SYSTEMATIC DESCRIPTIONS FOR THE ORDER CYSTOPORATA

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New photographs of primary types are used when possible. Some primary types are silicified, and new photographs of topotypes are used. Where neither primary types nor topotypes were available for study, specimens of nearly the same age from nearby areas were used. Some photographs were furnished by other paleontologists. For a few genera, drawings based on original published illustrations had to be used. Some reported geologic and geographic ranges cited for genera are difficult to evaluate, and I included only those in which I had reasonable confidence.

Order CYSTOPORATA Astrova, 1964

[Cystoporata ASTROVA, 1964, p. 28]

Zoarial growth form variable. Autozooecia tubular; short and lacking diaphragms or long and with diaphragms. Walls laminated, granular, or granular-prismatic. Some (ceramoporines) with communication pores and exilazooecia in exozone. Some (fistuliporines) with extrazooidal vesicular tissue between autozooecia. Most with lunaria. Few with acanthostyles, except in vesicles. *Ord.-Perm.*

Suborder CERAMOPORINA Bassler, 1913

[*nom. correct.* herein, *pro* Ceramoporoidea BASSLER, 1913, p. 326, suborder]

Zoarial growth form encrusting to massive, ramose, frondose, or bifoliate frondose. Monticules low or flush with zoarial surface. Autozooecia originating at basal layer or mesotheca or by interautozooecial budding in growing tip or in exozone. Autozooecia in full contact with one another at basal layer. Diaphragms generally sparse. Walls well laminated; with communication pores or gaps in most genera. Lunaria usually well developed, composed of hyaline calcite. Exilazooecia in exozone in most genera, few to abundant, restricted to monticules in a few forms. *M.Ord.-L.Dev.*

Family CERAMOPORIDAE Ulrich, 1882

[Ceramoporidae ULRICH, 1882, p. 156] [=Ceramoporellidae SIMPSON, 1897, p. 481]

Zoaria discoidal, encrusting, hemispherical, massive, ramose, hollow ramose, frondose, or bifoliate frondose. Monticules commonly low or flush with zoarial surface. Lunaria partly to completely radially arranged around monticules in most genera. Basal layer commonly dense calcite in lower half, laminated in upper half. Autozooecia tubelike, small to large; diaphragms generally few or absent. Walls commonly longitudinally laminate in endozone; generally with broadly curved laminae and amalgamate appearance in outer endozone and exozone. Walls in exozone generally thick. Communication pores few to abundant, absent in some genera. Lunaria extending from endozone to zoarial surface. Lunarial deposits commonly dense, light-colored calcite; locally, in many genera, indistinctly laminated. Wall laminae generally absent on distal side of a lunarium. Exilazooecia (cystopores) tubular; developed only in exozone; few to abundant; wall microstructure similar to that of zooecia. Acanthostyles present in some genera. *M.Ord.(Chazy.)-L.Dev.*

Characters of particular importance are well-laminated walls, communication pores, exilazooecia in the exozone, lunaria, and absence of extrazooidal vesicular tissue.

Ceramopora HALL in SILLIMAN, SILLIMAN, & DANA, 1851, p. 400 [**C. imbricata* HALL, 1852, p. 169; SD HALL & SIMPSON, 1887, p. xviii; Niagaran Gr., M. Sil. (Niag.), Lockport, N.Y., USA]. Zoarium thin discoidal expansions; encrusting, free, or a combination. Zoarium having attached central area with basal layer and free margins with celluliferous base made up of basal zooecia, or basal layer throughout, or free celluliferous base throughout. Small zoaria with one central monticule. Monticules with depressed center; exilazooecia of central cluster larger, more angular than intermonticular exilazooecia. Lunaria in perfect radial arrangement around central monticule; partial to complete radial arrangement around marginal monticules. Autozooecia large, commonly rhombically arranged; cavity ovate to rhomboidal in cross section. Communication pores abundant, most commonly just distal to ends of lunarium. Lunaria small in inner exozone, large at zoarial surface. Diaphrams absent. Exilazooecia few to abundant in intermonticular areas, generally small and subcircular in cross section; lacking diaphrams; with walls commonly oblique to zooecial walls. [Most zoaria of *C. imbricata* have a celluliferous base throughout or in the lateral margins beyond a central encrusting attachment area. Tubular basal zooecia commonly are directed downward or downward and outward; a few are directed downward and toward the center of the zoarium. Thick, poorly laminated walls of basal zooecia have laminae broadly curved and convex toward the base. Configuration of the laminae of basal zooecia indicates that soft tissue was present under the basal zooecia on the underside of the zoarium as well as on the upper surface.] *U.Ord.(Richmond.)-M.Sil.(Niag.),* N.Am., Eu.——FIG. 156,*1a–c.* **C. imbricata; a,* celluliferous base (below), zooecial walls, lunarial deposits, and no diaphragms; long. sec., lectotype, AMNH 1737-A, ×30; *b,* rhombic arrangement of large ovate autozooecia, large lunarial deposits in proximal (lower) half of zooecia, abundant communication pores, and virtual absence of exilazooecia; tang. sec., lectotype, ×30; *c,* abundant communication pores and small, subcircular exilazooecia in intermonticular area; tang. sec., paralectotype, AMNH 1737-B, ×30.

Acanthoceramoporella UTGAARD, 1968b, p. 1451 [**Ceramoporella granulosa* ULRICH, 1890, p. 466; OD; "Fernvale F.," U. Ord., Wilmington, Ill., USA]. Zoarium encrusting expansions, less commonly hollow ramose. Autozooecia with cavity in exozone elliptical or ovate, less commonly, trilobate in cross section. Thin zooecial lining locally present. Communication pores abundant, large; perpendicular to wall and circular to elliptical in cross section. Local gaps in walls in some species. Beadlike wall segments between closely spaced pores may have a short acanthostyle or subspherical body of poorly laminated, light-colored calcite surrounded by thin layer of laminae proximally and laterally and thicker layer distally. Lunaria small in inner endozone; nearly as large at zooecial bend as at zoarial surface. One to several ill-defined cores in some lunaria. Locally, distal side of lunarium bordered by thin laminated layer. Diaphragms abundant, straight or curved; a few abutting wall and very few lacking laminations and curving proximally along wall. Exilazooecia irregular in size and shape, partially to completely isolating autozooecia; diaphragms few to abundant, thick to thin. Exilazooecial walls with more communication pores than autozooecial walls. Acanthostyles generally abundant, short to long; core hyaline, large; collar of core-in-cone laminae, thin. Monticules with central cluster of exilazooecia and more acanthostyles and light-colored spherical bodies. [DONALD DEAN, National Museum of Natural History, has noted that a suite of specimens I thought (UTGAARD, 1968b, p. 1452, 1454) were cotypes of *Acanthoceramoporella granulosa* (ULRICH) are topotypes. Also, an old slide figured by ULRICH (1890) is the holotype, not a cotype. Thus, USNM 43227 are thin sections of the holotype and USNM 159715, 159716, and 159717 are topotypes, not the lectotype and paralectotypes.] *M.Ord.(Mohawk.)-U.Ord.(Richmond.),* E.N.Am., Eu.——FIG. 157,*1a–h.* **A. granulosa* (Ulrich); *a,* monticule (upper left) with partial radial arrangement of lunaria, abundant exilazooecia with many communication pores, and acanthostyles; tang. sec., topotype, USNM 159715, ×27; *b,* lunarial deposits, irregular diaphragms, communication pores, and beadlike wall segments; long. sec., topotype, USNM 159715, ×27; *c,* irregular diaphragms in inner exozone; long. sec., topotype, USNM 159732, ×27; *d,* basal layer (left), abundant diaphragms, and acanthostyles; long. sec., holotype, USNM 43227, ×27; *e,* large monticular zooecia (lower half), lunaria, acanthostyles, and exilazooecia; tang. sec., holotype, ×27; *f,* lunarial deposits, wall laminae, communication pore, and light-colored subspherical body immediately distal to pore (left of center); long. sec., topotype, USNM 159717, ×90; *g,* poorly laminated lunarial deposits, irregular exilazooecia, abundant acanthostyles; tang. sec., topotype, USNM 159717, ×90; *h,* communication pores, spherical, light-colored bodies in beadlike wall segments, and acanthostyle (left of center); transv. sec., topotype, USNM 159716, ×90.

?**Amsassipora** YAROSHINSKAYA, 1960, p. 394 [**A. simplex*; OD; U. Ord., Altai Mts., USSR]. Zoarium massive with smooth surface, autozooecia with cavity circular to irregularly subangular, variable in size. Walls unevenly thickened, questionably with communication pores. Diaphragms sparse, planar to slightly concave. Lunaria lacking. Acanthostyles at zooecial corners; associated with autozooecial budding. Exilazooecia absent. [Lack of lunaria and of undoubted communication pores as well as presence of acanthostyles associated with budding, which resembles the situation in rhombotrypids,

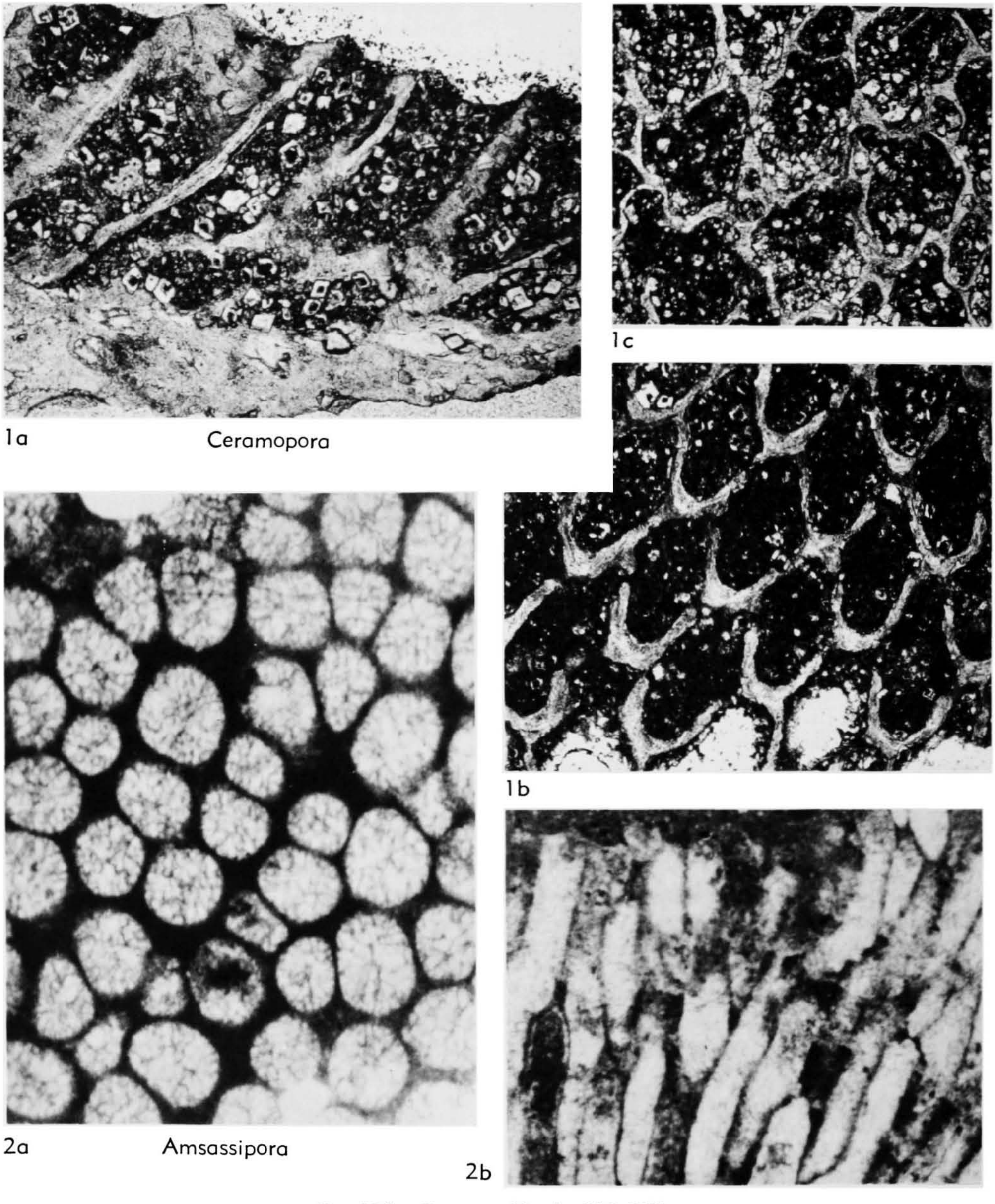


FIG. 156. Ceramoporidae (p. 358–359).

suggests that this genus may be a trepostomate. It is questionably retained in the Ceramoporidae, where it was placed by YAROSHINSKAYA and ASTROVA.] *U.Ord.,* USSR.——FIG. 156,*2a,b.* **A. simplex,* paratype, SNIIGGIMS 951/523a, 523b; *a,* subcircular to subangular autozooecia, acanthostyles at zooecial corners; tang. sec., ×40; *b,* irregular thickness of autozooecial walls, sparse diaphragms, acanthostyles associated with budding loci; long. sec., ×20 (photographs courtesy of G. G. ASTROVA).

Ceramophylla ULRICH, 1893, p. 331 [**C. frondosa*; OD; Decorah Sh., M. Ord. (Mohawk.), St. Paul, Minn., USA] [=*Coeloclema* ULRICH, NICKLES, & BASSLER, 1900, p. 24, 211; BASSLER, 1953, p. G82, *non* ULRICH, 1883, p. 258; *Coeloclema* NICKLES & BASSLER, ELIAS, 1954, p. 53, *non* ULRICH, 1883, p. 258]. Zoarium bifoliate or encrusting expansions or hollow ramose. Monticules small. Mesotheca locally absent in some bifoliate zoaria. Autozooecia with cavity subcircular to circular. In exozone, walls thick, bound-

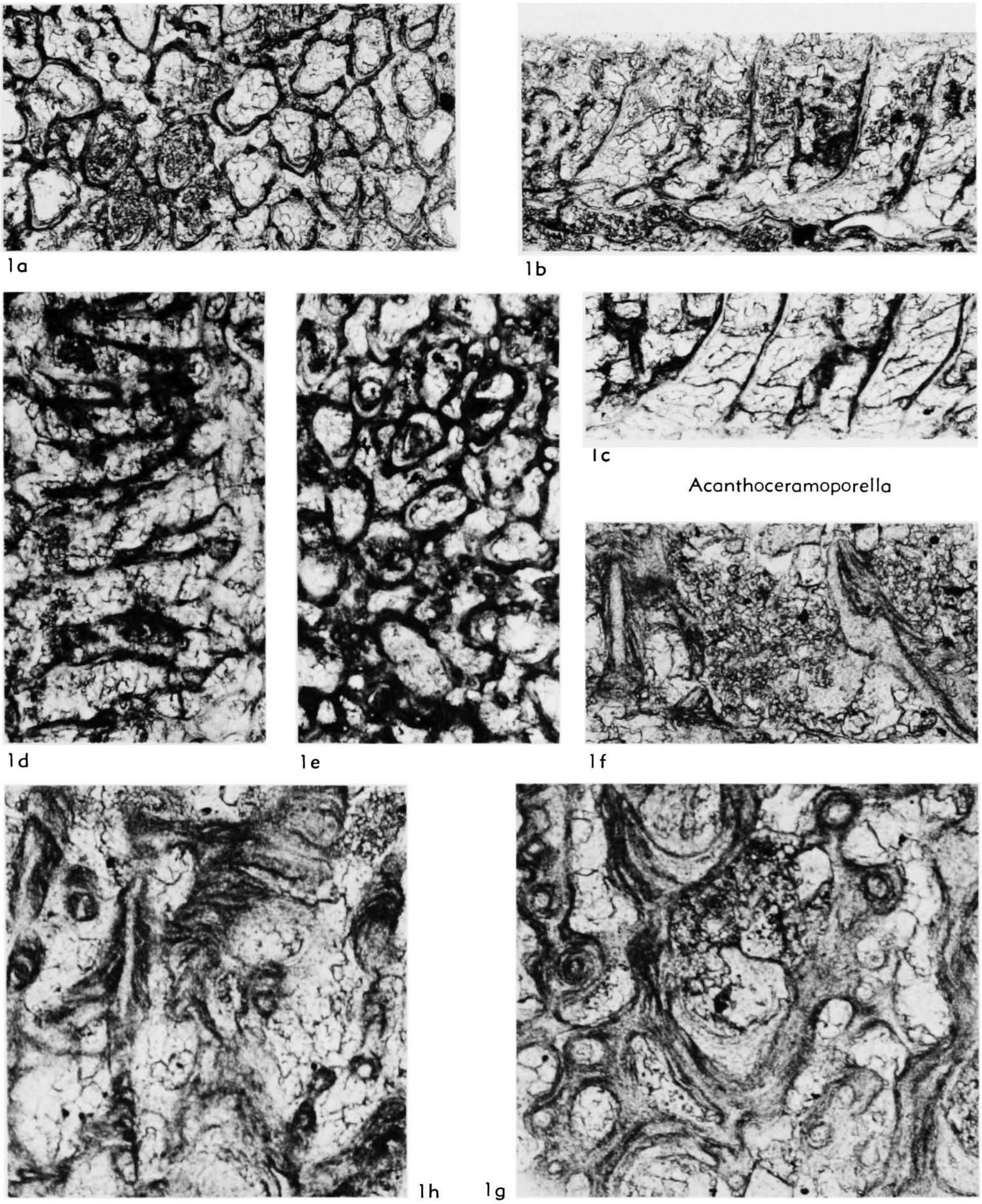
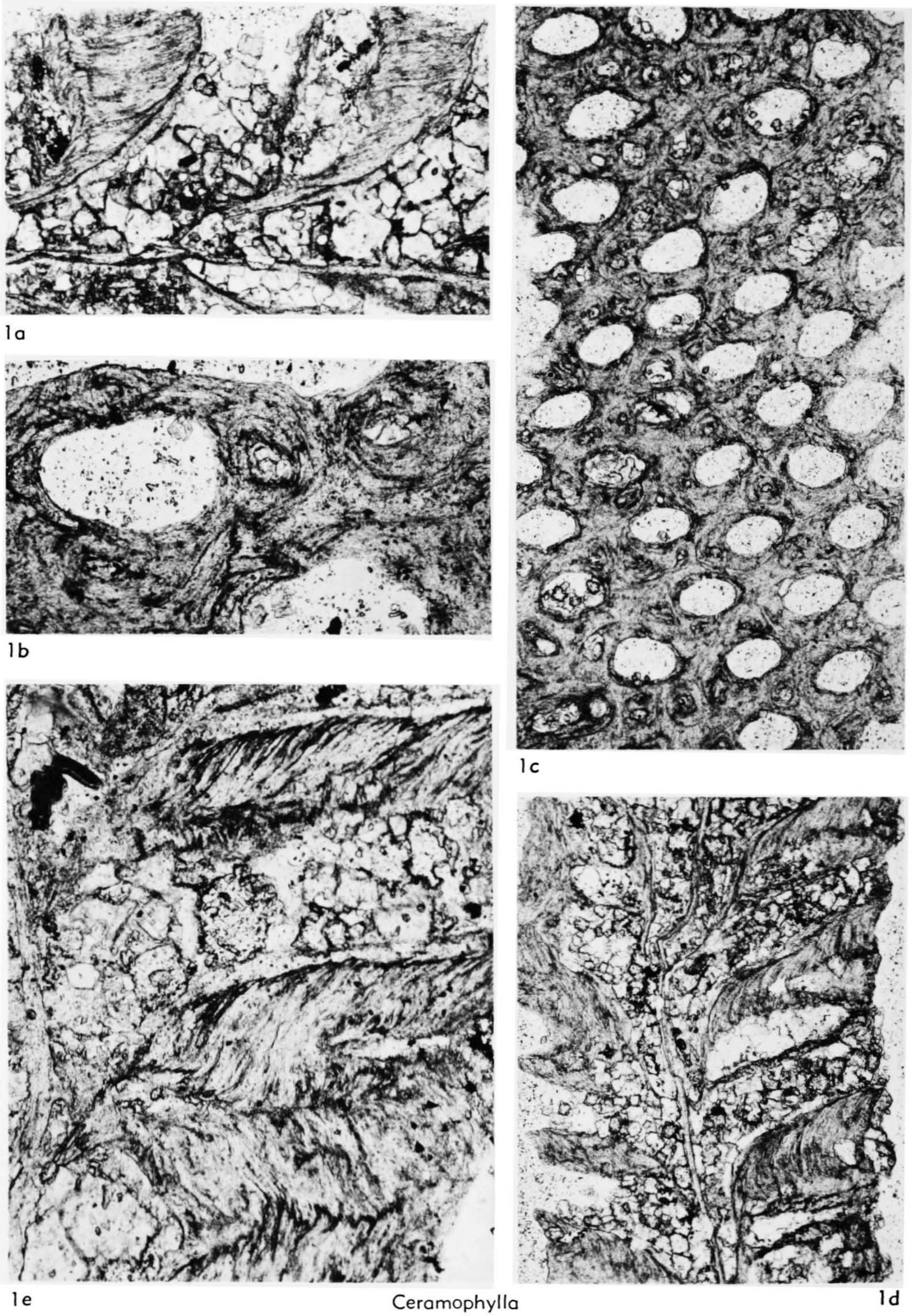


FIG. 157. Ceramoporidae (p. 359).

ary jagged or indistinct. Irregular bundles of wall laminae intertonguing between boundary and cavity, producing mottled appearance in tangential section. Communication pores few, generally in inner exozone. Lunaria small in inner endozone; nearly as large at zooecial bend as at zoarial surface. One to a few cores in many lunaria. Laminae lining distal side of some lunaria. Diaphragms absent. Exilazooecia generally abundant, reduced in diameter toward zoarial surface and in some pinched out or filled with laminated deposit; walls thinner than autozooecial walls; diaphragms absent. Monticular cluster of exilazooecia having thicker walls; monticular center locally subsolid. Lunaria not in radial arrangement or only slightly skewed toward monticular center in autozooecia on flanks of monticule. Zooecia in some slightly larger in monticules. [*Diamesopora vaupeli* ULRICH, 1890, is here reassigned to *Ceramophylla*. *C. vaupeli* has



Ceramophylla

FIG. 158. Ceramoporidae (p. 360).

widely but erroneously been cited as the type species of *Coeloclema* Ulrich (Utgaard, 1968b, p. 1453). *Coeloclema* Ulrich, 1883 is a fistuliporine with a Silurian type species. *C. vaupeli* and several other species differ from *C. frondosa* mainly by having a hollow ramose growth habit with a basal layer rather than encrusting laminar or bifoliate growth habits with basal layers or mesothecae. Several zoaria of *C. frondosa* have a relatively sharp boundary between clear and muddy cavity fillings in some zooecia, but no remnant of a skeletal diaphragm was observed.] *M.Ord.(Mohawk.)-U.Ord. (Eden.),* E.N.Am., Eu. ——Fig. 158,*1a–e*. **C. frondosa*; *a,* mesotheca, lunarial deposits, wall laminae, and exilazooecia; long. sec., lectotype, USNM 159721, ×50; *b,* poorly defined core in lunarium (left) and irregular wall laminae in mottled amalgamate wall; tang. sec., lectotype, ×100; *c,* thick, irregularly laminated walls and small exilazooecia and lunarial deposits; tang. sec., lectotype, ×30; *d,* mesotheca, thickening of walls at zooecial bend, sparse communication pores, and no diaphragms; long. sec., lectotype, ×30; *e,* intertonguing of laminae in walls, irregular dark zooecial boundary (below), and lunarial deposits; long. sec., paralectotype, USNM 159722, ×100.

Ceramoporella Ulrich, 1882, p. 156 [**C. distincta* Ulrich, 1890, p. 464; SD Ulrich, 1890, p. 380; McMicken Mbr., Eden F., U. Ord. (Eden.), Cincinnati, Ohio, USA] [=*Cheiloporella* Ulrich, 1882, p. 157; *Chiloporella* Miller, 1889, p. 297, incorrect subsequent spelling; *Ceramporella* Cumings & Galloway, 1913, p. 427, incorrect subsequent spelling]. Zoarium encrusting or frondescent. Monticules circular to elongate. Autozooecial cross-sectional area reduced from outer endozone to exozone, particularly in frondose zoaria. Autozooecia moderately small in exozone, cavity ovate to subcircular. Zooecial lining local. Communication pores rare. Lunaria increasing in size distally in endozone; nearly as large at zooecial bend as at zoarial surface; ends locally projecting into cavity; cores commonly one, rarely more, per lunarium; thin laminated layer locally on distal side. Commonly one, rarely more, convex or planar diaphragms of dense, light colored calcite per autozooecium. Most diaphragms abutting wall or curving proximally along wall; a few curving distally along wall. Diaphragms commonly at same level in adjacent zooecia. Exilazooecia partially to completely isolating zooecia; large and subangular in cross section in inner exozone, smaller and more circular distally. Lining commonly lacking. Diaphragms few, similar to zooecial diaphragms. Monticular exilazooecia, commonly of serial origin, clustering on semiprostrate proximal wall of autozooecium. [*Fistulipora flabellata* Ulrich, 1879, p. 28, which was subsequently designated as the type species of *Cheiloporella* Ulrich (1882, p. 257), is consistent with the emended definition of *Ceramoporella. C. flabellata* may have a frondose as well as an encrusting growth habit. Frondose zoaria commonly have longer and larger autozooecia in the endozone than do encrusting zoaria. Some zoaria of *C. flabellata* have thicker walls and autozooecial linings than do those of *C. distincta,* and display only slight or partial radial arrangement of lunaria around the monticules.] *M.Ord.(Mohawk.)-U.Ord.(Richmond.),* E.N. Am.——Fig. 159,*1a–d*. **C. distincta; a,* parts of three encrustations; lunarial deposits and diaphragms at nearly same level; transv. sec., lectotype, USNM 159710, ×30; *b,* radial arrangement of lunaria around monticular center; tang. sec., lectotype, ×30; *c,* large lunaria, thin walls, and abundant exilazooecia in intermonticular area; tang. sec., paralectotype, USNM 159711, ×30; *d,* basal layer (below), lunarial deposit, wall laminae, and exilazooecia in exozone; note light-colored, proximally curved diaphragm (left); long. sec., paralectotype, USNM 159712, ×100. ——Fig. 159, *1e–g*. *C. flabellata* (Ulrich), U. Ord., Ohio, USA, topotype, USNM 159714; *e,* exilazooecia in monticular center; tang. sec., ×30; *f,* encrusting overgrowths showing sparse diaphragms, lunarial deposits, and secondary overgrowths on right; transv. sec., ×30; *g,* basal layer, lunarial deposit, wall laminae, and remnant of a diaphragm; long. sec., ×50.

Crepipora Ulrich, 1882, p. 157 [**Chaetetes venusta* Ulrich, 1878, p. 93; SM Ulrich, 1882, p. 257; Economy Mbr., Eden F., U. Ord. (Eden.), W. Covington, Ky., USA]. Zoarium encrusting expansions, hollow ramose or solid ramose with conspicuous monticules. Autozooecia with cavity subangular to subcircular, moderately small, commonly rhombically packed. Wall laminae short, irregular; not concentric around living chamber. Boundary irregular, sinuous; forming broad, dark zone. Communication pores abundant in outer endozone and exozone; subcircular in cross section. Proximal surface of pore perpendicular to wall, distal surface commonly oblique, pores with larger diameter at one end; locally, both surfaces parallel and oblique to wall. Lunaria moderately large in endozone of ramose zoaria, moderately small in inner endozone of zoaria with basal layer; lunaria becoming slightly larger in outer exozone, ends in some projecting into autozooecial cavity. Radius of lunarium conspicuously smaller than radius of autozooecium. Central core or cores in many lunaria. Diaphragms thin to thick, irregularly spaced. Exilazooecia never abundant, commonly rare or absent in intermonticular areas; walls commonly thinner than in autozooecia. Communication pores present but less common in walls between adjacent autozooecia. Diaphragms rare in exilazooecia. Acanthostyles small, few to many in monticular exilazooecial

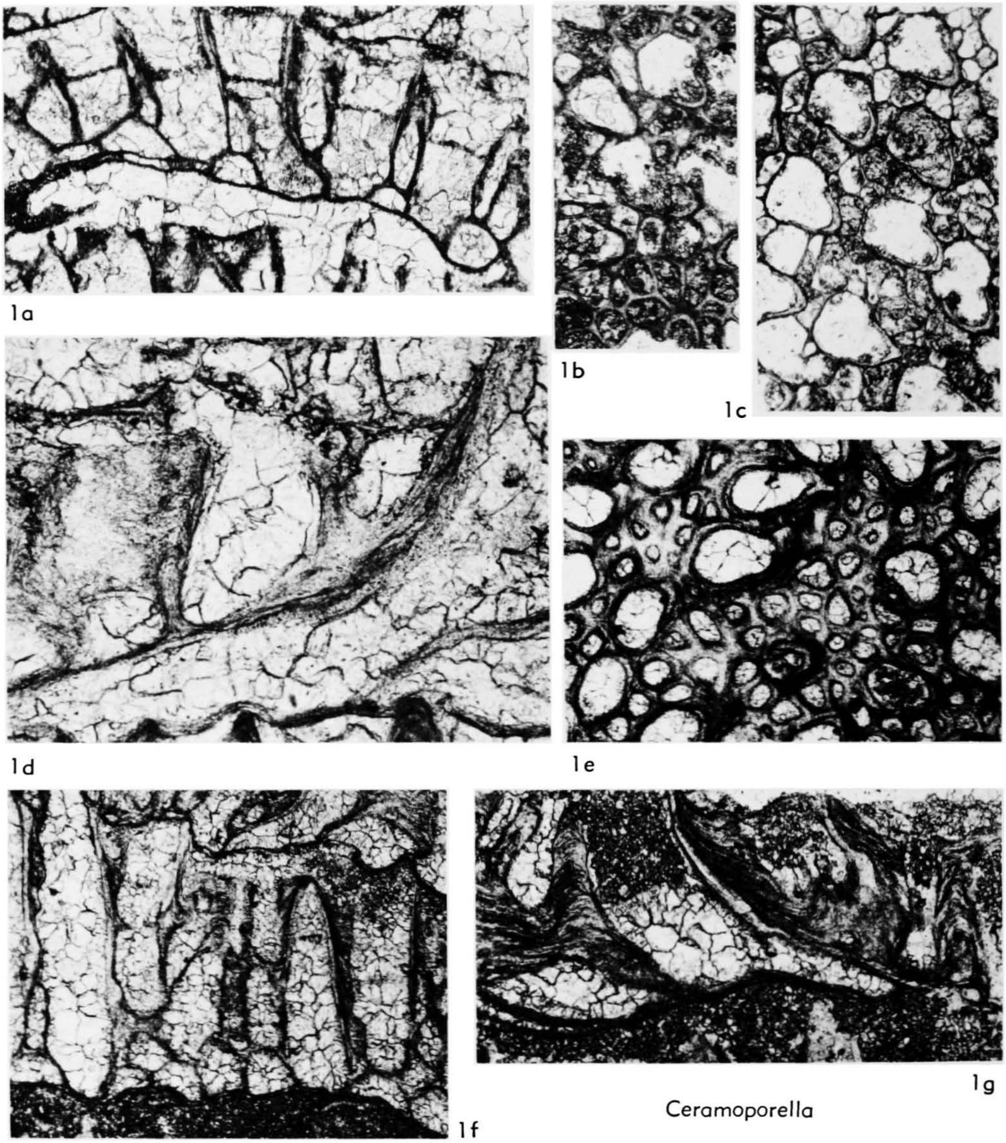


FIG. 159. Ceramoporidae (p. 363).

walls, rare, usually lacking in autozooecial walls in intermonticular areas. Monticules having core of small to large, circular to irregularly shaped exilazooecia, acanthostyles, and ring of marginal zooecia slightly larger than intermonticular autozooecia. Lunaria in some areas partly radially arranged. Monticular centers rarely subsolid. *M. Ord.(?Chazy., Mohawk.)-U.Ord.(Richmond.)*, E.N.Am., Eu.——FIG. 160, *1a–i*. **C. venusta* (ULRICH); *a*, lunarial deposit (left) and exilazooecia and acanthostyles in monticule; transv. sec., paralectotype, USNM 159707, ×50; *b*, cluster of exilazooecia in monticule and some exilazooecia in intermonticular area; tang. sec., paralectotype, USNM 159707, × 30; *c*, acanthostyles in exilazooecial walls in monticule; tang. sec., paralectotype, USNM 159708, ×100; *d*, core in lunarial deposit; tang. sec., paralectotype, USNM 159708, ×100; *e*, basal layer in hollow ramose zoarium and diaphragms in endozone and inner exozone; long. sec., lectotype, USNM 159706, ×30; *f*, exilazooecia with few acanthostyles in monticule and partial radial arrangement of lunaria; tang. sec., lectotype, ×50; *g*, basal layer and increase in size of lunarial deposit from endozone to inner exozone; transv.

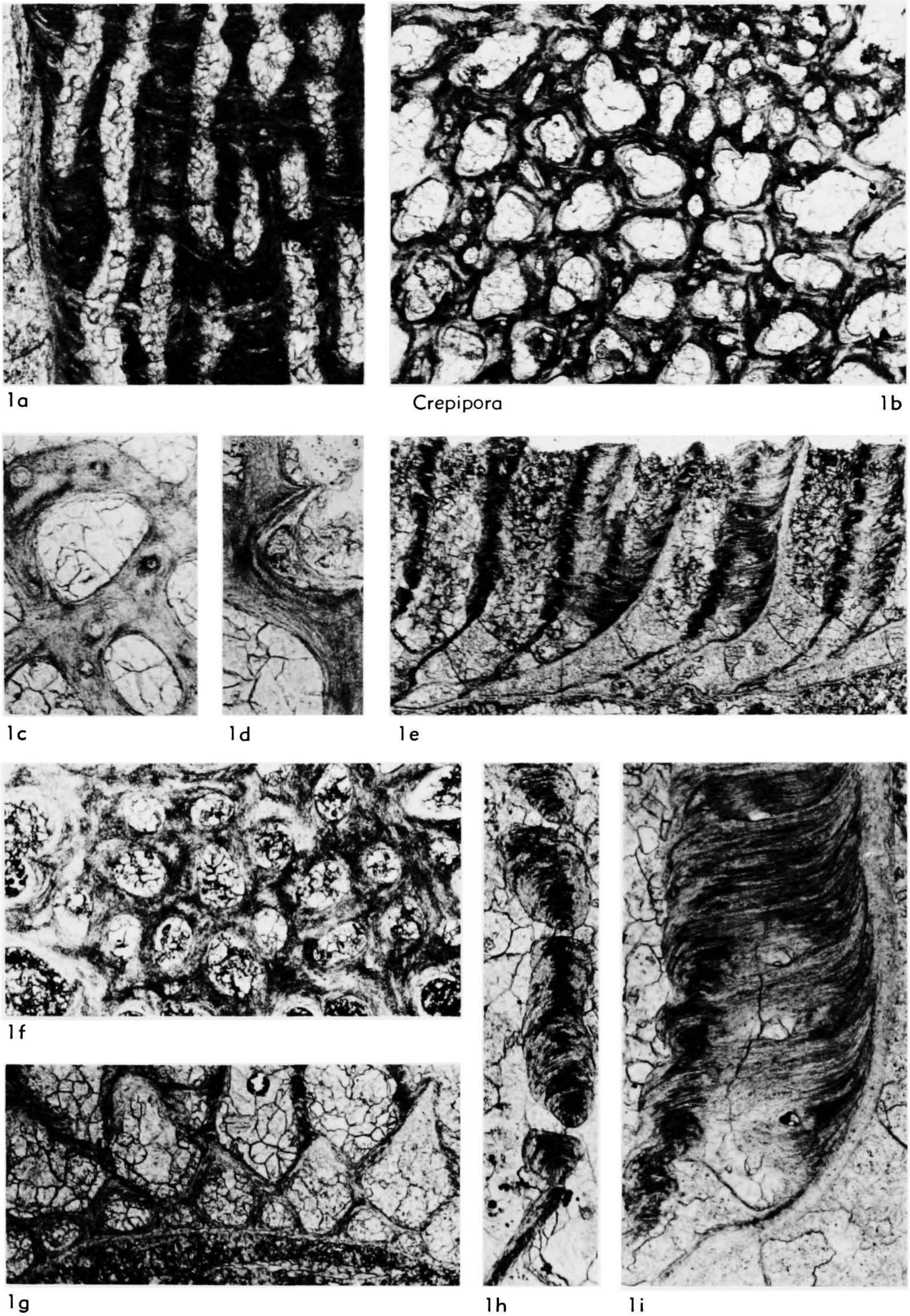
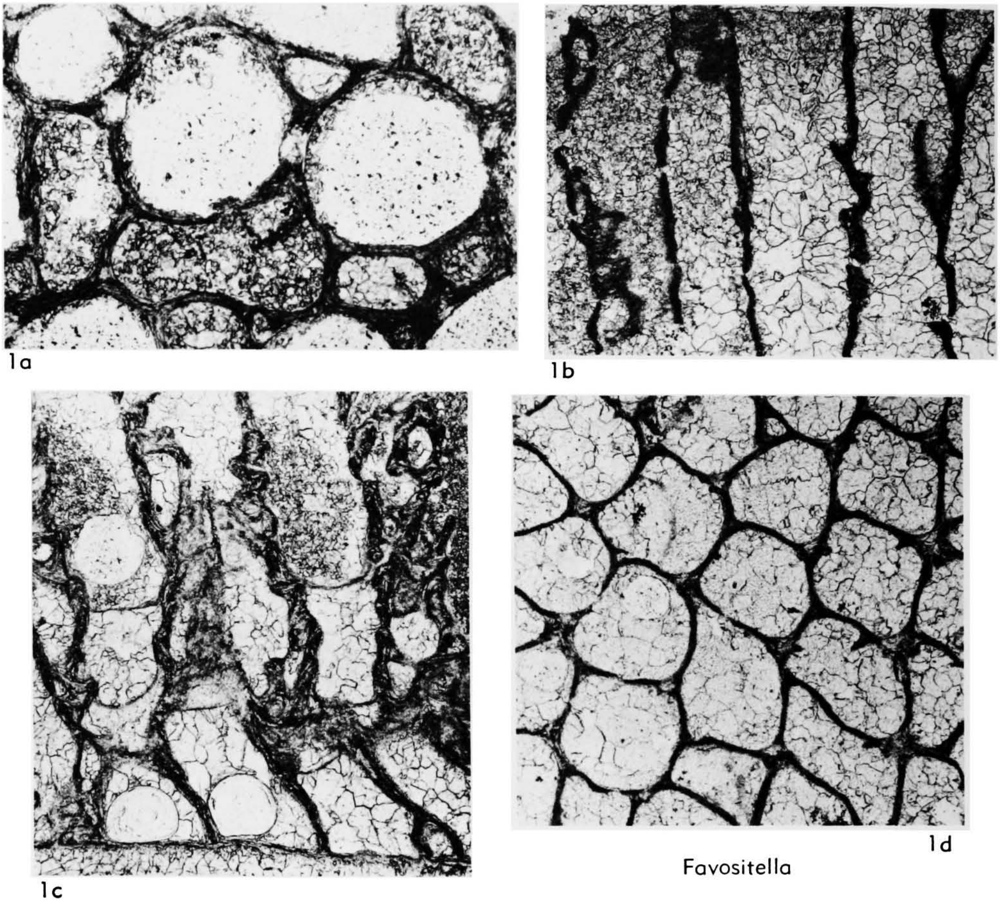
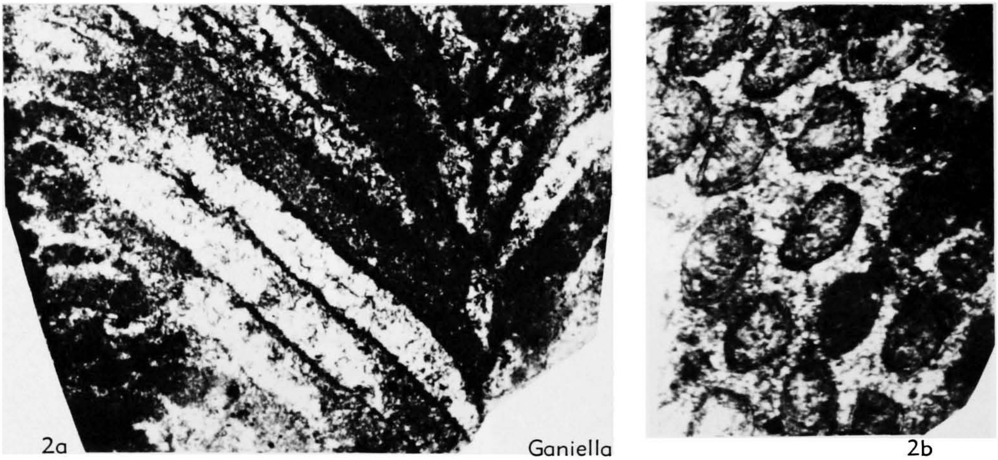


Fig. 160. Ceramoporidae (p. 363).



Favositella

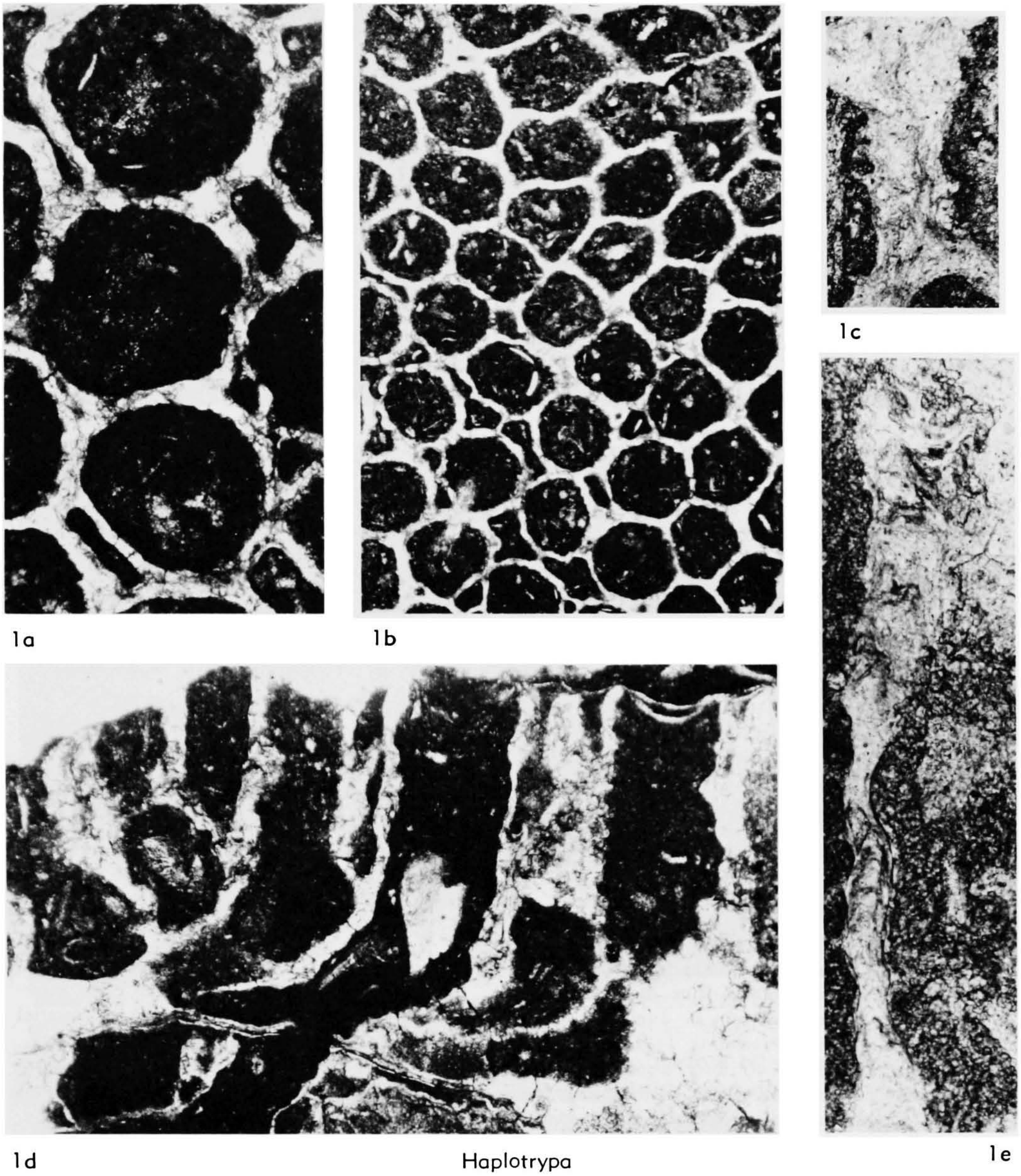


Ganiella

FIG. 161. Ceramoporidae (p. 366–368).

sec., lectotype, ×50; *h,* wall laminae and communication pores in exozone; long. sec., lectotype, ×100; *i,* lunarial deposit, wall laminae, and communication pores in exozone; long. sec., lectotype, ×100.

Favositella ETHERIDGE & FOORD, 1884, p. 472 [**Favosites interpunctus* QUENSTEDT, 1878, p. 10; OD; M. Sil. (?Wenlock.), Dudley, Eng.]



Haplotrypa

FIG. 162. Ceramoporidae (p. 369).

[=*Dnestropora* ASTROVA, 1965, p. 130]. Zoarium encrusting to massive, less commonly discoidal or hemispherical; with monticules. Autozooecia large, irregular in size and shape, cavity commonly with subangular to subrounded cross section in exozone. Walls undulatory or crenulated, moderately thick throughout. Locally, wall laminae irregular; with large mural lacunae. Generally short, curved, rod- to platelike protrusions (some resembling incomplete septa having broadly curved laminae) may extend outward (locally inward) at acute angle to zooecial wall, protrusions commonly in contact with one side of autozooecium. Communication pores common, small, subcircular. Diaphragms thin, moderately abundant. Lunaria small and subcircular to crescentic in endozone and inner exozone; increasing in size in outer exozone; small to large at zoarial surface. Laminated lining common on distal side of lunarial deposit. Wall laminae on

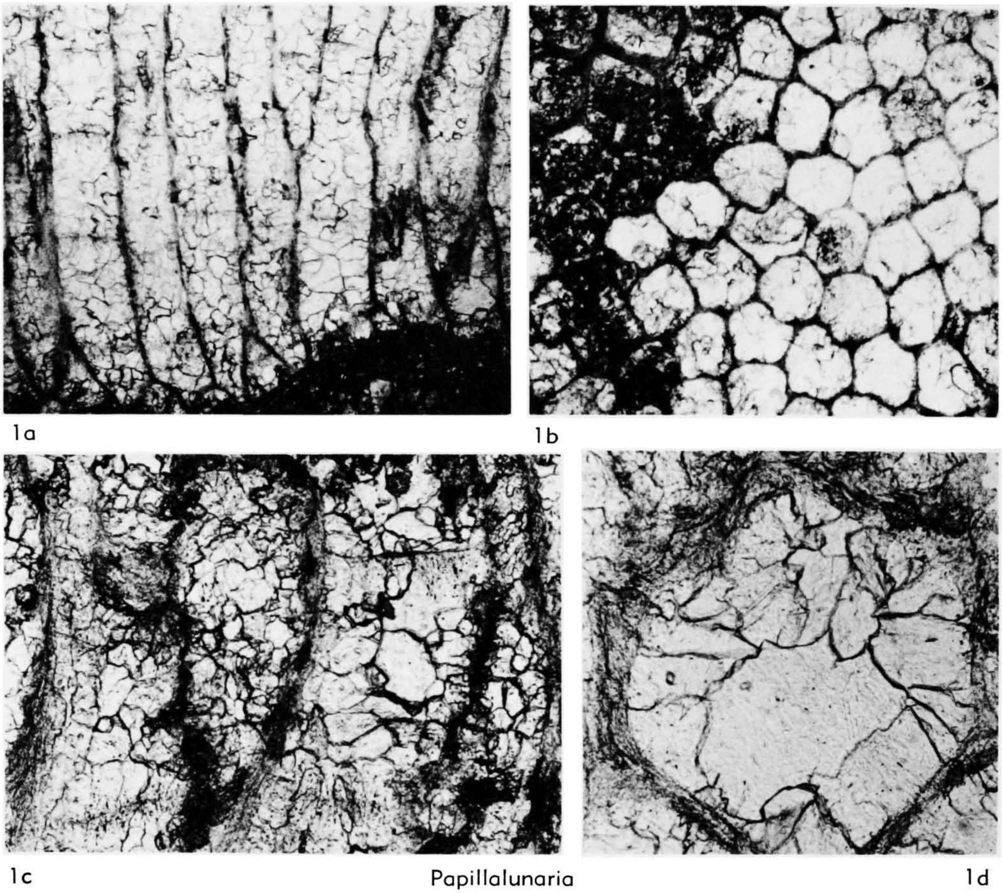


FIG. 163. Ceramoporidae (p. 369).

proximal side of some lunaria, particularly near monticules, with cone-in-cone flexures nearly perpendicular to lunarium or directed slightly outward. Flexures extending proximally from lunarium for short to long distance, locally inflecting autozooecial cavity. Exilazooecia few in intermonticular areas, irregular in shape; diaphragms may be thicker than autozooecial diaphragms; walls irregularly undulatory, with more communication pores and platelike protrusions than in autozooecia. Monticules irregular and ill defined; center of slightly larger monticular zooecia and abundant exilazooecia. [Middle Ordovician species from Estonia that were assigned to *Favositella* by Bassler (1911) do not fit the emended definitions of *Favositella* or *Bythotrypa*. They resemble *Favositella* more closely but probably represent an undescribed genus. *Dnestropora mirabilis* Astrova, 1965, p. 130, the type species by original designation of *Dnestropora* Astrova, 1965, p. 130, agrees well with the emended definition of *Favositella*, and *Dnestropora* is considered to be a junior subjective synonym of *Favositella*.] *M.Sil.-U. Sil.*, E.N.Am., Eu.——FIG. 161,*1a-d*. **F. interpuncta* (Quenstedt); *a*, small, ovate lunarial deposits and abundant exilazooecia; tang. sec., USNM 159729, ×50; *b*, irregular exilazooecium (left), communication pores, and protrusions from walls; long. sec., USNM 159729, ×30; *c*, spheroliths, undulatory walls, communication pores, and irregular exilazooecia; long. sec., USNM 159730, ×30; *d*, small lunarial deposits in some autozooecia (left), large lunarial deposits with proximal flexures (right), and few exilazooecia; tang. sec., USNM 159728, ×30.

?Ganiella Yaroshinskaya in Astrova & Yaroshinskaya, 1968, p. 51 [**G. frequens*; OD; L. Dev., Altai Mts., USSR]. Zoarium encrusting or bifoliate, branching. Mesotheca undulatory, thin. Autozooecia with sparse diaphragms; elongate to subcircular in cross section. Wall variable in thickness, questionably with small communication pores; microstructure indistinct, questionably laminated. Lunaria with shorter radius of curvature, indistinct. Questionable exilazooecia in outer exozone. [Indistinct lunaria, lack of vesicular tissue, and possible exilazooecia in the outer exozone suggest that *Ganiella* belongs in the Ceramoporidae, where Yaroshinskaya originally placed it; however, the indistinct microstructure and lack of obvious communication pores make the placement of this poorly known genus uncertain.] *L.Dev.,* USSR.——Fig. 161, *2a,b.* **G. frequens*; *a,* bifoliate zoarium, long autozooecia with no diaphragms, ?exilazooecia in outer exozone (left); long. sec., holotype, (SNIIGGIMS 952/T-20-5, ×40; *b,* elongate autozooecia with lunaria; indistinct microstructure; tang. sec., ?paratype, ×40 (negatives courtesy of A. Yaroshinskaya).

?Haplotrypa Bassler, 1936, p. 157 [**H. typica*; OD; Osgood F., M. Sil., Osgood, Ind., USA]. Zoarium encrusting. Autozooecia polygonal to subcircular in cross section. Wall laminae containing mural lacunalike structures and irregular acanthostylelike flexures that are subcircular in cross section. Wall irregular in thickness; irregular spinelike structures projecting into autozooecial cavity, some hooked proximally. Undoubted communication pores not observed. Diaphragms few. Lunaria not observed. Exilazooecia tubelike, subcircular to highly elongate in cross section; few in intermonticular areas. Monticules with more exilazooecia and slightly larger zooecia. [This doubtful genus, known only from the holotype, is questionably placed in the Ceramoporidae.] *M.Sil.,* E.N.Am.——Fig. 162,*1a–e.* **H. typica,* holotype, USNM 92132; *a,* mural lacunalike structures and flexures, no lunarial deposits; tang. sec., ×48; *b,* subangular to subcircular autozooecia and irregular exilazooecia in monticule (lower left); tang. sec., ×19; *c,* irregular flexures, spinelike protuberances, and mural lacunalike structures; tang. sec., ×96; *d,* basal layer, thick and irregular walls, and exilazooecia; long. sec., ×29; *e,* spinelike projections and irregularly flexed laminae (proximal, left); long. sec., ×96.

Papillalunaria Utgaard, 1969, p. 290 [**Crepipora spatiosa* Ulrich, 1893, p. 323; OD; "Trenton," M. Ord. (Mohawk.), Harrodsburg, Ky., USA]. Zoarium discoidal, hemispherical or irregularly massive; base concave or irregularly convoluted. Autozooecia moderately large, generally angular or subangular in cross section, a few subcircular. Walls generally undulatory, in some crenulated; generally thin, and some with monilalike swellings. Wall laminae indistinct, broadly to sharply curved. Boundary thin, dark, crenulated, and commonly not in center of compound wall, producing integrate appearance, or boundary obscure and walls amalgamate. Communication pores few, commonly absent. Lunaria small in inner exozone, nearly as large at zooecial bend as at zoarial surface. Ends of lunaria projecting into cavity. Cores in some lunaria. Knob- to rodlike protrusions on proximal side of lunaria in zooecia adjacent to monticules, rarely in intermonticular autozooecia. Laminated layer on proximal side of lunarium thin to absent; where present, laminae flexing around protrusions of lunarial deposit. Diaphragms abundant, thin, tabular, commonly at same level in adjacent autozooecia. Diaphragms laminated or displaying no discernable microstructure. Exilazooecia few. Monticules with few exilazooecia interspersed among autozooecia, monticular autozooecia much larger than intermonticular autozooecia. *M.Ord. U.Ord.,* E.N.Am.——Fig. 163,*1a–d.* **P. spatisoa* (Ulrich), lectotype, USNM 159723; *a,* thin basal layer, lunarial deposits, slightly moniliform walls, and thin diaphrams; transv. sec., ×20; *b,* larger zooecia in monticule (upper left), small lunarial deposits, and sparse exilazooecia; tang. sec., ×20; *c,* lunarial deposits with protrusions and laminae on proximal (left) side and diaphragms; long. sec., ×50; *d,* lunarial deposit (top) with protuberances on proximal side (toward top), indistinct wall laminations, and thin walls; tang. sec., ×100.

Suborder FISTULIPORINA
Astrova, 1964

[*nom. correct.* herein, *pro* Fistuliporoidea Astrova, 1964, p. 29, suborder]

Zoarial growth form variable; encrusting, hemispherical, massive, ramose, hollow ramose, bifoliate frondose, bifoliate with narrow straplike branches, bifoliate cribrate, articulate with bifoliate straplike branches, trifoliate, multifoliate, and fenestrate or pinnate with a vertical mesotheca and an obverse and reverse side. Monticules in most genera except some narrow bifoliate forms. Autozooecia short to long; diaphragms generally sparse. Walls laminated, granular or granular-prismatic. Distal and lateral sides of autozooecia bounded by superimposed vesicle walls in many genera. Communication pores absent. Autozooecia budded at basal layer, mesotheca, in endozone, or on vesicular tissue in exozone; partly to widely isolated by vesicles at budding surface. Crescentic to subcircular lunaria in exozone in most genera; granular, granular-prismatic, hyaline, or laminated. Exilazooecia absent. Vesicular tissue (cystopores) in all genera; tubelike with compound walls, like mesozooecia, in a few genera; generally boxlike to blisterlike with simple walls and roofs; granular, granular-prismatic, or laminated. Zones of thick vesicle roofs or stereom in many forms. Gonozooecia in few. Acanthostyles in some forms; most in vesicle roofs or stereom. *Ord.-Perm.*

Family ANOLOTICHIIDAE Utgaard, 1968

[Anolotichiidae UTGAARD, 1968a, p. 1035]

Zoaria encrusting, hemispherical, saucer shaped, massive or irregularly ramose. Monticules regularly spaced, rarely absent or poorly defined. Autozooecia large, tubular, with thin, distantly spaced diaphragms, commonly at same level in adjacent autozooecia. Wall structure indistinct, granular, or having dark granular zooecial boundary and cortex of light-colored layers of irregular rodlike or blocklike crystals or crystal aggregates perpendicular to boundary. Autozooecial walls incomplete; partly composed of superimposed vertical walls of interzooecial vesicles. Lunaria extending at least from outer endozone to zoarial surface, with microstructure similar to that of autozooecial walls but thicker in some. Interzooecial spaces (cystopores) in endozone and exozone; variable and irregular in shape in a zoarium, resembling tubular exilazooecia with compound walls, or, more commonly, tubelike, boxlike, or cystlike vesicles with simple walls; some originating at basal layer, partially isolating zooecia. Microstructure indistinct, granular or granular-prismatic. Monticules with central cluster of interautozooecial spaces. Acanthostyles absent except in *Lamtshinopora* and *Profistulipora*. Undoubted communication pores not observed. *Ord., M.Dev.*

Characters of particular importance are: granular or granular-prismatic wall microstructure; large autozooecia; tubelike, boxlike, or cystlike vesicular tissue that is irregular; lunaria; and absence of acanthostyles and stereom.

Anolotichia ULRICH, 1890, p. 381 [**A. ponderosa*; OD; "Fernvale F.," U. Ord. (Richmond.), Wilmington, Ill., USA]. Zoarium encrusting, massive, or irregularly ramose. Monticules poorly defined or absent. Cross section of autozooecial living chamber angular or subangular in endozone, subangular in exozone where interzooecial spaces few, subcircular where interzooecial spaces abundant. Axes commonly not parallel in adjacent autozooecia. Autozooecial walls undulatory, thin, locally thickened in bands. Transverse bands light colored where wall thinner, commonly at same level in adjacent zooecia. Rod-shaped crystals in thicker walled bands fanning out from subjacent thinner walled band. Two to six clear calcite rods extending for length of lunarium. Rods irregular in diameter and cross-sectional shape, in some with perpendicular extensions connecting rods in same lunarium. Rods enlarged distally, merging in some at zoarial surface to occupy entire thickened lunarium. Interzooecial spaces rare to abundant, angular to subangular, may be subcircular in cross section in exozone. *M.Ord.-U.Ord.*, N.Am.——FIG. 164,*1a–f*. **A. ponderosa*; *a,* enlarged partially to completely fused rods in lunaria close to zoarial surface; tang. sec., lectotype, USNM 159693, ×50; *b,* autozooecia, light-colored rods in lunaria, and interzooecial spaces; tang. sec., paralectotype, USNM 159696, ×30; *c,* rods in lunarium having lateral projections, some of which extend to adjacent rod; long. sec., lectotype, ×50; *d,* large angular autozooecium, lunarium with rods, and angular interzooecial spaces in endozone; transv. sec., paralectotype, USNM 159697, ×50; *e,* irregular interzooecial spaces and rods in lunaria; long. sec., paralectotype, USNM 159695, ×30; *f,* alternating dark- and light-colored bands in wall, outward fanning of crystal aggregates in thicker walled bands; long. sec., paralectotype, USNM 159694, ×100.

Altshedata MOROZOVA, 1959b, p. 7 [**Fistulipora belgebaschensis* NEKHOROSHEV, 1948, p. 50; OD; *M.Dev.* (Givet.), Altai Mts., Kuznetsk basin, USSR]. Zoarium encrusting or massive. Monticules with large zooecia and more abundant interzooecial spaces. Autozooecial living chamber subangular to subrounded in cross section; ends of lunaria commonly indenting living chamber. Autozooecial walls thick, undulatory; indistinct granular microstructure. Diaphragms closely spaced, oblique, concave, and thin. Interzooecial spaces generally one row of high, narrow blisterlike vesicles, angular in cross section; larger and more abundant in monticules. Lunaria thicker near zoarial surface; projections into zooecial cavity moderately long and thin in inner exozone to short, tapering in outer exozone. *M.Dev.*, USSR. ——FIG. 165,*1a–c*. **A. belgebaschensis* (NEKHOROSHEV), Kuznetsk basin, USSR, PIN 1204/9 a.B; *a,* oblique, closely spaced diaphragms in autozooecia, narrow interzooecial spaces with one row of vesicles, and undulatory, thick autozooecial walls; long. sec., ×30; *b,* thin diaphragms, thick autozooecial wall, and indistinct granular microstructure of

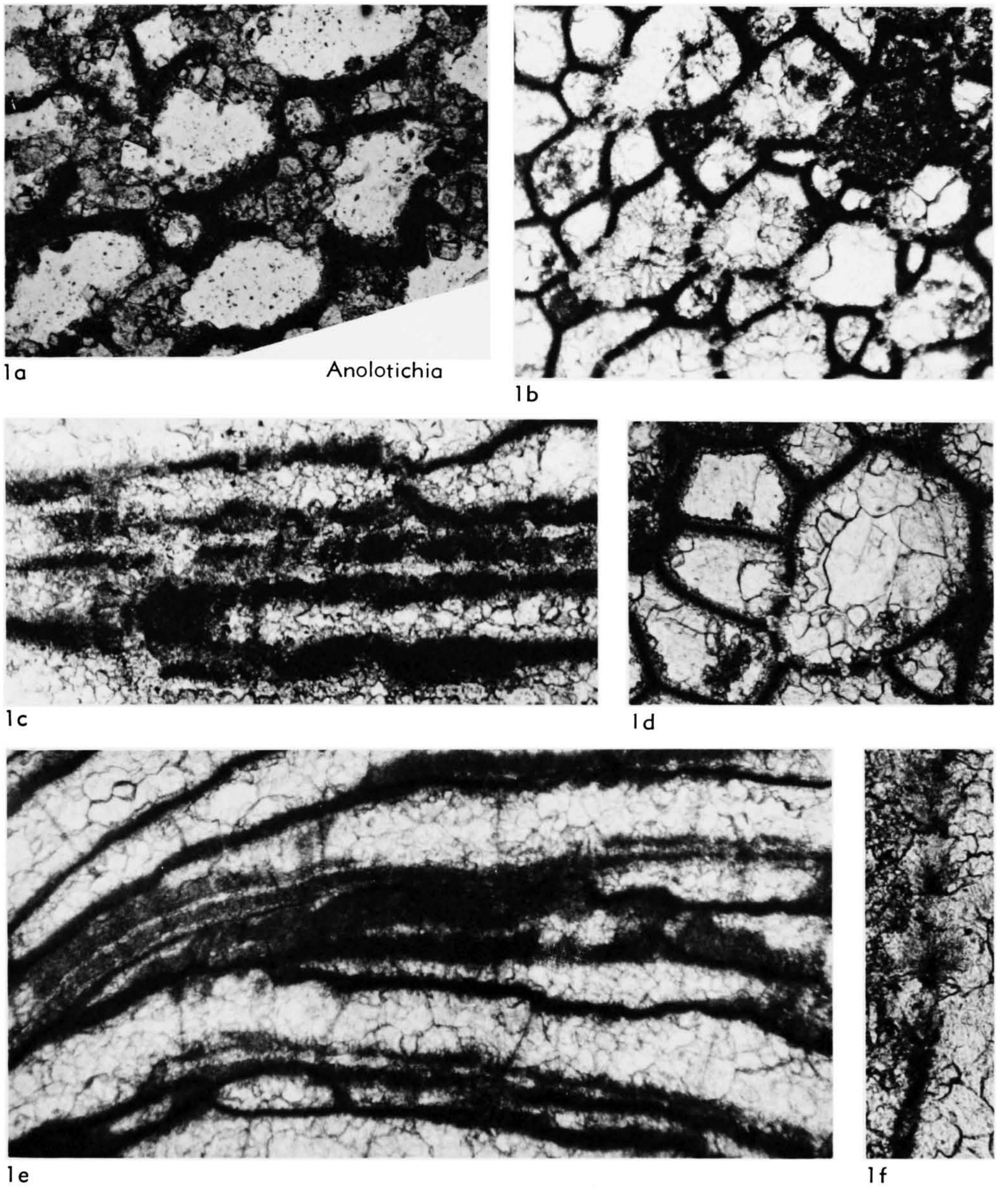
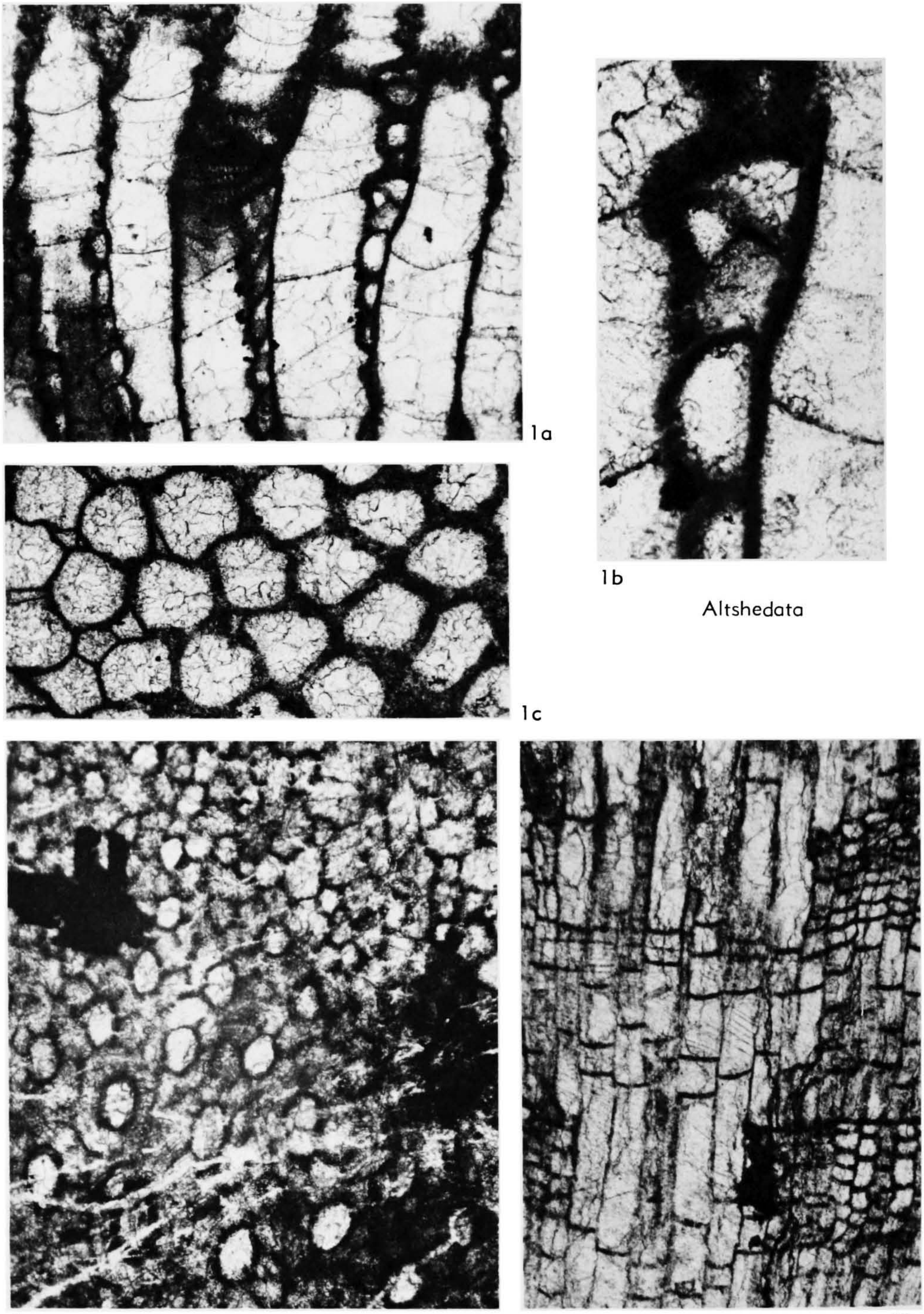


FIG. 164. Anolotichiidae (p. 370).

high, narrow, curved plates of cystose interzooecial spaces; long. sec., ×100; *c,* angular interzooecial spaces (above), some lunaria with ends projecting into zooecial cavity; tang. sec., ×30.

Bythotrypa Ulrich, 1893, p. 324 [**Fistulipora? laxata* Ulrich, 1889, p. 37; OD; "Trenton Gr.," M. Ord., Manit., Can.]. Zoarium encrusting, massive, or hemispherical. Monticules inconspicuous, depressed to slightly elevated. Axes commonly not parallel in adjacent autozooecia in exozone. Walls on distal or lateral sides of autozooecia commonly formed by vertical portions of walls of cystlike interzooecial vesicles; these walls scalloped in longitudinal view and straight in tangential section, producing angular autozooecial cavities. Other zooecia subrounded in cross section. Walls relatively thin throughout, straight to crenulated; granular. Zooecial boundary commonly obscure and walls uniform in appearance. Wall thickenings local with fan-shaped bundles of crystals. Lunaria moderately large in outer endozone, large at zoar-



Altshedata

Profistulipora

Fig. 165. Anolotichiidae (p. 376).

