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External Morphology of the Paleozoic Stromatoporoidea: Shapes and Growth Habits

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PART E, REVISED, VOLUME 4, CHAPTER 9B: EXTERNAL MORPHOLOGY OF THE PALEOZOIC STROMATOPOROIDEA: SHAPES AND GROWTH HABITS

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INTRODUCTION

NICHOLSON (1886, 1889, 1891, 1892), in his great pioneering work on British Paleozoic stromatoporoids about 120 years ago, was the first to differentiate clearly between basic shapes and growth habits in stromatoporoids, despite the overwhelmingly wide range of variability in external form they exhibit. He illustrated a number of forms, based mainly on rather incomplete, fragmentary skeletons, ranging from moundlike and laminar to dendroid and cylindrical forms (Fig. 1). NICHOLSON (1886, p. 27) also recorded the presence of “a concentrically wrinkled imperforate epitheca” and noted a small centralized attachment area on some bases of moundlike and laminar stromatoporoids, comparable with the holothecate massive or laminar species of favositid and alveolitid tabulate corals. These overall similarities suggested to NICHOLSON (1886) that stromatoporoids, like colonial corals, adopted similar modes of life, some being mainly free-living forms, and others living as habitual encrusters. Also, a few individual species were considered to have switched between free-living and encrusting modes of growth, depending on changes in environmental conditions. The cylindrical and dendroid stromatoporoids adopted another lifestyle category that NICHOLSON (1886) compared with the growth of some ramose species of tabulate corals. Few later workers on stromatoporoids followed NICHOLSON’s (1886) lead of differentiating between basic shapes (descriptive features) and growth habit categories (mainly interpretative) in assessing their data on external form. It is important that descriptive and interpretative aspects of external growth form of stromatoporoid skeletons be recorded separately, and as far as possible through their growth histories.

The Stromatoporoidea have only been featured once previously in a *Treatise* volume; that was some 50 years ago, and in a coelenterate volume. At the time, LECOMPTE (1956) recognized the group as being an extinct, problematic, reef-forming order, exhibiting closest relationships to the coelenterate class Hydrozoa, and having a calcareous skeleton described as variable, composed of “irregular rounded masses, relatively thin sheetlike expansions, and branched or unbranched subcylindrical structures” (LECOMPTE, 1956, p. 108). In other words, the external morphology was typified by mainly domical and laminar shapes, as well as unbranched to branching forms. LECOMPTE also reported the layered appearance of latilaminae showing where the skeleton was broken or weathered, the presence of stellate grooves or ridges representing traces of astrorhizae on terminal growth surfaces, and astrorhizae, sometimes in association with mamelons (LECOMPTE, 1956, fig. 89–90, 92.1). Both astrorhizae and mamelons are now interpreted as integral parts of the exhalant water system (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 9F, Functional Morphology, STEARN, 2010).

The calcareous skeleton of stromatoporoids represents a base that was precipitated from the underside of the thin, mantling veneer of living tissue, or from within the living part of the uppermost growth surface (STEARN, 1975; and see *Treatise Online,* Part E, Revised, vol. 4, Chapter 9F, Functional Morphology, STEARN, 2010). As it grew upward, the living tissue became progressively elevated above the substrate, and this facilitated the sponge’s filter-feeding activities. The pattern of growth, however,

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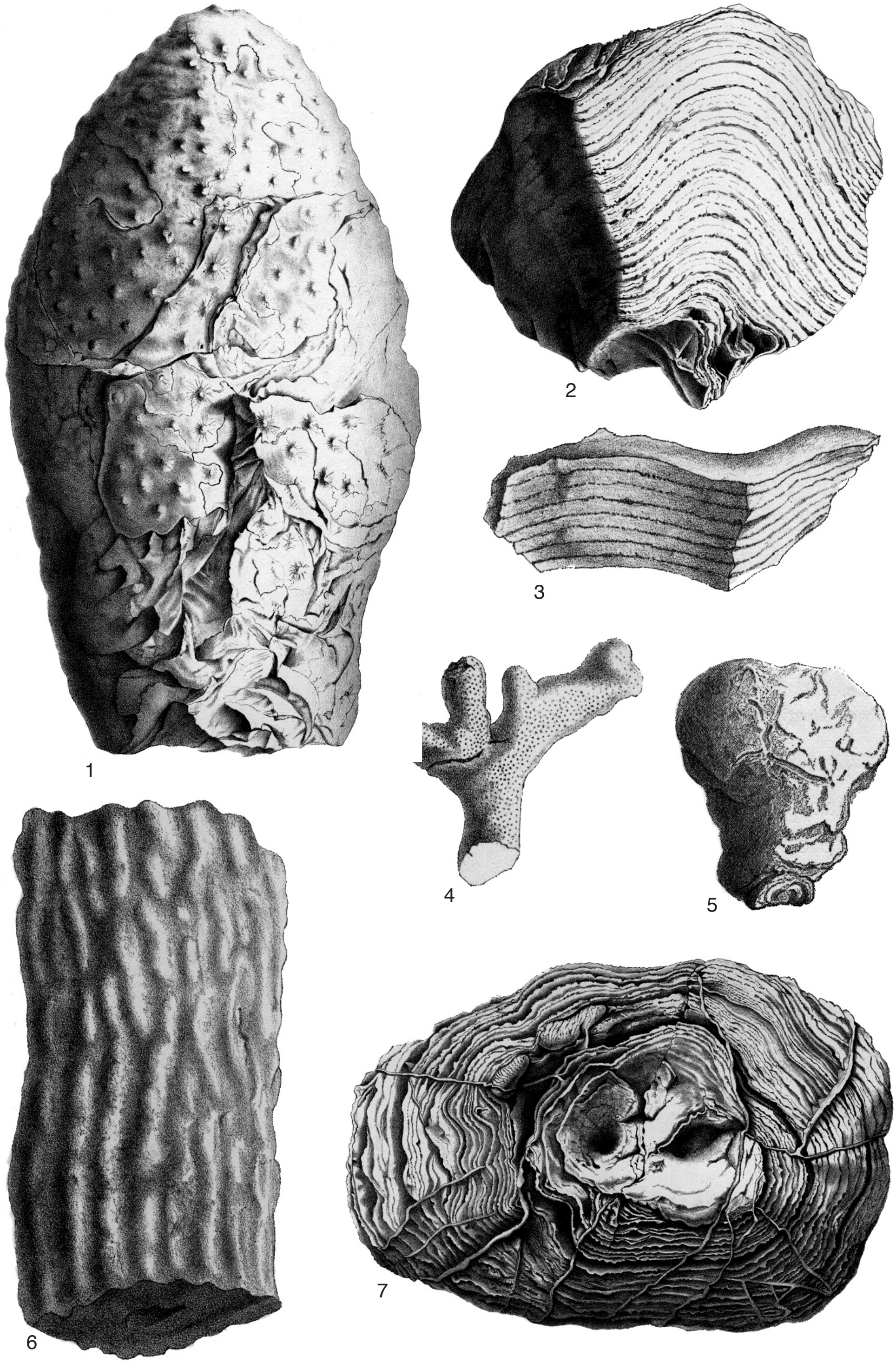

FIG. 1. *(For explanation, see facing page).*

was commonly disrupted by physical disturbance, such as sediment influx and turbulence, and sometimes by competition or predation pressures from associated organisms. The stromatoporoid animal produced a skeletal form that was governed largely by a combination of the sponge's functional and genetic makeup and its response to the environment. The external shape of the skeleton was, at least in part, an expression of the existing environmental controls, and therefore, of some potential for analyzing and interpreting paleoecological changes (Kershaw, 1984, 1990).

This contribution includes a full range of topics on the external morphology of stromatoporoids, the more descriptive parts being concerned with gross morphology (overall shapes) and surface features; some interpretative aspects of growth, development, and living habits are also considered, which impinge for the most part on the paleoautoecology of the group.

APPROACHES TO STUDY

Since the late 1960s, paleoecologists and sedimentologists have been largely responsible for advancing the studies of external stromatoporoid shapes, especially in developing field-based paleoecological and paleobiological approaches. The most common practice has been to study the stromatoporoid-bearing carbonate outcrops in the field and record the outcrop details of their shapes from exposed surfaces of broken or cut skeletons. Commonly, the skeletons are sectioned, usually longitudinally, in quarries and cliffs. This contrasts markedly with the main emphasis of work on stromatoporoids through nearly a century and a half, which has been taxonomically based, concentrating primarily on internal features using oriented thin sections to define and classify the taxa.

Where outcrops expose stromatoporoid morphologies in only two-dimensional views, it is commonly not easy to classify the three-dimensional shapes of skeletons; this applies particularly to reef-building forms (Kershaw, 1984). There are also practical difficulties in extracting large skeletons from matrices of well-lithified carbonate rocks intact, so, unfortunately, whole specimens are rarely collected. Where skeletons are intersected in cores of subsurface carbonate reefs, they are invariably incomplete, and their overall shape is often difficult to interpret from the core surfaces alone. Hence, some caution needs to be exercised in interpreting results of studies of external shapes of stromatoporoids, for example, based only on cores drilled in oil exploration work of subsurface reservoirs in Devonian carbonate reefs (Murray, 1966; Fischbuch, 1968; Noble, 1970; Embry & Klovan, 1971).

Stearn (1975, 1982) has previously reviewed aspects of studies of stromatoporoid

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Fig. 1. Representative stromatoporoid growth forms illustrated by H. A. Nicholson using lithographs and wood engravings that were published between 1886 and 1891; *1,* large, tall, bulbous form with external surface covered by small mamelons marking centers of astrorhizae in *Actinostroma stellulatum* Nicholson, Middle Devonian, Chircombe Bridge Quarry, Newton Abbott, Devon, England, ×0.5 (Nicholson, 1889, pl. 15, originally reproduced at ×1); *2,* incomplete specimen of a domical representative of *Stromatopora concentrica* Goldfuss, showing well-defined latilaminae on broken surfaces, but the overall shape is difficult to determine, Middle Devonian, Gerolstein, Germany, ×0.5 (Nicholson, 1891, pl. 21,*1,* originally published at ×1); *3,* fragmentary specimen of presumed low profile (laminar or low domical) sample of *S. concentrica* that exhibits flat-lying latilaminae; from the same stratigraphic interval and locality as view *2,* ×1 (Nicholson, 1886, pl. 11,*15,* ×1); *4,* portion of a branching, probably dendroid, stromatoporoid identified by Nicholson as *Stachyodes verticillata* McCoy; Middle Devonian, Hebborn, Paffrath district, Germany, ×1 (Nicholson, 1886, pl. 8,*9,* ×1); *5,* bulbous, somewhat pyriform-shaped stromatoporoid that Nicholson assigned to *Parallelopora capitata* Goldfuss, same stratigraphic interval and locality as view *4,* ×1 (Nicholson, 1891, p. 197, fig. 26, ×1); *6,* segment of the cylindrical stromatoporoid *Aulacera nodulosa* (Billings) exhibiting large, elongated nodes in slightly sinuous, vertical rows, Upper Ordovician, Cincinnati Group, Marion County, Kentucky, United States, ×1 (Nicholson, 1886, pl. 8,*1,* ×1); *7,* undersurface view of stromatoporoid *Actinostroma clathratum* Nicholson that has been weathered and eroded to expose a concave central part, and flatter, outer part of concentric ridges representing growth layers; nature of central area suggests that initial growth developed on a topographic high of more lithified sediment and/or skeletal debris, Middle Devonian, Dartington, Devon, England, ×.05 (Nicholson, 1889, pl. 12,*1,* ×1).

shapes in applications by a number of workers through the late 1950s to 1970s of paleoecological zonations in the Devonian reef facies of western Canada. Fischbuch (1962), for example, differentiated reef, forereef, and lagoonal facies on the basis of the stromatoporoid shapes and lithological types. Attempts were also made to apply concepts of gross shape differences to recognize bathymetric changes in these Devonian reefs, viewing the so-called massive stromatoporoids as best adapted to the most highly turbulent environment of the reef crest, in contrast to lamellar stromatoporoids that were considered to be more indicative of deeper, quieter, forereef settings. However, in the bank-type model of Laporte (1967), lamellar stromatoporoids were interpreted as occupying a position inshore from the massive stromatoporoids (see Dolphin & Klovan, 1970, p. 325). Although some workers established that shapes change in a systematic way across reef complexes (Murray, 1966; Fischbuch, 1968; Leavitt, 1968), controversy remains on the issue of the environmental significance of laminar forms. Stearn (1975, p. 1637) considered that acceptable conclusions could be drawn about the following: (1) that dendroid *Amphipora ramosa* occupied lagoonal environments, but probably did not act as a sediment baffle; (2) small, bulbous stromatoporoids lived in quiet waters; (3) large, domical (massive) forms of irregular shape were associated with the reef crest; and (4) the more robust dendroid genus, *Stachyodes,* was thought to have occupied positions on both sides of the reef crest. However, the status of laminar forms remains equivocal, not necessarily restricted to either quiet-water forereef or turbulent reef-crest settings. These laminar shapes are more likely to remain *in situ* in more turbulent conditions, but then they can also be reworked into forereef slopes.

Stearn (1982) further questioned the validity of using shapes to interpret the paleoenvironments of Paleozoic reef complexes, given that, in terms of the shapes of modern reef organisms (e.g., scleractinian corals), such complex patterns of distribution existed and they were not specific guides to the environments. The patterns of distribution of stromatoporoid shapes across ancient reefs may similarly have rather doubtful paleoenvironmental significance, unless the analyses are properly focused on the documentation of individual species: the taxonomic identification based on internal structures, and the shape related to paleoenvironmental factors, as well as the genetic make up of the species. Ideally, environmental analyses using the shapes of stromatoporoids should be combined with taxonomic identification of species based on their internal features and an understanding of the genetic composition of the species.

Kershaw's (1981) study of the taxonomically well-defined stromatoporoid species and the range of shapes they exhibit in one specific environmental setting (a Silurian biostrome in Gotland), allowing genetic inheritances to be differentiated from environmental influences in these species, is a good example of the type of research that is needed. The three most abundant species in the Gotland biostrome reflect two markedly different genetic responses by the species in the one biostromal habitat: one shows laminar to low domical shapes, and the other two exhibit high domical to bulbous forms. Each species also exhibits a range of specimen shapes within the biostrome that represents the ecophenotypic plasticity, or the individual responsiveness, of each species to the localized environmental fluctuations within the biostrome.

Stromatoporoids from shallower biostromal deposits, and deeper, level-bottom, argillaceous (marly) limestones, like those exposed along coastal sections in the Silurian of Baltoscandia (the successions on the Swedish island of Gotland and in northwestern Estonia) are uniquely well preserved and accessible. The skeletons can be relatively easily extracted whole for study in three dimensions in places, because they are preserved in thin carbonate units interbedded within a friable argillaceous matrix. These stromatoporoid-bearing Paleozoic carbonate sequences have proved particularly useful for establishing the range of skeletal morphotypes, and for defining models that employ stromatoporoid shapes in paleoenvironmental analyses (Kershaw, 1984, 1990; Kershaw & Keeling, 1994), though the results cannot be completely validated until the genetically related influences on these stromatoporoid species are more fully understood (Stearn, 1982).

RECOGNIZING STROMATOPOROID SHAPES

GENERAL RELATIONSHIPS

Many workers have attempted to establish an acceptable terminology for classifying the chief skeletal shapes (e.g., Noble, 1970; Abbott, 1973; Kershaw & Riding, 1978, 1980; Stearn, 1983, 1984; Kershaw, 1998), singling out a comparatively small number of major groups of forms. The scheme recognized by Kershaw (1998) included the terms: laminar, tabular, domical, columnar, bulbous, dendroid, expanding-conical, digitate, and irregular. Russian and Chinese workers have also restricted the number of names to more basic shapes. Bogoyavlenskaya (1984) identified laminar, approximately hemispherical, subspherical, irregular, subcylindrical, and dendritic; and Dong (2001) recognized broadly: massive (including a variety of spherical, hemispherical, columnar, or digitate) and tabular (single- to multilayered laminar or lens-shaped) forms. However, in a more detailed study of external forms of stromatoporoids from Middle Devonian reefs, Liu and Dong (1991) identified as many as 25 different shapes—massive forms (excluding columnar) that included both discrete (single-layered) and compound or composite (multilayered) types, as well as columnar, tabular (=laminar), dendritic (=dendroid) types, and encrusting types as a separate category—but most of these were just variations of more basic shapes. No completely consistent worldwide usage of terms for the description of external shapes has been adopted previously. It is hoped therefore that the following set of proposals for a Paleozoic stromatoporoid shape classification will be widely accepted.

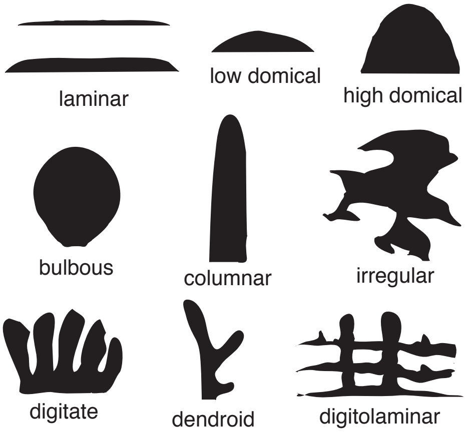

Fig. 2. Main shapes of Paleozoic stromatoporoids depicted as silhouettes in longitudinal section. Eight principal categories are recognized, and the domical shapes are further subdivided into two subgroups (see text for further discussion; Webby & Kershaw, new).

It is important here to characterize the bulk of Paleozoic skeletons consistently in terms of one or another of the six basic, geometrically distinct shapes (**laminar, domical, bulbous, columnar, digitate,** and **dendroid**), or as composites of these basic forms, for example, **digitolaminar** and **irregular** (Fig. 2). Only one other distinctive composite is known, an inferred foliaceous shape (Wood, 2000). This has a restricted Upper Devonian occurrence in Paleozoic sequences (see below). Most skeletons exhibit predominantly one type of external morphology through all mature stages of growth, but sometimes gradational relationships exist between two or more distinctly different shapes in the one skeleton, making such a classification difficult to apply. In a sense, the shapes are part of a continuum from laminar through various intermediates to columnar, digitate, and dendroid, reflecting differences in the relative rates of skeletal growth being secreted between its

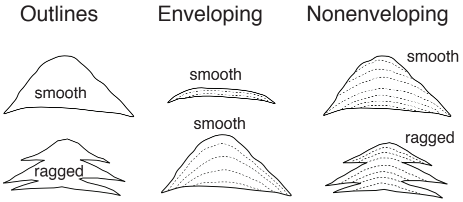

FIG. 3. Schematic representations in longitudinal section that illustrate relationships at lateral margins of stromatoporoid skeletons between smooth or ragged types of external surface growth and enveloping or nonenveloping styles of internal latilaminate growth (adapted from Kershaw, 1998, fig. 7, *partim*).

central axis and extremities by the mantling living tissue of the organism. The simple computer simulations presented by SWAN and KERSHAW (1994) are perhaps illustrative of the growth patterns.

The term laminar should apply mainly to comparatively thin, laterally extensive, flattened to undulating, sheetlike forms. It should also include sheetlike skeletons that were classified previously as tabular bodies. Where possible, older, more mature stages of growth should be identified, because many stromatoporoid skeletons developed initially from a laminar base and then grew to maturity as different shapes (e.g., domical, columnar, digitate, or irregular). The term domical is recognized here as further subdivided into two groups: the **low domical** and **high domical** subgroups (Fig. 2). The high domical subgroup here combines the previously separated high and extended domical categories of KERSHAW and RIDING (1978) and KERSHAW (1990, 1998), and the separated high, extended and highly extended subdivisons of LUCZYNSKI (2005). LUCZYNSKI also proposed low and high subgroups for the bulbous category. The wider utility of LUCZYNSKI's subdivisions, however, have yet to be demonstrated. Irregular is a composite morphotype derived by renewed growth in different orientations after successive environmental disturbances on the sea floor. Digitolaminar is another composite shape involving alternations of laminar and columnar growth that may reflect episodic environmental events (possibly sudden changes in rates of sedimentation) or, in a few cases following WOOD (2000), may be related to an inherent growth style (see discussion of Primary Cavities, herein, p. 57).

In general, domical to laminar forms are characteristically the most abundant (and the largest) Paleozoic stromatoporoid shapes; irregular and bulbous forms are also moderately common, and columnar, digitate, dendroid, and digitolaminar types are overall much less abundant. One other distinctive, though very rare shape is also known to occur (see foliaceous shape in section on Combinations, herein, p. 39). Laminar to low domical forms are usually preserved intact with little or no evidence of transportation, whereas high domical and bulbous forms show a greater susceptibility to overturning and other sorts of disturbance due to current activity. Dendroid and columnar forms apparently grew in relatively quiet water environments, although they are mainly preserved as fragmentary stem or postlike skeletons, and their attachment bases are rarely found. The few specimens recognized as attachment bases suggest that the forms lived only partially stabilized on an unconsolidated substrate. The majority of these skeletons were broken from their bases and either locally toppled or swept away to other depositional sites, dependent on the intensity of the intermittent storm activity.

SMOOTH AND RAGGED SKELETAL MARGINS

KERSHAW and RIDING (1978) characterized all laminar and domical stromatoporoids as having either **smooth** or **ragged** skeletal outlines (Fig. 3). The mainly laminar and low domical forms developed a ragged appearance, as seen in longitudinal cross section, when successive influxes of sediment caused growth interruptions of the lateral margins of skeletons (KERSHAW, 1993, fig. 2c,e–f). For example, the well-developed ragged margins of stromatoporoids from certain level-bottom depositional settings were attributed to a pattern of episodic sedimentary influxes (KERSHAW, 1984). The structures are superficially like the rejuvenescences of corals (SCRUTTON, 1998) caused by episodes of stress-influenced growth, perhaps related to annual cyclicity. The rhythmic changes in stromatoporoids are apparently related to discontinuities that bounded latilaminae, but these have not been demonstrably shown to represent annual accretion events (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 9F, Functional Morphology, STEARN, 2010). YOUNG and KERSHAW (2005, pl. 1,*6;* pl. 4,*4,6*) illustrated a few examples of stromatoporoids that clearly show these skeletal relationships, each latilamina being bounded above and below by growth interruption surfaces that can usually be traced laterally into the ragged, sediment-filled, tongue- or wedgelike inclusions at the margin (Fig. 4, Fig. 5.1). High domical (stacked, inverted, saucer, bell, and mushroom shaped), bulbous, columnar, and irregular morphotypes (KAPP, 1974) occasionally also exhibit ragged margins, but such elevated shapes more commonly display smooth outlines.

WOOD (2000, p. 700) suggested that raggedness (or production of laminar outgrowths) in Devonian stromatoporoids may, alternatively, be part of an inherent growth strategy. WOOD referred to cases of laminar and domical stromatoporoid individuals that had responded to localized death of areas of their living surface by producing laterally updomed growth structures with accompanying large primary cavities over the substrate (Fig. 5.2; and see Fig. 10). Such features, and the characteristic raggedness, developed in response to the intrinsic growth style, with the episodic engulfment of sediment initiating the development of complex, variable, and elevated patterns of growth. The other ragged forms were subjected to episodic swamping of sediment onto flanks of their skeletons, and they mainly produced phases of lateral growth (Fig. 5.1). KERSHAW, WOOD, and GUO (2006) have shown them, in general, to include the ragged-margin Silurian stromatoporoids. They do not form large primary cavities, so laminar outgrowths did not grow above the substrate, although partial scouring did occur beneath skeletal margins; and in some places, whole skeletons were moved, with associated secondary subskeletal voids forming as a result of storm-generated events (KERSHAW, 1980; and see section on Cavity Spaces, herein, p. 57).

ENVELOPING AND NONENVELOPING STYLES

Relationships across successive latilaminae at the margins of the skeleton may be either enveloping or nonenveloping (Fig. 3). The **enveloping** condition occurred where a succeeding latilamina entirely overlapped a previous latilamina at the lateral margin (i.e., the skeleton is enveloping with smooth margins). The smooth enveloping form developed where the living surface of the stromatoporoid sponge completely mantled the top and lateral surfaces of the skeleton (Fig. 6). The condition was maintained as long as the sponge continued its upward and outward growth, and the lower parts of the lateral margin remained free of accumulating sediment. The **nonenveloping** condition occurred when the succeeding latilamina failed to completely overlap a preceding latilamina (i.e., the skeleton is nonenveloping, with either smooth or ragged margins). These nonenveloping associations formed when the living surface: (1) became more localized, possibly as sediment accumulation around the lower parts of lateral margins, restricting the overlap of successive growth units, as in smooth or ragged low-domical shapes; or (2) became more elevated and laterally restricted to form high domical, bulbous, or columnar morphs to localize the living surface at higher levels where nutrients and oxygen from the water column could be more readily accessed. Laminae may also exhibit enveloping–nonenveloping relationships, and along their edge zones, they were capable of sealing off adjoining gallery spaces from the associated sediment. The enveloping–nonenveloping terminology is, however, not always easy to apply, unless substantially complete stromatoporoid skeletons are collected and sectioned longitudinally (vertically) though their centers.

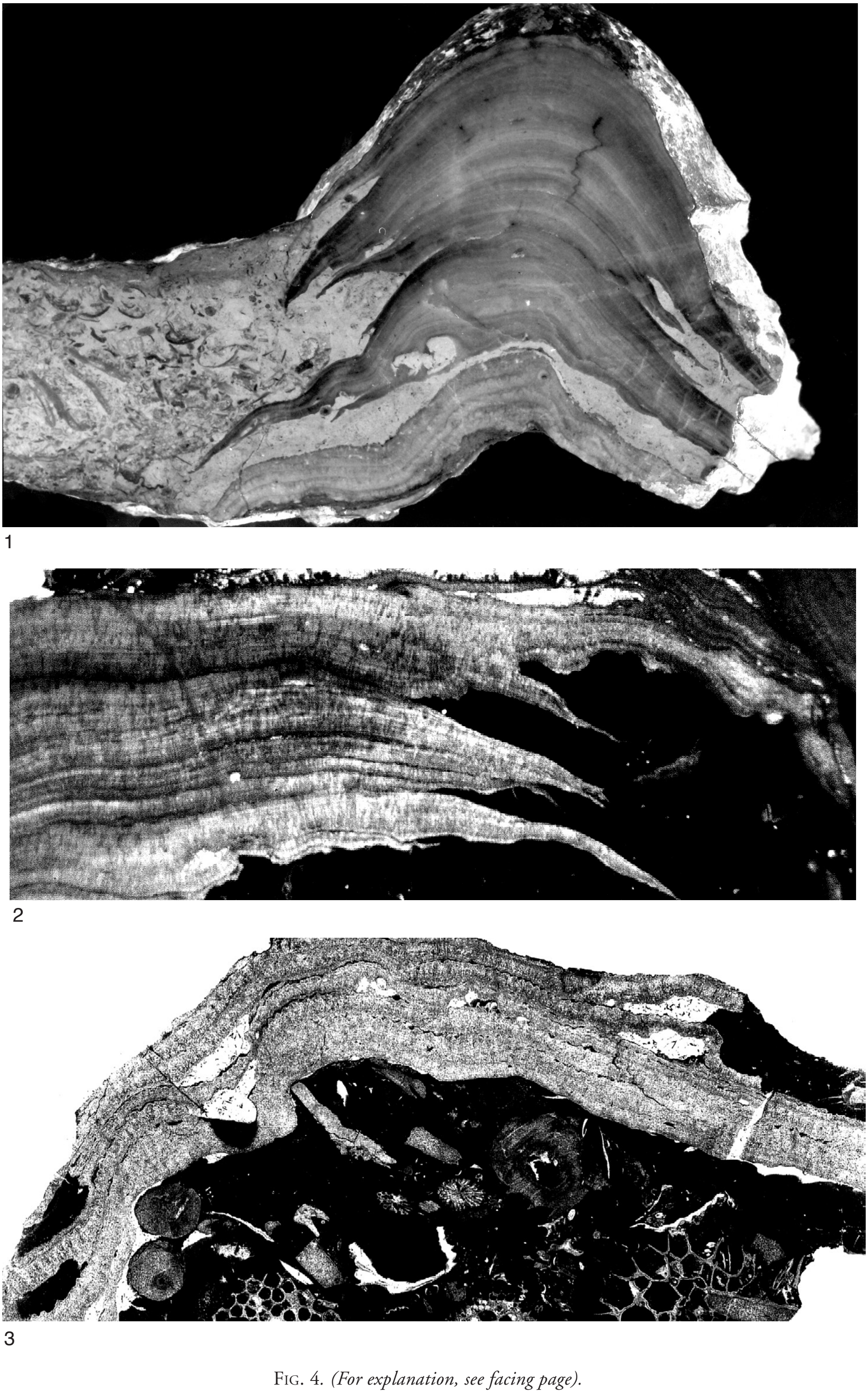

FIG. 4. *(For explanation, see facing page).*

James and Bourque (1992, p. 328, fig. 9) depicted the enveloping and nonenveloping forms as resulting from different positions of the living surface of the organism at the time of growth. The nonenveloping, ragged skeleton continued to maintain its living surface near the substrate, and remained more stable because it was being progressively buried by sediment as it grew, whereas the enveloping smooth skeleton was capable of maintaining a more elevated living surface, though it was less stable, and consequently more likely to be displaced. Most smooth-margined stromatoporoids, however, exhibit an enveloping style in their lower portions, and then a nonenveloping type in upper parts; consequently, they cannot be classified exclusively as belonging to either one type or the other. The reasons for this change are not entirely clear, but it seems that: (1) initial enveloping-type growth was mainly associated with stabilization and establishment of the skeleton on the substrate; and then, (2) the focus narrowed to topographically more elevated, nonenveloping growth, perhaps owing to lower parts suddenly becoming engulfed or swamped by sediment.

Most stromatoporoid growth forms can be subdivided broadly into two groups, based on: (1) whether they have a ragged margin with a nonenveloping style of growth; or (2) whether they show a smooth margin with enveloping and/or nonenveloping styles of growth. Many ragged types are laminar or low domical shapes, but they also include some high domical, and a few columnar or irregular forms. Smooth types are dominantly high domical, bulbous, and columnar shapes, as well as digitate and dendroid branching forms. What distinguishes most shapes with ragged margins from the shapes with smooth margins is the inclination of lateral ends of their latilaminae (and laminae): the latilaminae-laminae on the lateral flanks of ragged skeletons tend to be gently inclined, with angles up to 45° from the horizontal, whereas latilaminae-laminae at the lateral sides of smooth skeletons are characteristically inclined at angles greater than 45°, sometimes developing beyond 90° in bulbous forms so that the laminae curved inward, effectively becoming overhanging. Ragged margins developed because of growth interruptions between latilaminae, and episodic influxes of sediment accumulated as lateral tongues because the angle of repose of the sediment was less than 45°. Skeletons with smooth margins usually formed because sediment was unable to accumulate on steeply inclined lateral slopes; no sedimentation occurred on the adjoining substrate during the formation of the enveloping growth style, whereas episodic influxes of sediment were added to the adjacent sea floor during the production of a nonenveloping style.

The development of **coalescences** is another feature that was recorded by Kershaw (1990, p. 695, fig. 11) in the Silurian stromatoporoid species of the Kuppen biostrome on Gotland. A number of closely spaced, but initially separated, small specimens of one species merged as

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Fig. 4. *1,* Superposed laminar and domical stromatoporoid skeletons, separated by a thin, continuous layer of sedimentary rock; the first (*Pachystroma hesslandi*) has a gently upwardly arched, laminar shape, and the second (*Densastroma pexisum*), a ragged, domical form, composed of superimposed low domical growths; longitudinal section, Visby Formation, Wenlock, Kneippbyn, Gotland, Sweden, ×1.5 (Kershaw & Riding, 1978, fig. 2); *2,* laminar stromatoporoid skeleton of *Densastroma pexisum* (Yavorsky), with very ragged (or frayed) lateral margin; note growth interruptions associated with tapering wedges of sedimentary rock may be traced into interior of specimen, where they define successive latilaminae. Longitudinal section, BU-V-I-SK120, Visby Formation, Wenlock, Ireviken, Gotland, ×3 (adapted from Young & Kershaw, 2005, pl. 4,*4*); *3,* laminar skeleton of stromatoporoid *Pachystroma hesslandi* (Mori) is draped over a mud- and bioclast-rich substrate, incorporating a few crinoid ossicles, a rodlike skeletal clast, and possibly an intraclast; note also inferred primary cavities with sparite and geopetal infills, and more bluntly wedged margins that apparently relate to growth interruption bands and intervening latilaminae within the skeleton; thin section, BU-V-I-46, Visby Formation, Ireviken, Gotland, ×3 (adapted from Young & Kershaw, 2005, pl. 1,*6*).

