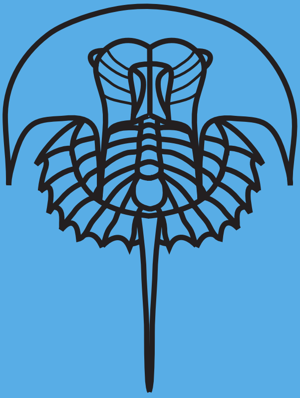

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Part V, Second Revision, Chapter 4: Morphology of the Pterobranch Tubarium

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PART V, SECOND REVISION, CHAPTER 4: MORPHOLOGY OF THE PTEROBRANCH TUBARIUM

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INTRODUCTION

The housing of the Pterobranchia, the tubarium, is a complexly organized organic structure with an extensive fossil record. However, the soft-bodied inhabitants of the tubarium are virtually unknown from the fossil record. Therefore, the anatomy of the Pterobranchia is based on the few extant members (*Atubaria* Sato, 1936; *Cephalodiscus* M'Intosh, 1882; *Rhabdopleura* Allman in Norman, 1869). The variation and evolutionary changes of the tubarium through time are useful for the biostratigraphy in the planktic graptolites (Graptoloidea). A detailed knowledge of the construction of the tubarium is also important for the understanding of graptolite taxonomy. Basic terminology for the pterobranch tubarium is introduced in this chapter (see *Treatise Online,* Part V, Chapter 12, for glossary of terms), with special features of individual groups discussed in more detail in the taxonomic chapters.

Nearly all known Pterobranchia produce a housing structure from an organic material (Fig. 1), secreted in modern pterobranchs largely by the cephalic shield of the individual zooids and produced in distinct increments called the fuselli. The poorly known extant cephalodiscid *Atubaria* appears to be the only taxon that does not produce a tubarium. The initial part of some benthic colonies (e.g., *Rhabdopleura; Epigraptus* Eisenack, 1941a), the sicula, was secreted by dermal glands of a larval organism prior to the development of the preoral shield of the mature zooid (see Lester, 1988). All subsequent housing development is by secretion from the preoral shield of the zooids. This housing was termed a tubarium by Lankester (1884) in the extant *Rhabdopleura,* while Hyman (1959) referred to it as the coenecium in modern Pterobranchia. Törnquist (1890) termed the homologous construction of the fossil groups of the graptolites the rhabdosome. This unique organic development has often been identified as an exoskeleton, but it represents a secreted housing for the pterobranch zooids and, thus, the term skeleton is inappropriate.

The pterobranch tubarium originally may have been highly translucent, as is seen in modern *Rhabdopleura* and *Cephalodiscus*, either colorless or slightly brownish or yellowish in color. Sometimes organic and sediment particles are incorporated in the construction of the tubes and the interconnecting tissue, especially in *Cephalodiscus* tubaria (see *Cephalodiscus agglutinans* Harmer & Ridewood, 1913). The organic material of the tubaria appears to darken with time, and Paleozoic material in general is dark brown to black in color. Sometimes the fossil tubaria are still partly translucent, as, for example, shown by Maletz (1994) in *Pterograptus* Holm, 1881, in which most specimens are not artificially bleached. It is not clear, however, whether this translucency is an effect of weathering of the sample.

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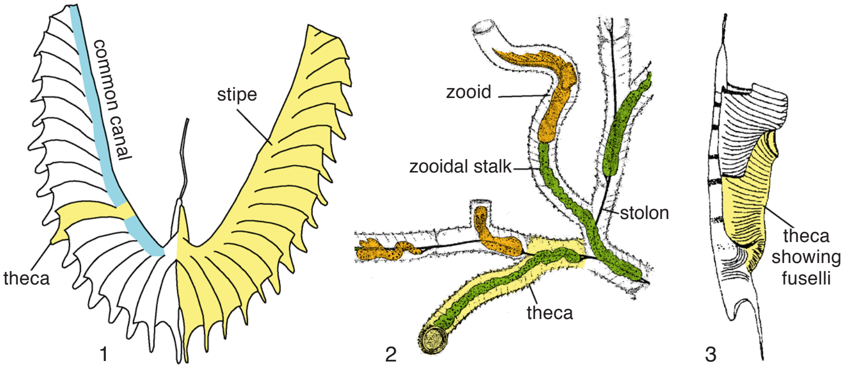

FIG. 1. The structure of the tubarium. *1, Isograptus mobergi* MALETZ, 2011a, tubarium showing two reclined stipes formed from numerous overlapping thecae; common canal indicates colonial organization (adapted from Maletz, Carlucci, & Mitchell, 2009, fig. 5E); *2, Rhabdopleura normani* ALLMAN in NORMAN, 1869, part of extant tubarium, showing thecal tubes and interconnected zooids, with one thecal tube highlighted in yellow, (adapted from Ridewood, 1907, fig. 7a); *3, Heisograptus micropoma* (JAEKEL, 1889), small tubarium showing fusellar construction (adapted from Maletz, 1999).