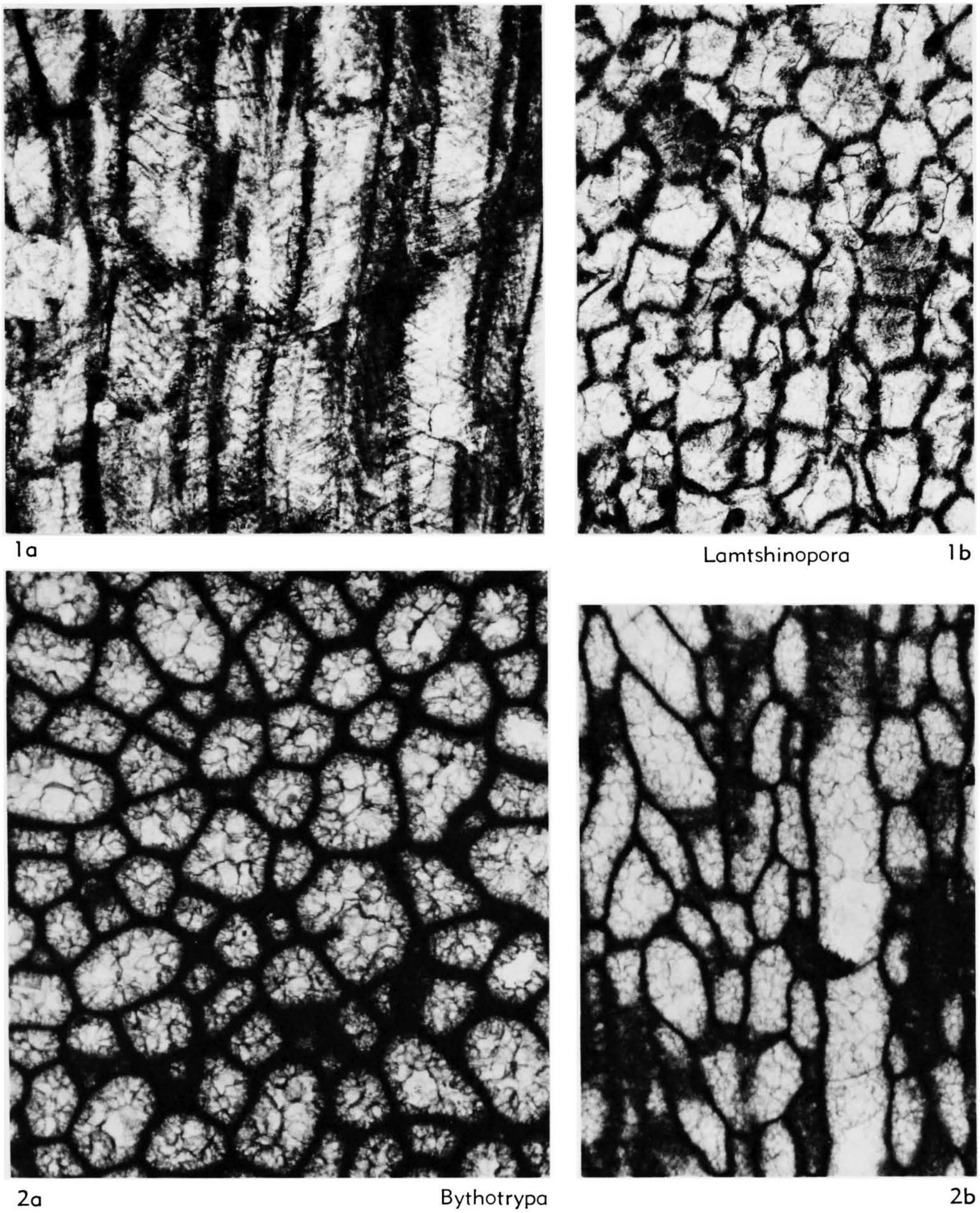


FIG. 166. Anolotichiidae (p. 371).

ial surface. Vesicular tissue abundant, partially isolating autozooecia; polygonal, boxlike, or cystlike; commonly elongated parallel to axes of autozooecia, locally obliquely, particularly in monticules. Locally top of curved wall of vesicular tissue diaphragmlike. Vesicular tissue in monticular centers commonly more variable in size and shape, obliquely elongated. Lunaria radially arranged around monticular centers. *M.Ord.*, E.N.Am.——FIG. 166,*2a,b*. **B. laxata* (ULRICH), holotype, USNM 43241; *a*, central cluster of vesicular tissue and autozooecia radially arranged with lunaria nearest monticular center; tang. sec., ×30; *b*, boxlike to obliquely elongated vesicular tissue in monticule (left); long. sec., ×20.

Crassaluna UTGAARD, 1968a, p. 1039 [**Crepipora epidermata* ULRICH, 1890, p. 471; OD; "Fern-

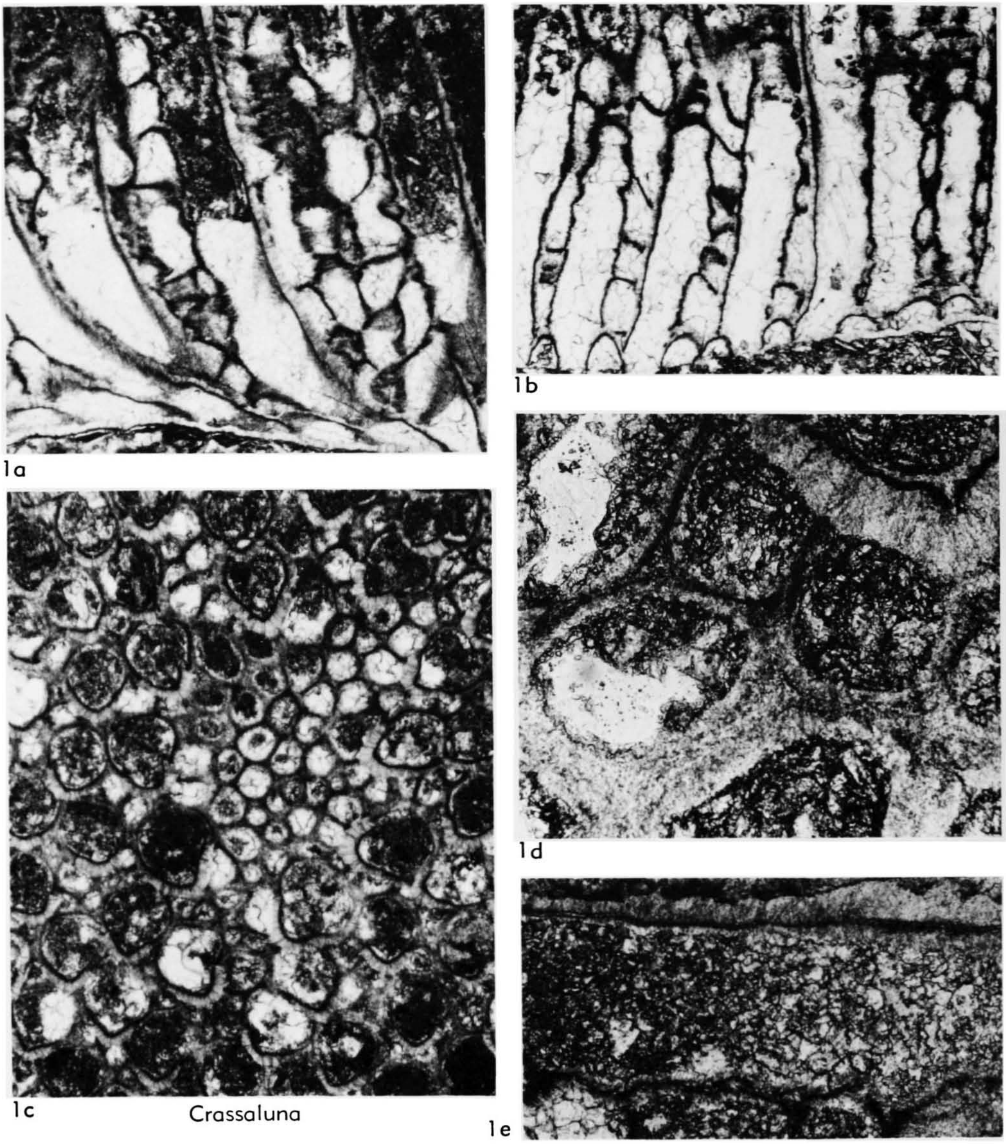


FIG. 167. Anolotichiidae (p. 373).

vale F.," U. Ord., Wilmington, Ill., USA}. Zoarium thin expansions, flat to convoluted. Monticules small to large, slightly elevated to slightly depressed. Recumbent portion of autozooecia short to long. Axes generally parallel in adjacent autozooecia. Autozooecia angular to subangular in cross section at zooecial bend, subangular to subrounded in outer exozone. Lateral and distal sides commonly composed of overlapping vertical portions of vesicular tissue. Autozooecial walls moderately thick, granular to granular-prismatic. Zones of thicker wall lacking distinct boundary and with crystal aggregates fanning outward, producing minutely spotted amalgamated appearance. Lunaria becoming larger and thicker in outer exozone; proximal side with uneven nodes and ridges; most lunaria with one minute longitudinal corelike structure near center. Walls of adjacent autozooecia and vesicular tissue unconformably abutting proximal side of lunarium. Vesicles variable but generally small, subangular to subrounded in cross section. Monticular centers with irregular tubelike and oblique vesicles surrounded by larger zooecia. Lunaria locally and in part radially arranged around monticules. *U.Ord.,* N.Am.——FIG.

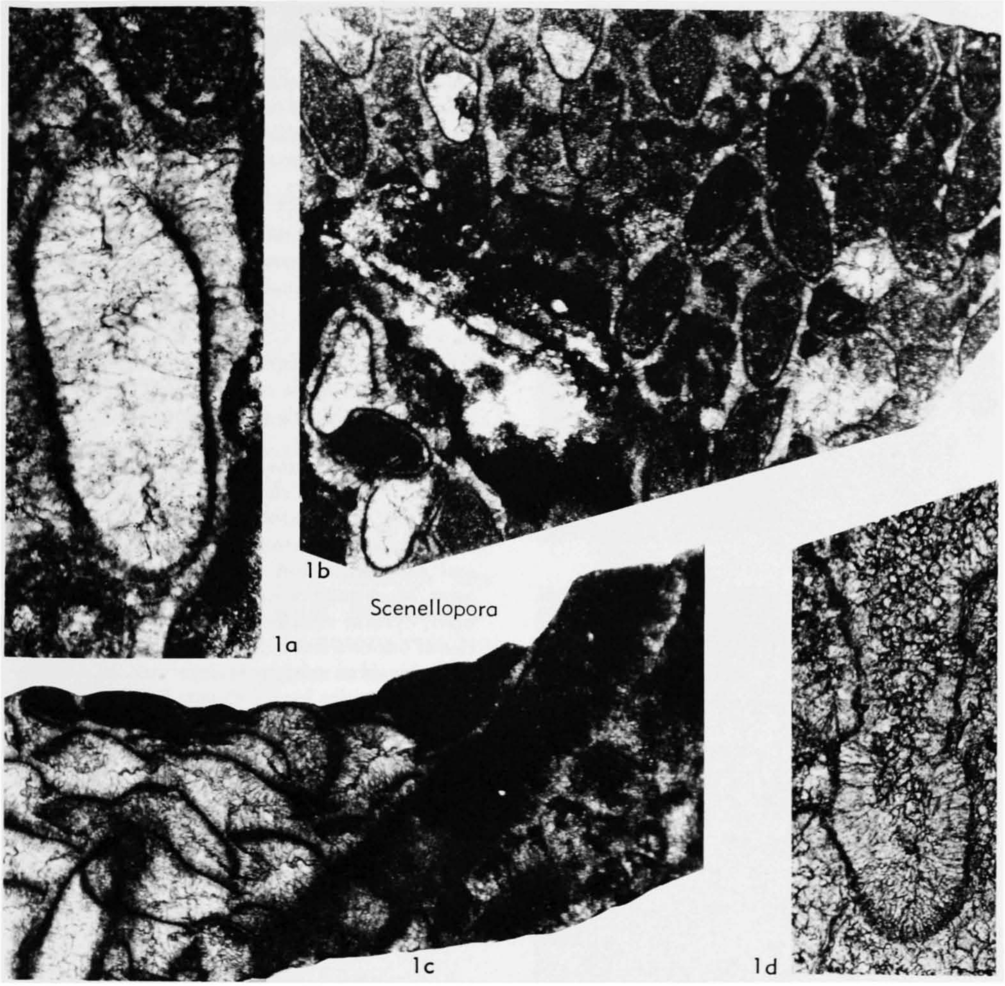


FIG. 168. Anolotichiidae (p. 376).

167, *1a–e.* **C. epidermata* (ULRICH); *a,* overlapping cystlike vesicles forming wall on distal side of autozooecia and serrated proximal sides of lunarial deposits; long. sec., lectotype, USNM 159700, ×20; *b,* basal layer, recumbent sinuses, and variation in shape of vesicular tissue; transv. sec., paralectotype, USNM 159701, ×20; *c,* monticule and partial radial arrangement of zooecia; tang. sec., lectotype, ×20; *d,* lunarium (upper right) with indistinct central corelike structure and thinner walls (center) with dark granular primary layer, and thicker walls (bottom) in vesicular tissue; tang. sec., paralectotype, USNM 159701, ×100; *e,* corelike structure in lunarium (top) and boxlike to cystlike vesicles (bottom); long. sec., paralectotype, USNM 159702, ×50.

?Lamtshinopora ASTROVA, 1965, p. 124 [**L. hirsuta*; OD; L. Ord., Vaigach Is., near N. Zemlya, USSR]. Zoarium encrusting, laminated or massive. Monticules either poorly defined areas of larger zooecia or absent. Cross section of autozooecial living chamber angular to irregularly subangular. Autozooecial walls thick; microstructure granular; light areas in walls may represent pores. Lunaria not readily apparent; poorly developed or absent. Numerous granular acanthostyles in autozooecial walls indenting living chamber, producing pseudoseptate appearance in some autozooecia. Interzooecial spaces apparently tubelike; cross section irregular in size and shape. [Extensive recrystallization makes it difficult to observe communication pores, which apparently are lacking. Similarly, lunariumlike structures are difficult to evaluate. Granular acanthostyles are not present in other Anolotichiidae, and *Lamtshinopora* is placed in this family with reservation.] *L.Ord.,* USSR.——FIG.

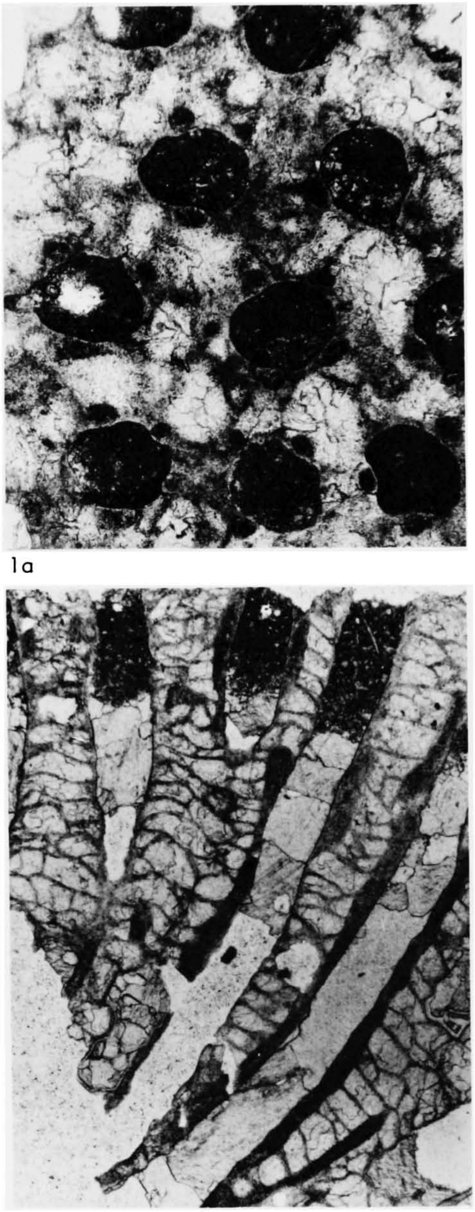


FIG. 169. Xenotrypidae (p. 377).

166,*1a,b*. **L. hirsuta*; *a*, autozooecia with sparse diaphragms and tubelike interzooecial spaces; long. sec., paratype, PIN 1393/382b, ×30; *b*, irregular interzooecial spaces and angular to subangular autozooecia; tang. sec., paratype, PIN 1393/382a, ×30.

Profistulipora ASTROVA, 1965, p. 144 [**P. arctica*; OD; L.-M. Ord., N. Urals, N. Zemlya, USSR]. Zoarium encrusting to massive, surface smooth. Monticules with slightly larger zooecia, lunaria not radially arranged. Autozooecia ovate in cross section, widely isolated by interzooecial spaces; diaphragms sparse. Wall granular, some small acanthostyles. Lunaria indistinct, granular. Interzooecial spaces tubular, irregular in height; zones of shorter tubular vesicles in monticules; cross section polygonal; walls and roofs granular; small acanthostyles in walls. *L.Ord.-M.Ord.*, USSR. ——FIG. 165,*2a*. **P. arctica*, paratype, PIN 1245/57a; monticule with larger zooecia (lower left), ovate autozooecia isolated by moderately large polygonal interzooecial spaces; tang. sec., ×30.——FIG. 165,*2b*. *P. menneri* ASTROVA, M. Ord., N. Urals, USSR, paratype, PIN 1606/16B; sparse diaphragms in autozooecia, tubelike interzooecial spaces, and zones of lower tubular vesicles in monticule (right); long. sec., ×20.

Scenellopora ULRICH, 1882, p. 150, 158 [**S. radiata*; OD; Trenton Gr., M. Ord., Knoxville, Tenn., USA]. Zoarium small, saucer shaped, commonly with central basal protrusion and one monticule; or thin irregular expansions with several monticules and broadly undulating basal layer. Monticular centers containing large, irregularly cystlike vesicles. One or two sets of fascicles of one or a few irregular rows of autozooecia radiating from margin of depressed monticular center. Fascicles highly elevated and distinct if zooecia tightly packed, low and indistinct if loosely packed. Autozooecial cavity generally oval but distal side may be angular. Walls moderately thin, straight to crenulated. Walls granular-prismatic in holotype; in some, wall granular-prismatic and locally indistinctly laminated. Lunaria moderately large; in most zoaria, some lunaria with one to several light-colored longitudinal rods, locally inflecting autozooecial cavity; rods with widely spaced, curved laminations convex outward; remainder of lunarium granular-prismatic or indistinctly laminated. Lunaria radially arranged and closest to monticular centers. Vesicular tissue irregular in size and shape, with microstructure similar to that of autozooecial walls. *M.Ord.*, N.Am.——FIG. 168,*1a–d*. **S. radiata*; *a*, lunaria on proximal (bottom) side of autozooecia, subcircular rod near center of upper lunarium; tang. sec., holotype, USNM 43289, ×100; *b*, irregular fascicles of zooecia radiating from central monticule; tang. sec., holotype, ×30; *c*, cystlike vesicles in depressed central monticule (left) and zooecia with few diaphragms (right); long. sec., holotype, ×30; *d*, radial disposition of autozooecia from ancestrula, near base of colony; deep tang. sec., topotype, USNM 159704, ×100.

Family XENOTRYPIDAE
Utgaard, new

Zoaria encrusting, hemispherical, or ramose. Monticules with central cluster of vesicles. Autozooecia large, living chamber inflected by large acanthostyles. Diaphragms few. Wall microstructure indistinct, granular. Lunaria absent. Vesicles large, irregular, blisterlike; large acanthostyles in vesicle walls. *?L.Ord.(Arenig.), M.Ord.-M.Sil.*

Characters of particular importance are: large autozooecia; indistinct, granular, wall microstructure; large, irregular vesicles; large acanthostyles in vesicle walls and inflecting autozooecia; and absence of lunaria.

Xenotrypa and *Hennigopora* have previously been included in the Constellariidae but differ from other genera in the family in lacking star-shaped monticules and laminated walls and in having large acanthostyles that inflect autozooecial living chambers. Thus, a new family is established here for these unusual forms. They resemble late Paleozoic Actinotrypidae in having large acanthostyles inflecting the autozooecia but differ from the Actinotrypidae in having large autozooecia, an indistinct granular microstructure, and large acanthostyles in vesicle roofs.

Xenotrypa Bassler, 1952, p. 381 [**Fistulipora primaeva* Bassler, 1911, p. 109; OD; Glauconite Ls., M. Ord., B2, Pawlovsk, USSR]. Zoarium high hemispherical. Monticules large, flush; center a cluster of vesicles. Autozooecia large, slightly indented by acanthostyles. Walls indistinctly granular. Vesicles irregular, isolating zooecia; indistinct microstructure. Acanthostyles large, generally in autozooecial walls, some in vesicle walls; centers light to dark in color; projecting as spines. *?L.Ord. (Arenig.). M.Ord.*, Eu.——Fig. 169,*1a,b*. *X. *primaeva* (Bassler), holotype, USNM 57208; *a*. autozooecia isolated by vesicles, large acanthostyles in zooecial walls and vesicles; tang. sec., ×30; *b*. autozooecia with few diaphragms, irregular vesicles, and large acanthostyles; long. sec., ×20.

Hennigopora Bassler, 1952, p. 382 [**Callopora florida* Hall, 1852, p. 146; OD; Niagaran Gr., Rochester Sh., M. Sil., Lockport, N.Y., USA]. Zoarium encrusting or ramose, base unattached in some. Monticules slightly elevated, having slightly larger zooecia. Autozooecia large, acanthostyles inflecting living chambers; diaphragms few, straight to oblique. Microstructure indistinct; granular, local indistinct laminations. Lunaria lacking. Vesicles large, subrectangular to cystlike; partially to completely isolating autozooecia in exozone. Acanthostyles few in vesicle walls. *U.Ord.(Richmond.)-M.Sil.*, E.N.Am., Eu.

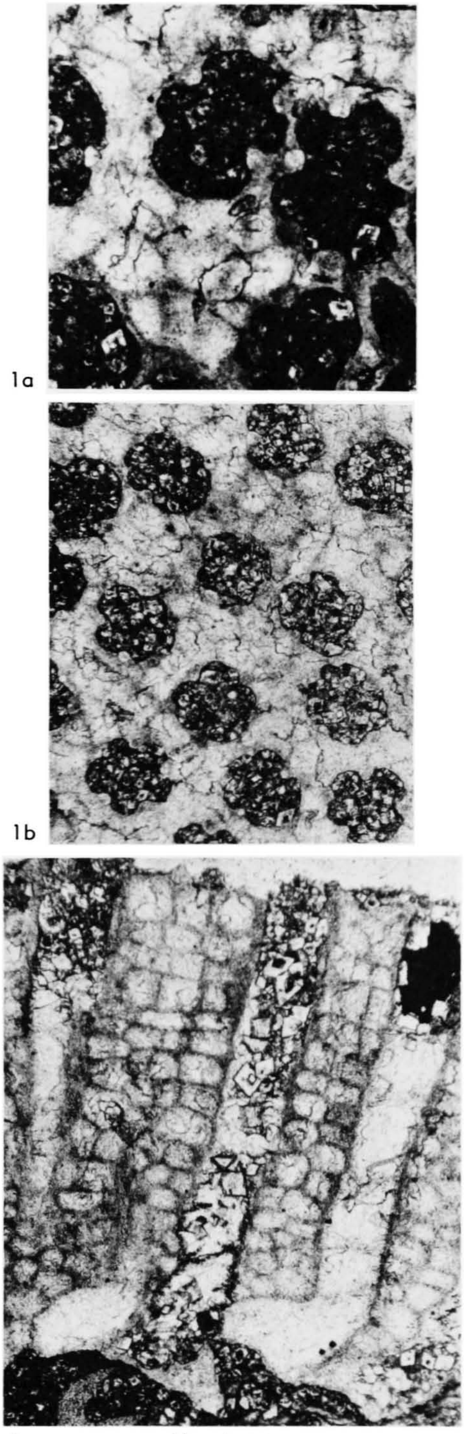


Fig. 170. Xenotrypidae (p. 377).

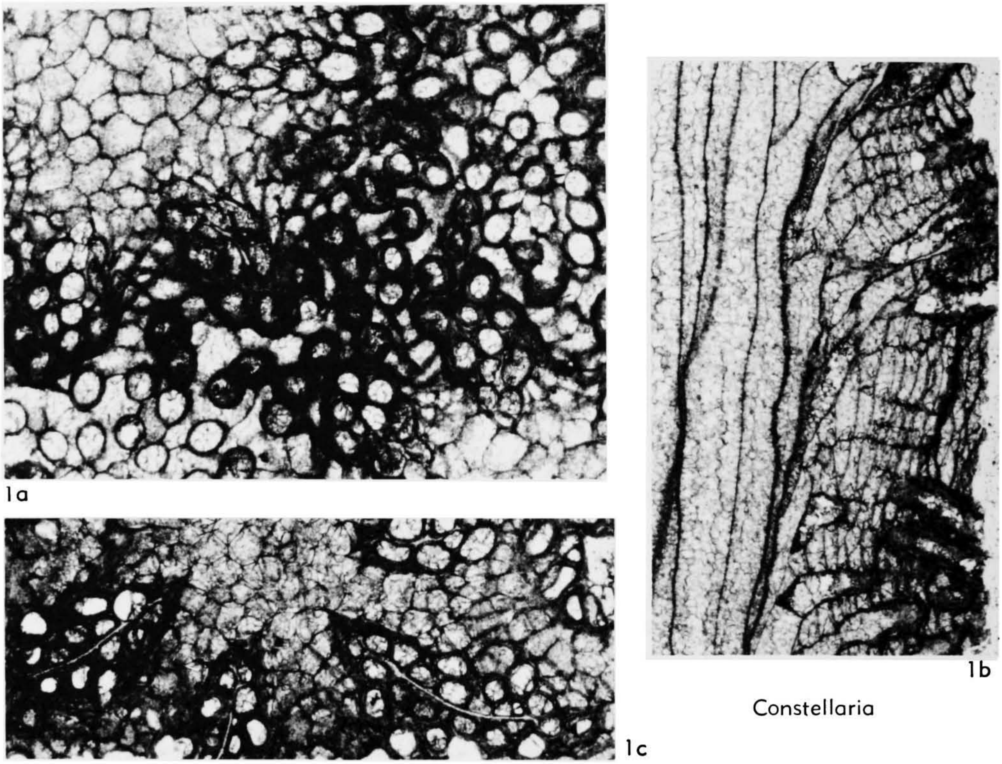


FIG. 171. Constellariidae (p. 378).

——FIG. 170, *1a–c*. **H. florida* (HALL); *a,* acanthostyles with light and dark centers in autozooecial and vesicle walls; tang. sec., syntype, AMNH 1744/1, ×48; *b,* acanthostyles indenting autozooecia, few in vesicles; tang. sec., USNM 159763, ×29; *c,* autozooecia with few diaphragms, acanthostyles (left side), and vesicles; long. sec., USNM 159763, ×29.

Family CONSTELLARIIDAE Ulrich, 1896

[Constellariidae ULRICH, 1896, p. 267] [=Stelliporidae MILLER, 1889, p. 169]

Zoaria encrusting, ramose, or frondose. Monticules star shaped; composed of central cluster and radiating interrays of vesicles (cystopores) between rays of loosely to tightly packed zooecia, with or without midray partitions. Lunaria present in one genus.[1] Wall structure indistinctly and transversely laminated. Acanthostyles small; in zooecial walls and vesicular tissue. Vesicles quadrate to blisterlike or commonly irregular and variable in zoarium. Local zones having thick vesicle roofs. *M.Ord.(Chazy.)-U.Ord. (Richmond.), ?L.Sil.*

Characters of particular importance are stellate to substellate monticules, indistinctly laminated wall microstructures, irregular quadrate to blisterlike vesicles, and small acanthostyles.

Constellaria DANA, 1846, p. 537 [**C. constellata* DANA, 1849, pl. 52; SM; ?U. Ord., ?Ohio, USA] [=*Stellipora* HALL, 1847, p. 79]. Zoarium encrusting, ramose, or frondose. Monticules stellate to subcircular; primary plus secondary rays of zooecia flush or elevated; monticular center and interrays of vesicles depressed, flush, or elevated. Autozooecia larger, with irregular polygonal cross section in endozone, smaller, with subcircular cross section in exozone; generally isolated by vesicles in intermonticular areas; lunarium lacking but some autozooecia with thicker proximal wall. Walls indistinctly and transversely laminated; diaphragms few to many, straight to curved. Vesicles boxlike and super-

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[1] *Lunaferamita* UTGAARD, 1981, described too late for inclusion in this *Treatise*. See J. Paleontol., v. 55, p. 1058–1070. Type species: *L. bassleri* (LOEBLICH); range: M.Ord. (Chazy.), Nev., Okla., Va.

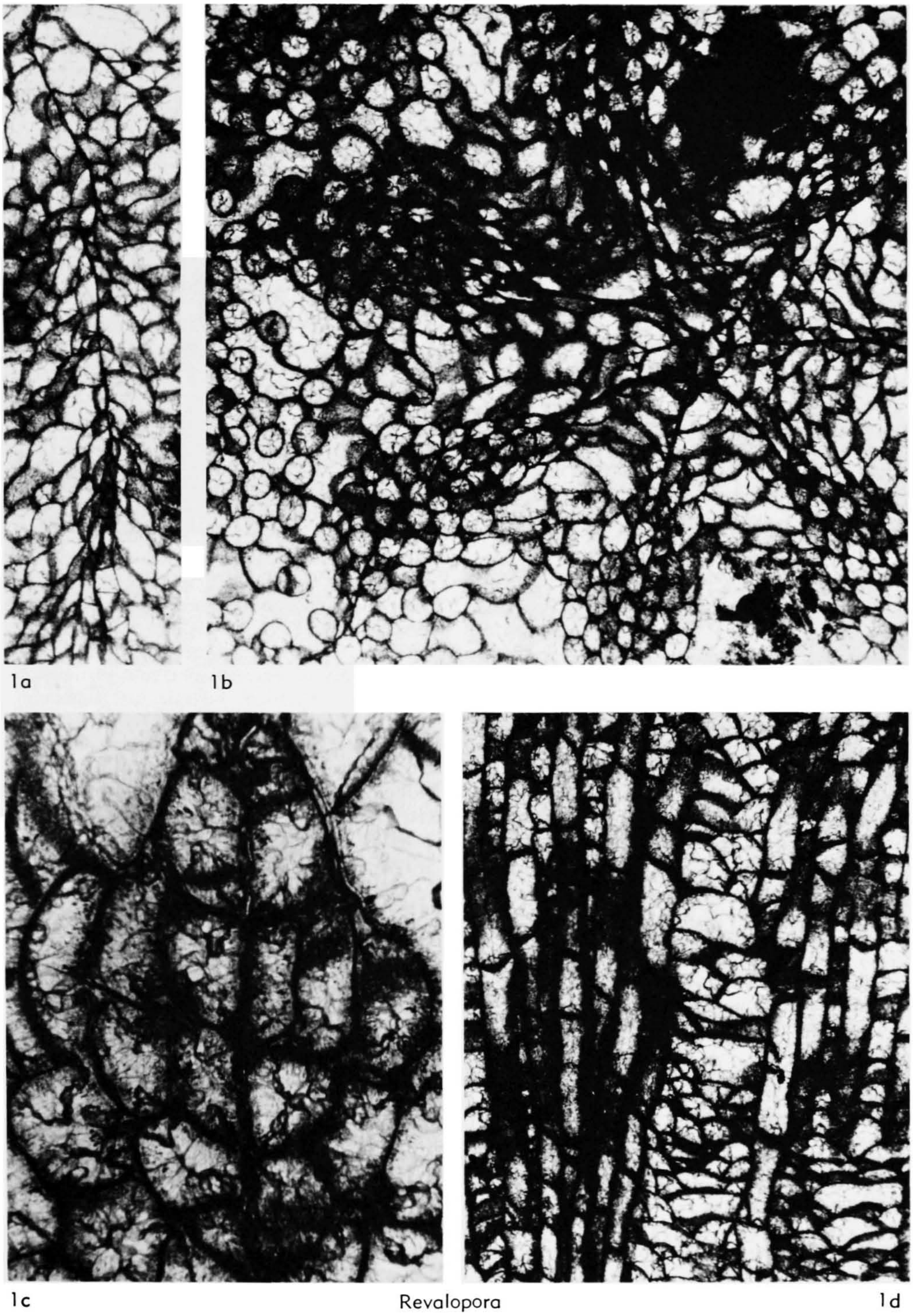


FIG. 172. Constellariidae (p. 380).

imposed (resembling mesozooecia) to irregular blisters; poorly laminated, containing pustules; vesicle roofs thickened in zones. Midray partitions of hyaline calcite; acanthostyles in vesicule and autozooecial walls. [The type species of *Stellipora* (*S. antheloidea* HALL, 1847, p. 79, by monotypy) is a *Constellaria.* The type species of *Constellaria* has been widely but erroneously assumed to be *C. florida* ULRICH, 1882. Whereabouts of the type of *C. constellata* is not known and it is presumed to be lost.] *M.Ord.(Chazy.)-U.Ord.(Richmond.),* E.N.Am., Eu. [*?L.Sil.,* Sib., see ROSS, 1963a]. ——FIG. 171, *1a,b. C. florida* ULRICH, Maysville Gr., U. Ord., Ky., USA, lectotype, USNM 159760; *a,* monticular centers (upper left, lower right) of vesicles, rays of zooecia radiating from monticule; tang. sec., ×30; *b,* simple endozone and autozooecia and vesicles in exozone; long. sec., ×30.——Fig. 171, *1c. C. florida prominens* ULRICH, McMicken Mbr., Eden F., U. Ord. (Eden.), Ohio, USA; paratype, USNM 159762; vesicles in monticular center and interrays, ray zooecia, and hyaline midray partitions; tang. sec., ×30.

Revalopora VINASSA DE REGNY, 1921, p. 220 [**Stellipora revalensis* DYBOWSKI, 1877, p. 44; OD; CI or CII, M. Ord., Est.]. Zoarium encrusting. Monticules large, star shaped; rays clusters of generally smaller zooecia; interrays and center depressed, containing vesicles. Autozooecia with straight to curved diaphragms; walls thin, indistinctly laminated. Lunaria not observed. Vesicles large and irregular in monticules and intermonticular areas; walls and roofs poorly laminated; isolating autozooecia in intermonticular areas. Midray partitions laminated, with acanthostyles, extending through vesicles to monticular center and inward in zoarium. *M.Ord.(?Llanvirn., Llandeil.-Caradoc.),* Eu.(Est.).——FIG. 172,*1a-d.* **R. revalensis* (DYBOWSKI), Kuckers Sh., Caradoc., C2, near Jewe, Est., USNM 57303; *a,* laminated midray partition and vesicles in monticular center; long. sec., ×20; *b,* monticule, midray partitions, ray zooecia, subcircular intermonticular autozooecia, and large, irregular vesicles; tang. sec., ×20; *c,* poorly laminated walls, midray partition with acanthostyles and subquadrate to subcircular ray zooecia; tang. sec., ×100; *d,* autozooecia with straight to curved diaphragms, superimposed vesicle walls forming part of autozooecial walls, and irregular vesicles; long. sec., ×20.

Family FISTULIPORIDAE
Ulrich, 1882

[Fistuliporidae ULRICH, 1882, p. 156] [=Chilotrypidae SIMPSON, 1897, p. 480; Favicellidae SIMPSON, 1897, p. 556; Fistuliporinidae SIMPSON, 1897, p. 480; Odontotrypidae SIMPSON, 1897, p. 481; Selenoporidae SIMPSON, 1897, p. 557; Cheilotrypidae MOORE & DUDLEY, 1944, p. 266]

Zoaria encrusting, massive, ramose or hollow ramose. Monticules in most genera. Autozooecia partly to completely isolated at budding surface by vesicular tissue. Blister- to boxlike vesicular tissue in exozone in all genera. Walls and vesicular tissue indistinctly laminated or granular or granular-prismatic. Acanthostyles in vesicle walls, roofs, or stereom in most genera. Lunaria in most genera; hyaline or granular-prismatic. *Sil.-Perm.*

Characters of particular importance are: blister- to boxlike vesicles in exozone; acanthostyles in vesicle roofs or stereom; thin, local zones of stereom; and lunaria.

Fistulipora MCCOY, 1849, p. 130, *nom. conserv.* ICZN Opinion 459, *non* RAFINESQUE, 1831 [**F. minor*; SD MILNE-EDWARDS & HAIME, 1850, p. lix, *non* CUMINGS, 1906, p. 1293, *ut F. spergensis minor*; L. Carb. Ls., Miss., G. Brit.] [?=*Cucumulites* GURLEY, 1884, p. 2]. Zoarium encrusting or massive, rarely ramose. Monticules elevated or flush, central cluster of vesicles and ring of larger zooecia with lunaria partly to altogether radially arranged, on side of zooecia nearest monticular center. Autozooecia long, tubular, with closely spaced planar or curved diaphragms; partially to completely isolated by vesicular tissue; microstructure granular or granular-prismatic. Lunaria through endozone and exozone, granular or granular-prismatic; radius of curvature shorter than that of autozooecial wall. Vesicles moderately large, angular; thin granular or granular-prismatic walls and roofs; rarely boxlike, commonly polygonal or subquadrate blisters. Local zone of thicker vesicle roofs at zoarial surface. [Many species in this large genus are in need of restudy. Early species tend to have larger, more boxlike vesicles, whereas many late Paleozoic species have smaller, polygonal or cystlike vesicles. *Cucumulites tuberculatus* GURLEY, 1884 is the type species of *Cucumulites* GURLEY, 1884, by original designation. The holotype is silicified and has not been sectioned. Its apparent synonym, *C. tricarinatus* GURLEY, 1884, though mostly silicified and poorly known, has features that are most similar to those of *Fistulipora,* and *Cucumulites* is tentatively placed in synonymy with *Fistulipora.*] *Sil.-Perm.,* worldwide.——FIG. 173,*1a-d.* **F. minor,* paratype, SM 315; *a,* angular to blisterlike vesicles and closely spaced diaphragms in autozooecia in outer exozone, granular to granular-prismatic microstructure; transv. sec., ×30; *b,* lunaria with short radius of curvature and granular microstructure in rounded autozooecia partially isolated by moderately large polygonal vesicles; tang. sec., ×30; *c,* subangular autozooecia with lunaria, partially

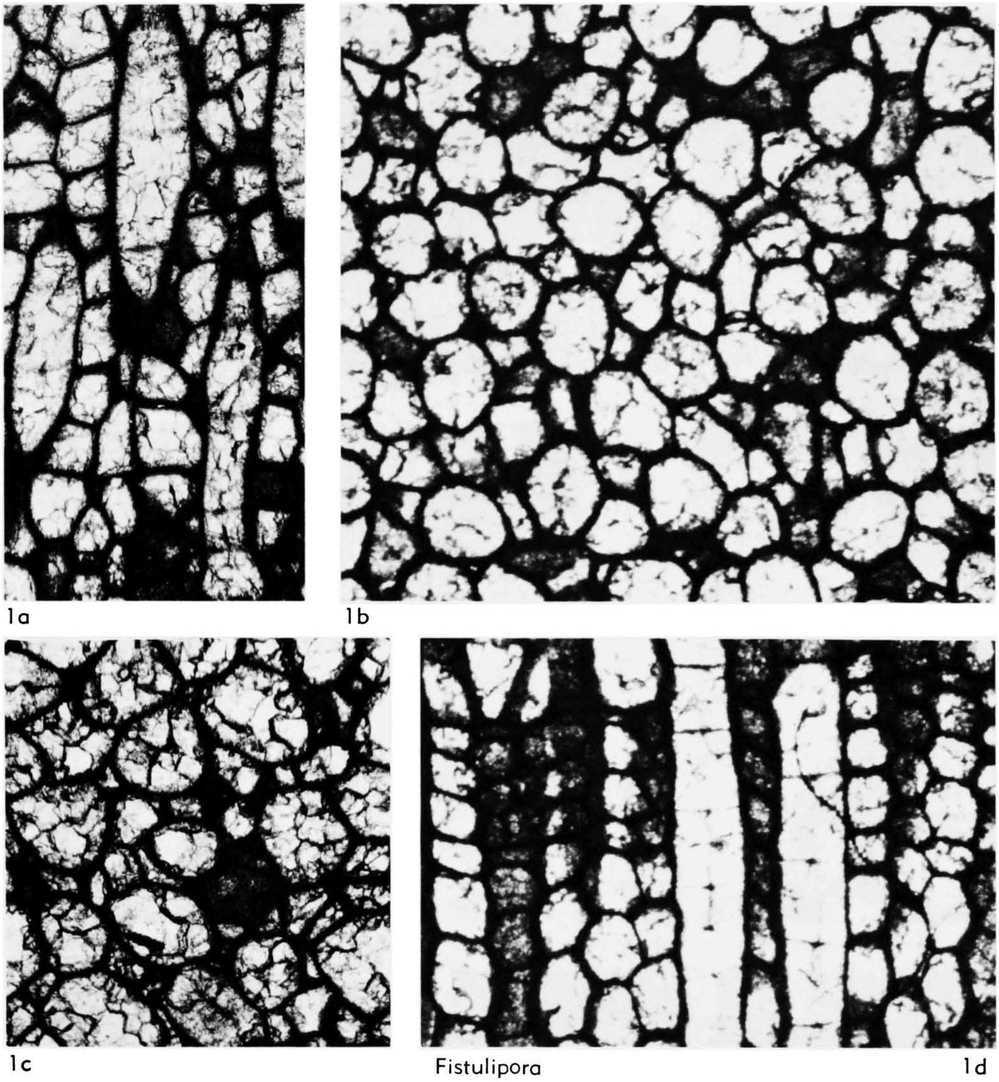


FIG. 173. Fistuliporidae (p. 380).

isolated by polygonal vesicles in endozone; transv. sec., ×30; *d,* tubular autozooecia with closely spaced planar diaphragms isolated by boxlike to polygonal vesicles; long. sec., ×30 (*a* and *c* are photographs of a section figured by BASSLER, labeled SM 315; *b* and *d* are photographs furnished by A. G. BRIGHTON of presumably the same paratype, SM 315, W. Hopkins Coll., bearing the additional number E5373b).

Buskopora Ulrich, 1886b, p. 22 [**B. dentata*; OD; "U. Helderberg?," M. Dev., Falls of the Ohio, Jeffersonville, Ind., USA]. Zoarium encrusting. Monticules small, elevated clusters of vesicles surrounded by larger zooecia with large, hood-shaped lunaria. Autozooecia with peristomes. Basal layer with dark, granular, primary layer and light-colored, granular-prismatic layer. Autozooecia recumbent for short distance, erect in exozone; diaphragms thick, throughout endozone and exozone. Autozooecia partially to completely isolated by small angular to subrounded vesicles; circular to oval in cross section, deeply indented by bifid lunaria. Walls of autozooecia and lunaria granular-prismatic; dark, granular, central zone of lunarium not continuous with dark, granular boundary of autozooecial wall. Vesicles blister-like, granular-prismatic, local zones of thick vesicle roofs with minute acanthostylelike tubuli. *M.Dev.,* E.USA.——FIG. 174, *1a–g.* **B. dentata*; *a,* topotype, USNM 43273, *b–g,* specimens from Jeffersonville F., Ind.; *a,* peristomes and lunaria projecting into

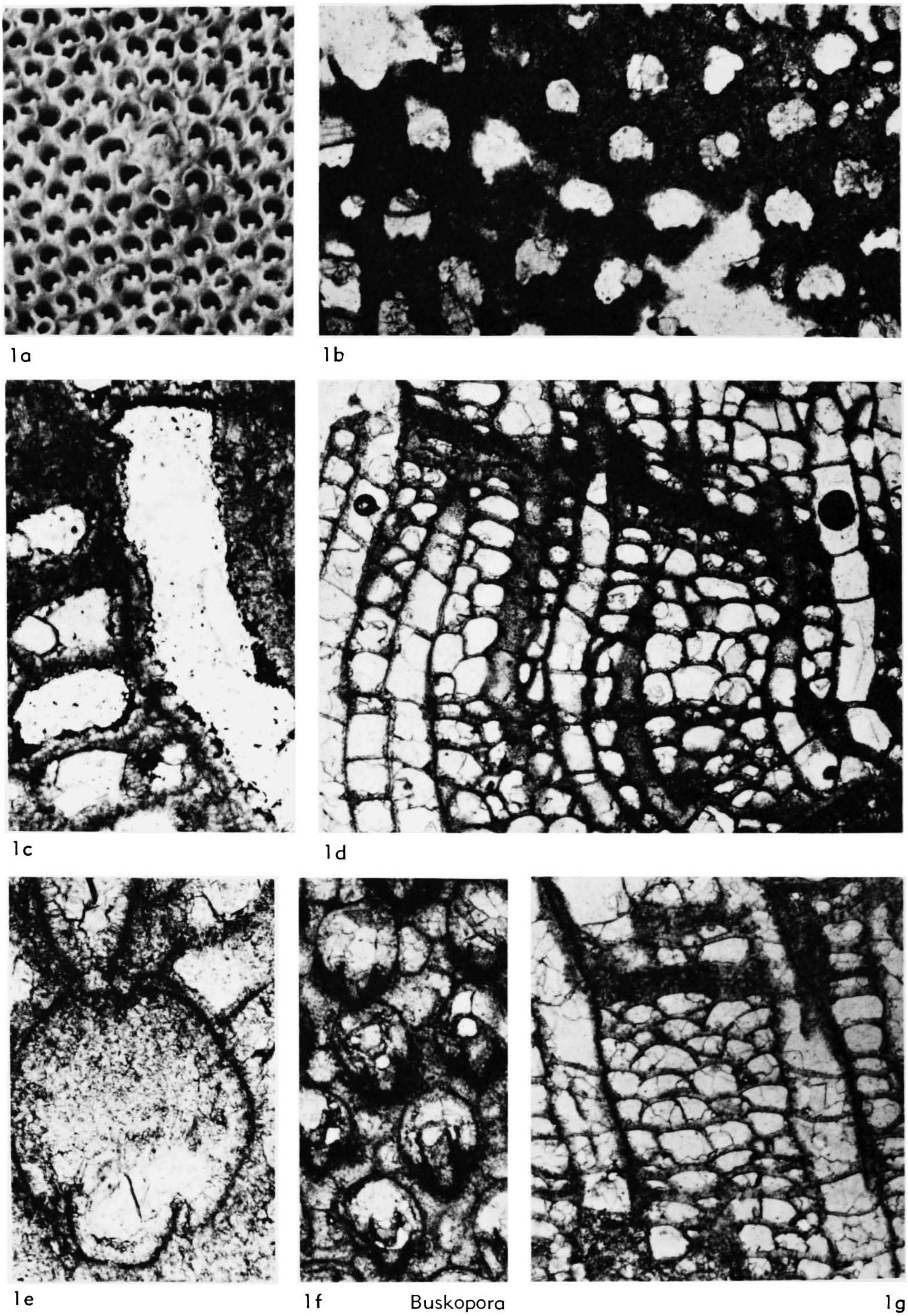


Fig. 174. Fistuliporidae (p. 381).

subcircular autozooecia like bifid teeth, and large, hoodlike lunaria in monticular zooecia (center), ×10; *b,* subcircular autozooecia indented by bifid lunaria and isolated by small vesicles having thick roofs with minute acanthostylelike structures; tang. sec., SIUC 3003, ×30; *c,* compound autozooecial wall with dark, granular, boundary zone and granularprismatic cortex; thicker, granular-prismatic lunarium on proximal side (right), and granular-prismatic vesicles (left); note simple, granular-prismatic subterminal diaphragm in autozooecium (above); long. sec., SIUC 3004, ×100; *d,* tubular autozooecia with planar diaphragms isolated by boxlike to blisterlike vesicles with two zones of thicker roofed vesicles; long. sec., SIUC 3004, ×30; *e,* granular-prismatic microstructure of autozooecial wall and projecting lunarium (below), light-colored corelike structure in lunarium (above) and granular vesicle walls (upper right); tang. sec., SIUC 3005, ×100; *f,* autozooecia narrowly isolated by small, angular vesicles and indented by lunaria; tang. sec., SIUC 3005, ×30; *g,* autozooecia with thick planar diaphragms and projecting end of lunarium and blisterlike vesicular tissue with zone of thick vesicle roofs containing minute acanthostylelike structures, transv. sec., SIUC 3006, ×30.

Canutrypa Bassler, 1952, p. 382 [**C. francqana*; OD; U. Dev., Ferques, France]. Zoarium ramose. Low monticules with central clusters of vesicles and ring of slightly larger zooecia. Autozooecia long, tubular; few diaphragms; proximal side rounded, distal side angular or with keel and sinuses in endozone. Wall granular-prismatic to indistinctly laminated. Gentle curve from endozone into exozone where walls thicken, containing minute tubuli perpendicular to boundary. Thin, straight or curved or partial diaphragms in inner exozone. One hemicylindrical cystlike structure with axis perpendicular to zooecial axis in many autozooecia in exozone; granular-prismatic microstructure. Lunaria in exozone; dark boundary and thick, light-colored distal deposit, poorly laminated, with minute tubuli perpendicular to boundary. Vesicular tissue in exozone; partially isolating autozooecia; small subquadrate blisters, subangular to subrounded in cross section; indistinctly laminated or granular-prismatic. Vesicle roofs thickening into solid stereom with minute tubules in outer exozone. *U.Dev.,* Eu.——Fig. 175,*1a–e*. **C. francqana*; *a,* thick lunarial deposits with tubuli perpendicular to zooecial walls and stereom with tubuli; tang. sec., paratype, USNM 113984, ×24; *b,* thin-walled contiguous autozooecia with diaphragms in endozone (left) and vesicular tissue from zooecial bend to zoarial surface, where stereom developed; long. sec., paratype, USNM 113984, ×24; *c,* thin-walled contiguous autozooecia with rounded proximal side and angular distal side, some with keel and sinus; transv. sec., paratype, USNM 113982-1, ×16; *d,* subcircular autozooecia with thick, light-colored lunarial deposit (below) and nearly straight wall of hemicylindrical cyst; vesicle roofs thickened to form stereom; tang. sec., holotype, USNM 116417, ×40; *e,* autozooecia with closely spaced and straight to curved and incomplete diaphragms in inner exozone, hemicylindrical cystlike structure on distal wall, thick and light-colored lunarial deposit on proximal side, and cystlike vesicular tissue in exozone; long. sec., holotype, ×24.

Cheilotrypa Ulrich, 1884, p. 49 [**C. hispida*; OD; Glen Dean F., U. Miss. (Chester.), Sloans Valley, Ky., USA) [=*Chilotrypa* Miller, 1889, p. 297, incorrect subsequent spelling]. Zoarium slender, hollow ramose or solid ramose, less commonly encrusting. Monticules small, with central cluster of vesicles, flush with surface; few surrounding zooecia conspicuously larger. Autozooecia narrow in endozone with narrower distal side. In exozone, autozooecia with ovate cavity, wider at proximal end. Walls with dark, granular, boundary zone and granular-prismatic cortex with tubuli. Lining local, laminated on distal side in outer exozone. Diaphragms sparse. Vesicles small, subrounded; autozooecia narrowly isolated; small blisters in inner exozone, granular-prismatic vesicle roofs merging to form stereom in outer exozone; tubuli in stereom. Lunaria in exozone, on wider proximal side, dark granular zone merging with granular zooecial boundary; thick, proximal granular-prismatic layer with tubuli perpendicular to boundary. *Miss.,* N.Am. ——Fig. 175,*2a–h*. **C. hispida*; *a,* hollow ramose zoarium with narrow autozooecia in endozone and vesicular tissue and stereom in exozone; transv. sec., paralectotype, USNM 159754, ×40; *b,* lunaria at wide end of autozooecia (below) and stereom between autozooecia; tang. sec., paralectotype, USNM 159759, ×24; *c,* hollow ramose zoarium, subtriangular autozooecia becoming wider outward in endozone; transv. sec., paralectotype, USNM 159759, ×24; *d,* lunaria with dark zone continuous into zooecial boundary and proximal (below dark zone), thick granular-prismatic zone, small subrounded vesicles (above) narrowly isolating autozooecia; tang. sec., lectotype, USNM 159757, ×40; *e,* granular-prismatic walls, questionable distal lining (above) in autozooecium on right, and stereom with tubuli; tang. sec., paralectotype, USNM 159758, ×80; *f,* hollow axis with constrictions, thin wall resembling basal layer, and thick walls and vesicular tissue in exozone; long. sec., lectotype, ×24; *g,* irregular hollow center (below), thin-walled autozooecia in endozone becoming wider in outer endozone and exozone, vesicles thickening into stereom in exozone; long. sec., paralectotype, USNM 159753, ×24; *h,* stereom isolating

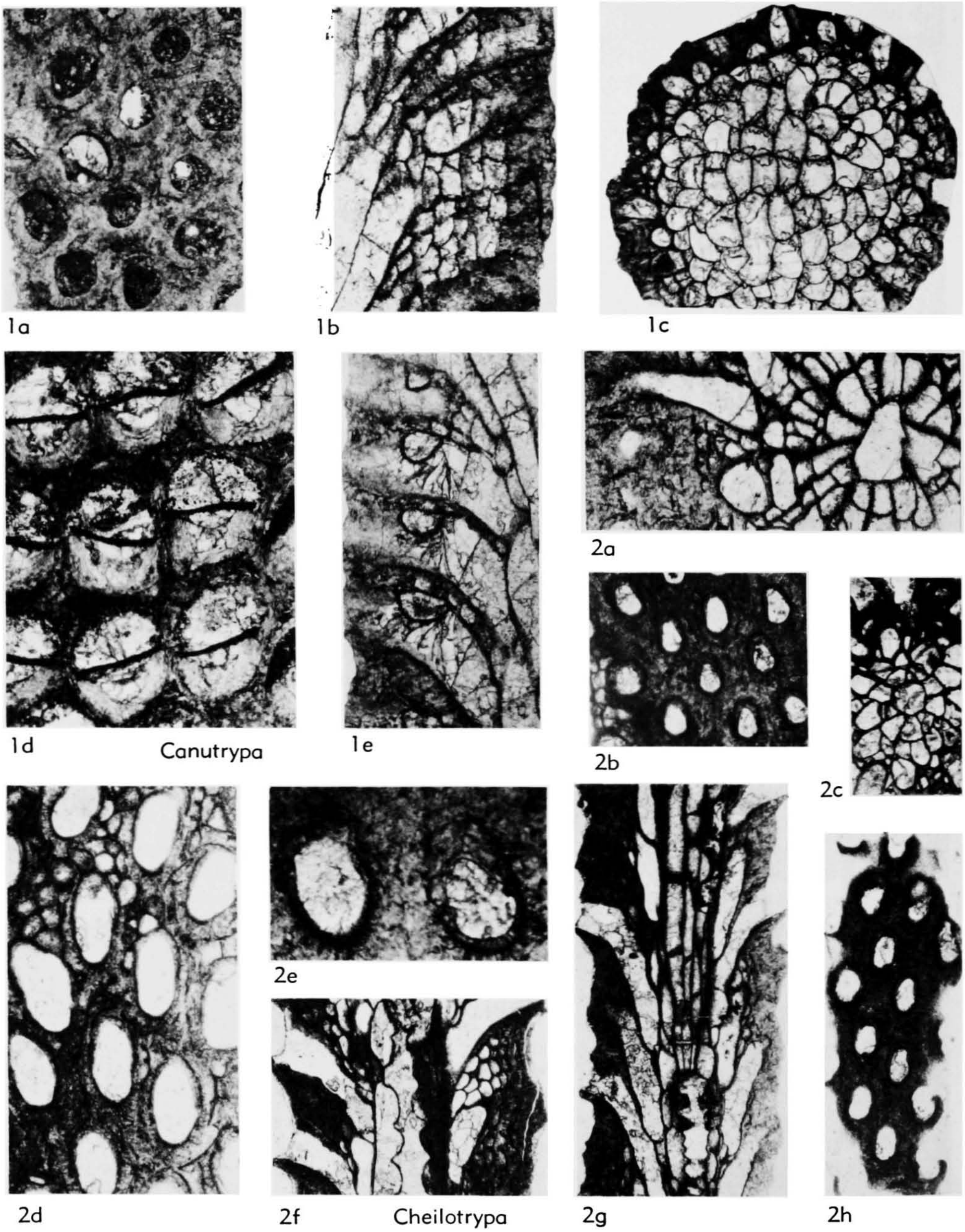


FIG. 175. Fistuliporidae (p. 383).

elongate autozooecia; tang. sec., paralectotype, USNM 159753, ×24.

Cliotrypa ULRICH & BASSLER IN BASSLER, 1929, p. 49 [**C. ramosa* ULRICH & BASSLER IN BASSLER, 1936, p. 160; SM; New Providence F., L. Miss., Kings Mt., Ky., USA]. Zoarium ramose, encrusting overgrowths. Monticules flush; center stereom, ring of slightly larger autozooecia with lunaria radially arranged. Autozooecia in endozone narrow, with proximal side rounded and distal side subangular to sinus-and-keel shaped; cavity subcircular in exozone. Walls transversely laminated; dark boundary, tubuli in cortex perpendicular to boundary. Lunaria in outer endozone and exozone; hyaline with one or two proximal projections. Diaphragms thin, sparse.

Hemiphragms proximally curved, triangular to spinelike; alternating on proximal and distal walls in outer endozone and in exozone. Gonozooecia, as bulbous swellings of autozooecia, in exozone. Vesicles in outer endozone and exozone; blisterlike cysts decreasing in height outward; stereom in most of exozone. Walls and roofs poorly and longitudinally laminated. Acanthostyles in vesicle walls and roofs. *L.Miss.*, N.Am.——Fig. 176,*1a–f.* **C. ramosa*; *a,* small, thin-walled autozooecia in endozone, rounded proximal sides and angular distal sides, some with keel and sinus, vesicles and stereom in exozone, autozooecia and bulbous gonozooecial swellings in exozone, hemiphragms; transv. sec., holotype, USNM 92133, ×20; *b,* large gonozooecia, smaller autozooecia with hyaline lunaria isolated by stereom with abundant acanthostyles; tang. sec., holotype, ×20; *c,* monticular center (right) of stereom with acanthostyles, radial arrangement of hyaline lunaria, and two large gonozooecia (left); tang. sec., holotype, ×20; *d,* narrow autozooecia with diaphragms in endozone (left), vesicles decreasing in height outwardly in exozone, and autozooecia with hemiphragms, long. sec., topotype, USNM 159799, ×30; *e,* poorly laminated vesicle walls and roofs with acanthostyles; transv. sec., topotype, USNM 159800, ×100; *f,* laminated autozooecial walls with tubules (top, center), lunaria with short radius of curvature, and subrounded vesicles; tang. sec., topotype, USNM 159801, ×100.

Coelocaulis Hall & Simpson, 1887, p. xvi [**Callopora venusta* Hall, 1874, p. 101; OD; New Scotland F., L. Dev. (Helderberg.), Clarksville, N.Y., USA]. Zoarium ramose, hollow. Monticules absent. Autozooecia contiguous at basal layer, with narrow keel and sinus in outer endozone. Autozooecia oblique to zoarial surface, cavity ovate; walls poorly laminated; diaphragms few; lunaria absent. Vesicular tissue in outer endozone and exozone; blisterlike cysts; vesicle roofs locally thicker; laminated. Vesicles elongate in cross section, partially isolating autozooecia. [*Coelocaulis* is similar in most respects to *Diamesopora* Hall, 1852. Apparent lack of well-defined lunaria and tubules in the laminated walls may result from silicification of the type specimens of *Coelocaulis venusta*.] *L.Dev.*, USA.——Fig. 177,*2a–d.* **C. venusta* (Hall), holotype, NYSM 635; *a,* ovate autozooecia and protruding vesicle walls, ×10; *b,* poorly laminated basal layer (right), walls, and vesicles, planar diaphragm in one autozooecium; long. sec., ×30; *c,* autozooecia isolated by elongate vesicles and vesicle roofs in exozone; tang. sec., ×50; *d,* hollow ramose zoarium; autozooecia narrow at basal layer, keel and sinus in outer endozone, autozooecia larger and isolated by vesicular tissue in exozone, transv. sec., ×20.

Cyclotrypa Ulrich, 1896, p. 269 [**Fistulipora communis* Ulrich, 1890, p. 476; SD Nickles & Bassler, 1900, p. 219; Cedar Valley F., M. Dev., Buffalo, Iowa, USA]. Zoarium encrusting; multiple overgrowths common. Monticules low; central cluster of vesicles and ring of larger autozooecia. Basal layer with granular lower part and granular-prismatic upper part. Autozooecia recumbent for short distance; hemispherical in cross section and achieving full width at basal layer; isolated by vesicular tissue; walls with granular boundary zone, granular-prismatic cortex generally thicker outside boundary. Autozooecia erect in exozone, circular in cross section, with thin diaphragms. Lunarium absent. Vesicular tissue granular-prismatic, low blisterlike cysts decreasing in height outward, commonly in repeated cycles, capped by zone of thicker vesicle roofs. Acanthostyles in vesicle walls and some in vesicle roofs. *M.Dev.-U.Dev., ?L.Miss.,* N.Am., Eu., USSR.——Fig. 177,*1a–d.* **C. communis* (Ulrich); *a,* basal layer with granular lower zone and granular-prismatic upper layer, autozooecium with hemispherical cross section in endozone, blisterlike vesicles with roofs thicker at surface, and acanthostyles light-colored; transv. sec., lectotype, USNM 159802, ×50; *b,* large vesicles in monticule, circular autozooecia isolated by medium-sized subangular to subrounded vesicles; tang. sec., lectotype, ×30; *c,* thick outer granular-prismatic layer of autozooecial walls, granular-prismatic vesicle walls; tang. sec., paralectotype, USNM 159803, ×100; *d,* long tubular autozooecia isolated by vesicular tissue, several cycles of outward decreasing of vesicle height and increasing thickness of vesicle roofs; long. sec., paralectotype, USNM 159804, ×30.

Cystiramus Morozova, 1959a, p. 79 [**C. kondomensis*; OD; Vassinskie Beds, U. Dev. (*Frasn.*), Kondoma River, Kuznetsk basin, USSR]. Zoarium ramose, bifurcating. Monticules not reported but small areas of larger zooecia are present. Endozone with short zooecia, rounded proximal side and angular distal side, cyclically budded in hemispherical zones on a curved wall; wall granular. Autozooecia in exozone isolated by vesicular tissue; wall thickening rapidly in inner exozone; boundary granular and granular-prismatic cortex thick with some distally diverging tubuli; diaphragms in inner exozone. Lunaria in exozone, dark boundary zone continuing into lateral autozooecial walls; proximal, light-colored, granular-prismatic layer thickest, with some perpendicular tubuli. Vesicles in exozone; granular-prismatic; subquadrate blisters thickened to stereom through most of exozone; ?tubuli few. *U.Dev.*, USSR.——Fig. 178,*1a–d.* **C. kondomensis*; *a,* endozonal zooecia with curved proximal side and subangular distal side, autozooecia with diaphragms isolated by vesicular tissue in exozone; transv. sec., paratype, PIN

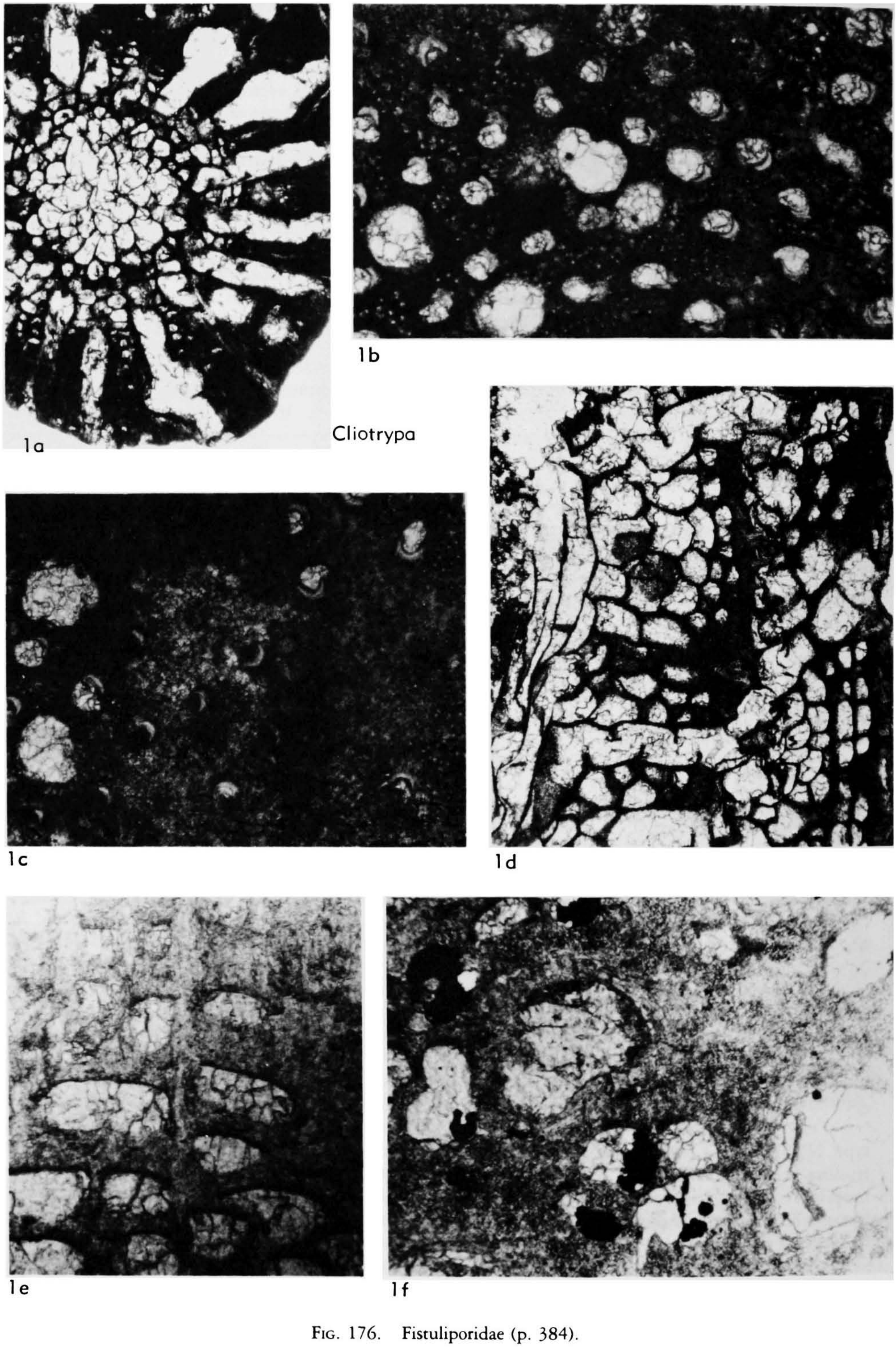


FIG. 176. Fistuliporidae (p. 384).

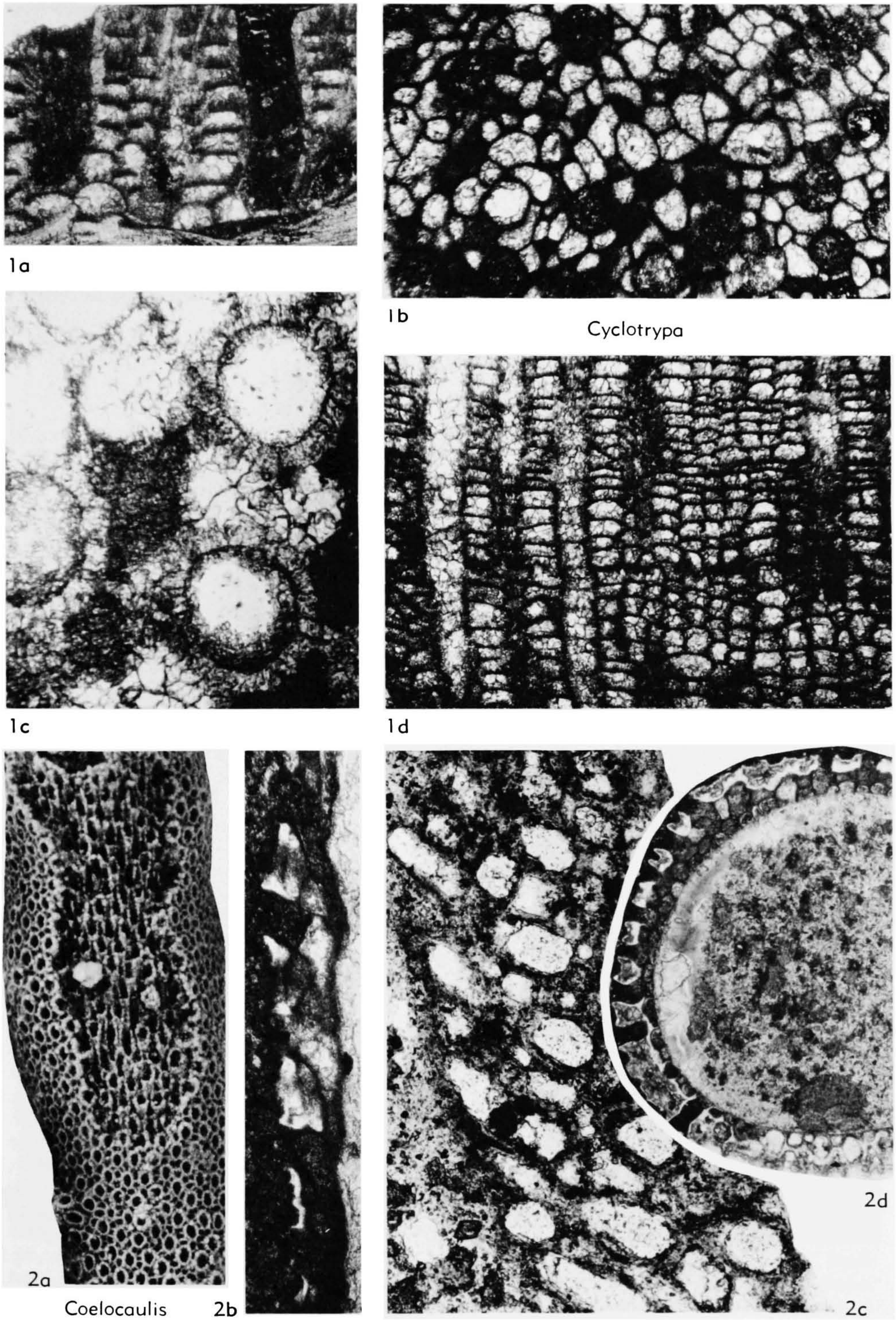


FIG. 177. Fistuliporidae (p. 385).

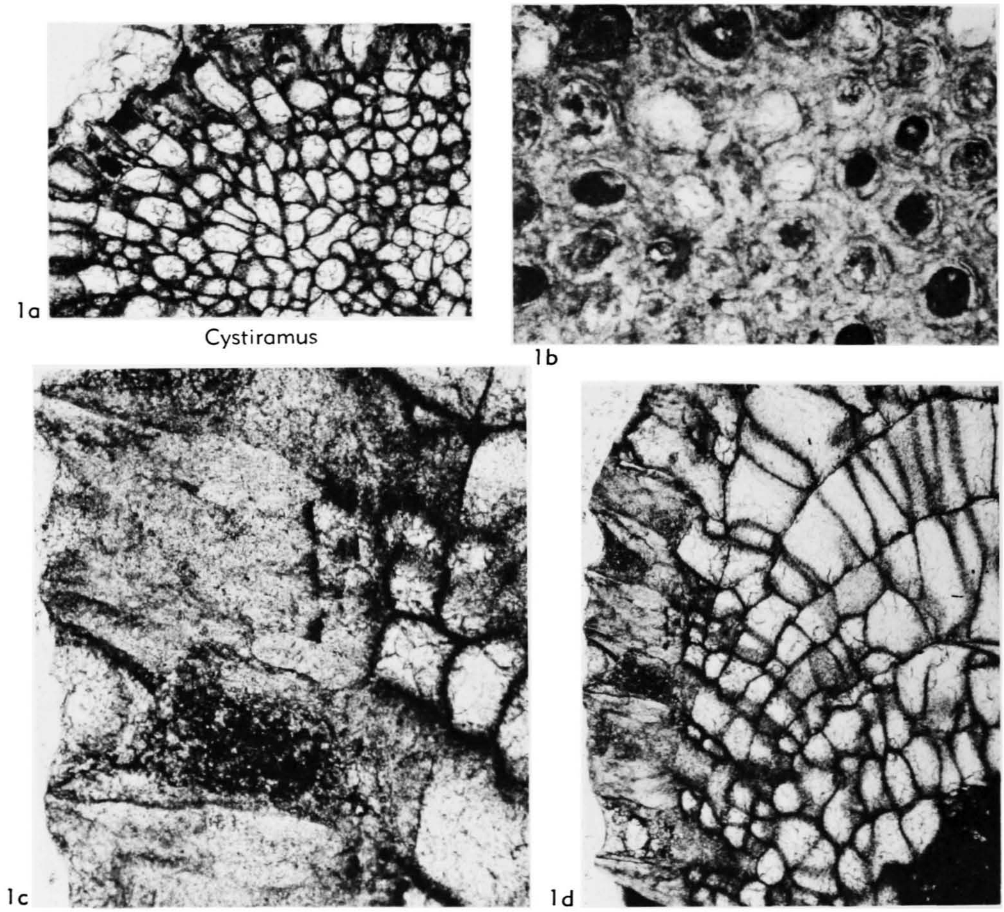


FIG. 178. Fistuliporidae (p. 385).

