a–d.* **C. pleasantensis,* holotype, YPM 25462; *a,* autozooecia aligned across mesotheca, relatively wide endozone; transv. sec., ×30; *b,* subrhomboidal autozooecia in endozone, subelliptical to subcircular autozooecia in exozone, mesotheca below; deep to shallow tang. sec., ×30; *c,* irregular and blunt spines, lining in some chambers, pustules in autozooecial boundary (left); tang. sec., ×100; *d,* crenulated mesotheca, shape of autozooecial chambers, superior hemisepta, thick basal diaphragms, autozooecial walls slope proximally in exozone; long. sec., ×30.

Chazydictya Ross, 1963b, p. 587 [**C. chazyensis*; OD; Chazy Ls., M. Ord., Isle La Motte, Vt., USA]. Zoarium branched or unbranched and explanate. Mesothecae generally straight; autozooecial ranges partly aligned across mesothecae. In exozones, autozooecia form angles between 55° and 65° with mesothecae. Autozooecia subelliptical in cross section. Pustules abundant along autozooecial boundaries and in extrazooecial stereom, scattered in autozooecial walls. Living chambers elliptical to subcircular in cross section. Basal diaphragms common, thin, slightly curved; regularly arranged in outer endozones and base of exozones. Exilazooecia and monticules absent. Locally, extrazooecial stereom laminae irregularly crinkled. *M.Ord.,* USA.——FIG. 246,*1a–c.* **C. chazyensis*; *a,* serrated autozooecial boundary, crinkled stereom laminae with pustules in exozone; long. sec., paratype, YPM 22098, ×100; *b,* abandoned chambers near base of exozone, thin basal diaphragm in outer endozone and base of exozone; long. sec., paratype, YPM 22069, ×30; *c,* subcircular living chambers, abundant pustules in extrazooecial stereom; tang. sec., holotype, YPM 22067, ×30.

Graptodictya ULRICH, 1882, p. 165 [**Ptilodictya perelegans* ULRICH, 1878, p. 94; OD; Waynesville Sh., U. Ord., Clarksville, Ohio, USA] [=*Arthropora* ULRICH, 1882, p. 167]. Zoarium branched, anastomosing irregularly in some species. Mesothecae slightly sinuous in longitudinal section, may zigzag in transverse section. Autozooecial ranges generally alternating across mesothecae. In exozones, autozooecia form angles between 80° and 90° with mesothecae, subelliptical in cross section. Pustules abundant along autozooecial boundaries and throughout exozonal walls and extrazooecial stereom. Living chambers subelliptical to subcircular in cross section. Superior hemisepta common, generally short and blunt, rarely thin and long, curving proximally; usually scattered in zoaria, but may

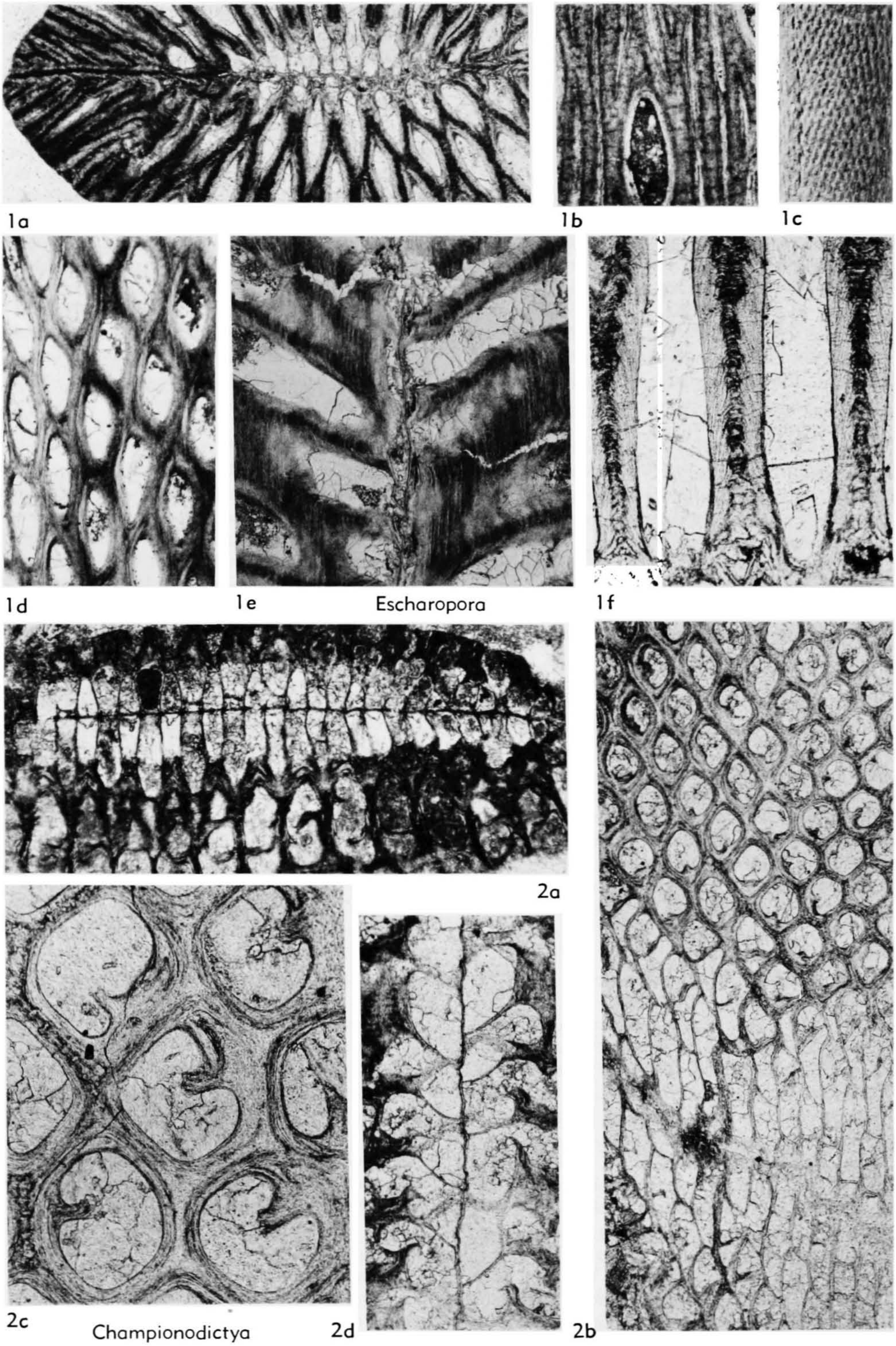


FIG. 245. Escharoporidae (p. 498–499).

be regularly arranged. Exilazooecia absent to rare, generally subelliptical in cross section, commonly closed by thickened walls. Monticules absent to rare, generally flat. Extrazooecial stereom laminae commonly crinkled, forming abundant and longitudinally sinuous striae between autozooecia, and along zoarial margins and proximal zoarial parts. *M.Ord.-L.Sil.*, USSR(Est.), Morocco, France, ?Austria, India.——Fig. 247,*1a–f*. **G. perelegans* (Ulrich); *a,* microstructure of autozooecial wall and extrazooecial stereom in exozone; transv. sec., holotype, USNM 137607, ×200; *b,* curved autozooecial walls in endozone; transv. sec., holotype, ×30; *c,* branching pattern, striae along zoarial margins; external view, holotype, ×5; *d,* indistinct blunt hemisepta, shape of living chambers; long. sec., holotype, ×50; *e,* autozooecia in rhombic pattern, sinuous striae between autozooecia and in zoarial margin; tang. sec., holotype, ×30; *f,* sinuous and continuous longitudinal autozooecial walls in endozone, extrazooecial stereom with striae in margin; tang. sec., USNM 242619, ×30.

Oanduella Männil, 1958, p. 340 [**O. bassleri*; OD; Oandu horizon, D3, Oandu bed, M. Ord., Oandu River, Est., USSR]. Zoarium cribrate; fenestrules ovate to subcircular, variable in size, surrounded by exilazooecia or extrazooecial stereom. Mesothecae slightly sinuous in longitudinal section. In exozones, autozooecia form angles between 50° and 70° with mesothecae, subelliptical to irregularly polygonal in cross section. Pustules common in exozonal walls and stereom. Living chambers subelliptical to subcircular in cross section. Inferior hemisepta common, long, thin, extending from mesothecae or distal autozooecial walls, regularly arranged or scattered in zoaria. Basal diaphragms and superior hemisepta absent. Exilazooecia common, subelliptical to polygonal in cross section, scattered in zoarial midregions, regularly arranged in zoarial margins or absent. Monticules probably absent. [Rhombic arrangement and skeletal microstructure of autozooecia in the exozone indicate a zoarial development similar to that in *Escharopora* Hall (Männil, 1958, p. 341) and other genera herein assigned to the Escharoporidae.] *M.Ord.*, USSR(Est.).——Fig. 247,*2a–c*. **O. bassleri*; *a,* arrangement and shape of autozooecia, fenestrules surrounded by zone of exilazooecia; external view, holotype, ×5; *b,* arrangement of autozooecia; tang. sec., ×25; *c,* sinuous mesotheca, inferior hemisepta; long. sec., ×25 (Männil, 1958).

?Proavella Männil, 1958, p. 345 [**Gorgonia proava* Eichwald, 1842, p. 44; OD; ?Vasalemma, M. Ord., Est., USSR]. [Männil (1958, p. 345) erected *Proavella* and designated *Gorgonia proava* as its type species, but did not figure a type. According to Männil, *Proavella* is similar in internal structure to *Graptodictya* Ulrich, but differs from it in having a cribrate growth habit. Ross (1964a, p. 13) questioned the validity of *Proavella* because type material is inadequately documented, and she noted similarities between *Proavella* and *Stictoporellina* Nekhoroshev in growth habits and arrangement of exilazooecia. The concept of *Proavella* and its taxonomic assignment will remain questionable until the type material becomes available for description and further comparison. Herein *Proavella* is tentatively assigned to the Escharoporidae because of its similarity in internal zoarial structure to *Graptodictya*, as noted by Männil (1958)].

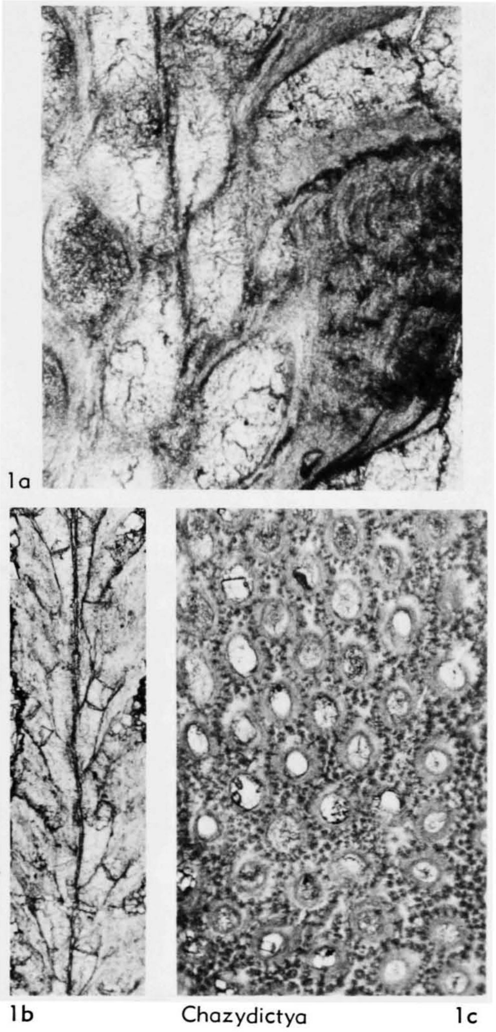


Fig. 246. Escharoporidae (p. 499).

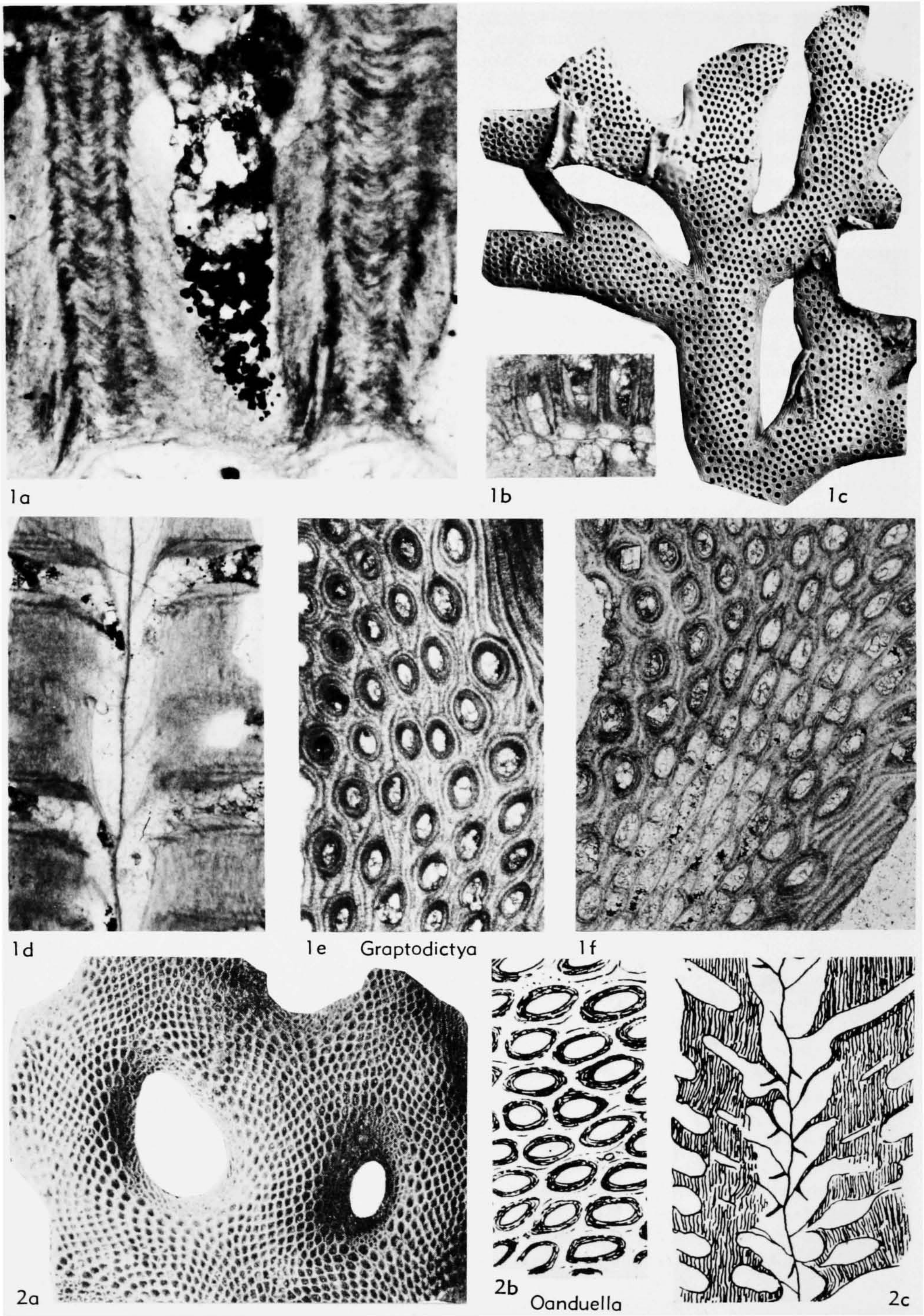


FIG. 247. Escharoporidae (p. 499–501).

Family INTRAPORIDAE Simpson, 1897

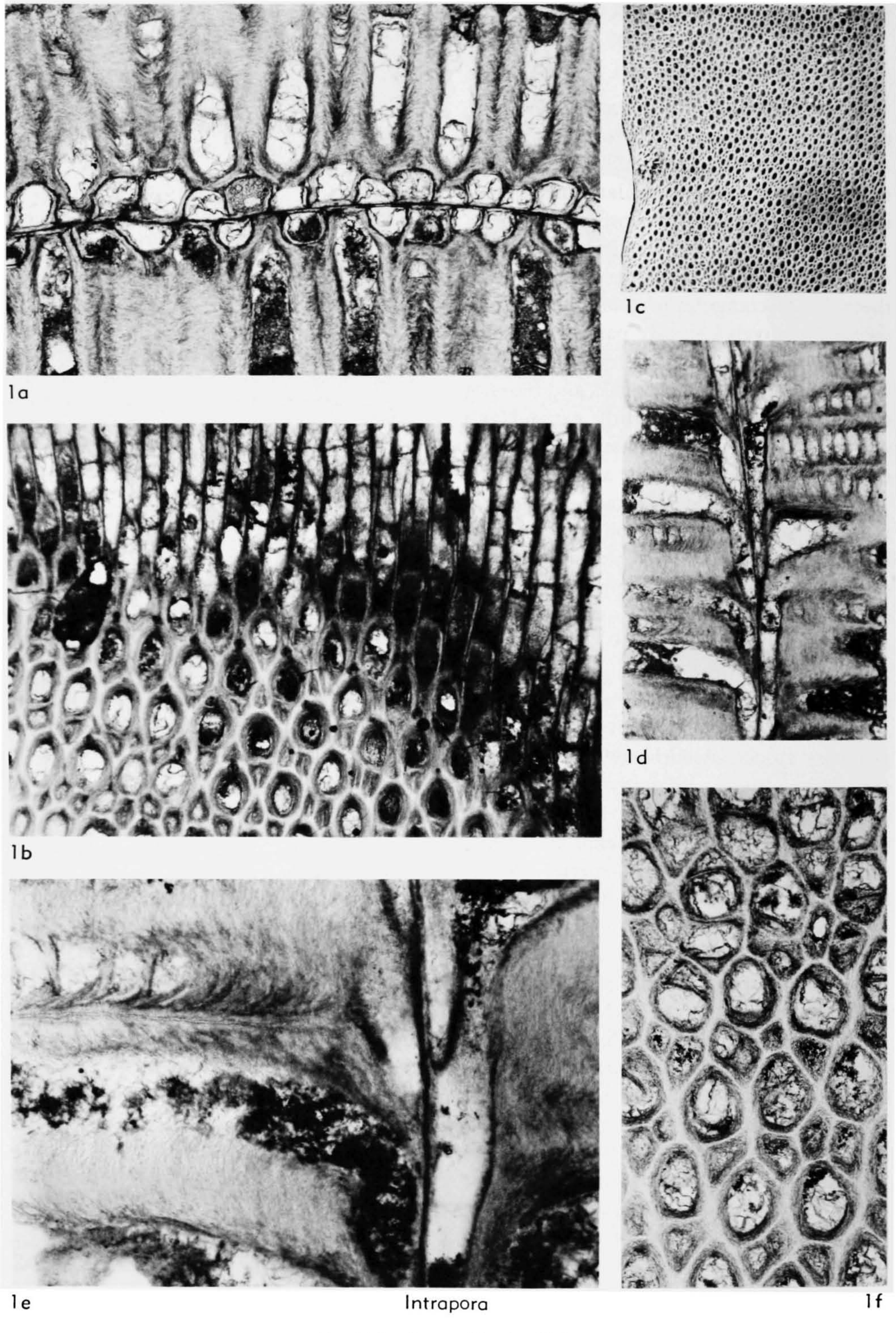
[Intraporidae SIMPSON, 1897, p. 543]

Zoaria branched or unbranched and cribrate or explanate. Zoarial attachments generally continuous skeletally. Mesotheca straight with median granular zone extending to edge of zoarial margins. In endozones, autozooecia arranged in straight ranges, generally alternating on opposite sides of mesothecae, subrectangular to rhomboid in cross section, relatively elongate parallel to mesotheca, contiguous with continuous longitudinal walls. In outer endozones and bases of exozones, autozooecia slightly expand and narrow alternately in adjacent ranges. In exozones, autozooecia form angles between 75° and 90° with mesothecae, arranged in rhombic pattern without continuous longitudinal walls, irregularly polygonal to subcircular in cross section, contiguous, partly separated by mesozooecia, or completely separated by pitted extrazooecial stereom. Autozooecial wall laminae curved and broadly U-shaped, may form striae at zoarial surface. Autozooecial boundaries not visible; pustules generally absent. Acanthostyles few. Living chambers subrectangular to subrhomboidal in cross section in endozones, subelliptical to subcircular in cross section in exozones. Superior hemisepta scattered in zoaria; inferior hemisepta lacking; chamber lining generally lacking. Basal diaphragms and abandoned chambers few. Mesozooecia, monticular and basal polymorphs in some genera. Monticules common to absent. *M.Dev.-U.Dev.*

The family Intraporidae SIMPSON, 1897, differs in skeletal microstructure and presence of mesozooecia from the Stictoporellidae NICKLES and BASSLER, 1900, and is removed from synonymy (BASSLER, 1953, p. G137) with that family. The Intraporidae is similar to the Stictoporellidae and Escharoporidae in the rhombic arrangement of autozooecia in the exozone. *M.Dev.-U.Dev.*

Intrapora HALL, 1883b, p. 157 [**I. puteolata*; M; Jeffersonville Ls., M. Dev., Falls of Ohio River, Ky.-Ind., USA]. Zoarium branched or unbranched and explanate. In exozones, autozooecia usually form angle between 75° and 80° with mesothecae, contiguous or separated partially by mesozooecia. Acanthostyles rare to common, consisting of straight cores of cryptocrystalline particles and thin laminar sheaths. Sheath laminae abut cores at low angle. Acanthostyles irregularly arranged, originating at base of exozone, terminating in outer exozones or as low protuberances at zoarial surfaces. Living chambers broadly subelliptical in cross section. Superior hemisepta indistinct, short, blunt. Mesozooecia abundant, polygonal to subcircular in cross section, variable in size. Mesozooecial diaphragms closely spaced, commonly thickening distally, rarely filling mesozooecial chambers. Monticules rare to common, generally raised; consisting of irregularly shaped, somewhat larger zooecia and some mesozooecia; common in species with explanate zoaria. *M.Dev.-U.Dev.*, N.Am., USSR.——FIG. 248,*1a–f*. **I. puteolata*; *a,* median granular zone in mesotheca, autozooecial boundaries in endozone, broadly curved laminae in exozone; transv. sec., USNM 242620 from Alpena Ls., Mich., ×50; *b,* shape and arrangement of autozooecia in endo-exozone, acanthostyles and mesozooecia in exozone; tang. sec., USNM 242620, ×30; *c,* arrangement of autozooecia and mesozooecia, mesozooecia in zoarial margins; external view, syntype, FMNH 13987 from Jeffersonville Ls., Ky.-Ind., ×5; *d,* shape of living chambers, indistinct superior hemiseptum, mesozooecia with diaphragms; long. sec., USNM 242621 from Alpena Ls., Mich., ×30; *e,* broadly curved laminae of autozooecia and mesozooecia, core and sheath of an acanthostyle, median granular zone in mesotheca; long. sec., USNM 242621, ×100; *f,* zooecia and mesozooecia in monticule; tang. sec., USNM 242622 from Alpena Ls., Mich., ×50.

Coscinella HALL, 1887, p. xix [**C. elegantula*; OD; Hamilton Gr., M. Dev., Widder, Ont., Can.]. Zoarium cribrate; fenestrules subelliptical to subcircular or irregularly shaped, generally smaller in middle and proximal regions than in distal and lateral regions, rarely closed partly by extrazooecial stereom. Zoarial and fenestrule margins of pitted extrazooecial stereom. Monticules absent. In exozones, autozooecia usually at right angles to mesothecae, elliptical to subcircular in cross section, generally surrounded by pitted extrazooecial stereom. Living chambers broadly elliptical to subcircular in cross section, may be closed locally by diaphragm at zoarial surface. Superior hemisepta short, blunt, indistinct. [Zoarial surfaces contain numerous pits (Fig. 249,*1e*) formed by concave laminae that are skeletally continuous with those of autozooecia, but they are extrazooecial. Shape and structure seem to indicate concurrent growth of these laminae in the autozooecia and the exozone. Specimens also possess scattered cavities in



Intrapora

FIG. 248. Intraporidae (p. 503).

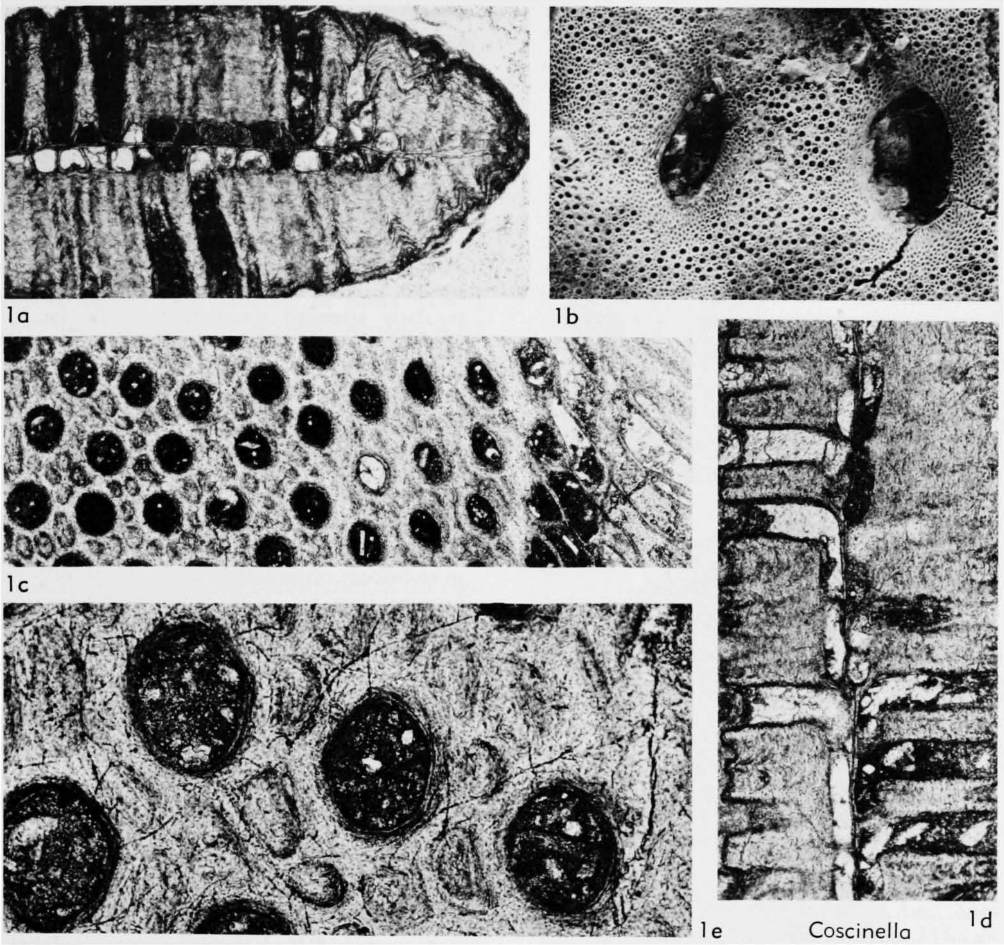


FIG. 249. Intraporidae (p. 503).

walls at the base of the exozone, which may have been unfilled portions of extrazooecial skeleton.] *M.Dev.*, Can.——FIG. 249,*1a–e*. **C. elegantula*, holotype, NYSM 641,6220/1; *a*, broadly curved laminae of autozooecia in exozone, extrazooecial stereom of zoarial margin; transv. sec., ×30; *b*, wide zone of pitted extrazooecial stereom surrounding fenestrules; external view, ×5; *c*, shape of autozooecia in endo-exozone, pitted extrazooecial stereom in exozone; tang. sec., ×30; *d*, shape of living chambers, indistinct hemisepta, median granular zone in mesotheca; long. sec., ×30; *e*, pitted extrazooecial stereom surrounding autozooecia, subcircular living chambers; tang. sec., ×100.

Family PHRAGMOPHERIDAE
Goryunova, 1969

[Phragmopheridae GORYUNOVA, 1969, p. 129]

Zoaria branched. In endozones, autozooecia in ranges alternating across mesotheca, contiguous, with continuous longitudinal walls. Walls slightly flexed at base of exozone in transverse section. In exozones, autozooecia arranged in rhombic pattern, without continuous longitudinal walls, generally polygonal to subcircular in cross section. Autozooecial wall laminae curved; autozooecial boundaries narrowly serrated. Mural styles common. Living chambers broadly elliptical to subcircular in cross section, variable in length. Cystiphragms and basal diaphragms common. Polymorphism expressed by mesozooecia. Extrazooecial stereom laminated and irregularly delineated. Acanthostyles present. *U.Carb.*

Capillaries of GORYUNOVA (1969, p. 129,

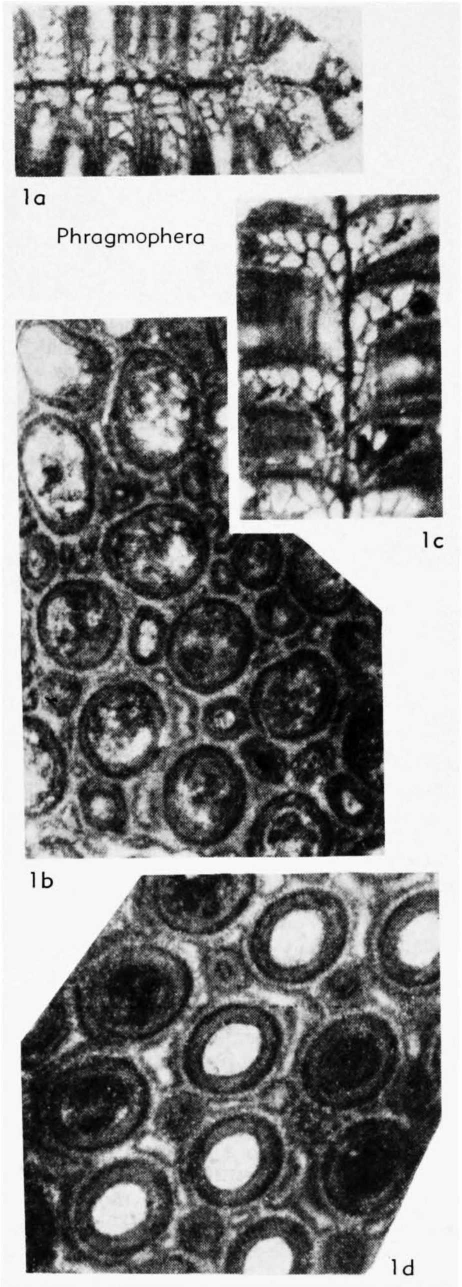


FIG. 250. Phragmopheridae (p. 506).

130) are interpreted here as mural styles, secondary zoarial deposits as extrazooecial stereom, and tubercles as acanthostyles.

Phragmophera GORYUNOVA, 1969, p. 129 [**P. eximia*; OD; U. Carb., C. Urals, USSR]. In exozones, autozooecia usually at right angles to mesothecae, irregularly subcircular in cross section, only locally contiguous, generally separated by mesozooecia. Mural styles aligned along autozooecial boundaries. Autozooecial walls extend into peristomes on zoarial surface. Living chambers generally broadly elliptical in cross section. Cystiphragms closed; in late endozones and exozones of autozooecia, in regular series. Basal diaphragms thin, slightly curved, regularly spaced in endozones and exozones. Mesozooecia abundant, irregularly polygonal to subcircular in cross section, variable in size, with few diaphragms, regularly arranged throughout zoaria, locally filled by stereom. Mesozooecial walls extending into peristomes at zoarial surface. Acanthostyles variable in size. *U.Carb.,* USSR(C. Urals).——FIG. 250,*1a–d.* **P. eximia,* holotype, PIN 389/654; *a,* mesotheca, autozooecial boundaries, and cystiphragms in chambers in exozone; transv. sec., ×20; *b,* arrangement of autozooecia, mesozooecia, and acanthostyles in exozone; tang. sec., ×40; *c,* abandoned chambers, basal diaphragms in endozone, cystiphragms along distal walls in exozone; long. sec., ×20; *d,* subpolygonal autozooecia, polygonal mesozooecia, indistinct mural styles along autozooecial boundaries, acanthostyles; tang. sec., ×40 (Goryunova, 1969).

Family RHINIDICTYIDAE Ulrich, 1893

[*nom. correct.* BASSLER, 1953, p. G140, *pro* Rhinidictyonidae ULRICH, 1893, p. 124]

Zoaria branched or unbranched and explanate, rarely cribrate. Basal attachments generally continuous skeletally with erect parts of zoaria. Mesothecae straight, sinuous, or bifurcated. Median granular zones extending throughout mesothecae. Median rods usually present, closely spaced, generally straight; consisting of cryptocrystalline cores and thin, laminated sheaths; subelliptical to circular in cross section; extending throughout median granular zone, diverging gradually into zoarial margins. In endozones, autozooecia in ranges alternating on opposite sides of mesothecae; commonly rectangular to subrhomboid in cross section parallel to mesothecae, contiguous, with continuous longitudinal walls and straight to slightly curved transverse walls; may be partially contiguous, without continuous longitudinal walls and separated by extrazooecial skeleton. Autozooecial boundaries extending into exozone, becoming narrowly serrated. In exozones, autozooecia usually form angle between 50° and 80° with mesothecae; commonly aligned in straight and distinct ranges; subrectangular to subelliptical in cross section, with straight to curved, generally indistinctly delineated longitudinal walls; may be aligned in indistinct ranges, subelliptical to subcircular in cross section, partially contiguous or separated by extrazooecial deposits, and without continuous longitudinal walls. Autozooecial wall laminae in most genera slightly curved and V-shaped. Autozooecial boundaries narrowly serrated. Autozooecial walls commonly vesicular in inner exozone in some genera. Mural styles rare to common, consisting of tightly curved segments of wall laminae; rarely with small, indistinct and discontinuous cores; usually variable in size, may be relatively large. Mural styles may be present in autozooecial boundaries or diverge from them; may be single or aligned in dark zones in zooecial walls and extrazooecial stereom; generally oriented perpendicular to zoarial surface, terminating in walls or at zoarial surface. Dark zones in walls and extrazooecial stereom rare to common, generally aligned longitudinally. Living chambers usually variable in length, elliptical to subcircular in cross section. Superior hemisepta rare to common, generally scattered in zoaria; may be regularly arranged. Inferior hemisepta rare and scattered. Chamber lining usually rare to lacking, but may be common. Intrazooecial cysts rare. Basal diaphragms absent to common, generally scattered in zoaria, may be regularly arranged. Polymorphism expressed by marginal, basal, and monticular zooecia. Monticules absent to common, consisting of extrazooecial skeletal deposits and few zooecia. Exilazooecia and mesozooecia absent. Extrazooecial skeletal deposits rare to common, consisting of laminar and vesicular portions in inner exozone or endozone in some genera. Distribution of extrazooecial skeletal deposits variable. *L.Ord.-M.Sil.*

Stictopora Hall, 1847, p. 73 [**S. fenestrata*; SD Ulrich, 1886a, p. 67; Chazy Gr., M. Ord. (Chazy.), N.Y., USA] [=*Sulcopora* d'Orbigny, 1849, p. 499, obj.; *Rhinidictya* Ulrich, 1882, p. 152; *Dicranopora* Ulrich, 1882, p. 166; *Hemidictya* Coryell, 1921, p. 303]. Zoarium branched or unbranched and explanate, rarely cribrate. Mesothecae generally straight, may be locally sinuous in longitudinal section. Median rods subelliptical in cross section. In endozones, autozooecia subrectangular to subrhomboidal in cross section, contiguous, with straight continuous longitudinal walls. In exozones, autozooecia in straight ranges, generally contiguous, with straight to slightly sinuous longitudinal walls, subrectangular in cross section, walls locally may be vesicular in inner exozone. Mural styles common, mostly in autozooecial boundaries or scattered in walls. Living chambers generally elliptical in cross section. Superior hemisepta rare to common, regular, thin, curved proximally, variable in length. Inferior hemisepta in few species; short, thin, generally projecting from mesotheca, scattered in zoaria. Basal diaphragms thin, slightly curved, variable in spacing, absent in some. Monticules common, generally scattered in zoaria. Extrazooecial stereom laminated, may be sparse in zoarial midregion. [The status of *Stictopora* Hall, 1847 and *Rhinidictya* Ulrich, 1882 is controversial. Ross (then Phillips, 1960; see also Ross, 1961a, 1966b) reviewed the nomenclature of *Stictopora* and considered *Rhinidictya* to be a synonym. More recently, Kopayevich (1973) has argued for retention of *Rhinidictya* as an independent genus. Because of poor preservation of type specimens, skeletal differences noted by Kopayevich in *S. fenestrata* (type species of *Stictopora*) and *R. nicholsoni* (type species of *Rhinidictya*) cannot be verified, and *Rhinidictya* is retained herein as a synonym of *Stictopora*.] *L.Ord.-L.Sil.*, USSR, N.Am., Australia, India, Burma, G.Brit.——Fig. 251,*1a–f*. *S. nicholsoni* (Ulrich), Tyrone Ls., High Bridge Gr., M. Ord., Ky.; *a,* indistinct laminae in autozooecial walls, superior hemisepta, mural styles in outer exozone; long. sec., paralectotype, USNM 137615, ×30; *b,* elliptical living chambers, sinuous longitudinal walls, mural styles in boundaries and walls; tang. sec., paralectotype, USNM 137615, ×50; *c,* mural styles in boundary between longitudinal walls; tang. sec., paralectotype, USNM 137615, ×200; *d,* median rods in mesotheca, autozooecial boundaries in longitudinal walls; transv. sec., paralectotype, USNM 137615, ×30; *e,* branching zoarium, autozooecia in linear ranges; external view, lectotype, USNM 137622, ×3; *f,* autozooecial boundaries in transverse walls, shape of living chambers, superior hemisepta; long. sec., USNM 242623, ×50.——Fig. 251,*1g–k*. **S. fenestrata*; *g,* sinuous mesotheca; long. sec., lectotype, NYSM 915, ×30; *h,* autozooecia in broadly curved ranges, shape of autozooecia, median rods in mesotheca (left); tang. sec., lectotype, ×30; *i,* mural styles in boundaries between longitudinal walls, elliptical living chambers; tang. sec., lec-

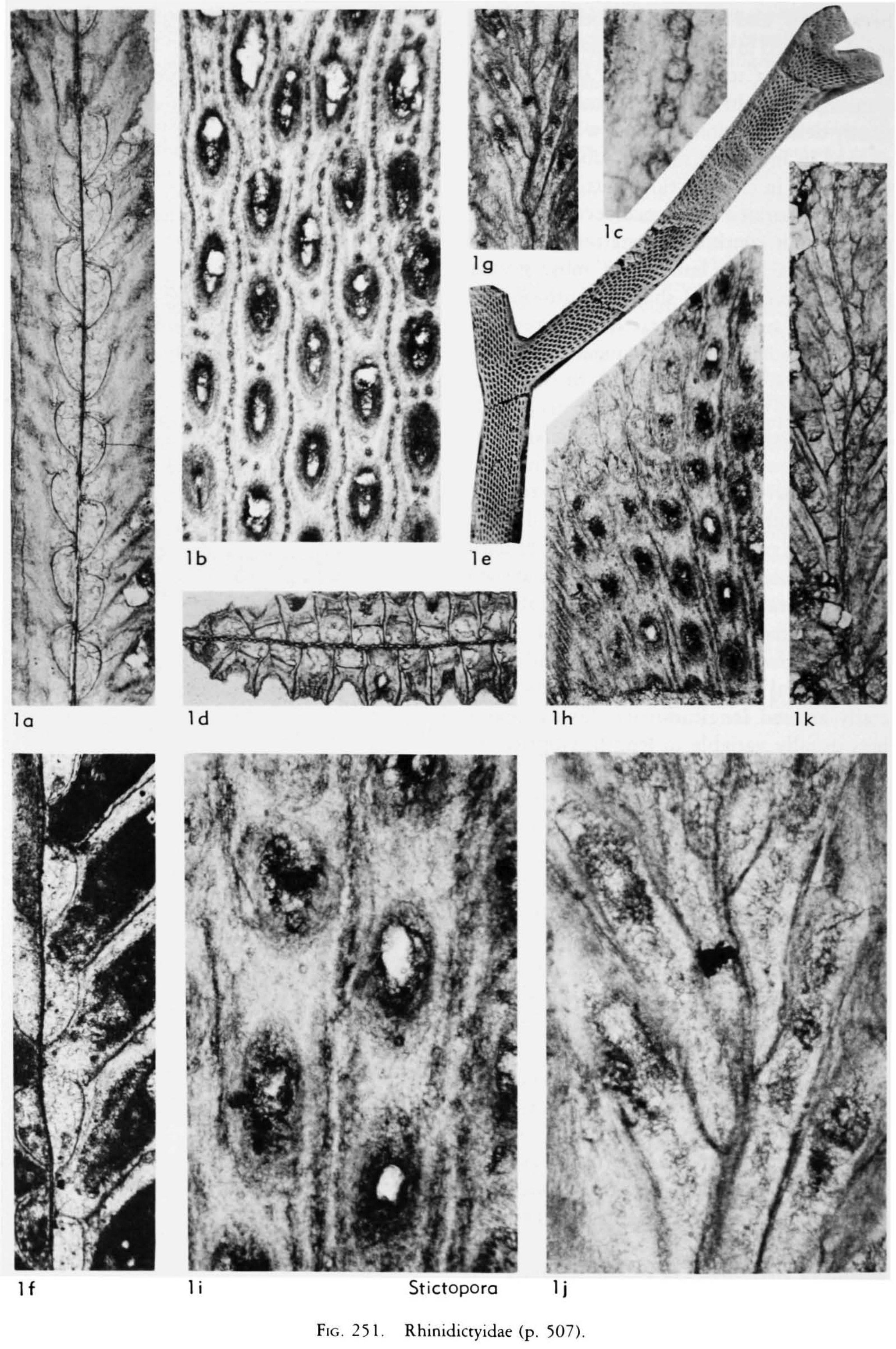


FIG. 251. Rhinidictyidae (p. 507).

totype, ×100; *j,* granular zone in mesotheca, indistinct autozooecial boundaries in endozone; long. sec., lectotype, ×100; *k,* basal diaphragms in endozone and exozone, segment of median rods in median granular zone of mesotheca; long. sec., YPM 22158, ×30.

Athrophragma KARKLINS, 1969, p. 61 [**Pachydictya foliata* ULRICH, 1886a, p. 73; OD; Spechts Ferry Sh. Mbr., Decorah Sh., M. Ord., St. Paul, Minn., USA]. Zoarium explanate, slightly lobate and undulating. Mesotheca straight to slightly sinuous. Median rods subcircular in cross section, diameter greater than width of median granular zones. In endozone, autozooecia in indistinct ranges, subelliptical to subcircular in cross section, locally contiguous, generally separated by extrazooecial vesicles, and without continuous longitudinal walls. In exozones, autozooecia in indistinct ranges, subelliptical to subcircular in cross section, without continuous longitudinal walls, generally separated by extrazooecial vesicles and stereom. Autozooecial walls relatively thin. Mural styles indistinct or lacking; locally in autozooecial boundaries and in dark, longitudinally aligned, discontinuous zones in extrazooecial stereom. Mural styles generally absent in autozooecial walls. Living chambers broadly elliptical to subcircular in cross section; lateral chamber structures absent. Basal diaphragms straight to slightly curved, regularly spaced. Monticules common, flat and raised, arranged in rhombic pattern; generally vesicular in inner exozones, having stereom in outer exozones. Extrazooecial skeleton common, consisting of stereom and vesicles. Vesicular structures common in endozones and inner exozones; stereom present throughout exozones. *M.Ord.-U.Ord.,* N.Am., USSR(W. Arctic).——FIG. 252,*1a–c.* **A. foliata* (ULRICH), lectotype, USNM 163111; *a,* broadly elliptical autozooecia and their chambers, stereom between autozooecia, monticule with larger zooecium and dark zones in stereom; tang. sec., ×30; *b,* basal diaphragms at regular intervals, vesicles in inner exozone, thin autozooecial walls; long. sec., ×30; *c,* extrazooecial vesicles between autozooecia in endozone and inner exozone, numerous thin, dark zones in exozonal laminar stereom; transv. sec., ×30.

Carinodictya ASTROVA, 1965, p. 287 [**Rhinidictya carinata* ASTROVA, 1955, p. 157; OD; M. Ord. (Mangaze.), Podkamennaya Tunguska River, Sib., USSR]. Zoarium branched. Mesotheca generally straight; median rods indistinctly delineated. In exozones, autozooecia in straight ranges, subelliptical in cross section, contiguous, with regularly sinuous and continuous longitudinal walls. Autozooecial walls generally vesicular in inner exozones. Mural styles common in autozooecial boundaries, rare in wall laminae. Living chambers elliptical in cross section. Supe-

FIG. 252. Rhinidictyidae (p. 509).

rior hemisepta rare, short, blunt, and scattered. Inferior hemisepta lacking. Basal diaphragms rare, scattered in zoaria, or absent. Monticules rare or absent. Extrazooecial stereom laminated, sparse in zoarial midregions. *M.Ord-U.Ord.*, USSR (Sib.).——Fig. 253,*1a–c*. **C. carinata* (Astrova), PIN 1242.150; *a,* autozooecial ranges, sinuous longitudinal walls, elliptical living chambers; tang. sec., ×30; *b,* mesotheca with median granular zone and segments of median rods; long. sec., ×50; *c,* V-shaped laminae of autozooecial walls (mesotheca obscured); transv. sec., ×30.

Eopachydictya Ross, 1963b, p. 591 [**E. gregaria*; OD; Chazy Ls., M. Ord., Isle La Motte, Vt., USA]. Zoarium branched. Mesotheca straight. Median rods subcircular in cross section. In endozones, autozooecia in straight ranges, generally subelliptical in cross section, contiguous, with slightly curved and continuous longitudinal walls. In exozones, autozooecia in indistinct ranges, subelliptical in cross section, partially contiguous or locally separated by extrazooecial stereom. Walls may be vesicular in inner exozones. Mural styles common along autozooecial wall boundaries and in extrazooecial stereom. Living chambers elliptical in cross section; lateral chamber structures absent. Basal diaphragms generally straight, rare to common. Monticules rare, generally flat, locally vesicular in inner exozones, with mural styles in stereom in outer exozones. Monticules scattered in zoaria. Extrazooecial skeleton of stereom and vesicles. Vesicles locally present in inner exozones, stereom irregularly arranged throughout exozones. *M.Ord.*, USA.——Fig. 253,*2a–d*. **E. gregaria*; *a,* indistinct autozooecial boundaries, mural styles in extrazooecial stereom between autozooecia and in monticule; tang. sec., holotype, YPM 22076, ×100; *b,* general shape of living chambers; long. sec., paratype, YPM 22079, ×30; *c,* indistinct vesicles in inner exozone, shape of chambers in endozone; long. sec., paratype, YPM 22079, ×100; *d,* mesotheca with median granular zone and indistinct median rods, autozooecial boundaries and extrazooecial stereom in exozone; transv. sec., paratype, YPM 22080, ×100.

Eurydictya Ulrich in Miller, 1889, p. 301 [**E. montifera* Ulrich, 1890, p. 521; OD; U. Ord. (Richmond.), Wilmington, Ill., USA]. Zoarium explanate. Mesotheca straight, median rods elliptical in cross section. In endozones, autozooecia rectangular in cross section, contiguous, with straight continuous longitudinal walls and generally straight transverse walls. In exozones, autozooecia usually forming an angle of about 80° with mesothecae. Autozooecia generally in indistinct ranges, contiguous to partly contiguous, locally separated by extrazooecial stereom. Longitudinal walls slightly curved, continuous or merging with extrazooecial stereom. Mural styles common in autozooecial boundaries and locally in walls. Vesicles absent in walls. Living chambers broadly elliptical to subcircular in cross section; lining thin, generally discontinuous. Superior hemisepta common, short or long, blunt, curving proximally. Basal diaphragms rare and scattered in zoaria. Monticules common, may be arranged in rhombic pattern. Monticular zooecia commonly filled by stereom, which is laminated and contains scattered mural styles. *M.Ord.-U.Ord.*, USA, USSR(Sib.).——Fig. 254,*1a–d*. **E. montifera*; *a,* irregularly conical monticules, alignment of autozooecia; external view, holotype, ISGS 2668, ×5; *b,* autozooecial boundaries (granular zones) in endozone, autozooecial boundaries and mural styles in exozone, median rods in granular zone in mesotheca; transv. sec., USNM 137614, ×50; *c,* shape of living chambers, hemisepta at base of exozone; long. sec., holotype, ×30; *d,* autozooecia in indistinct ranges, shape of living chambers, monticule with extrazooecial stereom, filled zooecia, and mural styles; tang. sec., USNM 137614, ×30.

