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PART G, REVISED, VOLUME 2, CHAPTER 8A: ORDER FENESTRATA: MORPHOLOGY AND GROWTH

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ORDER FENESTRATA

> *I now leave the question as to the mode of development of the whole of the Fenestrate Polyzoa of the Palaeozoic era to the unprejudiced judgment of the palaeontologist. When I began the study, I never thought that the investigation would have taken me into so many of the by-ways of life; but, bit by bit, the great mystery which had hitherto enveloped these forms began to unfold itself, and for months past my mind and thoughts have been occupied, and my leisure time devoted to an endeavour to comprehend the secret of this particular life* (VINE, 1879b, p. 249).

The Order Fenestrata (ELIAS & CONDRA, 1957) is an exclusively Paleozoic group, characterized with very few exceptions by erect colonies (Fig. 1). The vast majority are made up of unilaminate, bifurcated, or pinnate branches that are either free beyond the point of branch division or laterally linked by dissepiments or anastomosis (Fig. 2); branch width and thickness typically are under 2 mm and commonly under 0.5 mm. Zooecia in the branches usually are divided into a distinct inflated portion in the endozone with a narrower distally placed tube that extends through extensively developed extrazooecial laminated skeleton. Generally, in almost all but the most primitive representatives, the autozooecia are very regularly shaped and distributed. Heterozooecia are present in relatively few members of the order, and where they occur they may be either regularly or irregularly distributed.

GENERAL MORPHOLOGY

Fenestrate bryozoan colonies usually consist of a net of branches in which well-developed rows of autozooecial apertures are located on one side, the obverse (frontal) surface of each branch (Fig. 2.1,5; Fig. 3). Adjacent branches face the same general direction, and therefore the zoarium as well as individual branches may be said to have an obverse surface. The opposite, barren surface is termed the reverse surface (Fig. 2.2–2.4). Branches, and the autozooecia contained within them, have their proximal end closest to the point of colony origin as traced back skeletally, and their distal end is in the direction of growth. Colonies exceeding a half meter in height are known in *Fenestella s.l.* LONSDALE in MURCHISON, 1839 (SHRUBSOLE, 1879), *Archimedes* OWEN, 1838 (MCKINNEY & GAULT, 1980; SNYDER, 1991a), and *Acanthocladia* KING, 1849 (D. B. SMITH, date unknown, personal communication).

Fenestrules, the skeletally surrounded openings through colonies, may be produced by anastomosis of sinuously grown branches (Fig. 2.3), by essentially parallel branches that are linked at intervals by autozooecia-free skeletal bars termed dissepiments (Fig. 2.5), or by obliquely grown branches (pinnae) that are fused with other pinnae or with adjacent branches that are parallel with parent branches (Fig. 2.1–2.2). Colonies in the Fenestrata that possess fenestrules are structurally fenestrate, whereas forms that lack dissepiments, fused sinuous branches, or fused pinnae are not structurally fenestrate but instead have continuous open slots between adjacent branches. Most colonies that are not structurally fenestrate are characterized by pinnate branching (Fig. 2.4), although some early

McKinney, Frank K., and Patrick N. Wyse Jackson. 2015. Part G, Revised, Volume 2, Chapter 8A: Order Fenestrata: Morphology and Growth. Treatise Online 66:1–91, 54 fig.

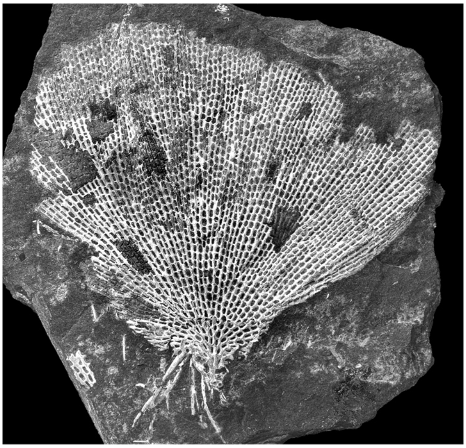

FIG. 1. Zoarium of *Fenestella (s.l.) plebia* M'COY, 1844, that grew as an erect fan from a small encrusting base (bottom center) and that was partially stabilized by skeletal pillars that originated near the base and extended down toward the substratum Mississippian, Halkyn Mountain, Flintshire, UK, NHMUK D11688, ×1.2 (adapted from Taylor, 2005).

forms without lateral branch linkage were characterized by bifurcation.

Within the branches of all but a few fenestrates, there is a continuous, longitudinal, planar to transversely curved basal plate (*bp,* Fig. 3.3,5) composed of granular calcite, from which one (rarely) or more typically two or more rows of autozooecia are developed on the obverse side of the plate. If there are but two rows of zooecia, a well-developed wall of granular calcite separates the rows, follows or crosses back and forth through the branch axial plane, and is referred to as the axial wall (*aw,* Fig. 3.3,6). The axial wall typically extends to the obverse surface, where it is expressed as a longitudinal keel (*k,* Fig. 3.1–3.3), that may be surmounted by variably developed, variably shaped, and variably spaced spines (if height exceeds width) or nodes (if width approximately equals or exceeds height).

Autozooecial chambers are divided into two portions. A proximal chamber-shaped portion adjacent to the basal plate typically is inflated laterally and/or frontally, and a cylindrical distal tube of smaller cross-sectional diameter extends from the chamber to an aperture on or near the obverse surface (*a,* Fig. 3.5–6, Fig. 4).

The chamber-shaped portion commonly is referred to as the living chamber. It is bounded on the reverse side by the basal wall (a portion of the basal plate plus inner laminar wall if present), on the proximal and distal ends by transverse walls (so called because they are obliquely transverse to the direction of branch elongation), on the obverse side by the frontal wall (use of the term here is quite different from its use for tubuliporates), and on the sides by lateral walls (*tw, fw,* and *lw,* Fig. 3.3,5,6). The median lateral walls in autozooecia of biserial branches are part of the axial wall. The axis of growth at the distal end of an autozooecial chamber typically reoriented towards the obverse surface as a new partition—a transverse wall—arose at some angle from the basal plate to divide the autozooecium from the one that would form next distally (Fig. 3.5, Fig. 4). Autozooecia within a row, therefore, overlap to a greater or lesser degree depending on the angle formed between the basal plate and the wall separating successive autozooecia. Autozooecia may lack internal skeletal structures, or one or more plates may extend from walls to change the cross-sectional shape or to divide the autozooecial chamber. Incomplete plates are termed hemisepta. Superior hemisepta (*sh,* Fig. 5.1) extend toward the basal wall from the inside of the bend where the frontal wall of the autozooecial chamber and the distal tube meet. Inferior hemisepta (*ih,* Fig. 5.1) extend up into the chamber from the distal portion of the basal wall or the base of the transverse wall. Diaphragms are complete plates (Fig. 5.2) that occur within the chambers of several phylloporinid fenestrates but otherwise are rare, although terminal diaphragms across apertures are common (see below).

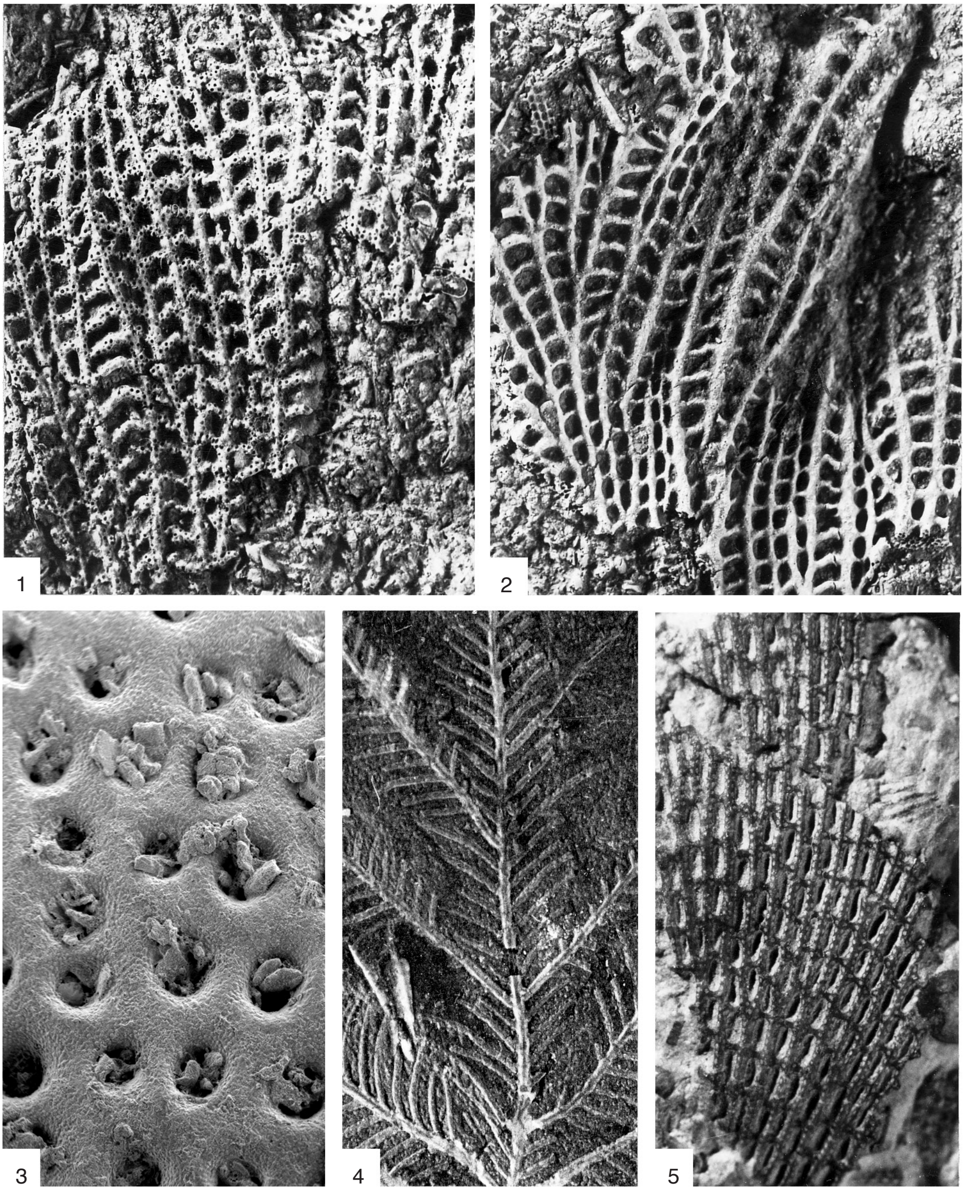

Fig. 2. Basic categories of branching in fenestrate bryozoans; *1–2*, main branches linked by closely spaced, short, lateral pinnae in *Septopora subquadrans* Ulrich, 1890, Mississippian, Big Stone Gap, Virginia, USA, *1*, obverse surface, USNM 98140b, ×2; *2*, reverse surface, USNM 98140b, ×2; *3*, sinuous branches joined by anastomosis, reverse surface of *Semicoscinium rhomboideum* Prout, 1859, Devonian (Eifelian), Falls of the Ohio, Indiana, USA, USNM 535118, ×15; *4*, main branches with closely spaced lateral pinnae that do not typically fuse, reverse surface of *Penniretepora elegans* (Young & Young, 1875), Pennsylvanian, High Blantyre, Scotland, HMAG 01-53wg, ×3; *5*, bifurcated branches linked by dissepiments, obverse surface of *Fenestella subantiqua* d'Orbigny, 1850, Silurian, Dudley, England, HMAG D-229, ×5 (new).

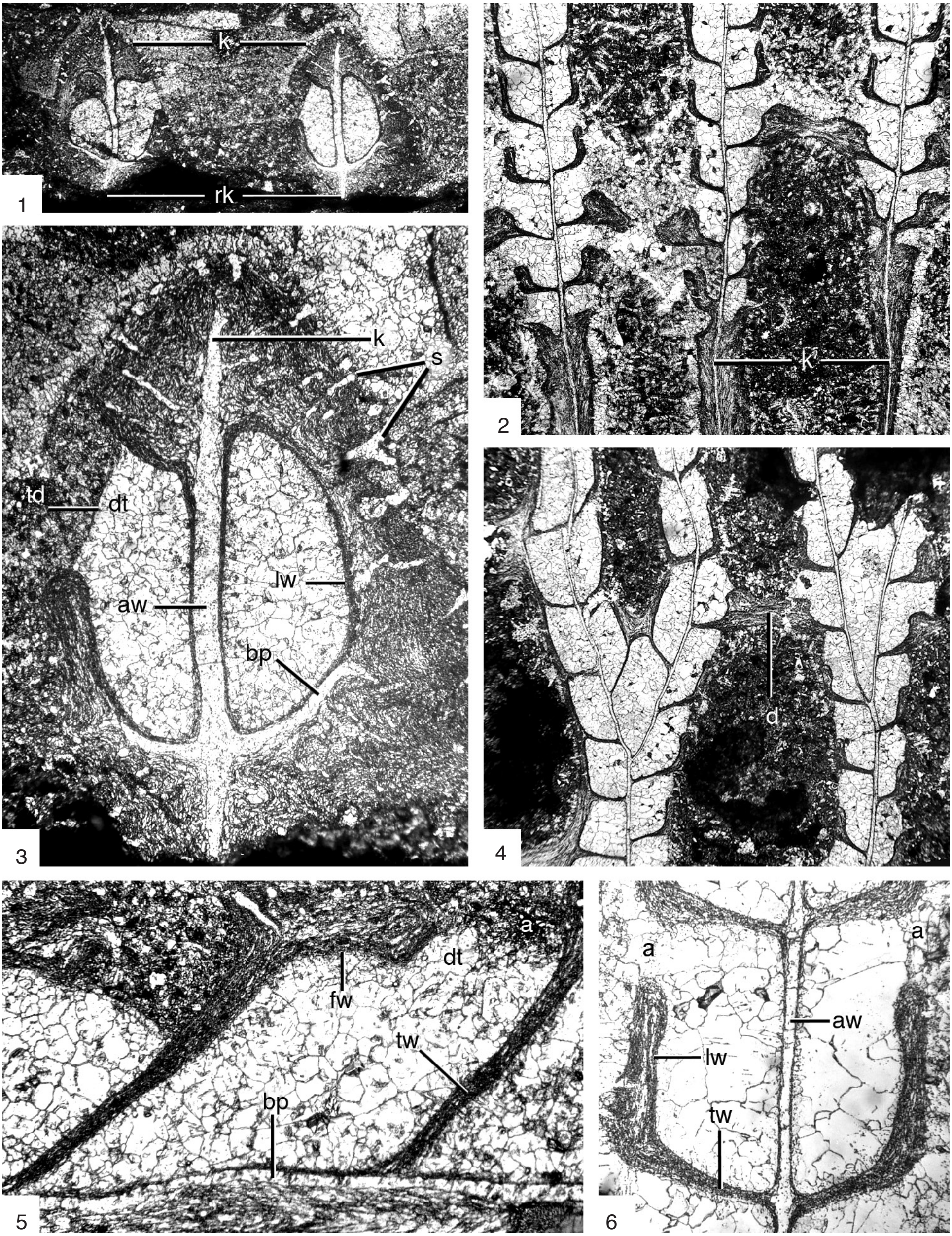

Fig. 3. Basic skeletal elements of fenestrates as seen in *Fenestella parvulipora* Hall, 1879, Silurian, Pegram, Tennessee, USA; *1*, transverse section of two biserial branches, with labels indicating outer surface of laminated skeleton of broad obverse keels *(k)* and single keel-shaped ridge *(rk)* of granular skeleton at center of basal plate, USNM 528951, ×30; *2*, tangential section cutting through broad obverse keels *(k)* and in upper portion through zooecial chambers, USNM 528966, ×30; *3*, transverse section of a single branch, with labels indicating axial wall *(aw),* reverse walls continuous as a basal plate *(bp),* and lateral walls *(lw)* defining the endozonal portion of autozooecia, the distal tube *(dt)* extending through the exozone and sealed by a terminal diaphragm *(td),* the granular core of the obverse keel *(k),* and the large microstyles *(s)* that extend through the laminated exozonal skeleton, USNM

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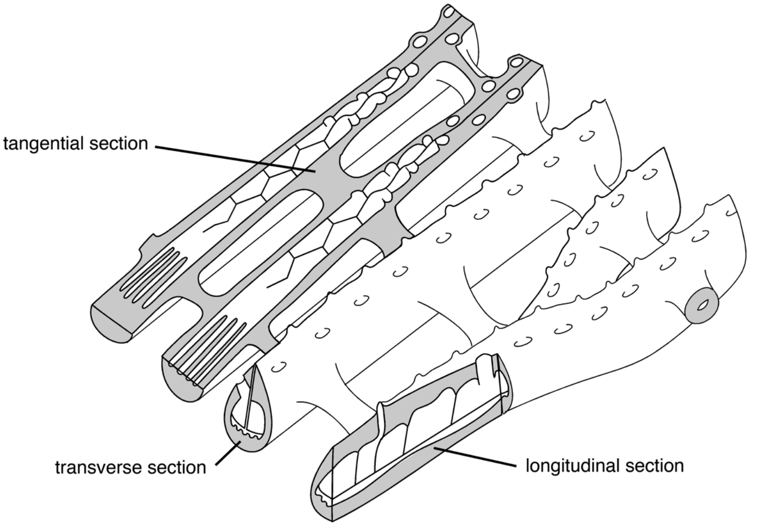

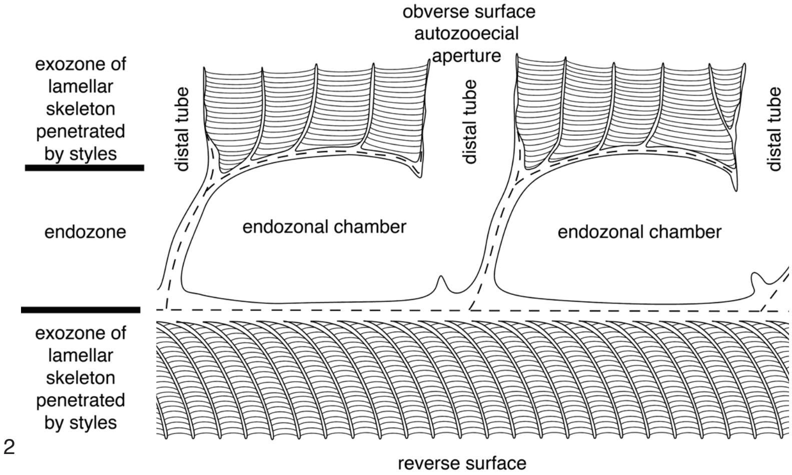

FIG. 4. Relation of typical internal structures to skeletal surface in fenestellid fenestrates; *1,* line drawing of several branches partially cut away as three oriented sections; *2*, location of endozone and exozone as seen in a longitudinal section along a row of zooecia, with zooecial boundaries approximated by dashed lines; see Figures 3 and 5 for names of specific zooecial skeletal features (new).

FIG. 3. (*Continued from facing page.*)

528951, ×100; *4*, tangential section through endozone of two bifurcating branches linked by a dissepiment *(d)* and with unusually large median zooecium immediately preceding each of the bifurcations, USNM 528966, ×30; *5*, longitudinal section through zooecial chambers with labels indicating reverse wall (*bp*, a portion of the granular basal plate) below which is laminated skeleton of the reverse exozone, transverse wall *(tw)* between successive zooecia along the branch, distal tube *(dt)* that penetrates the frontal wall *(fw)* and terminates in an open aperture *(a),* USNM 528951, ×100; *6*, tangential section with labels indicating axial wall *(aw),* transverse wall *(tw)* and lateral wall *(lw)* defining endozonal portions of zooecia, plus the aperture *(a)* at the end of the short zooecial distal tube through the laminated skeleton of the exozone, USNM 528966, ×100 (new).

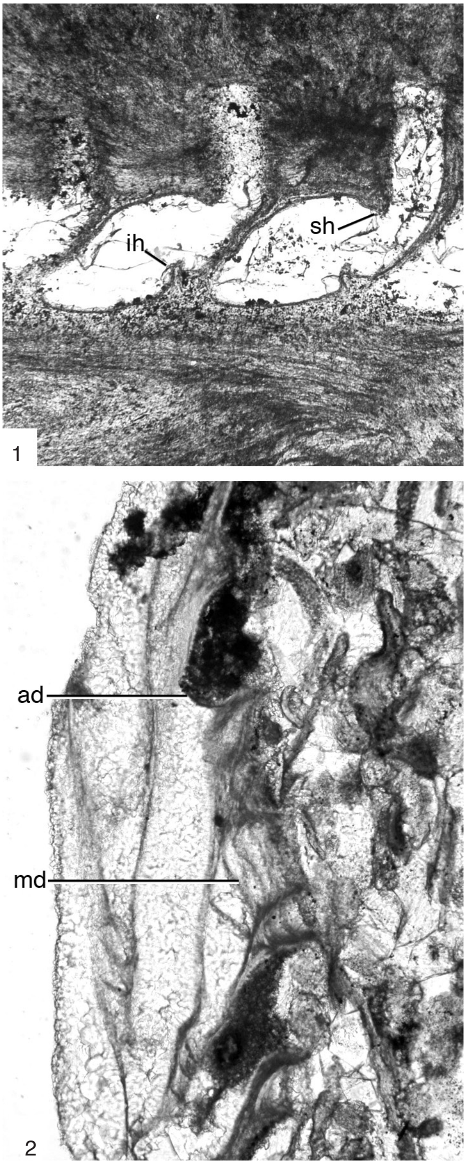

FIG. 5. Skeletal structures within fenestrate autozooecial chambers; *1,* superior hemisepta *(sh)* and inferior hemisepta *(ih)* projecting into distal portions of endozonal chambers of *Lyroporella quincuncialis* (HALL, 1857), Mississippian, Chester, Illinois, USA, USNM 483516, ×100 (adapted from McKinney, 1994); *2,* autozooecial diaphragm *(ad)* at transition from endozone to exozone and stacked diaphragms *(md)* in mesozooecia, *Phylloporina trentonensis* (NICHOLSON, 1875), Ordovician, Trenton, Belleville, Ontario, Canada, USNM 52847, ×60 (adapted from McKinney & Wyse Jackson, 2010).

Distal tubes most commonly have circular cross sections and terminate in circular apertures, although the angle at which they are viewed or at which a shallow tangential section intersects them can cause them to appear oval. Their length depends upon the extent of skeletal thickening on the obverse surface of the branch. The aperture either lies roughly at the level of the general skeletal surface or is slightly elevated above the general surface on a complete or partial low tubular peristome (Fig. 6). Peristome completion generally is related to whether the local skeletal surface is perpendicular or inclined relative to the axis of the distal tube. The perimeter of peristomes is interrupted in a few taxa by a proximal notch that extends down to the general skeletal surface (e.g., STRATTON & HOROWITZ, 1977a, pl. 4, fig. 1–2)

The endozone is that portion of the branch occupied by the inflated autozooecial chambers and characterized by granular skeleton (Fig. 4) that in some instances is lined on the inner surface by thin laminate wall. The exozone is that portion of the branch surrounding the endozone and composed of extrazooecial laminated skeleton. Distal tubes are the exozonal portion of autozooecia and extend through the obverse portion of the exozone.

Most fenestrates lack heterozooecia, but in some taxa autozooecia may be replaced either regularly or in an irregular pattern by them. In others, heterozooecia occur in other positions. Heterozooecia are described and illustrated in a later section (see p. 51).

Branches typically have a well-developed extrazooecial skeleton, which entirely envelops the branch except for zooecial apertures (Fig. 3, Fig. 4). Generally, this extrazooecial skeleton is especially thick on the reverse side. Many taxa are characterized by special structures constructed of extrazooecial skeleton, as described below (see p. 18).

Although phenotypic plasticity in fenestrate bryozoans is low, zoarial form is quite diverse

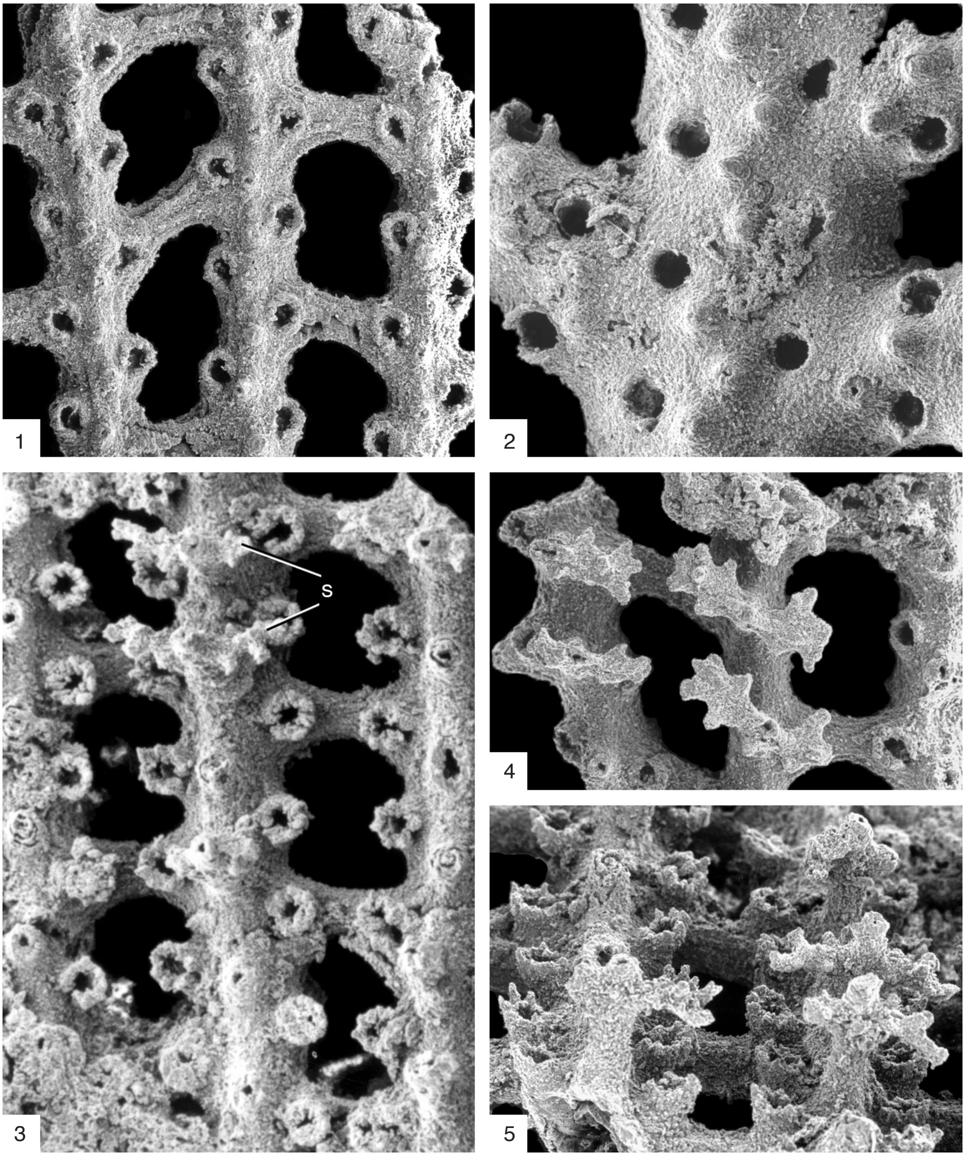

Fig. 6. Obverse surface morphology of silicified Pennsylvanian (Kasimovian?) bryozoans from the Cantabrian Mountains, Asturias, Spain, all ×50; *1, Fabifenestella*? *plummerae* (Moore, 1929), RGM 211 514b, branches with low median keel bearing zigzag row of moderately small nodes and separating two rows of zooecial apertures with incomplete peristomes, many of which appear to have a narrow, short proximal slot; *2, Ptiloporella*? *irregularis* Nikiforova, 1938, RGM 211 507a, main and lateral branches with median zigzag row of nodes on ill-defined keel separating two rows of zooecial apertures that vary from being flush with the branch surface, because of no (possibly not preserved) peristome, to having incomplete peristomes; *3–5, Cervella* Chronic, 1953; *3,* branches with low median keel bearing linear row of robust spines, all but two of which *(s)* have had the complex crests broken off and have hollow centers where the non-silicified granular cores have dissolved, separating two rows of zooecial apertures that have complete peristomes with eight styles, RGM 211 520c; *4,* region with good preservation of complex crests at outer ends of keel spines, RGM 211 530a; *5,* oblique view of region with well preserved crests at outer ends of keel spines above complete peristomes that curve toward the obverse and are serrated by long style tips, RGM 211 520c (adapted from Ernst & Winkler Prins, 2008).

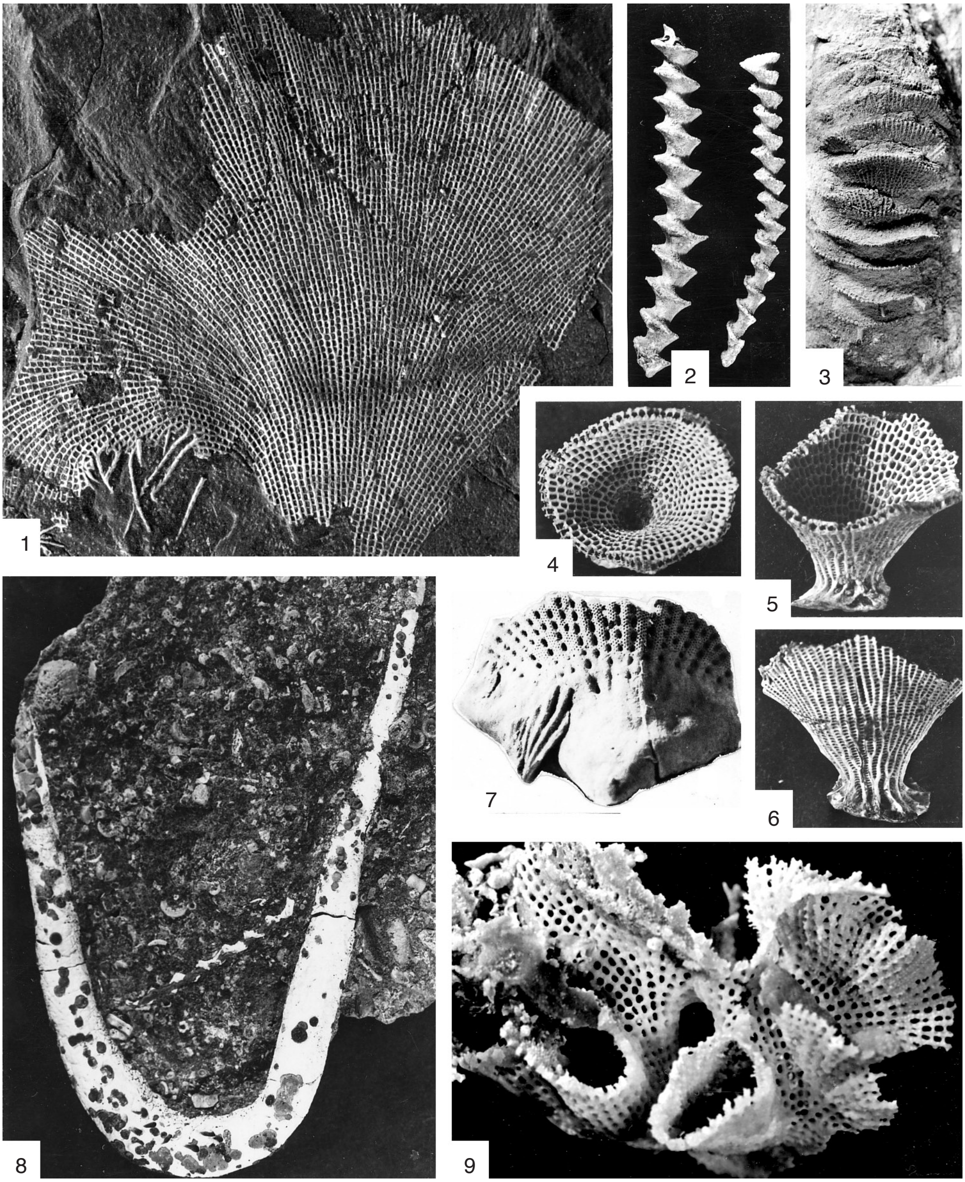

FIG. 7. Representative growth habits; *1,* simple fan-shaped zoarium, *Actinostoma fenestratum* Young & Young, 1874a, Pennsylvanian, Blantyre, Scotland, HMAG 01-53aah, ×2 (new); *2,* heavily calcified inner axial margins of helical zoaria, *Archimedes intermedius* Ulrich, 1890, Mississippian, Colbert County, Alabama, USA, USNM 304202, 304203, ×1 (adapted from McKinney & Gault, 1980); *3,* peripheral margin of helical zoarium, *A. intermedius*, Mississippian, Colbert County, Alabama, USA, USNM 304205, ×1 (new); *4–6,* simple conical zoarium, *Unitrypa acaulis* (Hall, 1883), Devonian, Falls of the Ohio, Indiana, USA, FMNH(UC) 14068, ×2 (new); *7,* obverse surface of lyre-shaped zoarium with heavily calcified proximal margin, *Lyropora* sp., Mississippian, Chester, Illinois, USA, USNM 241513, ×2 (McKinney, 1977); *8,* thickened margin of lyre-shaped zoarium, *Lyroporella quincuncialis* (Hall, 1857), Mississippian, London, Kentucky, USA, USNM 304211 (adapted from McKinney & Gault, 1980), ×1; *9,* complex irregular zoarium, unidentified fenestellid, Cathedral Mountain Formation, Permian (Kungurian), Cooper & Grant (1972), locality 702 or 702un, Hess Canyon quadrangle, Glass Mountains, Texas, USA, USNM 316125, ×2 (new).

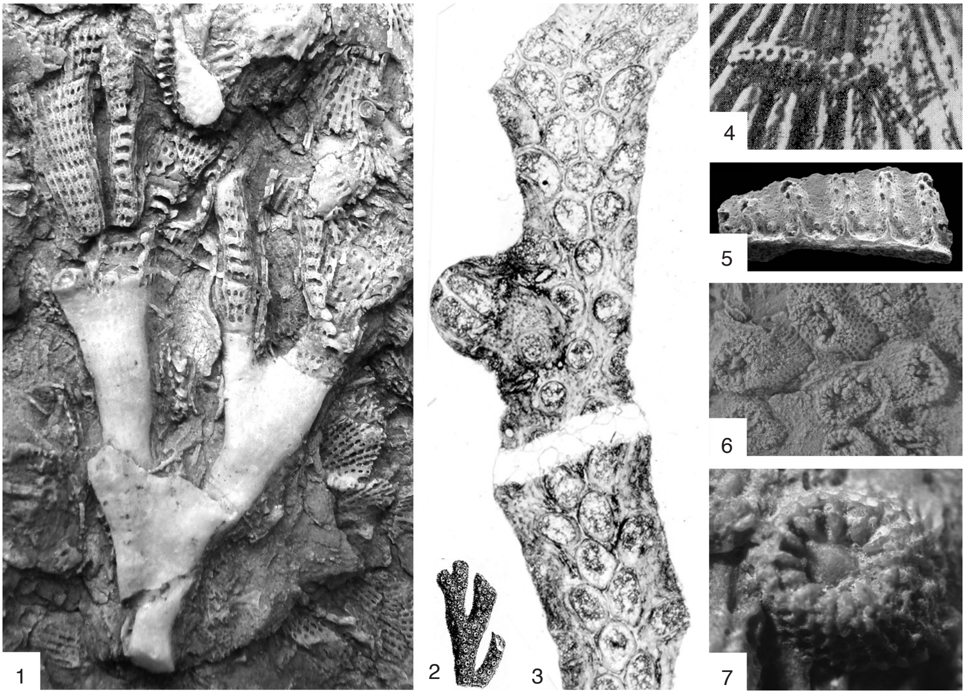

FIG. 8. Representative growth habits; *1,* erect compound zoarium of *Bigeyina* Suárez Andrés & McKinney, 2010, that grew as a series of bifurcating, narrow, hollow cones, the lowermost of which tend to be filled with a complex of thin-walled vesicles, Arnao Formation, Devonian (Emsian), Asturias, northwestern Spain, outcrop specimen, ×2 (adapted from Suárez Andrés & McKinney, 2010); *2–3,* non-fenestrated zoarial-form in *Ramipolypora crassa* (Lonsdale in Murchison, 1839), Silurian (Wenlock), Dudley, West Midlands, UK; *2,* original drawing, ×1 (adapted from Lonsdale in Murchison, 1839, pl. 41, fig. 13a), *3,* tangential section through obverse exozone showing branch shape, USNM 543544,×30 (adapted from McKinney, 2011); *4–5,* encrusting habit in *Schischcatella* Waschurova, 1964; *4, S. concreta* Waschurova, 1964, colony encrusting brachiopod valve, Lower Devonian, Shishkat, Kshtut River basin, Zeravshan Mountains, Tajikistan, UGT 17/412, paratype, ×3 (adapted from Waschurova, 1964), *5, S. heinorum* Ernst & Bohatý, 2009, lateral view of small colony composed of several rami on each side, separated by continuous median lamina, Loogh Formation, Middle Devonian (lower Givetian), Rhenish Massif, Mühlenwäldchen locality, Rhineland-Palatinate, Germany, paratype SMF 20.174, ×10 (adapted from Ernst & Bohatý, 2009); *6–7,* encrusting habit in *Ernstipora mackinneyi* Suárez Andrés & Wyse Jackson, 2014, Devonian, Arnao, Asturias, Spain; *6,* several circular sub-colonies forming done-shaped zoaria, holotype, DGO-12800, ×3 (new), *7,* single sub-colony showing outer superstructure and top of internal domed basal wall, paratype, DGO-12803, ×10 (new).

within the limitations imposed by pinnate, fenestrate, and rarer encrusting growth modes. The simplest colony form is a single erect sheet (Fig. 7.1), composed of either pinnate or laterally joined branches, with the latter arrangement characterizing the majority of the meshwork fenestellids. Such sheets may be essentially planar, up to tens of centimeters in height and width; curved, typically toward the reverse surface; or variably warped.

Erect growth around the entire radius of the base of attachment produces conical, paraboloid, or tubular colonies (Fig. 7.4–7.6), which may be simple and single, replicated, or changed upward into various other configurations. In addition, zoarial form may be lyre-shaped (Fig. 7.6), having gentle to strong transversely convex curvature of the obverse surface and heavy calcification along V- or U-shaped colony margins (Fig. 7.8). The calcification may be thickest near the colony base and taper distally; helical (Fig. 7.3), with one margin of the colony incorporated in a calcified, solid, screw-like axis (Fig. 7.2); or complexly convoluted, large undulose sheets (Fig. 7.9).

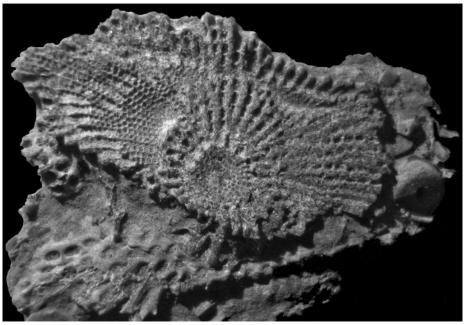

Fig. 9. Secondary encrusting meshwork in *Hemitrypa adversa* Suárez Andrés & Ernst, 2015, with low open cone, superstructure on inner surface, and secondary encrusting meshwork developed from center of older, lower meshwork, Moniello Formation, Devonian (Emsian–Eifelian), Arnao, Asturias, northwestern Spain, NHMUK PI BZ 5834, ×2.5 (adapted from Suáres Andrés, Wyse Jackson, & Sendino, 2014).

In *Bigeyina* Suárez Andrés & McKinney, 2010, a rare mode of erect branching growth occurs, where a series of elongate fenestrated cones develop from a skeletally thickened branching basal portion (Suárez Andrés & McKinney, 2010) (Fig. 8.1). A similar growth pattern is seen in the Permian polyporid *Bicorbis* Condra & Elias, 1945b, in which a tubular zoarium, consisting of a fenestrated meshwork on the outside with an internal substructure developed from the reverse of branches, forms lateral tubular branches (Condra & Elias, 1945a; McKinney, 1983a). Additionally, a similar pattern is known in rare specimens of *Fenestrapora* Hall, 1885, from the Devonian of Germany (Ernst in Suárez Andrés & McKinney, 2010).

Non-fenestrated zoarial forms are seen in several phylloporinids, including *Ooeciophylloporina* Bassler, 1952 and *Ralfinella* Lavrent'eva, 1985, a group which may be the ancestral clade to the more typical fenestrate bryozoans (McKinney, 2000). Similarly, the Silurian polyporid genus *Ramipolypora* McKinney, 2011, exhibits an unusual zoarial form, where branches with a typical fenestrate skeletal structure divide to produce an erect, non-fenestrated colony (McKinney, 2011; Fig. 8.2–8.3). Many of the pinnate acanthocladiids (such as *Ichthyorachis* M'Coy, 1844, and *Penniretepora* d'Orbigny, 1849) form zoaria whose lateral branches are not joined but diverge away from a central main stem (Fig. 2.4); in others (such as *Baculopora* Wyse Jackson, 1988, *Kalvariella* Morozova, 1970a, and *Matheropora* Bassler, 1953), zoaria generally develop by branch bifurcation and lack branch connections.