198/12, ×20; *b,* dark boundaries in subcircular autozooecia with lunaria of same radius of curvature on right side, stereom (with ?tubuli) isolates autozooecia; tang. sec., paralectotype, PIN 918/316a, ×30; *c,* thick granular-prismatic walls in autozooecia isolated by boxlike vesicles and stereom in exozone; long. sec., paralectotype, PIN 918/317B, ×100; *d,* hemispherical cycles of thin-walled autozooecia in endozone; vesicular tissue and thick-walled autozooecia in exozone; long. sec., paralectotype, PIN 918/317B, ×30.

Diamesopora HALL, 1852, p. 158 [**D. dichotoma*; M; "Niagaran Ls.," M. Sil. (Niag.), Lockport, N.Y., USA] [=*Coeloclema* ULRICH, 1883, p. 258, *non* ULRICH, NICKLES, & BASSLER, 1900, p. 24, 211; *nec* NICKLES & BASSLER, ELIAS, 1954, p. 53]. Zoarium ramose, hollow. Monticules absent. Basal layer granular-prismatic with indistinct tubuli. Autozooecia contiguous at basal layer, hemispherical in cross section, recumbent; keel and sinuses well developed in endozone; autozooecia elongate diamond shaped, rhombically packed in deep tangential view; diameter narrowing in exozone with distal spur in outer exozone; cavity subelliptical, isolated by stereom and in diagonally intersecting rows. Walls transversely laminated; boundary zone indistinct; tubuli outside boundary. Lunaria in exozone, small, most with small hyaline center; laminated distal lining continuous with lining of wall. Vesicular tissue in exozone; low, broad blisters, polygonal in cross section; laminated stereom with tubuli or small acanthostyles; stereom at lower level than autozooecial walls at surface. Diaphragms and subterminal diaphragms few. [*Trematopora osculum* HALL, 1876, is the type species of *Coeloclema* ULRICH, 1883, by subsequent designation (UTGAARD, 1968b, p. 1454). It does not differ significantly from *Diamesopora dichotoma* (HALL).] *M.Sil.,* N.Am.——FIG. 179,*1a–c. D. osculum* (HALL), Waldron Sh., M. Sil., Ind., USA, lectotype, AMNH 1916; *a,* basal layer (left) with thin, dark, lower zone and granular-prismatic upper layer with tubuli, vesicles containing laminated stereom and tubuli isolating autozooecia with subterminal diaphragms;

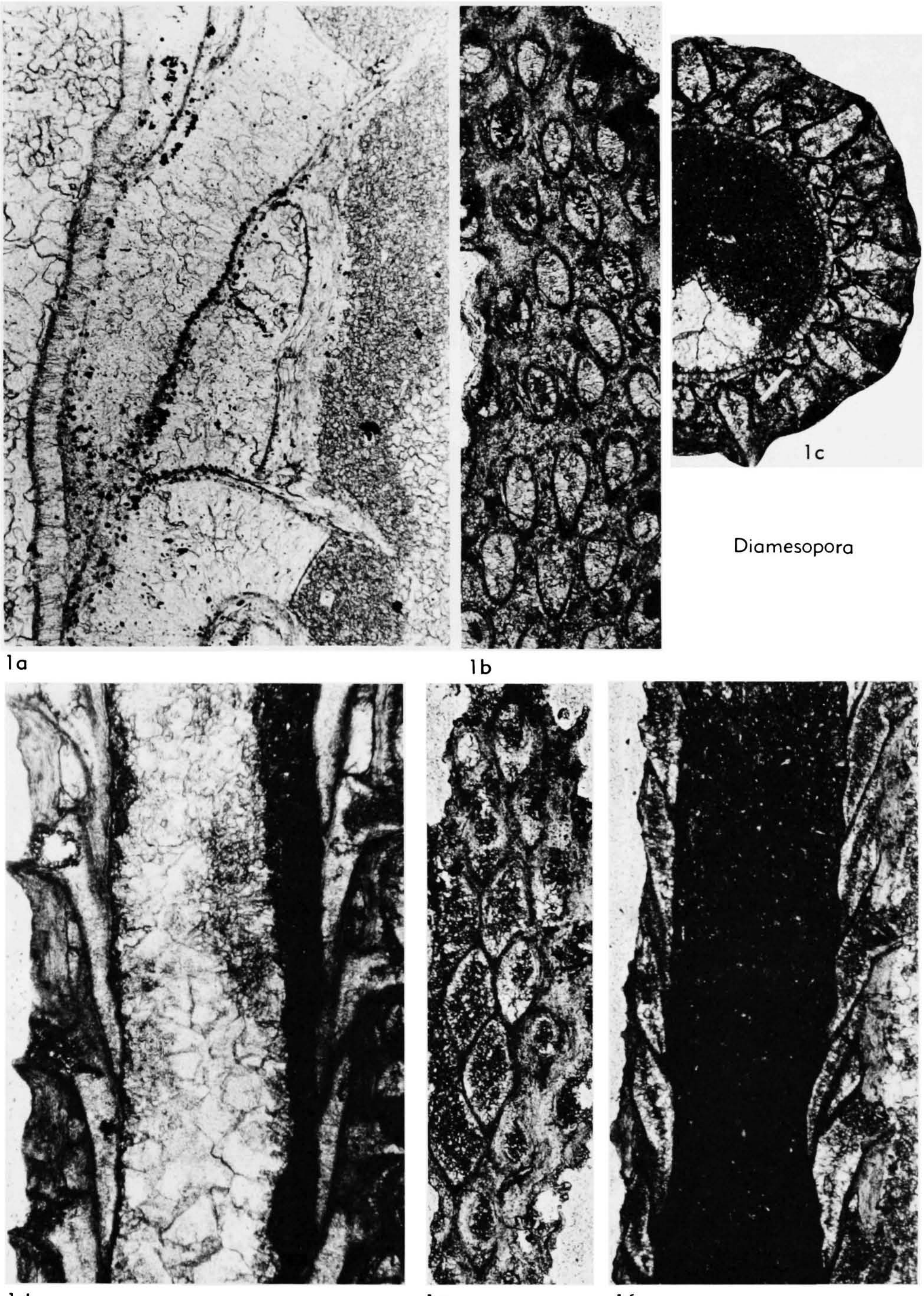


FIG. 179. Fistuliporidae (p. 388).

long. sec., ×100; *b,* laminated autozooecial walls, lunaria (lower side of autozooecia), vesicles in inner exozone (below) and stereom in exozone; tang. sec., ×30; *c,* hollow zoarium, granular-

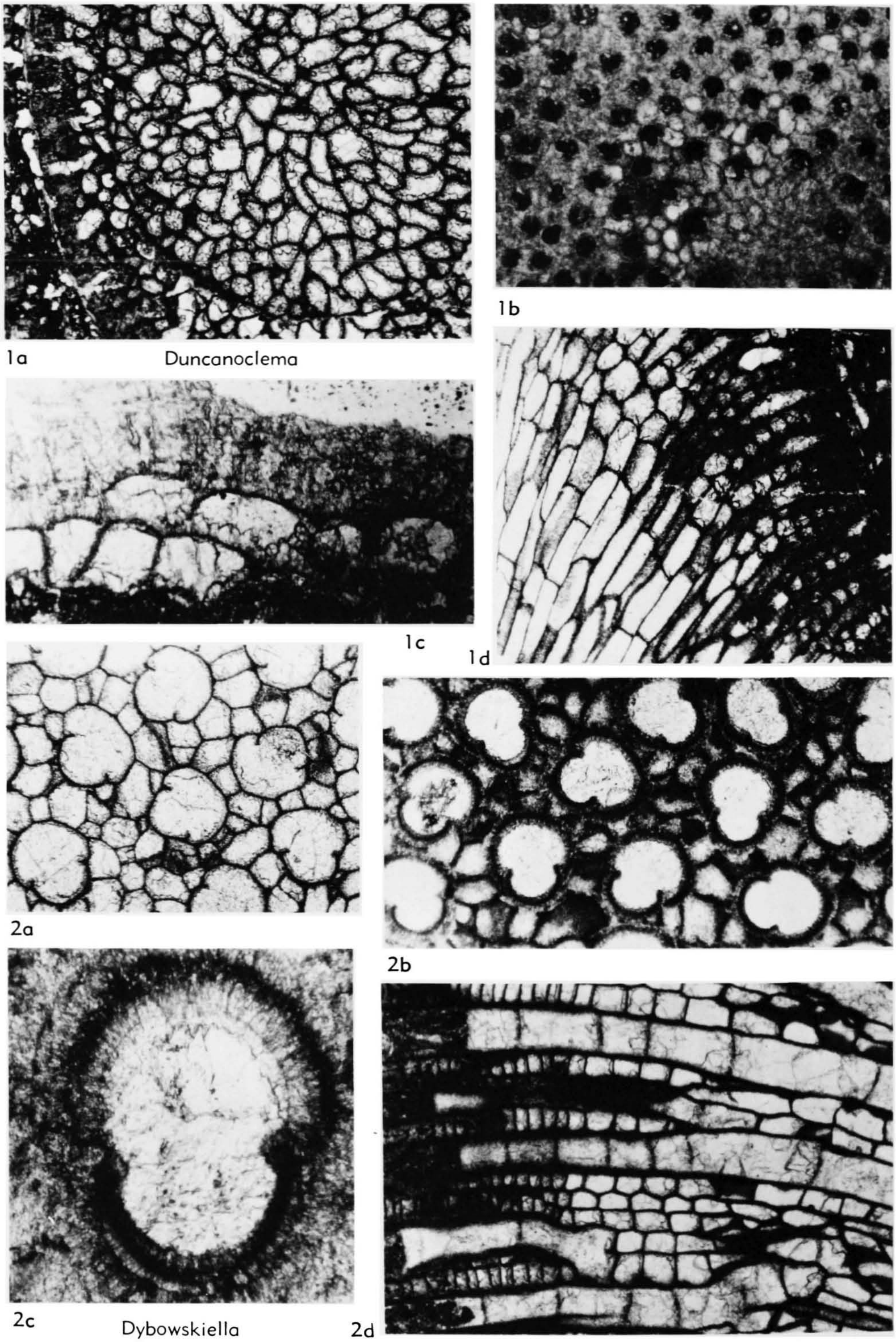


FIG. 180. Fistuliporidae (p. 391).

prismatic basal layer, hemispherical autozooecia at basal layer, keel and sinuses in outer endozone, vesicles and laminated stereom in exozone; transv. sec., ×30.——Fig. 179, *1d–f.* **D. dichotoma*; *d,* hollow zoarium, narrowing of autozooecia in exozone, vesicular tissue as low blisters in inner exozone; long. sec., topotype, USNM 159806, ×30; *e,* rhombic arrangement of autozooecia and smaller diameter in exozone than in endozone; tang. sec., holotype, AMNH 1760, ×30; *f,* hollow ramose zoarium, vesicular tissue becoming laminated stereom in exozone; long. sec., holotype, ×30.

Duncanoclema Bassler, 1952, p. 381 [**Fistuliporella marylandica* Ulrich & Bassler, 1913, p. 266; OD; Keyser Ls., U. Sil. (Cayug.), "L. Dev., Helderbergian," Cash Valley, Md., USA]. Zoarium ramose, with encrusting overgrowths. Monticules flush, central cluster of small vesicles; ring of larger zooecia with lunaria radially arranged. Autozooecia isolated at basal layer or in endozone of ramose zoaria by irregular, long, tubelike vesicles with curved roof. Autozooecia subcircular in cross section in endozone; wall thin, granular or granular-prismatic; thicker walled in exozone; diaphragms few. Lunaria in exozone; solid or discontinuous hyaline; some with cores; radius of curvature short and ends inflecting autozooecia. Vesicles becoming lower and more blisterlike in outer endozone and inner exozone; granular-prismatic; roofs thickening to stereom in outer exozone; small acanthostyles or tubuli in walls, roofs, and stereom; widely isolating autozooecia. *U.Sil.,* N.Am.——Fig. 180,*1a–d.* **D. marylandica* (Ulrich & Bassler); *a,* small subrounded autozooecia isolated by large irregular vesicles in endozone, encrusting overgrowth with hemispherical autozooecia at basal layer, stereom in outer exozone; transv. sec., paralectotype, USNM 159750, ×20; *b,* monticular center of smaller vesicles (lower right) and ring of larger zooecia with lunaria radially arranged, rhombic arrangement of isolated autozooecia; tang. sec., lectotype, USNM 159749, ×20; *c,* granular-prismatic vesicles and stereom with small acanthostyles or tubuli in outer exozone; long. sec., paralectotype, USNM 159751, ×100; *d,* long, tubelike vesicles in endozone and shorter, blisterlike vesicles with thicker roofs in exozone; long. sec., lectotype, ×20.

Dybowskiella Waagen & Wentzel, 1886, p. 916, *nom. subst. pro Dybowskia* Waagen & Pichl, 1885, p. 771, *non* Dall, 1877 [**Dybowskiella grandis*; OD; mid.-up. *Productus* Ls., Perm., Salt Ra., Pak.] [=*Triphyllotrypa* Moore & Dudley, 1944, p. 291]. Zoarium ramose, hollow ramose, encrusting, hemispherical, or massive. Monticules elevated or flush, central cluster of small polygonal vesicles surrounded by larger zooecia with lunaria partly to completely radial in arrangement. Autozooecia full width, hemispherical in cross section at basal layer or where budded on vesicular tissue. Basal layer with dark, granular, primary layer and thick, light-colored, granular-prismatic layer. Autozooecia subcircular in cross section in endozone and exozone; isolated by many small polygonal vesicles; wall with granular boundary zone and light-colored granular-prismatic cortex. Diaphragms straight, curved, oblique, or incomplete. Lunaria in endozone and exozone, ends inflecting autozooecial cavity; dark granular zone not continuous with dark boundary zone in wall; thick distal and proximal granular-prismatic zones. Vesicular tissue in endozone and exozone; isolating autozooecia; vesicles subrectangular with straight superimposed or zigzag walls and flat to slightly curved roofs at same level in adjacent vesicles; small and polygonal in cross section. Roofs thickening into stereom at zoarial surface in some species. Small acanthostyles or tubuli in some vesicle roofs or stereom (a few appear to be central "pores"). Vesicles granular-prismatic. [*Triphyllotrypa speciosa* Moore & Dudley, 1944, p. 291, is the type species of *Triphyllotrypa* Moore & Dudley, 1944, by original designation. Like other species assigned to *Triphyllotrypa,* it differs from *Dybowskiella grandis* Waagen & Wentzel, mainly in growth habit: encrusting, hemispherical, or massive in *T. speciosa* and ramose or hollow ramose in *D. grandis.* In addition, species assigned to *Triphyllotrypa* may have a thick prolongation on the proximal side of lunaria in monticular zooids, and little or no development of stereom. These differences are judged to be too minor for generic separation, and *Triphyllotrypa* is considered to be a synonym of *Dybowskiella.*] *Perm.,* Asia, N.Am., Australia.——Fig. 180,*2a–d.* **D. grandis,* "*?Carb.,*" USNM 61314; *a,* thin-walled autozooecia with inflecting ends of lunaria, isolated by small polygonal vesicles in inner exozone; tang. sec., ×30; *b,* thick-walled autozooecia with lunaria, dark acanthostyles in some vesicle roofs (above center); tang. sec., ×30; *c,* dark granular central zone in lunarium (below) not continuous into dark granular autozooecial boundary, thick, light-colored, granular-prismatic layers in autozooecial wall and lunarium; tang. sec., ×100; *d,* diaphragms in autozooecia in endozone and exozone (left) (above), autozooecia budded on vesicular tissue (below) in endozone and exozone, polygonal to boxlike vesicles isolate autozooecia, vesicles decrease in height in outer exozone; long. sec., ×20.

Eofistulotrypa Morozova, 1959b, p. 9 [**E. manifesta*; OD; U. Dev. (*Frasn.*), Kuznetsk basin, USSR]. Zoarium ramose. Endozone with thin-walled polygonal autozooecia. Autozooecia with granular wall, sparse diaphragms in exozone; subrounded in cross section. Lunarium in exozone, large, thin, generally indistinct. Vesicular

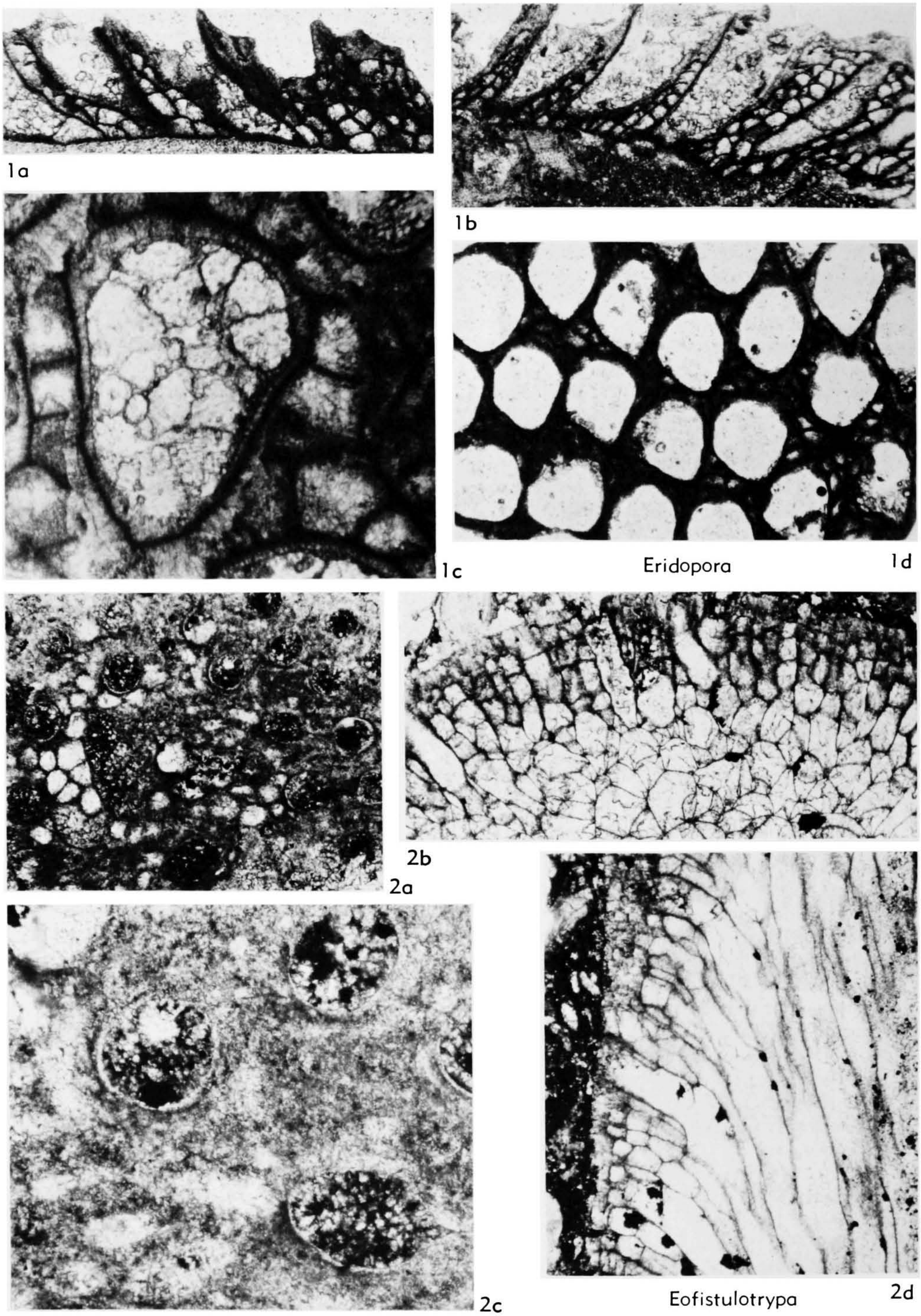


FIG. 181. Fistuliporidae (p. 391–393).

tissue in exozone; small, subrounded in cross section, isolating autozooecia; boxlike, decreasing in height outward in exozone; thin stereom at zoarial surface. *U. Dev. (Frasn.),* USSR.——FIG.

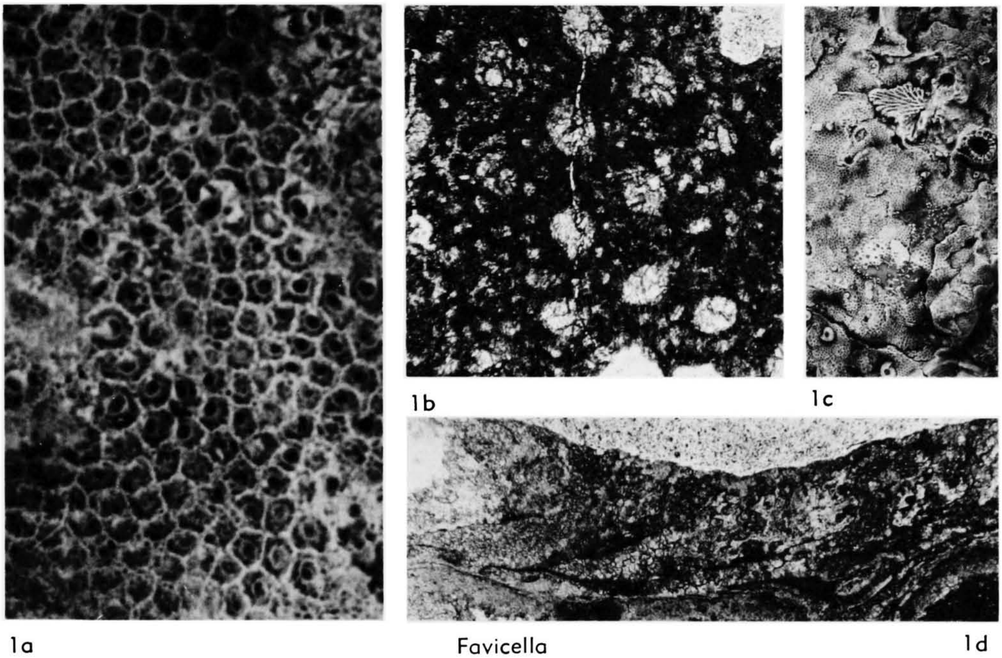


FIG. 182. Fistuliporidae (p. 393).

181,*2a–d*. **E. manifesta,* paratype, PIN 918/175; *a,* autozooecia with large lunaria (lower left) isolated by subrounded vesicles and stereom (top); tang. sec., ×30; *b,* polygonal autozooecia in endozone (below) and boxlike to polygonal vesicles isolating autozooecia in exozone (above); transv. sec., ×30; *c,* large lunaria (left) in autozooecia isolated by small vesicles and stereom; tang. sec., ×100; *d,* thin-walled autozooecia with no vesicular tissue in endozone (right), sparse diaphragms, angular vesicles becoming shorter in exozone and thin stereom at zoarial surface (left); long. sec., ×30.

Eridopora ULRICH, 1882, p. 137 [**E. macrostoma*; OD; Glen Dean F., U. Miss. (*Chester.*), Sloans Valley, Ky., USA] [=*Erydopora* NIKIFOROVA, 1927, p. 256, incorrect subsequent spelling]. Zoarium encrusting. Monticules small, flush; cluster of vesicles central. Basal layer granular-prismatic. Autozooecia in cross section hemispherical at basal layer, isolated by vesicular tissue; wall with dark, granular, boundary zone and granular-prismatic cortex; many distal and lateral walls formed of simple, superimposed vesicle walls; in exozone, autozooecia either oblique to zooarial surface and opening pyriform, or subperpendicular to surface and opening more circular; narrowly isolated by small vesicles. Lunarium in endozone and exozone, large; dark central zone continuing into dark zone in autozooecial wall; proximal granular-prismatic layer thick, may have irregular nodes. Vesicles in endozone and exozone; small, low blisters; stereom thin at surface, inner dark granular layer and outer granular-prismatic layer with tubuli. [*Eridopora* (*Discotrypella*) *stellata* ELIAS, 1957, p. 393, is the type species, by original designation, of the subgenus. The type of *E.* (*D.*) *stellata,* from the Eskeridge Shale (L. Perm.) at Roca, Nebraska, cannot be located and the status of this subgenus is doubtful.] *U.Miss.,* N.Am., USSR.——FIG. 181,*1a–d*. **E. macrostoma*; *a,* vesicular tissue isolating autozooecia from basal layer to zoarial surface; long. sec., lectotype, USNM 159738, ×30; *b,* recumbent to oblique autozooecia lacking diaphragms and isolated by small, blisterlike vesicles; long. sec., paralectotype, USNM 159737, ×30; *c,* simple autozooecial walls (above) and compound lunarial deposit (below) with thick, proximal, light-colored layer, simple to (a few) compound vesicle walls; tang. sec., lectotype, ×100; *d,* large autozooecia with large lunaria, in intersecting rows and narrowly isolated by small vesicles and stereom; tang. sec., paralectotype, USNM 159736, ×30.

Favicella HALL & SIMPSON, 1887, p. xviii [**Thallostigma inclusa* HALL, 1881, p. 188; OD; "Hamilton beds," M. Dev., York, N.Y., USA]. Zoarium encrusting. Monticules elevated; cluster of vesicles in center and encircling ring of slightly larger zooecia; lunaria obscure, radially arranged. Peristome elevated, ridges of vesicle walls in polygon shape surrounding each zooecium. Autozooecia with long recumbent portion at

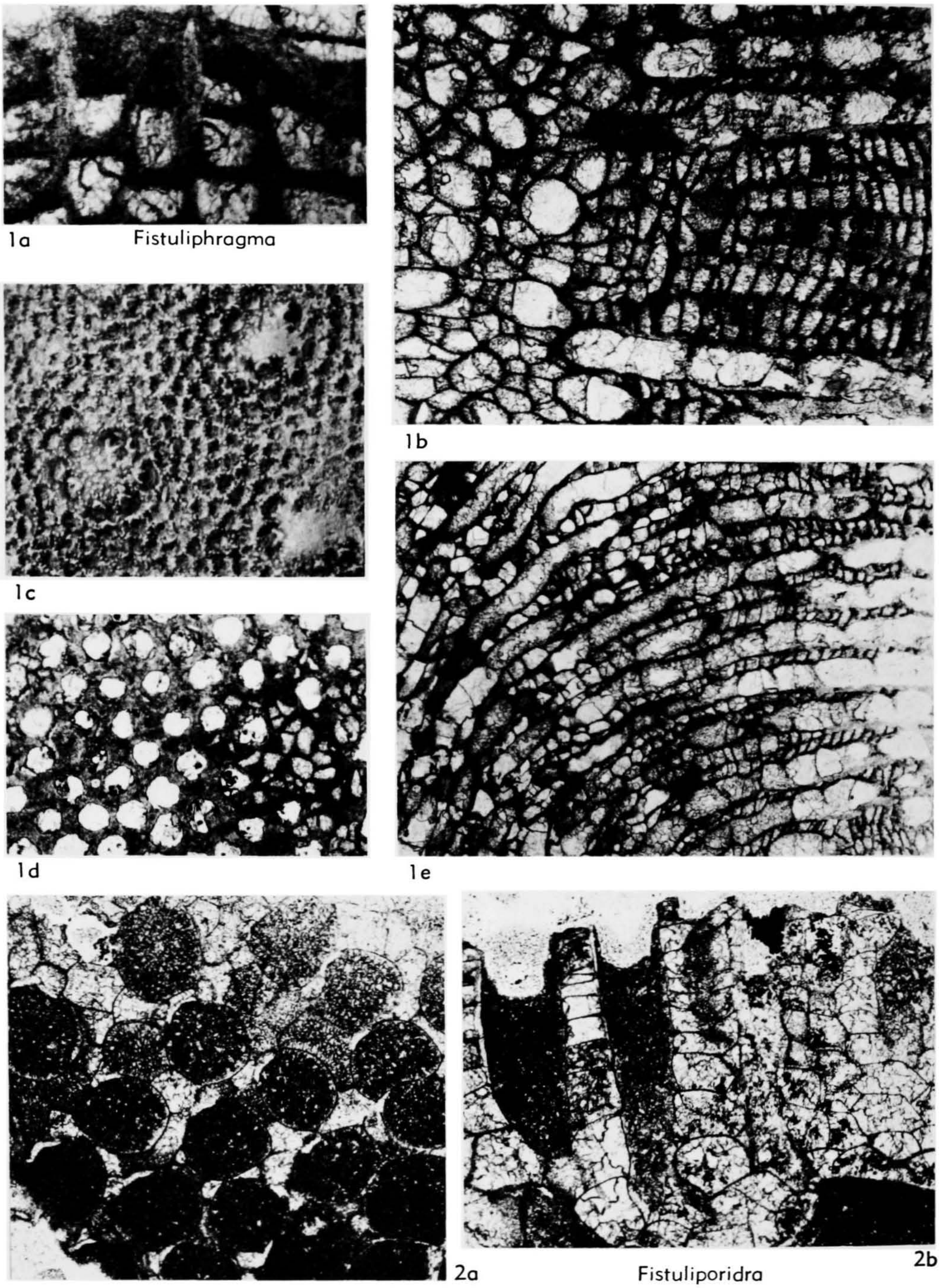


FIG. 183. Fistuliporidae (p. 395).

basal layer; contiguous; hemispherical cross section with keel and sinuses. Wall indistinctly granular-prismatic. Diaphragms not seen. Lunaria obscure. Vesicles small, blisterlike, widely isolating autozooecia. [The holotype is silicified and many characters are obscure, but the polygonal ridges of vesicle walls that surround each zooecium are distinctive.] M.Dev-

N.Am.——Fig. 182,*1a–d.* **F. inclusa* (Hall), holotype, NYSM 655; *a,* monticule (left, center), obscure lunaria and peristomal ridges and prominent polygonal ridge of vesicle walls surround each zooecium; ×10; *b,* subcircular autozooecia with obscure lunaria and granular-prismatic walls widely isolated by small vesicles; tang. sec., ×30; *c,* elevated monticules, ×1; *d,* recumbent autozooecia in endozone and vesicles in exozone; long. sec., ×30.

Fistuliphragma Bassler, 1934, p. 407 [**Fistulipora spinulifera* Rominger, 1866, p. 121; OD; Traverse Gr., M. Dev., Thunder Bay, Mich., USA]. Zoarium ramose, some encrusting overgrowths. Monticules elevated, cluster of vesicular tissue central, lunaria radially arranged. Autozooecia subrounded to subangular in cross section in endozone, isolated by vesicular tissue; subrounded in exozone. Diaphragms common. Hemiphragms few in endozone, closely spaced in exozone, alternating on proximal and distal sides; spinelike and curved to platelike. Walls indistinctly laminated. Lunaria small in endozone, large in exozone; light-colored dense deposit, some ends inflecting autozooecial cavity. Vesicles laminated, high blisters in endozone, subquadrate to low blisterlike to boxlike in exozone; acanthostyles in vesicle walls; walls superimposed; in some with thin stereom at zoarial surface. *M.Dev.,* N. Am.——Fig. 183,*1a–e.* **F. spinulifera* (Rominger); *a,* large, light-colored acanthostyles in vesicle walls in monticule, walls superimposed, roofs flat, indistinctly laminated; long. sec., paralectotype, USNM 159740, ×100; *b,* ovate autozooecia isolated by vesicles in endozone (left), boxlike vesicles with superimposed walls and acanthostyles in monticule (right, center); transv. sec., paralectotype, USNM 159740, ×30; *c,* elevated monticules with stereom at center, lunaria radially arranged, spinelike acanthostyles; lectotype, USNM 159742, ×10; *d,* monticule (right), autozooecia narrowly isolated by stereom; tang. sec., lectotype, ×20; *e,* vesicular tissue decreasing in height from endozone to exozone (right), spinelike hemiphragms and diaphragms in autozooecia, light-colored lunarial deposits on proximal side; long. sec., lectotype, ×20.

Fistuliporella Simpson, 1897, p. 560 [**Lichenalia constricta* Hall, 1883b, p. 183; OD; Hamilton Gr., M. Dev., Leroy, N.Y., USA]. Zoarium encrusting. Monticules elevated, cluster of vesicles or stereom central; ring of larger zooecia with lunaria radially arranged. Autozooecia isolated by vesicular tissue at granular-prismatic basal layer. Autozooecia subcircular in cross section; walls thin, granular or granular-prismatic; distal and lateral parts commonly made of superimposed vesicle walls; diaphragms straight to curved; mural spines in some species. Lunarium in endozone and exozone, of dense hyaline calcite. Vesicles high blisters in endozone, becoming low blisters in exozone; walls and roofs thin, granular or granular-prismatic, small acanthostyles in vesicle walls, zones of thicker vesicle roofs local; vesicles small, subangular to subrounded in cross section. *Sil.-Dev.,* N.Am., Eu. ——Fig. 184,*1a–f.* **F. constricta* (Hall), holotype, NYSM 736; *a,* solid, elevated monticular center with lunaria radially arranged; ×10; *b,* subcircular autozooecia isolated by small subangular vesicles; tang. sec., ×30; *c,* hyaline lunarial deposit (lower right side of autozooecia) and granular vesicular tissue; tang. sec., ×50; *d,* granular-prismatic basal layer, autozooecia isolated by vesicular tissue; long. sec., ×30; *e,* autozooecia bounded by superimposed vesicle walls, hyaline lunarial deposit (left, center), vesicles with thin granular walls and roofs, small acanthostyle in vesicle walls (center); transv. sec., ×50; *f,* autozooecia isolated at basal layer by vesicular tissue, vesicles decrease in height outward in exozone; transv. sec., ×30.

Fistuliporidra Simpson, 1897, p. 606 [**Lichenalia tessellata* Hall & Simpson, 1887, p. 207; OD; Hamilton Gr., M. Dev., Genesee Valley, N.Y., USA]. Zoarium encrusting, monticules elevated; cluster of vesicular tissue central, lunaria radially arranged. Autozooecia partially isolated at basal layer by vesicular tissue. Autozooecia subcircular in cross section in exozone, narrowly isolated; walls thin, indistinctly laminated or granular. Superimposed vesicle walls making up lateral and distal zooecial walls. Diaphragms not seen. Lunaria in endozone and exozone, small, of dense hyaline calcite, short and barlike with little curvature. Vesicular tissue blisterlike or boxlike; vesicles decreasing in height outward in exozone; walls and roofs thin, granular or indistinctly laminated. *M.Dev.,* N.Am.——Fig. 183,*2a,b.* **F. tessellata* (Hall & Simpson), holotype, NYSM 5060/1; *a,* subcircular autozooecia with thin walls narrowly isolated by moderately large, thin-walled vesicles, light-colored lunarial deposit (upper left side of autozooecia); tang. sec., ×30; *b,* thin granular-prismatic basal layer, autozooecia isolated by vesicular tissue; oblique long. sec., ×30.

Fistuliramus Astrova, 1960b, p. 362 [**F. sinensis*; OD; U. Sil., Arctic Urals, USSR]. Zoarium ramose. Monticules with ring of larger zooecia; lunaria in part radially arranged. Autozooecia thin-walled in endozone, isolated by vesicular tissue; subcircular in cross section in exozone, narrowly isolated by vesicles; walls laminated; thick laminated lining in exozone, some mural tubuli in lining. Diaphragms closely spaced in outer endozone and exozone, thin, flat to concave. Lunaria in outer endozone and exozone, of light-colored and dense calcite. Vesicular tissue long blisters in endozone, becoming more subquadrate at zooecial-bend region, decreasing

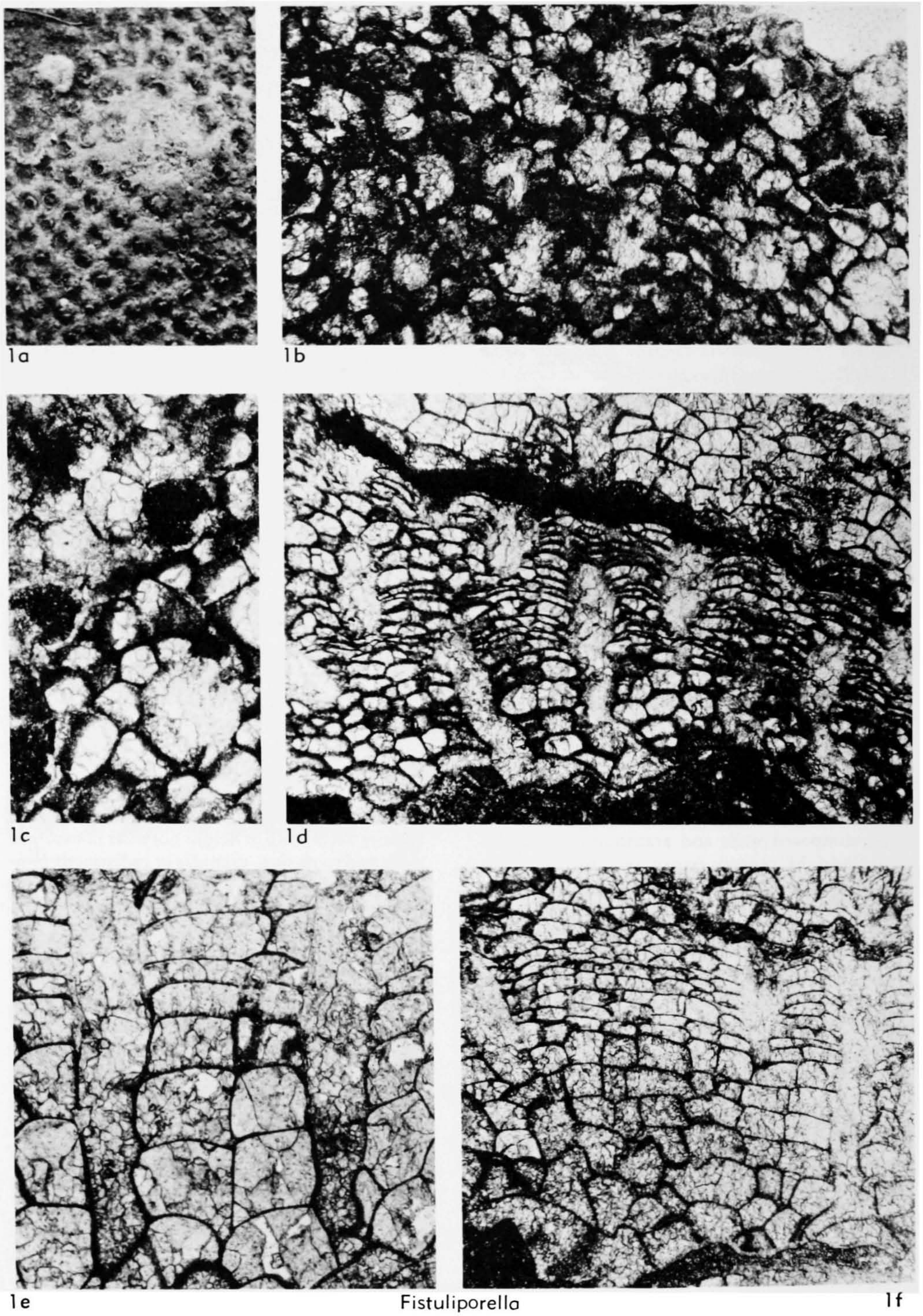


FIG. 184. Fistuliporidae (p. 395).

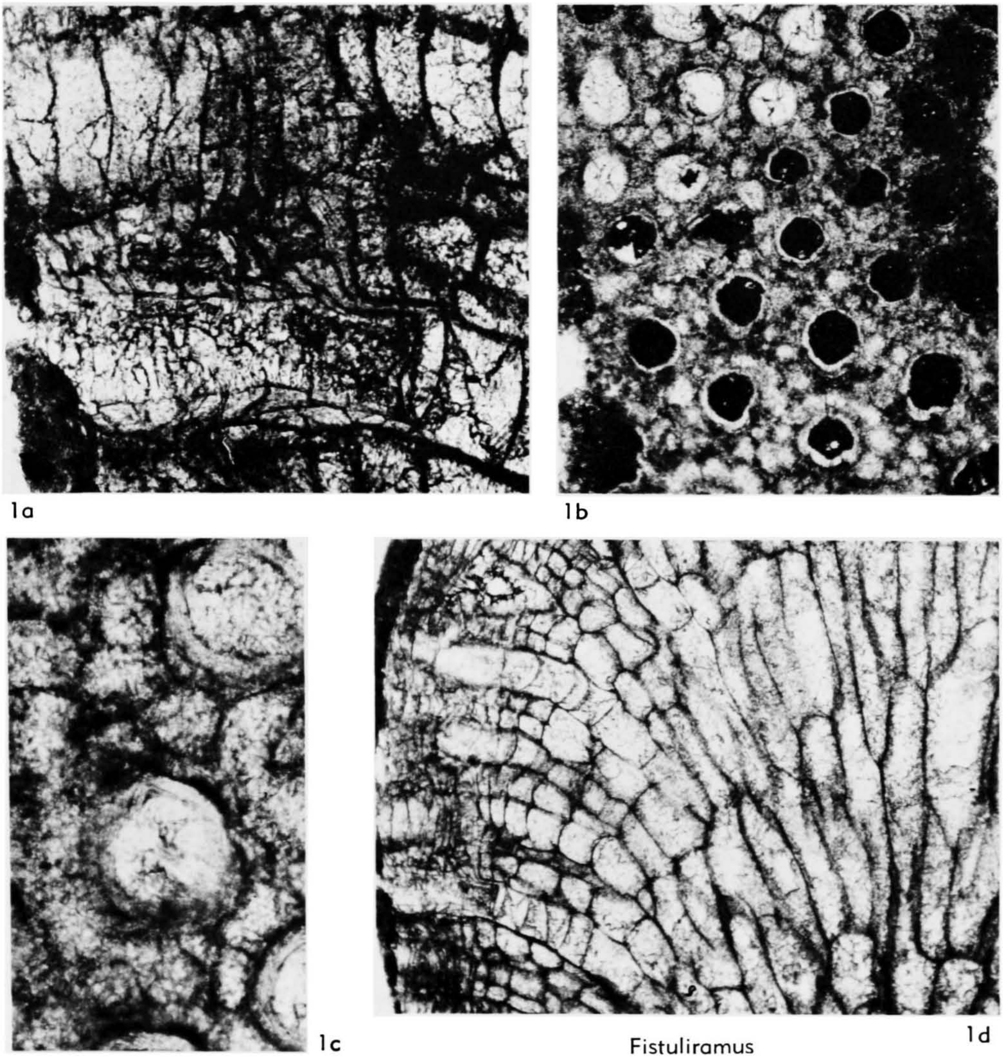


FIG. 185. Fistuliporidae (p. 395).

in height outward in exozone; walls and roofs laminated, containing small acanthostyles or tubuli. *U.Sil.-L.Dev.,* USSR.——FIG. 185,*1a–d.* **F. sinensis,* paratype, PIN 124-7/32; *a,* autozooecium with closely spaced diaphragms and laminated lining with tubules in living chamber (below, left), low, blisterlike vesicles with zone of thicker roofs (above, center); long. sec., ×100; *b,* autozooecia with light-colored lining and hyaline lunaria isolated by small subcircular vesicles; tang. sec., ×30; *c,* laminated autozooecial lining, light-colored lunaria, and small vesicles; tang. sec., ×100; *d,* thin-walled autozooecia and long, blisterlike vesicles in endozone (right), closely spaced diaphragms in inner exozone and decrease in vesicle height in exozone; long. sec., ×30.

Fistulocladia BASSLER, 1929, p. 49 [**F. typicalis*; OD; Perm., Noil Boewan, Timor]. Zoarium slender ramose; perpendicular branches form by encrusting main branch. Monticules flush, inconspicuous; lunaria not radially arranged. Central endozone a cylinder of narrow, round tubelike vesicles with flat roofs and cyclic zones of stereom. Autozooecia circular in cross section and narrowly isolated by stereom at origin on central cylinder; walls thick, granular-prismatic; basal diaphragms lacking, terminal diaphragms common; ovate in cross section in endozone and widely isolated by vesicles or stereom. Lunaria in endozone and exozone; dark distal layer continuing into dark zone in wall, proximal granular-prismatic layer thick, with irregular proximal projections in some. Vesicular tissue in small blisters; lower layer dark, granular, gran-

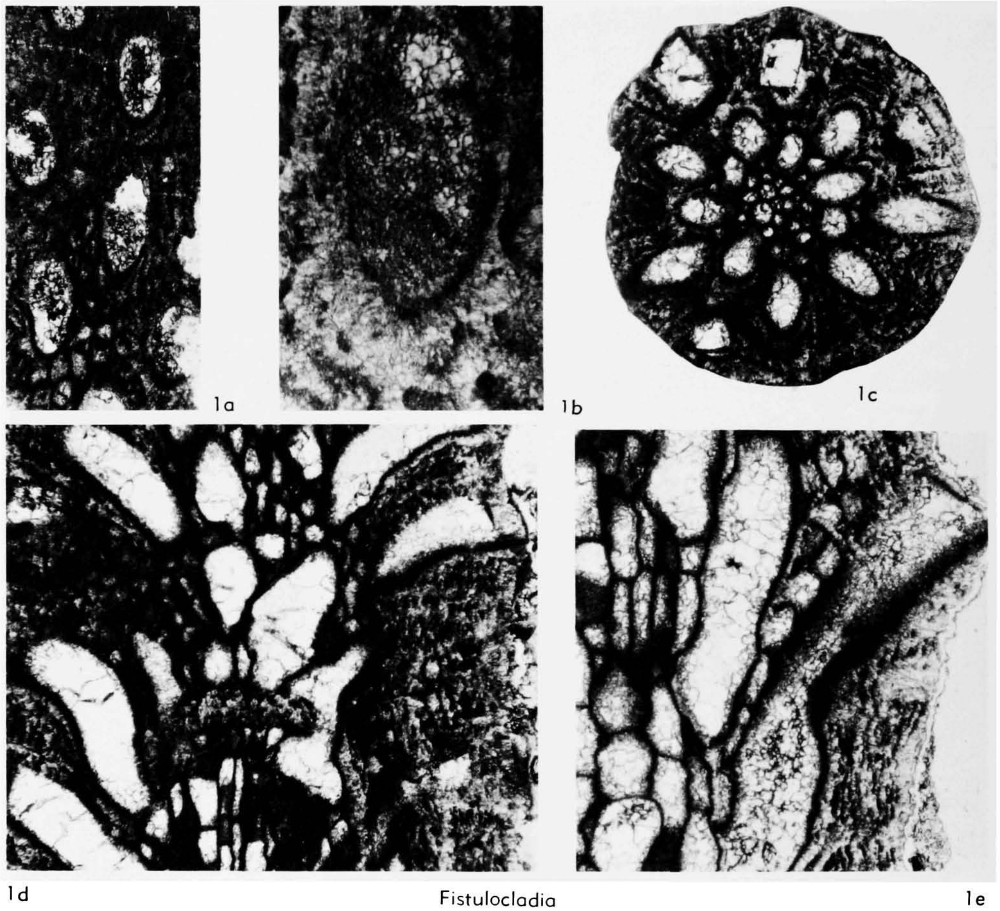


FIG. 186. Fistuliporidae (p. 397).

ular-prismatic layer light colored and with small tubuli; vesicle height very low in exozone, producing nearly solid stereom. *Perm.,* Timor.——FIG. 186,*1a–e.* **F. typicalis; a,* ovate autozooecia with lunaria (below) isolated by small vesicles and stereom; tang. sec., topotype, USNM 159745, ×27; *b,* granular-prismatic autozooecial wall, lunarium with thick granular-prismatic layer (below) and granular-prismatic stereom; tang. sec., topotype, USNM 159748, ×90; *c,* axial cylinder (center), autozooecia subcircular, narrowly isolated by vesicular tissue and with large lunaria in endozone, stereom in exozone; transv. sec., topotype, USNM 159744, ×27; *d,* axial cylinder of tubelike vesicles (below) and zone of stereom in axis, autozooecia budded from axial cylinder, low vesicle height in nearly solid stereom in exozone, thick terminal diaphragm (top, right); long. sec., topotype, USNM 159743, ×27; *e,* axial vesicles (top left) and autozooecia budded from axial cylinder (right and bottom), blisterlike vesicles and stereom, terminal diaphragm in autozooecium; long. sec., topotype, USNM 159746, ×45.

Fistulotrypa BASSLER, 1929, p. 48 [**F. ramosa*; OD; Perm., Basleo, Timor]. Zoarium ramose; monticules flush, center of stereom; peristomes elevated. Autozooecia in endozone contiguous; walls thin, granular; diaphragms few. Autozooecia in exozone isolated by vesicles; oval in cross section; diaphragms closely spaced. Wall with dark, granular, boundary zone and thick, granular-prismatic cortex. Lunaria in exozone; inconspicuous; dark, granular zone commonly not continuous into dark, zooecial boundary; distal granular-prismatic zone thick. Vesicles in outer endozone and exozone; low, broad blisters, large and subangular in tangential view, decreasing in height outward; stereom at surface; granular-prismatic structure with tubuli in vesicle roofs and stereom. *Perm.,* Timor.——FIG. 187,*2a–c.* **F. ramosa,* type, USNM 159822; *a,* dark granular boundary, granular-prismatic cortex and lunarium (lower side) in autozooecium; tang. sec., ×100; *b,* dark granular zooecial boundaries and subcircular vesicles; tang. sec., ×30; *c,* large,

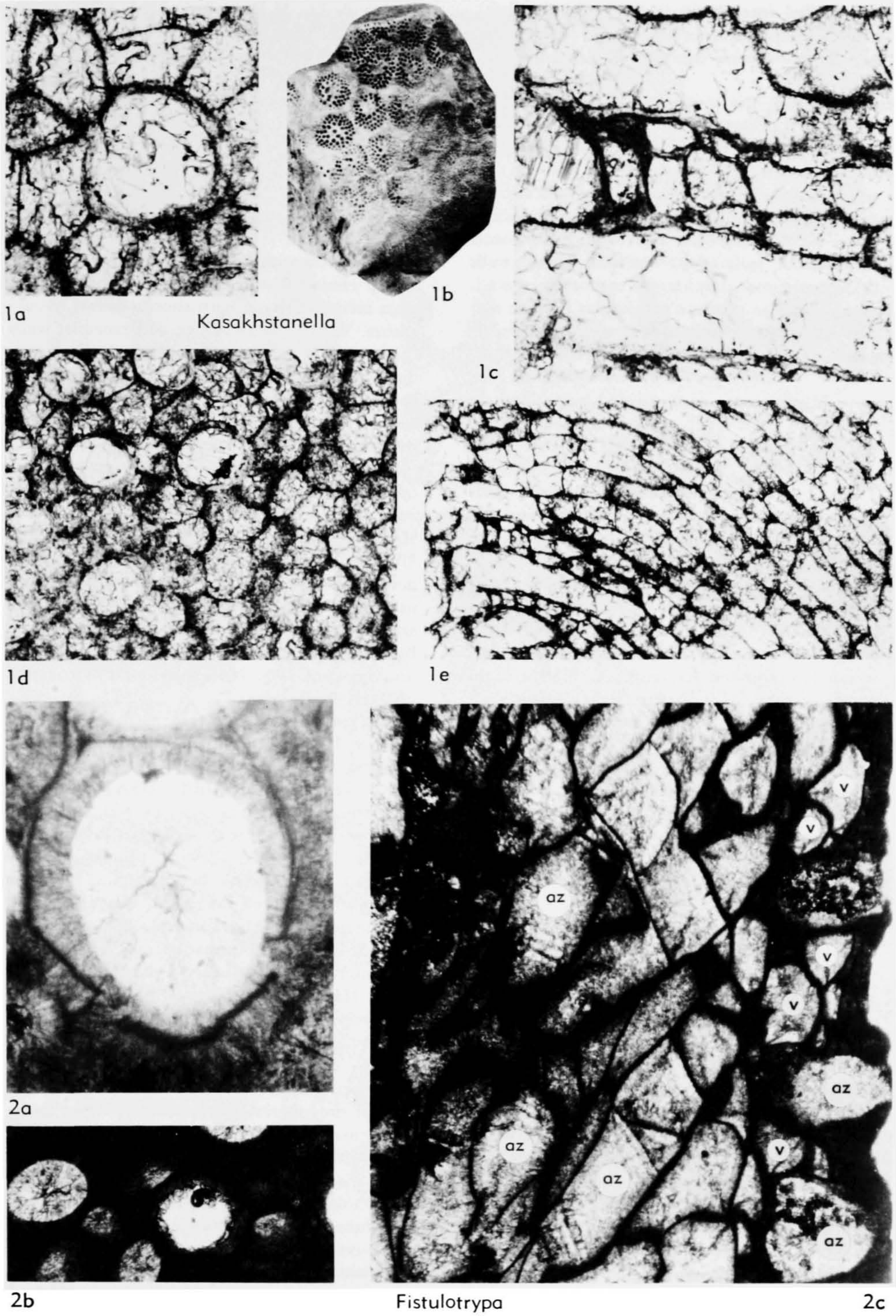


FIG. 187. Fistuliporidae (p. 398–400).

thin-walled autozooecia (az) in endozone (left), thicker-walled autozooecia (az) and vesicular tissue (v) in exozone (right); oblique long. sec., ×30.

Kasakhstanella NEKHOROSHEV, 1956a, p. 42 [**K. ramosa*; OD; Dev., D2^2, C. Kazakh., USSR]. Zoarium ramose, encrusting overgrowths. Monticules elevated; cluster of vesicular tissue in center and ring of larger zooecia with lunaria radially arranged. Large subhexagonal ridges in vesicular tissue surrounding each monticule. Autozooecia in endozone isolated by vesicular tissue; walls thin, laminated; diaphragms uniformly spaced. Autozooecia in exozone subcircular in cross section and isolated by vesicles; walls thin, laminated. Lunaria in endozone and exozone; thin, hyaline. Vesicular tissue in endozone and exozone; blisters high, decreasing in height in exozone; local zones of thicker vesicle roofs; laminated. *M.Dev.-U.Dev.,* USSR.——FIG. 187,*1a-e.* **K. ramosa,* paratype, USNM 158360; *a,* indistinctly laminated vesicle walls and autozooecium, hyaline lunarium (lower left); tang. sec., ×100; *b,* monticules surrounded by ridges forming a large subhexagon; ×2; *c,* laminated autozooecial walls, hyaline lunarial deposit, laminated vesicle walls and roofs; long. sec., ×100; *d,* monticular center (right), autozooecia with hyaline lunaria (near monticule), isolated by large vesicles; tang. sec., ×50; *e,* high, narrow vesicles in endozone (right), lower vesicles in exozone (left); long. sec., ×30.

Lichenotrypa ULRICH, 1886b, p. 23 [**L. cavernosa*; M; "U. Helderberg?," M. Dev., Falls of the Ohio, Jeffersonville, Ind., USA]. Zoarium encrusting; monticules flush, central cluster of vesicular tissue ringed by larger zooecia with lunaria radially arranged; peristome elevated; ridges in vesicular tissue in irregular curved to polygonal shapes surrounding most autozooecia. Autozooecia hemispherical in cross section, isolated by vesicles at granular-prismatic basal layer. Subcircular autozooecia with lunate to spinelike hyaline lunaria isolated by small subangular vesicles in exozone. Autozooecial boundary dark granular zone; cortex granular-prismatic. Diaphragms few. Vesicles in endozone and exozone; boxlike to low blisters, decreasing in height in exozone; thin stereom at surface; granular-prismatic. Large hyaline acanthostyles in vesicle walls or autozooecial walls; some sublunate and in position of lunarium. *M.Dev.,* N.Am.——FIG. 188,*1a,c,d.* **L. cavernosa*; *a,* monticular center (right), lunaria radially arranged, peristomes and irregular ridges on vesicular tissue; topotype, USNM 159812, ×10; *c,* subcircular autozooecia and large acanthostyles; tang. sec., topotype, USNM 159813, ×30; *d,* low blisterlike vesicles and large acanthostyles; long. sec., topotype, USNM 159813, ×30. ——FIG. 188,*1b,e,f. L.* sp. cf. *L. cavernosa,* Jeffersonville Ls., M.Dev., Ind., USA, SIUC 3007; *b,* large acanthostylelike lunaria; tang. sec., ×100; *e,* granular-prismatic vesicular tissue, tubuli in vesicle roofs; long. sec., ×100; *f,* autozooecia with lunaria and acanthostyles replacing lunaria isolated by small subangular vesicles; tang. sec., ×30.

Metelipora TRIZNA, 1950, p. 99 [**M. monstrata*; OD; L. Perm., Ural Mts., USSR]. Zoarium encrusting, discoidal. Monticules with central cluster of small vesicles surrounded by slightly larger zooecia with lunaria on side nearest monticular center. Autozooecia large, subcircular in cross section; lunaria with shorter radius of curvature. Vesicles in endozone and exozone; walls thick, roofs distantly spaced; superimposed, producing tubelike vesicles; small and subcircular in cross section. One to three vesicles isolating autozooecia in exozone. [Specimens of *Metelipora* were not available for study. V. P. NEKHOROSHEV informed me that existing thin sections of *Metelipora monstrata* TRIZNA, 1950 are thick and microstructure of the skeleton is unknown.] *?U.Carb., L.Perm.,* USSR.——FIG. 188,*2a,b.* **M. monstrata,* holotype, VNIGRI 2/135; *a,* autozooecia, indistinct wall structure, small tubelike vesicles; long. sec., ×40; *b,* rhombic arrangement of subcircular autozooecia isolated by vesicles, monticule in lower left, indistinct lunaria; tang. sec., ×40 (photographs courtesy of L. Nekhorosheva).

Odontotrypa HALL 1886, pl. 30 [**Lichenalia alveata* HALL, 1883b, p. 152; SD HALL & SIMPSON, 1887, p. xvii; M. Dev., Falls of the Ohio, Jeffersonville, Ind., USA]. Zoarium encrusting; monticules low, central cluster of solid vesicular tissue surrounded by ring of slightly larger zooecia with lunaria radially arranged. Autozooecia hemispherical in cross section at basal layer, isolated by vesicular tissue. Autozooecia subcircular in cross section in exozone. Lunarium in outer endozone and exozone. Vesicular tissue low blisters in endozone and exozone. [Holotype and available topotypes of *Odontotrypa alveata* (HALL) are silicified. This poorly known genus resembles *Buskopora* ULRICH, 1886 in many respects but lacks well-developed peristomes and deep inflection of the ends of the lunaria. With study of better material, it may prove to be a synonym of *Buskopora.*] *M.Dev.,* USA.——FIG. 189,*1a-d.* **O. alveata* (HALL); *a,* thin colony encrusting fenestrate bryozoan; holotype, WM 13991, ×1; *b,* monticules with lunaria radially arranged, autozooecia narrowly isolated; holotype, ×10; *c,* hemispherical autozooecia on basal layer, blisterlike vesicles; transv. sec., topotype, USNM 67689, ×30; *d,* subcircular autozooecia with lunaria narrowly isolated by vesicles; tang. sec., topotype, USNM 67689, ×30.

?Pholidopora GRUBBS, 1939, p. 552 [**P. concen-*

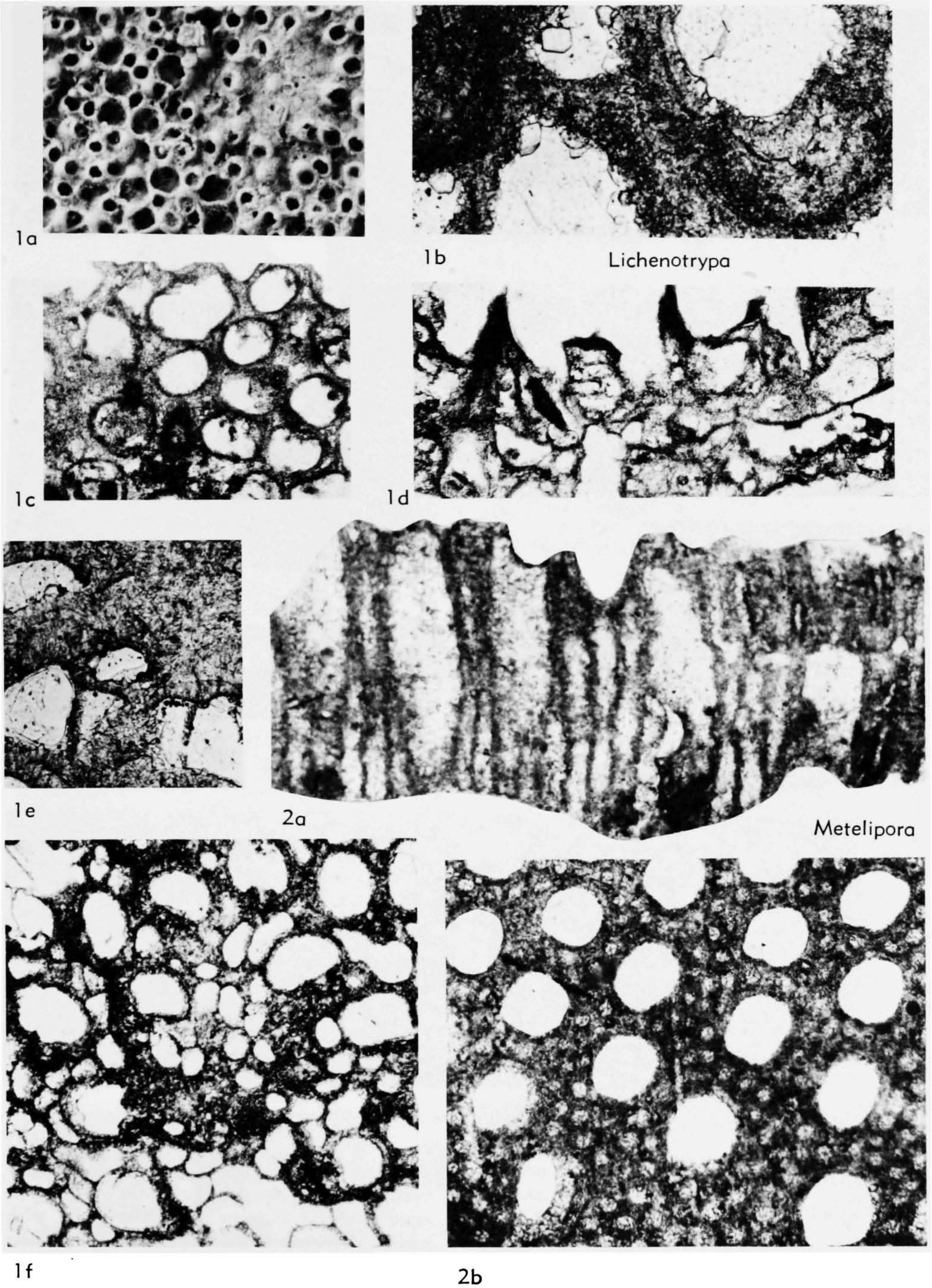


FIG. 188. Fistuliporidae (p. 400).

trica; OD; "Niagaran ls. nodules," M. Sil., Chicago, Ill., USA]. Zoarium encrusting; monticules depressed, cluster of vesicular tissue central, lunaria radially arranged. Autozooecia elongate with low peristomes and small, highly elevated lunaria; diaphragms closely spaced, concave. Vesicles isolating autozooecia. [The type specimens of *Pholidopora concentrica* are silicified and

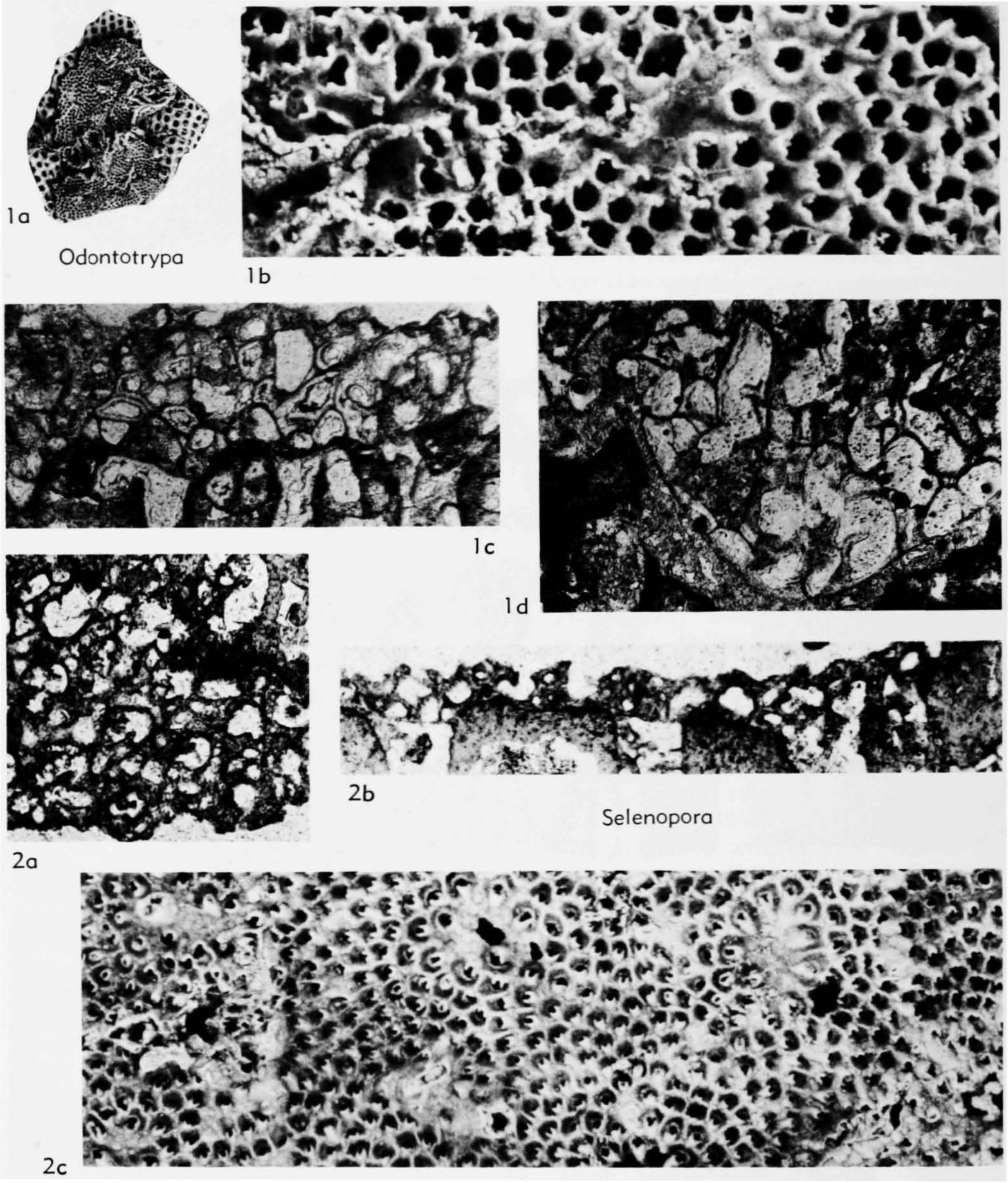


FIG. 189. Fistuliporidae (p. 400–404).

small. Virtually nothing is known of the internal anatomy of this genus, which is questionably placed in the Fistuliporidae.] *M.Sil.*, USA.——FIG. 190,*2*. **P. concentrica,* holotype, WM 46033; monticular center with lunaria radially arranged, elongate autozooecia, with highly elevated lunaria, isolated by vesicular tissue; ×10.

Pileotrypa HALL, 1886, pl. 30 [**Lichenalia denticulata* HALL, 1883a, pl. 24; SD HALL & SIMPSON, 1887, p. xvi; M. Dev., Falls of the Ohio, Jeffersonville, Ind., USA]. Zoarium encrusting; monticules elevated; lunaria highly elevated, radially arranged. Autozooecia isolated at basal layer by vesicular tissue, elongate; hemiphragms in outer endozone and exozone; lunarium large with markedly shorter radius of curvature. Vesicular tissue large, irregular blisterlike; no stereom. [Cotypes and available topotypes of *Pileotrypa denticulata* (HALL) are silicified and nothing is known of the microstructure.] *M.Dev.*, N.Am. ——FIG. 190,*1a–d*. **P. denticulata* (HALL); *a,* autozooecia widely isolated by vesicular tissue at basal layer; transv. sec., topotype, USNM 55071, ×30; *b,* monticule (lower right) with

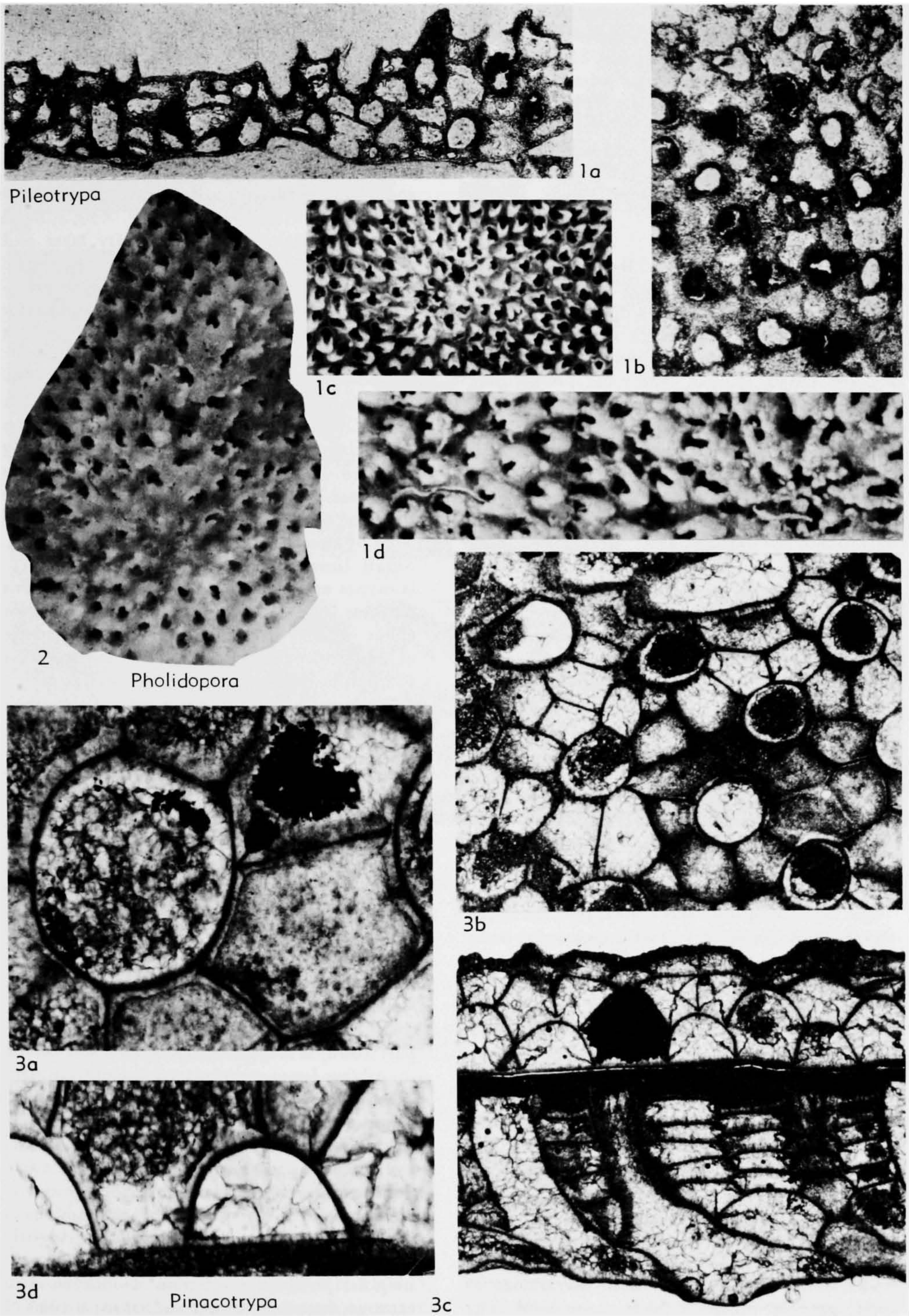


Fig. 190. Fistuliporidae (p. 400–404).

lunaria radially arranged, elongate autozooecia with large lunaria isolated by large subangular vesicles; tang. sec., topotype, USNM 55071, ×30; *c,* monticule with lunaria radially arranged; cotype, WM 13993, ×10; *d,* highly elevated, hood-shaped lunaria; cotype, WM 13993, ×20.