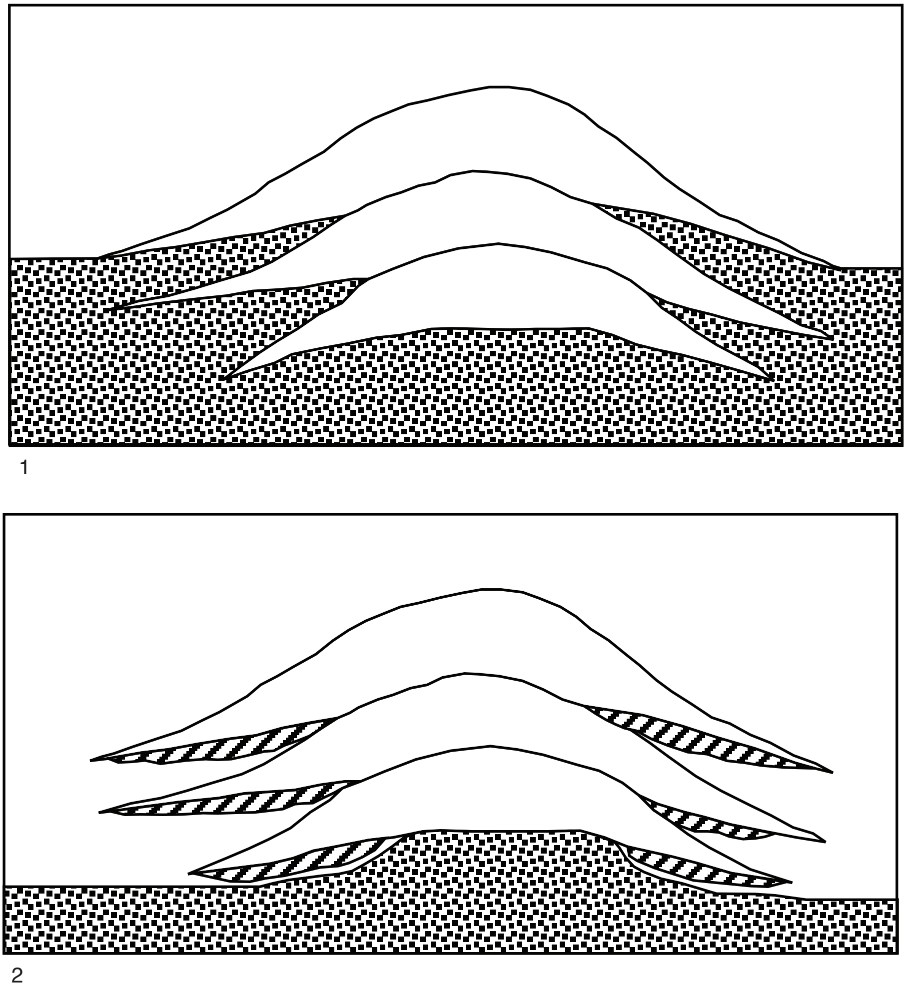

FIG. 5. Contrasting representations of how ragged margins of stromatoporoid skeletons may have formed. *1,* Marginal sediment wedges may be produced by periodic sediment swamping over lateral margins of the stromatoporoid, with consequent cessations of lateral growth. In recovery, after each phase of episodic sedimentation, the stromatoporoid grows laterally again over the newly accumulated sediment wedge. Each cycle of episodic sedimentation and renewed growth is repeated a number of times to produce the superimposed domical reconstruction shown; *2,* stromatoporoid developed three superposed low domical growths with ragged margins by the successive growth of raised, laterally extended outriggers above the substrate after each wholesale swamping episode. Apparently this type of growth developed in some stromatoporoids, for intrinsic reasons related to their genetic inheritance, and they can be identified because they created open undersurface sites (shelters or cavities) for the colonization of cryptic organisms (*oblique hachure*). Recognition of associated cryptic assemblages is therefore important in differentiating between the two growth styles of stromatoporoids (Kershaw & Webby, new).

they grew to form a much larger, coalesced skeleton. Examples included one species that produced a large, low, domical form, and another that established itself as a large, high, domical form. Neighboring specimens belonging to other species did not participate in these coalescences; they were either species specific (KERSHAW, 1998, p. 523), or perhaps even infraspecific, given that coalescences in some living sponges (e.g., CURTIS, 1979) only occur between individuals with matching strain types.

PARAMETERIZATION OF SHAPES

A few simple parameterization schemes have been proposed to assess external shapes in stromatoporoids (and other skeletal forms), but each has limited value because of sampling problems, large specimen size, and preservation of stromatoporoids. There are only a few localities, like Gotland, where oriented, uniquely well-preserved material can be sampled, sectioned, and measured (see KERSHAW & RIDING, 1978; KERSHAW, 1984). To be useful, whole specimens must be cut longitudinally along the growth axis, and this is seldom possible in more typical field occurrences. Selected specimens intersected on polished Devonian limestone blocks in public buildings of the city of Warsaw were the basis for LUCZYNSKI's (2005) study, not carefully oriented specimens from the field. Consequently, because solid limestones in the field or in public building facing stones limit the choice of orientation of section through a stromatoporoid, these approaches remain largely of theoretical value, but they are briefly outlined below.

KERSHAW and RIDING (1978) employed a triangular array to quantify, in two-dimensional profiles, the laminar, domical, and bulbous morphotypes (Fig. 7), on the basis that the three-dimensional shapes of stromatoporoid skeletons were approximately symmetrical about a vertical axis. The three parameters employed to measure the cross-sectional profiles were the vertical height (V), the basal length or diameter (B), and, arbitrarily at an angle of 25° to the vertical, the diagonal distance (D). This numerical scheme allowed the various morphs to be separated, using ratios of their vertical height to basal diameter, as follows: ratios of vertical height to basal diameter (V/B) of less than 0.1 grouped as the laminar forms, ratios between 0.1 and 0.5 classified as low domical, and ratios between 0.5 and 2.0 defined as high domical forms. The overall skeletal shape of the whole specimen could be determined using this method, but it remained impossible to quantify branching stromatoporoids using the given parameters.

Another comparatively simplified, shape-discriminating, parameterization method was introduced by YOUNG and SCRUTTON (1991, fig. 2–3) and SCRUTTON (1993, 1994, 1998, fig. 23) for depicting similarly shaped, compound Paleozoic corals (and stromatoporoids). A triangular diagram was also used, but with a different set of parameters, allowing the branching forms to be included in the array. Their three parameters were based on measuring the widths (W), overall heights (H), heights to the widest point (N), and lengths around the perimeter of the skeleton (P) of specimens. In their triangular diagram, the corals were depicted as having a continuum of variation and clearly differentiated main shape fields. The range of variation and differentiation mirrored the distribution of stromatoporoid shapes, and even the growth-form categories bore close similarities. Furthermore, it was possible to plot laminar and domical forms with a concave base in fields of the triangular diagram below the base line (as negative values)—an additional advantage for plotting stromatoporoid shapes.

LUCZYNSKI (2005) proposed a number of other ways of measuring stromatoporoid shape based on KERSHAW and RIDING's (1978) parameterization method. The parameters not only took account of the dimensions of the whole skeleton, but also changes in shape during successive phases of growth. This also involved specimens presumed to be oriented longitudinally (or vertically) through central axes and, where latilaminae were visible, allowing the way successive latilaminae were added (either in enveloping or nonenveloping growth units) above the basal surface, and their relationship to inferred levels of accumulating sediment on the adjacent sea floor, to be determined. The changes in skeletal growth of a specimen could be recorded by measuring length and height parameters for each successive latilamina. In addition, the burial ratio, that is, the proportion

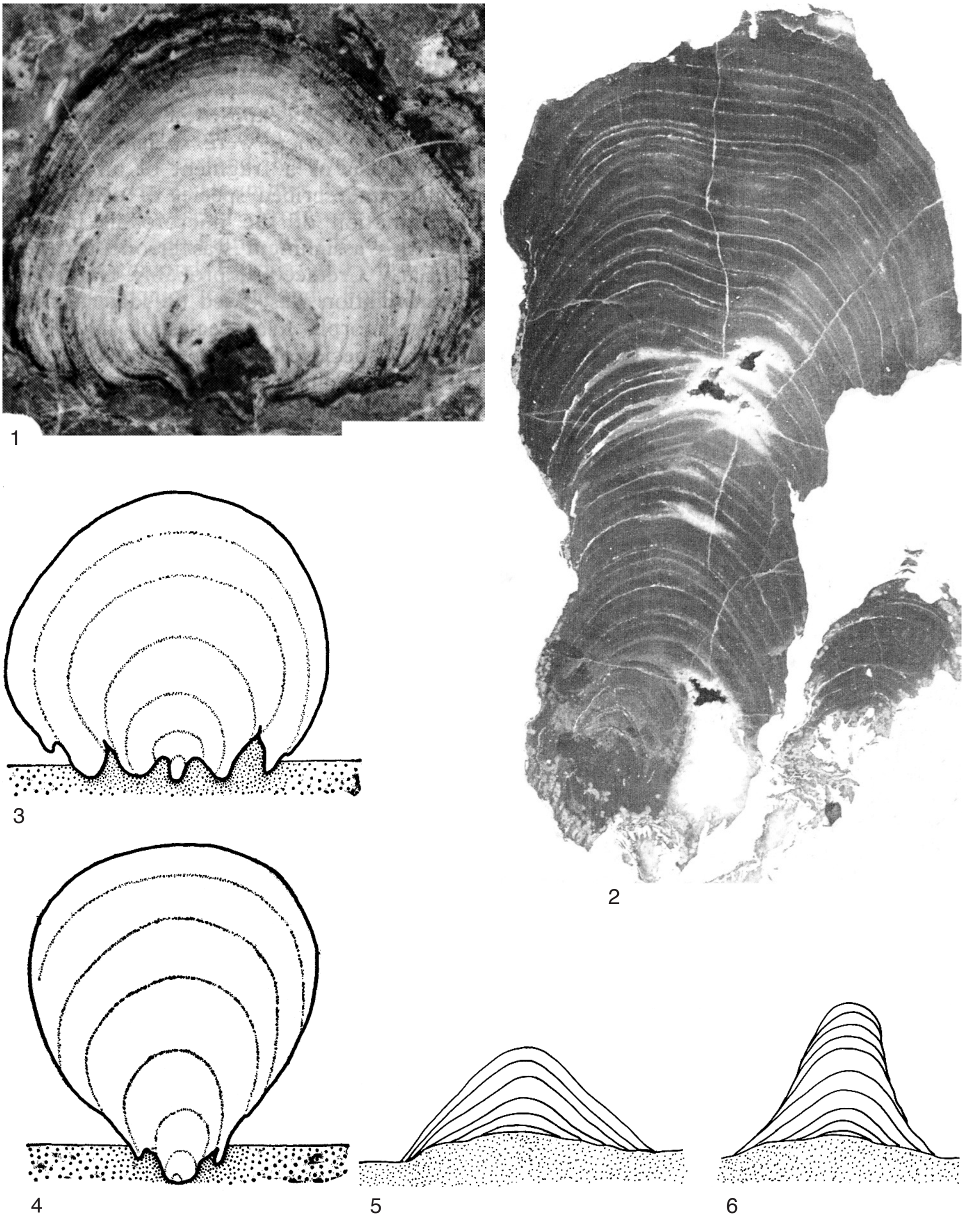

Fig. 6. Examples of some characteristic smooth-margined, bulbous, and domical stromatoporoid growth forms. *1,* Longitudinal section of typical smooth, bulbous stromatoporoid that shows concentrically arranged, internal skeletal banding (mainly enveloping, though toward the base it exhibits nonenveloping relationships); it occupied a somewhat irregular substrate, with its initial growth apparently centered on a small, rounded topographic high, perhaps of more lithified sediment and/or skeletal debris; *Stromatopora undata* Riabinin, Upper Devonian, Poland, ×0.75 (adapted from Kaźmierczak, 1976, fig. 1a; adapted by permission of Macmillan Publishers Ltd., *Nature*); *2,* large, high profile, relatively smooth stromatoporoid grew as an extended bulbous form; note latilaminae defining skeleton as a mainly nonenveloping form, suggesting that sediment accumulated in support of its *in situ* skeletal growth; longitudinal section, Lockport Group, Ludlow, Brockport, Monroe County, New York, United States, ×0.45 (adapted from Brett, 1991, fig. 7D); *3,* enveloping, *(continued on facing page).*

of the skeleton buried under sediment at each phase of latilaminate growth, could be plotted, in addition to the final burial shape when all skeletal growth ceased (LUCZYNSKI, 2005). Another important consequence of these studies was to demonstrate how the development of skeletons changes during growth, for example, from low domical to high domical and bulbous forms. However, currently none of the approaches toward using parameterization techniques allows the analysis of stromatoporoid form to be completely resolved. Consequently this remains an ongoing area of research.

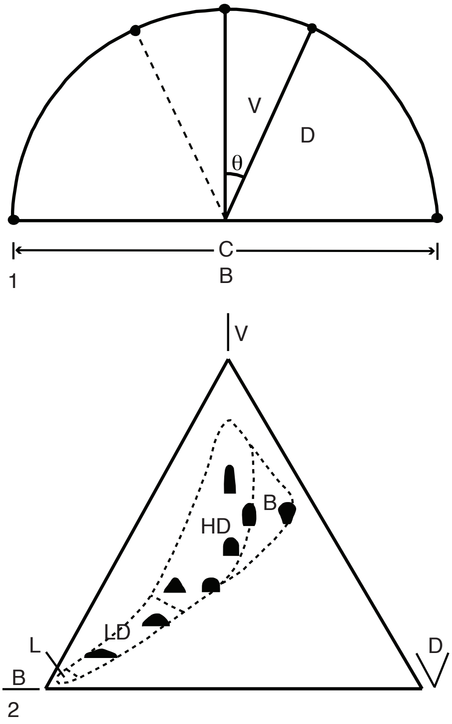

FIG. 7. Simplified parameterization approach for measuring and plotting stromatoporoid shapes, based on using skeletons oriented (or cut) in longitudinal section, as proposed by KERSHAW and RIDING (1978); *1,* three parameters are employed: basal (*B*), vertical (*V*), and diagonal (*D*). V and D are plotted from a central point (*C*), and the angle (θ) subtending D is set at 25 degrees (adapted from Kershaw & Riding, 1978, fig. 6); *2,* simple measurements of B, V, and D were plotted in a triangular diagram of stromatoporoid shapes, with the various fields being represented by the basic laminar (*L*), low domical (*LD*), high domical (*HD*), and bulbous (*Bl*) morphotypes (adapted from Kershaw & Riding, 1978, fig. 11).

SHAPE SUBDIVISIONS

JACKSON (1979) recognized six basic subdivisions of shape in sessile animals, and four of these—sheets, mounds, plates, and trees—are broadly applicable to the study of shapes in stromatoporoids (Fig. 8). Sheets differ from most other growth forms (except runners) in limiting the animal to the substrate surface, and hence, access to resources in the water column. Mounds give greater access to the water column and isolate most surface tissues from deleterious processes close to the substrate, though they may still maintain a major commitment to lateral spreading across the substrate. This gives mounds resistance to water movements and other sorts of bottom instability. Plates are rare growth forms in stromatoporoids; their raised, tierlike forms usually project laterally, more or less parallel to the substrate, from a limited area of attachment, but do not grow as tall as trees. Trees provide greater access to resources in

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FIG. 6 *(Continued from facing page).*
bulbous form that formed presumably on a supportive though uneven substrate, little affected by transport of sediment (either by erosion or deposition) during growth. The base is shown as having a corrugated surface, perhaps including concentric growth ridges where they project downward, and these seem to coincide with the ends of successive latilaminae (adapted from Kaźmierczak, 1971, fig. 6b); *4,* nonenveloping, bulbous form with a narrow base that was capable of maintaining its *in situ* orientation, owing to the effect of progressive burial by sediment during growth (adapted from Kaźmierczak, 1971, fig. 6c); *5,* characteristic smooth, enveloping, domical form that was unlikely to have been affected by small-scale transport of sediment during growth (adapted from Kershaw, 1993, fig. 2A); *6,* typical smooth, nonenveloping, domical form that may have been produced while slow accumulation of sediment occurred but alternatively may have been capable of concentrating its growth axially, for some reason other than being related to sediment influx (adapted from Kershaw, 1993, fig. 2B).

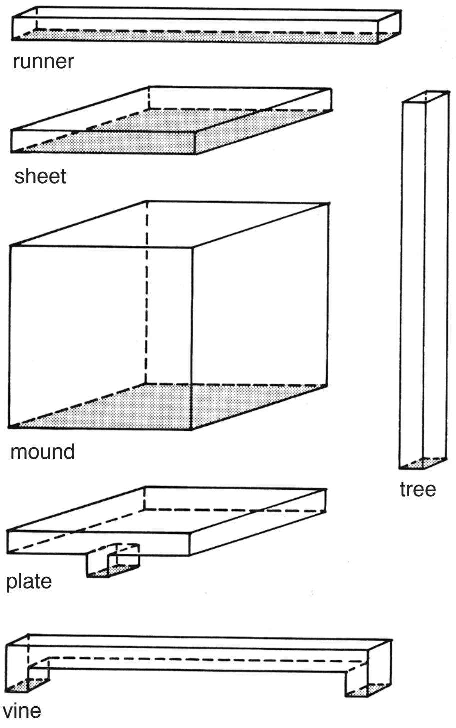

FIG. 8. Simple rectangular conceptions of the six basic sessile animal growth forms. Areas of attachment to substrate are *stippled* (adapted from Jackson, 1979, fig. 4).

the water column, and the soft tissues probably became well isolated from the substrate, but they have a much more limited area of attachment, with consequent loss of structural integrity at their basal attachment. Sheets and mounds are the most common growth forms in stromatoporoids. Like a number of other groups of sessile animals, the stromatoporoids developed particularly variable growth forms that often formed composites of more than one major growth morphotype. Most commonly, these are sheet-mound combinations, but some comparatively rare composites of raised, tierlike plates and mounds may also occur. Here we have adopted these broad subdivisions for convenience in describing the main stromatoporoid shapes.

SHEETS

Sheets are defined as thin layers that spread laterally (tangentially) in all directions.

Laminar

The laminar morphotype is flat, thin, sheetlike layer that grew laterally outward with accretionary growth in all directions away from an initial settlement point. It may be only a few millimeters thick (Fig. 9.1), or may, provided a component of upward growth was maintained across the skeleton, form a tabular body to tens of centimeters in thickness (Fig. 9.2–9.3). It may spread freely across an unconsolidated substrate or encrust a hard surface such as another skeletal object. It usually remains in contact with the underlying surface but may, in places, be separated by primary, cement-filled cavities (Fig. 10). Irrespective of size and complexities of relationships with sediments, it is recommended that the general term laminar is preferred to all other names used to refer to sheetlike or platy structures, including the following: sheetlike, stratiform, lamellar, discoidal, platy, and tabular. These are all now regarded as obsolete. The laminar morphotype is the simplest and one of the most common stromatoporoid shapes, especially in reef complexes. It may have flattened, undulating, or wavy, up-domed or saucer-shaped (concave upward) orientations, dependent on the nature of the substrate. The shape exhibits smooth lateral margins when no episodic sedimentation is associated with growth (Fig. 9.2), or ragged lateral margins when sediment periodically interferes with growth (Fig. 9.3) (KERSHAW & RIDING, 1978); the terms smooth and ragged are features of lateral surfaces, not shapes. Note that the term encrusting does not apply, as it is not a shape; it signifies attachment to a surface, usually a hard (but not a soft) substrate. It is important, in addition, to emphasize that earliest growth stages of many stromatoporoids are laminar, as they grew from an initial laminar base, so the term should apply mainly to more mature stages of growth.

KERSHAW (1984) noted that laminar shapes were well suited to developing on unconsolidated muddy substrate, because the skeletal weight was low and evenly spread.

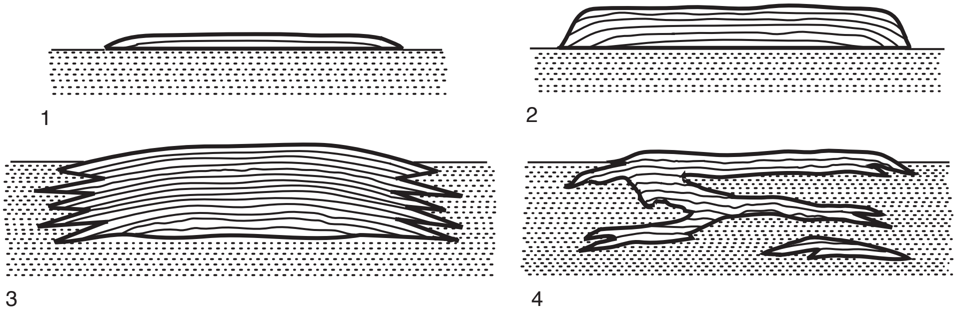

Fig. 9. The main laminar shapes dependent on the various interactions between growth, substrate, and sedimentary influx, particularly the possible effects of sedimentation on the development of the final form. The exception (see Fig. 10) is where sediment swamping causes partial mortality of a laminar skeleton, and parts were able regenerate to produce new outgrowths that spread laterally, but also tended to up-dome over newly accumulated sediment, producing primary cavities (not shown here); *1,* initial stages of predominant lateral spreading laminar growth (adapted from Kershaw, 1990, thin laminar morphotype part of fig. 7); *2,* successive laminar growth where the skeleton was able to maintain smooth lateral margins, perhaps because very limited sediment was accumulating on the substrate (adapted from Kershaw, 1990, thicker laminar, formerly tabular, morphotype part of fig. 7); *3,* laminar shape with ragged lateral margins where there may have been more frequent, small-scale influxes of sediment that disrupted growth, especially along lateral margins (adapted from Stearn, 1983, fig. 1E); *4,* anastomosing pattern may have developed because persistent movement of sediment from place to place made it difficult for growth to be consistently maintained across entire growth surface; at any one time, parts of a skeleton remained alive, while other parts had become swamped by sediment (adapted from Stearn, 1983, fig. 1A).

The fact that they were able to develop intact suggests that there was little or no sedimentary influx for most of the time. However, they were more susceptible to being overwhelmed by sedimentation than the domical shapes, especially at the margins. Laminar crusts formed also over large skeletal objects, though where the initial colonization occurred on smaller, ephemeral patches of hard substrate or skeletal debris, skeletons were likely to spread rapidly and widely to other areas with an unconsolidated substrate (Kershaw, 1998, fig. 5). Meyer (1981) suggested lateral spreading rates of individual stromatoporoid growth of about 10–23 mm/yr.

Intermittent burial by influxes of sediment caused severe impacts on the lateral spread and vertical continuity of laminar growth, resulting in **anastomosing,** laminar to low domical sheets or crusts (Fig. 9.4). Kershaw (1998, p. 522, fig. 7) noted that with such episodic patterns of rapid spread of sediment, the successive layers of such skeletons did not necessarily maintain continuity of growth across their entire surfaces; at one time parts may have remained alive, while other parts became swamped by sediment. Representatives of a species of *Lophiostroma,* possibly allied to *L. schmidti,* illustrated by Bogoyavlenskaya (1982, p. 117, fig. 5; 1984, fig. 2), from the Silurian of Podolia, shows unusual examples of splayed or imbricated laminar sheets (Fig. 11.2) of large size (up to 2 m across) between sediment layers. These structures developed as a consequence of successive interactions of sediment influx and rapid spread of lateral growth (see Substrate Preferences section, herein, p. 43). Good examples of cavities have not yet been recorded from undersurfaces of anastomosing, laminar crusts of Silurian age.

The laminar stromatoporoids of the Middle Devonian reef complex of South Devon (Kershaw & Riding, 1980) exhibit some of the largest sizes, reaching dimensions of 5.5 m across and up to 0.20 m thick; however, they could not be identified taxonomically because of their state of recrystallization. Also, the laminar crusts of *Stachyodes australe* and *Clathrocoilona spissa* in different Upper Devonian reef habitats

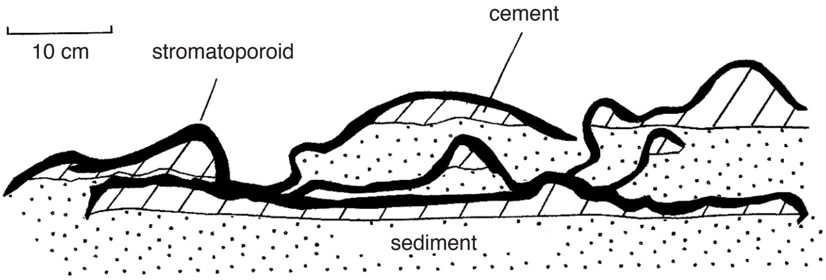

FIG. 10. Representation based on a tracing showing how a laminar stromatoporoid skeleton could possibly regenerate after partial mortality owing to sediment swamping. Both the initial laminar growth and the subsequent development of lateral outgrowths tend to up-dome over sediment-forming primary cavities that later became cement filled; Frasnian, Upper Devonian, Pillara Limestone, Bugle Gap, Canning Basin, Western Australia (adapted from Wood, 1999, fig. 6.20).

of the Canning Basin (Western Australia) are about 1.5 m across and often less than a centimeter thick (WOOD, 1998, 2000). They also exhibit remarkable developments of primary cavities on their undersurfaces (Fig. 10, Fig. 12.1–12.2; and see discussion of Primary Cavities, herein, p. 57; after WOOD, 1998, fig. 2; 1999, fig. 6.19c, 6.20).

Euryamphipora platyformis KLOVAN, from the Devonian Redwater reef complex in Alberta, is another species with an unusual explanate growth form. The species is the only amphiporid taxon to exhibit a laminar shape, being variously interpreted as a horizontal, sheetlike form (KLOVAN, 1966; MISTIAEN, 1985; STEARN, 1997, p. 842) and an erect, vertically elevated plate (COCKBAIN, 1984, fig. 10). However, MISTIAEN's (1985, p. 207, fig. 129, pl. 20,*9*) recognition of *Euryamphipora* sp., as a small, 1-mm-thick specimen encrusting a brachiopod shell (Fig. 11.3), seems to establish the taxon, with its complex internal amalgamate network of laminae and slightly zigzagged pillars, as a low-lying, laminar form.

Case studies show that laminar shapes are more commonly associated with more energetic Paleozoic reef regimes. Some also exhibit large sizes. For example, KERSHAW (1990, 1993, 1997) and KERSHAW and KEELING (1994) documented distribution patterns of stromatoporoid shapes from biostromal and biohermal habitats in Gotland. Detailed studies of the content and distribution of the two different biostromes at Kuppen and Grogarnshuvud (KERSHAW, 1990, 1997) demonstrated significant differences in proportions of low-profile (laminar to low domical) stromatoporoids relative to high-profile types (mainly the high domical to bulbous forms), whereas in the Holmhällar bioherm (KANO, 1989; KERSHAW & KEELING, 1994), only low-profile (laminar to low domical) and anastomosing forms were developed.

MOUNDS

Mounds are defined as three-dimensional domical and bulbous shapes that arose from combinations of lateral (tangential) and vertical (longitudinal) growth.

Domical

A domical shape is typically a skeletal mound combining outward (lateral) and upward growth from an initial laminar base; may appear as a simple hemisphere with a smooth, arcuately curved, upper part (Fig. 2), or may develop a more bell-shaped (campaniform) shape because of its ragged (zigzagged or skirted) extensions of lateral margins toward the base (Fig. 4.1, Fig. 5.1). Like laminar morphologies, the relationships at the base are largely dependent on substrate characteristics. The base may be relatively flat lying, but on soft substrates may vary from slightly convex downward, where lateral growth developed on an aggrading substrate, to convex upward, where the lateral growth formed while sediment was being winnowed away, more or less contemporaneously (Fig. 13; and see examples based on bryozoan colony shapes, in Spjeldnaes, 1996, fig. 2D–E). On firm substrates, the base may be convex upward, where lateral growth occurred over a preexisting local high or encrusted a large skeletal object with positive relief. The preferred term domical is more or less equivalent to the previous terms: hemispherical, domal, bun-shaped, bell-shaped, conical, mamelon, massive *partim,* and ?pyriform, which are now all regarded as obsolete.

As noted earlier (see Recognizing Stromatoporoid Shapes, p. 5), the domical shape is further subdivided into **low domical** and **high domical** subgroups (Fig. 2) (the latter combining the high and extended categories of Kershaw & Riding, 1978; Kershaw, 1990). In part, we follow Kershaw and Riding, arbitrarily subdividing the low and high domical forms on the basis of whether their ratios of vertical height to basal diameter (V/B) are between 0.1 and 0.5, or 0.5 to 2.0, respectively. High domical shapes commonly develop from continued growth to maturity of a low domical skeleton; and this low domical stage may, or may not, have commenced initial growth from a laminar base. Hence, it is important in future growth analysis surveys that the nature of changes in skeletal shape within skeletons is evaluated through all stages of growth (Luczynski, 2005).

Smooth and ragged types of margins are well represented in the low domical morphs (Fig. 2, Fig. 4.1, Fig. 5, Fig. 6.5), whereas smooth associations are more commonly developed in the high domical subgroup (Fig. 6.6). Sometimes ragged domical shapes (some are composite domical types) developed asymmetrical appearances as they grew on the substrate, in association with unidirectional current activity (Fig. 14, Fig. 15.2). A divergence of views exists as to whether these asymmetrical skeletons grew inclined toward the direction of current flow (Broadhurst, 1966) or away from the current flow (Kapp, 1974).

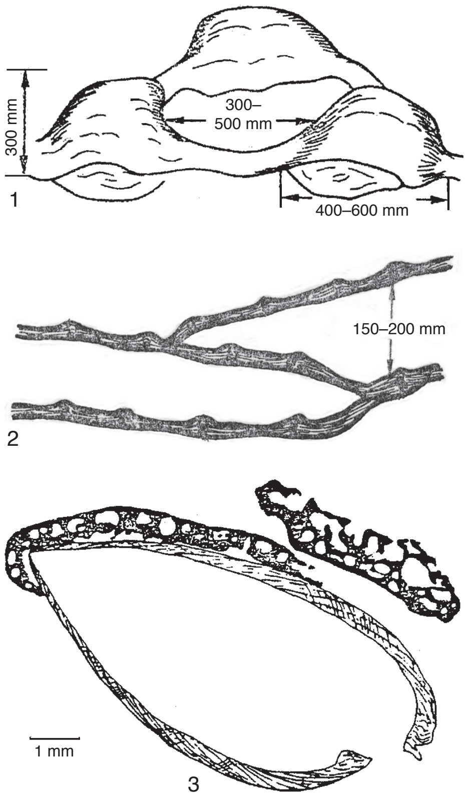

Fig. 11. *1,* Field sketch of a portion of a complex, composite intergrowth of domical and laminar forms of *Parallelostroma malinovzyensis* (Riabinin), Silurian, Podolia, Ukraine; interconnected, multiskeletal structures grew on substrate to large sizes, measuring up to 5 m^2 (adapted from Bogoyavlenskaya, 1982, fig. 4); *2,* field sketch of a fragment of the anastomosing laminar sheets of a species of *Lophiostroma,* Silurian, Podolia, Ukraine; laminar shapes of such forms repeatedly split in response to episodic sediment swamping events and may extend to lengths of at least 1.2 m and heights of up to 0.6 m (adapted from Bogoyavlenskaja, 1982, fig. 5); *3,* sketch of thin laminar growth of *Euryamphipora* sp., encrusting a slightly disarticulated brachiopod shell, including parts of both dorsal and ventral valves close to the anterior commissure; Dewal Formation, Givetian, Dewal section, Central Mountains, Afghanistan, based on specimen GFCL 4135 (thin sections: AF 76 D 83/4) (adapted from Mistiaen, 1985, vol. 2, fig. 128).