Goniotrypa Ulrich, 1889, p. 40 [**G. bilateralis*; OD; Stony Mountain F., ?U. Ord., Manitoba, Can.]. Zoarium small, probably unbranched; consisting of 2 to 4 autozooecial ranges and longitudinal ridge along middle of branch. Mesothecae straight; median rods apparently lacking. In endozones, autozooecia in straight ranges, contiguous, subrhomboid in cross section, with straight and continuous longitudinal walls. Endozones relatively wide. In exozones, autozooecia in straight ranges, subcircular in cross section, contiguous; ranges probably separated laterally by longitudinal ridge along center of branch. Longitudinal walls straight and continuous. Mural styles and vesicular structure apparently absent. Exozones relatively narrow. Living chambers with relatively long endozonal and short exozonal portions subcircular in cross section in exozones. Superior hemisepta short, blunt, regularly arranged. Inferior hemisepta and other lateral structures absent. Basal diaphragms and monticules absent. Extrazooecial stereom laminated in longitudinal ridge along middle of zoarium. [*Goniotrypa* is based on poorly preserved material and its assignment to the Rhinidictyidae is tentative. The budding pattern and shape of autozooecia in the endozone is similar to that in *Stictopora*; however, *Goniotrypa* differs from *Stictopora* and other rhinidictyids in having narrow, probably unbranched zoaria, and in having a relatively thin exozone with a median ridge along the middle of the branch.] *?U.Ord.*, Can., ?N.Ire.——Fig. 254,*2a–d*. **G. bilateralis, a,* mesotheca, wide endozone, narrow exozone; long. sec., syntype, USNM 242625, ×100; *b,* continuous longitudinal wall; tang. sec., syntype, USNM 242626, ×100; *c,* autozooecial range, straight longitudinal walls; tang. sec., USNM

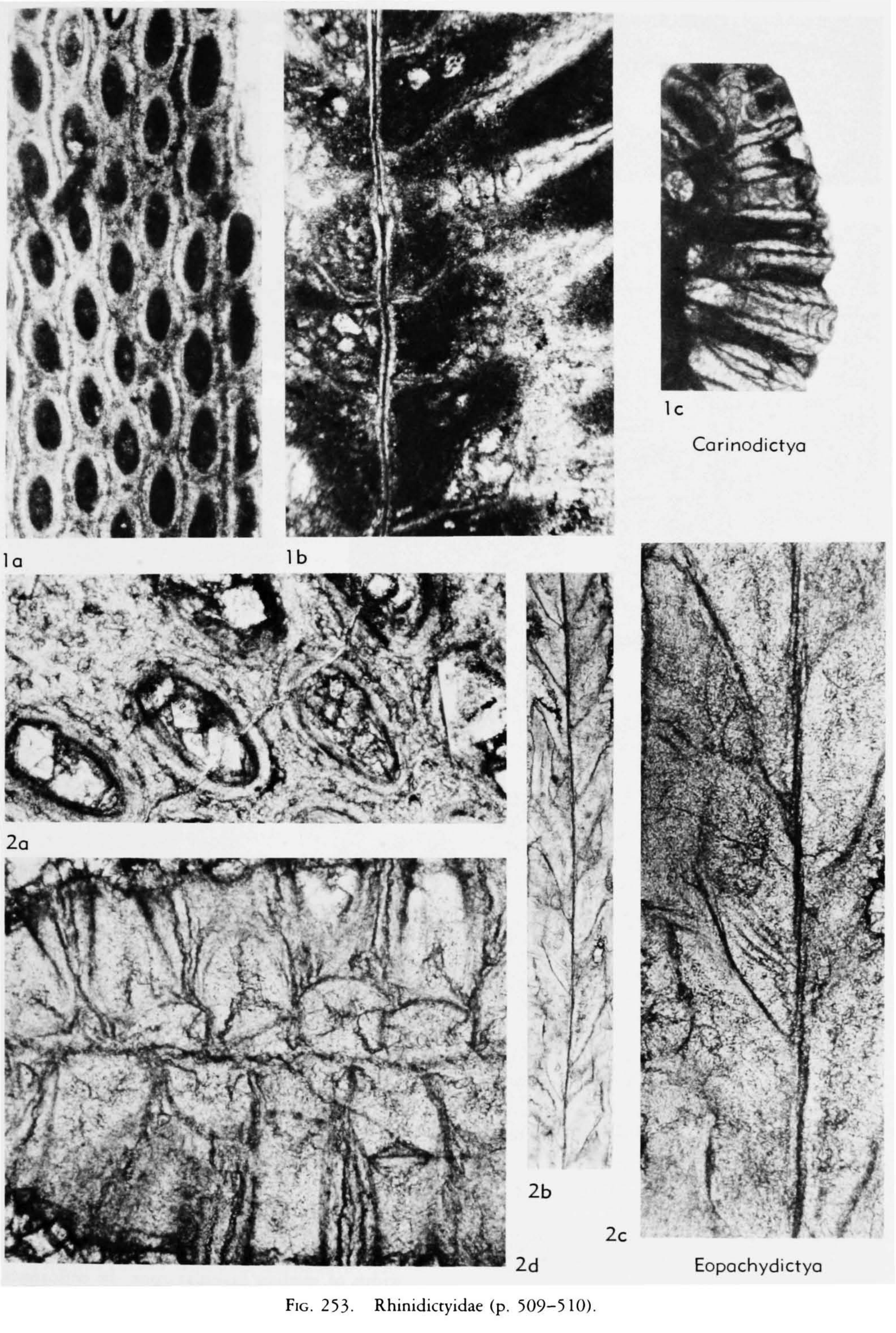


FIG. 253. Rhinidictyidae (p. 509–510).

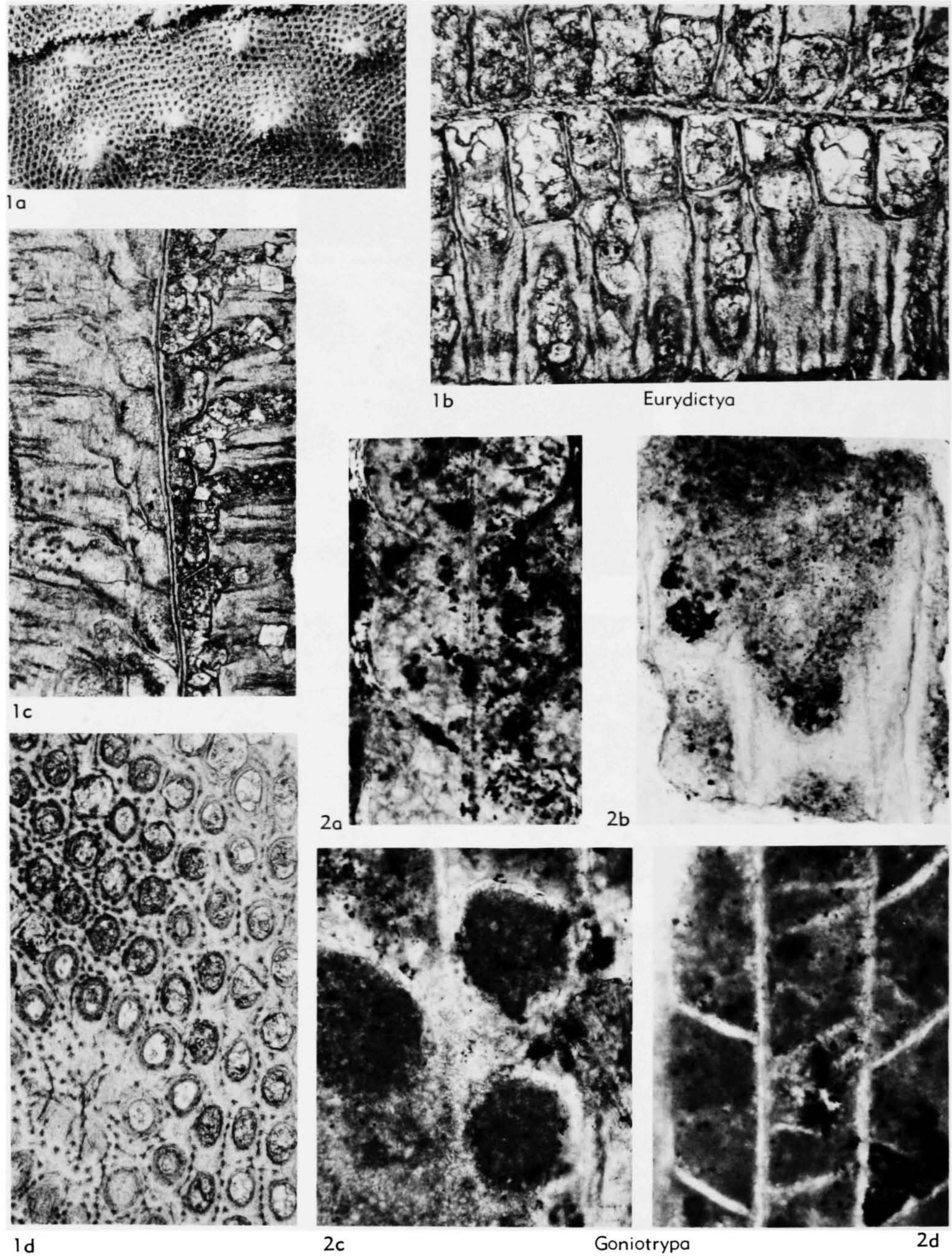


Fig. 254. Rhinidictyidae (p. 510).

242627, ×100; *d,* rhomboid autozooecia in endozone; tang. sec., syntype, USNM 242628, ×100.

Pachydictya Ulrich, 1882, p. 152 [**P. robusta*; OD; "Trenton Gr.," M. Ord., Knoxville, Tenn., USA]. Zoarium branched; branches commonly with wide margins. Mesothecae generally straight. Median rods subcircular in cross section, commonly with diameter greater than width of median granular zone. In endozones, autozooecia in indistinct ranges, subelliptical to subcircular in cross section, partly contiguous, partly separated by extrazooecial stereom, and lacking continuous longitudinal walls. In exozones, autozooecia in relatively distinct ranges, broadly elliptical in cross section, partly contiguous or separated by extrazooecial stereom and lacking continuous longitudinal walls. Autozooecial walls locally vesicular in inner exozones. Mural styles common, mostly in autozooecial boundaries, also scattered in walls and laminar stereom. Living chambers subelliptical to subcircular in cross section. Chamber lining common, relatively thick. Other lateral chamber structures absent. Basal diaphragms straight to curved, generally common. Monticules common, flat or raised, locally with scattered zooecia. Monticules commonly vesicular in inner exozones, with mural styles singly or in indistinct rows in outer stereom. Extrazooecial skeleton common; vesicles localized in endozones and inner exozones, stereom scattered throughout exozones. *M.Ord.-L.Sil.*, USSR, Austria.——FIG. 255,*1a–d*. **P. robusta*; *a,* branched zoarium with wide zoarial margins, flat monticules, aligned autozooecia; external view, lectotype, USNM 137608, ×5; *b,* shape of living chambers, vesicles in inner exozone, chamber lining; long. sec., lectotype, ×30; *c,* mural styles in autozooecial boundaries, walls and in stereom of outer exozone, distinct lining along chambers, monticule with scattered mural styles; tang. sec., paralectotype, USNM 137609, ×30; *d,* autozooecial boundaries in exozone, vesicles in endozone; transv. sec., paralectotype, USNM 137625, ×30.

Phyllodictya ULRICH, 1882, p. 153 [**P. frondosa*; OD; High Bridge Gr., M. Ord., High Bridge, Ky., USA]. Zoarium explanate, irregularly lobate locally. Mesotheca slightly sinuous in longitudinal section. Median rods elliptical to subcircular in cross section. In endozones, autozooecia in straight to curving ranges, subrectangular to subrhomboid in cross section, contiguous, with straight to slightly sinuous and continuous longitudinal walls. In exozones, autozooecia commonly form angles between 45° and 50° with mesothecae; in straight to curved and indistinct ranges, contiguous or partly contiguous, separated partly by extrazooecial stereom locally. Longitudinal walls regularly sinuous, generally continuous or locally merging with extrazooecial stereom. Transverse walls slightly raised proximal to autozooecial chambers in some species. Autozooecial walls commonly vesicular in inner exozones. Mural styles common in autozooecial boundaries, walls, and extrazooecial stereom. Living chambers elliptical in cross section, without lateral structures. Basal diaphragms straight to slightly curved, common; scattered, or may be regularly arranged. Monticules rare to common, generally scattered in zoaria. Monticular zooecia commonly filled with stereom. Extrazooecial skeleton consisting of stereom and vesicular portions; vesicular structures local in inner exozones; laminated stereom localized throughout exozones, with mural styles arranged singly or in discontinuous rows. *?L.Ord.-M.Ord.*, ?USSR(Est.), USA.——FIG. 255,*2a–c*. **P. frondosa*; *a,* median granular zone with median rods, autozooecial boundaries and mural styles in exozone; transv. sec., lectotype, USNM 242630, ×50; *b,* subelliptical autozooecia, elliptical living chambers, mural styles in boundaries, monticule with open and filled zooecia; tang. sec., lectotype, ×30; *c,* median rods in granular zone of mesotheca, mural styles in autozooecial walls, shape of chambers; long. sec., paralectotype, USNM 242634, ×50.

Sibiredictya NEKHOROSHEV, 1960, p. 277 [**S. usitata*; OD; M. Ord. (Mangaze.), Rybokupchaya River, Sib., USSR]. Zoarium cribrate; fenestrules irregularly shaped, variable in size, surrounded by extrazooecial stereom with mural styles. Mesothecae sinuous in longitudinal section. Median rods poorly delineated or lacking. In endozones, autozooecia in straight to slightly curving ranges, irregularly subrectangular to subrhomboidal in cross section, with continuous longitudinal walls. In exozones, autozooecia in straight ranges in midregions between fenestrules, in curving ranges around fenestrules, subelliptical to subrectangular in cross section, contiguous to partly contiguous, separated locally by extrazooecial skeleton. Longitudinal walls continuous in midregions, merging locally with extrazooecial stereom in lateral regions. Mural styles rare in zoarial boundaries and walls, common in extrazooecial stereom in zoarial margins. Living chambers subelliptical to subcircular in cross section, without lateral structure. Basal diaphragms not observed. Monticules absent. Extrazooecial skeleton generally of laminated stereom, vesicular locally in inner exozone; vesicle walls relatively thick. Extrazooecial skeleton may encrust proximal parts of zoaria. *M.Ord.*, USSR(Sib.).——FIG. 256,*1a–e*. **S. usitata,* Amutkan Cr., Sib., paratype, USNM 171740; *a,* median granular zone in mesotheca, autozooecial boundaries, indistinct extrazooecial vesicles in inner exozone; transv. sec., ×30; *b,* irregular shape of fenestrules, arrangement of autozooecia; external view, ×5; *c,* longitudinal autozooecial walls, subelliptical living chambers; tang. sec., ×50; *d,* subrectangular autozooecia in endozone, mural styles in extrazooecial stereom adjacent to fenestrule; tang. sec., ×50; *e,* sinuous mesotheca, extrazooecial vesicles in inner exozone; long. sec., ×50.

Trigonodictya ULRICH, 1893, p. 160 [**Pachydictya conciliatrix* ULRICH, 1886a, p. 76; OD; Decorah Sh., M. Ord., Cannon Falls, Minn., USA] [= *Astreptodictya* KARKLINS, 1969, p. 49]. Zoarium irregularly branched or unbranched and explanate; ridgelike expansions lateral to general growth planes of zoaria in some. Mesothecae

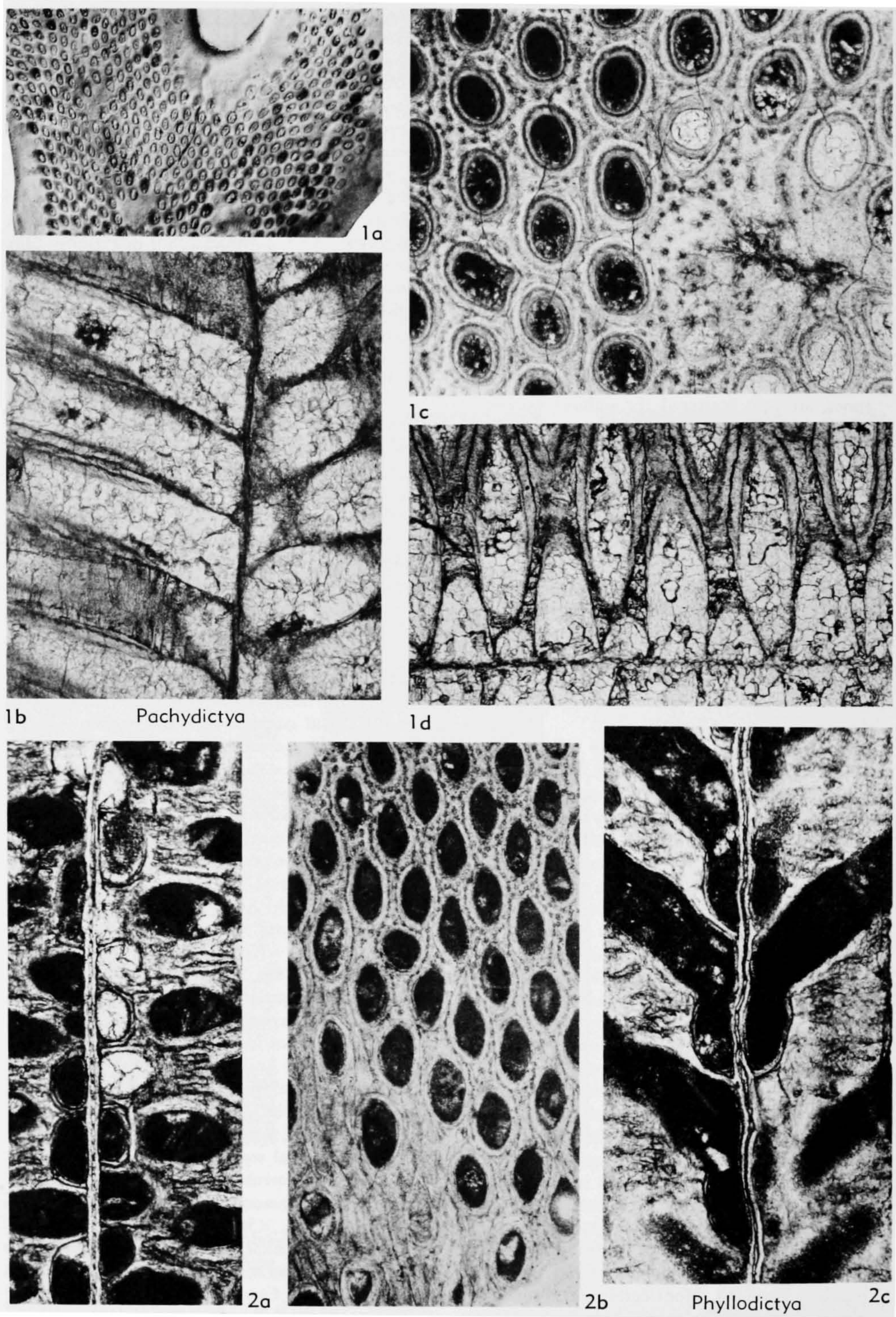


FIG. 255. Rhinidictyidae (p. 512–513).

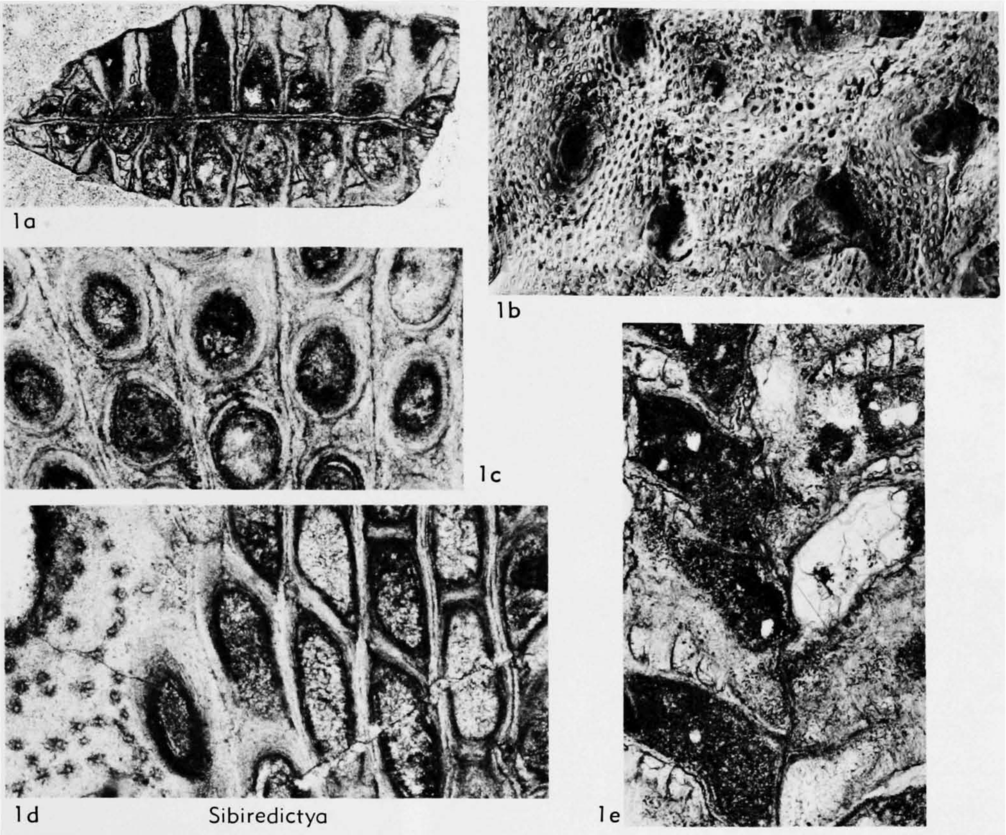


FIG. 256. Rhinidictyidae (p. 513).

straight to sinuous in longitudinal section, locally zigzag in transverse section; bifurcating where branches or ridgelike expansions form lateral growth planes. Median rods circular in cross section, commonly with diameter greater than width of median granular zones. In endozones, autozooecia in straight ranges, subrectangular to subrhomboidal in cross section, generally contiguous laterally, locally separated by extrazooecial vesicles within ranges, with straight and generally continuous longitudinal walls. In exozones, autozooecia in straight ranges without continuous longitudinal walls, separated by extrazooecial skeletal deposits, elliptical in cross section, walls generally without vesicular structure. Mural styles indistinct; common in autozooecial boundaries and in dark zones in extrazooecial stereom, generally absent in autozooecial walls. Living chambers elliptical in cross section, without lateral chamber structures. Basal diaphragms straight to slightly curved, generally scattered in zoaria, but may be regularly arranged. Monticules rare to common, flat or raised, may be irregularly ridgelike, generally scattered in zoaria. Monticules commonly vesicular in inner exozones, laminar in outer exozones; laminar part commonly with mural styles aligned in dark zones, locally discontinuous. Extrazooecial skeletal deposits common, consisting of laminar and vesicular portions. Vesicular structures common in inner exozones, locally in endozones, and between longitudinally aligned autozooecia. Extrazooecial stereom aligned in straight to slightly curving ridgelike range partitions that are delineated laterally by continuous dark zones and autozooecial boundaries. Extrazooecial stereom between range partitions and autozooecia consisting of laminae inclined proximally relative to those in autozooecial walls and range partitions; laminar stereom commonly with dark zones, longitudinally aligned, locally with indistinct mural styles. *M.Ord.-M.Sil.,* N.Am., G.Brit., USSR, Swed. ——FIG. 257,*1a,b*. *T. acuta* (HALL), Trenton Gr., M. Ord., N.Y., holotype, AMNH 666/1; *a,* autozooecial boundaries, extrazooecial stereom with vesicles at base of exozone, dark zones within laminar stereom in exozone; transv. sec., ×100; *b,* elliptical autozooecia and chambers, microstructurally continuous dark zones along middle of extrazooecial stereom of range partitions; tang. sec., ×100.—FIG. 257,*1c–e*. **T. conciliatrix* (ULRICH); *c,* sub-

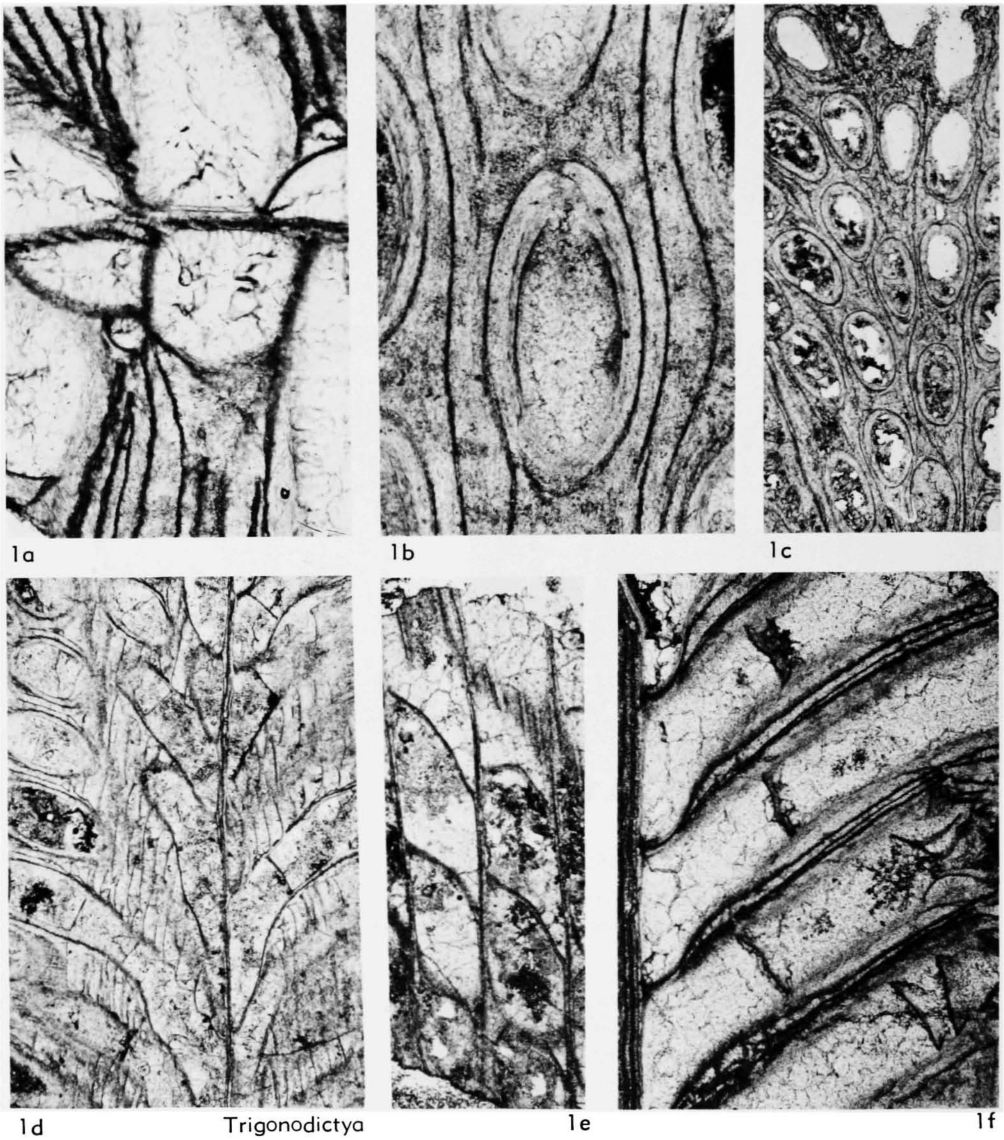


Fig. 257. Rhinidictyidae (p. 513).

elliptical autozooecia, range partitions of extrazooecial stereom, and mural styles in dark zones in stereom; tang. sec., paralectotype, USNM 242652, ×30; *d,* abandoned chambers, extrazooecial vesicles in endozone and inner exozone, granular zone with median rods in mesotheca; oblique long. sec., lectotype, USNM 242650, ×30; *e,* median rods in mesotheca (near top), subrhomboidal autozooecia with structurally continuous longitudinal autozooecial walls in endozone; deep tang. sec., paralectotype, USNM 242653, ×50.——Fig. 257,*1f. T. fenestelliformis* (Nicholson), U. Ord. (Richmond.), Ill.; basal diaphragms, probable remnants of brown body in chamber closed by monticule (middle right), extrazooecial stereom with dark zone between autozooecia; long. sec., USNM 242624, ×50.

Family STICTOPORELLIDAE Nickles & Bassler, 1900

[Stictoporellidae Nickles & Bassler, 1900, p. 46]

Zoaria branched or unbranched and cribrate or explanate. Zoarial attachments continuous skeletally with erect parts of zoaria. Mesothecae straight to slightly sinuous with

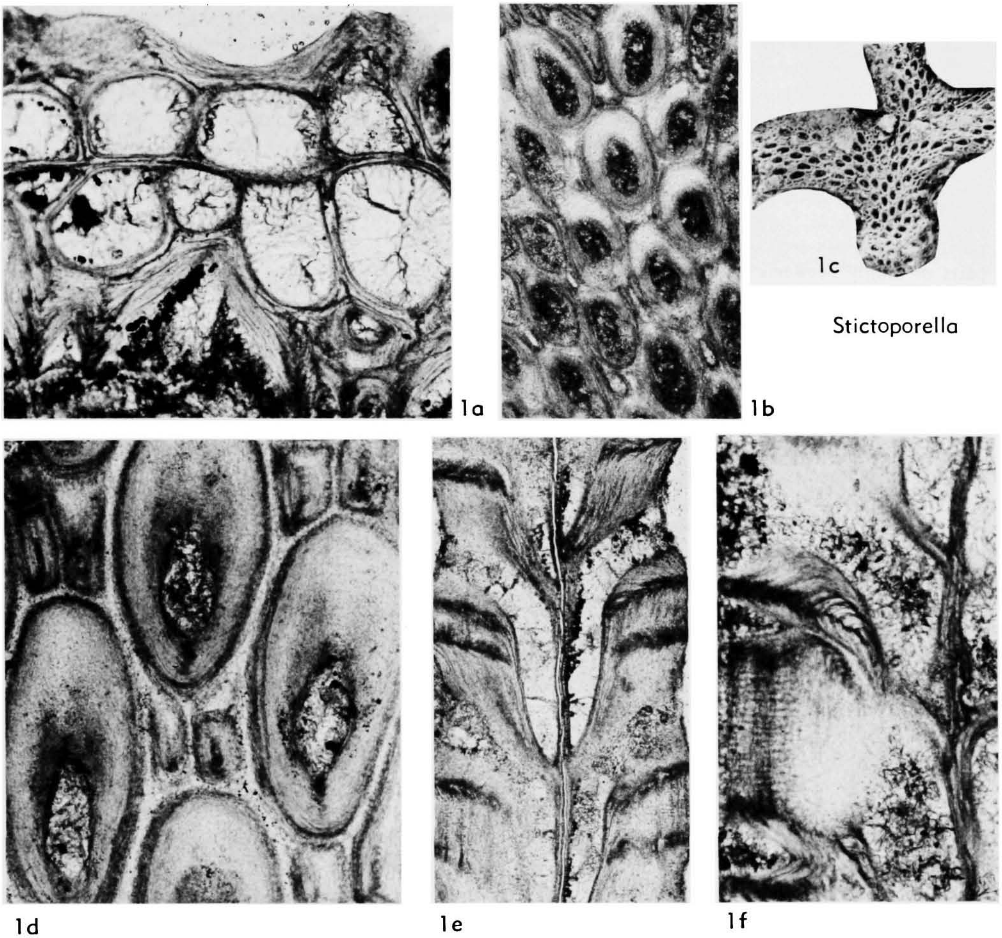


FIG. 258. Stictoporellidae (p. 517).

median granular zone generally extending to zoarial margins. In endozones, autozooecia in straight ranges, alternating on opposite sides of mesothecae; contiguous with continuous longitudinal walls, subrectangular to subrhomboidal in cross section, slightly expanded and narrowed alternately in adjacent ranges in outer endozones and base of exozones. In exozones, autozooecia form angles with mesothecae ranging between 50° and 80°, contiguous or separated by exilazooecia, generally polygonal to subcircular in cross section, not in linear ranges, with lateral walls restricted to individual autozooecia. Autozooecial wall laminae broadly V-shaped. Autozooecial boundaries narrowly serrated. Pustules common in exozonal walls and extrazooecial stereom. Living chambers subrectangular to subrhomboidal in cross section in endozones, elliptical to subelliptical in cross section in exozones. Basal diaphragms and lateral chamber structures absent. Exilazooecia common. Monticules absent to common, consisting of exilazooecia and zooecia of variable sizes. Extrazooecial stereom laminated, sparse in midregions of zoaria. *L.Ord.-M.Sil.*

The Stictoporellidae resemble Escharoporidae and Intraporidae in rhombic arrangement of autozooecia in the exozone, but differ in microstructure, cross-sectional shape of autozooecia, and distribution of exilazooecia in exozones.

Stictoporella ULRICH, 1882, p. 152 [**S. interstincta*; OD; "Economy" Mbr., "Eden" F., U. Ord., West Covington, Ky., USA; =*Ptilodictya* *flexuosa* James, 1878, p. 4] [=*Lemmatopora* Počta, 1894, p. 102]. Zoarium branched. In exozones, autozooecia subpolygonal in cross section, generally contiguous, or locally separated by exilazooecia or extrazooecial stereom. Pustules common; scattered along autozooecial boundaries, in exozonal walls, and extrazooecial stereom. Living chambers elliptical in cross section. Exilazooecia subelliptical to irregularly polygonal in cross section; regularly arranged in pairs or singly between successive autozooecia, or in groups along zoarial margins. Monticules rare to absent, flat or slightly raised, irregularly arranged in zoaria; consisting of exilazooecia and few zooecia of variable size. [The type specimens of *Lemmatopora* Počta are poorly preserved (Prantl, 1935a) and were unavailable for study. Thus, I follow Bassler (1953, p. G138) in considering *Lemmatopora* to be a synonym of *Stictoporella*.] *M.Ord.-M.Sil.*, N.Am., USSR, ?Czech. ——Fig. 258,*1a–f*. **S. interstincta*; *a*, mesotheca with discontinuous median granular zone, microstructure of autozooecial walls; transv. sec., paralectotype, USNM 137613, ×100; *b*, polygonal autozooecia, elliptical living chambers in outer exozone; tang. sec., paralectotype, USNM 137613, ×30; *c*, branching pattern; external view, lectotype, USNM 137612, ×5; *d*, shape of autozooecia and exilazooecia in exozone; tang. sec., USNM 242635, ×100; *e*, shape of living chamber, microstructure of autozooecial walls; long. sec., USNM 242635, ×100; *f*, serrated autozooecial boundaries in exozone; long. sec., paralectotype, USNM 137613, ×100.

Pseudostictoporella Ross, 1970, p. 376 [**P. typicalis*; OD; Selby Mbr., Rockland F., M. Ord., Napanee, Ont., Can.]. Zoarium branched or unbranched and explanate. In exozones, autozooecia irregularly hexagonal in cross section, contiguous or partly separated by exilazooecia. Pustules common along autozooecial boundaries, scattered in exozonal walls. Living chambers subelliptical in cross section. Exilazooecia polygonal to irregularly subcircular in cross section, scattered in zoaria; arranged in groups, singly or in short rows. Exilazooecia commonly closed locally by thickened walls. Monticules common, generally flat; consisting mostly of exilazooecia, few zooecia, and some extrazooecial stereom. Monticules generally scattered in zoaria; may be regularly arranged in some species with explanate zoaria. *M.Ord.*, N.Am.——Fig. 259,*2a–c*. **P. typicalis*; *a*, narrowly serrated autozooecial boundaries in exozone, median granular zone of mesotheca in zoarial margin; transv. sec., paratype, YPM 25455, ×100; *b*, polygonal autozooecia, open and closed exilazooecia in exozone; tang. sec., holotype, YPM 2545, ×100; *c*, sinuous mesotheca, shape of living chambers; long. sec., holotype, ×30.

Stictoporellina Nekhoroshev, 1956a, p. 48 [**Stictoporella? cribrosa* Ulrich, 1886a, p. 69; OD; Decorah Sh., M. Ord., Minneapolis, Minn., USA]. Zoarium cribrate; fenestrules subelliptical to subcircular, generally elongate distally. Fenestrule margins with numerous exilazooecia. In exozones, autozooecia irregularly subpolygonal to subcircular in cross section, contiguous or locally separated by exilazooecia. Autozooecial boundaries locally not visible in some species. Pustules common along autozooecial boundaries, scattered in exozonal walls. Living chambers elliptical to subelliptical in cross section. Exilazooecia irregularly polygonal to subcircular in cross section, variable in size, locally closed by thickened walls, arranged singly or in scattered groups in zoaria. Monticules common to absent, generally raised and irregularly shaped, consisting mostly of exilazooecia and extrazooecial stereom. *Ord.*, USSR(?Est.), USA.——Fig. 259,*1a–f*. **S. cribrosa* (Ulrich); *a*, mesotheca with median granular zone, V-shaped laminae in exozone; transv. sec., paralectotype, USNM 162023, ×50; *b*, irregularly sinuous mesotheca, shape of living chambers; long. sec., lectotype, USNM 162015, ×30; *c*, arrangement of autozooecia and exilazooecia, shape of fenestrules; exterior view, lectotype, ×5; *d*, autozooecia alternating across mesotheca; transv. sec., lectotype, ×30; *e*, subpolygonal autozooecia, pustules in autozooecial boundaries, open and filled exilazooecia; tang. sec., lectotype, ×100; *f*, autozooecia in indistinct rhombic pattern, distribution of exilazooecia in exozone; tang. sec., lectotype, ×30.

Family VIRGATELLIDAE
Astrova, 1965

[Virgatellidae Astrova, 1965, p. 290]

Zoaria branched or unbranched and explanate. Mesothecae straight to sinuous. Median granular zone discontinuous, without median rods. In exozones, autozooecia arranged in indistinct rhombic pattern, without continuous longitudinal walls or in linear ranges with continuous longitudinal walls partly contiguous or separated by extrazooecial stereom, subelliptical to subcircular in cross section, with indistinct wall laminae. Autozooecial boundaries narrowly serrated. Mural styles abundant, relatively large, consisting of distinct cores and thin sheaths. Living chambers subelliptical to subcircular in cross section, variable in length. Superior and inferior hemisepta common. Basal diaphragms common. Exilazooecia and mesozooecia absent. Monticules common, con-

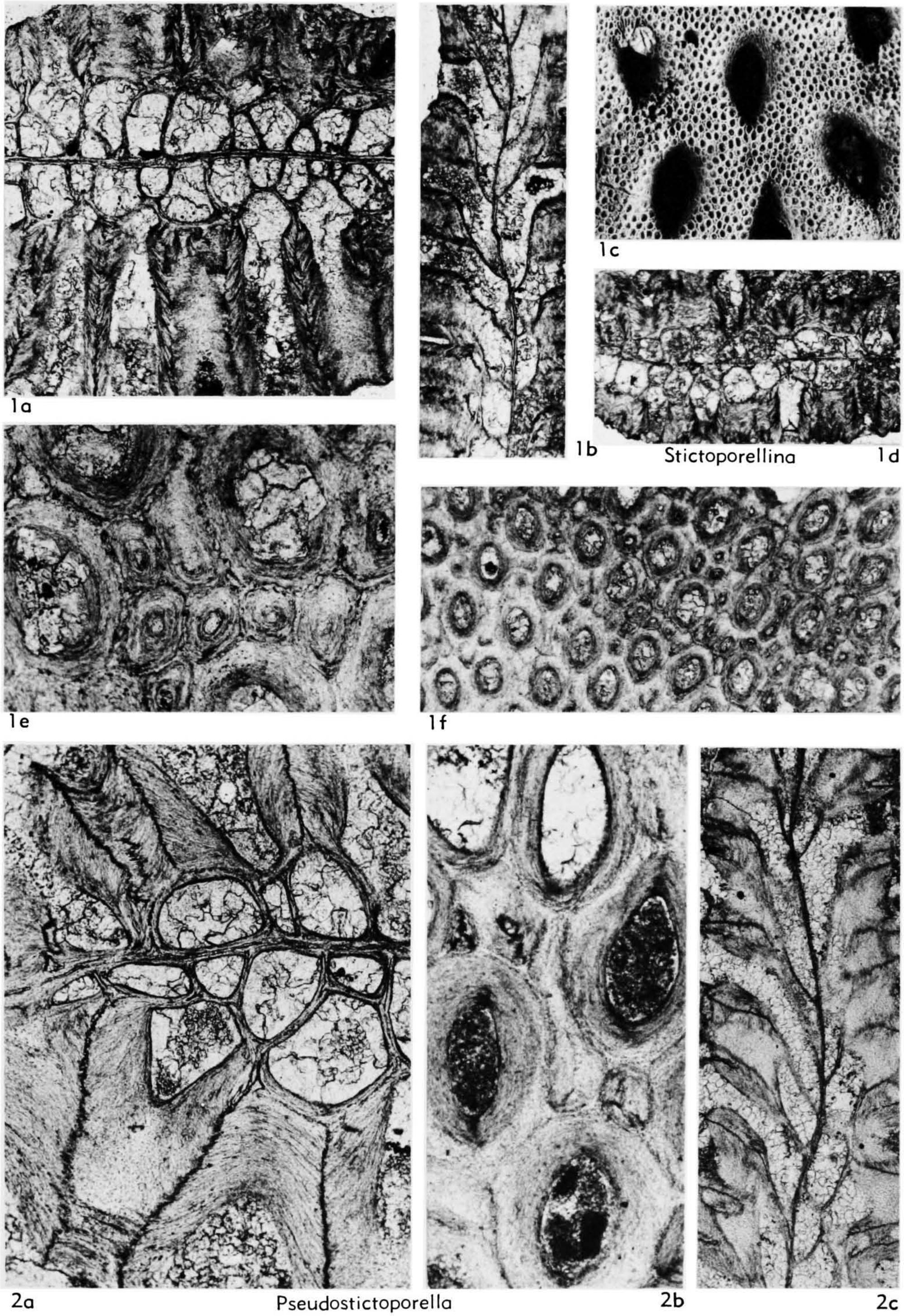


FIG. 259. Stictoporellidae (p. 518).

sisting of extrazooecial stereom. Extrazooecial skeleton common; consisting of vesicular portion in inner exozones, laminar stereom in parts of outer exozones. *M.Ord.*

According to ASTROVA (1965, p. 290), Virgatellidae are more similar to the Rhinidictyidae than to other ptilodictyines in skeletal microstructure, shape of autozooecia in exozones, and in presence of abandoned chambers. Of the Rhinidictyidae, *Athrophragma* (Fig. 252,*1a*) and *Pachydictya* (Fig. 255,*1c*) possess autozooecia that are similar in arrangement and shape to those in *Virgatella* (Fig. 260,*2b*). *Stictopora* has autozooecia similar to those in *Pseudopachydictya*; however, *Pseudopachydictya* differs in arrangement and shape of autozooecia (Fig. 260,*1a*) in exozones from that in *Virgatella* (Fig. 260,*2b*). Thus, morphological relationship between the Virgatellidae and Rhinidictyidae can be inferred only to a degree because the arrangement and shape of autozooecia at mesothecae and in endozones of the Virgatellidae is not determinable in available material. Virgatellids differ from most other ptilodictyines in having autozooecia commonly surrounded by extrazooecial stereom, in rhombic and linear arrangements of autozooecia in exozones, and in kind and distribution of mural styles (ASTROVA, 1965, p. 290).

Virgatella ASTROVA, 1955, p. 158 [**V. bifoliata*; OD; M. Ord. (Mangaze.), Podkamennaya Tunguska River, Sib., USSR]. Zoarium branched or unbranched and irregularly explanate. Mesotheca slightly sinuous in longitudinal section. In exozones, autozooecia subelliptical to subcircular in cross section, aligned in indistinct rhombic pattern, generally separated by extrazooecial stereom. Autozooecial boundaries discontinuous locally. Mural styles common throughout laminar part of autozooecial walls and stereom; arranged singly and in irregularly curving series and clusters, bifurcating frequently. Living chambers subelliptical in cross section. Superior hemisepta thin, long, curving proximally; inferior hemisepta short, blunt, extending from mesothecae; both hemisepta indistinct, regularly arranged. Basal diaphragms scattered near base of exozones, relatively thick, slightly curved, may be incomplete in outer exozone. Monticules flat, irregularly arranged. Extrazooecial stereom arranged regularly in exozones throughout zoaria. *M.Ord.,* USSR(N. Zemlya,Sib.).——FIG. 260,*2a,b*. **V. bifoliata,* PIN 1242/30; *a,* microstructure of bifurcating mural styles in exozone, mesotheca with indistinct median granular zone; long. sec., ×100; *b,* rhombic pattern of subelliptical to subcircular autozooecia in inner exozone; tang. sec., ×30.

Pseudopachydictya ASTROVA, 1965, p. 293 [**Pachydictya multicapillaris* ASTROVA, 1955, p. 155; OD; M. Ord. (Mangaze.), Podkamennaya Tunguska River, Sib., USSR]. Zoarium branched. In exozones, autozooecia in straight ranges or laterally in ranges oblique to zoarial midregion. Autozooecia subrectangular to subelliptical in cross section, generally contiguous in midregions, partly separated by extrazooecial stereom in lateral regions. Longitudinal walls slightly sinuous and continuous, locally merging with extrazooecial stereom, relatively thick; vesicular structure absent. Mural styles common, relatively large with distinct cores and thin sheaths, present in autozooecial boundaries and throughout walls. Mural styles gradually curve and some bifurcate. Living chambers elliptical in cross section, relatively small, locally narrowed or closed by thickened walls in outer exozones. Superior hemisepta short, blunt, regularly arranged. Inferior hemisepta thin, long, generally arising from mesothecae, scattered in zoaria. Basal diaphragms generally straight, scattered to common in zoaria. Monticules common, irregularly spaced, generally flat and irregularly shaped. Extrazooecial stereom laminated, common in lateral regions, sparse in midregions; containing mural styles. *M.Ord.,* USSR(W. Arctic, Sib.).——FIG. 260,*1a,b*. **P. multicapillaris* (ASTROVA), Vaygach, W. Arctic, PIN 1393/269; *a,* autozooecia in linear ranges in midregion (right), ranges in lateral region (left) oriented obliquely to midregion; tang. sec., ×30; *b,* indistinct wall laminae, diverging mural styles; long. sec., ×50.

Family Uncertain

Euspilopora ULRICH in MILLER, 1889, *Ptilotrypa* ULRICH in MILLER, 1889, *Ptilotrypina* ASTROVA, 1965, *Stictotrypa* ULRICH, 1890, *Taeniodictya* ULRICH, 1888, and *Trepocryptopora* YANG, 1957, are not assigned to revised families. These genera, however, are retained in the Ptilodictyina because they possess features of the suborder but differ from the type genera of the families and among themselves. Because most include only one species, and each species is represented by only a few specimens in varying states of preservation, these genera are not

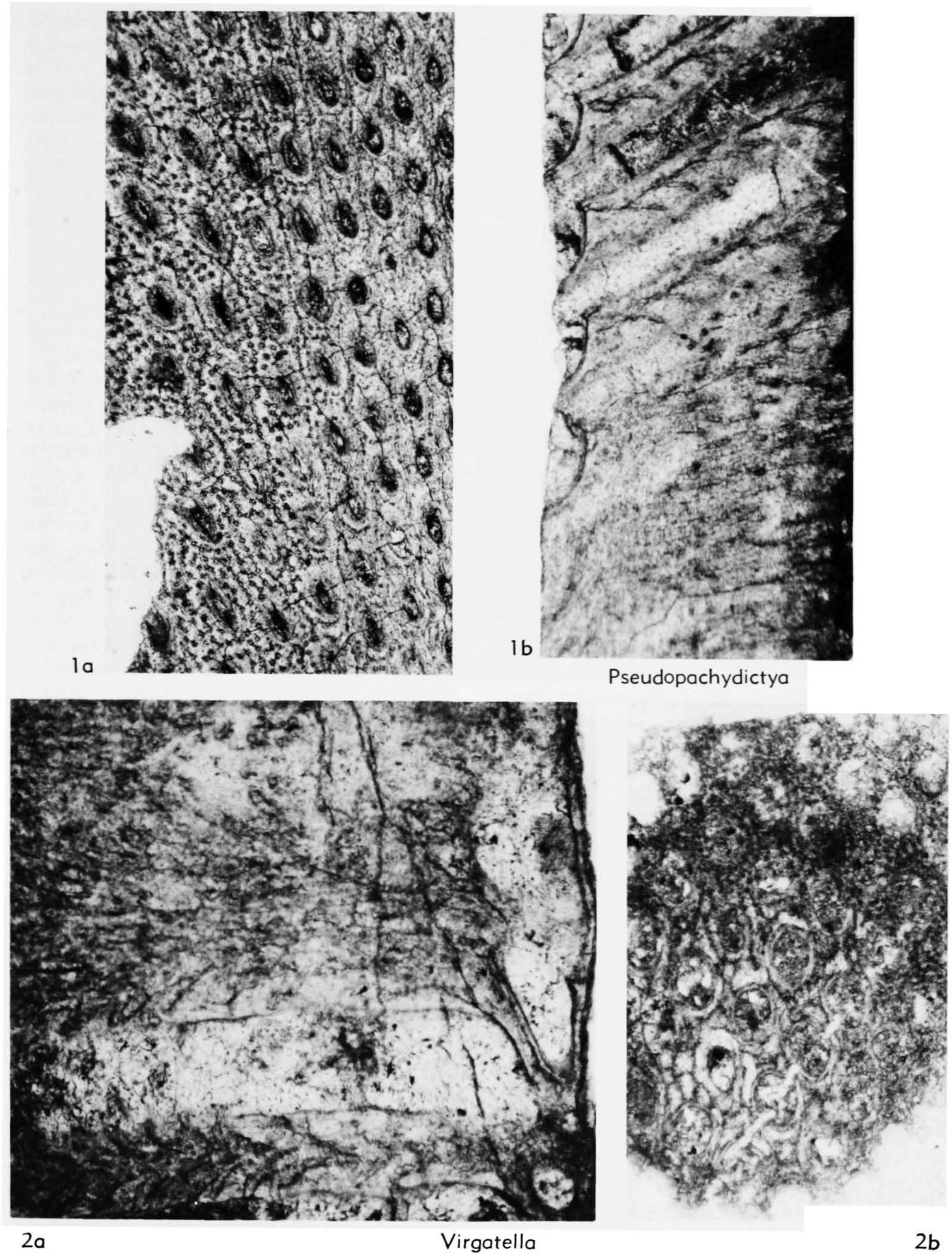


FIG. 260. Virgatellidae (p. 520).

sufficiently well known to establish new families.

Euspilopora ULRICH in MILLER, 1889, p. 301 [**E. serrata* ULRICH, 1890, p. 526; OD; Cedar Valley Ls., M. Dev., Buffalo, Iowa, USA]. Zoarium branched or unbranched and explanate, margins broadly crenulated. Mesothecae straight or slightly sinuous locally in longitudinal section. Median granular zone extends throughout mesothecae, may contain scattered median rods. In endozones, autozooecia arranged in straight to slightly curving ranges, aligned or alternating on opposite sides of mesothecae, irregularly subelliptical in cross section parallel to mesothecae, mostly contiguous, with continuous longitudinal walls, only locally separated by extrazooecial stereom. In exozones, autozooecia usually forming angles between 80° and 90° with mesothecae; ranges straight to slightly curved; broadly elliptical to subcircular in cross section, contiguous laterally, with continuous longitudinal walls extending into ridges at zoarial surface; separated locally by transverse extrazooecial vesicles. Autozooecial wall laminae indistinct and broadly curved. Autozooecial boundaries narrowly serrated in inner exozones, generally not visible in outer exozones. Mural styles abundant in walls and laminated stereom, closely spaced and very small, consisting of closely curved segments of skeletal laminae or locally containing minute and discontinuous cores. Mural styles generally in indistinct series usually at right angles to zoarial surface. Acanthostyles common, small, generally with straight cores; present in outer exozones, scattered in zoaria; rarely arranged at regular intervals along longitudinal walls. Living chambers broadly elliptical in cross section, without lateral structures. Basal diaphragms absent. Polymorphism expressed by modified marginal, basal, and monticular zooecia. Monticules common, generally depressed; consisting mostly of extrazooecial skeleton and few zooecia; extrazooecial skeleton locally vesicular in inner exozone. Monticules in branched zoaria regularly arranged near zoarial margins, locally extending into margins. Monticules in explanate zoaria furrowlike, elongated parallel to growth direction of zoaria; at relatively regular intervals throughout zoaria. Extrazooecial skeleton common, irregularly delineated, consisting of vesicular and laminar portions. Vesicles with relatively thick walls, variable in size, commonly elongated longitudinally; mostly in inner exozone, rarely in endozone. Laminar stereom with numerous mural styles; acanthostyles rare in outer exozones. [*Euspilopora* is similar to rhinidictyids in having autozooecia in relatively straight ranges and median rods in the mesotheca; however, it differs from rhinidictyids and most other ptilodictyines in cross-sectional shape of autozooecia (Fig. 261,*1b,d*), irregular presence or lack of median rods in some species, general appearance and abundance of mural styles, presence of acanthostyles (Fig. 261,*1d*), and abundance and appearance of monticules. In skeletal microstructure as well as presence and kind of mural styles, *Euspilopora* is similar to *Taeniodictya* Ulrich.] *M.Dev.*, USA.——Fig. 261,*1a–e*. **E. serrata*; *a*, autozooecial boundaries in endozone and inner exozone, extrazooecial vesicles with relatively thick walls in exozone; long. sec., lectotype, USNM 242639, ×100; *b*, acanthostyles aligned in longitudinal walls; tang. sec., paralectotype, USNM 242638, ×30; *c*, mesotheca with median granular zone; transv. sec., paralectotype, USNM 242637, ×50; *d*, autozooecia in curving ranges, monticule in margin, numerous mural styles throughout exozone; tang. sec., paralectotype, USNM 242636, ×50; *e*, living chambers with mesotheca as basal wall, numerous mural styles in autozooecial walls; including same long. sec. as *a*, ×50.