Pinacotrypa Ulrich in Miller, 1889, p. 315 [**Fistulipora elegans* Rominger, 1866, p. 122; OD; Hamilton Gr., M. Dev., Hamburg, N.Y., USA]. [=*Fistulicella* Simpson, 1897, p. 606; *Fistuliporina* Simpson, 1897, p. 555]. Zoarium encrusting. Basal layer thin, wrinkled; lower primary layer granular, upper layer granular-prismatic. Monticules flush, center with large vesicles. Autozooecia with peristome, circular, isolated by six to eight large polygonal vesicles in petal-like array around zooecia. Autozooecia with long recumbent portion, keel and sinus, erect in exozone; diaphragms sparse, thin. Autozooecial walls having granular boundary zone and granular-prismatic cortex; cortex in some with light-colored, pustulelike areas that form minute nodes on peristome. Vesicular tissue partly isolates zooecia at basal layer; vesicles becoming shorter and more regular outward in exozone, boxlike with superimposed walls, some walls compound, protruding as ridges above vesicle roofs at zoarial surface. Vesicle roofs flat, simple, at same level in adjacent vesicles. Small tubuli (?acanthostyles) in vesicle roofs (some appear porelike in tangential section). Lunaria poorly developed, slightly thicker than remainder of wall, or absent. [*Thallostigma plana* Hall, 1881, p. 187, the type species of *Fistulicella* Simpson, by original designation, does not differ significantly from *Pinacotrypa elegans* (Rominger). Therefore, *Fistulicella* Simpson is here considered to be a junior subjective synonym of *Pinacotrypa* Ulrich. *P. plana* has a weakly developed lunarium, or no lunarium, and minute pustules in the granular-prismatic cortex of autozooecial walls that can be expressed as protuberances on the peristome. *Thallostigma serrulata* Hall, 1883b, p. 185, the type species of *Fistuliporina* Simpson by original designation, does not differ significantly from *Pinacotrypa plana* or *P. elegans.* Thus, *Fistuliporina* Simpson, 1897, is here considered to be a junior subjective synonym of *Pinacotrypa* Ulrich. *Pinacotrypa serrulata* (Hall) has several zooecia with abundant, pustulelike, light-colored areas and a poorly developed lunarium or no discernable lunarium. In addition, *P. serrulata* may have operculumlike covers at the zooecial orifice.] *M.Dev.,* N.Am.——Fig. 190,*3a–d.* **P. elegans* (Rominger); *a,* dark granular zooecial boundary in subcircular autozooecia, granular-prismatic layer, compound construction of some vesicle walls, and vesicle roofs with minute tubuli; tang. sec., paralectotype, UMMP 6667-1, ×100; *b,* petal-like array of vesicles around subcircular autozooecia, poorly developed lunarium (thicker portion of autozooecial wall) on proximal (left) side of autozooecia; tang. sec., lectotype, UMMP 6667-3, ×30; *c,* basal layer and contiguous autozooecia in endozone, autozooecia isolated by low, boxlike vesicles in exozone (of lower encrusting sheet), hemispherical autozooecial cross section at basal layer and keel and sinus in outer endozone (in upper encrustation); long. sec. (below) and transv. sec. (above), lectotype, ×30; *d,* basal layer with dark, granular, primary layer and lighter colored, secondary, granular-prismatic layer; hemispherical and keel-and-sinus cross-sectional shapes in endozone, note discontinuity in granular layers in autozooecial walls (upper left); transv. sec., lectotype, ×100.

Selenopora Hall, 1886, pl. 25 [**Lichenalia circincta* Hall, 1883b, p. 153; M; M. Dev., Falls of the Ohio, Jeffersonville, Ind., USA]. Zoarium encrusting; monticules flush, lunaria radially arranged. Lunaria highly elevated; subcircular to polygonal pattern of ridges on vesicular tissue surround each autozooecium. Autozooecia isolated by small vesicles in endozone and exozone. Small lunaria indent autozooecial cavity. [Cotypes and available topotypes of *Selenopora circincta* (Hall) are silicified and little is known about internal anatomy of this genus. Presence of subcircular ridges in the vesicular tissue that surrounds each autozooecium distinguishes *Selenopora* from *Buskopora* Ulrich. The small lunarium with inflecting ends separates it from *Favicella* Hall & Simpson.] *M.Dev.,* USA.——Fig. 189,*2a–c.* **S. circincta* (Hall); *a,* elongate autozooecia, with indenting lunaria, isolated by vesicles; tang. sec., topotype, USNM 2935, ×30; *b,* autozooecia isolated by small vesicles at basal layer; transv. sec., topotype, USNM 2935, ×30; *c,* monticules with lunaria radially arranged, subcircular to polygonal ridges on vesicles surround autozooecia; cotype, WM 13975, ×10.

Strotopora Ulrich in Miller, 1889, p. 326 [**S. foveolata* Ulrich, 1890, p. 487; SD Ulrich, 1890, p. 383; Keokuk Gr., L. Miss., Bentonsport, Iowa, Warsaw, Ill., USA]. Zoarium ramose to subfrondose, endozone commonly crushed; anastomosing branches; encrusting overgrowths. Monticules elevated, lunaria radially arranged. Autozooecia subcircular in cross section, isolated by vesicular tissue; wall laminated, boundary dark to obscure, tubuli in cortex perpendicular to boundary. Diaphragms few. Hemiphragms in exozone; thick and spinelike to platelike. Lunaria in outer endozone and exozone; hyaline with irregular proximal projections. Gonozooecia in exozone; funnel- to blister-shaped expansions of autozooecia; subrounded to polygonal in cross section; roofs with abundant tubuli. Vesicular tissue in endozone and exozone; vesicles blisterlike and polygonal to subrounded in cross sec-

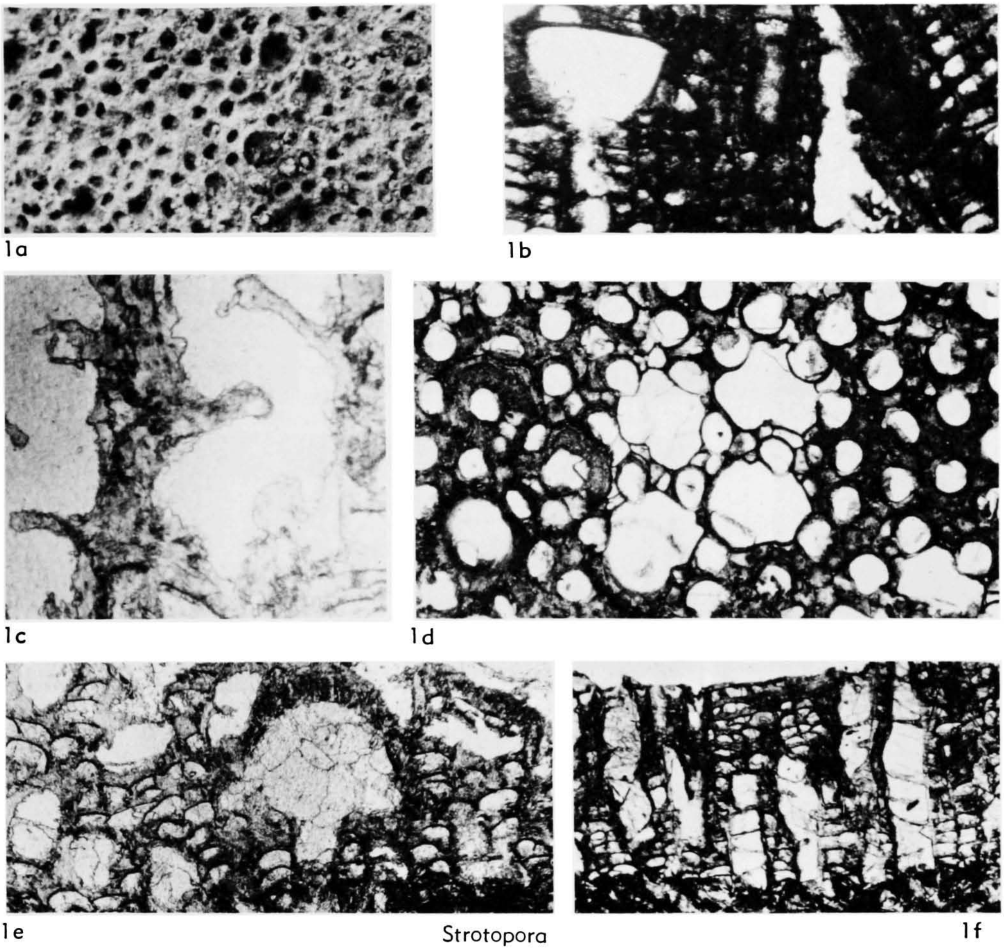


FIG. 191. Fistuliporidae (p. 404).

tion; decreasing in height in exozone; zones of thick vesicle roofs or stereom. Acanthostyles in laminated vesicle walls and roofs; some appearing porelike in tangential section. [*Strotopora* differs from the closely related genus *Cliotrypa* ULRICH & BASSLER by having gonozooecia that are more polygonal in cross section and vesicular tissue throughout the endozone. Crushed endozones in some zoaria may indicate that they were originally hollow ramose.] *L.Miss.*, N.Am.——FIG. 191,*1a–f*. **S. foveolata*; *a,* monticule (lower right), autozooecia isolated by vesicular tissue, and large, open (broken or eroded) gonozooecia; topotype, USNM 55060, ×10; *b,* funnel-shaped gonozooecium and vesicular tissue with acanthostyles; long. sec., topotype, USNM 159815, ×30; *c,* hemiphragms in autozooecia; transv. sec., "topotype" (Warsaw, Ill.), USNM 159795, ×100; *d,* gonozooecia, one with shelflike partition (upper left), hyaline lunaria in autozooecia, stereom with acanthostyles; tang. sec., topotype, USNM 159814, ×20; *e,* blisterlike gonozooecium having thick roof with acanthostyles, blisterlike vesicular tissue; transv. sec., "topotype," USNM 159795, ×30; *f,* autozooecia with hemiphragms and diaphragms, blisterlike vesicles with zones of thicker vesicle roofs; long. sec., topotype, USNM 159814, ×20.

Family RHINOPORIDAE
Miller, 1889

[Rhinoporidae MILLER, 1889, p. 290]

Zoaria thin; encrusting or bifoliate fronds. Monticules lacking. Autozooecia elongate in cross section, with hyaline lunaria; isolated at surface by vesicular tissue. Tunnels covered by rounded roof on vesicular tissue; standing as elevated, anastomosing ridges on zoarial surface. Walls laminated or granular-

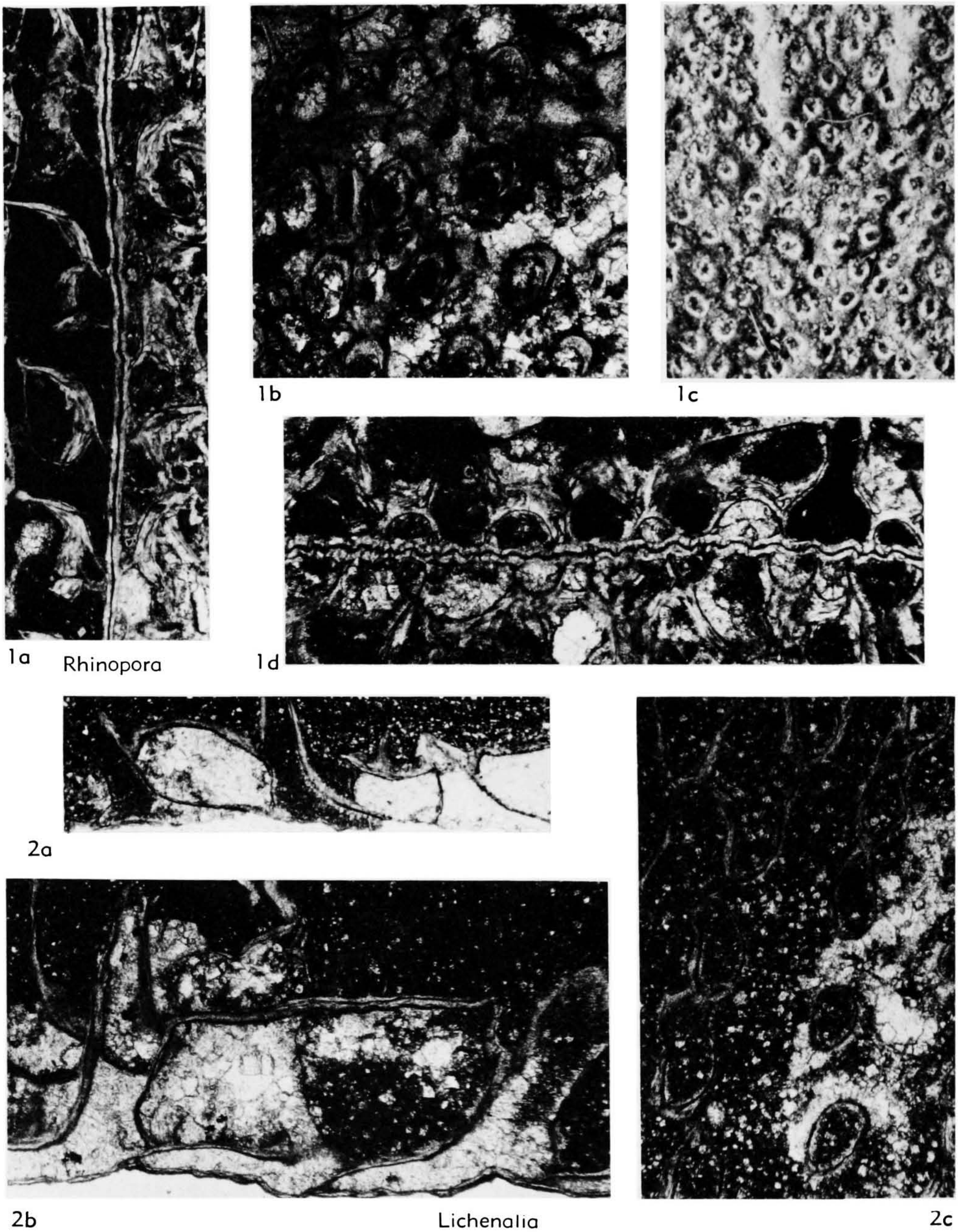


Fig. 192. Rhinoporidae (p. 406–407).

prismatic. Autozooecia narrowing from endozone to exozone, with semirecumbent distal spur in endozone. Vesicular tissue in outer endozone and exozone; large blisters; generally only one vesicle high. *L.Sil.-M.Sil.*

Characters of particular importance are: few, large vesicles; hyaline lunarium; tunnels; and lack of monticules and acanthostyles.

Rhinopora Hall in Silliman, Silliman, & Dana, 1851, p. 399 [**R. verrucosa* Hall, 1852, p. 48; SD; Clinton Gr., Sil., Hill Mill, N.Y., USA].

Zoarium bifoliate fronds. Lunaria highly elevated. Mesotheca thick, crenulated; median layer dark and poorly laminated to granular-prismatic layers light colored. Autozooecia short, almost completely contiguous at mesotheca; hemispherical in cross section; keel and sinuses in outer endozone. Diaphragms lacking. Wall indistinctly laminated. Large hyaline lunarium in exozone. Large blisterlike vesicles isolating autozooecia in exozone; laminated with tubuli in vesicle roofs. *L.Sil.*, E.N.Am.——Fig. 192,*1a–d*. **R. verrucosa*; *a,* trilayered mesotheca, distal prong on autozooecia in endozone, hyaline lunaria and laminated walls and large blisterlike vesicles; long. sec. of specimen from Ohio, USNM 79326, ×30; *b,* elongate autozooecia with laminated walls and hyaline lunaria isolated by vesicles, branched tunnel in exozone; tang. sec., USNM 79326, ×30; *c,* elevated lunaria and elevated anastomosing covered tunnels; lectotype, AMNH 1492/2-1, ×10; *d,* thick, crenulated mesotheca, hemispherical autozooecia in endozone; transv. sec., USNM 79326, ×30.

Lichenalia Hall in Silliman, Silliman, & Dana, 1851, p. 401 [**L. concentrica* Hall, 1852, p. 171; SM; Rochester Sh., M. Sil., Lockport, N.Y., USA]. Zoarium encrusting. Lunaria highly elevated. Autozooecia with long recumbent portion on laminated basal layer; walls thin, laminated. Diaphragms few. Lunaria hyaline; variable in size and shape. Large blister- to boxlike vesicles in outer endozone and exozone; partly isolating autozooecia; thick, laminated roofs with indistinct tubuli. *M.Sil.*, E.N.Am., Eu.——Fig. 192,*2a–c*. **L. concentrica*; *a,* autozooecia elevated above large blisterlike vesicles; long. sec., topotype, USNM 159817, ×20; *b,* thin laminated basal layer (below), recumbent autozooecia with distal spur in endozone, thin diaphragm, large laminated vesicles; long. sec., topotype, USNM 159816, ×30; *c,* elongate autozooecia isolated by vesicular tissue and tunnel (filled with clear calcite); tang. sec., topotype, USNM 159816, ×30.

Family BOTRYLLOPORIDAE
Miller, 1889

[Botrylloporidae Miller, 1889, p. 290]

Zoaria encrusting circular discs with central monticule or encrusting sheets of coalesced discs. Primary and, in some forms, secondary and tertiary elevated fascicles of two rows of small autozooecia radiating from depressed central region of monticule. Vesicular tissue in interfascicle areas, monticular center, and coalesced margins of monticules. Walls laminated. No lunaria or acanthostyles. Proximal hemiseptum at zooecial bend; diaphragms few, thin. *M.Dev.*

Characters of particular importance are: radiating fascicles of autozooecia; fascicles of two rows of autozooecia; narrow, long autozooecia; large vesicles; proximal hemiseptum; and lack of acanthostyles.

Botryllopora Nicholson, 1874a, p. 133 [**B. socialis* Nicholson, 1874c, p. 160; SM; Hamilton F., M. Dev., Arkona, Ont., Can.]. Zoarium encrusting, single disc or multiple, coalesced discs each with depressed central monticule. Approximately 10 primary, raised fascicles of autozooecia radiating from central depressed area; secondary and tertiary fascicles in larger zoaria. In each fascicle, an elevated dense, light-colored, median rib separates two rows of zooecia. Autozooecia small, ovate in cross section, with few thin diaphragms; proximal hemiseptum at zooecial bend. Walls transversely laminated; minute porelike structures perpendicular to laminae. Vesicular tissue from basal layer to surface of colony in monticular centers, interrays, and coalesced margins of multimonticular colonies. Vesicles short, wide, blisterlike, and polygonal in cross section to boxlike and subcircular. Monticular vesicles larger than interray vesicles; vesicles at coalesced margins very large. Vesicle roofs thicker and nearly at same level near zoarial surface. Vesicles longitudinally laminated; laminae lapping distally on autozooecial walls. *M.Dev.*, E.N. Am.——Fig. 193,*1a–e*. **B. socialis*; all but specimen in *e* from "Widder Beds"; *a,* fascicle with two rows of autozooecia and median rib (above), laminated wall microstructure and vesicular tissue (below); tang. sec., USNM 66192, ×100; *b,* small, coalescing discoidal colonies; USNM 159797, ×1; *c,* monticular center and radiating autozooecia; tang. sec., USNM 159796, ×20; *d,* fascicles of autozooecia and large blisterlike vesicles between discoidal monticules; oblique transv. sec., USNM 159798, ×20; *e,* monticular center with vesicles flanked by fascicles of autozooecia; long. sec., topotype, USNM 96862, ×30.

Family ACTINOTRYPIDAE
Simpson, 1897

[Actinotrypidae Simpson, 1897, p. 479]

Zoaria bifoliate or encrusting. Autozooecia isolated by vesicular tissue; granular-prismatic structure. Lunaria lacking. Acanthostyles in autozooecial walls inflecting autozooecial cavity, producing petaloid appearance. *L.Miss., Perm.*

Characters of particular importance are autozooecia isolated by vesicles; large acan-

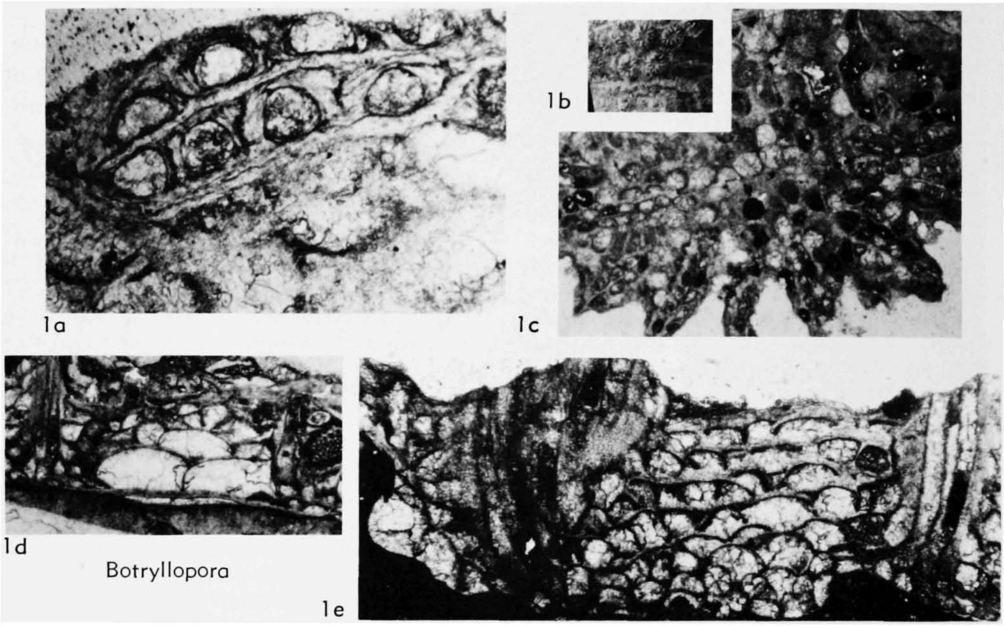


FIG. 193. Botrylloporidae (p. 407).

thostyles (canaliculi) indenting autozooecia, small acanthostyles in vesicle roofs, and no lunaria.

Actinotrypa ULRICH in MILLER, 1889, p. 291 [**Fistulipora peculiaris* ROMINGER, 1866, p. 123; OD; Keokuk Gr., L. Miss. (Osag.), La Grange, Mo., USA]. Zoarium bifoliate or encrusting. Monticules raised, with central cluster of vesicular tissue and encircling ring of slightly larger zooecia. Basal layer granular-prismatic. Mesotheca thin to thick; central granular layer dark, flanking granular-prismatic layers lighter colored. Autozooecia with long recumbent portion in endozone, erect in exozone, basically circular in cross section but idented by 5 to 11 acanthostylelike septa (canaliculi) extending through exozone; canaliculi centers granular to hyaline, with indistinct laminated sheath; diaphragms few and thin; funnel-cystiphragms off center. Autozooecia isolated by blisterlike vesicular tissue with granular inner and granular-prismatic outer layer. Vesicle walls and roofs one thick curved plate; zones of thicker roofs local; roofs with small acanthostyles expressed as bumps on surface. *L.Miss.(Osag.),* C.N.Am.——FIG. 194,*1a–e*. **A. peculiaris* (ROMINGER); *a,* autozooecia with peristomes and canaliculi isolated by vesicular tissue with projecting acanthostyles; paralectotype, UMMP 6409-7, ×9; *b,* dark vesicle walls, vesicle roofs with obscure acanthostyles, and indented autozooecia; tang. sec., lectotype, UMMP 6409-3, ×30; *c,* crushed endozone with obscure mesotheca, recumbent autozooecium (right) in endozone, blisterlike vesicular tissue with thick roofs near surface, obscure acanthostyles in vesicle roofs; long. sec., lectotype, ×30; *d,* granular- to hyaline-centered acanthostylelike canaliculi in autozooecial wall (left) and small acanthostyles in vesicle roof (right); tang. sec., topotype, USNM 97238, ×100; *e,* well-developed indenting acanthostylelike canaliculi, some with hyaline centers, dark, curved vesicle walls and dense vesicle roofs; tang. sec., specimen from Keokuk F., L. Miss. (Osag.), Iowa, USA, USNM 159761, ×30.

Actinotrypella GORYUNOVA, 1972, p. 149 [**A. mira*; OD; Sebisurkhskaya suite, L. Perm., Darvaz Ra., USSR]. Zoarium bifoliate, lenticular in cross section, parallel sided, ribbonlike, branched in some. Monticules lacking. Mesotheca thin, trilayered. Autozooecia isolated by dense stereom in exozone, in ranges and rows that intersect diagonally. Perforated operculum in some zooecia. Autozooecia recumbent at mesotheca, short proximal hemiseptum at zooecial bend, erect in exozone. Seven to 10 acanthostyles (canaliculi) in each autozooecium in exozone inflecting living chamber as would septa; having hyaline core and laminated sheath. Vesicular tissue small, blisterlike vesicles in endozone; nearly solid stereom in exozone. Small acanthostyles in thick vesicle roofs and stereom. *L.Perm.,* USSR.——FIG. 195,*1a–d*. **A. mira,* holotype, PIN 2351/418; *a,* hemispherical autozooecia on mesotheca, vesicles in endozone, stereom in exozone; transv. sec., ×10; *b,* trilayered mesotheca,

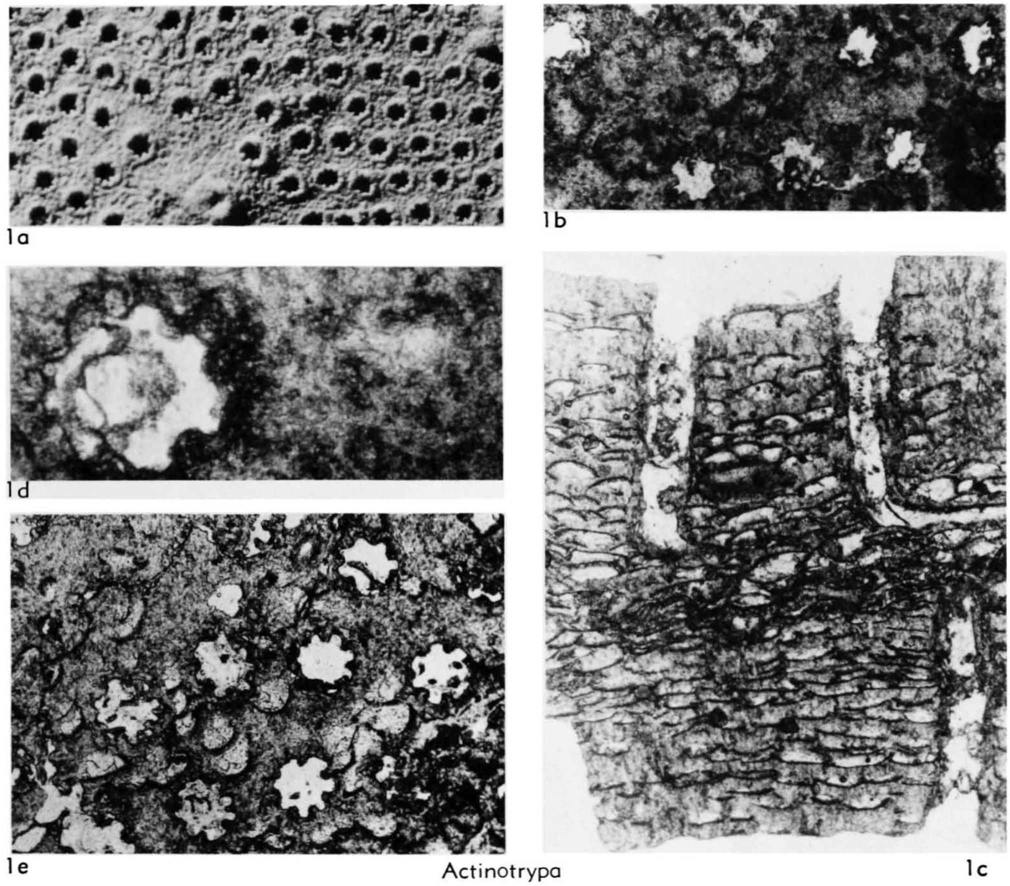


FIG. 194. Actinotrypidae (p. 408).

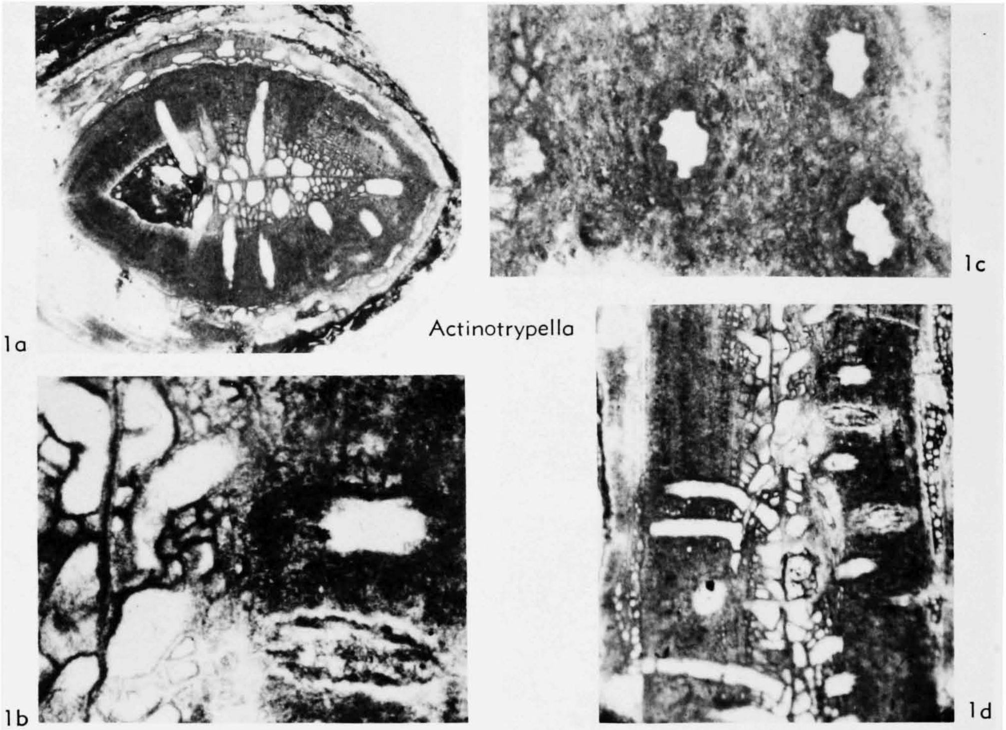
autozooecium with short recumbent portion and hemiseptum at zooecial bend (upper left), vesicles in endozone; long. sec., ×30; *c,* autozooecia indented by canaliculi and widely isolated by stereom with tubules; tang. sec., ×40; *d,* autozooecia partially isolated by vesicles in endozone, isolated by stereom in exozone; long. sec., ×10 (photographs in *a,c,d* courtesy of R. V. Goryunova, in *b,* courtesy of Alan Horowitz).

Epiactinotrypa KISELEVA, 1973, p. 68 [**E. flosculosa*; OD; Chandalazy suite, U. Perm., Partizanskiy distr., Maritime Terr., USSR]. Zoarium encrusting. Autozooecial apertures with peristome, isolated in exozone by vesicular tissue, 12 to 16 acanthostylelike canaliculi in exozone inflecting living chamber. Monticules lacking. Autozooecia recumbent in endozone, proximal hemiseptum at zooecial bend, erect with sparse, thin diaphragms in exozone. Small, angular vesicles isolating autozooecia. Vesicle walls straight, thin to thick, commonly superimposed; roofs flat to curved, thin; boxlike vesicles wider than high. Local zones of thicker roofed vesicles. *U.Perm.,* USSR.——FIG. 195,*2a,b.* **E. flosculosa,* holotype, PGU 187/48, drawings made from KISELEVA, 1973, pl. 6, fig. 2; *a,* tubular autozooecia isolated by boxlike to blisterlike vesicles, autozooecium budded on vesicular tissue (left); long. sec., ×25; *b,* subcircular autozooecia indented by acanthostyles (canaliculi), isolated by small subangular vesicles; tang. sec., ×50.

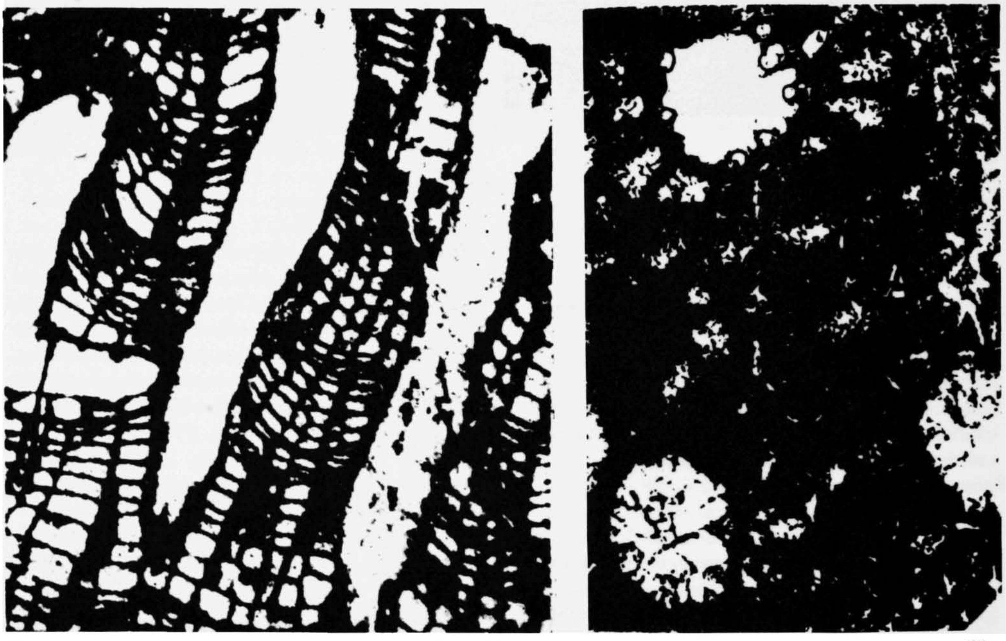
Family HEXAGONELLIDAE
Crockford, 1947

[*nom. transl.* BASSLER, 1953, p. G87, *ex* Hexagonellinae CROCKFORD, 1947, p. 7]

Zoaria if bifoliate, then frondose or narrow and regularly to irregularly branched or cribrate; if trifoliate, then regularly or irregularly branched; if multifoliate, then with bifoliate branches radiating from multifoliate center of colony. Monticules subcircular, elongate, or absent. Some genera with noncelluliferous,



Actinotrypella



Epiactinotrypa

FIG. 195. Actinotrypidae (p. 408–409).

solid branch margins or with a hexagonal pattern of ridges in vesicular tissue surrounding each monticule. Symmetrical arrangement of lunaria on branches in many genera. Mesotheca thin, trilayered; median tubules rare. Few, short, longitudinal ridges on mesotheca in a few genera. Autozooecia recumbent on mesotheca, in endozone hemispherical in cross section; erect in exozone and circular in cross section. Autozooecia clavate to teardrop shaped on mesotheca in a few genera; partly contiguous to isolated by vesicular tissue at mesotheca. Distal hemiseptum at zooecial bend in one genus; diaphragms absent or few. Walls granular-prismatic or laminated. Lunaria well developed to inconspicuous; granular-prismatic or hyaline or laminated. Vesicular tissue low blisters; zones of stereom or solid stereom in exozone; many genera with small acanthostyles in vesicle roofs or stereom. *L.Dev.-U.Perm.*

Characters of particular importance are: bifoliate, trifoliate, or multifoliate colonies; vesicular tissue in endozone; zones of stereom or solid stereom in exozone; lunaria; and small acanthostyles in vesicle roofs and stereom.

Hexagonella WAAGEN & WENTZEL, 1886, p. 911 [**H. ramosa*; SD NICKLES & BASSLER, 1900, p. 291; *Productus* Ls., Perm., Salt Ra., Pak.]. Zoarium bifoliate, compressed to subcylindrical. Monticules flush, central cluster of vesicular tissue and radiating rows of autozooecia with lunaria radially arranged. Each monticule surrounded by elevated hexagonal pattern of ridges in vesicular tissue. Mesotheca thin, straight, granular in middle endozone; thicker, trilayered, with granular central layer and granular-prismatic outer layers in lateral endozone. Autozooecia recumbent, widely isolated by vesicular tissue from mesotheca to zoarial surface. Wall granular-prismatic; diaphragms sparse, planar. Lunaria from outer endozone to zoarial surface; proximal layer thick, granular-prismatic; dark central zone not continuous into zooecial boundary in some autozooecia. Vesicles large, irregular in endozone, boxlike in inner exozone, blisterlike and low in outer exozone. Zones of thicker vesicle roofs and stereom at surface; granular-prismatic; tubuli in vesicle roofs and stereom. Vesicles small, subangular in cross section. *Perm.,* Asia, Australia. ——FIG. 196,*2a–d*. **H. ramosa*; Kalabagh Mbr., Wargal Ls., Salt Ra.; *a,* solid monticular centers, hexagonal ridge surrounds each monticule; USNM 159831, ×1.7; *b,* subcircular autozooecia with lunaria, isolated by small subangular vesicles; tang. sec., USNM 159829, ×30; *c,* thin mesotheca in central endozone, thick mesotheca in lateral endozone (right), autozooecia isolated at mesotheca by vesicular tissue, vesicle height decreases outward in exozone, sparse diaphragms in autozooecia; transv. sec., USNM 159833, ×30; *d,* autozooecium (upper), cycles of decreasing vesicle height upward in exozone, thin zones of stereom; long. sec., USNM 159832, ×30.

Ceramella HALL & SIMPSON, 1887, p. xix [**C. scidacea*; OD; Hamilton Gr., M. Dev., Cayuga Lake, Darien Center, N.Y., USA] [=*Caramella* MOROZOVA, 1960, p. 87, incorrect subsequent spelling]. Zoarium bifoliate fronds. Monticules elongate, depressed, with center of vesicular tissue; zooecia larger around margin. Mesotheca thin; central zone dark and outer layers laminated. Autozooecia hemispherical in cross section in endozone, partially isolated, some with keel and sinus; recumbent portion long; slightly oblique at zoarial surface; diaphragms few; walls with dark, thin boundary and laminated cortex. Lunaria in exozone; radius of curvature short; laminated, with thick, light-colored distal layer. Vesicular tissue in endozone and exozone; vesicles blisterlike, of moderate size, thin stereom at surface; isolating autozooecia in exozone; laminated; tubuli in vesicle roofs. *M.Dev.,* N.Am. ——FIG. 196,*1a–e*. **C. scidacea*; *a,* bifoliate frondose zoarium; lectotype, NYSM 623, ×1; *b,* elongate, depressed monticule; lectotype, ×10; *c,* pyriform autozooecia (lunaria to bottom) isolated by moderately large vesicles; tang. sec., paralectotype, NYSM 622, ×30; *d,* autozooecia partly isolated at mesotheca, blisterlike vesicles in endozone and exozone, monticule (upper left); transv. sec., lectotype, ×30; *e,* undulatory mesotheca, long recumbent portion of autozooecia, vesicles in exozone isolate autozooecia; long. sec., lectotype, ×30.

Coscinium KEYSERLING, 1846, p. 191 [**C. cyclops*; SD ULRICH, 1884, p. 38; L. Perm., Timan, USSR]. Zoarium bifoliate, cribrate. Autozooecia with peristome and lunarium, isolated at surface by stereom. Mesotheca trilayered; central zone granular and outer layers granular-prismatic; few, short longitudinal ridges on mesotheca. Autozooecia recumbent, in rows at mesotheca; hemispherical in cross section, some with keel and sinuses; teardrop shaped and mostly contiguous at contact with mesotheca. Diaphragms sparse. Autozooecial walls with granular boundary and granular-prismatic cortex. Lunaria in outer endozone and exozone; granular-prismatic. Vesicular tissue forming small, low blisters; stereom through most of exozone; some discontinuous compound range walls with dark granular boundary; numerous tubuli in vesicle roofs and stereom. *Perm.,* USSR.——FIG. 197,*1a–f*. **C. cyclops,* paratype, USNM 171739; *a,* dark, granular, autozooecial boundary continuous into granular layer in lunarium (below); tang. sec., ×100; *b,* elongate to circular autozooecia isolated by vesicular tissue; tang. sec., ×30; *c,* mesotheca, stereom with tubuli, terminal diaphragm in

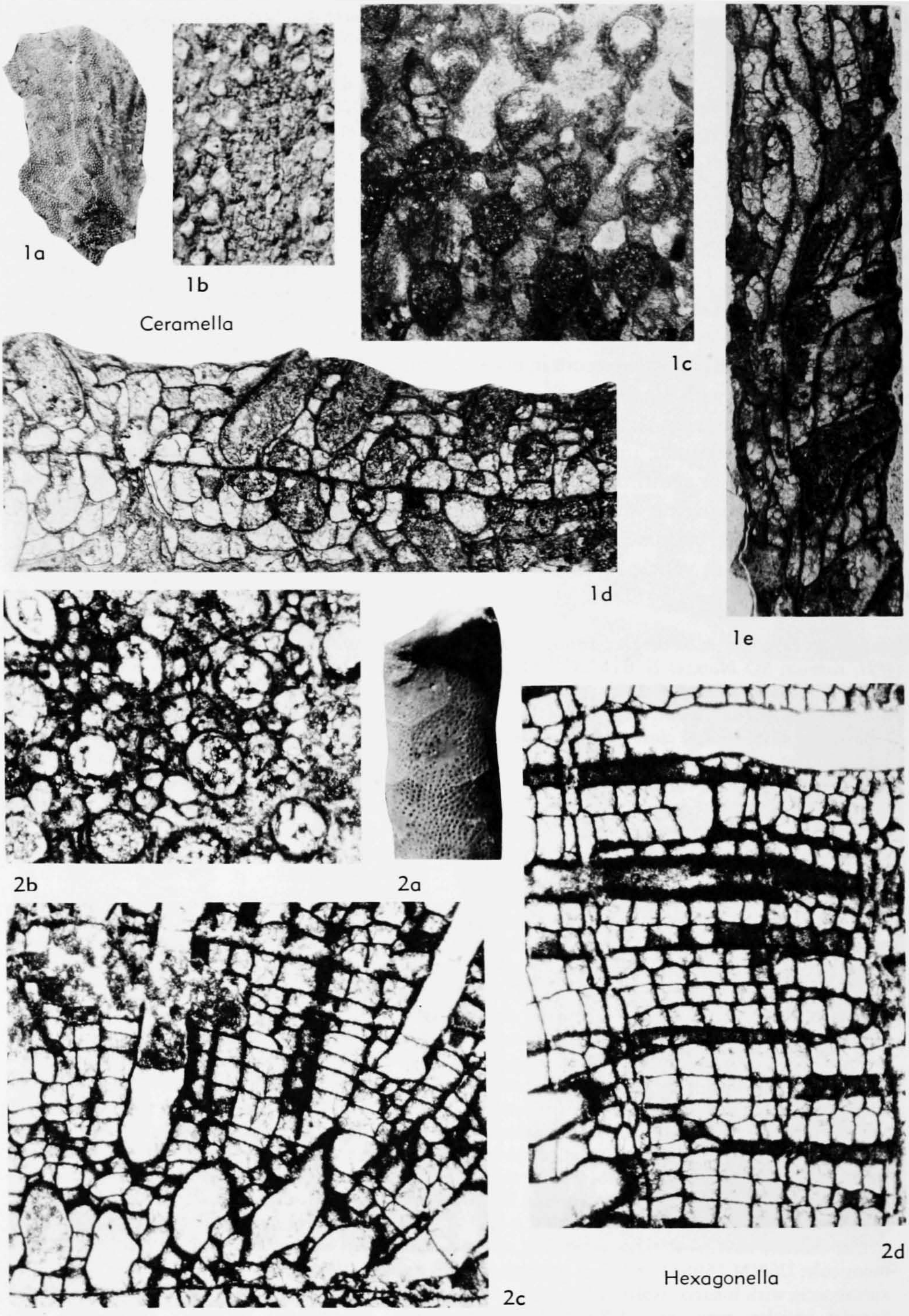


FIG. 196. Hexagonellidae (p. 411).

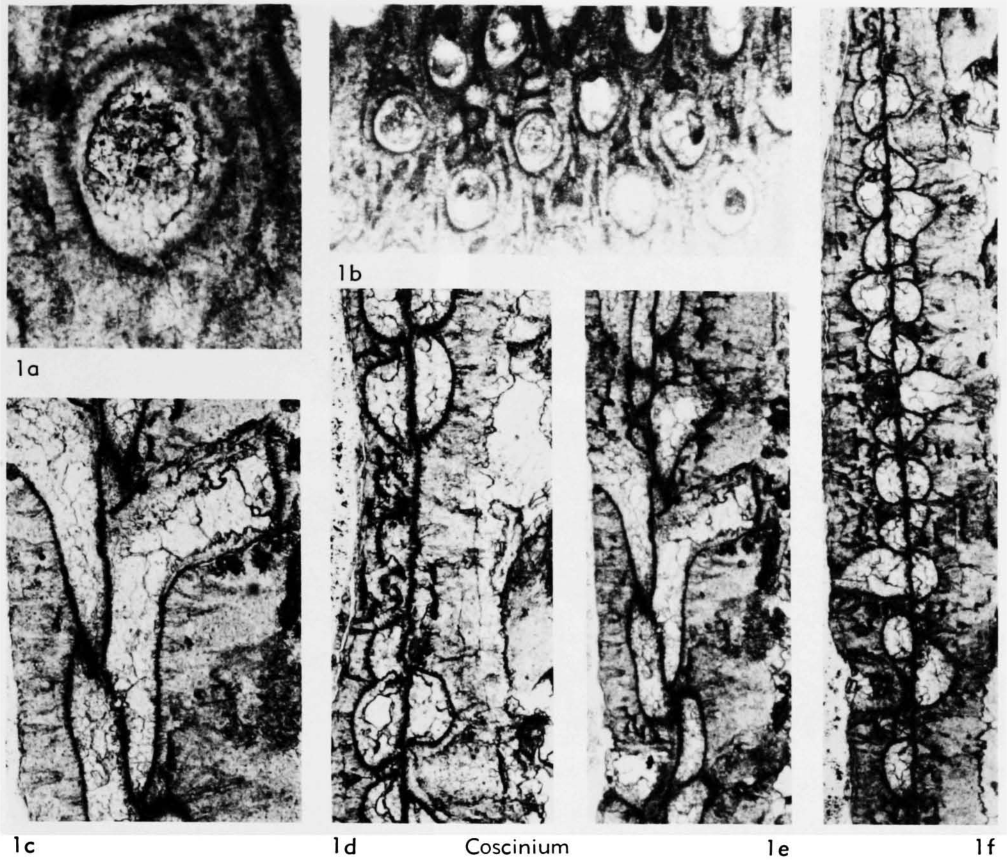


FIG. 197. Hexagonellidae (p. 411).

autozooecium; long. sec., ×50; *d,* thin, granular-prismatic mesotheca, autozooecia mostly contiguous at mesotheca, dark, granular boundary in some range walls in stereom and tubuli in stereom; transv. sec., ×50; *e,* undulatory mesotheca, recumbent autozooecia in endozone, small vesicles in inner exozone, stereom in exozone; long. sec., ×30; *f,* autozooecia contiguous to isolated at mesotheca, stereom in exozone; transv. sec., ×30.

Coscinotrypa HALL, 1886, pl. 29 [**Clathropora carinata* HALL, 1883a, pl. 26; M; M. Dev., Falls of the Ohio, Jeffersonville, Ind., USA]. Zoarium bifoliate, cribrate; fenestrules bordered by rim of solid stereom; lunaria radially arranged around fenestrules; branches symmetrical with lunaria on side of autozooecia away from branch center. Mesotheca trilayered; median layer dark, lateral layers laminated and having tubuli. Mesotheca regularly undulatory in transverse view. Autozooecia contiguous at mesotheca; hemispherical in cross section, with keel and sinuses; size decreasing from endozone to exozone. Walls laminated, with tubuli. Lunaria in outer endozone and exozone; radius of curvature short, producing trilobed autozooecial cross section; hyaline or distinctly laminated. Vesicular tissue forming large blisters in outer endozone, low blisters in inner exozone; stereom in most of exozone; laminated, with numerous small acanthostyles. *M.Dev.,* N.Am.——FIG. 198,*1a–g.* **C. carinata* (HALL); *a,* frond with small fenestrules and broken branch; cotype, WM 13986:no fragment number, ×1; *b,* frond with large fenestrules; cotype, WM 13986:f.33, ×1; *c,* branch with lunaria on side of autozooecium away from branch centerline; cotype, WM 13986:f.32, ×10; *d,* undulatory mesotheca, branch at high angle to frond, stereom in exozone; transv. sec., cotype, WM 13986:f.35, ×30; *e,* thick, undulatory mesotheca, hemispherical autozooecia with keel and sinuses in outer endozone; transv. sec., Jeffersonville F., Ind., SIUC 3010, ×30; *f,* laminated walls, laminated stereom with acanthostyles, lunaria on side of autozooecia away from branch midline (horizontal); tang. sec., Jeffersonville F., SIUC 3009, ×30; *g,* thick mesotheca, autozooecia decrease in diameter from endozone to exozone; long. sec., cotype, WM 13986:f.35, ×30.

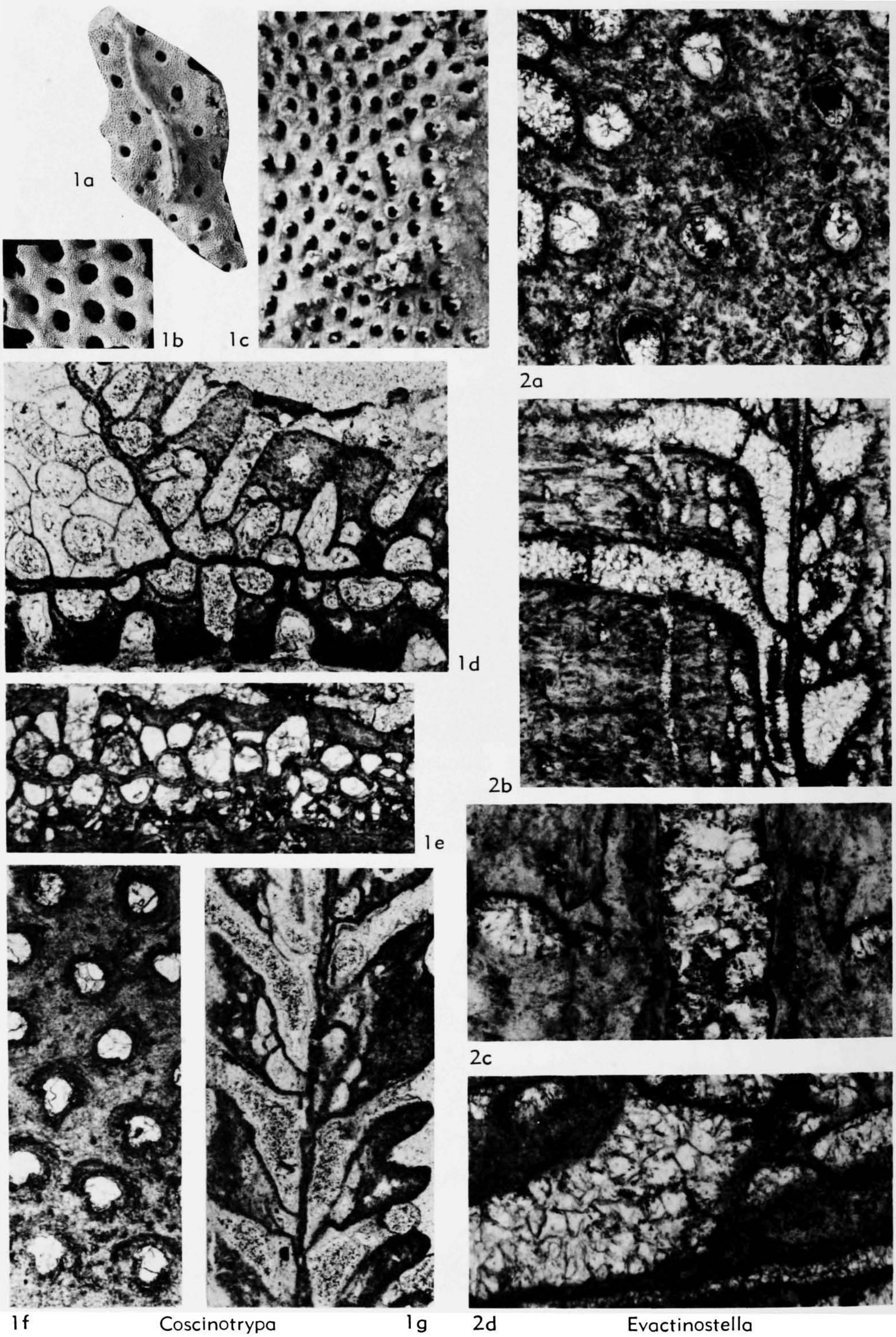


FIG. 198. Hexagonellidae (p. 413–417).

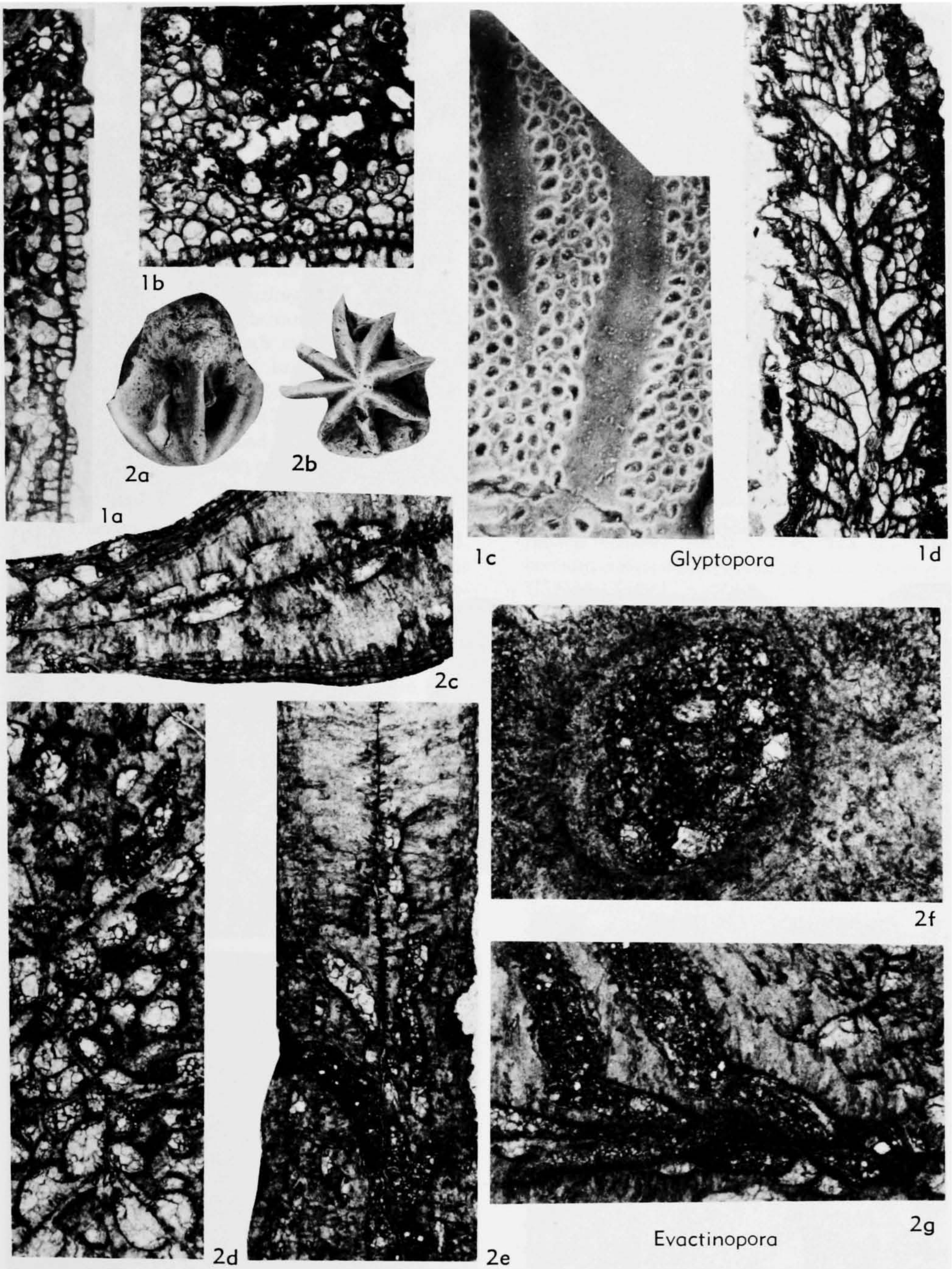


Fig. 199. Hexagonellidae (p. 415–417).

Evactinopora Meek & Worthen, 1865, p. 165 [**E. radiata*; OD; Miss., Mo., USA]. Zoarium multifoliate; 4 to 8 vertical bifoliate branches radiating from center; base and some branch tips of solid stereom. Monticules lacking. Autozooecial cavity subcircular, widely isolated by stereom. Mesotheca thin, laminated in central endozone; thick, trilayered in branches, with central layer dark and laminated layers light-colored with tubuli near margins resembling granular-prismatic microstructure. Autozooecia isolated at mesotheca by vesicular tissue; recumbent portion

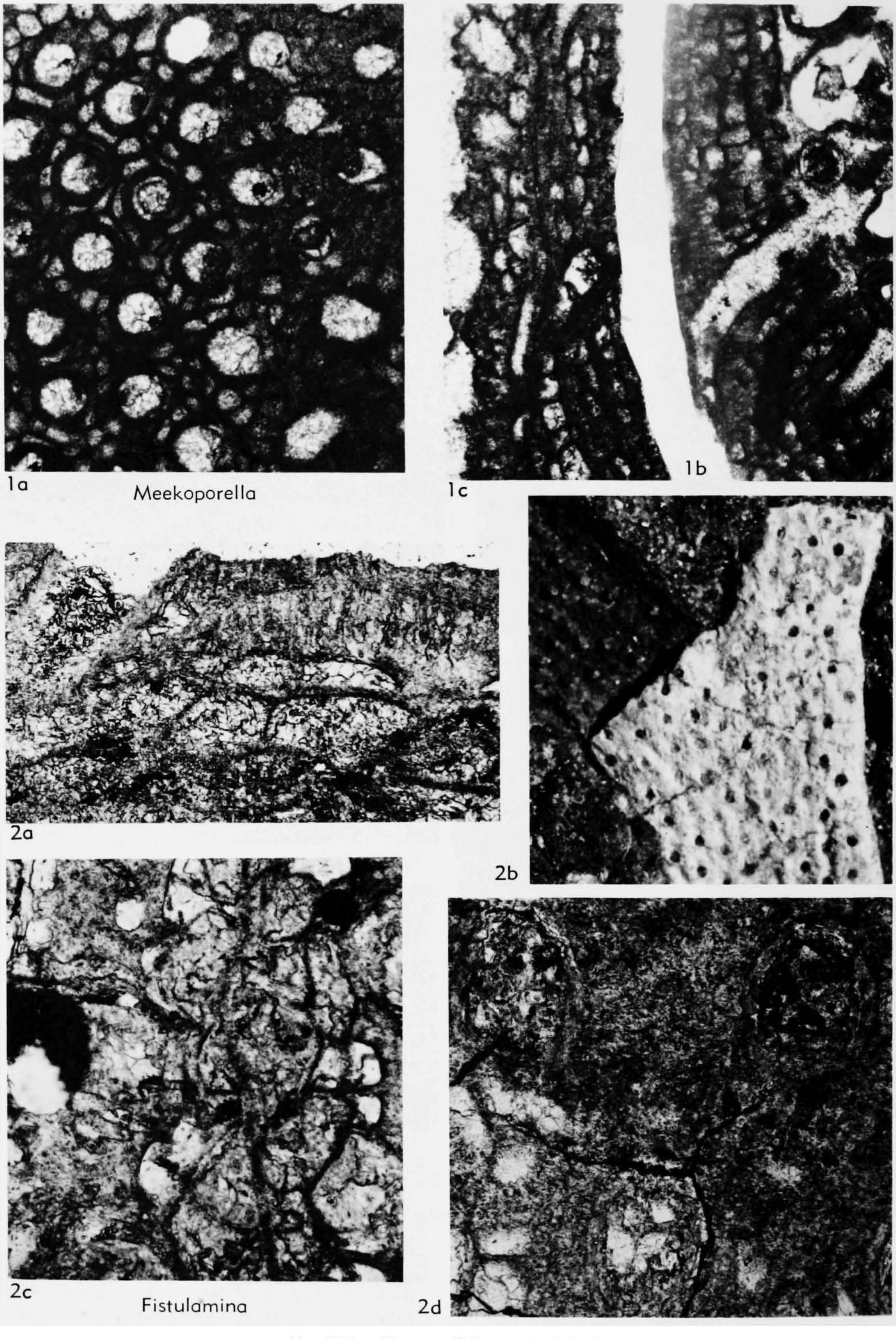


FIG. 200. Hexagonellidae (p. 417–418).

long; short hemiseptum at zooecial bend in some autozooecia. Wall with dark boundary zone and laminated cortex having tubuli. Lunarium in exozone; hyaline or laminated. Vesicular tissue blisterlike in central endozone; stereom throughout most of branch endozones and exozone; laminated, with numerous small acanthostyles. *Miss.*, N.Am.——FIG. 199,*2a,b*. **E. radiata*, holotype, ISGS(ISM) 10784; *a*, noncelluliferous base and branch margins, ×1; *b*, bifoliate branches radiating from center of colony, ×1. ——FIG. 199,*2c–g*. *E. sexradiata* MEEK & WORTHEN, St. Joe Mbr., Burlington Ls., L. Miss., Mo., USA; *c*, thick vesicle roofs and stereom with acanthostyles near branch margin; transv. sec., USNM 159819, ×30; *d*, branching mesothecae and large, blisterlike vesicles in central endozone; transv. sec., USNM 159820, ×30; *e*, autozooecia, vesicles (below), and stereom (above, near branch margin) adjacent to mesotheca; long. sec., USNM 159820, ×30; *f*, laminated lunarium (below), laminated wall with tubuli, acanthostyles in stereom; tang. sec., USNM 159818, ×100; *g*, autozooecia with short hemiseptum at zooecial bend, thick walls and stereom in exozone; long. sec., USNM 159819, ×30.

Evactinostella CROCKFORD, 1957, p. 27 [**Evactinopora crucialis* HUDLESTON, 1883, p. 593; OD; L. Perm., Fossil Ra., Australia]. Zoarium multifoliate, 4 or 5 bifoliate branches radiating from center; branches bifurcating in plane of mesotheca. Monticules low, substellate central cluster of small vesicles or stereom surrounded by larger zooecia with lunaria radially arranged. Low, broad ridges on vesicular tissue surrounding each autozooecium. Mesotheca thick, central layer dark and outer layers laminated. Autozooecia with long recumbent portion, isolated by vesicular tissue at mesotheca; diaphragms few; walls thick, laminated, with indistinct boundary. Lunaria large, laminated, light colored; thicker than remainder of autozooecial wall, with proximal tubuli. Vesicular tissue with vesicles blisterlike, small in cross section; cyclic zones of decreasing vesicle height and stereom in exozone; inner layer dark and outer layer thick, laminated, with tubuli and large, indistinct acanthostyles. *L.Perm.(Artinsk.)*, Australia.——FIG. 198, *2a–d*. **E. crucialis* (HUDLESTON), Callytharria F. (low. Artinsk.), W. Australia, USNM 159823; *a*, autozooecia widely isolated by small vesicles and stereom; tang. sec., ×30; *b*, mesotheca, recumbent autozooecia, sparse diaphragms, vesicles, and stereom with acanthostyles; long. sec., ×30; *c*, laminated autozooecial walls, dark lower layer and laminated outer layer in stereom; long. sec., ×100; *d*, indistinct laminations in autozooecial walls and vesicular tissue at zooecial bend; long. sec., ×100.

Fistulamina CROCKFORD, 1947, p. 10, 28 [**F. inornata*; OD; Miss. (low Burindi), Glen William, Australia]. Zoarium ribbonlike, bifoliate, branching in plane of mesotheca; monticules lacking; margins thin, solid. Autozooecia with fairly long recumbent portion, isolated by vesicular tissue; diaphragms lacking; walls indistinctly laminated. Lunaria laminated, indistinct; on proximal side in endozone and inner exozone, toward lateral side near branch margin and at zoarial surface. Vesicular tissue low blisters; stereom through most of exozone; laminated with tubuli. *Miss.(Visean)*, Australia, USSR.——FIG. 200,*2a–d*. **F. inornata*; *a*, autozooecial walls (left), laminated vesicles and stereom with tubuli (right); long. sec., topotype, USNM 147232, ×100; *b*, bifurcating ribbonlike branches, autozooecia in rows isolated by vesicular tissue, lunaria on side of autozooecia near branch margin (left); holotype, SU 6431, ×10 (photograph by Robin E. Wass); *c*, mesotheca (vertical), vesicles in endozone, laminated stereom in exozone; transv. sec., topotype, USNM 147232, ×100; *d*, ovate autozooecia, laminated walls, indistinct lunaria (below), small vesicles and laminated stereom isolate autozooecia; tang. sec., topotype, USNM 147232, ×100.

Glyptopora ULRICH, 1884, p. 39 [**Coscinium plumosum* PROUT, 1860, p. 572; OD; St. Louis Gr., U. Miss. (Meramec.), Warsaw, Ill., Barretts Station, Mo., USA] [=*Glyptotrypa* MILLER, 1889, p. 307, incorrect subsequent spelling]. Zoarium bifoliate fronds, branches nearly at right angles; "monticules" low, long and narrow, solid stereom; autozooecia elongated oblique to monticular margin; lunaria on end nearest monticule. Mesotheca thin to thick, central zone dark with median tubuli, poorly laminated layers lighter colored; narrow longitudinal ridges on mesotheca paralleling budding direction. Autozooecia semirecumbent in endozone, slightly oblique to zoarial surface; diaphragms sparse, thin; walls indistinctly laminated. Lunaria hyaline or laminated. Vesicular tissue isolating autozooecia in endozone and exozone; blisters low; stereom in outer exozone; laminated with numerous tubuli or small acanthostyles. *U.Miss.*, N.Am., USSR, Australia.——FIG. 199,*1a–d*. **G. plumosa* (PROUT), Warsaw F., Ill., USA; *a*, thin bifoliate frond, mesotheca with longitudinal ridges, autozooecia and vesicles at mesotheca; transv. sec., USNM 159824, ×20; *b*, mesotheca with median tubuli and longitudinal ridges (below), autozooecia isolated by vesicular tissue (above); deep tang. sec., USNM 159825, ×20; *c*, depressed, elongate monticules of solid stereom, rows of elongate autozooecia with lunaria on end nearest monticule; USNM 159827, ×10; *d*, autozooecia with sparse diaphragms, blisterlike vesicles, stereom at surface; long. sec., USNM 159825, ×20.

Meekopora ULRICH in MILLER, 1889, p. 312 [**Fistulipora? clausa* ULRICH, 1884, p. 47; M; U.

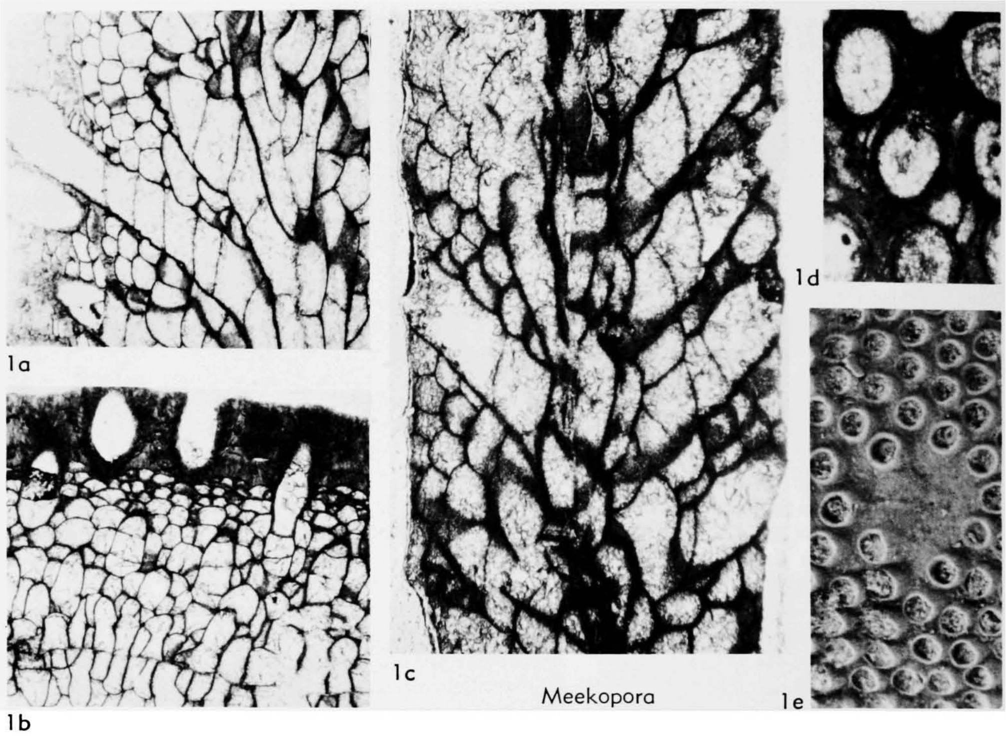


FIG. 201. Hexagonellidae (p. 417).