The majority of stromatoporoids exhibit low-profile (that is, laminar to low domical) shapes. This is probably largely because they were hydrodynamically the most stable growth forms; that is, the most resistant to current activity in both reef and nonreef


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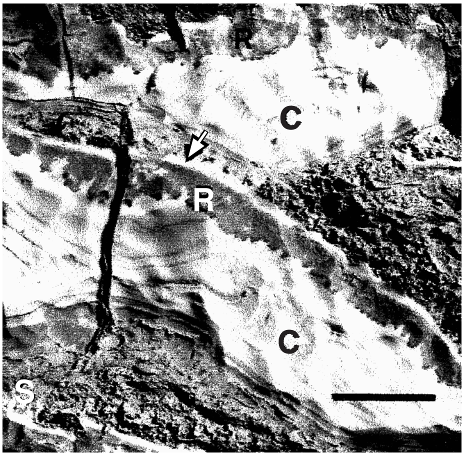

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FIG. 12. Unusual, widely spreading, thin, laminar stromatoporoid growth forms that produce large primary cavities; *1,* stromatoporoid *Stachyodes australe* (WRAY), slope-margin facies, Frasnian, Canning Basin reefs, Western Australia, exhibiting expansive, very thin, laminar crusts (continuous, wafer-thin, light colored bands shown in photo); laminar stromatoporoids are gently updomed over large primary cavities that largely became filled with lighter-colored, lens-shaped bodies of zoned calcite cement (also shown), and growths of cryptic calcimicrobe *Shuguria* also commonly preserved directly beneath stromatoporoid crusts, ×0.15 (adapted from Wood, 1999, fig. 6.19c; reproduced from *Reef Evolution,* Rachel Wood, 1999, p. 230, by permission of Oxford University Press); *2,* in more detail, an extensive, thin, gently doming, laminar sheet of *S. australe* (WRAY) as a thin, light-colored band (*arrowed*) that obliquely spans field of view, and more than 20 mm above dark-colored sedimentary rock (*S*) shown at bottom left. Originally, a large primary cavity formed in the space between and was first colonized by pendent growths of encrusting calcimicrobe *Shuguria* (*R*) as dark, sheetlike bands on underside of stromatoporoid, then the rest was infilled with light-colored, zoned, radiaxial calcite cement (*C*); Frasnian outcrop is in slope-margin facies, near Sheep Camp Yard, Geikie Gorge, on Fitzroy River, Canning Basin, Western Australia, scale bar, 20 mm (adapted from Wood, 1998, fig. 2D; reproduced with permission of and copyright Elsevier).

settings (KERSHAW, 1998, p. 511). The high domical forms were mechanically less stable—that is, more prone to disturbance by current activity (unless sediment later accumulated around them)—but, because of their raised living surface, were better able to access nutrients higher in the water column.

The conical shape (apex upward) is distinctive (Fig. 16.1), although comparatively rare; it may be regarded as a subtype of the high domical forms, either where successive units (latilaminae) of skeletal growth were inclined sharply away from a central (vertical) axis (the enveloping condition), or where successively higher, more gently convex latilaminae became more withdrawn from lateral margins (the nonenveloping condition); see also Columnar Shape (herein, p. 25).

The reef limestones of the Gotland succession generally have comparatively large, domical-shaped specimens (MORI, 1970). For example, the Kuppen biostrome, which has a high proportion of domical stromatoporoids relative to other shapes (KERSHAW, 1990), has low domical forms that are commonly up to 1 m across and 0.3 m high, and high domical shapes, typically up to 0.3 m across and 0.5 m in height. Few of them have a ragged appearance. Though many high domical shapes are toppled, the biostrome is interpreted to have been formed in a comparatively low to moderate energy regime, subject to episodic storms (KERSHAW & KEELING, 1994). Other reef deposits exhibit even larger high domical forms, such as the *in situ*, 1-m-high skeleton (Fig. 17) now exposed in a single *rauk* (sea stack) at Fågelhammar (KERSHAW & RIDING, 1978).

Domical stromatoporoids are the dominant growth forms of the marly, deeper, level-bottom Visby Formation (Silurian) of Gotland (KERSHAW, 1984), and they are of comparatively small size, normally 50 to 150 mm in diameter and up to 70 mm in height. About 20% of the skeletons have ragged lateral margins th at testify to the intermittent influxes of sediment during growth (Fig. 4.1). The mainly encrusting species *Peridiostroma simplex* also occurs in this habitat and produces

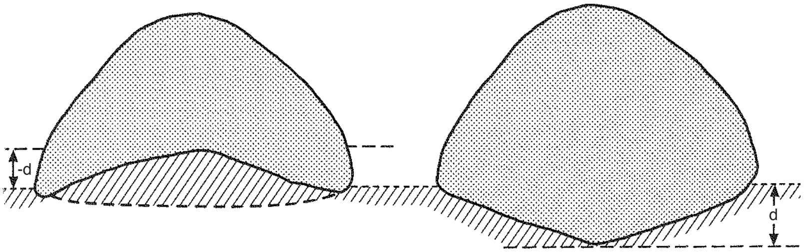

FIG. 13. Two longitudinally oriented sections, based on domical-shaped bryozoans, Lower Ordovician, Öland, Sweden, showing same basal morphology as many domical stromatoporoids that lived on soft substrates; specimen (left side) has a concave base; specimen (right side), a convex base. Growth of each example was initiated from a central point on base; sample on left then continued to grow outward and somewhat downward, to adjust for loss of sediment from surrounding substrate (*-d,* total amount of sediment removed during lifetime of its active growth); sample on right continued to grow outward and slightly upward to adjust to amount of sediment being added to surrounding substrate (*d,* total amount of sediment that must have been added during lifetime of its active growth) (Spjeldnaes, 1996, fig. 2D–E).

another important shape variant of small, predominantly smooth, domical composites that may become interlinked by short lateral projections near their bases, giving them an irregularly lumpy, conjoint form overall (Fig. 18–19). Only a few laminar and bulbous shapes are additionally found in this habitat.

Another type of composite domical shape developed in the Silurian of Podolia. BOGOYAVLENSKAYA (1982, p. 117, fig. 3V, 4) illustrated this combination (Fig. 11.1) as an arrangement of three, conjoined, domical skeletons (each about 0.5 m in diameter and 0.3 m in height) that are linked by laminar projections (about 0.4 m in length) of *Parallelostroma malinovzyensis* (RIABININ). This large, partially coalescent growth form seems to have formed an approximately triangular array on the substrate.

Other domical variants are the ragged mushroom-type shapes that also formed as composites, first as an extended series of comparatively narrow growth units (latilaminae) forming a columnar base, and then overtopped abruptly by laterally expanded, convexly shaped, domical, upper growth units (Fig. 15.1; see also KAPP, 1974, fig. 1). This composite shape has a distinctive morphology but only occurs rarely. It reflects a rapid change from narrow columnar to laterally spreading growth. This apparently relates to a sudden change during growth, from a stressed to a less-stressed environmental condition, as the rate of sediment influx dramatically declined (see later discussion of Combinations of columnar and explanate patterns of growth, herein, p. 37).

Large domical stromatoporoids also occur in Devonian reef facies. For example, KERSHAW and RIDING (1980) recorded a specimen from South Devon measuring 1.7 m across. WOOD (2000) reported other large examples from the Upper Devonian back reef community of the Canning Basin (Western Australia), including skeletons of *Actinostroma papillosum* that have a highly unusual, large, apparently composite (mound and plate-type), domical shape with extended lateral (tiered) platy outgrowths from domical centers (Fig. 20, see also Fig. 32). Overall skeletal dimensions are up to 1 m in width and 1 m in height. Primary cavities may be developed on undersurfaces of the successive, outwardly tapering extensions of these domical forms. It remains uncertain whether this complex form represents an intrinsic growth style or if the lateral outriggers with their accentuated raggedness developed as a consequence of repeated influxes of sediment (WOOD, 2000).

Other large domical stromatoporoids may exhibit upper surfaces that are covered by multiple peaks (or cones) that represent a part of the tops or sides of mamelon columns, as in a very large and complex, domical specimen of *Parallelostroma typicum*

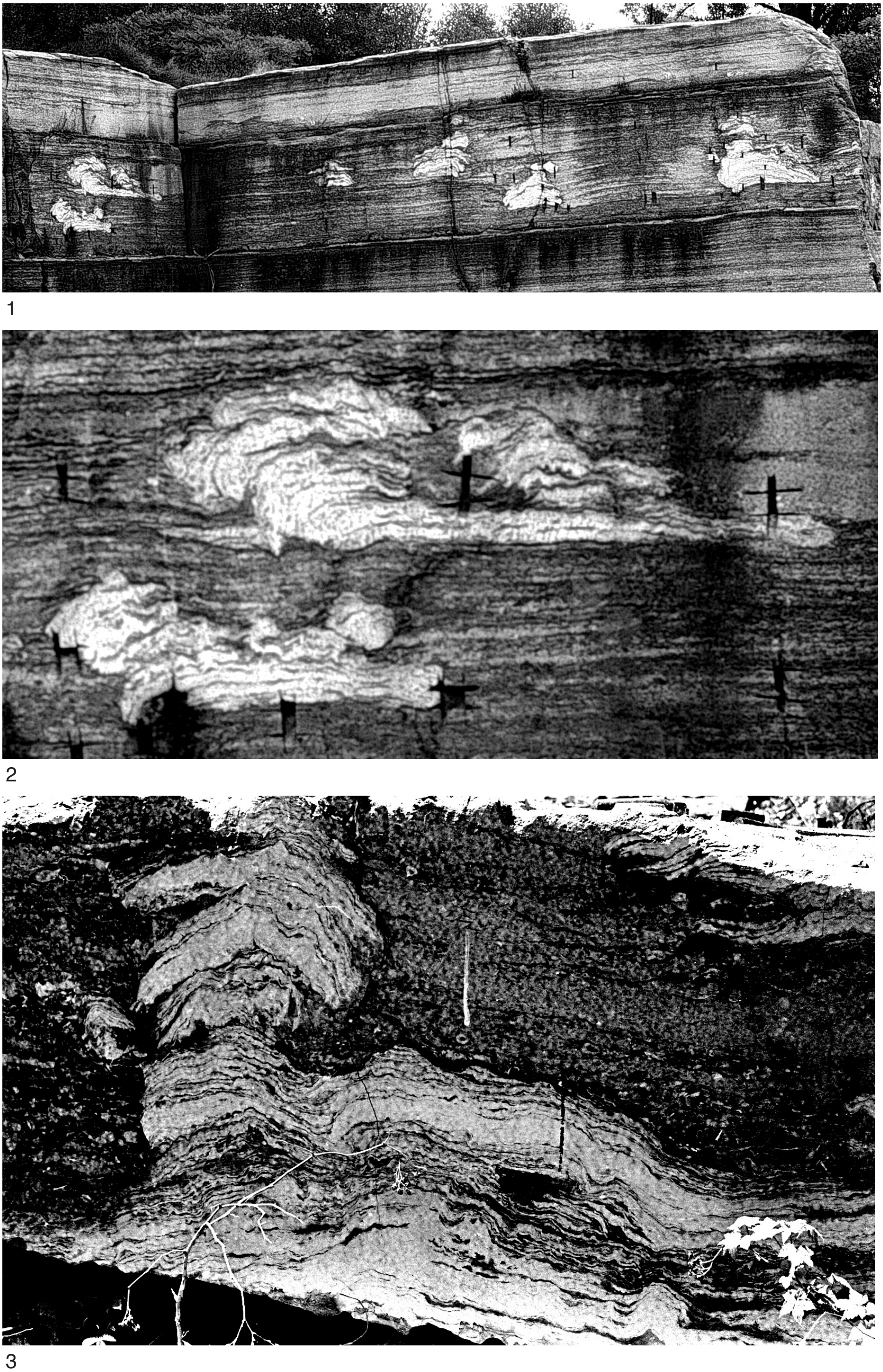

FIG. 14. *(For explanation, see facing page).*

in the *rauk* (sea stack) area at Fågelhammar, in the Folhammarn nature reserve (see Sandstrom, 1998) on Gotland (Fig. 17, Fig. 21.1). Kershaw (1990, 1998) recognized many similar mamelated structures in species from the Gotland Silurian succession, including examples from the Kuppen biostrome (Fig. 21.2).

In a Middle Devonian reef core of the Rhenish Schiefergebirge in Germany, Braun and others (1994, p. 360, fig. 7) have recorded many large mamelated high domical to irregular specimens in the vertical and horizontal walls of a quarry (Fig. 21.3). Unfortunately, they regarded one of their growth forms as a mamelon morphotype. The term mamelon (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 8, Glossary, Webby, 2010), however, applies only to the upward skeletal extensions on the upper growth surface and should not be denoted as a stromatoporoid shape. The well-defined mamelon columns of specimens shown on the cut walls of the quarry are highlighted by distinctive, cone-in-cone, or zigzag-shaped, patterns of the latilaminae, but these represent internal (not external shape) features of the skeletons. Nevertheless, these large, prominently zigzag-mamelated skeletons are of interest, because, as shown by Braun and others (1994, p. 361, fig. 8b, 9, 10, pl. 5, 7, 8), in the central reef, they are more commonly reoriented than other high domical stromatoporoids, though in the interpreted reef growth center, an appreciable number of larger zigzag-mamelated specimens remain *in situ* or have only been slightly disturbed. Such structures have previously been termed protuberants by Kershaw (1998, p. 522, fig. 7).

Bulbous

This form usually has a near-spherical outline, except for a relatively narrow, flattened base (Fig. 2, Fig. 6.1, 6.3–6.4). It is widest at the midpoint between bottom and top, and characteristically has a smooth outline as a consequence of an enveloping-type growth. Sometimes, with continued upward growth, a skeleton may develop as an extended bulbous form (Fig. 6.2). While many bulbous forms developed from a narrow laminar base, others appear to have grown from a single settlement point, such as a hard object on the substrate, with both upward and outward spreading from the initial attachment site. The shape was regarded by Kershaw and Riding (1978) as an end member of the more or less continuous laminar–domical–bulbous series. However, in terms of the three morphological variables of their parameterization scheme, the bulbous shape is only produced when the dimensions of the basal length remain low compared to the other (vertical and diagonal) dimensions. The term bulbous should take precedence over the more or less equivalent terms, such as globular, oblate, cabbage-shaped, nodular, subspherical, and spheroidal. All these latter should now be treated as obsolete.

The high center of gravity and narrow base resulted in the bulbous morphs being more susceptible to current activity (including

Fig. 14. Cut walls showing many longitudinal sections of large, laminar to domical skeletons of the stromatoporoid *Pseudostylodictyon lamottense* (Seely), Fisk quarry, Isle La Motte, Vermont, United States (Kapp, 1974); exposures in the quarry are from middle part of Chazy Group, lower Crown Point Formation, Middle Ordovician, Darriwilian; *1,* large skeletons of *P. lamottense* occur at scattered intervals along two particular bedding planes spaced about 0.6 m apart, and some of the specimens have a noticeable asymmetry, with steeper slopes to the left. About 4.5 m sequence of the gently inclined, stromatoporoid-bearing limestone deposits shown in photo. Kapp (1974, fig. 5, 8) previously illustrated parts of this outcrop (new, photo by B. D. Webby); *2,* enlarged view of two large, ragged, low domical skeletons of *P. lamottense* (also illustrated at left end of exposure in view *1*). Both show a similar asymmetry, with successive layers (latilaminae with ragged lateral ends) displaced toward their steeper sides that, according to Kapp (1974), probably represented the direction of current flow. The upper specimen has an overall length of 2 m (about 0.7 m in height), and the lower specimen is 1 m long at the base (about 0.4 m high) (new; photo by B. D. Webby; Kapp, 1974, fig. 8, previously provided a more generalized illustration that included these two skeletons); *3,* large, ragged, composite skeleton of *P. lamottense,* with lower half developing as laterally extended, undulating, laminar form, and upper half continuing into a narrowly constricted, high domical shape. Specimen is about 2 m long at the base and approximately 1.5 m high (new; based on photo kindly supplied by C. W. Stearn).

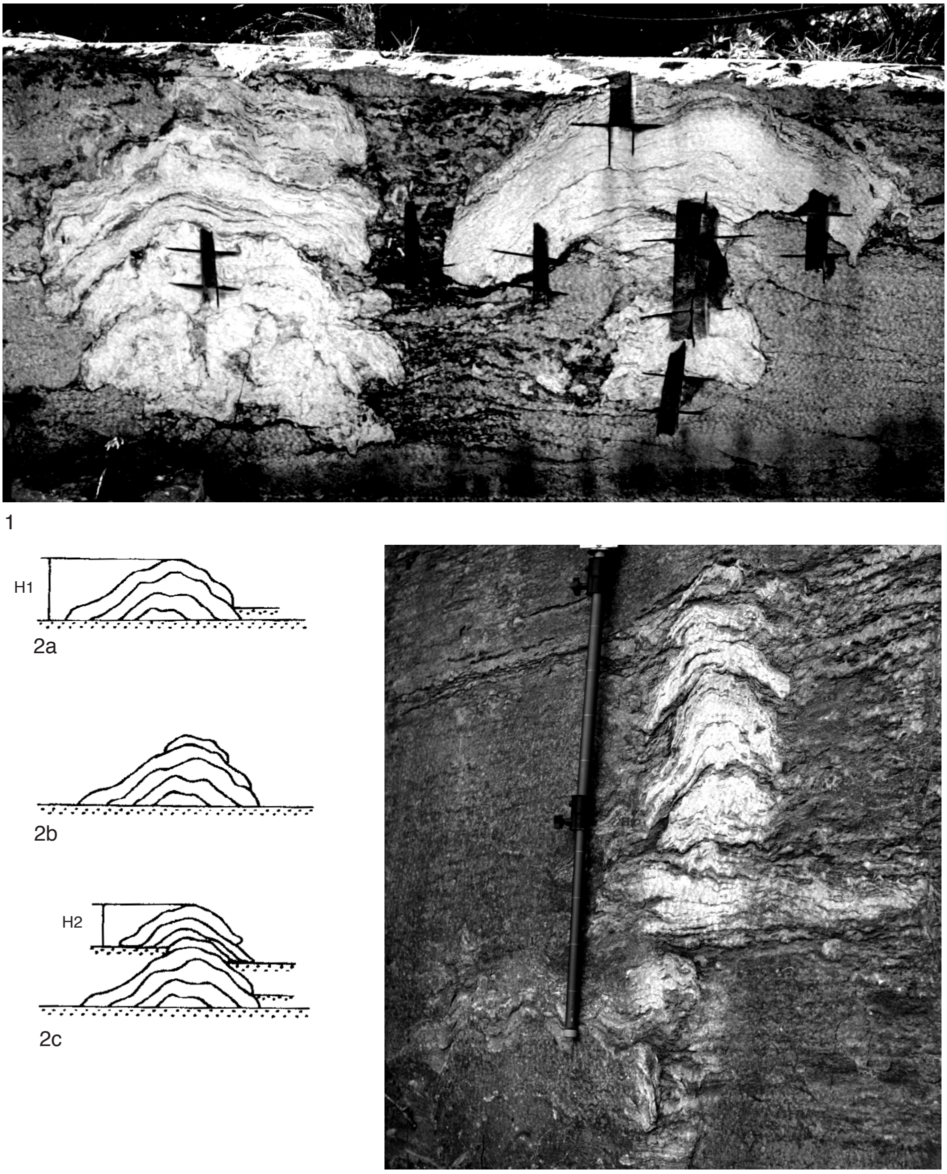

FIG. 15. *1,* Large, ragged, high domical and mushroom-shaped skeletons of *P. lamottense*, Goodsell quarry, lower Crown Point Formation, Chazy Group, uppermost Middle Ordovician, Darriwilian, Isle La Motte, Vermont, United States; mushroom-shaped form is a composite that may have developed when rate of sedimentary influx suddenly declined, although it is puzzling that the adjacent columnar form does not show the same pattern (new, photo by B. D. Webby; similar image previously figured by Kapp, 1974, fig. 1); *2a–c,* diagrammatic representation of successive growth phases in a domical skeleton; *2a,* in first growth phase (*H1*), three domelike layers were added, maintaining contact on both sides with original substrate, but fourth layer was raised on one side because of small influx of sediment on that side; *2b,* sediment influx increased, causing most of skeleton to be buried, except a small area at top; *2c,* the small area then became site for a second growth expansion of new layers (*H2*), although the substrate levels were different on either side. *H1,* relief of skeleton during first growth phase; *H2*, relief achieved in second *(continued on facing page.)*

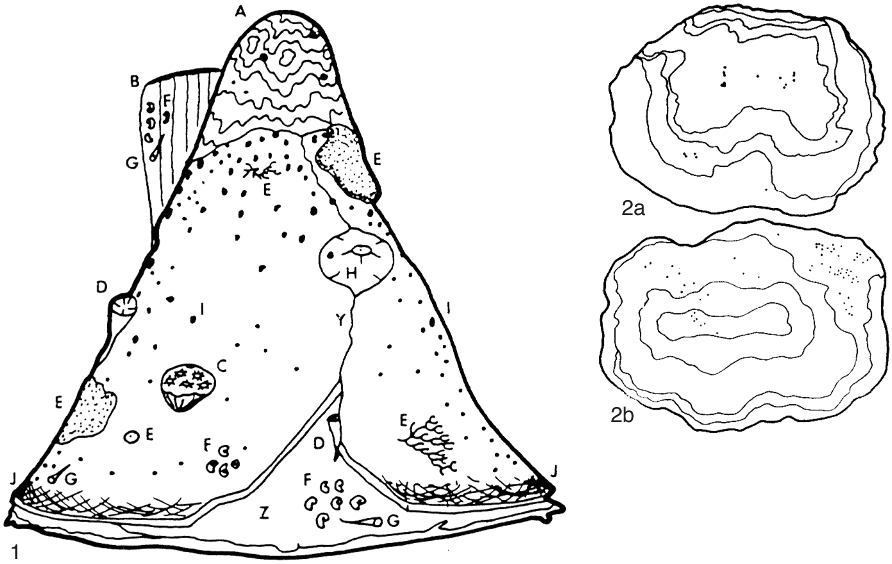

FIG. 16. Distribution of encrusters on high domical Silurian stromatoporoids, upper Visby Formation, Gotland, Sweden; *1,* sharply cone-shaped, high domical skeleton in lateral view showing varied distribution of mainly small, open surface epibionts; coverage of encrusters was greater toward top, suggesting progressive burial from base; *A,* stromatoporoid; *B,* halysitid coral; *C,* heliolitid coral; *D,* rugose coral; *E,* bryozoan; *F,* spirorbid worms; *G,* cornulitid; *H,* crinoid attachment base; *I, Trypanites; J, Allonema; Y,* hairline-type fracture; *Z,* exfoliated area, ×0.75 (adapted from Nield, 1986, fig. 3); *2a–b,* flattened undersurfaces of two high domical skeletons of specimens *a,* Hä6 and *b,* HäS8 that show patterns of clustering of tiny encrusting spirorbid worms, perhaps suggesting they colonized short-lived secondary cavities, ×0.23 (adapted from Nield, 1986, fig. 2A–B).

overturning), and they seldom grew to larger sizes (greater than 0.3 m across), as did the laminar and domical forms. Overall, they occur less commonly than laminar and domical forms. The fact that some were able to grow to maturity and sustained little movement suggests they occupied relatively quiet-water environmental conditions, perhaps in back-reef habitats (KERSHAW & RIDING, 1980); though for such mature, enveloping-type skeletons to be preserved intact, it possibly requires their rapid engulfment in periodic sediment-laden storm surges.

The shape illustrated by STEARN (1983, fig. 1F; 1984, fig. 1F) as bulbous expands upward from a narrow base and differs somewhat from typical bulbous morphs in having nonenveloping, ragged lateral edges. The shape is strictly obconical rather than bulbous. The skeletons appear to have grown in relationships with episodic sedimentation and maintained their stability

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FIG. 15 *(Continued from facing page).*

growth phase. Such changes in growth are dependent on small-scale fluctuations in sedimentary input; local currents may have influenced the symmetry of vertical growth, for example, if they were maintained in one direction for a time, with a noticeable asymmetry developing as a consequence of successive layers being displaced in the direction of current flow (adapted from Kapp, 1974, fig. 6); *3,* large, ragged, predominantly columnar skeleton of *P. lamottense,* Fisk quarry, lower Crown Point Formation, Chazy Group, uppermost Middle Ordovician, Darriwilian, Isle La Motte, Vermont, United States; in detail, however, this complex skeleton has an irregular, steeply tilted (possibly disturbed), narrow base, then successive, 0.5 m long, laminar outgrowths, one undulating more to the left, and the other being more regularly layered and tapering to the right, followed by the upper, columnar part composed of stacked and ragged domical growths, about 0.3 m in diameter to the top; overall this complex, composite, stromatoporoid skeleton has a considerable number of laterally associated, sedimentary-rock–filled wedges and some internal sedimentary rock inclusions; the part of the monopod measuring stick shown in the photo is 1.05 m long (new; photo courtesy of Frank R. Brunton).

FIG. 17. High domical skeleton of *Parallelostroma typicum* (ROSEN) exposed on the coast, forming a small isolated *rauk* (sea stack), Hemse Group, Ludlow, Fågelhammar, Folhammarn nature reserve, Gotland, Sweden, showing areas of exfoliation of laterally exposed wavy latilaminae, especially in low to middle parts, although it retains a relatively smooth outer surface in the upper part; specimen is 1.35 m high; note also scale bar = 8 cm (Kershaw digitized photo no. DCP-9400; previously illustrated by Mori, 1970, pl. 28,*2*; Manten, 1971, fig. 223; Riding, 1981, fig. 42; Fagerstrom & West, 2010, fig. 1A–B).

as they progressively became engulfed. However, because this obconical shape only occurs rarely, it is perhaps best regarded as a subgroup of the more typical bulbous forms. An apparently obconical, or cuplike, skeleton of *Labechia conferta* was illustrated by NICHOLSON and MURIE (1878, fig. 5), and other species from the Halla and Sundre formations of Gotland also exhibit this shape (Mori, 1970; Kershaw, 1998).

TREES

Trees are defined as erect to inclined, unbranched columns, or branching (digitate or dendroid, rarely both branching types occurring in the same species). Treelike shapes are not common growth forms among Paleozoic stromatoporoids, and have limited real significance as taxonomic entities. Only a few taxonomic groupings have adopted predominantly treelike growth forms, among them, the small order Amphiporida, the moderate-sized family Aulaceratidae (order Labechiida), and the two small families, Idiostromidae (order Stromatoporellida) and Stachyodidae (order Syringostromatida). There are, in addition, a few genera with predominant treelike forms that are grouped within orders and families dominated by laminar and dendroid growth habits, e.g., clathrodictyid genera *Labechiina*, *Neobeatricea*, and stromatoporellid genus *Dendrostroma.* These may have taxonomic integrity, though some specialists may prefer to treat such forms as growth-form variations of related genera.

Columnar

This form is erect, unbranched, with lateral sides parallel to subparallel, and where the vertical height is more than twice the basal diameter (V/B > 2.0) or width (Fig. 2). In some cases, the unbranched columnar shapes may be linked to members of the laminar–domical–bulbous series of Kershaw and Riding (1978), with high domical and columnar forms developing from similar relatively narrow laminar bases (see Kershaw, 1998, fig. 7). Also, some extended bulbous forms are difficult to distinguish from columnar forms where they grow from a point rather than a laminar base (Fig. 6.2; and Harrington, 1987, fig. 6). Some columnar shapes represent broken fragments of larger branching growth forms, so some care is needed to establish that the skeletons were unbranched through all stages of their growth. The columnar growth form may exhibit smooth or ragged margins and either an enveloping or nonenveloping habit. Equivalent terms unbranched and subcylindrical are regarded as obsolete.

Both types of columnar shapes appear to have grown rapidly upward with limited lateral spreading. The smooth, enveloping forms (e.g., species of genus *Aulacera* of the family Aulaceratidae, order Labechiida) may have grown predominantly in quiet-water conditions but then were collapsed and completely engulfed in sediment by a major storm surge event (Fig. 22–23). In contrast, the ragged (irregularly notched, rejuvenated), nonenveloping forms may have grown in more episodic, turbulent (rough water) conditions, resulting in alternations between columnar (upward) growth, when the restricted growing surface was able to maintain pace with progressive burial by sediment, and pauses in sediment supply, when localized laminar outgrowths were able to develop (Fig. 15.3; see also Cuffey & Taylor, 1989, p. 297, fig. 2E). These two types of columnar growth responses developed from quite different sets of environmental conditions and probably from stromatoporoid organisms that had markedly different inherited growth programs.

The most striking examples of columnar stromatoporoids are the large, unbranched, postlike columns from the latest Ordovician (Hirnantian) successions of Anticosti Island, Canada (Petryk, 1981; Cameron & Copper, 1994). These are mainly referred to species of *Aulacera*. Most specimens (Fig. 22.1–22.2) are preserved as broken logs that are scattered randomly on bedding planes, or current aligned, typically 1–2 m in length and up to 0.3 m in diameter, although one specimen is 1.6 m long and only 0.13 m in diameter (Cameron & Copper, 1994, fig. 3C). The length-to-diameter ratios are estimated to range between 12:1 and 6:1. Most specimens show very limited taper along their lengths, but Plummer's (1843, fig. 8) originally figured, vertically fluted, 1-m-long specimen has a marked taper, from a point at one end to a maximum diameter of 6–7 cm at the other (see *Treatise Online*,

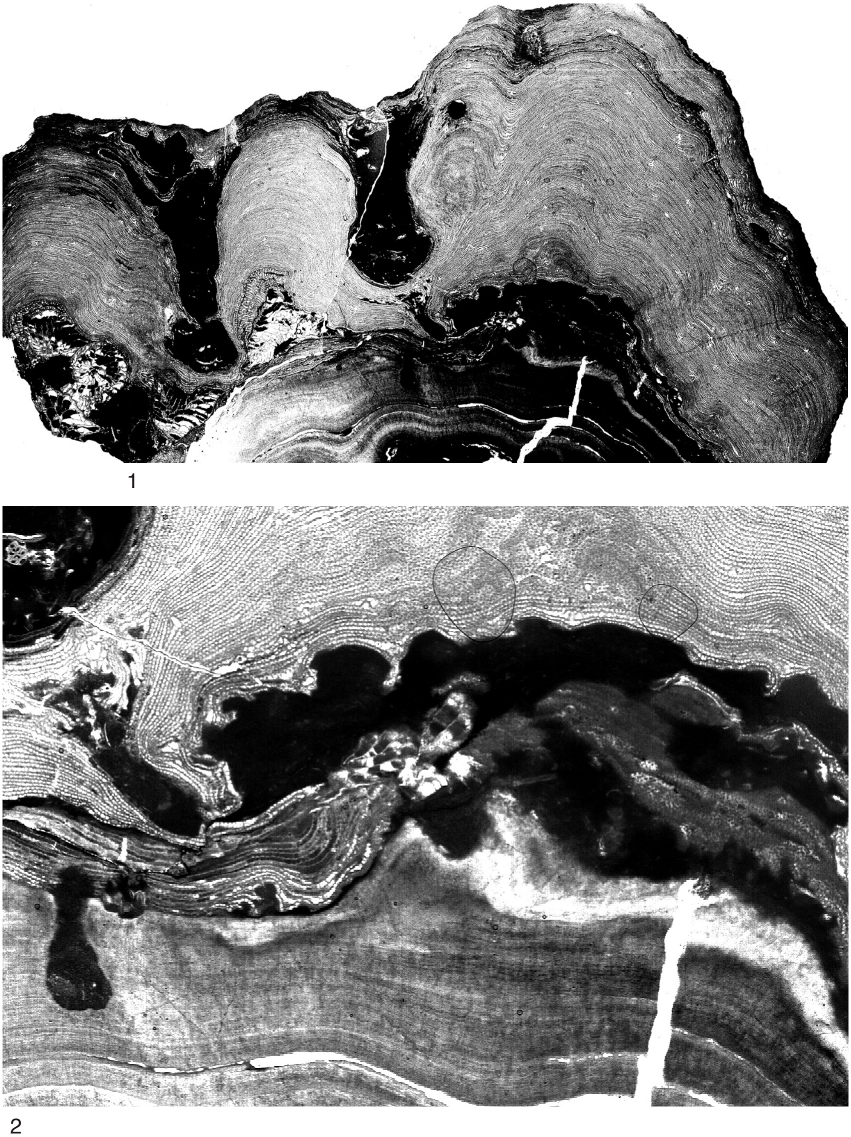

Fig. 18. *1,* longitudinal thin section of two stromatoporoid species, *Densastroma pexisum* (Yavorsky) and *Petridiostroma simplex* (Nestor), Visby Formation, Gotland, Sweden, sample 1-23, locality Ireviken 3 (Note: faint circles near base of right domical mass of *P. simplex* are air bubbles in thin section). *D. pexisum* is the gently updomed laminar stromatoporoid at the bottom, and *P. simplex* is the smooth, composite skeleton of three domical masses in middle to upper parts. Note that the three domical masses have laterally interconnected thin, irregular, laminar outriggers in their basal and topmost parts. Also note the complex and varied encrusting relationships between *P. simplex* and the underlying rugose coral and small bryozoan (left side; for details, see Fig. 19), as well as its relationships with the underlying, irregularly elongate tongue of dark sedimentary rock, ×0.9 (right side; for details, see view *2*); *2,* enlarged view of base of skeleton of *P. simplex* beneath right domical mass showing particularly complex and irregular arrangement of contacts with underlying dark sedimentary rock tongue. This suggests that either a large cavity originally existed beneath this part of the skeleton and that cavity was only later backfilled with sediment; or, alternatively, the sedimentary material predates the basal growth; i.e., it became lithified and irregularly eroded, perhaps even in part burrowed, before being overgrown by the stromatoporoid organism. Note well-defined, flask-shaped *Trypanites* boring in the upper part of the underlying, fine-textured, laminar skeleton of *D. pexisum* (lower left part of figure), ×3.6 (adapted from Kershaw, Wood, & Guo, 2006, fig. 3a).