Ptilotrypa Ulrich in Miller, 1889, p. 320 [**P. obliquata* Ulrich, 1890, p. 531; OD; U. Ord. (Richmond.), Wilmington, Ill., USA]. Zoarium generally large and branched. Mesothecae irregularly crenulated locally in longitudinal section, gradually thickening toward lateral zoarial margins; thickened margins with curved laminae forming narrowly serrated zone beyond central median granular zone. Median rods absent. In endozones, autozooecia generally in straight ranges, alternating on opposite sides of mesothecae, subrectangular to subelliptical in cross section parallel to mesotheca, contiguous, with slightly sinuous and continuous longitudinal walls. In exozones, autozooecia usually forming angles between 40° and 50° with mesothecae, arranged in indistinct rhombic pattern, subelliptical in section, partly contiguous, separated laterally by local extrazooecial stereom, without continuous longitudinal walls. Autozooecial wall and stereom laminae narrowly to broadly curved and U-shaped, locally forming striae at zoarial surface. Autozooecial boundaries narrowly to broadly serrated, walls locally crenulated in inner exozones. Pustules rare or lacking. Mural styles absent. Living chambers elliptical in cross section, variable in length. Chamber lining thin and discontinuous. Mural spines rare, short, and blunt. Cysts rare, spherical to irregularly shaped. Cystiphragms common, variable in size, locally in discontinuous series along distal walls. Polymorphism expressed by modified marginal, basal, and rare monticular zooecia. Monticules rare to common, scattered, generally flat; consisting mostly of extrazooecial stereom, commonly with striae at zoarial surface. [*Ptilotrypa* is somewhat similar to escharoporids in structure of the mesotheca (Fig. 262,*1a*) as well as arrangement and cross-sectional shape of autozooecia (Fig. 262,*1d*); however, it differs from escharoporids and ptilodictyoids in autozooecial angle with the mesotheca, gradual thickening of autozooecia at the base of the exozone (Fig. 262,*1c*), longitudinal shape of autozooecia (Fig. 262,*1c*), presence and shape of scattered cystiphragms, and general appearance of skeletal laminae.] *U.Ord.*, USA.——Fig. 262,*1a–d*. **P. obliquata*, lectotype, USNM 242640; *a*, median granular zone merging with mesothecal laminae in zoarial margin, autozooecial boundaries in endozone; transv. sec., ×30; *b*, arrangement of

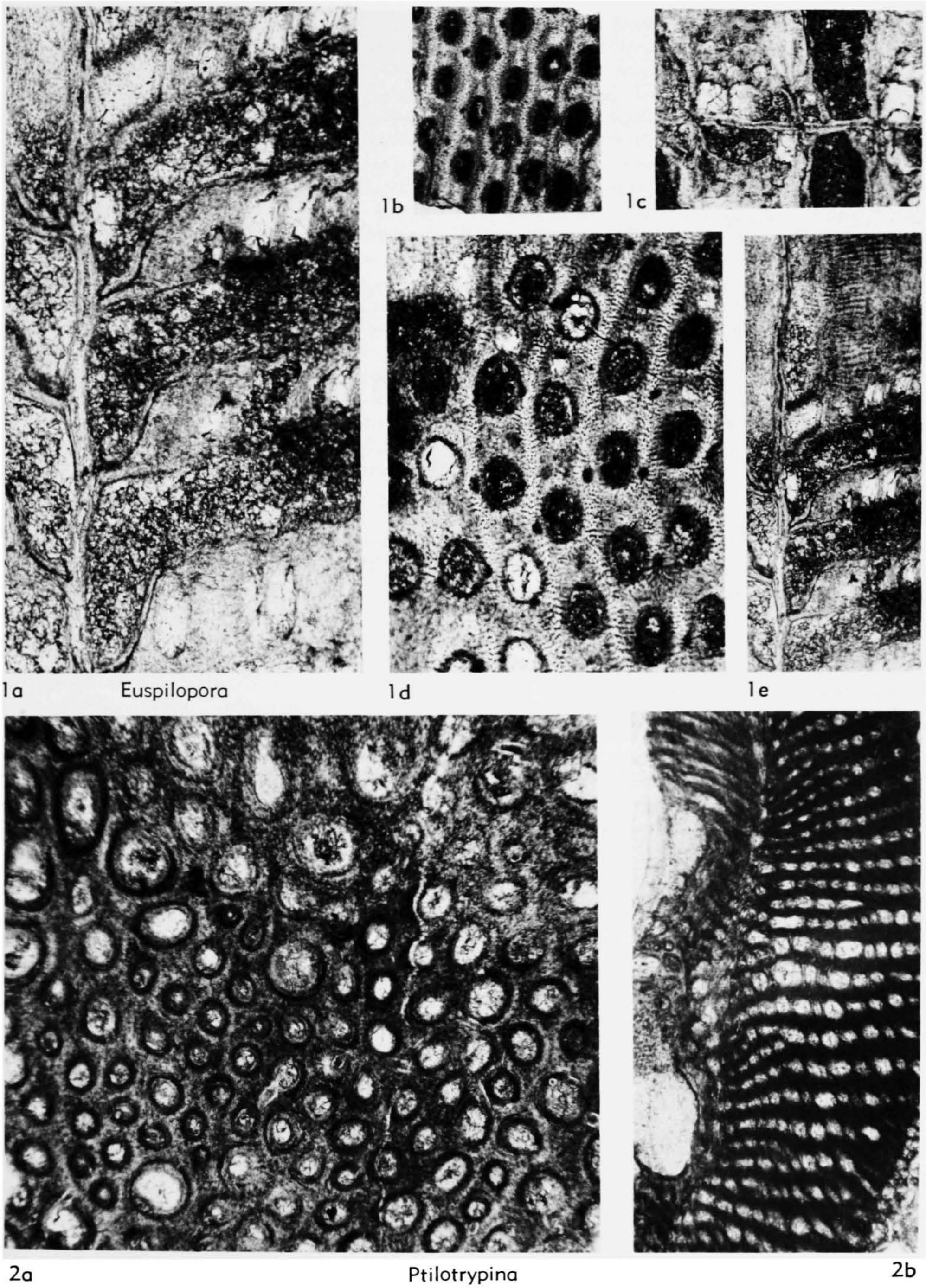


FIG. 261. Family Uncertain (p. 521–522).

autozooecia, scattered monticules; external view, ×5; *c,* mesotheca locally crenulated, living and few abandoned chambers, irregularly shaped cystiphragms at base of exozone; long. sec., ×30; *d,* autozooecia in indistinct rhombic arrangement, extrazooecial stereom in lateral walls between some autozooecia; tang. sec., ×30.

Ptilotrypina ASTROVA, 1965, p. 249 [**P. semibi-*

foliata; OD; M. Ord. (Mangaze.), Podkamennaya Tunguska River, Sib., USSR]. Zoarium generally bifoliate and irregularly explanate with local unifoliate and encrusting segments. Mesothecae broadly sinuous in longitudinal section. Endozones narrow and indistinctly delineated. In exozones, autozooecia relatively few, slightly curving, usually forming angles between 60° and 80° with mesothecae, subelliptical to subcircular in cross section, arranged singly or in groups, irregularly aligned and distributed, partly contiguous, mostly separated by mesozooecia or extrazooecial stereom. Zooecial walls irregularly nodular and variable in thickness, consisting of broadly curved and irregularly U-shaped laminae. Autozooecial boundaries broadly serrated. Pustules abundant, present throughout exozone. Living chambers irregularly subelliptical to subcircular in cross section, variable in length, apparently without lateral structures. Basal diaphragms common, relatively thick, straight to slightly curved. Mesozooecia abundant, constituting most of zoarium, subelliptical to subcircular in cross section, variable in size, commonly with scattered diaphragms, arranged locally in indistinct ranges, apparently arising locally from mesothecae. Extrazooecial stereom common, irregularly delineated; forming irregularly shaped, monticulelike flat areas and low protuberances at zoarial surface. [*Ptilotrypina* is characterized by zoaria with combined bifoliate and unifoliate growth habit, different mode of development of zooecia, and a nodular zooecial wall structure that suggests a different configuration of skeletal laminae (Astrova, 1965, p. 249). Zoaria consist of a few, scattered zooecia with large skeletal apertures and numerous zooecia with small skeletal apertures. Those with large apertures (regular zooecia of Astrova), which I consider to be autozooecia, occur singly or in irregular groups. Those with small apertures (pseudomesoporelike of Astrova), which I consider to be mesozooecia, constitute the major part of a zoarium, and some may arise from the mesotheca. Available material is not adequate for determining microstructure of the mesotheca and zooecial walls, and the structural relationship between autozooecia and mesozooecia in the endozone and base of the exozone.] *M.Ord.-U.Ord.*, USSR(Sib.).——Fig. 261,*2a,b*. **P. semibifoliata,* U. Ord. (Dolbor.), Sib., paratype, PIN 1242/230; *a,* irregular distribution of autozooecia and mesozooecia; tang. sec., ×50; *b,* bifoliate (upper) and local unifoliate (lower) segments of zoarium; oblique long. sec., ×30.

Stictotrypa Ulrich, 1890, p. 393 [**Stictopora similis* Hall, 1876, p. 122; OD; Niagara Gr., M. Sil., Waldron, Ind., USA]. Zoarium branched. Mesothecae slightly sinuous in longitudinal section. Median granular zone discontinuous locally, without median rods. In endozones, autozooecia in straight ranges, alternating on opposite sides of mesothecae, subrectangular to subrhomboid in cross section, contiguous, with slightly sinuous and continuous longitudinal walls. Endozone relatively wide. In exozones, autozooecia usually at right angles with mesothecae, in indistinct ranges, locally sloping proximally, broadly elliptical in cross section, partly contiguous, separated by extrazooecial stereom, without continuous longitudinal walls. Autozooecial walls consisting of broadly curved laminae, locally forming low peristomes around autozooecial apertures. Autozooecial boundaries narrowly serrated. Acanthostyles rare to common, small, generally with straight cores; mostly in outer exozones in extrazooecial stereom near autozooecial boundaries, scattered in zoaria. Living chambers subelliptical in cross section, without lateral structures. Basal diaphragms absent. Polymorphism expressed by modified marginal and basal zooecia. Extrazooecial stereom occurring regularly throughout exozones. Stereom laminae usually broadly curved, concave to zoarial surface. Stereom may contain single cavities at base of exozones. [*Stictotrypa* is similar to genera of the Escharoporidae, Intraporidae, and Stictoporellidae in having longitudinal autozooecial walls that are continuous in the endozone, but become restricted to autozooecia in the exozone. It differs from those genera, however, in having a relatively wide endozone (Fig. 262,*2b*), in microstructure of autozooecial walls and autozooecial boundaries, in shape of autozooecia, in lack of exilazooecia or mesozooecia, and somewhat in distribution of extrazooecial skeleton in the exozone.] *M.Sil.,* USA.——Fig. 262,*2a–d.* **S. similis* (Hall), lectotype, AMNH 1926-1; *a,* autozooecia alternate across slightly curved mesotheca; transv. sec., ×30; *b,* indistinct autozooecial boundaries, median granular zone in mesotheca; long. sec., ×100; *c,* microstructure of intermittent median granular zone in mesotheca, indistinct serrated autozooecial boundaries in exozone; transv. sec., ×100; *d,* autozooecia in indistinct ranges at base of exozone; tang. sec., ×30.

Taeniodictya Ulrich, 1888, p. 80 [**T. ramulosa* Ulrich, 1890, p. 528; OD; Keokuk Ls., L. Miss., Nauvoo, Ill., USA]. Zoarium branched, rarely unbranched and explanate, with skeletally continuous basal attachments. Mesothecae relatively thick, slightly sinuous, crenulated locally in longitudinal section, containing small and abundant mural styles at right angles to median granular zone, merging with extrazooecial stereom in zoarial margins. Median granular zone discontinuous through mesothecae. In endozones, autozooecia in ranges, alternating or aligned on opposite side of mesothecae, irregularly subrhomboid in cross section, contiguous with slightly sinuous, continuous, relatively

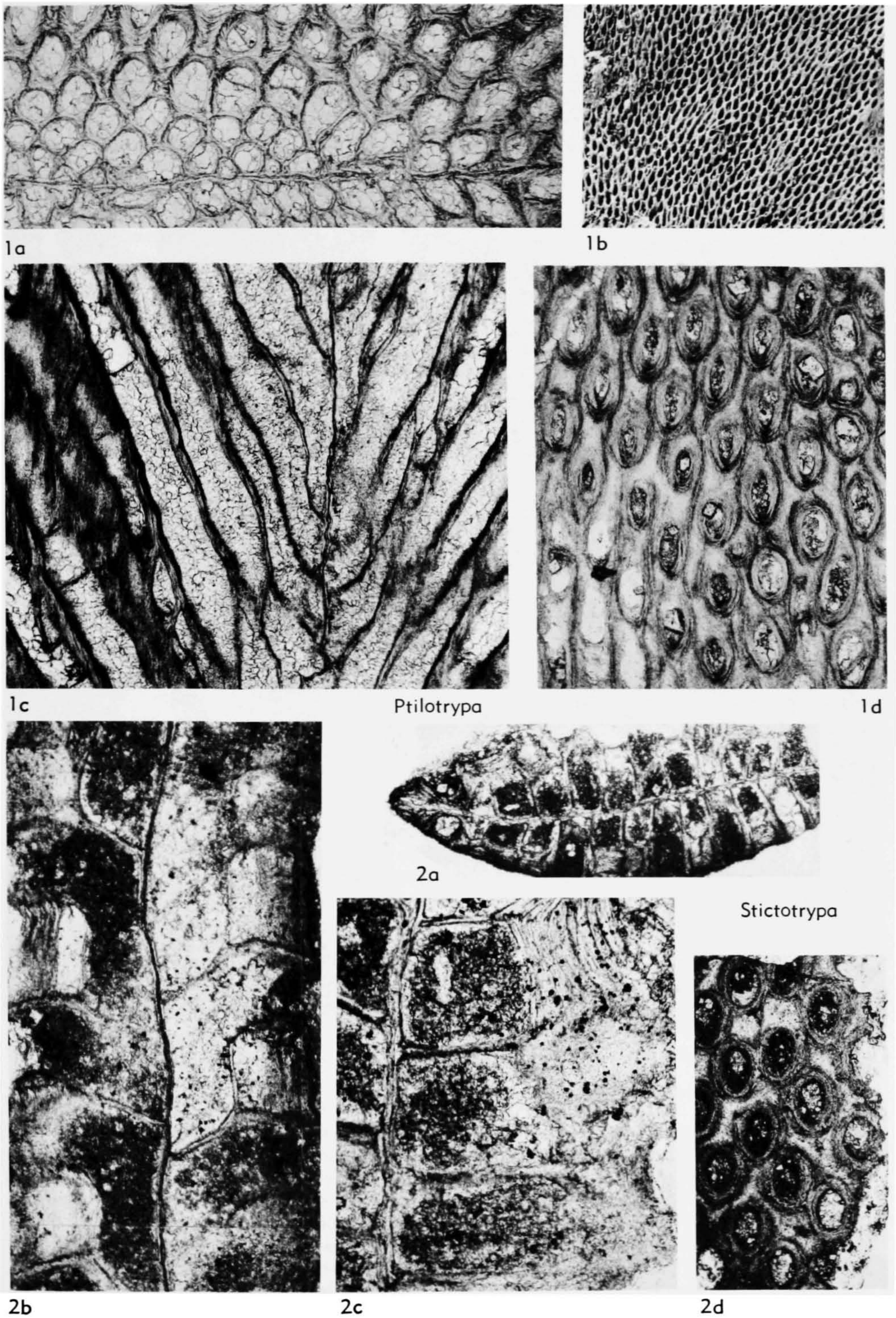


FIG. 262. Family Uncertain (p. 522–524).

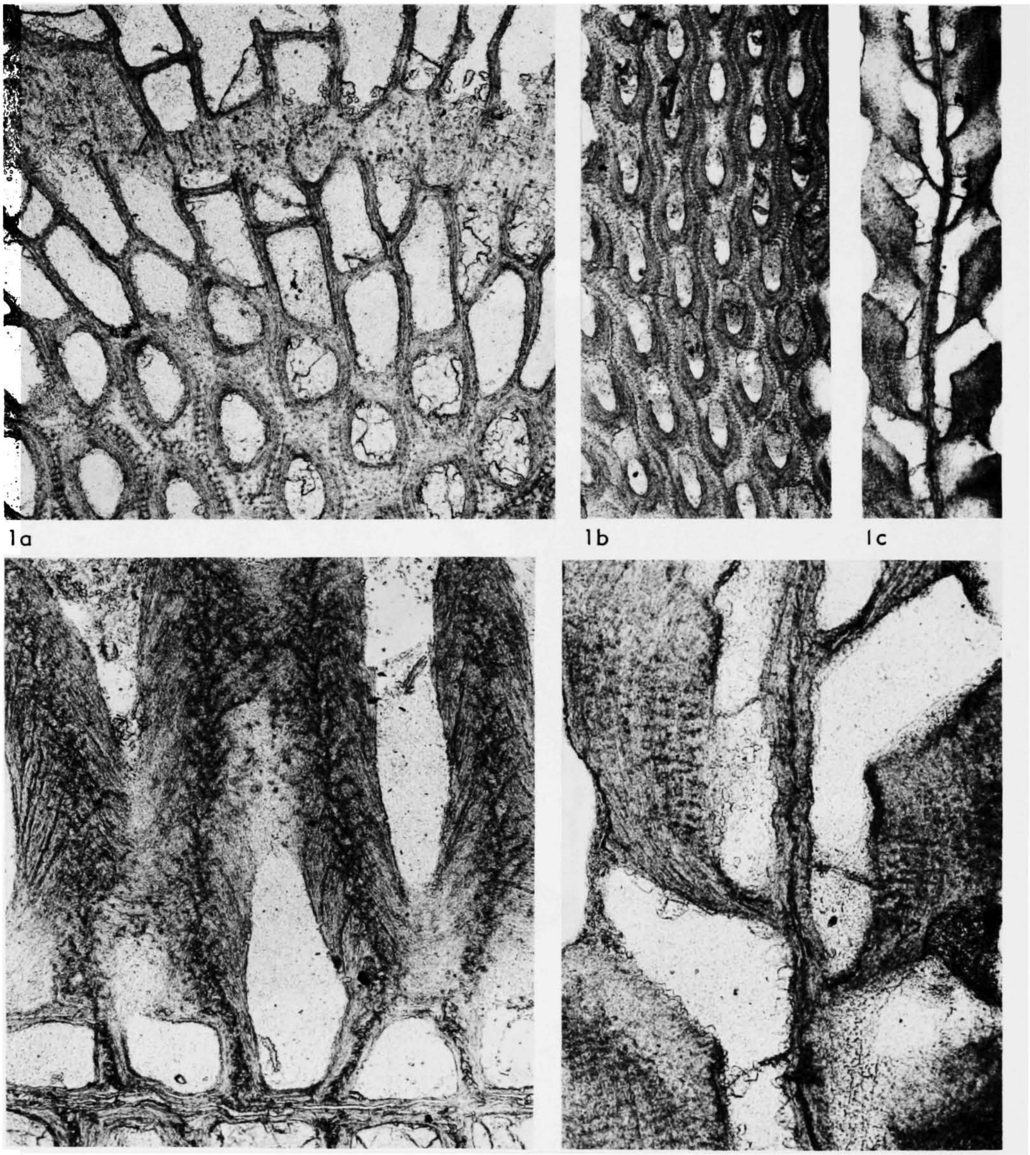


FIG. 263. Family Uncertain (p. 524).

thick, longitudinal walls. In exozones, autozooecia usually forming angles between 45° and 60° with mesothecae, in slightly curving to straight ranges, elliptical in cross section, generally contiguous, separated partly by extrazooecial stereom within ranges. Autozooecial wall and stereom laminae curved and broadly U-shaped. Autozooecial boundaries broadly serrated, commonly absent. Mural styles abundant, small, closely spaced, consisting of tightly curved segments of wall laminae or minute and discontinuous cores or granules, generally curved, arranged in diverging pattern along middle of longitudinal walls, terminating in walls at angles to chambers or zoarial surface. Living chambers narrowly elliptical in cross section, variable in length. Superior hemisepta common, short, blunt, generally scattered in zoaria. Basal diaphragms rare, thin, irregularly curved, spaced irregularly through zoarium. Polymorphism expressed by marginal and basal zooecia. Extrazooecial stereom common, indistinctly delineated, generally between successive autozooecia in zoarial midregions. Stereom laminae commonly forming striae at zoarial surface in margins, containing abundant mural styles. [*Taeniodictya* is similar to rhinidictyids in arrangement and shape of autozooecia in the endozone and to a lesser degree in the exozone, but differs from rhinidictyids and other ptilodictyines in skeletal structure. In microstructure, *Taeniodictya* is similar to *Euspilopora,* but differs in shape of autozooecia and presence of abandoned chambers (Fig. 263,*1c*), in having mural styles in the mesotheca (Fig. 263,*1a*), in configuration of mural styles in the exozone (Fig. 263,*1d*), and lack of acanthostyles and monticules.] *?M.Sil., Miss.,* USA.——FIG. 263,*1a–e.* **T. ramulosa*; *a,* subrhomboid autozooecia in endozone, mural styles in mesotheca and exozone; tang. sec., paralectotype, USNM 242644, ×50; *b,* contiguous and regularly curved longitudinal walls in exozone; tang. sec., paralectotype, USNM 242642, ×30; *c,* abandoned chambers, thin and irregularly curved basal diaphragms; long. sec., USNM 242642, ×30; *d,* mural styles in diverging pattern along middle of longitudinal walls in exozone; transv. sec., paralectotype, USNM 242645, ×100; *e,* slightly crenulated mesotheca with mural styles perpendicular to the median granular zone, basal diaphragms; long. sec., USNM 242642, ×100.

Trepocryptopora YANG, 1957, p. 7 (English summary) [**T. dichotomata*; OD; up. L. Ord., S. Shaanxi, China]. Zoarium branched or unbranched and explanate. Mesothecae straight to slightly sinuous, may be crenulated locally in transverse section. In endozones, autozooecia arranged in rhombic pattern, elliptical in cross section, contiguous, without continuous longitudinal walls. Endozones narrow, indistinctly delineated; autozooecial walls thickening only slightly at base of exozones. In exozones, autozooecia usually at right angles to mesothecae, arranged in rhombic pattern, elliptical in cross section, only partly contiguous locally, generally separated by exilazooecia. Autozooecial walls relatively thin, wall and stereom laminae indistinct. Autozooecial boundaries apparently narrowly serrated. Living chambers broadly elliptical in cross section, relatively short, with thin and indistinct lining locally. Basal diaphragms thin, straight to curved, commonly cystoidal, at relatively regular intervals throughout zoarium. Exilazooecia common, very small, indistinctly delineated, generally subelliptical to subcircular or irregularly shaped in cross section, may have scattered diaphragms, present throughout exozones. [*Trepocryptopora* appears to be one of the earliest ptilodictyines. It possesses a distinct mesotheca but differs in other ptilodictyine characters, as noted by YANG (1957). The endozone is indistinctly delineated because of different autozooecial growth. Autozooecia are subtubular throughout a zoarium, arising from the mesotheca at right angles and changing only slightly in shape and thickness at the base of the exozone. Autozooecial living chambers are very short because abandoned chambers are abundant. Basal walls of abandoned chambers are commonly cystoidal diaphragms, which are uncommon in ptilodictyines. *Trepocryptopora* also differs in kind of polymorphism by having very small zooecia (mesopores of YANG) with a few scattered diaphragms. I consider these polymorphs to be exilazooecia. Microstructure of the

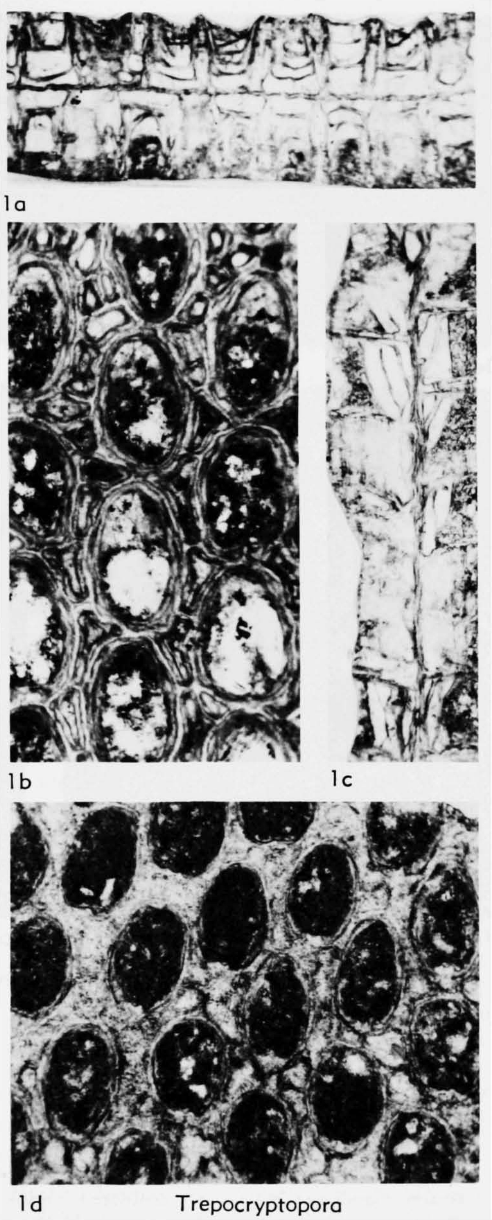


FIG. 264. Family Uncertain (p. 527).

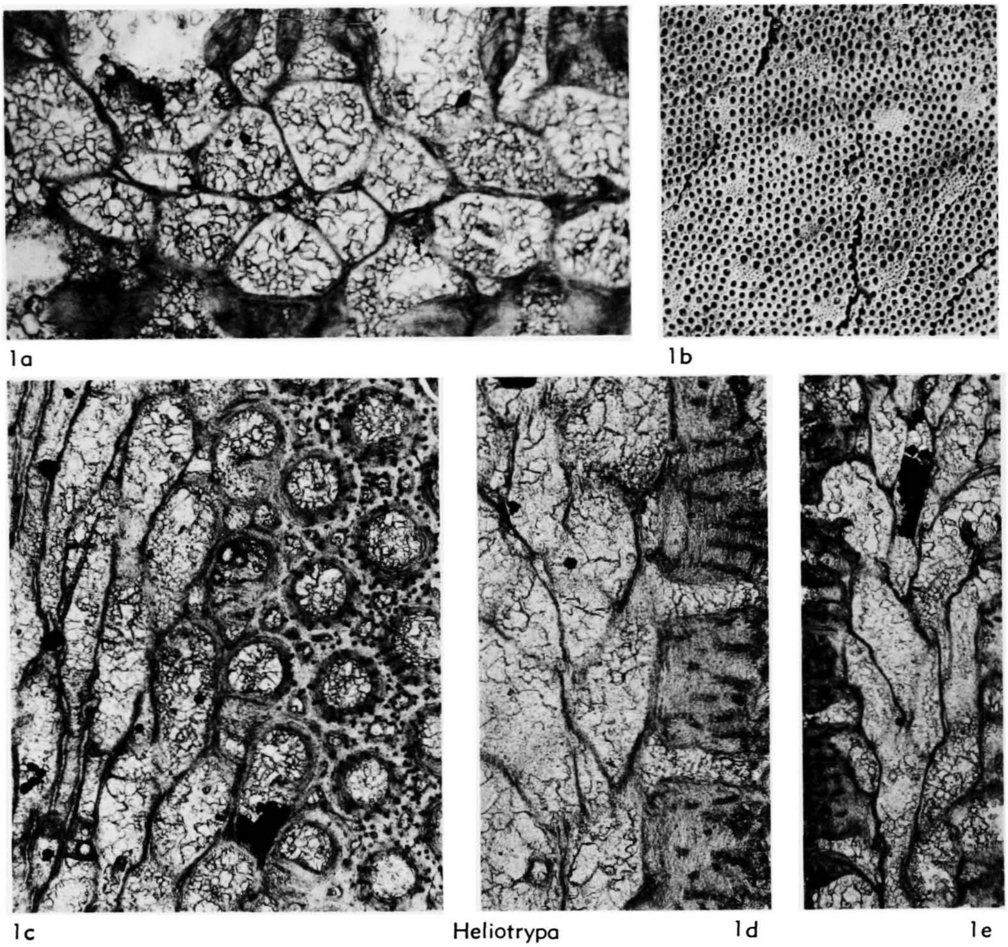


FIG. 265. Suborder Uncertain (p. 528).

mesotheca and configuration of laminae in the exozone are not determinable in available specimens. If the Early Ordovician age of *Trepocryptopora* can be verified, it is a ptilodictyine that differs considerably from those of younger ages.] *up.L.Ord.,* China(S. Shaanxi).——FIG. 264,*1a–c*. **T. dichotomata,* holotype, Northwest University Catalogue 8950; *a,* crenulated mesotheca, curved basal diaphragms, indistinct chamber lining; transv. sec., ×20; *b,* partly contiguous autozooecia, irregularly shaped exilazooecia; tang. sec., ×40; *c,* relatively thick, sloping basal diaphragms near mesotheca and in exozone, autozooecia arising from mesotheca without forming distinct endozone; long. sec., ×20 (photographs courtesy of King-Chih Yang).——FIG. 264,*1d*. *T. flabelata* YANG, up. L. Ord., S. Shaanxi, holotype, Northwest University Catalogue 8953; subelliptical autozooecia with narrowly serrated boundaries, indistinct exilazooecia; tang. sec., ×40 (photograph courtesy of King-Chih Yang).

Suborder Uncertain

Heliotrypa ULRICH, 1883, p. 277 [**H. bifolia*; M; U. Miss. (Chester.), Ky., USA]. Zoarium irregularly explanate and undulating, may self-encrust locally. Autozooecia budded in relatively straight ranges from medial zones, ranges partly aligned across medial budding zones. Autozooecial basal walls contiguous proximally, irregularly sinuous vertically, alternating in adjacent ranges, continuous planar mesothecae not formed. Granular median zones having discontinuous median rods of variable size, locally coalescing, extending into autozooecial walls of endozones in some. In endozones, autozooecia contiguous with sinuous longitudinal walls, irregularly subrectangular to subelliptical in cross section, elongated parallel to medial budding zones, alternately expanded and narrowed in adjacent ranges, becoming subelliptical and abruptly thickened at base of exozones. In exozones, autozooecia irregularly contiguous and locally separated by exilazooecia or extrazooecial stereom, irregularly subcircular in cross section with lateral walls restricted to individual autozooecia, and longitudinal linear ranges not formed. Autozooecial boundaries broadly serrated. Autozooecial walls slightly variable in thickness, consisting of broadly U-shaped laminae. Mural styles abundant throughout exozones, straight or irregularly diverging, locally indenting autozooecial chambers; consisting of broadly curved segments of skeletal laminae and discontinuous small cores; may bifurcate locally. Living chambers irregularly subrectangular to subelliptical in cross section in endozones, subcircular in cross section in exozones. Basal diaphragms rare to absent, scattered in autozooecia of outer exozones, locally present under self-encrusted zoarial parts. Superior hemisepta common, irregularly shaped with blunt terminal edges. Inferior hemisepta absent. Intrazooecial cysts common, generally scattered in endozones, circular in cross section or irregular in shape. Exilazooecia abundant throughout exozones, variable in size, subcircular or irregularly shaped in cross section. Monticules common, generally flat, irregularly shaped, arranged in rhombic pattern; consisting of numerous exilazooecia with abundant mural styles. Extrazooecial stereom laminated, irregularly delineated, sparse throughout outer exozones. [*Heliotrypa* is similar to ptilodictyines in having flattened and bifoliate zoaria, but differs in mode of budding of autozooecia and in other zoarial features. Autozooecia bud from a medial zone (Fig. 265,*1a,c,d*) without delineating a planar mesotheca because basal autozooecial walls, although contiguous proximally, are limited in structural continuity. As in some ptilodictyines (Rhinidictyidae), median rods are formed in basal walls of autozooecia, but are variable in width, are in an irregular pattern, and may extend into autozooecial walls in endozones. Microstructurally, however, median rods in *Heliotrypa* are similar to those in the Rhinidictyidae. *Heliotrypa* differs from other ptilodictyines in shape of autozooecia and their living chambers, appearance of skeletal laminae, microstructure and abundance of mural styles (Fig. 265,*1c*), and in abundance and kind of exilazooecia. *Heliotrypa* resembles rhabdomesines in mode of autozooecial budding, but differs in having planar medial budding zones instead of axial zones. It also differs from rhadomesines in distribution of autozooecia and exilazooecia in exozones, and in skeletal microstructure. Because of its different growth habit, *Heliotrypa* is not assigned to a suborder, but is tentatively retained in the Cryptostomata until its taxonomic affinities are better established.] *U.Miss.*, USA.——FIG. 265,*1a–e*. **H. bifolia*; *a,* medial budding zone of autozooecia, irregularly shaped median rods, shape of autozooecia in endozone; transv. sec., lectotype, USNM 242646, ×100; *b,* arrangement of autozooecia and exilazooecia, distribution of monticules with exilazooecia; external view, paralectotype, USNM 242647, ×5; *c,* shape of autozooecia in endozone and exozone, medial budding zone with rods and intrazooecial cyst (lower left); tang. sec., paralectotype, USNM 242648, ×50; *d,* microstructure of autozooecial walls and mural styles; long. sec., paralectotype, USNM 242648, ×100; *e,* shape of living chambers, superior hemisepta in some chambers, sinuous basal autozooecial walls; long. sec., paralectotype, USNM 242647, ×50.

Invalid and Unconfirmed Generic Names Applied to the Ptilodictyina

The following names are considered to be invalid or unconfirmable, and are either available or unavailable.

Crateriopora ULRICH, 1879, p. 29, *nom. dub.* [**C. lineata*]. Name applied to encrusting parts of zoaria that ULRICH (1882, p. 151) subsequently recognized as encrusting bases of bifoliate cryptostomates with proximally tapering parts of zoaria. *U.Ord.*, USA.

Disteichia SHARPE, 1853, p. 146, *nom. oblit.* [**D. reticulata*; M]. According to NILS SPJELDNAES (pers. commun., March 17, 1971), it is not a ptilodictyine, but probably a phylloporinid. Skeletal microstructure is obliterated and species is not recognizable. *Ord.*, Port.

Fimbriapora ASTROVA, 1965, p. 254, *nom. dub.* [**Ptilodictya fimbriata* JAMES, 1878, p. 8]. Skeletal microstructure of type material is almost obliterated and species is not recognizable. *M.Sil.*, USA.

Graptopora ULRICH, 1882, p. 148, *nom. nud.* (*non* SALTER, 1858, p. 63; *non* LANG, 1916, p. 405). Diagnosis not given, species not named. *Ord.*, USA.

Hemipachydictya KOPAYEVICH, 1968, p. 128, *nom. dub.* [**Stictopora crassa* HALL, 1852, p. 45]. Skeletal microstructure of type material is recrystallized and species is not recognizable (ROSS, 1961a, p. 337). *M.Sil.*, USA.

Nicholsonia WAAGEN & WENTZEL, 1886, p. 874. Specimens not located. *Ord.*, India.

Sladina REED, 1907, p. 208, *nom. dub.* [**S. cateniformis*]. Skeletal microstructure is recrystallized and species is not recognizable. Probably not a ptilodictyine (for contrasting view see SPJELDNAES, 1957, p. 367). *U.Ord.*, G.Brit.

Stictoporina HALL & SIMPSON, 1887, p. xx [**Trematopora claviformis* HALL, 1883b, p. 181]. Repository of species not known; concept of genus not verifiable. *M.Dev.*, USA.

INTRODUCTION TO THE SUBORDER RHABDOMESINA

By Daniel B. Blake

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The cryptostomate suborder Rhabdomesina includes many of the slender dendroid bryozoans found in Paleozoic marine sediments. Although specimens are known from much of the world, research has been concentrated in North America, the Soviet Union, Australia, and parts of Asia. The suborder ranges from the lower Middle Ordovician to the Upper Permian.

A large number of taxonomic characters are available, but recognition of the limits of the suborder has proven difficult because no unique suite of characters is recognized. Convergence with other groups, in particular the trepostomates, apparently has been common.

Six families are recognized here. The Arthrostylidae is dominant in Ordovician and Silurian rocks, and then declines. A few genera are known from younger Paleozoic rocks of the Soviet Union. Arthrostylids have been described mainly from North America, Europe, and western and central portions of the Soviet Union. They are poorly known because their small size renders them inconspicuous in the field and difficult to study in the laboratory. The Bactroporidae includes a single Devonian genus known only from North America. The remaining families, Rhabdomesidae, Rhomboporidae, Hyphasmoporidae, and Nikiforovellidae, are geographically widespread and primarily found in middle and upper Paleozoic rocks.

Acknowledgments.—I am grateful to the following individuals for making available specimens under their care, or for providing illustrations or information on specimens and publications: Roger Batten, J. L. H. Bemelmans, B. M. Bell, C. Blotwijk, R. S. Boardman, Krister Brood, Robert Conrad, P. L. Cook, Donald Dean, J. M. Edwards, Julia Golden, R. V. Goryunova, W. G. E. Graham, A. H. Kamb, O. L. Karklins, A. Kellermeyer, Lois Kent, Marie Kiepura, W. J. Kilgour, J. S. Lawless, D. B. Macurda, R. V. Melville, I. P. Morozova, V. P. Nekhoroshev, M. H. Nitecki, Eugene Richardson, Paul Siegfried, F. M. Swain, and R. F. Wise. The figures were prepared by D. R. Phillips. R. S. Boardman, R. J. Cuffey, and J. R. P. Ross read portions of the manuscript and made useful suggestions.

GROWTH PATTERNS

Rhabdomesines formed encrusting holdfasts, generally attached to such firm substrate as shell material. The period of encrusting growth was probably brief, for known holdfasts are small relative to overall zoarial size (Fig. 266, *10a*).

Most members of the suborder developed relatively slender (0.5–3.0 mm) cylindrical branches of fairly constant diameter between bifurcations. In many genera, especially earlier ones, zooecial apertures are arranged at the surface in a rhombic pattern that is mostly uninterrupted by polymorphs, monticules, or apparent microenvironmental influences (Fig. 266, *9,10*). However, branches of a number of upper Paleozoic genera (e.g., *Rhombopora,* see Fig. 286,*3b*) are wider (up to about 5 mm) and have lost the constancy of diameter between bifurcations and regularity of apertural arrangement.

Although large silicified specimens are rare, available material shows that thickening of the exozonal wall and partial or complete closing of apertures was possible during colony life.

The growing tip may be attenuated in zoaria with steeply ascending zooecia (Fig. 266,6), but generally it is blunt. Intracolony

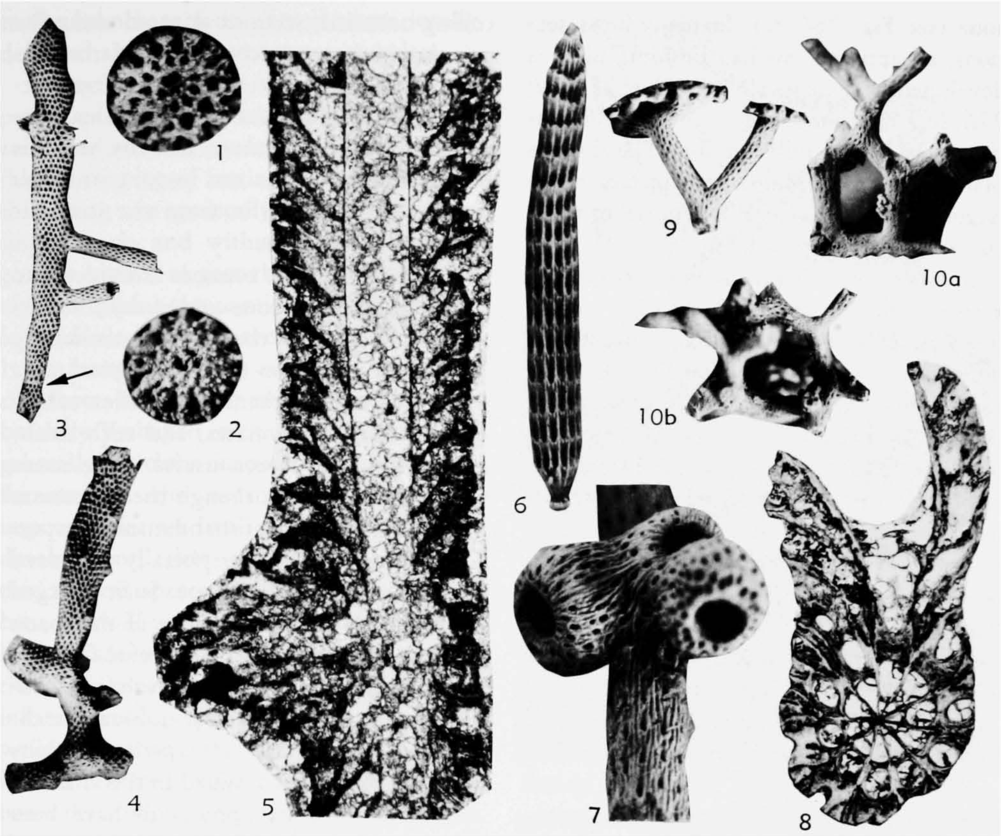

FIG. 266. Growth habits and articulation structures in Rhabdomesina.——*1–4. Rhabdomeson* sp., Perm., Texas; colonies that survived breakage and resumed growth elsewhere; *1,* broken branch base in early stage of healing with stylets developed but zooecia still open; USNM 240829, ×15.0; *2,* later stage of healing with zooecia mostly closed; USNM 240830, ×15.0; *3,* conical branch that resumed growth in former proximal direction at level of arrow after breaking from parent (compare with *5*); USNM 222647, ×2.5; *4,* conical branch arising from cylindrical parent branch; USNM 240831, ×2.5.——*5. Rhabdomeson* sp., Hamilton Gr., M. Dev., N.Y.; hollow axial cylinder; zooecial orientation is reversed at level of branch; specimen was apparently broken but survived to resume growth; long. sec., USNM 249311, ×30.——*6–8. Ulrichostylus* aff. *U. spiniformis* (ULRICH), Bromide F., M. Ord., Okla.; *6,* slender branch with growing tip and weakly developed exozone; proximal tip is spherical surface of joint; USNM 249332, ×10; *7,* parent stem and three cup-shaped proximal joints; USNM 249328, ×10.0; *8,* transverse section of branch and longitudinal section of cup-shaped proximal joint; hollow of cup continuous with one zooecium from main stem, lined with weakly laminated skeletal layer; USNM 249336, ×30.0.——*9. ?Acanthoclema* sp., ?Jeffersonville Ls., M. Dev., Falls of the Ohio near Louisville, Ky.; exterior view of colony with fenestellid colony partially encrusted and used as brace; USNM 178558, ×8.0.——*10a,b. ?Orthopora* sp., ?Jeffersonville Ls., M. Dev., Falls of the Ohio near Louisville, Ky.; interconnected growth habit at colony base provides strength without significant thickening of exozonal walls; *a,* lateral and *b,* top views, USNM 178559, ×8.0.

overgrowths are uncommon. The ramifying growth pattern was maintained throughout life, except where branches encountered foreign objects, which they partially encrusted to brace the colony (Fig. 266,*9*).

Study of sectioned zoarial bases suggests that the zone of astogenetic repetition was established after only a few founding zooids were developed. Zooecia were budded about a varied but generally well-defined, one- or two-dimensional median axis. In some early arthrostylids, the axis is sharply defined (see Fig. 281, *1b–d*), but in many later rhabdomesines it is an irregular, slender budding zone (see Fig. 286,*3c*). In many cross sections, an apparent median budding plate is developed at least locally (see Fig. 274,*1d*; 276,*1c*), but none is structurally differentiated, as in the Ptilodictyina. The median plate in the Rhabdomesina appears to be largely a product of local alignment of zooecial walls during growth.

In other taxa, the axial region may contain a small undifferentiated bundle of zooecia (see Fig. 269), a more or less enlarged and differentiated axial bundle (see Fig. 283,*1a*), or a hollow axial cylinder (Fig. 266,*5*). In these taxa, budding of nonaxial zooecia is from the outer surface of the axial structure.

Zooecia are typically added in a spiral pattern about the axis, and the spiral is reflected in apertural arrangement at the branch surface. Such addition is probably largely a response to geometric growth restraints, as outlined by Gould and Katz (1975) for receptaculitids. Locally, on branches showing typical spiral budding, a number of zooecial tiers may be added in an annular pattern.

A few authors have described spiral growth with terms implying that each zooecial tube is helically wrapped about the axis; if dissected from a zoarium, the shape of such a zooecium would broadly resemble that of an openly spiraled gastropod shell. Longitudinal thin sections show spiraling is limited, if it occurs at all. In these sections, individual zooecia commonly can be traced from the median axis to the zoarial surface. That is, the entire length of the tube lies within a single, flat plane of section and does not curve more than a few degrees because it does not pass out of the plane of section. If extensive coiling occurred, sections oriented along the axis should show zooecia in oblique cross section, which has not been observed. Cross sections of zooecia appear in longitudinal sections only near the centers of branches; this results from sections not passing through branch axes, as well as from the irregular nature of many zoaria.

The rhabdomesine zoarium is divided into a thin-walled endozone and a thick-walled exozone. Generally, the boundary is sharply defined. Cheetham (1971) argued that peripheral-wall thickening provides colony support in cheilostomates, and such thickening would have been useful in Paleozoic bryozoans as well. Although the exozone is well developed in most rhabdomesines, specimens showing walls peripherally thickened to an unusual degree are rare. Such enlarged stems developed near the base of the zoaria seemingly would have been useful for support of a large colony. Extensively interconnected stems may be present in basal attachment areas (Fig. 266,*10*); perhaps colony support usually was attained in this manner.

Growth generally appears to have been rather continuous with few indications of periodicity. Periodicity in bryozoans is recognized by skeletal banding in the exozone, seen in a few rhabdomesines, or by signs of temporary growth termination and exozone development across a branch axis, as in many trepostomates, or by annular growth banding, as in certain cheilostomates (e.g., *Myriapora*). Lack of such indications suggests that rhabdomesine colonies usually developed in a continuous growth period.

SKELETON

Skeletal wall materials and wall growth sequences in rhabdomesines are little studied but appear generally similar to those in trepostomates and other cryptostomates. Tavener-Smith and Williams (1972) published observations made with the scanning electron microscope. Other authors (e.g., Brood, 1970; Blake, 1973a) have discussed development of specific skeletal features.

Most of the rhabdomesine wall is constructed of laminated calcite (Fig. 267,*3*). The laminae are made of lenticular platelets arranged in clearly defined layers of approximately constant thickness. The layers are usually oriented approximately parallel to the surface of zooecial chambers or parallel to the branch surface, except where locally deflected about such structures as stylets.

Ontogenetic changes in wall thickness and profile, primarily between endozone and exozone, are effected by local addition rather than thickening of laminae. Patterns of wall thickening are generally consistent within single zoaria and within genera, implying genetic control of growth, and thereby providing a useful taxonomic character. Lamellar profile is defined as the outline of a lamellar plane between adjacent zooecial chambers. In rhabdomesines, this outline is basically V-shaped in the early exozone and generally becomes increasingly rounded or flattened as the exozone thickens. Two important factors, wall thickness and stylet development, alter the profile. As walls thicken and spaces expand between chambers, the wall profile becomes flatter. Sheath laminae around stylets are deflected toward the zoarial surface and commonly cause an inflated profile, especially in relatively thin-walled taxa with a narrow stylet field approximately centered between chambers. In diagnoses that follow, emphasis is placed on the outline as seen in transverse view because the distance between laterally adjacent chambers is commonly less than that between longitudinally successive chambers, and the profile is easier to evaluate. Both views are considered in diagnoses of genera in which longitudinal spacing is significantly different from lateral spacing, as in many arthrostylids.

Another skeletal material, nonlaminated calcite, is present but limited in rhabdomesine zoaria (Fig. 267,*2,3*). Under the scanning electron microscope, nonlaminated material differs from laminated wall platelets only in crystal size and shape, the nonlaminated crystals being relatively enlarged and irregular. A well-defined and continuous nonlaminated layer is developed along zooecial boundaries in a few arthrostylids; however, the layer is discontinuous and weakly differentiated from the enclosing laminated skeleton in other families. Small, equidimensional, nonlaminated granules are common along zooecial boundaries of many rhabdomesines.

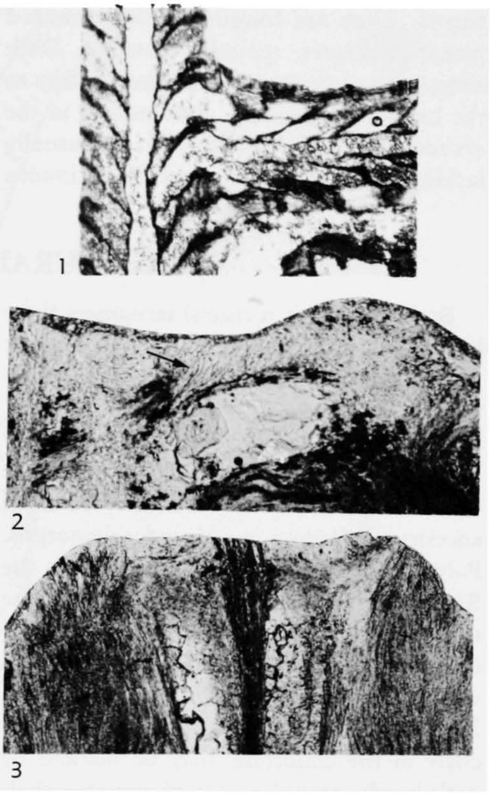

FIG. 267. Growth, wall materials in Rhabdomesina.——*1. Rhabdomeson noinskyi* SHISHOVA, U. Perm. (Kazan.), Nemda River basin, USSR; hollow part of branch continuous with autozooecium, suggesting relatively simple derivation of the axial cylinder; long. sec., ×15.——*2. Cuneatopora bellula* (BILLINGS), Jupiter F., L. Sil., Anticosti Is., Can.; articulation surface of distal branch tip (compare with *3*); wall material generally nonlaminated but some weak growth lines are present (arrow); USNM 249327, ×154.——*3. Arthroclema angulare* ULRICH, Fort Atkinson Ls., U. Ord., Ill.; walls mostly constructed of laminated calcite, distal tip with articulation surface of nonlaminated skeletal material; long. sec., USNM 249326, ×77.