THE TUBARIUM CONSTRUCTION

The pterobranch tubarium consists of variably developed independent chambers or communal living compartments for the individual zooids or of interconnected tubes. The two groups of the Pterobranchia, the Cephalodiscida and the Graptolithina (MITCHELL & others, 2013), produce similarly developed tubaria, but those of the Cephalodiscida do not show the interconnection and seriality of the tubes in the colonial Graptolithina. The individual zooidal tubes of the tubarium are termed the thecae (Fig. 1.1) in fossil graptolites. The term is here also used for the individual tubes of extant pterobranchs (Fig. 1.2, Fig. 2.6).

The tubaria of the Cephalodiscida (Fig. 2.1–2.2) differ in a number of aspects from those of the derived colonial Pterobranchia. They are quite variable in development, ranging from completely separate, proximally closed tubes for the individual zooids with their developing buds to an array of interconnected structures with a common internal cavity inhabited by the zooids. In forms with individual tubes, these are usually embedded in a coarse cortical mass or are laterally in contact, at least for part of their length. In one subgenus (*Acoelothecia* JOHN, 1931), the housing consists of a network of branched spines and bars without a common cavity. As the tubaria of *Cephalodiscus* are formed from social groups of clonally developing organisms, they, unlike the Graptolithina, do not show a recognizably differentiated housing tube for the founder of the colony. A dome or a sicula, as in the derived colonial Pterobranchia, does not exist (MITCHELL & others, 2013).

The thecal tubes of all Graptolithina are interconnected and form a communicating housing system through the common canal (Fig. 1.1). The tubes of *Rhabdopleura,* the only extant genus of the Graptolithina, and interpreted as a fairly ancient and primitive taxon, are formed from creeping parts with a dorsal zigzag suture and an erect part with fusellar full rings (Fig. 2.5–2.6). The erect parts of each tube originate through a lateral resorption foramen from the creeping tubes (LANKESTER, 1884); thus, tube building differs considerably from tube growth in more derived graptolithines, in which an initial, primary opening is left for the emergence of the zooids. The development and differentiation of thecae is not well known in most dendroid graptolites, as tips of stipes with growing ends are difficult to obtain. In many benthic graptolites and in the planktic Anisograptidae, the thecae are bundled into