Miss., Sloans Valley, Ky., USA]. Zoarium narrow, bifoliate, branching. Monticules depressed; central cluster of vesicular tissue or stereom and ring of slightly larger zooecia. Autozooecia with peristomes and lunaria. Mesotheca thin, granular-prismatic. Autozooecia at mesotheca narrow, boxlike to hemispherical in cross section, partially to completely isolated by vesicular tissue. Walls granular-prismatic, tubuli in cortex; locally, lateral and distal walls replaced by superimposed vesicle walls. Diaphragms thin, closely spaced in endozone and inner exozone; planar to cystoidal; some off-centered funnel cystiphragms. Lunaria in endozone and exozone; dark granular boundary continuous into boundary of autozooecial wall; granular-prismatic layer slightly thicker proximally, may have tubuli. Vesicular tissue decreasing in height to low blisters in exozone; local zones of thicker vesicle roofs and thin stereom; granular-prismatic, with tubuli in roofs and stereom. *Miss.,* N.Am., Asia. ——FIG. 201,*1a–e*. **M. clausa* (ULRICH); *a,* closely spaced diaphragms in endozone and inner exozone, vesicles decreasing in height outward, stereom at surface; long. sec., lectotype, USNM 159834, ×20; *b,* thin mesotheca, boxlike to hemispherical autozooecia, large vesicles in endozone, stereom at surface; transv. sec., lectotype, ×20; *c,* crushed endozone, autozooecia isolated by blisterlike vesicles in exozone, distal "wall" of autozooecium (right center) of superimposed vesicle walls; long. sec., paralectotype, USNM 159835, ×30; *d,* elongate autozooecia narrowly isolated by small vesicles; tang. sec., paralectotype, USNM 159836, ×30; *e,* solid monticular center, autozooecia with peristomes and lunaria; paralectotype, USNM 159837, ×10.

Meekoporella MOORE & DUDLEY, 1944, p. 304 [**M. dehiscens*; OD; Stanton Ls., U. Penn. (Missour.), Fredonia, Kans., USA]. Zoarium bifoliate sheets joining at 120° and diverging distally. Monticules with central cluster of vesicles and ring of larger zooecia; lunaria, in part, radially arranged. Mesotheca thick to thin; central layer granular, outer layers granular-prismatic. Autozooecia isolated at mesotheca by vesicles, curving gently into exozone. Wall granular-prismatic; diaphragms few. Lunaria large, slightly indenting, thick, granular-prismatic. Vesicular tissue with vesicles box- to blisterlike; granular-prismatic; local zones of thicker vesicle roofs or stereom. Vesicles small in cross section, locally forming ring around autozooecium. Acanthostyles at some junctions of vesicle walls and in vesicle roofs. *U.Penn.-L.Perm.,* N.Am.——FIG. 200,*1a–c*. **M. dehiscens*; *a,* autozooecia with lunaria, isolated by small vesicles, vesicles locally forming ring around autozooecium (upper left); tang. sec., paratype, KUMIP 32393, ×30; *b,*

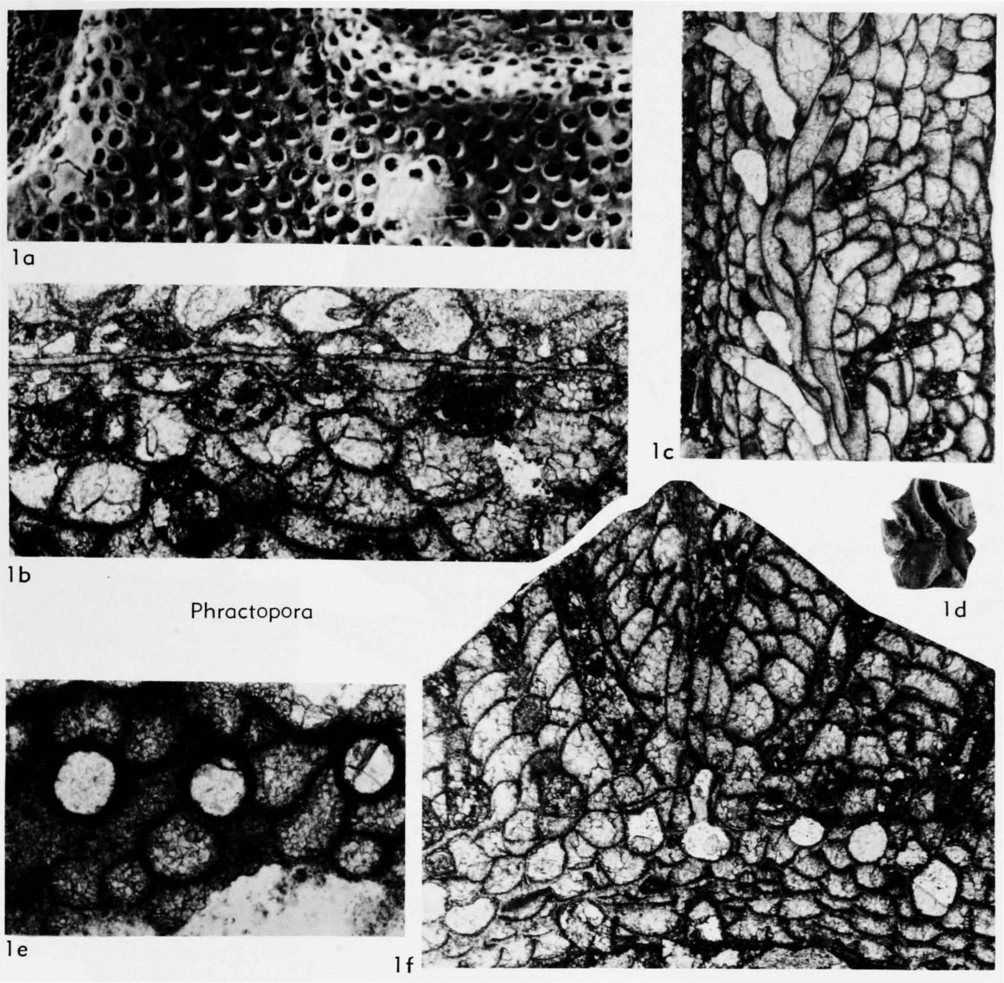


Fig. 202. Hexagonellidae (p. 419).

autozooecium, parted mesotheca (left), zones of thick vesicle roofs with acanthostyles (left); long. sec., paratype, KUMIP 32393, ×30; *c,* thick mesotheca (vertical), granular-prismatic microstructure, boxlike to blisterlike vesicles; long. sec., paratype, KUMIP 32396, ×30.

Phractopora Hall, 1883b, p. 154 [**Lichenalia (Phractopora) cristata*; OD; M. Dev., Falls of the Ohio, Jeffersonville, Ind., USA]. Zoarium bifoliate, bifurcating branches nearly at right angles to main branch. Monticules low; central cluster of large vesicles or stereom and ring of slightly larger zooecia. Autozooecia with peristomes and lunaria. Mesotheca with granular central zone and granular-prismatic outer layers; thin. Autozooecia isolated at mesotheca by vesicular tissue; walls granular-prismatic; diaphragms sparse; locally, distal side made of superimposed vesicle walls. Lunaria in outer endozone and exozone; radius of curvature slightly smaller than that of lateral-distal autozooecial wall; inconspicuous; granular-prismatic. Vesicular tissue in endozone and exozone; large, low blisters decreasing in height outward in exozone; granular-prismatic; thin stereom at surface. *M. Dev.,* N.Am.——Fig. 202, *1a–f.* **P. cristata*; *a,* branches expressed as ridges, monticular center, peristomes and lunaria; syntype, WM 14002, ×10; *b,* granular-prismatic mesotheca, blisterlike vesicles isolate autozooecia in endozone of branch; transv. sec., topotype, USNM 159838, ×50; *c,* undulatory mesotheca, autozooecia with sparse diaphragms, isolated by vesicular tissue; long. sec., topotype, USNM 159838, ×20; *d,* bifurcating branches diverge from main branch at nearly right angles; syntype, WM 14002, ×1; *e,* indistinct lunaria (lower side) in subcircular autozooecia, large vesicles; tang. sec., topotype, USNM 159838, ×50; *f,* undulatory mesotheca, granular-prismatic vesicles (below), low branch

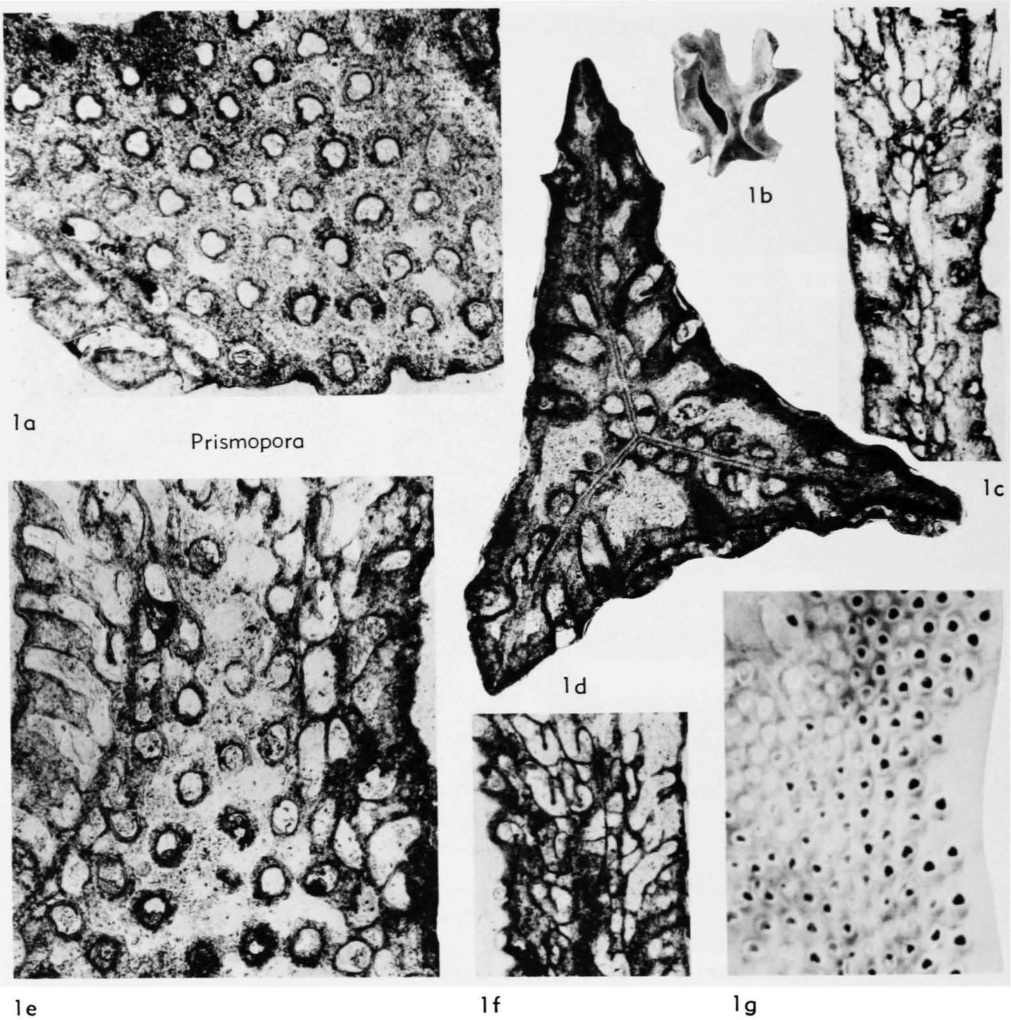


FIG. 203. Hexagonellidae (p. 420).

(above); transv. sec., topotype, USNM 159838, ×30.

Prismopora HALL, 1883b, p. 158 [**P. triquetra*; SD HALL & SIMPSON, 1887, p. xxi; M. Dev., Falls of the Ohio, Jeffersonville, Ind., USA]. Zoarium trifoliate, irregularly branching. Branches narrow, parallel-sided; faces concave; margins solid, noncelluliferous. Monticules lacking. Autozooecia with peristomes and lunaria; lunaria on proximal side of autozooecia in row in center of branch; rotated to progressively more lateral position in rows of autozooecia toward branch margin. Mesotheca with central layer granular, outer layers granular-prismatic. Autozooecia partially isolated at mesotheca by vesicular tissue; clavate at contact with mesotheca, expanding distally, with recurved distal hemiseptum near zooecial bend; subcircular in cross section in exozone. Wall granular-prismatic; tubuli in outer granular-prismatic layer. Lunaria in exozone; radius of curvature short; ends may inflect slightly; microstructure granular-prismatic. Vesicular tissue forming small, low blisters in endozone and inner exozone; granular-prismatic; stereom in most of exozone, with acanthostyles. *Dev.-Perm.*, N.Am., Australia.——FIG. 203, *1a–g*. **P. triquetra*; *a,* autozooecia isolated by stereom, lunaria on proximal side of autozooecia near branch center, on lateral sides of autozooecia near branch margins; tang. sec., topotype, USNM 159839, ×30; *b,* bifurcating trifoliate branches; cotype, WM 13985:f.10, ×1; *c,* undulatory mesotheca, autozooecia and vesicles in endozone, stereom in exozone; long. sec., topotype, USNM 159839, ×20; *d,* granular central layer in mesothecae, trifoliate zoarium, stereom in exozone; transv. sec., topotype, USNM 159841, ×30; *e,* two mesothecae flank tangential view of concave

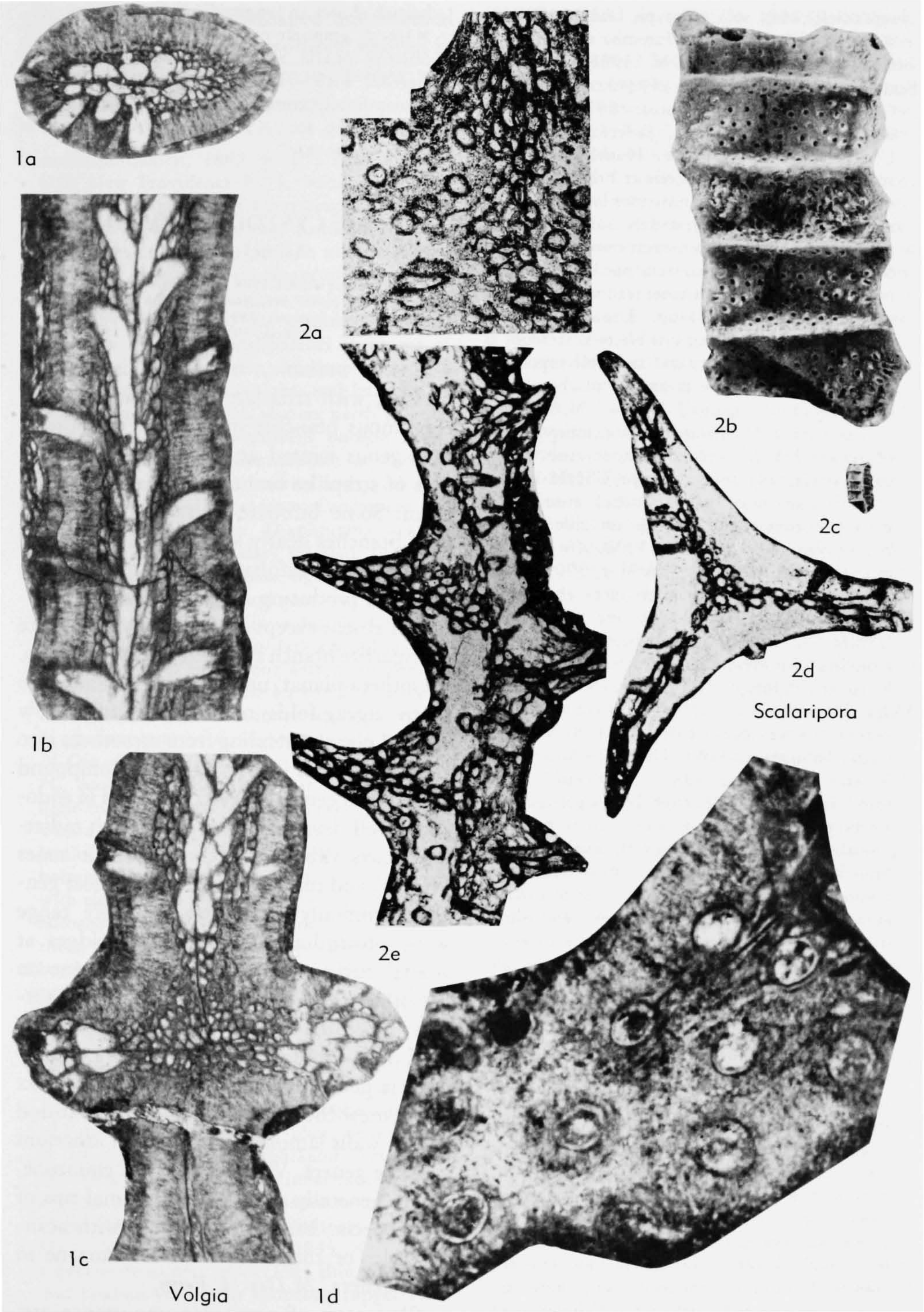


FIG. 204. Hexagonellidae (p. 422).

branch face; distal hemisepta in longitudinal view of autozooecia (left); tang. and long. sec., topotype, USNM 159839, ×30; *f*, recumbent autozooecia and vesicles in endozone, distal hemisepta (left); long. sec., topotype, USNM 159840, ×20; *g,* peristomes and lunaria, solid branch margin (right); cotype, WM 13985, ×10.

Scalaripora HALL, 1883b, p. 159 [**S. scalariformis*; OT, also SD HALL & SIMPSON, 1887, p. xxi; M. Dev., Falls of the Ohio, Jeffersonville, Ind., USA]. Zoarium trifoliate, branches parallel-sided with concave faces; short branches transverse to main branch. Monticules lacking. Autozooecia with peristomes; widely isolated; lunaria on side of autozooecium nearest center of branch. Mesotheca thin. Autozooecia partly isolated at mesotheca by vesicular tissue; recumbent portion long; diaphragms lacking. Lunaria obscure. Vesicular tissue forming low blisters; stereom at surface thin. [The types and available topotypes are silicified and little is known of the microstructure of this genus.] *M.Dev.,* N.Am.——FIG. 204,*2a–e*. **S. scalariformis*; *a,* mesotheca in transverse branch, vesicular tissue, subcircular autozooecia; tang. sec., topotype, USNM 55275, ×24; *b,* transverse, short branches, autozooecia with peristomes and lunaria on side nearest branch center; cotype WM 13990, ×8; *c,* small, triangular branch; cotype, WM 13990, ×1; *d,* triangular branch with concave faces, thin mesotheca, autozooecia; transv. sec., topotype, USNM 55275, ×16; *e,* main branch, short, side branches with mesotheca and blisterlike vesicles; long. sec., topotype, USNM 55275, ×16.

Volgia STUCKENBERG, 1905, p. 31 [**Coscinium arborescens* STUCKENBERG, 1895, p. 173; OD; U. Carb., Samarskaya Luka, USSR] [=*Ramiporina* SHULGA-NESTERENKO, 1933, p. 40, obj.]. Zoarium bifoliate, branches slightly compressed; secondary branches and some short tertiary branches, with mesotheca at right angles to main branch. Monticules lacking. Mesotheca thin, granular-prismatic. Autozooecia partly isolated at mesotheca, curving gently into exozone. Short, discontinuous compound range walls in endozone. Walls with dark granular boundary and granular-prismatic cortex; tubuli in outer granular-prismatic layer. Diaphragms lacking. Lunaria obscure, granular-prismatic; granular middle layer continuous into autozooecial boundary. Vesicular tissue forming small, low blisters in endozone; granular-prismatic stereom throughout exozone, with small acanthostyles. *Penn.,* USSR. ——FIG. 204,*1a–d*. **V. arborescens* (STUCKENBERG), River Don, USSR, PIN 436/119; *a,* hemispherical autozooecia at mesotheca, stereom in exozone; transv. sec., ×16; *b,* thin mesotheca, autozooecia partially isolated by low, small, blisterlike vesicles in endozone, stereom with acanthostyles in exozone; long. sec., ×16; *c,* secondary branch at right angles to primary branch, mesothecae and small vesicles at branch junction, autozooecia at both ends of primary branch shown in transverse view, vesicles in endozone and stereom in exozone in secondary branch shown in longitudinal view; transv. sec., ×16; *d,* granular-prismatic autozooecial walls, obscure lunaria, autozooecia; widely isolated by stereom with acanthostyles; small vesicles and discontinuous compound range wall in endozone (right); tang. sec., ×32 (photographs courtesy of G. G. Astrova).

Family CYSTODICTYONIDAE Ulrich, 1884

[Cystodictyonidae ULRICH, 1884, p. 34] [=Arcanoporidae VINE, 1884, p. 203 (part); Acrogeniidae SIMPSON, 1897, p. 480; Thamnotrypidae SIMPSON, 1897, p. 480; Sulcoreteporidae BASSLER, 1935, p. 21]

Zoaria variable, many bifoliate, compressed, with straplike dichotomous or trichotomous branches in plane of mesotheca. One genus jointed at dichotomous branchings of straplike branches in plane of mesotheca. Some bifoliate frondose or trifoliate with branches nearly at right angles to main branch. One bifoliate with anastomosing branches producing large fenestrules. Monticules absent except in *Dichotrypa.* Bipartite or tripartite branch symmetry in most genera. Mesotheca planar, undulatory, or folded into sharp, zigzag folds; no median tubules. Low vertical plates extending from mesotheca into zooecial cavities in a few genera. Compound range walls generally well developed in endozone; well developed and thick, with radiating arrays (libria) of branched dark zones (valvae) and tubules in exozone in most genera; commonly one, three, or more range walls protruding as conspicuous ridges at zoarial surface. Autozooecia recumbent on mesotheca, oblique or direct at zoarial surface; short, diaphragms lacking; proximolateral hemiseptum in a few genera. Autozooecia generally teardrop shaped at contact with mesotheca; right- and left-handed forms; walls laminated. Laminated lunarium in some genera. Vesicles sparse in endozone, small, generally adjacent to proximal tips of autozooecia. Laminated stereom with acanthostyles or tubules in most of exozone in most genera. *M.Dev.-L.Perm.*

Characters of particular importance are: bifoliate or trifoliate colonies; compound range walls in endozone; thick, compound range walls with branched dark zones in exozone; teardrop or club-shaped autozooecial outline at contact with mesotheca; vesicles in endozone; laminated stereom in exozone; and small acanthostyles in stereom.

Cystodictya Ulrich, 1882, p. 152 [**C. ocellata*; OD; New Providence F., L. Miss., Somerset, Ky., USA]. Zoarium bifoliate, straplike, branching in plane of mesotheca. Autozooecia with peristomes and lunaria on side nearest branch margin. Ridges between ranges of autozooecia lacking. Mesotheca thin to moderately thick; indistinctly laminated to granular-prismatic; with low ridges running parallel to ranges of autozooecia. Autozooecia teardrop-shaped at contact with mesotheca; right- and left-handed in form; quadrate in cross section; partly isolated by boxlike vesicles; recumbent portion short; blunt proximolateral hemiseptum at zooecial bend, indenting zooecial cavity and producing slight hook-shaped appearance of autozooecia in deep tangential section. Diaphragms lacking. Walls laminated; boundary serrated; tubuli in cortex. Lunarium in exozone; light colored, laminated, some with core and proximal rib. Compound range walls thin in endozone with dark boundary continuous into dark central layer of mesotheca; thick in exozone with many flexures and irregular tubuli. Vesicles small, boxlike in endozone; low blisters in inner exozone; stereom in exozone; laminated, with tubuli and flexures. *M.Dev.-U.Miss.,* N.Am.——Fig. 205, *1a–h*. **C. ocellata*; *a,* laminated autozooecial walls, light-colored laminated lunaria (right), each with a core and a proximal projection, tubuli in laminated stereom and range walls; tang. sec., holotype, USNM 43650, ×100; *b,* range walls with elongate tubules, lunaria on lateral sides of autozooecia; tang. sec., holotype, ×30; *c,* mesotheca (below), blunt hemiseptum at zooecial bend, laminated walls, larger vesicles in endozone, small, blisterlike vesicles in inner exozone, laminated stereom with flexures and tubuli; long. sec., holotype, ×100; *d,* short, recumbent autozooecia and vesicles in endozone, erect autozooecia isolated by stereom in exozone; long. sec., holotype, ×30; *e,* short recumbent portion of autozooecia in endozone, blunt hemiseptum at zooecial bend, no diaphragms, vesicles in endozone, smaller vesicles in inner exozone, stereom in exozone; long. sec., specimen from U. Miss. (Merimec.), "Lower Division; St. Louis Gp.," Mo., USA, USNM 159843, ×30; *f,* low ridges on mesotheca (upper left), thin range walls and boxlike vesicles in endozone (upper left), autozooecia slightly hooked at zooecial bend where proximolateral hemiseptum is present; tang. sec., USNM 159843, ×30; *g,* planar mesotheca with short ridges, boxlike autozooecia and vesicles in endozone, flexures and tubuli in range walls; transv. sec., USNM 159843, ×30; *h,* mesotheca with possibly recrystallized granular-prismatic outer layers, range walls continuous with dark central layer of mesotheca, boxlike vesicles in endozone, stereom with flexures and tubuli in range walls (left, right) in exozone; transv. sec., USNM 159843, ×100.

Acrogenia Hall, 1883b, p. 193 [**A. prolifera*; M; "Hamilton Beds," M. Dev., Vincent, N.Y., USA]. Zoarium bifoliate, narrow, compressed; jointed at dichotomous branches, in plane of mesotheca; base of colony with cylindrical branches; noncelluliferous, longitudinally striated, jointed. Autozooecia in ranges; arrangement reticulate to slightly rhombic; branches bilaterally symmetrical; midrib more prominent than other range walls. Border narrow, noncelluliferous. Lunaria elevated, on proximal side of autozooecia; slightly rotated to side of autozooecium away from branch center. Mesotheca thick, trilayered; median zone dark and outer layers laminated. Autozooecia subtriangular, with rounded distal portion, in contact with mesotheca; forms right- and left-handed. Autozooecia triangular in cross section in endozone, near proximal tip; hemispherical to subquadrate toward distal margin. Compound range walls with dark boundary zone continuous with boundary zone in mesotheca; dark zones branched in range walls in exozone. Autozooecia erect in exozone; walls laminated, with tubuli; diaphragms lacking. Lunaria in outer endozone and exozone; hyaline with laminated lining. Vesicles irregular in endozone; between range walls adjacent to proximal tip of autozooecia partially isolating autozooecia; low blisters at zooecial bend; stereom with acanthostyles in exozone. *M.Dev.,* N.Am.——Fig. 206, *1a–f*. **A. prolifera,* holotype, NYSM 594; *a,* stereom in exozone (lower left), vesicles in endozone (upper right), slightly elevated range walls and lunaria near zoarial surface (below); tang. sec., ×30; *b,* subcylindrical, longitudinally striated branches with joints near base of colony; ×2; *c,* thick, trilayered mesotheca, triangular to hemispherical autozooecia in endozone, range wall boundary continuous to dark, central zone of mesotheca, stereom with small acanthostyles in exozone; transv. sec., ×100; *d,* laminated mesotheca, vesicles at zooecial bend, laminated stereom with acanthostyles in exozone; transv. sec., ×100; *e,* planar mesotheca, hemispherical to subquadrate autozooecia in endozone, small vesicles at zooecial bend, stereom in exozone; transv. sec., ×30; *f,* slightly undulatory mesotheca, long recumbent portion of autozooecia in endozone, vesicles in inner exozone, stereom; long. sec., ×30.

Dichotrypa Ulrich in Miller, 1889, p. 300 [**Fistulipora flabellum* Rominger, 1866, p. 122; M; "Warsaw Ls.," U. Miss. (Meramec.), Spergen Hill, Ind., USA]. Zoarium bifoliate fronds; in

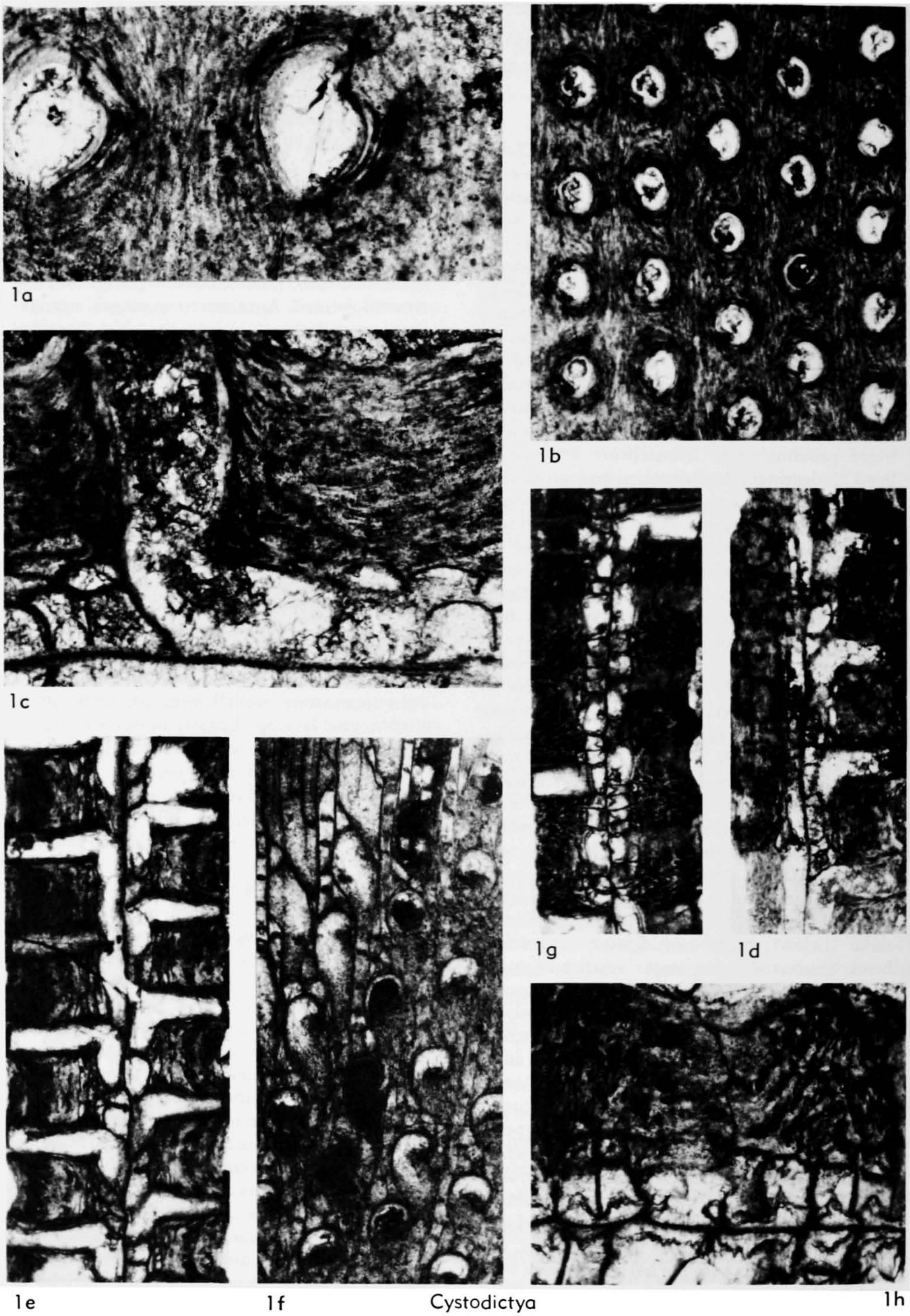


FIG. 205. Cystodictyonidae (p. 423).

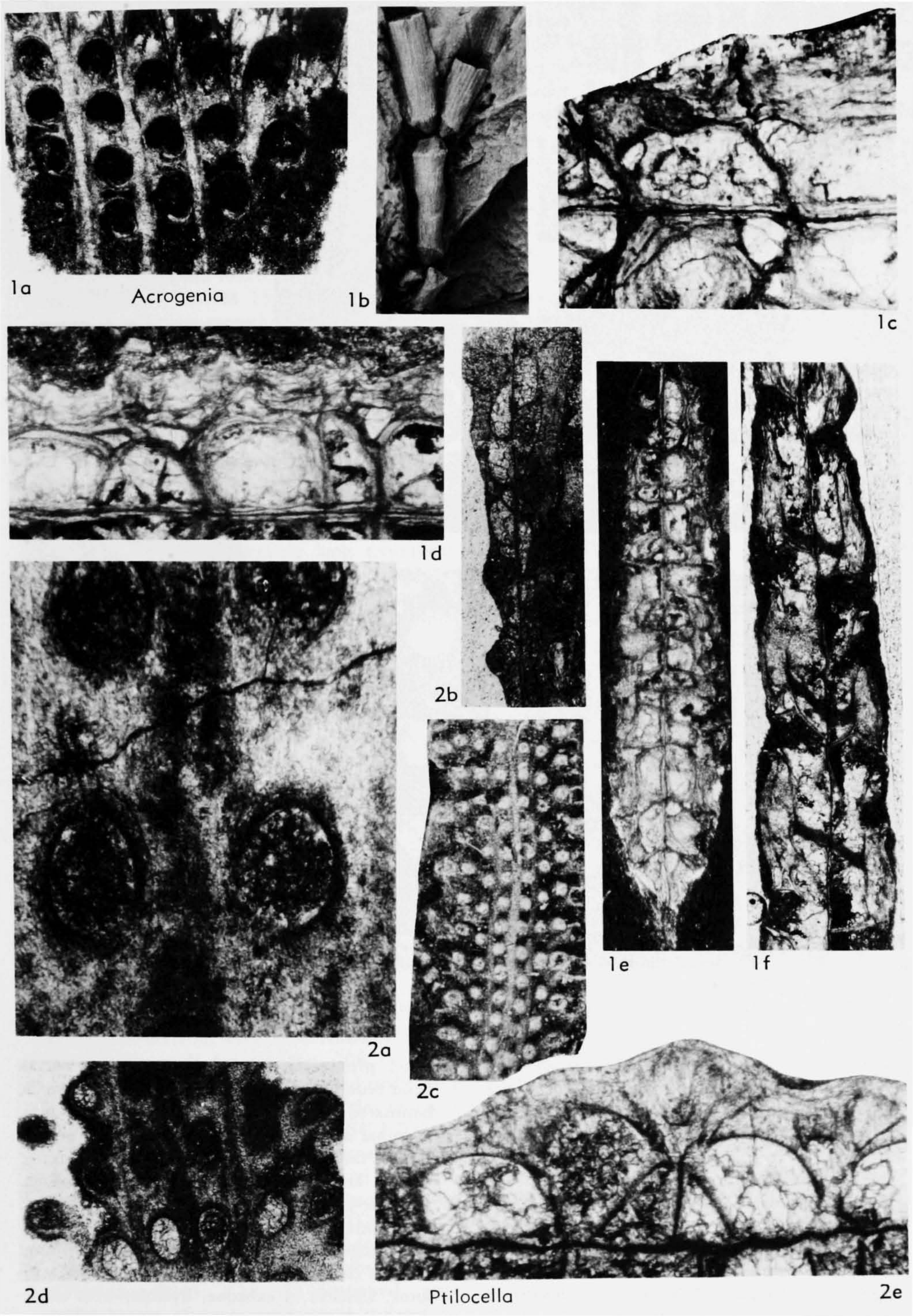


FIG. 206. Cystodictyonidae (p. 423–427).

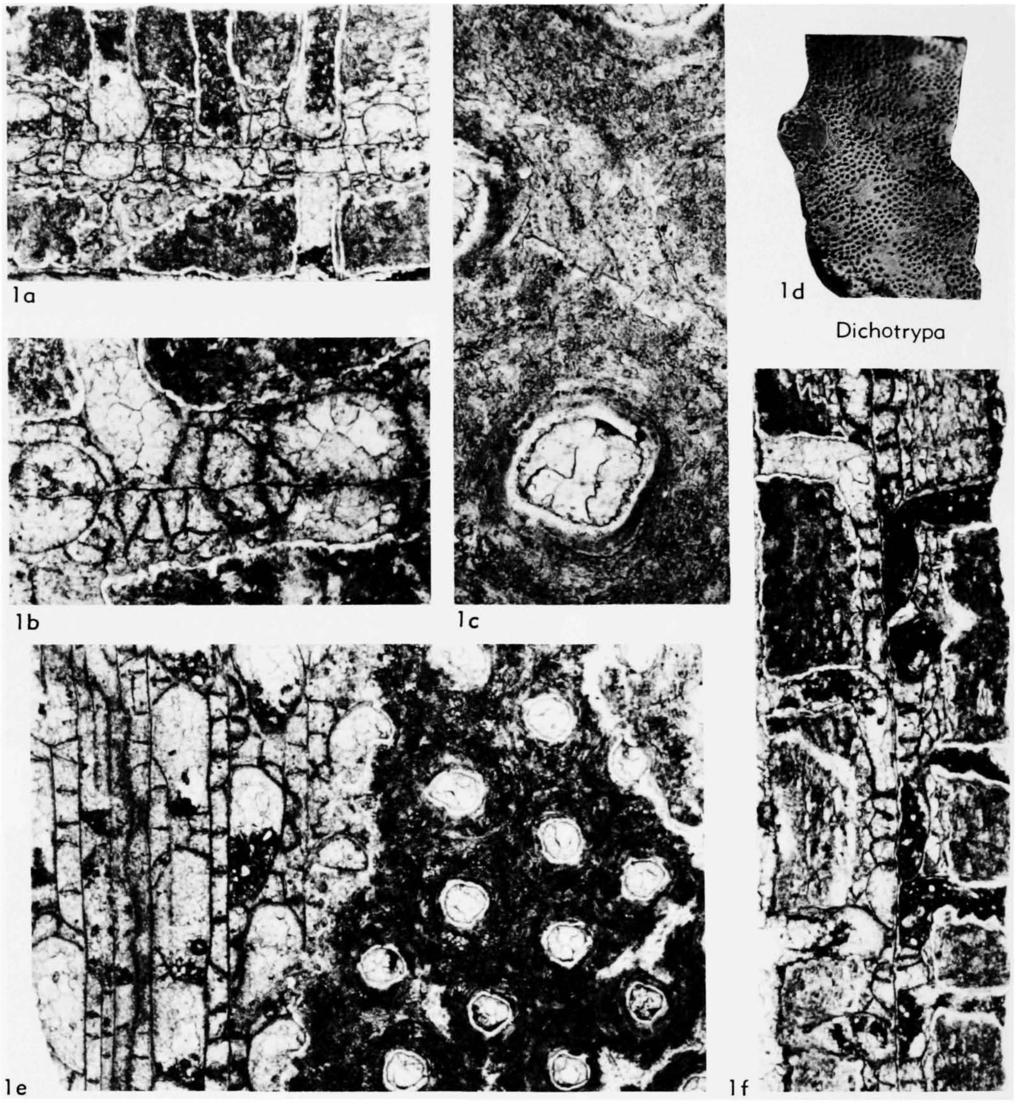


FIG. 207. Cystodictyonidae (p. 423).

some with irregular branches. Monticules elevated or flush; central cluster of small, angular vesicles or stereom surrounded by ring of slightly larger zooecia with lunaria radially arranged. Peristomes low and lunaria elevated. Mesotheca thin, trilayered, granular-prismatic; with several low, longitudinal ridges per autozooecium. Autozooecia in ranges on mesotheca, rhombically arranged over several ranges, teardrop shaped in outline at junction with mesotheca, right- and left-handed forms. Autozooecia in endozone triangular to hemispherical to quadrate in cross section; partly isolated by vesicles; recumbent portion moderately long, lacking diaphragms; walls granular-prismatic in inner endozone; proximolateral hemiseptum at zooecial bend blunt. Autozooecia erect in exozone; walls laminated with lining; basal diaphragms lacking; terminal diaphragms in some. One or two thin simple range walls separating ranges of autozooecia and subquadrate vesicles in endozone; granular-prismatic; range walls losing identity and continuity in exozone in most species; indistinct range walls and ranges of vesicles forming sinuous trace between ranges of autozooecia in some. Lunaria in exozone, hyaline, with thick distal lining continuous with zooecial lining. Vesicles in endozone high, boxlike to blisterlike, quadrate in cross section, in ranges and adjacent to proximal end of autozooecia, granular-prismatic in inner exozone, low, blisterlike, angular in cross section, laminated. Laminated stereom in exozone, with small acanthostyles. [*Dichotrypa* lacks well-defined compound range walls in the exozone and has monticules. In these characters it resembles members of the Hexagonellidae. In all other characters, it more closely resembles members of the Cystodictyonidae; hence, it is retained in this family with some reservation.] *?M.Dev.,Miss.,* N.Am., USSR.——FIG 207,*1a–f.* **D. flabellum* (ROMINGER); *a,* mesotheca with short vertical plates, subquadrate autozooecia and vesicles in endozone; transv. sec., topotype, USNM 159857, ×30; *b,* thin, granular-prismatic mesotheca, autozooecia partially isolated by vesicles; transv. sec., topotype, USNM 159857, ×50; *c,* autozooecium with lunarium, stereom with acanthostyles; tang. sec., topotype, USNM 159857, ×100; *d,* zoarium with large monticules; syntype, UMMP 6505-14, ×2 (negative courtesy of A. Horowitz); *e,* teardrop-shaped autozooecia, vesicles and range walls in endozone (left), subcircular autozooecia in exozone (right); tang. sec., topotype, USNM 159857, ×30; *f,* moderately long recumbent portion of autozooecia in endozone, autozooecia partially isolated by vesicles in endozone, smaller vesicles and stereom in exozone; long. sec., topotype, USNM 159857, ×30.

Filiramoporina FRY & CUFFEY, 1976, p. 4 [**F. kretaphilia*; OD; Wreford Ls., L. Perm. (Wolfcamp.), Kans., USA]. Zoarium bifoliate; dichotomous branching in plane of mesotheca; branches slender, slightly compressed. Ridges low, present only locally between ranges of autozooecia, with sparse nodes. Mesotheca relatively thin. Autozooecia in endozone irregularly hemispherical in cross section, recumbent portion moderately long, microstructure granular-prismatic, zooecial bend sharp. Terminal diaphragms sparse, others absent. In exozone, autozooecia ovate in cross section, lunaria apparently absent. Compound range walls thin in endozone; thick, with radiating dark, granular zones in exozone. Vesicles in outer endozone irregular, small, blisterlike. Stereom with small ?tubules in exozone. *L.Perm.,* N.Am.——FIG. 208,*1a–f.* **F. kretaphilia*; *a,* mesotheca, compound range walls in endozone (left and right), vesicles in outer endozone; transv. sec., paratype, PSU PT06Aa-p-7012, ×188; *b,* recumbent autozooecia on mesotheca in endozone, sharp zooecial bend, vesicles in outer endozone, stereom in exozone; long. sec., paratype, PSU PT06Aa-p-7012, ×20; *c,* mesotheca, small vesicles in outer endozone, stereom in exozone; long. sec., holotype, PSU CH10Ab-p-7043, ×38; *d,* compound range walls, ranges of ovate autozooecia isolated by stereom; tang. sec., paratype, PSU CH10Ab-p-7105, ×33; *e,* mesotheca, subhemispherical cross section of autozooecia in endozone, compound range walls with branching dark zones (valvae); transv. sec., paratype, PSU CH10Ab-p-7001b, ×56; *f,* mesotheca, small vesicles in outer endozone, stereom in exozone; transv. sec., paratype, PSU PT06Aa-p-7019, ×56.

Lophoclema MOROZOVA, 1955, p. 567 [**L. semichatovae*; OD; U. Carb., River Don, USSR]. Zoarium bifoliate; branches narrow, lenticular, with marginal noncelluliferous keels, anastomosing in plane of mesotheca; fenestrules large, subpolygonal; median range wall forming prominent ridge. Mesotheca thick, planar; dark (?granular) central layer and (?granular-prismatic) light-colored outer layers. Autozooecia subtriangular in contact with mesotheca; proximal end pointed, distal end rounded to subangular; hemispherical to subquadrate in cross section; diaphragms sparse in exozone. Autozooecia ovate in cross section in exozone; lunaria obscure. Compound range walls thin in endozone with dark boundary zone and light-colored (?granular-prismatic) lateral zones; branching dark zones and tubuli in exozone. Vesicles small, near proximal end of autozooecia in endozone; partially isolating autozooecia; small blisters in inner exozone; stereom (?laminated) with acanthostyles through most of exozone. *U.Carb.,* USSR.——FIG. 208,*2a–c.* **L. semichatovae,* holotype, PIN 436/57; *a,* planar, trilayered mesotheca, hemispherical to subquadrate autozooecia, stereom and range walls with branching dark zones in exozone; transv. sec., ×14; *b,* narrow branches, large fenestrules, prominent medial range wall, ovate autozooecia; deep tang. sec., ×14; *c,* compound range walls, subtriangular autozooecia in endozone, small subangular vesicles, ovate autozooecia and stereom with acanthostyles in exozone; tang. sec., ×38 (photographs courtesy of G. G. Astrova).

Ptilocella SIMPSON, 1897, p. 605 [**Ptilodictya parallela* HALL & SIMPSON, 1887, p. 270; OD; Hamilton Gr., M. Dev., Fall Brook, N.Y., USA] [=*Stictoporidra* SIMPSON, 1897, p. 532, NICKLES & BASSLER, 1900, p. 425; *Stictoporina* SIMPSON, 1897, p. 532 (*non* HALL & SIMPSON, 1887, p. xx), multiple original spelling]. Zoarium straplike, bifoliate; dichotomously branched in plane of mesotheca. Range walls protruding as one prominent median rib or as median rib with one rib on either side. Autozooecia with peristomes, no lunaria; reticulate arrangement in central two or three ranges and rhombic arrangement on lateral margins; margins thin, wide to narrow, noncelluliferous. Mesotheca slightly undulatory; central layer dark and outer layers light colored, laminated to granular-prismatic. Autozooecia subtriangular near branch center to hemispherical in cross section in endozone; circular in exozone; teardrop shaped at junction with mesotheca. Range walls compound; boundary zone continuing into dark zone of mesotheca in some;

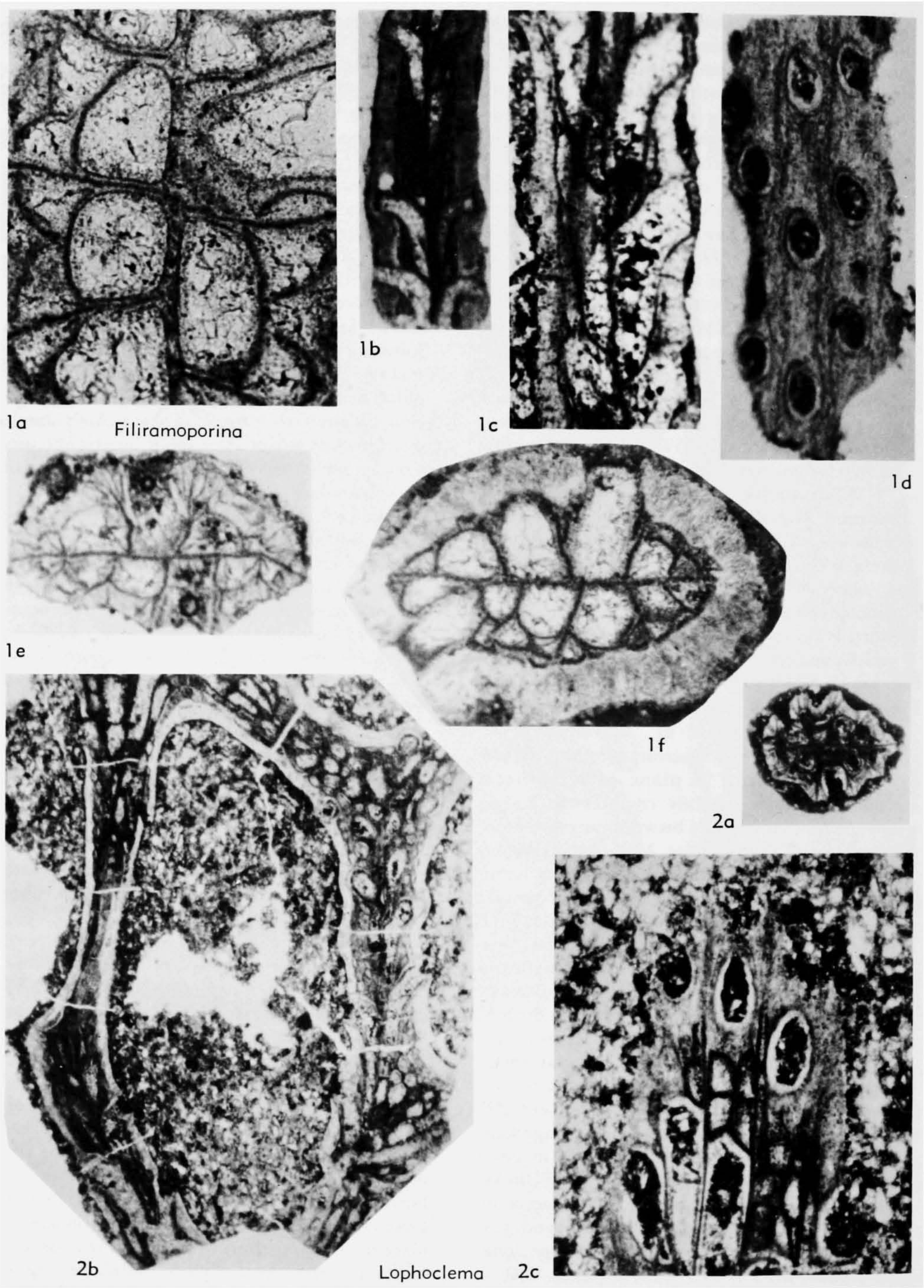


FIG. 208. Cystodictyonidae (p. 427).

indistinct branched dark zones and tubuli in range walls in exozone. Vesicles on mesotheca near proximal tips of autozooecia; small, blister-like; stereom laminated, with tubuli in exozone. [*P. subcarinata* (HALL & SIMPSON), the type species of *Stictoporidra* SIMPSON, 1897 by original designation, is consistent with the emended definition of *Ptilocella.*] *M.Dev.,* N.Am.——Fig. 206,*2a–e*. **P. parallela* (Hall & Simpson), holotype, NYSM 889; *a,* thick range walls with tubuli, laminated autozooecial walls, stereom; tang. sec., ×100; *b,* autozooecia and vesicles in endozone, stereom in exozone; oblique long. sec., ×30; *c,* midrib and two other prominent ribs at range walls, rhombic arrangement of lateral autozooecia; ×10; *d,* three prominent range walls at branch center, rhombically arranged and slightly oblique autozooecia near branch margins; tang. sec., ×30; *e,* trilayered mesotheca, triangular autozooecia near branch center, few vesicles in endozone, laminated stereom with tubules in exozone, indistinct branched dark zones and tubules in range walls in exozone; transv. sec., ×100.

Semiopora Hall, 1883b, p. 193 [**S. bistigmata*; M; Hamilton Gr., M. Dev., W. Williams, Ont., Can.]. Zoarium straplike, bifoliate; branches dichotomous or trichotomous in plane of mesotheca. Range walls prominent, distal and proximal ridges elevated; lunaria on side of autozooecia away from middle of branch. Mesotheca thin, undulatory, trilayered, laminated. Autozooecia subtriangular or subquadrate in cross section in endozone, aligned across mesotheca; teardrop shaped outline at contact with mesotheca, right- or left-handed in form. Walls laminated, with minute tubules perpendicular to thin, dark, zooecial boundary. Proximolateral, blunt hemiseptum at sharp zooecial bend. Lunaria laminated, ends projecting slightly. Compound range walls with dark boundary continuous into dark middle zone in mesotheca; dark zones branching in inner exozone, obscure in outer exozone; small tubules in range walls. Sparse, high vesicles near proximal tips of autozooecia in endozone; stereom laminated, with tubules in exozone. *M.Dev.,* N.Am.——Fig. 209,*2a–c*. **S. bistigmata,* holotype, NYSM 958; *a,* laminated walls and lunaria with ends projecting, prominent range walls with dark boundaries and tubules; tang. sec. ×100; *b,* thin mesotheca, subtriangular to subquadrate autozooecia and sparse vesicles in endozone, laminated stereom with tubules in exozone, range walls with branched dark zones in inner exozone; transv. sec., ×100; *c,* undulatory mesotheca, proximolateral hemiseptum at zooecial bend (upper left), sparse vesicles in endozone, laminated stereom in exozone; long. sec., ×100.

Stictocella Simpson, 1897, p. 532 [**Stictopora sinuosa* Hall, 1883b, p. 190; OD; Hamilton Gr., M. Dev., Union Springs, N.Y., USA]. Zoarium straplike, bifoliate. Range walls elevated, sinuous; peristomes present. Mesotheca thin; median layer dark, laminated or granular-prismatic layers light colored. Autozooecia hemispherical in cross section in endozone, some with sinuses, ovate in cross section in exozone. Walls with dark boundary and perpendicular tubules in laminated cortex. Range walls with dark boundary branching in exozone. No discernable lunaria but proximal portion of autozooecial wall thicker and with more tubules. Vesicles in outer endozone, boxlike. Stereom laminated, with tubules in exozone. *M.Dev.,* N.Am.——Fig. 209,*1a–c*. **S. sinuosa* (Hall), holotype, NYSM 1005; *a,* thin mesotheca, low vesicles in outer endozone, stereom in exozone; long. sec., ×100; *b,* laminated autozooecial walls with tubules, range walls and stereom with tubules; tang. sec., ×100; *c,* hemispherical autozooecia, some with keels, in endozone, low vesicles in outer endozone, stereom with tubules in exozone, range walls with branched dark zones; transv. sec., ×100.

Sulcoretepora d'Orbigny, 1849, p. 501 [**Flustra? parallela* Phillips, 1836, p. 200; OD; L. Carb., Yorkshire, Eng.] [=*Arcanopora* Vine, 1884, p. 204, obj.; *Acanthopora* Vine, Morozova, 1960, p. 86, incorrect subsequent spelling; *Mstaina* Shulga-Nesterenko, 1955, p. 175]. Zoarium narrow bifoliate ribbons, dichotomously branched in plane of mesotheca; elongate, rounded autozooecia in ranges, rhombically arranged on lateral sides of branch; lunaria elevated on proximolateral side of autozooecia; range walls elevated; monticules absent; branch margins narrow, noncelluliferous. Mesotheca with dark central layer and laminated outer layers; sharply folded in center, undulatory near branch margins. Autozooecia full width and rectangular to parallelogram-shaped in deep tangential section; contiguous; alternating across mesotheca. Compound range walls with dark median zone continuous into boundary zone in mesotheca; lateral zones laminated; branched dark zones and tubules in thickened range walls in exozone. Autozooecia subquadrate to subhemispherical in cross section at mesotheca; angular teardrop shaped in deep tangential section in mid exozone and partially isolated between range walls by small, blisterlike vesicles. Walls laminated with minute tubules. Lunaria laminated, indistinct. Vesicles adjacent to mesotheca only at noncelluliferous branch margins. Stereom laminated with tubules in exozone. [*Mstaina laminicurvis* Shulga-Nesterenko, 1955, p. 176, from the Lower Carboniferous (Visean) at the River Msta, Vitsa, USSR, is the type species of *Mstaina* Shulga-Nesterenko, 1955, by original designation. Because it is similar to species of *Sulcoretepora, Mstaina* is considered to be a junior subjective synonym of *Sulcoretepora.*] *L.Carb.,* Eu., USSR.——Fig. 210,*1a–f*. **S. parallela* (Phillips), Carboniferous Ls., Scot.; *a,* undulatory mesotheca, sharp zooecial bend, thin exozone; long. sec., HM D-113-2, ×30; *b,* ovate autozooecia between range walls in exozone;

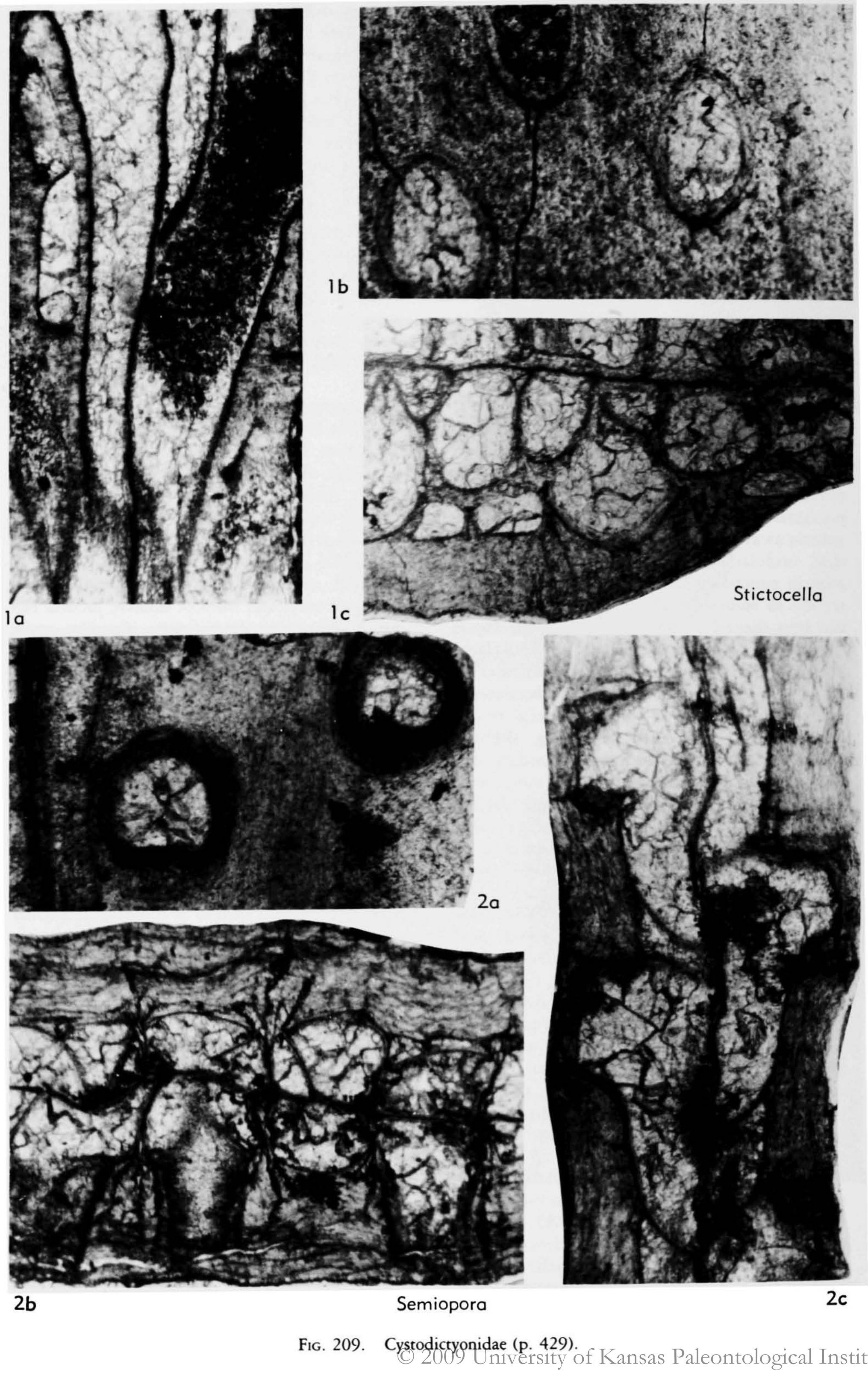


FIG. 209. Cystodictyonidae (p. 429).

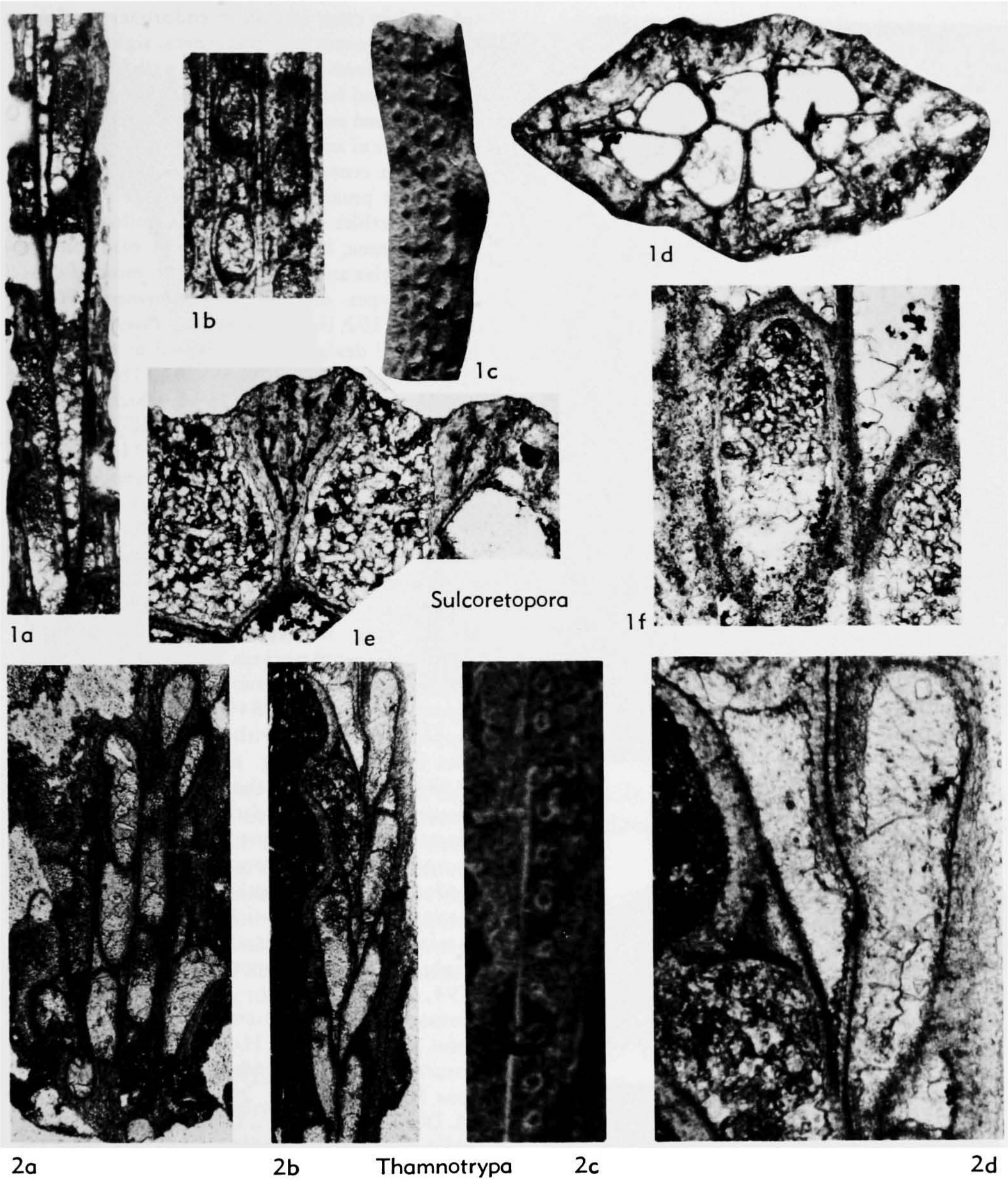


FIG. 210. Cystodictyonidae (p. 429–432).

tang. sec., HM D-113-4, ×30; *c,* straplike zoarium with elevated range walls and lunaria; HM D-113, ×3; *d,* autozooecia alternating across folded mesotheca, vesicles in outer endozone and inner exozone, stereom in exozone; transv. sec., HM D-113-3, ×50; *e,* mesotheca (lower left), range wall with branched dark zones and tubules; transv. sec., HM D-113-2, ×100.

Taeniopora NICHOLSON, 1874a, p. 133 [**T. exigua* NICHOLSON, 1874b, p. 122; SD HALL & SIMPSON, 1887, p. xii; Hamilton Gr., M. Dev., Bartlett's Mills, Arkona, Ont., Can.] [=*Pteropora* HALL, 1883b; p. 192, *non* EICHWALD, 1860, p. 395]. Zoarium straplike, bifoliate; diamond shaped in cross section; branching trichotomous. Median rib on each branch prominent, elevated, rounded, noncelluliferous; branch margin narrow, noncelluliferous. Peristomes elevated. Mesotheca moderately thick, trilayered; central zone dark and laminated or granular-prismatic outer layers light colored. Midrib a prominent, thick, compound range wall, branching dark zones and tubules in exozone. Other range walls loosing identity in exozone. Autozooecia hemi-

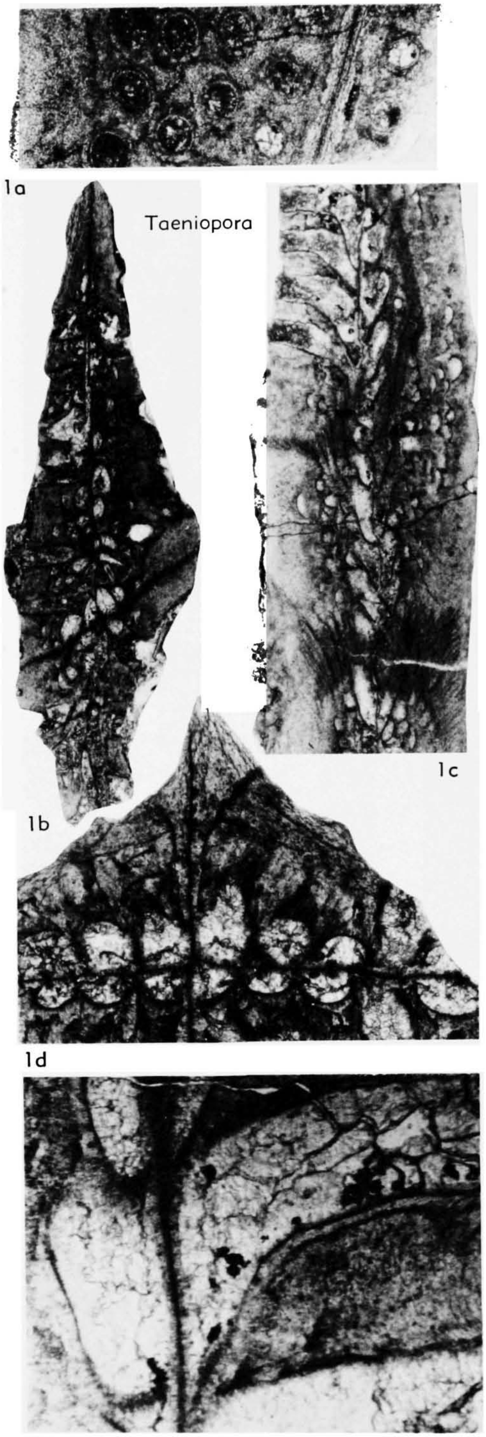


Fig. 211. Cystodictyonidae (p. 431).

spherical in cross section in endozone, teardrop shaped at contact with mesotheca, right- or left-handed in form. Autozooecial walls with dark boundary and laminated cortex. Lunaria in outer endozone and exozone; thick, laminated; rotated toward side of autozooecia nearest branch margin away from center of branch. Vesicles on mesotheca near proximal tips of autozooecia; small, low, blisterlike vesicles in outer endozone and inner exozone; laminated stereom with minute acanthostyles and tubules through most of exozone. [Types of *Pteropora duogeneris* Hall, 1883b, p. 192, the type species of *Pteropora* Hall by original designation, are listed as hypotypes of *Taeniopora exigua* Nicholson, 1874b. Two specimens from Unadilla Forks, which possibly were the specimens originally described by Hall as *P. duogeneris,* are impressions. In external characters, they agree well with *Taeniopora exigua,* and *Pteropora* Hall, 1883b, is considered to be a junior synonym of *Taeniopora.*] *M.Dev.,* N.Am.——Fig. 211,*1a–e.* **T. exigua*; *a,* prominent midrib (right), circular autozooecia, small vesicles, no well-defined range walls lateral to midrib; tang. sec., topotype, USNM 159844, ×28; *b,* planar mesotheca (vertical), thick midrib, stereom in exozone; oblique transv. sec., topotype, USNM 159844, ×19; *c,* autozooecia (upper left), stereom with acanthostyles and vesicles in exozone; long. sec., topotype, USNM 159845, ×19; *d,* mesotheca (horizontal), midrib (vertical) with several dark zones, hemispherical autozooecia in endozone, laminated stereom in exozone; transv. sec., topotype, USNM 159847, ×47; *e,* trilayered mesotheca with granular-prismatic outer layers, vesicles in endozone (left), laminated autozooecial walls and stereom (right); long. sec., topotype, USNM 159846, ×94.