Nonlaminated skeletal material also is present in the axial region of stylets and, in some arthrostylids and early hyphasmoporids, as rods along the branch axis (see Fig. 276,*2c*).

Under the light microscope, thin irregular bands termed dark zones (KARKLINS, this revision) are seen in the exozone of some forms. They are longitudinally oriented planar structures, typically clustered. Dark zones arise at or near zooecial boundaries at the base of the exozone, then radiate in the exozone. Distinct skeletal layers are usually lacking although granular and discontinuous nonlaminated intervals are present in some genera. The exozonal wall in *Ulrichostylus* shows changes in lamellar orientation at positions of dark zones, but no disruption of the laminated wall when studied with the scanning electron microscope.

STRUCTURAL CATEGORIES

BOARDMAN (this revision) recognizes three basic structural elements in stenolaemates: zooids, multizooidal structures, and extrazooidal structures.

Zooids are minimally defined as body walls enclosing coelomic space (BOARDMAN & CHEETHAM, 1973), the definition covering ancestrulae, feeding zooids, and polymorphs. Polymorphs are relatively uncommon in the Rhabdomesina; most zooids probably were typical feeding autozooecia. BOARDMAN's (this revision) description of vertical zooidal walls is applicable to the Rhabdomesina. Zooecial boundaries in the suborder, especially in the endozone, may be marked by dark bands, granular or nonlaminated skeletal zones, or laminae apparently extending uninterrupted between zooecial chambers.

Multizooidal structures are grown by the colonies, and eventually become parts of zooecia. These parts include walls from which zooids bud as well as budding zones (BOARDMAN, this revision). Encrusting basal walls, either at the level of the ancestrula or beneath overgrowths, are examples.

Extrazooidal structures grown by colonies are never included within zooecial boundaries (BOARDMAN, this revision). Recognition of extrazooidal material is contingent upon recognition of zooecial boundaries, but a clearly defined boundary is generally lacking in rhabdomesines. The boundary is considered to lie close to the zooecial chamber, and most of the exozonal wall is considered to be extrazooidal.

AUTOZOOECIA

Polymorphism is limited in the Rhabdomesina. Axial and monticular polymorphs are developed in some taxa; all other larger tubes are considered to be autozooecia. Autozooecia bud from a linear or cylindrical locus and are consistently oriented within a genus. Pores through walls linking zooecia are unknown.

Autozooecial shapes are varied in the suborder (Fig. 268) but relatively constant within genera and species, and therefore taxonomically useful. Most zooecia are angular or sigmoidal. In the majority of taxa, the initial axis of the zooecium is oriented approximately normal to the axis of the stem (Fig. 268,*2,3,5*). After a relatively short interval, the axis is deflected in the distal direction (Fig. 268,*1,4*). Most of the endozonal length of the zooecium is in this second interval. In a relatively few species, after deflection, the zooecial axis parallels the budding locus rather than diverging from it, and the zooecium is recumbent in the endozone (Fig. 268,*5*). In some taxa, the zooecial axis is straight in the endozone and the base of the zooecium is attenuated (Fig. 268,*4*) or flattened (Fig. 268,*6,7*) in longitudinal section. At the base of the exozone, the zooecial axis is generally deflected more (Fig. 268,*2*) or less (Fig. 268,*3,4*) abruptly toward the branch surface, a change reflected in both the proximal and distal zooecial outline (Fig. 268,*6*) or in only the proximal outline (Fig. 268,*7*). In a few species, the axis does not change orientation at the exozonal boundary (Fig. 268,*1*).

Position of the zooecial boundary in the endozone of rhabdomesines lies near the midline of the wall and is generally a distinct, irregular, commonly granular zone. The position in the exozone typically is obscure, especially in later genera, but is readily seen

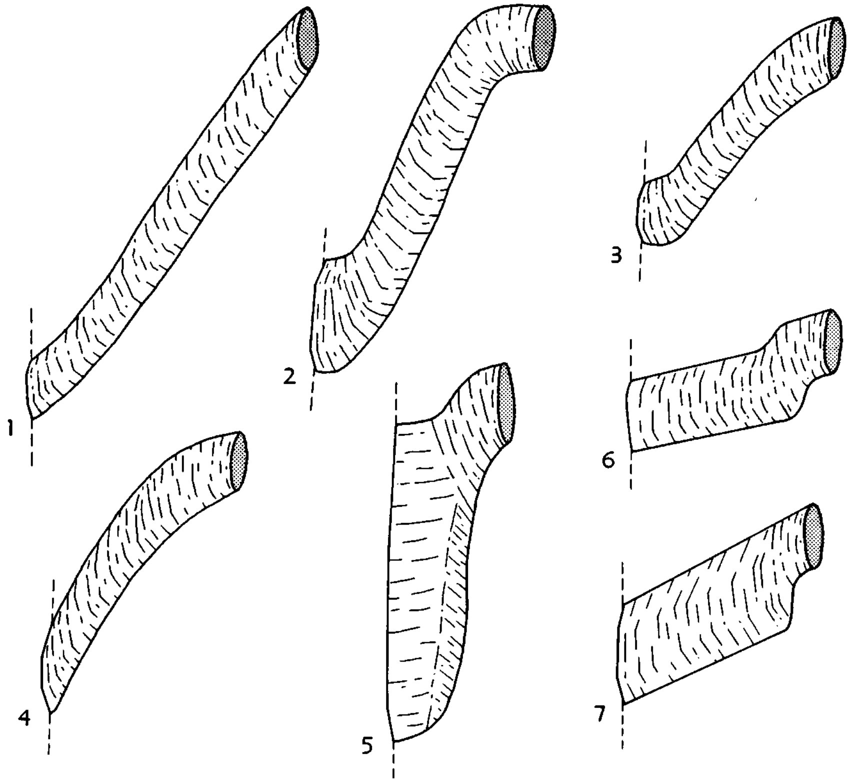

FIG. 268. Diagrams of zooecial shape in some rhabdomesines. Vertical dashed lines represent position of budding axes, stippled ellipses are apertures, zooecial shape changes from polygonal to rounded at the endozonal-exozonal boundary.——*1.* Sublinear, weakly inflated zooecial base in *Ulrichostylus.*——*2.* Weakly inflated zooecial base and abrupt zooecial bend in *Streblotrypella.*——*3.* Inflated zooecial base and rounded zooecial bend in *Rhabdomeson.*——*4.* Attenuated zooecial base and rounded zooecial bend in *Rhabdomeson.*——*5.* Inflated zooecial base, recumbent endozone, and abrupt zooecial bend in *Nematopora.*——*6.* Linear endozone in *Cuneatopora,* with abrupt deflection at zooecial bend.——*7.* Linear endozone in *Acanthoclema,* with distal wall not deflected at zooecial bend.

near to the autozooecial opening in such genera as *Nematopora* (see Fig. 276,*2*) and *Arthrostylus* (see Fig. 271).

In the exozone of later rhabdomesines, the position of the zooecial boundary appears to correspond to that in *Nematopora* and *Arthrostylus.* Indications of the zooecial boundary are seen in walls of endozones and the proximal part of exozones of such genera as *Orthopora, Tropidopora* (see Fig. 280,*1e*), *Rhabdomeson* (see Fig. 282,*1d*), *Arthroclema* (see Fig. 272,*2e*), *Osburnostylus* (see Fig. 277,*1d*), *Hyphasmopora* (see Fig. 293,*1c,d*), and *Streblotrypa* (see Fig. 293,*2d*). The apparent position of the boundary close to the zooecial chamber is also seen in tangential views of such genera as *Ascopora* (see Fig. 283,*1c*), *Rhombopora* (see Fig. 286,*3e*), and *Arthroclema* (see Fig. 272,*2g*).

The wall beyond the zooecial boundaries is considered to be extrazooidal. Although apparently limited in a few genera (e.g., *Helopora, Cuneatopora*), extrazooidal wall generally is extensive, forming most of the thick exozonal wall.

Position of the zooecial boundary in rhabdomesines corresponds with that in such ptilodictyines as *Athrophragma* (KARKLINS, 1969, p. 25), close to the zooecial chamber. In *Athrophragma,* at the base of the exozone, the wall between zooecial boundaries is filled by a cystose and hence extrazooidal material.

This cystose interval is followed by the development of laminated wall. In rhabdomesines, the extrazooidal wall is laminated throughout.

Different interpretations can be made of zooecial-boundary position. Where obscure, BOARDMAN (this revision; BOARDMAN & CHEETHAM, 1973) suggested placing the boundary at the first break in lamellar curvature from the zooecial chamber. In rhabdomesines this position typically is dictated by the location of stylets. Following this hypothesis, many zooecial boundaries would be polygonal in outline and extrazooidal wall either absent or localized. BOARDMAN's suggestion is not followed here because of the lack of independent skeletal evidence in the exozone of later rhabdomesines and because the typical irregular placement of stylets would provide an apparently effective tissue support system but an irregular zooecial boundary.

Polypide size must have been quite varied if size was correlated with chamber diameter. DUDLEY (1970) and RYLAND (1970) both suggested that food resources are not the same in modern bryozoan species of different tentacular crown sizes. It seems likely that different rhabdomesine species also exploited different food resources.

AXIAL ZOOECIA

In some genera, **axial zooecia** are elongate polymorphs that may form a distinct axial bundle (see Fig. 283,*1a,b*). Four morphologic changes may contribute to the development of an axial bundle: (1) axial zooecia become more slender than neighboring autozooecia; (2) axial zooecia become thinner walled than neighboring autozooecia; (3) axial zooecia infrequently diverge from the axial region; and (4) outer surfaces of marginal axial zooecia become curved to produce the cylindrical axial surface.

That axial zooecia are derived phylogenetically from autozooecia is indicated by the existence of many intermediate morphologies. Axes may be well defined and linear; zooecia may parallel a poorly defined axis for varying distances; two or three zooecia may be present along the axis, regularly turning toward the surface to be replaced by newly budded individuals; or there may be a well-defined central bundle (e.g., *Ogbinopora*).

As the axial bundle develops, dimorphism of zooecial length appears because shorter, more typical zooecia continuously bud from the outer surface of the bundle. Intrazooecial structures are rare in axial zooecia, although diaphragms may be present. Axial zooecia provide a means of thickening the stem and increasing the area of budding locus, thus increasing the maximum possible number of autozooecia around the branch without requiring major changes in autozooecial shape or orientation. Axial zooecia become more clearly differentiated and the axial bundle better defined during the history of the Rhabdomesina.

Whether or not axial zooecia contained polypides, and if so, their possible functions, are unknown. However, those axial zooecia reaching the lateral surfaces of branches show typical autozooecial morphology.

AXIAL CYLINDERS

The axial cylinder is a hollow tubular polymorph in the axial region of one genus, *Rhabdomeson*. The cylinder is usually wider than neighboring autozooecia and has typical stenolaemate compound walls; diaphragms may be developed. Structural discontinuity has not been recognized between walls of cylinders and of autozooecia. Rather, lamellar planes can be traced from the cylinder into the endozonal walls of autozooecia, proving that the cylinder walls were part of the colony. The presence of diaphragms and compound walls demonstrates that the cylinder was not produced by simple encrustation of a foreign substrate, but was a part of the colony body cavity. True encrusting rhabdomesines, however, have been described (NEWTON, 1971).

As seen in a few ideally oriented specimens, the axial cylinder of a daughter branch was produced as a longitudinal extension of an autozooecium in the parent stem (Fig. 267,*1*). Goryunova and Morozova (1979) have described the growth relationship.

In some specimens, the axial structure is conical rather than cylindrical. These conical specimens previously were assigned to *Coeloconus,* but that genus was synonymized with *Rhabdomeson* after the discovery of conical stems extending as branches from typical cylindrical *Rhabdomeson* zoaria (Blake, 1976).

Rhabdomeson branches that were broken and survived to resume growth, with new zooecia directed in the former proximal direction, have been recognized from Devonian (Fig. 266,*5*), Mississippian, and Permian rocks (Blake, 1976). It seems likely that cylinder development was linked to fragmentation as a mode of colony increase.

SKELETAL DIAPHRAGMS

Skeletal diaphragms in rhabdomesines are generally thin and calcified on their outer surfaces. They most commonly developed well below zoarial surfaces and in taxa with elongate zooecia. It has not been established if differences in diaphragm frequency were ecologically controlled, for example by recurring unfavorable conditions that induced frequent polypide degeneration.

Thickened terminal diaphragms, commonly clustered, have been observed in some species. Because rhabdomesine zooecia generally reached a maximum length in a given species, the presence of such diaphragms seems to indicate a termination of polypide activity. Silén and Harmelin (1974) have described analogous inactive areas in the central portions of circular encrusting colonies of modern tubuliporates.

HEMISEPTA

Hemisepta in rhabdomesines are centered either on the proximal or distal wall, but not on lateral walls (Fig. 269). They occur singly, in offset pairs, or in multiple proximal wall series. A single hemiseptum on the proximal wall at the zooecial bend is common. In cross section, hemisepta range from low and rounded to thin and extended. Typically, hemisepta on proximal walls are thicker than those on distal walls. Hemisepta were secreted from both sides and apparently originated through a simple fold in epidermal tissues.

Functionally, hemisepta seem related to polypide position because multiple hemisepta occur in taxa with elongate zooecia, suggesting that addition of new hemisepta was associated with the degeneration-regeneration cycle. In *Orthopora,* the zooecial chamber is commonly curved about the hemisepta (see Fig. 285,*2e*), suggesting a polypide position either lateral to or behind these structures. In such positions, the hemisepta may have served to protect the polypide, to provide muscle and ligament attachment points, or to guide the polypide during protrusion. Hemisepta probably were not zooecial floors because: (1) the partitions are incomplete and would not serve to isolate the new polypide; (2) in the case of paired hemisepta, the distal-wall member of the pair would lie behind the zooecial floor and would seem to be without function; and (3) in such taxa as *Rhabdomeson,* the space distal to the hemiseptum appears to be insufficient for a functioning polypide.

STYLETS

The term stylet is applied here to any rodlike skeletal structure oriented approximately perpendicular to the zoarial surface and parallel to the zooecium. Stylets formed more or less prominent spines, or low, hemispherical knobs on zoarial surfaces. Structurally, they possess an axial component, the core, and a concentric bundle of sheath laminae that enclose the core. The core may be constructed of nonlaminated material or of laminae oriented subparallel to the zoarial surface but arched toward the surface, or a combination of both. The sheath laminae are simply zoarial laminae deflected toward the zoarial sur-

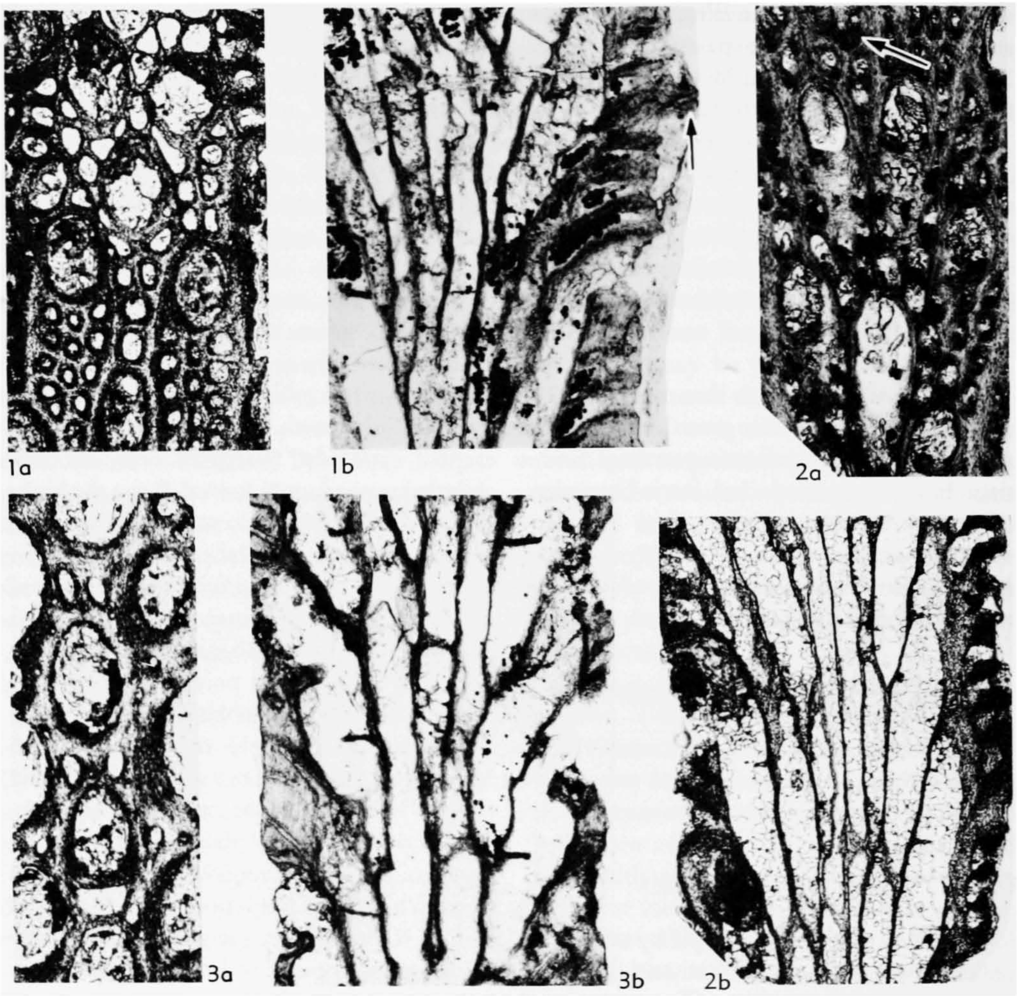

FIG. 269. Population variation in Hyphasmoporidae.——*1–3. Streblotrypa nicklisi* VINE, U. Miss. (Chester.), Ill.; USNM 249315–249317, all ×75; *1a,* metapores in fields, stylets present, tang. peel; *1b,* typical interior, stylets (arrow) present, long. sec.; *2a,* metapores in fields and one questionable stylet (arrow), tang. sec.; *2b,* typical interior, stylets absent, long. sec.; *3a,* stylets present, metapores not in distinct field, tang. peel; *3b,* typical zooecia but shorter than those in *1* and *2,* long. sec.

face about the core. A growth discontinuity is lacking between sheath and zoarial laminae, but a discontinuity is present between the core and the sheath laminae, except for small diaphragmlike lamellae that extend across cores in some forms.

Most, and probably all, stylets were solid during colony life, containing no soft tissues. In rhabdomesines, most stylets are restricted to exozones. Although some stylets arise very close to zooecia, axial structures appear to be isolated from the zooecial chambers by at least a few laminae.

Paurostyles (Fig. 219,*4*; 270,*1*) are the simplest type of stylet. The paurostyle core is an irregular cylinder of nonlaminated material, usually crossed by rare laminae and commonly offset along its length. The sheath lamellar bundle is narrow, and typical lamellae are weakly deflected in the distal direction. Paurostyles are approximately 0.02 to 0.04 mm in diameter. Many of the micracanthopores of earlier workers are paurostyles; however, morphologically diverse structures were included under the older term.

Heterostyles (Fig. 219,*5*; 270,*2*) differ from paurostyles in having a core of distinct lenses of nonlaminated material separated by bands of sheath laminae that arch across the axis. The sheath is narrow and deflection of laminae is weak to strong. Heterostyles are slender (approximately 0.02 to 0.04 mm) and of nearly constant diameter, but irregular outline.

Stylets approximating traditional acanthopore morphology are termed acanthostyles (Fig. 219,*9*; 270,*1*). In these structures, the axial core is a continuous, clearly defined cylinder of nonlaminated material, usually uninterrupted, but in places crossed by thin lamellar bands. The sheath laminae are well developed, forming a broad bundle usually strongly deflected away from the zoarial axis (e.g., *Acanthoclema,* Fig. 218,*4*). Therefore acanthostyles form prominent structures on zoarial surfaces. In a few taxa, the enclosing laminae are only weakly deflected (e.g., *Pamirella,* see Fig. 288,*1c*) and apparently form only low surficial structures. Most acanthostyles range in diameter from approximately 0.02 to 0.12 mm, some tapering along their length.

Morphology is transitional between paurostyles and acanthostyles, but the axial core is more clearly defined in acanthostyles and the sheath lamellar bundle is wider and more strongly deflected. Paurostyles also are generally smaller.

Aktinotostyles (Fig. 219,7; 270,*3*) are a type of stylet with a core formed by a broad band of distally arched laminae. Laterally, these laminae are deflected into cones pointing away from the aktinotostyle axis. Irregular scattered granules of clear material are common along the axis, and in some a distinct cylinder resembles that of acanthostyles. Typically, the sheath lamellar bundle is relatively narrow. Surrounding laminae may be either strongly or weakly deflected toward the zoarial surface. The deflected interval is small, and does not prominently affect the surface. Branching aktinotostyles have been observed in few specimens. Aktinotostyle diameter ranges from approximately 0.02 to 0.13 mm, commonly with distal increase.

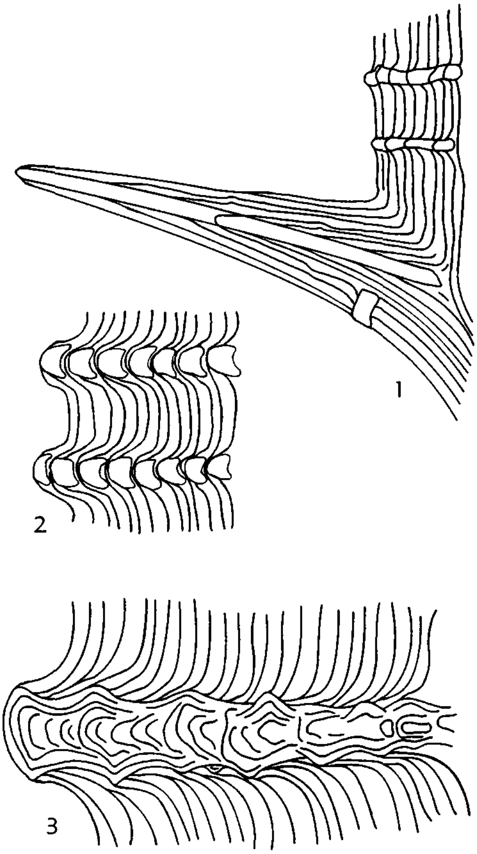

FIG. 270. Diagrams of stylets.——*1.* Two paurostyles (above) showing irregular cores and weakly deflected sheath laminae; acanthostyle (below) showing cylindrical core, conically deflected sheath laminae, and one lamellar surface crossing the core; a mural spine is present in the sheath laminae below the acanthostyle.——*2.* Two heterostyles showing discontinuous core of lenticular nonlaminated material, and sheath laminae.——*3.* Aktinotostyle, showing laminated, spinose core containing several nonlaminated fragments near base of the structure; the sheath lamellar bundle is narrow and individual lamellae are strongly deflected. All approximately same scale.

In a few zoaria, stylets have been observed to change longitudinally from aktinotostyles to acanthostyles. The nonlaminated cylinder of the acanthostyle extends from the lamellar core of the aktinotostyle, and the sheath laminae abruptly change, becoming much more strongly deflected in the outward direction. Although the structural change is abrupt, there is no indication of fracture or other disruption of growth.

The stellatopores of ROMANCHUK (1966) superficially resemble aktinotostyles; however, they were described as hollow structures containing diaphragms, and skeletal walls around the stellatopore contain a ring of capillaries. This description does not fit aktinotostyles and I consider the two structures to be distinct.

Mural spines are styletlike structures that generally grow into zooecial chambers. The core of a mural spine is nonlaminated and clearly differentiated from enclosing laminae, which are weakly deflected in the direction of growth. Unlike true stylets, mural spines are very short, arising within the exozonal wall during late ontogeny. BOARDMAN and CHEETHAM (1969) suggested that mural spines may have functioned as polypide attachment structures.

Usage of the term "capillary" has been reviewed by KARKLINS (this revision). The term has been employed primarily by Soviet authors for a variety of smaller skeletal structures, most of which I here refer to as paurostyles, mural spines, deflections in the sheath laminae of acanthostyles, or deflections in the core laminae of aktinotostyles.

Various Soviet workers have suggested that capillaries may represent a form of open communication system. I have seen no evidence either under the light microscope or with the scanning electron microscope for open passages within the exozonal wall beyond the zooecia or metapores. The small size of most capillarylike structures in rhabdomesines, combined with their irregular outline and common lack of well-defined continuous cores, seem greatly to limit their function as communication structures. In contrast, the open links among neighboring autozooecia and interzooecial areas across the hypostegal coelom would appear to provide effective communication.

Interpretation of stylet morphology, much of it derived from trepostomate species, has differed among various authors. Because stylets are very similar between orders, arguments based on members of one group may be pertinent to others. Important is whether the core of stylets, especially acanthostyles, was solid or open during colony life. If solid, stylets could have functioned only for strengthening support. If hollow, some communication function may have been performed, or a zooidal polymorph may have been present. ASTROVA (1971) found diaphragms and sedimentary particles in larger trepostomate acanthostyles and interpreted these as having been originally open. The distinct, well-defined core may also indicate an open axis. BLAKE (1973b) illustrated scanning electron micrographs showing core material sharply defined from enclosing laminae. BLAKE and TOWE (1971) dissolved the zoarial laminae from a specimen of *Idioclema,* showing that the core material could be removed intact from the skeleton, and therefore was cohesive and not interrupted by laminae or foreign material. ARMSTRONG (1970) believed that calcite in the stylet core of two species of the trepostomate *Stenopora* was secreted by specialized zooidal epithelium, and BROOD (1970) preferred an originally solid core in his interpretation of two species of *Orthopora.* BLAKE (1973c) argued in favor of an originally solid stylet, largely because of the relationships between the sheath laminae and the core. The laminae abut and were intergrown in irregular patterns with the core, without indication of a lining in an open cavity. Laminae rarely enclose organic materials and are directed distally as they cross the core. These layers follow orientation of the sheath laminae and were apparently deposited on a firm (core) substrate.

It has been argued that certain acanthostyles opened into autozooecial chambers. Although sheath laminae are commonly thin near the base of stylets, in most examples the bases are clearly enclosed by laminae. A few are equivocal because of the plane of section. There is no clear evidence that the core of rhabdomesine acanthostyles opened into autozooecia.

Stylet function.—Interpretations of stylet function must be consistent with a number of observations of rhabdomesines. (1) Stylets are present in a majority, but not all rhabdomesine species or all members of some populations. (2) More than one stylet type may be present in a species. (3) Although stylets may be no more numerous than autozooecia, they are usually abundant, and more or less fill the exozonal wall between apertures. (4) Although in many specimens enlarged stylets are immediately proximal to the zooecia, relatively few of these are associated with only a single zooecium. (5) Evidence of other associated structures (e.g., a spine) is lacking. (6) Although usually arising at the base of the exozone, many stylets developed as the exozone enlarged and some originated during endozonal development. (7) All stylets were apparently solid structures during colony life, with no opening into zooecial chambers. Lack of internal coelomic space and physical isolation seem to preclude stylet association with such vital functions as respiration and reproduction.

It has long been argued that prominent acanthostyles would provide protection (e.g., Cumings & Galloway, 1915). The inclined orientation of the acanthostyles, and their grooved, hoodlike appearance in a few species (e.g., *Helopora inexpectata* McNair) suggest that acanthostyles may also have functioned as a guide during lophophore protrusion. Recognizing that the bryozoan colonies were covered with living tissue during life, Tavener-Smith (1975) suggested that low stylets may have provided support for surficial tissue, a function seemingly particularly appropriate for the spinose aktinotostyles.

Because paurostyles seem too small to provide effective protection and acanthostyles more prominent than necessary for simple support of soft tissue, stylets may be an example of bryozoan structures that originated for one function (tissue support) and became adapted to a new one (protection).

SKELETAL RIDGES

Skeletal ridges are elongate skeletal folds developed on rhabdomesine branches (see Fig. 266,*7*; also see 272,*1*). Such ridges are common in the suborder, and are developed in several patterns. In some genera, especially earlier ones, straight to somewhat sinuous longitudinal ridges separate rows of zooecia. Short ridges may separate successive apertures or border the proximal margins of apertures. The ridges then flare distally and join to form longitudinal ridges (see Fig. 275,*1*). Peristomes, ridges surrounding apertures, are common in older genera. In later genera, ridges are less clearly defined or absent, although the crest of the wall separating neighboring zooecia has at times been referred to as a ridge.

Skeletal ridges and derivation of stylets.—Skeletal ridges are best developed in early Rhabdomesina, in which stylets are weakly developed. Ridges probably supported soft tissue and provided strength for slender-stemmed colonies. Later in the history of the suborder, stylets apparently assumed tissue support functions, whereas thicker branches provided structural support.

The various stylet types appear to be of common origin because they intergrade morphologically and are constructed of similar materials. When they first appear in the fossil record, stylets are found along skeletal ridges, and ridge morphology provides a suitable stylet precursor. Nonlaminated calcite, typical of stylet cores, occurs in thin, locally discontinuous bands along ridge midzones. Laminated layers on either side of wall midzones are directed toward the zoarial surface and abut the midzone, suggesting the enclosing laminae of a stylet. Stylets appear to have originated by development of continuous linear cores and of sheath laminae enclosing the cores. Weakly differentiated, styletlike structures are present along the wall midzone in *Moyerella,* which provides a suitable morphological precursor to the relatively small paurostyles found in many arthrostylids.

METAPORES

Several types of small open cavities have been recognized in Paleozoic bryozoans (Fig. 269). The term "exilapore" of Dunaeva and Morozova (1967) was applied to short, hollow tubes lacking diaphragms, which arise in the exozone of some trepostomates. Utgaard (1973) and Boardman and McKinney (1976) changed the term to "exilazooecia." At least some exilazooecia were budded as a part of the normal autozooecial pattern.

The term metapore was applied by Shishova (1965) to tubular cavities arising in the basal exozone in genera of the Hyphasmoporidae (herein the Nikiforovellidae and Hyphasmoporidae). These cavities were described as either filling spaces between apertures or, more rarely, surrounding zooecial apertures. In *Acanthoclema,* only a simple metapore is developed for each autozooecium, and in such genera as *Streblotrypella* and *Nikiforovella,* metapores are scattered in the exozone. Where closely spaced, metapores are angular in transverse outline, but they are circular where widely spaced. In some specimens, metapores appear in the late endozone (Morozova, 1970, pl. 28). Although initially used only for hyphasmoporid genera, the term "metapore" is here also applied to similar structures (i.e., slender, tubular cavities arising near the base of the exozone) in *Trematella* (Rhabdomesidae) and *Rhombopora* and its allies (Rhomboporidae).

Autozooecial budding in the Rhabdomesina generally takes place at or near the axis of the branch, whereas metapores arise at the base of the exozone. Metapores are not a part of the autozooecial budding pattern of the suborder and, as open tubular structures, they are not homologous with autozooecia. Therefore, there is no reason to hypothesize the presence of polypides, a conclusion supported by the large number and small volume of metapores in some genera.

The most reasonable function for metapores seems to be as space-filling structures separating zooecia. Spacing of polypides would provide neighboring individuals with enough room for effective feeding, and skeletal material would be conserved without seriously weakening the zoarium.

The metapore-bearing *Trematella* and *Rhombopora* are not assigned to the Hyphasmoporidae or the Nikiforovellidae because the sum of their characters suggest affinities with other families.

Some metapores (e.g., in *Rhombopora* and most species of *Nikiforovella*) are superficially indistinguishable from trepostomate exilazooecia that arose in the exozone. The term "metapore" is retained in the rhabdomesines because there is no evidence that these structures arose as polymorphs, as they apparently did in trepostomates.

Mesozooecia are typical of older trepostomates. They typically arose in the outer endozone or exozone, and they contain closely spaced diaphragms. Similar structures are present in a few arthrostylids (e.g., *Helopora*); however, the term metapore is retained in the arthrostylids because no clear information is available as to their possible common origin.

OVICELLS

Brood (1970) interpreted large swellings on the stems of some specimens of *Orthopora* (=*Saffordotaxis* of Brood) *ludlowensis* (Brood) to be gonozooids. These bulbous structures are internally open and are covered by stylet-bearing, laminated, skeletal wall. They are linked to the interior of the zoarium by a zooecium. Possible gonozooids are present in other rhabdomesines, but these structures are subject to varied interpretations (e.g., pathological reactions or overgrowths on foreign objects). In most rhabdomesine species, it has not been possible to recognize brood chambers. Goryunova (1975) suggested that this implies direct development, without a brooding phase, in these bryozoans.

MONTICULES

Monticules, broadly defined as areas of modified zooecia, are relatively uncommon in the Rhabdomesina. An example in *Nicklesopora* is a specimen (Fig. 284,*1a*) with a much enlarged polymorph surrounded by a group of enlarged, angular, thin-walled polymorphs. In *Nemataxis* (see Fig. 284,*2f*), monticulelike annular bands are developed in which the zooecia are closed by terminal diaphragms. In *Rhombopora simplex* (Ulrich), described in *Bactropora* by Ulrich (1890), raised, semiannular bands were developed by elongation of exozonal intervals of zooecia, combined with minor deflections in zooecial orientations but no other apparent changes in zooecial shape.

Attenuated and, in some specimens, branchlike monticules consisting of elongate but otherwise typical autozooecia (Fig. 216, 6) have been described in conical branches of *Rhabdomeson* (Blake, 1976). The pointed tips of these monticules are apparently formed of fused stylets, and the monticules are regularly spaced in alternating rows along convex surfaces of the curved branches.

Banta, McKinney, and Zimmer (1974) hypothesized a chimneylike exhaust function for monticules in some Ordovician bryozoans, a function appropriate in the rhabdomesines. Other functions, or combinations of functions, are possible. For example, the prominent monticules of *Rhabdomeson* may have been protective or may have served as initiation points for branches (Blake, 1976). The much enlarged polymorph in *Nicklesopora* may have been reproductive or protective, as in some polymorphs in modern bryozoans, and as suggested by various authors for fossil polymorphs. Anstey, Pachut, and Prezbindowski (1976) discussed monticules as budding centers and polar points maintaining morphogenetic gradients within subcolonies.

The morphologically diverse and taxonomically isolated occurrences of monticulelike structures imply phylogenetically independent origins.

ARTICULATED ZOARIA

Articulated zoaria, in which discrete segments were linked by noncalcified material, are typical of the Arthrostylidae. Most colonies were disarticulated prior to burial, but original relationships can be seen in a few specimens (see Fig. 272,*2c*). Jointing developed both along unbranched stems and at dichotomies.

In most arthrostylids, the articulation surface on the proximal end of each zoarial segment is convex, and in most specimens there is a series of low concentric or radial ridges on the apex. The surface on the distal end of the segment is similar but usually flattened or slightly concave. Therefore, the surfaces usually were subparallel and mobility of the joint would have been limited. Articulation surfaces were solid and communication through the skeleton between segments was impossible. Many ends of segments are enlarged, so that branch diameter at the joint was greater than that along the stem. Skeletal material forming the joint surfaces is weakly laminated or nonlaminated in spite of its occurrence in the exozone, where lamination is typical. Although generally nonlaminated, faint growth lines approximately perpendicular to the articulation surface have been detected in a few specimens. These growth lines are subparallel to the zoarial surface and parallel to the overall exozonal growth surface (Fig. 267,*2,3*). This implies that the uncalcified joint material of arthrostylids was secreted in layers parallel to the growing zoarial surface, in the same orientation as that of more typical calcified walls.

Two joint patterns developed in a single Ordovician species of *Ulrichostylus*. Typical, low, conical joint surfaces are associated with a ball-and-socket pattern (Fig. 266, 7). The sockets are on the sides of branches, but have not been observed on ends of branches. A single zooecium from the parent stalk opened to form the hollow interior of the socket joint (Fig. 266,*8*); hence, the opening is a polymorph of a zooecium. The interior of the cup is lined with weakly laminated skeletal material, and radial ridges are developed on the wall surface. The remainder of the structure appears to be built of autozooecia. The ball joint forms the distal portion of the complete joint structure, and therefore occurs on the proximal end of zoarial segments. The ball consists of a steeply conical surface terminated by a commonly perforated spherical tip (Fig. 266,6). The surface bears linear ridges. The ball-and-socket joint probably was more flexible than the typical joint.

Articulated joints comparable to the arthrostylid patterns are absent from most members of later families, but may be present in Devonian *Bactropora* (see Fig. 290,*1b*) and Mississippian *Rhombopora.*

Borg (1926a) described jointing in the modern stenolaemate *Crisia.* In this genus, organic matrix of the joint is continuous with that of the calcified wall, and joint mobility is limited. Probably, rhabdomesines were similarly constructed.

FRAGMENTATION AND ZOARIAL DIMORPHISM

Some rhabdomesines were capable of increase by means of colony fragmentation. Blake (1976) described *Rhabdomeson* branches of Permian age that had apparently broken free of parent colonies and survived to resume growth elsewhere (Fig. 266,*2,4*). This is shown by healed breakage scars, some extending across individual zooecia, at the bases of many branches (Fig. 266,*1,3*). These specimens show different stages of repair, ranging from fresh breaks to near closure of the zooecial tubes and formation of an exozonal surface. The appearance of a regrown base is very different from that of a surface grown entirely against a foreign substrate. In some specimens, after breakage, a new branch developed in alignment with the axis of the old, but with the growth direction reversed (Fig. 266,*2*). The hollow axial cylinder, typical of *Rhabdomeson,* appears to be characteristic of increase by fragmentation in rhabdomesines because a Devonian *Rhabdomeson* (Fig. 266,*5*) also was broken and budding direction reversed.

Colony fragments that were subject to breakage are typically conical with the central axial cavity expanding distally as the remainder of the zoarium, the endozone and exozone, remain constant in dimensions. Such zoarial parts (Fig. 266,*3,4*) were previously assigned to a distinct genus, *Coeloconus.*

Fragmentation may have provided an effective mode of increase in higher energy environments. For example, reproduction could have been accomplished without larval loss to predation in densely populated communities dominated by suspension feeders.

The expanded, conical shape of the branch may have helped trigger fragmentation under higher energy conditions. Commonly, bases of the cones are slightly constricted immediately distal to branching points. This constriction may have provided a mechanism for local weakening of the branch in order to induce fragmentation.

Modes to increase fragmentation have been reported in modern bryozoans. Boardman and Cheetham (1973, p. 173) pointed out that in some cheilostomates, especially such free-living genera as *Cupuladria,* "fragmentation may be so common as to provide an important means of colony reproduction." Some modern fragmentation appears to be environmentally controlled. In the cheilostomate bryozoan *Discoporella umbellata* (Defrance), Marcus and Marcus (1962, p. 301) reported colonies produced by fragmentation only in depths from 3 to 4 meters, and ancestrular colonies only from depths over 70 meters. These authors suggested, "Perhaps the settlement of larvae is difficult in irregularly agitated shallow waters. However by budding the species succeeds to populate this biotope." Following fragmentation in *Discoporella umbellata,* budding begins to occur around the proximal margins of the preexisting colony, with the polarity of the new zooecia reversed from that of the old. This reversed direction of growth is not near the prefragmentation budding zone but in a previously inactive area, and the new zooecia are somewhat irregular in development. Both of these patterns are present in fragmented *Rhabdomeson.*

BIOLOGY AND DISTRIBUTION OF RHABDOMESINA

Position of epidermal tissue layers.—Growth models of Borg (1926b, 1933) have been profoundly important in reconstructing various Paleozoic bryozoans (see Boardman, Karklins, Utgaard, this revision), including the Rhabdomesina (Brood, 1970; Blake, 1973a). Critical to these interpretations is the observation that skeletal laminae in most Paleozoic bryozoans are so oriented as to necessitate secretion over skeletal surfaces, rather than from the interior of the skeleton, as in brachiopods. In these colonies, the skeleton was apparently covered by two tissue layers that were in turn separated by coelomic space. The tissue layers not only overlay the outer skeletal surface, but lined the zooecia at least to the depth of any basal diaphragm. Because skeletal walls were secreted from both sides, they have been termed compound walls, and comparable growth patterns were described by Borg (1926b) in modern tubuliporates. A second wall type, in which skeletal walls were secreted exclusively from the interior, much as in brachiopods, apparently is present only in basal walls in rhabdomesines. Such walls most commonly form basal attachment surfaces, but may also have developed where rhabdomesines encrusted foreign objects above the base of the colony. This second growth pattern, yielding so-called simple walls, is common in post-Paleozoic tubuliporates.

Apparent epidermal tissues have been discovered in the type suite of *Rhombopora simplex* (Ulrich). These brown traces form a continuous layer over the zoarial surface, lying close to the tips of the stylets in most areas, but somewhat above the tips in others. The organic layer is quite similar to that illustrated by Boardman and Cheetham (1973, fig. 36B) in a ramose trepostomate. The rhabdomesine tissues are not preserved beneath an overgrowth or other protective structure, thereby suggesting crystallization of the enclosing calcite must have taken place very early.

Rhabdomesine polypides.—Brown, apparently organic structures that seemingly represent preserved remnants of polypides (as well as other soft tissues) have been described in diverse Paleozoic bryozoans (Cumings & Galloway, 1915; later authors). Such well-preserved polypidelike remains are not known from rhabdomesines, although probable organic matter of unrecognizable shape is present in some zooecia of many zoaria. Fossils with recognizable structures in the zooecia are massive cystoporate and trepostomate bryozoans. In these groups, organic material was protected by overgrowths and diaphragms. Thus, lack of preserved remains in rhabdomesines may have resulted from the small, relatively exposed nature of the zoaria rather than from any basic original difference in polypide structure.

Reconstruction of rhabdomesine polypides must be based on comparisons with Paleozoic and modern materials, combined with information provided by the zooecial outline. Reconstructions have been presented by Newton (1971) and Tavener-Smith (1974).

Brown, spherical, possibly organic bodies occur in some zooecia. Distribution of these bodies and associated diaphragms suggest that rhabdomesines were subject to degeneration-regeneration cycles, and that polypide position advanced with ontogeny in at least those taxa in which brown bodies occur. Brown bodies have not been observed in metapores.

Astogeny.—Available information on

early astogenetic stages in the Rhabdomesina is limited. TAVENER-SMITH (1974) interpreted some small, conical structures as young rhabdomesine zoaria, although his reasons for this taxonomic assignment are not clear. TAVENER-SMITH's fossils are 1.3 to 3.0 mm in length and 0.7 to 0.9 mm in width. Surfaces of the conical zoarial bases are covered by a wrinkled material that proved to be microgranular when studied with the scanning electron microscope. Zooecia are present within the microgranular wall, where they originated near the pointed tip and grew approximately parallel to the axis of the cone. New individuals were added medially as growth proceeded. The conical, proximal, attachment area was very small. TAVENER-SMITH (1974) believed that these colonies gained added support by encrusting foreign objects as well as by enlargement of the base. In a few available thin sections of basal attachments, I observed no such conical structures as those described by TAVENER-SMITH.

Colony integration.—Following BOARDMAN and CHEETHAM (1973), colony integration in terms of interrelationships among autozooecia was quite high in the Rhabdomesina, but integration was low in terms of astogeny and polymorphism. Moreover, there was no significant change in level of integration during the known history of the group.

Ecology.—Rhabdomesines generally are associated with diverse marine faunas typically dominated by suspension-feeding epifaunal organisms (e.g., crinoids, brachiopods, bryozoans). Generally, the most abundant, largest, and best-preserved fragments occur in slabs of little-disturbed skeletal debris in fine-grained clastic rocks. Because of these associations, rhabdomesines seem to have preferred generally open, marine waters of normal salinity and perhaps of low turbulence. Influx of fine clastic material was common, but not enough sediment was introduced to preclude development of a diverse suspension-feeding fauna. The rhabdomesines are primarily present within patches of abundant shelly epifauna, probably in large part because of a need for firm attachment surfaces. Some rhabdomesines appear to have lived in nearshore, possibly open, lagoonal environments (NEWTON, 1971). BROOD (1975a) described rhabdomesines of Gotland from inferred shallow-water (20 to 50 m), soft-bottom sediments. Algae were believed to have been common.

Biogeography and biostratigraphy.—Lack of comprehensive studies have limited the use of rhabdomesines in biogeographic and biostratigraphic work, but many of the better known genera have been recognized from widely separated areas of the world. Long generic ranges appear to limit biostratigraphic usefulness; however, rhabdomesines have been extensively used in the Soviet Union.

TAXONOMIC CONCEPTS WITHIN THE RHABDOMESINA

Formal taxonomic recognition of the suborder Rhabdomesina (*nom. correct.* herein) has been relatively recent (ASTROVA & MOROZOVA, 1956), although affinities among component families were recognized earlier (e.g., MCNAIR, 1937). Most family-level taxa, including five of the six employed here, were proposed during the late nineteenth century. For many years, however, only the names Arthrostylidae and Rhabdomesidae were generally used. The content of the Arthrostylidae here remains basically unchanged from the usage of BASSLER (1953) and other earlier workers. SHISHOVA (1965) redefined the Hyphasmoporidae of VINE (1886), assigning to it those rhabdomesine genera with abundant metapores. GORYUNOVA (1975) recognized the Nikiforovellidae for those hyphasmoporid genera lacking axial zooecia and possessing abundant stylets.

Even with removal of the Hyphasmoporidae and Nikiforovellidae, the Rhabdomesidae remained a morphologically diverse family. The Rhomboporidae of Simpson (1897) is recognized here for genera sharing strong similarities of axial development, zooecial shape and arrangement, and stylet development. The Bactroporidae of Simpson (1897) is employed for a single genus. The Rhabdomesidae is characterized by a trend toward development of axial zooecia, zooecial shape, and stylet development.

Generic recognition in the suborder has been hampered by a lack of adequate illustration, and as a result, characters have remained obscure. In general, genera have been based on a small number of often rather narrowly defined characters, leaving little room for either population variation or evolutionary convergence.

Species concepts have been largely based on statistics, including average size of apertural openings or aperture spacing along a stem, number of stylets or polymorphs per square millimeter, and so on. Relatively little effort has been made to establish the taxonomic value of such information by careful comparison within and between populations, both at inter- and intraspecific levels. Intraspecific variation can be significant (Fig. 266,*3,4*; 269). Some characters used in species definition are questionable. For example, because most rhabdomesines are slender and cylindrical, only a relatively few zooecial chambers can be oriented perpendicular to the plane of section; lateral rows will have apparent apertural diameters less than their actual diameter. Even sections slightly offset from perpendicular can have an apparent diameter beyond the accuracy in hundredths of a millimeter cited in many taxonomic descriptions. Stylets, especially aktinotostyles, arise in different parts of the exozone, becoming more abundant near the zoarial surface. Therefore, numbers measured per square millimeter will change with the position of the section in the exozone.

Growth changes can be readily overlooked because available material generally is fragmentary. Relatively complete silicified specimens from the Permian of West Texas (USNM collections) commonly have relatively thin exozonal walls near growing tips, whereas older intervals typically are thicker walled, with apertures commonly either closed or much reduced. Branching in some of the West Texas zoaria is irregular, with one stem passing near to another. In these specimens, facing apertures were nearly closed by skeletal material, presumably because the proximity of the neighboring branch precluded effective lophophore function. Apertures on opposite sides of the branches are of more typical, open outline. Thus, apparent wall development and apertural size may depend not only on position in a zoarium but even on side of the branch.

Morphologic characters stressed here in the recognition of family- and genus-level taxa in the Rhabdomesina include: (1) presence of jointed zoaria (family level), nature of jointing (genus level), and zoarial growth habit (primarily genus level); (2) nature of budding locus and development of axial region (family and genus levels); (3) shape, orientation, and regularity of arrangement of autozooecia (family and genus levels); (4) presence and development of hemisepta (family and genus levels); (5) width of exozone relative to branch radius (of limited value at both family and genus levels); (6) lamellar profile in the exozone (genus level); (7) presence and abundance of metapores (family and genus levels); and (8) development of stylets (family and genus levels). Evolutionary trends are evident within some of these characters; however, taxon boundaries are based on character presence and development rather than on hypotheses of character evolution.

Discussion of evolutionary trends and comments on diagnostic characters follows.

1. Zoarial form and branching patterns provide some useful taxonomic characters, especially in older members of the suborder and within the Arthrostylidae. Various authors have noted that in stenolaemates, zoarial form may vary within genera or species. Harmelin (1973, 1975) described

significant, microenvironmentally controlled variation in colony form in several modern tubuliporate species. This variation included both encrusting and erect growth habits within single species.

Based on total characters known to me, all zoaria clearly of rhabdomesine affinities are erect, and most are dendroid. Encrusting holdfasts, both basal and in erect portions of zoaria, have been described, but these are apparently small relative to overall colony size. A number of nonramose genera possess characters suggesting both trepostomates and cryptostomates, but more research is needed to determine their affinities.

Articulated colonies may have been primitive in the Arthrostylidae and the growth pattern was largely restricted to this family. Because individual arthrostylid segments were apparently linked only by soft tissues, few colonies are preserved intact and zoarial habit is usually difficult to determine. Development of articulation facets is a guide to zoarial form, and most arthrostylids were jointed at fairly regular intervals. Clear evolutionary trends in jointing are not apparent.

Branches in most earlier genera appear to have approximately constant mature diameters, although enlarged ?basal intervals are known. Also in earlier taxa, zooecial apertures were generally arranged at the surface in regular rhombic or annular patterns. In many later genera, for example in younger rhomboporids, both branch diameter and apertural arrangement were quite irregular, even over short branch intervals. These changes took place within families; for example, diameter is constant and apertural arrangement regular in *Saffordotaxis* (see Fig. 289,*1*) and some older species of *Rhombopora,* whereas later species of *Rhombopora* (see Fig. 286,*3*) and *Megacanthopora* (see Fig. 287) are more irregular in habit. Regularity changed within genera as well; for example, zooecia are quite regular in *Helopora fragilis* Hall (see Fig. 274,*1*) from the Silurian but irregular in *Helopora inexpectata* McNair from the Devonian.

Variations in zoarial habit, noted by Harmelin (1973, 1975), are correlated with both environmental and microenvironmental changes. In the Rhabdomesina, in general, greater flexibility in zoarial habit is associated with younger genera and species. If zoarial habit in the Rhabdomesina also reflects environmental control and breadth of habitat tolerance, then seemingly later genera possessed generally broader environmental tolerance.

2. The budding locus is linear and well defined in primitive taxa. Evolutionary trends away from a sharply defined axis took place in different, but not all rhabdomesine lineages. The process began with loss of axial regularity and development of weak alignment of basal portions of zooecia within the axial region. The process continued with the development of increasingly well-defined axial bundles of zooecia. These changes are best seen in the Rhabdomesidae and Hyphasmoporidae. In the Rhomboporidae, Nikiforovellidae, and Bactroporidae, axial zooecial development is weak or absent, but the budding locus may be irregular to somewhat planar. Although irregular in some taxa, a more or less well-defined linear, planar, or cylindrical budding locus is one of the unifying conservative features of the Rhabdomesina.

3. Clearly defined evolutionary trends in zooecial shape have not been recognized.

4. Hemisepta developed independently in different lineages, being generally present in the Hyphasmoporidae and Rhabdomesidae but absent in the Arthrostylidae, Rhomboporidae, and Nikiforovellidae.