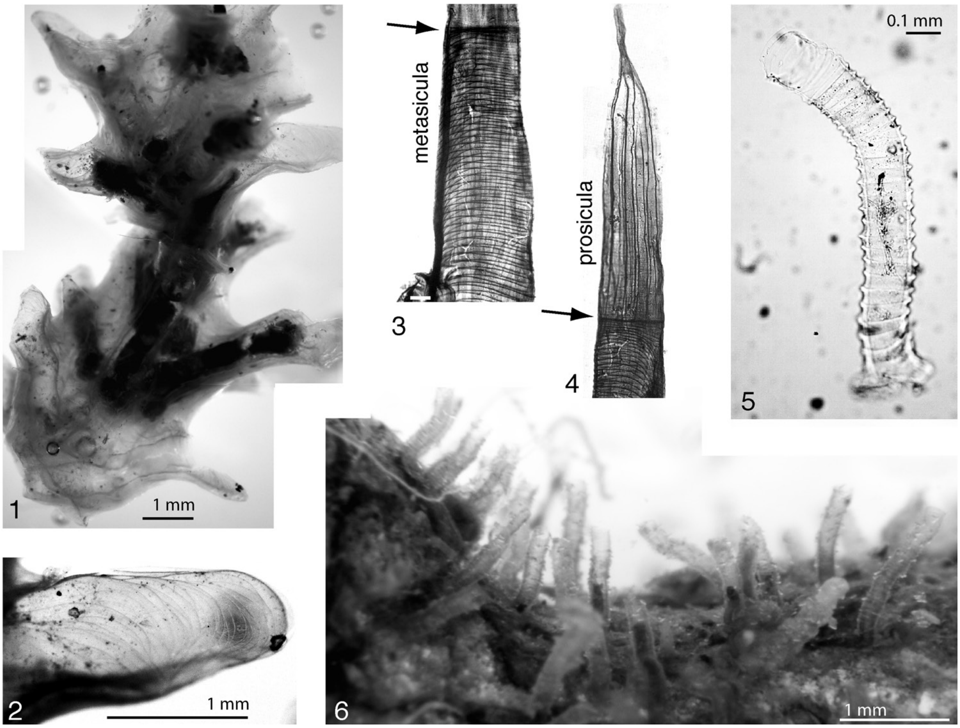

Fig. 2. Colony form and structure in the Pterobranchia. *1–2, Cephalodiscus (Idiothecia) levinseni* Harmer, 1905, origin unknown, extant; *1,* fragment of a tubarium showing isolated tubes inhabited by zooids (darker matter); *2,* enlarged view of aperture of thecal tube showing irregular fuselli (adapted from Mitchell & others, 2013, fig. 3); *3–4,* isolated and bleached prosicula and metasicula of the Graptoloidea, *arrows* mark boundary between prosicula and metasicula (adapted from Palmer & Rickards, 1991, pl. 13–14); *5–6, Rhabdopleura normani* Allman in Norman, 1869; *5,* individual erect tube showing fuselli, extant (new); *6,* MB.G. 1122, Jaeger collection, Museum für Naturkunde, Berlin; large colony growing on coral, extant, Heltjefjord near Bergen, Norway, ~100 m depth (new).

triads with lateral origin of new autothecae and bithecae.

COLONY SHAPES

The shapes of pterobranch colonies vary considerably, based on numerous factors (some genetically controlled, others due to ecological interactions of the organisms with their environments). Ecophenotypic variation is most frequently developed in benthic forms, in both encrusting and erect taxa. Planktic taxa are less strongly affected by environmental conditions and, thus, generally show a lower amount of ecologically controlled variation. Instead, they possess more highly symmetrical colony shapes, presumably useful for maintaining a stable position in the water column. The main factor determining colony shape is the number of stipes in multiramous colonies. Graptolithines can produce two-dimensional (sheetlike) and three-dimensional (bushy) colonies. Sheetlike colonies can develop secondary three-dimensional shapes, from curved fans to conical colonies, in erect benthic forms and in planktic colonies.

BENTHIC ENCRUSTING COLONIES

Encrusting colonies can form only two-dimensional shapes (Fig. 2.6), but still the amount of variation may be high, depending on the shape of the overgrown surface. Thigmophilic colonies form dense masses of zooidal tubes connected to hardground