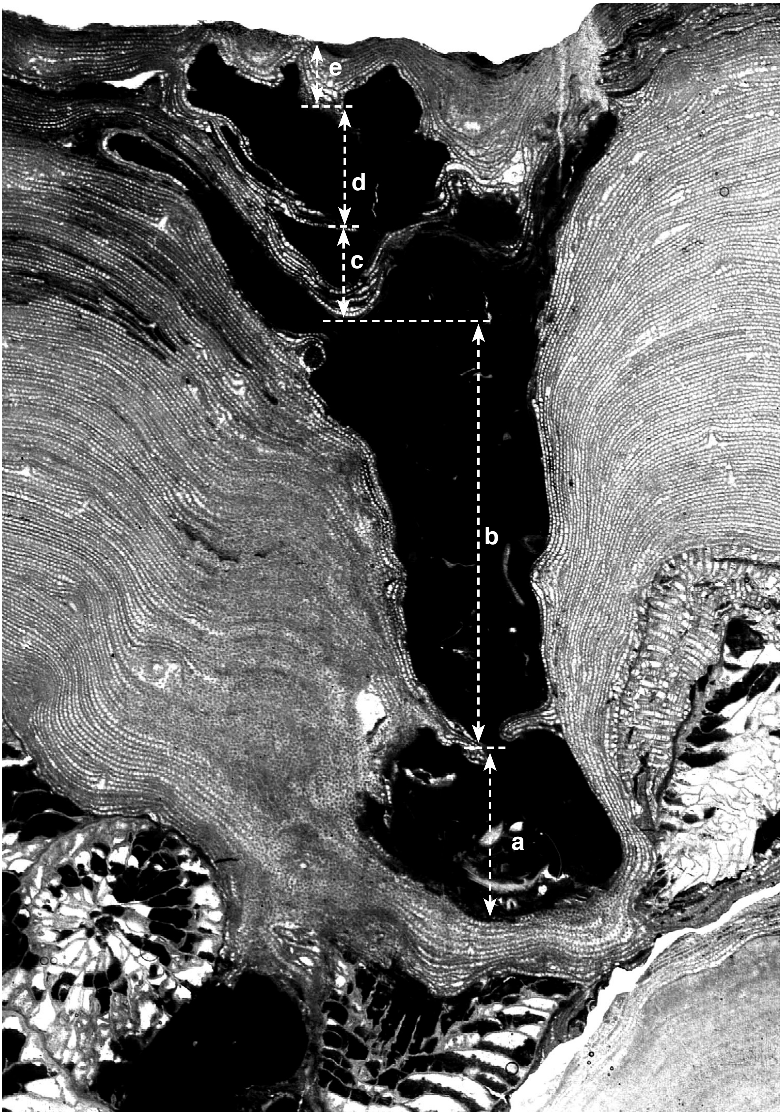

FIG. 19. Enlarged view of Figure 18.1 to show organism-organism and organism–sediment relationships associated with the left and central domical masses of the *P. simplex* skeleton. Note the encrusting basal contacts with the rugose coral to the left, and superposed coral and bryozoan colonies to the right. A delicate balance existed between the growth of the domical masses and the sedimentary infilling of intervening cavity spaces. The organism–sediment relationships may be traced through five separate phases (*a–e*), as follows: *a,* sediment infilling lower cavity, and then a pause in rate of sediment influx, allowing slender lateral offshoots, each with a few laminae to extend inward, almost closing off space; *b,* a more continuous period of sediment influx, allowing nonenveloping relationships of successive laminae to develop along sides of adjacent domical masses as cavity became progressively infilled; *c,* cessation of sedimentary input then permitted lateral spread of undulating, ragged strands of laminar growth, and in this case, the gap was bridged by a few irregular, sinuous laminae that formed across the cavity, although some localized swamping by sediment also continued to produce small, sediment-filled spaces; *d,* slightly increased rate of sedimentary input probably allowed the next, larger, sediment-filled cavity to form; *e,* in this last sediment-starved phase, lateral outriggers of growth were able to completely mantle the upper surface of skeleton, closing off all infilled cavity spaces between formerly separated left and central domical masses, ×5 (Kershaw & Webby, new).

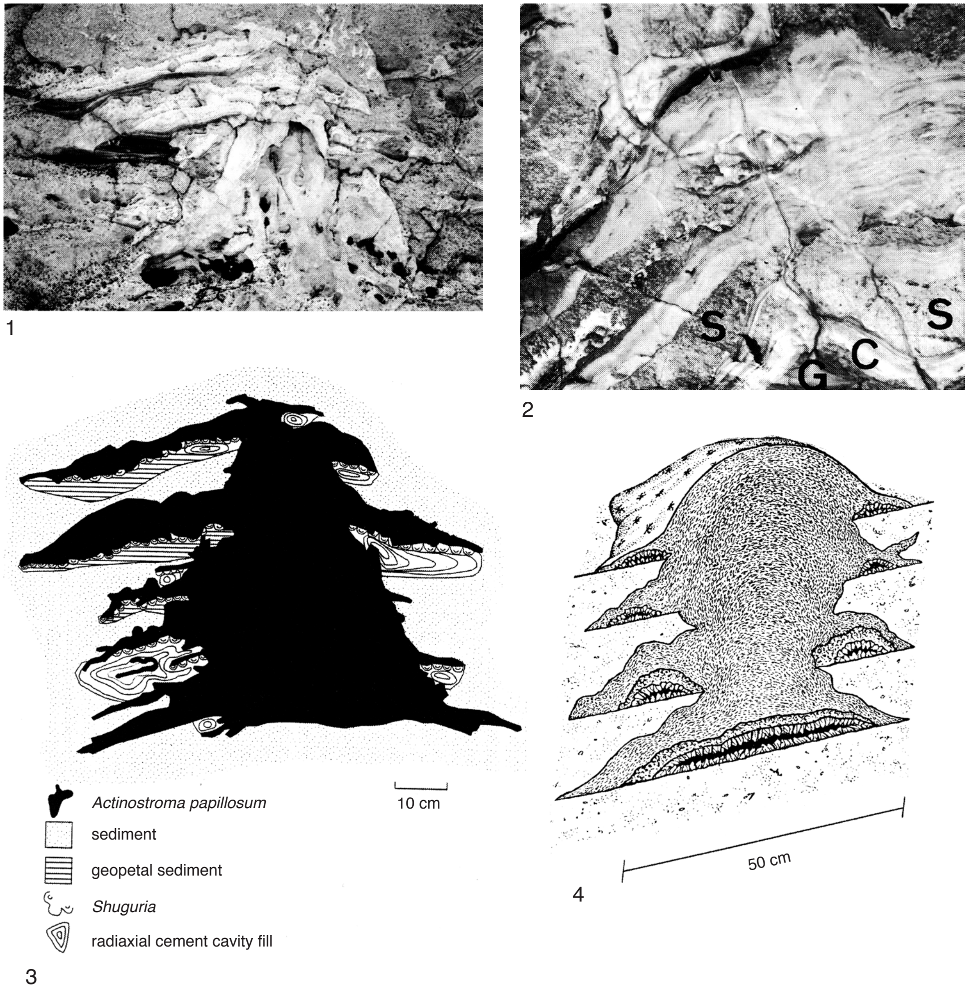

Fig. 20. Large, complex, free-standing, domical stromatoporoid that developed unsupported lateral outriggers off an elevated skeleton and was also colonized by cryptic organisms; these encrusted the sheltered sites beneath the extended outriggers, and the primary spaces were subsequently infilled by a combination of geopetal sediments and early marine cements. However, Wood (2000, p. 678) inferred that at any one time during growth, the overall relief above the substrate would rarely be more than about one-third the total height of skeleton. The stromatoporoid adopting this growth form is *Actinostroma papillosum* Bargatzsky, Frasnian, Upper Devonian, Pillara Limestone, Windjana Gorge, Canning Basin, Western Australia (see also Fig. 32; adapted from Wood, 1999, fig. CS 3.5b, copyright John Sibbick); *1,* a large domical specimen of *A. papillosum* Bargatzsky, ×0.05 (Wood, 2000, fig. 6A); *2,* part of a skeleton showing lateral outriggers of *A. papillosum* Bargatzsky with lower surfaces encrusted by *Shuguria* (*S*), and cavities filled with sedimentary rock that form geopetal structures (*G*), and fibrous cement (*C*), ×0.2 (Wood, 2000, fig. 6B); *3,* outline drawn from the same large domical specimen (see view *1*) to illustrate the nature of attached cryptic growth of *Shuguria* and cavities beneath lateral outgrowths containing geopetal structures and early marine cement (Wood, 2000, fig. 7A); *4,* schematic drawing depicting inferred mode of growth of large domical stromatoporoid, with its important role in generating cryptobiont-bearing cavity spaces (Wood, 2000, fig. 6C; drawing courtesy of John Sibbick).

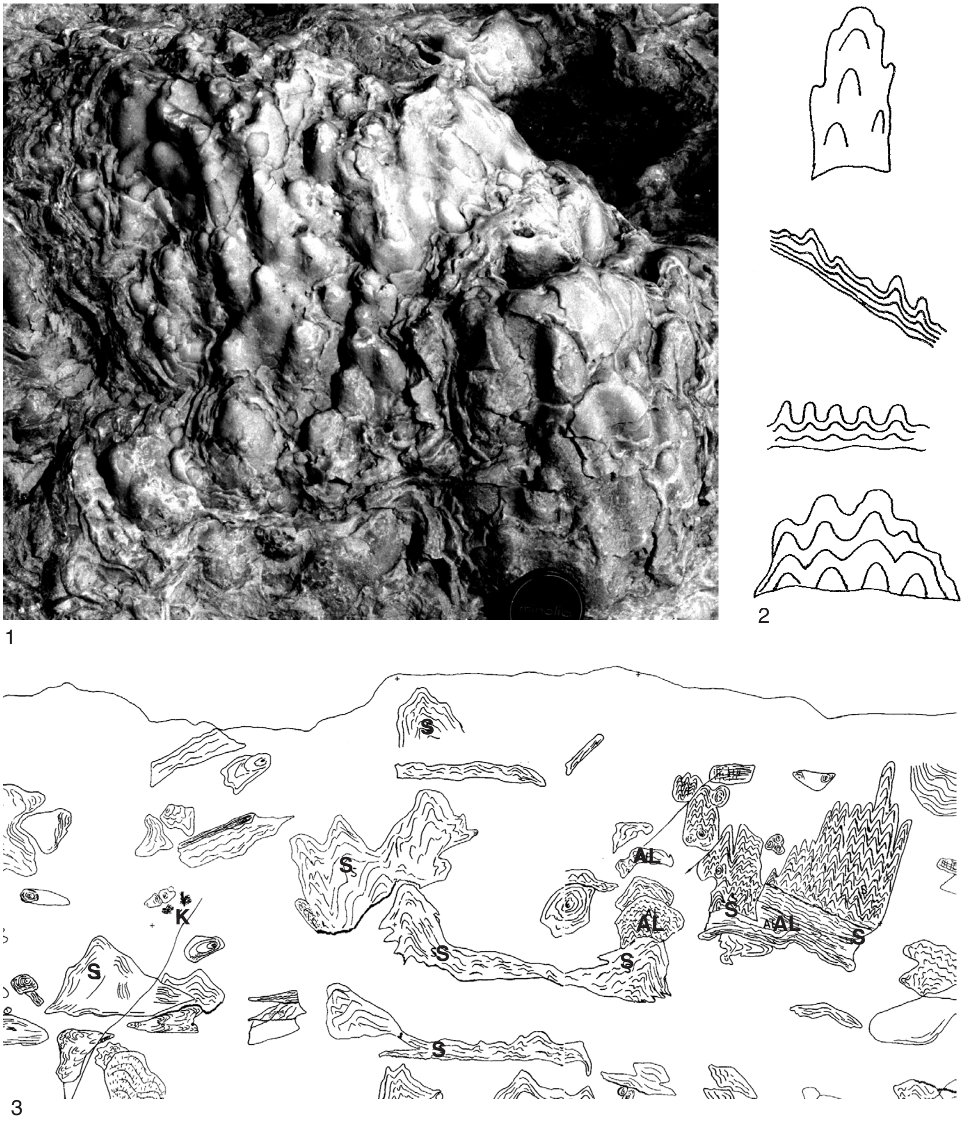

FIG. 21. *1,* Oblique view of part of a large, mamelated, domical specimen of *Parallelostroma typicum* (ROSEN), Hemse Group, Ludlow, Fågelhammar, Gotland, Sweden, showing smooth, conelike peaks of mamelons, and in some, inclined, exfoliated areas, examples of discontinuity surfaces between latilaminae, ×0.2 (Webby, new; similar specimen from same locality and stratigraphic level was illustrated by Mori, 1970, pl. 28,*3;* and by Fagerstrom & West, 2010, fig. 1C); *2,* diagrammatic sketches of mamelons on upper surfaces and their counterparts as mamelon columns in longitudinal section from the Kuppen Biostrome, Gotland; at the top are two examples of mamelons (or mamelon columns) that exhibit oblique relationships to lateral slopes; one is a large mamelon that shows very small, secondary cones on its slopes. The other two examples at the bottom show mamelon columns that developed on flat or updomed surfaces (adapted from Kershaw, 1990, part of fig. 7); *3,* tracing showing details of part of outcrop (mainly part of the reef growth center) at the center of 15-m-long cut wall A, Villmar reef complex, Givetian, Middle Devonian, Germany; detailed section is 4 m long and only top half (upper 1.5 m) of 3-m-high cut wall; it shows distributions of main components of reef: the bulk are stromatoporoids (only some are marked *S*), and others, much less common: one coral (*K*) and three laminar algae (*AL*); stromatoporoids include forms that are *in situ* (near horizontal in outcrop) and reworked forms (tilted in outcrop); shapes are mainly laminar, low, and high domical; additionally, there are prominently mamelated domical stromatoporoid skeletons—see upper right part of figure (adapted from Braun & others, 1994, part of pl. 5).

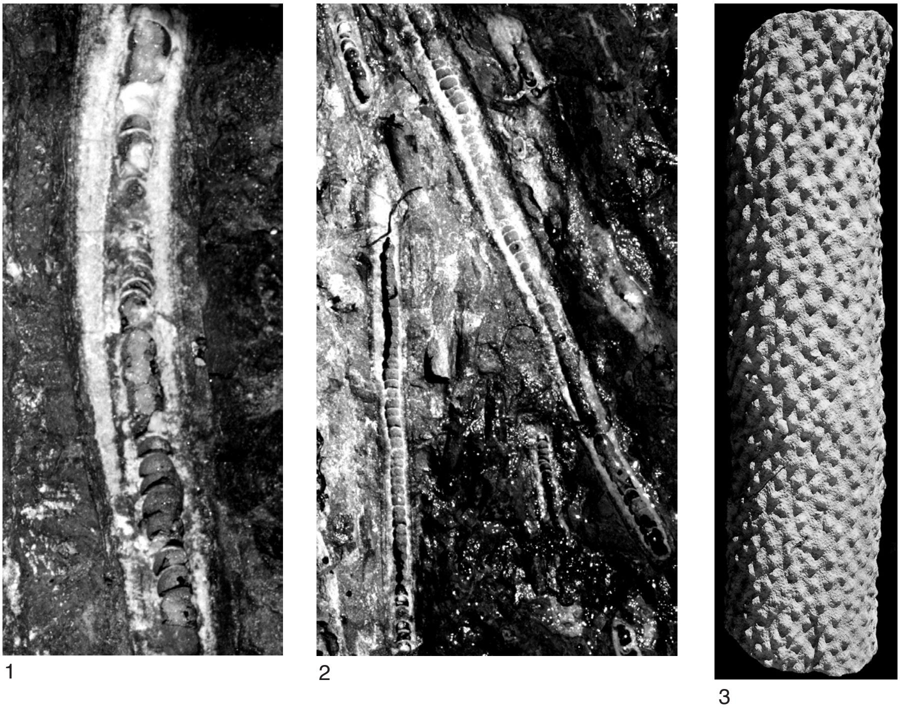

FIG. 22. Photographs of relatively slender, columnar, aulaceratid stromatoporoids, Vaureal Formation, Upper Ordovician, Anticosti Island, Canada. Specimens in views *1* and *2* are from exposed bedding surfaces, whereas specimen in view *3* has been isolated from the sedimentary rock; *1,* characteristic columnar shape of *Aulacera* sp., showing internal structures, especially arcuate axial cysts, of abraded specimen, Anse aux Fraises, western Anticosti Island, ×0.5 (Webby, new); *2,* toppled, current aligned, slender, columnar skeletons of *Aulacera* sp., exhibiting some internal axial and peripheral features in abraded specimens, Anse aux Fraises, western Anticosti Island, ×0.25 (Webby, new); *3,* columnar aulaceratid specimen, probably *Aulacera nodulifera* (FOERSTE, 1909), Anticosti coast, east of Rivière-aux-Saumons, showing the distinctive nodular external surface, AMF.134347, ×0.3 (Webby, new).

Part E, Revised, Vol. 4, Chapter 16B, genus *Aulacera,* view h).

During life, the aulaceratids are inferred to have grown vertically to at least a meter above the carbonate-mud substrate before being toppled by a storm event (Fig. 23). Some broken skeletal bases are preserved *in situ*, up to 0.25 m in height (part-embedded and part-exposed above the substrate), and occasionally grouped in nestlike clusters. They do not appear to develop a separately differentiated laminar base. The initial (basal) unit of growth, i.e., the part embedded in the substrate, has the same skeletal structure of large axial cyst plates and lateral rows of small lateral cyst plates, as does the rest of the aulaceratid skeleton. Only one feature apparently helped to stabilize these large specimens on the unconsolidated substrate: a concretionary growth ring that probably developed by synsedimentary processes around the unmodified base (see CAMERON & COPPER, 1994, fig. 4). BOGOYAVLENSKAYA, VASSILJUK, and GLEBOV (1990, p. 70), however, argued that the columnar skeletons of aulaceratids lacked traces of attachment, that they were spindle-like in shape, and hence, skeletons grew by adopting a rolling back-and-forth motion on nearshore substrates. This interpretation is discounted in favor of the group more typically exhibiting symmetrically arranged, erect, columnar shapes that represent upright growth, and internally composed of an axial core of large, superposed, horseshoe-shaped cyst plates and a surrounding, uniformly

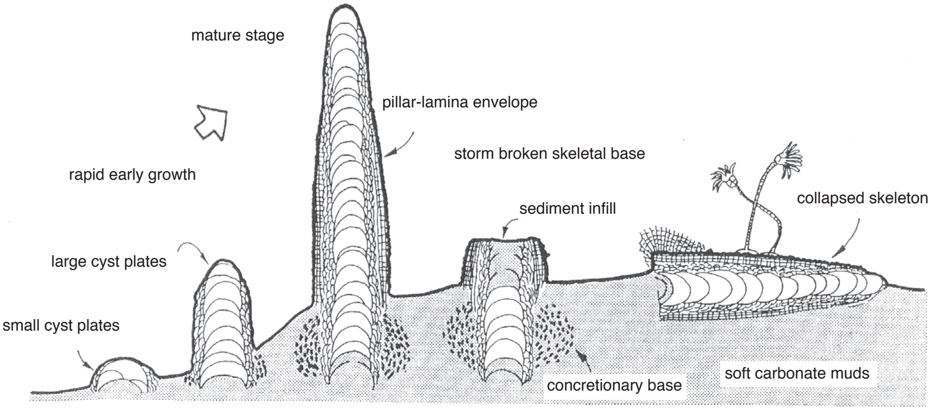

FIG. 23. Schematic reconstruction of life and death of large, columnar, aulaceratid stromatoporoids, Late Ordovician, Ellis Bay Formation, Anticosti Island, Canada (Cameron & Copper, 1994, fig. 4).

continuous, peripheral zone of smaller, imbricated cyst plates (see BOLTON, 1988, pl. 2.5, fig. 4, 6; WEBBY, 1991, fig. 11A–C, 12A, E; CAMERON & COPPER, 1994, fig. 3e; and see also *Treatise Online,* Part E, Revised, vol. 4, Chapter 9C, p. 4, Fig. 2,*4*, STEARN, 2011, and Chapter 16B, genus *Aulacera,* views a–h).

Outer lateral surfaces of the columnar aulaceratids on Anticosti Island show markedly different features. For example, they may be smooth, undulose, nodular (Fig. 22.3), or pustular. Some of these characters have been used to define the different taxonomic species of the genus. The aulaceratids of Anticosti Island are not closely associated with reef complexes. They grew in forests on muddy, unconsolidated substrates in relatively undisturbed deeper water conditions above storm wave base and were subjected to periodic severe storm events (LONG & COPPER, 1987; CAMERON & COPPER, 1994; KERSHAW & BRUNTON, 1999). Other aulaceratid genera (e.g., *Ludictyon, Cryptophragmus)* exhibit unbranched, columnar shapes, but the nature of initial growth in these forms remains unknown.

A feature of a species of *Cryptophragmus* from western North America and the Siberian Platform (RAYMOND, 1914; GALLOWAY & ST. JEAN, 1961; BOGOYAVLENSKAYA, 1977) is the presence of a mud or sparry, calcite sheath between the axial column with its large, superposed cysts and a lateral zone appearing as rows of small cyst plates (like the structure of *Cystostroma)* or a combination of cyst plates and pillars (as in *Labechia*). The lateral zone of *C. antiquatus* RAYMOND was interpreted by GALLOWAY and ST. JEAN (1961, p. 18) as representing "growth downward from the top of the column, after . . . the mud was deposited, making latilaminae" (Fig. 24). However, the latilaminae appear to be integral parts of the *Cryptophragmus* skeleton. The intervening mud (or sparry calcite) sheaths are between 1 and 2 mm thick, and may, in some specimens be repeated up to three times between successive latilaminae. Each mud sheath was implied by GALLOWAY and ST. JEAN (1961) to have been deposited during a nongrowing season. The problem remains how the mud sheaths formed as a relatively uniform layer on near-vertical slopes of the cylindrical skeleton. Possibly, with seasonal changes, there was partial mortality of the skeleton, allowing sediment-trapping, binding, or precipitating activities of microbial communities to preferentially mantle and then trap the mud on the outer surface before the next growing season allowed a new latilamina to be secreted over the mud layer. A study of better preserved specimens is needed to check whether the mud sheaths

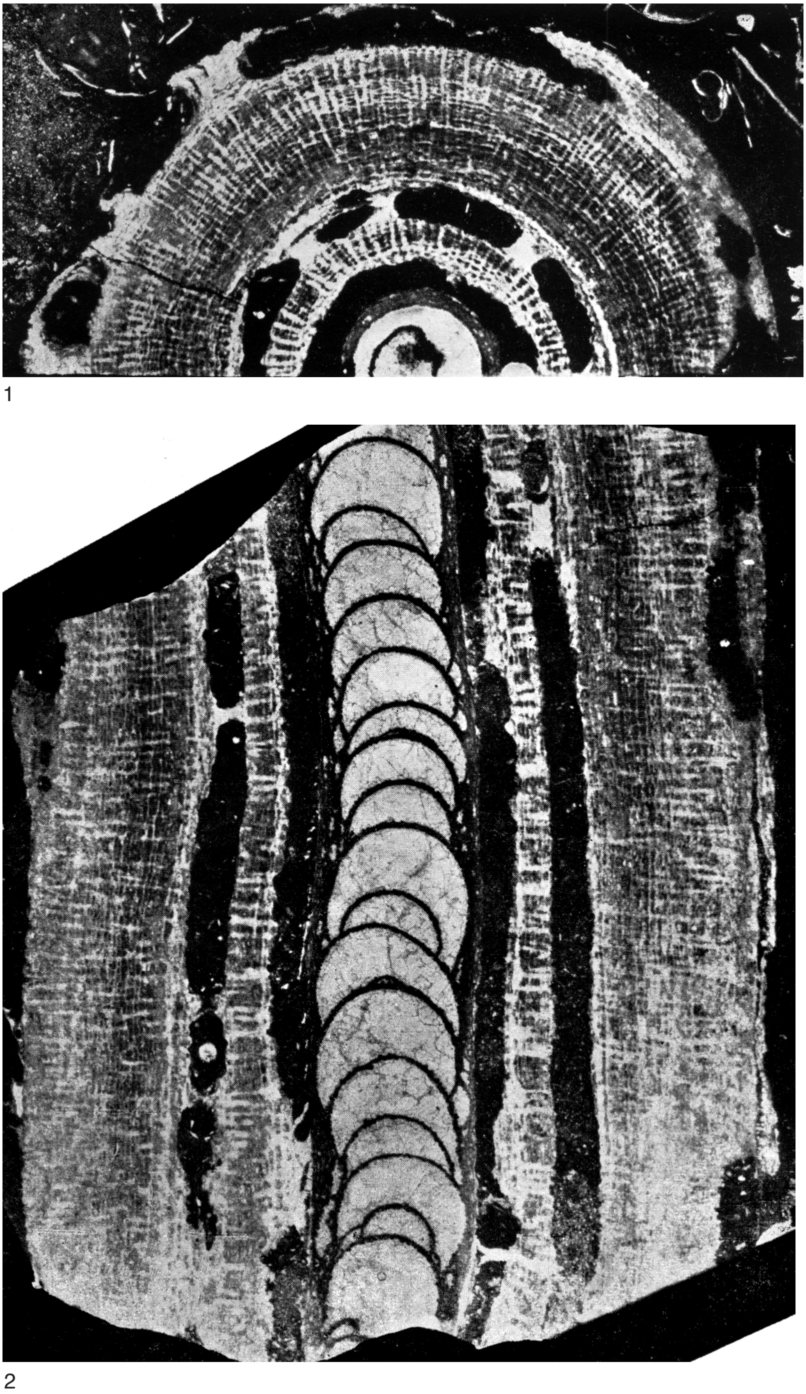

FIG. 24. *(For explanation, see facing page).*

show evidence of mat or biofilm (microbial) communities or not.

The clathrodictyid genera *Labechiina* and *Neobeatricea* and problematic genera *Clavidictyon* and *Shirdagopora* also show predominantly columnar growth.

Digitate

The term digitate is preferred to describe shapes with subparallel, multibranched columns (Fig. 2, Fig. 25). Other related terms are multicolumnar, multiprotuberant, fingerlike, stachyodiform, and fasciculate, but these are all now regarded as obsolete. The term stachyodiform was restricted by Cockbain (1984, p. 9) to more robust-type branching forms (diameters greater than 5 mm) but was only applied to species of a few genera besides *Stachyodes*. Some of the examples of protuberant, multicolumnar growth reported by Kershaw (1998, p. 522, fig. 7) represent digitate growth forms as described here.

Digitate shapes are characteristically erect, subparallel, close-spaced, fingerlike, or occasionally expanding-upward columns, off a laminar base. Comparatively smooth and nonenveloping types are commonly associated. In its simplest representation, the shape is depicted by the syringostromatid species *Syringostroma cylindricum* Fagerstrom (Bjerstedt & Feldman, 1985, fig. 6, 8), appearing as a number of discrete columns spreading upward and outward from a laminar base (Fig. 25.1). Bjerstedt and Feldman (1985) identified a succession of growth forms (and taxa) through a 1.5-m-thick, upward-shoaling, Middle Devonian

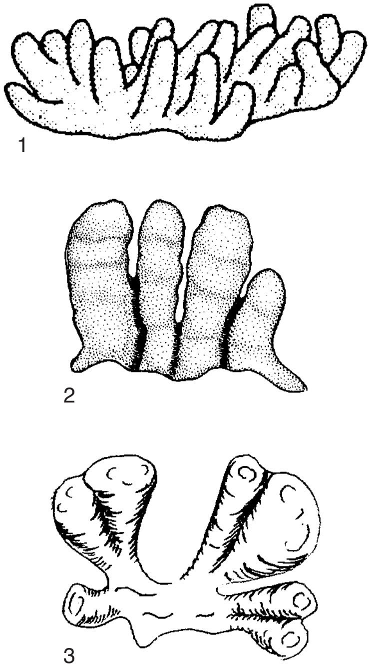

Fig. 25. Examples of stromatoporoids that exhibit digitate growth forms; *1,* schematic representation of digitate form of *Syringostroma cylindricum* Fagerstrom, north lakeshore site of the stromatoporoid bioherm, lower Eifelian, Middle Devonian, uppermost Lucas Dolostone, uppermost Detroit River Group, Kelleys Island, Ohio, United States (adapted from Bjerstedt & Feldmann, 1985, see parts of fig. 6, 8, no scale); *2,* drawing of digitate morphotype of species *Parallelostroma kudrinzyensis* (Riabinin), of subparallel columns raised above a broad laminar base, Pridoli, upper Silurian, Skal'skiy horizon, Podolia, Ukraine, ×2.5 (adapted from Bogoyavlenskaya, 1984, fig. 1v, ×5); *3,* field sketch of digitate shape of *Parallelostroma typicum* (Rosen), though it is not typical in being more openly radiating and with branches expanding outward; Ludlow, upper Silurian, Malinovetskiy horizon, Podolia (adapted from Bogoyavlenskaya, 1982, fig. 7, no scale).

Fig. 24. Columnar labechiid *Cryptophragmus antiquatus* Raymond from beds equivalent to upper Pamelia formation, north of Aylmer, Quebec, Canada, in thin sections illustrating the specimen, with a narrow axial column of superposed, horseshoe-shaped cyst plates, and a broad lateral zone of very fine, outwardly radiating pillars intersecting very closely spaced rows of long, low cyst plates, as well as including three mud-filled (possibly in part sparry calcite) sheaths; *1,* transverse section of the columnar specimen showing main features of three mud-filled sheaths—two in inner part of the lateral zone and a third close to outer margin of this specimen. These concentrically arranged sheaths maintain parallel relationships with adjacent, much finer pillar and cyst plate structures, they have similar thicknesses, and in a few places, they show breaks in continuity of mud fill where a few, much thicker, hour-glass–shaped structures (possibly composed of sparry calcite) occur, ×4 (Raymond, 1914, pl. 2,*1*); *2,* longitudinal section exhibits similar features, although the outermost mud sheath appears to have a very limited continuity along length of specimen, ×4 (Raymond, 1914, pl. 2,*2*).

biohermal package that developed on a stabilized bindstone substrate at Kelleys Island, Ohio. The digitate growth form (they called it fasciculate) of *S. cylindricum* appeared in the topmost part of the bioherm, therefore representing the end member of their laminar→domical→irregular→digitate series of shapes.

Species of the syringostromatid genus *Parallelostroma,* from the Silurian of Podolia, also exhibit digitate growth (see Bogoyavlenskaya, 1982, p. 120, fig. 7; 1984, fig. 1c). The growth form of *P. kudrinzyensis* (Riabinin) has a very characteristic digitate shape arising off a laminar base (Fig. 25.2), and *P. typicum* (Rosen) shows radiating columns that progressively expand away from the laminar base, with more vertically directed columns being larger than the more laterally directed columns (Fig. 25.3). Many species of the genus *Stachyodes* (family Stachyoditidae) exhibit a digitate growth form, and the skeletons usually have robust branch diameters of 5 mm or more. However, a few have a more completely integrated meshwork of columns and laminar elements, as shown in *S. fasciculata* Heinrich from Middle Devonian reef complexes of Bergisches Land, Germany, and *S. costulata* Lecompte from the Upper Devonian Canning Basin reef complexes (Cockbain, 1984; Wood, 2000). *S. fasciculata* has a laminar base and a more continuous laminar fusion of adjacent columns (Stearn, 1966, p. 118; see also *Treatise Online,* Part E, Revised, vol. 4, Internal Morphology, Chapter 9C, p. 17, Stearn, 2011), while *S. costulata* (Fig. 26, and see Fig. 32) exhibits more irregularly reticulated meshes of lateral bridges interlinking adjacent columns. These stachyodid species exhibiting combinations of the two morphologies (digitate and laminar) were capable of exhibiting more flexible growth strategies (perhaps they were less constrained by their genetic make up). It appears that the subparallel columnar growth was maintained during episodes of sediment swamping, and development of lateral offsets (laminar growth) relates to the pauses between the periodic influxes of sediment. Where meshworks of interlinked lateral bridges are more complete, the growth form should be described as digitolaminar (previously named digitate by Kershaw, 1998, fig. 7); see further discussion of Digitolaminar shapes, herein, p. 37).