Encrusting growth forms in the Order Fenestrata are extremely rare and confined to two genera, *Schischcatella* (see Fig. 8.4–8.5) and *Ernstipora* (see Fig. 8.6–8.7). The former encrusted Devonian brachiopods where, from a strap-like basal wall, the zooecial-bearing portion developed as a series back-to-back rami that formed a short bifoliate erect portion (Waschurova, 1964; Ernst & Bohatý, 2009). In *Ernstipora* colonies comprise circular, distally-tapering cones that develop from an encrusting basal wall. Zooecial-bearing walls arise directly from the encrusting base and are not interlinked by dissepiments; a keel node–supported superstructure supports the internal circlet of branches, and it is often fused with the superstructure of adjacent subcolonies (Suárez Andrés & Wyse Jackson, 2014). These unusual encrusting forms have developed unique feeding and water-hydrodynamic patterns.

In *Hemitrypa adversa* Suárez Andrés & Ernst, 2015, development of a secondary encrusting meshwork is known from a single zoarium from the Devonian (Emsian–Eifelian) of Asturias, northwest Spain (Fig. 9) (Suárez Andrés, Wyse Jackson, & Sendino, 2014). This colony comprises an open, flattened cone with the superstructure covering branches on the inside of the cone, a pattern which is the reverse of the normal pattern in this genus. The open cone grew subparallel to the sediment surface, and centrally within it a second meshwork lies directly above the lowermost primary meshwork; the open cone was budded from the older portion of the colony.

The fenestrate colony form has evolved in bryozoan groups several times during the

Phanerozoic (Cuffey & McKinney, 1978; Bigey, 1981; Taylor, 1987). However, aside from gross external similarities, the differences at zooecial level and the presence or otherwise of different heteromorphs differentiates members of the Paleozoic Order Fenestrata from younger taxa. The Cretaceous cyclostome *Meliceritella schneemilichae* Taylor, 1987, and the Recent cheilostome *Jaculina parallelata* (Waters, 1895) are just two such examples of post-Paleozoic bryozoans that have developed a fenestrate zoarial form (Waters, 1895; Taylor, 1987). The former superficially resembles some phylloporinids such as *Mooreophylloporina* Bassler, 1952, where branches anastomose, while the latter takes after the fenestellids, with hollow dissepiment-like extensions that join zooid-bearing branches. These cross-bars are produced by hollow trabeculae and are not composed of the kind of skeletal material that is typical of true members of the Order Fenestrata. Another striking example of homeomorphy is that observed in the lyre-shaped zoaria of the cyclostome *Hornera reteramae* Canu & Bassler, 1920, from the Castle Hayne Limestone of North Carolina (McKinney, Taylor, & Zullo, 1993) and the Late Mississippian fenestrate genera *Lyropora* Hall, 1857, and *Lyroporella* Simpson, 1895 (McKinney, 1994).

METHODS OF STUDY

Although use of thin sections had been reported earlier (e.g., Waters, 1878, p. 462, fig. 4, 7, 8; Vine, 1884, p. 189), Ulrich (1890) was the first to systematically use thin sections in the study of Paleozoic bryozoans (see Boardman, 1983), including fenestrate forms. Ulrich's use of thin sections in the study of fenestrates, however, was less vigorous than for the other Paleozoic orders; with few exceptions, they were not generally used in studies of fenestrates outside of the Soviet Union until the late 20th century. New taxa, both genera and species, have been erected in various studies throughout the world—excepting the Soviet Union and its descendant states—on the basis of externally observed features. Many of the fenestrate genera thus erected are based on silicified specimens freed from carbonate rocks in acid baths (see Tavener-Smith, 1973a, p. 397–398 for technique). Important fenestrate faunas have been described (e.g., Chronic, 1949; Tavener-Smith, 1973a; Wyse Jackson, 1996; Gautier, Wyse Jackson, & McKinney, 2013) on exterior observation of silicified material, although Wyse Jackson (1996), and Gautier, Wyse Jackson, and McKinney (2013) use supplementary thin sections and peels of associated non-silicified specimens. Tavener-Smith (1973a) included observation and measurement of some internal features, and Gautier (1972) and Gautier, Wyse Jackson, and McKinney (2013) provided much information on growth of an acanthocladiid genus. Taxa based on silicified materials are most often insufficiently characterized because observations of internal structure (zooecial features and wall structure) commonly cannot be made.

Thin sections or acetate peels should be prepared following external observation of specimens that have at least one surface free or as an initial step in the study of specimens embedded in matrix (Fig. 4). At minimum, a tangential section or peel should be prepared from each specimen. Ideally, such a section should in part graze the outermost edges of the obverse side of branches, pass through the superstructure (if present), and in other areas should cut down locally to the laminated skeleton on the reverse side of the budding plate. In such sections, zooecia are cut through at varying, roughly determinable levels, and extrazooecial features at all levels are included as well. Most fragments are not precisely planar and tangential sections that cut through all levels with branches result because of the curved surface. In fragments that are essentially planar, a very slight lateral obliquity will achieve the same results. It is preferable that two additional thin sections or peels also be prepared: (1) a transverse section cutting perpendicularly across the branches and (2) a longitudinal section that is perpendicular to the obverse and reverse surfaces along the length of a branch, preferably near the bisecting plane of a row of zooecia.

Several accounts of the preparation of thin sections of bryozoans have been given (e.g., Ulrich, 1890, p. 292–293; Nekhoroshev, 1932, p. 280–283; Bassler, 1953, p. G17–18; Astrova & Shishova, 1963, p. 28–32; Ross & Ross, 1965, p. 43–44), with quite similar objectives. The primary differences are the nature of supplies and equipment available to the various authors. Basic procedures are as in preparation of petrologic thin sections, except that a particular depth of cut within a specimen is desired in bryozoans and extreme care must be in initial preparation. After the specimen is mounted on the glass slide, the preferred thickness to which it is ground varies with the nature of the features to be studied and with the translucency of the material; a uniform thickness of 0.003 mm is not necessary in all cases. The area of the slide should be sufficiently larger than the specimen, so that it may be fully labeled with curatorial information.

Acetate peels may be made in lieu of or in addition to thin sections, following the method described by Boardman & Utgaard (1964). The advantages of acetate peels include the following: (1) they are more quickly prepared than thin sections, (2) they replicate a single surface of extremely low relief so that they contain no thickness of specimen and thereby exhibit many microstructural details not visible in sections, (3) several peels may be made from a single surface, and (4) serial peels may be more closely spaced than serial sections. With a finely calibrated parallel grinder, closely spaced serial peels may be accurately spaced and oriented (Taylor, 1978). The disadvantages of acetate peels are as follows: (1) mineralogy is not reflected well in them, so that wall composition and presence of organically derived brown deposits cannot be determined; (2) friable specimens may break apart on release from the peel or adhere to the peel surface; (3) the soft plastic surfaces are easily scratched; and (4) dust and other debris are more difficult to remove safely than from sections. Friable specimens may be strengthened and small specimens made made easier to manipulate by embedding them in epoxy blocks, as described by Nye, Dean, and Hinds (1972).

Casts may be prepared for specimens of fenestrates that exist only as molds. Many sets of plaster casts of fenestrates were made in James Hall's laboratories during the latter half of the 19th century, and latex casts (Engel, 1975) have been more recently used. The obvious problem of assessing validity of taxa based on casts is that no internal structures are included, except for those fortuitous spots where zooecial chambers had been infilled and the filling lithified before the original skeleton was destroyed. The auality of casts depends on both quality of the original surface and casting medium, as well as the technical skill of the preparator.

An interesting pictorial system to display variations in distance from dissepiment to dissepiment was devised by Elias (1964, p. 376–377, pl. 1). Photographs of fenestrate meshworks were reproduced and enlarged to a standard scale with the midlines of branches and dissepiments carefully traced. The distance between adjacent dissepiment midlines was measured, divided by the scale of the photograph, and written within the fenestrule delineated by the two dissepiments. Each space within the gridwork was then coded on a finely graded color scale, according to length. The colored plat of the frond could then be examined for astogenetic gradient, repetitive bands, and local anomalies. Elias (1964, p. 376) claimed to be able to correlate the Tournaisian-Visean boundary between Russia and North America by this method, but it has not come into general use partly because of skepticism that beyond the primary zone of astogenetic change such changes along the growth direction were largely influenced by irregularly fluctuating local environmental conditions.

Exposed specimens of fenestrates are found most frequently with their reverse surface visible and their obverse surface adhering to the substrate. This is due, in large part, to the greater topography of the obverse surface, so that cracks parallel to bedding tend to pass along the smoother, less adherent, reverse side of specimens. Where observation of the obverse surface of such specimens in shale is desired, a method of lifting the specimens free of matrix was devised by Young (1877). The well-dried specimens were covered with heated asphalt (Young, 1877) or other adherent fluid that can set hard and then overlain by paper (Graham, 1975). After the covering material hardened, the shale was disintegrated by soaking in water and picking it away from the surface of the specimen. More intractable shales may be disintegrated by addition of cleaning or chelating agents as long as they do not react significantly with the imbedded fossil material.

CT-microtomography, a relatively new tool in paleontologic studies (See Chapter 3), has allowed for the visualization of the internal features of *Polyfenestella* Bancroft, 1986b (Wyse Jackson & McKinney, 2013). Future use of the technique in the study of fenestrate morphology is dependent on there being a sufficient difference in density between the skeleton and the infilling matrix. In many cases with fenestrate bryozoans, both are calcitic, which reduces the fidelity of the images being produced and the effectiveness of the technique.

SKELETAL STRUCTURE

BRANCHES

As recognized by Ulrich (1890, p. 352) and subsequent investigators, bryozoans of the order Fenestrata have two types of wall structure as seen in microscopic study: granular and laminar. Earlier, Nicholson (in Nicholson & Lydekker, 1889, p. 608) reported a "punctate" structure of the outer laminated layer, based on microscopic observation.

Both the granular and laminar skeletal material seem to have been originally of low-magnesium calcite, as recrystallization has been relatively minor in most specimens and overall wall structure is well preserved (as a result in most stenolaemates: Sandberg, 1977, p. 148; Smith, Key, & Gordon, 2006). The calcitic skeletons of fenestrate bryozoans are organized into three zones: a sporadically developed inner laminar layer; a granular layer; and a thickened, outer laminated layer (Fig. 3–4, Fig. 10). The distribution of these layers varies between the phylloporinids and fenestellids, on one hand, and the acanthocladiids, on the other.

The granular wall is composed of "coarsely granular calcite" (Tavener-Smith & Williams, 1972, p. 150) and constitutes the basal plate (where present); the transverse and longitudinal intrazooecial walls, including the axial wall (where present); the medial portions of most elevated elements derived from the axial wall; and the core of skeletal pillars that may extend from branches. Tavener-Smith (1969, p. 285) suggested that organic films originally encased the crystals in granular skeleton, based on grain shape and on analogy with similar condition in modern tubuliporates.

The granular wall delimits the zooecia, except in some taxa in which it may thin to zero in certain portions of distal tubes and frontal walls and, more rarely, distolateral walls (McKinney, 1980a). Within the exozone, it occurs in the cores of microstyles and nodes. Tavener-Smith and Williams (1972, p. 150–152) reported that the granular skeleton in *Carinophylloporina typica* Bassler, 1952, is 3 µm or less in thickness in transverse zooecial walls, up to 10 µm thick in the axial wall, and up to 4 µm thick in granular cores of microstyles. They found the granular wall in *Pustuloporina corticosa* (Ulrich, 1890) to be much more robust, forming a sheath around the zooecia, 10 µm to 30 µm in thickness, with crenulations of 15 µm wavelength on the reverse surface of the granular layer that extend parallel to the branch axis, from which microstyle cores, about 5 µm in thickness, originate. The presence of such crenulations and their reflection

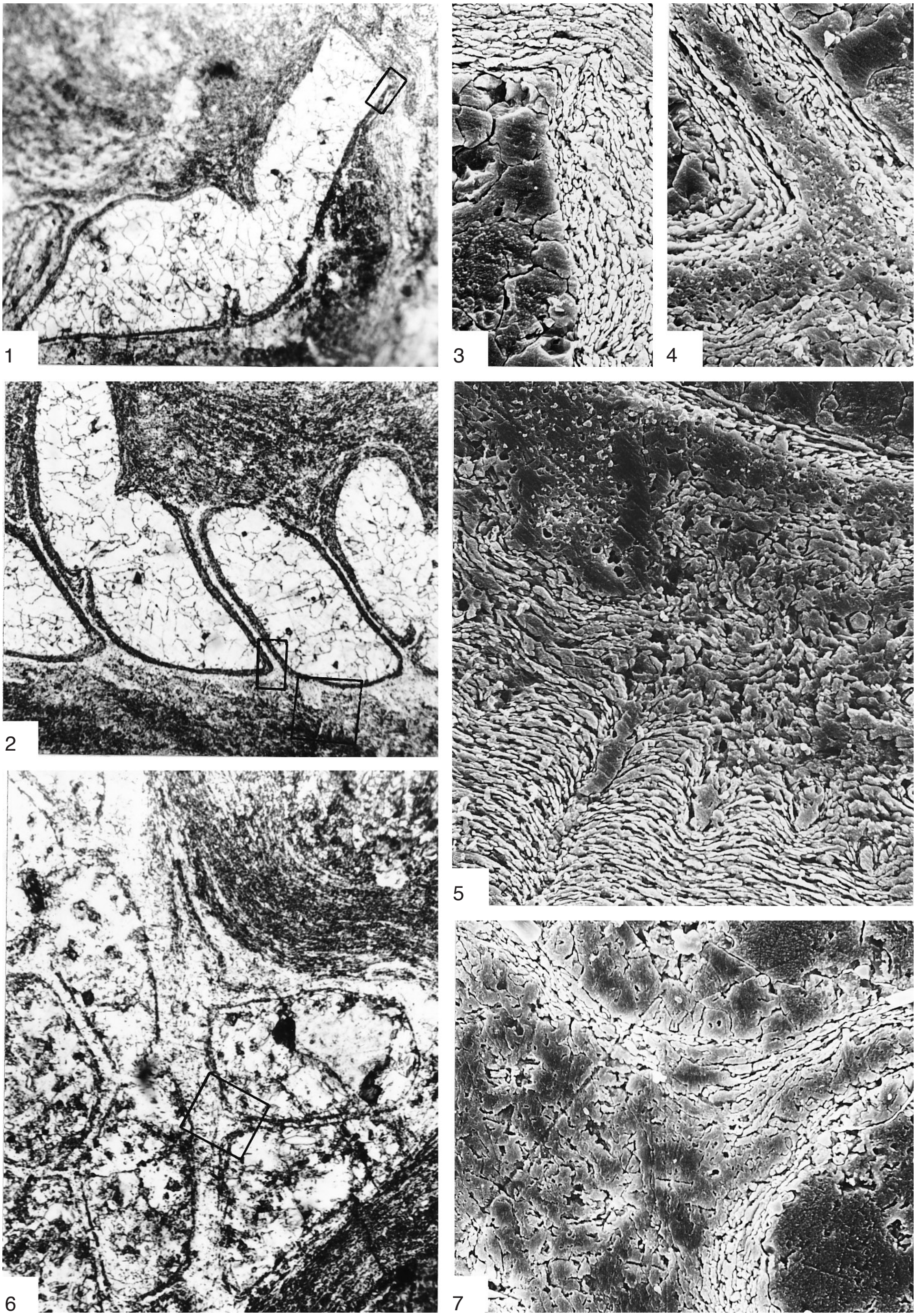

FIG. 10. *For explanation, see facing page.*

in the enveloping laminae have been considered fundamental unifying features in the fenestellids (Tavener-Smith, 1975, p. 3, 9), although in a few taxa they are minimally expressed or absent.

Styles originate predominantly from the crests or flanks of crenulations in the thick granular skeleton of the basal zooecial wall (Fig. 11.1; Elias & Condra, 1957, p. 4; Tavener-Smith, 1969, p. 301) and also from the granular skeleton sheathing other zooecial surfaces. Styles also have diverse extrazooecial origins, such as keel ridges and spines (Fig. 11.2), and they can proliferate by sequential bifurcations (Fig. 1.3). In some instances they seem to originate *de novo* from individual laminae in extrazooecial laminated skeleton (Fig. 11.4).

The laminated skeleton externally sheathes the granular skeleton in fenestrates. The laminated skeleton is composed of calcite fibers that are approximately 1 µm thick in a specimen assigned to *Carinophylloporina typica,* 650 nm to 850 nm thick in *Semicoscinium rhombicum*, irregularly 450 nm to 900 nm thick in *Pustuloporina corticosa*, and 400 nm thick in *Archimedes terebriformis* Ulrich, 1890 (Tavener-Smith & Williams, 1972, p. 150–153). Earlier, Tavener-Smith (1968, p. 87; 1969, p. 286) and Brood (1970, p. 189–190) interpreted components of laminae as plates rather than fibers, based on the similar flat shape in both longitudinal and transverse sections. Brood surmises that the original fibrous texture was modified by recrystallization. Olaloye (1974, p. 485) recorded platy components of laminae in *Penniretepora* d'Orbigny, 1849. The laminae of the outer laminated skeleton are deflected outwardly and lap up against granular cores of microstyles. The laminae and units therein were probably originally separated by proteinous layers (Tavener-Smith, 1968, p. 89; 1969, p. 286), as skeletal crystal seeding requires such matrix in living skeletal invertebrates.

Occasionally, numerous cycles of thick to thin laminae occur in thick deposits of extrazooecial skeleton (Fig. 11.6). Presumably, such cyclic sequences reflect iterative environmental changes that were expressed in changes in rate of skeletal accretion.

Elias and Condra (1957, p. 37) noted that skeletal laminae are embedded in a "structureless substance." The interval of "structureless substance" between laminae was reported as several times the thickness of the laminae, given as typically 0.8–0.9 µm. No other investigators have recorded such material. Ross and Ross (1962, p. 48) state that in *Polypora* M'Coy, 1844, "laminae of adjacent zooecial walls intertongue and the laminae are convex distally."

Laminated skeleton may locally or fully line the interior surface of granular skeleton surrounding zooecial chambers, varying from 0 µm to at least 4 µm (Tavener-Smith & Williams, 1972, p. 152). Tavener-Smith

Fig. 10. Skeletal microtexture; *1–5*, *Archimedes intermedius*, Mississippian, Reid Gap, Blount County, Alabama, USA, USNM 528953; *1–2*, boxes indicate areas shown at higher magnification in parts *3–5*, ×125; *3*, outer end of locally ill-defined wall of autozooecial distal tube, capped by a terminal diaphragm, with zooecial laminated skeleton thinly developed on the interior surface of distal tube and with thick, but similarly textured, laminated skeleton enveloping the outer surface of distal tube and terminal diaphragm, ×1200; *4*, continuous granular skeleton across the junction of transverse and basal zooecial walls, with transitional boundaries between the granular skeleton and the laminated wall lining the endozonal zooecial chamber and with the laminated texture of the reverse-side extrazooecial skeleton, ×1200; *5*, granular skeleton of the zooecial basal wall and of the cores of microstyles that arise from the basal wall, with laminae of the reverse-side extrazooecial skeleton deflected toward the reverse surface by the microstyle cores, ×1200; *6–7, Septopora cestriensis* Prout, 1859, Mississippian, Johnson County, Illinois, USA, USNM 528954*; 6*, box indicates area shown at higher magnification in part 7, at junction between main branch (left) and lateral pinnate branch, ×125; *7,* granular core of lateral zooecial wall in main branch and of thinner axial wall between zooecia in lateral branch, with a broader transition between granular wall and laminated lining of zooecia in lateral branch than between granular and laminated wall of *A. intermedius*, ×1000 (new).

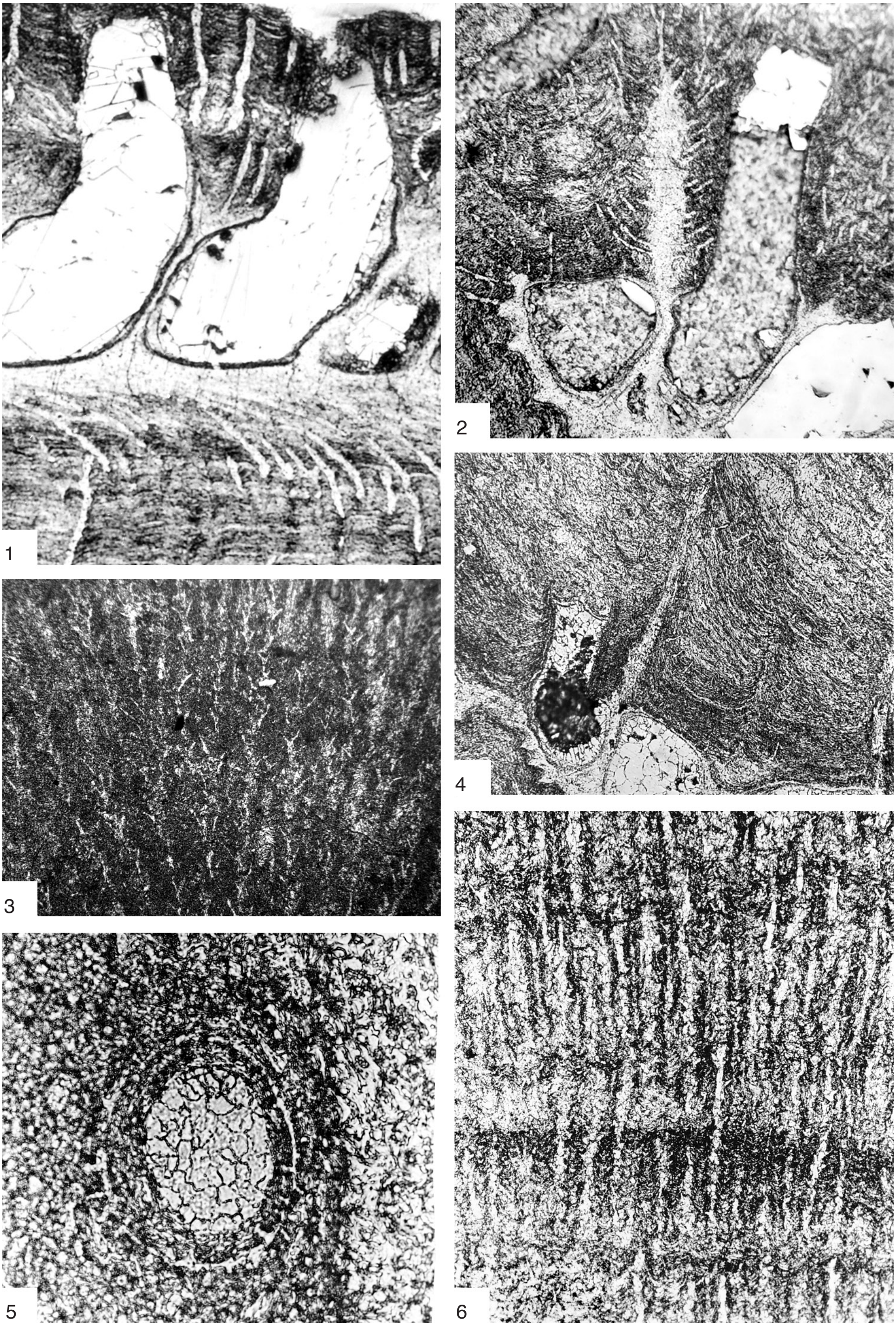

FIG. 11. *For explanation, see facing page.*

(1968, p. 87; 1969, p. 288) interpreted this skeletal layer as a fundamental part of the wall, based on an inference of a decreasing rate of addition through time and analogy with a similar zone in the modern tubuliporate *Hornera frondiculata* Lamouroux, 1816, that develops immediately proximal to growing tips of branches.

Boundaries between the granular layer and the laminated layer on either side most commonly are defined sharply, as seen in light microscope observations. As seen in electron photomicrographs (Tavener-Smith, 1968, p. 87; 1969, pl. 55, fig. 1, 3, 5), the boundaries within *Hemitrypa hibernica* M'Coy, 1844, may be transitional on a fine scale, with the granular layer made of progressively more elongate grains nearer the boundary and with the units of the laminae progressively more elongated away from the boundary. A similarly gradational contact occurs in *Pseudohornera bifida* (Eichwald, 1855) (Brood, 1970 p. 191), *Archimedes intermedius* and *Septopora cestriensis* (Fig. 10). Specimens of *Penniretepora* sp. illustrated by Olaloye (1974, pl. 15, fig. 3–6) appear to have more abrupt, nontransitional boundaries between granular and laminated layers.

In fenestrates, including most phylloporinids, a continuous basal plate extends the length of the reverse side of each branch and is the skeletal unit from which erect zooecial walls arise toward the obverse surface. The granular wall of the basal plate and of the erect zooecial walls forms one continuous structure (Fig. 3.3, Fig. 10.2,4; Tavener-Smith, 1969, p. 288, text-fig. 1; Brood, 1970, p. 189, fig. 1; Gautier, 1973, p. 274, fig. 1C).

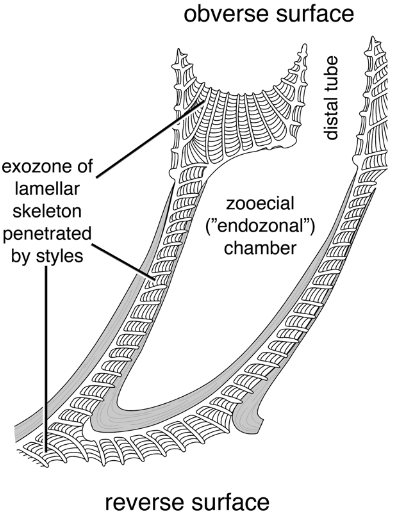

Fig. 12. Separation of autozooecia from previously formed autozooecia by extrazooecial laminated skeleton in *Adlatipora* Gautier, Wyse Jackson, & McKinney, 2013. Each new autozooecium originated *de novo* against the reverse edge of the distal tip of the branch and extended toward the obverse surface, with extrazooecial laminated skeleton providing the reverse wall of the autozooecial chamber (adapted from Gautier, Wyse Jackson, & McKinney, 2013).

Skeletal organization, at least in some acanthocladiids, differs in that no basal plate is present. On the distal side of granular wall that defines the distal side of zooecial chambers, there is a thin zone of laminated skeleton traversed by microstyles (Fig. 12;

Fig. 11. Examples of microstyle cores penetrating extrazooecial laminar skeleton; *1,* large microstyle cores based on longitudinal ridges on the reverse side of the granular-textured zooecial basal plate and from granular skeleton at the transition from endozone to frontal exozone, *Polypora maccoyana* Ulrich, 1890, Keokuk Formation, Mississippian, Nauvoo, Illinois, USA, USNM 528952, ×100; *2–3, Lyroporella quincuncialis*, Paragon Formation, Mississippian, near London, Kentucky, USA, USNM 528955, *2,* narrow microstyle cores derived from granular skeletal core of obverse spine, ×100; *3,* bifurcated fine microstyle cores in the thick proximo-lateral margin of the colony, ×100; *4, L. quincuncialis*, short narrow microstyle cores developed from discrete laminae within the thick proximo-lateral margin of zoarium, Mississippian (Visean–Serpukhovian), Chester, Illinois, USA, USNM 241521, ×100; *5–6, Lyropora subquadrans* (Hall, 1857), Mississippian (Visean–Serpukhovian), Southward Pond, Mississippi, USA, USNM 483520; *5,* tangential section cutting across distal tube defined by a nearly complete thin ring of granular skeleton, lined internally by microstyle-bearing laminae, ×80; *6,* transverse section through thick skeletal deposits along proximo-lateral margin of zoarium, with microstyles through relatively coarse to fine laminae comprising several cycles, ×80 (new).

Gautier, 1973, p. 271–273, fig. 2; Gautier, Wyse Jackson, & McKinney, 2013), which at one time formed the distal tip of the branch. Each additional zooecium was budded against the thin zone of extrazooecial laminated skeleton on the outer surface of the preceding zooecia. Therefore, autozooecial granular skeleton exists as discrete units, each of which defines the distal limit of a zooecium. The proximal surfaces of zooecia are the outer surfaces of microstyle-bearing extrazooecial laminated skeleton that covered outer surfaces of preceding zooecia. Acanthocladiid zooecia may contain an inner lining of laminated skeleton over both granular and microstyle-bearing laminated surfaces. Intervention of the outer laminated skeleton between zooecial walls of granular skeleton also has been observed (McKinney, 1978, p. 85) in the primary zone of astogenetic change in the fenestellid *Lyroporella quincuncialis* (Hall, 1857).

ZOOECIAL-EXTRAZOOECIAL SKELETON DISTINCTION

The distinction between the zooecial and the extrazooecial skeleton in stenolaemate bryozoans is based on those skeletal elements originally associated with a specific zooid (zooecial skeleton) and those that were not (extrazooecial skeleton) (Boardman & Cheetham, 1969, p. 213; 1973, p. 149–151; Tavener-Smith, 1969, p. 300). Decisions relating skeletal deposits to these two categories are based in large part on position of the skeleton relative to zooecial chambers (Boardman & Cheetham, 1973, p. 149). The recognition of the zooecial-extrazooecial boundary, where present, is often "... drawn at the first break or reversal of direction of zooecial laminae outward from the longitudinal axis of the zooecium" (Boardman & Cheetham, 1973, p. 150).

Given that the majority of the wall that defines zooecial chambers in fenestrates is granular rather than laminated, the criterion of change in orientation of adjacent laminae can be used only locally to divide zooecial from extrazooecial skeleton. Instead, zooecial boundaries in fenestrates are considered to be approximately along the midplane of the granular wall that surrounds inflated portions of zooecial chambers and in its projection—either as a continuous granular sheet or as an abrupt reversal in inclination of laminae—around distal tubes (Fig. 4, Fig. 11.5). Laminae on the other side of the granular wall from the zooecial chamber diverge gently from it proximally, overlying distal edges of earlier-formed laminae. The inclination of laminae lining zooecial chambers is difficult to determine; the laminae are basically parallel to the surface of the granular wall or may overlap one another distally. Therefore, there is a very strong reversal of inclination of laminae (locally approaching 360°) where laminated skeleton is present on both sides of the granular wall, which is why we consider the midplane of the granular wall to approximate the zooecial boundary. In this concept, all the microstyle-bearing laminated wall, including that which occurs between zooecial chambers in certain acanthocladiids (Fig. 12), but excepting that which lines the distal tube in some acanthocladiids, is considered extrazooecial.

Thus defined, zooecial skeleton in fenestrates is only a few µm thick and generally includes granular skeleton and, where developed, inner generally non-style-bearing laminae. The bulk of fenestrate skeletons are extrazooecial, consisting of the half of granular skeleton outward from zooecial cavities, the relatively small volume of granular skeleton that exists in places not adjacent to zooecial chambers, and the abundantly developed microstyle-bearing laminated skeleton on outer sides of granular skeleton.

EXTRAZOOECIAL SKELETON AND VESICULAR TISSUE

Extrazooecial skeleton is present in fenestrates to a much higher degree than in any other bryozoan group and is one of the most characteristic features of fenestrates. Such robust structures as the thickened colony margins in lyre-shaped (*Lyropora*) and spiral forms (*Archimedes*), thickened deposits—

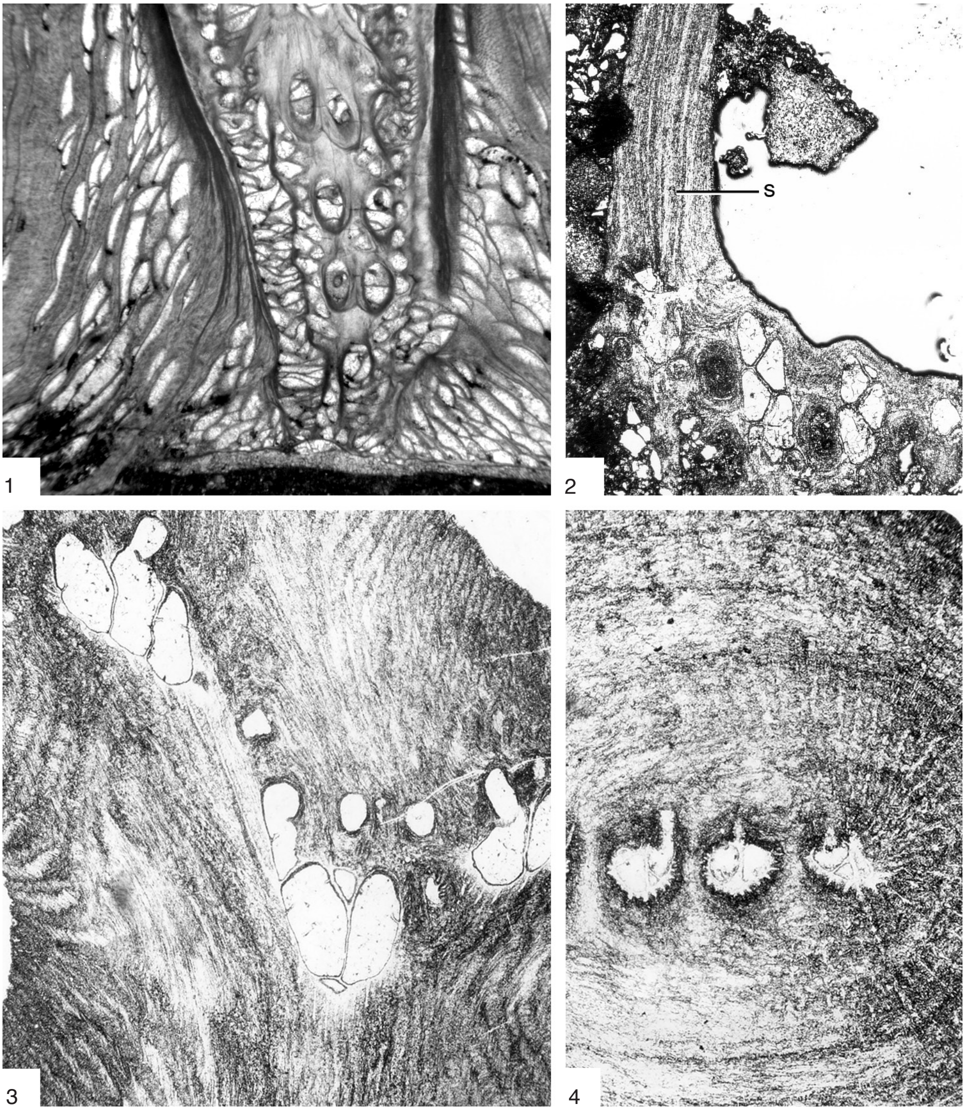

FIG. 13. Sections through robust extrazooecial skeletal structures; *1,* base of conical *Bigeyina winteri* (BORNEMANN, 1884), centered on the ancestrular region and surrounded by substrate-attachment ring of vesicular extrazooecial skeleton grading outward to continuous laminated deposits, Geeser Sichten, Devonian (Eifelian), Trilobite Felder, Gees, Germany, UBKr 1b, ×10; *2,* laminar skeleton of robust pillarlike structure *(s)* extending from the edge of a fenestellid colony, USNM 528956, Mississippian (Visean–Serpukhovian), near Russellville, Alabama, USA, ×38; *3*, helical axis of *Archimedes intermedius,* consisting largely of extrazooecial laminated skeleton surrounding branches of the inner edge of the zoarium, Mississippian (Visean–Serpukhovian), Reid Gap, Blount County, Alabama, USA, USNM 528953, ×38; *4*, extrazooecial laminated skeleton surrounding cross sections of branches in the heavily calcified proximal margin of *Lyroporella quincuncialis*, Mississippian, Chester, Illinois, USA, USNM 528968, ×38 (new).

both solid and vesiculose—associated with colony attachment, and anchoring spines or other processes extending from fronds are composed entirely of microstyle-bearing, laminated extrazooecial skeleton (Fig. 10.1,2,7,8; Fig. 13; TAVENER-SMITH, 1968, p. 91–92; 1969, p. 304–307; BOARDMAN & CHEETHAM, 1973, fig. 36E–G; MCKINNEY, 1978, p. 85–86). Vesicular tissue frequently is distributed in older proximal portions of colonies, particularly, but not exclusively, in members of the Family Semicoscinidae Morozova, 1987. In some Devonian species of *Bigeyina*, *Hemitrypa,* and *Hemitrypella* Nekhoroshev, 1948 (Suárez Andrés & McKinney, 2010; Ernst, 2012), this tissue infills part of the interior of conical zoaria and wraps around the exterior of bases forming a wide area of attachment. In *Bigeyina* extensive extrazooecial tissue seals the older proximal external portions of branches, forming an unusual branching zoarium; this skeleton is initially vesiculose in proximal postion, becoming laminated in more distal and lateral portions of zoaria (Suárez Andrés & McKinney, 2010). In *Pseudoisotrypa* Prantl, 1932 extrazooecial tissue may be 1 mm thick on the reverse surfaces of branches and well-developed on crests of keel-laths (Suárez Andrés & McKinney, 2010).

DISSEPIMENTS

Dissepiments are bars of extrazooecial skeleton that link adjacent branches in many fenestellid and polyporid fenestrates (Fig. 14) and that, most commonly, are regularly spaced. They consist of a median zone of granular skeleton, which may contain a "trail of dark granules" (Tavener-Smith, 1969, p. 300) and thickly developed outer laminar skeleton containing microstyles like those of main branches. Granular cores of the microstyles within the laminar dissepimental skeleton originate from the median zone of granular skeleton (Fig. 14.2,6).

Dissepiments apparently formed "by lateral expansions from contiguous sides of adjacent branches, meeting midway between the branches" (Simpson, 1895, p. 690). Narrow, hourglass-shaped dissepiments may be found just proximal to growing tips of branches, where they appear to have been established quite rapidly. Innermost laminae in dissepiments extend outwardly at high angles from adjacent branches, lapping onto the narrow granular dissepiment core (Fig. 14.2,4,5). The high angles of the innermost laminae also suggest that the dissepiments were quite rapidly established as narrow elements, rather than bulging out as rounded to blunt protuberances from adjacent branches. The almost universal unerring accuracy of junctions from adjacent branches and smooth continuity across the point of juncture in the middle of dissepiments further suggests that cuticles had joined and fused, and the colonial envelope of tissue first became continuous across dissepiments as calcification commenced. Errors were uncommon (Fig. 14.3). Calcification generally continued on dissepiments as they were stranded behind the growing edge: those that are positioned proximally are thicker than are those that are more distal.

Some specimens of a single species, especially commonly in the Devonian, show variation among anastomosis, short dissepiments connecting sinuous branch segments, and longer dissepiments connecting linear branch segments (Simpson, 1895, p. 691–692). Dissepiments apparently developed phylogenetically by maintaining skeletal cross connections as lineages evolved from having anastomosed to having linear branches (Fig. 15; Tavener-Smith, 1975, p. 14). The consistent size and placement of dissepiments and their generation by coordinated extensions from adjacent branches indicate that their development reflects a high degree of colony control.