Thamnotrypa Hall & Simpson, 1887, p. xxi, *nom. subst. pro Thamnopora* Hall, 1883b, p. 158, *non* Steininger, 1831, p. 10 [**Thamnopora divaricata* Hall, 1883a, pl. 26; OD; Onondaga Ls., M. Dev., Buffalo, N.Y., USA]. Zoarium narrow, trifoliate, subtriangular in cross section; branches nearly at right angles to main portion. Median rib rounded, conspicuous; other range walls not expressed as ridges. Autozooecia in rows, with peristomes; lunaria not observed. Mesotheca thin, undulatory along branch axis; trilayered, central zone dark and lateral zones light colored. Autozooecia subhemispherical in cross section in endozone; ovate teardrop shaped in outline at contact with mesotheca, right- or left-handed in form. Walls with thin dark boundary and laminated cortex with tubules perpendicular to boundary. Compound range walls with branching dark zones in exozone. Vesicles high blisters, subtriangular in cross section in endozone. Stereom laminated, with tubules in exozone. *M.Dev.,* N.Am.——Fig. 210,*2a–d.* **T. divar-*

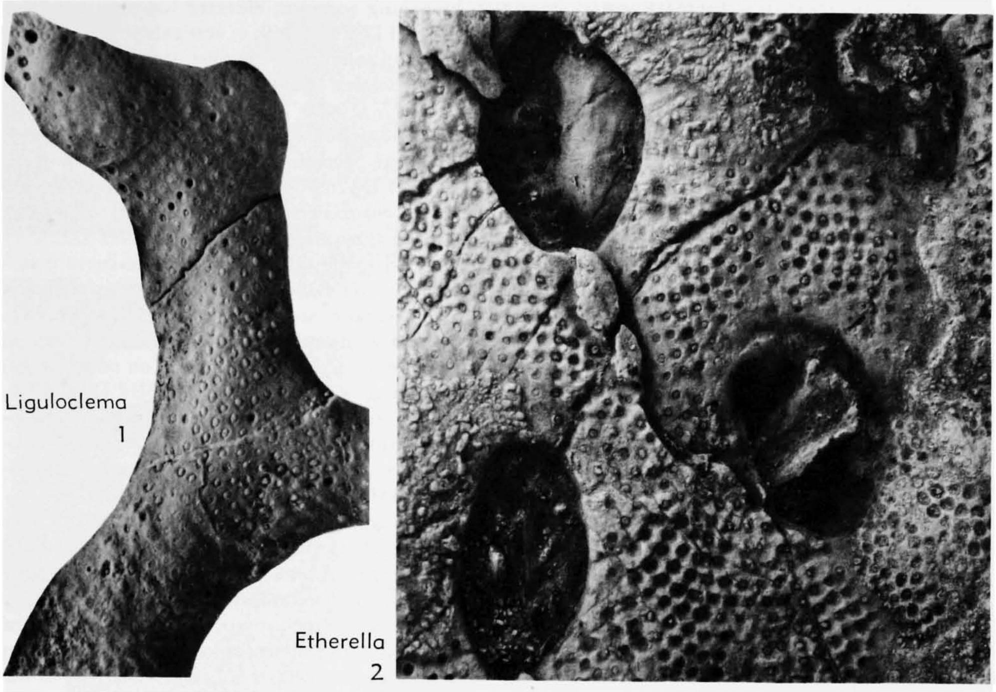


FIG. 212. Etherellidae (p. 433).

icata (HALL), holotype, NYSM 1039; *a,* right- and left-handed autozooecia aligned between compound range walls; deep tang. sec., ×30; *b,* undulatory mesotheca, autozooecia, sparse vesicles, stereom in exozone; long. sec., ×30; *c,* prominent midrib, autozooecia with peristomes; ×10; *d,* trilayered mesotheca, sparse vesicles in endozone, laminated stereom with tubules in exozone; long. sec., ×100.

Family ETHERELLIDAE
Crockford, 1957

[Etherillidae CROCKFORD, 1957, p. 30]

Zoaria bifoliate, compressed; form cribrate or branching straplike. Monticules lacking. Margins on branches narrow, noncelluliferous. Autozooecia recumbent on mesotheca, recurved with hook-shaped appearance at zooecial bend; erect in exozone. Lunaria present or possibly absent. Small vesicles in endozone, stereom in exozone. [Genera in the Etherellidae are poorly known owing to lack of thin-sectioned specimens. The recurved, hook-shaped appearance of the autozooecia at the zooecial bend is presumed to be the diagnostic feature of the family, but further study may reveal a close relationship to the Cystodictyonidae.] *Perm.*

Etherella CROCKFORD, 1957, p. 32 [**E. porosa*; OD; Noonkanbah F., Perm., Fitzroy basin, W. Australia]. Zoarium bifoliate, cribrate. Mesotheca trilayered. Autozooecia partially isolated at mesotheca by vesicular tissue; recumbent portion relatively long; hooked around oblique vertical plate at zooecial bend. Lunaria not apparent. Stereom narrowly isolating autozooecia in exozone. [Internal features and microstructure of this genus are poorly known.] *Perm.,* Australia.——FIG. 212,*2.* **E. porosa,* holotype, CPC 1102 A; cribrate zoarium, rhombic arrangement of autozooecia narrowly isolated by stereom, hook-shaped autozooecia in weathered portion (above), ?lunaria in unweathered portion (lower right); ×5 (photograph courtesy of R. E. Wass).

Liguloclema CROCKFORD, 1957, p. 35 [**L. typicalis*; OD; Noonkanbah F., Perm., Fitzroy basin, Australia]. Zoarium bifoliate, compressed, straplike, irregularly branching. Autozooecia with lunaria. Stereom widely isolating autozooecia in exozone. [Internal anatomy of this genus is poorly known.] *Perm.,* Australia.——FIG. 212,*1.* **L. typicalis,* holotype, CPC 1106 A; zoarium, indistinct lunaria in less weathered portion (below); ×5 (photograph courtesy of R. E. Wass).

Family GONIOCLADIIDAE Waagen & Pichl, 1885

[*nom. transl.* Nikiforova, 1938, p. 195, *ex* Goniocladiinae Waagen & Pichl, 1885, p. 775]

Zoaria bifoliate, mesotheca vertical in cylindrical to laterally compressed branches. Primary branches with paired secondary branches at right angles, or distolaterally directed; or with alternating distolaterally directed secondary branches, some with tertiary branches; secondary or tertiary branches fused in some genera to produce large fenestrules. Obverse side with one to six rows of autozooecia on flanks dipping moderately to steeply away from median carina. Reverse side noncelluliferous, with or without keel. Monticules absent. Autozooecia with or without sparse diaphragms; walls generally well laminated, with laminated lunarium in most genera. Vesicles small, generally sparse in inner endozone, more abundant in outer endozone; replaced by generally laminated stereom, with tubules or acanthostyles, in exozone or outer exozone. *Miss.-Perm.*

Characters of particular importance are the vertical mesotheca, the celluliferous obverse side, and the noncelluliferous reverse side.

Goniocladia Etheridge, 1876, p. 522, *nom. subst. pro Carinella* Etheridge, 1873, p. 433, *non* Johnston, 1833, p. 232 [**Carinella cellulifera* Etheridge, 1873, p. 433; OD; "Low. Ls. Gr.," L. Carb., Braidwood, Eng.]. Zoarium bifoliate; narrow, curved dichotomous branches in some anastomosing to form large fenestrules; vertical mesotheca protruding as ridge on rounded, noncelluliferous reverse side and as sharp keel on peaked obverse side. Autozooecia in two to three rows on either side of median carina; subcircular apertures opening upward and indented by ends of lunaria on side of autozooecia away from branch center. Mesotheca thin; median layer dark, outer layers laminated. Autozooecia hemispherical in cross section at mesotheca, partially isolated by small vesicles; curving upward and outward; diaphragms sparse. Walls with thin, dark, serrated boundary and laminated cortex having minute tubules perpendicular to boundary. Lunaria laminated, with numerous tubules in proximal side. Vesicles forming small blisters, laminated; stereom laminated, with numerous tubules and small, indistinct acanthostyles in most of exozone and noncelluliferous reverse side. *Miss.-Perm.*, Eu., Asia, Australia.——Fig. 213,*1a–h*. **G. cellulifera* (Etheridge); *a*, branching zoarium, elevated lunaria; topotype, BMNH D32637, ×9; *b*, vertical mesotheca, vesicles and stereom in exozone, stereom on reverse side (below); transv. sec., topotype, BMNH D32637-3, ×50; *c*, laminated walls and lunaria with tubules on outer side (right), stereom with numerous acanthostyles; tang. sec., topotype, BMNH D32637-2, ×100; *d*, solid reverse side (left), autozooecia and vesicles in endozone; oblique long. sec., topotype, BMNH D32637-7, ×50; *e*, mesotheca, autozooecia curve distolaterally, vesicles in outer endozone, stereom in exozone; tang. sec., topotype, BMNH D32637-5, ×30; *f*, mesotheca (left), autozooecia isolated by stereom and vesicles, lunaria on outer (right) side; tang. sec., topotype, BMNH D32637-4, ×50; *g*, subcircular autozooecia; tang. sec., topotype, BMNH D32637-7, ×30; *h*, wall microstructure, vesicles and stereom; long. sec., topotype, BMNH D32637-7, ×100.

Aetomacladia Bretnall, 1926, p. 21 [**A. ambrosioides*; M; Carb., Fossil Hill, Australia]. Zoarium of slender branches, each with vertical mesotheca; paired secondary branches at right angles to primary branch, perpendicular to mesotheca. Obverse with prominent keel at mesotheca, steep flanks; autozooecia in rows with lunarium on side away from branch center. Reverse side rounded with weak striations and median rib where mesotheca protrudes. Mesotheca trilayered; median tubules (?acanthostyles) clear, vertical. Autozooecia hemispherical in cross section at mesotheca; curving outward and upward toward flanks of obverse side. Walls laminated with minute tubules; diaphragms sparse in endozone. Lunaria laminated, thick, with tubules on proximal side. Vesicles low blisters in endozone and inner exozone; stereom laminated, with acanthostyles and tubules through most of exozone. *Carb.-Perm.*, Australia.——Fig. 214,*2a–e*. **A. ambrosioides*, Callytharra F., Perm., W. Australia; *a*, primary branch with secondary branches nearly at right angles, autozooecia with lunaria, median rib on each branch; USNM 159850, ×10; *b*, vertical mesotheca running from obverse (top) to reverse (bottom), hemispherical autozooecia in endozone; transv. sec., USNM 159849, ×30; *c*, autozooecia and vesicles in endozone, stereom with acanthostyles and tubules in exozone; oblique long. sec., USNM 159851, ×30; *d*, autozooecia with diaphragms in endozone, blisterlike vesicles in outer endozone, stereom in exozone; long. sec., USNM 159848, ×50; *e*, median rib formed by mesotheca with median tubules (below), rows of autozooecia, with lunaria on side away from median rib, widely isolated by stereom; tang. sec., USNM 159848, ×30.

Goniocladiella Nekhoroshev, 1953, p. 166 [**G. kasakhstanica*; M; L. Carb., Kazakh., USSR]. Zoarium bifoliate, vertical mesotheca, noncel-

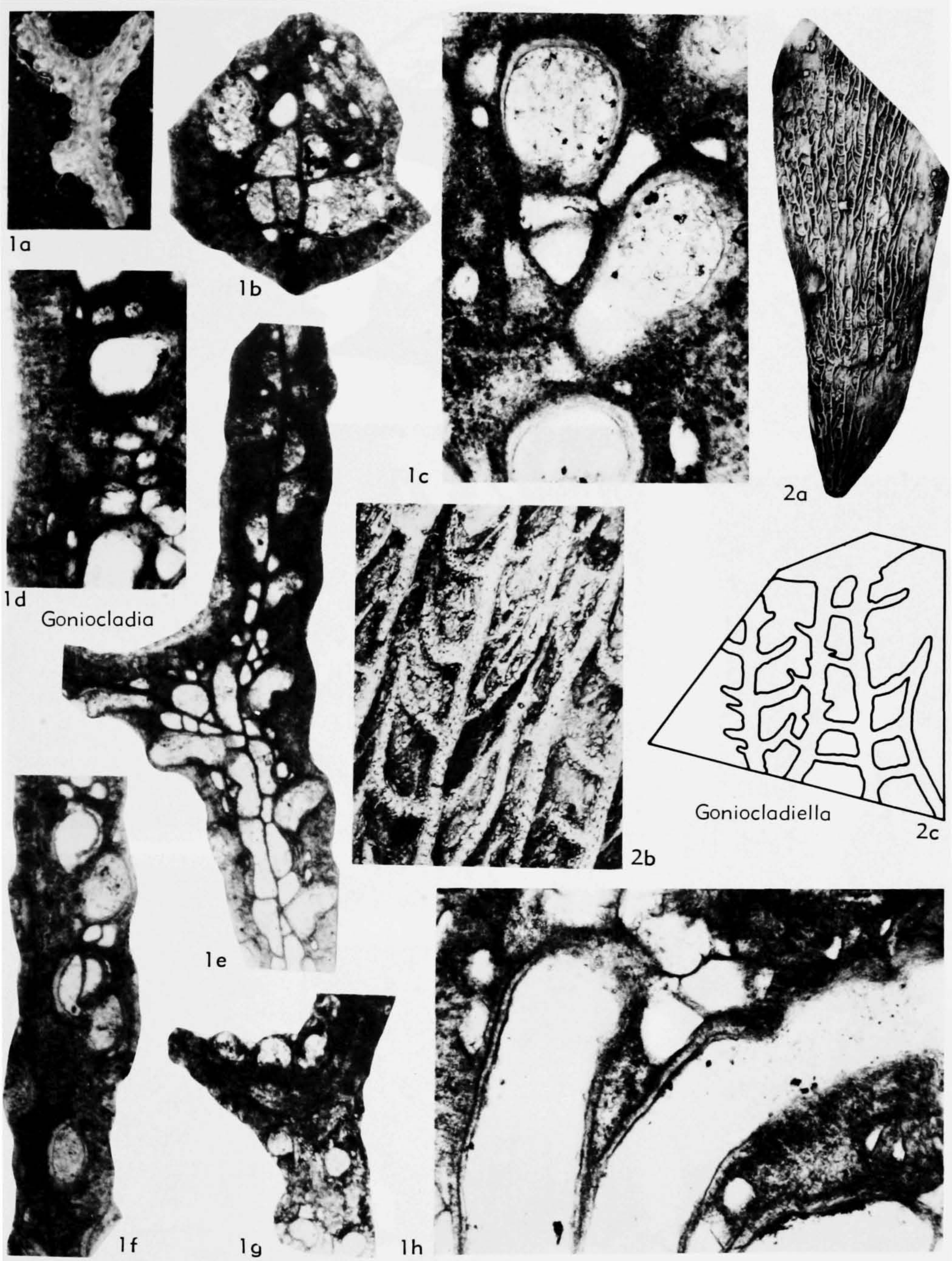


Fig. 213. Goniocladiidae (p. 434).

luliferous reverse and few rows of autozooecia on rounded obverse side. Main branches subparallel, undulatory; side branches diverging distolaterally, fusing to form frond with polygonal fenestrules in some. [Types of the type species of *Goniocladiella* are impressions and the internal anatomy is not known. *G. parallela* Nekhoroshev, 1956, has been erroneously cited as the type species, but it too is known only from surface features. Thin sections of species of this genus were not available for study.] *L.Carb.*, USSR. ——Fig. 213,*2a,b*. *G. parallela* Nekhoroshev, L. Carb., $C^2{}_1$, Altai, USSR, type; *a*, fenestrate zoarium with polygonal fenestrules;

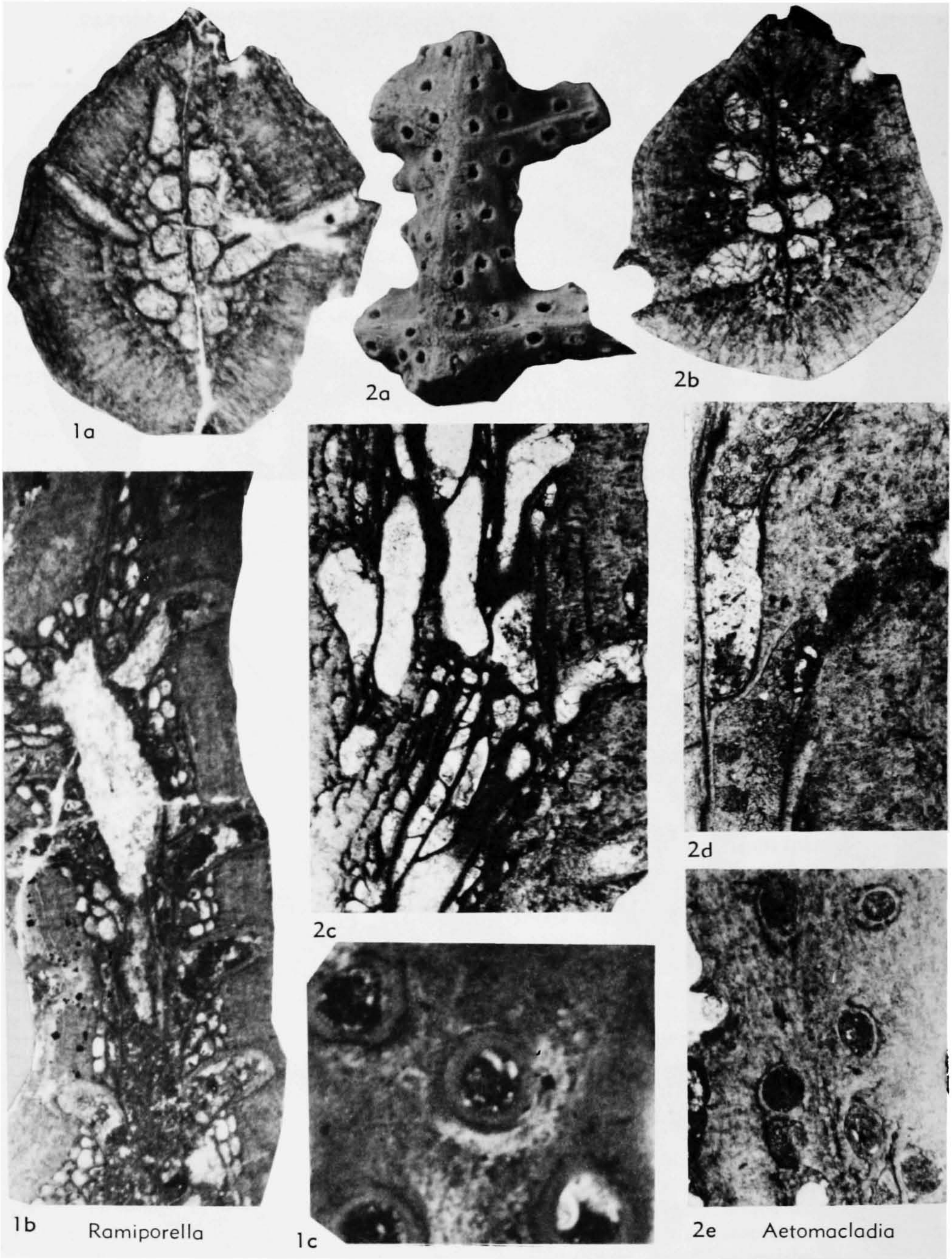


FIG. 214. Goniocladiidae (p. 434–438).

×0.5; *b*, undulatory branches, irregular fenestrules, few rows of autozooecia; ×3.0 (photographs courtesy of V. P. Nekhoroshev).——FIG. 213,*c*. **G. kasakhstanica*, holotype; fenestrate colony; ×1.5 (after Nekhoroshev, 1953, pl. 24, fig. 4a).

Ramipora TOULA, 1875, p. 230 [**R. hochstetteri*; OD; Perm.-Carb. (?L. Perm.), Spits.]. Zoarium bifoliate; branches rounded, with vertical mesotheca forming keel on noncelluliferous reverse side and on celluliferous obverse side. Main branches with secondary and tertiary branches

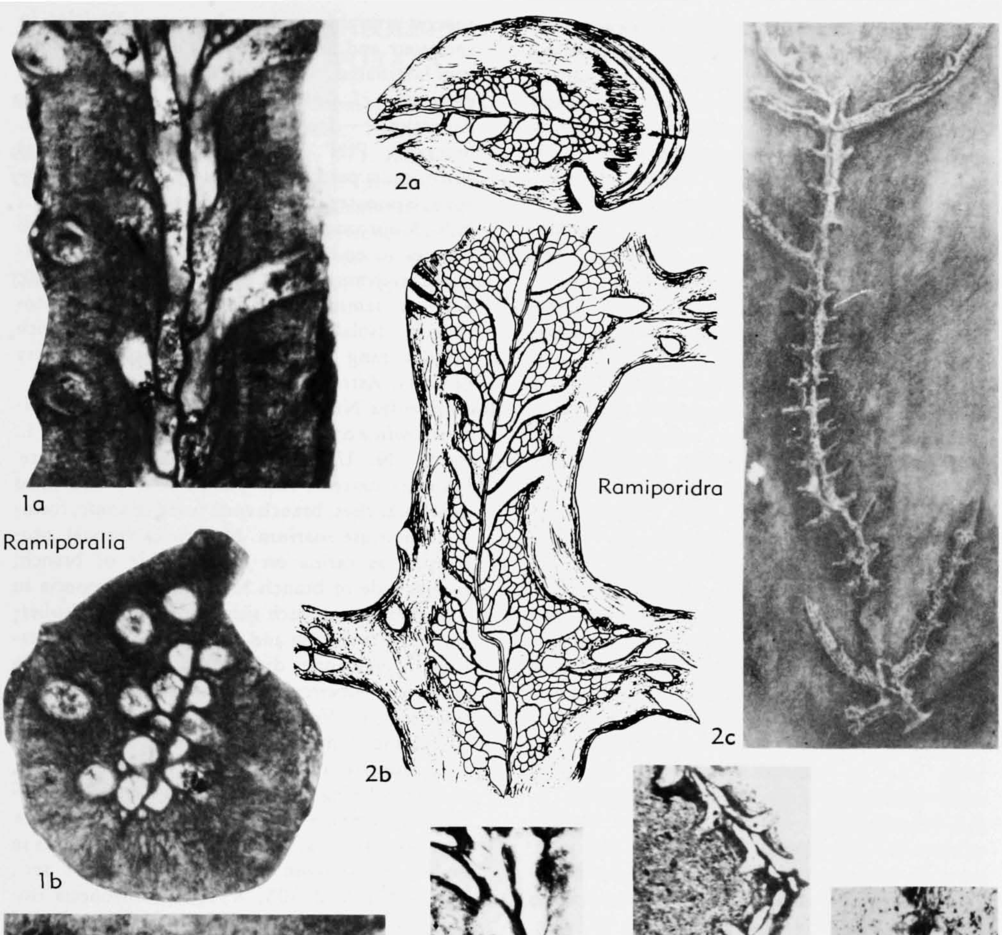


FIG. 215. Goniocladiidae (p. 436–438).

diverging distolaterally, commonly in pairs, and joining to form frond with large, polygonal fenestrules. Autozooecia partially isolated at mesotheca, hemispherical in cross section; recumbent portion long, erect in exozone; diaphragms sparse. Few rows of subcircular autozooecia with lunaria, isolated by stereom. Vesicles in endozone and exozone, blisterlike; stereom laminated, with tubules through most of exozone. *Perm.,* USSR, Spits.——FIG. 215,*3a–c*. **R. hochstetteri,* U. Perm., Starostinskaja Suite, Spits.; *a,* fusion of secondary branches, laminated stereom isolates autozooecia in exozone; deep tang. sec., PIN 2237/254, ×10; *b,* long recumbent portion of autozooecia, sparse vesicles at zooecial bend, stereom in exozone; deep tang. sec., PIN 2237/255, ×15; *c,* branched zoarium with large polygonal fenestrules, vertical mesotheca with one range of autozooecia on each side; deep tang. sec., PIN 2237/255, ×10 (photographs courtesy of I. P. Morozova).

Ramiporalia SHULGA-NESTERENKO, 1933, p. 42 [**R. dichotoma*; OD; L. Perm., N. Urals, USSR]. Zoarium bifoliate; branches dichotomous and subcylindrical, each with vertical mesotheca protruding as low carina on celluliferous obverse side, reverse side noncelluliferous. Autozooecia hemispherical in cross section at mesotheca, partially isolated by tiny vesicles; recumbent portion long, erect in exozone; diaphragms not seen; walls laminated, with laminated lunarium on side of zooecia away from branch center. Vesicles extremely small blisters in endozone and inner exozone. Laminated stereom with tubules in exozone isolating intersecting rows of autozooecia with subcircular apertures. *L.Carb.-U.Perm.,* USSR, Australia.——FIG. 215,*1a–c*. **R. dichotoma,* holotype, PIN 2985/0636; *a,* undulatory mesotheca, long recumbent portion of autozooecia, small vesicles in endozone and inner exozone, stereom in exozone; long. sec., ×20; *b,* mesotheca, hemispherical autozooecia and small vesicles in endozone, stereom with numerous tubules (reverse side below); transv. sec., ×20; *c,* subcircular autozooecia, with laminated walls and lunaria (left), isolated by laminated stereom with tubules; tang. sec., ×40 (photographs courtesy of G. G. Astrova).

Ramiporella SHULGA-NESTERENKO, 1933, p. 39 [**R. asimmetrica*; OD; L. Perm., N. Urals, USSR]. Zoarium bifoliate; branches subcylindrical; primary branch straight or undulatory, with alternating right and left secondary branches and some tertiary branches. Mesotheca vertical, thin, protruding as low carina on subrounded obverse side; reverse side more rounded. Autozooecia in endozone hemispherical in cross section, partially isolated by vesicles; erect in exozone, subcircular in cross section. Walls laminated, with laminated lunarium on side of autozooecia away from branch center. Vesicles in endozone and exozone; small, low blisters; stereom laminated, with numerous tubules, in outer exozone. *?L.Carb.,U.Carb.-U.Perm.,* USSR, Australia.——FIG. 214,*1a–c*. **R. asimmetrica,* holotype, PIN 2985/115; *a,* hemispherical autozooecia partially isolated by vesicles in endozone, laminated stereom in exozone; transv. sec., ×20; *b,* autozooecia isolated by moderately small vesicles in endozone and inner exozone, laminated stereom in outer exozone; long. sec., ×20; *c,* thick, laminated walls and lunaria in autozooecia, isolated by laminated stereom with tubules; tang. sec., ×40 (photographs courtesy of G. G. Astrova).

Ramiporidra NIKIFOROVA, 1938, p. 197 [**Ramipora uralica* STUCKENBERG, 1895, p. 169; OD; L. Perm., N. Urals, USSR]. Zoarium bifoliate; branches narrow, with paired second and third order branches; branch ends fused in some, forming fenestrate zoarium. Mesotheca vertical, protruding as carina on obverse side of branch; reverse side of branch rounded. Autozooecia in 5 or 6 ranges on each side of carina; hemispherical in cross section and partially isolated by vesicles in endozone; diaphragms absent; erect in endozone, subcircular in cross section with indistinct lunaria. Vesicles low blisters in endozone, decreasing in height into exozone. Stereom possibly laminated, with tubules, in outer exozone, widely isolating autozooecia. *?L.Carb., U.Carb.-U.Perm.,* USSR.——FIG. 215,*2a–c*. **R. uralica* (STUCKENBERG); *a,* vertical mesotheca, vesicles in endozone, stereom in exozone; transv. sec., TsGM No. 982/305, ×11; *b,* autozooecia isolated by vesicular tissue at mesotheca, laminated stereom in outer exozone; deep tang. sec., TsGM No. 982/305, ×11; *c,* primary, secondary, and tertiary branches, median carina, few ranges of autozooecia on obverse side; holotype, Museum, State University of Kazan, ×1 (photograph courtesy of V. P. Nekhoroshev).

GENERIC NAMES OF INDETERMINATE OR UNRECOGNIZABLE STATUS ASSIGNED TO CYSTOPORATA

Anellina GREGORIO, 1930, p. 33 [**Eschara (Anellina) parvula*; M]. *Perm.,* Italy.

Archaeotrypa FRITZ, 1947, p. 435 [**A. prima*; OD]. *U.Cam.,* Alberta, Can.

Cycloidotrypa CHAPMAN, 1920, p. 366 [**C. australis*; OD]. *L.Carb.,* Moorowarra, Australia.

Diptheropora DEKONINCK, 1873, p. 13 [**D. regularis*; OD]. *Carb.,* Bleiberg, Ger.

Tuberculopora RINGUEBERG, 1886, p. 21 [**T. inflata*; OD]. *M.Sil.,* Lockport, N.Y., USA.

GENERIC NAMES ERRONEOUSLY ASSIGNED TO CYSTOPORATA

Bolopora LEWIS, 1926, p. 420. Chemogenic or bacteriogenic dubiofossil (HOFMANN, 1975).

Cambroporella KORDE, 1950, p. 371. Alga.

Coenites EICHWALD, 1829, p. 179. Tabulate coral. Specimens of this genus lack vesicular tissue and the "lunaria" are proximal projections of oblique corallites developed during late ontogeny.

Dianulites EICHWALD, 1829, p. 180. Trepostomate.

Glossotrypa HALL, 1886, pl. xxxi. Trepostomate.

Revalotrypa BASSLER, 1952, p. 382. Trepostomate.

Solenopora DYBOWSKI, 1878, p. 124. Alga.

Spatiopora ULRICH, 1882, p. 155. Trepostomate.

NOMINA NUDA

Diaphragmopora MCFARLAN, 1926, p. 223.

Didymopora ULRICH, 1882, p. 156.

Pakridictya MÄNNIL, 1959, p. 38.

THE ORDER CRYPTOSTOMATA

By Daniel B. Blake

[University of Illinois, Urbana]

The Cryptostomata was first proposed as a bryozoan suborder by Vine (1884). Only five genera were assigned to the suborder. Of these, two have since been considered bifoliate cryptostomates (*Ptilodictya* and *Stictoporella*) and two, rhabdomesine cryptostomates (*Glauconome,* now *Glauconomella,* and *Rhabdomeson*). One is now assigned to the Cystoporata (*Arcanopora,* now *Sulcoretepora*). The fenestellines were not included in the original concept. According to Vine, cryptostomates are distinguished by the tubular to subtubular longitudinal outline of zooecia, their angular cross section, and the vestibule concealing the orifice.

In ensuing years, Ulrich (1890, 1893) placed additional families including the fenestellids in the group, which he raised to ordinal rank. He provided a diagnosis and a list and descriptions of component families. Ordinal diagnoses since Ulrich have stressed a limited number of characters, the most important being zooecial shape; presence of a vestibule; a well-developed, generally abruptly arising exozone; and, in many taxa, the presence of hemisepta.

Ulrich was much concerned with relationships among cryptostomates. Many morphological similarities mentioned here were first noted by him (1890, 1893), and he expressed such relationships as those between phylloporinids and fenestellines in phylogenetic terms. Ulrich (1890) stressed the importance of what now would be called a polythetic classification (". . .in the aggregate of characters is found the true test of relationship," p. 329); and in various points in his text, he suggested phylogenetic relationships among taxa (p. 357) and the problems evolution imposes upon the recognition of taxa (p. 328).

McNair (1937) informally recognized three zoarial types in the cryptostomates, a unilaminate group including the phyllopo-

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Fig. 216. Morphology of the Cryptostomata.——*1. Rhabdomeson* sp., Rhabdomesina; Cathedral Mt. F., M. Perm., Texas; cryptostomate holdfast, rapid development of erect growth habit; USNM 222618, ×5.6.——*2. Arthrostyloecia nitida* Bassler, Rhabdomesina; Edinburg F., M. Ord., Va.; reverse, ridge-bearing surface to left, obverse surface to right; apertures enclosed by prominent peristomes; syntype, USNM 240802, ×9.2.——*3. Ulrichostylus* sp., Rhabdomesina; Bromide F., M. Ord., Okla.; a primitive cryptostomate showing cylindrical growth habit, apertural alignment, longitudinal ridges, and extrazooecial skeleton developed as a basal articulation process; USNM 214196, ×9.2.——*4. Orthopora regularis* (Hall), Rhabdomesina; M. Dev., N.Y.; ramose dichotomous growth habit; cylindrical branches, aligned apertures, and stylet development; syntype, AMNH 35758B, ×3.6.——*5. Saffordotaxis incrassata* (Ulrich), Rhabdomesina; New Providence F., L. Miss., Ky.; spiral arrangement and elliptical outlines of apertures, stylet development, UI X-5380, ×5.6.——*6. Rhabdomeson* sp., Rhabdomesina; Word F., Perm., Texas; conical growth habit, extreme monticule development, apertural arrangement; USNM 222620, ×2.3.——*7. Rhinidictya grandis* Ulrich, Ptilodictyina; Platteville Gr., M. Ord., Ill.; ramose growth habit, flattened branch outline; linear and spiral arrangement of apertures; syntype, USNM 43606, ×9.2.——*8. Hemitrypa proutana* Ulrich, Fenestellina; Warsaw F., mid. Miss., Ill.; reticulate growth habit and a fragment of netlike extrazooidal skeletal superstructure (arrow); ISGS 2818-1, ×5.6.——*9. Phylloporina clathrata* (Miller & Dyer), Fenestellina; Mt. Hope F., U. Ord., Ky.; fenestrate growth and apertural arrangement in a primitive fenestellid; USNM 214213, ×9.2.——*10. Phylloporina variolata* Ulrich, Fenestellina; Eden Gr., U. Ord., Ohio; reverse surface in a phylloporinid; syntype, USNM 214214, ×9.2.——*11. Archimedes* sp., Fenestellina; Pennington F., U. Miss., Ky.; extrazooidal skeleton in form of an axial column and basal struts (arrow); UI X-5381, ×1.6.——*12. Lyropora divergens* Ulrich, Fenestellina; U. Miss., Ill.; fenestrate growth habit and extrazooecial basal keel; syntype, ISGS 2783, ×3.6.——*13. Acanthocladia fruticosa* Ulrich, Fenestellina; Penn., Ill.; pinnate growth habit, development of surficial ridges, small peristomes enclosing apertures; ?syntype, ISGS 4471-1, ×3.6.

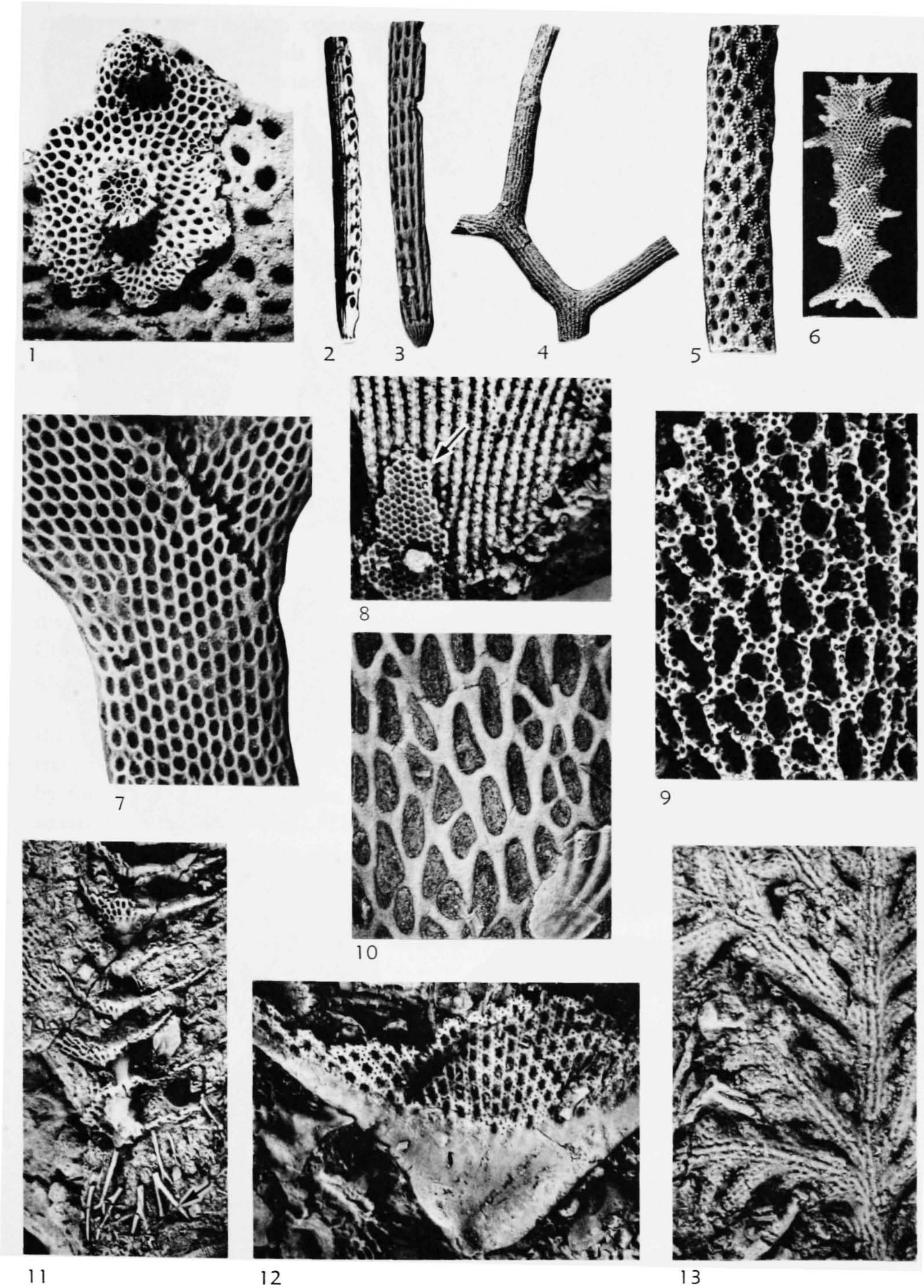

FIG. 216. *(For explanation, see facing page.)*

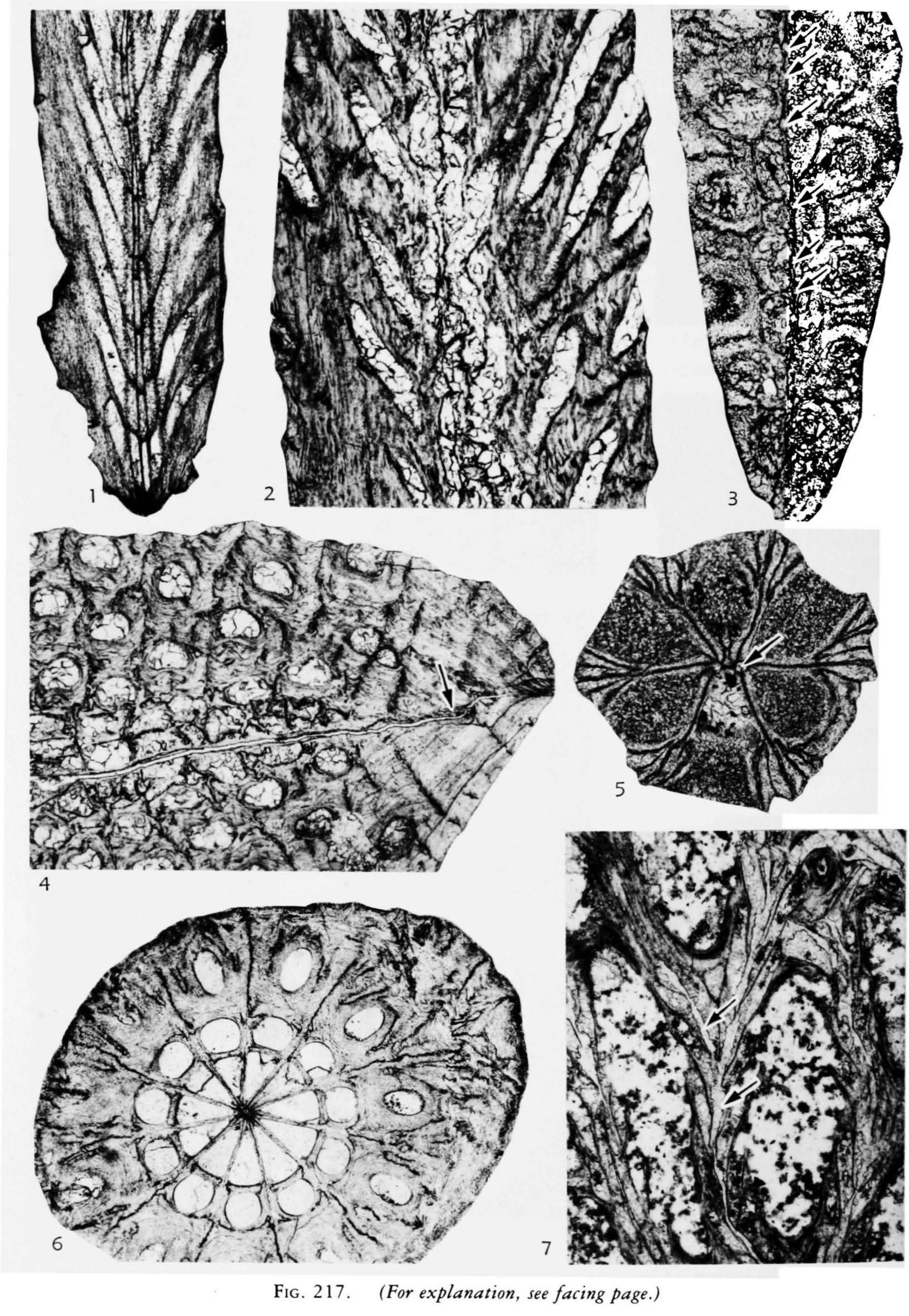

FIG. 217. *(For explanation, see facing page.)*

rinids and fenestellids, a cylindrical group including the arthrostylids and rhabdomesids, and a bifoliate group including the rhinidictyids, ptilodictyids, and sulcoreteporids. McNair (1937, p. 154) did not consider the three divisions to be taxonomically significant: "There is little evidence to indicate that these three divisions based on zoarial forms should be considered taxonomic units or that members within such divisions are related phylogenetically; it seems more probable that similar zoaria were evolved by a number of stocks."

Astrova and Morozova (1956) formally recognized the three groups of McNair (1937) as suborders, interpreting each as a natural phylogenetic branch. Subsequently, Morozova (1966) established the Timanodictyoidea for certain Permian bryozoans. Termier and Termier (1971) interpreted the three original suborders as phylogenetically distinct, and they thought that the order Cryptostomata represents an evolutionary grade.

The Cryptostomata was subdivided first through the recognition of the order Fenestrata by Elias and Condra (1957) and then by the recognition of the order Rhabdomesonata by Shishova (1968). These changes left only the Ptilodictyoidea and the Timanodictyoidea in the Cryptostomata. The Fenestrata of Elias and Condra was based largely upon the presence of a "colonial plexus," expressed as a clear granular calcite layer. Also important in the concept of the Fenestrata were inferred homologies between the colonial plexus and the cyclostomate common bud. Shishova (1968), in considering the fenestellids, further emphasized zooecial shape, budding pattern, microstructure, the presence of peristomes, and in some cases, lunaria and ovicells. The Rhabdomesonata of Shishova was based primarily upon zoarial form, zooecial shape, and budding pattern. Shishova did not consider the three traditional cryptostomate suborders to be closely related.

The new ordinal concepts of Fenestrata and Rhabdomesonata have not been universally accepted. For example, following the classification of Astrova and Morozova (1966), Tavener-Smith and Williams (1972) considered the three major groups to be suborders. Cuffey (1973), in a numerical taxonomic study, retained the unified Cryptostomata. Within the order, he concluded that the rhabdomesines and ptilodictyines were closer to each other than either were to the fenestellines. He recognized two suborders with the rhabdomesines and ptilodictyines as infraorders in one and the fenestellines alone in the other.

Blake (1975, 1980) argued for retention of the three traditional branches as suborders within an order Cryptostomata because of morphological similarities among the Ordo-

Fig. 217. Comparison of Arthrostylidae and Stictoporellidae.——*1. Ulrichostylis* sp., Rhabdomesina; Bromide F., M. Ord., Okla.; long, slightly curved zooecia in an early arthrostylid; long. sec., USNM 214205, ×28.——*2. Stictoporellina gracilis* (Eichwald), Ptilodictyina; Ranicips Ls., L. Ord., Öland, Swed.; long, slightly curved zooecia in an early ptilodictyid; long. sec., USNM 214207, ×28.——*3. Stictopora* sp., Ptilodictyina; McLish F., M. Ord., Okla.; median wall bearing mural rods (arrows), granular zones, and fine laminae; transv. sec., USNM 222627, ×28.——*4. Stictoporellina gracilis* (Eichwald), Ptilodictyina; same data as *2*; median wall, granular zones, extrazooecial skeleton at lateral margin of zoarium, small interval of laminated median wall (arrow), and extensive wall constructed of fine laminae; prominent clear line is a crack following median wall; transv. sec., USNM 214207, ×28.——*5. Nematopora lineata* Billings, Rhabdomesina; Sil., Anticosti Is., Can.; median rods (arrow); granular zones along midline of endozonal wall, radiating in the exozone; fine laminae and trend toward development of a median wall; transv. sec., USNM 43384, ×92.——*6. Ulrichostylus* sp., Rhabdomesina; same data as *1*; sharply defined central axis; granular zones along zooecial boundaries in endozone, then radiating in exozone; fine laminae; transv. sec., USNM 214211, ×28.——7. Unidentified genus and species, Phylloporinidae, Fenestellina; Bromide F., M. Ord., Okla.; long attenuated zooecia, thickened and nonlaminated layer (arrows); long. sec., USNM 214217, ×28.

FIG. 218. *(For explanation, see facing page.)*

vician members of the Arthrostylidae (Rhabdomesoidea), Phylloporinidae (Fenestelloidea) and some genera of the Rhinidictyidae and Stictoporellidae (Ptilodictyoidea).

THE ORDER CRYPTOSTOMATA

The Cryptostomata are an order of almost entirely erect stenolaemate bryozoans with generally limited bases of attachment (Fig. 216,*1*). Zoaria may be unbranched, bushlike, pinnately branched, or reticulated (Fig. 216,*2–13*). Stem cross sections are approximately cylindrical or flattened. Zooecia generally are arranged in regular longitudinal or spiral rows, and the apertures are elliptical, subcircular, or rectangular in outline (Fig. 216,*2,3,5–9*). Zooecial apertures may be present on all surfaces, or a barren reverse surface may be developed (Fig. 216,*2,10*). Surfaces are commonly ornamented with striae or ridges, peristomes (Fig. 216,*2–4*), and stylets or similar structures (Fig. 216,*5*). Extrazooecial skeletal material may be extensive, developed as rootlike attachment structures, as thickened deposits between zooecia or along the reverse surfaces of zoaria, in the form of a netlike superstructure, or in other patterns (Fig. 216,*2,3,8,11,12*). Multizooecial skeletal deposits are present within the reverse wall of some taxa.

Budding took place from linear or planar loci (Fig. 217,*3–6*). Zooecia generally are short (Fig. 218,*2*), but can be long and attenuated, especially in earlier representatives (Fig. 217,*1,2*). In most genera, the endozonal walls are thin and the exozonal walls relatively thick (Fig. 218,*1*). The transition between the two zones usually is abrupt and marked by a distinct zooecial bend, a change in orientation in which the zooecial axes turn from approximately parallel to the branch axis to essentially perpendicular to the branch surface (Fig. 218,*1,6*). The body cavity within the exozone, the so-called vestibule, commonly is constricted. One or more hemisepta are common on the proximal wall at the zooecial bend, and one or more may be present on the distal wall, in the outer endozone (Fig. 218,*6*). Other intrazooecial structures include mural spines and diaphragms (Fig. 219,*2*), the latter most commonly in genera with elongate zooecia.

Cryptostomate walls are constructed primarily of microscopically laminated deposits, but microscopically nonlaminated material usually is present, and may be extensively developed in the Fenestellina (Fig. 217,*7*; 221,*1*). Nonlaminated material forms the interior of walls, usually along zooecial boundaries. It may be discontinuous, appearing as intermittent granules. Nonlaminated material forms the axes of various types of stylets (Fig. 219,*4–6,8,9*). Walls in erect portions of zoaria apparently were entirely compound in nature, and diverse polymorphs and nonpolymorphic openings were developed (Fig. 216,*6*; 218,*3–5*; 219,*1,3*).

FIG. 218. Comparison of Arthrostylidae and later Rhabdomesina.——*1. Cuneatopora lindstroemi* ULRICH, Rhabdomesina; Sil., Gotl.; arthrostylid morphology; note zooecial shape and well-defined central axis; ?paratype, USNM 214193, ×28.——*2. Nematopora fragilis* ULRICH, Rhabdomesina; Sil., Ill.; short, robust zooecia and median rod representative of some arthrostylids; long. sec., ?syntype, USNM 214222, ×91.——*3. Streblotrypa* cf. *S. marmionensis* ETHERIDGE, Rhabdomesina; Perm. (Callytharra), W. Australia; multiple metapores (arrows) associated with each zooecium; long. sec., USNM 112466, ×91.——*4. Acanthoclema scutulatum* HALL, Rhabdomesina; Ludlowville Sh., M. Dev., N.Y.; stylet and single metapore (arrows) associated with each zooecium; long. sec., USNM 214200, ×91.——*5. Helopora* sp., Rhabdomesina; Jupiter River F., Sil., Anticosti Is., Can.; single metapore (arrows) with each zooecium; long. sec., USNM 214199, ×55.——*6. Orthopora* sp., Rhabdomesina; Keyser Ls., Sil.-Dev., W. Va.; zooecial form in early member of the suborder; well-developed zooecium in the plane of section (arrow); in distal and proximal parts of section, central axis is passing out of plane of view; well-developed hemisepta and acanthostyles also evident; long. sec., USNM 222625, ×68.——*7. Ulrichostylus* sp., Rhabdomesina; Bromide F., M. Ord.; irregular nonlaminated skeletal layer (arrow) near colony axis and in the midline of the wall, enclosed by thicker laminated layer; transv. sec., USNM 222626, ×182.

Space-enclosing vesicles occur in bifoliates (Fig. 219,*2*). Structurely diverse stylets are developed (Fig. 219,*4–9*). Cryptostomates only rarely show development of overgrowths, and interzooecial pores are lacking.

A traditional argument for grouping the three cryptostomate suborders is reflected in the ordinal name, "hidden mouth." Various earlier workers believed the terminal membrane to be beneath the skeletal surface of the branch at the base of the vestibule, which is that portion of the zooecium within the exozone. The only evidence for a terminal-membrane position at the base of the vestibule appears to be the complex shape of the zooecium. Although recessed terminal diaphragms have been recognized in modern tubuliporates, these diaphragms are near the aperture in most taxa. There is no strong evidence that cryptostomate terminal membranes were recessed.

The order Cryptostomata contains the suborders Rhabdomesina, Fenestellina, Ptilodictyina, and Timanodictyina. Some subordinal grouping, such as that suggested by CUFFEY (1973), seems desirable but is deferred until completion of *Treatise* revision of stenolaemate taxa. Affinities of the Cryptostomata within the phylum have been a matter of some controversy, and in different classifications the order has been included within both the stenolaemates and the gymnolaemates. BOARDMAN (this revision) discusses the subject in his historical review of stenolaemate studies.

The Timanodictyina is not further considered here because of its exclusively upper Paleozoic range.

COMPARISON OF EARLY CRYPTOSTOMATE FAMILIES

Subordinal status for each of the three long-ranging groups of cryptostomates is based largely on the distinctive nature of later families; however, the morphology of early cryptostomates strongly suggests a common ancestry for the three. As stenolaemate history is presently understood, these affinities should be reflected in classification by inclusion of all branches in a single order. The early families are compared in Table 5.

The ancestral cryptostomate probably separated from earlier bryozoan stocks through the evolution of either a one- or two-dimensional budding locus (Table 5, no. 4; see BLAKE, 1980). The three major cryptostomates lineages subsequently were founded on the development of individual budding-loci patterns and growth habits (Table 5, no. 1). Phylogenetic relationships among the three have not been studied, and their approximately simultaneous appearance in the stratigraphic record does not aid in the determination of sequence. The Arthrostylidae, however, is morphologically intermediate and therefore the other two stocks are compared to it. Because of their diversity, the arthrostylids may be of disparate ancestry. As presently understood, this seems unlikely because the family is unified by a number of common features, most important of which

FIG. 219. Comparison of Rhabdomesina and Ptilodictyina.——*1. Streblotrypa* cf. *S. marmionensis* ETHERIDGE, Rhabdomesina; Perm. (Callytharra), W. Australia; metapore appearance (arrow); tang. view, USNM 112446, ×91.——*2.* Unidentified genus and species, Rhinidictyidae, Ptilodictyina; McLish F., M. Ord., Okla.; slender, elongate zooecia, diaphragms, and vesicles; long. sec., USNM 222621, ×28. ——*3. Helopora fragilis* HALL, Rhabdomesina; Clinton Gr., Sil., Hamilton, Ont.; tabulated metapore (arrow); USNM 222622, ×68.——*4. Nicklespora elegantula* (ULRICH), Rhabdomesina; Keokuk Gr., Miss., Ky.; small stylet; syntype, USNM 168365, ×360.——*5. Stictoporellina gracilis* (EICHWALD), Ptilodictyina; Ranicips Ls., L. Ord., Öland, Swed.; small stylets; USNM 214207, ×91.——*6. Ulrichostylus* sp., Rhabdomesina; Bromide F., M. Ord., Okla.; stylets in an early arthrostylid; USNM 222623, ×180. ——*7. Rhombopora* cf. *R. lepidodendroides* MEEK, Rhabdomesina; Catacora Marl, L. Perm., Yauichambi, Bol.; stylet; UI X-5382, ×180.——*8. Nikiforovella* sp., Rhabdomesina; Ludlowville coral bed, Dev., Ont.; small stylets; USNM 222619, ×912.——*9. Acanthoclema scutulatum* HALL, Rhabdomesina; Ludlowville Sh., M. Dev., N.Y.; stylets (arrow); USNM 222624, ×360.

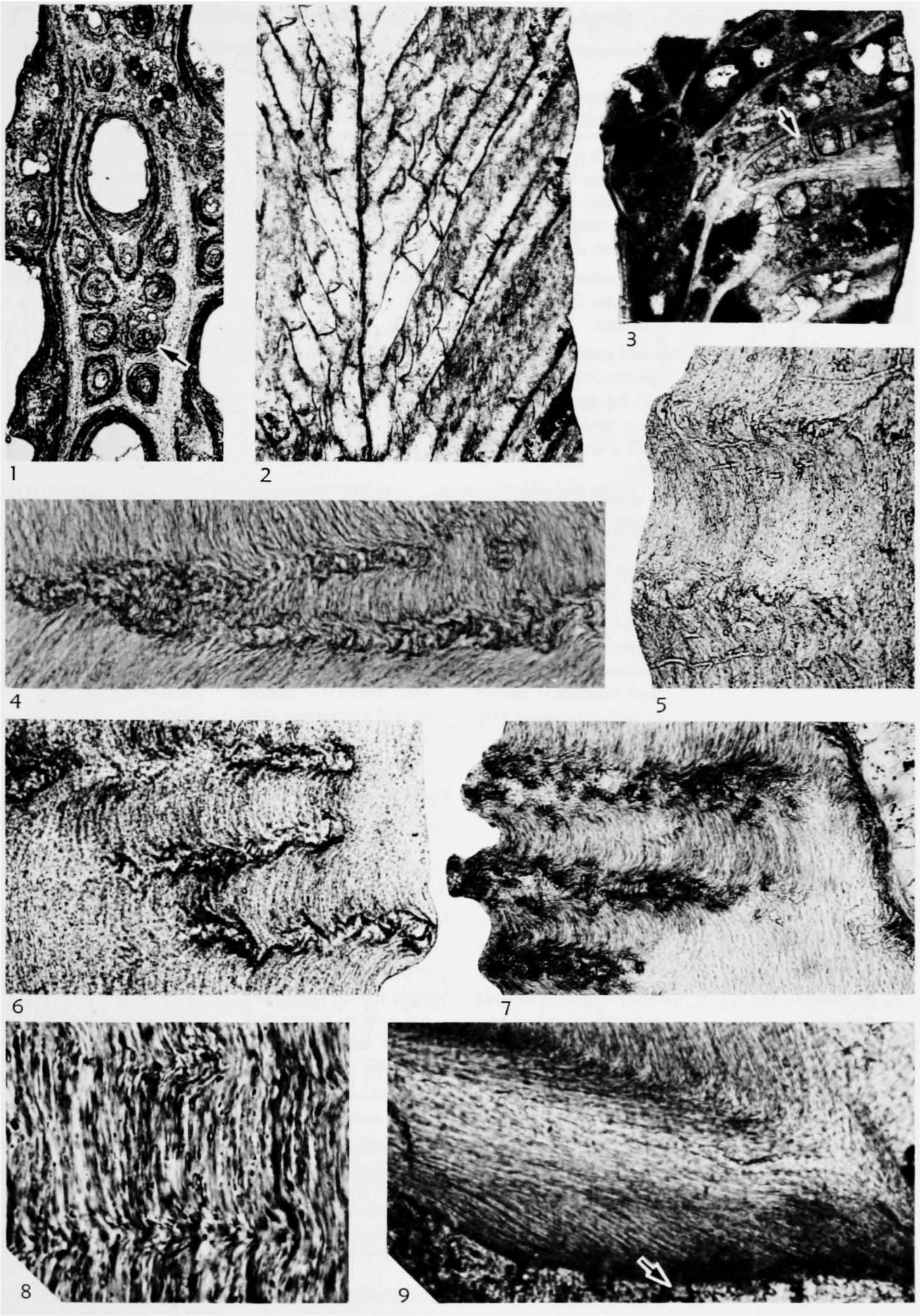

FIG. 219. *(For explanation, see facing page.)*

Table 5. *Comparison of Early Cryptostomate Families.*

Character	Arthrostylidae (Rhabdomesina)	Phylloporinidae (Fenestellina)	Rhinidictyidae Stictoporellidae (Ptilodictyina)
1. Zoarial habit	Erect; most species branching but not anastomosing; stems cylindrical, some species articulated throughout	Erect; anastomosing; stems cylindrical, not articulated	Erect; most species branching, anastomosing in some; stems flattened, some species with basal articulation
2. Stem diameter	Early representatives may be under 0.5 mm; to 1.0 mm	Commonly 0.5 to 0.75 mm	Early representatives may be 0.75 to 1.0 mm
3. Zooecial distribution	Around stem axes in most species; one surface lacking apertures in some species; these with 2 to 5 apertural rows	One surface lacking apertures; with 2 to about 8 apertural rows	Two dimensional
4. Budding locus	One dimensional; at least locally in some species, the axis widens to form a two-dimensional budding surface	One dimensional or narrow two dimensional	Two dimensional
5. Zooecial shape	Elongate in early species; shorter in most later species; zooecia angular, with distinctive pattern of wall thickening (Fig. 220)	Elongate in most species; somewhat shortened in a few; zooecia angular, with distinctive pattern of wall thickening (Fig. 220)	Elongate in certain early species, somewhat shortened in others; zooecia angular with distinctive pattern of wall thickening (Fig. 220)
6. Nature of apertures	Elliptical, peristomes present in some	Elliptical to circular; peristomes present in some	Elliptical, subcircular, rectangular; peristomes present in some
7. Intrazooecial structures	Diaphragms and hemisepta present in some	Diaphragms and hemisepta present in some	Diaphragms and hemisepta present in some
8. Polymorphs or similar structures	Lacking in most species, metapores in a few later species	Lacking in some species, mesoporelike structures in others	Vesicular skeletal material and mesoporelike structures in a few species
9. Secondary skeletal structures	Diverse stylets; longitudinal surficial ridges present in some	Simple stylets; longitudinal surficial ridges present in some	Usually simple stylets; longitudinal surficial ridges present in some
10. Skeletal microstructure	Laminated wall dominant, nonlaminated wall commonly thick but discontinuous; laminae fine, bearing radiating, planar, irregular zones in some species; median rods in a few species	Laminated wall dominant, nonlaminated wall in some well developed, continuous; laminae fine, bearing radiating, planar, irregular zones in some species; median rods lacking	Laminated wall dominant; nonlaminated wall commonly thick but discontinuous; laminae fine, bearing radiating, planar irregular zones in some species; median rods in some species

are zoarial form and the nature of budding loci.

Among arthrostylids and bifoliates, two of the most similar taxa are the oldest known representatives of each, *Ulrichostylus spiniformis* (Ulrich) (Arthrostylidae) and *Stictoporella gracilis sensu* Bassler, 1911 (Stictoporellidae). Similarities include zooecial

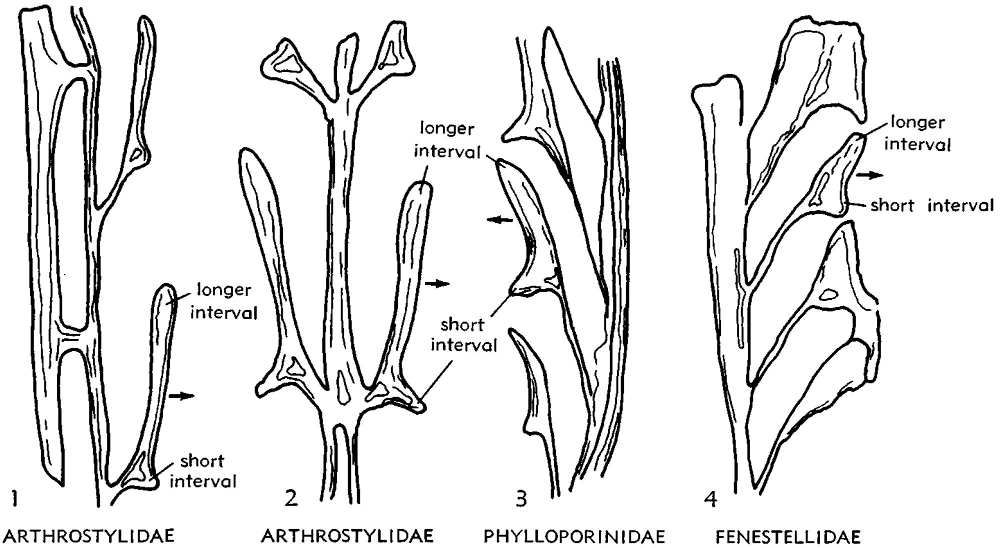

FIG. 220. Cryptostomate exozone development, based on specimens in Figure 221,*6–9*. *1,2,* Arthrostylidae; *3,* Phylloporinidae; *4,* Fenestellidae. Zooecial shapes are similar among the specimens, and endozonal walls are thin. Endozonal walls branch at the base of the exozone; the branch is marked by thickening of nonlaminated skeletal material. A short interval, thickened on both sides of the zooecial boundary, is directed proximally and forms the distal wall of a zooecium. A longer interval is directed distally, approximately paralleling the zooecial and zoarial axes. This wall is thickened primarily on the outer skeletal surfaces (arrows).

shape (Fig. 217,*1,2*), skeletal structures (Fig. 217,*4,6*; 218,*7*), and the presence of simple stylets (Fig. 219,*5,6*). Major differences are in zoarial size and budding pattern (Fig. 217,*4,6*).

Other shared characters among some early members of the two stocks (Table 5) include an overlapping range of stem diameters, presence of zoarial articulation, nature of apertural development, similar zooecial shapes (Fig. 220), presence of median rods (Fig. 217,*3,5*), and, in some arthrostylids, an indication of a two-dimensional budding locus (Fig. 217,*5*).

Each lineage developed its own distinctive characters, including vesicular skeletal structures and anastomosing growth habits in the bifoliates and extensive articulation in the arthrostylids.

The Phylloporinidae is poorly understood. Ross (1963, p. 592) pointed out, "All the genera. . .in the Family Phylloporinidae . . .require critical study to determine their systematic positions." In order to avoid inconsistency with future taxonomic arrangement, no attempt has been made here to update names used in illustrations.

Characters that phylloporinids and arthrostylids have in common (Table 5) include the presence of a reverse surface (Fig. 216,*2,10*; 221,*1,2*), similar numbers of apertural rows, and the presence of longitudinal ridges and peristomes. Members of both families have well-developed nonlaminated skeletal deposits along the midlines of lateral and reverse walls and forming axes of ridges on zoarial surfaces. The layer, however, is weak or absent from the front of zooecia (Fig. 217,7; 221,*1*). Thin, dark, irregular skeletal zones occur in both (Fig. 217,*6*; 221,*2*), and similar stylets may occur (Fig. 221,*3,4*). Distinctive, irregular polymorphs are present in certain phylloporinids; however, small polymorphlike structures are present in a few arthrostylids (Fig. 219,*3*). The Phylloporinidae is most readily distinguished on the basis of growth habit.

COMMENTS ON OTHER BRYOZOANS

Some authors (e.g., Ulrich, 1890; Ross, 1964b; Shulga-Nesterenko & others, 1972) have described similarities between the Phylloporinidae and the Fenestellidae, placed them together in classifications, and noted the possibility of a close phylogenetic relationship; however, other authors (for example Bassler, 1953) considered the two not to be closely related. Dunaeva and Morozova (1975) removed the Phylloporinidae from their Fenestelloidea, emphasizing different zooecial shapes, the presence of "specific heterozooids" in the phylloporinids, and the absence of ovicells from that family. Thus, a brief review of the similarities between the two families is necessary because the phylloporinids occupy a critical position in present interpretations.

Characters common to the phylloporinids and the fenestellids include zoarial habit, skeletal-layer development, wall thicknesses, and stylet development. Zooecial similarities between the phylloporinids and fenestellids are important. Some early fenestellids possess elongate zooecia, shorter than but suggestive of shapes seen in the phylloporinids (*Fenestella granulosa* Whitfield, Fig. 220; 221,*5,9*; compare with Fig. 221,*8*). Zooecia in a few phylloporinids appear quite short and resemble those of more typical fenestellids, but this pattern is uncommon in the family. In both families, the zooecia are basally attentuated, endozonal walls are thin, and the exozone is relatively narrow and sharply differentiated from the endozone. Exozonal thickening of the wall is almost entirely on the branch-surface side of the zooecial boundary line. Reduction in zooecial length appears to have evolved primarily after the origin of the Fenestellidae.

Fenestella granulosa is a fenestellid with many similarities to phylloporinids; however, this species is correctly assigned to the Fenestellidae because: (1) its zooecia are relatively short compared to those of typical phylloporinids (Fig. 221,*8*); (2) it is of regular growth habit with subparallel branches of constant diameter linked at frequent intervals by crossbars lacking apertures; (3) the nonlaminated deposits along the branch midline are relatively regular in development, as in other fenestellids and unlike typical phylloporinids (Fig. 217,*7*); and (4) the spiny keel separating the rows of zooecia is similar to that in typical members of *Fenestella.*

Thus, members of the Phylloporinidae and Fenestellidae are very similar, yet readily distinguished. A hypothesis of close phylogenetic relationships is accepted here, and linking the Phylloporinidae and Arthrostylidae links the Fenestellina to the Arthrostylidae.

I have argued that the earliest known cryptostomate families share many characters, thus implying a close common ancestry. In

Fig. 221. Comparison of Arthrostylidae and Fenestellina.——*1. Arthrostylus* cf. *A. obliquus* Ulrich, Rhabdomesina; Sevier Sh., M. Ord., Tenn.; well-developed nonlaminated skeleton (arrow) in an arthrostylid, reverse surface directed down; transv. sec., USNM 222628, ×92.——*2. Phylloporina aspera* (Hall), Fenestellina; Chazy Ls., M. Ord., Can.; granular bands, finely laminated skeletal wall, and nonlaminated skeletal wall (arrow); transv. sec., USNM 43438, ×56.——*3.* Unidentified genus and species, Phylloporinidae, Fenestellina; Bromide F., M. Ord., Okla.; reverse surface illustrating stylet development and spacing; tang. sec., USNM 214217, ×56.——*4. Nematopora* sp., Rhabdomesina; Dev., Ohio; basal attachment, fusion of branches, apertural shape, stylet development; external view, USNM 214215, ×13.——*5. Fenestella granulosa* Whitfield, Fenestellina; Waynesville F., U. Ord., Ohio; parallel branches, barren crossbars, regular development of median nonlaminated wall (arrows), and elongate zooecia in the Fenestellidae; deep tang. sec., USNM 214221, ×56.——*6. Arthrostylus tenuis* (James), Rhabdomesina; Eden Gr., U. Ord., Ky.; zooecial shape, wall development; long. sec. oriented perpendicular to reverse surface (left), USNM 222629, ×184.——*7. A. tenuis* (James), Rhabdomesina; same data as *6*; zooecial shape and wall development; long. sec. oriented parallel to reverse surface, USNM 222630, ×184.——*8. Phylloporina dawsoni* Ulrich, Fenestellina; Trenton Gr., M. Ord., Quebec, Can.; zooecial shape, wall development; long. sec., USNM 222631, ×184.——*9. Fenestella granulosa* Whitfield, Fenestellina; Whitewater Sh., U. Ord., Ind.; zooecial shape, wall development; long. sec., USNM 222632, ×92.

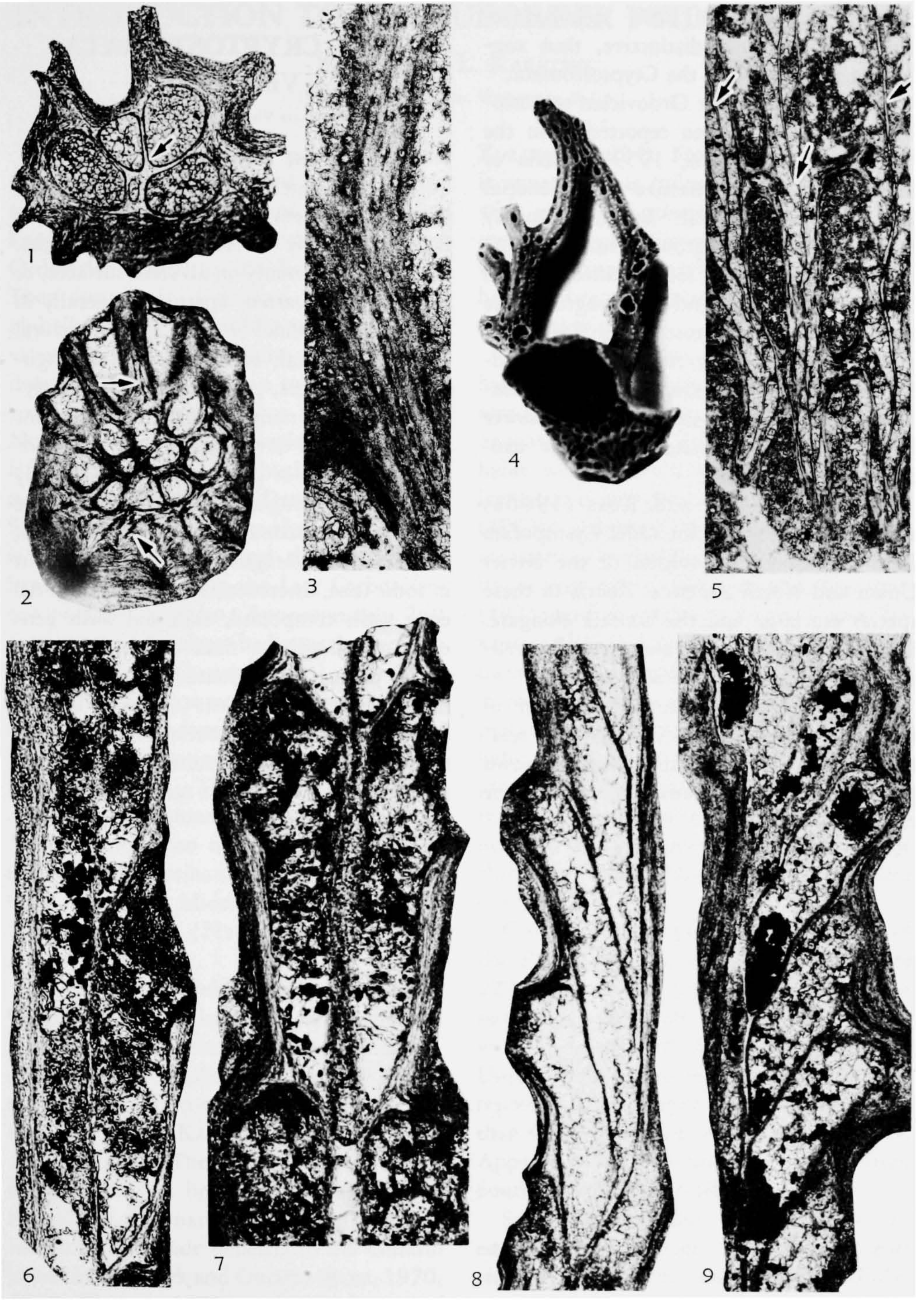

FIG. 221. *(For explanation, see facing page.)*

contrast, members of other stenolaemate orders appear quite distinctive, thus suggesting isolation from the Cryptostomata.