The species *S. costulata* also exhibits, at widely spaced intervals, acutely dichotomous branches (Fig. 26.4), which suggests an even greater plasticity of growth in the species. This branching type is a feature of the more exclusively dendroid forms (see below), but in *S. costulata,* the dividing branches remained acutely aligned because so little space existed between the subparallel columns of its skeletal growth, as compared with more typical, open branching, dendroid forms.

Dendroid

The term dendroid is maintained for shapes that are typically produced by erect, open-spreading, laterally free, arborescent branches (Fig. 2, Fig. 27.1), and may have a smooth exterior and nonenveloping habit. The branching is usually dichotomous (Fig. 27.2–27.4), but offsets having the appearance of lateral buds may also be present (Fig. 27.5). The dendroid, thicket-like clusters grew initially from attachments to small skeletal grains on soft substrates, apparently developing some stability as they sank into muddy substrates under their own weight (adopting a mud-sticking strategy; Brett, 1991, p. 330). Other terms have been used to identify this growth form, but they should now be regarded as obsolete (e.g., ramose, arborescent, twiglike, amphiporiform). The term amphiporiform has been applied only to slender-branching, *Amphipora*-like fossils with stemlike branches, usually less than 5 mm in diameter (Cockbain, 1984, p. 9).

The presence of dendroid branching has been used taxonomically to recognize some stromatoporoid genera of the Labechiida, Stromatoporellida, and Amphiporida. In the labechiid family Aulaceratidae, for

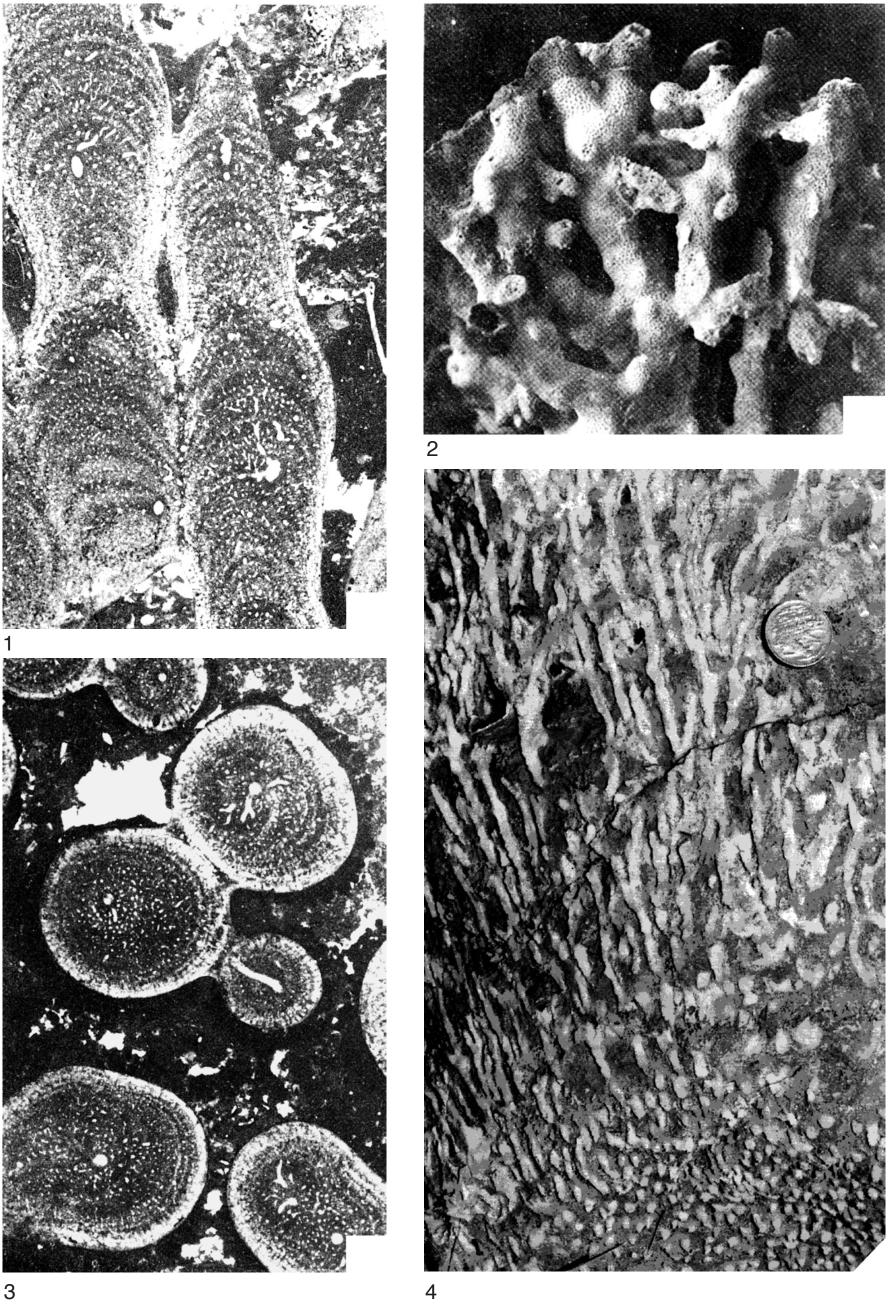

FIG. 26. Digitate shapes of *Stachyodes costulata* LECOMPTE, Frasnian, Upper Devonian, Canning Basin, Western Australia; *1,* longitudinal section, Pillara Limestone, Emanuel Range, fossil loc. no. NOB 33 (registered fossil no. GSWA F10625), ×3.2 (adapted from Cockbain, 1984, pl. 19A); *2,* general view of silicifed skeleton, Sadler Limestone, Emanuel Range Kudata Gap, fossil loc. no. NOB 32, showing dichotomous branching and lateral bridges (registered fossil no. GSWA F 7885), ×1.6 (adapted from Cockbain, 1984, pl. 19B); *3,* transverse section, Pillara Limestone, Emanuel Range, fossil loc. no. NOB 33 (registered fossil no. GSWA F10625), ×3.2 (adapted from Cockbain, 1984, pl. 19C); *4,* longitudinal section of a densely branching (digitate) thicket, Pillara Limestone, Baralama Spring; note also examples of dichotomous (dendroid) branching in middle upper part of figure, ×0.25 (adapted from Wood, 2000, pl. 3,*1*).

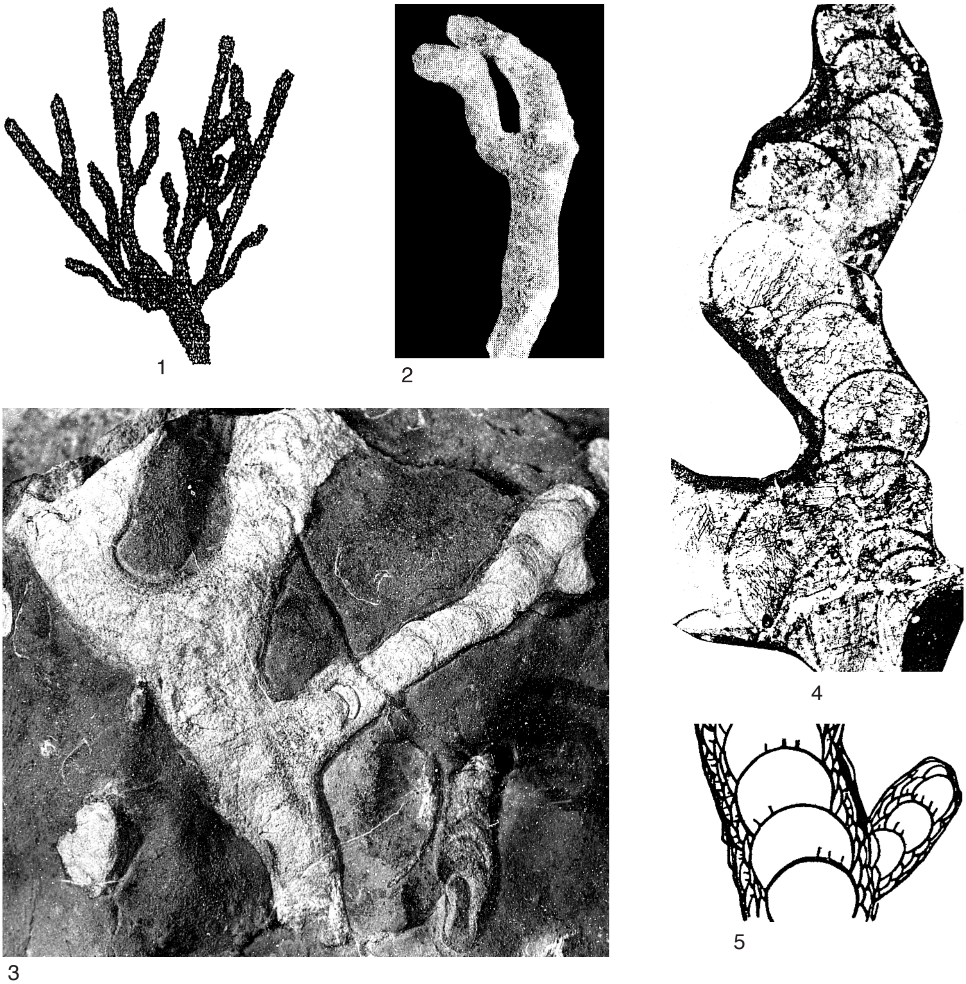

FIG. 27. Examples of branching, mainly dendroid-shaped stromatoporoids; *1,* hypothetical representation of skeleton of a slender, dendroid, amphiporid stromatoporoid (adapted from Kershaw & Brunton, 1999, fig. 3C); *2,* branching, silicified fragment of *Clavidictyon? sokolovi* (Riabinin), Hamra Formation, upper Ludlow, Burgsvik, Gotland, Sweden (loc. no 150), ×2 (Mori, 1970, pl. 22,*8*); *3, Thamnobeatricea gouldi* Webby, Upper Ordovician, Sandbian, Gordon Group, Bubs Hill, Tasmania, showing typical lateral branching form, specimen no. UTGD90454, ×1 (Webby, 1991, fig. 16B); *4,* longitudinal section of incomplete, dichotomously branching specimen of *Pararosenella cylindrica* (Vassilyuk), Upper Devonian, Famennian, Donetsk Basin, Donbass, Ukraine, specimen no. 4, Sverdlovsk Mining Institute, ×5 (adapted from Bogoyavlenskaya, Vassilyuk, & Glebov, 1990, pl. 26,*1*); *5,* sketch showing a lateral branch (like a lateral bud) in a part of skeleton of *Pararosenella cylindrica;* incorrectly labelled as *Rosenella lissitzini* forma *cylindrica* Vassilyuk by Bogoyavlenskaya, Vassilyuk, & Glebov, 1990, p. 73 (adapted from Bogoyavlenskaya, Vassilyuk, & Glebov, 1990, fig. 7 *partim*).

example, about half the genera (*Sinodictyon, Thamnobeatricea, Alleynodictyon, Pararosenella*) exhibit dendroid (dichotomous or lateral) branching forms (others show columnar shapes). Other genera that developed mainly dendroid growth forms are: *Dendrostroma* (family Stromatoporellidae), *Idiostroma* (family Idiostromatidae), *Amphipora, Clathrodictyella, Novitella,* and *Paramphipora* (order Amphiporida), and the problematic genus *Praeidiostroma,* but this latter has been interpreted as a growth variant of the clathrodictyid genus *Gerronostroma* (Stearn & others, 1999).

COMBINATIONS

Digitolaminar

This composite shape comprises a complex, boxwork structure of laterally extensive, successive, platelike tiers (or floors) above a laminar base and separated to more coalescent, vertical, postlike columns (or lobes) that may be continuous or incomplete, the latter dependent on sediment-filled interruptions to vertical continuity (Fig. 2, Fig. 28–29, Fig. 43). The shape was termed digitate by Kershaw (1998, p. 520, fig. 7) and platy-multicolumnar by Wood (2000, p. 678), but the term digitate is inappropriate, because it exhibits the well-developed, laminar-shaped tiers, and the term platy-multicolumnar is not consistent with other basic descriptive shape terminology used here. Hence, the combined term digitolaminar is preferred to maintain conformity with the single laminar and digitate usages employed in this shape classification. The modern scleractinian coral, *Porites lichen* Dana, which is widely distributed in lagoons and reef slopes of the tropical Indo-Pacific from the Red Sea to Samoa, shows a strikingly similar growth form combination of laminar and digitate shapes (Fig. 28.1; see also Veron & Pichon, 1982, p. 43, fig. 61–62; and Veron, 1986, p. 228, fig. 3). The generalized digitolaminar shape is also exhibited within the growth form variations of the Silurian heliolitid coral, *Stelliporella parvistella* (Roemer) from Gotland and England (Young & Scrutton, 1991). This plastic species exhibits an extraordinarily wide range of growth forms (laminar, domical, bulbous to columnar, and branching), as well as alternations (or switches) between discrete units of laminar and digitate growth.

Examples of digitolaminar growth develop in a number of Paleozoic stromatoporoids. In *Ecclimadictyon stylotum* (Parks), the growth combination comprises successive growth units, each exhibiting a laminar tier from which a number of erect, bulbous to columnar lobes arise (Fig. 28.2–28.3). In the large, highly complex, composite growth form of *Actinostroma windjanicum* Cockbain, a boxwork structure develops from a centralized area of more or less parallel to slightly coalescent, vertical columns, and more laterally extensive, tiered, laminar outgrowths (Fig. 29, Fig. 32), as depicted by Wood (2000, p. 678, fig. 8–9). Another specimen identified by Riabinin (1953, p. 49, pl. 19, *1*) as *Stromatopora* n. sp., from the Silurian of Podolia, possibly another growth variant of *Parallelostroma typicum* (Rosen), also appears to show a digitolaminar phase of growth, with its broadly open, reticular form of lateral extensions and partially interconnected, postlike offshoots (Fig. 28.4). A digitolaminar habit also appears to be present in the specimens of *Stachyodes australe* described by Mistiaen (1991) and Lachkhem and Mistiaen (1994) that exhibit predominantly laminar crusts (Fig. 30), including the vertical to steeply inclined offshoots that may be preferably interpreted as representing columnar or chimneylike branches.

The units of growth that produced the composite digitolaminar shapes were probably capable of developing in two different ways, either: (1) the skeletal shapes were produced when marked changes in rates of sedimentation occurred, while both laminar and digitate types of growth were forming close to the substrate; or (2) the structures developed while rates of sediment influx were more uniform, with the laminar growth (with primary cavities) produced above the substrate, and the digitate growth close to the substrate. Consequently, the laminar part of the unit formed either on a substrate when sedimentation was reduced, or it was produced by lateral growth above the substrate, away from more continuous sediment influx on the sea floor. Presence of sparite cement beneath laminar growth portions of some lower Wenlock examples from Gotland suggest that primary cavities may have existed. The branching, digitate

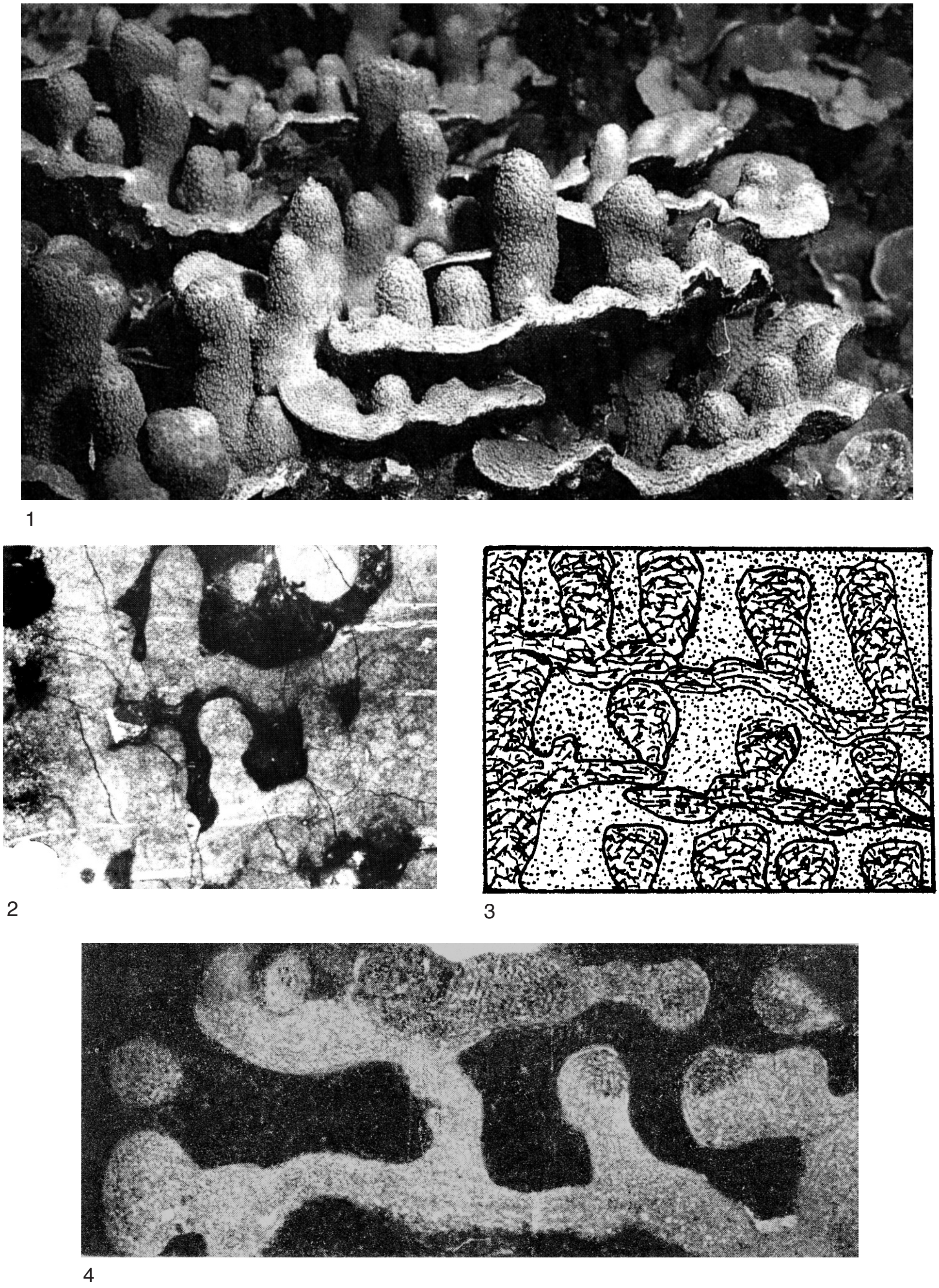

FIG. 28. Examples of Paleozoic digitolaminar stromatoporoids and a living scleractinian coral; *1,* digitolaminar-shaped skeleton of living, tropical, Indo-Pacific coral *Porites lichen* DANA (photo courtesy of Ron and Valerie Taylor, reproduced in Veron, 1986, p. 228, fig. 3); *2,* digitolaminar shape of skeleton of *Ecclimadictyon stylotum* (PARKS), Lake Aylmer Formation, upper Silurian, Marbleton area, southeastern part of Quebec Appalachians, Canada, ×2.8 (adapted from Hughson & Stearn, 1989, pl. 2L); *3,* thin section showing digitolaminar growth of *E. stylotum* *(Continued on facing page.)*

part of the growth, in contrast, probably formed near the substrate where moderate levels of sedimentary influx were maintained. These views are consistent with the suggestions made by YOUNG and SCRUTTON (1991, p. 380–381) for the digitolaminar shapes displayed by the heliolitid coral *Stelliporella parvistella*. In their survey of a number of heliolitid corals, they noted that, whereas the others had marked genetic controls on their growth form variation, *S. parvistella* was a very plastic species that exhibited ecophenotypic responses, particularly to changes in the sedimentation rate. They commented: "A modest, nonlethal increase in sedimentation could stimulate branching (=digitate) growth," but growth returned "to tabular or domal (=laminar) form when sedimentation reverted to background rates" (YOUNG & SCRUTTON, 1991, p. 381). Similarly, WOOD (2000, p. 700) noted that digitolaminar forms were possibly "indicative of growth under stressed conditions, such as episodic siliciclastic-sediment input, and that episodic sediment swamping may have initiated the formation of elevated structures which provided escape from such a threat." However, some workers (e.g., C. W. STEARN, personal communication, September 2006) maintained that these rare, complex growth forms, with such regular, rhythmic, repetitions, must be genetically controlled.

Foliaceous

A few specimens of *Actinostroma* sp., from the Upper Devonian of the Canning Basin (Western Australia), were described by WOOD (2000, p. 680) as exhibiting an unusual, highly complex, "inferred, whorl-forming, foliaceous" shape (Fig. 31). WOOD (2000, fig. 18) reconstructed the growth form (Fig. 32) as a large, elevated, free-standing shape, with a stacked, open, cuplike assembly of up to four, well-separated, thin, inwardly inclined, laminar layers or tiers (interpreted as parts of foliaceous whorls). The inferred shape was noted by WOOD as resembling the foliaceous growth form of the modern scleractinian coral, *Acropora palmata*.

Irregular (syn., massive *partim*)

This combination is not a geometrically distinct basic shape, and it is not easy to categorize, either by sampling whole specimens or, where this is not feasible because of their size, by accurately determining their three-dimensional form from oriented cross sections alone. Irregular shapes may vary in size from small to large, reaching sizes of more than a meter across and up to one meter in height. They commonly represent combinations of two or more basic growth forms, including the laminar, domical, bulbous, or even rarely, columnar forms (Fig. 2). The margins of skeletons are more often ragged than smooth. However, care must be taken when studying these irregular forms, because a good number prove to be composites of more than one growth form and may involve different species growing more or less contiguously with one another. The term irregular may sometimes be used with qualification to group shapes that cannot otherwise be accommodated into other main subdivisions, but adequate supplementary descriptions of the geometries and associations of these assigned forms should also be presented.

In some places, irregular shapes formed as *in situ* growths on hard substrates, where the stromatoporoid species encrusted irregular topographic highs of uneven rocky or reef areas or large skeletal objects. The irregular-shaped composites may have resulted from complex intergrowths of

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FIG. 28 *(Continued from facing page).*

(PARKS), with columnar lobes arising from successive laminar bases and intervening spaces surrounded by sediment (*dotted areas*), ×2.2 (adapted from Stearn, 1983, fig. 6A); *4,* photograph of digitolaminar "*Stromatopora* sp." (probably a species of *Parallelostroma,* like *P. typicum*), Malinovetskiy horizon, upper Silurian, Ludlow, Zbruch River, Podolia, Ukraine; polished surface of specimen no. 105a in collection of O. I. Nikiforova, ×5 (adapted from Riabinin, 1953, pl. 19,*1*).

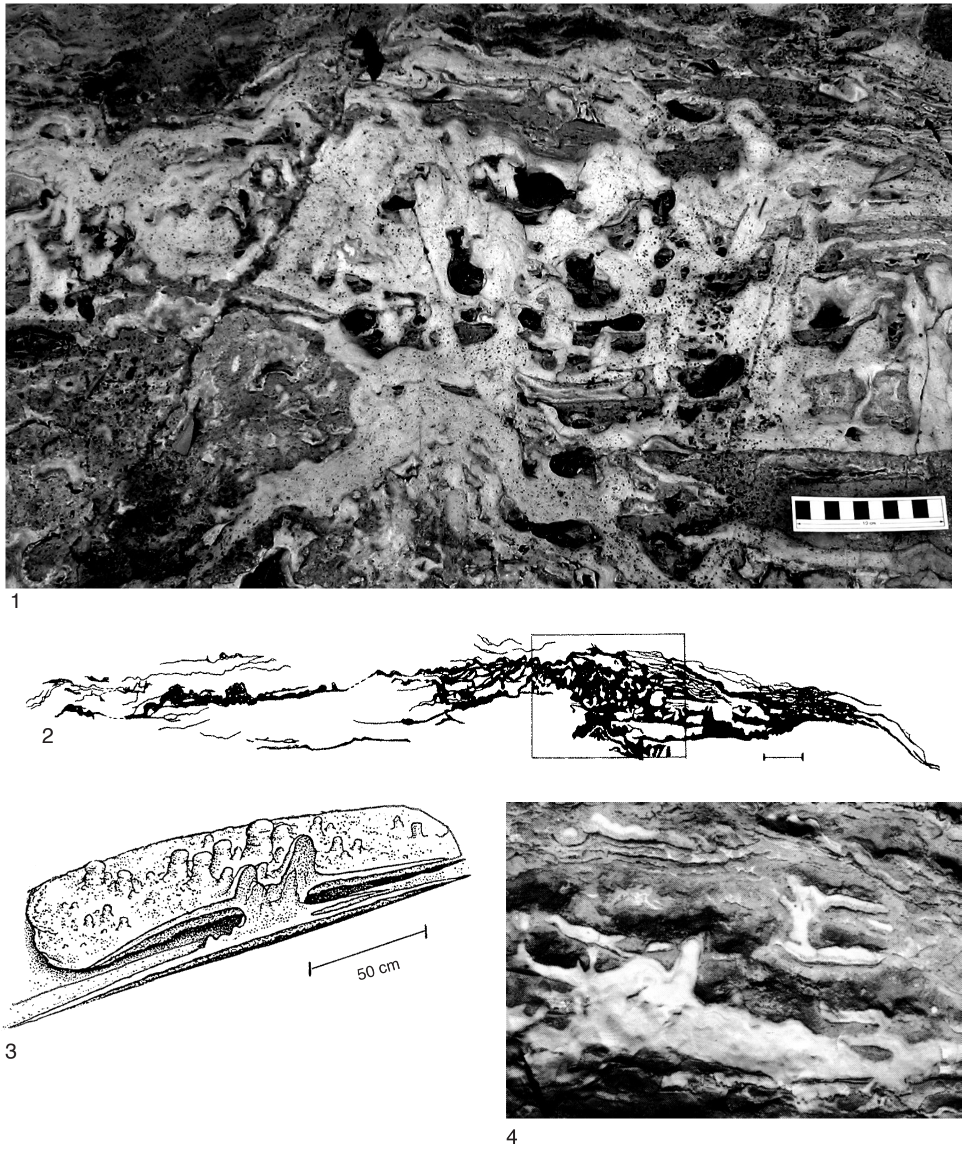

FIG. 29. Large, composite, digitolaminar stromatoporoid skeleton of *Actinostroma windjanicum* COCKBAIN, and other laminar stromatoporoid skeletons (possibly smaller specimens of the same species) with an incipient development of digitolaminar shape, Frasnian, Upper Devonian, Pillara Limestone (back reef facies), Windjana Gorge, Canning Basin, Western Australia; *1,* central columnar part of skeleton with extensive development of intersecting, stacked, lateral bridges (or domes) above substrate, leaving elevated undersurfaces as primary shelters or cavities available for encrusting *Shuguria*; scale bar, 10 cm (photograph courtesy of Rachel Wood; digitized photo IMG-0007); *2,* silhouette of very large, complete, digitolaminar-shaped skeleton of *A. windjanicum* from outcrop in gorge; note especially widely spread lateral outriggers (or plates), away from central part of specimen (*rectangular box*), shown in the outcrop photograph of view *1,* scale bar, 0.2 m (Wood, 2000, fig. 8B); *3,* reconstruction of the digitolaminar growth form based on the stromatoporoid *A. windjanicum* (Wood, 2000, fig. 9B; drawing courtesy of John Sibbick); *4,* other laminar skeletons may exhibit distinctive, columnar-shaped upgrowths off laminar bases; in a few places these upgrowths bear lateral offshoots, producing overall a rather rudimentary, digitolaminar shape, ×0.1 (Wood, 2000, fig. 15F).

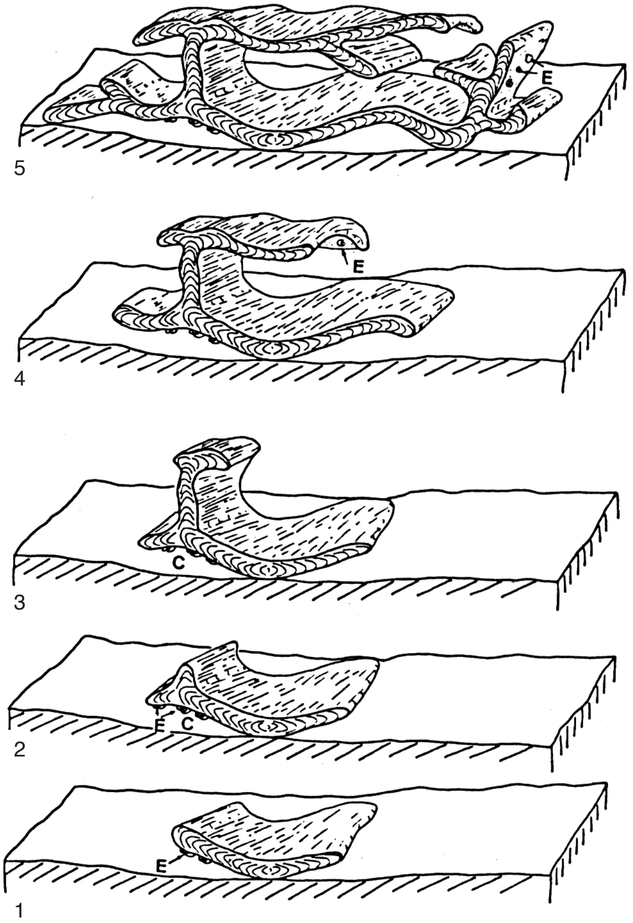

Fig. 30. Schematic representation of the morphology and five-stage growth development of *Stachyodes australe* (Wray). The sequence as interpreted by Lachkhem and Mistiaen (1994) comprises: (1) establishment as a free, recumbent, laminar sheet lying on the substrate, with a few cryptic organisms or so-called epizoans (*E*) becoming attached beneath a sheltered site; (2) initiation of vertical as well as continued lateral growth, with the sheltered site developing as a primary cavity (*C*) bearing a larger epizoan population; (3–4) extension of vertical growth and then lateral spread of an elevated outgrowth, with another sheltered site becoming available on its undersurface for colonization of cryptobionts (*E*); (5) continuation of the patterns of branching lateral, vertical, and oblique laminar growth, producing an anastomosing, wavy, sheetlike network, again with cryptobionts (*E*) colonizing some raised undersurfaces (Lachkhem & Mistiaen, 1994, fig. 4).

one, or more than one, stromatoporoid species or overgrowths of dead stromatoporoid surfaces, by the same or different encrusting stromatoporoid species. These shapes probably developed mainly in more turbulent conditions of the reef crest (Stearn, 1975; Braun & others, 1994), though irregular combinations were capable of being formed in a variety of other environmental settings.