PSEUDODISSEPIMENTS

The term pseudodissepiment (Fig. 16) was introduced by Miller (1962, p. 541–542, text-fig. 2, pl. 77, fig. 2) for structures in a Wenlockian fenestellid. These structures are formed of a shorter, blunt branch generated at some bifurcations that either meets and fuses with a neighboring branch or is met by an

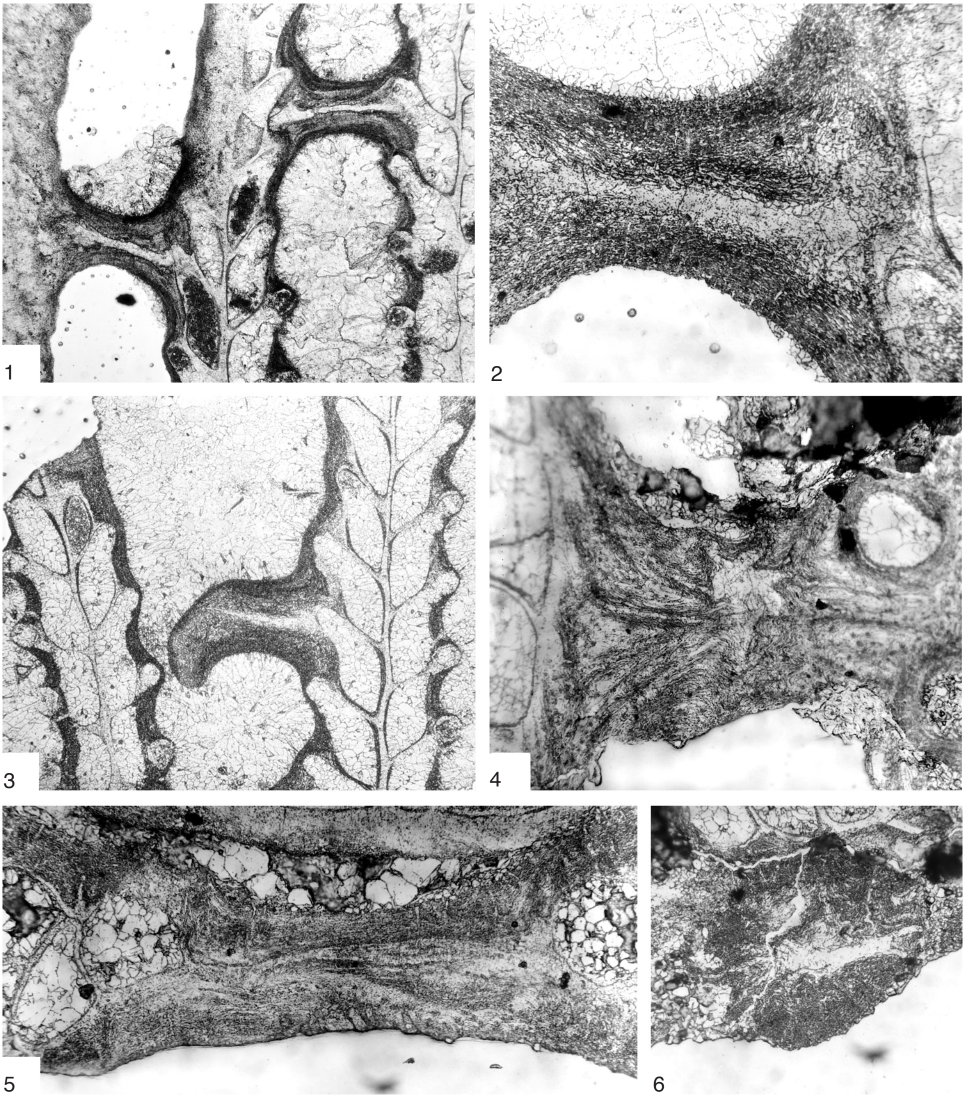

Fig. 14. Structure of dissepiments. *1–3, Utropora nobilis* Barrande in Počta, 1894, Lower Devonian (Pragian), Koněprusy, Prague Basin, Czech Republic, NMCR L17872; *1*, intermediate to deep tangential section through two normally developed dissepiments of laminated skeleton surrounding a core of granular skeleton, ×30; *2,* tangential section through mid-depth of dissepiment illustrating microstyles from granular core of dissepiment and extending through surrounding laminated skeleton, ×100; *3,* tangential section through incomplete, malformed dissepiment developed from a single branch, ×30; *4–6, Pustuloporina cestriensis* (Ulrich, 1890), Mississippian (Visean–Serpukhovian), Sloans Valley, Kentucky, USA; *4,* tangential section through a dissepiment that developed a complexly ridged structure of granular skeleton at approximately the midpoint, USNM 528973, ×100; *5,* transverse section that cuts through laminated skeleton, barely missing the granular core of a single dissepiment connecting branches at each end of the photograph, USNM 528972, ×100; *6,* portion of a zoarial longitudinal section that consists of a cross section of a dissepiment with a flat granular core, USNM 528973, ×100 (new).

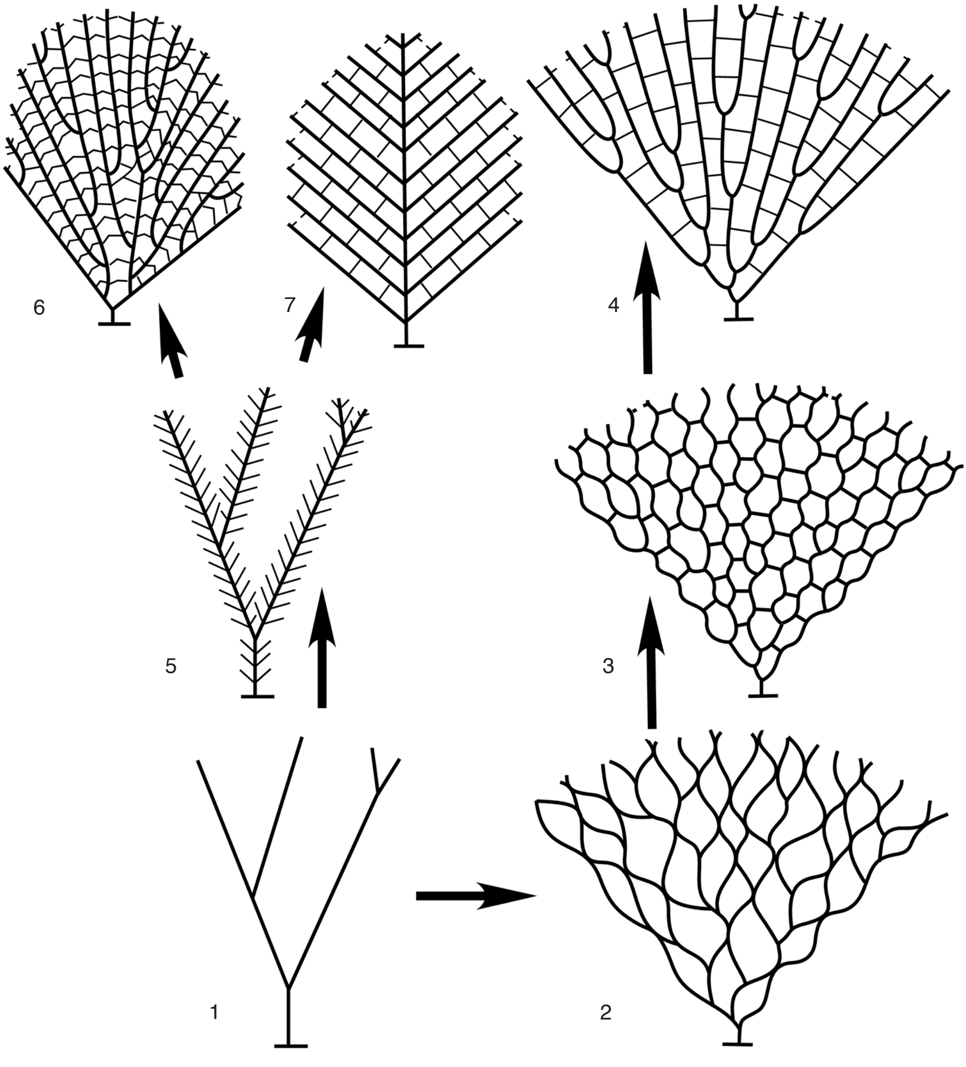

FIG. 15. Possible character state sequences in evolution of fenestrate meshwork types; *1,* erect colony of narrow, bifurcated unilaminate branches; *2,* uniformly sinuous, bifurcated unilaminate branches that contact at random and fuse; *3,* regularly sinuous, bifurcated unilaminate branches that contact at regular intervals and fuse along branch margins; *4,* linear, bifurcated unilaminate branches connected at regular intervals by skeletal dissepiments (*2–4* have the same number of branches at the distal margin); *5,* bifurcated unilaminate primary branches with regularly spaced, zooid-bearing short pinnae; *6,* unilaminate primary branches that arise as unusually long pinnae that are closely spaced and connected by fused, short, regularly spaced secondary pinnae; *7,* main branch with long, regularly spaced pinnae connected by regularly spaced skeletal dissepiments (new).

extension of extrazooecial laminated skeleton from that branch. Therefore, they consist of a short, zooecium-bearing branch, which may be fused onto another short branch or a short segment of typical dissepimental structure.

CARINAE AND CARINAL NODES

In most genera and species with two rows of zooecia per branch, the obverse edge of the axial wall forms a keel (the carina) down the branch midline from which regularly spaced nodes or spines may project (Fig. 6). These

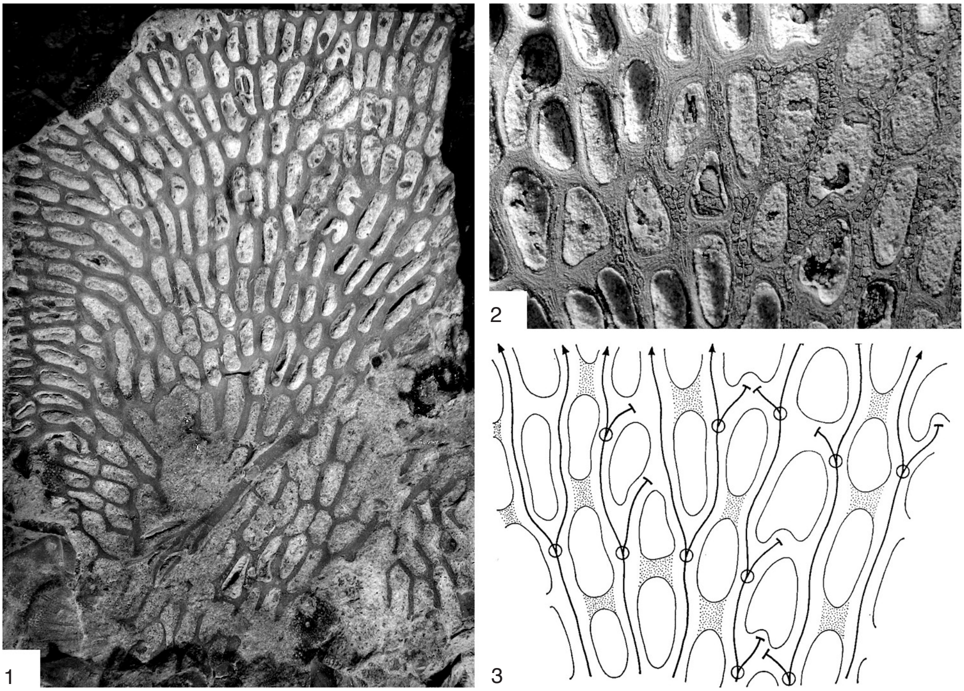

FIG. 16. So-called pseudodissepiments in fenestellid species *"Reteporina" reticulata* (HISINGER, 1837), from the Much Wenlock Limestone, Silurian (Wenlock), Dudley, England, each composed of a branch segment that intersects and fuses with the neighboring branch or dissepiment within a short distance of its origin at a bifurcation; *1,* almost complete zoarium characterized by fenestrules with irregular sizes and shapes, due to variations in placement of branch bifurcations and dissepiments, BU 3250, ×3 (new); *2,* polished surface of specimen that is basis for diagram in *3,* BU 3252, ×8 (new); *3,* diagram highlighting the bifurcation points and branch terminations seen in part *2* (adapted from Miller, 1962).

spines are termed carinal or keel nodes. They have a core of granular wall sheathed by laminated skeleton (LIKHAREV, 1926; ELIAS & CONDRA, 1957, p. 19; TAVENER-SMITH, 1969, p. 302; 1975, p. 11). The laminated skeleton is penetrated by microstyles derived from the core of the keel nodes (Fig. 11.2; TAVENER-SMITH, 1969, p. 289; 1975, p. 11).

Except for somewhat variable thickening by additional laminated skeleton and taxa in which two distinct sizes alternate, keel nodes on a given specimen (and within a species) are of roughly equal size (Fig. 6.1–6.2). They may be robust and high, at least 0.2 mm wide by 1.5 mm high in some taxa, or they may be smaller than 0.03 mm wide with equivalent height. From taxon to taxon, spacing of keel nodes may be related to branch junctions (in acanthocladiids), to branch-dissepiment junctions (in fenestellids), to zooecial spacing, or to unknown factors that produce regular or occasionally irregular spacing. Two sizes of keel nodes regularly alternating with one another are not common, although occasionally recorded (e.g., SHUL'GA-NESTERENKO, 1951, p. 23; SAKAGAMI, 1962, p. 328; TAVENER-SMITH, 1973a, p. 456).

Some keel nodes expand and ramify at their distal tips, producing umbrella- or treelike structures (Fig. 6.3–5). Such highly developed processes have been used as generic characters (CHRONIC, 1953; ERNST & WINKLER PRINS, 2008); see MALONE and PERRY (1965, p. 44) for a dissenting view.

SIMPSON (1895, p. 697–699) identifies six combinations of features in fenestellid keels. These include (1) a row of nodes on a low

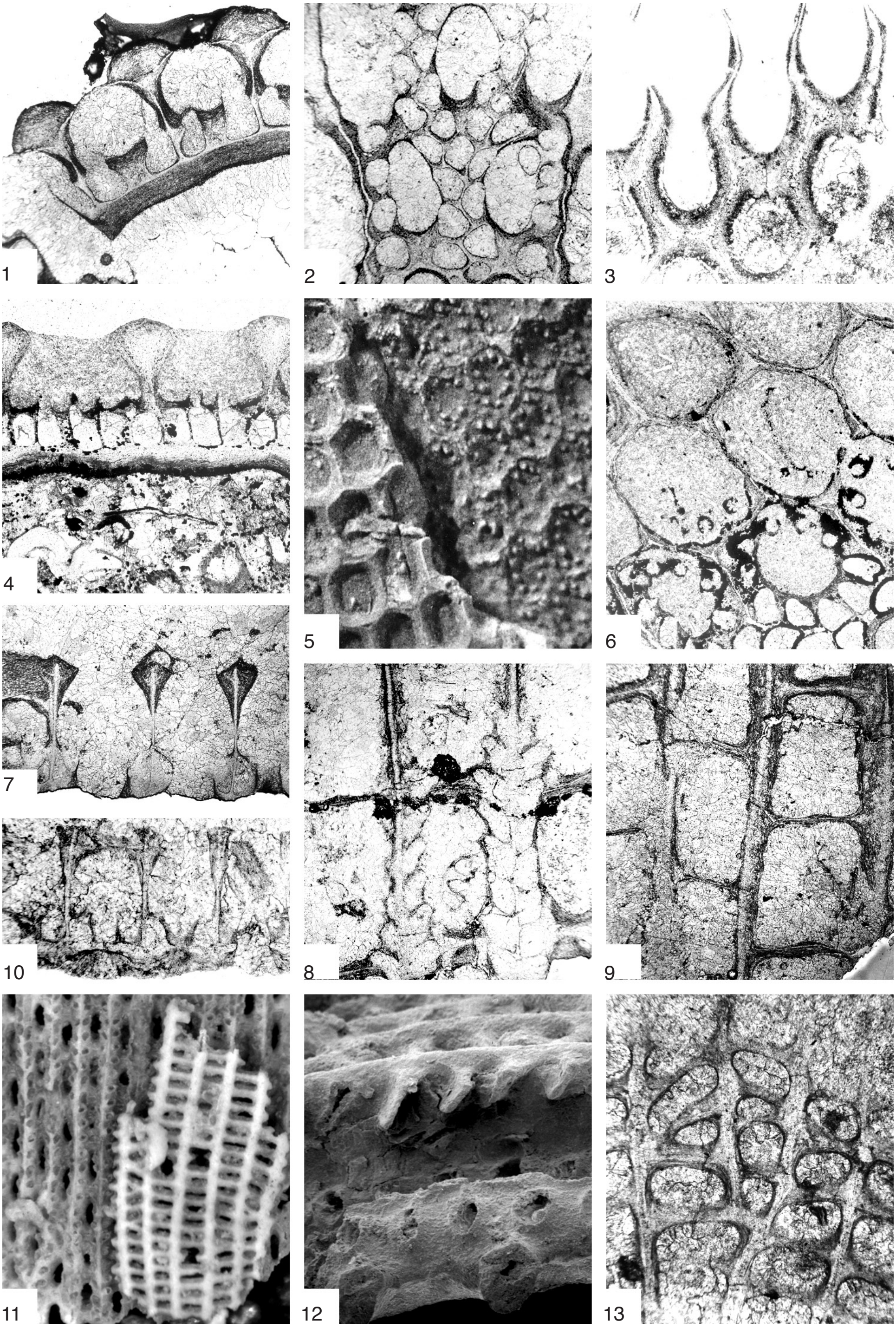

FIG. 17. *For explanation, see facing page.*

or suppressed keel; (2) a smooth keel; (3) a high keel expanded midway up, usually with small conical nodes along margins of the expanded portion; (4) a high keel expanded at the summit, with a smooth surface; (5) a prominent keel expanded at the summit, with nodes; and (6) a prominent keel with the same thickness throughout.

Keel nodes and spines have typically been cited as defensive structures intended to deter predators (e.g., Tavener-Smith, 1969, p. 302; 1973a, p. 443; 1975, p. 11). The keels themselves have often been interpreted as defensive (e.g., Nekhoroshev, 1928, p. 515), and Cumings (1904, p. 65) suggested that they "... afford a very efficient means of protection against the snipping off, by some obnoxious visitor, of the tentacles of the polypides." A strengthening function (Cumings, 1904, p. 75) has also been attributed to keels, particularly to those with expanded summits such that their cross sections resemble I-beams (Elias & Condra, 1957, p. 31).

SUPERSTRUCTURES

Elaborate extrazooecial superstructures occur in some fenestrate taxa with typically two rows of zooecia per branch. The superstructures consist of obverse extensions of the granular axial wall above the surfaces of the branches, microstyle-bearing laminated skeleton that encases the obverse extensions, and lateral processes that consist either of granular and laminated skeleton or solely of laminated skeleton (Fig. 17; Tavener-Smith, 1969, p. 302). The superstructures are continuous elevations above branches and are interconnected in various patterns over the spaces between branches. They develop either as lateral extensions from upper margins of high keels or from tips of keel nodes that extend well above low keels.

Various types of superstructures, all elaborated from keel elements, have been recorded. These keel-borne and node-borne superstructures are described below:

1. Keel-borne superstructures
   a. branches sinuous and anastomosed; keels expanded at summits, coalesced above points of anastomosis; keels restricted to centers of branches (genera such as *Bigeyina*) (Fig. 17.1–17.3);
   b. branches sinuous and anastomosed; keels formed into a continuous hexagonal network, passing along branch

Fig. 17. Superstructures based on high keels. *1–3,* Keels with laterally expanded summits that locally join over underlying points of branch convergence; *1–2, Bigeyina sacculus* (Barrande, in Počta, 1894), Koněprusy Limestone, Lower Devonian (Pragian), Koněprusy, Czech Republic, NMCR L18479, transverse section *(1)* through three branches with high keels and their laterally expanded summits and tangential section *(2)* through sinuous branches, ×20; *3, Pseudoisotrypa bohemica* Prantl, 1932, Zlíchov Limestone, Zlíchovian, Lower Devonian, Kaplička, near Prague, Czech Republic, NMCR L40798, tangential section through expanded keel summits, ×20. *3–6, Loculipora perforata* (Hall, 1884), Hamilton beds, near Darien, New York, USA, NYSM 6580/1, continuous hexagonal meshwork of keels with expanded summits over anastomosed branches; *4,* longitudinal section including cross sections of three keels, ×20; *5,* obverse view of keel meshwork (left) and underlying branches where keels are broken away (right), ×10; *6,* tangential section through expanded keel summits (upper left), thinner underlying portions of keels, and (lower right) obverse region of branches, ×20. *7–9, Tectulipora pannosa* (Počta, 1894), Koněprusy Limestone, Lower Devonian (Pragian), Koněprusy, Czech Republic, continuous rectangular meshwork of keels along branches and across dissepiments; *7,* transverse section through three branches with high keels and their laterally expanded summits, NMCR L18545, ×20; *8,* tangential section through lower portions of keels *(top)* and obverse region of branches *(bottom),* NMCR L18584, ×20; *9,* tangential section through expended keel summits, NMCR L18484, ×20. *10–13,* Keels along relatively straight branches, laterally joined by bars spaced along keel summits; *10, Unitrypa subcircularis* Stewart, 1922, Little Saline Limestone, Lower Devonian, Little Saline Creek, Missouri, USA, FMNH(UC) 27655; *j,* transverse section through three branches with high keels and their laterally expanded summits, ×20; *11, Unitrypa* sp., Onondaga Formation, Devonian, Falls of the Ohio, Indiana, USA, USNM 528970, obverse view of keel summits and connecting bars, with two rows of connecting bars broken away, revealing narrow median keel and portions of underlying branches, ×10; *12, Unitrypa acaulis,* Eifelian, Jeffersonville, Indiana, FMNH(UC) 57428, lateral breakaway view of branch (below), high keel, and connecting bars (top), ×35; *13, U. subcircularis,* Little Saline Limestone, Lower Devonian, Little Saline Creek, Missouri, USA, FMNH(UC) 27655; tangential section through keel summits (extending bottom to top of figure) and laterally connecting bars, ×20 (new).

centers and across between zooecial pairs at points of anastomosis; keels widened at summits (*Loculipora* HALL, 1885) (Fig. 17.4–17.6);

c. branches connected by dissepiments; keels organized into a continuous rectangular network along branch and dissepiment centers, expanded at summits, connected above dissepiments by broad lateral processes (*Tectulipora* HALL, 1888) (Fig. 17.7–17.9);

d. branches connected by dissepiments; keels along branches but not across dissepiments, narrow or widened at summits, connected by thin, inclined, lateral processes equal to or less than distance between dissepiments. Much more closely spaced than dissepiments such that superstructure openings are slit-like and as wide as distance between carinae (*Unitrypa* HALL, 1885) (Fig. 17.10–17.13).

2. Node-borne superstructures

a. branches connected by dissepiments; node crests extended and fused into narrow longitudinal bars over branch centers that are connected by closely spaced, thin processes that meet midway between branches and coalesce, forming a longitudinal element there, such that the superstructure meshwork is fine-grained, with each opening essentially centered over a zooecial aperture (*Hemitrypa*) (Fig. 18.1–18.3);

b. branches connected by dissepiments; node crests expanded as broad, proximally tilted, thin bars; bars extended horizontally, joining midway between adjacent branches to fuse into a sinuous, longitudinal bar located above the midline of fenestrules and dissepiments, rather than above branch centers; therefore superstructure openings are the same width as branch spacing but are centered over branches rather than over fenestrules (*Pseudounitrypa* NEKHOROSHEV, 1926) (Fig. 18.4).

PILLARS

Robust pillar-shaped to spinose outgrowths of laminated skeleton, with or without a central core of granular skeleton, are common on obverse, reverse, and marginal surfaces of fenestrates. These deposits are most common from reverse surfaces of branches in proximal portions of colonies.

The outgrowths have a wide variety of shapes and surface sculpture. They vary from narrow and highly elongate to broad and short. They range from single shafts to variously bifurcated and ramified, and to compound. Where present, bifurcations may be variously placed along the length of proximally directed structures that taper away from their point of origin, resulting in a rootlike appearance (Fig. 19.1). Other pillar structures consist of single shafts that divide at one point into several arms extending at high angles to the primary shaft (Fig. 19.6–19.7). Surface sculpture may include grooves or series of reverse barbs (Fig. 19.2–19.3).

Robust outgrowths that originate at the zoarial margin (Fig. 7.1, Fig. 13.2) extend in essentially the same direction as a supporting branch but commonly have slightly smaller diameter than the supporting branch (TAVENER-SMITH, 1969, p. 303; 1973a, p. 442, 464). The majority of barbed spinose outgrowths originate along zoarial margins.

Many of the pillars with origins on reverse surfaces of zoaria may be seen to extend to a substrate or to an inferred position of former substrate. They affix to the substrate by cementation, by wrapping around small elements of the substrate, or apparently by extending into soft substrates where present. They are interpreted as strengthening or support structures (e.g., KING, 1850, p. 37; YOUNG & YOUNG, 1874b; VINE, 1885, p. 85; CUMINGS & others, 1906, p. 1200; NEKHOROSHEV, 1932, p. 289–290; SHUL'GA-NESTERENKO, 1941, p. 27–28; FERGUSON, 1963, p. 158; TAVENER-SMITH, 1969, p. 302; 1973a, p. 443). ELIAS & CONDRA (1957, p. 53) commented that "distribution of encrustations, pillars, and other external structures

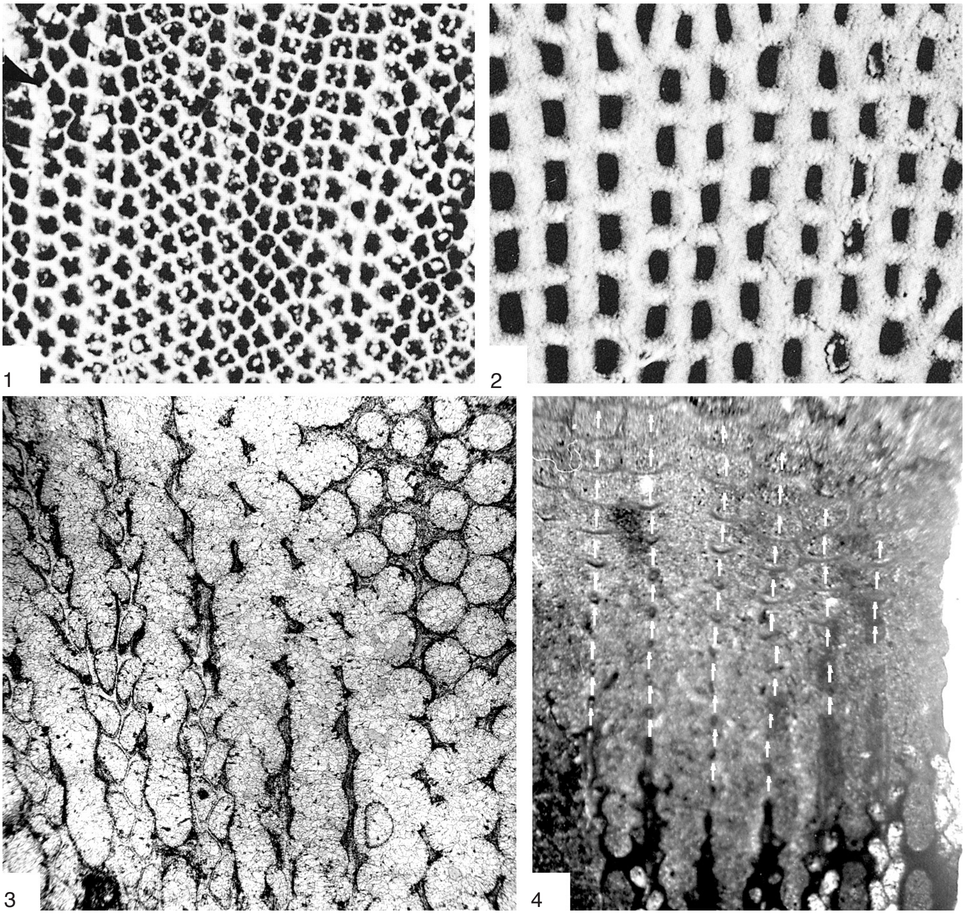

FIG. 18. Superstructures based on high keel nodes; *1–3,* narrow extensions from node crests bifurcated and coalesced, generating a fine-meshed superstructure with a single opening over each zooecial aperture; *1–2, Hemitrypa aprilae* SNYDER, 1991a, Warsaw Formation, Mississippian (Visean), Dennis Hollow, near Valmeyer, Illinois, UI X-6867, obverse surface of superstructure mesh with a small node extending into the meshwork opening from each segment of its skeletal wall; *2,* reverse surface showing size of underlying fenestrate meshwork in part *1,* both ×15 (adapted from Snyder, 1991a); *3, Hemitrypa tenella* BARRANDE in POČTA, 1894, Koněprusy Limestone, Lower Devonian (Pragian), Koněprusy, Czech Republic, NMCR L18558-A, tangential section passing through superstructure meshwork *(upper right),* supporting nodes with triangular cross sections, and obverse region of underlying branches *(lower left),* ×30 (adapted from McKinney & Křìž, 1986); *4,* narrow extensions from node crests coalesced along fenestrule midlines and forming transversely elongate superstructure openings centered over branch midlines; tangential section through endozone *(bottom)* to superstructure (top), with small arrows between successive keel nodes along branch axis, continuing into region of superstructure to indicate alignment with centers of transverse meshwork openings, *Pseudounitrypa sibirica* NEKHOROSHEV, 1926, Mississippian (Tournaisian), Tom' River near Roiskaya village, Kuznets basin, Russia, CNIGRI 644/115, ×20 (new).

on zoaria does not suggest purposefulness. They develop haphazardly, and their service in anchorage and reinforcement is apparently accomplished in irregular hit or miss manner."

Under some conditions, pillars grown from one part of a zoarium may extend to another part of the zoarium (Fig. 19.1,4,5). If the point of contact occurred where the cuticle was decayed or was senescent, the tip of the extension may retain its integrity and "form a number of discrete dactylose processes that clasp the branch and firmly secure the spine to it" (TAVENER-SMITH,

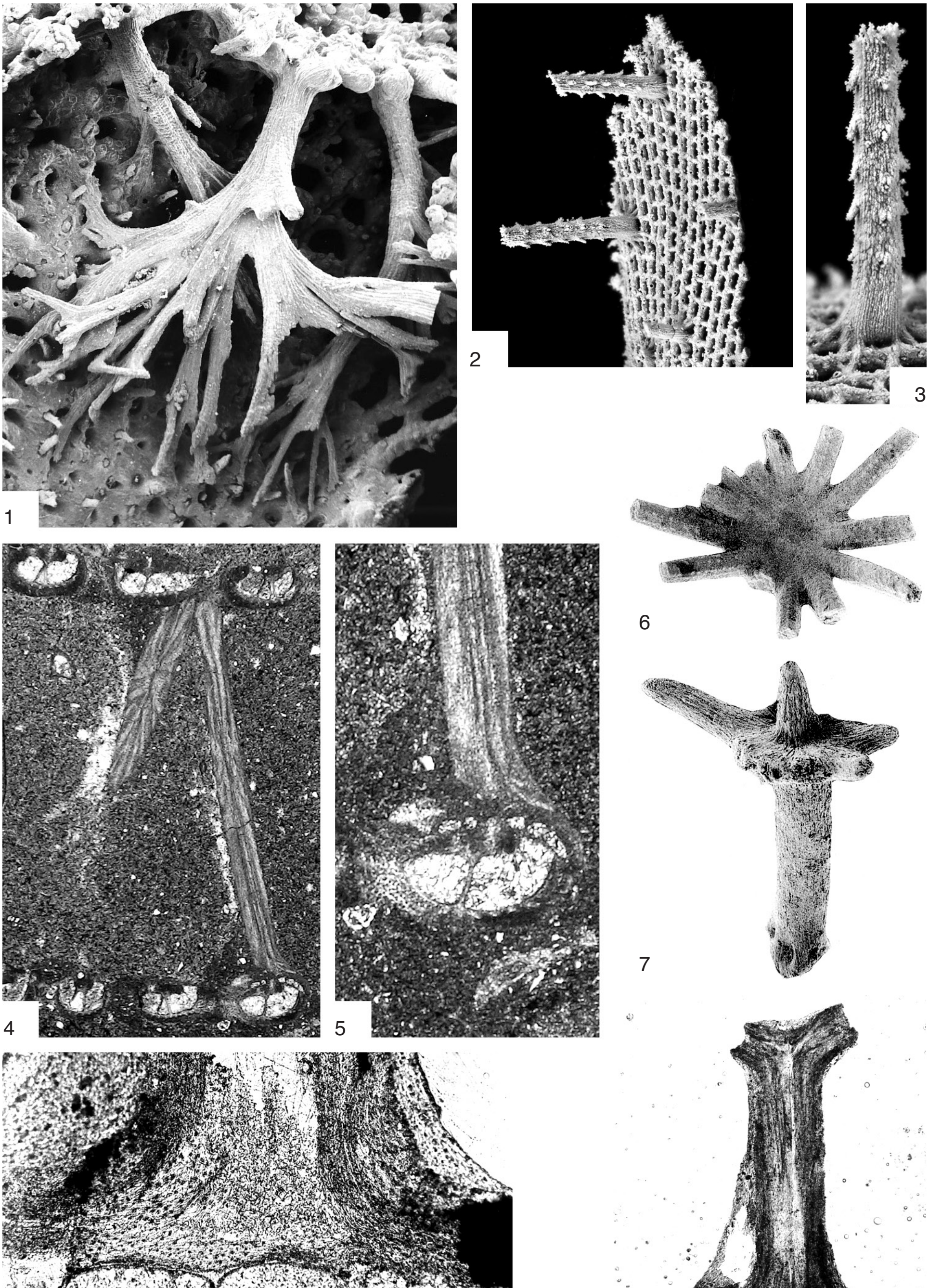

FIG. 19. *For explanation, see facing page.*

1973a, p. 442), a relationship similar to contact with any other substratum. If, however, the point of contact was made where the colony was alive and the cuticle still responsive, the pillar may have skeletally fused with the newly contacted part, may be thickened by lamellar skeleton in continuity with the area of contact, and may ramify along branches and dissepiments as attenuated chords (TAVENER-SMITH, 1969, p. 303). The surface sculpture of the ramified pillar tip often does not coincide with the surface with which it has fused (TAVENER-SMITH, 1969, p. 303). This lack of coincidence between skeletal structure of the pillar and the region of the zoarium where it made contact may have contributed to earlier workers' interpretation of the spines as belonging to independent organisms.

Some forms of extrazooecial skeletal development, such as marginal thickenings of lyre-shaped and spiral forms and deposits associated with zoarial attachment (Fig. 7), overspread many branches and filled fenestrules between, resulting in occlusion of zooecial apertures in the areas affected. The Permian genus *Bicorbis* is a polyporid fenestrate that has a skeletal meshwork formed entirely of microstyle-bearing laminated skeleton arising from the reverse sides of branches (Fig. 20). Zoaria are cylindrical, with obverse surfaces of branches outermost and the derived skeletal structure present as a smaller cylinder within, supported by and continuous with columns of laminated skeleton extending from the reverse sides of branches and typically situated at branch-dissepiment junctions. This structure is composed of longitudinal and transverse elements that are less regularly disposed than the branch-dissepiment meshwork but that correspond in general to the main meshwork of zooecia-bearing branches and dissepiments.

Palaeocoryne

Some varieties of solid skeletal extensions have been considered independent organisms by some investigators. DUNCAN and JENKINS (1869) erected *Palaeocoryne* for pillars with terminal arms that extend at high angles to the shaft and that issue from or obverse surfaces of *Fenestella s.l.* (Fig. 19.6–19.7). FERGUSON (1961) added the generic concept *Claviradix* for those that he considered to have a hollow base, while NELSON and BOLTON (1980) added *Magowanella*, which has an identical structure to *Palaeocoryne*.

These pillarlike structures have been considered as Hydrozoa (DUNCAN & JENKINS, 1869; DUNCAN, 1873), algae (CONDRA & ELIAS, 1944, p. 45; ELIAS, 1946, p. 285), a combination of algae and bryozoan skeleton (ELIAS & CONDRA, 1957, p. 43), *incertae sedis* (FERGUSON, 1961, p. 146), and as independent bryozoans that typically attached to obverse surfaces of fenestellids but that could live independently (FERGUSON, 1963,

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FIG. 19. Skeletal pillars extending from fenestrate branches. *1, Hemitrypa* sp., Middle Permian (Kungerian), Glass Mountains, Texas, USA, USNM 32151, branched pillars extending from reverse side of branch meshwork, ×8 (adapted from McKinney, 1981a); *2–3, Fenestella (s.l.) frutex* M'COY, 1844, limestone is equivalent to uppermost Glencar Limestone and lowermost Dartry Limestone, Mississippian (Visean), south side of Carrick Lough, County Fermanagh, Northern Ireland, NHMUK PD5006, barbed pillars extending from obverse surface; *2,* ×5 (new); *3,* detail of barbed pillar, ×12 (new); *4–5, Archimedes intermedius*, Mississippian (Visean–Serpukhovian), Colbert County, Alabama, USA, USNM 528957, section through pillars extending from reverse side of a more distal whorl of branches (cut in cross section at top of part *4*) to the next-proximal whorl (cut in cross section at bottom of part *4*); *4,* ×10 (new); *5,* detail of contact and fusion of a pillar with a branch of the more proximal whorl, ×50 (new); *6–9,* pillars (so-called *Palaeocoryne*) from obverse surface of fenestellids; *6–7,* Main Limestone, Mississippian (Serpukhovian), Hurst, Yorkshire, UK, NHMUK PD7802; *6,* low central boss with lateral spines radiating from top of obverse pillar, ×15 (adapted from Bancroft, 1988); *7,* lateral view of obverse pillar with spines radiating from near distal end, ×20 (adapted from Bancroft, 1988); *8–9,* Lower Limestone Series, Mississippian (Visean), Craigenglen, Boghead, Scotland, HMAG Young Collection 01-53adb; *8,* section through branch (bottom) and base of pillar, with laminated skeleton continuous from branch into pillar, ×100 (new); *9,* section through entire length of pillar, from originating branch (bottom) to radially branched tip of pillar (top of figure), ×30 (new).

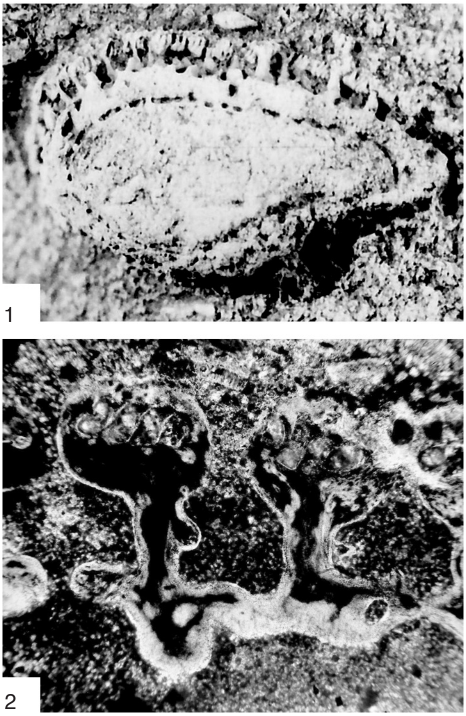

Fig. 20. Reverse-side structural meshwork of the polyporid *Bicorbis arizonica* (Condra & Elias, 1945a) resulting from the laminar wall of the reverse side of branches, composed of pillarlike laminar skeletal extensions that ramify and fuse at their tips to form a coarse net, Kaibab Limestone, Lower Permian, Grand Canyon National Park, Arizona, USA. *1,* eroded cross section across silicified tubular zoarium, with obverse surface of branches forming the perimeter of the cross section and the reverse-side parallel structure forming the inner skeletal ring, FMNH PE 13877-2, ×4; *2,* thin section of silicified zoarium cutting branches at top and reverse-side skeletal extensions at bottom, FMNH PE 24298, ×20 (adapted from McKinney, 1983a).

p. 161). However, skeletal continuity was demonstrated as early as the late 19th century (Young & Young, 1874b), and the majority of investigators have considered so-called *Palaeocoryne* structures to be part of the fenestellids from which they extend (e.g., Young & Young, 1874b; Vine, 1879b; Nickles & Bassler, 1900; Nekhoroshev, 1932, p. 289; Bassler, 1953; Tavener-Smith, 1973a, p. 443; Bancroft, 1988). The putative genus *Palaeocoryne* is retained informally here and, together with the synonymous genera *Claviradix* and *Magowanella* and other robust skeletal extensions, it is considered here also as part of the bryozoans on which it is found.

ASTOGENY

Metamorphosis of fenestrate larvae typically occurred on solid substrata such as brachiopods, other bryozoans, echinoderms, rocks, and occasionally smaller particles such as ostracode valves. The initial portion of a fenestrate colony is an ancestrula consisting of a hemispherical to slightly elongate hemi-ovoid basal disc, the protoecium, from which a central to subcentral narrow distal tube extends perpendicularly or obliquely (Fig. 21; Cumings, 1904, 1905; Gautier, 1972, 1973; McKinney, 1978).

The diameter of the basal discs ranges from about 0.1 mm (Cumings, 1904, p. 59) to about 0.6 mm (Cumings, 1905, p. 171), but it has been determined for very few taxa. Cumings's figures are for *Fenestella s.l.;* Gautier (1972) has determined a range of 0.20 mm to 0.50 mm for basal discs of the acanthocladiid *Adlatipora* Gautier, Wyse Jackson, and McKinney, 2013. *Polyporella* Simpson, 1895, from the Devonian of Michigan have hemispherical basal discs (Fig. 22.1–22.2), ranging from 0.15 mm to almost 0.30 mm. The basal disc of a paratype of *Semicoscinium couviniensis* (Dessilly & Kräusel, 1963) is approximately 0.20 mm in diameter. Hemi-ovoid basal discs of *Lyroporella* (Fig. 22.3–22.4) are about 0.21 mm by 0.15 mm.

Distal tubes arising from basal discs range from sharply differentiated (Cumings, 1905, fig. 37; Gautier, 1972) to less abruptly differentiated (Fig. 22.2). Their diameters are greatly reduced from those of basal discs, approaching the diameters of the distal tubes of asexually produced zooecia.