A number of Lower Ordovician trepostomate genera have been reported from the Baltic region (MÄNNIL, 1959). Zoaria of these tend to be massive and zooecial arrangements, irregular. Budding usually took place across the growing surface rather than from a restricted locus. Exozonal walls tend to be thinner and diaphragms more abundant than in cryptostomates. Somewhat younger trepostomates, from the lower Middle Ordovician Simpson Group of Oklahoma, are generally similar to the Lower Ordovician trepostomates, although exozones are more varied.

ASTROVA (1965) and ROSS (1966a) described members of the order Cystoporata from the Lower Ordovician of the Soviet Union and North America. Zoaria in these species are large and the zooecia elongate. Exozonal walls are thin, and generally well-developed vesicular material is present.

The Tubuliporata, the fourth order of Paleozoic stenolaemates, consists of a relatively small number of inadequately known genera and cannot be readily compared to the cryptostomates.

Order CRYPTOSTOMATA Vine, 1884

[Cryptostomata VINE, 1884, p. 184, suborder]

Zoaria almost always erect; unbranched, bushlike, pinnately branched, or reticulated; jointing rare; stem cross section cylindrical or flattened; rarely developing overgrowths. Apertures commonly on all stem surfaces, or some surfaces barren; apertures generally in regular longitudinal or spiral rows, apertural outlines elliptical, subcircular, or rectangular. Striae, ridges, peristomes, stylets, polymorphs, small nonpolymorphic depressions commonly well developed on surface. Budding loci linear or planar. Zooecia generally short, rarely elongate; usually with zooecial bend at endozonal-exozonal boundary; hemisepta, diaphragms, mural spines present in some taxa, interzooecial pores lacking. All erect walls compound, exozonal walls generally much thicker than endozonal walls; walls primarily laminated, nonlaminated material generally present (extensive in Fenestellina); in some taxa, extrazooecial skeletal material extensive and multizooecial skeletal material present. Vesicles rare. *Ord.-Perm.*

INTRODUCTION TO THE SUBORDER PTILODICTYINA

By Olgerts L. Karklins

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The Ptilodictyina are a suborder of the Cryptostomata characterized chiefly by an erect, bifoliate growth habit. The earliest known Ptilodictyina are from upper Lower Ordovician strata of the Estonian region. They apparently diversified and dispersed globally during the Middle and Late Ordovician and then gradually diminished in diversity from the Silurian to the Carboniferous periods. Except for a few studies in North America and the Soviet Union, little is known about the distribution of ptilodictyines in the Silurian and Devonian systems. Even less is known about their distribution in the Carboniferous, and they apparently became extinct during the Late Carboniferous or Early Permian. Approximately 260 species have been described, mostly from the Ordovician and Silurian systems.

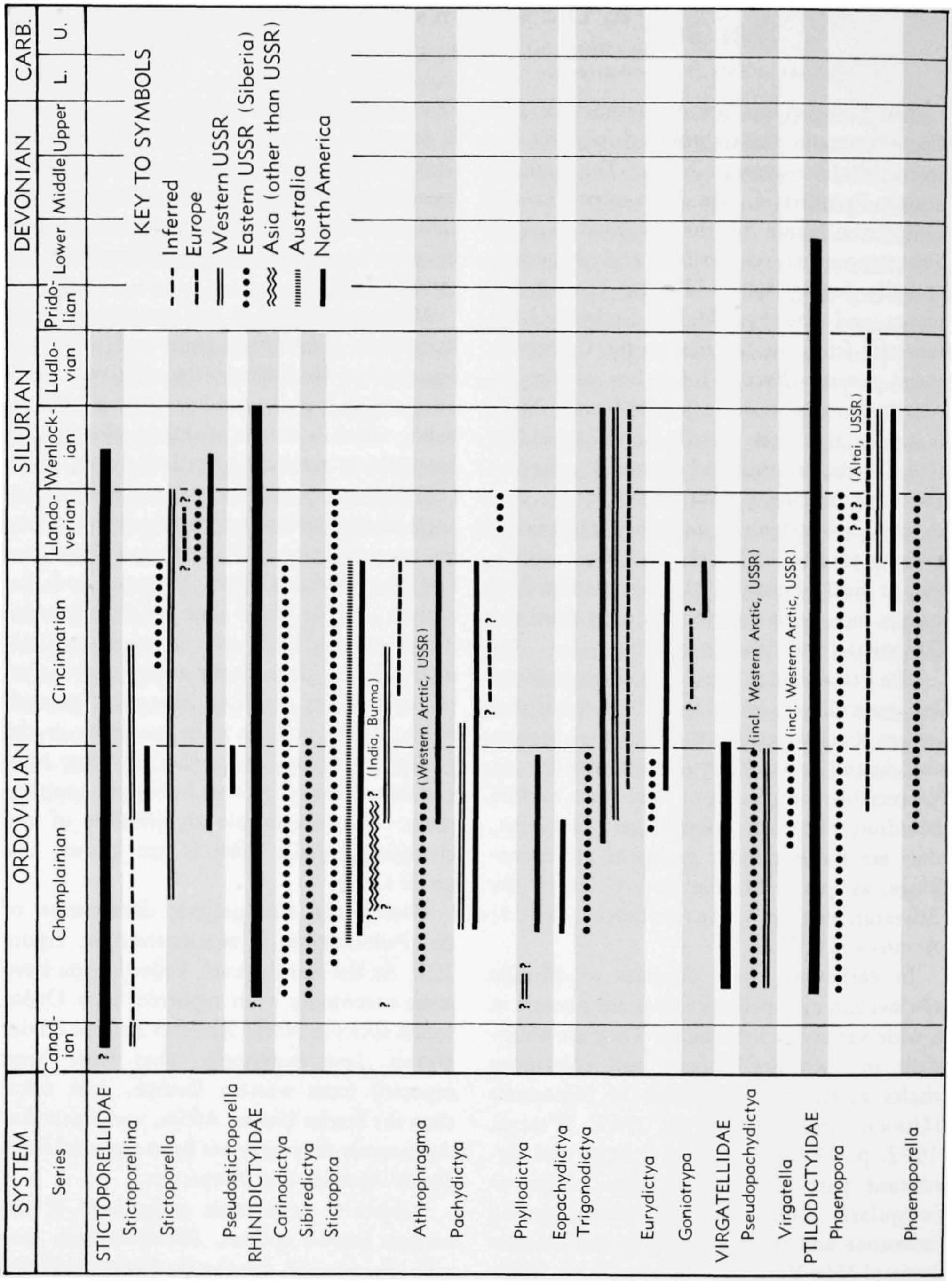
The Ptilodictyina were exclusively marine, and generally are found in carbonates deposited in shallow basins of continental shelves and inland seas. They commonly are an appreciable component of lower and middle Paleozoic bryozoan assemblages. In places, they are the dominant group of an assemblage, as in the Middle Ordovician of the Siberian region (Nekhoroshev, 1961; Astrova, 1965).

In carbonate shelf deposits of Middle Ordovician age, ptilodictyines are present in a wide variety of lithologies. They are abundant in such argillaceous and calcareous shales as the Decorah Shale of Minnesota (Ulrich, 1893; Karklins, 1969; Webers, 1972, p. 479). They form a large and significant part of bryozoan assemblages in irregularly alternating and intertonguing limestone and shale deposits in the Ontario basin of New York and Ontario (Ross, 1970, 1972; Walker, 1972), and in reef tracts of northern New York and Vermont (Ross, 1963b) and Tennessee (Walker & Ferrigno, 1973; Alberstadt, Walker, & Zurawski, 1974). From these examples, it is apparent that ptilodictyines thrived in a wide variety of relatively shallow environments; however, distinct ptilodictyine associations within larger bryozoan assemblages have not been recognized in different carbonate lithologies.

Most ptilodictyines had an erect growth habit that is variously expressed, and they attached to the substrate by relatively small encrusting bases. An encrusting growth habit, which is common among other stenolaemates, is rare among ptilodictyines. Ross (1963b) indicated that some ptilodictyines occasionally evolved encrusting growth habits in reef tracts. Walker and Ferrigno (1973) and Alberstadt, Walker, and Zurawski (1974) noted that encrusting ptilodictyines are indeed rare, being found only in reef cores; throughout a reef tract, other ptilodictyines retained the erect growth habit. These are the only examples in the group demonstrating a relatively clear relationship between growth habit and environment. The taxonomic significance of the changing growth habit is not known and needs study.

Global and stratigraphic distribution of the Ptilodictyina is summarized in Figure 222. At the family level, Ptilodictyina have most commonly been reported from Ordovician rocks in North America and the Soviet Union. Less commonly, they have been reported from western Europe, Asia other than the Soviet Union, Africa, and Australia. Apparently they have not been reported from South America and Antarctica.

Subject to taxonomic assignment of the earliest known species, *Stictoporellina gracilis* (Eichwald), the family Stictoporellidae appears to have originated during the late Early Ordovician in the Estonian region. It became dispersed globally during the Middle Ordovician and ranged into the Silurian. The


SYSTEM
Series
ORDOVICIAN
Canad-ian
Champlainian
Cincinnatian
SILURIAN
Llando-verian
Wenlock-ian
Ludlo-vian
Prido-lian
DEVONIAN
Lower
Middle
Upper
CARB.
L.
U.
KEY TO SYMBOLS
Inferred
Europe
Western USSR
Eastern USSR (Siberia)
Asia (other than USSR)
Australia
North America
STICTOPORELLIDAE
Stictoporellina
Stictoporella
Pseudostictoporella
RHINIDICTYIDAE
Carinodictya
Sibiredictya
Stictopora
(India, Burma)
Athrophragma
(Western Arctic, USSR)
Pachydictya
Phyllodictya
Eopachydictya
Trigonodictya
Eurydictya
Goniotrypa
VIRGATELLIDAE
Pseudopachydictya
(incl. Western Arctic, USSR)
Virgatella
(incl. Western Arctic, USSR)
PTILODICTYIDAE
Phaenopora
(Altai, USSR)
Phaenoporella
?

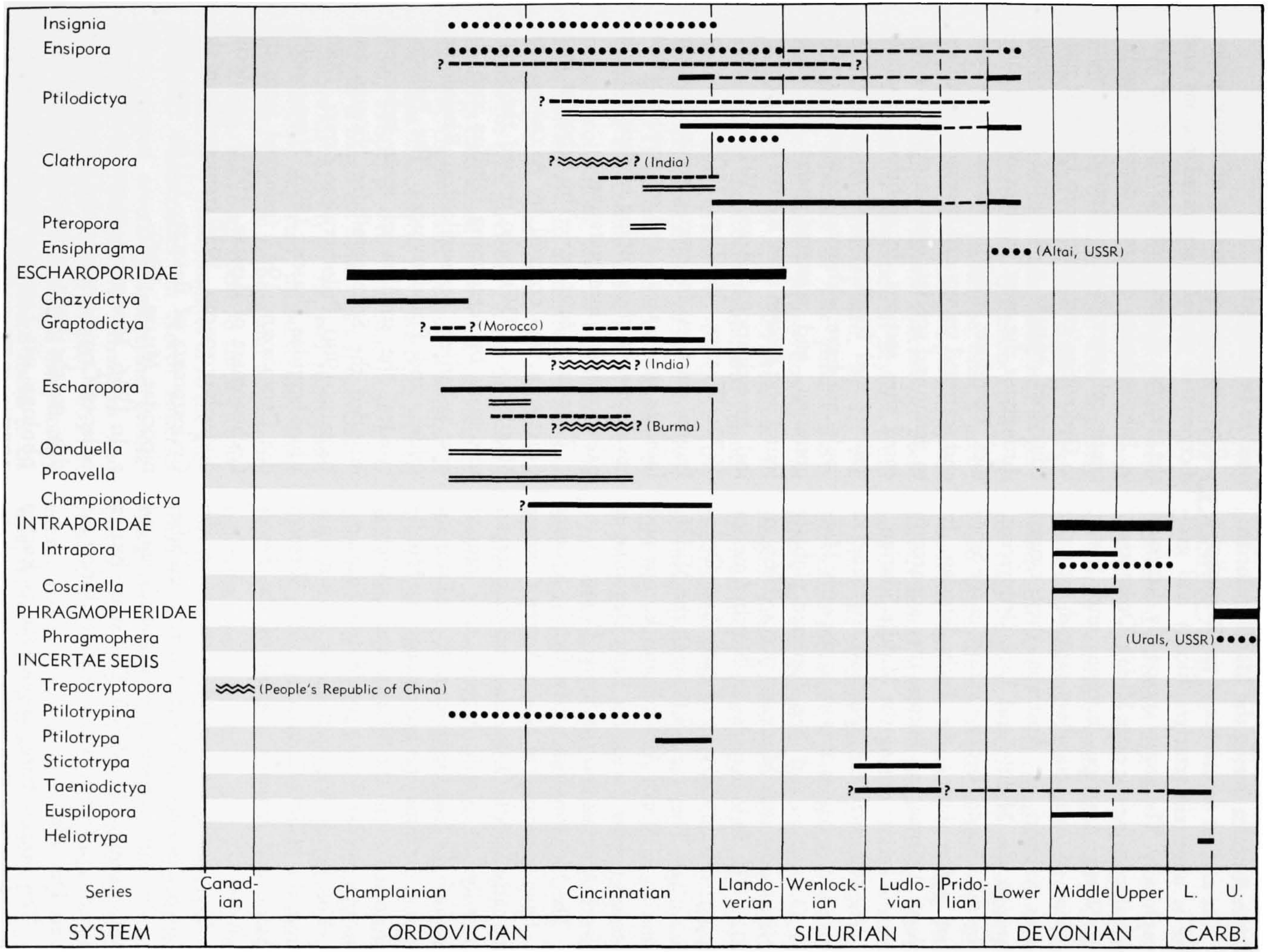


FIG. 222. Summary of stratigraphic and geographic distribution of the suborder Ptilodictyina and the cryptostomate genus *Heliotrypa*.

Stictoporellidae apparently became extinct in Europe during the Early Silurian and in North America during the Middle Silurian.

The earliest occurrence of the Rhinidictyidae is uncertain stratigraphically and geographically. The group apparently dispersed globally during the early Middle Ordovician. In North America, Europe, and Soviet regions of Asia members ranged into the Early Silurian; in Australia they ranged through the Middle and Late Ordovician. The rhinidictyids became extinct in the Siberian region during the Early Silurian. In North America and Europe they apparently became extinct during the Middle Silurian.

The Ptilodictyidae reportedly originated in the Siberian region at least by the early Middle Ordovician and then dispersed globally (Nekhoroshev & Modzalevskaya, 1966, p. 101). The Ptilodictyidae in North America appear first in deposits of early Late Ordovician age. They ranged through the Middle Silurian in North America and Europe and became extinct during the Early Devonian in North America and the Soviet Union.

The Escharoporidae, new family, appears to have originated in North America during the early Middle Ordovician and then spread globally. In North America they ranged through the Late Ordovician. In the Estonian region, the family ranged through the Middle Ordovician into the Silurian and apparently became extinct during the Middle Silurian.

The family Virgatellidae is known only from the Middle Ordovician of the Western Arctic and Siberian regions of the Soviet Union.

The family Intraporidae occurs in the Lower Devonian of North America and Siberia. In North America the intraporids ranged only through the Middle Devonian, but in Siberia apparently became extinct during the Late Devonian.

The family Phragmopheridae is known only from late Carboniferous strata of the Uralian region of the Soviet Union.

Occurrences of certain genera of the families Ptilodictyidae, Escharoporidae, and Rhinidictyidae in Ordovician and Silurian strata of the Indian subcontinent (Fig. 222) need to be verified.

The common occurrence of many ptilodictyines in globally separated regions and the presence of comparable ptilodictyine taxa in lithologically different deposits significantly enhances their biostratigraphic value in Ordovician and Silurian rocks. Most ptilodictyines possess a uniform morphology throughout the erect portions of their colonies. Therefore, small fragments of a broken and scattered colony can be easily identified to genus and species, even in randomly oriented thin sections. In addition, generally delicate and fragile ptilodictyine skeletons could not have withstood significant transportation, and scattered parts are likely found near growth sites. Recent paleoecological investigations (Ross, 1970, p. 361; 1972; Walker, 1972, p. 2509, 2511) of fragile colonies in erect-growth positions indicate quiet, clear, and relatively shallow environments, thus adding to their value in paleoecological interpretations.

Taxonomic position.—The suborder Ptilodictyina was erected by Astrova and Morozova (1956), who revised the Cryptostomata by regrouping families into the new suborders Fenestelloidea, Rhabdomesoidea, and Ptilodictyoidea. The Ptilodictyoidea, the smallest of these suborders, included the Stictoporellidae Nickles and Bassler, 1900, Ptilodictyidae Zittel, 1880, Rhinidictyidae Ulrich, 1893, Hexagonellidae Crockford, 1947 (removed from the Cyclostomata of Bassler, 1953), Goniocladiidae Nikiforova, 1938 (removed from the Cyclostomata of Bassler, 1953), and Rhiniporidae Miller, 1889.

In 1966, Morozova erected another suborder of Cryptostomata, the Timanodictyoidea, on the basis of the contrasting morphology of *Timanodictya* Nikiforova, 1938, and *Timanotrypa* Nikiforova, 1938, which she removed from the family Rhinidictyidae. The Timanodictyina (=Timanodictyoidea) comprise a special group of

Permian Bryozoa (SHISHOVA, 1968, p. 129) consisting of genera with erect bifoliate and radial modes of zoarial construction, or of single layered encrusting zoaria.

HISTORY OF CLASSIFICATION

In early works, the ptilodictyines were usually grouped, perhaps because of their small size and delicate form, with similarly delicate modern forms now classed as cheilostomate Bryozoa, or less commonly as gorgonacean Coelenterata. GOLDFUSS (1829, p. 104, pl. 37, fig. 2) published what is probably the earliest illustration of a ptilodictyine, which he named *Flustra lanceolata.* Soon after the formal separation of Bryozoa from the Coelenterata (EHRENBERG, 1831), the zoological affinities of the ptilodictyines began to be questioned. MILNE-EDWARDS (in LAMARCK, 1836, v. 2, p. 229) retained *F. lanceolata* in the Coelenterata, but considered the assignment to be doubtful. LONSDALE (in MURCHISON, 1839, p. 676, pl. 15, fig. 11) noted similarities between *F. lanceolata* and certain other fossils in MURCHISON's collections, and he established the genus *Ptilodictya* to accommodate his and the GOLDFUSS specimens. *F. lanceolata* became the type species of *Ptilodictya,* which LONSDALE considered to be a unique form of Paleozoic coelenterate. Because the figured specimens of GOLDFUSS have not been located (ROSS, 1960a, p. 440), the concept of *Ptilodictya* is based on LONSDALE's specimens.

EICHWALD (1842, p. 39, and subsequent publications) reported ptilodictyines from Ordovician strata in Estonia and northwestern Russia, assigning them to the escharid- and flustrid-like cheilostomates or to the gorgonacean coelenterates. In North America HALL erected several ptilodictyine genera, including the well-known *Stictopora* and *Escharopora.* HALL (1847, p. xxii; 1852, p. 354) noted the unusual external morphology of these genera and considered them to be coelenterates or bryozoans. Later, in an endeavor to classify known Bryozoa, D'ORBIGNY (1849, p. 499) recognized *Stictopora* and *Ptilodictya* as fossil bryozoans of undoubted Paleozoic age.

McCOY (1851–1855, p. 45), in his work on British Paleozoic fossils, revised the diagnosis of *Ptilodictya* and assigned it to the family Escharidae (not recognized now) of the class Polyzoa. McCOY noted the subtubular construction of the autozooecia and described the wall structure as being uniformly continuous from the mesotheca to the zoarial surface.

Since the investigations of D'ORBIGNY and McCOY, assignment of *Ptilodictya* and *Stictopora* to the Bryozoa has not been challenged. These genera have been regarded as typical fossil bryozoans, and numerous, superficially similar specimens were assigned to them until the introduction of thin-sectioning methods. NICKLES and BASSLER (1900) listed approximately 100 species of *Ptilodictya* and 80 species of *Stictopora* that were included in these genera at one time or another. Most have since been reassigned.

During the latter part of the nineteenth century, paleontologists studying Bryozoa were involved in a controversy concerning zoological affinities of the fossil Trepostomata, then included with the tabulate corals. NICHOLSON, a leading worker on fossil Bryozoa, at the time was actively involved in the study of the Trepostomata and noted (1874b, p. 123) that *Clathropora,* a ptilodictyine, was a bryozoan, and (1875b, p. 34) that *Ptilodictya* might be a transitional form between tabulate corals and bryozoans. In a subsequent publication, NICHOLSON (1879, p. 11) considered *Ptilodictya* and related forms to be undoubted fossil bryozoans, and later published (1881, fig. 15) what is probably the first illustration of a thin section from a ptilodictyine.

ZITTEL (1880, p. 603) established the family Ptilodictyidae with *Ptilodictya* as the type genus. According to ZITTEL, the family comprised genera in which autozooecia grew back to back. It included known ptilodictyines, some bifoliate fistuliporines, an arthrostylid, and some poorly known and generally unrelated genera. Zittel assigned the Ptilodictyidae to the suborder Cyclostomata.

Ulrich, in a series of outstanding papers on fossil Bryozoa, argued (see 1882, p. 121) for the classification of the Monticuliporidae, consisting mostly of the trepostomates with some fistuliporid and ceramoporid genera, as Bryozoa. He discussed the comparative morphologies of a recent tubuliporate, *Heteropora,* and selected trepostomatous bryozoans, and compared them with *Ptilodictya* and *Stictopora.* Using thin-sectioning methods introduced by Nicholson, Ulrich (1882, p. 151–152) recognized morphologic differences between *Ptilodictya* and *Stictopora* by making a new family Stictoporidae (now Rhinidictyidae) that, in addition to *Stictopora,* included his genera *Pachydictya* and *Phyllodictya.*

Ulrich (1882) also erected the suborder Trepostomata to accommodate some Bryozoa of controversial phylum affinities, and thereby differentiated them from the suborder Cyclostomata (now order Tubuliporata). The original concept of the suborder Trepostomata included the Ptilodictyidae and Stictoporidae as first and second groups. The Monticuliporidae, Fistuliporidae, and Ceramoporidae completed the suborder.

During the same period in England, Vine published several papers on the British Paleozoic Bryozoa, which included reviews of the existing bryozoan classification. Vine (1884, p. 184, 196) accepted Ulrich's suborder Trepostomata, but he proposed a new suborder, the Cryptostomata, with *Ptilodictya* as the type genus. Vine's (1884, fig. 4) published illustrations show *Ptilodictya* with what appear to be exilazooecia, suggesting that his material may also have included specimens of *Phaenopora* (Ulrich, 1890, p. 344). Exilazooecia are generally lacking in *Ptilodictya* (mesopores of Ross, 1960c, p. 1064). Vine (1884, p. 203) also proposed a new family, Arcanoporidae (not recognized now) for *Ptilodictya* and two other genera, *Arcanopora* (now *Sulcoretepora*) and *Glauconome* (now *Glauconomella*). The family Rhabdomesidae (Rhabdomesontidae of Vine, 1884), a group of small branching forms, completed the Cryptostomata.

Ulrich (1890) emended the diagnoses of the Ptilodictyidae Zittel and Rhabdomesidae Vine, and enlarged the Cryptostomata by adding the families Acanthocladiidae, Fenestellidae, Phylloporinidae, and Cystodictyonidae.

In 1893, Ulrich published a monograph on Paleozoic Bryozoa from Minnesota. In this work he erected the family Rhinidictyidae, comprising most genera that were previously assigned to the Stictoporidae. This monograph is probably the most important single work on skeletal morphology of bifoliate cryptostomates and still has a bearing on taxonomy of the families.

Nickles and Bassler (1900) presented a synopsis of the classification of known Bryozoa, and added the family Stictoporellidae to the Cryptostomata. The Stictoporellidae together with the Ptilodictyidae and Rhinidictyidae constitute the basic group of the Ptilodictyina, as it is used now. These three ptilodictyine families contain the most abundant and widely distributed genera of the oldest known Cryptostomata (Astrova & Morozova, 1956; Astrova, 1965).

After the extensive work by Ulrich, the concept of the Cryptostomata was not reexamined until 1937, when McNair noted critically that the Cryptostomata comprised phylogenetically unrelated groups. He indicated that the order included three general zoarial types. The first is unilaminate with autozooecia opening only on one side, and is found in the Fenestellidae, Phylloporinidae, and Acanthocladiidae. The second type, found in the Arthrostylidae and Rhabdomesidae, has autozooecia opening on all sides. The third type is bifoliate with autozooecia opening on two sides and growing back to back from the mesotheca. This third type, found in the Ptilodictyidae, Stictoporellidae, Rhinidictyidae, Sulcoreteporidae, and Actinotrypidae, was considered to be most characteristic of the Cryptostomata.

In the first edition of this *Treatise,* BASSLER (1953) presented a synopsis of the bifoliate cryptostomate genera. The order Cryptostomata and the contents of the bifoliate families remained essentially unchanged from the arrangement of NICKLES and BASSLER (1900), except for transfer of the Phylloporinidae from the Fenestellidae to the Trepostomata.

In 1956, ASTROVA and MOROZOVA proposed a major revision of the Cryptostomata. They cited the work of MCNAIR (1937) and concluded that the three types of Cryptostomata recognized by him differed not only in zoarial growth but also in microstructure of skeletal walls and internal morphology of autozooecia. ASTROVA and MOROZOVA considered these to be naturally segregated groups that diverged phylogenetically during Late Cambrian or Early Ordovician time. They redefined the order Cryptostomata and subdivided it on morphological and possible phylogenetic grounds into three suborders: the Fenestelloidea (including the Phylloporinidae), Ptilodictyoidea, and Rhabdomesoidea.

ASTROVA (1960a) reviewed the general history of bryozoan studies, including investigations in the Soviet Union, and gave a synopsis of the families and genera of the Ptilodictyoidea. She illustrated genera occurring in the Soviet Union, and others were mentioned and assigned to appropriate families.

Ross (then PHILLIPS, 1960) restudied type material and additional specimens from several ptilodictyine genera, including *Stictopora* HALL, 1847, *Escharopora* HALL, 1847, and *Pachydictya* ULRICH, 1882. On the basis of zooecial construction in the type species of these genera, she established three informal taxonomic categories: the escharoporids, stictoporids, and pachydictyids. These categories were differentiated on the configuration of laminae in zooecial walls, mode of growth of zooecia from the mesotheca (budding surface), presence of exilazooecia (mesopores of Ross), and features in zooecial chambers. In subsequent publications, Ross (1960a,b,c, 1961a,b; 1963b, 1964a,b) considered other ptilodictyine genera, recognized some new genera, and included them in her classification.

On the basis of zoarial morphologies, Ross (1964b) interpreted the informal escharoporid, stictoporid, and pachydictyid groups to be phylogenetic lineages within the early ptilodictyines. Genera forming the three lineages overlapped families in the classification of BASSLER (1953), ASTROVA and MOROZOVA (1956), and ASTROVA (1960a). Ross (1964b) briefly reviewed some biological features of Bryozoa and considered the Hexagonellidae CROCKFORD, 1947, and Goniocladiidae NIKIFOROVA, 1938 (placed by ASTROVA & MOROZOVA, 1956, in the Ptilodictyoidea) as families of the then cyclostomate suborder Ceramoporina BASSLER, 1913.

In a comprehensive work, NEKHOROSHEV (1961) described the Middle Ordovician to Lower Silurian bryozoans of the Siberian platform. The Cryptostomata are represented by the fenestelline Phylloporinidae and Fenestellidae, the rhabdomesine Arthrostylidae, and the ptilodictyine Ptilodictyidae, Stictoporellidae, and Rhinidictyidae. NEKHOROSHEV recognized about 70 cryptostomate species, of which 61 were assigned to ptilodictyine genera. Of the ptilodictyines, *Phaenopora* and *Phaenoporella* are the most common genera; both diversify at the base of the upper Middle Ordovician (Mangazeian Stage), with many species ranging through the Upper Ordovician and some into the Lower Silurian. NEKHOROSHEV noted that the Middle and Upper Ordovician of the Siberian platform is not only remarkable in having a large and diversified ptilodictyid component, but also in having a relatively small trepostomatous component (ASTROVA described the Trepostomata in 1965). NEKHOROSHEV concluded that the Middle and Upper Ordovician fauna of the Siberian platform is distinctly different from that of North America and the Baltic region, and must have inhabited a separate marine basin, which he designated as the "*Phaenopora* province."

ASTROVA (1965), in a major work on the Paleozoic Bryozoa of Siberia, discussed at length the ptilodictyine families Ptilodictyidae, Stictoporellidae, and Rhinidictyidae because they are the most abundant representatives of the earliest cryptostomates and constitute a large part of the Ordovician and Silurian fauna in Siberia. She described the astogeny and ontogeny of zoaria and the structure of skeletal matter, and suggested possible functions for zoarial and zooecial structures. She also outlined the phylogeny of the Ptilodictyidae, recognizing two closely related evolutionary lineages that she used as the basis for the new subfamilies Ptilodictyinae and Phaenoporinae. The Ptilodictyinae, originating in the upper Lower Ordovician of the Soviet Union, is the older of the two subfamilies. Morphologically, ASTROVA's Ptilodictyinae and Phaenoporinae appear to form a part of the escharoporid lineage of ROSS (1964b). ASTROVA also recognized the family Virgatellidae, which she considered to be related to the Rhinidictyidae.

GORYUNOVA (1969) erected the family Phragmopheridae, found in Carboniferous strata, and assigned it to the Ptilodictyina. The Phragmopheridae is distinctly different from older families of the Ptilodictyina and its relationship to them is uncertain.

The suborder Ptilodictyina as described herein includes seven families: Ptilodictyidae ZITTEL, 1880, Escharoporidae new, Intraporidae SIMPSON, 1897, Phragmopheridae GORYUNOVA, 1969, Rhinidictyidae ULRICH, 1893, Stictoporellidae NICKLES and BASSLER, 1900, and Virgatellidae ASTROVA, 1965. The Intraporidae of SIMPSON is restored.

In addition, the Ptilodictyina also includes six genera that are presently unassigned to families: *Euspilopora* ULRICH in MILLER, 1889, *Ptilotrypa* ULRICH in MILLER, 1889, *Ptilotrypina* ASTROVA, 1965, *Stictotrypa* ULRICH, 1890 (removed from Rhinoporidae MILLER, 1889), *Taeniodictya* ULRICH, 1888, and *Trepocryptopora* YANG, 1957. These genera are ptilodictyine in general mode of budding and zoarial morphology but differ from representatives of established families in the shape and arrangement of zooecia, configuration of wall laminae, and other skeletal structures. The insufficient material on which these genera are based does not warrant assignment to suprageneric categories. *Heliotrypa* ULRICH, 1883, is also discussed herein, but is not considered to be a ptilodictyine and therefore is removed from the Stictoporellidae.

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MORPHOLOGY

BASAL ZOARIAL ATTACHMENTS

Basal attachments of zoaria in the Ptilodictyina are of two basically different kinds. In one, fully developed zoaria are skeletally continuous with their bases (Fig. 223,*2–4*) and are rigidly fixed in their growth position. This type of basal attachment prevails among the ptilodictyines and, in general, is characteristic of the families Intraporidae, Rhinidictyidae, and Stictoporellidae. In the other kind of basal attachment, fully developed zoaria include skeletally detached bases (Fig. 224,*2*; 225,*2*) that are thought to have been separated from distal parts of the zoaria by flexible articulating joints (Ulrich, 1882, p. 151; Bassler, 1927, p. 164, pl. 11, fig. 9; Phillips, 1960, p. 18; Ross, 1960a, p. 441; Nekhoroshev, 1961, p. 69; Astrova, 1965, p. 95). Flexible joints are known in recent species of both gymnolaemates and stenolaemates. They also occur in the family Ptilodictyidae, *Escharopora* of the Escharoporidae, and probably in other fossil bryozoans.

The basal attachment in both rigid and jointed colonies consists of two parts, an encrusting expansion on the substrate (Fig. 223,*2–4*; 224,*2,5*) and a vertical extension (Fig. 223,*2–4*; 225,*2,5*) between the fully developed zoarium and its base, here called the **connecting segment**. General shape of the encrusting base appears to be determined in part by the nature of the substrate, but areal extent of the base may be related to height and thickness of a fully developed zoarium (Fig. 223,*2,3*). Connecting segments rise vertically from the approximate centers of the bases and expand distally into fully grown zoaria of bifoliate growth habit.

Basal attachments of both types are fragile. The rigid type is only rarely found unbroken. Jointed attachments are not known to be connected, even if bases and connecting segments are found together in the same deposits. The flexible material between bases and connecting segments in the unjoined type is thought to have consisted of organic tissues (Astrova, 1965, p. 95; others) that were not preserved.

In available ptilodictyines, only a few specimens possess reasonably well-preserved basal zoarial attachments that are suitable for thin sectioning or peeling. Several serial peels and a few thin sections were prepared from bases of species of *Stictopora* (Fig. 223, *1,5,6*) and *Trigonodictya* (Fig. 223,*3,4*; 225,*4*; 226,*1*), both Rhinidictyidae, and from an encrusting base that may belong to an escharoporid (Fig. 224,*1–3,5*) and from a connecting segment of a ptilodictyid (Fig. 225,*1–3,5*).

Microstructure of zoarial attachments is the same as in the main erect part of a zoarium. The laminae are similar in size and configuration, but granular zones or zooecial boundaries are relatively indistinct or not visible. The three-dimensional arrangement and shape of basal zooecia were determined from a series of peels taken at intervals between 0.1 and 0.5 mm upward from the encrusting base and tangentially to it. Because the encrusting bases slope away from their centers, zooecia are ontogenetically younger toward the edge of the encrustation. Because of small size, longitudinal sections paralleling the mesotheca could not be obtained from the specimen of *Stictopora,* but a few, slightly oblique sections are available from *Trigonodictya*.

By analogy to modern bryozoans (Ryland, 1970), encrusting bases in the ptilodictyines probably contain ancestrulae. Tavener-Smith (1975) has speculated on possible growth in the basal attachment of a generalized ptilodictyine.

Basal attachments of rigid zoaria.— Encrusting bases in most species are irregularly explanate, rarely subcircular to indistinctly elongate (Fig. 223,*2–4*). A group of zooecia constituting the center of a base, as determined from serial peels, are regarded as the first generation of basal zooecia because of their position and alignment in the base (Fig. 223,*1d*; 226,*1b*). The first generation of zooecia arise concurrently with the formation of a basal layer and align in a preferred direction (Fig. 223, *1c,d*). Orientation of the first generation establishes the mesothecal plane for a zoarium and preferred elongation for the encrusting base.

Growth of the mesotheca in the base appears to have been initiated between a pair of aligned zooecia in the first generation, and not from the basal layer. Once growth of the mesotheca was initiated, subsequent zooecia arose both from the mesotheca as it extended laterally and vertically (Fig. 223, *1b–d*) and from the basal layer (Fig. 223, *1c,d*). The basal layer is laminar, very thin, and generally of uniform thickness through the central part of the base.

In *Trigonodictya fenestelliformis* (Nicholson), the basal layer consists of a thin laminar part at the base and a vesicular part above (Fig. 225,*4*; 226, *1c*). The first generation of zooecia in this species arises from the vesicular structure and aligns in an indistinct spiral pattern (Fig. 226, *1b*). Subsequent generations of zooecia reoriented in a preferred direction while initiating the mesotheca (Fig. 226, *1a*) and also reoriented while arising from the laterally expanding basal layer (Fig. 226, *1d*). The vesicular structure fills most of the space between basal zooecia and extends into the connecting segment (Fig. 225,*4*; 226, *1a*).

Connecting segments are generally variable in length, subtubular (Fig. 223,*2*) to flattened, and without distinct zoarial margins. They formed with the vertical extension of the mesotheca. Zooecia in the connecting segment arise from the mesotheca in patterns characteristic for species (Fig. 223, *1a,b*), but are commonly closed by thickened walls or extrazooecial stereom in the exozone.

In general, zooecia in basal attachments of rigid zoaria are similarly shaped but smaller in size than autozooecia in the main erect part of the same zoarium. Endozones are poorly defined and of variable width in the base (Fig. 223, *1c,d*; 225,*4*), but are distinct and of uniform width in the connecting segments (Fig. 223, *1a,b*; 226, *1a*).

Basal attachments of jointed zoaria.—Encrusting bases of jointed colonies are generally irregularly subcircular (Ulrich, 1879, p. 29; 1882, p. 151; Bassler, 1927, pl. 11, fig. 9; Nekhoroshev, 1961, p. 69) with

Fig. 223. Basal attachments of rigid zoaria (*1–4*) and autozooecial budding pattern at mesotheca in erect part of zoarium (*5,6*).——*1a–d. Stictopora* sp., Lexington Ls., M. Ord., Burgin, Ky.; serial peels of basal attachment; *a,* distal part of connecting segment; mesotheca with median rods and regularly arranged zooecia proximally of fully expanded zoarium; transv. peel; *b,* narrowest part of connecting segment, approximately in middle between encrusting base and expanded zoarium; median rods in mesotheca generally visible, zooecia indistinctly aligned (toward left) and irregularly shaped; transv. peel; *c,* distal portion of first generation of zooecia (upper right) from which mesotheca extends and subsequent zooecia align in preferred direction (toward left), median rods not visible; peel parallel to basal layer of zoarial base; *d,* first generation of zooecia (ancestrula inferred) from which mesotheca (upper right) extends laterally and vertically; subsequent zooecia align in preferred direction toward left; extensive extrazooecial deposits containing numerous mural styles form margin of base; peel in plane of base of first generation of zooecia; all USNM 242610, ×30.——*2. Intrapora puteolata* Hall, Onondaga Ls., M. Dev., Ohio; basal attachment, consisting of encrusting base and connecting segment, expands into branched zoarium; external view, USNM 242611, ×5.——*3,4. Trigonodictya pumila* (Ulrich), Decorah Sh., M. Ord., Cannon Falls, Minn.; *3,* subcircular base and subtubular connecting segment of zoarium; external view, USNM 163096, ×5; *4,* irregular encrusting base with preferred orientation toward right, connecting segment expands into branched zoarium; external view, USNM 163095, ×5.——*5. Stictopora mutabilis* Ulrich, Decorah Sh., M. Ord., Rochester, Minn.; transverse walls arise from mesotheca, both sides of longitudinal wall (center), and one side (facing zoarial margins) of subsequently added longitudinal walls; curved transverse walls incline toward zoarial margins (to left and right from center); tang. sec. of endozone of fully developed branch, USNM 242612, ×50.——*6. Stictopora neglecta* (Ulrich), Lexington Ls., M. Ord., Burgin, Ky.; area of branching, longitudinal walls arise from mesotheca and junction of transverse walls of enlarged zooecium (lower right), marginal zooecia and extrazooecial stereom in margin (upper right); tang. sec., USNM 242613, ×50.

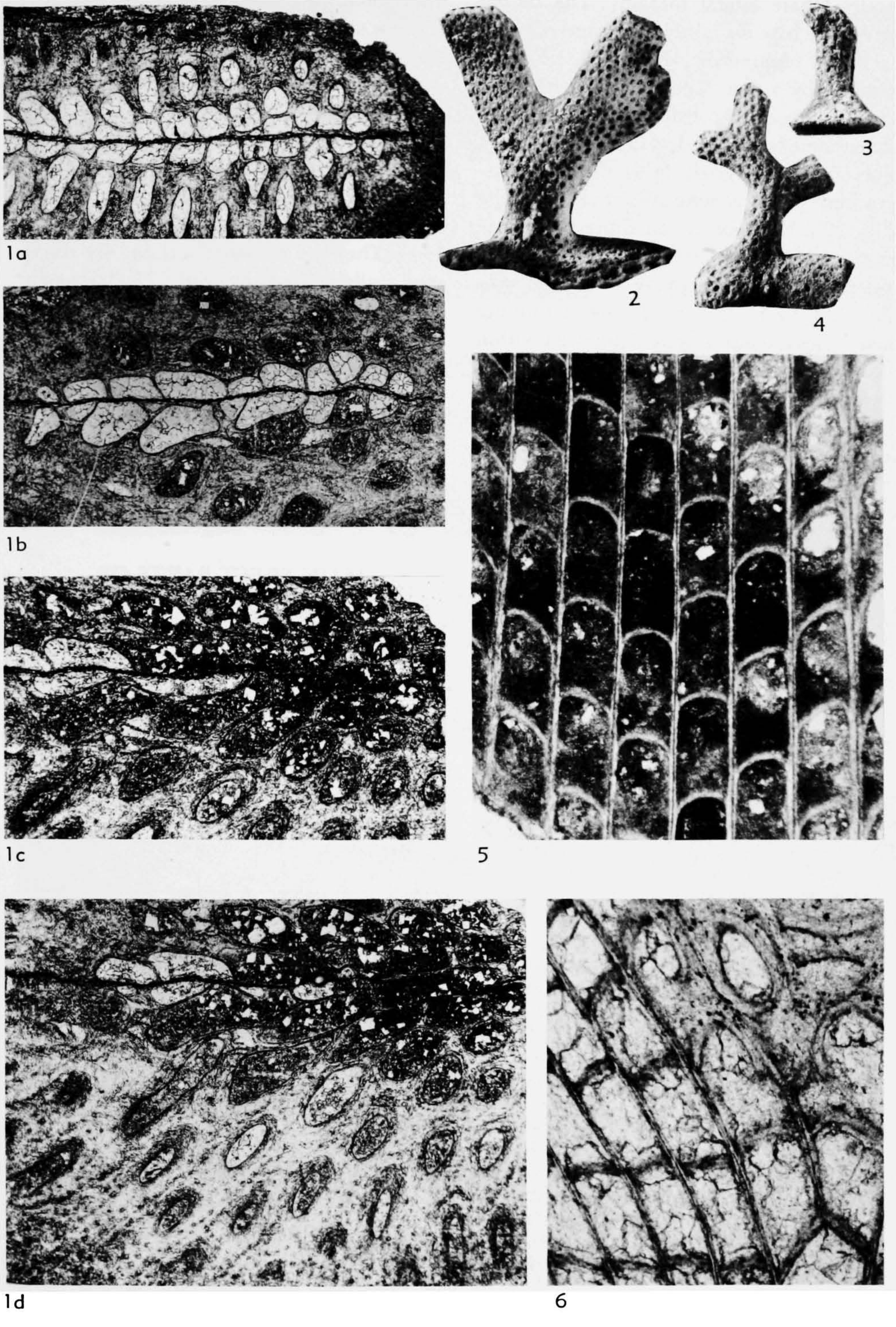

FIG. 223. *(For explanation, see facing page.)*

locally lobate lateral margins. The central part of the base is slightly raised and contains a circular depression (Fig. 224,*2,5*) surrounded by a rim. The first generations of zooecia apparently constitute this depression as they arise from the basal layer. Subsequent zooecia arise in a relatively regular radial pattern from the basal layer as it extends radially (Fig. 224,*5*). Zooecia constitute fine striae on the surfaces of these bases (Fig. 224,*1,2*) and are locally overlapping in the margins (Fig. 224,*3a,5*). In general, zooecia forming these bases are indistinctly delineated within the same range (Fig. 224,*1*) and irregularly shaped in cross section (Fig. 224,*3a,5*).

The mesotheca, or similar structure, is absent in the encrusting bases of jointed zoaria. The basal layer consists of indistinctly laminar calcite and is uneven in thickness (Fig. 224,*3*).

Connecting segments of the main part of a zoarium taper to proximal tips (PHILLIPS, 1960, p. 17; ROSS, 1960a, p. 440; 1960c, p. 1064; ASTROVA, 1965, p. 95), which fit into approximately matching circular depressions of their bases. The proximal part of connecting segments is generally subtubular. Connecting segments apparently originated at or within the depression of a corresponding base. A mesotheca is present in the tip (ROSS, 1960a, p. 441) (Fig. 225,*1,3,5*) and extends throughout the connecting segment, but does not link skeletally with the depression of an encrusting base. The mesotheca originates with the inception of the connecting segment.

For each species, zooecia in the connecting segment are in a regular pattern at the mesotheca, but are smaller than those in the fully developed zoarium of the same specimen (PHILLIPS, 1960, p. 18; ROSS, 1960a, p. 441). They are commonly closed by thickened walls or stereom (Fig. 225,*3,5*), as in rigid attachments. In some species, an annular ridge (ROSS, 1960a, p. 441) surrounds the connecting segment at some distance above its tip. This ridge consists of extrazooecial stereom that closes the zooecia (Fig. 225,*5*); however, regular arrangement of zooecia is generally maintained across the ridge (Fig. 225,*3,5*).

MAIN ERECT PARTS OF ZOARIA

The main erect part of a zoarium is bifoliate, consisting of two layers of autozooecia facing in opposite directions. Each layer forms one side of a zoarium and the proximal walls of the autozooecia constitute the mesotheca (Fig. 227), which extends throughout the erect part of the zoarium.

Mesotheca.—The mesotheca, or multi-

FIG. 224. Basal attachments in jointed zoaria (*1–3,5*) and autozooecial budding pattern in erect part of zooarium (*4,6*) of *Escharopora.*——*1. Escharopora?* sp., U. Ord. (Maysvill.), Cincinnati, Ohio; encrusting zoarial base; longitudinal walls, serrated zooecial boundaries along median of longitudinal walls, elongated and relatively narrow zooecial chambers with few cross partitions, basal walls (portions of skeletal calcite in center); tang. sec., USNM 242600, ×100.——*2a,b. E. acuminata* (JAMES)?, U. Ord. (Eden.), Covington, Ky.; *a,* encrusting base with striae radiating from rim of hollow depression, ×15; *b,* approximate extent of base encrusting a monticuliporine trepostomate, ×5; both external views, USNM 242601 from USNM 56077.——*3a,b. E. pavonia* (D'ORBIGNY)?, U. Ord. (Maysvill.), Cincinnati, Ohio; *a,* basal zooecia in cross section at edge of an encrusting base, massive calcitic layer forms basal layer; peel at right angle to edge of base, ×50; *b,* undifferentiated bottom layer of base; indistinct contact between zoarial base and underlying monticuliporine trepostomate; sec. at right angle to edge of base, ×100; both USNM 242602.——*4. E. subrecta* (ULRICH), Decorah Sh., M. Ord., Minn.; slightly curved continuous longitudinal walls and transverse walls at mesotheca in main erect part of zoarium; sec. just above mesotheca, USNM 163176, ×50.——*5,6. E. falsiformis* (NICHOLSON)?; *5,* U. Ord. (Cincinnat.), Cincinnati, Ohio; zoarial base; zooecia radiate from hollow depression in center, becoming less regularly arranged toward margin; tang. sec., USNM 242603, ×30; *6,* U. Ord. (Maysvill.), Covington, Ky.; regularly curved longitudinal walls, autozooecial chambers widen and narrow alternately in adjacent ranges at junctions between longitudinal and transverse walls (walls at mesotheca, upper right), and along endozone-exozone boundary (left); deep tang. sec., USNM 242604, ×30.

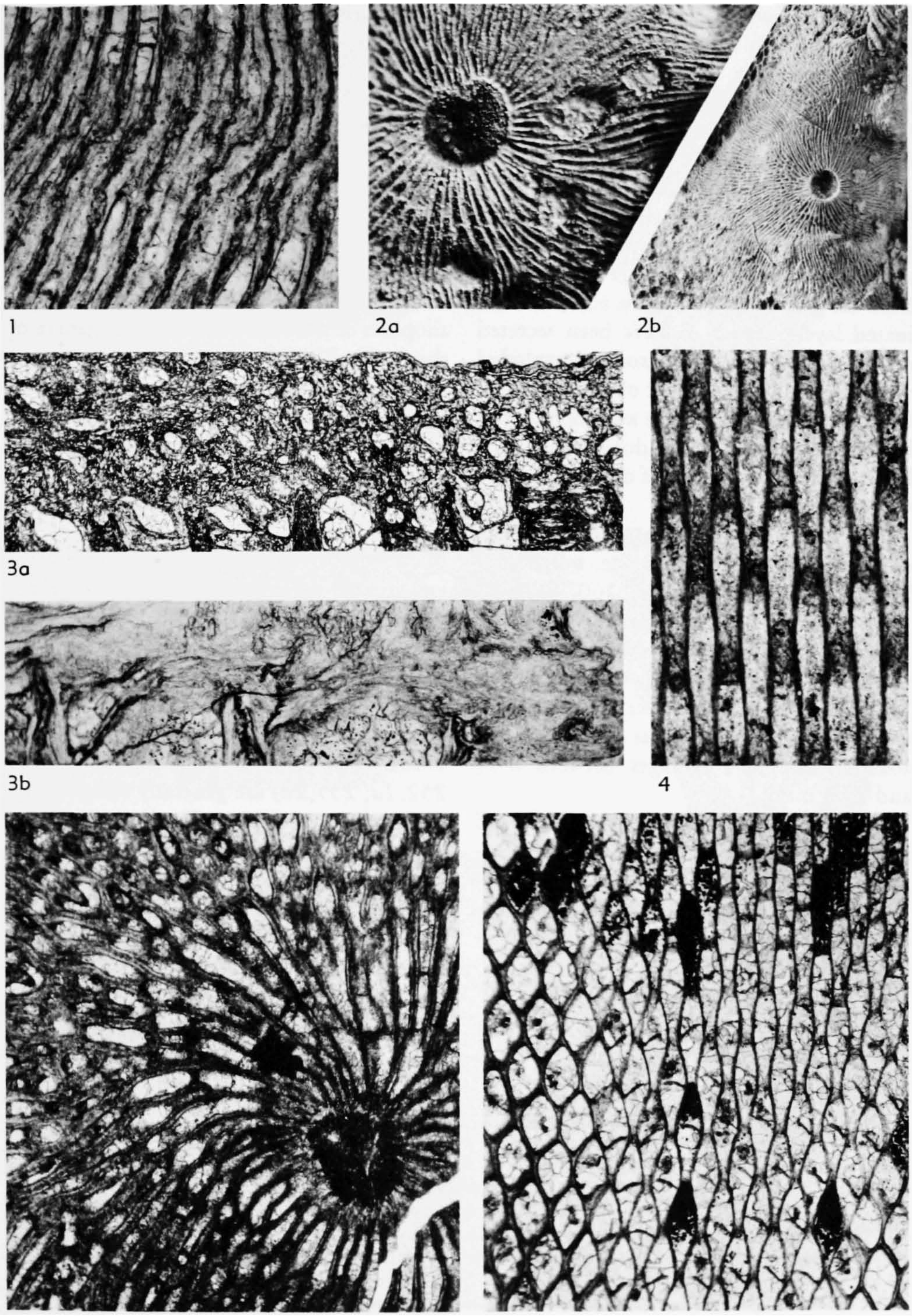

FIG. 224. *(For explanation, see facing page.)*

zooecial median wall, forms the budding surface from which autozooecia arise in characteristic patterns. Except in the zoarial margin, the mesotheca consists of laminated layers that are separated by a **median granular zone** (Fig. 227, 228; see also 240,*1h*).

In laminated layers of the mesotheca, laminae parallel the granular zone as far as the margins, where they adjoin in a broadly or narrowly serrated zone (see Fig. 240,*1f*). Both the granular zone and the adjacent laminated layers appear to have been secreted concurrently while the mesotheca extended vertically and laterally. Part of the mesotheca forms the basal walls of the autozooecia, but laminae of the mesotheca do not appear to be continuous with those of the autozooecial wall.

The mesotheca in most ptilodictyines developed in one growth plane, but it may bifurcate (Ulrich, 1893, p. 160; Phillips, 1960, p. 16; Ross, 1964a, p. 23) (Fig. 229,*3*). The mesotheca is generally straight (see Fig. 240,*1e*) to slightly undulating (see Fig. 244,*1d*); in a few taxa it is zigzag in transverse section. Thickness of mesotheca in zoarial midregions averages between 0.01 and 0.03 mm.

The median granular zone is sheetlike and may be locally discontinuous. At zoarial margins it coalesces with skeletal laminae (Fig. 230,*2*). The zone consists of irregularly shaped crystalline particles that are approximately three microns in diameter (Tavener-Smith & Williams, 1972, p. 149).

The granular zone in the mesotheca may contain rodlike structures called **median rods** (Fig. 227, 231), which are segregated from the crystalline particles. These rods (median tubuli of Ulrich, 1893, p. 98; Bassler, 1953, p. G12; median tubuli or acanthopores of Phillips, 1960, p. 3; median tubuli of Ross, 1964a, p. 24; 1964b, p. 934; Karklins, 1969, p. 17; capillaries of Astrova, 1965, p. 101; Kopayevich, 1968, p. 128; zoarial canals of Kopayevich, 1973, p. 59; acanthopores, lenticles of Tavener-Smith & Williams, 1972, p. 149; acanthopores of authors) occur in most genera of the family Rhinidictyidae.

Median rods consist of calcite cores enclosed by dark-colored, laminated sheaths (see Fig. 251,*1d,h*). Calcite in the cores is finely crystalline and the particles are densely packed (Tavener-Smith & Williams, 1972, pl. 28, fig. 184). As observed in the light microscope, the particles are equidimensional and smaller than those in the granular zone. In some specimens, the rods merge locally into a continuous, thin layer (Tavener-Smith, 1975, p. 3) that replaces or merges with particles of the granular zone.

Laminated sheaths enclose individual cores. The laminae (see Fig. 251, *1h*; 252,*1a*; 255,*2a*) are generally thinner than those of the mesotheca. The sheath laminae merge indistinctly with those of the mesotheca, but appear to be discontinuous with particles forming the granular zone.

The median rods are elliptical to subrounded in cross section and generally less than 0.01 mm in diameter. They appear to originate within the upper part of encrusting zoarial bases. As the zoarium grows distally

Fig. 225. Basal attachments of jointed (*1–3,5*) and rigid (*4*) zoaria.——*1–3,5. Clathropora frondosa* Hall, Niagara Gr., M. Sil., N.Y.; *1,* mesotheca and regularly arranged zooecia in tapered connecting segment slightly distal of proximal tip; transv. sec., USNM 242605, ×30; *2,* tapered connecting segment (proximal tip broken or abraded), expands into fully developed zoarium; external view, USNM 242606, ×5; *3,* intrazooecial deposits constitute annular ridge around connecting segment a short distance above its proximal tip; zooecia closed by thickened walls or stereom deposits in exozone; transv. sec., USNM 242607, ×30; *5,* extrazooecial stereom in annular ridge (upper part), regularly arranged zooecia throughout the connecting segment, mesotheca in the proximal tip (lower part); long. peel, USNM 242608, ×30. ——*4. Trigonodictya fenestelliformis* (Nicholson), U. Ord. (Richmond.), Wilmington, Ill.; margin of encrusting zoarial base; basal layer laminar adnate to substrate (a brachiopod, bottom) and vesicular above it; a few zooecia arise from vesicular portion, vesicles in indistinct zones; peel at right angle to edge of encrusting base, USNM 242609, ×30.

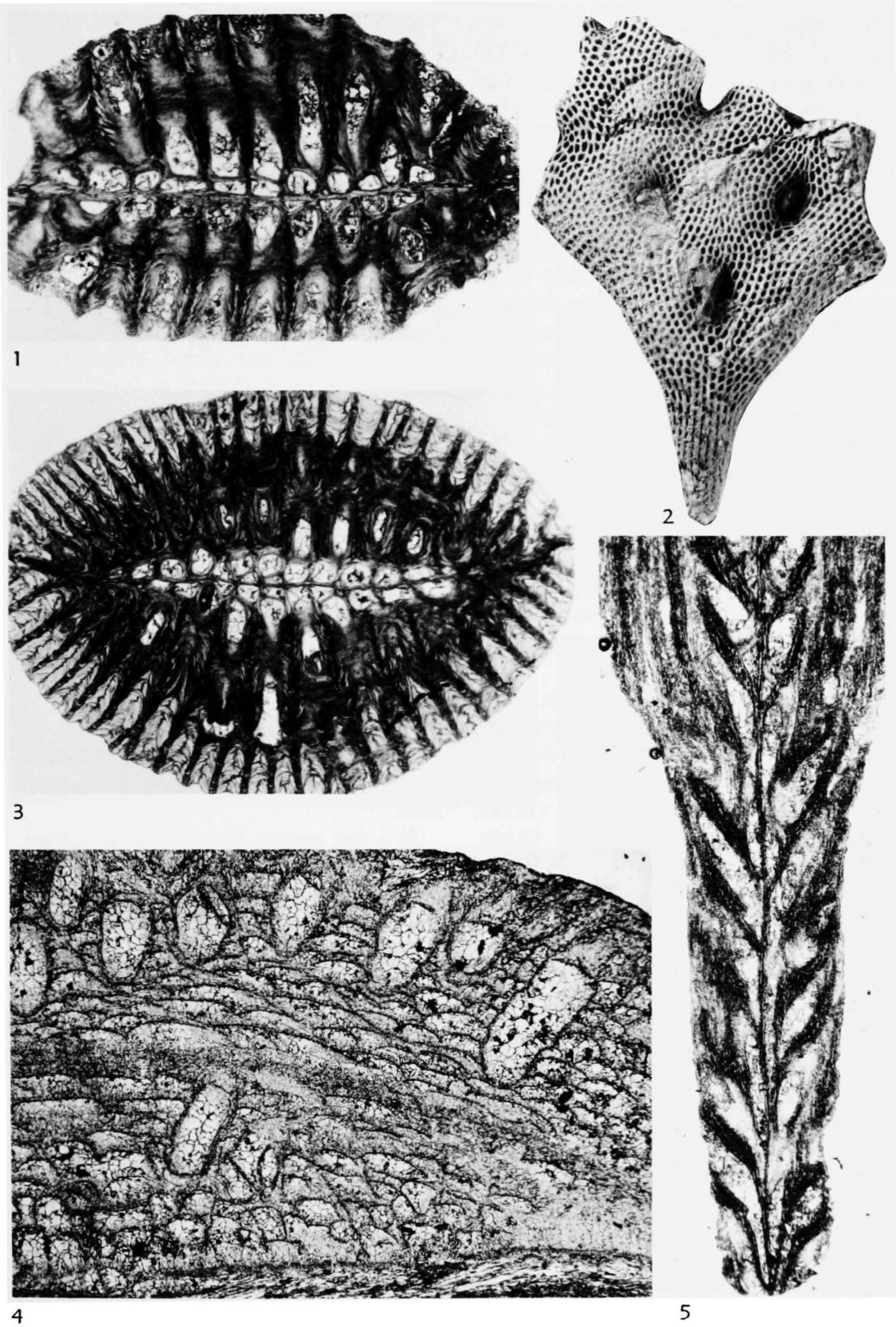

FIG. 225. *(For explanation, see facing page.)*

while expanding laterally, the rods are continuously added along the margins and between previously formed rods. They arise within the granular layer and do not bifurcate. As observed in transverse (see Fig. 252,*1c*) and deep tangential (see Fig. 251,*1b*; 257,*1e*) sections, the rods are evenly spaced and are continuous for appreciable distances. They curve broadly (Fig. 231) toward zoarial margins, where many terminate. In areas of zoarial branching, rods may curve into a new branch or terminate within the granular zone as new rods arise in the new branch. In general outline, the median rod complex in a zoarium is fan shaped and confined to the median granular zone of the mesotheca. I have not observed structural breaks in laminae of a mesotheca, which could indicate extension of the median rods into zooecial walls in the endozone, as reported by PHILLIPS (1960, p. 3, 5). Thus, the median rods do not appear to be associated directly with individual autozooecia, but appear to be extrazooecial.

Autozooecia.—In the Ptilodictyina, autozooecia are comparable in structure, size, shape, and distribution to those in the trepostomates (BOARDMAN, 1971), cystoporates (UTGAARD, 1973), rhabdomesines (BLAKE, 1973c), and cyclostomates (BORG, 1926b, 1933; BROOD, 1972). They are also similar to those in the fenestellines (TAVENER-SMITH, 1969a, 1975) but are larger.

In most ptilodictyines, autozooecia arise from the mesotheca in linear ranges of uniform width (Fig. 223, 231, 232). Junctions between mesothecal and autozooecial wall laminae are usually irregular discontinuities (see Fig. 240,*1b*; 257,*1e*).

Autozooecia are usually delineated laterally by longitudinal walls and distally by transverse walls (Fig. 228, 231, 232). Longitudinal walls are continuous until they bifurcate or a new wall arises from within a widened range (Fig. 228). Longitudinal walls delineate the zooecial ranges at precise lateral intervals and either preceded the transverse walls (Fig. 231) or arose concurrently with them (Fig. 228, 232). Transverse walls (Fig. 228, 231, 232) separate successive autozooecia within a range at regular intervals and alternate in position with those of adjacent ranges (rhombic budding of BOARDMAN & UTGARRD, 1966, p. 1083). The shape of a resulting autozooecium in cross section is that of a subrectangle or subparallelogram of constant size (Fig. 228, 231). Width of the autozooecium averages between one-third and half its length at the mesotheca, with longer dimension in the zoarial growth direction. With few exceptions, this ratio is maintained in the endozone.

In a few genera, longitudinal and transverse walls are only partially contiguous, and the longitudinal walls are not linearly continuous. Extrazooecial skeletal deposits between autozooecia are laminar or vesicular

FIG. 226. Basal attachment of a rigid zoarium (*1*) and autozooecial budding pattern in erect zooecia (*2,3*). ——*1a–d. Trigonodictya fenestelliformis* (NICHOLSON), U. Ord. (Richmond.), Wilmington, Ill.; serial peels of basal attachment; *a,* proximal part of connecting segment with fully developed mesotheca containing abundant median rods and regularly aligned zooecia, narrow endozone, vesicular extrazooecial stereom arises locally from the mesotheca; transv. peel, ×50; *b,* encrusting zoarial base; first generation of zooecia in spiral pattern (lower center), zooecia generally separated by vesicles of basal layer, mesotheca not present; peel from base of first generation of zooecia just above bottom of basal layer, ×50; *c,* vesicular portion of basal layer from which first generation of zooecia arises, subsequent zooecia in margin of encrusting base (upper left); peel in plane of vesicular portion of basal layer parallel to substrate (at right angle to margin of encrusting base, Fig. 225,*4*), ×50; *d,* regularly arranged basal zooecia in margin of encrusting base; peel in plane parallel to substrate, ×30, all USNM 242609.——*2. Athrophragma foliata* (ULRICH), Decorah Sh., M. Ord., St. Paul, Minn., paralectotype; subtubular autozooecia surrounded by vesicular and laminar extrazooecial stereom in inner exozone, distinct autozooecial boundaries; tang. sec., USNM 163112, ×30.——*3. Athrophragma grandis* (ULRICH), U. Ord. (Richmond.), Wilmington, Ill.; subtubular autozooecia in relatively straight ranges surrounded by vesicular extrazooecial stereom just above mesotheca, distinct autozooecial boundaries, median rods (near top); tang. sec., USNM 242614, ×30.

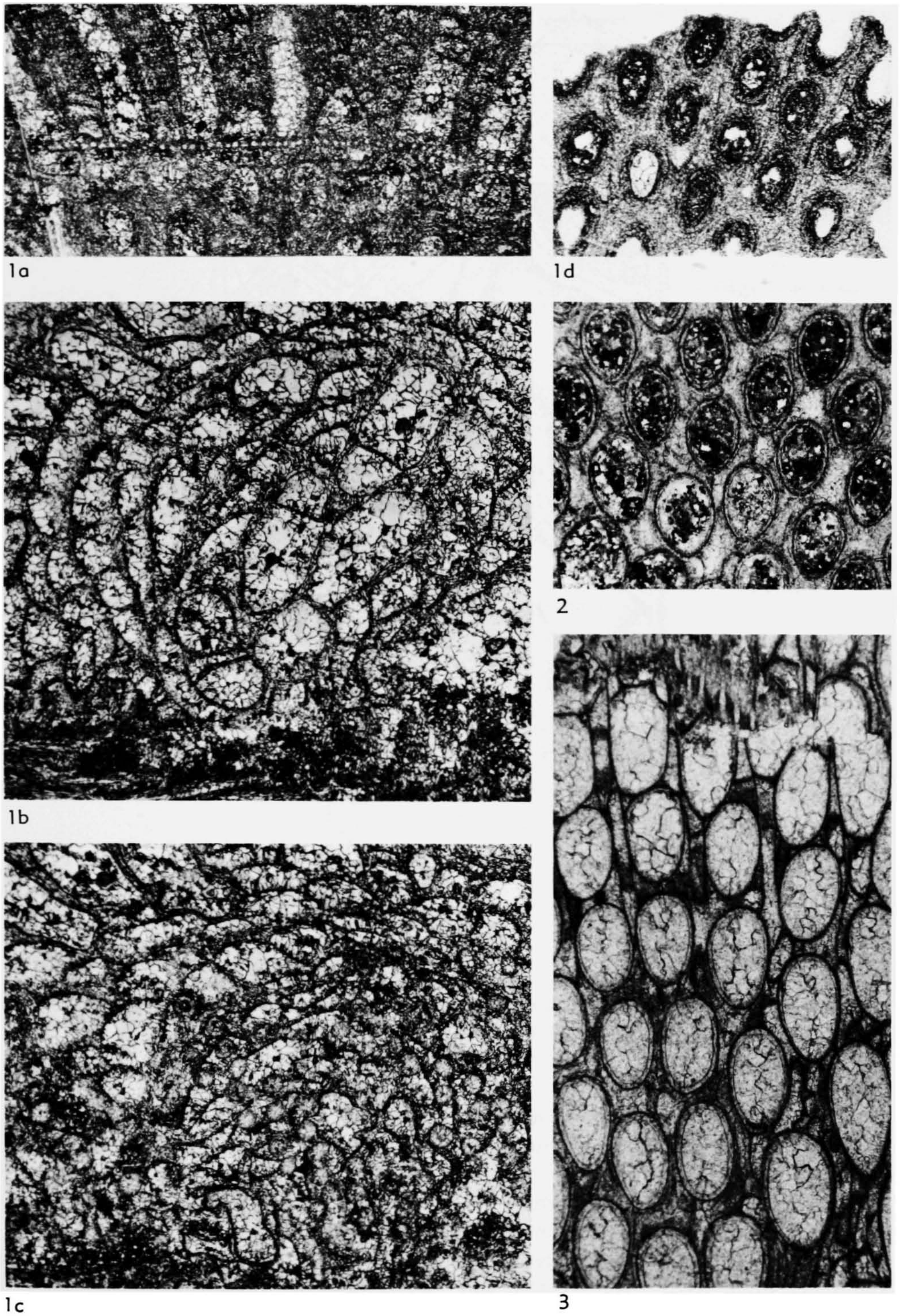

FIG. 226. *(For explanation, see facing page.)*

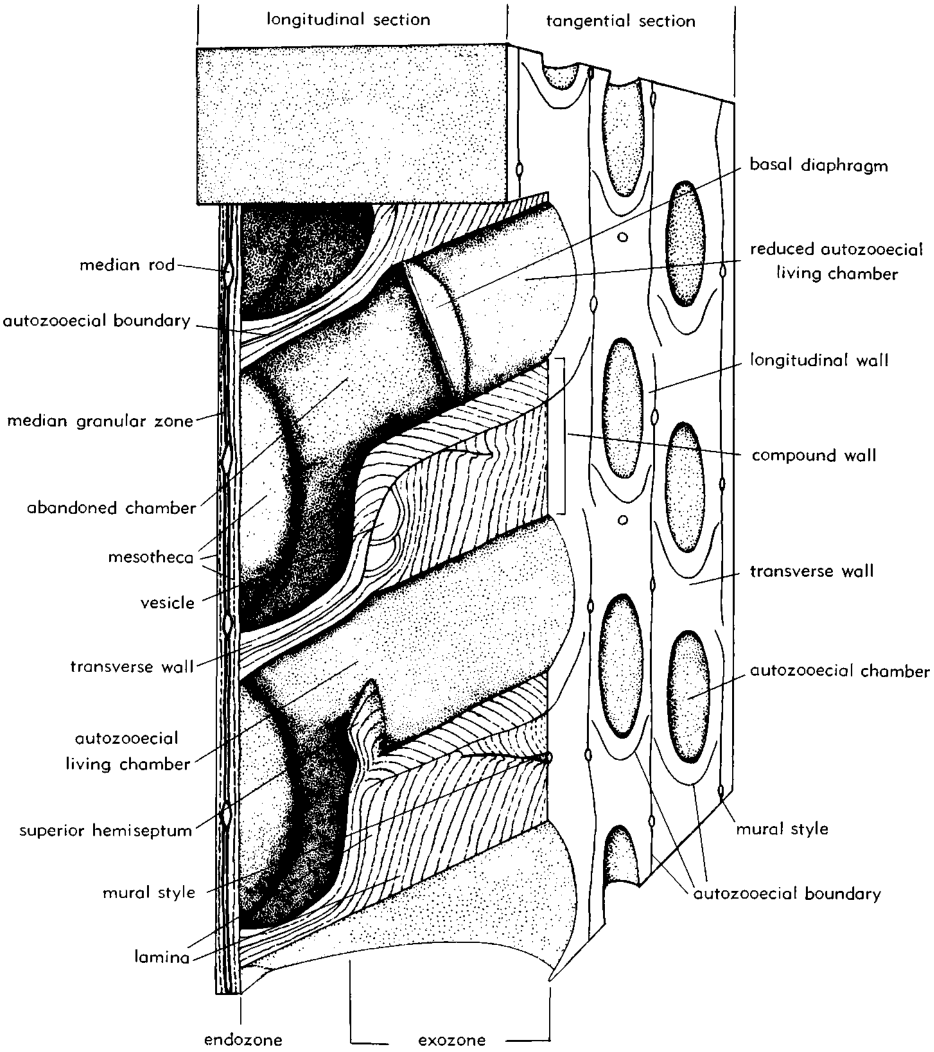

FIG. 227. Zoarial structure of generalized *Stictopora*, family Rhinidictyidae. Longitudinal section at right angle to mesotheca and parallel to length of zooecia from mesotheca to zoarial surface in midregion of erect zoarium. Tangential section parallel to and slightly under surface of zoarium and parallel to plane of mesotheca. Only one side of bifoliate zoarium is shown.

(Fig. 226,*3*; 233; 234; see also 252,*1a*). Generally, the autozooecia are irregularly subelliptical to subcircular in cross section at the mesotheca (Fig. 234).