Irregular forms were also produced on unconsolidated substrates where skeletons, especially high-profile domical to bulbous shapes, were affected by periodic current movements, causing them to be repeatedly tilted, rolled, and even, at times, partially fragmented, prior to successive resumptions of growth. Each disruptive event produced changes to the attitude of the skeleton, and hence a different orientation for the

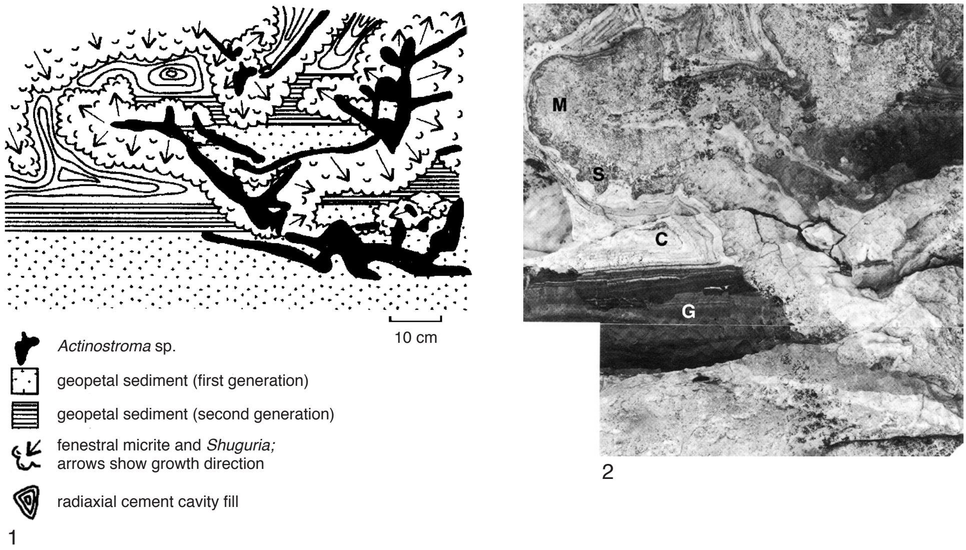

FIG. 31. Skeletal components for reconstructing the inferred foliaceous growth form of stromatoporoid *Actinostroma* sp., Frasnian, Upper Devonian, Pillara Limestone (back-reef facies), Windjana Gorge, Canning Basin, Western Australia, as shown in Figure 32.3 (Wood, 1999, fig. CS 3.5b); *1,* field tracing from a fallen block in gorge showing an incomplete skeleton of *Actinostroma* sp. It forms a complex, obliquely angled, open mesh of tierlike plates that WOOD (2000) infers to have been whorl-forming and foliaceous; lower surfaces of whorls were especially heavily encrusted by fenestral micrites and crusts or bushlike *Shuguria,* then one or two generations of geopetal sediment was added to remaining cavity spaces before final void-filling by banded calcite cements (adapted from Wood, 2000, part of fig. 11); *2,* longitudinal section through a series of stacked, whorl-like tiers (or plates) of the inferred foliaceous growth form of stromatoporoid *Actinostroma* sp. Note that the tiers or foliose plates are first encrusted by fenestral micrite (*M*), then by calcimicrobe *Shuguria* (*S*); large cavities that remain around plates are subsequently partly filled with dark-layered geopetal sedimentary rock (*G*) and the remaining void by banded radiaxial calcite cement (*C*), ×0.08 (Wood, 2000, fig. 12).

renewed growth. Sometimes thin layers of sediment were added during pauses between the renewed phases of growth, so in some cases, the regrowth could have included almost entirely ambitopic stromatoporoids (forms that largely occupied soft substrates). In other cases, a mixture of ambitopic and encrusting stromatoporoids may have been involved, even associations of different species. Consequently, shape analyses of skeletons that assumed irregularly shaped composites always need to be carried out with great care, and preferably in conjunction with the taxonomic identification of the species involved, based on their internal structures.

BJERSTEDT and FELDMANN (1985, p. 1044, fig. 6, 8) recognized an irregular shape as the penultimate member of their inferred stromatoporoid growth series through the upward-shoaling bioherm from the Middle Devonian of Ohio. The irregular shapes occur in the upper part of the bioherm, between the low domical (broadly hemispherical) and digitate (fasciculate) members of their growth series. The irregular skeletal shape is a more or less broadly arching combination of partly fused and partly anastomosing low, domical shapes, with sediment-filled, wedgelike invaginations around the margins of the structure. BJERSTEDT and FELDMANN (1985) considered the irregularity of these tongues of sediment to suggest that early growth became interrupted by episodes of high turbidity and/or influxes of sediment, and that some initial substrate instability may have existed as well, such as differential settling or sinking of skeletons into the soft substrate. Then, as the developing irregular skeletons grew upward, they

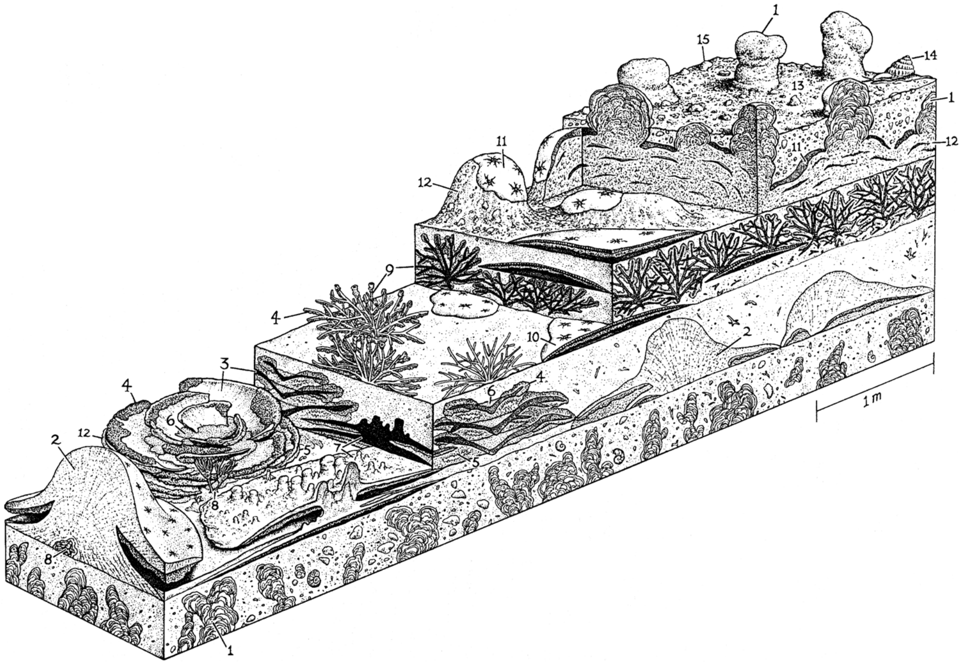

FIG. 32. Reconstruction of four successive back-reef communities based on data, Frasnian, Late Devonian, Windjana Gorge, Canning Basin, Western Australia: *1,* columnar growths of calcimicrobe *Rothpletzella*; *2,* domical stromatoporoid (*Actinostroma papillosum*); *3,* inferred whorl-forming foliaceous stromatoporoid (*Actinostroma* sp.); *4,* calcimicrobe *Shuguria*; *5,* fibrous cement; *6,* geopetal sediment; *7,* digitolaminar stromatoporoid (*Actinostroma windjanicum*); *8,* crinoids; *9,* digitate to dendroid stromatoporoid (*Stachyodes costulata*); *10,* laminar stromatoporoid (?*Hermatostroma* spp.); *11,* encrusting stromatoporoid (?*Clathocoilona spissa*); *12,* inferred microbialite; *13,* coarse siliciclastic sediment; *14,* gastropods; *15,* oncolites (Wood, 1999, fig. CS 3.5b; drawing courtesy of John Sibbick).

may have become more prone to turbulence in the water column and hence developed more pronounced upper-surface irregularities in the skeletons.

SUBSTRATE PREFERENCES

Growth of the calcareous skeleton apparently commenced from a single point, where the larva first settled (STEARN, 1983), then spread laterally in all directions across the substrate, unless constrained by proximity to other living organisms or influxes of sediment. A view favored by some workers (e.g., FAGERSTROM in KERSHAW, 1998, p. 514) is that stromatoporoids preferred to colonize dead skeletal material rather then living organisms. A wide range of hard and soft substrates were suitable, though in order to guarantee larval settlement, NESTOR (1984, p. 278) considered that the muds needed to be intermixed with at least 10% of skeletal grains to provide enough rigidity for settlement, and the more lithified the substrate, the better. According to NESTOR (1984), the most favorable hard-bottom sites were carbonate reefs, lithified sediments, and skeletal remains, but KERSHAW (1998, p. 513) has noted that the many examples of initial growth over soft substrates show little evidence of a hard object underlying the point of settlement. NICHOLSON (1886, p. 27) referred to an initial attachment by "a narrow peduncle," but the structure has not been confirmed in Paleozoic stromatoporoids. BOGOYAVLENSKAYA's (1984, p. 7, fig. 1b) illustration of such a structure apparently belongs to a Mesozoic stromatoporoid (based on STEINER, 1932, p. 17). Stromatoporoids, like a wide range of other sedentary

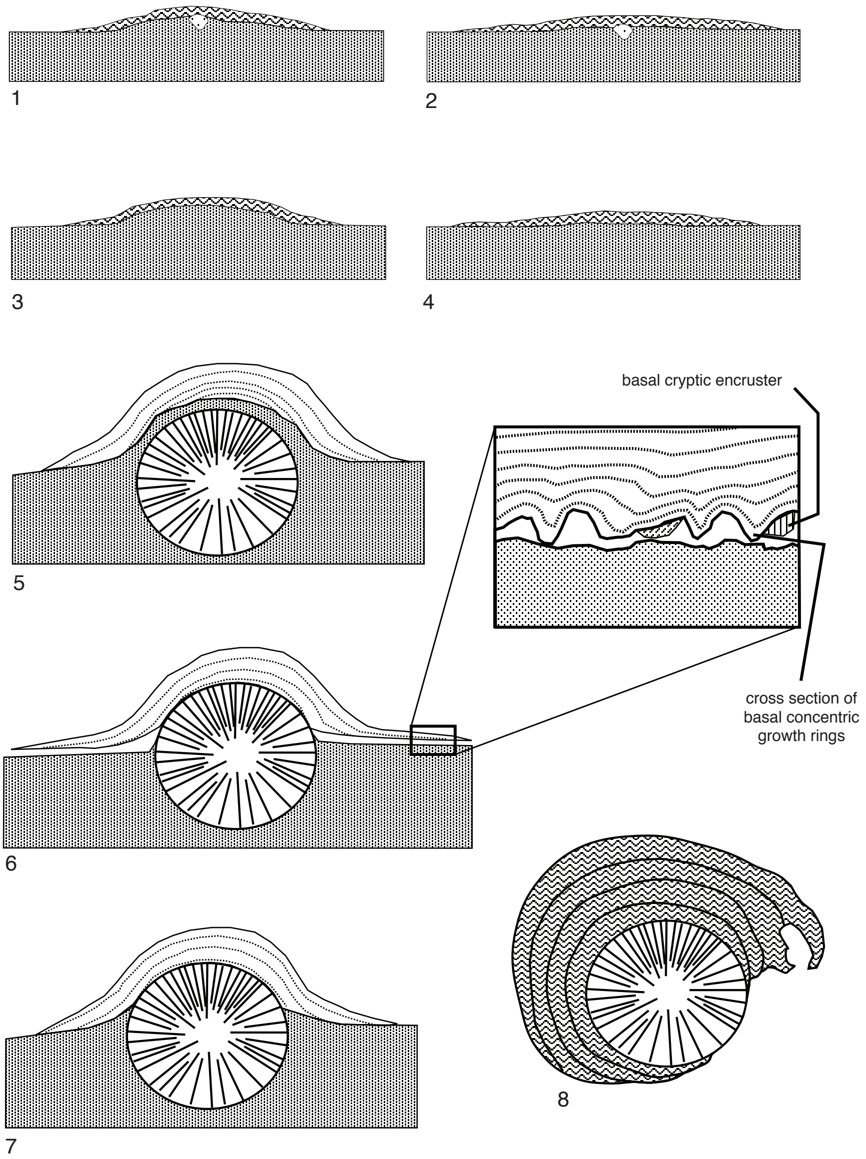

FIG. 33. Schematic representations of the likely range of interactions between stromatoporoids and the substrate during initial settlement of larvae and early skeletal growth, based on known examples of Paleozoic laminar, domical, and bulbous stromatoporoids. Identification of primary cavities is undoubted in Devonian stromatoporoids, but evidence remains equivocal for Ordovician and Silurian forms. *1–7,* ambitopic organisms, *8*, encrusting stromatoporoid; *1–2,* settlement on a small hard object, with and without a topographic high, then early growth spreading laterally over surrounding unconsolidated sediment; *3–4,* settlement on unconsolidated sediment, then early lateral spreading growth, with and without a topographic high (evidence of a tiny hard object for the initial larval settlement is lacking); *5,* establishment on a topographic high (possibly a large skeletal object) that has a thin layer of sediment draped over it; *6,* establishment directly on a hard skeletal object (no associated sediment), and then over the substrate, lateral outriggers develop, which have concentric growth rings on their undersurfaces, and small primary cavities form in spaces between rings (see details in enlargement); *7,* initiation occurs on a hard object and then lateral spread is over sediment without formation of primary cavities; *8,* initiation and subsequent growth is entirely encrusting over hard surface of a large bioclast (rugose coral) (adapted from Kershaw, 1998, fig. 5, and Kershaw, Wood, & Guo, 2006, fig. 1).

organisms (e.g., tabulate and rugose corals, certain brachiopod groups and bryozoans), as NICHOLSON (1886) first recognized, adopted two different benthic lifestyles, depending on whether they occupied mainly hard or soft substrates (see also BRETT, 1991, p. 329). The terms used to differentiate between these lifestyles are: **ambitopic** (Latin, *ambo*, both; Greek, *topos*, place; see JAANUSSON, 1979, p. 269–270), for organisms that were attached in early growth, but then lived essentially freely on unconsolidated substrates through their remaining life (Fig. 33.1–33.7), and **encrusting,** for organisms that remained in occupation of hard substrates through most of their life (Fig. 33.8).

The majority of Paleozoic stromatoporoids seem to have adopted an ambitopic life habit during later stages of their growth, whereas only a relatively few of all the designated orders of the class have representatives that maintained encrusting habits through all stages of their growth history. In most cases, it is difficult to establish whether the encrusting lifestyle existed across the full range of the distribution of a species in time and place, but probably not. It seems likely that most species switched from encrusting to ambitopic life modes because of changing substrate characteristics, but they were probably controlled also, to a significant degree, by their inherited growth program. When the switch occurred during initial growth, the stromatoporoid is recognized as having an ambitopic lifestyle, but when the change occurred during later, more mature stages of growth, the stromatoporoid species should be regarded as having an encrusting mode of life. Though determinations of these changes tend to be somewhat arbitrary and conditional on the quality of preservation of whole skeletons, initial growth is usually taken to represent the first one, or perhaps two, recognizable sets of latilaminae at the base of the skeleton.

AMBITOPIC STROMATOPOROIDS

Most Paleozoic stromatoporoids grew like many tabulate corals, as almost completely free, unattached organisms on soft to partially consolidated substrates. As noted by JAANUSSON (1979, p. 270), this contrasts with modern reef constructions that formed on hard substrates. For attachment of their free-living larvae, the stromatoporoid sponges probably required at least some small (or larger) skeletal grains, or reworked pieces of lithified mud, or microbial mat on the substrate, and then after initial settlement and metamorphosis as encrustations, they adapted through more mature stages of growth to a predominantly unattached, freely colonizing lifestyle over wide expanses of soft substrate (Fig. 33.1–33.2, 33.7).

A feature in some stromatoporoids is the broad, very thin, compact, concentrically wrinkled basal layer (Fig. 33.6, and further description below) and analogues in chaetetids and corals, that some authors (e.g., THAYER, 1975; BRETT, 1991) considered may have acted like a snowshoe. It maintained support for the stromatoporoid skeleton with its spread across a relatively large surface area of soft substrate, while also helping to stabilize the underlying substrate. However, this basal structure is rarely well preserved, and consequently remains poorly understood. Other skeletons do not appear to preserve any traces of a hard object for initial settlement, or the object is mantled by a thin layer of mud (Fig. 33.3–33.5), which may suggest these forms could grow directly on soft substrates without settling initially on hard objects (KERSHAW, 1998, p. 513), especially where there is some topographic expression. However, as alternatives: (1) the preserved hard objects may have been too small to be identified beneath the comparatively large skeletons, especially given how difficult whole specimens are to adequately sample and study; or (2) their absence may relate to the poor quality of preservation; perhaps the integrity of the hard objects was lost or destroyed due to differential compaction or selective dissolution (possibly originally aragonitic grains) along the interface between sediment and the overlying skeleton.

Kershaw and Brunton (1999) recognized ambitopic stromatoporoids occupying a number of types of unconsolidated substrates, from calcareous sands to muds: (1) *Solenopora*-dominated, bank-type calcareous sands that, under steady current activity, caused low to high domical morphotypes to become partially buried; (2) cohesive, muddy substrates with associated flat-based laminar to low domical shapes that easily became displaced to other sites on the sea floor; (3) mixed mud and silt substrates that retained unbroken, *in situ* skeletons; and (4) calcareous mudstone substrates that apparently became bioturbated, more consolidated (though possibly less cohesive), with associated columnar shapes that became broken. The bulk of these laminar to low domical stromatoporoids assisted very effectively in stabilizing extensive areas of unconsolidated substrate. This is supported by results of Kershaw's (1998) modeling work on the effects of unattached stromatoporoid shapes in differing current velocities, across sand and mud substrates showing: (1) low domical stromatoporoids as relatively more stable than other forms; and (2) laminar to low domical shapes less susceptible than other forms to current scour and reorientation. The elevated shapes, especially those with smaller attachment bases (e.g., bulbous, columnar, and branching morphs), were more easily displaced on unconsolidated substrates. The large aulaceratid columnar shape, however, developed bulbous, ringlike, concretionary ballast at its base (Cameron & Copper, 1994), and this may have helped it sink under its own weight into the soft sediment, developing what Brett (1991, p. 330) called a "mud-sticking" response.

Few attempts have been made to record substrate selectivity of stromatoporoid species, or to determine whether the stromatoporoid species of a particular assemblage maintained consistent relationships to the substrate types of a given habitat. Some writers (e.g., Kershaw, 1998, p. 513) claimed that, in general, stromatoporoids did not apparently discriminate between specific substrates. However, in one detailed study of a Silurian assemblage of four species from Gotland, Kershaw (1984) examined substrate relationships on a species-by-species basis and was able to show that preferential selection did exist. Three of the named species (*Densastroma pexisum, Pachystroma hesslandi, Eostromatopora impexa)* grew predominantly freely as ambitopic forms on the calcareous muddy substrate (though not exclusively, as they could facultatively encrust when settling by chance on a hard substrate). The other species, *Peridiostroma simplex* (Nestor) is dominantly an encruster (see below). The shapes of all four species varied from laminar to high domical, but the three ambitopic, muddy substrate-dominant species include forms with ragged margins and overall larger sizes, compared with *P. simplex,* which has a comparatively smooth margin and smaller size.

ENCRUSTING STROMATOPOROIDS

In the Gotland assemblage, *Peridiostroma simplex* encrusted the skeletons of other stromatoporoids, as well some corals, gastropods, and orthoconic nautiloids (Mori, 1968, p. 57, pl. IV,*2–3*, pl. 19,*1;* Kershaw, 1984, pl. 20,*3–4,6,8;* cf. Nestor, 1999, p. 118, fig. 1b). It seems therefore, that this species had a different genetic inheritance from the other three ambitopic, muddy substrate-dominant species mentioned immediately above. *P. simplex* maintained a different growth program preferentially, but not exclusively, through its more mature stages of growth, favoring an encrusting mode of life, as a predominantly attached stromatoporoid (Fig. 18–19, Fig. 34). *P. simplex* is one of a number of stromatoporoid species that adopted a mainly encrusting mode of life, in preference to the majority of species that exhibited an ambitopic mode of life. It represented a minor, encrusting component (usually one or two species) of the level-bottom assemblage dominated by the ambitopic stromatoporoids that grew on the unconsolidated (muddy) substrate, but where there were also localized patches of skeletal debris representing a firm substrate for encrusters.

The encrusting stromatoporoids were more commonly represented in assemblages that occupied reef habitats (especially bioherms) with higher energy conditions and greater access to coarse skeletal debris, such as larger skeletal objects, intraclasts, or perhaps rigidly, microbially bound and/or cemented (early lithified) pavements for their settlement and continued fixosessile growth. Some had no difficulty growing around vertically oriented solitary rugose corals (KERSHAW, 1998, p. 514, fig. 5B), or overgrowing large gastropod or nautiloid shells (see below). It is not easy to prove whether stromatoporoids interacted in competitive, confrontational strategies with other living organisms on these hard substrates, or whether the successive overgrowths occurred dominantly as postmortem events over dead skeletal debris (KERSHAW, 1998, p. 514; FAGERSTROM & others, 2000, p. 10). Examples of repeated encrustations of different stromatoporoid genera (and species) are well known; see the specimen illustrated by ST. JEAN (1971, p. 1408, fig. 25), where species of three genera (*Stromatopora, Stromatoporella, Clathrocoilona*) took part in forming a multilayered composite of seven, successive, overgrowing laminar crusts.

Another multiple encrustation depicted by NESTOR (1984, p. 268, fig. 1) includes stromatoporoids, a bryozoan, and a heliolitid coral, the stromatoporoid component, *Eostromatopora impexa,* being overgrown by *Clathrodictyon delicatulum* (in part directly encrusting and in part overgrowing a thin sediment tongue), and *C. delicatulum,* then substantially encrusted by *Petridiostroma simplex* (Fig. 35). This specimen is instructive because it emphasizes the need for caution in interpreting substrate contacts. Sometimes a thin layer of unconsolidated sediment may accumulate on the hard surface of the underlying stromatoporoid prior to the next overgrowth, so this overgrowing stromatoporoid may be ambitopic rather than an encrusting form. In the case of *C. delicatulum,* however, the growth was mixed, initially encrusting a hard substrate, then once established, it switched to an ambitopic mode and spread laterally over the unconsolidated substrate (see also KERSHAW, 1998, p. 514, fig. 5A). SCRUTTON (1997, p. 180) reported similar examples of thin sediment layers occupying intergrowth relationships between successive tabulate coral colonies.

Many of the species of the Devonian stromatoporellid genus *Clathrocoilona* have been recognized as adopting an encrusting-type lifestyle, species such as *C. spissa, abeona, crassitexta lemisca, obliterata*, and *saginata* (LECOMPTE, 1951; ZUKALOVA, 1971; COCKBAIN, 1984; MISTIAEN, 1985; COOK, 1999). Some show striking examples of overgrowth relationships with other stromatoporoids (Fig. 36.1), rugose, and tabulate corals (LECOMPTE, 1951, pl. 27,*3–4,* pl. 28,*4;* ST. JEAN, 1971, fig. 23; ZUKALOVA, 1971, pl. 14), and occasionally large nautiloid specimens (COOK & WADE, 1997). COOK and WADE (1997, p. 81) claimed that the growth of *C. spissa* "commenced and flourished while (the cyrtoconic) nautiloids were in an upright living position." The sheathlike overgrowth was apparently thickest along the ventral margin (Fig. 36.2) and thinner inside its open coil. Encumbered by this encrustation, it is unlikely that the nautiloid *Diademoceras submamillatum* (WHITEAVES) could have been capable of more than limited motion above the substrate. These nautiloids are of variable heights (102 to 180 mm) and diameters (35 to 90 mm). Growth interruption surfaces within the stromatoporoid skeleton indicate repositioning of the nautiloid on the substrate. A thin section illustrated by COOK and WADE (1997, fig. 4B) shows a 12-mm-thick laminar encrustation of *C. spissa* on the ventral surface of the nautiloid. WOOD (2000, p. 695, fig. 18) referred to domical or laminar stromatoporoids, most notably, *C. spissa,* that encrusted a community of moundlike structures (fenestral micrites that are inferred to be microbialites) in the Upper Devonian (Frasnian) reef

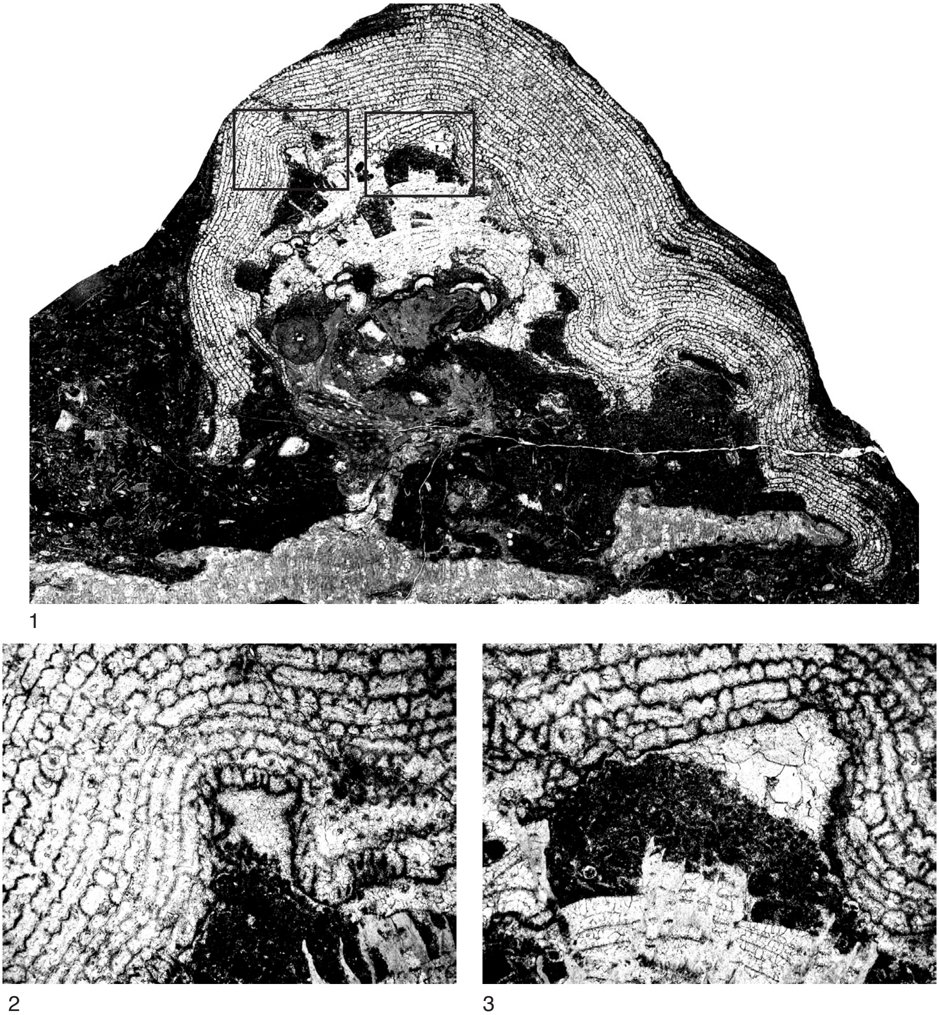

Fig. 34. Longitudinal thin section of another skeleton of stromatoporoid *Petridiostroma simplex* (Nestor), Visby Formation, Gotland, Sweden, sample ST46; Ireviken 3; *1,* specimen grew as an irregularly undulating, laminar to low domical skeleton centered on a ball-like cluster of organisms, including a probable heliolitid coral colony (light colored at the top), calcimicrobes, a crinoid ossicle, and other bioclastic debris, as well as some sedimentary rock that is peloidal; *left and right boxes* are enlarged views 2 and 3, respectively, ×2.5; *2–3,* two enlarged areas at contact between *P. simplex* and underlying coral exhibit cavities with geopetal and calcite spar infills. It is uncertain whether cavities were primary or secondary; orientation of geopetal structures suggests whole skeleton of *P. simplex* may have been rotated clockwise about 45 degrees after initial burial, ×6 (adapted from Kershaw, Wood, & Guo, 2006, fig. 5).

flat and back reef settings of the Canning Basin (Fig. 32). These sheetlike, encrusting, stromatoporoid skeletons may be more than 1 m across and up to 80 mm thick. The species may also be intergrown within the mounds of fenestral micrites and with other stromatoporoids.

The lophiostromatid stromatoporoids are also of interest, being mainly an encrusting group (Webby in Stearn & others, 1999). Only two genera (*Lophiostroma* and *Dermatostroma*) are assigned to the group. The type and best-known species of *Lophiostroma*, *L. schmidti*, occurs in the Ludlow of various parts of Europe, notably Gotland, Estonia, and possibly Podolia (Ukraine) (NESTOR, 1966; MORI, 1970; BOGOYAVLENSKAYA, 1984). In Gotland and Estonia, the skeletons of *L. schmidti* are typically encrusting, laminar to low domical, and may form rather complex intergrowth associations with other stromatoporoids, tabulate corals, bryozoans, and calcareous algae (NESTOR, 1984; KERSHAW, 1990). They occur in reef habitats (e.g., biostromes), where larger skeletal remains or lithified sediments are available for overgrowth. According to MORI (1970, p. 143), individuals usually avoided marly bottoms, that is, they only exceptionally colonized soft substrates. On Gotland, the species size ranges vary from 9 mm to 0.5 m across and from 1 to 40 mm in thickness (MORI, 1970, p. 141).

Other occurrences of the same or a similar species of *Lophiostroma* from the biohermal deposits of the Malinovetskiy horizon in Podolia (BOGOYAVLENSKAYA, 1982, 1984) exhibit a markedly different skeletal shape, being composed of laterally extensive, composite growth in thin, splayed, or imbricated, anastomosing, laminar sheets (Fig. 11.2), with individual crusts up to 2 m across and 50 to 60 mm thick. Episodic sedimentation apparently played a significant part in the development of these anastomosing crusts. Initial growth may have encrusted a lithified substrate or associated skeletal objects, but then, following successive influxes of sediment, the stromatoporoid developed the free living, lateral-spreading, anastomosing, laminar growth form, that is, the species switched to an ambitopic (free-living) lifestyle over unconsolidated substrates. The successive interactions involved: (1) the organism first rejuvenating from small, surviving, less-elevated crusts after swamping with sediment and in places accompanying erosion; and then (2) rapid lateral spread to form a new laminar crust over all areas of the recently accumulated soft sediment and former substrate, acting to effectively stabilize and seal off these extensive areas beneath the laminar crust, which for a time represented a new sea floor. The switch from a more characteristic encrusting life habit of *L. schmidti*, as seen in the Gotland and Estonian occurrences, to an ambitopic, anastomosing Podolian skeleton, seems to suggest that the species had a more plastic or flexible growth program than may have been suspected from study of Gotland and Estonian specimens alone. However, alternatively, BOGOYAVLENSKAYA (1984, fig. 2c) incorrectly identified the large anastomosing specimens from Podolia as belonging to *L. schmidti*. The specimens may, instead, belong to a different species of *Lophiostroma*, possibly *L. smotrischiense,* which was reported previously by RIABININ (1953) from the same stratigraphic interval (Malinovetskiy horizon). Further work is required to resolve the taxonomic status of these East European species. The other lophiostromatid genus is *Dermatostroma*. It only comprises a few species, and virtually all are small encrusting stromatoporoids that overgrew other organisms. For

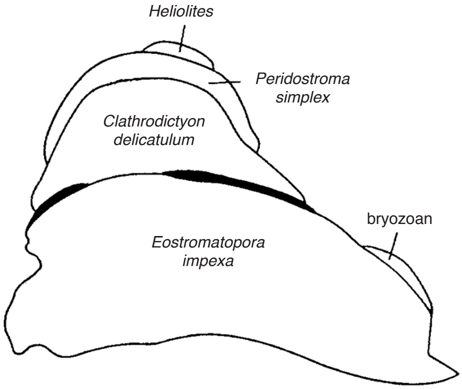

FIG. 35. Schematic longitudinal section of multiple encrustation of three different stromatoporoid species, a bryozoan, and a heliolitid coral, Jaani Stage, Wenlock, Suuriku, Estonia; of the three species, *Eostromatopora impexa* (NESTOR*)* is overgrown by *Clathrodictyon delicatulum* NESTOR, but much of the contact is separated by a thin layer of fine-grained sedimentary rock, suggesting it may be ambitopic, whereas *Peridiostroma simplex* completely overgrew *C. delicatulum,* supporting its predominantly encrusting role (adapted from Nestor, 1984, fig. 1).

example, the Late Ordovician species *D. papillatum* encrusts the brachiopod *Hebertella,* and *D. scabrum* overgrows the bryozoan *Escharopora pavonia* (see GALLOWAY, 1957; GALLOWAY & ST. JEAN, 1961).

The following genera (including representatives of all the Paleozoic stromatoporoid orders) have been identified as having one or more encrusting stromatoporoid species.

Labechiida: *Cystistroma, Cystostroma, Labechia, Labechiella, Stratodictyon, Lophiostroma, Dermatostroma*
Clathrodictyida: *Atelodictyon, Clathrodictyon, Ecclimadictyon, Gerronostroma, Hammatostroma, Plexodictyon*
Actinostromatida: *Plectostroma*
Stromatoporellida: *Clathrocoilina, Hermatostroma, Stictostroma, Stromatoporella, Synthetostroma, Trupetostroma*
Stromatoporida: *Ferestromatopora, Salairella, Stromatopora, Taleastroma*
Syringostromatida*: Habrostroma, Parallelostroma*
Amphiporida*: Euryamphipora*

The labechiids, clathrodictyids, stromatoporellids, and stromatoporids have proportionally greater numbers of encrusting species than the other groups. At present, it is only possible to speculate on the possible reasons for these different patterns. By analogy with the epitheca of some corals (SCRUTTON, 1998), the basal layer seems to be less commonly preserved in encrusting stromatoporoids, perhaps allowing them to more readily, opportunistically, overgrow other skeletal organisms on hard substrates (see further discussion of the basal layer, next section). The ambitopic stromatoporoids, on the other hand, may have needed to secrete a basal layer in order to seal off their undersurfaces from the deleterious effects of normal seawater (CLARK, 1976), or from being contaminated by small sedimentary particles or attacked by organisms associated with the substrate (STEARN, 1983). However, some of the stromatoporoids that grew across finer muddy substrates do not preserve a basal layer either.