The walls of basal discs and the surmounting distal tubes in *Fenestella s.l.* have been reported (Cumings, 1905, p. 171) as consisting of a granular layer enveloped by

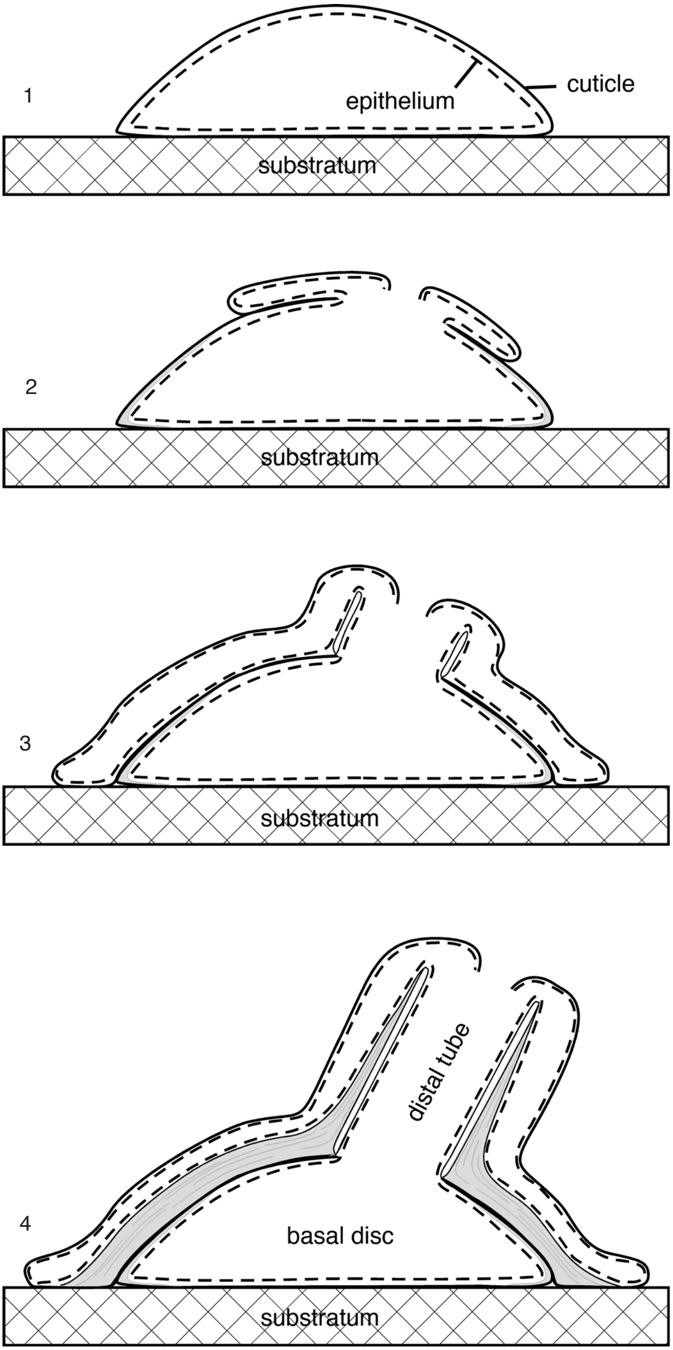

FIG. 21. Development of ancestrula in fenestrates from initial transition of settling larva into a hemispherical disc on the substratum *(1),* through near-apical folding and lateral expansion of the cuticle *(2)*, secretion of shape-defining skeleton *(3)*, and development of surrounding extrazooecial laminar wall *(4)* (adapted from Gautier, Wyse Jackson, & McKinney, 2013).

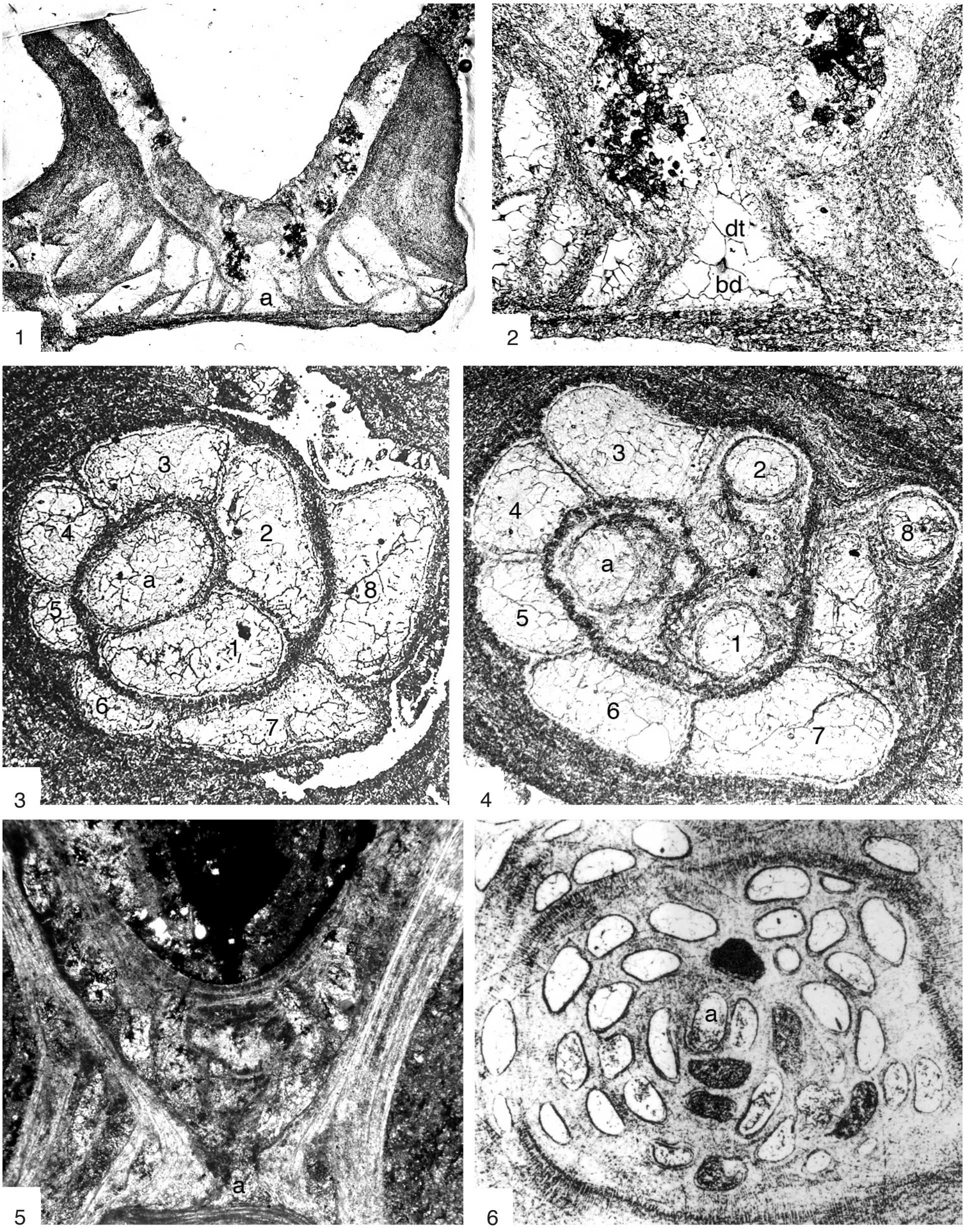

FIG. 22. Ancestrulae and primary zones of change of representative fenestrates. *1–2, Polyporella* sp., Petoskey Formation, Traverse Group, Middle Devonian, Norwood, Michigan, USA, USNM 528971; *1,* section through axis of conical specimen in which only ancestrula *(a)* and extrazooecial laminated skeleton are in contact with substratum, ×30 (new); *2,* enlargement of ancestrula in which the basal disc *(bd)* is surmounted by a broad distal tube *(dt)* that is only moderately well differentiated from the underlying basal disc, ×100 (new); *3–4, Lyroporella quincuncialis* (HALL, 1857), Mississippian (Visean–Serpukhovian), M&O Okan Bridge, Illinois, USA, USNM 242723; *3,* section tangential to and just above substratum cutting primary (endozonal) chambers of ancestrula *(a)* and surrounding ring of sequentially budded *(numbered 1–8)* zooecia in the primary zone of astogenetic change, ×100 (adapted from McKinney, 1978); *4,* tangential section slightly higher than that in part *3,* cutting through distal tubes of ancestrula and zooecia *1, 2,* (*Continued on facing page.*)

microstyle-bearing laminar skeleton. Study of *Adlatipora* revealed a different, two- or three-part structure of skeleton around the ancestrula (Fig. 21). This structure includes (1) an inner thin, dark layer in the basal disc that terminates abruptly at the base of the distal tube and slightly overlaps the substratum, and an inner granular layer in the distal tube but not in the basal disc; (2) an outer microstyle-bearing laminar layer with microstyles directed away from the thin, dark layer; and (3) in some, a thin layer of granular or poorly laminated skeleton, interior to the thin, dark layer (Gautier, Wyse Jackson, & McKinney, 2013). A granular layer seems absent in the basal disc of *Polyporella* (Fig. 22.1–22.2) but is present in *Lyroporella* (Fig. 22.3; McKinney, 1978, p. 84, pl. 2, fig. 1–2) as is a very thin clear layer, similar to the thin granular zooecial walls in surrounding zooecia, but defined on its inner surface by an even thinner dark layer.

The inner thin, dark layer in the basal disc of *Adlatipora* apparently represents, in part, the outer cuticular membrane of the metamorphosed larva after it settled on the substrate. This interpretation (Gautier, Wyse Jackson, & McKinney, 2013) is based on (1) a reflected lip on the underside that overlaps the underlying substratum, which suggests secretion from the interior; (2) a different textural appearance from typical zooecial linings; (3) a limitation to the basal disc walls and the slight continuity onto the substratum; (4) its absence from the distal tube; and (5) a position that would be occupied by cuticle doubled by evagination from the aperture at which the distal tube eventually formed (Fig. 21; Tavener-Smith, 1968, p. 89–90; 1969, p. 295–296; Gautier, Wyse Jackson, & McKinney, 2013). The deposition of the microstyle-bearing laminar outer skeleton of the basal disc occurred from the outer surface, which requires the presence of extrazooidal tissues, the most logical origin being the spread of an external colonial envelope, which was bounded by cuticle and epithelium both above and below, from the subcentral aperture where the dark layer is abruptly terminated. The microstyle-bearing laminated wall of the basal disc was, therefore, deposited on outer cuticles and is part of an exterior wall. Although the doubling of the cuticle over the larva seems a prerequisite for exterior calcification, evidence for its doubled status has not been found. This lack may be due to the original back-to-back appression and fusion of the cuticles or to the destruction of evidence during preservation. A granular wall that defines the distal tube is interpreted as an interior wall deposited after origination of the outer colonial envelope of cuticle and tissues.

The innermost very thin, dark layer of *Lyroporella* is interpreted as homologous with that of *Adlatipora*. The two-layered wall (granular and microstyle-bearing laminar) encompassing it is inferred to be an exterior wall secreted on the inner surface of evaginated cuticle that then spread over the underlying substratum. It is not known whether the colonial envelope began before or after the establishment of the distal tube of the ancestrula in *Lyroporella*. In *Polyporella*, the colonial envelope perhaps began to develop only after the short ancestrular distal tube formed, as there is no apparent discontinuity in the skeletal microstructure at the base or within the distal tube.

Fig. 22. (*Continued from facing page.*)

and *8,* ×100 (adapted from McKinney, 1978); *5,* section through axis of conical specimen in which only ancestrula *(a)* and extrazooecial laminated skeleton are in contact with substratum, *Semicoscinium couviniensis* (Dessilly & Kräusel, 1963), Devonian (Eifelian), Chemin de Boussu, Couvin, Belgium, IRSN 27260A, ×100 (new); *6,* section tangential to and just above substratum cutting primary (endozonal) chambers of ancestrula *(a)* and surrounding zooecia in the primary zone of astogenetic change, *Adlatipora fossulata* Gautier, Wyse Jackson, & McKinney, 2013, Cathedral Mountain Formation, Permian (Kungurian), Glass Mountains, Texas, KU 54146, ×40 (adapted from Gautier, Wyse Jackson, & McKinney, 2013).

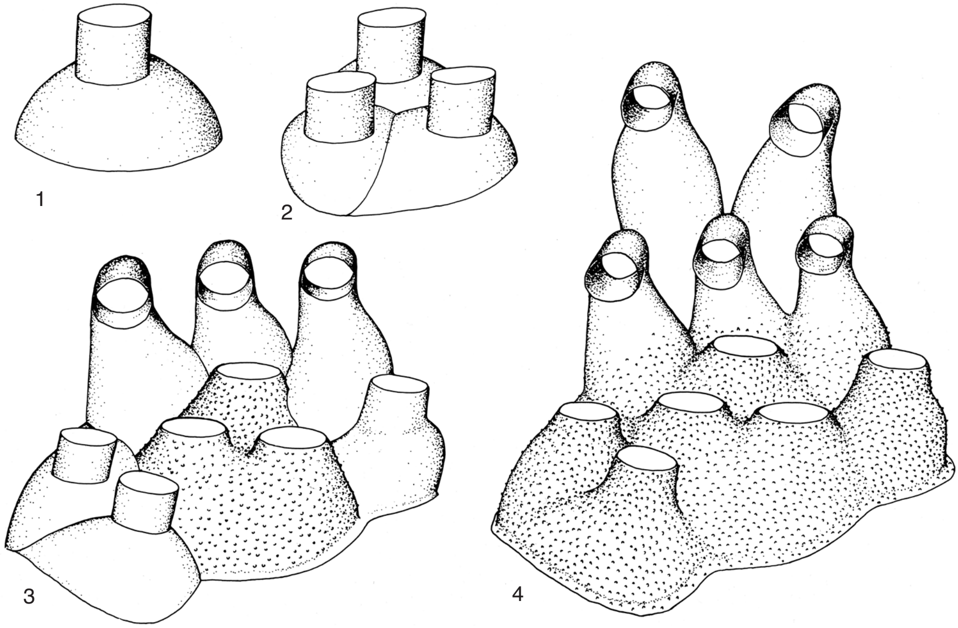

FIG. 23. Initial development of a colony of *Lyroporella quincuncialis* (HALL, 1857), based on a series of 13 peels through the primary zone of astogenetic change of USNM 242723, two of which are illustrated in Fig. 20.3–20.4; *1,* ancestrula; *2,* ancestrula and first two asexually budded autozooecia; *3,* ancestrula surrounded by complete set of basal autozooecia, three of which are oriented upright rather than adnate on the substratum; *4,* the three upright basal zooecia succeeded by the first two autozooecia budded above the level of the substratum (adapted from McKinney, 1978).

PRIMARY ZONES OF ASTOGENETIC CHANGE

The first few asexually budded zooids in different fenestrates had markedly different shapes and placement. In some, the ancestrula is the only zooecium in contact with the substrate (Fig. 22.2). In others, the ancestrula is surrounded by encrusting autozooecia (Fig. 22.3, Fig. 23).

An outwardly deposited, microstyle-bearing laminated skeleton surrounds the basal disc in *Adlatipora* (Fig. 21.4; GAUTIER, WYSE JACKSON, & MCKINNEY, 2013) and *Lyroporella* (Fig. 22.3; MCKINNEY, 1978, p. 84–85, pl. 2, fig. 1), demonstrating the presence of a colonial envelope. It was from within this colonial envelope that subsequent zooids were produced asexually. Therefore, in fenestrates, beginning with zooids derived from the ancestrula and extending throughout the colonies, there was no zooid-zooid, parent-offspring relationship (GAUTIER, 1973, p. 273), as is described by CUMINGS (1904, 1905) and by TAVENER-SMITH (1969, p. 296, text-fig. 4B–D).

In *Polyporella* sp. from the Devonian of Michigan and *Semicoscinium couviniensis*, the first asexually budded autozooecia were generated within the colonial envelope in the vicinity of the distal tube of the ancestrula (Fig. 22.1,5), so that only the basal disc and eventually the extrazooecial skeleton affixed the colony to the substratum. In these forms the primary zone of astogenetic change was very short, as the typical zooecial form and size was reached and repeated by the second or third generation above the substratum.

CUMINGS (1904, 1905) described the primary zone of astogenetic change for a species, which he placed in *Fenestella* LONSDALE in MURCHISON, 1839. NEKHOROSHEV (1928, p. 486, 514) concluded that CUMINGS had worked with a species of *Semicoscinium*

PROUT, 1859, rather than with *Fenestella*, a conclusion supported by MOROZOVA (1962, p. 104) and herein. However, MOROZOVA (1962) reported that her work on initial growth stages of *Fenestella s.l.* and *Polypora s.l.* from Carboniferous deposits of the Russian platform generally support CUMINGS's description.

The ancestrula in CUMINGS's material is marginal in the basal group, which spreads symmetrically in two uniserial strands of zooecia that typically, but not in all cases, join opposite the ancestrula to complete a ring with the apertures opening outward (CUMINGS, 1904, p. 60). The basal group of zooecia, including ancestrula, typically totals 10 but varies from 5 to 14. The basal zooecia are organized into pairs by carinae that appear to originate as upgrowths of folds of the basal plate (CUMINGS, 1904, p. 64). The absence of any indication of a median cuticle within the axial walls that produce the carinae seems to eliminate the possibility of the axial walls being exterior walls.

Additional zooecia were budded in series above the ring-shaped basal group, for a total of as many as 50 or 60 in the primary zone of astogenetic change (CUMINGS, 1904, p. 59). Successive generations exhibit a gradient from elongate tubular, slightly divergent zooecia with slightly developed distal tubes of the first suprabasal generation to normal fenestellid zooecial shape above (CUMINGS, 1905, p. 172–173). CUMINGS (1904, p. 65) noted that in his material, in funnel-shaped colonies that developed from a ring-shaped basal series, zooecia apparently always open on the outer surface of the funnel. ELIAS & CONDRA (1957, p. 49), however, noted that for *Fenestella s.l., Polypora s.l.*, and *Hemitrypa* about as many funnel-shaped zoaria have apertures opening on the inside as the outside. MOROZOVA (1962) supported ELIAS and CONDRA's observations.

The angle of divergence of the bilateral series of basal zooecia extending from the ancestrula in some colonies was too great, apparently, for the ends to recurve and meet; in these instances, an upright, sheetlike zoarial form developed rather than cone-shaped form. If the edges of the zoaria became concave on the obverse surface and fused during growth, then, in some, zooecia opened on the inside of funnel-shaped zoaria (CUMINGS, 1904, p. 65).

The primary zone of astogenetic change in *Unitrypa* was reported (CUMINGS, 1904, p. 67–70) to be similar to that of his *Fenestella,* except that a spreading extrazooecial basal sheet encrusts the substratum for some distance, then turns up abruptly around the edges and extends upward with a bell-shaped flare, leaving a 0.2–0.3 mm space (as measured from CUMINGS's figures) between it and the approximately three tiers of zooecia encompassed. The axial wall in the young branches was not seen by CUMINGS as arising from the base but as developing with the first or second tier of suprabasal zooecia and extending out and down to fuse with the upturned basal sheet. Above the edge of the upturned basal sheet (which is an exterior wall including outer cuticle), diamond-shaped flanges of interior wall grew laterally and fused, initiating the zoarial superstructure.

Information on the primary zone of astogenetic change in *Polypora s.l.* also is derived from CUMINGS's (1904, p. 70–74) studies. The ancestrula is subcentrally placed among the basal zooecia, which CUMINGS interpreted to be budded in two pairs, with one final single zooecium, around the ancestrula. However, their arrangement could also be interpreted as a single curvilinear series wrapped around the ancestrula. Additional work is needed on their relationships as seen at higher magnifications than those figured by CUMINGS. Suprabasal zooecia originated against the outer, reverse sides of the basal zooecia and curved axially so that it is typical for zooecial apertures to be placed toward the interior in funnel-shaped colonies of *Polypora*. However, as CUMINGS reported, a more linear arrangement of basal zooecia may give rise to sheetlike zoarial form with edges curled toward the reverse and then fused, causing zooecia to open on the outside of a funnel-shaped zoarium.

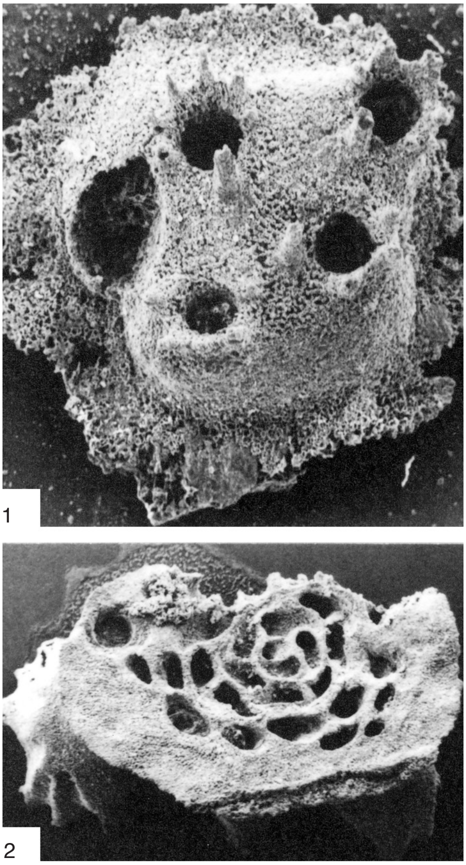

FIG. 24. Initial development of acanthocladiid colonies; *1,* young colony consisting of ancestrula (probably top center of figure) and three zooecia in the primary zone of astogenetic change, unidentified silicified acanthocladiid, Cathedral Mountain Formation, Permian (Kungurian), Glass Mountains, Texas, KU 54246, ×95 (adapted from Gautier, Wyse Jackson, & McKinney, 2013); *2,* underside of young colony of *Adlatipora* with silicified skeleton and empty zooecial chambers, with small ancestrula surrounded by ring of zooecia and additional basal zooecia roughly organized into clusters where upright branches would develop, Cathedral Mountain Formation, Permian (Kungurian), Glass Mountains, Texas, KU 54572, ×20 (adapted from Gautier, 1972).

In *Lyroporella* the entire group of seven or eight basal zooecia originated uniserially around the perimeter of the ancestrula in about one and a half revolutions (Fig. 22.3–22.4; McKINNEY, 1978). The first and last basal zooecia were recumbent on the substratum, but the three or four zooecia in the middle of the series that originated on the substratum-colony margin had growth axes oriented upward and apertures directed toward the axis of the ancestrula (Fig. 23). Suprabasal zooecia were budded against the reverse surfaces of the upright basal zooecia and with apertures also oriented toward the axis of the ancestrula, establishing the orientation of the obverse surface of the branch system that developed above. The primary zone of astogenetic change is interpreted to include only the basal zooecia and the first tier of suprabasal zooecia, as no differences in morphology and geometric relationships (other than bifurcation points and ontogenetic changes) were noted among successive generations of suprabasal zooecia.

Kingopora ehrenbergi (GEINITZ, 1846) is illustrated by KORN (1930, fig. 6) as having nine radially arranged zooecia in the basal disc, each having the base of its chamber located perimetrically and extending upward and inward, tapering into a distal tube. KORN's material was a mold, including internal fillings, with the presumed central ancestrula missing due to state of preservation.

The base of attachment of acanthocladiids, such as *Adlatipora* (Fig. 24), is apparently a complex of zones of change and of repetition (GAUTIER, WYSE JACKSON, & McKINNEY, 2013). Basal zooecia were budded uniserially in a clockwise or counterclockwise direction around the ancestrula, four or five zooecia making a complete circle. The first asexual zooecium originated near the base of the distal tube of the ancestrula and extended to and partially around the margin of the basal disc. Less commonly, two oppositely directed uniserial rows developed. After completion of the uniserial row with up to two revolutions, additional basal zooecia were budded annularly, initiating an encrusting primary zone of astogenetic repetition. Annular budding was organized initially or shortly thereafter to produce four to seven radiating groups, some or all of which formed the bases of branches. Beyond the ancestrula, GAUTIER, WYSE JACKSON, and McKINNEY (2013) recognize change in form due to microenvironment rather than to astogeny, except for change in the pattern of right- and left-handed budding. The number of basal zooecia (exceeding 20) in the acanthocladiid *Adlatipora* contrasts with the lower number of basal zooecia described for fenestellids.

Two bases of attachment of Pennsylvanian *Thamniscus* (most likely not in this genus) have been illustrated (CUMINGS, 1905, fig. 35; ELIAS, 1973, fig. 30) but not described. Both indicate a uniserial row of recumbent zooecia encircling the ancestrula, and ELIAS's figure illustrates many additional, annularly budded basal zooecia organized along five radial budding axes. The basal portions of such *Thamniscus* more generally resemble those of *Adlatipora* than those of described fenestellids.

The primary zone of astogenetic change of *Sardesonina corticosa* (ULRICH, 1886a), as illustrated diagrammatically by CUMINGS (1905, fig. 33), has tubuliporate or trepostomatous aspect. A circular basal disc is at the initial point of a distinct wedge of budding of elongate zooecia. A line of discontinuity in orientation of zooecia along the margin of the wedge indicates that the exterior wall that laterally encompassed a trumpet-shaped cone was reflected back upon itself and spread proximally (with respect to growth direction of the ancestrula) as a base from which proximally oriented zooecia were budded. The primary zone of astogenetic change is not known for other phylloporinids.

The nature of growth in the fenestrate primary zone of astogenetic change, though similar in the mode of calcification, contrasts strongly in sequence of development and in geometry with the same zone described in other stenolaemates (BOARDMAN, 1983, p. 115). The differences are due to radial spread of the colonial coelom prior to asexual budding and include (1) the lack of an initial cone of growth encompassed by exterior wall and (2) the presence of extrazooecial skeleton between ancestrulae and subsequently budded basal zooecia.

ZONES OF ASTOGENETIC REPETITION

The major part of most fenestrate zoaria is within the primary zone of astogenetic repetition, in which successive generations of zooecia and other skeletal structures have similar ranges of morphology and distributions relative to one another. ELIAS (1964, p. 375) ascribes the generally increased spacing distally between dissepiments in some Mississippian (Lower Carboniferous) *Fenestella s.l.* species to astogenetic changes. However, consistent, progressive changes in measurements and counts, except proximal increase in the calcification of the dissepiments, have not been demonstrated in other studies testing for astogenetic changes in the meshworks of *Utropora* POČTA, 1894, *Archimedes*, or *Polypora s.l.* (STRATTON & HOROWITZ, 1977b; MCKINNEY, 1980a; MCKINNEY & STEDMAN, 1981). Apparently, fenestrate nets in general constitute zones of astogenetic repetition, with differences between regions likely due to microenvironment or temporal changes in the environment.

During astogeny the microstyle-bearing, extrazooecial laminated skeleton typically was added to the exterior proximal, earlier-formed skeletal surfaces as solid skeleton (Fig. 22.5–22.6) or, in some instances, as large vesicles (Fig. 13.1, Fig. 22.1). By the progressive thickening of branches and dissepiments, by the development of vesicles, or by both processes, the surfaces of proximal portions of colonies could become occluded and smoothed over. Similar heavy calcification extended variably along margins of sheet-like zoaria and constitutes the marginal supports of *Lyropora, Lyroporella* (Fig. 7.7–7.8; Fig. 13.4), and *Archimedes* (Fig. 7.2, Fig. 13.3).

SUBSEQUENT ZONES OF ASTOGENETIC CHANGE AND REPETITION

Subsequent zones of astogenetic change due to overgrowth are virtually or completely lacking in fenestrates.

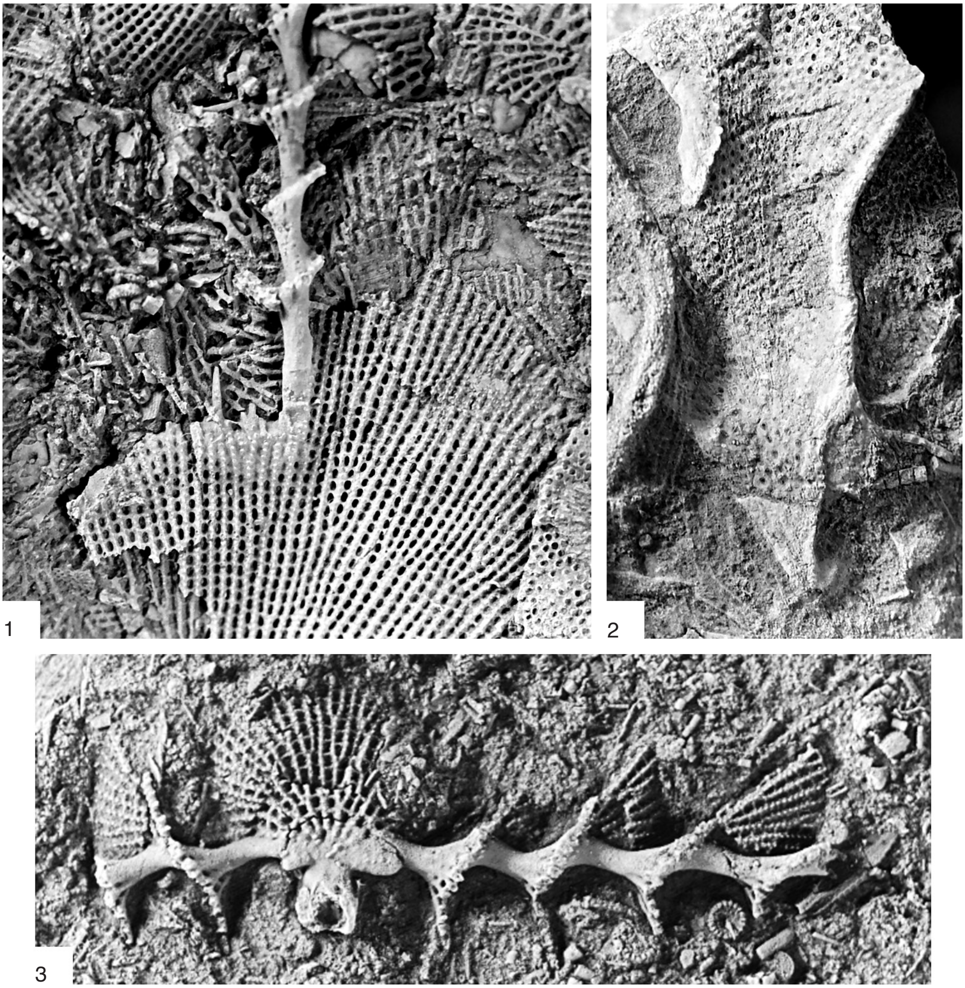

FIG. 25. Zones of astogenetic change in *Archimedes; 1,* secondary or subsequent zone of astogenetic change, where a single branch at the edge of a gently curved frond developed more rapidly than its neighbors and bifurcated frequently to establish a new helical axis from which a coiled meshwork of branches extended, *Archimedes intermedius*, Mississippian, Colbert County, Alabama, USA, USNM 356313, ×4 (adapted from McKinney, 1983b); *2,* primary zone of astogenetic change at base of colony, succeeded by the primary zone of astogenetic repetition that gave rise along both margins of the narrow fan to secondary zones of astogenetic change of slowly revolving helical axes, *Archimedes* aff. *A. moorei* CONDRA & ELIAS, 1944, Mississippian (Visean–Serpukhovian), Buncombe, Illinois, USA, USNM 356311, ×3 (adapted from McKinney, 1983b); *3,* initially broad fan-shaped colony with primary zone of astogenetic change at attachment to non-preserved cylindrical object that either gave rise directly to helical growth along both margins of the fan or, more likely, developed a short primary zone of astogenetic repetition before rotational growth began along the margins of the fan, *Archimedes intermedius*, Mississippian, Colbert County, Alabama, USA, USNM 509497, ×4 (adapted from McKinney & Burdick, 2001).

Secondary zones of astogenetic change that are followed by secondary zones of astogenetic repetition may be seen in numerous specimens of *Archimedes* in which the fronds are preserved (Fig. 25.1; CONDRA & ELIAS, 1944, pl. 5, fig. 3). In very few remarkable specimens, the primary zone of astogenetic change is associated with a small base of attachment, the primary zone of astogenetic repetition constitutes the

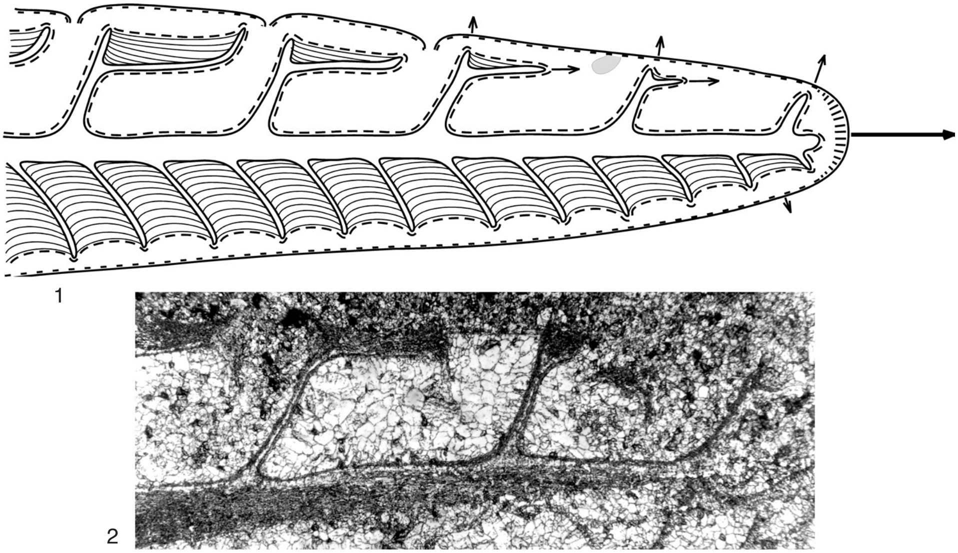

FIG. 26. Model and example of growing tips of fenestrate branches. *1,* inferred outer cuticle and epithelium distribution in a longitudinal section at the growing tip of a fenestellid branch; *arrows* indicate skeletal accumulation (*arrow length* approximates relative rate of extension, which decreases proximally from the branch tip), skeletal-secreting epithelium is indicated by *longer dashes,* and squamose epithelial cells underlying the outer cuticle by *short dashes;* palisade epithelial cells at the extending branch tip (on the *right*) constitute a zone of cell proliferation, as well as of cuticle and active cuticle extension and secretion by the palisade cells, indicated by short cuticle-perpendicular lines; *grey, oval-shaped patch* indicates polypide bud and represents local cell proliferation from the epithelium under the cuticle of the almost completely defined autozooecial chamber (second from branch tip); fully formed polypides of the more proximal autozooecia are not shown; *2,* branch tip with morphology consistent with growth model illustrated in part *1*, *Archimedes intermedius*, Bangor Limestone, Mississippian (Visean), Fox Trap, Alabama, USA, PRI 8865, ×125 (new).

fenestellid meshwork that arises from the base of attachment, the secondary zone of astogenetic change is associated with the twisting and local elongation of zooecia that initiate the helical axis of the screw (McKinney, 1980b), and the secondary zone of astogenetic repetition consists of the spiral portion, both screw and radiating meshwork, distal to the point of origin of the spiraling. Although very few bases of attachment of *Archimedes* (Fig. 25.2–25.3) are known, numerous examples are known of the origin of axes of spirals of *Archimedes* from edges of fragments of established fronds (Fig. 25.1), which are, in most instances, the margins of pre-existing spirals (McKinney, 1979, 1983b) rather than an initial fan. In these specimens, fragmentation prevents determination of the total number of zones of change and repetition.

SKELETAL GROWTH AND INFERRED TISSUE DISTRIBUTION

Above the encrusting bases, fenestrate bryozoans are interpreted to have been interior-walled forms with a continuous colony-wide envelope bounded at the seawater-colony interface by a flexible cuticle (Fig. 26.1). This interpretation is derived from analogy with the so-called double-walled growth in tubuliporates (Borg, 1926b, p. 596; Elias & Condra, 1957, p. 37–38; Boardman & Cheetham, 1969, p. 213) and is based on the inference of deposition on the outer surfaces of fenestrates (Tavener-Smith, 1968, p. 88; 1969, p. 290–291; 1971, p. 183; 1973b, p. 355; Brood, 1970, p. 189, 194, 195; Tavener-Smith & Williams, 1972, p. 151–153; Gautier, 1973, p. 271, 273).

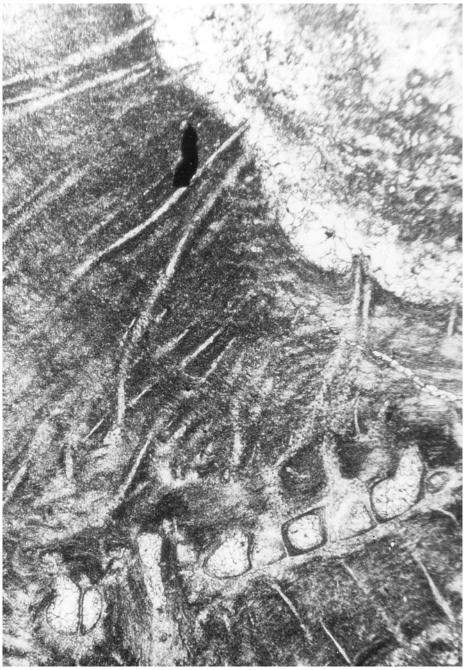

FIG. 27. Style cores projecting beyond general surface of laminar skeleton, *Archimedes lunatus* CONDRA & ELIAS, 1944, Pitkin Limestone, Mississippian (Visean–Serpukhovian), locality 1977-79, unit 5, Pitkin Quarry, Westfork, Washington County, Arkansas, USA, USNM 450589, ×50 (new).

Skeletal deposition on the outer surfaces of fenestrates is indicated by progressive thickening of branches proximally (Fig. 26.2), which in extreme development occluded and buried zooecial apertures. It is also indicated by the distal overlap of the superposed skeletal laminae and the presence of granular cores of microstyles that extend outward from other granular structures, with edges of laminae turned up around the cores.

Recognition that microstyle cores in fenestrates were originally solid structures has largely developed as the result of electron microscope studies (Fig. 10.1; TAVENER-SMITH, 1968, p. 87–88; 1969, p. 288–290; 1973b, p. 357; BROOD, 1970, p. 192; TAVENER-SMITH & WILLIAMS, 1972, p. 151–153; GAUTIER, 1973, p. 272–273; OLALOYE, 1974, p. 485), although ELIAS and CONDRA (1957, p. 20) and TERMIER and TERMIER (1970, p. 197) recognized their solid nature by light microscope observation. The various indications that microstyle cores were originally solid include (1) their protrusion beyond the general surface of the zoarium (Fig. 27), (2) the outward rather than inward deflection of laminae around them (Fig. 10.5), (3) their homogeneous granular texture rather than sparry infilling, and (4) the absence of a laminar lining as would be expected around an open chamber.

Style cores were interpreted originally as hollow tubules (e.g., VINE, 1884, p. 189; NICHOLSON in NICHOLSON & LYDEKKER, 1889, p. 608; ULRICH, 1890, p. 353; SIMPSON, 1897, p. 499; SHUL'GA-NESTERENKO, 1931, p. 50, 51, 77, 78; 1941, p. 26, 29–30; 1949, p. 33–38; RIGBY, 1957). Some later investigators still adhered to this interpretation (e.g., MOROZOVA, 1970a, p. 221; 2001, p. 11–14; DUNAEVA & MOROZOVA, 1975, p. 228; POPEKO & GORELOVA, 1975, p. 242). The interpretation of microstyle cores as algal filaments has generally been abandoned (CONDRA & ELIAS, 1944, p. 25–50; RIGBY, 1957); the bryozoan-algal consortium hypothesis is discussed below.

The secretion of the skeleton from the outer surface requires that the surface be covered by secretory epithelium (Fig. 26.1). NEKHOROSHEV (1928, p. 507) was apparently the first to imply that there must be widespread extrazooidal tissue for nourishment of nonfeeding areas of the colony that were covered by continuous skeletal deposits. The most reasonable reconstruction of enveloping soft tissues—as for virtually all other Paleozoic stenolaemates—is a colony-wide envelope of fluid and cells below an outer cuticle, corresponding to that present in modern free-walled tubuliporates (BORG, 1926b, p. 596; ELIAS & CONDRA, 1957, p. 32–33; TAVENER-SMITH, 1968, p. 88–89; 1969, p. 291–292; 1973b, p. 355; BROOD, 1970, p. 194–195; GAUTIER, 1973, p. 271–274; BOARDMAN & CHEETHAM, 1973, p. 149–150; NIELSEN & PEDERSEN, 1979; BOARDMAN, 1983). The sequence of tissues inward from the colony surface is inferred to have been cuticle, cuticle-secreting epithelium, fluid-filled space, calcite-secreting epithelium, extrazooidal calcitic skeleton, zooidal calcitic skeleton, zooidal secretory tissue (ectoderm), and other zooidal soft parts (Fig. 26.1; see Fig. 37). A suggestion (Cowen & Rider, 1972, p. 153, 158–159) that current-generating cilia seated in epithelium of the subcuticular envelope bordering fenestrules and over various other extrazooidal skeletal surfaces seems unnecessary.

Investigators agree that granular skeleton was deposited at a more reduced rate behind the growing margin, where skeleton was being thickened (Tavener-Smith, 1968, p. 87; 1969, p. 294–295; Gautier, 1973, p. 273). Brood (1970, p. 191) and Gautier (1973, p. 273) inferred secretion onto the granular layer in the direction of wall extension, based on exposure of the distal edge of the granular skeleton to the inferred colony-wide envelope and on the inference of growth lines across it based on tracing a line at high angle between successive microstyle axes (right end of Fig. 26.1–26.2). The zone of granular skeleton has been referred to as the colonial plexus (Elias & Condra, 1957, p. 25) and as the primary skeleton or shell (Tavener-Smith, 1968, p. 88; 1969, p. 291; Tavener-Smith & Williams, 1972, p. 150). Various authors (e.g., Cumings, 1904, p. 59; Elias & Condra, 1957, p. 40; Tavener-Smith, 1969, p. 291) have referred to the laminated skeleton as a secondary deposit. The various skeletal textures are referred to here by the descriptive terms granular and laminar, following the attitude of Sandberg (1977, p. 152) that ordinal naming is not applicable in all cases.