Ontogenetically, autozooecia formed two distinct growth stages, an early endozonal stage followed by an exozonal stage. In the endozone, autozooecial walls are thin and may curve (Fig. 223,*5*; 224,*4*; 232) regularly as they extend from the mesotheca. Width of the endozone is generally constant and may be characteristic of a group of species, as in *Stictopora*. With beginning of the exozonal growth stage, zooecial walls thicken considerably as autozooecia diverge from the general growth direction of the mesothecal plane. Morphological changes at the endozone-exozone boundary include adjustments in space between autozooecial chambers and thickened walls, modifications in configuration of wall laminae (Fig. 227), inception of other skeletal structures within

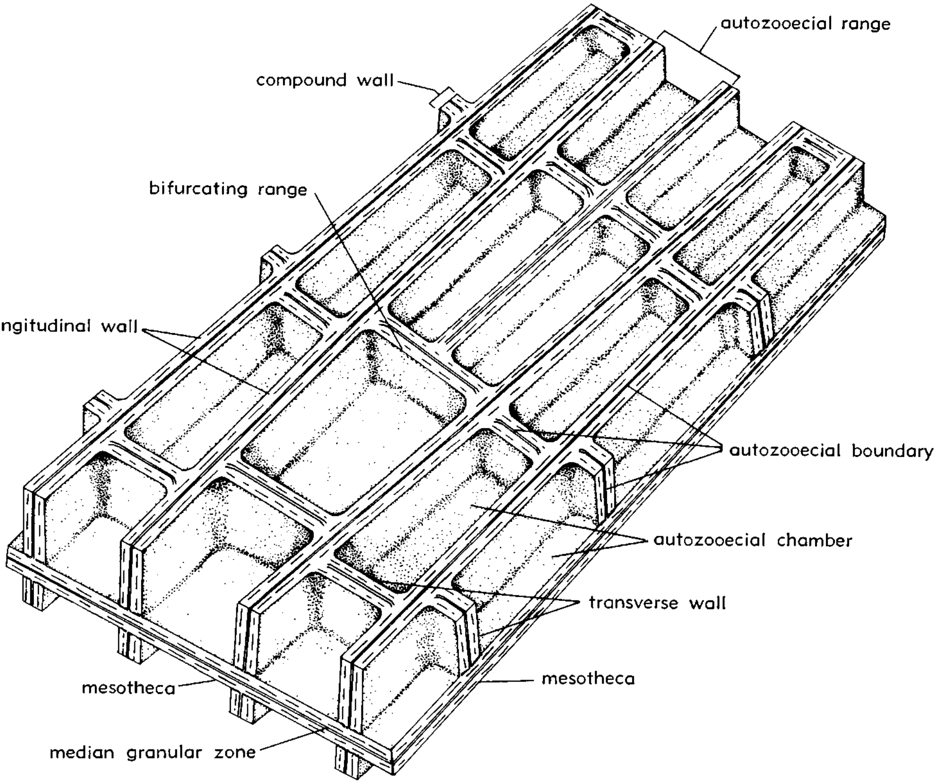

FIG. 228. Arrangement and shape of autozooecia in the endozone of generalized *Ptilodictya,* family Ptilodictyidae. Budding pattern at mesotheca in midpart of erect zoarium is characteristic of the ptilodictyines. Longitudinal walls are structurally continuous; transverse walls may be straight, as shown, or convex distally. One bifurcating range is shown.

laminae (Fig. 235,*3*), and the appearance of polymorphs (see Fig. 242,*2a*). Features typical of the zooecial endozone overlap with those of the exozone so that the endozonal-exozonal boundary describes a narrow, indistinct zone that is irregular in thickness (see Fig. 244,*1d*). At the zoarial margin, the boundary becomes indistinguishable (see Fig. 240,*1f*).

Linearity of zooecial ranges and skeletal continuity of longitudinal walls (see Fig. 240,*1d*) are maintained in the exozone of many taxa but may be obscured by extrazooecial stereom or modified by monticular areas (see Fig. 254,*1a,d*). In other taxa (see Fig. 245,*2b*), zooecial walls that are longitudinal in the endozone lack this alignment in the exozone, and autozooecia in some genera are in a distinct rhombic pattern (Fig. 224,6). Autozooecial chambers, regardless of zooecial shape, are usually subtubular with a subelliptical (see Fig. 253,*2a*) to subcircular (see Fig. 254,*1d*) cross section in the exozone.

Ptilodictyine autozooecia consist of structurally different granular and laminar calcareous materials. Granular zones (Fig. 227) constitute only a small part of the total skeletal mass, but they form the basic framework in ptilodictyine zoaria. The significance of the granular component and its bearing on possible phylogenetic relationships between ptilodictyines and other cryptostomate suborders has been only recently recognized (TAVENER-SMITH, 1975; BLAKE, this revision).

In most ptilodictyines, autozooecial

boundaries are granular in the endozone (Fig. 223, 231, 232), and are identical in microstructure to the granular zone in the mesotheca. Laminae in endozonal walls generally parallel the granular autozooecial boundaries, although this relationship is not always clear (see Fig. 259,*2a*). In most taxa, the interface between granular zones and adjacent laminae is abrupt.

With the beginning of the exozonal growth stage, zooecial boundaries may be obscured by merging zooecial wall laminae (see Fig. 240,*1b*), become broadly serrated zones (see Fig. 245,*1f*), or become narrowly serrated zones (see Fig. 259,*2a*) consisting of irregular discontinuities formed by intertonguing of all laminae along the approximate median between autozooecia (Fig. 229,*4,5*).

In the exozone, laminae in compound walls form different patterns in different families. In general, the laminae are either in an inverted U-shape (Fig. 229,*5*; 230,*1,2,4*) or V-shape (Fig. 227; 229,*4*; 236) toward the zoarial surface. Walls having a broadly U-shaped configuration possess autozooecial boundaries that are broadly serrated as a result of intertonguing with laminae in adjacent zooecia (see Fig. 240,*1b*). These boundaries vary from being well defined (see Fig. 245,*1f*) to indeterminate (see Fig. 242,*2a*), and are not visibly connected with the boundaries in the endozone. Walls having narrowly (see Fig. 255,*1d*) to broadly V-shaped laminae (see Fig. 259,*2a*) possess autozooecial boundaries that are on the average narrowly serrated. These boundaries are well defined in most genera and are continuous with boundaries in the endozone. In a few taxa, dark zones other than autozooecial boundaries may arise in autozooecial walls in the exozone and extend through the walls at approximately right angles to the zoarial surface.

In some ptilodictyines, autozooecial walls are divided into a relatively thick outer part and a much thinner inner part (Fig. 237,*1,3*). Configuration of laminae in the outer part of a wall is characteristic of a taxon. In the inner part of a wall, adjacent to the zooecial chamber, laminae may be parallel to the long axis of a zooecial chamber (Fig. 229,*5*) or oblique to the chamber axis (see Fig. 255,*1b*). The thin part of a wall lines zooecial chambers. Generally, both sets of wall laminae intertongue along a dark discontinuity, suggesting that they were secreted concurrently.

BOARDMAN (1971, fig. 1) described similarly divided zooecial walls in certain Trepostomata as consisting of a cortex (outermost unit of zooecial wall) and lining (wall unit between cortex and zooecial chamber).

The lining of zooecial chambers in ptilodictyines is generally indistinct. In autozooecia, it may be present or absent. When present, it is commonly discontinuous within a chamber.

Configuration of autozooecial wall laminae, together with relative thickness of lam-

FIG. 229. Miscellaneous morphology of ptilodictyines.——*1. Phaenopora twenhofeli* BASSLER, Becscie F., L. Sil., Anticosti Is., Can., holotype; probable remnants of soft parts occurring as elongated brown bodies around superior and inferior hemisepta (center and upper, right of mesotheca); long. sec., USNM 143032, ×50.——*2,3. Trigonodictya conciliatrix* (ULRICH), Decorah Sh., M. Ord., Cannon Falls, Minn., paralectotypes; *2,* extrazooecial stereom in autozooecial range partitions with median dark zones containing distinct mural styles in exozone; tang. sec., USNM 242615, ×50; *3,* mesotheca bifurcating at right angle (lower center), distinct median rods in granular zone, extrazooecial vesicles at base of exozone; transv. sec., USNM 242616, ×100.——*4. Pseudostictoporella typicalis* ROSS, float, M. Ord., Martinsburg, N.Y., paratype; compound autozooecial wall with V-shaped laminae, narrowly serrated and nongranular autozooecial boundary in exozone, indistinct dark layers between laminae; transv. sec., YPM 25455, ×400. ——*5. Phaenoporella transenna mesofenestralia* (SCHOENMANN), M. Ord. (Mangaze.), Podkamennaya Tunguska River, Sib., USSR; U-shaped laminae and broadly serrated autozooecial boundaries, exilazooecium (center) with lining of laminae parallel to chamber, indistinct dark layers between laminae; transv. sec., USNM 171741, ×400.

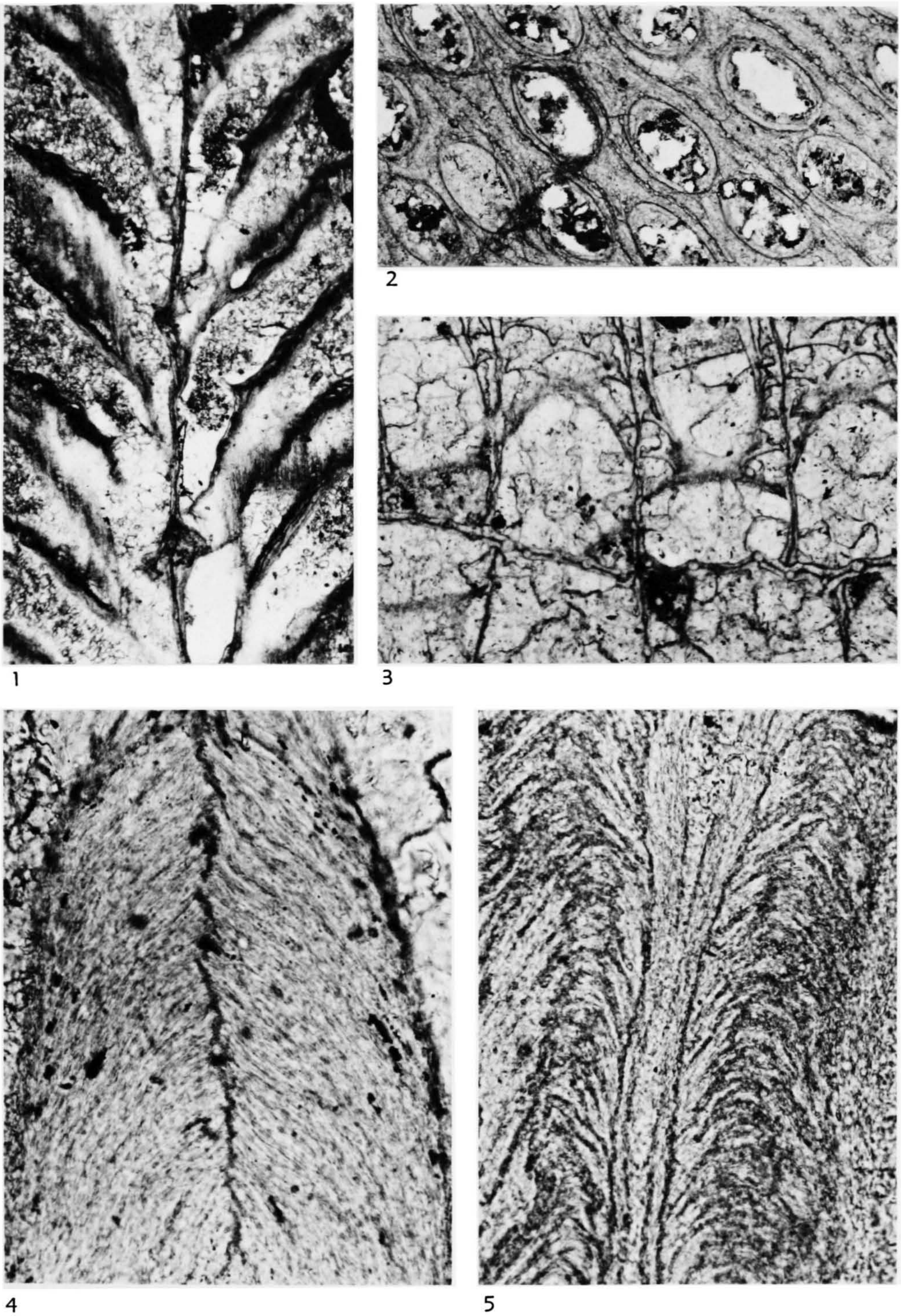

Fig. 229. *(For explanation, see facing page.)*

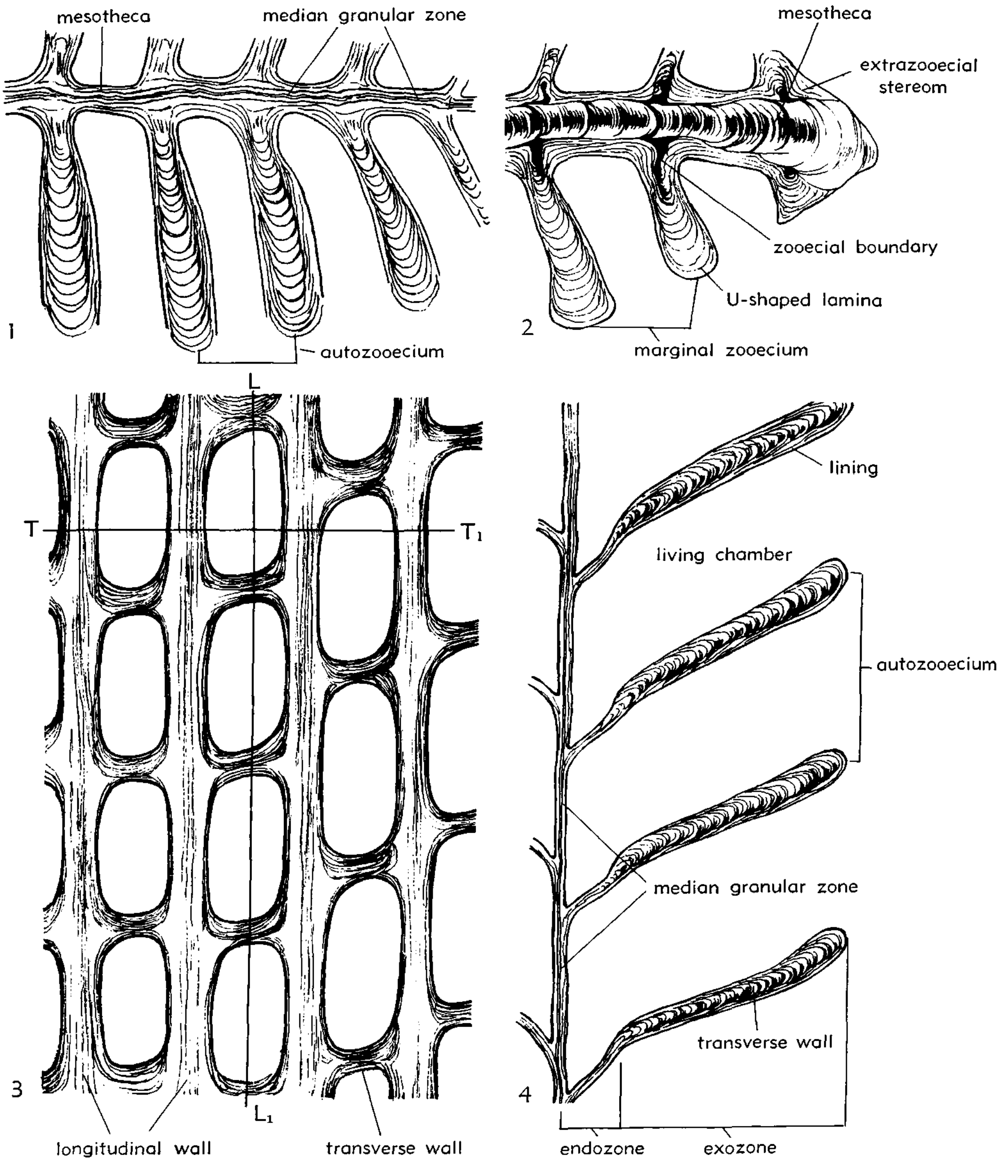

FIG. 230. Generalized *Ptilodictya,* family Ptilodictyidae.——*1.* Zoarial midregion, transv. sec. (along T–T_1 in *3*).——*2.* Zoarial margin and curved laminae in mesotheca, transv. sec.——*3.* Exozone in zoarial midregion, tang. sec.——*4.* Zoarial midregion, long. sec. (along L–L_1 in *3*).

inae, characterize various ptilodictyine families.

Autozooecia within a single erect zoarium are identically constructed and show only minor differences in shape, size, and ontogeny. In areas of zoarial branching, autozooecia are generally modified in shape from those in segments between branches. These autozooecia are commonly larger or smaller than regular zooecia and are subcircular in cross section (see Fig. 247,*1c*; 251,*1e*). If the branching results from widening of zooecial ranges at the mesotheca, the autozooecia are commonly larger (Fig. 223,*6*). If the branching results from bifurcating longitudinal walls at the mesotheca, the autozooecia are

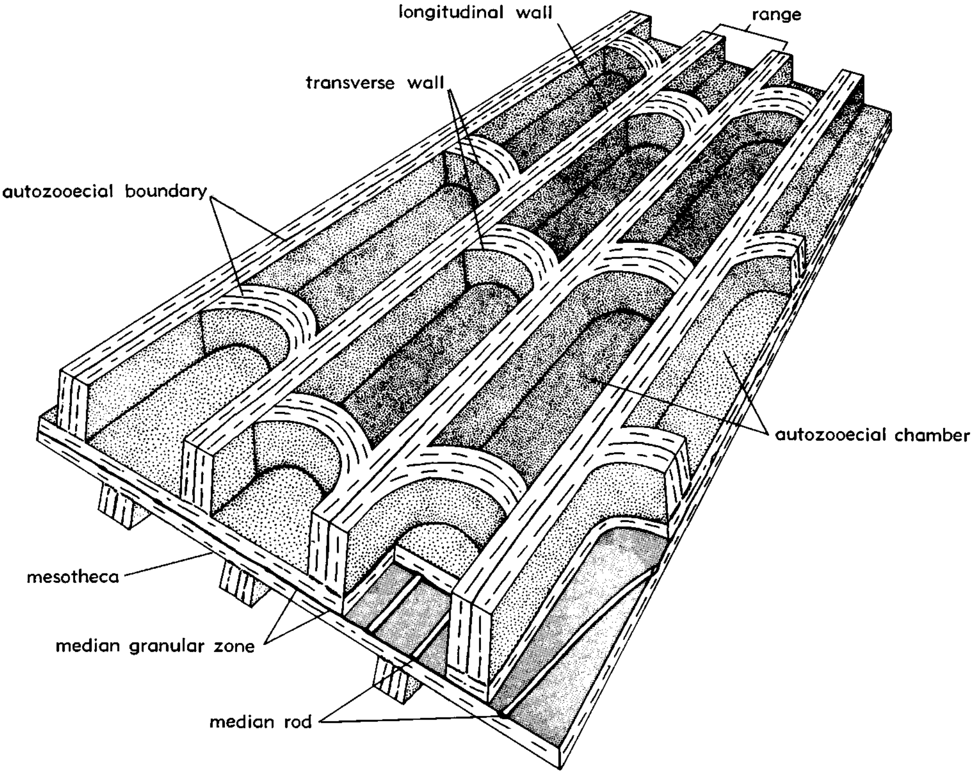

FIG. 231. Arrangement and shape of autozooecia in the endozone of a generalized *Stictopora,* family Rhinidictyidae. Structural relationship between autozooecial walls in the endozone suggests that longitudinal walls probably precede transverse walls during formation of a zooecium. This budding pattern appears to characterize some species of *Stictopora.*

commonly smaller and more elliptical in cross section than those in segments between branches (see Fig. 242,*2c*).

These are just a few examples of modified autozooecia that occur along with regularly formed autozooecia. All of these slightly modified zooecia are considered to be autozooecia because they are comparable to regular autozooecia in chamber size, structure, and origin.

Chambers of autozooecia.—Extant tubuliporate bryozoans possess subtubular chambers that house functional soft parts. In most Ptilodictyina, autozooecial chambers differ in size and shape from endozone to exozone. Endozonal segments are generally subrectangular to subrhomboid in cross section parallel to the mesotheca and are only rarely subelliptical (Fig. 227, 228, 231, 232, 234). Exozonal segments are subtubular throughout and subelliptical to subcircular in cross section.

Size, shape, and postulated growth of autozooecia and living chambers in the Ptilodictyina are comparable to those in autozooecia of the Tubuliporata and assumed autozooecia in Trepostomata (BOARDMAN, 1971, p. 18), Cystoporata (UTGAARD, 1973, p. 327), and Rhabdomesidae (BLAKE, 1973c, p. 363).

Basal diaphragms are common in the Ptilodictyina, but occur irregularly. They may be present in some autozooecia of a zoarium or in most autozooecia in some groups of taxa. Basal diaphragms consist of a few laminae that are structurally continuous with autozooecial wall laminae. Diaphragms may be straight or curved (Fig. 227; see also

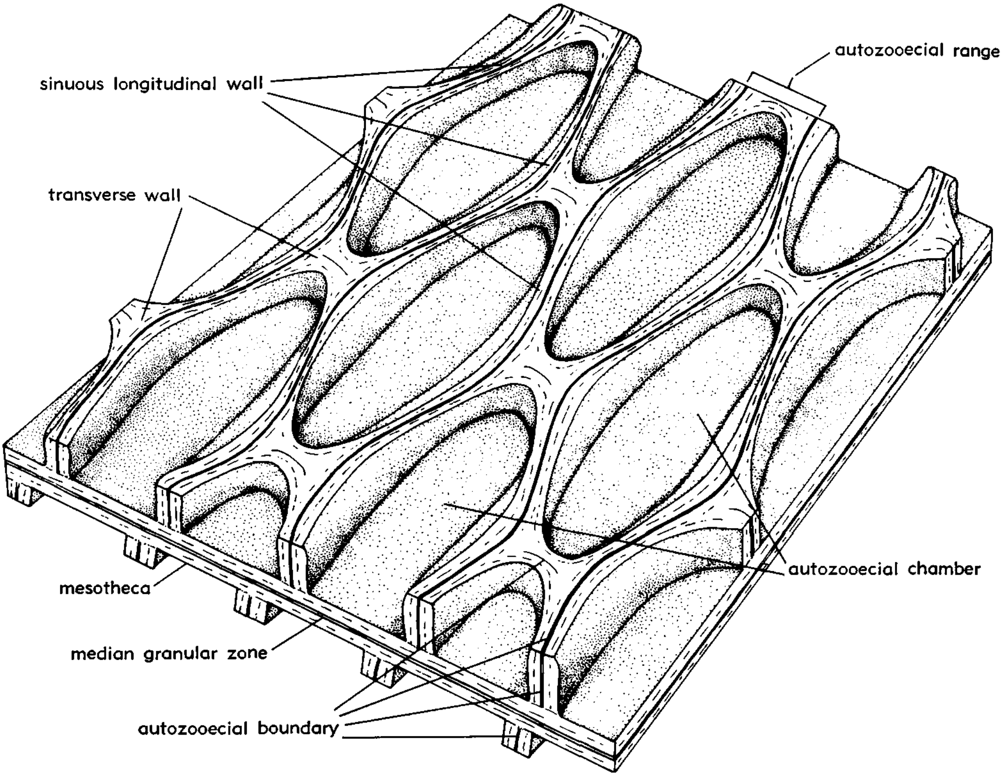

FIG. 232. Arrangement and shape of autozooecia in the endozone of a generalized *Escharopora,* family Escharoporidae. Autozooecia expand and narrow alternately in adjacent ranges. Development in the endozone characterizes the family and approximates that of the Intraporidae and Stictoporellidae.

252,*1b*). At junctions with autozooecial walls they curve sharply outward toward zoarial surfaces (Fig. 233, 236).

In some species, basal diaphragms are regularly spaced (see Fig. 252,*1b*). In others they are scattered. In a few taxa they are present only at the base of the exozone (see Fig. 246,*1b*), and in others they may occur anywhere in a chamber. In general, variation among taxa in spacing of basal diaphragms suggests that some species differ in length of their living chambers.

In numerous species, diaphragms are absent and there is no evidence for their presence at any time during the growth of a zoarium (Fig. 230, 237–239). Therefore, it is assumed that in these taxa the mesotheca formed the basal proximal wall (floor) of the living chamber throughout the growth of a zoarium (Fig. 229,*1*).

If abandoned chambers (see Fig. 252,*1b*) can be considered as part of the evidence for degeneration-regeneration cycles in colonies, these cycles are irregular in the Ptilodictyina. However, the general lack or rare occurrence of abandoned chambers may not be indicative of the absence of cycles. Perhaps the basal diaphragms were not preserved, or degeneration-regeneration cycles occurred without secretion of diaphragms.

Autozooecial chambers in the Ptilodictyina contain several kinds of skeletal features that project from the walls into the chambers without forming a complete cross structure. Similar structures in the trepostomatous bryozoans have been termed lateral structures (BOARDMAN, 1971, p. 18). In the ptilodictyines lateral structures include hemisepta (Fig. 227), mural spines of varying shapes (see Fig. 240,*1g*; 245,*2c*), and such

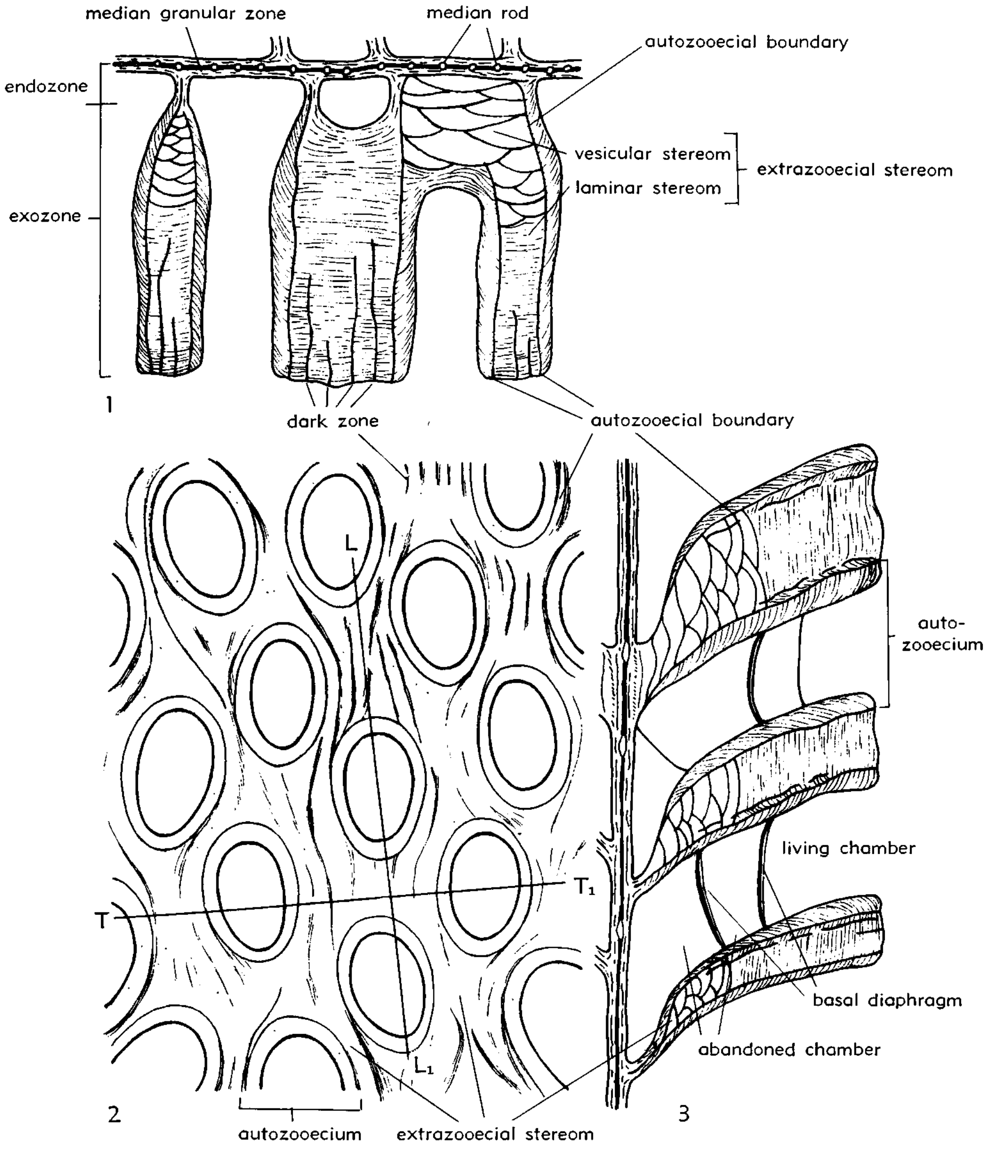

FIG. 233. Generalized zoarial midregion in *Athrophragma,* family Rhinidictyidae.——*1.* Transverse section (along T–T$_1$ in *2*).——*2.* Tangential section of exozone.——*3.* Longitudinal section (along L–L$_1$ in *2*).

uncommon structures as cysts (Ross, 1960a, p. 441) and cystiphragms (see Fig. 241,*2c*). Lateral structures modify the sizes and shapes of autozooecial living chambers.

Hemisepta are the shelflike, straight or curved projections (Fig. 237,*3*) that extend from the wall partway into autozooecial chambers. The projections are formed as extensions of wall laminae and are of varying shapes. They generally arise from walls at the base of the exozone and project into the endozonal part of a chamber. In Ptilodictyina, a hemiseptum that projects from a proximal wall into the endozonal part of a chamber is called a superior hemiseptum (Fig. 227); one extending from the mesotheca or a distal wall

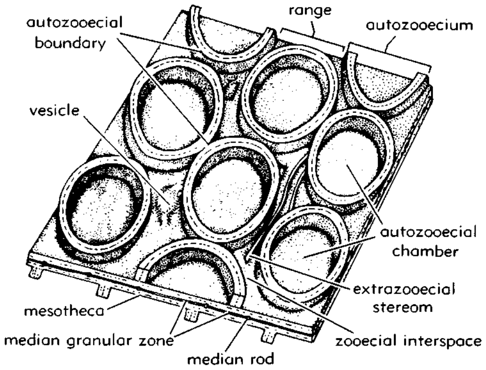

FIG. 234. Arrangement and shape of autozooecia in the endozone of generalized *Pachydictya* and *Athrophragma,* family Rhinidictyidae. Autozooecia are subtubular, partly separated by extrazooecial skeleton or space, and laterally without structurally continuous longitudinal walls.

is called an inferior hemiseptum (Fig. 237,*3*). Both kinds of hemisepta may occur in the same chamber, arranged alternately, or they may occur singly. Inferior hemisepta are commonly straight (see Fig. 242,*2a*). Superior hemisepta vary in shape, and may be straight or curved (see Fig. 251,*1f*). Most superior hemisepta are slightly curved, hooklike in cross section, or knoblike (see Fig. 244,*1b*). Although hemisepta conventionally have been regarded as one of the most characteristic features of the ptilodictyines, their distribution is uneven within a zoarium or a species, and numerous taxa lack them. In general, hemisepta are more common in taxa that lack basal diaphragms.

Mural spines are thin extensions of zooecial wall laminae that project into autozooecial chambers. They generally curve proximally (see Fig. 240,*1g*), but may extend at a right angle to the chamber axis. Spines have not been observed in endozonal parts of chambers. In exozones, spines generally occur irregularly; however, in some species (Ross, 1960c, p. 1066) they arise from walls at regular alternating intervals and are closely spaced. In specimens with closely spaced spines, the volume of each living chamber is reduced and soft parts probably curved around tips of the spines.

Cystiphragms are uncommon and of minor significance in ptilodictyines. They are present in one or two Ordovician genera (see Fig. 262,*1c*), one Devonian genus (see Fig. 241,*2c*), and one Carboniferous genus (*Phragmophera*).

Cysts are laminated, hollow, irregularly shaped spheres that project inward from zooecial walls. They are generally rare in the ptilodictyines. Ross (1960a, p. 441) described cysts in species of *Ptilodictya* and suggested a possible association with reproductive functions.

Polymorphic zooecia.—Ptilodictyine zoaria contain several kinds of polymorphic zooecia that differ from the autozooecia in ontogeny, size, or shape. They include zooecia near margins of zoaria and fenestrules, exilazooecia (exilapores of DUNEAVA & MOROZOVA, 1967, p. 87; term modified by UTGAARD, 1973, p. 339), mesozooecia (ROSS, 1964b, p. 940), and zooecia near or in monticules.

Marginal zooecia are those near free margins of branching (see Fig. 251,*1e*) or explanate zoaria, or along margins of fenestrules in cribrate zoaria (see Fig. 244,*1c*). These zooecia are considered to be polymorphic because they arise from the mesotheca without forming distinct endozonal chamber portions. Thus, they commonly are shorter and have only an exozonal stage of development (Fig. 230). Marginal zooecia are subtubular and generally oriented oblique to the vertical growth direction of a branch. Because of the different orientation, cross-sectional shape of the zooecia is commonly elongated distally and narrowed laterally. In some taxa, however, marginal zooecia are more rounded than autozooecia (see Fig. 255,*1a*). Such features as basal diaphragms are also present in marginal zooecia, if present in autozooecia of a taxon. In general, marginal zooecia vary more in shape than do regular autozooecia in a specimen.

In microstructure, marginal zooecia are the same as autozooecia. As marginal zooecia arise from the mesotheca, they form thicker walls than those in a regular endozone, and the walls thicken gradually while forming the

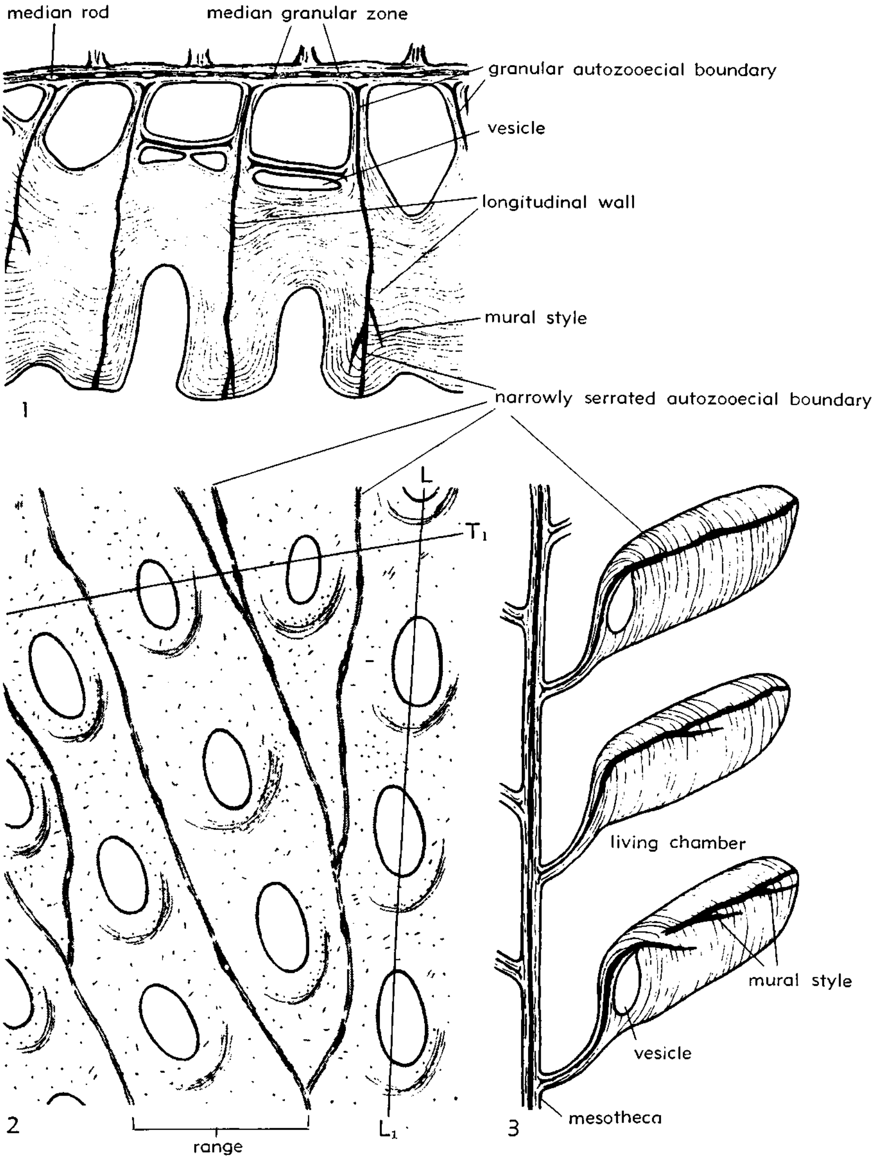

Fig. 235. Generalized zoarial midregion in *Stictopora,* family Rhinidictyidae.——*1.* Transverse section (along T–T_1 in *2*).——*2.* Tangential section of exozone showing bifurcating ranges.——*3.* Longitudinal section (along L–L_1 in *2*).

margins (see Fig. 245,*1a*). Wall laminae are in structural continuity with laminae of extrazooecial deposits in the margins (see Fig. 249,*1a*).

In general appearance, marginal zooecia are similar to autozooecia forming areas of bifurcation and to zooecia forming the basal attachments of a zoarium. Soft parts in the marginal zooecia probably performed all normal functions but at different rates, which resulted in a modified mode of development and appearance of the marginal zooecia.

Exilazooecia (Dunaeva & Morozova, 1967, p. 87) are polymorphs that are appreciably smaller than regular autozooecia in the same zoarium (Fig. 229,*5*; 237; 239,*2*).

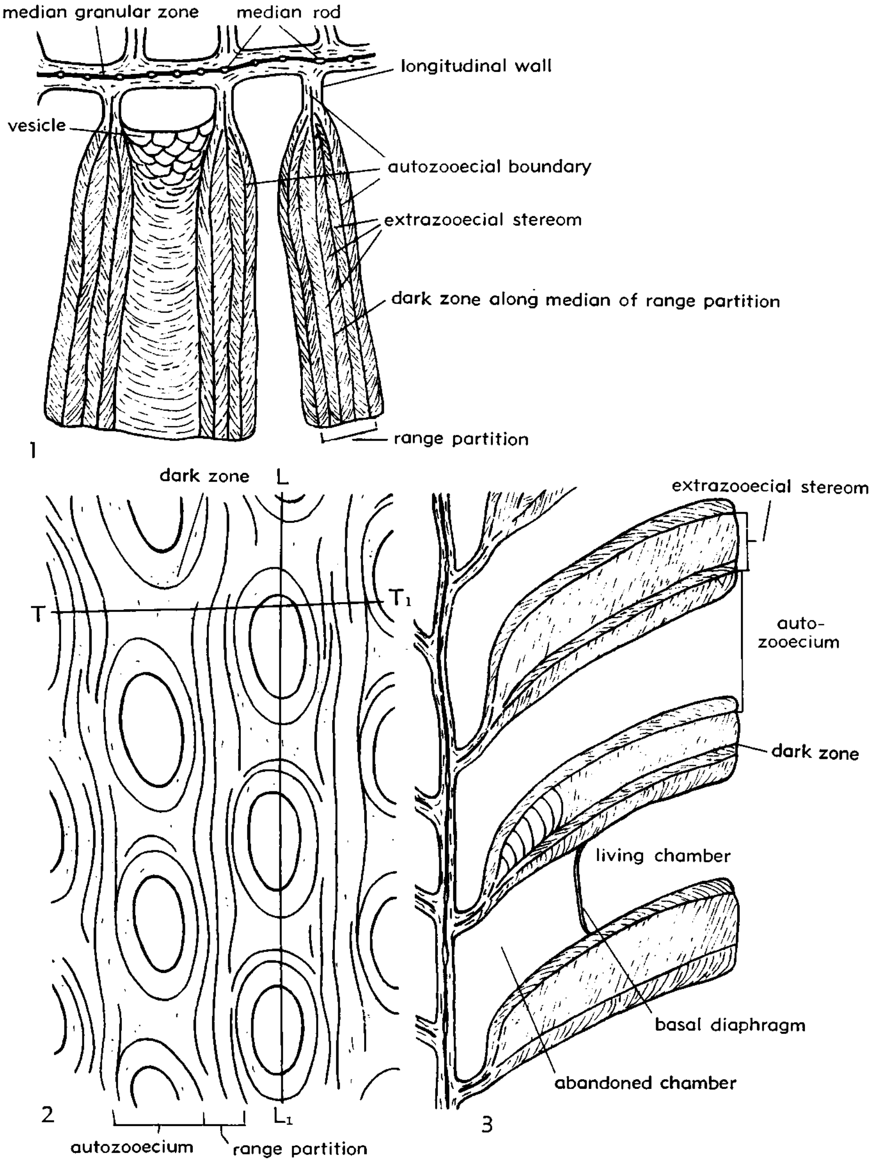

FIG. 236. Generalized zoarial midregion in *Trigonodictya*, family Rhinidictyidae. Extrazooecial stereom between range partitions and autozooecial walls consists of laminae that are reversed in direction from those in autozooecial walls.——*1*. Transverse section (along T–T$_1$ in *2*).——*2*. Tangential section of exozone.——*3*. Longitudinal section (along L–L$_1$ in *2*).

They are subtubular skeletal sacs that are irregularly polygonal to subrounded in cross section (see Fig. 259,*1f*). Diaphragms generally are lacking or few. Exilazooecia developed in exozones, but in certain taxa they budded in endozones (see Fig. 264,*1b*). Exilazooecia commonly constitute monticules or occur throughout a zoarium. They are common in some ptilodictyine families, but are absent in the Rhinidictyidae and Virgatellidae.

Exilazooecia in the ptilodictyines have

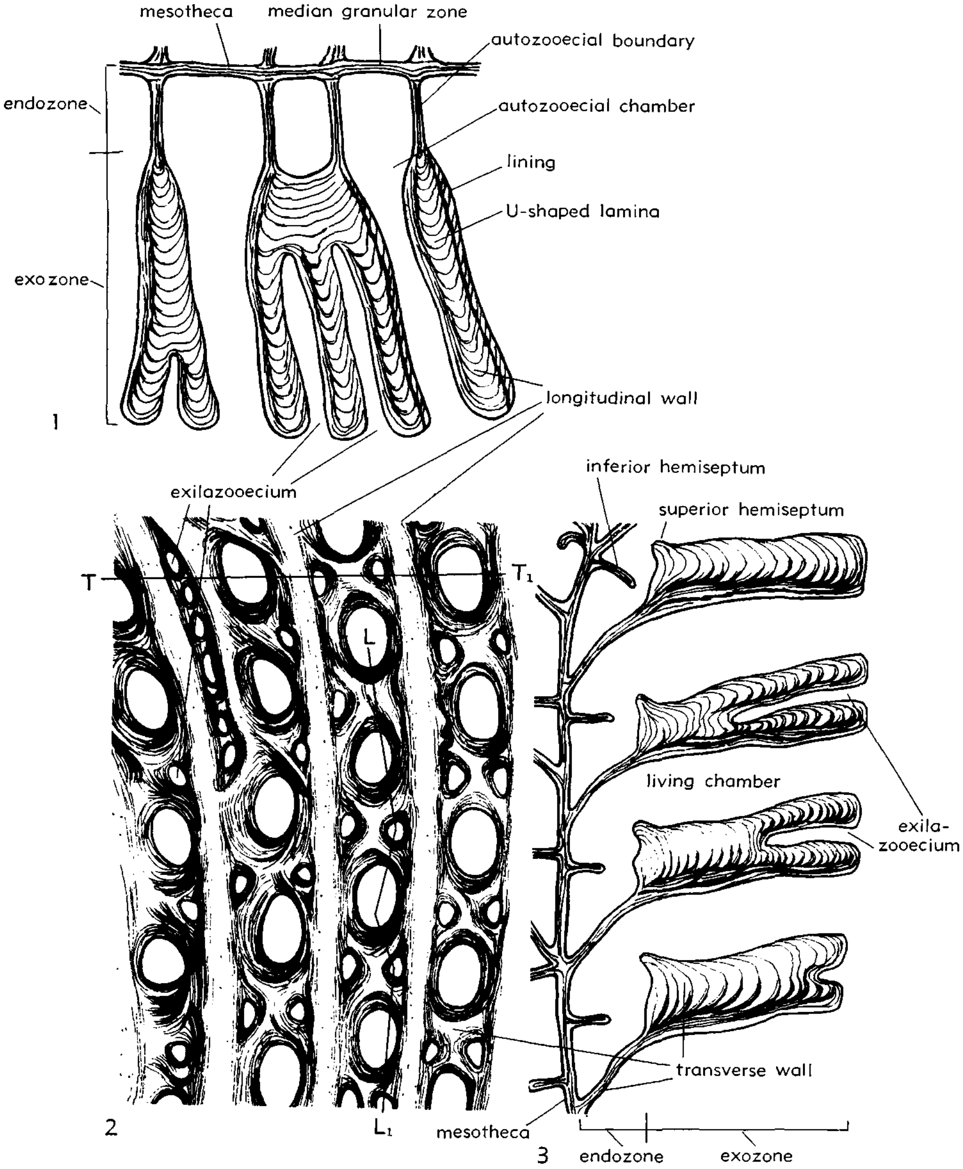

FIG. 237. Generalized zoarial midregion of *Phaenopora,* family Ptilodictyidae.——*1.* Transverse section (along T–T₁ in *2*).——*2.* Tangential section of exozone.——*3.* Longitudinal section (along L–L₁ in *2*).

been commonly described as mesopores (ULRICH, 1890, 1893; BASSLER, 1953; PHILLIPS, 1960; ROSS, 1960c), as mesozooecia (ROSS, 1964b), and as pseudomesopores (ASTROVA, 1965; KOPAYEVICH, 1972). KOPAYEVICH (1972) in a study of polymorphism in the family Ptilodictyidae recognized at least two kinds of pseudomesopores, which she distinguished as primary and substituting. Both kinds appear to be skeletally identical but differ in their locus of origin. Primary pseudomesopores originated at the base of the exozone and continued to grow concurrently with the autozooecia. Substituting pseudomesopores originated from living chambers of autozooecia in inner exozones

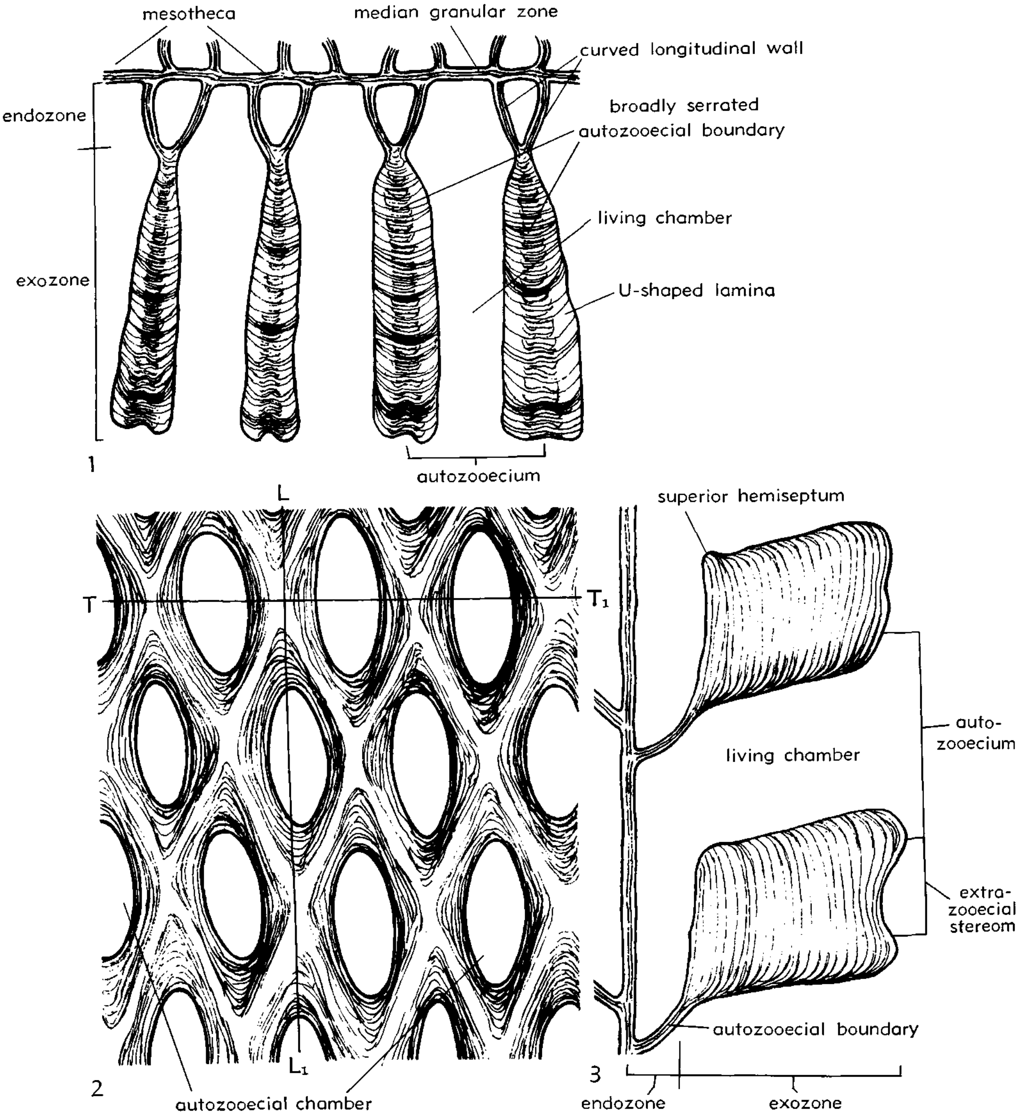

FIG. 238. Generalized zoarial midregion in *Escharopora*, family Escharoporidae.——*1*. Transverse section (along T–T$_1$ in *2*).——*2*. Tangential section of exozone.——*3*. Longitudinal section (along L–L$_1$ in *2*).

and replaced or aborted them in outer exozones or at zoarial surfaces. KOPAYEVICH also reported that groups of substituting pseudomesopores resulted in slightly raised areas at zoarial surfaces, and postulated that these could have been associated with brooding functions in certain ptilodictyids.

Only one kind of exilazooecia is recognized here, and it appears to be the equivalent of KOPAYEVICH's primary pseudomesopore. The second kind could not be distinguished with certainty in available material.

Mesozooecia are comparable to exilazooecia in size, locus of origin, and pattern of distribution in a zoarium, but possess numerous diaphragms. ROSS (1964b, p. 940) proposed the term mesozooecium for the small zooecia, with or without diaphragms, that are

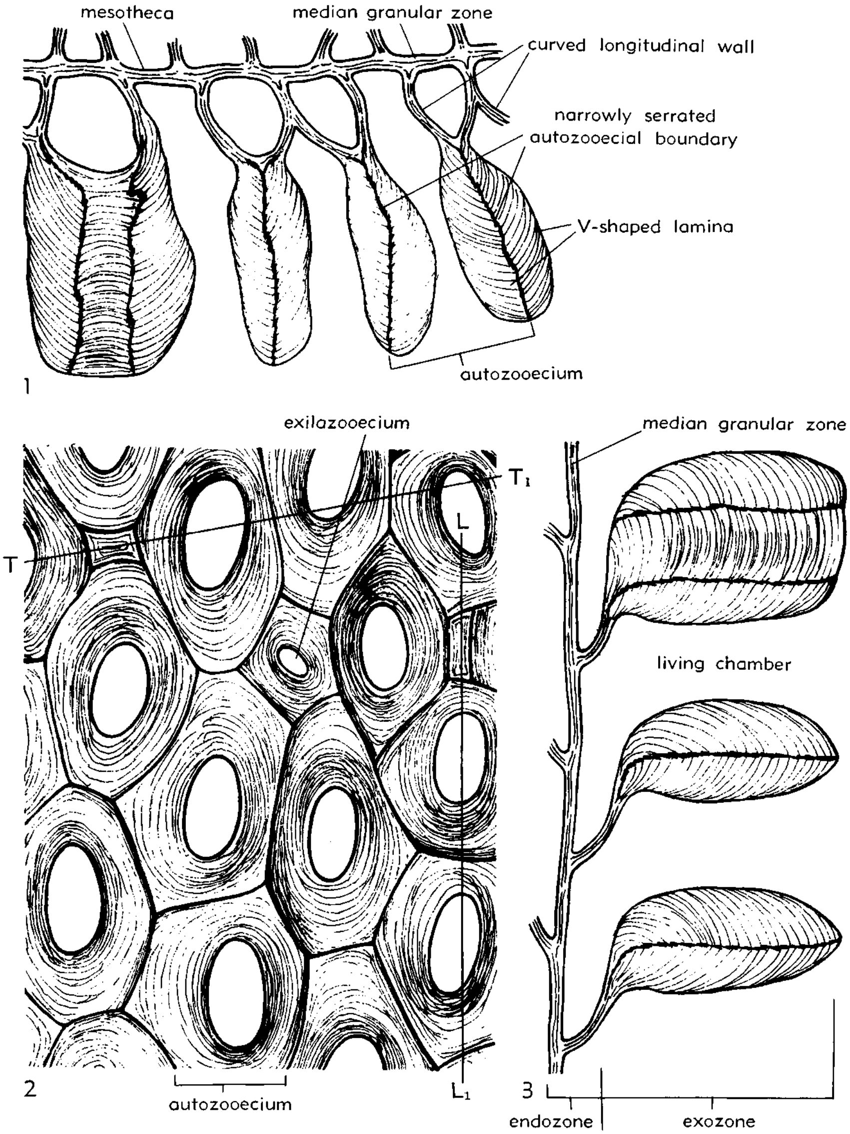

FIG. 239. Generalized zoarial midregion in *Pseudostictoporella*, family Stictoporellidae.——*1.* Transverse section (along $T–T_1$ in *2*).——*2.* Tangential section of exozone.——*3.* Longitudinal section (along $L–L_1$ in *2*).

generally known as mesopores in the Trepostomata, Cystoporata, and some Cryptostomata. Herein, the term is used only for small zooecia with numerous diaphragms.

In the Ptilodictyina, mesozooecia are known in only three genera. Two of these, ***Ensiphragma*** (see Fig. 241,*2c*), a ptilodictyid, and ***Intrapora*** (see Fig. 248,*1d*), an intraporid, both Devonian in age, are from two morphologically unrelated families. The third, ***Ptilotrypina,*** is without present family assignment but is of Middle Ordovician age.

In numerous ptilodictyine species the regular zooecial arrangement is commonly modified by clusters of polymorphs that are irregular in size and shape. These clusters may be flat, slightly depressed, or projected above the zoarial surface (see Fig. 254, *1a*;

262,*1b*), and are termed monticules. Their diameter is generally small, ranging from less than 1 mm to rarely more than 2 mm. Commonly, monticules are irregularly subcircular or elongate (see Fig. 255,*1a*), and are irregularly conical or ridgelike when projected above the zoarial surface. Their zooecia differ in shape and size from intermonticular autozooecia, exilazooecia, or mesozooecia, and they may consist of extrazooecial stereom (see Fig. 254,*1d*). Monticules with different constituents may occur separately or in various combinations in zoaria, and are generally differentiated only in exozones. Similar modified zoarial segments occur in numerous other Paleozoic stenolaemate bryozoans and analogous structures appear to be present in recent tubuliporates (BANTA, MCKINNEY, & ZIMMER, 1974).

Monticular zooecia are larger than regular autozooecia but have larger or smaller chambers. Most occur around outer edges of monticules and generally are gradational in size with adjacent intermonticular autozooecia (see Fig. 252,*1a*). They rarely occur in the middle of a monticule. Monticular zooecia may also be less regular in shape than intermonticular autozooecia.

In monticules with mostly exilazooecia (see Fig. 242,*2c*) in the exozone, autozooecia arose from the mesotheca, but were replaced at the base of the exozone by exilazooecia. In some genera of Ptilodictyidae, exilazooecia reportedly arose from autozooecia in the midpart of the exozone (substituting pseudomesopores of KOPAYEVICH, 1972).

Monticules consisting of extrazooecial stereom in the exozone began apparently as zooecia at the mesotheca and then were replaced or filled with the extrazooecial skeletal deposits (see Fig. 257,*1f*) in exozones.

Monticules are common zoarial features in the Ptilodictyina, but their presence is irregularly variable in most taxa. In general, monticules are more abundant in larger or more robust zoaria in the same taxon. Monticules are generally present in explanate zoaria, but are absent in small zoaria with delicate branches. The pattern of distribution of monticules within zoaria appears to be determined by the areal extent of the zoaria. In zoaria with an explanate growth habit, monticules may occur at alternate, regular intervals, forming a rhombic pattern (see Fig. 254,*1a*). In zoaria with a branching growth habit in which branches are relatively wide, monticules are arranged along the median of branches at relatively regular intervals. In some taxa with explanate growth habits, distances between adjacent monticules may vary from 2 to 4 mm, measured from center to center of a monticule. Single monticules commonly occur in branching areas or at random in zoarial branches.

Extrazooecial skeletal deposits.—Extrazooecial skeleton is common in the Ptilodictyina (Fig. 233, 234, 236), its extent being variable in different families. Skeletal deposits comprise zoarial segments that are generally laminated, but may include vesicular structures (vesicular tissue of ULRICH, 1890, p. 298), such structures as median rods in the mesotheca, and thin dark zones in some exozones. Except for median rods in the mesotheca and some vesicular structure in the endozone, skeletal deposits are generally formed during the exozonal growth stage.

Extrazooecial vesicles in ptilodictyines occur in overlapping series (Fig. 233). Most vesicles originated near bases of exozones. In the few genera where autozooecia are only partially contiguous at the budding surface, vesicles arise at the mesotheca (see Fig. 252,*1c*; 255,*1d*) because longitudinal walls are lacking in the endozone. Vesicles terminate in the exozone by merging with stereom. Vesicles are common in the Rhinidictyidae and are absent or rare in other ptilodictyine taxa.

Dark zones in extrazooecial stereom generally arise in exozones (Fig. 233), and only rarely in endozones (Fig. 234). In exozones the dark zones delineate extrazooecial stereom between and around zooecia (see Fig. 257).

In *Trigonodictya* of the Rhinidictyidae, extrazooecial stereom forms distinct longitudinal partitions between autozooecial ranges (Fig. 236; see also 257,*1b*). These straight to slightly sinuous structures are termed **range partitions** (Karklins, 1969, p. 26). Extrazooecial stereom between aligned ranges of autozooecia consists of laminae that are reversed in direction in adjacent dark zones (Fig. 236). Such reversal of laminae is uncommon among other Paleozoic bryozoans.

Zooecial wall laminae intertongue with those of the extrazooecial skeleton. Resulting boundaries are variable in shape, or the laminae may be continuous, without visible structural discontinuities (Fig. 238). In a few ptilodictyines, extrazooecial stereom encrusts the zoarial surface (Fig. 225,*5*). In these forms, and in those with relatively distinct autozooecial boundaries, extent of the extrazooecial deposit can generally be delineated. In zoaria where zooecial boundaries are not visible, extent of the stereom can be approximately inferred from the symmetry of the autozooecia and the generally uniform thickness of their walls. Thus, wider than usual interzooecial spaces in some regions of a zoarium, accompanied by reversal in direction of laminae, suggest the presence of extrazooecial skeleton, although no precise physical boundaries exist (Fig. 238).

Extrazooecial stereom probably constitutes a considerable part of the skeletal mass in zoarial basal attachments (Fig. 225,*4*). In all zoaria, stereom constitutes the main part of lateral zoarial and fenestrule margins. There it merges with the mesotheca (Fig. 230,*2*) and forms edges of the margins. Intermittent discontinuities between laminae of the stereom and mesotheca outline approximately the extent of stereom in lateral margins of some taxa (Fig. 230,*2*). In other taxa, stereom is confluent with the mesotheca, but extent of the mesotheca in a margin is generally indicated by the median granular zone.

In general, extent of extrazooecial stereom in exozones in zoarial midregions can be related to the mode of autozooecial budding at the mesotheca, and to subsequent zooecial adjustments in space along endozone-exozone boundaries. Because development of zoaria is slightly different in different families, distribution of extrazooecial stereom characterizes families to a degree.

Other skeletal structures.—**Pustules** (mural lacunae of Boardman, 1960, p. 22; pustules or granules of Ross, 1964b, p. 939; small capillaries of Astrova, 1965, p. 103; granules of authors), as understood here, are the very small, irregular dark spots in skeletal laminae, approximately 0.01 mm or less in diameter (Ross, 1963b, p. 588). These structures lack cores and are not clearly separable in wall laminae. As seen in the light microscope, pustules are crinkled parts (Ross, 1964b, p. 940) of a few laminae (see Fig. 246,*1a*), as if resulting from a local discontinuity within laminae. These discontinuities may reflect minute changes in the laminae during secretion. Pustules may also be remnants of impurities that were entrapped in skeletons during the process of secretion; however, they are more prevalent and more regularly arranged in some taxonomic groups than in others. They commonly occur within zooecial boundaries or align along the boundaries (see Fig. 246,*1c*). Pustules are also scattered at random, mostly in the outer exozone (see Fig. 259,*1e*). In tangential sections, pustules rarely may resemble mural styles; however, they differ from mural styles in being equidimensional and in lacking distinguishable cores.

Mural styles are elongate, straight to slightly curved, small, rodlike, somewhat irregular structures in the zooecial skeleton. In the Ptilodictyina, mural styles are found in most genera of the Rhinidictyidae and Virgatellidae as well as some genera without family assignment.

With few exceptions (see Fig. 263,*1a*), mural styles arise in the exozone of a zoarium. They may arise from zooecial boundaries (see Fig. 255,*2c*) or appear within walls at random (see Fig. 253,*2a*). They occur singly or are aligned in short, dark zones (see Fig. 251,*1c*). Mural styles originating in outer exozones commonly terminate at zoarial surfaces as small, low protuberances in well-preserved specimens. Mural styles originating in inner exozones generally terminate within the skeleton (see Fig. 255,*2a*). They do not connect with zooecial chambers.

Mural styles consist of indistinct cores surrounded by sheaths of tightly curved, very thin laminae. Because of small size of the mural styles, it is not always possible to establish the presence of a core when using a light microscope. Cores, when distinguishable, appear to be finely laminated, but configuration of the laminae cannot be clearly observed (see Fig. 251,*1a–c*). Cores may also be absent or consist of discontinuous segments separated by a few skeletal laminae or crossing sheath laminae.

Sheath laminae merge with regular skeletal laminae, abut cores, or extend irregularly across them. In tangential sections (see Fig. 251,*1b,c*) sheaths appear as dark rims surrounding the cores.

Mural styles are generally of similar size in a zoarium and vary little within a group of taxa. In most genera, the diameter of a style is less than 0.01 mm, but may range to 0.02 mm. ASTROVA (1965, p. 102) described mural styles in which the diameter ranged between 0.008 and 0.005 mm, with a few less than 0.005 mm. The smallest mural styles probably lack cores (see Fig. 261,*1e*).

Biological significance of median rods, mural styles, and pustules.—Differences in structure and distribution of median rods, mural styles, and pustules suggest different biological functions. Median rods and mural styles have commonly been compared with or regarded as kinds of acanthostyles (acanthopores of ROSS, then PHILLIPS, 1960; others). BLAKE (1973a,b; this revision) reviewed the various functions that have been postulated, and agreed with CUMINGS and GALLOWAY (1915) and TAVENER-SMITH (1969b) that acanthostyles could perform a protective function for soft parts enveloping the zoaria. Whatever the function, it could not have been a major one in the Ptilodictyina, because acanthostyles are rare in representatives of the suborder. Median rods and mural styles, however, differ from the acanthostyles in abundance, pattern of distribution, and general structure, suggesting differences that are presently unknown.

ASTROVA (1965, p. 102) and KOPAYEVICH (1973, p. 59) suggested that median rods together with mural styles or pustules formed parts of a capillary or canal system in colonies. ASTROVA compared these capillaries with similar structures in the fenestellids (SHULGA-NESTERENKO, 1931, p. 77; 1949) and considered the capillaries in the rhinidictyids as being more primitive than those in the fenestellids. Structure of these capillaries in the fenestellids and other cryptostomates were considered to be granular by several investigators (in ASTROVA, 1965, p. 102), including V. P. NEKHOROSHEV, A. N. NIKIFOROVA, and M. I. SHULGA-NESTERENKO. ASTROVA postulated that the inferred capillaries might be analogous to pseudopores in the Tubuliporata and may have functioned as part of a communication system among zooids and between zooids and the external environment.

KOPAYEVICH (1968, p. 127; 1973, p. 60) described mural styles as capillaries that formed parts of a zoarial canal system. In the Rhinidictyidae, median rods in the mesotheca and dark zones in the exozone complete the suggested canal system. In the family Ptilodictyidae, mural pustules in the exozone, a median granular zone in the mesotheca, and granular zones in endozones (autozooecial boundaries herein) constitute a similar system of zoarial canals. Both authors suggested that this canal complex may have connected individual autozooecia within the zoarium and the zoarium to the external environment, and may have functioned for the passage of biologic, probably gaseous, substances.

Detailed structure of median rods, mural styles, and pustules indicates that they are uniformly solid and may not have been tubelike. Structure of median rods suggests (TAVENER-SMITH & WILLIAMS, 1972, p. 149) that they are original deposits that were formed concurrently with secretion of growing edges of mesothecae and granular zones.

Mural styles in most genera occur only in exozones where they arise from autozooecial boundaries, or from within dark zones or wall laminae. The regular intergrowth of mural styles with skeletal laminae indicates that mural styles also developed concurrently with laminated walls and were solid from their point of origin to their terminal end. That they were not tubelike is also suggested by the general absence of internal, clay-sized, terrigenous particles.

Mural styles and median rods are not structurally connected.

The only taxon in which mural styles could have terminated in autozooecial chambers appears to be the Virgatellidae (see Fig. 260,*2a*). Although mural styles in this family are distinctly different in growth form, size, and possibly structure, additional specimens are needed to verify a possible connection at the chamber-wall interface. In some taxa (see Fig. 252,*1a*), mural styles are not present in autozooecial walls but only in extrazooecial stereom in exozones. Thus, they do not connect autozooecia.

Pustules are structurally discontinuous within exozonal laminae (see Fig. 246,*1a*) and do not extend to zooecial walls in endozones or to granular zones in the mesotheca.

It seems that no median rods, mural styles, or pustules could have been parts of an interconnected zoarial canal system for passage of biological substances. Furthermore, it is unlikely that these structures, consisting of solid calcitic material, could have transmitted biologic substances, even by diffusion (Boardman & Cheetham, 1973, p. 130).

Median rods, mural styles and, to a degree, pustules are interpreted to be discrete zoarial structures. Median rods are extrazooecial structures confined to the mesotheca, and they do not extend into zooecial walls. Mural styles and pustules are zooecial and extrazooecial structures that, except in *Taeniodictya* (see Fig. 263,*1a*), are confined to the exozone. Their biological significance remains conjectural.

In the ptilodictyines, median rods and mural styles characterize the Rhinidictyidae and some unassigned genera. Relatively large mural styles characterize the Virgatellidae. Pustules occur mostly in the Ptilodictyidae, Escharoporidae, Stictoporellidae, and some unassigned genera.

TAXONOMIC CHARACTERS OF FAMILIES

The suborder Ptilodictyina, as described herein, includes the families Ptilodictyidae, Escharoporidae (new), Intraporidae (restored), Phragmopheridae, Rhinidictyidae, Stictoporellidae, Virgatellidae, and the unassigned genera *Euspilopora, Ptilotrypa, Ptilotrypina, Stictotrypa, Taeniodictya,* and *Trepocryptopora*. *Heliotrypa* is not considered to be a ptilodictyine but is retained tentatively in the Cryptostomata.

Until a few decades ago (Bassler, 1953), certain growth habits were commonly used as the main criteria for differentiating families, although skeletal structures were reasonably well known in several genera. Nicholson (1881, fig. 15) showed the laminar nature of a ptilodictyine skeleton. Ulrich (1890, p. 308–331; 347–349; 1893, p. 124–187) described and illustrated the main kinds of skeletal structures in several ptilodictyines, mostly Rhinidictyidae, which partly form the morphological basis for families described herein.

Ross reviewed the ptilodictyine genera in a series of publications beginning in 1960. Skeletal morphology in *Ptilodictya* (Ross, 1960a, p. 441, 444, text-fig. 1; 1960c, p. 1062–1072, text-fig. 2) and *Phaenopora* (Ross, 1961a, p. 332; 1962, text-fig. 4) is characteristic of the family Ptilodictyidae. Astrova (1965) considered these genera to be representative of two distinct phylogenetic lineages within the family.

The revised concept (herein) for the family

Stictoporellidae is largely based on skeletal development in *Stictoporella* (Phillips, 1960, p. 23; Ross, 1960c, p. 1072–1074; 1964a, p. 19), *Pseudostictoporella* (Ross, 1970, p. 378), and *Stictoporellina* (Karklins, 1970).

The concept for the Escharoporidae, new family, is based on skeletal development in *Championodictya* (Ross, 1964a, p. 18), *Chazydictya* (Ross, 1963b, p. 587), *Escharopora* (Phillips, 1960, p. 17–19, text-fig. 1; Ross, 1964a, p. 17), and *Graptodictya* (Phillips, 1960, p. 19–23; Ross, 1960b, p. 859).

In the Rhinidictyidae, reinterpreted or new material has been described for *Stictopora* (Phillips, 1960, p. 6–8, text-fig. 2; Ross, 1961a, p. 336; 1961b, p. 76–83; 1964a, p. 24–28); *Eopachydictya* (Ross, 1963b, p. 591), *Eurydictya* (Phillips, 1960, p. 12), and *Pachydictya* (Phillips, 1960, p. 13–17; Ross, 1961a, p. 337–342; 1964a, p. 21–24).

Revised concepts of families are mostly based on erect parts of zoaria. The following characters have been used extensively: (1) structure of mesothecae and median granular zones; (2) modes of budding of autozooecia from mesothecae, and autozooecial shapes in endozones; (3) changes in autozooecial shape from endozone through exozone, including shape of living chambers; (4) changes in microstructure of zooecial walls, including autozooecial boundaries from endozone through exozone; (5) nature of any such additional structures in autozooecial walls as pustules or mural styles; (6) kinds of any polymorphic zooecia in exozones; and (7) relative amounts and structures of any extrazooecial skeletal deposits in exozones.

Zoarial growth habits and basal attachments are, to a degree, characteristic of families. However, care should be exercised in the taxonomic use of these features.

Zoarial development and structures in those genera not included in families are ptilodictyine in general appearance, but differ in the modified growth modes of autozooecia at the mesotheca, in the exozone, and in modified skeletal structures.

Until recently, descriptions and interpretations of skeletal structures have been based on observations using the light microscope. Introduction of the scanning electron microscope in the study of the stenolaemate bryozoans (Boardman & Towe, 1966; Boardman in Boardman & Cheetham, 1969; Tavener-Smith, 1969a,b, 1975; Armstrong, 1970; Tavener-Smith & Williams, 1972; Brood, 1972; Blake, 1973a,b) has just begun. In general, data obtained on ptilodictyines by using the scanning electron microscope (Tavener-Smith & Williams, 1972; Tavener-Smith, 1975) appear to confirm interpretations made by using the light microscope. Further use of the scanning electron microscope will undoubtedly provide additional information of value in refining taxonomy.