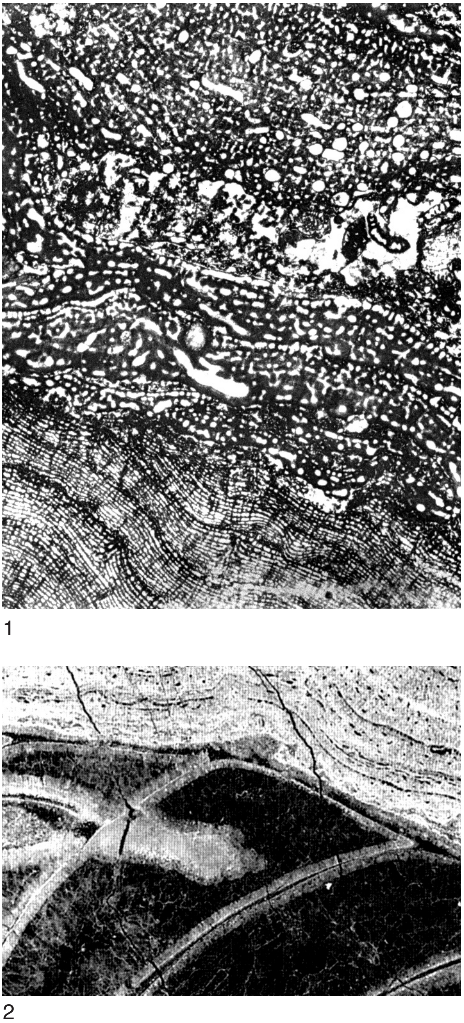

FIG. 36. Examples of stromatoporoid *Clathrocoilona spissa* (LECOMPTE) that encrusted other stromatoporoids and large organisms such as nautiloids; this species seems to encrust other organisms directly without intervening layers of fine-grained sedimentary material; *1,* longitudinal thin section of a latilaminate specimen of *C. spissa* that encrusts discordantly the underlying latilaminate species of *Actinostroma;* from a paratype of the type species, specimen no. 7174, Givetian, Surice 51e, Dinant Basin, Belgium, ×3 (adapted from Lecompte, 1951, pl. 27,*4*); *2,* longitudinal thin section of specimen of laminar stromatoporoid *Clathrocoilona spissa* (LECOMPTE) encrusting the ventral side of nautiloid *Diademoceras submamillatum* (WHITEAVES); note the nautiloid also shows septa and part of the siphuncle; Papilio Formation, Middle Devonian, Storm Dam, Broken River area, northern Queensland, Australia; photo in negative relief, ×2.4 (adapted from Cook & Wade, 1997, fig. 4B).

BASAL LAYER

The term **basal layer** was proposed by Riding (1974, p. 572) to represent the structurally modified basal part of a single skeletal crust of stromatoporoid *Stachyodes australe* (Wray). It was previously interpreted as a crustose alga, named *Keega,* by Wray (1967). The layer normally overlies the sediment (or a cavity) directly, is usually less than 4 mm thick, and is composed of arcuate laminae and microlaminae as well as subhorizontal canals. In other stromatoporoids, the basal layer may be represented by initial growth over the substrate by skeletons that may exhibit latilaminae or not; the term does not apply to renewed (successive) growth within latilaminae. It only includes the start of growth in nonlaminate and latilaminate skeletons over areas of new (mainly unconsolidated) substrate, not the resumptions of growth within latilaminate skeletons, which are the basal phases of Stearn (1989).

Riding (1974) did not regard the basal layer based on *S. australe* as strictly comparable to the thin, dense, wrinkled epithecal structure of Galloway (1957), but he did acknowledge that basal layers were present in other stromatoporoids, and Cockbain (1984) extended the list to a variety of typical laminar to domical stromatoporoids, including those with latilaminate skeletons. The basal layer is more typically a much thinner (less than 1 mm thick), compact skeletal structure, but it may occasionally develop thicker, irregularly reticulated or cystose structures above the dense basal surface, as in a few forms like *S. australe*. Both Riding (1974) and Cockbain (1984) adopted the term basal layer in preference to epitheca and suggested it may have been an adaptation that aided rapid lateral spread of stromatoporoids (mainly ambitopic forms) across unconsolidated substrates.

Cockbain (1984) also recognized that a silicified specimen of *Actinostroma papillosum* with preservation of a recognizable basal layer had concentric wrinkles on its undersurface, this feature being long reported as associated with the basal layer. Whether the basal layer became well developed or not depended largely on variables such as the nature of the substrate and rate of spreading growth (Cockbain, 1984, p. 12). Kershaw (1998, p. 515) also preferred the use of the term basal layer, as it is a neutral term with no cnidarian connotations.

Nevertheless, many sponge workers have continued, in some cases, perhaps uncritically, to refer to the initial growth layer of stromatoporoids, and other hypercalcified sponges, as an epitheca, using Edwards and Haime's (1848, p. 46) long-established cnidarian term for Paleozoic stromatoporoids (see Rosen, 1867, p. 32; Nicholson, 1886, p. 58; Stearn & others, 1999, p. 6), for Mesozoic stromatoporoids (see Wood, 1987, p. 87), and for those studying living hypercalcified sponge taxa (see Hartman, 1983, p. 121; Boury-Esnault & Rützler, 1997, p. 36, fig. 203). Stearn (1983, p. 144–145) noted that stromatoporoids exhibit a "distinct epitheca . . . like that found in tabulate corals" and referred to the irregular basal structures as enclosing voids that had spread laterally along the substrate. Stearn (1983, p. 145) added that these "epithecae" are rarely visible "in stromatoporoids enclosed in carbonate sediment but are conspicuous in stromatoporoids that weather free from argillaceous limestones and calcareous shales."

Two North American stromatoporoid workers (Galloway, 1957; Galloway & St. Jean, 1957; St. Jean, 1971, 1986), preferred the term peritheca to epitheca, although peritheca also has the drawback of an earlier use in coral terminology (Hill, 1935). Galloway (1957, p. 387) referred to stromatoporoid specimens that grew on a substrate of clay or lime mud, producing a less than one millimeter thick "wrinkled, thin, compact, lower layer." This was a finer and denser structure than the normal overlying skeletal elements, but he also noted some cases where the basal structure consisted of cyst plates. Galloway and St. Jean (1957, p. 45) additionally recorded occasional foreign bodies called protocoenostea, also interpreted as a part of the peritheca. STEARN's (1983, p. 144) enclosing voids appear to be analogous to the spaces associated with GALLOWAY's (1957, p. 387) cyst plates, and contrast markedly with the regular, laminated structures of mature (normal) phases of growth. ST. JEAN (1971, 1986), in his use of the term peritheca, emphasized its varied form, and (1971, fig. 34) added renewed growth between successive latilaminae as perithecal structures. Use of the term peritheca should now be discontinued.

In its original context as a term for cnidarians, epitheca represented a thin, calcareous skeletal structure (or investment) surrounding a corallite laterally, as an extension of the basal plate (HILL, 1935; MOORE, HILL, & WELLS, 1956). The structure may have a similar development in hypercalcified sponges, being related to initial primary growth of the basal surface of the rigid calcareous skeleton by incremental outward (lateral) spreading over the substrate, sometimes with concentrically wrinkled surfaces that have been represented as growth ridges. These latter may have sealed off the living parts of the mantling sponge from seawater, sedimentary particles, and/or boring organisms associated with the substrate, as in stromatoporoids. But in other hypercalcified sponge groups (e.g., living demosponges, such as *Ceratoporella, Acanthochaetetes, Astrosclera,* and *Calcifibrospongia*), where the living part of the sponge and its edge zone become raised well above the substrate, the epitheca is associated with lateral surfaces. Where these living forms exhibit a thin, compact epithecal layer, with concentric ridges resembling growth lines on lateral surfaces, HARTMAN and GOREAU (1972, p. 135) and HARTMAN (1983, p. 121) have compared this structure to similar features in scleractinian corals. Though precise data are lacking on the structure and mode of formation of the epitheca, in extant hypercalcified sponges, it is currently regarded as a secondary structure (J. VACELET, personal communication, 2007), not an initial primary growth layer, as in fossil representatives such as the stromatoporoids and chaetetids.

According to WOOD (1998, p. 154), the epitheca (including holotheca) limited the ability of mid- to late Paleozoic tabulate corals to encrust, except for a few taxa (e.g., *Alveolites, Aulopora*) that opportunistically encrusted other skeletal metazoans. Similarly, she noted that most stromatoporoids did not settle actively on hard substrates, except for a few encrusting-type stromatoporoids that were capable of overgrowing repeatedly other large skeletal metazoans (tabulates and bryozoans). WOOD (1998, p. 154), in consequence, considered it difficult to envisage that such stromatoporoids could have lived in "the highly turbulent, surf zone that reef corals and coralline algae occupy today," because they lacked the means to achieve "secure and permanent attachment to a hard substrate…." However, it is likely, judging from the record of abundant, large stromatoporoids in megabreccias derived from the Upper Devonian (Frasnian) reef margins of western Canada (MOUNTJOY, 1967; SRIVASTAVA, STEARN, & MOUNTJOY, 1972; COOK & others, 1972) that stromatoporoids did have a dominant role in building wave-resistant structures into the zone of turbulence, like counterparts in the modern reef.

Both the basal layer (or epitheca) of hypercalcified sponges and the epitheca of corals appear to have played pivotal roles in facilitating the initiation of calcification in the skeleton. CLARK (1976) has proposed that for corals, based mainly on the work of BARNES (1972), the first stages of epithecal growth were confined within an envelope (fold or lappet) of soft tissue at the margins of the skeleton, preventing exposure to the surrounding seawater. In chaetetids, this similar thin, sheetlike epithecal growth is now termed a basal layer, and it is compositionally organic rich (R. R. WEST, personal communication, 2006; *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Introduction to Chaetetid-type Porifera, p. 21, fig. 24, West, 2011a; and Chapter 2B, Functional Morphology of Chaetetid-type Porifera, p. 8–9, West, 2011b). The basal layer grew chiefly as a support for the rest of the skeleton, and as a barrier to seawater and extraneous small objects on its basal and/or perimeter sides.

In addition, archaeocyath workers (Debrenne & Zhuravlev, 1992, p. 59; Debrenne, Zhuravlev, & Kruse, 2002, p. 1690, fig. 1–2) have also abandoned use of the term epitheca in favor of a new term, radicatus, and they regard this structure as a secondary growth layer (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 8, Glossary, Webby, 2010; and Chapter 18A, General Features of the Archaeocyatha).

Kershaw, Wood, and Guo (2006), in their study of stromatoporoids from level-bottom muddy substrates from the mid-Silurian Visby Formation of Gotland, concluded that the basal layer was not clearly differentiated from overlying laminae of the skeleton and no epithecal-type structures were found. Two main types of basal surface were depicted: smooth and corrugated (Fig. 33). The smooth growth developed initially on a topographic high formed by a bioclast (shell fragment) that had already been mantled by partially consolidated mud, and then spread laterally with no apparent disturbance to adjacent muds, perhaps because these too had already started to lithify (Fig. 37.1). Growth of this smooth type may be disrupted by periodic influxes of sediment, as shown in Figure 37.1. The corrugated growth type extended laterally, forming a concentrically arranged pattern of ridges and grooves, with the grooves sometimes interpreted as small-scale primary cavities. The ridge-and-groove structure is considered to have formed by the growing edge of the stromatoporoid pushing soft sediment into wavelike ridges as it grew, then it became well settled on the substrate as skeletal mass increased (Fig. 37.2–37.3, Fig. 38). A variant of the corrugated growth type also developed where episodic sedimentation interrupted its continuity of growth, producing intertonguing sediment wedges. In a longitudinal section across the corrugated basal surface of one specimen (Fig. 18.2), there is no evidence that an independent basal layer formed, though there are a number of downward-trending prolongations of the basal surface, including the first one or two laminae, that may be interpreted as representing an initial basal layer. However, a clearly defined basal layer is not that often differentiated, either because the structure is not preserved, or it never became secreted originally, as in some level-bottom muddy substrate occurrences (see Kershaw, Wood, & Guo, 2006).

Attempts to characterize early stages of skeletal development as ontogeny of the stromatoporoid organism, in terms of phylogeny, have not been successful (Galloway, 1957; Bogoyavlenskaya, 1984). Galloway (1957, p. 392), for example, found that the structurally modified initial growth in his skeletons preserved in limestones was “nearly always lost in freeing the specimens from the matrix,” and he was equally unsuccessful in preparing specimens to show the initial growth of skeletons preserved in shale, probably because of weathering processes. Bogoyavlenskaya’s (1984) efforts to demonstrate that the initial growth represented the first part of an ontogenetic (or astrogenetic) succession were similarly in vain. Stearn (1983, 1989, p. 46), in referring to the different growth changes through the skeleton, concluded that they were not part of an ontogenetic succession.

Stearn (1986, 1989, p. 46) proposed a process-oriented approach to the study of variability of skeletal growth in stromatoporoids, employing phase changes, rather than using the more conventional basic descriptions of alternations in internal structures. He referred to rhythmic structural changes as units of growth that replaced each other on a number of occasions during the developmental (=growth) history of the skeleton. The successive phase changes were subdivided into basal, spacing, and

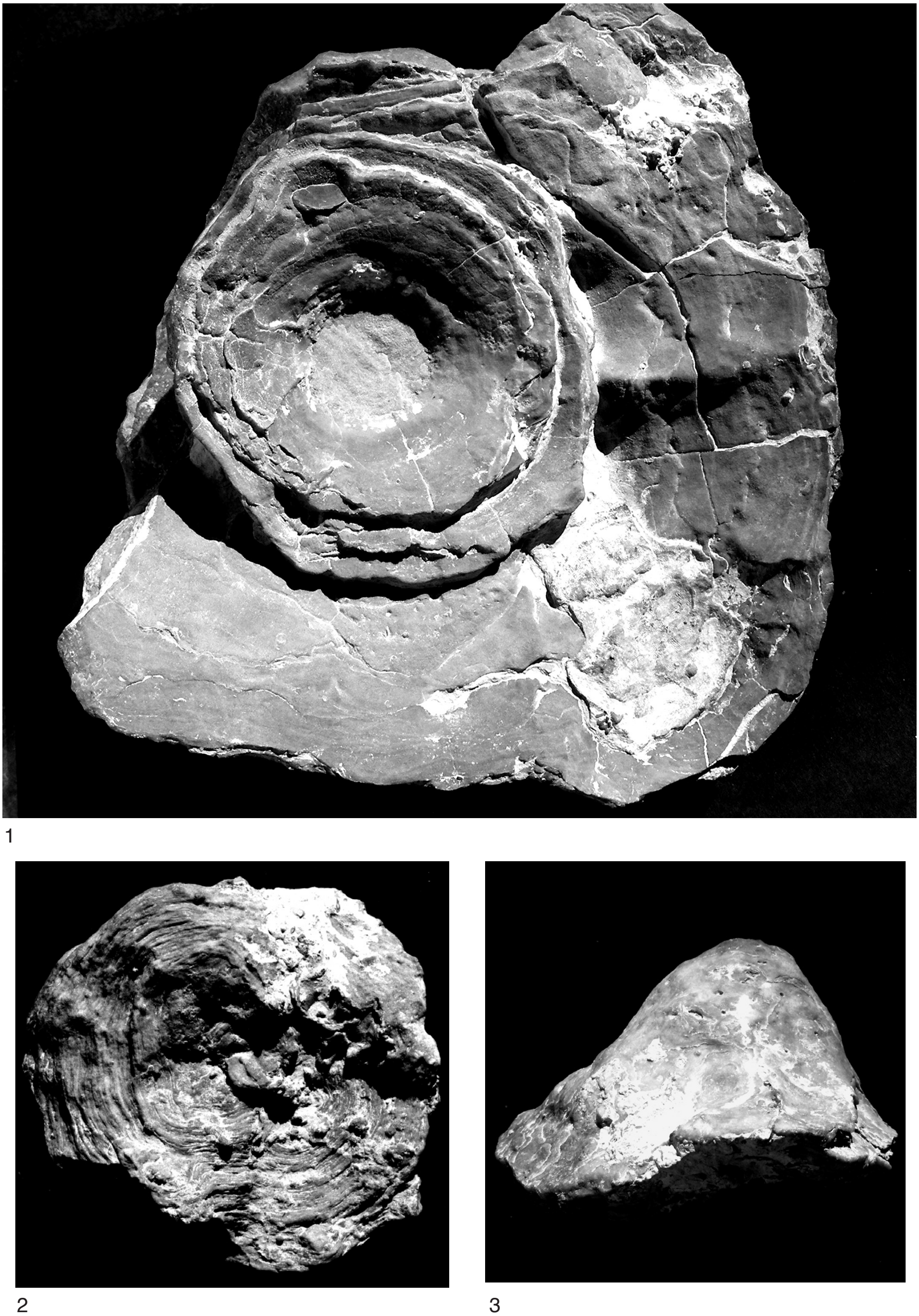

FIG. 37. *(For explanation, see facing page).*

terminal phases (Stearn & others, 1999; see also *Treatise Online,* Part E, Revised, vol. 4, Chapter 9C, Internal Morphology, p. 25–29, Stearn, 2011). He applied the term basal phase to initial growth, as well as to restarts of growth at bases of successive latilaminae within the stromatoporoid skeleton (Stearn, 1989, p. 47); though no examples of characteristic units of growth representing a basal phase have been described. Here we prefer to view the basal phase as more conceptual and interpretative than focused on the basic description of a skeletal structure. The feature (basal layer) developed as a product during the initial (basal) phase of growth, but no strictly comparable feature appears to accompany restarts of growth of successive latilaminae.

The basal layer of Paleozoic stromatoporoids remains inadequately known; a more intensive approach to the study of this structure is needed across main taxonomic groups, substrate types, lifestyles, and preservation states (for example, in response to processes such as differential compaction, dissolution and replacement, pressure solution, and weathering) and, as well, to a better understanding of its relationships to cavity spaces (see below). As currently understood, the basal layer (syn., epitheca, peritheca) of Paleozoic stromatoporoids is a structurally modified unit, either a very thin, dense or compact, wrinkled layer representing the basal growth surface, or a composite layered interval comprising both the thin, dense layer and one or more, somewhat disordered, rows of small, irregular, cystlike plates, with sometimes even a few associated inclusions (though some of these are probably foreign bodies, like the protocoenostea of Galloway & St. Jean, 1957, p. 45).

Where the stromatoporoid basal layer grew over the substrate, it sometimes developed broad concentric wrinkles on its undersurface. These may be: (1) related to the lateral growing edge pushing soft sediment into waves; or (2) they may have developed where each successive layer (laminae) at the base slightly overgrew the preceding layer along its lateral edge, producing a similar concentric pattern across the base; or (3) due to a more pronounced pattern of concentric rings, which sometimes developed between such layers when episodic sedimentation intervened (Kershaw, Wood, & Guo, 2006). These wrinkled basal surfaces have not been noted specifically at the bases of resumptions of internal growth in latilaminate skeletons, nor recorded apparently from the bases of encrusting-type stromatoporoids. The basal layer encompasses all the structural elements associated with the basal surface that rest on the substrate, as well as bases of upraised lateral outgrowths above the substrate (see discussion of Cavity Spaces, herein, p. 57), prior to the start of more orderly, layered, normal growth of the mature skeleton, irrespective of whether the skeleton is latilaminate or not. It may be concluded that basal layers are important in helping stromatoporoids colonize soft substrates by acting to seal off their bases

Fig. 37. Views of the bases of typical domical stromatoporoids, Silurian, Gotland, Sweden; *1,* smooth basal surfaces beneath a ragged, domical, stromatoporoid skeleton, Hemse Group, Ludlow, Snoder, AMF.134348; specimen apparently commenced its growth on a topographic high and continued, successively, after each growth interruption to maintain its concave base. Consequently, overall the slightly curved to flattened surfaces are gently tilted outward; outer areas also show a few widely spaced, gentle undulations (or radial folds). The exposed smooth surfaces possibly formed from initial growth after each growth interruption over unconsolidated sediment and appear to be equivalent internally to bases of latilaminae; overall shape of skeleton is high domical but basically composed of superimposed, low, domical growths; in profile, it resembles ragged domical skeleton illustrated in middle to upper part of Figure 4.1, ×0.67 (Webby, new); *2–3,* basal and lateral views of a smooth, enveloping, high domical stromatoporoid, Visby Formation, Wenlock, Södra Backen; basal surface is gently undulating to flattened and has well-developed fine, concentric growth ridges, but the surface is not completely exposed because calcareous mudstones, encrusting organisms, and skeletal debris mask a few small areas of the surface, and growth ridges also in a few places have become a little weathered. Nevertheless, because an enveloping type of growth is represented, it appears that the successive latilaminae (and/or laminae) of the skeleton terminate on the basal surface, with their ends more or less coinciding with outer edges of successive concentric growth ridges, AMF. 134349, ×0.5 (Webby, new).

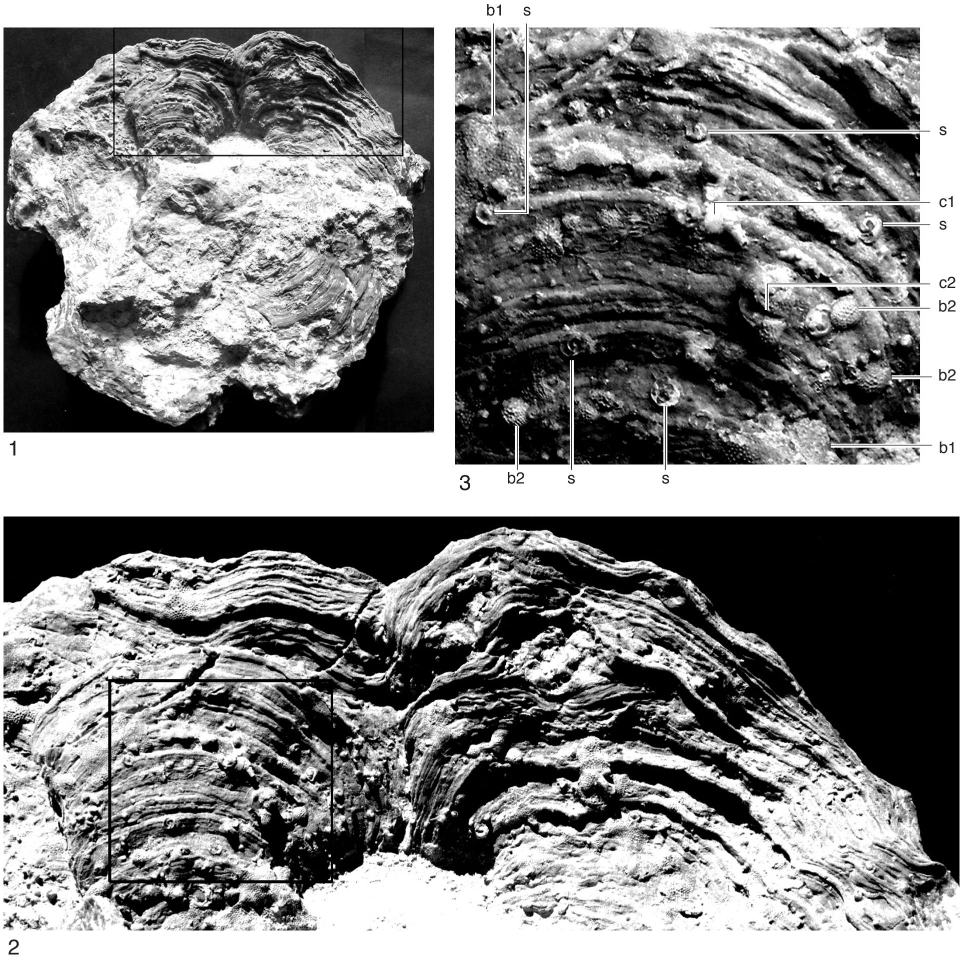

FIG. 38. Views at various magnifications of undersurface of a large, apparently coalescent, nonenveloping, low domical specimen of *Parallelostroma* sp., AMF.134350, Hamra Formation, Ludlow, Kettelviken, Gotland, Sweden. One area near margins of basal surface is well exposed and shows much detail of nature of corrugated base with growth rings and an abundance of cryptic encrusters (see views *2* and *3*); upper surface is undulose and encrusted by a variety of organisms, including small, solitary rugosans and auloporoid corals; *1,* general view of entire base of stromatoporoid *Parallelostroma* sp.; note the area outlined in black exhibits best-exposed part of basal surface (for more detail, see view *2*), ×0.25 (Webby, new); *2,* corrugated basal surface of part of skeleton of stromatoporoid *Parallelostroma* sp.; note the two convex-outward sets of concentric growth ridges and an intervening zone with a locally sinuous, concave-outward, as well as upwardly steplike trend of growth ridges that seems to have formed in response to coalescing growth of specimen; in outer part of zone, growth ridges have continuity through sinuous and steplike changes of direction—steplike rise is from right to left; basal growth ridges appear to equate with distal ends of successive latilaminae (and/or laminae) within skeleton; a large number of cryptic encrusters are scattered over corrugated basal surfaces; *box* shows location of part illustrated in view *3,* ×0.85 (Webby, new); *3,* enlargement depicting some of randomly distributed cryptic encrusters on corrugated underside of *Parallelostroma* sp. skeleton; they are completely randomly distributed over the corrugated basal surface; they did not preferentially occupy narrow groovelike hollows (potentially small primary occupation sites; see Fig. 33.6, inset) between individual growth ridges. Consequently, it is likely that these encrusters were predominantly colonizers of a large secondary shelter (overhang or cavity); *b1,* sheetlike bryozoan; *b2,* button-shaped bryozoan; *c1,* crinoid with articulated plates; *c2,* crinoid holdfast partly overgrown by bryozoan; *s, Spirorbis,* ×1.8 (Webby, new).

(and sides) from entry of seawater, sedimentary particles, and invading organisms, both from underlying surfaces and from the adjacent water column.

CAVITY SPACES

Spaces are mainly present beneath the stromatoporoid bases, but they may also develop at levels above initial bases, either representing secondary cavities that formed on lateral sides beneath ragged margins, in association with episodic sedimentation, or as primary cavities produced beneath upraised lateral outgrowths (or outriggers) of some larger, composite, Late Devonian growth forms (Wood, 1998, 2000; Kershaw, Wood, & Guo, 1999, 2006). Good examples of internal spar- and sediment-filled cavities may be associated with growth interruption surfaces (Fig. 4.3, Fig. 34; Stearn, 1983, fig. 3; Young & Kershaw, 2005, pl. 1,*6*). The cavities exhibited in the illustrated specimen of the stromatoporoid *Pachystroma hesslandi* from the Silurian (Visby Formation) of Gotland (Fig. 4.3), are apparently, according to Kershaw, Wood, and Guo (2006, fig. 4), primary structures.

It is not always an easy matter to discriminate between primary and secondary cavities, because of the complex interactions between stromatoporoid growth and sedimentary processes (e.g., multiple phases of erosion and sedimentation). For example, a ragged, low domical skeleton may have lateral outgrowths, produced by intrinsic growth above the substrate, that create primary shelters for occupation of cryptobionts (Fig. 5.2). However, a similar ragged skeletal structure may result from growth that was interrupted by episodic sediment swamping of marginal areas of the skeleton (Fig. 5.1), and then much of the accumulated, unconsolidated sediment was removed in an erosive phase, leaving the successive lateral outgrowths exposed for colonization by crypt faunas (Fig. 5.2), but this time the reexposed sites are technically secondary shelters.

PRIMARY CAVITIES

Riding (1974) first recognized that parts of the widely spreading laminar growth of Devonian stromatoporoids *Stachyodes australe* and ?*Hammastroma* sp. maintained contact with the sediment surface, while other parts grew slightly upraised above the substrate, resulting in cavities that subsequently became cement filled (see illustrations in Riding, 1974, pl. 86,*4;* Cockbain, 1984, pl. 18,*B,D*). Pratt (1989) also recognized small primary cavities in the Lower Devonian reefs of southwestern Ontario that include an encrusting, cryptic, tabulate coral and bryozoan fauna. These cavities were apparently produced by "sediment settling and shrinkage" (Pratt, 1989, p. 508).

Mistiaen (1991) and Lachkhem and Mistiaen (1994) also studied examples of *S. australe* from Upper Devonian (Frasnian) successions of the Ardennes (Belgium) and the Boulonnais area (northern France). These include specimens (up to 0.15 m long) with laminar sheets that grew across the substrate, as well as developing a broadly reticular mesh of vertical to inclined platy upgrowths that interconnect with raised, platelike, lateral outgrowths above the substrate. Lachkhem and Mistiaen (1994, fig. 4) identified primary cavities on the undersides of the platy upgrowths from the Ardennes that were colonized by cryptobionts, then infilled with early cement (Fig. 30). Skeletons were also recognized from the Boulonnais area (Mistiaen, 1991, fig. 2, pl. 1,*2*), indicating that *S. australe* may have been exposed to storm activity and overturning prior to final burial.

Wood (1998, 1999, fig. 6.20), studied a number of spectacularly large specimens of *Stachyodes australe* from marginal slope settings of the Upper Devonian Canning Basin, Western Australia, that were laminar platy crusts less than a centimeter thick and laterally extensive (up to 1.5 m wide); these thin sheets were typically upwardly arched over the substrate, forming primary cavities on their undersurfaces that were up to

0.3 m in height (Fig. 10, Fig. 12.1–12.2). This rather unique type of growth and cavity formation was largely a response to parts of the living surface becoming overwhelmed by episodic sedimentation, and this stimulated limited areas of living tissue at skeletal margins to produce upward-arching laminar growth, especially away from the sediment source. Cavities formed beneath the thin laminar outgrowths of stabilized stromatoporoids, with these crusts capable of extending laterally for distances of up to 1 m without coming into contact with the substrate (Wood, 1998, p. 154, 1999; Kershaw, Wood, & Guo, 2006). It was a novel and versatile solution for these stromatoporoids to maintain continued growth despite being subjected to periodic sedimentary events. The skeletons achieved a level of stability once the lateral outgrowths had developed into extensive dome-shaped crusts, affording them a measure of protection from further physical disturbance. These crusts then achieved some rigidity, as the underlying cavity spaces became infilled by geopetal sediment and early marine cement during burial processes (Fig. 10). There is little evidence of collapse of cavities associated with compaction or related breakage of the laminar crusts. The large primary framework cavities became attractive crypt dwelling sites. The invading cryptobionts included abundant pendent growths of the calcimicrobe *Shuguria,* a few lithistid sponges, spiny atrypid brachiopods, and ostracodes. Generations of geopetal sediment and pervasive early marine cements then filled the remaining space.

The widest range of complex laminar and domical stromatoporoids that developed primary cavities supporting cryptic communities, however, occurs in the back reef (and reef flat) settings of the Canning Basin (Wood, 2000). Three species of *Actinostroma*, a species attributed to *Hermatostroma*, and the digitate-dendroid growth form of *Stachyodes costulata,* were described by Wood (2000). Some of these are discussed briefly here (Fig. 32).

1. Skeletons of *Actinostroma papillosum* have a large size (up to 1 m in width and height), a broadly domical, ragged form, a tiered arrangement of tapering (up to 0.5 m long), lateral outgrowths from a centralized, updomed core, and open cavities on undersurfaces of the lateral outgrowths. These latter were colonized by the encrusting, cryptic growths of calcimicrobe *Shuguria* (Wood, 2000, p. 678; Fig. 20.1–20.4).

2. Spectacularly large (up to 5 m wide and 1.5 m high), complex, composite, digitolaminar *Actinostroma windjanicum* (Wood, 2000, fig. 9B) also developed shelters on undersides of extensive, vertically stacked, lateral outgrowths or plates (up to 1.5 m across and spaced 50 to 150 mm apart), and a digitate (or multicolumnar) central area, which was differentiated with partially separated to coalescent, lateral connecting bridges (sometimes looking like a boxwork structure). The lateral outgrowths arch upward or downward at distal ends, away from or toward the substrate, or form semi-enclosed overhangs, occupied by bushy growths of *Shuguria* above the substrate, which then became infilled with geopetal sediment and early cement (Fig. 29.1–29.4).

3. A third species of *Actinostroma* (*A.* sp.) interpreted by Wood (2000) as a complex, elevated, free-standing, foliaceous (whorl-forming to tiered) form (about 1 m in diameter and 0.6 m high), has successive encrustations of fenestral micrite (probably derived from microbes), cryptic *Shuguria,* and rare solitary rugosans that developed on the inclined foliose plates, especially undersurfaces, and intertier spaces, which were infilled by generations of geopetal sediment and early cement (Fig. 31.1–31.2).