The process of secretion of calcitic skeletons in fenestrates has produced a series of ideas, the earlier of which have been well summarized by Elias and Condra (1957, p. 15–22) and by Tavener-Smith (1969, p. 282–284). Shul’ga-Nesterenko (1931, p. 50–51, 77–78; 1941, p. 26, 29–30) inferred a capillary system permeating branches of *Lyrocladia* Schul'ga-Nesterenko, 1931 and other fenestellids, consisting of canals situated within the striae (elongate ribbing) on the reverse side of the basal plate and on the lateral and frontal sides of zooecia, and capillary tubules extending from the crests of the striae toward the surface through the skeleton. The capillary system was thought to carry “skeletal substance” from zooids to branch surfaces, where it was deposited in layers (note that Shul’ga-Nesterenko recognized the existence of skeletal deposition in fenestrates on the branch surface). Later, she considered (1949, p. 33–38) that the capillary system carried nutrients to a peripheral ectodermal secretory epithelium, apparently conceived as a single layer immediately upon the skeletal surface (Tavener-Smith, 1969, p. 283).

A hypothesis of a bryozoan-algal symbiosis in the production of laminated skeleton of fenestrates was developed by Condra and Elias (1944, p. 25) and followed in some later papers (Condra & Elias, 1945a, p. 122–125; Elias, 1946, 1973; Rigby, 1957; Elias & Condra, 1957, p. 19–22, 40–45). Condra and Elias thought that the microstyle cores were unrelated to the granular skeleton sheathing zooecial cavities. They inferred that fenestrate skeletons were variably flexible during the life of the colony, becoming calcified at some distance behind the growing margin, and that algal filaments were responsible for calcification. The algal filaments were thought to be preserved as the structures now known as microstyle cores. Symbionts were thought to be brown algae in some taxa and red algae in others. In the view of Condra and Elias (1944), only the granular layer surrounding zooecial cavities was a direct bryozoan skeletal deposit; all the outer laminated skeleton was thought to have “been initiated by the bryozoan symbiont and extended to the intimately connected algal partner, while the latter precipitated little or no lime by its metabolic activity” (p. 48).

The bryozoan-algal symbiosis hypothesis was immediately criticized by Easton (1944, p. 407–408), who pointed out several inconsistencies in the concept and noted that "two or more different kinds of skeletal tissue occur commonly in many organisms" (p. 408). Haas (1945) and Shul'ga-Nesterenko (1949) also were quick to criticize the idea of bryozoan-algal symbiosis.

The granular skeleton of fenestrates (except the skeleton of microstyle cores) was termed the "colonial or germinal plexus" by Elias and Condra (1957, p. 25–40). The general continuity of the granular skeleton in fenestrates was recognized by Vine (1884, p. 190) but interpreted as an originally fluid-filled interspace. The continuity of the granular skeleton, except in some taxa such as *Adlatipora*, and its reported unit extinction in polarized light (Elias, 1956, p. 321, 323; Elias & Condra, 1957, p. 28) convinced Elias and Condra that the granular skeleton has a role of holding together the zooecia (p. 26). They concluded that there is homology between the colonial plexus of fenestrates and the common bud recognized in tubuliporates by Smitt (1865) and by Borg (1926a, p. 328). As Boardman and Cheetham (1969, p. 219) indicated, the concept of a common bud has been poorly formulated and inconsistently applied and should be replaced by standard histological terminology.

As part of their inference of homology in growth between fenestrates and tubuliporates, Elias and Condra (1957, p. 40) emphasized that adjacent zooecia in fenestrates have a "common primary wall"—that is, in the terminology used here, they apparently lacked a median cuticle and are, therefore, interior walls as is the norm for tubuliporates. Elias and Condra are also correct in envisioning the granular wall (their colonial plexus) as being secreted in a zone of active growth and extension at branch tips (Fig. 26) where partitions arose from the basal plate that subdivided the expanding subcuticular space at the growing tips into discrete zooecial chambers.

The colonial plexus relates to the inferred zone of active epithelium proliferation, cuticle intussusception, and zooid differentiation in fenestrates, the zone homologous with that in the tubuliporates that Elias and Condra (1957) and Brood (1970, p. 189) apparently interpreted as the common bud. However, the zone at the growing tips of branches is only a small part of the colony-wide subcuticular envelope, which is interpreted to have covered the entire—or at least the non-senescent portion of—fenestrate zoaria above the basal wall of the encrusting base, serving as a colonial distribution system for nutrients and skeletal-building materials.

In some earlier interpretations of skeletal development in fenestrates, the presence of a single or doubled cuticle was inferred between the laminated and granular zooecial wall (Tavener-Smith, 1968, p. 89; 1969, p. 293–294). This interior cuticle was thought to have developed as an invagination of the outer cuticular membrane and involved back-to-back zooidal and colonial epithelia. This interpretation was later (Gautier, 1973; Tavener-Smith, 1973b) discarded in favor of interpretations that involve no cuticle within the calcified skeleton. The growth model preferred here (Fig. 26.1) is similar to that of Gautier (1973), who envisions skeletal calcification extending to the distal tips of branches, with edgewise calcification of the basal plate and other granular skeletal elements at or near the distal tips of branches. This appears to have been accomplished by a single epithelial sheet that differentiated into zooidal epithelium frontally and extrazooidal epithelium on the reverse and eventually between zooidal apertures as the growing tip migrated beyond. A contrasting model (Tavener-Smith, 1973b, fig. 4) would have calcification lagging behind zooidal (and polypide) definition at the growing tip and back-to-back zooidal and extrazooidal epithelia that were eventually separated by their own lateral secretion product, the basal plate. Well-preserved tips of *Archimedes* branches (Fig. 26.2) support Gautier's model.

The interpretation of fenestrate skeletons as originally soft and flexible appears to be incorrect (Condra & Elias, 1944, p.

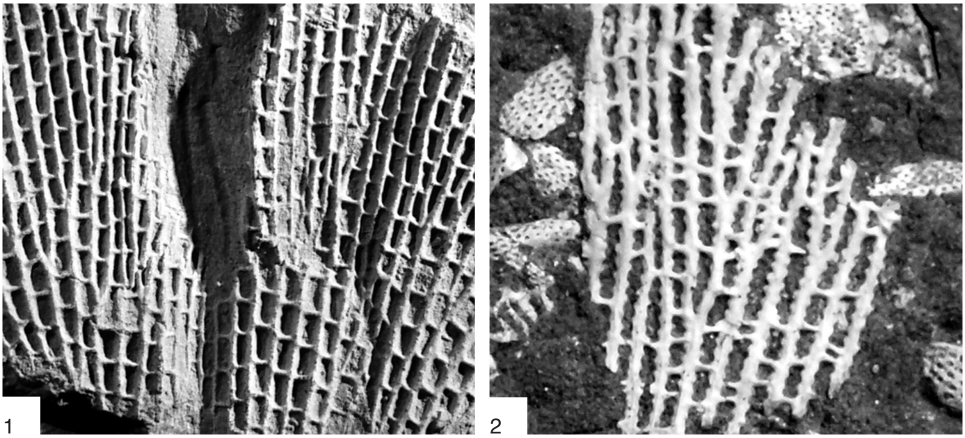

FIG. 28. Regularity of spacing between successive dissepiments; *1,* low variation in distance between successive dissepiments in *Fenestralia sanctiludovici* PROUT, 1858, St. Louis Limestone, Middle Mississippian, near Princeton, Kentucky, USA, USNM 49928, ×5 (new); *2,* unusually high variation in distance between successive dissepiments in *Esthonioporina quadrata* (BEKKER, 1921), Kukruse horizon, Middle Ordovician (Darriwilian), Kukruze, Estonia, TU 1110-5, ×5 (new, courtesy of Tartu University).

36–37; ELIAS & CONDRA, 1957, p. 32; ELIAS, 1973, p. 450). It is true that crystallites in fenestrate skeletons were almost certainly sheathed in a very thin proteinous sheet (TAVENER-SMITH, 1968, p. 89; 1969, p. 285), but that is the general case of organisms with rigid carbonate skeletons.

Dissepiments are formed by simultaneous lateral bulging of facing surfaces of two adjacent branches near the growing tip (SIMPSON, 1895, p. 690; ELIAS & CONDRA, 1957, p. 29–30; TAVENER-SMITH, 1968, p. 91; 1969, p 300–301). The granular wall extended laterally with progressive taper until two similar extensions met about midway between branches. Then the covering cuticles fused allowing tissue continuity, and the skeletal elements merged. ELIAS (1956, p. 323) recorded the granular structural core of dissepiments in *Fenestella subantiqua* as 3–6 µm thick. Laminated skeleton, locally showing twisting adjustment of the oppositely formed sides at the median contact, formed around the granular core as the dissepiment thickened and continued to be added, producing progressively thickened dissepiments. Microstyles—with cores derived from the granular core of the dissepiment—grew radially, extending slightly beyond the surface of laminated skeleton to form a pustulose surface similar to that on branches.

Varying degrees of regularity in the spacing of dissepiments were attained by different taxa. In some genera dissepiments could be closely and very regularly spaced (Fig. 28.1); in others they were widely and irregularly placed (Fig. 28.2). Whatever stimulated their formation typically affected the two adjacent branches involved at about the same position and level of development, for most are essentially perpendicular to branches and are built evenly from both sides. In forms with more widely spaced dissepiments, however, they more commonly were begun at two different positions along the branch lengths, so that they are inclined rather than perpendicular to the branches, though the two portions unerringly extended toward one another with few exceptions, indicating a very close control of the growth stimulus. An exception is illustrated in Figure 14.3.

The laminae lining the zooecial chamber presumably were deposited by zooidal epithelium. Such interior laminae are typically relatively thin to only moderately thickened and were added preferentially in certain portions of the zooecium (Fig. 10.4,6). Their

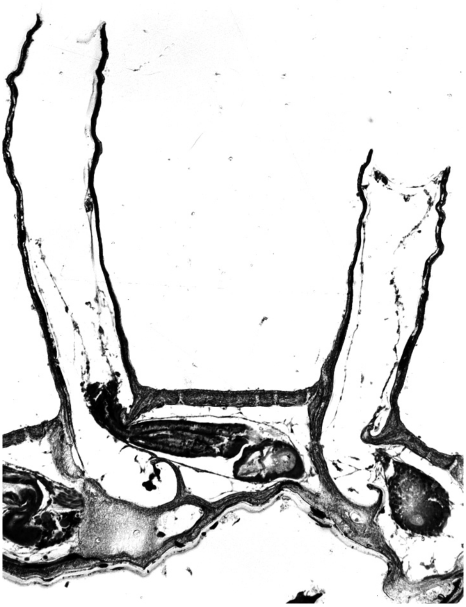

FIG.29. Thin section of the modern tubuliporate *Harmelinopora indistincta* (CANU & BASSLER, 1929), with epoxy-impregnated soft tissues; in both zooids, the membranous sac and tentacle attach high in the erect peristome, and inferior and superior hemisepta define a proximal chamber *(right)* from a smaller portion *(left)* that is continuous with the erect peristome *(above)* and is comparable to the distal tube in fenestrates; the polypide of the left zooid is almost completely retracted into the proximal chamber, and the proximal chamber of the right zooid contains either a brown body comprising the remains of the former polypide or a small, regenerating polypide replacing the former polypide, Mediterranean Sea, Port Cros, Gabinère, Hyères, France, ×80 (adapted from Boardman, 1998, fig. 5).

effect, and presumably their major function, was to modify shape of the zooecial chamber.

The distal tube has traditionally been described as a vestibule (ULRICH, 1890, p. 352, and subsequent authors) until more recent work (e.g., zooecial neck of GAUTIER, 1972; and distal tube beginning with MCKINNEY, 1977, 1978, 1980a). The term vestibule implies that it is an entrance chamber that is exterior to the so-called hidden mouth (the basis for the ordinal name Cryptostomata, in which the Fenestrata were included prior to 1957) formed by the hemiseptum along its projecting edge or by the change in diameter from distal tube to inflated endozonal portion of the chamber. Although the distal tubes of fenestrates are indeed analogous in position with vestibules of modern tubuliporates, herein we prefer to use distal tube for fenestrates, rather than a term suggesting that its function is firmly known.

Hemisepta were noted in the late 19th century (WATERS, 1878, p. 462, fig. 7; YOUNG, 1882, p. 215) as enigmatic structures within zooecia. ULRICH (1890, p. 350–351, fig. 10) very accurately described and illustrated the form and placement of superior and inferior hemisepta; he noted (ULRICH, 1890, p. 351) that their functions were unknown, “unless it acted as a support to the cell front.” A contrasting hypothesis was put forward by NEKHOROSHEV (1977, p. 4), who “assumed that to them were attached muscles which ... drew tentacles inside ....”

In representatives of the modern tubuliporate *Harmelinopora* BROOD, 1976, from the Mediterranean (Fig. 29), there are short chambers to which polypides retract, bounded distally by hemisepta to which retractor muscles attach and beyond which an elongate peristome extends. The peristome is significantly longer than the length of the refuge chamber, so the elasticity of the muscles and elasticity or pleating of the membranes must be high for the polypide to be extended to a position where its tentacles protrude beyond the aperture. Overall geometry of the chambers and peristomes of *Harmelinopora* is similar to that of the endozonal chambers and distal tubes of fenestrates, and the autozooidal soft structures of fenestrates likely functioned and perhaps were positioned similarly.

Unusual calcified structures preserved in the apertures of many specimens of *Thamniscus colei* WYSE JACKSON, 1988, appear to be paired opercular plates (Fig. 30; WYSE JACKSON, 1994). The plates hinge near the base of the distal tube, on opposite sides of the tube, and close medially along their outer edges. They are inferred to be locally calcified regions of the zooidal terminal membrane that opened when the zooidal

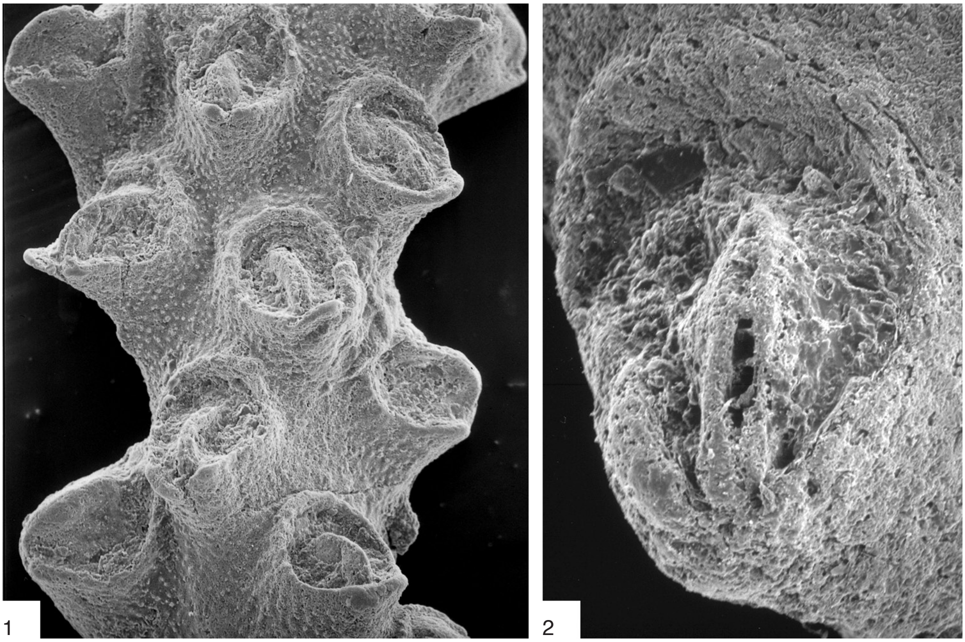

FIG. 30. Possible operculae made up of two plates, which touch opposite sides of the distal tube wall at their lower edges but converge outwardly to meet along a common edge that projects approximately to the preserved zooecial aperture, *Thamniscus colei* WYSE JACKSON, 1988, shales above Main Limestone, Pennsylvanian (Bashkirian), Hurst, North Yorkshire, England, TCD.37224; *1,* section of branch with the possible operculae visible in almost all zooecial apertures, ×80; *2,* aperture of single zooecium with line of contact of the paired plates clearly visible, ×300 (new).

polypide was extended to the feeding position and were closed when the polypide was retracted into the zooecial chamber (Fig. 31). Opercula, some of which are calcified, are characteristic of cheilostome bryozoans and are present on heterozooids in a few distantly related living and fossil tubuliporates (ROBERTSON, 1910; TAYLOR, 1985).

Stellate apertures have been widely reported in many fenestrate taxa (e.g., YOUNG & YOUNG, 1874a; WATERS, 1878; SHRUBSOLE, 1879; YOUNG, 1880, 1882; ULRICH, 1888, 1890, p. 315, fig. 5a; MCNAIR, 1938; NIKIFOROVA, 1938; CROCKFORD, 1949; SHUL'GA-NESTERENKO, 1951; ELIAS, 1956; CAMPBELL, 1961; TAVENER-SMITH, 1971; FLEMING, 1972; ENGEL, 1975, 1979; STRATTON & HOROWITZ, 1977a; ERNST & KÖNIGSHOF, 2010; ERNST, 2012). Such apertures have variably developed scallops around the margin, with the septa between adjacent scallops pointed toward the midpoint of the aperture (Fig. 32). Development of the scallops and intervening septa varies from minimal to septa extending up to one-third the diameter of the aperture, at which stage they typically coalesce along their inner margins, leaving an axial opening one-third the original diameter of the aperture (Fig. 32.4). Septa extend only partially down the distal tube from the aperture.

Typically, eight septa ring an aperture, this number having been observed in *Actinostoma* YOUNG & YOUNG, 1874a, *Archimedes; Cavernella* MOROZOVA, 1974; *Laxifenestella* MOROZOVA, 1974*; Minilya* CROCKFORD, 1944; *Rectifenestella* MOROZOVA, 1974; *Spinofenestella* TERMIER & TERMIER, 1971; *Polypora; Penniretepora;* and *Septatopora* ENGEL, 1975. Less frequently, seven indentations have been noted, in a fenestellid (SHUL'GA-NESTERENKO, 1951, p. 70), *Semicoscinium,* and a polyporid (MCNAIR,

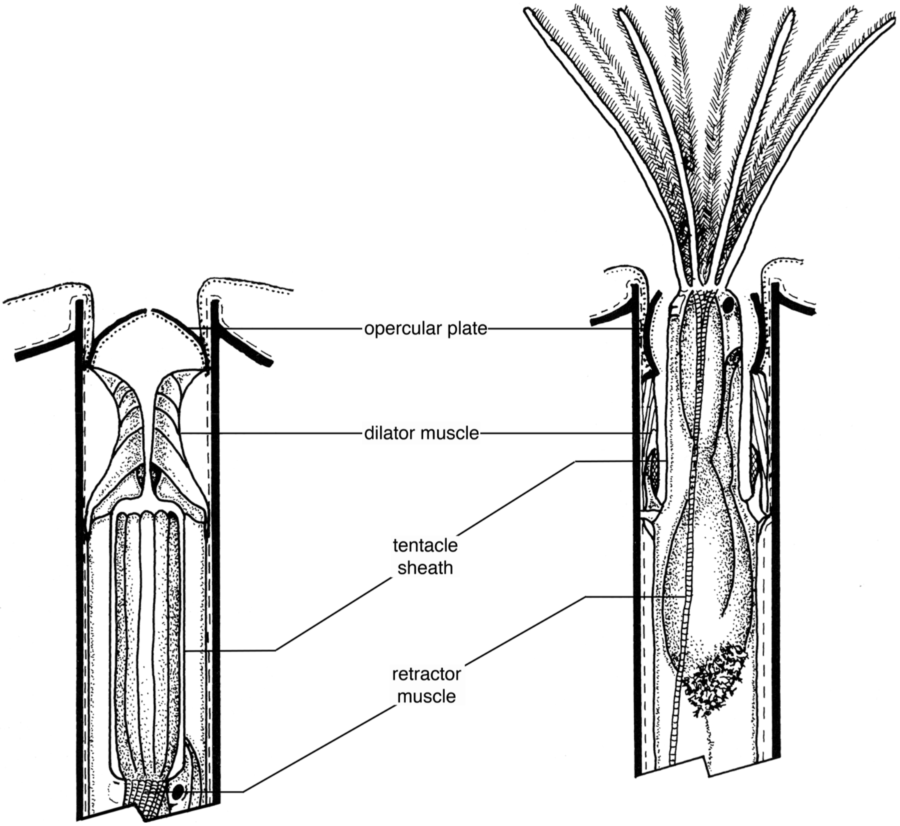

FIG. 31. Position of paired, apparent opercular plates in *Thamniscus colei* relative to probable distribution of zooecial soft tissues in the *(left)* closed and *(right)* open position (adapted from Wyse Jackson, 1994).

1938). MCNAIR (1938) also noted that some specimens of the latter two genera may have only six septa in apertures, and ENGEL (1979, p. 138) recorded up to 16 septa in Australian Carboniferous polyporids.

Presence of septa in apertures apparently represents an ontogenetic stage at which partial aperture closure occurred while polypides still functioned. Some investigators (e.g., YOUNG & YOUNG, 1874a; ENGEL, 1975, 1979) have considered the presence of the septa to have taxonomic significance, but this has been challanged (first by SHRUBSOLE, 1879, p. 277) and is not well established. General taxonomic usefulness of septate apertures is improbable, given their widespread but spotty occurrence in diverse genera.

Scalloped apertural calcification may relate to position of extended tentacles (TAVENER-SMITH, 1971, p. 182; ENGEL, 1975, p. 574–576). This seems reasonable, inasmuch as fenestrates are related to living tubuliporates, in which eight is a common number of tentacles (WINSTON, 1977; 1978, p. 9; 1979, p. 260) and in which tentacles barely clear the apertures (NIELSEN, 1970, fig. 2, 37; SILÉN & HARMELIN, 1974, fig. 1; COOK, 1977, p. 33; WINSTON, 1978, p. 4–5; 1979, p. 260; MCKINNEY, 1988). The nearest-neighbor spacing of zooecial apertures in fenestrates most commonly is 200–300 µm, which is typical nearest neighbor spacing for eight-tentacled lophophores of living tubuliporates (MCKINNEY & JACKSON, 1989, p. 127, fig. 6.5). If the

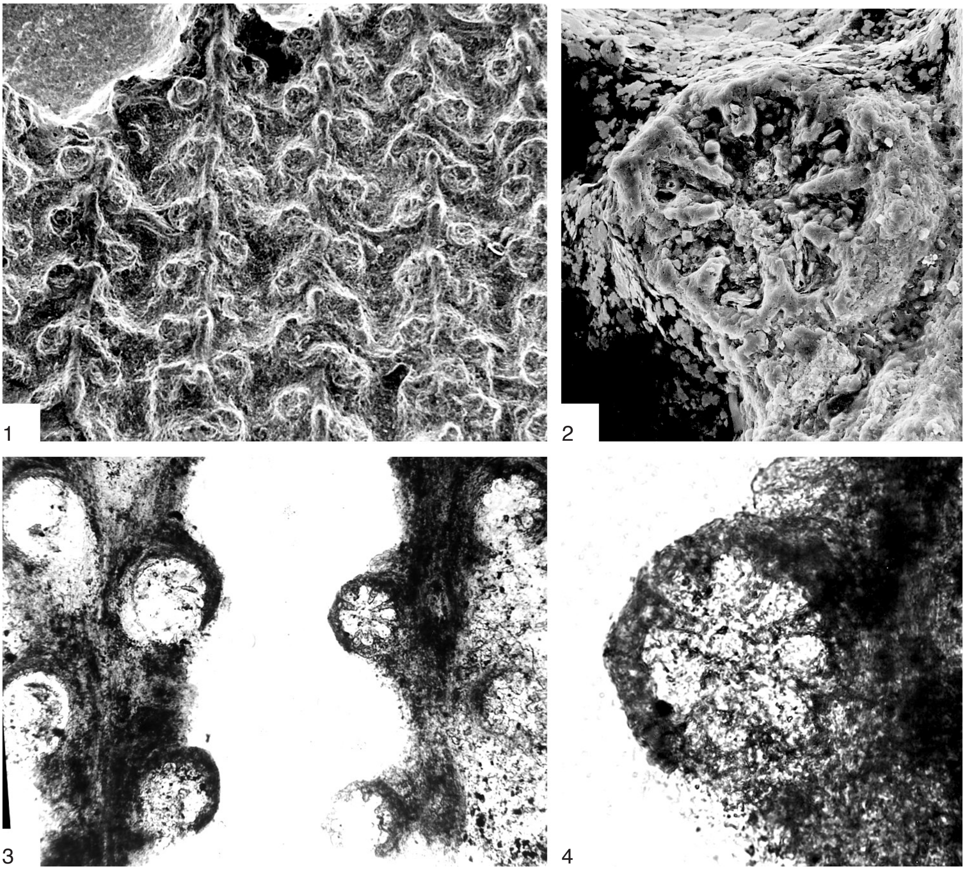

FIG. 32. Stellate apertures in *Actinostoma fenestratum* YOUNG & YOUNG, 1874a, Upper Limestone Series, Pennsylvanian, Boghead near Hamilton, Lanarkshire, Scotland (new); *1–2,* HMAG 01-53aao; *1,* obverse surface of specimen with zooecium having a variably well preserved stellate aperture, ×60; *2,* a single, well-preserved stellate aperture, ×400; *3–4,* HMAG 01-53aap; *3,* acetate peel passing at and barely below level of stellate apertures in right branch but slightly deeper through distal tubes in left branch, below the shallow septa that cause the stellate appearance of apertures, ×125; *4,* single stellate aperture with inner ends of septa joined at a central apertural ring, ×400.

peripheral slots in fenestrate stellate apertures were for tentacle exsertion, the central opening apparently was centered over the mouth.

Where apertural stylets projected as spines above the aperture (Fig. 6.5), tentacles would necessarily have been confined to the spaces between the spines, if the base of the lophophore was at or below the aperture as is typical for living stenolaemates. Twenty of 34 fenestellid and polyporid species in a Mississippian fauna are found by SNYDER (1991a) to have apertural stylets, with species averages from 2 to 30 stylets per aperture. Although the number of apertural stylets in some species may equal the number of tentacles in individual lophophores, it seems unlikely that there is a universal correspondence, given that living stenolaemate species have a range only of 8 and 16 tentacles (MCKINNEY & JACKSON, 1989). This includes *Cinctipora elegans* HUTTON, 1873, which has relatively huge zooids (BOARDMAN, MCKINNEY, & TAYLOR, 1992). The extremely low and high values in number of stylets per aperture found by SNYDER (1991a) probably do not correspond directly with number of tentacles.

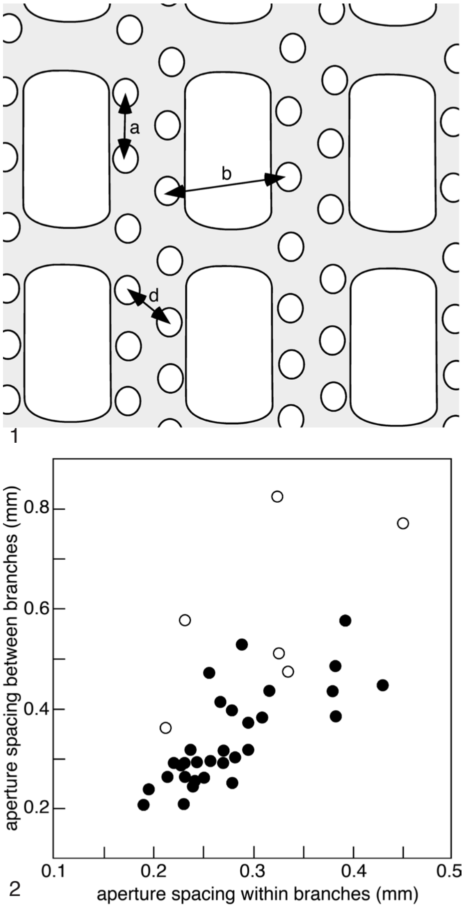

FIG. 33. Average spacing between centers of zooecial apertures within branches and between branches in 37 species of Middle Mississippian fenestrate bryozoan fauna (Snyder, 1991a). *1,* diagram showing entities measured between branches *(b)* and combined measurements within branches made along *(a)* and diagonal *(d)* to axis of growth; *2,* plot of results for 31 biserial species and 6 multiserial species (new).

The distance between apertures along and across branches probably correlated with the diameter of lophophores, as is the case in living bryozoans (Winston, 1977; McKinney & Jackson, 1989). Apertures are very regularly spaced in fenestrate branches, especially in biserial taxa. The distance between apertures across fenestrules of biserial taxa is also relatively uniform and usually not much more than the spacing of apertures within a branch (Fig. 32.1,3; Fig. 33). This suggests that lophophores were circular in plan and slightly overlapped (Snyder, 1991a). However, Starcher and McGhee (2000), from a measure of branch morphologies and aperture spacing in some fenestellids and polyporids, suggested that lophophore shape may be controlled by the number or rows of autozooecia developed. They noted that in biserial colonies (those with two rows of autozooecia on branches), lophophores were equitentactular with a circular plan, whereas in polyporid multiserial colonies, hetermorphic lophophores developed. In these multiserial varieties, symmetrical lophophores were positioned on central rows, with asymmetrical lophophores positioned on laterally rows. Asymmetrical lophophores developed shorter tentacles inwards of branches with longer tentacles outwards towards fenestrules. Apertural spacing, as well as autozooecial diameter, can be used as proxy measures for lophophore diameter. In the Warsaw fenestrates of North America, apertural spacing varies between approximately 0.2 mm to 0.8 mm, and this variation may reflect the exploitation of

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FIG. 34. (*Continued from facing page.*)
Mountain Formation, Permian (Kungurian), Glass Mountains, Texas, USA; *1,* growing tip of branch with fossulate apertures, KU 54578, ×25; *2,* region near growing tip of branch where partial skeletal closure of the fossula at the aperture end has nearly isolated a proximal pore, with isolation complete in the lower left zooecium, KU 54602, ×100; *3, Adlatipora* sp., Poplar Tank Member, Skinner Ranch Formation, Permian (Sakmarian–Kungurian), Glass Mountains, Texas, USA, USNM 543121, silica molds of zooecial chambers where skeleton has been etched away, showing distal tubes with narrower proximal tube differentiated at the base of the distal tube, leading to the pore proximal to the aperture, ×45 (adapted from Gautier, Wyse Jackson, & McKinney, 2013).

different trophic levels (Snyder, 1991a, p. 166–167).

A pore, roughly one-third the diameter of the aperture, occurs consistently in some taxa (*Diploporaria* Nickles & Bassler, 1900, and *Adlatipora*) and in association with apertural septa in others (some fenestellids, *Polypora s.l., Dissotrypa* Ernst & Königshof, 2010, *Septatopora,* and *Penniretepora*) (Young & Young, 1874a, 1875; Young, 1880; Ulrich, 1890, p. 351; Fleming, 1972; Tavener-Smith 1971; Engel, 1975; Ernst, 2012). The pore extends through the obverse laminated wall to communicate with the endozonal zooecial chamber, approximately at the base of the distal tube (Fig. 34.3; Engel, 1975, p. 572; Gautier, Wyse Jackson, & McKinney, 2013, fig. 6.3–6.8). In *Anastomopora clara* Ernst & Königshof, 2010, several such pores are associated with each autozooecial chamber (Ernst & Königshof, 2010, p. 27, pl. 24–25). In *Adlatipora* the pore is a remnant of a proximal fossula of the zooecial aperture in which the fossula has been partially filled with laminated skeleton (Fig. 34.1–34.2; Gautier, Wyse Jackson, & McKinney, 2013) and has laminae that lap into it, suggesting that the external cuticle folded down into the pore. A gradient from pear- or keyhole-shaped apertures to isolated proximal pores, as in *Fenestella s.l. polynodosa* Miller, 1961a (Miller, 1961a, text-fig. 1b) and *Diploporaria* (Young & Young, 1875), suggested that these taxa may have had zooidal ontogenies similar to that of *Adlatipora*. In *Polypora s.l. stenostoma* Tavener-Smith , 1971, a proximal pore is an intermediate stage between an apertural fossula and a continuously calcified obverse wall (Fig. 35; Tavener-Smith, 1971, p. 181–182).

Aside from the unlikely suggestions that proximal pores result from taphonomy (Ulrich, 1890, p. 351–352) or served avicularia (Young & Young, 1874a, p. 683), there are at least three possible interpretations of their function: (1) hydropores, (2) oviducts, or (3) anal pores that served for hydrostatic compensation during tentacle protrusion. They may have served a combination of

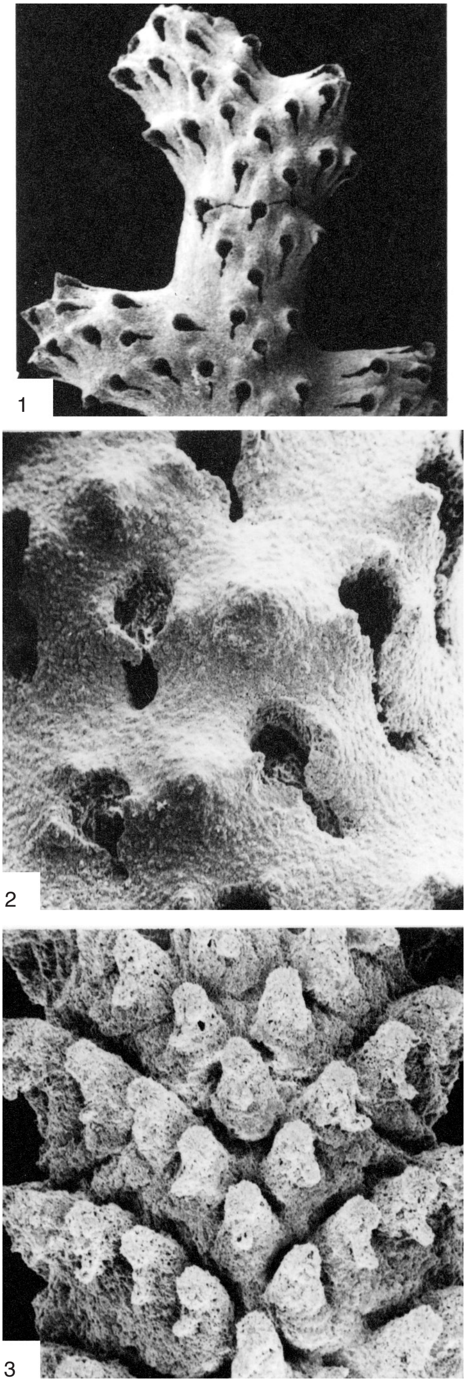

Fig. 34. Aperture-proximal pore development from keyhole-shaped apertures in *Adlatipora*; *1–2, A. fossulata* Gautier, Wyse Jackson, & McKinney, 2013, Cathedral (*Continued on facing page.*)

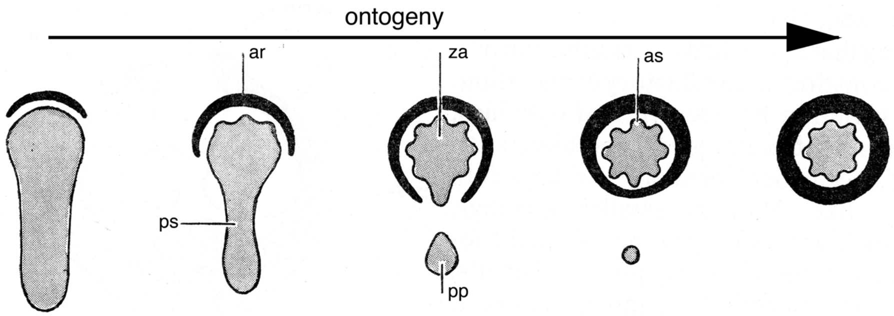

FIG. 35. Ontogenetic changes in apertures of *Polypora s.l. stenostoma,* from an elongate keyhole-shaped frontal opening with incipient distal apertural rim *(left)* to reduction in width of proximal slit and incipient apertural scallops; complete constriction of part of the proximal slit so that a proximal pore is isolated from the aperture; completion of the apertural rim around an aperture with eight, equal apertural scallops and reduction in size of the proximal pore; and, finally, to complete closure of the proximal pore. *ar,* apertural rim; *as,* apertural scallop; *pp,* proximal pore; *ps,* proximal slit; *za,* zooecial aperture (adapted from Tavener-Smith, 1971).

these and other functions. Regardless of the function of proximal pores, the penetration of the frontal wall of the zooid by a single large pore is a significant departure from zooecial morphology—and presumably zooidal organization—of other stenolaemates.

Entrance to a hydrostatic compensation sac as a function for the proximal pores has been dismissed as unlikely by TAVENER-SMITH (1971, p. 186), and ENGEL (1975, p. 575–576). GAUTIER (1972, p. 102–104, fig. 31A) noted that an awkward sharp bend in a compensation sac would be required at the base of the fossula or proximal pore if that were its function. TAVENER-SMITH (1971, p. 184–186) considered the pore in *Polypora s.l. stenostoma* to represent a penultimate ontogenetic stage in calcification of the earlier hydrostatically functional, depressible frontal wall. However, he considered that hydrostatic function had ceased by the stage at which the pore was established and suggested no alternative function. CROCKFORD (1949), FLEMING (1972, p. 6–7), and ENGEL (1975, p. 575–576) noted that the proximal pores in two Australian polyporids open at broad, shallow depressions on the obverse surface. ENGEL (1975), therefore, suggested that the depressions may be the bases of brood chambers and that the pores functioned in part for passage of fertilized eggs to the chambers (see discussion below of heterozooecia and gynozooecia).

A final suggestion, both consistent with skeletal morphology and biological function, is that a pore completely separated from and proximal to the zooecial aperture functioned as a passageway for fecal products (ENGEL 1975, p. 575–576; GAUTIER, 1972, p. 100–102, fig. 31B). GAUTIER, WYSE JACKSON, and MCKINNEY (2013, p. 453) noted that the association of a proximal pore with apertures divided by septa constitutes the most compelling basis for interpreting the proximal pores as anal pores. Apparently, the only way a zooid could function, in those instances in which eight septa extend to a ring around a central apertural opening, would have been for tentacles to protrude through the eight peripheral openings, the mouth to be situated below the central opening, and the anus to empty below the aperture. This proposal also accomodates the pear-shaped apertures from which the proximal lobe may eventually become separated by development of a transverse partition. Fecal products could then have travelled through the proximal pore to the exterior of the colony, if the outer cuticle folded in to line the pore. GAUTIER, WYSE JACKSON, and MCKINNEY (2013, p. 453; see also GAUTIER 1972, p. 100–102, fig. 31B) proposed a model in which the anus opened through the fossula or proximal pore and was not located on the tentacle sheath as in other bryozoans. If this model is correct, then the fenestrates as a whole had the plasticity to develop the unique zooidal soft-part arrangment several times, for it appears independently in fenestellids, polyporids, pennireteporids, and acanthocladiids. Although possibly correct, Gautier's model does not seem to be universally necessary, in that some living bryozoans defecate below the zooid's aperture and push the fecal pellet out through the aperture and into the ambient water as the lophophore is protruded (M. J. McKinney, 1997).

Exozonal tubes, which have a small circular to oval openings and parallel sides, are scattered randomly on obverse and reverse surfaces, and are known in several species of the phylloporinid *Enallopora* d'Orbigny, 1850 (Ernst & Carrera, 2012). Their function remains unknown.

Red-brown granules (Fig. 36) that presumably represent organic remains of zooids are not common in fenestrates. Their occurrence requires protection from complete oxidation, and this occurs most commonly where apertures have been sealed by massive extrazooecial skeletal deposits such as in spiral axes and lyre-shaped supports. Less commonly red-brown granules may be found where complete, thin terminal closures or large external skeletal cysts protected zooidal soft parts from decay. Where they occur, the red-brown granules typically are concentrated into spherical to ovoid masses roughly 50 µm in diameter. They occur in living chambers (Fig. 36.1–36.2) or in distal tubes (Fig. 36.3–36.5). The round to ovoid red-brown masses probably represent remains of brown bodies. Less frequently lines of red-brown granules may be seen in sections and appear to reflect zooidal membranes such as the membranous sac (Fig. 36.6).

No more than one set of red-brown granules has been seen per zooecium. If successive generations of zooids occupied each zooecium, then the resultant successive generations of brown bodies were removed from the zooecial cavities rather than accumulating, as is the case in some cheilostomes (e.g., Palumbi & Jackson, 1983; McKinney & Jaklin, 1993). Fenestrates and cheilostomes have shortened zooecia, in contrast to trepostomes and tubuliporates in which brown bodies can accumulate as a series in zooecia proximal to the diaphragm-floored, outermost space available to be occupied by a polypide (Boardman, 1998, p. 3, fig. 2–3).