5. Although exozonal walls thicken with ontogeny, zooecia in many taxa appear to have attained an approximate mature size, as in the cheilostomates. Therefore, mature branch diameter and relative thickness of the exozone is more or less constant within a genus, and exozonal wall thickness provides some indication of affinities. Considerable variation may be seen, however, among species, among zoaria, or among branches within zoaria. Relatively thicker exozonal walls are commonly associated with later Paleozoic genera.

6. Evolutionary trends in lamellar profile have not been recognized.

7. Metapores are present in at least one genus of all recognized families except the Bactroporidae, but they are most prevalent in the Hyphasmoporidae and the Nikiforovellidae. Metapores first appear in *Cuneatopora* (Arthrostylidae) and closely related genera. Once established, metapores were conservative in development and occurrence, for only in *Cuneatopora* have populations been found in which metapores are present in some zooaria, absent in others, although abundance may vary significantly (Fig. 269). In rhabdomesines, metapore presence, especially in large numbers, or in taxa with regular arrangement of zooecia, is therefore considered to be strongly indicative of hyphasmoporid or nikiforovellid affinities.

In the Rhomboporidae and in *Trematella* of the Rhabdomesidae, metapores are developed in relatively small numbers. These genera are of somewhat irregular growth mode and the metapores appear to have functioned largely as space-filling mechanisms.

8. Stylets of different types are believed to have had a common origin along the skeletal ridges as surficial tissue support structures. Simple stylets (paurostyles) are present in primitive arthrostylids, and during the history of the suborder stylets became more strongly differentiated and more clearly defined.

Position of the zooecial boundary has been inferred to be relatively constant within the suborder and generally not of taxonomic value within the group. In some relatively primitive arthrostylid genera, the position of the boundary is clear near to and paralleling the zooecial chamber. In many genera (e.g., *Streblotrypa, Orthopora, Nemataxis*) in later families, a similar position can be detected. Position of the zooecial boundary is interpreted to be constant and to lie close to the zooecial chamber in almost all members of the suborder, which implies that extrazooecial wall is virtually ubiquitous, the amount depending on wall thickness. In *Ulrichostylus* and *Helopora,* zooecial boundaries are atypical for the suborder. In *Ulrichostylus,* the zooecial boundary is clearly defined proximal to the apertures, but the boundaries appear to flare distally, joining longitudinal dark zones. Lamellar orientation in longitudinal section still implies a probable boundary position near the chamber and the development of thick extrazooidal walls. In *Helopora,* the zooecial boundary is near the middle of the wall, and extrazooidal material is limited but does seem to be present near some zooecial junctions.

Genera of uncertain affinities.—A number of genera: *Anisotrypa, Callocladia, Coeloclemis, Dyscritella, Hyalotoechus, Idioclema, Linotaxis, Nikiforopora, Stenocladia,* and *Syringoclemis,* possess characters typical of both trepostomates and cryptostomates. Budding patterns, zooecial shapes and arrangements, zoarial growth habits, and polymorph budding positions tend to resemble trepostomates whereas lamellar profiles and development of stylets and hemisepta resemble cryptostomates. Ordinal assignment must await the future review of the trepostomates and comparative assessment of all Paleozoic genera planned for this *Treatise* revision of Bryozoa.

SYSTEMATIC DESCRIPTIONS FOR THE SUBORDER RHABDOMESINA

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Suborder RHABDOMESINA Astrova & Morozova, 1956

[*nom. correct.* herein, *pro* Rhabdomesoidea Astrova & Morozova, 1956, p. 664, suborder] [=Rhabdomesonata Shishova, 1968, p. 131, order]

Zoaria erect, generally dendroid, rarely pinnate, some unbranched. Branch jointing common in one family, otherwise rare. Branch diameters 0.1 to 6.0 mm; generally constant between bifurcations, some irregular; in jointed taxa, expanding distally along segments. Most branches subcircular in outline, few polygonal. Apertures generally in rhombic pattern, or in longitudinal rows; rarely confined to one side of branch. Longitudinal and peristomial ridges well developed to absent. Metapores present or absent; where present, ranging from few to densely spaced in exozonal walls between autozooecia. Metapores generally arising at bases of exozones, cross sections rounded where widely spaced, angular where closely spaced, diaphragms may be present. Axial regions containing linear axes, planar walls, axial cylinders, or axial bundles of zooecia. Planar walls, where developed, restricted to endozone. Walls of axial zooecia commonly thinner than neighboring endozonal walls; mural rods parallel to branch length, present in planar walls of some taxa. Zooids budded at or near axial structures or reverse surface. Zooecial bases attenuated, inflated, or flattened in longitudinal profile. Zooecial cross sections generally polygonal in endozone. Zooecia may be recumbent in endozone or diverge from 10° to 70°. Zooecial bends broadly rounded to abrupt. Living chambers generally elliptical in exozones, may be subcircular; living chambers usually oriented 70° to 90° to branch surfaces, but may be as low as 30°. Zooecial lengths 2 to 15 times diameter in late endozone. Longitudinal arrangements of zooecia regular to irregular. Hemisepta present or absent; where present, generally developed near zooecial bend; hemisepta commonly paired. Diaphragms absent to common. Exozonal widths of mature stems ranging from about one-fifth to four-fifths of branch radius. Zooecial boundaries variable; locally not visible, especially in exozone, or marked by irregular, narrow, dark zone; granular or nonlaminated material present in some areas along zooecial boundaries. Dark zones present in exozones of some taxa, similar in structure to zooecial boundaries. Lamellar profiles varying from V-shaped to flattened or concave. Extrazooecial wall material usually well developed in exozones between zooecia. Polymorphs and monticules rare. Stylets usually abundant, more than one type in many taxa; usually approximately paralleling zooecial chambers. Mural spines may be present. *Ord.-Perm.*

KEY TO GENERA OF RHABDOMESINA

Multiple routes are provided for certain genera because of character state variation within taxa and the probability of incomplete information for many fossil suites.

1 Zoaria divided into segments articulated at least terminally, in some taxa also laterally, or zoaria articulated only at base of branch; reverse surface developed in some genera (most genera of the Arthrostylidae) 2
– Zoaria not obviously articulated; reverse surface never developed 16
2(1) Reverse surface developed 3
– Reverse surface not developed 7
3(2) Branching on alternate sides of primary stem, lateral arms developed at regular intervals; articulated only basally, if at all .... *Glauconomella* (Fig. 274, *2*)
– Branching varied but not regularly alternating 4
4(3) Articulated rarely if at all; branch cross

section usually polygonal, apertures elliptical, not flaring distally *Heminematopora* (Fig. 275, *1*)

– Zoarium jointed at regular intervals 5

5(4) Apertures flaring distally, zooecia usually in 4 rows . . *Hemiulrichostylus* (Fig. 275, *2*)

– Apertures elliptical, zooecia usually in 3, sometimes 2 or 4 rows 6

6(5) Peristomes prominent *Arthrostyloecia* (Fig. 272, *1*)

– Peristomes subdued . . *Arthrostylus* (Fig. 271)

7(2) Articulated only basally, if at all 8

– Articulated at regular intervals 9

8(7) Cross section of zooecia triangular, zooecia arranged in 3-fold annular pattern; zooecia elongate .... *Hexites* (Fig. 275, *3*)

– Cross section varied but distinct, triangular, 3-fold pattern lacking; zooecia short *Nematopora* (Fig. 276, *2*)

9(7) Zooecia arranged in distinct cycles, with prominent peristomes *Osburnostylus* (Fig. 277)

– Distinct cyclic arrangement of zooecia, prominent peristomes lacking 10

10(9) Individual branch segments flaring strongly in distal direction *Sceptropora* (Fig. 279)

– Individual zoarial segments flaring weakly, if at all, in distal direction 11

11(10) Zoaria highly branched, with articulated primary, secondary, and tertiary branches (in disarticulated suites, look for different size classes and lateral articulation sockets) . . *Arthroclema* (Fig. 272, *2*)

– Zoaria rarely branched, usually articulated only terminally 12

12(11) Some zoarial segments weakly expanded distally; zooecial apertures arranged in rhombic pattern in which spiral rows appear dominant; zooecia arranged in numerous rows; true acanthostyles, metapores usually present ... 13

– Zoarial segments generally cylindrical, not expanded; zooecial apertures arranged in either annular or rhombic patterns such that longitudinal rows appear dominant; zooecia arranged in few to numerous rows; metapores absent, paurostyles usually only of stylet type 15

13(12) Diaphragmed metapores, interconnected peristomial ridges present; zoaria articulated basally .... *Moyerella* (Fig. 276, *1*)

– Diaphragmed metapores, interconnected peristomial ridges absent 14

14(13) Zooecia generally short, diverging sharply from stem axis; metapores not diaphragmed . . . *Cuneatopora* (Fig. 273, *2*)

– Zooecia generally elongate, gradually divergent; metapores diaphragmed *Helopora* (Fig. 274, *1*)

15(12) Zoaria robust, some specimens jointed only rarely, apertures flaring; zooecia sublinear, elongate, diverging gradually from central axis . . *Ulrichostylus* (Fig. 281)

– Zoaria slender, closely jointed, apertures elliptical; zooecia short, recumbent in endozone ...... *Nematopora* (Fig. 276, *2*)

16(1) Metapores almost always present 17

– Metapores absent (Arthrostylidae, Bactroporidae, Rhabdomesidae, Rhomboporidae) 27

17(16) One or more metapores present for each autozooecium (Nikiforovellidae, Hyphasmoporidae) 18

– Metapores present, but in numbers smaller than 1 for each autozooecium (Rhomboporidae, Rhabdomesidae) 33

18(17) Central axis linear or axial zooecia weakly developed, but no distinct central bundle of zooecia present; stylets usually present; zooecia generally short, length approximately 5 times diameter; zooecial base inflated (Nikiforovellidae) 19

– Few axial zooecia present or a distinct bundle of axial zooecia (possibly linear axis in one genus); stylets usually lacking; zooecia generally elongate, length approximately 10 or more times diameter, but shorter where a distinct axial bundle is present (Hyphasmoporidae) . . 23

19(18) One metapore for each zooecium; stylets present, median axis well defined *Acanthoclema* (Fig. 292, *1*)

– Metapores either absent or more than 1 metapore for each zooecium 20

20(19) Zooecia of varied lengths, with some individuals following axial region for varying distances; axis poorly defined . . 21

– Zooecial shapes constant, arrangement regular, metapores always present 22

21(20) Zooecial outline irregular, exozonal walls thin ...... *Pinegopora* (Fig. 291, *2*)

– Zooecial outline rounded, exozone robust *Nikiforovella* (Fig. 291, *1*)

22(20) Zooecia elongate, exozonal interval of living chamber oriented perpendicular to branch surface, stylets may be lacking, exozone in mature stems relatively narrow .... *Streblotrypella* (Fig. 292,*2*)

– Zooecia shorter, may be inclined to surface, stylets apparently always present, exozone in mature stems relatively wide *Nikiforovella* (Fig. 291, *1*)

23(18) Distinct axial bundle lacking, or axial region formed by about 10 or fewer axial zooecia 24

– Axial region formed by more than about 10 axial zooecia 26

24(23) Axis linear or possibly formed by very few axial zooecia . *Petaloporella* (Fig. 295)

– At least some axial zooecia forming axial region 25
25(24) Radiating dark zones present in exozone .... *Hyphasmopora* (Fig. 293, *1*)
– Radiating dark zones absent *Streblotrypa* (*Streblotrypa*) (Fig. 293, *2*)
26(23) Axial bundle large; single hemiseptum usually present on distal wall in late endozone, proximal wall inflated at zooecial bend .... *Ogbinopora* (Fig. 294, *1*)
– Axial bundle small to moderate in size, hemisepta absent *Streblotrypa* (*Streblascopora*) (Fig. 294, *2*)
27(16) Branch outlines commonly polygonal; zooecia commonly radially aligned as viewed in transverse section; endozonal interval of zooecia may be recumbent (Arthrostylidae) 28
– Branch outlines not polygonal; zooecia not radially aligned as viewed in transverse section; endozonal interval of zooecia not recumbent (Bactroporidae, Rhomboporidae, Rhabdomesidae) 33
28(27) As viewed in transverse section, zooecia in well-defined radial rows 29
– Zooecia not in well-defined radial rows ... 32
29(28) Axial zooecia present *Heloclema* (Fig. 273, *1*)
– Axial zooecia absent 30
30(29) Zooecia elongate .. *Hexites* (Fig. 275, *3*)
– Zooecia short 31
31(30) Skeletal cysts present *Pseudonematopora* (Fig. 278)
– Skeletal cysts absent . *Nematopora* (Fig. 276, *2*)
32(28) Median axis regular, well defined, linear or planar; zooecia regular in shape and arrangement ... *Nematopora* (Fig. 276, *2*)
– Median axis irregular, linear; zooecia somewhat irregular in shape and arrangement *Tropidopora* (Fig. 280)
33(27) Axial zooecia or axial cylinder generally more or less well developed; zooecia generally elongate; zooecial base more or less attenuated; paurostyles or acanthostyles, or both, present; aktinotostyles, heterostyles absent; hemisepta usually present (Rhabdomesidae) 39
– Axial zooecia and axial cylinder absent; zooecia short, zooecial base more or less inflated; aktinotostyles usually present, acanthostyles may be present, or well-developed acanthostyles present alone; heterostyles and hemisepta absent (Rhomboporidae) 34
– Axial zooecia and axial cylinder absent; zooecia elongate; exozonal intervals of living chambers inclined to stem surface; aktinotostyles, paurostyles, acanthostyles absent; heterostyles present; hemisepta present or absent (Bactroporidae) *Bactropora* (Fig. 290)
34(33) Aktinotostyles absent, well-developed acanthostyles present .. *Pamirella* (Fig. 288)
– Aktinotostyles present, acanthostyles present or absent 35
35(34) Metapores more or less common *Megacanthopora* (Fig. 287)
– Metapores absent or rare 36
36(35) Zooecial arrangement more or less regular; metapores may be present 37
– Zooecial arrangement more or less irregular; metapores absent 38
37(36) Acanthostyles present, metapores may be present ..... *Rhombopora* (Fig. 286, *3*)
– Acanthostyles and metapores absent *Saffordotaxis* (Fig. 289, *1*)
38(36) Exozone generally narrow in mature stems, endozonal walls thin; zooecia may be budded from more or less clearly defined planar axial surface *Klaucena* (Fig. 286, *1*)
– Exozone wide in mature stems, endozonal walls thick ..... *Primorella* (Fig. 289, *2*)
39(33) Median axis formed by well-defined bundle of zooecia . *Ascopora* (Fig. 283, *1*)
– Median axis varied but not formed by well-defined bundle of zooecia 40
40(39) Median axis formed by well-defined cylinder of diameter usually greater than that of zooecia; or axis open, conical *Rhabdomeson* (Fig. 282)
– Median axis varied but not enlarged, cylindrical or conical 41
41(40) Branch diameter 2 mm or greater; zooecia highly elongate, regular in arrangement; zooecial bend abrupt, monticules may be present 42
– Branch diameter usually 2 mm or less; zooecia of varied lengths but usually not highly elongate, and when elongate, zooecia of irregular arrangement; zooecial bend more or less gradual; monticules absent 43
42(41) Zooecial rows not separated by well-defined longitudinal ridges; zooids budded from somewhat irregular axis of one or more longitudinal zooecia; monticular areas of enlarged apertures may be present .... *Nicklesopora* (Fig. 284, *1*)
– Zooecial rows separated by well-defined longitudinal ridges; zooids budded from more or less clearly defined longitudinal axis; zooecia in annular bands and closed by terminal diaphragms *Nemataxis* (Fig. 284, *2*)
43(41) Zooecia short or moderately elongate, with median axis generally well defined, linear or somewhat planar; at least one pair of closely overlapping hemisepta generally present at zooecial bend *Orthopora* (Fig. 285, *2*)
– Zooecia elongate, typically following cen-

tral axis for varying distances before diverging toward exozone; median axis more or less ill defined 44

44(43) One pair of overlapping hemisepta present ....*Orthopora* (Fig. 285, *2*)

– Overlapping hemisepta absent 45

45(44) Median axis irregular but quite well defined; zooecial arrangement somewhat irregular........*Trematella* (Fig. 285, *1*)

– Median axis weakly defined, zooecial arrangement very irregular *Mediapora* (Fig. 283, *2*)

Family ARTHROSTYLIDAE
Ulrich, 1882

[*nom. correct.* ULRICH, 1888, p. 230, *pro* Arthronemidae ULRICH, 1882, p. 151] [=Arthroclemidae SIMPSON, 1897, p. 546]

Zoaria erect; generally dendroid; some unbranched; rarely planar, branching. Branch jointing usually present. Branch diameters from about 0.1 to 2.5 mm; relatively constant between bifurcations, or expanding distally along segment in jointed taxa. Branch cross sections rounded or polygonal. Apertures in longitudinal rows or rhombic pattern; reverse surfaces may be present. Longitudinal and peristomial ridges usually present; ridge development varied. Metapores may be present, with or without diaphragms. Axial regions formed by well-defined linear axes, except in taxa with reverse surfaces; planar budding surfaces and axial zooecia uncommon in a few taxa. Zooids budded near axial region or from reverse surfaces. Zooecial bases attenuated to inflated in longitudinal profile. Zooecial cross sections in endozone polygonal, usually triangular. Zooecia initially recumbent in many taxa, diverging only at zooecial bend; zooecial divergence in other taxa approximately 15° to 70°. Zooecial bends generally rounded to abrupt, but may be weakly developed. Living chamber usually elliptical in exozone, subcircular in cross section; usually oriented between 70° and 90° to surface, but may be as low as 30°. Zooecial lengths approximately 3 to 12 times diameter. Proximal wall at zooecial bend more angular and inflated than distal wall in some taxa; true hemisepta absent. Diaphragms generally rare to few. Exozonal width varied, commonly about half branch radius. Zooecial boundaries generally well developed, especially in endozone; usually dark, of granular or nonlaminated material, commonly more or less irregular. Boundaries locally not visible. Radiating dark zones arising at or near zooecial boundaries at base of exozone in some taxa. Lamellar profile in exozone generally V-shaped to rounded in transverse section; V-shaped, rounded, flattened, or concave in longitudinal section. Development of extrazooecial skeleton varied. Paurostyles or acanthostyles usually present, perpendicular to branch surface or parallel to zooecia. *L.Ord.-L.Perm.*

Arthrostylus ULRICH, 1882, *nom. subst.* ULRICH, 1888, p. 230, *pro Arthronema* ULRICH, 1882, p. 151; *non* ESCHSCHOLTZ, 1825 [**Helopora tenuis* JAMES, 1878, p. 3; OD; Economy Mbr., Eden Sh., U. Ord., Cincinnati, Ohio, USA]. Zoarium dendroid, jointed, branching at ends of segments only. Individual segments straight or slightly curved, segment diameters approximately 0.3 mm, diameters usually constant between joints except for terminal enlargement at joint surfaces. Segment cross section polygonal. In segments from single populations, apertures in 2 to 4 longitudinal rows on obverse surfaces, offset in adjacent rows. Prominent longitudinal ridges developed on reverse surfaces, between rows of apertures, and between successive chambers; peristomes present. Lateral zooecia budded from walls of reverse surfaces; medial zooecia, where developed, budded from walls of lateral zooecia. Zooecial bases inflated. Zooecia recumbent in endozone, diverging from reverse surface at zooecial bend; rounded to subpolygonal in cross section. Zooecial bends abrupt, living chambers in exozones about 90° to segment surfaces. Zooecial length from 4 to 6 times diameter; arrangement of zooecia regular. One or two thin diaphragms common near base of zooecia. Exozonal width between ridges approximately one-quarter zooecial diameter. Zooecial boundaries well defined, nonlaminated wall locally well developed between zooidal wall along reverse surface and extrazooidal wall, and along zooecial boundaries in endozone. Nonlaminated material locally forming endozonal wall; zooecial boundaries elsewhere irregular, or locally not visible. Lamellar profiles rounded over longitudinal ridges, between laterally adjacent zooecia; flattened between longitudinally successive zooecia. Paurostyles present, weakly developed. [*Arthrostylus* is distinguished on budding pattern, zooecial shape and orientation, development of nonlaminated wall, and paurostyle development. Although distinctive in growth habit and devel-

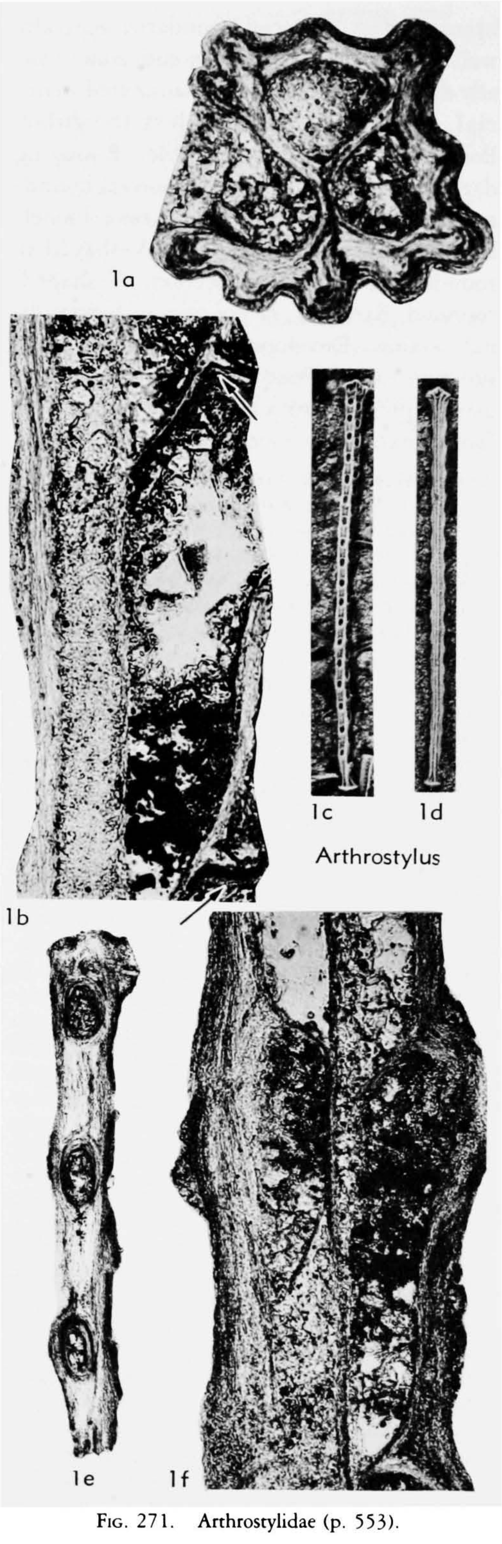

Fig. 271. Arthrostylidae (p. 553).

opment of nonlaminated walls, it resembles some other arthrostylid genera in jointing pattern and stylet development. Simpson (1897) suggested separation of *Arthrostylus* from other arthrostylid genera at the family level. Budding patterns and wall development suggest affinities between *Arthrostylus* and the Phylloporinidae.] *M.Ord.(Blackriv.)-U.Sil.(Wenlock.* or *?Ludlov.),* N.Am., Greenl., Baltic region.——Fig. 271,*1a–f.* **A. tenuis* (James); *a,* obverse surface (top), three zooecial rows, left zooecium at aperture, dark zones; transv. sec., USNM 240789, ×240; *b,* reverse surface (left), one complete zooecium and portions of two others; long. sec., USNM 240790, ×240; *c,* articulation facets, apertural arrangement, longitudinal ridges; external obverse view, USNM 240785, about ×11; *d,* articulation facets, longitudinal ridges; external reverse view, USNM 240786, about ×11; *e,* apertural arrangements; shallow tang. sec., USNM 240787, ×80; *f,* two rows of zooecia; deep tang. sec. parallel to reverse surface and perpendicular to orientation of *b,* USNM 240792, ×160.

Arthroclema Billings, 1865, p. 54 [**A. pulchellum*; M; Trenton Ls., M. Ord., Ottawa, Ont., Can.]. Zoarium branching, with well-defined axial stem and alternate secondary and tertiary branches; jointed longitudinally, laterally. Primary segments up to about 1 mm in diameter. Segment diameters generally constant except for terminal flanges in some specimens; cross sections subcircular. Apertural arrangement predominantly longitudinal, locally weakly rhombic. In most species, sinuous or straight longitudinal ridges separate apertural rows and longitudinally successive apertures. Proximal and lateral margins of aperture commonly bordered by peristome. Metapores absent. Axial region formed by well-defined linear axis. Zooecial bases weakly to moderately inflated longitudinally. In endozone, zooecial cross section subtriangular, rounded; zooecia recumbent, diverging at rounded zooecial bend. Living chambers oriented from 30° to nearly 90° to branch surface; angle increasing with exozonal thickening. Zooecial length varied, commonly 4 to 5 times diameter, up to about 10 times in primary and secondary segments. Longitudinal arrangement of zooecia regular. Diaphragms few in some species. Exozonal width varied, depending in part on segment type. Zooecial boundaries usually narrow, irregular; granular or nonlaminated material locally developed; longitudinal dark zones, similar to zooecial boundaries, developed in exozonal wall between longitudinal rows of apertures and longitudinally successive apertures. Extrazooecial skeleton well developed. Lamellar profile in exozones V-shaped against dark zones, flattened between longitudinally successive apertures. Paurostyles scattered to com-

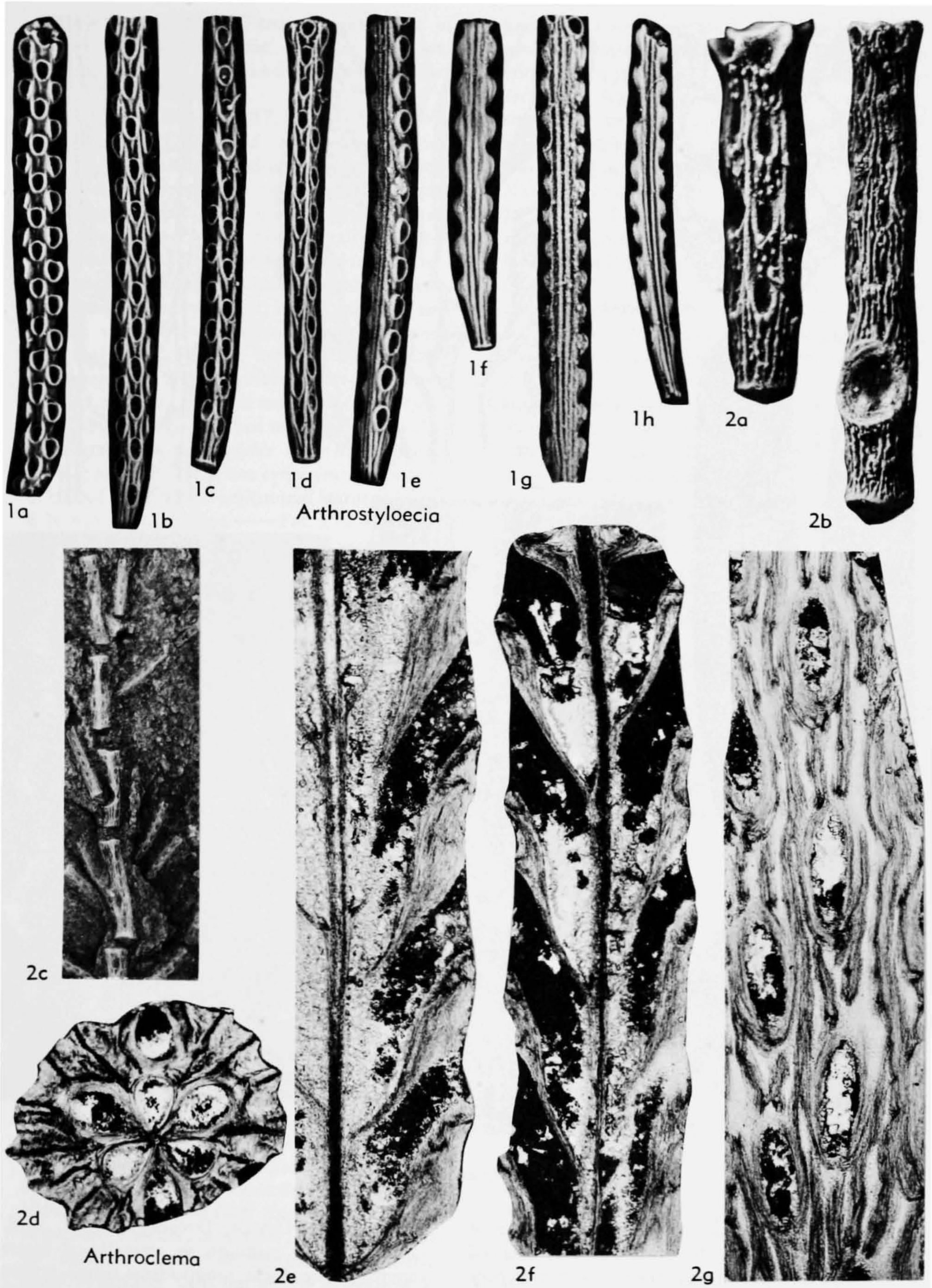

FIG. 272. Arthrostylidae (p. 554–557).

mon, usually developed on ridges. [*Arthroclema* is distinguished by zoarial form, zooecial shape, and wall structure. Tertiary segments may resemble branches of *Nematopora* and *Ulrichostylus*, and distinct size classes are necessary for differentiation (ULRICH, 1893). *Arthroclema* resembles

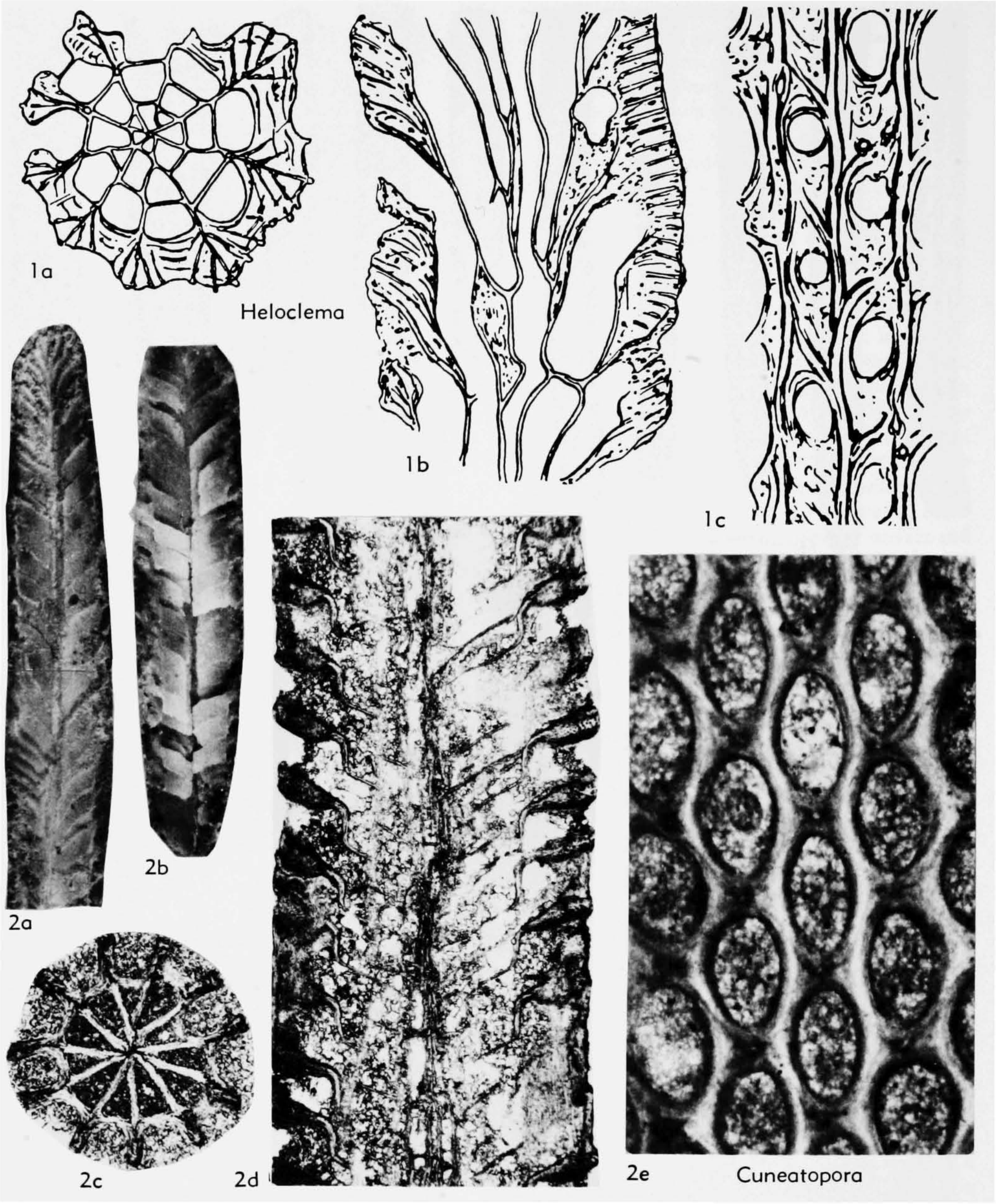

Fig. 273. Arthrostylidae (p. 557–559).

Ulrichostylus in wall structure and presence of lateral articulation joints but differs in zooecial orientation. *Arthroclema* resembles *Nematopora* in zooecial form and orientation but differs in growth habit. Bassler (1911) reported a few specimens of the Trentonian species *A.* cf. *A. armatum* from the Lower Ordovician (B_2) of Estonia, but that report is questionable.] *?L.Ord., M.Ord.(Blackriv.)-U.Ord.(Richmond.),* N.Am., Baltic region.——Fig. 272,*2a,b*. *A.* cf. *A. cornutum* Ulrich, Decorah Sh., M. Ord., Minn., USA; variation in articulation facets, apertural alignment, longitudinal ridges, stylets; probable secondary segments, USNM 240859 and 240857, both ×17.——Fig. 272,*2c–g*. **A. pulchellum,* USNM 240862; *c,* branching zoarium; exterior view, ×4; *d,* zooecial cross section and dark zones in secondary segment; transv. sec., ×75; *e,* zooecial shapes and boundaries, thick exozone; long. sec., ×75; *f,* zooecial shapes, thin exozone, and distal articulation surface in tertiary segment; long. sec., ×75; *g,* apertural arrangement, dark zones, and stylets in secondary segment; tang. sec., ×75.

Arthrostyloecia Bassler, 1952, p. 384 [**A. nitida*; OD; Edinburg F., M. Ord., Strasburg Junction, Va., USA]. Zoarium dendroid, jointed, branching at ends of segments only. Individual segments straight or slightly curved. Segment diameters approximately 0.3 mm, usually constant except for terminal enlargement. Apertures alternate in three longitudinal rows on obverse surface. Peristomes prominent; some branching and joining to form longitudinal ridges between apertural rows, between longitudinally successive apertures, and on reverse surface. Zooecia budded at or near reverse surface. [*Arthrostyloecia* is known from silicified material. Externally, it differs from *Arthrostylus* only in peristome development, but it is not synonymized because of lack of information on internal features.] *Ord.,* E.N.Am., Baltic region.——Fig. 272,*1a–h.* **A. nitida,* all about ×16; *a,* apertural arrangement and peristomes; holotype, USNM 116409; *b–h,* apertural arrangement, longitudinal ridges, reverse surfaces, and peristomes; paratypes, USNM 240795, 240798, 240799, 240802, 240803, 240805, and 240806.

Cuneatopora Siegfried, 1963, p. 138 [**C. erratica*; OD; in clasts of possible M. Ord. age from glacial deposits, Baltic region]. Zoarium erect, not known to branch, jointed longitudinally. Segments usually straight, approximately 0.5 to 2.5 mm in diameter. Segments generally expanding distally; circular in cross section. Apertural arrangement rhombic. Longitudinal ridges and peristomes absent. Metapores present or absent; where developed, arising in exozone, usually at junction of three autozooecia, diaphragms absent. Zooecia inflated or flattened; at bases cross section in endozone polygonal, commonly triangular. Zooecial divergence from axis between 35° and 70°. Zooecial bend abrupt, zooecial axis in exozone commonly parallel to axis of endozone. Living chambers generally inclined between 80° and 90° to segment surface, may be as low as 60°. Zooecial length approximately 3 to 6 times diameter. Longitudinal arrangement of zooecia regular. Diaphragms absent from zooecia. Exozonal width usually about half branch radius. Zooecial boundaries commonly obscure; or narrow, irregular, granular material locally developed. Extrazooecial skeleton limited. Lamellar profile in exozone V-shaped to weakly rounded. Acanthostyles well developed. Prominent conical or cylindrical deflections common in sheath laminae. [*Cuneatopora* is distinguished on zoarial habit, budding pattern, zooecial shape and orientation, presence of metapores and acanthostyles, and reduction of extrazooidal skeleton. Longer zooecia in this genus are similar to the shorter zooecia of *Helopora* in shape, growth habit, stylets, and presence of metapores.] *?M.Ord.,Sil.(Llandov.-Wenlock.),* N.Am., Eu.——Fig. 273,*2a,b.* **C. erratica*; *a,* broken, relatively elongate, proximal zooecia; holotype, Münster B523a, ×10; *b,* zooecial shapes in broken paratype; Münster B523d, ×10.——Fig. 273,*2c. C. bellula* (Billings), Jupiter F., L.Sil., Anticosti Is., Can.; zooecial shapes and exozonal development; transv. sec., USNM 240780, ×70.——Fig. 273,*2d,e. C. lindstroemi* (Ulrich), Sil., Gotl., Swed.; *d,* zooecial outlines; long. sec., ?paratype, USNM 240863, ×35; *e,* apertural arrangement, shapes, stylets; tang. sec., ?paratype, USNM 214193, ×70.

Glauconomella Bassler, 1952, p. 384 [**Glauconome disticha* Goldfuss, 1831, p. 217; OD; Wenlock Ls., equals Dudley of Goldfuss, U. Sil., Eng.]. Zoarium pinnate; primary, secondary branches only; jointing unknown. Branch diameters approximately 0.5 mm, constant between bifurcations; branch cross section rounded on reverse side, angular on obverse side. On obverse surface, apertures aligned in 4 longitudinal rows, 2 on each side of median keel; reverse surface bearing fine ridges. Metapores absent. Median zooid rows budded from walls of lateral zooids; lateral zooid rows budded from reverse surface. Zooecial bases inflated. Zooecial cross section in endozone polygonal to rounded. Zooecia recumbent in endozone, diverging only at zooecial bend; apertures large. Zooecia short, flask-shaped, length approximately 4 times diameter, longitudinal arrangement regular. Diaphragms present in some species. Zooecial boundaries well defined, wide, irregular, usually containing granular material, nonlaminated material locally developed, especially between zooecial rows. Planar dark zones, similar to zooecial boundaries, radiating in exozone from zooecial boundaries; exozonal dark zones paralleling branch axis. Extrazooecial skeleton well developed. Lamellar profile in exozone V-shaped against dark zones, rounded to flattened away from dark zones. Stylets absent. [*Glauconomella* is distinguished on branching pattern, presence of a reverse surface, zooecial and apertural shapes, and wall structure. Limits and affinities of the genus are uncertain. Some species of *Glauconomella* and *Penniretepora* are superficially similar and, in general, the post-Silurian species have been assigned to *Penniretepora.* Whether or not these genera are distinct is uncertain, and a Silurian limit to *Glauconomella* is arbitrarily accepted here. *Glauconomella* is very similar to *Nematopora* in zooecial shape and wall structure, but differs in budding and branching patterns.] *U.Ord.-U.Sil.(Wenlock.),* Eu., N.Am.——Fig. 274,*2a–e.* **G. disticha* (Goldfuss), *a–c* from Eng. and *d,e* from Gotl.; *a,* branching pattern

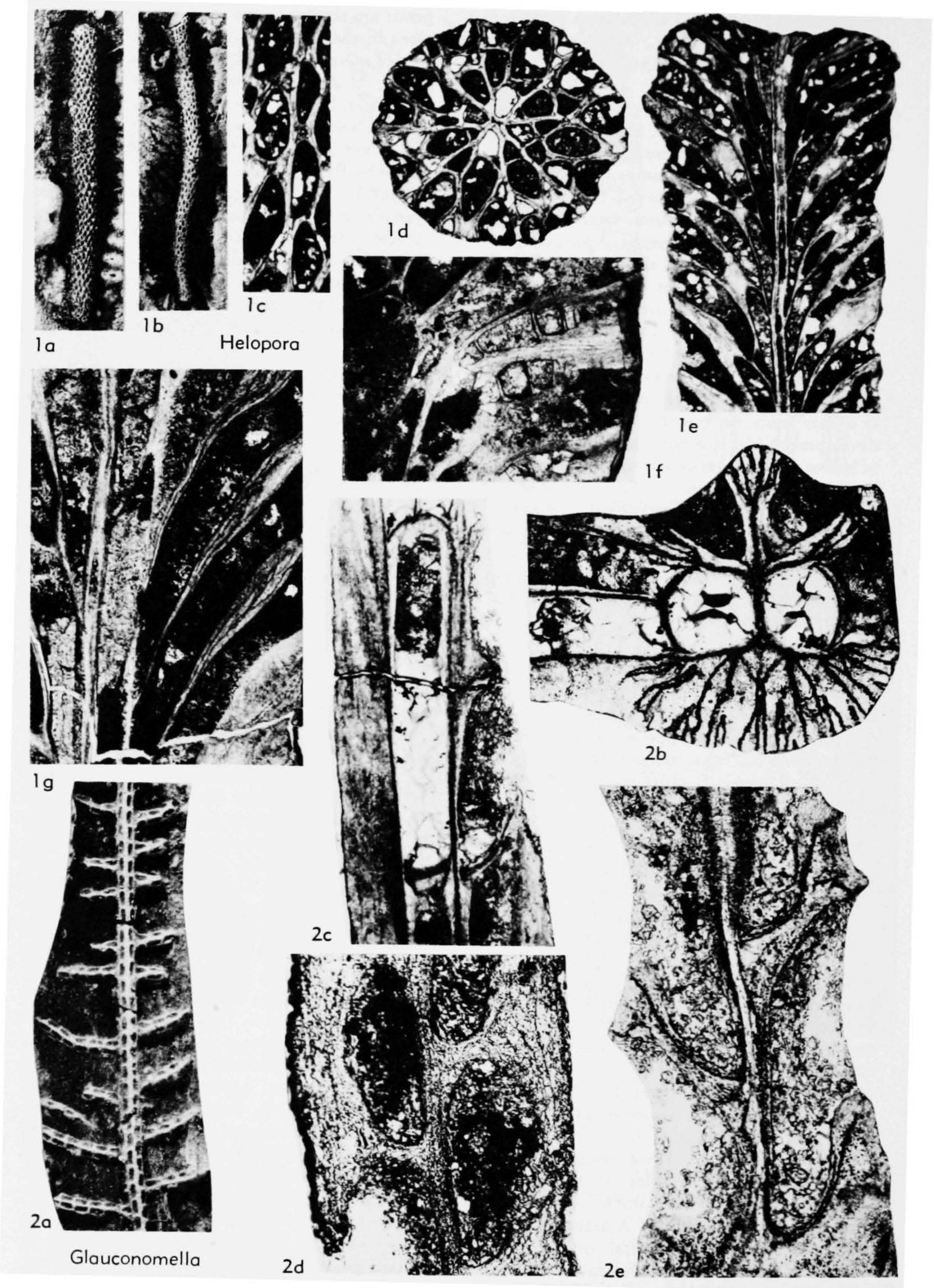

FIG. 274. Arthrostylidae (p. 557–559).

and apertural arrangement on obverse surface; USNM 240808, ×6; *b,* lateral branch (left), zooecial cross section and arrangement, dark zones; transv. sec., USNM 240810, ×75; *c,* reverse surface (left); deep tang. sec. of left zooecial row, long. sec. of right zooecial row, USNM 240810, ×50; *d,* apertural arrangement and shapes; deep tang. sec., USNM 240811, ×75; *e,* zooecial outlines; long. sec. parallel to reverse surface, USNM 240811, ×75.

Heloclema Shulga-Nesterenko, 1955, p. 139 [**H. spiralis*; OD; Steshevskij Level, L. Carb., Oka River, Luzhki Village, Russ. plat., USSR]. Zoarium dendroid, jointing unknown. Branches 0.55 to 0.70 mm in diameter, subcircular in cross section. Apertures in 7 to 9 longitudinal rows, separated by ridges; metapores absent. Axial region formed by few axial zooecia. Zooecial bases attenuated to weakly inflated. Zooecial cross section in endozone polygonal, initially triangular. Zooecial divergence from axial region approximately 15° to 30°; zooecial bend abrupt. Living chambers oriented from 70° to 90° to branch surface. Autozooecial length generally about 10 times diameter. Longitudinal arrangement of autozooecia somewhat irregular. Proximal wall angular at zooecial bend; diaphragms rare. Exozonal width varied, generally about half branch radius. Zooecial boundaries well defined, narrow; nonlaminated material locally developed. Planar, longitudinal, dark zones radiating through exozone from approximate position of zooecial boundaries at base of exozone. Extrazooecial skeleton well developed. Lamellar profile in exozone V-shaped against dark zones. Stylets developed on longitudinal ridges between apertures. [*Heloclema* is distinguished by zooecial shape and orientation, arrangement of stylets, and development of the exozonal wall. It resembles *Nematopora* in development of the exozonal wall and arrangement of stylets.] *L.Carb. (Visean),* USSR.——Fig. 273,*1a–c.* **H. spiralis*; drawings of zooecial shapes and arrangements; *a,* transv. sec.; *b,* long. sec.; *c,* tang. sec., ×55 (Shulga-Nesterenko, 1955).

Helopora Hall in Silliman, Silliman, & Dana, 1851, p. 398 [**H. fragilis*; M; ?Cabot Head Sh., Cataract Gr., equals Clinton Gr. of Hall, L. Sil., Flamborough Township, near ?Hamilton, Ont., Can.]. Zoarium erect, not known to branch, jointed longitudinally. Individual segments generally straight, diameters 0.5 to 2.0 mm. Segments expanding distally along length, or enlarged terminally at joint surfaces; cross sections circular. Apertural arrangement basically rhombic. Longitudinal ridges, peristomes absent. Metapores with diaphragms common in some species, especially at expanded ends of segments. Metapores narrower than zooecia, arising in exozone, paralleling zooecia; diaphragms thickened, irregularly spaced. Axial region formed by more or less well-defined linear axis. Zooecial bases weakly inflated, or attenuated. Zooecial cross section polygonal in endozone, initially triangular. Zooecial divergence from axis ranging from 25° to 70°; zooecial bend rounded. Living chambers oriented from 60° to 90° to zoarial surface. Zooecial length from 6 to 10 times diameter. Longitudinal arrangement of zooecia regular to irregular. Zooecial diaphragms few. Exozonal width about half segment radius. Zooecial boundaries locally obscure; where developed, usually narrow, irregular, commonly granular; nonlaminated material may be developed. Extrazooecial skeleton limited. Lamellar profile in exozone V-shaped to somewhat rounded. Acanthostyles large, well developed, common on zooecial boundaries, arising near base of exozone; prominent conical deflections common in sheath laminae. [*Helopora* is distinguished on segment shape, apertural arrangement, budding pattern, zooecial shape and orientation, presence of acanthostyles and metapores with diaphragms, and reduction of extrazooecial skeleton.] *L.Sil. (Llandov.)-L.Dev., ?M.Dev.(Eifel.), U.Dev.,* E.N.Am., S.Am., USSR.——Fig. 274,*1a–g.* **H. fragilis*; *a,b,* stem shapes and apertural arrangement; syntypes, AMNH 30718, 30722, both ×6; *c,* apertural arrangement, stylet development; deep tang. sec., USNM 240814, ×50; *d,* zooecial and metapore cross sections; transv. sec., USNM 240814, ×50; *e,* expanded distal end of stem, zooecial shapes, acanthostyles; long. sec., USNM 240818, ×30; *f,* distal end of segment, metapore; long. sec., USNM 222622, ×75; *g,* zooecial shapes and boundaries, lamellar profile; long. sec., USNM 240816, ×75.

Heminematopora Bassler, 1952, p. 384 [**H. virginiana*; OD; Edinburg F., M. Ord., Strasburg Junction, Va., USA]. Zoarium dendroid, not known to be jointed. Branch diameters approximately 0.25 mm, constant between joints. Apertures alternating in 5 to 7 longitudinal rows on obverse surface; lateral rows discontinuous, some apertures separated by barren intervals continuous with reverse surface. Ridges in varied patterns on obverse surface; peristomial ridges usually complete about apertures; some peristomes branching and joining to form sinuous longitudinal ridges between apertural rows or between longitudinally successive apertures. Converging longitudinal ridges developed on reverse surface. Zooecia budded at or near reverse surface; exozonal interval of living chamber inclined to branch surface. [Known only from silicified material, *Heminematopora* is distinguished on budding pattern, development of ridges, and zooecial orientation.] *Ord.,* E.N.Am., Baltic region.——Fig. 275,*1a–f.* **H. virginiana,* all about ×16; *a,* zooecial arrangement, longitudinal ridges; holotype, USNM 116411; *b–f,* zooe-

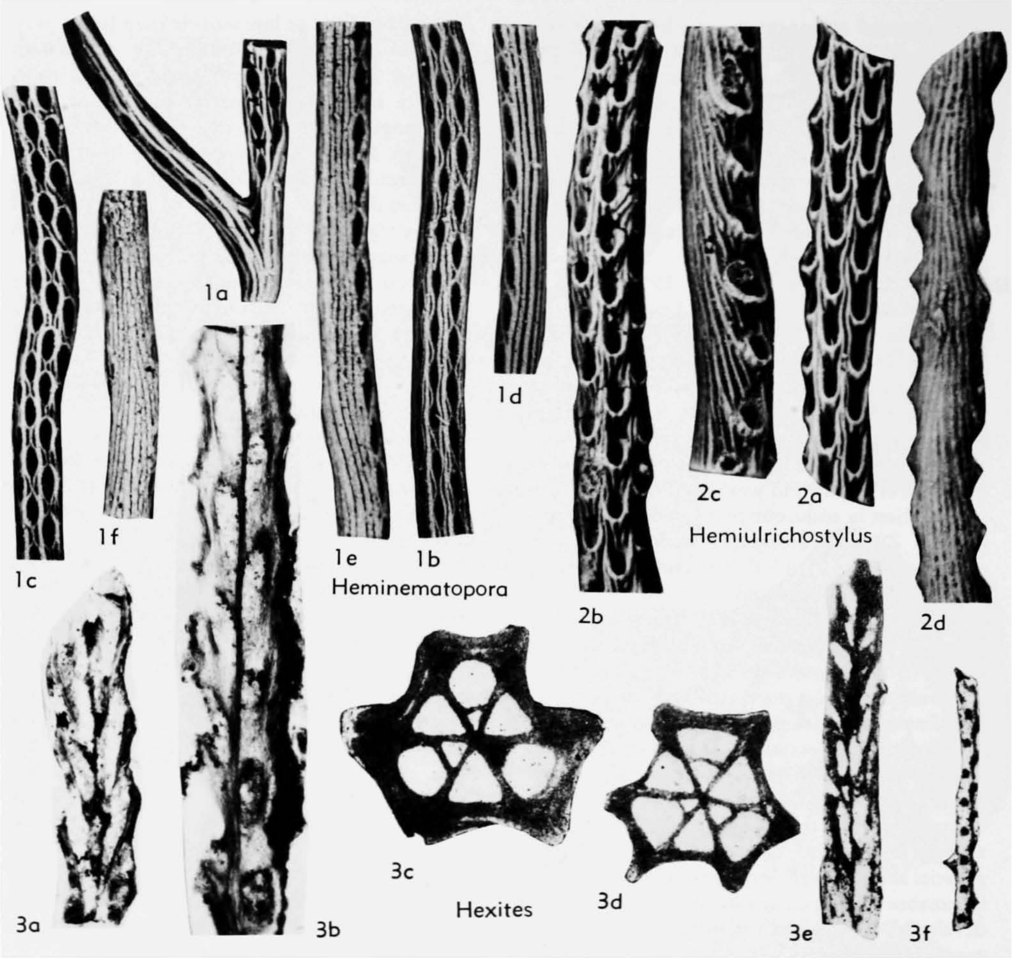

FIG. 275. Arthrostylidae (p. 559–560).

cial arrangement, longitudinal ridges, reverse surfaces; paratypes, USNM 240822–240826.