4. Dense, multibranched (digitate to dendroid), monospecific thickets of *Stachyodes costulata*, up to 0.3 m in height (Fig. 26.1–26.4), have some interconnected, lateral bridges between adjacent branches. These latter may be preferentially encrusted on undersurfaces by *Shuguria* and contain geopetal structures as well (Wood, 2000).

In upper Silurian reefs of Gaspé Peninsula and the Brunswick area of eastern Canada, Bourque and Amyot (1989) and Noble (1989) reported cavities partly or completely infilled by dark sedimentary rock and sparry calcite cement, that were, in places, occupied by cryptic faunas such as corals and brachiopods. However, these cavities occur beneath bases of laminar to irregularly low domical stromatoporoid skeletons that average only about 6 cm in diameter, and they are unusual in being separated by a thin, micritic, microbially generated veneer, rather than directly in contact with skeletal bases.

The primary cavities known to occur beneath stromatoporoid bases in the Silurian of Gotland are comparatively small structures (Kershaw, Wood, & Guo, 2006). They are represented by small, groovelike cavities that lie between concentric rings on the basal surfaces of stromatoporoids, occupying the muddy substrates of the Visby Formation. Additionally, Spjeldnaes (1975, fig. 2A–C) illustrated relationships between a Silurian bryozoan-dominated crypt fauna and the coral and stromatoporoid skeletons of the Visby Formation, that suggest cryptic bryozoans occupied undersurfaces of skeletal bases and sheltered sites beneath the tonguelike lateral outgrowths (or ragged margins) of possible domical stromatoporoids (Fig. 39.1–39.2). Spjeldnaes (1975) did not specifically identify whether his diagrammatic representations of domical growth forms were stromatoporoids or corals, but his figured outlines show typical stromatoporoid shapes. The bryozoans either colonized the sheltered (or shaded) undersurfaces areas as the vertically successive lateral outgrowths grew above the substrate, suggesting they were primary sites for settlement, or the successive outgrowths (or ragged margins) formed first during episodic buildup of sediments around the skeleton, and then much of the sediment was washed away, exposing the ragged margins with their undersurfaces available as secondary shelters. However, Kershaw, Wood, and Guo (2006) considered that encrusters rarely occupied the bases of ragged outgrowths in the Visby stromatoporoids, because their skeletons seldom prove to be unequivocally *in situ* forms.

SECONDARY CAVITIES

Other laminar to low domical stromatoporoids from the same deeper, level-bottom Visby Formation (Wenlock) of Gotland, have been recognized by Kershaw (1980, p. 327) as comparatively small (50 to 150 mm diameter), isolated skeletons that lived on a carbonate-mud substrate, “not a part of a reef framework where the growth could have created overhangs or primary cavities.” These skeletons formed secondary cavities beneath their basal surfaces, either: (1) by partial scouring of unconsolidated deposits from beneath skeletal margins of *in situ* stromatoporoids; or (2) by movements of whole skeletons in storm-generated currents across an uneven substrate, and then imperfect (probably differential) settling to produce subskeletal voids for a cryptic community to colonize (Fig. 40). The sheltered undersides of stromatoporoid bases were occupied by a variety of encrusting bryozoans, tabulate corals, strophomenid brachiopods, and spirorbid worms.

Another Gotland survey (Nield, 1986) of encrusting faunas on mainly high domical upper Visby stromatoporoids noted a much greater diversity of encrusters on exposed apical and lateral surfaces than on skeletal bases (Fig. 16.1). The organisms on the bases were mainly spirorbid worms and tended to occur in clusters (Fig. 16.2), suggesting they may have been largely inhabitants of localized, short-lived (secondary) cavities. However, it is frequently impossible to differentiate unequivocally between the original cryptic, shade-loving (sciaphilic) forms of stromatoporoid bases and the open-surface encrusting forms that formed on the same bases after these high domical skeletons had been rolled and/or broken before final burial.

Another study of the diversity, distribution, and abundance of open-surface and

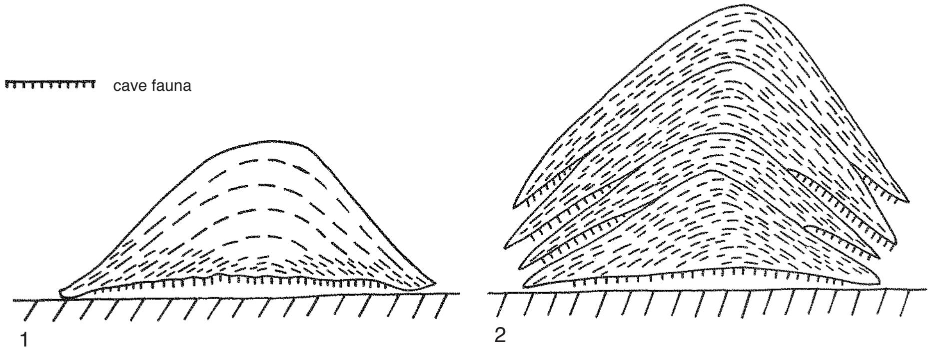

FIG. 39. A diagnostic cryptic bryozoan fauna was recognized by SPJELDNAES (1975) as encrusting undersurfaces of domical growth forms of stromatoporoid and coral bases in marly deposits of the Silurian Visby Formation, Gotland, Sweden; he noted the so-called cave fauna as occurring mainly on the bases of specimens but also, less commonly, beneath raised, lateral outriggers of certain specimens. Two of his diagrammatic longitudinal sections are reproduced here to show how SPJELDNAES (1975) conceived the distribution of the bryozoan cave fauna; *1,* smooth, enveloping, domical growth form that typically developed a slightly updomed basal surface over the substrate, leaving a cavity for colonization of the encrusting bryozoan cave dwellers (adapted from Spjeldnaes, 1975, fig. 2A); *2,* composed of four stacked, or superimposed, low domical growths, with the ragged margins resulting from lateral extensions (or outriggers) of the skeleton, like the example shown in Figure 5.2; cavity that formed beneath basal surface of this form was encrusted by cryptic organisms (mainly bryozoans), and sheltered undersurfaces of successive lateral outriggers were also colonized, although rather more spasmodically (adapted from Spjeldnaes, 1975, fig. 2B).

cryptic encrusting communities of the upper Silurian (Ludlow) stromatoporoids from the reef-forming Hamra Beds of Gotland was presented by SEGARS and LIDDELL (1988). The stromatoporoid skeletons were laminar, low domical, and bulbous shapes; more than 30 specimens were collected from the lower part of the reef where individuals were surrounded by argillaceous sediment. SEGARS and LIDDELL (1988) recorded the abundance and diversity of cryptic and open-surface encrusters on lower and upper surfaces, respectively. The encrusting organisms were also differentiated on whether they came from inner or outer parts of these surfaces. The encrusting (cryptic and open surface) bryozoans were the most diverse component (18 species), and occupied proportionally the most space. Other organisms included: spirorbids, crinoids, tabulates (cryptic and open surface), brachiopods (cryptic only), tentaculitids, and rugosans (open surface only).

Lower surfaces exhibit overall abundances of cryptobionts, declining from 18% coverage in outermost parts to 6.6% in the interiors, and the number of species dropping, correspondingly, from 29 to 18 toward the centers. SEGARS and LIDDELL (1988) suggested that the lower abundances in interiors relative to marginal areas reflected the lesser influences of currents scouring toward the center as compared to areas near the margins. Though they accepted KERSHAW's (1980) proposal that the scouring process more commonly produced secondary cavities by removing sediment from areas in proximity of the margins, SEGARS and LIDDELL's (1988, fig. 4) reconstruction of the stromatoporoid specimen gave a misleading interpretation of how the cryptic colonization of the stromatoporoid skeletons took place (Fig. 41.1–41.2). They show a low domical stromatoporoid before death as almost completely undercut by secondary scouring processes, leaving it counterbalanced on a slender, centralized pedestal of presumed consolidated or cemented substrate, without apparently any evidence of collapse of this attachment support or of associated subsidence into the substrate. Yet, the stromatoporoids prior to sampling were "surrounded by argillaceous sediment [sic]" allowing easy removal of specimens (SEGARS

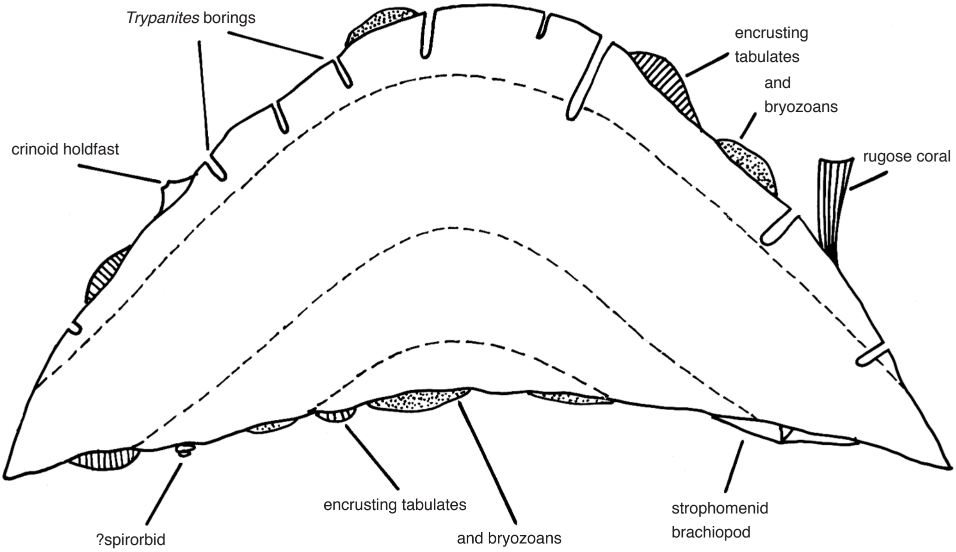

FIG. 40. Diagrammatic representation of a longitudinal section of a domical stromatoporoid showing differential distribution of encrusting and boring organisms on upper and lower surfaces; middle Silurian, Gotland, Sweden (Kershaw, 1980, fig. 3).

& LIDDELL, 1988, p. 392), which suggests the original substrate was a uniform muddy, probably mainly unconsolidated (soft) sediment. The repeated winnowing processes of the sediment from beneath the rigid stromatoporoid bases allowed encrusting cryptic faunas to progressively colonize the skeletal undersurfaces, producing records of complete coverage, even beneath central interiors of the stromatoporoid specimens. This seems impossible to reconcile with the maintenance of a centralized pedestal of hard sedimentary rock (see SEGARS & LIDDELL, 1988, fig. 4) during the lifetime of the cryptobiont community.

An alternative explanation is required to explain the relationships, and one that is consistent with KERSHAW's (1980) earlier views. First, these stromatoporoids grew almost entirely on soft substrates, in contrast to the cryptic fauna that encrusted hard undersurfaces of stromatoporoid skeletons. A repeated series of episodic sedimentation, erosion, colonization, and early cementation events are required to explain the overall patterns of distribution, diversity, and abundance of cryptic encrusters on the stromatoporoid bases, as recorded by SEGARS and LIDDELL (1988). It seems likely that cryptic organisms first colonized the undersurface of the stromatoporoid when it was still actively growing, once the first cavities had formed by marginal scouring or winnowing of sediment from under the skeletal base, and/or after wholesale displacement of the skeleton in storm-generated activity across the substrate. The cavities existed long enough for a first wave of encrusters to settle and become well established, and then an episodic sedimentation, or combined sedimentation–early cementation event may have overwhelmed the initial population (Fig. 42.1–42.3). Successive phases of current scouring (or winnowing) and/or displacement movement were followed by waves of cryptic faunas again settling and thriving in the newly formed cavities (Fig. 42.3–42.5). These cycles of scouring at skeletal margins, and/or whole displacement of specimens that produced new cavities and cryptic recolonization, were preserved by further sedimentary events that caused the

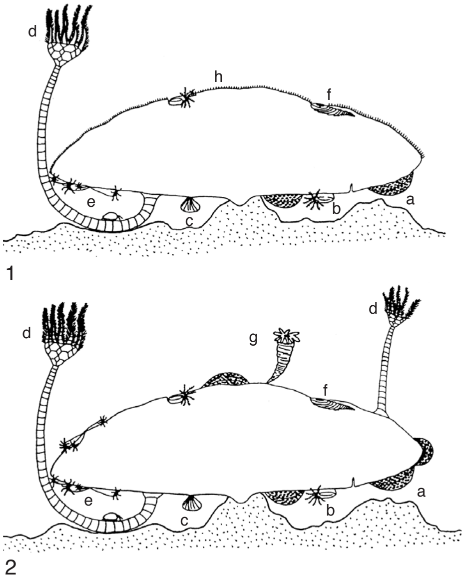

FIG. 41. Representation of record of epibionts that became encrusters on hard external surfaces of a smooth, low domical stromatoporoid, Ludlow, upper Silurian, Hamra Formation, Gotland, Sweden, both before its death and after death. The stromatoporoid was also shown as having an extensive, open, subskeletal cavity with a very small pedestal of sediment for attachment that was maintained for support of weight for some time (at least from before to after death), implying that the sediment was much lithified; see text for further discussion of this interpretation; *1,* encrusting epibionts on the stromatoporoid before death; note presence of living tissue mantling virtually entire upper surface of stromatoporoid; *2,* encrusting epibionts on stromatoporoid after death; note epibiont inhabitants now cover both upper and lower surfaces; *a,* bryozoans; *b,* spirorbids; *c,* brachiopods; *d,* crinoids; *e,* tabulate corals; *f,* tentaculitids; *g,* corals; *h,* area of surface with stromatoporoid living tissue (Segars & Liddell, 1988, fig. 4A–B).

cavities to be sealed off and then infilled by early cements and geopetal sediments. The repetitions of these events occurred on the undersurfaces of a rigid stromatoporoid skeleton as it grew, and perhaps continued briefly after death, that is, prior to its final entombment in the succession. It is possible that the cavity infills of early cements and geopetal sediments imparted rigidity to areas immediately beneath many skeletons of individual stromatoporoids while they continued to grow.

LATERAL AND TERMINAL GROWTH SURFACES

Like the basal surfaces, the lateral margins of stromatoporoids need to be more carefully examined in the wider context of unraveling before-death interactions of growth in association with sediment and the water column, and after-burial impacts of diagenetic change. In general, the stromatoporoid organism was capable of sealing off its skeletal interior from intruding sedimentary particles and stopping sediment settling on the growth surface (Stearn, 1983, p. 143; see also *Treatise Online,* Part E, Revised, vol. 4, Chapter 9C, Internal Morphology, p. 7, Stearn, 2011). However, sometimes growth interruptions occurred after sediment engulfed and necrotized parts of the growing surface. The cover of sediment then became a sediment inclusion as new, more continuous, lateral growth developed (Young & Kershaw, 2005). In broad outline, a wide range of marginal features occur, from smooth surfaces with no notching or raggedness, to extremely ragged or skirted margins, these latter exhibiting growth interruptions that are represented by sediment-filled tongues, or, less commonly, spar-filled cavities (Young & Kershaw, 2005, p. 643). Domical shapes are commonly bell shaped: smooth, convex tops that arch gently downward, becoming steeper on midslopes, then more flattened into ragged, lateral margins toward the base. Laminar forms are commonly extensive, flattened sheets with splayed, ragged, lateral margins, likely to develop at any successional level from bottom to top.

The main skeletal features capable of being preserved on upper surfaces are the mamelons, astrorhizae, and papillae. These are further detailed in chapters on the Internal Morphology and Functional Morphology of Paleozoic stromatoporoids (*Treatise Online,* Part E, Revised, vol. 4, Chapter 9C [Stearn, 2011] and 9F, respectively [Stearn, 2010]). Only a few comments on surface characteristics of these features are included here.

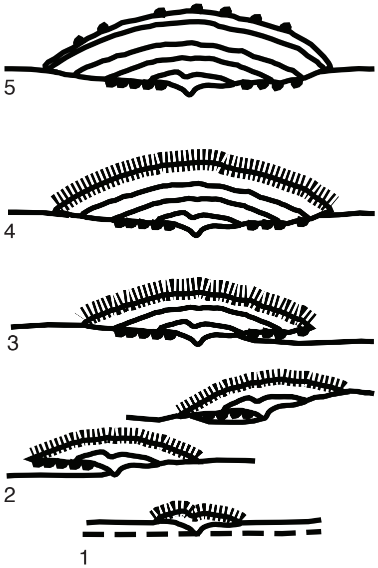

Fig. 42. This alternative model employs a stromatoporoid similar in shape to that represented by Segars and Liddell (1988), but it is based on the understanding that stromatoporoids of the Hamra Formation grew almost entirely on soft substrates. A rather different five-stage succession of events is proposed: stages *1–4*, growth of stromatoporoid, with its living tissue mantling the upper surface, and cryptobionts colonizing partially exposed areas of basal surfaces progressively during different stages, dependent on intermittent secondary scouring activity (before the death of the stromatoporoid); stage *5,* death of the stromatoporoid and the immediately following initial occupation of the upper surface by most of the encrusting epibiont organisms; meanwhile all the former encrusters of the basal surface had probably been overwhelmed by sediment influx and had probably died. The five-stage succession of events is summarized as follows; *1,* initiation of a small, low domical stromatoporoid, with upward and outward growth matching slow accumulation of sediment from a point coinciding with initial level of soft substrate (*dotted line*); *2,* larger, low domical stromatoporoid has grown, and on one side, soft muddy substrate has been scoured to form a large basal cavity for cryptic organisms to inhabit; first example (left side) is shown remaining upright, supported by substrate sediment to right side, or second example (right side) has become tilted to, in effect, cantilever the specimen over cavity (now supported on either side); *3,* with changed conditions—influx of sediment—the cavity on the left side may have been blocked off (or filled) by sediment, and then in another current scouring event, a new cavity (and site for cryptic organisms) may have been produced on right side; *4,* stromatoporoid continued to grow and then in another phase of sedimentary influx, cavity on right side was also blocked off, or filled; at this stage there had been two different generations of cryptic organisms that had lived and died on different parts of the stromatoporoid base. Many more cycles of episodic sedimentation and current scouring or movement of stromatoporoid individuals by storm-generated activity may have produced additional phases (or opportunities) for colonizing coverage of undersurfaces until the history of events was complete; *5,* after death, stromatoporoid skeleton was available for colonization by open surface encrusters, until final entombment of skeleton in sedimentary column (Webby & Kershaw, new).

These structures were probably secreted from modified cells at the base of the organism's mantling sheet of living tissue, prior to termination of skeletal growth and probable death of the organism. Sometimes, a wide variety of hard-substrate-encrusting organisms colonized the terminal growth surface after death (for example, see Segars & Liddell, 1988, fig. 4B), and remained in occupation during a sediment-free interval on the terminal surface, until episodic sedimentation resumed and finally engulfed the skeleton completely.

The **mamelons** (Lecompte, 1956; Galloway, 1957; Stearn & others, 1999) are the updomed extensions or prolongations of the upper growing surface, being typically represented within the skeleton by vertically oriented mamelon columns. The terms mamelon and monticule were

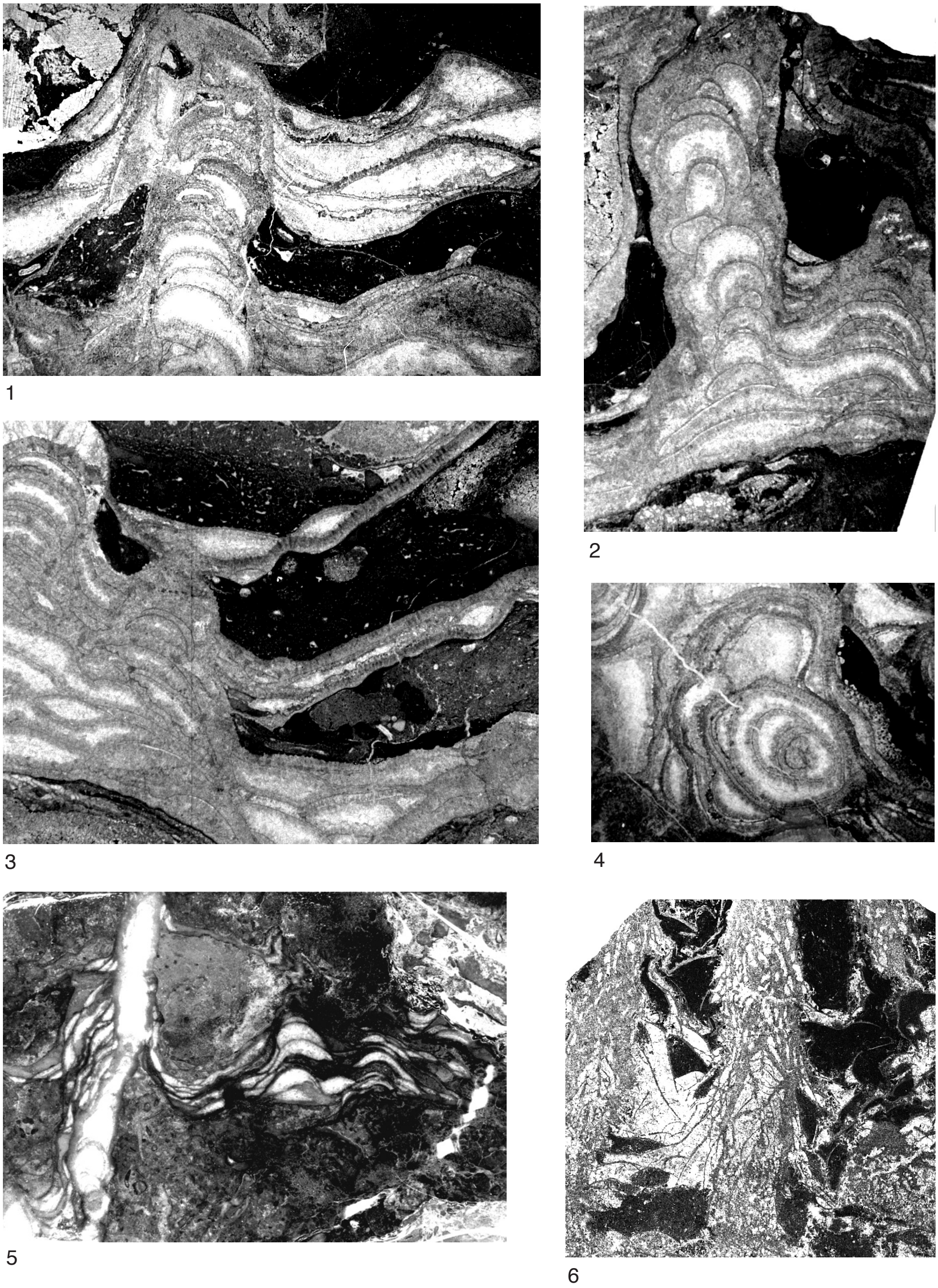

FIG. 43. Labechiid stromatoporoid skeletons in successions that exhibit digitolaminar shapes, lower Katian, Upper Ordovician; *1–5,* coarsely cystose species of *Rosenella*, with some affinities to *R. woyuensis* OZAKI, but it exhibits a more complex development of laterally extended, laminar growth units that may alternate in places with sediment-filled spaces, and commonly intersecting vertically persistent, mamelate-like, columnar upgrowths; just west of Boonderoo shearing shed, lower Fossil Hill Limestone, Cliefden Caves Limestone Group, central New South Wales, Australia,

(Continued on facing page).

used interchangeably by Nicholson (1886) in the first part of his monograph on the British stromatoporoids, but in later parts, Nicholson (1889, 1891, 1892) used only the term mamelon. Much later, Galloway (1957, p. 356) restored the use of monticule for a small mamelon. Kershaw (1990, p. 702, fig. 7; 1998, fig. 6) recognized that mamelons maintained vertical orientations, even though they occupied sites on steep slopes of cone-shaped, high domical types (Fig. 21.1), or tilted laminar shapes lying on a sloping substrate (Fig. 21.2). In both cases, the mamelons were aligned vertically upward toward the light or a particular upward pattern of current flow, though they were tilted with respect to the growing surface. The mamelons were usually evenly spaced across the upper surface of the skeleton, ranging from a few millimeters in height and diameter to exceptionally large dimensions, with vertical continuity up to 150 mm in height and 25 mm or more in diameter. Some Ordovician labechiids have comparatively extended mamelon columns, such as a *Rosenella* from New South Wales. This form has a composite digitolaminar shape (Webby, Zhen, & Percival, 1997, p. 170, pl. 2C; see also Fig. 43.1–43.5), and the mamelon columns are continuous vertically, up to 100 mm in height and about 10 mm in diameter, but the successive laminar phases are never more than about 3 cm apart, meaning that that columns probably did not rise as isolated columns more than that height above the sedimentary interface during growth. Such an example of digitolaminar growth demonstrates the ease with which environmental switches can occur in a few plastic, probably ecophenotypic species, of alternating phases of mainly coalesced, laterally extended laminar growth and the predominantly separated, erect, digitate upgrowths (multicolumnar protruberants of Kershaw, 1998, p. 522) that represent the mamelon columns. Another example of elevated mamelon columns is seen in large domical skeletons of *Pachystylostroma surculum* from the Mjøsa Limestone in Norway (Fig. 43.6). Some authors (Stearn, 1966; Webby, 1971; Cockbain, 1984) have noted that separated digitate skeletal growth tends to develop from extensions of mamelon columns off laminar bases.

Sometimes **astrorhizae** are associated with the mamelons of stromatoporoids (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 9C, Internal Morphology, Fig. 10,*3*, Stearn, 2011). They may be represented by astrorhizal traces (grooves or ridges) that converge in a stellate pattern toward one or more osculum-like opening(s) at the summit of a mamelon, or they may also be present on smooth terminal growth surfaces of stromatoporoids where there are no clearly differentiated mamelons (Fig. 44.2–44.3; and see *Treatise Online,* Part E, Revised, vol. 4, Chapter 9C, Internal Morphology, Fig. 10,*1*, Stearn, 2011). Some stromatoporoids, like many labechiids, do not show

Fig. 43. *(Continued from facing page).*

AMF.12952; *1,* longitudinal section showing vertically upraised columnar growth that appears to have continued to grow, while the laminar growth units appear to have been disrupted at least twice by sediment incursions, ×2.5 (Webby, Zhen, & Percival, 1997, pl. 2C); *2,* longitudinal section illustrating that initial cystose growth of specimen developed over a relatively flat laminar base, then columnar growth took over as successive, large axial cyst plates were added to the column, ×2.5 (Webby, new); *3,* longitudinal section of skeleton also formed on a relatively flat laminar base, and again lower-lying laminar units appear to have been disrupted a number of times by sediment influxes, while broadly raised columnar area to left maintained a continuity of growth, ×2.5 (Webby, new); *4,* tangential section showing columnar nature of vertical growth, ×2.4 (Webby, new); *5,* longitudinal view illustrating remarkable continuity of a vertical column relative to lateral growth; note pattern of lateral extensions initially draping off main column, perhaps because sediment was already piled up against rapidly upgrowing column, ×0.75 (Webby, new); *6,* longitudinal section, *Pachystylostroma surculum* Webby, holotype, PMO 97112, Mjøsa Limestone, Bergevika, Norway, showing strongly mamelate nature of large domical skeleton, especially close to its upper surfaces, where many sediment-filled inclusions seem to occur; with respect to near-surface growth of such skeletons, they may be described also as locally digitolaminar, ×3.5 (Webby, 1979, fig. 2C).

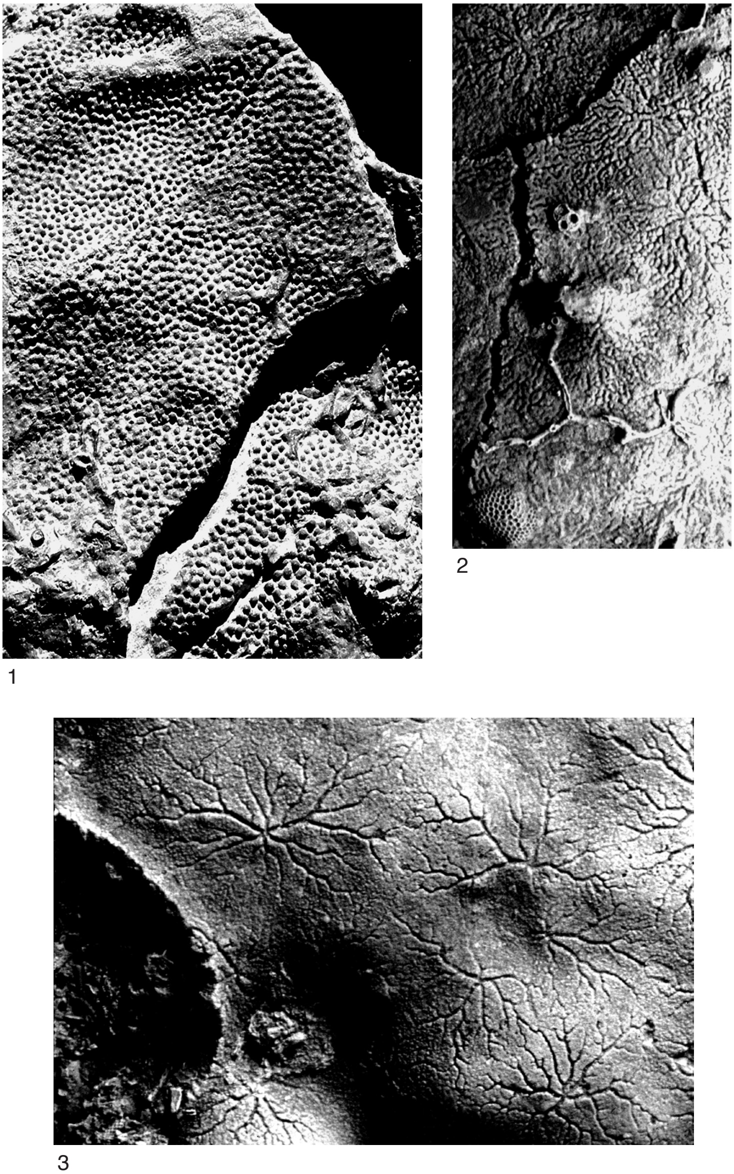

FIG. 44. *1,* Laminar skeleton of *Labechia conferta* (Londsdale), Silurian, Wenlock, Dudley, England, showing well-developed papillae representing tops of individual pillars on terminal growing surface; in places, papillae exhibit alignments into paired, slightly sinuous rows; rarely the paired rows vaguely radiated away from one or two centers; consequently, intervening grooves may be interpreted as original pathways for tubes of living tissue of astrorhizal system that failed to calcify; AMF.134351, a specimen originally presented to the Sydney University paleontology collection by T. W. Edgeworth David, now transferred to the Australian Museum, ×2 (Webby, new); *2–3,* two unidentified stromatoporoid skeletons, possibly *Eostromatopora* sp. (×2.5), and *Pachystroma hesslandi* (Mori) (×3), respectively, Visby Formation, Wenlock, Gotland, Sweden, showing terminal growing surfaces with well-preserved astrorhizal grooves, but no associated mamelons; note also the prominent encrusters in view *2*: a branching, reptant, auloporid coral, and a button-shaped bryozoan (views *2* and *3* courtesy of P. Copper, new).

traces of preserved astrorhizae, though they may exhibit mamelons. In the labechiids, astrorhizae are rarely preserved, because canals of the exhalant current system were probably almost completely confined to the living tissue that lay above the secreted structural elements of successive growing surfaces (Stearn, 1975, fig. 4).

A few stromatoporoids exhibit small, raised, rounded surface cones or bosses on the terminal growing surface, named **papillae** (Galloway, 1957, p. 356; Mori, 1968, p. 17, fig. 5c); these represent the tops of pillars, denticles, or pillarlike structures (they are not growth forms). They were originally termed tubercles by Nicholson (1886, p. 60; see also Nestor, 1964, 1966) but this term is best abandoned, given its potential confusion with the spelling of the chaetetid term tubercule (defined as spine-like projections at junctions between two or more tubules; see *Treatise Online,* Part E, Revised, vol. 4, Chapter 8, Glossary, Webby, 2010). In stromatoporoids, papillae are well developed in some labechiids, most notably *Labechia (L. conferta*) and *Lophiostroma* (*L. schmidti*), and some actinostromatids (Galloway & St. Jean, 1957, p. 149). In *L. conferta,* the papillae are usually separated and rounded (Fig. 44.1) but may be partially confluent, forming sinuous rows (Nicholson, 1886, p. 60, pl. 3,*12–15*). The discrete structures recorded by Prosh and Stearn (1996, pl. 3,*3*) as protuberances are not like papillae (cf. Kershaw, 1998, p. 522), but domal inflexions of laminae that are apparently the result of a response from a stromatoporoid to a "foreign intruder or trauma" (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 9C, Internal Morphology, Fig. 14,*2*, Stearn, 2011).

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