Figure 37 is a hypothetical reconstruction of fenestrate zooids. The reconstruction assumes close phylogenetic relationship of fenestrates and tubuliporates and, therefore, similar tissue organization is inferred—that is, the presence of an external, colony-wide subcuticular envelope linking zooids and covering extrazooecial regions. The reconstruction is based in large part on information presented by Borg (1926a), Nielsen (1970, fig. 13), and Nielsen & Pedersen (1979) for tubuliporate zooids, as well as on thin sections through hard and soft structures of *Harmelinopora*, a modern tubuliporate with zooid shape and structures very much like that of typical fenestrates (Fig. 29; Harmelin, 1976, pl. 16; Boardman, 1998, fig. 3). The model differs from that of Tavener-Smith (1971, p. 185, text-fig. 5b–d) in that the vestibule-widening muscles are restricted to the distal tube rather than inserting on the proximal wall of the endozonal chamber.

HETEROZOOECIA

Most fenestrate bryozoan colony fragments have only one kind of zooecia, the autozooecia, preserved in the branches. In fenestrates in which only one type of zooecium occurs, the zooecia are considered to be autozooecia, meaning that they feed and apparently carry on other necessary life functions of the colony. Although more than one kind of zooecium is not typical for fenestrates, they do occur in a number of species. Where more than one type of zooecium occur in a species, those similar to zooecia in monomorphic fenestrates are considered to be autozooecia and the other zooecial type(s) to be heterozooecia.

Heterozooecia are highly diverse considering their relatively limited distribution across

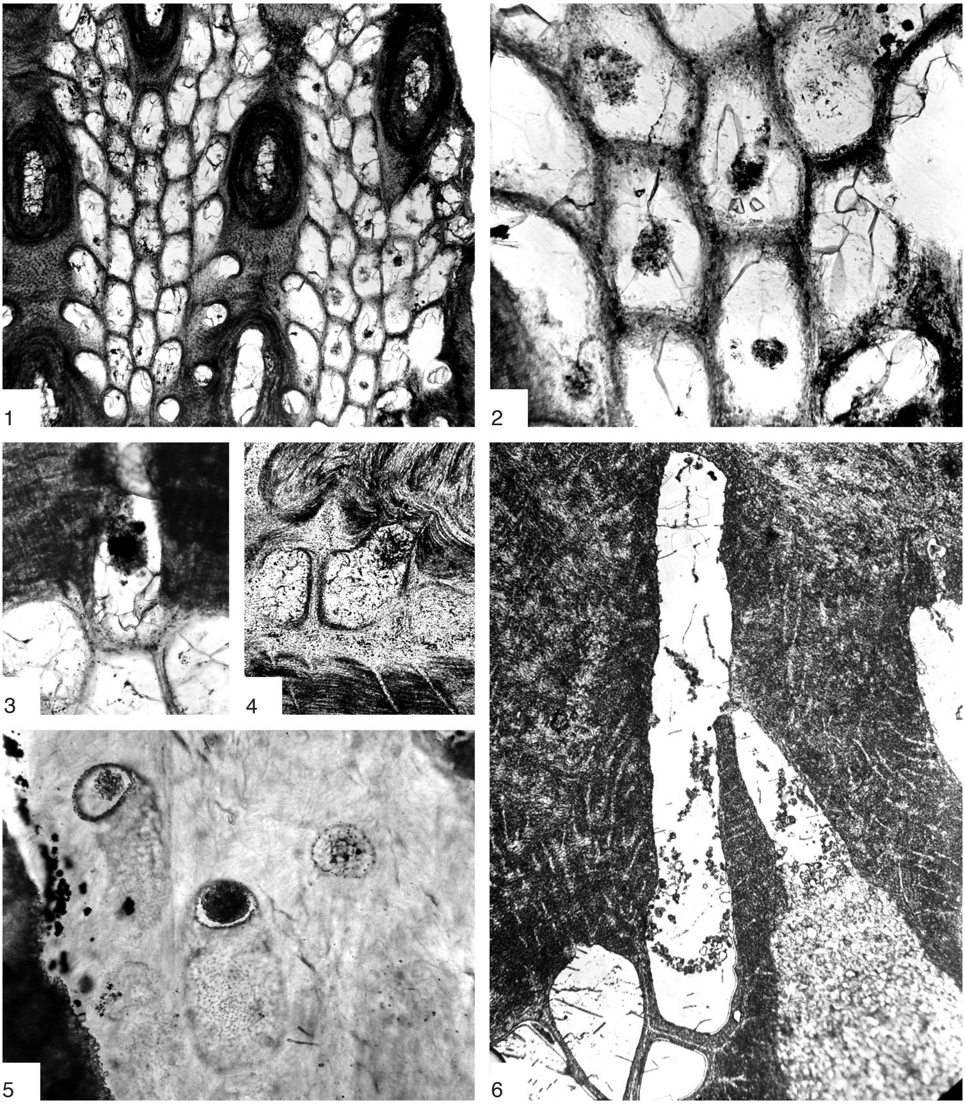

FIG. 36. Mineralized inferred soft tissue remains in zooecia of fenestrate bryozoans; *1–3,* spherical to oval clusters of reddish brown granules inferred to represent brown bodies in endozonal chambers in a tangential section *(1–2)* and in a distal tube in a tangential section *(3)* in *Lyropora subquadrans*, Mississippian (Visean), Chester, Illinois, USA, AMNH 30077-1; *1,* ×30; *2–3,* ×100; *4,* inferred remnant of brown body in distal tube cut in a longitudinal section, *Archimedes* sp., Bangor Limestone, Mississippian (Visean), Fox Trap, Alabama, USA, USNM 182789, ×100; *5,* well-defined inferred remnants of brown bodies in distal tubes in a silicified section of a thick section with zooecial chambers visible as ghosts, *Lyroporella quincuncialis*, Paragon Formation, Mississippian (Visean–Serpukhovian), near London, Kentucky, USA, USNM 528958, ×100; *6,* inferred remnants of membranous sac and other zooidal membranes in a transverse section, *L. subquadrans*, Glen Dean Limestone, Mississippian (Serpukhovian), Leitchfield, Kentucky, USA, FMNH PE54109, ×100 (new).

fenestrates. Functions of heterozooecia in fenestrates are problematic. However, one widespread class of heterozooecia in the normal zooecial position but with an unusually inflated endozonal chamber, or less commonly with some indication of an expanded exozonal region, is interpreted as a brood chamber–bearing gynozooecia. The following descriptions

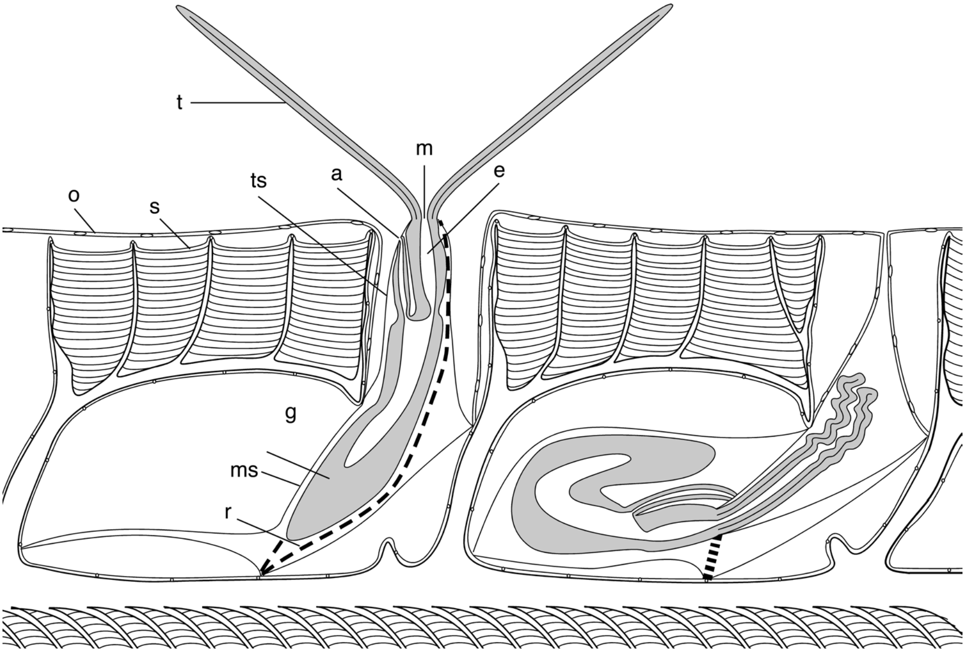

FIG. 37. Hypothetical distribution of soft tissues in two fenestrate autozooids, the one on the right extended to the feeding position and the one on the left retracted into the endozonal chamber; *a,* anus; *e,* esophagus; *g,* gut; *m,* mouth; *ms,* membranous sac; *o,* outer cuticle and epithelium; *r,* retractor muscle; *s,* skeletal-secreting epithelium; *t,* tentacle; *ts,* tentacle sheath (new).

begin with the types of apparent gynozooecia and then cover the diverse enigmatic heterozooecia.

GYNOZOOECIA

The gynozooids are heterozooids specialized for egg and subsequent larval production. Many tubuliporate gynozooids produce enlarged chambers (gynozooecia) in which embryos are brooded before being released as non-feeding larvae. The brood chambers form near the distal end of the tubular gynozooid and range in shape from simple spherical to pear-shaped expansions that do not physically overlap onto adjacent zooids, and also to enormous chambers through which peristomes of neighboring zooids extend or that ramify between fasciculate rows of zooidal apertures. A large diversity of tubuliporate brood chamber morphologies is illustrated in BORG (1926a), HARMELIN (1976), and HAYWARD & RYLAND (1985).

Descriptions and illustrations of inflated structures interpreted as brood chambers are common in the literature on fenestrates. Most commonly, such structures in fenestrates have been referred to as ovicells, but they are not homologous with ovicells in cheilostome bryozoans. We use the term brood chambers because of their apparent homology with similar structures of that name in post-Paleozoic tubuliporate stenolaemates. Early illustrations and brief descriptions of brood chambers were given by M'COY (1844, p. 201), ETHERIDGE (1873, p. 101), VINE (1884, p. 191), HALL & SIMPSON (1887, p. 105, pl. 45, fig. 23; pl. 47, fig. 24), ULRICH (1886b, p. 7; 1890, p. 557), MCNAIR (1937), NIKIFOROVA (1938, p. 245, 248, 251), and by many others from the 1950s onwards.

The first detailed interpretation (TAVENER-SMITH, 1966a) of inflated structures in

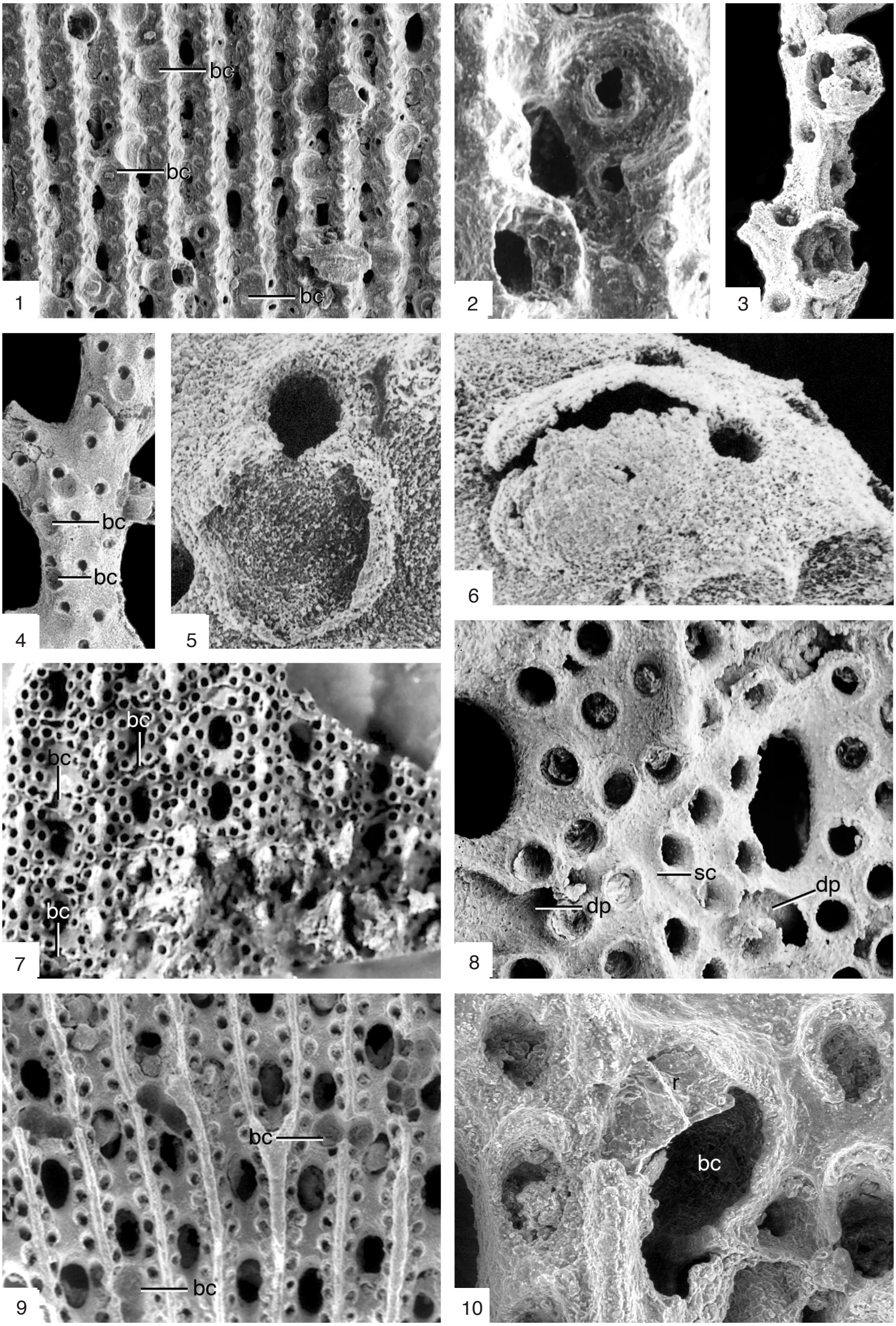

FIG. 38. *For explanation, see facing page.*

fenestrates as brood chambers was based on two species of *Fenestella s.l.* and one of *Hemitrypa*. Twenty years later, Bancroft (1986a) reviewed much of the recent literature and categorized brood chambers into a series of four types.

Type A brood chambers

Type A brood chambers consist of a large, globular chamber that communicates with the endozonal chamber of the gynozooecium through the distal tube (Fig. 38.1–3). The brood chamber surface was originally completely calcified except for the short tubular communication with the endozonal chamber of the gynozooid and an ooeciopore located above the general branch surface. Most commonly, the chamber has been taphonomically deroofed such that the ooeciopore is not preserved and the concave basal surface of the chamber, indenting the obverse surface of the branch, is the only portion preserved. Type A brood chambers can be roughly centered over the distal tube of the gynozooecium of which it is a part, or they may be somewhat offset toward the branch margin. Some are small enough not to interfere with structure of adjacent zooids. In some instances, however, especially those roughly centered over distal tubes, they may be large enough to distort or occlude neighboring autozooecia and to extend beyond both margins of biserial branches. Type A brood chambers were noted in *Fenestella s.l., Hemitrypa*, and *Penniretepora* by Bancroft (1986a), and they have been illustrated more recently for *Laxifenestella*? and *Fabifenestella*? (Ernst & Winkler Prins, 2008). In fragments of fertile colonies with Type A brood chambers, gynozooecia may make up at least 5% of the total zooecia, apparently without an ordered distribution (Fig. 38.1).

Type B brood chambers

A second set of structures inferred to represent brood chambers consist of smoothly concave depressions approximately 100–200 µm in diameter on the frontal surface of branches, each immediately proximal to the aperture of an apparent gynozooecium. The apertures of the zooecium are complete, without a proximal breach in the peristome or upper distal tube. There is no evidence of an original calcified roof extending over the depressions, although the colony-wide outer cuticle likely ballooned over them.

Type B brood chambers were noted by Bancroft (1986a) only for species assigned to *Septatopora*, in which each zooecium has a small auxiliary tube that extends from near

Fig. 38. Heterozooecia of fenestrates (part 1); *1–3,* type A brood chambers; *1–2, Fenestella s.l.*, Upper Helderberg Group, Jeffersonville, Indiana, USA, FMNH PE 78525-A; *1,* abundant de-roofed brood chambers represented as circular concave depressions *(bc),* ×20 (new); *2,* concave lower surfaces of two former brood chambers centered over distal tubes of gynozooecia, ×80 (new); *3,* substantial parts of brood chamber roofs preserved in *Laxifenestella*? *filistriata* (Ulrich, 1890), Las Llacerias Formation, Pennsylvanian (Moscovian–Kasimovian), Sotres, Asturias, Spain, RGM211 524a, ×30 (adapted from Ernst & Winkler Prins, 2008); *4–6,* type C chambers in acanthocladiids; *4,* several brood chambers *(bc)* in a branch of *Thamniscus octonarus* Ulrich, 1890, Las Llacerias Formation, Pennsylvanian (Moscovian–Kasimovian), Sotres, Asturias, Spain, RGM211 529c, ×20 (adapted from Ernst & Winkler Prins, 2008); *5,* a shallow chamber with broken roof contiguous with proximal notch in edge of aperture in unidentified acanthocladiid, Cathedral Mountain Formation, Permian (Kungurian), Glass Mountains, Texas, USNM 528972, ×140 (adapted from Gautier, Wyse Jackson, & McKinney, 2013); *6,* chamber contiguous with proximal rim of zooecial aperture, almost completely obscuring proximal fossula in aperture (medial break in roof post-mortem) in *Adlatipora fossulata* Gautier, Wyse Jackson, & McKinney, 2013, Cathedral Mountain Formation, Permian (Kungurian), Glass Mountains, Texas, USA, KU 54594, ×100 (adapted from Gautier, Wyse Jackson, & McKinney, 2013); *7–8,* type D brood chambers in *Polypora shumardi* Prout, 1858, Hamilton beds, Eifelian, Devonian, Falls of the Ohio, Indiana, USA, FMNH (UC) 57424; *7,* partially de-roofed portions of brood chambers *(bc)* visible on almost all dissepiments and extending as sinuous canals between zooecial apertures, ×10 (new); *8,* de-roofed sinuous canals *(sc)* leading to points at which the canals led to broader, dissepimental portions *(dp)* of brood chambers, ×40 (new); *9–10,* type E brood chambers in *Semicoscinium* sp., Jeffersonville Limestone, Devonian (Eifelian), Falls of the Ohio, Indiana, USA, USNM 535120; *9,* abundant de-roofed brood chambers *(bc)* represented as deeply concave depressions (adapted from McKinney, 2008); *10,* gynozooecium *(bc)* with roof *(r)* of chamber partially preserved, ×75 (new).

the base of the distal tube to the skeletal surface proximal to the aperture. Where apertures have associated proximal concave depressions, the outer end of the auxiliary tube terminates within the depression. The presence of the auxiliary tube in all zooecia suggests that it probably had some other primary function, but where it terminates into a concave depression it may also have served as a passageway for migration of fertilized eggs (Engel, 1975; Bancroft, 1986a). Several other authors have described very similar aperture-proximal depressions in other fenestrates, but apparently without an auxiliary tube present. Given that the auxiliary tube is ubiquitous for all zooecia in *Septatopora*, not just gynozooecia, the presence of an auxiliary tube does not seem necessary for recognition of Type B brood chambers.

Brood chambers that appear intermediate between Type A and Type B occur in *Laxifenestella fluctuata* Snyder, 1991 (Snyder, 1991a, p. 11, fig. 2, 4). Some zooecial apertures, along with a small area on the proximal side of each, are surrounded by a low, circular to slightly oval ridge. The enclosed area proximal to the aperture is concave, sloping down to a slight lip that defines the proximal edge of the aperture.

Type C brood chambers

As in Type B inferred brood chambers, this third type consists of smoothly concave depressions, approximately 150–200 µm in diameter, on the frontal surface of branches, each immediately proximal to the aperture of an apparent gynozooecium. In contrast with Type B brood chambers, associated zooecial apertures are incomplete, having a proximal breach in the upper part of the distal tube that continues down to the lower proximal edge of the peristome, and some preserve portions of a domal, thin, calcified roof (Fig. 38.4–38.6; Southwood, 1990). Type C brood chambers have been reported in *Acanthocladia*, *Adlatipora*, *Synocladia* King, 1849, and *Thamniscus* King, 1849 (Southwood, 1985; Bancroft, 1986a; Gautier, Wyse Jackson, & McKinney, 2013) and in *Penniretepora* (Southwood, 1990). In fragments of fertile colonies with Type C brood chambers, gynozooecia may compose almost 10% of the total zooecia, apparently without an ordered distribution (Fig. 38.4).

Type D brood chambers

Canal-like structures that are covered by a thinly calcified roof and occur in some polyporids also were interpreted as brood chambers (Fig. 38.7–38.8; Stratton, 1981; Bancroft, 1986a). The chambers meander between autozooecial apertures on the obverse surface of branches and extend across the obverse surface of dissepiments, where chamber width commonly increases substantially. The chambers commonly appear to terminate laterally against branch crests (Stratton, 1981), but they also commonly continue across the crests of low branches and constitute networks of unknown extent. Stratton (1981) reported that there are occasional zooecia entirely within a canal that have peristomes shorter than those that bound the canals, and he interpreted these as gynozooecia. Thus far, Type D brood chambers are known only in the Middle Devonian *Polypora (s.l.) shumardii*. Type D brood chambers can extend across almost all dissepiments and follow extended serpentine paths between autozooecial apertures over large areas of zoaria (Fig. 38.7), but determination of gynozooecia is difficult, and their frequency of occurrence is unknown.

Type E brood chambers

The Type E brood chamber goes beyond the four categories extablished by Bancroft (1986a) and covers additional features that also appear to have been brood chambers in fenestrates. The endozonal chambers of a small percent of zooecia in biserial fenestrates are conspicuously larger than their neighbors and appear to have been gynozooecia in which the endozonal chamber served as the brood chamber (Fig. 38.9–38.10). In some species the chambers are so inflated that they are essentially spherical and cause a conspicuous bulge on the branch surface that is covered by only a thin skeletal wall. An apparent variation of Type E brood chambers occurs in an unidentified fenestellid (Stratton, 1975). In these the lateral wall of the endozonal portion of the gynozooecium is present as a partial partition within the overall globular brood chamber, which consists of the endozonal portion of the gynozooecium and a lateral portion that is located within the adjacent fenestrule, with the two regions within the chamber in continuous communication over the crest of the incomplete lateral wall of the endozone. Type E brood chambers generally are widely scattered and infrequent in fertile colonies, although Stratton (1975) illustrated a region where over 25% of the zooecia are gynozooecia.

Patterned distributions of Type E gynozooecia have been seen in a few species. Ulrich (1886b) noted enlarged zooecia with atypically large apertures occurring as single medial zooecia immediately proximal to branch bifurcations in his new species *Fenestella bifurca* Ulrich, 1886b. Type E brood chambers of *Semicoscinium* have been noted to occur near the base of zoaria (McNair, 1937) or in well-defined transverse bands (McKinney, 2008).

Two inflated hollow structures in a branch fragment of *Phylloporina furcata* (Eichwald, 1854) were interpreted as brood chambers by Brood (1971). The chambers are 0.50 mm in length and 0.35 mm in width, are situated laterally on the branch fragment, and open to the reverse and reverse-lateral of the branch. One opens through a pore similar to autozooecial apertures; the other has about the same diameter, but opens through a high peristome similar to ooeciostomes in tubuliporates. In *Phylloporina trentonensis* (Nicholson, 1875), rare brood chambers (termed gynozooecia), with inflated triangular-shaped chambers in the exozone, are placed in the fork of branch bifurcations (McKinney & Wyse Jackson, 2010).

CYCLOZOOECIA

Cyclozooecia (Morozova, 1974, p. 64–67) are simple, typically hemispherical chambers with their own granular wall, which may be lined internally with laminae (Fig. 39.1–39.4). They were first noted during the 19th century (Etheridge, 1877, p. 117; Vine, 1880, p. 506; Hall, 1885, pl. 2, fig. 16–17) and referred to as dimorphic or accessory pores. Their diameters typically are a little smaller than—but can be as large as—those of autozooecial distal tubes. They occur more commonly on the reverse side of branches, generally near or at the junctions between branches and dissepiments or lateral branches. Cyclozooecia may occur on obverse sides as well, occurring within the space between successive autozooecial distal tubes.

Cyclozooecia are bounded on the skeletal surface by a low peristome. Their depth typically does not exceed one-half or two-thirds of their width, at which stage they are covered by a terminal diaphragm; if zoarial growth continues, they become buried by laminated skeleton. Most cyclozooecia developed against the basal plate, where it has been suggested (Elias & Condra, 1957, p. 41) that they originate in the regions between the longitudinal ridges. They also may originate at any depth within the laminated skeleton and, in some instances, occur in stacked series.

Cyclozooecia occur most frequently in acanthocladiids. They appear to be invariably and abundantly present in *Septopora* Prout, 1859 (Ulrich, 1890, p. 397, 627) and, according to Morozova (1973, p. 332–333), in *Acanthocladia*. They are less frequently, but not uncommonly, found in various other acanthocladiid genera and fenestellid genera including *Ignotifenestella* Morozova, 1974, and *Permofenestella* Morozova, 1974.

The variation in their abundance within zoaria and within species, their apparently haphazard phylogenetic distribution, and their general shape are consistent with them reflecting galls caused by parasitic infections, as happens in some marine nematode infestations (e.g., Ruiz & Lindberg, 1989; Huntley, 2007). Several features of

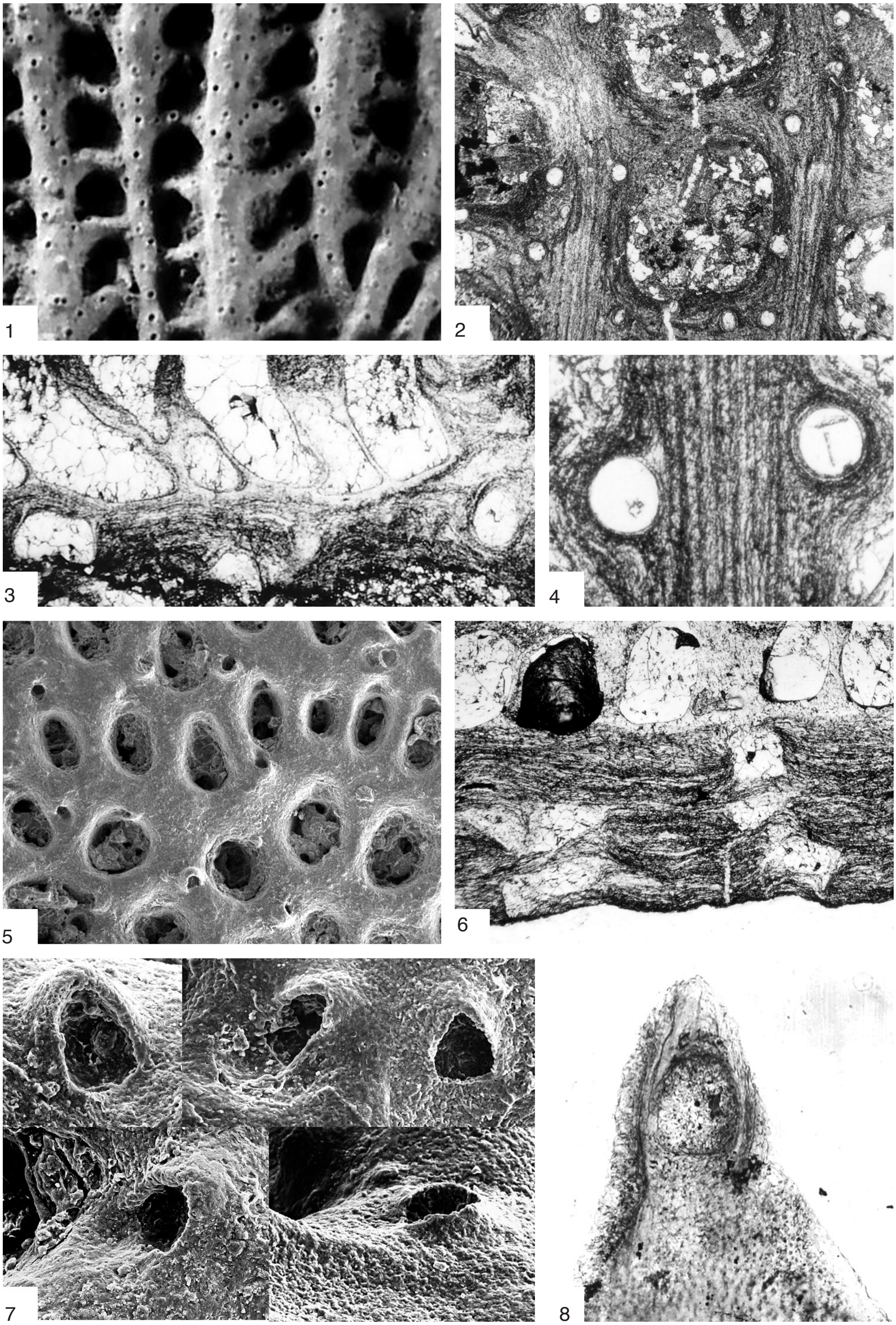

FIG. 39. *For explanation, see facing page.*

cyclozooecia, however, indicate that they are inherent structures generated by the bryozoan. These include the consistent hemispherical shape, definition by a thin wall of granular skeleton, common presence of laminae lining the interior of the thin granular skeleton, tendency to occur in certain locations within zoaria (e.g., reverse side of branch junctions in some species), and occurrence of terminal diaphragms. Also, some terminal diaphragms that cover cyclozooecia are centrally perforate (MOROZOVA, 1974, p. 64–65). This suggests that they probably contained tissues, perhaps even a diminutive polypide, that required communication with the colony-wide envelope or with the external environment. VINE (1880, p. 506) supposed that cyclozooecia between autozooecial apertures were analogous to bases of vibracula.

AVICULOMORPHS

Heterozooecia in *Fenestrapora* are structurally related to cyclozooecia, with shallow chambers defined laterally by thin granular walls, and have been referred to as aviculomorphs (MCKINNEY, 1998). These heterozooecia consist of a chamber that ends in a slightly elongate equilaterally triangular aperture. The aperture is usually tilted with respect to the local skeletal surface, with the hooded distal tip extending above the surrounding skeleton (Fig. 39.5,7). The two lateral sides of the chamber and aperture are slightly convex, but the shorter basal side is more nearly linear (Fig. 39.7–39.8). The orientation with respect to growth direction appears haphazard (Fig. 39.5).

As with the cyclozooecia, aviculomorphs may occur in stacked series; however, unlike cyclozooecia, their bases are flat (Fig. 39.6). They are most common on reverse sides of branches, although they can also occur in abundance on the surfaces of the high axial keels that extend from the obverse midline of branches in colonies of *Fenestrapora* (MCKINNEY, 1998). An abbreviated, shallow, concave region defined by a low, broad peristome commonly occurs adjacent to the short, lower side of the triangular aperture (Fig. 39.7).

The placement, size, and shape of reverse-side aviculomorphs are similar to avicularia on the reverse side of zoaria of some reteporid cheilostomes. These similarities include (1) the elevation of the distal tip; (2) a slight rim inset below the outer rim of the triangle, similar to the palate on which the mandible of an avicularium rests when closed; (3) a nearly straight proximal side of the aperture, similar to the straight fulcrum on which an avicularium's mandible

FIG. 39. Heterozooecia of fenestrates (part 1, continued); *1,* abundant cyclozooecia on reverse surfaces of main branches and pinnae of *Septopora intermedia* ULRICH, 1890, Mississippian (Visean–Serpukhovian),Tateville, Kentucky, USA, lectotype, USNM 43300, ×10 (new); *2,* circular cross sections of cyclozooecia in laminated skeleton near reverse surface of branches, *S. subquadrans*, Pitkin Limestone, Mississippian (Visean–Serpukhovian), Timbo, Arkansas, USA, USNM 528959, ×30 (new); *3*, longitudinal section cutting three cyclozooecia embedded in laminae of reverse side of branch, *S. intermedia*, Grayson Shale, Mississippian (Visean–Serpukhovian), Leitchfield, Kentucky, USA, paralectotype, USNM 496175, ×75 (adapted from McKinney, 2002); *4,* deep tangential section cutting two cyclozooecia with thin lining of laminated skeleton interior to thin sheet of granular skeleton that defines the perimeters of the cyclozooecia (also visible in view *3*), *S. intermedia*, Glen Dean Limestone, Mississippian (Serpukhovian), Grayson County, Kentucky, USA, USNM 496176, ×75 (adapted from McKinney, 1998); *5–8*, aviculomorphs in *Fenestrapora* spp.; *5,* reverse surface of zoarium with several haphazardly oriented aviculomorphs, *F. infraporosa* (ULRICH, 1886b), Jeffersonville Limestone?, Devonian (Eifelian), Falls of the Ohio, Indiana, USA, USNM 496172, ×20 (adapted from McKinney, 1998); *6,* longitudinal section through multiple layers of flat-bottomed aviculomorphs embedded in laminae of reverse surface of branch, *Fenestrapora* sp., Hamilton Group, Lower Devonian, Lambton, Bosanquet County, Ontario, Canada, USNM 496174, ×50 (adapted from McKinney, 1998); *7,* views of aviculomorphs, many with a shallow depression adjacent to the relatively straight lower edge of the aviculomorph aperture, *F. infraporosa*, Jeffersonville Limestone?, Devonian (Eifelian), Falls of the Ohio, Indiana, USA, collage from USNM 496172 and 496173, ×100 (new); *8,* deep tangential section through chamber of aviculomorph on reverse side of branch, *F. biperforata* HALL, 1885, Hamilton beds, Lower Devonian, Moscow, New York, USA, holotype?, NYSM 731, ×125 (adapted from McKinney, 1998).

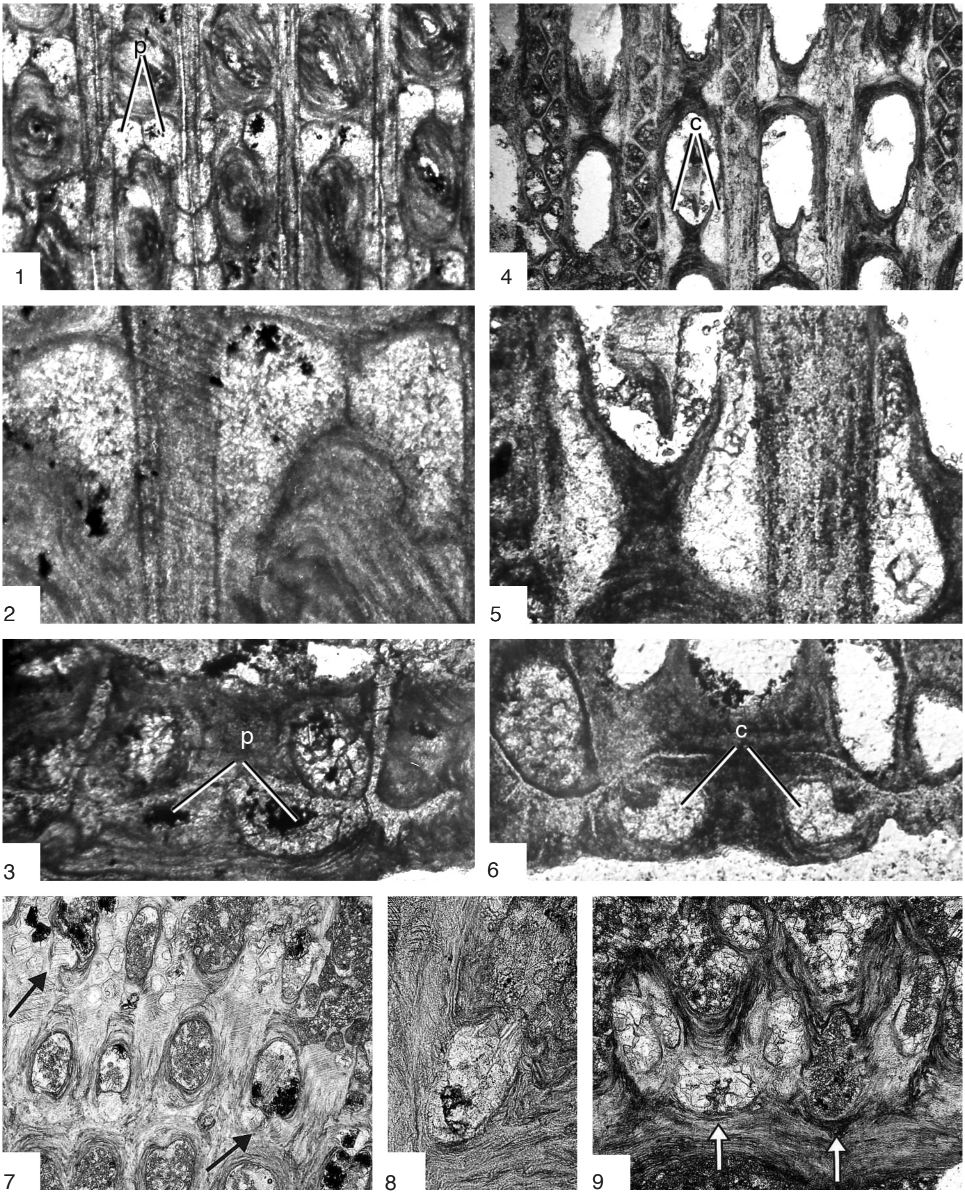

Fig. 40. Heterozooecia of fenestrates (part 2); *1–3,* parazooecia *(p)* in *Mirifenestella murengolensis* (Shishova, 1970), Middle(?) Devonian, Undur-Khan, Hentiy Aymag, Mongolia, holotype, PIN 2287/493; *1,* deep tangential section at transition from base of autozooecia to reverse laminated skeleton, cutting parazooecia at branch-dissepiment junctions, ×30 (new); *2,* detail of chamber shapes of abutting parazooecia, proximal taper to apertures that are directed proximally, and apparent skeletal closure of apertures, ×100 (new); *3,* cross section of two branches, the linking dissepiment, and chambers of two parazooecia bounded by basal plate and laminae of reverse extrazooecial wall, ×100 (new); *4–6,* cavernozooecia *(c)* of *Cavernella dvinensis* (Shul'ga-Nesterenko, 1951), Pennsylvanian (Kasimovian), Brin-Navolok, Arkhangelskaya Oblast, Russia; *4,* deep tangential section at transition from base of autozooecia to reverse laminated skeleton, cutting cavernozooecia at branch-dissepiment junctions, PIN 2935/179, ×30 (new); *5,* detail of chamber shapes of cavernozooecia and distal taper to apertures that are directed distally, PIN 2935/179, ×100 (new); *6,* cross section of two branches, the linking dissepiment, and chambers of two

(*Continued on facing page.*)

hinges; and (4) a shallow cavity proximal to the aviculomorph, analogous with where cheilostome avicularia have a depressible membrane covering the part of the avicularian zooidal chamber that is proximal to the mandible hinge. Whether or not a thickened, mandible-like section of cuticle covered the apertures of aviculomorphs, with hydrostatic or muscle systems for operation, is speculative at present (McKinney, 1998).

PARAZOOECIA

Parazooecia (Shishova, 1970, p. 30, pl. 12, fig. 3b; Morozova, 1973, p. 330, pl. 1, fig. 4; 1974, p. 58–59) are found in *Mirifenestella* Morozova, 1974 (Middle Devonian) and are not known in any other genus at this time. They consist of pyriform cavities larger than autozooecial chambers and are located in pairs on dissepiments (Fig. 40.1–40.3). The long axes of the parazooecia are, in essence, proximally–distally oriented. The cavities meet along the plane of lateral symmetry of the dissepiments, extend laterally to abut and extend under the basal plate of the adjacent row of autozooecia, and are centered just below the plane of the autozooecial base plate. They open to the exterior through a tube that is progressively restricted as it extends proximally and curves laterally (or obliquely toward the reverse) to the fenestrule margin.

CAVERNOZOOECIA

Cavernozooecia (Fig. 40.4–40.6;) are rather similar to parazooecia, occur in the Pennsylvanian (Upper Carboniferous)–Permian genus *Cavernella* Morozova, 1974, and are known in no other form. Shul'ga-Nesterenko (e.g., 1941, p. 82; 1951, p. 45) and Morozova (1973, p. 330; 1974, p. 65–66) initially refered to these features as caverns, and the term cavernozooecia was introduced by Goryunova & Morozova (1979, p. 64). Cavernozooecia occur at dissepiment-branch junctions and consist of elongate, distally tapered, somewhat distorted pyriform cavities with their long axis oriented parallel with branch axes. They typically occur in pairs, one at either end of a dissepiment. Cavernozooecia are situated laterally on the reverse side of the strongly curved autozooecial basal plates. In some transverse sections, the cavity is nestled against the adjacent basal plate, although in other sections there is a thin intervening zone of laminate skeleton. They typically do not swell to abut at mid-dissepiment. Morozova (1973, 1974) described hemiseptum-like structures near the proximal wall that defined a bend toward an aperture located on the reverse side of dissepiment-branch junctions. In tangential section, the narrowed distal ends appear (Fig. 40.4–40.5) to have a low peristome, which defines distally located apertures that opened laterally into the fenestrules at a point about one-third along the length of the fenestrule. More sections that include longitudinal cuts are needed to resolve geometry of the cavities more fully.