Hemiulrichostylus BASSLER, 1952, p. 384 [**H. lineatus*; OD; Edinburg F., M. Ord., Strasburg Junction, Va., USA]. Zoarium erect, not known to branch or to be jointed; diameters approximately 0.5 mm, constant. Apertures alternating in 4 longitudinal rows on obverse surface. Peristomes complete in some specimens or apertures proximally and laterally bordered by prominent ridges flaring distally to join longitudinal ridges between zooecial rows; some ridges converging distally on reverse surface. Ridges on sloping surfaces between longitudinally successive apertures. Exozonal interval of living chamber inclined to surface. Plane of aperture inclined to stem axis. [Known only from silicified material, *Hemiulrichostylus* is distinguished by budding pattern, development of ridges, and zooecial arrangement.] *M.Ord.(Blackriv.),* E.N.Am.——FIG. 275,*2a–d*. **H. lineatus,* all about ×20; *a,* zooecial arrangement, ridges; holotype, USNM 116412; *b–d,* obverse and reverse surfaces, zooecial arrangement, longitudinal ridges; paratypes, USNM 240819–240821.

Hexites SHULGA-NESTERENKO, 1955, p. 137 [**H. triangularis*; OD; Tul'skij level, L. Carb., Chekhurskij Village, Russ. plat., USSR]. Zoarium dendroid, jointing unknown. Branches with diameters 0.18 to 0.38 mm, cross sections polygonal. Apertures with peristomes in six longitudinal rows, separated by prominent ridges; metapores absent. Axial region formed by well-defined linear axis. Zooids budded around axis in groups of three. Zooecial bases attenuated or weakly inflated. Zooecial cross sections triangular in endozone. Zooecia initially recumbent in endozone, then diverging at approximately 25°. Zooecial bend weakly defined, proximal wall profile angular, distal wall profile more or less straight. Zooecial length about 7 times diameter. Longitudinal arrangement of zooecia regular.

Proximal wall swollen at zooecial bend, but true hemisepta not developed; diaphragms absent. Exozonal width approximately half branch radius at longitudinal ridge positions, one-fourth radius over zooecia or less. Extrazooecial skeleton well developed. Lamellar profile in exozone flattened between longitudinally successive zooecia. Small stylets present on longitudinal ridges. [*Hexites* is distinguished on budding pattern and zooecial shape.] *L.Carb.(Visean),* USSR.——FIG. 275,*3a–f*. **H. triangularis*; *a,* zooecial outlines, linear axis; long. sec., holotype, PIN 309/66, ×30; *b,* apertural outlines, longitudinal ridges; tang. to deep tang. sec., holotype, ×40; *c,* zooecial cross sections; transv. sec., holotype, ×80; *d,* zooecial cross sections; transv. sec., paratype, PIN 309/80, ×80; *e,* zooecial outlines; long. sec., paratype, PIN 309/32, ×25; *f,* external view; paratype, PIN 309/32, ×10 (Shulga-Nesterenko, 1955).

Moyerella NEKHOROSHEV, 1956b, p. 45 [*M. stellata*; OD; L. Sil. (Llandov.), Mojero, Kurejka rivers, Sib. plat., USSR]. Zoarium erect, not known to branch, jointed longitudinally; segment diameters from less than 0.5 to more than 1.5 mm. Segments expanding distally along length; circular in cross section. Apertural arrangement rhombic. Longitudinal ridges lacking except at tapered segment base; zooecial apertures lacking in base. Peristomes prominent, at least in type species; deflected distally and usually intersecting with peristome of next aperture. Metapores with diaphragms, parallel to zooecia, arising near base of exozone, usually at juncture of three zooecia. Axial region formed by linear axis or planar budding surface. Zooecial bases attenuated. Zooecial cross sections polygonal in endozone, commonly triangular. Zooecial divergence from axial region 30° to 45°. Zooecial bend rounded to abrupt; zooecial axis in exozone commonly subparallel to axis in endozone, offset distally. Living chambers usually oriented from 60° to 70° to zoarial surface. Zooecial length usually 3 to 5 times diameter. Longitudinal arrangement of zooecia generally regular. Diaphragms rare. Exozonal width varied, commonly about half stem radius. Zooecial boundaries typically narrow, locally irregular, granular. Nonlaminated material thin, discontinuous in endozone, somewhat thickened in exozone in peristomial ridges. Lamellar profile in exozone V-shaped. Large acanthostyles developed at junction of peristomes; prominent conical or cylindrical deflections present in sheath laminae. Small paurostyles present along peristomial ridges. [*Moyerella* is distinguished on zooecial shape and orientation, as well as metapore, stylet, and peristomial ridge development. It resembles *Cuneatopora* in zooecial shape and orientation and *Helopora* in budding pattern and metapore development.] *L.Sil.(Llandov.),* USSR.——FIG. 276,*1a–e*. **M. stellata,* paratypes; *a,* apertural arrangement, peristomial ridges; USNM 240832, ×20; *b,* apertural arrangement, peristomial ridges; tang. peel, USNM 240833, ×75; *c,* zooecial outlines, arrangement; transv. sec., USNM 240833, ×75; *d,* peristomial ridges; tang. sec., USNM 240833, ×200; *e,* zooecial shapes, arrangement; long. sec., USNM 240833, ×75.

Nematopora ULRICH, 1888, p. 231 [**Trematopora minuta* HALL, 1876, pl. 11; OD; Waldron Sh., M. Sil., Waldron, Ind., USA]. Zoarium dendroid, usually jointed only at base; unjointed in some species (specimens?); closely jointed in at least one species. Branch or segment diameters 0.1 to 0.7 mm; usually constant between bifurcations or joints. Branch cross section polygonal to subcircular. Apertures in 4 to 10 longitudinal rows. Prominent longitudinal ridges usually present between apertural rows and longitudinally successive apertures. Peristomes commonly present, metapores absent. Axial region usually formed by well-defined linear axis; planar median wall developed locally in some species. Two or three median rods developed in walls of some specimens. Zooecial bases inflated. Zooecial cross sections in endozone triangular. Zooecia recumbent in endozone, diverging from axis at zooecial bend; zooecial bend abrupt. Living chambers oriented 90° to branch surface. Zooecial length from 4 to 6 times diameter. Longitudinal arrangement of zooecia regular. Diaphragms absent. Exozonal width approximately half branch radius at ridges. Zooecial boundaries generally well defined, narrow; locally with granular or nonlaminated material. Planar, longitudinal dark zones, similar to zooecial boundaries, radiate through exozone from approximate position of zooecial boundaries. Lamellar profile in exozone V-shaped against dark zones in transverse section, flattened to slightly concave in longitudinal section. Extrazooecial wall material well developed. Paurostyles common on ridges in many species. [*Nematopora* is distinguished on branch and zooecial shapes, surficial features, and development of zooecial boundaries and exozonal dark zones. Its branches commonly resemble tertiary segments of *Arthroclema.*] *M.Ord.-L.Perm.,* N.Am., Eu., USSR, Asia.——FIG. 276,*2a*. **N. minuta* (HALL); zoarial form; syntype, AMNH 1919, about ×8.——FIG. 276,*2b*. *N. granosa* ULRICH, ?Decorah Sh., M. Ord., Minn., USA; branch shape, apertural arrangement, stylets, longitudinal ridges; USNM 240834, about ×20.——FIG. 276,*2c–e*. *N. lineata* (BILLINGS), Ellis Bay F., L. Sil., Anticosti Is., Can., all ×75; *c,* zooecial cross section, dark zones, median rods; transv. sec., USNM 240836; *d,* apertural arrangement, zooecial boundaries, dark zones; tang. sec., USNM 240838; *e,* zooecial shape, zooecial boundaries; long. sec. through apertures, USNM 240840.

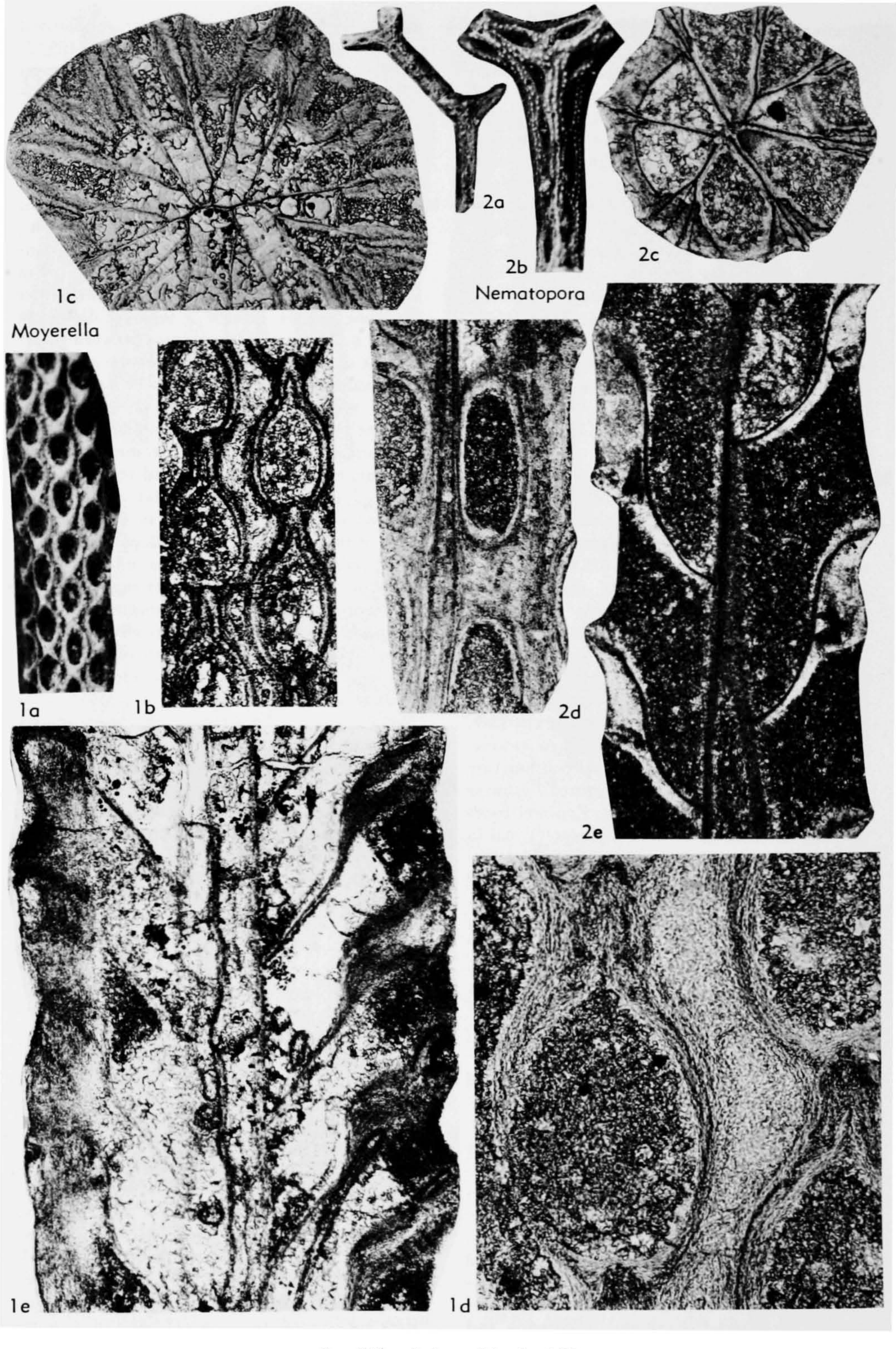

FIG. 276. Arthrostylidae (p. 561).

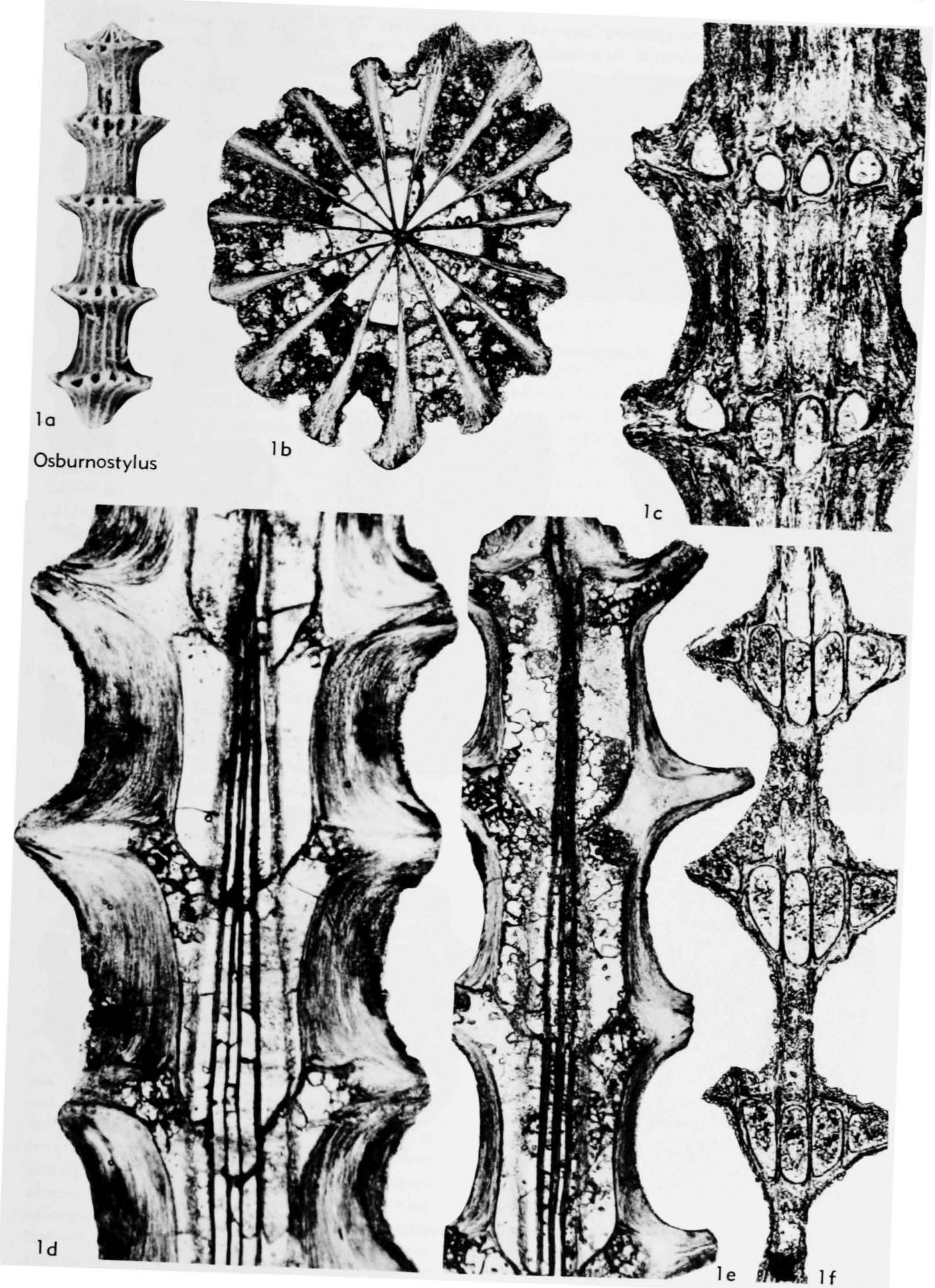

FIG. 277. Arthrostylidae (p. 563).

Osburnostylus BASSLER, 1952, p. 381 [**O. articulatus*; OD; Benbolt F., M. Ord., Rye Cove, Va., USA]. Zoarium erect, jointed longitudinally; branching not observed. Segments straight or

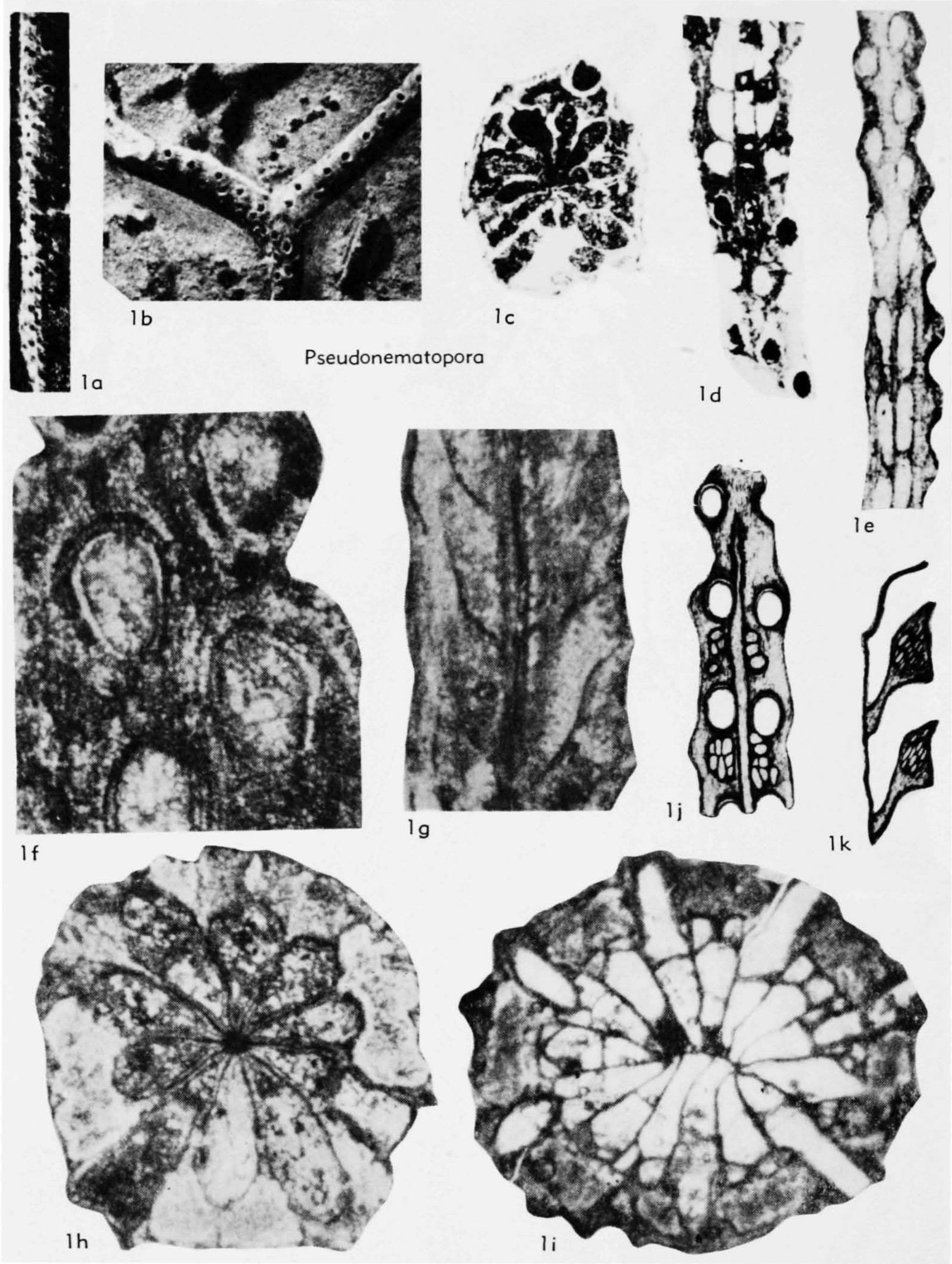

FIG. 278. Arthrostylidae (p. 565).

curved, diameters 0.5 to 1.0 mm, cross sections approximately circular. Apertures aligned in approximately 15 longitudinal rows; transversely, in prominent annular bands. Prominent longitudinal ridges separating apertural rows. Metapores absent. Axial region formed by well-defined linear axis. Zooecial bases inflated. Zooecial cross sections triangular in endozone. Zooecia recumbent in endozone, diverging from axis at zooecial bend; zooecial bend rounded. Living chambers oriented from 70° to 90° to segment surface. Zooecial length about 7 to 10 times diameter. Longitudinal arrangement of zooecia regular. Diaphragms present near base of some zooecia. Exozonal width varied. Zooecial boundaries usually well defined, locally obscure, narrow. Extrazooecial skeleton well developed. Lamellar profile in exozone V-shaped in transverse section at level of apertures; flattened to concave in longitudinal section. Acanthostyles well developed lateral to zooecial chambers. [*Osburnostylus* is distinguished by growth habit, budding pattern, zooecial shape and orientation, and presence of acanthostyles. It resembles *Nematopora* in zooecial orientation and shape, and *Helopora* in the large number of zooecia about the axis and the presence of acanthostyles.] *M.Ord.(Blackriv.),* E.N.Am.——FIG. 277,*1a–f*. **O. articulatus*; *a,* annular zooecia; paratype, USNM 240841, about ×15; *b,* zooecial outlines, linear axis; transv. sec., paratype, USNM 240842, ×75; *c,* thick exozone, apertural arrangement; tang. peel, paratype, USNM 240843, ×50; *d,* thick exozone, zooecial outlines and arrangement; long. sec., paratype, USNM 240843, ×50; *e,* thin exozone, zooecial outlines and arrangement; long. sec., paratype, USNM 240844, ×50; *f,* thin exozone; deep tang. peel, paratype, USNM 240845, ×50.

Pseudonematopora BALAKIN, 1974, p. 130 [**Nematopora? turkestanica* NIKIFOROVA, 1948, p. 39; OD; L. Carb. (low. Visean), W. Talas Alatau Ra., S. Kazakh., USSR]. Zoarium dendroid, unjointed. Branch diameters 0.8 to 2.8 mm; usually constant between bifurcations. Branch cross sections subcircular. Apertures in 8 to 16 longitudinal rows. Longitudinal ridges present or absent; peristomes complete or only on proximal sides of apertures, tapering distally. Metapores absent. Axial region formed by well-defined linear axis or planar median wall; median wall present in most branches between 1.3 and 2.6 mm in diameter; median rods absent. Zooecial base weakly inflated. Zooecial cross sections in endozone triangular (where budded along linear axis, or at ends of median wall) to polygonal (where budded along median wall). Zooecia initially recumbent, diverging from axis near gradual zooecial bend. Living chambers oriented from 55° to 90° to branch surface. Zooecial length about 3 to 5 times diameter. Longitudinal arrangement of zooecia regular. Diaphragms absent. Exozonal width approximately one-third of branch radius. Zooecial boundaries dark, well defined, narrow. Planar, longitudinal dark zones similar to zooecial boundaries, probably present in exozone. Lamellar profile in exozone flattened to slightly concave; extrazooecial wall material well developed. Skeletal cysts may be well developed at endozonal-exozonal boundary. Stylets absent. [*Pseudonematopora* is distinguished on the usual presence of skeletal cysts and a planar median wall. BALAKIN (1974) cited NIKIFOROVA (1948) as the original publication of *N.? turkestanica,* but NIKIFOROVA (1948) cited a 1936 date and the title "Lower Carboniferous Bryozoa from the western extremity of the Talaskian Alatau." No journal was cited, and I have been unable to trace the source.] *L.Carb.(low. Tournais.-low. Visean),* USSR.——FIG. 278,*1a–k*. **P. turkestanica* (NIKIFOROVA); *a,b,* Kassin strata, Karaganda region, and Irsu-Kazanchukur divide, respectively; exterior surfaces and zooecial arrangement; TsGM 5648, both ×4 (Nekhoroshev, 1953); *c–e,* Irsu-Kazanchukur divide; transv., deep tang., and tang. to deep tang. secs.; paratypes, TsGM 6548/808, all ×20; *f–i,* Kshikainda Suite, low. Visean (Balakin, 1974); *f,* tang. sec., MGU 409/513, ×59; *g,* long. sec., MGU 409/1950, ×20; *h,* linear axis, transv. sec., MGU 409/8552, ×30; *i,* planar median wall, transv. sec., MGU 409/1121, ×39; *j,k,* Dzhaltyrsky F., up. Visean; skeletal cysts; tang., long. secs., TsGM 184a, both ×20 (Nekhoroshev, 1956b; illustrated as *Nematopora peregrina*).

Sceptropora ULRICH, 1888, p. 228 [**S. facula*; M; Stony Mountain F., U. Ord., Stony Mt., Manit., Can.]. Zoarium dendroid, jointed longitudinally, bifurcations rare. Segments straight; slender proximally, expanding more or less abruptly in distal direction to form bulbous or discoid end; subcircular in cross section. Apertures aligned in 12 to 20 distal rows, absent proximally. Prominent longitudinal ridges separating apertural rows. Angular metapores with diaphragms may enclose zooecial chambers. Axial region formed by well-defined linear axis. Zooecial bases weakly inflated. Zooecial cross sections polygonal in endozone, commonly triangular. Zooecia recumbent in proximal interval of segment, diverging abruptly if budded distally. Zooecial outline broadly rounded, zooecial bend not distinct. Living-chamber orientation dependent on zooecial position. Zooecial length varied with position, from less than 4 to more than 10 times diameter. Longitudinal arrangement of zooecia regular to somewhat irregular. Zooecial diaphragms absent. Exozone forming most of branch radius near segment base, relatively narrow distally. Zooecial boundaries usually well defined, locally obscure; granular or nonlaminated material in some intervals. Extrazooecial skeleton well developed. Lamellar profile V-shaped in exozone. Paurostyles abundant on ridges. [*Sceptropora* is distinguished on segment shape, zooecial shape and orientation, and metapore and stylet development. It is similar to *Helopora* in budding pattern, zooecial shape and orientation, and presence of metapores, but differs in segment shape.] *U.Ord.(Richmond.)-L.Sil.(Llandov.);?U.Sil. (?Wenlock.),* N.Am.,

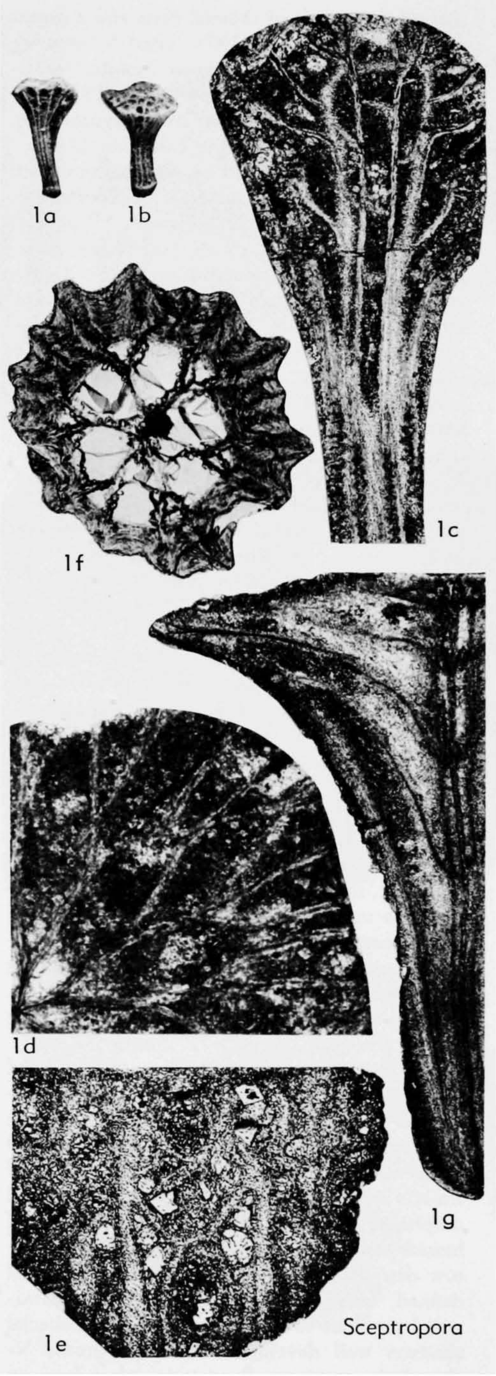

FIG. 279. Arthrostylidae (p. 565).

Baltic Region, USSR.——FIG. 279,*1a–f*. **S. facula*, *a–e* syntypes; *a*, segment shape, longitudinal ridges, apertures; USNM 240848, about ×6; *b*, surface of expanded distal end of segment; USNM 240849, about ×6; *c*, zooecial arrangement; deep tang. sec., USNM 240851, ×60; *d*, zooecial orientation, median axis; transv. sec. near distal end of segment, USNM 240850, ×60; *e*, zooecial apertures at distal end of segment; tang. peel, USNM 240846, ×80; *f*, U. Ord., Anticosti Is., Can.; zooecial arrangement; transv. sec. near proximal end of segment, USNM 240847, ×160; *g*, Elkhorn F., U. Ord., Ohio, USA; zooecial outlines and arrangement; long. sec., USNM 240852, ×60.

Tropidopora HALL, 1886, pl. 25 [**T. nana*; M; Onondaga Ls., equals Helderberg Gr. of HALL, M. Dev., Onondaga Valley, Erie Co., N.Y., USA]. Zoarium dendroid, jointing unknown. Branch diameters approximately 0.4 mm, constant between bifurcations; branch cross section subcircular. Apertural arrangement rhombic, somewhat irregular. Weak longitudinal ridges separating apertural rows; peristomes, metapores absent. Axial region formed by irregular linear axis. Zooecial bases attenuated to weakly inflated. Zooecial cross sections triangular, rounded in endozone. Zooecia recumbent in endozone, diverging from axis at abrupt zooecial bend. Living chambers oriented from 80° to 90° to branch surface. Zooecial length from 5 to 6 times diameter. Longitudinal arrangement of zooecia somewhat irregular. Diaphragms absent. Exozonal width about half branch radius. Zooecial boundaries narrow, granular; nonlaminated material locally developed. Extrazooecial skeleton well developed. Lamellar profile flattened in exozone. Paurostyles scattered on or near longitudinal ridges. Mural spines common in exozone. [*Tropidopora* is distinguished on branch size, surficial features, and zooecial shape and orientation. It is known from a single specimen.] *M.Dev.(Erian),* E.N.Am.——FIG. 280, *1a–e*. **T. nana*, holotype, NYSM 1053; *a*, paurostyles; long. sec., ×400; *b*, zooecial outline, lamellar profile; transv. peel, ×100; *c*, apertural arrangement; exterior, ×15; *d*, apertural arrangement, stylets; tang. sec., ×100; *e*, median axis, zooecial outlines and arrangement; long. sec., ×100.

Ulrichostylus BASSLER, 1952, p. 384 [**Helopora divaricatus* ULRICH, 1886a, p. 59; OD; ?Decorah Sh., equals Trenton shales of ULRICH, M. Ord., Minneapolis, Minn., USA]. Zoarium dendroid in some species, possibly unbranched in others. Jointed longitudinally, also laterally in dendroid branches; joint surfaces generally weakly concave-convex; ball-and-socket pattern present in at least one species. Segments straight or curved; diameters 0.5 to 1.0 mm, usually constant between joints; cross sections polygonal to subcircular. Apertures in 6 to 8 longitudinal rows. Prominent longitudinal ridges separating apertural rows; apertures bordered proximally and laterally by strong ridges that flare distally to join longitudinal ridges, forming inverted V-pattern.

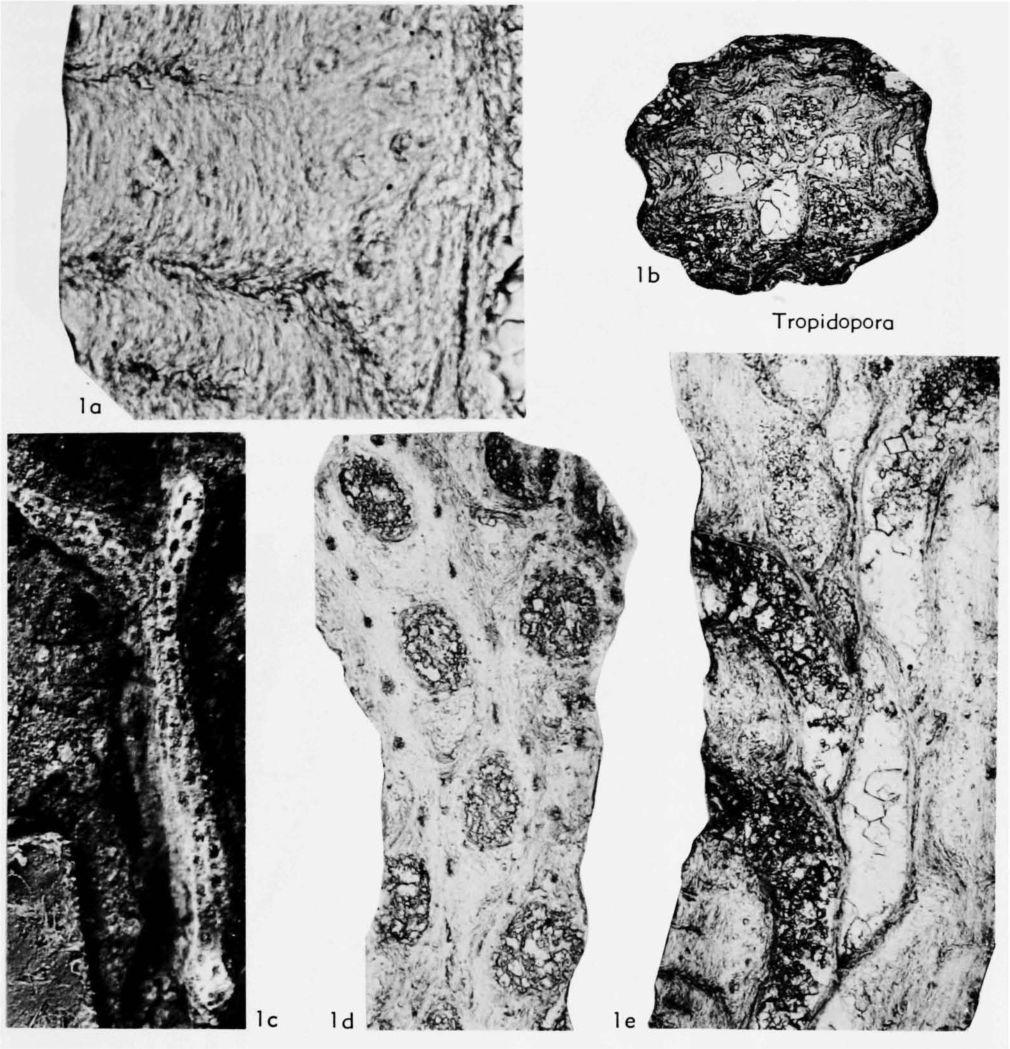

FIG. 280. Arthrostylidae (p. 566).

Ridges proximal to apertures sloping gradually into aperture below; 1 or 2 longitudinal ridges may be present on sloping surface. Metapores absent. Axial region formed by well-defined linear axis. Zooecial bases attenuated to weakly inflated. Zooecial cross sections triangular in endozone. Zooecial divergence from axis approximately 20° to 40°; zooecial bend weakly developed, broadly rounded. Living chambers in exozone elliptical in cross section, oriented from 60° to 70° to branch surface. Zooecial length 5 to 12 times diameter. Longitudinal arrangement of zooecia regular. Diaphragms scattered in elongate zooecia. Exozonal width more than half branch radius. Zooecial boundaries generally narrow in endozone, irregular, commonly with granular or nonlaminated material, locally not visible; well developed in exozone near proximal and lateral margins of chambers, positions obscure distal to chambers. Planar longitudinal dark zones radiating through exozone from near zooecial boundaries at base of exozone; appearance similar to that of zooecial boundaries. Lamellar profile in exozone rounded in transverse section, interrupted by radiating boundary zones; flattened in longitudinal section, sloping toward zoarially proximal zooecium. Exozonal wall material well developed. Paurostyles scattered, weakly developed, concentrated in wall between longitudinally successive zooecial chambers. [*Ulrichostylus* is distinguished on budding pattern, zooecial shape and orientation, and wall structure.] *M.Ord.(Chazy.-Blackriv.), ?U.Ord. (Richmond.),* E.N.Am., Baltic region.——FIG.

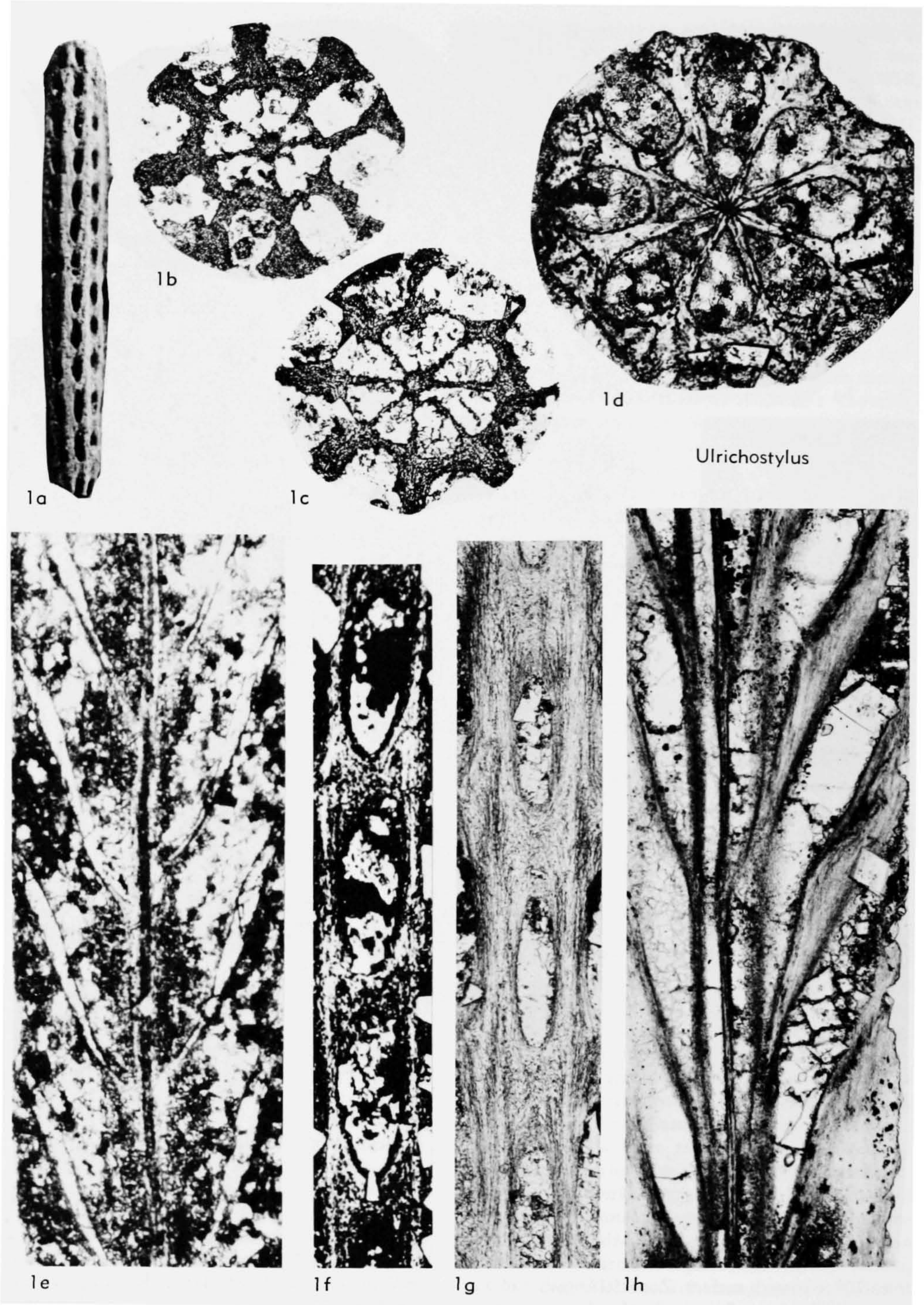

FIG. 281. Arthrostylidae (p. 566).

281,*1a–f*. **U. divaricatus* (ULRICH), syntypes (*a*, Univ. Minnesota 5928A; *b–f*, 5928B); *a*, apertural arrangement, longitudinal ridges; ×11; *b,c*, zooecial cross sections and arrangements, linear axes; transv. peels, ×70; *d*, radiating dark zones; transv. sec., ×94; *e*, zooecial shapes; long. sec.,

×85; *f*, apertural outlines, longitudinal ridges; tang. sec., ×85.——FIG. 281, *g,h*. *U. spiniformis* (ULRICH), Lebanon Ls., M. Ord., Tenn., USA, all USNM 240853, ×70; *g*, apertural outlines, longitudinal ridges; tang. sec.; *h*, zooecial outlines, lamellar profile; long. sec.

Nomen Nudum

Oandupora MÄNNIL, 1959, p. 39. Name not accompanied by characters differentiating taxon, Article 13a, ICZN.

Family RHABDOMESIDAE Vine, 1884

[*nom. correct.* BASSLER, 1953, p. G130, *pro* Rhabdomesontidae VINE, 1884, p. 205]

Zoaria generally dendroid; some zoaria, branches, or parts of branches conical; jointing unknown. Branch diameters approximately 0.5 to 6.0 mm, constant or varied between bifurcations. Branches subcircular in cross section. Apertural arrangement basically rhombic, somewhat irregular in some taxa or areas of some branches; ridges absent. Metapores rare. Axial region variable, from linear axes or a few weakly defined axial zooecia to large bundles of axial zooecia or enlarged axial cylinder. Diaphragms may be present in axial cylinders. Autozooecial bases attenuated to inflated in longitudinal profile; zooecial cross sections polygonal in endozone. Zooecial divergence from axial bundle 15° to 45°. Zooecial bends rounded to abrupt. Living chambers in exozone generally elliptical in cross section, rarely subcircular. Living chambers usually oriented from 80° to 90° to surface, may be as low as 50°. Autozooecial lengths approximately 4 to 15 times diameter. Hemisepta usually paired, mostly developed near zooecial bend; may be in multiple series or absent. Diaphragms few in most species, scattered in some; terminal diaphragms present in one genus. Exozonal width usually less than half branch radius, may range from about one-third to two-thirds branch radius in mature stems. Zooecial boundary narrow, dark; may contain granular or nonlaminated material; or locally, may not be visible. Lamellar profiles V-shaped in exozone, more or less flattened between stylets. Monticules of enlarged, thin-walled polymorphs rare. Paurostyles or acanthostyles always present, both in many species; few to common, but usually not densely spaced in exozonal walls. Stylets generally arising in exozone, paralleling zooecial chambers in most species. Mural spines present in some species. *U.Sil.-U.Perm.*

Rhabdomeson YOUNG & YOUNG, 1874, p. 337 [**Millepora gracilis* PHILLIPS, 1841, p. 20; OD; Carb., N. Devon, Eng.] [=*Coeloconus* ULRICH in MILLER, 1889, p. 298]. Zoarium usually dendroid; some zoaria, branches, or parts of branches conical. Cylindrical branch diameters 0.7 to 6.0 mm, constant between bifurcations. Apertural arrangement rhombic. Axial region formed by hollow, regular to somewhat irregular, axial cylinder; diameter of cylinder usually greater than that of autozooecia. Wall thickness of axial cylinder usually comparable to that of other endozonal walls; diaphragms present in axial cylinders of some species. Zooecial bases usually attenuated, inflated in some species; zooecia in endozone initially triangular in cross section, becoming hexagonal. Zooecial divergence 20° to 45° from axial surface in cylindrical stems; ascending along surface of axial cylinder to zooecial bend in conical stems. Zooecial bend generally abrupt, somewhat rounded in some species; living chambers oriented from 80° to 90° to branch surface. Zooecial length in cylindrical stems generally from 4 to 7 times diameter; longitudinal arrangement of zooecia usually regular. Inflated, recurved hemiseptum usually on proximal wall at zooecial bend; may be rare or multiple. Diaphragms rare. In cylindrical branches, exozonal width generally about half branch radius or less, rarely more. Zooecial boundary generally narrow, irregular, granular in some areas; locally not visible. Lamellar profile in exozone narrowly to broadly V-shaped. One or two acanthostyles occurring proximal to zooecial chambers, paurostyles few to common. Mural spines may be present in exozonal living chambers. Stylets arising in exozone, paralleling autozooecia. Monticulelike structures formed of fused stylets are present in at least one species. [*Rhabdomeson* has commonly been recognized on the presence of an axial cylinder. It resembles *Ascopora* in development of autozooecia, exozone, stylets, and hemisepta, but differs primarily in structure of the axial region. The synonymy of *Rhabdomeson* and *Coeloconus* has been discussed by BLAKE (1976). Location of the types of *R. gracilis* is unknown and they may be lost (SHERBORN, 1940).] *M.Dev.(Erian)-U.Perm.(Dzhulf.)*, N.Am., USSR, Asia, Australia.——FIG. 282, *1a,d-f*. *R. rhombicus* (ULRICH), Warsaw Sh., mid. Miss., Ill., USA; *a*, branch shape, apertural

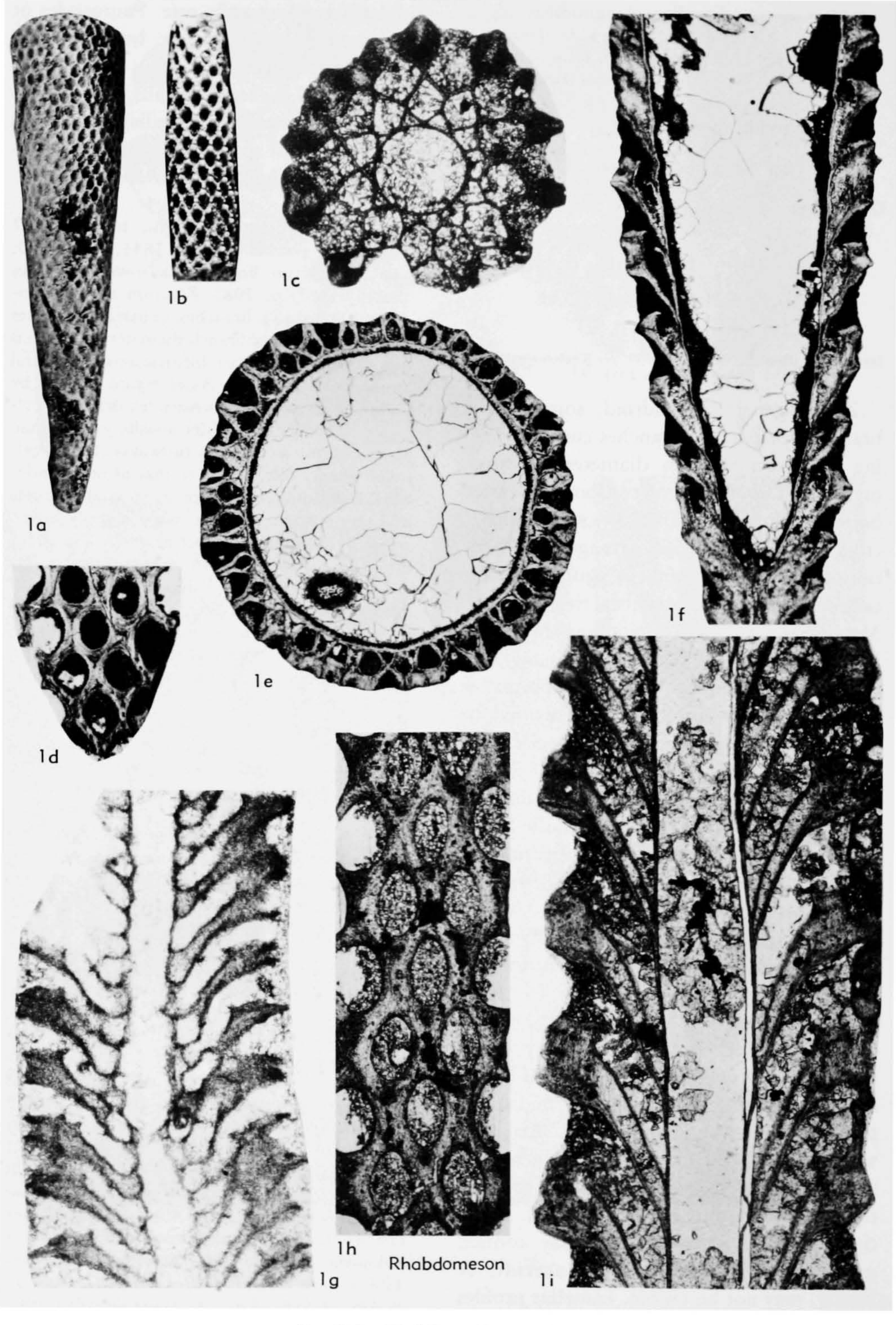

FIG. 282. Rhabdomesidae (p. 569).

arrangement; syntype, USNM 240827, ×6; *d*, apertural and stylet arrangements; tang. sec., syntype, USNM 43335, ×28; *e*, central cone, arrangement of zooecia; transv. sec., syntype, USNM 240828, ×28; *f*, zooecial shapes and arrangement, hemisepta, stylets; long. sec., syntype, USNM 43335, ×28.——Fig. 282,*1b,c,h,i*. **R. gracilis* (Phillips); *b*, aperture and stylet arrangements; USNM 240771, about ×8; *c*, axial cylinder, zooecial cross sections; transv. sec., USNM 121681, ×47; *h*, living chamber outlines, stylets; tang. sec., USNM 121681, ×47; *i*, zooecial shapes, axial cylinder; long. sec., USNM 121681, ×47.——Fig. 282,*1g*. *R. kansasensis* Sayre, Drum Ls., U. Penn., Mo., USA; irregular axial cylinder, inflated zooecial base, wide exozone; long. sec., syntype, KUMIP 125167, ×38.