METAXIZOOECIA

Metaxizooecia resemble cavernozooecia and are found in *Iberofenestella* Ernst, 2012, known only from the Lower Devonian of northwest Spain (Ernst, 2012). Metaxizooecia are unknown in any other genus. Morphologically, they form sub-spherical or elongate chambers situated between branches just on the distal margins of dissepiments (Ernst, 2012, p. 219, fig. 9B–E, 10A–D) (Fig. 40.7–40.9). Apertures open into the fenestrules.

Fig. 40. (*Continued from facing page.*)
cavernozooecia surrounded by laminae of reverse extrazooecial wall, PIN 2935/52, ×100 (new); *7–9,* metaxizooecia in *Iberofenestella wolfae* Ernst, 2012, from the La Vid Formation, Lower Devonian (Emsian) of Collada del Campo de la Puerta, Cantabrian Mountains, northwestern Spain; *7,* mid-tangential section indenting fenestrules *(see arrows)*, RGM 211 536-6-7, ×20; *8,* with aperture opening into fenestrule, RGM 211 536-6-6, ×75; *9,* oblique transverse section positioned between adjacent branches *(see arrows),* RGM 221 536-1-11, ×50 (adapted from Ernst, 2012).

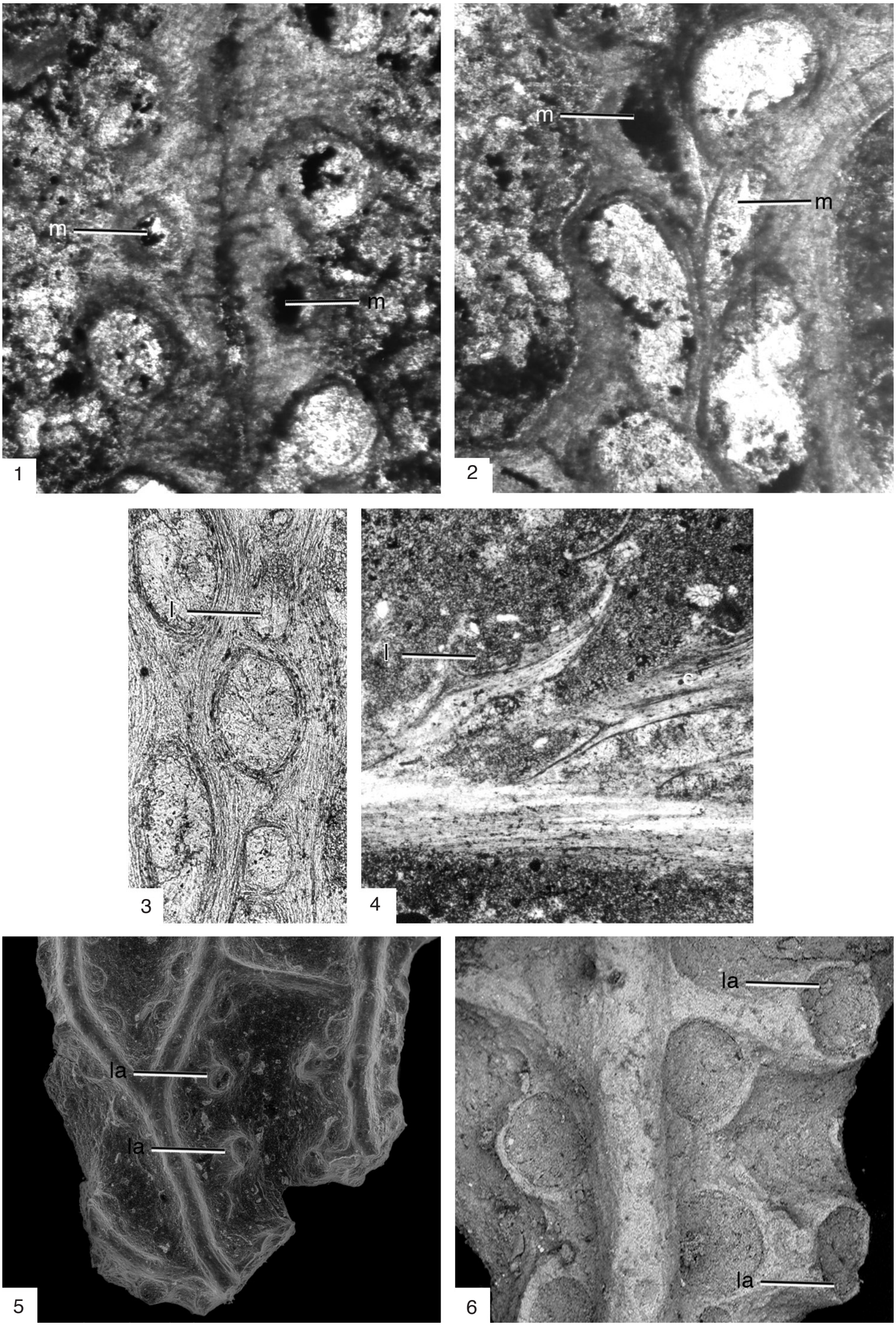

FIG. 41. *For explanation, see facing page.*

MICROZOOECIA

Diminutive zooecia, budded in the normal biserial sequence occur in the Permian genus *Permofenestella* (Fig. 41.1–41.2; Morozova, 1970b, p. 86–87, text-fig. 1, pl. 6, fig. 5; 1973, p. 332, pl. 2, fig. 7). These polymorphs, named microzooecia by Morozova in 1974 (p. 66), occur irregularly within the colony, either singly or in pairs on opposite sides of the axial wall. Their chambers are one-half (or less) of the volume of autozooecial chambers, and their distal tubes are approximately 0.06 mm in diameter. They have the position and relative size of primary nanozooecia in tubuliporates.

LEPTOZOOECIA

Leptozooecia are tubular structures that developed in exozones of some phylloporinid fenestrates (Lavrent'eva, 1985), most notably in the genus *Kallodictyon* Morozova, 1981 where they open to both obverse and reverse surfaces (Ernst & Nakrem, 2007), in *Lakkella* Ernst, Senowbari-Daryan, & Hamedani, 2006 (Fig. 41.3–41.4), and in some species of *Rhombocladia* Rogers, 1900, where they open only to the ventral (obverse) surface (Ernst & Minwegen, 2006; Ernst, Senowbari-Daryan, & Hamedani, 2006; Ernst & Königshof, 2010). Leptozooecia have smaller diameters than do autozooecia and vary from circular to rounded-triangular in cross section.

REVERSE-SIDE HETEROZOOECIA

Several phylloporinid genera *Phylloporina*, *Pseudohornera* Römer, 1876, and *Thamnocella* Simpson, 1897, have heterozooecia with a general morphology similar to autozooecia but with reduced size on the reverse side of branches (Tavener-Smith, 1975; Lavrent'eva, 1985; McKinney & Wyse Jackson, 2010). The reverse-side heterozooecia, referred to as "vestigial kenozooecia" (McKinney & Wyse Jackson, 2010, p. 452), may originate on the reverse side of a well-defined basal plate or may originate along a boundary near the reverse side of branches; this boundary is made of typical inter-zooecial skeletal endozonal skeletal walls. Tavener-Smith (1975, p. 7, 9, text-fig. 3) reported the reverse-side heterozooecia of *Pseudohornera diffusa* (Hall, 1852) arising from the median portion of the reverse side of the basal plate and termed them "suppressed zooecia." These heterozooecia in *P. diffusa* are laterally delineated by longitudinal ribbing on the basal plate and extend distally along the basal plate for some distance before curving toward the reverse surface, while maintaining their open tubular nature through successively deposited laminated layers. In *Thamnocella* these heterozooecia are restricted to the space between granular-wall ridges and are covered by laminar skeleton (McKinney & Wyse Jackson, 2010, p. 452).

LATERAL HETEROZOOECIA

Zooecia intercalated between autozooecia and offset laterally into fenestrules occur in the Carboniferous fenestellid *Polyfenestella* Bancroft, 1986b (Fig. 41.5–41.6; Bancroft, 1986b, type A-zooecia).

Fig. 41. Heterozooecia of fenestrates (part 3); *1–2,* microzooecia *(m)* of *Permofenestella labuensis* Morozova, 1974, Ufimian Stage, Permian (Guadalupian), near Labuya, North-East Russia, holotype, PIN 2830/2; tangential section through exozone *(1)* and through endozone-exozone transition *(2),* ×100 (new); *3–4, Lakkella jamalica* Ernst, Senowbari-Daryan, & Hamedani, 2006, Permian (Guadalupian), near Lakaftari, central Iran; *3,* leptozooecia *(l)* placed distally of autozooecia in tangential section through exozone, UEN 9-5-2, ×100 (adapted from Ernst, Senowbari-Daryan, & Hamedani, 2006); *4,* leptozooecia *(l)* as small pit in longitudinal section in exozone, holotype, SMF 2115 (1-2-1), ×70 (adapted from Ernst, Senowbari-Daryan, & Hamedani, 2006); *5–6, Polyfenestella fenestelliformis* (Young, 1881), Lower Limestone Group, Mississippian (Visean), High Blantyre, Scotland, GAGM 01-53xl; *5,* lateral heterozooecia *(la)* strongly indenting fenestrules, with small circular cyclozooecia scattered among the autozooecial apertures, ×22; *6,* lateral heterozooecia *(la)* showing lateral positioning and slightly smaller apertural diameters than autozooecia adjacent to central keel, ×80 (adapted from Wyse Jackson & McKinney, 2013).

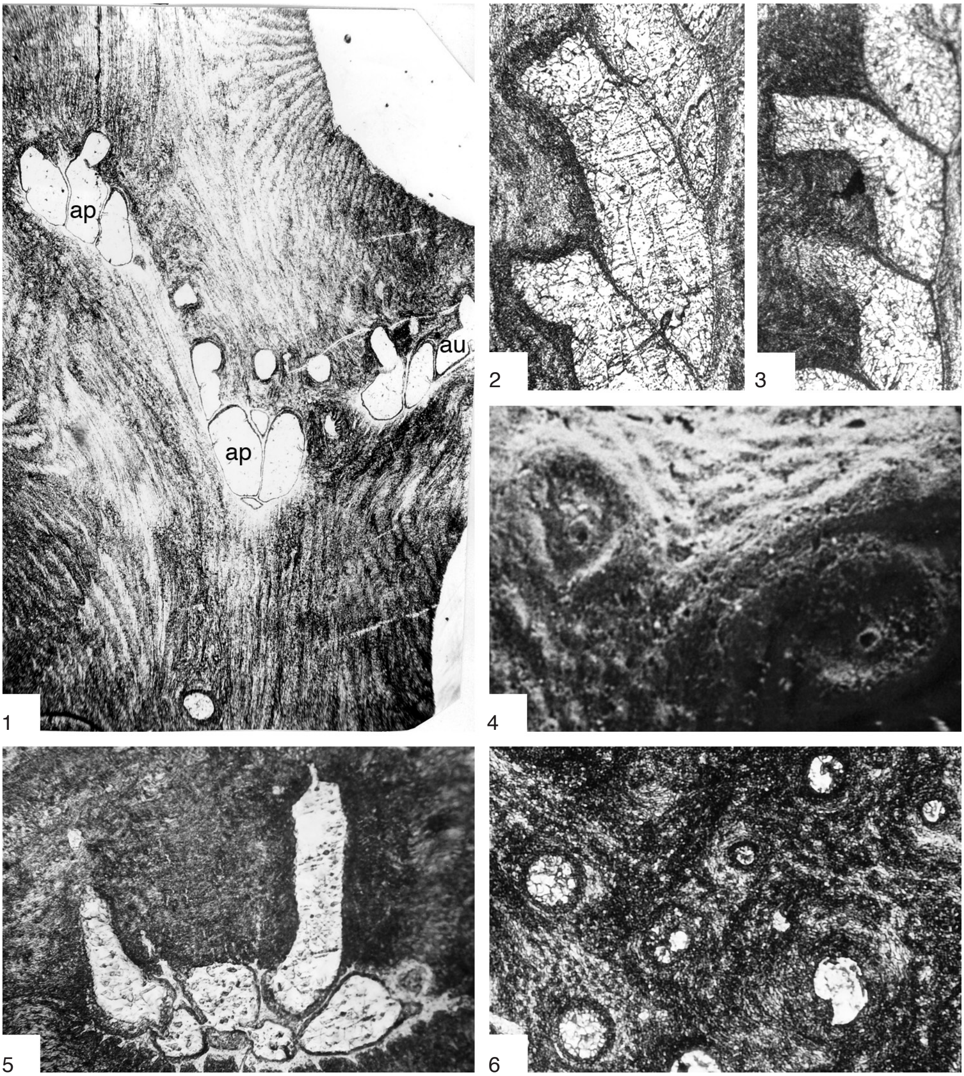

Fig. 42. Heterozooecia of fenestrates IV. *1–3,* large axial polymorphs *(ap)* and normal autozooecia *(au)* of *Archimedes intermedius; 1,* longitudinal section of thickened axial margin intersecting endozonal chambers of axial polymorphs in two portions of the helical colony margin, Bangor Limestone, Mississippian (Visean), Reid Gap, Blount County, Alabama, USA, USNM 528953, ×30 (new); *2–3,* axial polymorphs *(2)* and normal autozooecia *(3)* of the same specimen, Bangor Limestone, Mississippian (Visean), east of Huntsville, Alabama, USA, USNM 298659, ×80 (adapted from McKinney, 1980b); *4,* surface view of centrally perforated terminal diaphragms; these structures suggest change in function from autozooecia to secondary nanozooecia, *Penniretepora elegans* (Young & Young, 1875), Lower Limestone Group, Hosie Limestones, Mississippian (Visean), Hairmyres, East Kilbride, Scotland, NHMUK PD6282, ×150 (adapted from Bancroft, 1986c); *5–6,* intrazooecial polymorphism denoted by the inverted funnel-shaped skeletal closure in branches engulfed by thick laminated skeleton along the margins of zoaria of *Lyropora subquadrans* (Hall, 1857); *5,* funnel-shaped closure of a long distal tube (*upper right* of photograph) as seen in transverse section, Monteagle Limestone, Mississippian (Visean–Serpukhovian), near Burnside, Kentucky, USA, FMNH PE54110, ×80 (new); *6,* funnels cut in various stages of closure (*upper right* of photograph) as seen in shallow tangential section of branches, Glen Dean Limestone, Mississippian (Serpukhovian), Leitchfield, Kentucky, USA, USNM 528960, ×80 (new).

Bancroft described these heterozooecia as having irregular but generally conical chambers. Their apertures are identical to or only slightly smaller than autozooecial apertures, open on the obverse side of the lower parts of branches below the level of the autozooecial rows, and generally are tilted laterally toward the fenestrules (Bancroft, 1986b; Wyse Jackson & McKinney, 2013).

AXIAL HETEROZOOECIA

Enlarged zooecia occur in the branch that constitutes the inner helical colony margin of some species of *Archimedes* (Fig. 42.1–42.2; McKinney, 1980b, p. 605–606). These zooecia are about 50% longer and broader than autozooecia in the same zoaria, they have greatly enlarged apertures, and their chamber shape is quite variable (compare Fig. 42.1–42.2 with Fig. 42.3). Their unique size and shape probably are related to their generation at the rapidly extending tip of the spirally growing colony (see description of zoarial morphogenesis below).

INTRAZOOECIAL POLYMORPHISM

Intrazooecial polymorphism apparently occurs regularly in numerous fenestrates. Change in function from autozooids to specialized heterozooecia is indicated by closure of the distal tube by a centrally perforate terminal diaphragm (Fig. 42.4). The central apertural perforations of flat to slightly conical terminal diaphragms have a diameter of about 10–20 µm (Bancroft, 1986c; Ernst, Dorsch, & Keller, 2011).

Centrally perforated terminal diaphragms can be even more pronouncedly conical in such taxa as *Archimedes* and *Lyroporella,* in which heavy deposits of laminated skeleton develop (Fig. 42.5–45.6; Tavener-Smith, 1969, pl. 52, fig. 6; McKinney, 1977, p. 91). Where laminated skeleton builds thickly around zooecial apertures, distal tubes may become highly elongate. At some point, however, the aperture at the outer end of the distal tube is closed by an inverted, centrally perforate funnel-shaped diaphragm. The central perforation of approximately 20 µm diameter may then be maintained for some distance so that the tip of the funnel is greatly drawn out. The consistent development of the funnel with a central perforation of uniform, small diameter at the end of an extended distal tube is virtually identical with secondary nanozooids in the tubuliporate *Diplosolen obelium* (Johnston, 1838). It is inferred that the fenestrate zooecia that are capped by centrally perforate planar or funnel-shaped terminal diaphragms initially functioned as autozooids, but at the stage during which the diaphragm formed they functioned as nanozooids, with a reduced polypide bearing a single tentacle as in tubuliporate nanozooids (McKinney, 1977, p. 96; Bancroft, 1986c).

LARVAL DEVELOPMENT

The presence of inflated chambers associated with zooecia in some fenestrates suggests that, in these forms at least, larvae were brooded. Absence of inflated chambers, however, does not necessarily imply that larvae were not brooded. Lack of information about gynozooecia may be due to (1) original brood chambers having been non- or lightly calcified and thereby lost in fossilization; (2) larvae being brooded within confluent endozonal chambers where walls were incompletely formed or resorption occurred between two or more zooecia; (3) larvae having been brooded within skeletally unmodified gynozooecia; or (4) as in many tubuliporates, brood chambers may have been so uncommon within a species that they are unlikely to be found unless several hundred fragments are examined.

External fertilization of released eggs, typically produced in large numbers, results in planktotrophic larvae, whereas internal fertilization, asymmetrical cleavage, and retention of the zygotes at or in the parent result in lecithotropic larvae (Ström, 1977, p. 24). The latter pattern characterizes living bryozoans in general and is ubiquitous for the Tubuliporata (Ström, 1977), in which larvae are brooded within the membranous sac of the gynozoid. In all known instances, tubuliporate larvae are polyembryonic—that is, two or more larvae develop from a single primary embryo and are, therefore, genetically identical. In at least some living tubuliporates, over 100 embryos can develop from a single fertilized egg (Harmer, 1893; Borg, 1926a). Though based on few studies, tubuliporate larvae are known to settle and metamorphose in the laboratory within 15 minutes to 5 hours after release (Ryland, 1974, p. 241). Among living bryozoans, Eggleston (1972) found that the spread of a species across its potential habitat is a reflection of abundance of suitable substrata and of duration of the planktic stage of larvae. In addition, "most have short-lived, lecithotropic, ciliated larvae" (Eggleston, 1972, p. 259). The genetic structure of populations of a polyembryonic tubuliporate over very small scales indicates that, in natural conditions, offspring tend to settle close to the maternal colony (Pemberton & others, 2007). These conditions in living bryozoans, especially in the tubuliporates, raise the question of the prevalence of brooding, the presence of polyembryony, and larval longevity in fenestrates.

Since larvae of fenestrates are not directly preserved (though their metamorphosed product, the ancestrula, is preserved), their nature must be inferred indirectly and tentatively. Indirect evidence suggests that larvae of some fenestrates settled and metamorphosed within minutes or hours.

Larvae of living tubuliporates, which are polyembryonic, statistically are smaller than those of living gymnolaemates, which are not polyembryonic (McKinney, 1993; Pachut & Fisherkeller, 2010). The size of the ancestrula is determined by size of the larva from which it forms (review in Pachut & Fisherkeller, 2010), and ancestrulae of tubuliporates statistically are smaller than those of living gymnolaemates (Pachut & Fisherkeller, 2010). Ancestrulae of all extinct stenolaemate clades, including fenestrates, are statistically indistinguishable in size from those of tubuliporates, individually and collectively, but they are statistically smaller than those of gymnolaemates (Pachut & Fisherkeller, 2010). This, together with the presence of brood chambers in fenestrates, is consistent with the hypothesis that the Class Stenolaemata has been characterized by polyembryony throughout its history.

Species of *Hemitrypa*, *Polypora s.l.*, and *Septopora* in Permian deposits of western Texas were inferred to have had short-lived lecithotrophic larvae that settled near the maternal colony, based on localized distribution of the species, frequency of fused sibling colonies (Fig. 43), and the low probability that sibling colonies would have settled adjacent to one another had they been in the water column for long (McKinney, 1981a). Brood chambers occur in *Hemitrypa* and in *Polypora s.l.* (Bancroft, 1986a), but none have been found in *Septopora*, although they are known in its close relative, *Penniretepora* (Bancroft, 1986a). Fusion wherever these sibling colonies touched is consistent with the hypothesis that they were polyembryonic (McKinney, 1981a). Although fusion between young conspecific but genetically different colonies of living cheilostomes is known (Chaney, 1983; Craig, 1994; Hughes & others, 2004), it has not been demonstrated for tubuliporates. Fusion of young, equal-sized encrusting tubuliporates that are in close proximity with an apparent maternal colony is common, and tubuliporate polyembryony suggests that such cases are between genetically identical siblings.

ZOARIAL MORPHOLOGY AND BRANCHING

ZOARIAL MORPHOLOGY OF FENESTRATED FENESTRATES

Condra & Elias (1944, p. 56) devised a measure of meshwork density termed the meshwork formula, later renamed the micrometric formula (Miller, 1961b, p. 224), as a way of characterizing fenestrated fenestrates. This measure was employed in some studies

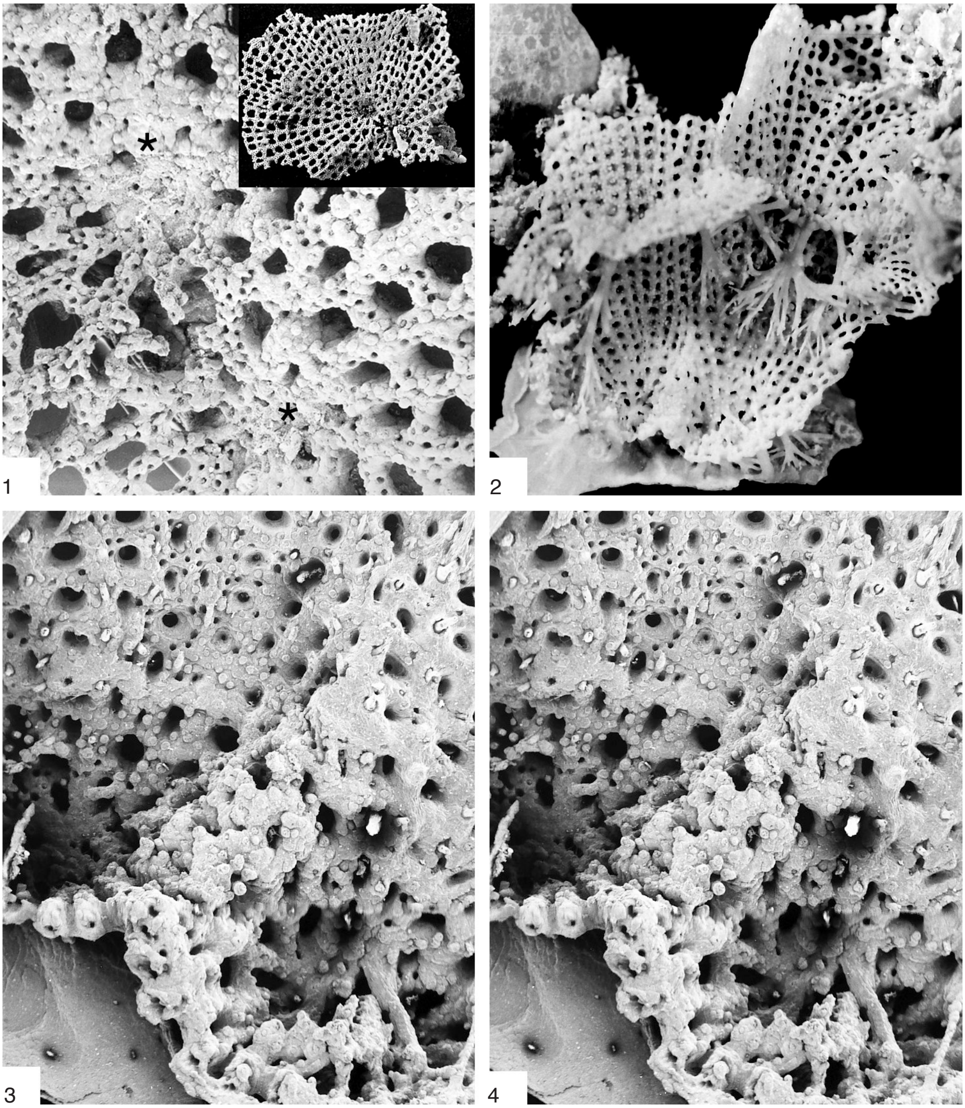

Fig. 43. Silicified compound colonies of *Septopora* Prout, 1859, formed by intraspecific fusion of young colonies established close to one another; *1,* young, minimally conical colonies that fused when their growing margins touched and continued growth as a single, essentially flat colony; inset shows colony origins in lower right; *asterisks*, points of origin; Bone Spring Formation, Permian (Kungurian), Glass Mountains, Texas, USA, USNM 312152, ×9 and ×1 *(inset)* (new); *2–4,* young, conical colonies that fused when their growing margins touched and continued growth as a single complex colony, Cathedral Mountain Formation, Permian (Kungurian), Glass Mountains, Texas, USA, USNM 312151; *2,* entire specimen with two separate conical regions of attachment to the shell substratum indicating points of establishment of the original colonies, within each of which branches radiate from the base of the cone, ×2; *3–4,* stereo pair of points of attachment *(upper right)* of the two original colonies and the boundary along which they fused, ×9 (adapted from McKinney, 1981a).

up until recently (Miller, 1961b, 1963; Tavener-Smith, 1966b, 1973a; Bancroft, 1985; Sakagami, 1995; Sakagami, Sciunnach, & Garzanti, 2006), despite the recognition of its limitations (Utgaard & Perry, 1960, p. 13; Miller, 1961b, p. 233) in not differentiating those taxa with a similar formula but gross-morphological characteristic and in allowing easily comparison between taxa (Tavener-Smith, 1973a). A combination of zoarial and zooecial characters is now used to produce rigorous generic assignments (Morozova, 1974; McKinney, 1980a; Hageman, 1991; Snyder, 1991a, 1991b; Gilmour & McColloch, 1995, chapter 7E). Although the micrometric formula was shown to be deficient, discrete patterns of meshwork densities have been shown to hold to *a priori* determined genera but should not be used as a basis to define genera (Hageman & McKinney, 2010). Starcher and McGhee (2002) showed that only a small proportion of morphospace available to meshwork fenestrates is expressed in the fossil record of fenestellids and polyporids. This, they argued, is due to phylogenetic constraints rather than limitations set by morphology. Meshwork porosity in fenestellids may reach 65%, compared to 50% in polyporids, and branches in fenestellids are typically narrower and fenestrule length shorter than in polyporids, which have more autozooecial rows (Starcher & McGhee, 2002). In some lyre-shaped bryozoans, fenestrule area can make up as little as 13% of the area of the meshwork sheet (McKinney,Taylor, & Zullo, 1993; Hageman & McKinney, 2010). Meshwork density (porosity) has implications for the feeding efficiency of fenestrated bryozoans.

ZOARIAL FORM IN PINNATE FENESTRATES

Pinnate fenestrates generally comprise either small, fan-shaped expansions with regular lateral pinnae developing from a mainstem (as in, for example, *Penniretepora* and *Kalvariella*; Fig. 2.7), irregular lateral pinnae (*Baculopora* and *Diploporaria*), irregular dichotomous branching (*Thamniscus*), or fusion of lateral pinnae to form a meshwork (*Septopora*) (Fig. 2.1). Distal expansion is frequently planar, and secondary lateral pinnae may develop tertiary pinnules that increase the areal extent of zoaria. Equally, some mainstems may bifurcate or lateral pinnae develop into so-called mainstems that diverge from the original. In *Acanthocladia* and *Adlatipora,* from the Permian of the Glass Mountains in Texas, zoaria are complex and frequently developed a bush-like zoarium up to 20 cm in height. Through curvature of mainstems, their bifurcation, and the development of lateral so-called mainstems, branches can grow beyond a flat-plane and produce a complex of branches that infill 3D space.

BRANCHING

With the exception of *Schischcatella* and *Ernstipora,* all fenestrates undergo branch proliferation above the base of attachment. This branch proliferation occurs only within a plane, which may be flat, curved in various ways, or complexly proliferated, but which invariably has an obverse and a reverse side. The component branches are unilamellar, have their own obverse surfaces toward which autozooecial apertures are oriented, and branch only in the plane parallel to the basal plate. Branching may be by bifurcation, or it may be by pinnation, with paired or alternating lateral branches arising from major branches; less commonly it may involve a programmed (Fig. 44.1–44.2) or microenvironmentally determined (Fig. 45) combination of the two.

BIFURCATION

In biserial forms, bifurcation is commonly accomplished by intercalation of one autozooecium (Fig. 46.2) or a series of autozooecia (Fig. 46.3) between the two original rows immediately preceding or at the point of branch division so that the medial, linear to sinuous budding path divides around the medial zooecium or zooecial row to continue into each descendant branch link. The median zooecium at the point of bifurcation serves as the base of the inside row of zooecia on both descendant links, while the two rows of autozooecia from the parent link continue as the outer row in the two descendants. In some instances, branch division occurs immediately after four autozooecial rows have developed, with two rows of zooecia passing into each descendant link.

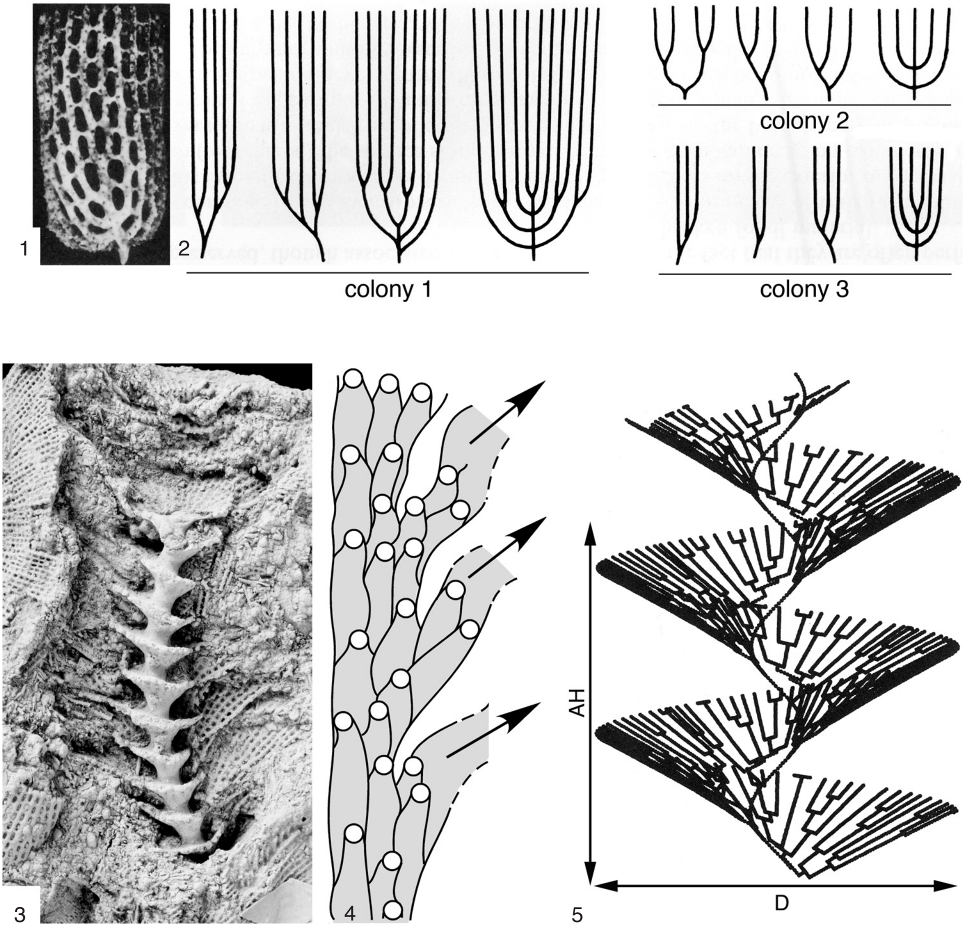

FIG. 44. Distinctive geometries resulting from patterned changes in rate or distribution of branch proliferation in fenestrates. *1–2,* branching and geometry of *Ptilofenestella carrickensis* TAVENER-SMITH, 1965; *1,* cylindrical colony with a hemispherical base developed by initial high rate of branch division rapidly diminishing to zero (no further branch divisions) at the transition from the hemispherical base to the upper cylindrical portion, Dartry Limestone equivalent, Mississippian (Visean), Carrick Lough, County Fermanagh, Ireland, NHMUK PD4478, ×8 (adapted from Tavener-Smith, 1965); *2,* branching patterns in three colonies (adapted from Tavener-Smith, 1965); *3–5,* branching and geometry of *Archimedes*; *3, Archimedes* cf. *A. invaginatus* ULRICH, 1890, eroded to level of helical, densely calcified colony axis with a portion of the radiating fenestellid meshwork visible, Bangor Limestone, Mississippian (Visean), near Russellville, Alabama, USA, USNM 71694, ×2 (new); *4,* diagram of zooecial distribution along the closely spaced bifurcations that define the axial margin *(left)* of the zoarium and initial portions *(right)* of branch systems that radiate from the axial margin, diagram shows a straightened (not rotated) view of zooecial and branch patterns (adapted from McKinney, 1980b); *5,* computer simulation of helical morphology and branching pattern in *Archimedes,* with *arrows* indicating a standardized diameter *(D)* and a portion of the height *(AH)* equivalent to the diameter, used for standardized volume comparison of zoarial morphologies in Fig. 52–53 (adapted from McKinney & Raup, 1982).

If the autozooecial basal shape is basically triangular and branches consist of an alternating series of zooecia that open on either side of the branch, there is no intercalation of zooecia preceding bifurcation (Fig. 46.1). Rather, the zooecium that forms the base of the bifurcation has its aperture placed medially and functions as an inward-opening zooecium for both descendant branch links. The first zooecium of each of the two new

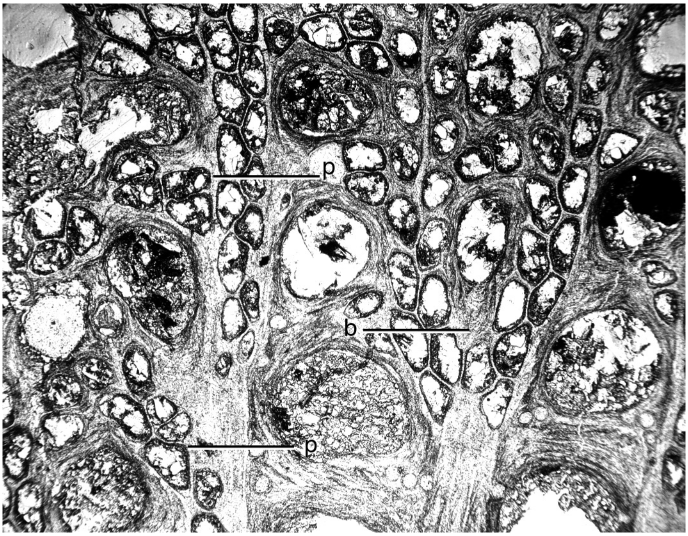

FIG. 45. A zoarium in which almost all branches originate as pinnae *(p),* some of which are microenvironmentally stimulated to transform into an effective branch bifurcation *(b)* producing two main branches from which additional pinnae bud, *Septopora cestriensis* PROUT, 1859, Mississippian (Visean–Serpukhovian), Chester, Illinois, USA, USNM 518286, ×30 (adapted from McKinney, 2002).

autonomous branch links is situated on a disto-lateral facet of the zooecium at the base of the bifurcation and opens toward the outer side of the branch.

Bifurcation of multiserial branches was initiated over a variable distance proximal to the point of bifurcation, by intercalation of one or more additional zooecial rows (Fig. 46.4). Where a branch reached a critical width, the zooecia added at the distal tip were oriented obliquely in two equal groups, growing disto-laterally toward their respective sides. No additional median rows formed, and the two groups separated into distinct descendant branch links. Each descendant link initially had about half as many zooecial rows as were present at the distal end of the parent link; additional rows were added distally at a rate dependent on genetic and/or microenvironmental stimuli.

At bifurcation points, newly established branch links diverged for short distances at angles up to 45°, or more, with respect to the axial plane of the parent link. As they approached the normal lateral branch spacing, the angle of departure diminished

FIG. 46. Increase in branch numbers. *1,* bifurcation of biserial branches without intercalation of a medial autozooecial row immediately proximal to branch division, *Spinofenestella inclara* (POČTA, 1894), Koněprusy Limestone, Lower Devonian (Pragian), Koněprusy, Czech Republic, NMCR L21452, ×30 (adapted from McKinney & Kříž, 1986); *2,* insertion of a single medial autozooecium *(m)* below bifurcation, *Utropora parallela* (BARRANDE in POČTA, 1894), Koněprusy Limestone, Lower Devonian (Pragian), Koněprusy, Czech Republic, NMCR L24652, ×30 (adapted from McKinney & Kříž, 1986); *3,* medial row of autozooecia *(left center)* proximal to bifurcation *(top center)* producing biserial branches, *Paucipora hemiseptata* (SHUL'GA-NESTERENKO,1951), Peski beds, Myachkiĭ Horizon, Pennsylvanian (Moscovian), Peski Station, Moscow Basin, Russia, holotype, PIN 136/56, ×40 (new); *4,* addition of multiple rows of autozooecia proximal to bifurcation of multiserial descendant branches, *Lyropora lyra* (HALL), Mississippian (Visean–Serpukhovian), Southward Pond, Mississippi, USA, USNM 483520, ×30 (adapted from McKinney, 1994); *5,* continuous main branch from which pinnae extend at approximately 45° angle, *Septopora intermedia* ULRICH, 1890, Glen Dean Limestone, Mississippian (Serpukhovian), Grayson County, Kentucky, USA, USNM 5528961, ×30 (new); *6,* successive, asymmetrical bifurcations producing short branches alternatively from side to side of a continuous central branch, *Adlatipora* sp., Word Formation, Permian (Guadalupian), Glass Mountains, Texas, USA, USNM 543120, ×8 (adapted from Gautier, 1972).

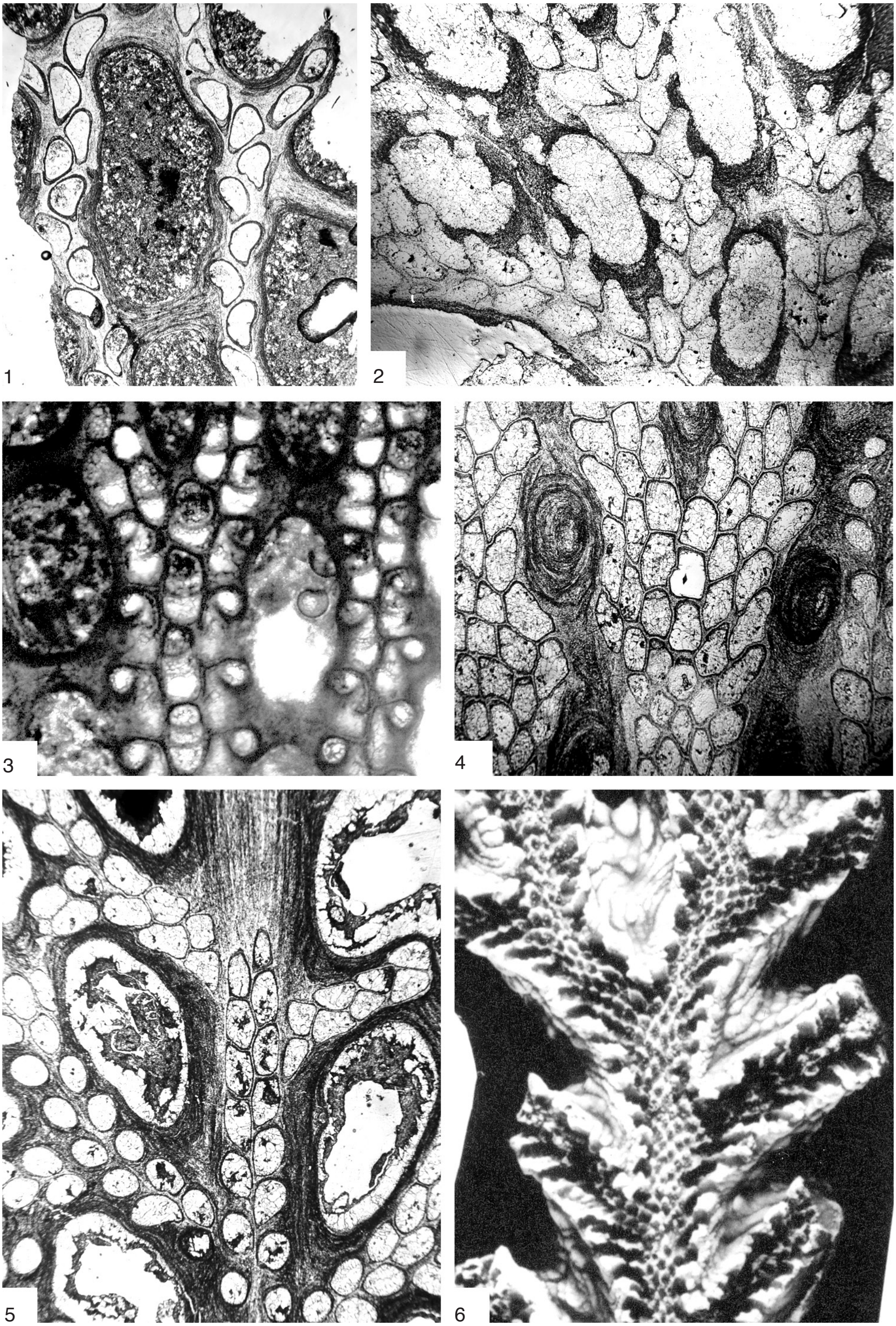

FIG. 46. *For explanation, see facing page.*

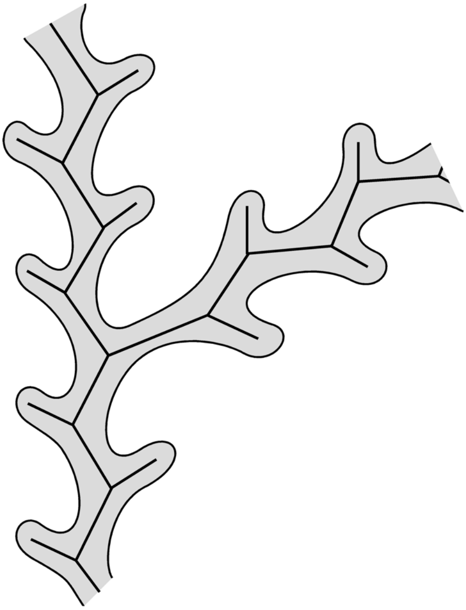

FIG. 47. Pattern of pinnation in the acanthocladiid *Adlatipora,* showing pinnae diverging alternately to right and left due to a slight shift in the boundary *(midline)* of right- versus left-hand zooecia (adapted from Gautier, Wyse Jackson, & McKinney, 2013).

so that their growth directions became almost parallel with the projected axis of the parent branch segment.