Ascopora Trautschold, 1876, p. 367 [**Millepora rhombifera* Phillips, 1836, p. 199; M; Carb., Yorkshire, Eng.]. Zoarium dendroid. Branch diameters 1.0 to 5.5 mm, usually constant between bifurcations. Apertural arrangement rhombic. Axial region formed by weakly to well-defined cylindrical bundle of 4 to 30 axial zooecia. Axial zooecia polygonal in cross section, walls commonly thinner than those of autozooecia; diaphragms usually absent, may be rare. Autozooecial bases attenuated to weakly inflated; autozooecia in endozone initially triangular in cross section, becoming hexagonal. Autozooecial divergence from axial bundle mostly between 20° and 45°. Zooecial bend generally abrupt; living chambers commonly oriented about 90° to branch surface. Autozooecial length mostly 5 to 10 times diameter. Longitudinal arrangement of zooecia usually regular. Single, massive, recurved hemiseptum may be present on proximal wall at zooecial bend; single, slender hemiseptum rarely present on distal wall in late endozone; multiple hemisepta rarely present on proximal wall; or hemisepta may be absent. Autozooecial diaphragms generally absent, may be rare. Exozonal width ranging from less than half branch radius in slender species to about two-thirds branch radius in robust species. Zooecial boundary generally narrow, irregular, granular in some areas; locally not visible; lamellar profile V-shaped in exozone. One or two acanthostyles proximal to each zooecial chamber; orientation relative to zoarial surface may be greater than zooecial angle. Paurostyles common to densely spaced; in single or double rows between apertures, or stylet fields may be present. Mural spines may be present in exozonal living-chamber wall. Stylets arising in exozone. [*Ascopora* is distinguished by an axial bundle of zooecia, zooecial shape, stylet development, and lack of metapores. Location of the types of *A. rhombifera* is unknown, and they may be lost (Sherborn, 1940).] *L.Carb. (Tournais.* or *Visean)-L.Perm.(?Artinsk.)*, USSR, N.Am., Asia.——Fig. 283,*1a,b*. *A. magniseptata* Shulga-Nesterenko, U. Carb., Russ. plat., USSR, holotype, PIN 136/95; *a*, axial bundle, zooecial outlines; transv. sec., ×20; *b*, zooecial shapes, hemisepta, axial zooecia; long. sec., ×20.——Fig. 283,*1c*. *Ascopora* sp., Penn.-Perm., Nev., USA; living chamber outlines, acanthostyles, paurostyles; tang. sec., USNM 240854, ×20.——Fig. 283,*1d*. *Ascopora* sp., Earp F., Cisco Gr., U. Penn-Perm., Ariz., USA; zooecial shapes, hemisepta, axial zooecia; long. sec., USNM 240855, ×30.——Fig. 283,*1e*. *Ascopora* sp., ?Brazier Ls., Carb. (?Penn.), Idaho, USA; zooecial shapes, stylets, axial zooecia; long. sec., USNM 240856, ×30.

Mediapora Trizna, 1958, p. 209 [**M. injaensis*; OD; Taidonskaya and Fominskaya zones, L. Carb. (Tournais.-Visean), Inya and Tykhta rivers, Kuznetsk basin, USSR]. Zoarium dendroid. Branch diameters 1.4 to 2.3 mm. Apertural arrangement rhombic, locally irregular. Metapores present in at least some species. Axial region formed by a few axial zooecia or possibly ill-defined linear axis. Axial zooecia not in distinct bundle; ascending variable distances along axial region before diverging toward surface. Axial zooecia weakly differentiated from autozooecia, except in length and probably diameter; diaphragms lacking. Autozooecial base attenuated to inflated; zooecial cross sections polygonal in endozone, irregular or hexagonal. Autozooecial divergence from axial region 20° to 40°. Zooecial bend usually rounded; living chamber outlines irregular, varied within single zoarium. Outer interval of exozone oriented about 90° to branch surface. Autozooecial length 8 to 15 times diameter; longitudinal arrangement of autozooecia irregular to highly irregular. Hemisepta absent, diaphragms scattered in most species. Exozonal width usually one-third to half branch radius. Lamellar profile probably V-shaped in exozone. Acanthostyles common, varied in size, arranged in linear series. [*Mediapora* is distinguished by the presence of axial zooecia and by zooecial shape and arrangement.] *?U.Sil.(Ludlov.), L.Carb.(Tournais.-Visean)*, USSR.——Fig. 283,*2a–c*. **M. injaensis*, all ×20; *a*, irregular zooecial arrangement; biased long. sec., holotype, VNIGRI 263/913; *b*, zooecial cross sections, development of exozone; transv. sec., holotype; *c*, apertural shapes, arrangement; tang. sec., paratype, VNIGRI 264/913 (Trizna, 1958).——Fig. 283,*2d*. *M. fragilis* Trizna, L. Carb.; axial zooecia; long. sec., paratype, VNIGRI 266/913, ×20 (Trizna, 1958).

Nemataxis Hall, 1886, pl. 25 [**N. fibrosus*; M; lithology suggests Springvale Ss. (W. A. Oliver, 1974, pers. commun.), equals up. Helderberg Gr. of Hall, L. Dev., Ont., Can.]. Zoarium dendroid. Branch diameters approximately 3 to 4 mm, constant between bifurcations. Apertural

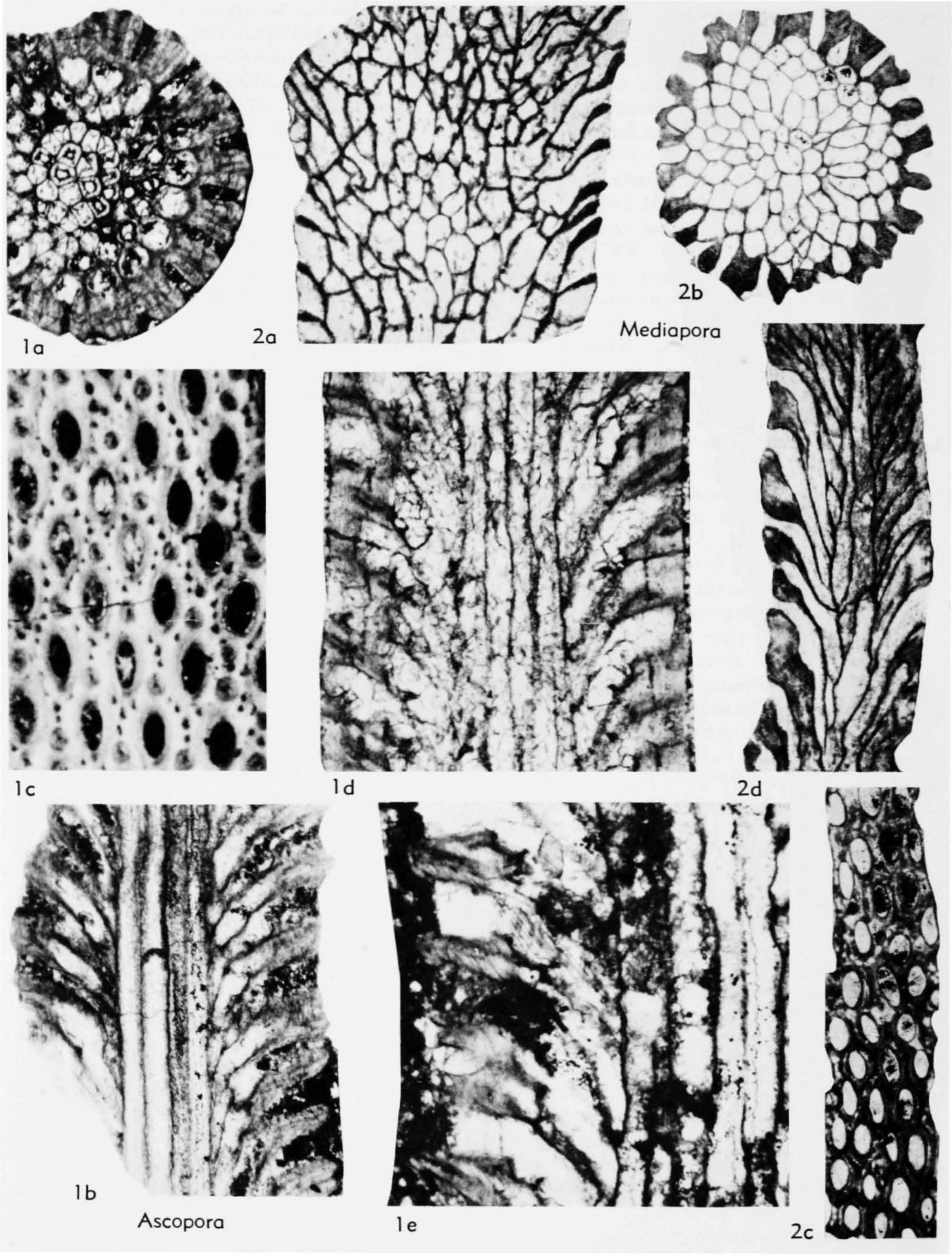

FIG. 283. Rhabdomesidae (p. 571).

arrangement rhombic. Axial region formed by linear axis. Zooecial bases inflated; zooecia initially polygonal, irregular in cross section, becoming hexagonal, then subrectangular. Zooecial divergence from axis about 45°. Zooecial bend abrupt. Living chambers oriented at 80° to 90° to branch surface. Zooecial length about 15 times diameter; longitudinal arrangement of zooecia regular. Single, massive, short, rarely recurved hemiseptum on proximal wall at zooe-

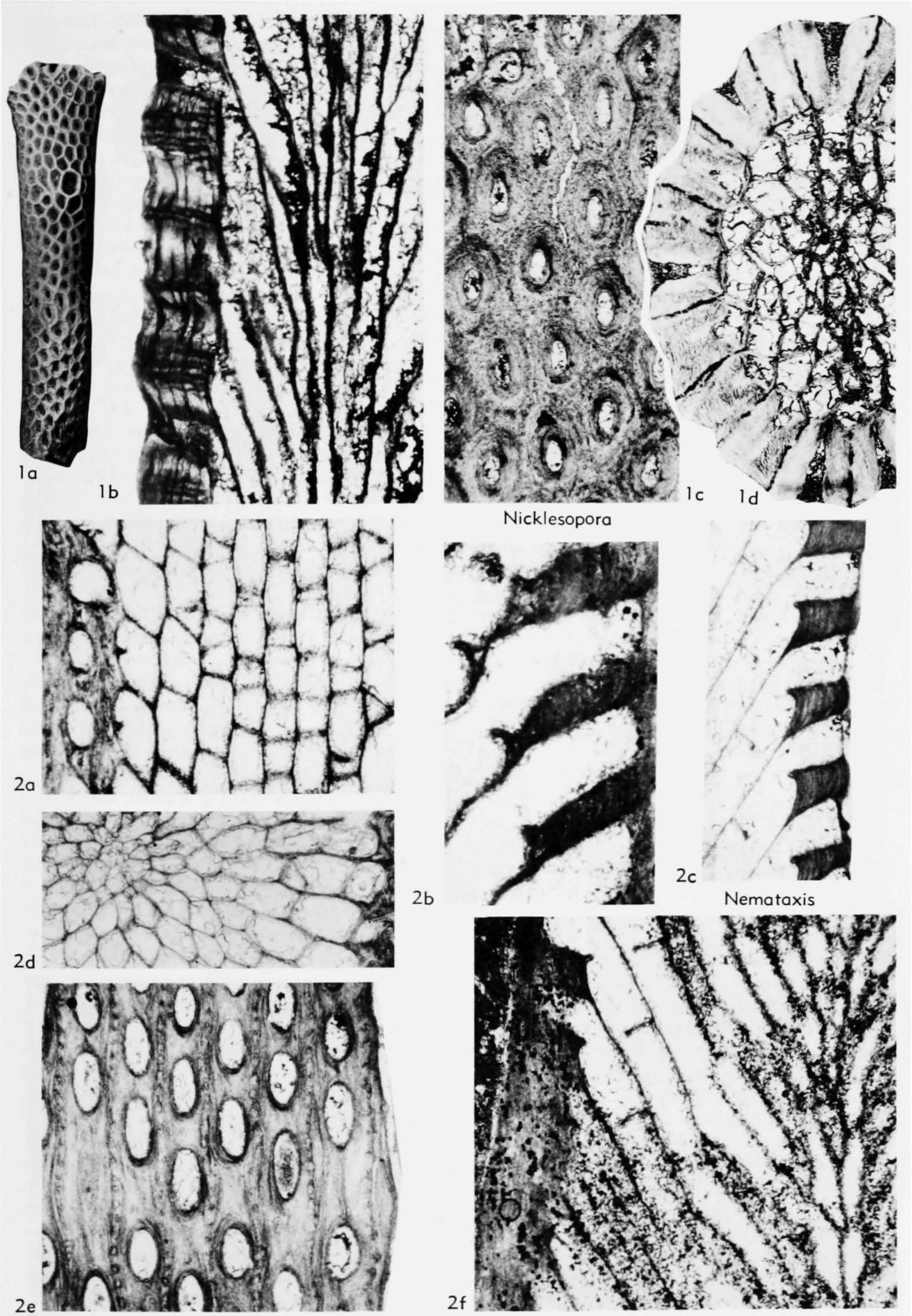

FIG. 284. Rhabdomesidae (p. 571–574).

cial bend in most zooecia; single, slender, straight hemiseptum with recurved margin on distal wall in late endozone; multiple pairs of hemisepta on either wall in some zooecia. Small chambers may be developed under hemisepta. Diaphragms scattered in endozone; thick terminal diaphragms locally in annular bands around branch. Exozonal width about one-third branch radius. Zooecial boundary narrow, irregular, locally not visible. Lamellar profile flattened in exozone, except where orientation of sheath laminae around closely spaced stylets has chevron profile. Small acanthostyles common, aligned between apertural rows; arising near base of exozone, approximately parallel to zooecia. Sheath laminae flaring, not closely parallel to core axis. [*Nemataxis* is distinguished on size of zoarium, presence of terminal diaphragms in annular bands, shape of zooecia, and development of hemisepta and stylets.] *L.Dev.(Ulster.),* E.N.Am. ——FIG. 284,*2a–f.* **N. fibrosus*; *a,* zooecial outlines, alignment; deep tang. sec., syntype, FMNH UC 23803, ×28; *b,* terminal diaphragms, lamellar profile, hemisepta, chambers beneath hemisepta; long. sec., syntype, FMNH UC 23803, ×46; *c,* lamellar profile, hemisepta; long. sec., USNM 240766, ×28; *d,* exozone (right), zooecial cross sections, axial region of branch; transv. sec., FMNH UC 23803, ×28; *e,* terminal diaphragms, stylet arrangement, living chamber outlines; tang. sec., USNM 240766, ×28; *f,* zooecial outlines, branch axis; long. sec., syntype, FMNH UC 23803, ×28.

Nicklesopora BASSLER, 1952, p. 384 [**Rhombopora elegantula* ULRICH, 1884, p. 33; OD; New Providence Sh., L. Miss., Kings Mt. at Halls Gap, Lincoln Co., Ky., USA]. Zoarium dendroid. Branch diameters 0.7 to more than 2.5 mm, may vary somewhat between bifurcations. Apertural arrangement basically rhombic; somewhat irregular, especially near monticules. Axial region formed by few axial zooecia, not in distinct bundle. Axial zooecia may be more slender, thinner walled than autozooecia. Axial zooecia ascending five or more zooecial ranks before diverging from axial region, assuming morphology of autozooecia. Zooecial bases attenuated; zooecia initially polygonal, irregular in cross section, becoming hexagonal. Autozooecial divergence from axial region approximately 15° to 30°. Zooecial bend abrupt; living chambers usually oriented about 90° to branch surface, some as little as 75°. Length of zooecia not arising in axial region 10 or more times diameter; longitudinal outline, arrangement of zooecia somewhat irregular. Single, short, commonly massive hemiseptum usually on proximal wall near zooecial bend; slender short hemiseptum may be present on distal wall in late endozone. Diaphragms rare. Exozonal width approximately one-third to half branch radius. Zooecial boundary generally narrow, irregular, granular; locally not visible. Lamellar profile in exozone broadly V-shaped. Monticules rare, consisting of one much enlarged, thin-walled polymorph surrounded by smaller, enlarged, thin-walled polymorphs. Paurostyles common, most in single well-defined linear series either enclosing zooecial apertures in polygonal pattern or extending longitudinally between rows of zooecia. Paurostyles arising in exozone paralleling zooecial chambers. [*Nicklesopora* is distinguished on zoarial size, zooecial shape, development of the exozone, and presence of monticules and paurostyles.] *U.Dev.-L.Carb.,?U.Perm.,* N.Am., Australia, USSR.——FIG. 284,*1a–d.* **N. elegantula* (ULRICH); *a,* zooecial arrangement and monticule; syntype, USNM 240768, about ×6; *b,* axial zooecia, zooecial shapes; long. sec., syntype, USNM 43716, ×28; *c,* living chamber outlines, stylet alignment; tang. sec., syntype, USNM 168365, ×28; *d,* zooecial cross sections, lamellar profile; transv. sec., syntype, USNM 168365, ×28.

Orthopora HALL, 1886, pl. 25 [**Trematopora regularis* HALL, 1874, p. 106; SD HALL & SIMPSON, 1887, p. xiv; New Scotland Ls., equals up. Helderberg Gr. of HALL, L. Dev., Clarksville, Albany Co., N.Y., USA]. Zoarium dendroid. Branch diameters 0.5 to 1.0 mm, constant between bifurcations. Apertural arrangement rhombic. Axial region usually formed by more or less well-defined linear axis. Axial bundle absent, but some autozooecia may ascend along axial region for short interval in endozone before diverging toward surface. Zooecial bases attenuated to inflated; zooecia initially polygonal, irregular in cross section, becoming hexagonal. Zooecial divergence usually 25° to 40°. Zooecial bend generally abrupt; living chamber oriented about 90° to branch surface. Zooecial length usually 4 to 6 times diameter, greater in species with zooecia ascending parallel to axis in endozone. Longitudinal arrangement of zooecia usually regular. Straight, moderately massive hemiseptum usually present on proximal wall at zooecial bend; slender, straight hemiseptum usually on distal wall in late endozone; overlap of hemisepta and changes in wall orientation commonly producing U-shaped zooecial outline near zooecial bend; second hemiseptum may be present on proximal wall in late endozone; rarely, hemisepta lacking. Diaphragms rare. Exozonal width one-third to half branch radius. Zooecial boundary narrow, irregular; granular, nonlaminated material may be present in intervals of endozone; locally not visible. Lamellar profile in exozone flattened. Paurostyles and acanthostyles commonly occurring together, with paurostyles more abundant. Stylets scattered to common in more or less well-defined rows; may be confined to longitudinal rows between lines of zooecial chambers; arising in exozone, parallel to zooecia. Sheath laminae

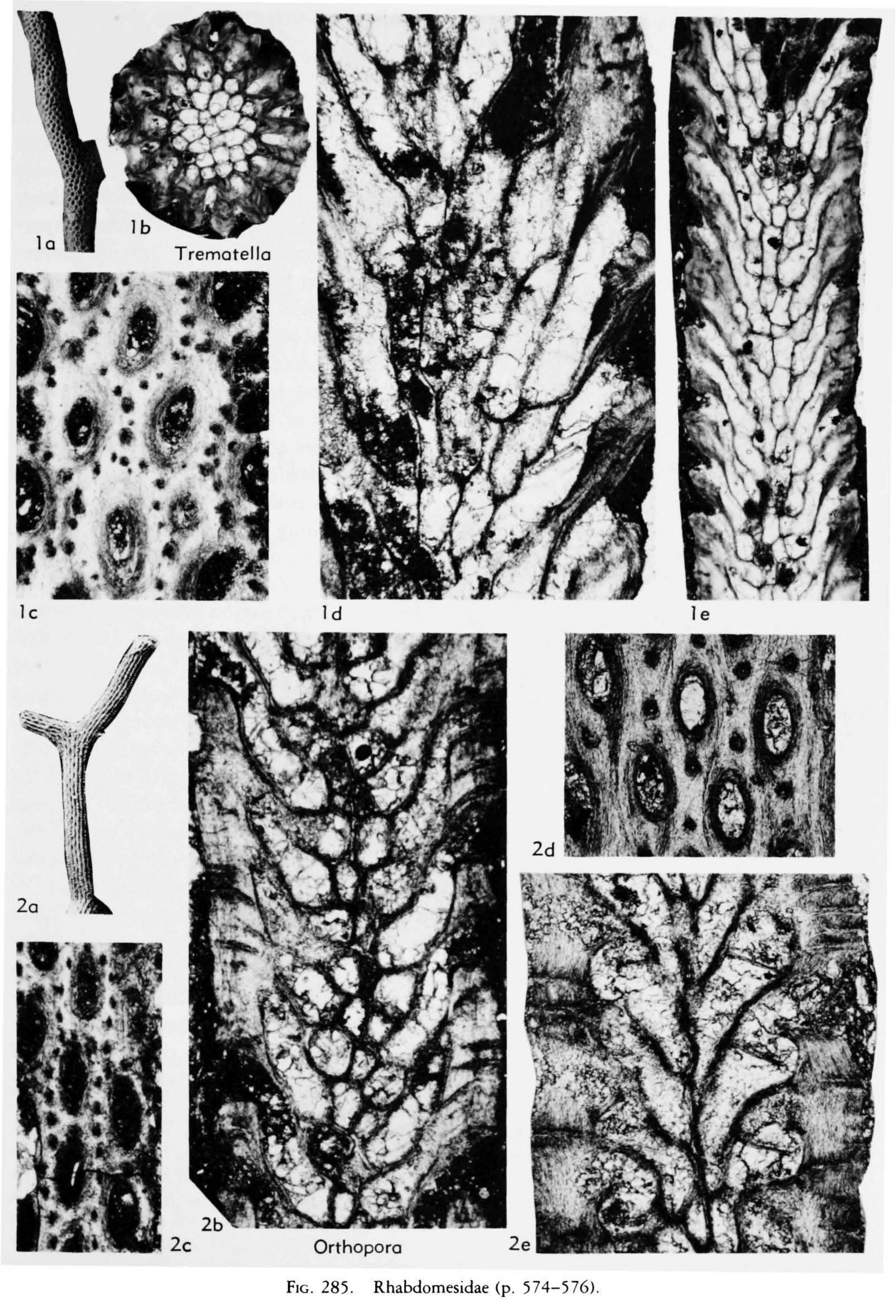

FIG. 285. Rhabdomesidae (p. 574–576).

commonly steeply ascending, oriented subparallel to core, distinct from zoarial laminae. [*Orthopora* is distinguished on apertural arrangement, zooecial shape, and development of hemisepta and stylets.] *U.Sil.(Ludlov.)-M.Dev.(Givet., Erian),* N.Am., Eu., USSR——Fig. 285,*2a–c*. **O. regularis* (Hall); *a,* branching pattern, apertural arrangement; syntype, AMNH 35758A, ×4; *b,* branch axis, zooecial shapes; long. sec., syntype, NYSM 942, ×50; *c,* apertural and stylet arrangements; tang. sec., syntype, NYSM 942, ×50.——Fig. 285,*2d,e*. *O. tonolowayensis*? Bassler, Keyser Ls., L. Dev., W. Va., USA; *d,* living chamber outlines, stylet arrangement; tang. sec., USNM 214197, ×75; *e,* zooecial shapes, hemisepta, stylets, lamellar profile; long. sec., USNM 214194, ×75.

Trematella Hall, 1886, pl. 25 [**T. glomerata*; SD Duncan, 1949, p. 133; Onondaga Ls., equals up. Helderberg Gr. of Hall, M. Dev., Onondaga Valley, Erie Co., N.Y., USA]. Zoarium dendroid. Branch diameters 1.2 to 2.0 mm, somewhat varied between bifurcations. Apertural arrangement rhombic, locally irregular. Metapores rare. Axial region generally formed by weakly defined linear axis; axial zooecia absent but autozooecia may ascend along axis in endozone for varying intervals before diverging from axis. Zooecial bases usually inflated, rarely attenuated; zooecia initially polygonal, irregular in cross section, becoming hexagonal. Zooecial divergence from axial region approximately 20° to 30°. Zooecial bend rounded; living chambers oriented 50° to 70° to branch surface. Zooecial length about 5 to 12 times diameter; longitudinal arrangement of zooecia usually irregular. Single, small to massive hemiseptum common on proximal wall at zooecial bend. Diaphragms rare in most species, scattered in some. Exozonal width approximately one-third to half branch radius. Zooecial boundary generally narrow, irregular, granular, with nonlaminated material in places; locally not visible. Lamellar profile in exozone narrowly to broadly V-shaped. Paurostyles and acanthostyles present, with paurostyles more abundant. Stylets in more or less well-defined rows, or scattered; arising in exozone, approximately parallel to autozooecia; two types gradational in form. Sheath laminae in some acanthostyles steeply ascending, oriented subparallel to core, distinct from zoarial laminae. [*Trematella* is distinguished on zooecial shape and arrangement, development of stylets, metapores and hemisepta.] *L.Dev.(Ulster.)-M.Dev.(Erian),* E. N.Am.——Fig. 285,*1a–e*. **T. glomerata,* holotype, NYSM 1040; *a,* apertural arrangement; ×5; *b,* zooecial arrangement, exozonal development; transv. sec., ×20; *c,* living chamber outlines, acanthostyles, paurostyles, metapores; tang. sec., ×50; *d,* zooecial outlines and arrangement; long. sec., ×50; *e,* zooecial outlines and arrangement; long. sec., ×20.

Family RHOMBOPORIDAE Simpson, 1895

[Rhomboporidae Simpson, 1895, p. 549]

Zoaria dendroid, jointing rare. Branch diameters 0.5 to about 4.5 mm, relatively constant or varied between bifurcations; branches subcircular in cross section. Apertural arrangement basically rhombic, somewhat irregular in some taxa or areas of some branches; ridges absent. Metapores may be present. Axial region generally formed by linear axis; median planar surfaces discontinuous in some species; weak trend toward development of axial zooecia in few species. Zooecial bases attenuated to inflated in longitudinal profile. Zooecial cross sections polygonal in endozone, irregular to triangular near budding locus, hexagonal away from locus. Zooecial divergence from axial region 20° to 30°. Zooecial bends rounded to abrupt; living chambers in exozones elliptical to subcircular in cross section, usually oriented about 90° to branch surfaces, but may be as low as 60°. Autozooecial lengths approximately 5 to 10 times diameters. Hemisepta absent; diaphragms rare to common. Exozonal width one-fifth to four-fifths branch radius in mature stems. Zooecial boundaries locally not visible; or narrow, dark; granular material and nonlaminated material in some areas. Lamellar profiles V-shaped to broadly rounded in exozones, more or less flattened between stylets. Aktinotostyles or acanthostyles always present, both in many species; stylets common to abundant, mostly arising in exozone; stylets usually parallel to zooecial chambers. Mural spines may be present. *?U.Dev.,L.Miss.-U.Perm.*

Rhombopora Meek, 1872, p. 141 [**R. lepidodendroides*; OD; ?Willard Sh., Penn., Nebraska City, Otoe Co., Neb., USA]. Zoarium with jointed branches in at least one species; branch diameters 0.7 to 4.5 mm, may vary between bifurcations. Apertural arrangement approximately rhombic, locally irregular. Metapores uncommon in some species; typically fewer than 1 metapore for every 15 zooecia. Axial region usually formed by irregular linear axis; intraspecifically, some zooecia parallel axis for short

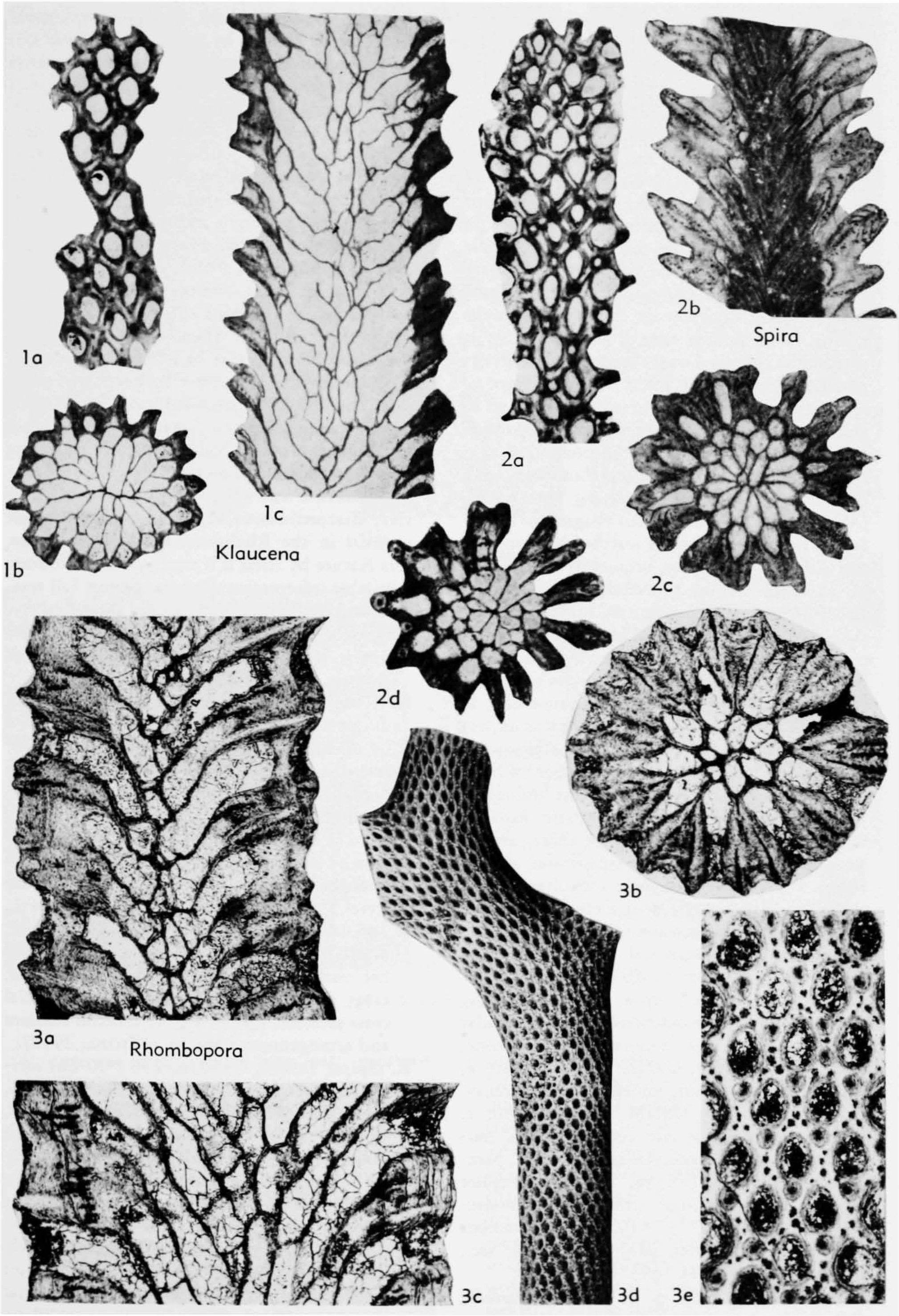

FIG. 286. Rhomboporidae (p. 576–578).

intervals, true axial zooecia not developed. Zooecial bases inflated; zooecia initially polygonal and irregular in cross section, becoming hexagonal. Zooecial divergence from axis approximately 30° to 50°. Zooecial bend generally rounded; living chambers oriented 80° to 90° to branch surface. Zooecial length varied, usually 5 to 9 times diameter; longitudinal arrangement of zooecia regular to somewhat irregular. Diaphragms uncommon. Exozonal width from one-fifth to more than half branch radius. Lamellar profile V-shaped in exozone. In one species, semiannular monticulelike ridge developed by elongation of some autozooecia; other polymorphs absent in annulations. One or two acanthostyles proximal to each zooecial chamber; most stylets parallel to zooecia, a few less steeply inclined to surface than zooecia. Aktinotostyles common to abundant; diameters generally constant through exozone. Mural spines may be present in exozonal wall of zooecia. Some acanthostyles arising in endozone, most stylets arising in exozone. [Many more species have been assigned to *Rhombopora* than can be readily justified by comparison with the type species, bearing in mind ranges of variation in other rhabdomesine genera. *Rhombopora* is distinguished on branch size and shape, zooecial shape and orientation, and presence of acanthostyles, aktinotostyles, and only a few metapores. In many later species of *Rhombopora,* size increases, zooecial arrangement is locally irregular, the median axis becomes less well defined, there is some tendency toward development of axial zooecia, the zone of budding is somewhat broadened, most endozonal walls become relatively thin, and the exozone becomes relatively narrow. These characters are similar to those of some trepostomates. *Rhombopora* and its allies are here considered to be rhabdomesines because of the restricted nature of the budding locus, zooecial shape, and similarity to such unequivocal rhabdomesines as *Orthopora.*] *?U.Dev.,L.Miss.(Osag.)-U.Perm.(Dzhulf.),* N.Am., Asia, S.Am.——FIG. 286,*3a–e.* **R. lepidodendroides*; *a,* irregular branch axis, zooecial shapes, broad exozone; long. sec., lectotype, USNM 168360, ×30; *b,* zooecial cross sections, lamellar profile; transv. sec., paralectotype, USNM 168360, ×30; *c,* elongate zooecia near axis, zooecial shapes, narrow exozone, stylet arrangement; long. sec., paralectotype, USNM 168359, ×30; *d,* irregular growth habit, apertural arrangement; paralectotype, USNM 240773, ×10; *e,* living chamber outlines, acanthostyles, paurostyles; tang. sec., paralectotype, USNM 168359, ×30.

Klaucena TRIZNA, 1958, p. 213 [**K. immortalis*; OD; Taidonskaya zone, L. Carb. (up. Tournais.), Kondoma River, Kuznetsk basin, USSR]. Zoarium dendroid, jointing unknown. Branch diameters 0.7 to 2.0 mm. Apertural arrangement rhombic, locally irregular. Metapores unknown. Axial region formed by well-defined linear axis or by median plate similar in structure to other endozonal walls. Zooecial bases inflated; zooecia initially polygonal, irregular in cross section, becoming hexagonal. Zooecial bend rounded; some living chamber outlines deflected by acanthostyles; chambers oriented 60° to 80° to branch surface, orientation varied within single specimens. Zooecial length approximately 6 times diameter; longitudinal arrangement of zooecia irregular. Hemisepta absent, diaphragms rare to scattered in some species. Exozonal width approximately one-third to half branch radius. Zooecial boundaries, lamellar profile unknown. Large acanthostyles may be scattered in exozone, possible aktinotostyles may be developed proximal and distal to zooecial chambers. [TRIZNA (1958) based *Klaucena* largely on the presence of a planar, median, budding surface in species of general rhabdomesine character. Two subgenera, *Klaucena* and *Spira,* were recognized. Similar, discontinuous, median plates are not unusual in the Rhabdomesina and, therefore, this feature by itself is a weak generic criterion. Available information does not permit full reassessment of affinities, but zooecial shape and stylet development, especially in *K.* (*Spira*), suggest affinities with the Rhomboporidae.] *L.Carb.(Tournais.-Visean),* USSR.

K. (Klaucena). Species of *Klaucena* with branch diameters 1.3 to 2.0 mm; axial region formed by median plate similar in structure to other endozonal walls. Scattered diaphragms may be present; exozonal width approximately one-third branch radius; large acanthostyles scattered in exozone. [Distinguished on the presence of a median plate, zooecial shape and arrangement, and development of acanthostyles.] *L.Carb.(Tournais.),* USSR.——FIG. 286,*1a–c.* **K.* (*K.*) *immortalis,* holotype, VNIGRI 271/913, all ×20; *a,* living chamber outlines and arrangement, large stylets; tang. sec.; *b,* planar median plate, zooecial cross sections, transv. sec.; *c,* zooecial outlines and arrangement; long. sec. (Trizna, 1958).

K. (Spira) TRIZNA, 1958, p. 218 [**K.* (*S.*) *altinodata*; OD; Taidonskaya zone, L. Carb. (up. Tournais.), Kondoma River, Kuznetsk basin, USSR]. Species of *Klaucena* with branch diameters 0.7 to 2.0 mm; axial region apparently formed by linear well-defined axis in which local alignment of zooecial walls forms a weak axial plate in some intervals. Diaphragms rare; exozonal width approximately half branch radius; possible aktinotostyles developed proximal and distal to zooecial chambers. [Distinguished by zooecial shape and arrangement, and stylet development]. *L.Carb.(Tournais.-Visean),* USSR.——FIG. 286,*2a–d.* **K.* (*S.*) *altinodata,* all ×20; *a,*

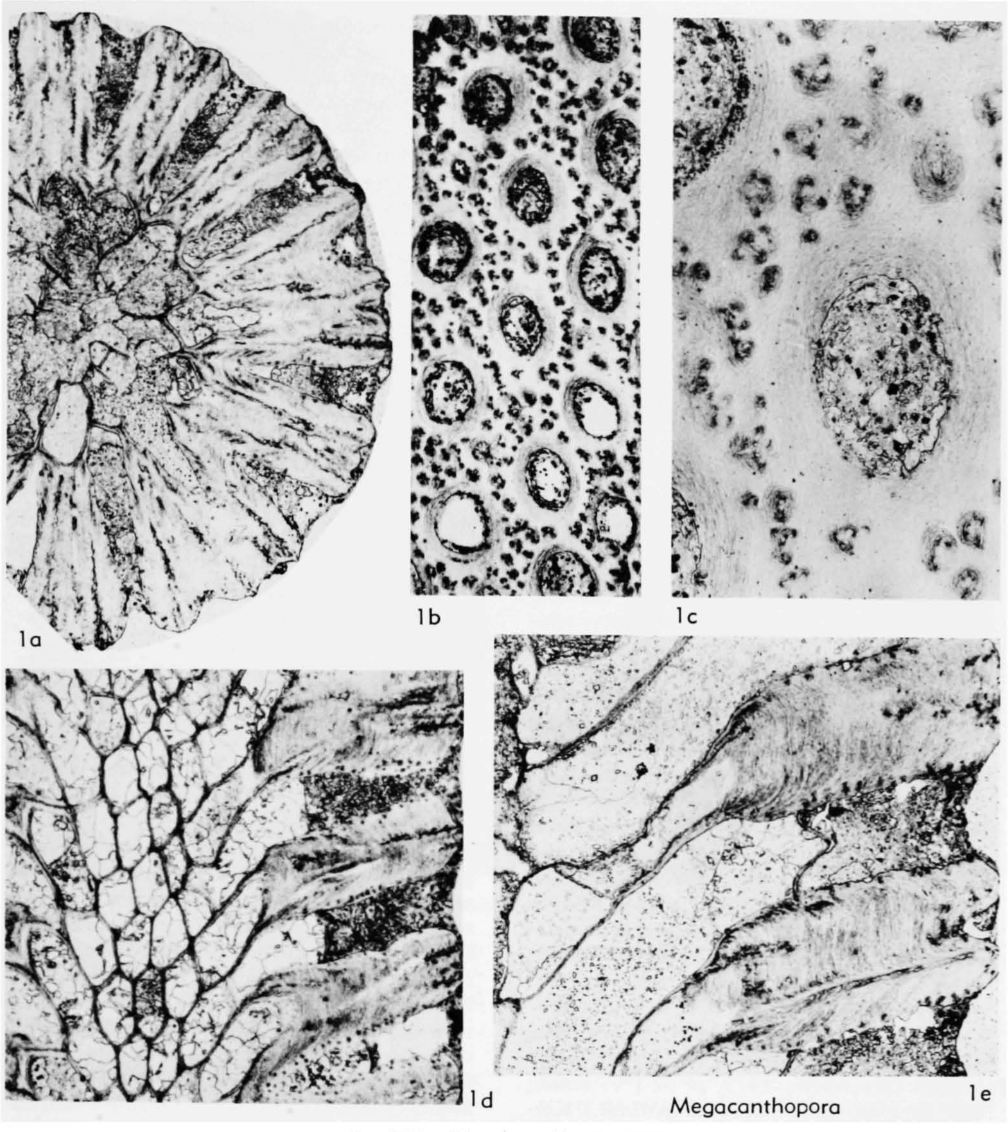

FIG. 287. Rhomboporidae (p. 579).

apertural arrangement; tang. sec., paratype, VNIGRI 276/913; *b,* zooecial shapes and arrangement, stylets; long. sec., holotype, VNIGRI 275/913; *c,* arrangement of zooecia, exozonal development; transv. sec., holotype; *d,* zooecial cross sections and arrangement; transv. sec., paratype, VNIGRI 277/913? (Trizna, 1958).

Megacanthopora MOORE, 1929, p. 10 [**M. fallacis*; M; Wayland Sh. Mbr., Graham F., Cisco Gr., U. Penn., Cisco, Texas, USA] [=*Neorhombopora* SHISHOVA, 1964, p. 55]. Zoarium with jointing unknown; branch diameters 0.7 to 4.5 mm, somewhat varied between bifurcations. Apertural arrangement basically rhombic, locally irregular. Metapores common. Axial region formed by irregular linear axis. Zooecial bases inflated; zooecia initially polygonal, irregular in cross section, becoming hexagonal. Zooecial divergence from axis commonly about 45°, rarely less. Zooecial bend generally rounded; living chambers oriented 80° to 90° to branch surface. Zooecial length usually 5 to 8 times diameter; longitudinal arrangement of zooecia varied, irregular. Diaphragms uncommon. Exozonal width about one-third to two-thirds branch radius. Lamellar profile broadly V-shaped in exozone. Acanthostyles uncommon, not localized, angle relative to zoarial surface may be greater than zooecial angle. Aktinotostyles abundant, generally closely spaced; diameter approximately constant through length. Mural spines regularly arranged in exozonal living-chamber wall. Stylets arising in exozone. [DUNAEVA (1973) assigned *Megacanthopora* to the Stenoporidae, apparently on the presence of two types of stylets and narrow tubular exozonal cavities, here termed metapores. More than one stylet type occurs within single specimens elsewhere in the Rhabdomesina (e.g., most genera of Rhabdomesidae), and slender, apparently nonhomologous cavities or depressions are widely distributed in the class Stenolaemata. Therefore, I do not consider these structures in *Megacanthopora* to indicate affinities with the Trepostomata, and I assign the genus to the Rhabdomesina because it possesses the restricted budding pattern and basic angular zooecial shape and orientation typical of the suborder. Distinctive generic features include zooecial shape and arrangement, development of the exozone, and presence and development of acanthostyles, aktinotostyles, and metapores. *Megacanthopora* is similar to *Rhombopora,* differing only in metapore abundance, and possibly relative exozonal width. *Neorhombopora* SHISHOVA (1964) was named for species lacking large acanthostyles; however, its type species, *Rhombopora crassa* (ULRICH), possesses large acanthostyles and differs little from *M. fallacis.* Therefore, *Neorhombopora* is here synonymized with *Megacanthopora.*] *U.Carb.(Namur.-Stephan.),* N.Am., USSR.——FIG. 287,*1a–e.* ***M. fallacis*; *a,* lamellar profile, stylets; transv. sec., paratype, KUMIP 58441, ×30; *b,* metapores, stylets; tang. sec., paratype, KUMIP 58441, ×30; *c,* aktinotostyles, acanthostyle, mural spines, metapores; tang. sec., paratype, KUMIP 58441, ×100; *d,* autozooecial shapes; biased long. sec., paratype, KUMIP 58441, ×30; *e,* autozooecial shapes, complexly arranged stylets; long. sec., paratype, KUMIP 58438, ×50.

Pamirella GORYUNOVA, 1975, p. 62 [**P. nitida*; OD; Bezardarinska F., L. Perm. (Artinsk.), Kur-Teka River, Pamir, USSR]. Zoarium with jointing unknown; branch diameters 0.5 to 2.5 mm, generally constant between bifurcations. Apertural arrangement rhombic. Metapores unknown. Axial region usually formed by well-defined linear axis; endozonal zooecia may parallel axis for short intervals, but true axial zooecia not developed. Zooecial bases attenuated to weakly inflated; zooecial cross sections polygonal, irregular in endozone. Zooecial divergence from axis approximately 20° to 40°. Zooecial bend rounded, living chamber outlines may be deflected by stylets, chambers oriented 70° to 90° to branch surface. Zooecial length generally ranging to about 10 times diameter; longitudinal arrangement of zooecia somewhat irregular. Diaphragms may be common. Exozonal width approximately half to two-thirds branch radius. Lamellar profile V-shaped in exozone. Acanthostyles common to abundant, filling exozone in some species, usually not aligned in well-defined series. Acanthostyles arising in exozone, parallel to zooecia; core typically large, well developed; sheath laminae commonly subparallel to core, sharply defined. [As originally described, *Pamirella* included the type species and *P.* (*ex Rhombipora*) *pulchra* (BASSLER); it is here extended to include *P. orientalis* (BASSLER), *P. nicklesi* (ULRICH), *P. minor* (ULRICH), and *P. asperula* (ULRICH), all previously assigned to *Rhombopora. Pamirella* is distinguished on development of the axial region, zooecial shape and orientation, acanthostyle development, and lack of hemisepta.] *L.Carb.(Osag.)-L.Perm.(Artinsk.),* USSR, Timor, N.Am.——FIG. 288,*1a–d.* **P. nitida*; *a,* zooecial cross sections, stylet development, lamellar profile; transv. sec., holotype, PIN 2351/215, ×25; *b,* branch axis, zooecial shapes, stylet development; long. sec., PIN 2351/99, ×25; *c,* branch axis, zooecial shapes, stylet development; long. sec., holotype, ×25; *d,* apertural and stylet arrangements; tang. sec., holotype, ×40.

Primorella ROMANCHUK & KISELEVA, 1968, p. 57 [**P. polita*; OD; Barabash Suite, U. Perm., Bol'shoy Mangugay River, Maritime Terr., USSR]. Zoarium with jointing unknown; branch diameters 1.0 to 1.5 mm, probably varied between bifurcations. Apertural arrangement basically rhombic, somewhat irregular. Metapores unknown. Axial region formed by linear, generally well-defined axis. Zooecial bases weakly inflated; zooecial cross sections polygonal, irregular in endozone. Zooecial divergence approximately 20° to 30°. Zooecial bend rounded. Living chambers generally oriented about 90° to branch surface. Zooecial length 5 to 8 times diameter; longitudinal arrangement of zooecia irregular. Diaphragms scattered. Exozone irregular, wide, ranging to four-fifths branch radius. Lamellar profile broadly V-shaped in exozone. Aktinotostyles abundant, in single or double series in exozone; arising near base of exozone, with diameters relatively constant with growth, parallel to zooecia. [*Primorella* was originally assigned to the Trepostomata (ROMANCHUK & KISELEVA, 1968), apparently because of overall growth habit. GORYUNOVA (1975) reassigned the genus to the Rhabdomesoidea (=Rhabdomesina), noting it differed from *Pamirella* only in stylet development. *Primorella* is here included in the Rhabdomesina because of the nature of the axial region, zooecial shape, and development of stylets. It is distinguished on apertural arrangement, zooecial shape and arrangement, development of exozone, and development of aktinotostyles as the only stylet type.] *U.Carb.(Stephan.)-U.Perm.,* USSR.——FIG. 289,*2a–c.* **P. polita,* PIN 2210/386; *a,* axial

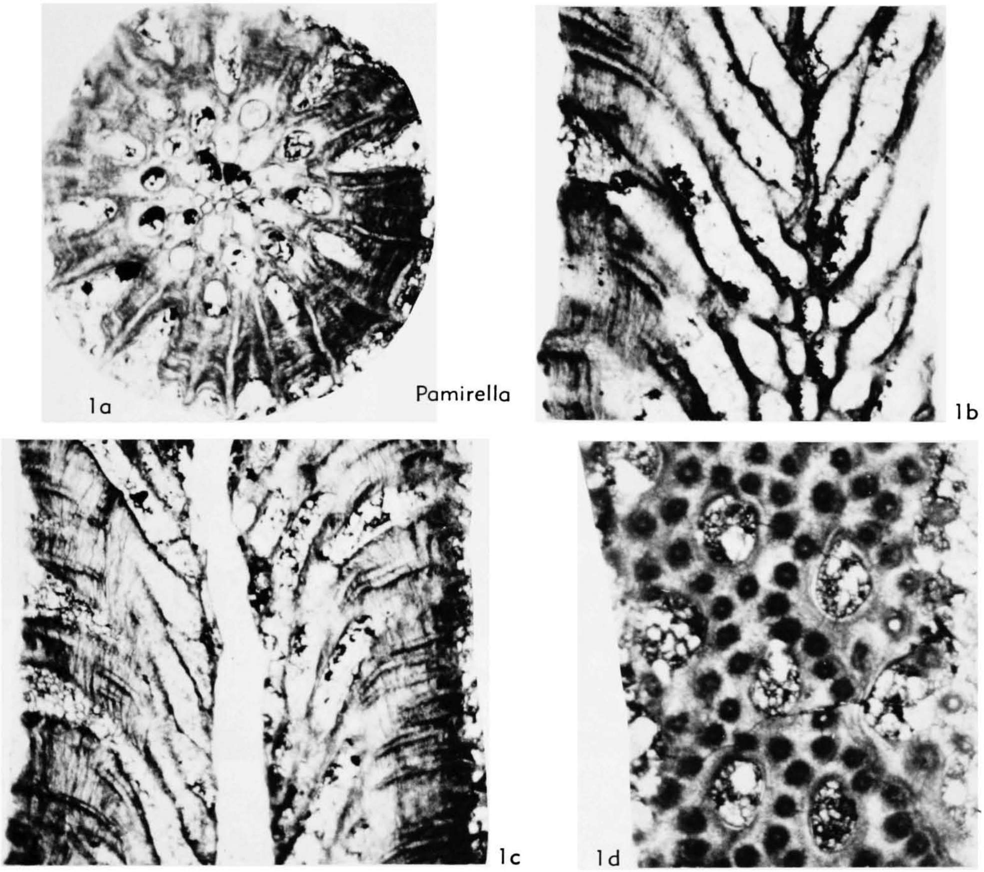

FIG. 288. Rhomboporidae (p. 580).

region, zooecial shapes and arrangement; long. sec., ×24; *b,* zooecial arrangement, lamellar profile, stylets; transv. sec., ×40; *c,* apertural arrangement, stylet development; tang. sec., ×40.

Saffordotaxis BASSLER, 1952, p. 385 [**Rhombopora incrassata* ULRICH, 1888, p. 89; OD; New Providence Sh., L. Miss., Kings Mt. at Halls Gap, Lincoln Co., Ky., USA]. Zoarium with jointing unknown; branch diameters 0.7 to 2.0 mm, constant between bifurcation. Apertural arrangement rhombic. Metapores unknown. Axial region usually formed by well-developed, linear axis; alignment of zooecial walls forming planar median surface in some intervals. Zooecial bases weakly inflated; zooecia initially polygonal, irregular in cross section, becoming hexagonal. Zooecial divergence approximately 20° to 30°. Zooecial bend abrupt; living chambers in exozone oriented about 90° to branch surface. Zooecial length about 8 times diameter; longitudinal arrangement of zooecia regular. Diaphragms rare. Exozonal width one-third to half branch radius. Lamellar profile broadly rounded in exozone. Aktinotostyles common to abundant, in single or multiple rows, arising near base of exozone, rarely with nonlaminated core near stylet base, typically expanding with growth, paralleling zooecia. [*Saffordotaxis* is distinguished on zooecial shape, and arrangement and presence of aktinotostyles as the only stylet type. Its characters are very similar to those in early species of *Rhombopora,* differing largely in stylet development. Intervals of nonlaminated core, as in acanthostyles, are present in very few stylets of *Saffordotaxis,* but otherwise, only typical aktinotostyles are present. In contrast, *Rhombopora* has one or two enlarged acanthostyles proximal to each zooecium.] *L.Miss.(Kinderhook.-Osag.),* E.N.Am.——FIG. 289,*1a–e.* **S. incrassata* (ULRICH); *a,* axial region, zooecial shapes, stylets; long. sec., syntype, USNM 43345, ×40; *b,* axial region, zooecial shapes, aktinotostyles; long. sec., syntype, USNM 240774, ×24; *c,* zooecial cross sections, exozonal development; transv. sec., syntype, USNM 240774, ×24; *d,* living chamber outlines, thick exozonal walls, stylets; tang. sec., syntype, USNM 43345, ×24; *e,* apertural arrangement, stylets; UI X-5272, about ×5.

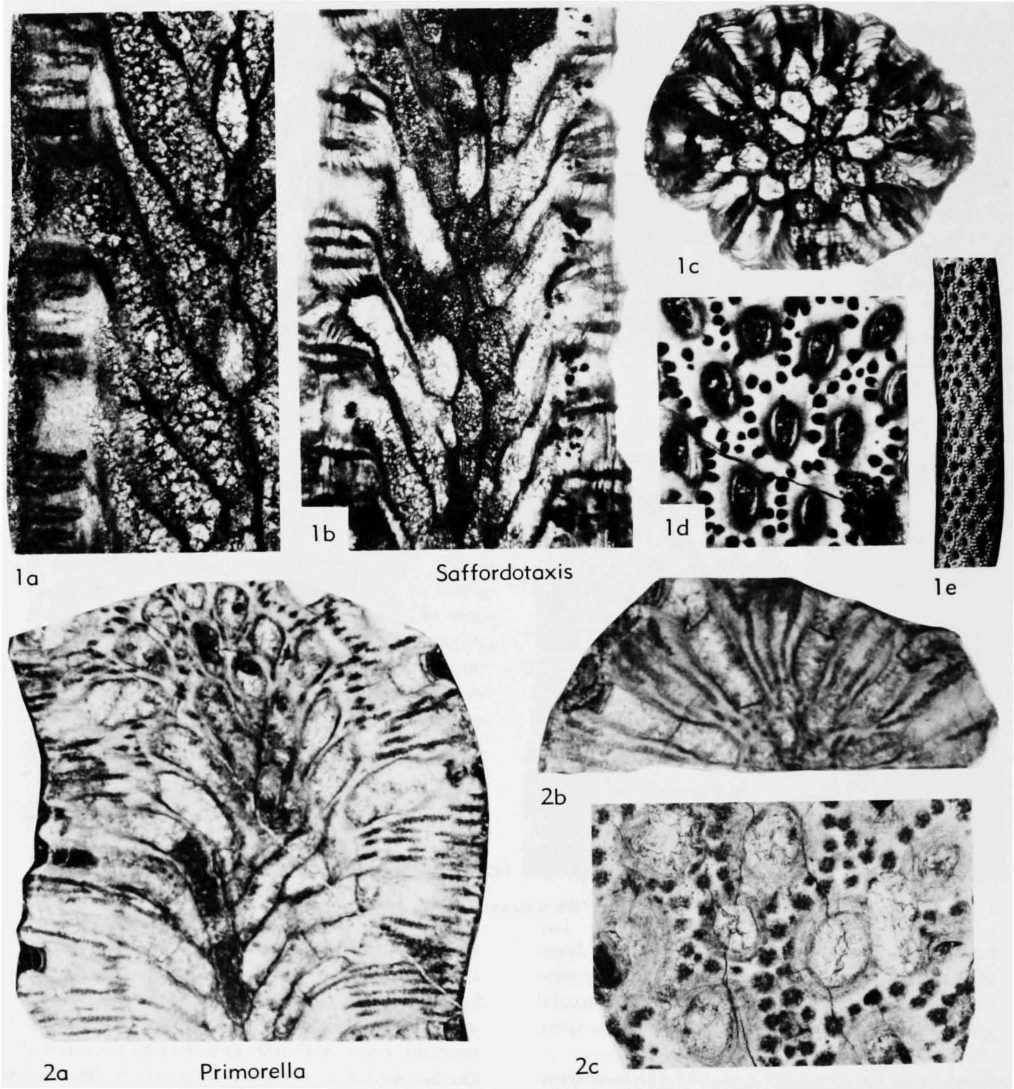

FIG. 289. Rhomboporidae (p. 580–581).

Family BACTROPORIDAE Simpson, 1897

[Bactroporidae SIMPSON, 1897, p. 553]

Zoaria erect, not known to branch; articulated basally in at least one species, proximal side of joint unknown; tapered basal interval lacking apertures, bearing nodose, discontinuous ridges. Stem diameters 1 to 2 mm, constant along length except for tapered base; cross sections subcircular. Apertural arrangement rhombic, ridges absent. Metapores absent. Axial region formed by narrow median plate; median rods questionably developed in some species. Zooids budded from median plate, divergence about 30°. Zooecial bases inflated in longitudinal sections. Zooecial cross sections polygonal, regular in endozone. Zooecial bends rounded; living chambers elliptical in cross section in exozone, oriented about 50° to 60° to stem surface. Zooecial lengths 7 to 10 times diameter. Single, prominent, straight hemiseptum on proximal wall at zooecial bend in one species; absent in others. Diaphragms absent. Exozonal width about half stem radius.

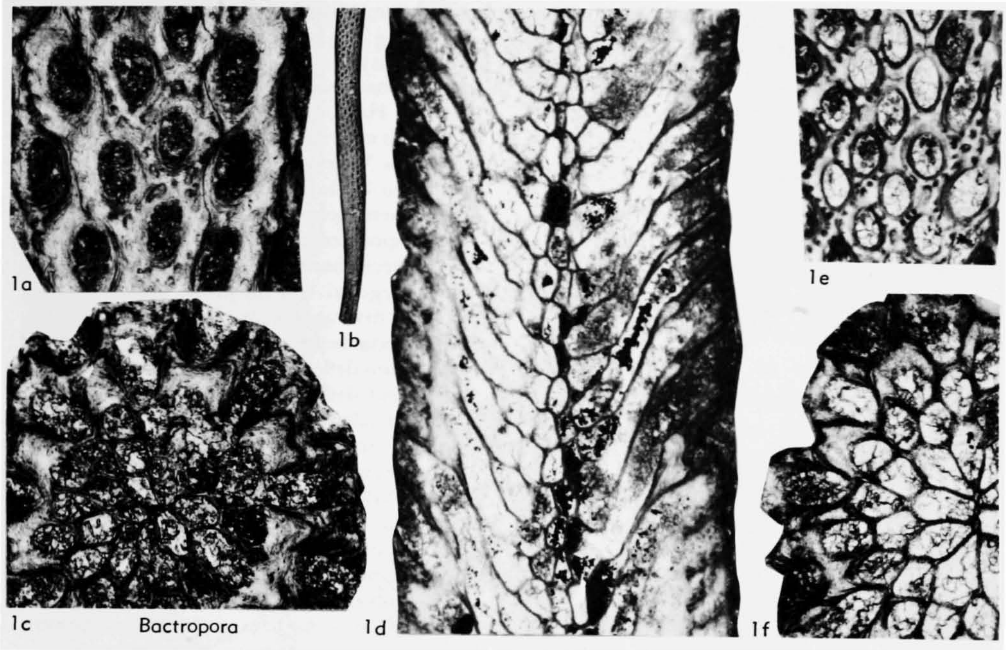

FIG. 290. Bactroporidae (p. 583).

Zooecial boundaries may not be visible; or narrow, irregular, dark with granular material in some areas. Lamellar profiles V-shaped in exozone, flattened between stylets. Heterostyles abundant, filling exozonal wall between zooecia, in linear series or irregular groups, arising in exozone, approximately parallel to zooecial chambers. Mural spines regularly arranged in exozone of one species. *M.Dev.*

Bactropora HALL & SIMPSON, 1887 p. xv [*?*Trematopora granistriata* HALL, 1881, p. 182; OD; ?Ludlowville Sh., Hamilton Gr., M. Dev., Darien Center, Genesee Co., N.Y., USA]. Characters of family. [*Bactropora* is distinguished on zoarial and zooecial shapes, development of exozone, and presence of heterostyles. It is similar to *Nematopora* and *Orthopora* in development of the axial region and zooecial shape, but distinctive in zooecial orientation, stylet development, and presence of basal articulation joints.] *M.Dev.(Erian),* E.N.Am.——FIG. 290, *1a–c.* **B. granistriata* (HALL), holotype, NYSM 599; *a,* living chamber outlines, stylet development; tang. sec., ×45.0; *b,* external form, apertural arrangement, stylet development; ×13.5; *c,* zooecial cross sections, lamellar profile; transv. sec., ×45.0——FIG. 290, *1d–f. B. simplex* (HALL) (named in *Nematopora* by ULRICH, 1886), ?Ludlowville Sh., Hamilton Gr., M. Dev., N.Y., USA, holotype, NYSM 817; *d,* axial region, zooecial shapes and arrangement; long. sec., ×27.0; *e,* living chamber outlines, stylet development; tang. sec., ×27.0; *f,* median plate, zooecial cross sections; transv. sec., ×45.0.

Family NIKIFOROVELLIDAE Goryunova, 1975

[Nikiforovellidae GORYUNOVA, 1975, p. 67]

Zoaria dendroid, jointing unknown. Branch diameters approximately 0.5 to 2.0 mm, relatively constant between bifurcations; branches subcircular in cross section. Apertural arrangement rhombic, longitudinal ridges present or absent. Metapores scattered, or closely spaced in exozonal walls between zooecia, or absent; metapores arising at base of exozone, diaphragms absent. Axial region formed by linear axes or planar walls; elongate zooecia may parallel axis, true axial zooecia not developed. Zooecial bases inflated to flattened in longitudinal section. Zooecial cross section usually polygonal in endozone, may be subhexagonal or rounded. Zooecial divergence from axial region 20° to 70°. Zooecial bends mostly rounded, may be abrupt or lacking. Living chambers in exozone usually elliptical in cross section, may be subcircular; outline may be deflected inward by stylets. Living chambers oriented at 50° to 90° to branch surface, orientation varied in some branches. Zooecial length 2 to 10 times diameter. Hemisepta usually absent, weakly developed in some species. Diaphragms generally few; terminal diaphragms rare. Exozonal width one-third to more than half branch radius. Zooecial boundaries locally not visible; or dark, irregular, with granular or nonlaminated wall material in some areas of most taxa. Lamellar profiles V-shaped or rounded in exozone; becoming flattened between widely spaced apertures. Paurostyles and acanthostyles common to abundant; aktinotostyles present in one genus; stylets generally arising at base of exozone, parallel to zooecial chambers. Mural spines may be regularly arranged in exozonal living chambers. *?L.Dev.,M.Dev.-U.Perm.*

Nikiforovella Nekhoroshev, 1948a, p. 56 [**N. alternata*; OD; L. Carb.; near Lake Baikal, USSR]. Branch diameters about 1 mm. Longitudinal ridges absent. Metapores relatively few in most species, densely spaced between autozooecia in few species. Axial region usually formed by well-defined linear axis or local planar wall. Axial zooecia absent, but endozone of zooecia may ascend near branch axis for short intervals before diverging; otherwise similar to typical autozooecia. Zooecial bases usually weakly inflated. Zooecial cross sections polygonal, commonly hexagonal in endozone. Zooecial divergence from axis approximately 30° to 45°. Zooecial bend usually rounded. Living-chamber walls may be deflected into chambers by stylets; chambers oriented 70° to 90° to branch surface, orientation varied within zoaria in some species. Zooecial length 4 to 8 times diameter; longitudinal arrangement of zooecia regular to irregular. Hemisepta usually absent; may be weakly developed. Diaphragms rare. Exozonal width mostly greater than half branch radius. Zooecial boundary commonly irregular, locally with granular or nonlaminated wall material, or locally not visible. Lamellar profile in exozone rounded between closely spaced apertures. Paurostyles and acanthostyles common to abundant, scattered; some acanthostyles large, well developed. Mural spines may be regularly arranged in exozonal living-chamber wall. *M.Dev.-L.Perm.*, USSR, S.E.Asia, N.Am.——Fig. 291,*1a–c*. **N. alternata*, holotype, TsGM 201, all ×40; *a*, zooecial shapes and orientation; long. sec.; *b*, scattered stylets, metapores; tang. sec.; *c*, linear axis, zooecial cross sections; transv. sec. (Nekhoroshev, 1948b).

Acanthoclema Hall, 1886, pl. 25 [**Trematopora alternata* Hall, 1883b, p. 148; OD; Onondaga Ls., equals up. Helderberg Gr. of Hall, M. Dev., Onondaga Valley, N.Y., USA]. Branch diameters 0.7 to 1.5 mm. Longitudinal ridges absent. Single metapore proximal to each zooecium. Axial region formed by generally well-defined axis. Zooecial bases flattened. Zooecial cross section polygonal, in endozone subhexagonal. Zooecial divergence from axis approximately 70°. Zooecial bend not developed, proximal wall of zooecium deflected abruptly at metapore, distal wall not deflected. Living chamber oriented approximately 70° to branch surface. Zooecial length 2 to 3 times diameter; longitudinal arrangement of zooecia regular. Hemisepta absent; shallow or terminal diaphragms may be developed, other diaphragms absent. Exozonal width about half branch radius. Zooecial boundary commonly irregular, locally not visible, or locally with granular or nonlaminated wall material. Lamellar profile in exozone rounded in transverse view, near metapore; flattened in longitudinal view. Paurostyles or acanthostyles few, concentrated between longitudinally successive apertures. Mural spines regularly arranged in exozonal living-chamber wall. [Differentiation of *Acanthoclema, Nikiforovella, Streblotrypa,* and *Streblotrypella* depends largely on the development of metapores, stylets, and median axes; however, these features may vary significantly within populations. Because of inadequate illustration, *Acanthoclema* was largely ignored during development of the concepts of *Nikiforovella* and *Streblotrypella. Acanthoclema* is here restricted to those nikiforovellid species with a single metapore developed proximal to each autozooecium. It is further characterized by regular arrangement of zooecia and metapores, development of a linear axis, zooecial shape, and nature of the stylets. *Acanthoclema* is also similar to the arthrostylid *Cuneatopora* in typical mature branch diameter, zooecial shape and orientation, axial definition, and presence of metapores, but *Cuneatopora* is articulated and its metapores are lateral to the autozooecia.] *M.Dev.(Erian),* E.N.Am.——Fig. 292,*1a–c*. **A. alternatum* (Hall), holotype, NYSM 579; *a,* linear axis, zooecial shapes, stylets; long. sec., ×47; *b,* median axis, zooecial cross sections; transv. sec., ×47; *c,* zooecial shapes, mural spines; long. sec., ×94.——Fig. 292,*1d,e*. *A. scutulatum* Hall, Hamilton Gr., M. Dev., N.Y., USA; *d,* linear axis, zooecial shapes, metapores; long. sec., USNM 240782, ×47; *e,* apertural arrangement, stylets, metapores; tang. sec., USNM 168344, ×94.

Pinegopora Shishova, 1965, p. 60 [**P. delicata*; OD; U. Perm. (Kazan.), Pinega River, Arkhan-

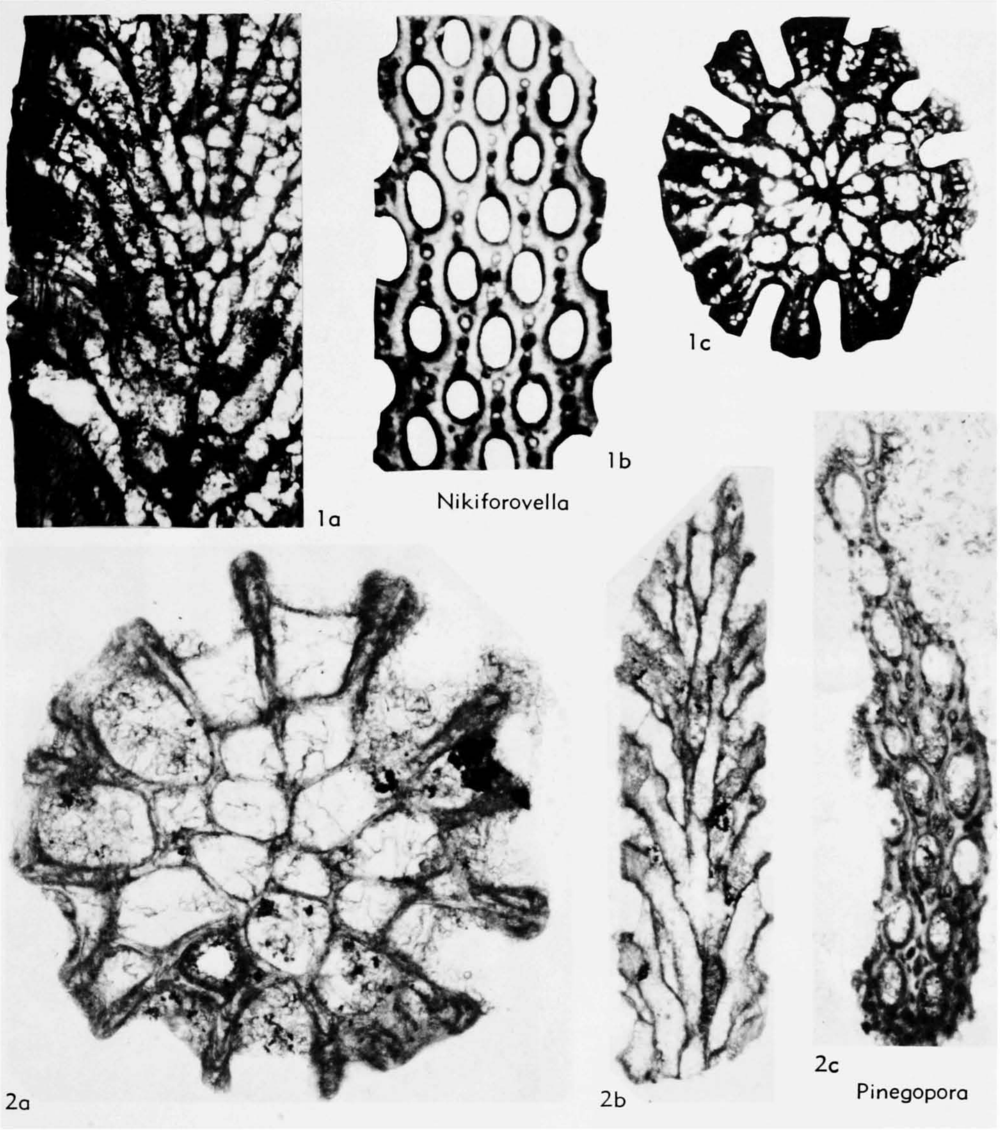

FIG. 291. Nikiforovellidae (p. 584).

gel'sk Prov., Russ. plat., USSR]. Branch diameters 0.6 to 0.7 mm. Longitudinal, tuberculate ridges separating apertural rows. Metapores scattered in exozone. Axial region formed by elongate endozonal intervals of some zooecia, undifferentiated except in length; shorter zooecia budded from surfaces of longer zooecia. Zooecial bases weakly inflated. Zooecial cross sections polygonal in endozone, usually irregular. Zooecial divergence from axis approximately 25°. Zooecial bend rounded. Living chamber orientation varied, usually about 50° to surface. Zooecial length varied, shorter zooecia approximately 7 times diameter. Longitudinal arrangement of zooecia irregular. Hemisepta absent, diaphragms scattered. Exozonal width approximately one-third branch radius; endozonal-exozonal boundary gradational. Zooecial boundary irregular, granular, locally not visible. Lamellar profile V-shaped in exozone. Acanthostyles scattered. [*Pinegopora* is distinguished on the nature of the axial region, zooecial shape and orientation, and development of the exozone.] *U.Perm.(Kazan.),* USSR.——FIG. 291,*2a–c.* **P. delicata,* holotype, PIN 1692/275; *a,* zooecial cross sections, lamellar profile; transv. sec., ×100; *b,* zooecial outlines, arrangement; long. sec., ×30; *c,* apertural arrangement; tang. sec., ×30.

Streblotrypella NIKIFOROVA, 1948, p. 41 [**Streblotrypa major* ULRICH in MILLER, 1889, p. 326; OD;

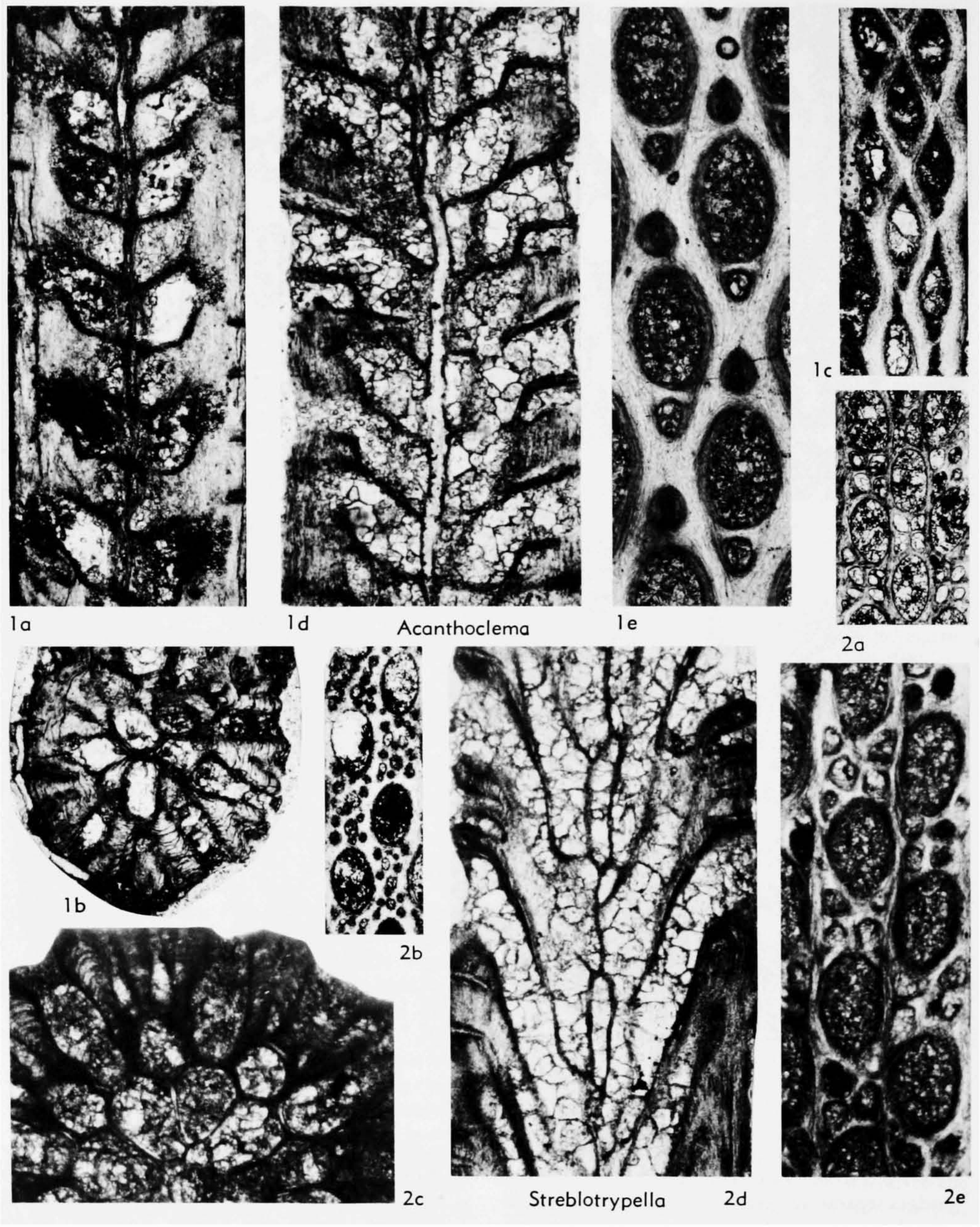

FIG. 292. Nikiforovellidae (p. 584–585).

New Providence Sh., L. Miss., Kings Mt. at Halls Gap, Lincoln Co., Ky., USA}. Branch diameters 0.7 to 1.5 mm. Longitudinal ridges may separate rows of apertures. Metapores few to densely spaced between autozooecia. Axial region formed by well-defined linear axis. Zooecial base weakly inflated. Zooecial cross sections polygonal in endozone, usually hexagonal. Zooecial divergence from axis approximately 20° to 30°. Zooecial bend abrupt. Living chambers usually oriented 80° to 90° to zoarial surface. Zooecial length 5 to 10 times diameter; longitudinal arrangement of zooecia generally regular. Hemisepta absent, diaphragms rare. Exozonal width approximately one third to half branch radius. Zooecial boundary commonly dark, irregular; locally granular, or with nonlaminated wall material, or not visible. Lamellar profile broadly flattened to V-shaped in exozone. Aktinotostyles or acanthostyles scattered, or stylets absent. [Compared to *Nikiforovella, Streblotrypella* usually has more elongate and steeply ascending zooecia, living chambers in the exozone are more perpendicular to the zoarial surface, and the exozone generally is narrower. *Streblotrypella* sometimes lacks stylets and has a correlated concentration of metapores in a cluster proximal to the zooecia.] *?Dev.,L.Carb.(Osag.)-L.Perm,?U. Perm.,* N.Am., USSR, S.E.Asia, Japan, Australia.——FIG. 292,*2a–e*. **S. major* (ULRICH); *a,* apertural and metapore arrangements; tang. peel, USNM 240790, ×28; *b,* apertural arrangement, stylets, metapores; tang. sec., USNM 240791, ×28; *c,* zooecial cross sections, lamellar profile; transv. sec., syntype, USNM 44095, ×47; *d,* zooecial shapes, metapore arrangement; long. sec., syntype, USNM 44095, ×47; *e,* apertural and metapore arrangements; tang. sec., USNM 240789, ×47.

Family HYPHASMOPORIDAE Vine, 1886

[Hyphasmoporidae VINE, 1886, p. 95] [=Streblotrypidae ULRICH, 1890, p. 365]

Zoaria dendroid, jointing unknown. Branch diameters 0.2 to 5.5 mm, relatively constant between bifurcations in most species; branches subcircular in cross section. Apertural arrangement rhombic, longitudinal ridges commonly separating rows of apertures. Metapores generally filling exozonal wall between autozooecia, but may be scattered; usually in longitudinal rows between successive apertures, present or absent beyond distolateral margins of zooecial apertures; arising in late endozone or at base of exozone; diaphragms absent. Axial region formed by weak to well-defined axial zooecia, or well-defined bundles of axial zooecia. Axial zooecia, especially those in bundles, typically with narrower and thinner walls than in endozones of autozooecia. Zooids budded from surfaces of axial zooecia, or near branch axis. Autozooecial bases attenuated to inflated in longitudinal section. Autozooecial cross sections polygonal in endozone, irregular to hexagonal. Zooecial divergence from axial region approximately 10° to 30°. Zooecial bends rounded to abrupt. Living chambers in exozone usually subcircular to elliptical in cross section, may be flattened proximally, usually oriented about 90° to branch surface. Autozooecial length 8 or more times diameter. Single, slender hemiseptum usually on distal wall in late endozone; proximal wall at zooecial bend commonly inflated, but not developed as true hemiseptum; hemisepta may be absent. Diaphragms scattered or absent. Exozonal width from one-third to over half branch radius. Zooecial boundaries narrow, dark, irregular, with granular or nonlaminated material in some areas; locally not visible. Lamellar profile V-shaped to rounded in exozone, zooecial lining may be present. Stylets rare, parallel to autozooecial chambers. *L.Carb.-U.Perm.*

Hyphasmopora ETHERIDGE, 1875, p. 43 [**H. buskii*; M; L. Carb., E. Kilbride, Scot.]. Branch diameters 0.2 to 0.4 mm, usually constant between bifurcations. Weakly developed longitudinal ridges separating apertural rows. Metapores densely spaced between autozooecia, absent beyond distolateral margins of zooecial apertures; arising at base of exozone. Axial region formed by weakly differentiated, narrow, axial zooecia paralleling axis for varying intervals before diverging toward surface, assuming autozooecial morphology. Zooecial bases attenuated. Zooecial cross sections polygonal in endozone, irregular. Zooecial divergence from axial region 10° to 20°. Zooecial bend rounded to abrupt. Living chamber orientation varied, inclined to branch surface. Zooecial length generally more than 10 times diameter; longitudinal arrangement of zooecia irregular. Single, straight, slender hemiseptum on distal wall in late endozone; proximal wall at zooecial bend inflated, true hemisepta lacking. Diaphragms apparently absent. Exozonal width approximately one-third to half branch radius. Zooecial boundary well defined, narrow, irregular, granular, ramifying into multiple planar dark zones at base of longitudinal ridges in exozone; thickened, nonlaminated wall material locally developed, especially at base of exozone. Lamellar profile in exozone V-shaped to subrounded between dark zones, rounded between metapores. Stylets absent. [*Hyphasmopora* is distinguished on zooecial shape and arrangement, and wall structure. It resembles *Streblotrypa* in nature of the zooecia, exozone, and metapores, but is distinctive in the presence of weakly defined axial zooecia and well-defined zooecial boundaries. Location of the primary types of *H. buskii* is unknown.] *L.Carb.,* Scot.——FIG. 293,*1a–f*. **H. buskii*; *a,* zooecial aperture, metapore arrangement; tang. sec., USNM 240779, ×75; *b,* metapores, zooecial

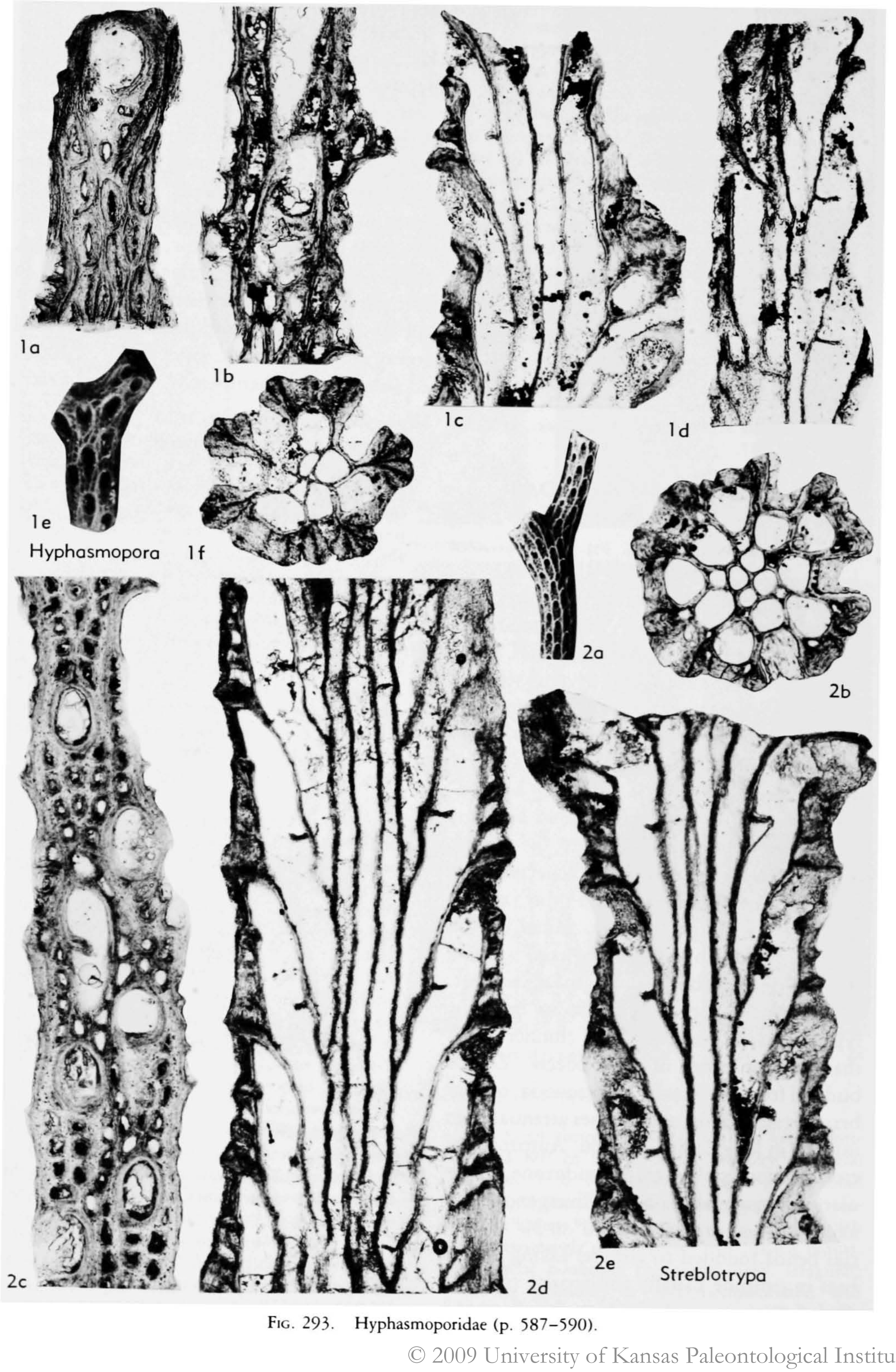

FIG. 293. Hyphasmoporidae (p. 587–590).

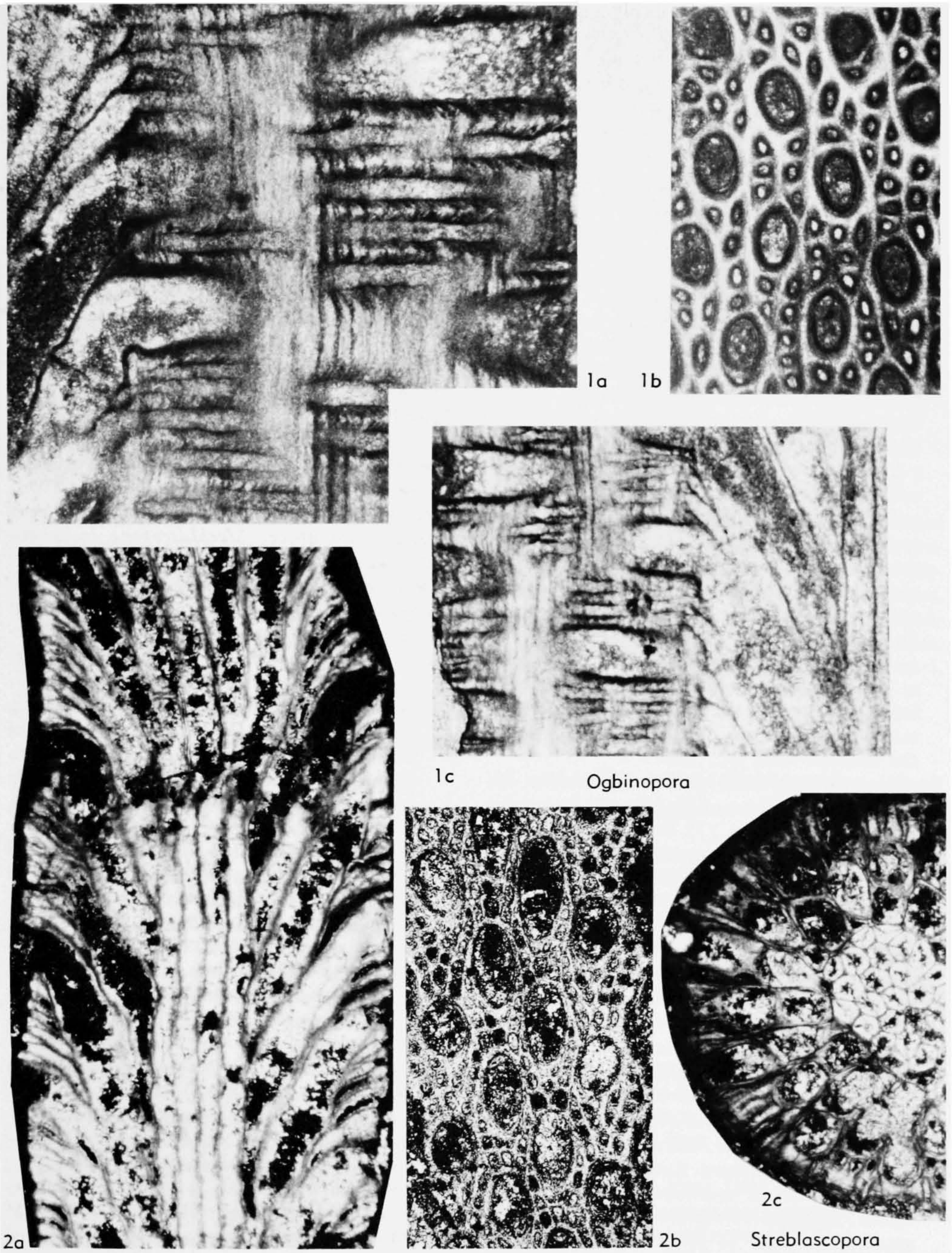

FIG. 294. Hyphasmoporidae (p. 589–590).

boundaries; tang. sec., USNM 240778, ×75; *c,* zooecial shapes and boundaries; long. sec., USNM 240777, ×75; *d,* zooecial shapes and arrangement, hemisepta; long. sec., USNM 240775, ×75; *e,* zooecial aperture and metapore arrangements; USNM 240780, ×20; *f,* dark zones in exozone; transv. sec., USNM 240779, ×75.

Ogbinopora SHISHOVA, 1965, p. 59 [**O. armeniensis*; OD; Gnishik horizon, U. Perm. (Guadalup.), Ogbin Village, Transcauc., USSR]. Branch diameters 2.5 to 5.5 mm, varied between bifurcations. Irregular longitudinal ridges separating apertural rows. Metapores densely spaced between autozooecia, present beyond distolateral margins of zooecial apertures, arising in late endozone or base of exozone. Axial region formed by large bundle of axial zooecia. Autozooecial base attenuated. Autozooecial cross sections hexagonal in endozone. Zooecial divergence from axial region approximately 20° to 30°. Zooecial bend abrupt. Living chambers oriented approximately 90° to branch surface. Autozooecial length approximately 12 times diameter; longitudinal arrangement of autozooecia regular. Single, straight hemiseptum usually on distal wall in late endozone; proximal wall at zooecial bend usually inflated and may form massive hemiseptum. Diaphragms sparse. Exozonal width one-third to half branch radius. Zooecial boundary generally not visible; locally a discontinuous dark zone. Lamellar profile generally rounded in exozone; zooecial lining in autozooecia thick, sharply defined, absent from metapores. Stylets absent. [*Ogbinopora* is distinguished by zoarial size, presence of a large bundle of axial zooecia, zooecial shape, broad exozone, and development of hemisepta.] *Perm.(Artinsk.-Guadalup.),* USSR, S.E.Asia.——FIG. 294, *1a–c. *O. armeniensis,* holotype, PIN 1613/126; *a,* lamellar profile, paired hemisepta at zooecial bend; long. sec., ×47; *b,* zooecial aperture and metapore arrangements; tang. sec., ×28; *c,* zooecial outlines, long. sec., ×28.

Streblotrypa VINE, 1885, p. 391 [**S. nicklisi*; M; Carb.; Yorkshire, Eng.] [=*Lanopora* ROMANCHUK, 1975, p. 77]. Branch diameters 0.7 to 2.5 mm, usually constant between bifurcations. Weak to well-developed longitudinal ridges separating apertural rows. Metapores usually densely spaced between autozooecia, rarely scattered in exozone; present or absent beyond distolateral margins of zooecial apertures, arising in exozone or rarely in late endozone. Axial region varied; ranging from few axial zooecia to large, well-defined axial bundles. Individual zooecia rarely diverging from well-defined axial bundles, but commonly diverging and developing morphology typical of autozooecia in species with few axial zooecia. Autozooecial bases attenuated to weakly inflated. Autozooecial cross sections polygonal in endozone, irregular or hexagonal. Zooecial divergence from axial region approximately 20° to 30°. Zooecial bend generally abrupt. Living chamber flattened proximally in exozone, chamber oriented about 90° to branch surface. Autozooecial length usually 8 to 12 times diameter. Longitudinal arrangement of autozooecia usually regular. True hemisepta rare or lacking; single, straight, slender hemiseptum may be present on distal wall in late endozone; proximal wall at zooecial bend inflated. Scattered diaphragms may be present. Exozonal width usually between one-third and half branch radius, rarely greater. Zooecial boundary usually well defined, irregular, rarely not visible; discontinuous, nonlaminated wall material may be present. Lamellar profile rounded in exozone. Stylets usually absent; paurostyles and weakly developed acanthosyles may be present. [VINE's (1885) one specimen of *S. nicklisi* from England is lost. DUNCAN (1949) recommended replacement of VINE's specimen by a suite of fossils in collections of the U.S. National Museum, but such replacement does not fulfill ICZN requirements for designation of a neotype. Nevertheless, the concept of *S. nicklisi* has been generally based on the North American specimens illustrated here. *Lanopora* ROMANCHUK (1975) differs from *Streblotrypa* only in presence of swellings on longitudinal ridges, a feature I consider to be of no generic significance, and *Lanopora* is herein synonymized with *Streblotrypa.* Some species of *Streblotrypa* and *Streblascopora* BASSLER, 1952, are distinct, but others combine features of both genera; therefore, *Streblascopora* is herein reduced to subgenus rank under *Streblotrypa. Streblotrypa* is similar to the nikiforovellid *Streblotrypella* in zooecial orientation, trend toward stylet loss, and concentration of metapores proximal to zooecial apertures.] *U.Miss.(Meramec.)-U.Perm.,* Eu., Asia, Australia, N.Am., S.Am.

S. (Streblotrypa). Species of *Streblotrypa* lacking distinct bundle of axial zooecia; about 10 or fewer axial zooecia at any level in branch. Hemisepta usually present, metapores usually restricted to rows between zooecial apertures, commonly absent beyond distolateral margins of apertures. [*S.* (*Streblotrypa*) is distinguished by its axial region, narrow exozone, and usual lack of stylets. It differs from *S.* (*Streblascopora*) primarily in development of hemisepta and axial zooecia. In *S.* (*Streblotrypa*), polymorphs are relatively less numerous than in *S.* (*Streblascopora*) and they are not set off in a distinct axial bundle.] *U.Miss.(Meramec.)-U.Perm.,* Eu., Asia, Australia, N.Am., S.Am. ——FIG. 293, *2a–e. *S.* (*Streblotrypa*) *nicklisi* VINE, U. Miss. (Chester.), Ill., Ala., USA; *a,* apertural and metapore arrangements, longitudinal ridges; USNM 240786, ×10; *b,* zooecial cross sections, lamellar profile; transv. sec., USNM 240788, ×75; *c,* apertural and metapore arrangements; tang. sec., USNM 240788, ×75; *d,* axial zooecia, autozooecial outlines, hemisepta, metapores; long. sec., USNM 240784, ×75; *e,* axial zooecia, autozooecial outlines, hemisepta, metapores; long. sec., USNM 240788, ×75.

S. (Streblascopora) BASSLER, 1952, p. 385 [**Streblotrypa fasciculata* BASSLER, 1929, p. 66; OD; Perm., Soefa, Timor, Indon.]. Species of *Streblotrypa* with more or less clearly defined bundle of axial zooecia and more than

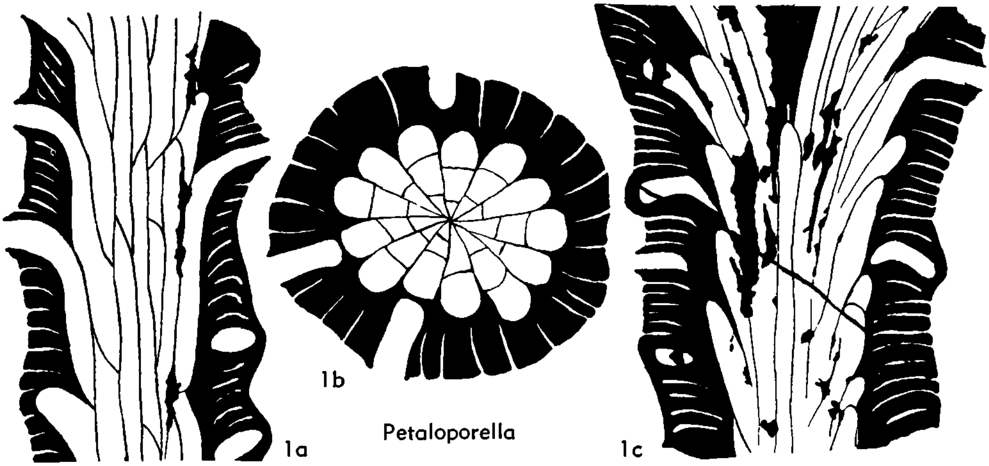

FIG. 295. Family Uncertain (p. 591).

about 10 axial zooecia at any level in branch. Hemisepta rare or absent, metapores common beyond distolateral margins of zooecial apertures. *L.Carb.-U.Perm.*, USSR, S.E.Asia, Japan, Australia, N.Am.——FIG. 294,*2a–c*. **S.* (*Streblascopora*) *fasciculata* BASSLER, holotype, Delft 12340KA, all ×28; *a,* axial zooecia, autozooecial outlines, metapores; long. sec.; *b,* apertural and metapore arrangements; tang. sec.; *c,* axial bundle, zooecial cross sections, lamellar profile; transv. sec.

Family Uncertain

Petaloporella PRANTL, 1935b, p. 4 [**P. bohemica*; M; Branik Ls., M. Dev., Branik, Czech.]. Zoarium dendroid, jointing unknown. Branch diameters 1.1 to 1.8 mm, apparently relatively constant between bifurcations. Apertural arrangement rhombic, longitudinal ridges absent, metapores more or less densely spaced in exozone between autozooecia. Axial region formed by linear axis or axial zooecia. Zooids budded around axis or from surface of axial zooecia. Zooecial base weakly inflated. Zooecial cross section in endozone triangular. Zooecial divergence from branch axis 10° to 20°. Zooecial bend rounded. Living chambers oriented about 90° to branch surface. Autozooecial length approximately 10 times diameter. Longitudinal arrangement of zooecia somewhat irregular. Hemisepta, diaphragms, stylets absent. [Type specimens of *Petaloporella bohemica* could not be located in the Narodini Museum (Prague) and may be lost (W. A. OLIVER, pers. commun. to R. S. BOARDMAN). The concept of *Petaloporella* cannot be refined because some features are unclear in the original illustrations. One drawing shows a well-defined median axis (Fig. 295,*1b*), whereas one appears to show axial zooecia (Fig. 295,*1c*), and another (Fig. 295,*1a*) is difficult to interpret. If axial zooecia are present, *Petaloporella* may be a synonym of *Streblotrypa*.] *M.Dev.*, Czech.——FIG. 295,*1a–c*. **P. bohemica*; *a,* zooecial shapes, metapores; drawing, biased long. sec.; *b,* budding; drawing, transv. sec.; *c,* axial zooecia; drawing, long. sec., approx. ×20 (Prantl, 1935b).

Summary of Recent Important Taxonomic Changes in Rhabdomesina

Acanthoclema HALL, 1886. Herein transferred from the Rhabdomesidae to the Nikiforovellidae; generic concept restricted in scope.

Bactropora HALL & SIMPSON, 1887. Herein returned from the Rhabdomesidae to the Bactroporidae, following SIMPSON (1897).

Bactroporidae SIMPSON, 1897. Family concept accepted herein; not in general usage since original description.

Coeloconus ULRICH, 1889. Synonymized with *Rhabdomeson*; see BLAKE (1976).

Cuneatopora SIEGFRIED, 1963. Some species have been transferred from *Helopora*; see KOPAYEVICH (1975).

Hyphasmoporidae VINE, 1886. Restricted in content by reassignment of some genera to the Nikiforovellidae by GORYUNOVA (1975).

Klaucena TRIZNA, 1958. Herein transferred from the Rhabdomesidae to the Rhomboporidae.

Lanopora ROMANCHUK, 1975. Herein synonymized with *Streblotrypa*.

Megacanthopora MOORE, 1929. Considered by some Soviet authors to belong to the Trepostomata, herein assigned to the Rhomboporidae.

Nematopora ULRICH, 1888. Generally regarded as including only species articulated basally or not at all, herein considered to include *N. harrisi* (James), a highly segmented species formerly assigned to *Helopora*.

Neorhombopora Shishova, 1964. Herein synonymized with *Megacanthopora*.

Osburnostylus Bassler, 1952. Herein transferred from the Tubuliporata to the Rhabdomesina.

Petaloporella Prantl, 1935b. Herein transferred from the Tubuliporata to the Rhabdomesina, family uncertain.

Primorella Romanchuk & Kiseleva, 1968. Originally assigned to the Trepostomata, herein assigned to the Rhabdomesina, following Goryunova, 1975.

Rhabdomesidae Vine, 1884. Herein restricted in scope by reassignment of some previously included genera to the Bactroporidae, Rhomboporidae, and Arthrostylidae.

Rhabdomesina {=Rhabdomesoidea} Astrova & Morozova, 1956. Recognized herein as a suborder; generally given ordinal rank by Soviet authors.

Rhabdomeson Young & Young, 1874. Includes conical branches previously assigned to *Coeloconus*; see Blake (1976).

Rhombopora Meek, 1872. Herein transferred from the Rhabdomesidae to the Rhomboporidae; concept of genus here much restricted.

Rhomboporidae Simpson, 1897. Family concept accepted herein; not in general usage since original description.

Saffordotaxis Bassler, 1952. Herein transferred from the Rhabdomesidae to the Rhomboporidae.

Streblascopora Bassler, 1952. Herein reduced to subgeneric rank and assigned to *Streblotrypa*.

Streblotrypella Nikiforova, 1948. Herein transferred from the Hyphasmoporidae to the Nikiforovellidae.

Trematella Hall, 1886. Herein transferred from the Trepostomata to the Rhabdomesidae.

Tropidopora Hall, 1886. Herein transferred from the Rhabdomesidae to the Arthrostylidae.

Vetofistula Etheridge, 1917. Transferred to the Coelenterata; see Ross (1961).

Different authors have included genera in the Rhabdomesina that I consider to have other or uncertain affinities. Some of these genera were reassigned by various authors prior to this work, and include: *Archaeomeson* Astrova, 1965; *Clausotrypa* Bassler, 1929; *Denmeadopora* Fleming, 1969; *Goldfussitrypa* Bassler, 1952; *Hayasakapora* Sakagami, 1960; *Hyalotoechus* McNair, 1942; *Idioclema* Girty, 1910; *Linotaxis* Bassler, 1952; *Maychella* Morozova, 1970; *Mongoloclema* Shishova, 1970; *Nemacanthopora* Termier & Termier, 1971; *Nemataxidra* Bassler, 1952; *Nematotrypa* Bassler, 1911; *Ottoseetaxis* Bassler, 1952; *Pesnastylus* Crockford, 1942; *Rhombocladia* Rogers, 1900; *Rhomboporella* Bassler, 1936; *Spirillopora* Gurich, 1896; *Streblocladia* Crockford, 1944; and *Syringoclemis* Girty, 1910.