PINNATION

Pinnae are sets of lateral branches that abruptly depart from the main branch from which they arise, usually at an angle of about 45° or more. Pinnate branching may be either simply or complexly patterned, depending upon whether the zooecial rows in the main branches are continuous with or are abutted by the point of origin of the lateral branches.

In many genera, such as *Ptylopora* M'COY, 1844*, Penniretepora, Ichthyorachis, Kalvariella,* and *Septopora*, lateral branches arise without disruption of budding sequence or shape of zooecia in the parent longitudinal branch (Fig. 46.5). The shape and orientation of the proximal walls of the initial autozooecia of the pinnae are determined by the morphology of the normal lateral walls of the adjacent autozooecia of the main branch, so that morphology of the initial autozooecia of pinnae is skewed. Subsequent autozooecia in the pinnae have normal morphology. Commonly, a thin layer of extrazooecial lamellar skeleton is present between the autozooecia of the main branch and the initial autozooecia of pinnae. The conformation of the initial autozooecia of the pinnae to the pre-existing morphology of the contiguous autozooecia of the parent main branch, and the common presence of intervening extrazooecial skeleton, indicate that the pinnae formed a short distance behind the advancing tip of their parent main branch.

A more complex pinnate branching pattern is typified by that of *Adlatipora* (Fig. 46.6; GAUTIER, WYSE JACKSON, & MCKINNEY, 2013). In this genus, autozooecia are organized into diagonal rows that originate alternately along branch midlines such that all zooecia in a branch may be designated as either right- or left-handed. The so-called main branch, from which the lateral branches apparently arise, is made up of a zigzag sequence of links, each of which is terminated by a bifurcation. Bifurcation is initiated by an interruption in the alternation of right- and left-handed zooecia along the branch following one another along the midline. This results in a shift in position and orientation of branch axis (e.g., toward the right if there is repetition of left-handed axial zooecia). Associated with the shift in branch-axis orientation and axial position, a lateral branch origin is located on the opposite side of the projection of the branch axis that precedes the shift. The lateral branch is initiated by establishment of a new path of alternately oriented zooecia, forming a new branch axis (Fig. 47; GAUTIER, WYSE JACKSON, & MCKINNEY, 2013, fig. 7.3).

BRANCH SPACING AND RATES

Regardless of details of branch proliferation—whether by dichotomous bifurcation or by various modes of pinnate branching—branches within any fenestrate bryozoan are

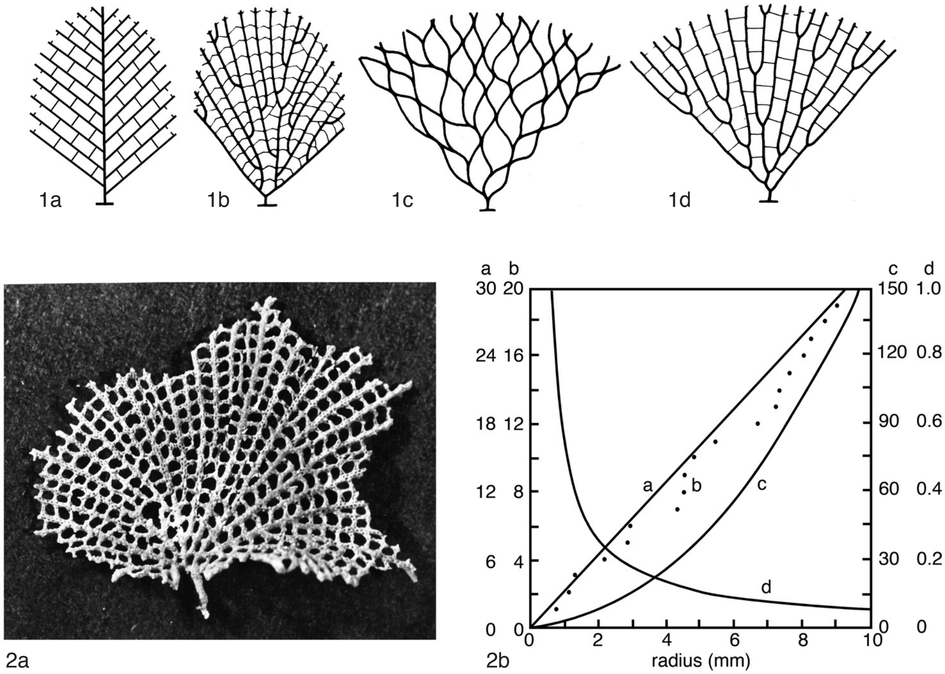

FIG. 48. Simple planar fenestrate colonies. *1a–d,* Diagram showing interaction of branching types and branch paths in colonies with the same number of terminal branches; *1a,* a central main stem with long pinnae linked by dissepiments; *1b,* short pinnae linking main branches that originate as pinnae from pre-existing main branches; *1c,* sinuous anastomosed branches in which branch proliferation points are difficult to distinguish; *1d,* dichotomous branches linked by dissepiments; *2a–b,* branch increase in a simple planar fenestrate bryozoan colony; *2a,* 180° planar, fan-shaped specimen of *Septopora* sp. from the Bone Spring Formation, Permian (Kungurian), Glass Mountains, Texas, USA, USNM 316123, ×2; *2b,* graph of the specimen's calculated arc length *(a)* in mm as the radius expanded, a plot of cumulative number of origins of main branches *(b)* against radius from the center of growth, increase in surface area *(c)* in mm^2 as the radius increased, and a curve *(d)* plotting the probability that any given single branch will give rise to a new main branch within a 0.5 mm increase in colony radius (curve can also be characterized as the proportion of existing branches that likely will produce a new main branch in the next 0.5 mm at a given colony radius) (adapted from McKinney, 1981b).

uniformly spaced in relation to neighboring branches. The variation in spacing between midplanes of adjacent branches within a colony of some species is less than 5% of the mean spacing (MCKINNEY & STEDMAN, 1981), and variation within a population sample of a species seldom exceeds 15% (e.g., SNYDER, 1991a; REID, 2003; ERNST & WINKLER PRINS, 2008). Filtration nets of laterally linked branches were typical for fenestrates characterized by dichotomous branching as well as many pinnate genera.

The branching rate—that is, the proximal-distal spacing between successive branch origins within a zoarium), the zoarial form, and, where applicable, the position within distally changing zoarial form, are mutually interdependent. This interrelatedness is indicated in part by ELIAS and CONDRA (1957, p. 49). Given that branch spacing and branch size within fenestrate colonies are essentially uniform, the overall zoarial shape primarily reflects the position and abundance of branch origins. Representatives of taxa that have rigidly set or narrowly varying zoarial form also have specifically determined positions at which branching must occur in order for the correct form to develop. These taxa were probably genetically programmed to react to certain stimuli (external or self-generated current, nutrient availability, etc.) so that a highly patterned sequence of branching events occurred. Branch increase, as used here, refers to bifurcation, which produces two essentially similar descendant branch segments (Fig. 48.1c–d) and to the origination of pinnae that characteristically are elongate or that are a subset of normally short pinnae that become elongate and themselves serve as main branches from which pinnae develop (Fig. 48.1a–b).

A relatively simple example may be seen in planar zoaria that expand at an arithmetic rate (Fig. 48.2; McKinney, 1981b). Where the zoarium expands distally as a planar wedge that subtends a constant arc as measured from origin of a specified set of branches, arc length and distance from origin to growing edge are related linearly:

$$l = 2r \times d / 360^\circ,$$

where l = arc length, r = branch system length (the distance from origin to growing edge), and d = arc subtended (in degrees) (Fig. 48.2b, see line a). Therefore, if the distance from the branch origin to first new branch origin is specified as unit length, there must, on average, be one new branch origin and an increase by one in total branch number per unit length within such distally extending zoaria (Fig. 48.2b, line b consisting of points). This is due to uniform branch spacing and the linear relationship between the arc length and the branch system length. The single branch origin per unit length in planar fenestrates can be programmed (Fig. 48.1a) or microenvironmentally allocated to any branch at that level (Fig. 48.1b–d). For an arithmetically uniform expansion rate, lateral placement of a bifurcation is not important, but regular placement in the proximal-distal sense is important. Simultaneously, frond surface area increases exponentially:

$$A = \pi r2 \times d / 360^\circ,$$

where A = frond surface area, and r and d are defined as above (Fig. 48.2b, line c).

The number of branches increases distally in the expanding planar branch system defined above. Since there is, on average, only one bifurcation per unit length, the chance of bifurcation terminating a branch segment at successively distant intervals decreases exponentially (Fig. 48.2b, line d) in the patterns where lateral placement of bifurcation points is not precisely patterned. Therefore, at progressively distal levels within such branch systems, branches are on average progressively longer (with the exception of those that originated just before final cessation of growth). The lack of appreciation of this geometric necessity for planar, uniformly widening fenestrate fronds has occasionally led to unnecessary or inaccurate taxonomic characterizations, such as the claims that branching rates decrease distally or that a taxon is characterized by frequent or by infrequent bifurcations based on small frond fragments.

The relationship specified above holds only for essentially planar feeding surfaces with

Fig. 49. *Archimedes* specimens from diverse Upper Mississippian (Visean–Serpukhovian,) facies of eastern North America; *1–2, Archimedes* sp., Indian Springs Shale Member, Big Clifty Formation, Mississippian, Sulphur, Indiana, USA, durable, heavily calcified axial screws from open-water muddy environments; *1,* sinistrally coiled screws (anticlockwise rotation with growth), TCD.60600b, and *2,* dextrally coiled screws (clockwise rotation with growth), TCD.60600a, ×0.6 (new); *3, Archimedes intermedius* Ulrich, 1890, from back-barrier argillaceous mudstones, Bangor Limestone, Mississippian (Visean), Fox Trap, Colbert County, Alabama, USA, NCSM 11761 (ex McK 6992), edges of complete branch systems of two toppled zoaria, the left zoarium with growth direction toward top of figure and the right with growth direction toward bottom of figure, ×0.6 (adapted from McGhee & McKinney, 2002); *4, Archimedes* sp., from a basinal lime packstone, Goreville Limestone Member, Kinkaid Formation, Mississippian, Goreville, Illinois, USA, NCSM 11762 (ex McK 6993), single, robust axial screw with high ELEV, and some delicate axial screws *(two indicated by arrows)* with low ELEV, ×0.6 (adapted from McGhee & McKinney, 2002); *5,* lightly calcified *Archimedes laxus* (Hall, 1857) with high ELEV and low BWANG from a back-barrier lime packstone accumulated at an unknown distance (but not contiguous) from the barrier, Mississippian (Serpukhovian), Glen Dean Formation, Leitchfield, Kentucky, USA, PRI 55116, ×0.6 (adapted from McGhee & McKinney, 2002).

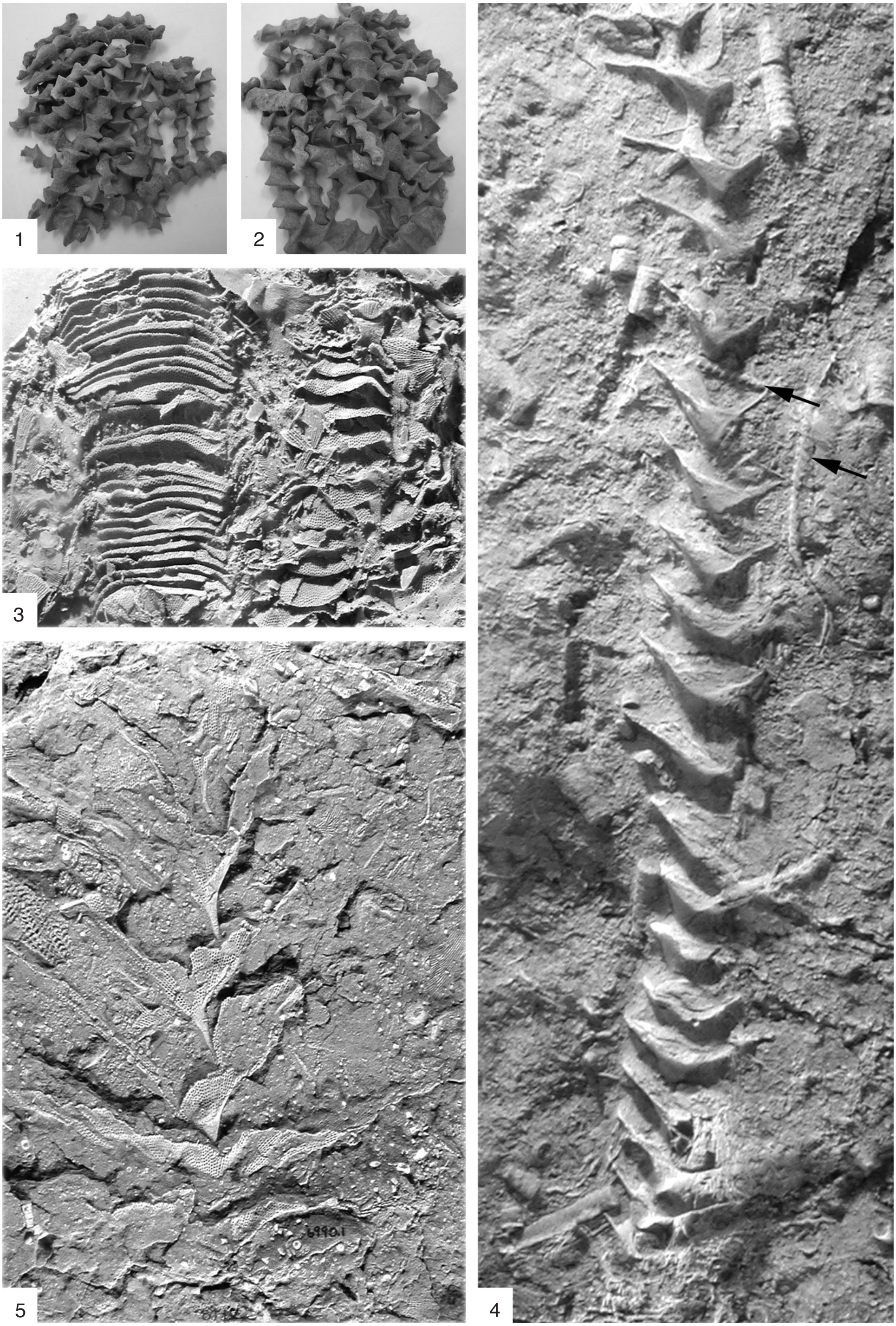

FIG. 49. *For explanation, see facing page.*

uniform space between branches growing in a uniform, nonvarying arc unit. Partial to complete simple conical forms also expand distally at an arithmetic rate and add branches uniformly at unit length. A departure from the simple expanding planar or conical condition—paraboloid, spherical, helical, or complex surfaces, or change in rate of widening of a sheet of branches—generates different relationships between branch system length, bifurcation rate, and surface area.

BRANCHING PATTERNS IN SPECIFIC TAXA

Ptilofenestella has simple, small cylindrical colonies with paraboloid or hemispherical proximal portions. Tavener-Smith (1965, p. 486–487) recognized that in the expanding proximal portion of a *Ptilofenestella* colony there are closely spaced branch divisions, while there are none in the cylindrical portion. The distally decreasing branching rate varies inversely with the increase and stabilization in number of branches (Fig. 44.1–44.2). That branch divisions in proximal portions of *Ptilofenestella* colonies are a combination of pinnate branching and of bifurcation is irrelevant to the rate of branch increase and precise proximal–distal placement of branch division: all branching could have been accomplished by bifurcation.

The characteristic helical zoaria of *Archimedes* were generated by closely spaced bifurcation along one rapidly extending margin of the colony; this edge produced a helically coiled axial margin (Fig. 44.3; Cowen & Rider, 1972, p. 157–158; McKinney, 1980b). The coiling may be dextral or sinistral (clockwise or anticlockwise rotation in the direction of growth) (Taylor & Sendino, 2014) (Fig. 49.1–49.2). As seen in serial sections through the skeletal screw that constitutes the zoarial axial region, the branch bifurcations along the axial margin are highly asymmetrical (Fig. 44.4). At each bifurcation point, the new marginal branch continues the helical trace followed by its predecessors, twisting through a few degrees of arc depending on the number of bifurcations per revolution of the helical margin. The other new branch diverges abruptly and is simultaneously bent toward its reverse surface so that it continues away from the zoarial axis at a high angle and by subsequent normal bifurcations contributes to construction of the spiraled meshwork (Fig. 44.5). In tightly coiled species of *Archimedes*, axial bifurcations follow immediately one upon the other so that the axial margin is basically triserial due to intercalation of a medial zooecium at each bifurcation (Fig. 44.4)). In more loosely coiled species, clearly biserial branch links may be seen between axial margin bifurcations. The shape and size of the zooecia in the branches that constitute the axial margin may be much more variable than for the autozooecia elsewhere in the zoarium.

Bifurcation along the marginal axis of *Archimedes* may be notable for its strong asymmetry and for the curvature, twisting, and variability in size and shape of constituent zooecia. Other aspects, however, clearly ally it with normal biserial branch bifurcation: intercalation of a zooecium or less commonly a short series of zooecia preceding bifurcation, and presence of a medial budding path that divides around the intercalated zooecium to continue smoothly as a medial budding path along the midline of each of the two descendant branches (McKinney, 1980b).

Aside from overall colony height and diameter, the essential morphological characteristics of *Archimedes* colonies were set at the helical axial margin (at the top center of the colony) and can be described by five measurable attributes (Fig. 50.1). These are (1) the radius of the helical path traced by the branch that constitutes the inner margin of the colony (RAD), (2) the distance along the central axis to complete one revolution of the helical margin (ELEV), (3) the angle between successive bifurcations along the inner margin (ANG), (4) the angle between the central axis and the whorls of branches that diverge from it (BWANG), and (5) the distance between three adjacent branches at which the central branch bifurcates as they

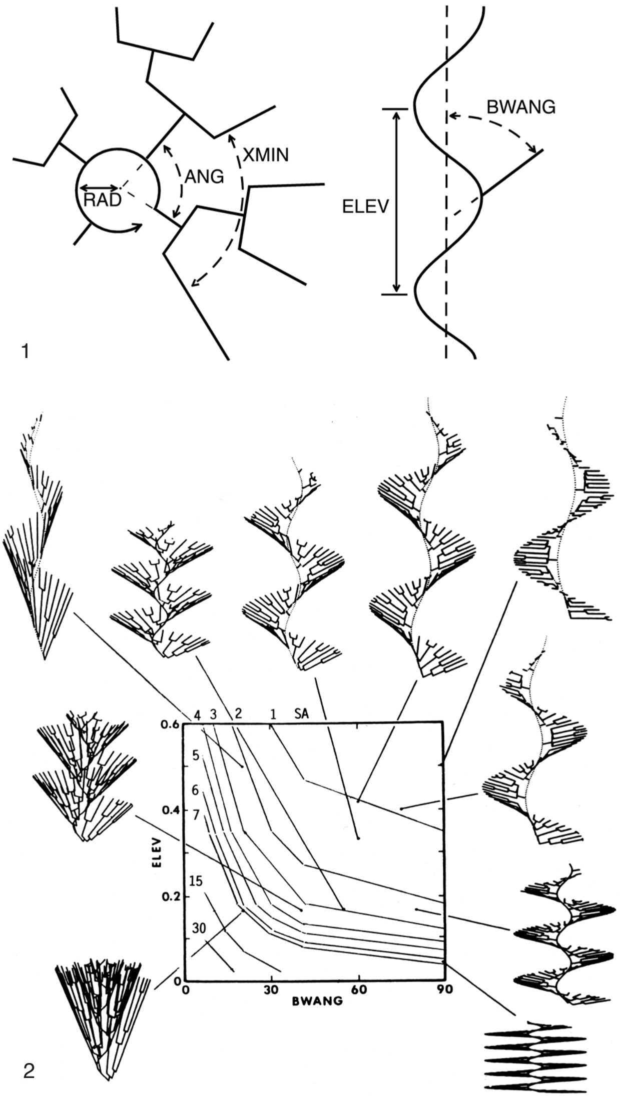

FIG. 50. Theoretical morphology of helical colonies (part 1); *1,* essential measured zoarial characteristics as portrayed by two simulations; see p. 76 for definition of RAD, ANG, XMIN, ELEV, and BWANG (new); *2,* a portion of the range of potential surface area *(SA)* of the filtration sheet comprising the branch whorls in this slice of morphospace in which XMIN is held constant and the variation is the result of interaction of BWANG and ELEV; see discussion on p. 76–79 (adapted from McGhee & McKinney, 2000).

extend away from the central axis (XMIN). These five attributes can be programmed as a suite of variables to simulate colony morphology of *Archimedes* and other helical colonies (McKinney & Raup, 1982; Raup, McGhee, & McKinney, 2006). Simulations demonstrated that overall colony morphology is most affected by changes in ELEV (Fig. 50.2, Fig. 51.2) and BWANG (Fig. 50.2–50.3, Fig. 51.1), and the openness per unit area on the branch filtration sheet is determined by XMIN (Fig. 51.1–51.2).

The total mesh surface area in any given colony is determined by several interacting

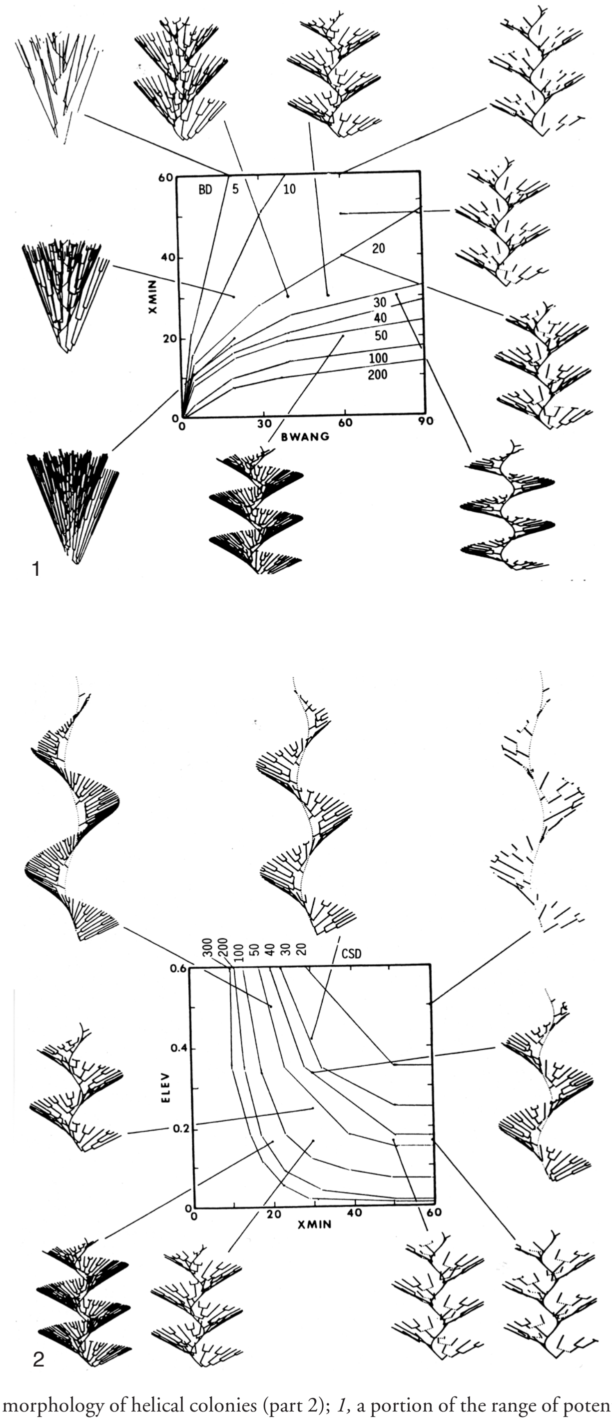

FIG. 51. Theoretical morphology of helical colonies (part 2); *1,* a portion of the range of potential branching density (*BD*) in this slice of morphospace in which ELEV is held constant and the variation is the result of interaction of BWANG and XMIN; *2,* a portion of the range of potential colony structural density (CSD) in this slice of morphospace in which BWANG is held constant and the variation is the result of interaction of ELEV and XMIN (see discussion on p. 76–79) (adapted from McGhee & McKinney, 2000).

attributes: diameter of the colony, total height of the colony, spacing between successive whorls of branches, and the angle between the branch whorls and the axis of the colony. For standardizing comparison of fundamental geometries among colonies of various sizes, characteristics of an equal cylindrical portion of space occupied within a colony can be compared by specifying a uniform diameter and height and computing different values for ELEV, BWANG, and XMIN within that volume. In the study that explored these issues (McGhee & McKinney, 2000), an arbitrarily chosen standard colony diameter (*D*) was used to define an equivalent length portion of the height (*AH*) of a colony (Fig. 44.5), and branch whorls were modeled as right-circular cones stacked at spacing equal to ELEV.

The least area occupied by a single branch whorl in the standardized cylinder would be generated when BWANG is 90° and can be approximated by a disk of diameter *D*. With progressive decrease of BWANG toward 0°, a cone of diameter *D* has greater and greater surface area that can be expressed as a dimensionless number (A_W) by dividing the calculated area of the cone by the area of the disk of diameter *D*. (Formulae for determining A_W and other dimensionless numbers used in Fig. 50.2 and Fig. 51 can be found in McGhee & McKinney, 2000.) The number of branch whorls per standardized cylinder (W_{AH}) is determined by dividing the distance *AH* by the measured length of ELEV characteristic of the colony. The surface area (*SA*) of the fenestrate meshwork within the standardized cylinder for any Archimedes or other helical colony is determined by the following equation: $SA = (W_{AH})(A_W)$.

Figure 50.2 has the *SA* field plotted within the theoretical morphospace for the full range of possible BWANG and a portion of possible ELEV. Note that the largest *SA* is found in the lower left, corresponding with closely spaced whorls that have a very small angle to the colony axis, and that *SA* decreases toward the upper right, corresponding with the increased distance between whorls that are nearly perpendicular to the colony axis.

The number of terminal branches within a whorl (B_W) is determined only by the distance maintained between adjacent branches and the diameter of the colony or of a specified cylindrical portion of the colony. For example, the planar *Septopora* colony illustrated in Figure 48.2 has a narrow range of variation in distance between centers of adjacent branches, so that as the colony grew, new branches were added at a constant rate relative to increase in the colony radius (Fig. 48.3, dot series b). If XMIN of the colony had been greater, there would be fewer branches along the colony perimeter, and if XMIN had been smaller there would have been more branches. If the *Septopora* colony had a 360° perimeter, as in an *Archimedes* branch whorl, rather than a 180° perimeter, there would have been double the number of branches. If one then conceives of the colony being a cone of the same diameter rather than as a disk, the number of branches remains the same even though the length of each branch segment must be longer in order to reach the top of the cone rather than it woiuld be in a flat plane (i.e., a disk). The number of branches is determined solely by the distance between branch tips at the colony perimeter, whether that perimeter is around a flat plane or at the top of a high cone.

Branching density (*BD*) within a helical colony was defined by McGhee and McKinney (2000) as "the number of branches contained in a filtration-sheet whorl divided by the surface area of the whorl," or $BD = B_W / A_W$.

The calculated *BD* field is superimposed on the theoretical morphospace for the full range of possible BWANG and a portion of possible XMIN in Figure 51.1. *BD* decreases with decreasing BWANG (best seen along the top edge of the field) and with increasing XMIN (best seen along the right edge of the field.)

Colony structural density (*CSD*) can be defined as the number of branches present

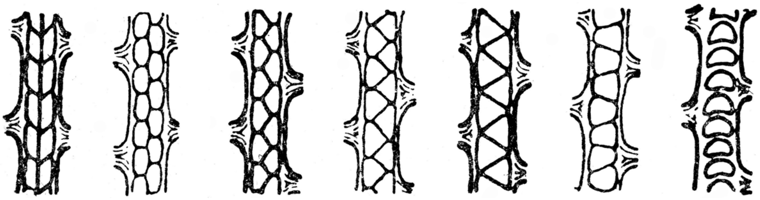

FIG. 52. Ranges of autozooecial shapes in biserial fenestellids, as seen in deep endozonal tangential sections (adapted from Nekhoroshev, 1932).

in a standardized cylindrical portion of a helical colony (McGHEE & McKINNEY, 2000). *CSD* is a function of the number of branches present in a whorl, which is determined by XMIN and the diameter of the standardized cylinder, and of the number of whorls present, which is determined by ELEV and height of the standardized cylinder, or *CSD* = $(B_W)(W_{AH})$.

The calculated *CSD* field is superimposed on the theoretical morphospace for a portion of possible ELEV and a portion of possible XMIN in Figure 51.2. *CSD* increases with decreased ELEV and XMIN and decreases with increased ELEV and XMIN. That is, the densest colonies occur in the lower left corner and the most open colonies in the upper right corner of Figure 51.2.

AUTOZOOECIAL CHAMBER SHAPE

Although ULRICH studied fenestrate bryozoans in thin section, he concluded (1890, p. 330–331) that their "individual zooecia ... are so uniform that no recognizable peculiarities can be said to distinguish those of one genus from those of another." By 1932, however, NEKHOROSHEV had illustrated a graded, and presumed evolutionary, sequence of endozonal chamber basal sections that ranged from elongate rectangular to transversely elongate crescentic (Fig. 52). Though depth of sections produces a limited range of differing cross-sectional shapes of chambers (Fig. 53), those who have studied fenestrates in thin section consider chamber shape as seen in tangential sections to be of taxonomic importance at the species and genus level (e.g., MOROZOVA, 1974, 2001; SNYDER, 1991a; REID, 2003).

Almost all fenestellids that are characterized by two rows of zooecia per branch have autozooecial endozonal chambers that are elongate parallel with the branch axis, have the shortest diameter perpendicular to the branch axial plane and parallel with the reverse wall (basal plate), and have an

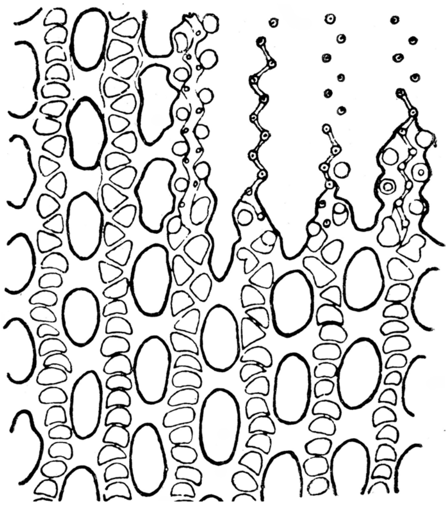

FIG. 53. Drawing of tangential thin section of *Lunofenestella ferganensis* (NEKHOROSHEV in NIKIFOROVA, 1933) that cuts through the deep endozone *(left and bottom)* and through the zigzag row of spines that project above the obverse surface *(upper right)*. The basal cross-sectional shape of autozooecia is transversely crescentic, but as seen in an arc-shaped band between the deep endozone and the obverse spines, autozooecia diverge alternately right and left and develop triangular cross sections in the shallow endozone before passing through the obverse exozone as distal tubes with circular cross sections (adapted from Nekhoroshev, 1932).

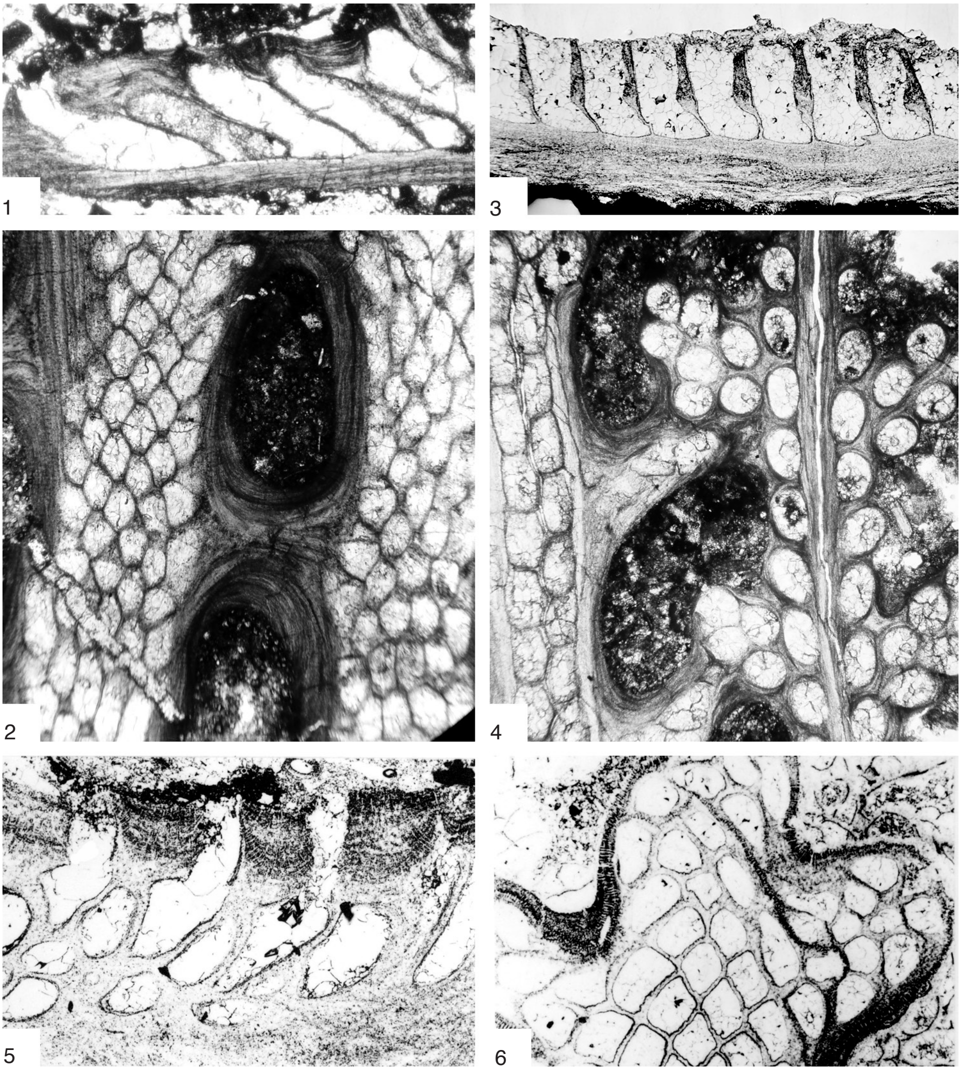

Fig. 54. Variation in non-fenestellid fenestrates. *1–2,* polyporids; *1, Parapolypora spinifera* (Ulrich, 1890), Mississippian (Visean–Serpukhovian), Sloans Valley, Kentucky, USA, USNM 542921, longitudinal section through tubular autozooecia extending at approximately 45° angle from reverse wall to obverse surface, ×30 (new); *2, Pustuloporina cestriensis* (Ulrich, 1890), Mississippian (Visean–Serpukhovian), Litchfield, Kentucky, USA, USNM 182787, tangential section through endozone filled with rhombic to variably polygonal cross sections of autozooecia, ×30 (adapted from Tavener-Smith, 1969); *3–6,* acanthocladiids; *3–4, Septopora intermedia* Ulrich, 1890, Mississippian (Visean–Serpukhovian), Litchfield, Kentucky, USA, USNM 496175; *3,* longitudinal section through autozooecia, extending almost vertically from reverse wall to obverse surface, ×30 (adapted from McKinney, 2002); *4,* tangential section through endozone *(left),* with pentagonal cross sections of autozooecia and exozone *(right),* where distal tubes of autozooecia have nearly the same cross sectional size as endozonal chambers, ×30 (new); *5–6,* amphora-shaped autozooecia of the acanthocladiid, *Adlatipora*; *5, Adlatipora* sp., Eiss Limestone, Permian (Sakmarian), Pottowatomie County, Kansas, USA, KU 54460aa, longitudinal section through autozooecia that expand in diameter from base to top of endozone and abruptly contract into a vertical distal tube through the obverse exozone, ×50 (adapted from Gautier, Wyse Jackson, & McKinney, 2013); *6, Adlatipora fossulata* Gautier, Wyse Jackson, & McKinney, Cathedral Mountains Formation, Permian (Kungurian), Glass Mountains, Texas, USA, KU 54603L, tangential section through endozone with rhombic to distally convex cross sections of autozooecia, ×30 (adapted from Gautier, Wyse Jackson, & McKinney, 2013).

intermediate diameter perpendicular to the reverse wall. A narrowed tube extends from the distal end of the inflated endozonal portion of the chamber, through the exozone, to open frontally (on the obverse surface). The wide diversity of chamber shapes (Fig. 52) were developed within this constructional limitation. The basal shape of fenestellid endozonal chambers is determined primarily by the degree of overlap of the zooecia across the branch midline, from forms with no overlap and quadrangular- or parallelogram-shaped basal shapes through progressively greater overlap resulting in pentagonal, trapezoidal, triangular, and transversely crescentic basal shapes. Crescentic basal shapes are characteristic of taxa with chamber bases placed uniserially along branch midplanes, though the chambers diverge alternately toward right and left sides in the vicinity of the transition from endozone to obverse exozone (Fig. 53).

At bifurcations, the endozonal portions of centrally placed fenestellid autozooecia do not have typical shapes. They have a tendency towards triangular or irregularly polygonal cross sections.

Endozonal portions of polyporid autozooecia tend to be elongate, extending directly at an acute angle from the basal plate or extending along the basal plate for only a short distance before reorienting toward the frontal surface, and they are polygonal in cross section (Fig. 54.1–54.2). Diameters parallel with the basal plate are roughly equal, or the proximal-distal diameter is slightly longer than the transverse. Most have hexagonal or rhombic cross section, with fewer having quadrangular cross sections.

The zooecia of pennireteporids and septoporids extend at or near 90° angles to the frontal surface, either arising directly or with a very short reclined portion (Fig. 54.3–54.4). The chamber shape in deep tangential sections varies from typically quadrangular or pentagonal to less commonly triangular crescentic or proximally tapered bean shaped.

Acanthocladiid zooecial chamber shapes are less well known than those of other fenestrate groups. In general, the endozonal portions of acanthocladiid zooecia are inflated, and the zooecia become narrower in the transition to the exozone, extending as a tube perpendicular to the obverse surface (Fig. 54.5–54.6). Endozonal chambers vary from highly inflated, with or without polygonal cross sections proximally and initially recumbent, to modified amphora shaped. The latter are virtually erect for their entire length with gentle inflation of the endozonal portion, closely appressed against the inflated distal wall of the preceding zooecia, and therefore concave on the proximal side.

The presence of hemisepta (Fig. 5.1) in some fenestellids results in variably constricted chambers depending on their placement and extent. The shape of zooecial chambers could also be modified by resorption (Gautier, 1972, p. 48; Gautier, Wyse Jackson, & McKinney, 2013, fig 2.6), or by local deposition of a laminar lining (Fig. 10.1–10.2).

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