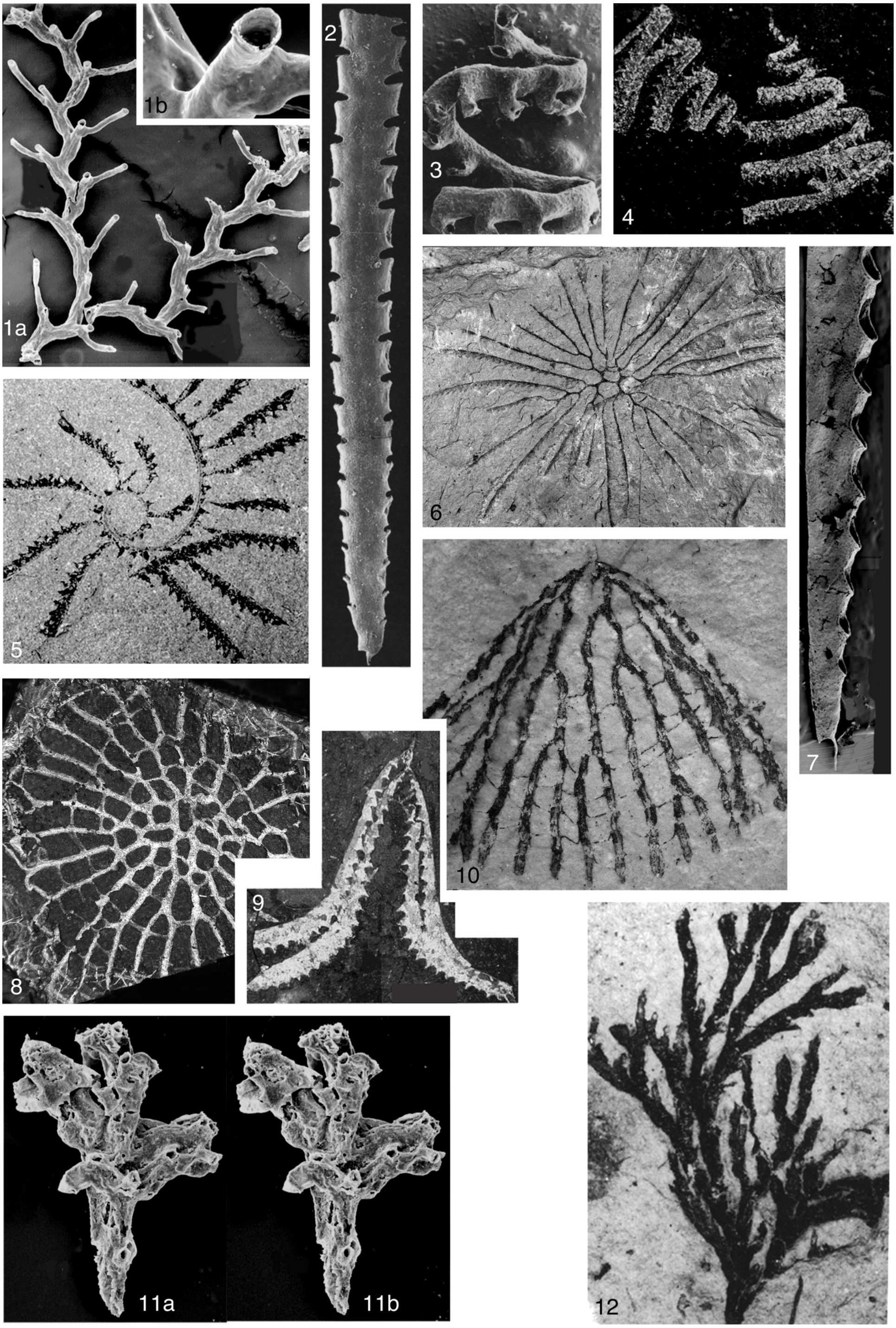

FIG. 3. *For explanation, see facing page.*

or other hard surfaces, be it rocks, shells of bivalves and brachiopods, or the corallites of corals. The individual tubes grow in close contact to each other and do not leave any vacant space between them. The extant *Rhabdopleura compacta* HINCKS, 1880, is a good example of this thigmophilic colony shape, but many other benthic pterobranchs possess a similar growth form (see KOZŁOWSKI, 1949). Another common benthic colony form is the runner-type colony of the extant *Rhabdopleura normani* or the Upper Ordovician *Bulmanicrusta*? sp. (MITCHELL, WILSON, & ST. JOHN, 1993), which loosely and quickly covers large areas, though not completely. The individual zooids keep a certain distance from each other and, thus, the stipes never touch. Through their repetitious branching, the colonies can become extremely large.

BENTHIC ERECT COLONIES

Erect benthic taxa do not develop into thigmophilic shapes, but usually branch at variable distances and form conical, as in planktic *Rhabdinopora* EICHWALD, 1855 (Fig. 3.10), fan-shaped, or bushy (Fig. 3.12) colonies. In conical colonies, the thecae have their openings on the inside of the cone, as can be seen from the few, available, well-preserved specimens (BULMAN, 1933). In fan-shaped colonies, all openings are oriented in the same direction, while in bushy forms, thecal openings can be variably oriented and the colonies are truly three-dimensional. However, in the Dendrograptidae, even in the bushy forms, the thecae appear to be oriented in the same direction on the individual stipes in a serial arrangement. The development of the stipes and the orientation of the thecal openings may be more complex in the Acanthograptidae, in which individual stipes are formed from a number of overlapping thecal tubes and thecal openings may point in various directions (Fig. 3.1).

PLANKTIC COLONIES

The colony shapes of planktic taxa are generally more symmetrical, due to the need for balance and orientation in the water column. Most multibranched, planktic graptolites grew into an essentially two-dimensional, planar shape (Fig. 3.6). This shape, however, could be transformed either into umbrella-shaped (Fig. 3.8) or strongly conical (Fig. 3.3–3.4,10) colonies. Their three-dimensionality is based on the modification of this original conical arrangement of the stipes in the early planktic genus *Rhabdinopora* (Fig. 3.10). A truly three-dimensional colony growth with highly irregular branching, as, for example, in benthic *Dendrograptus* HALL, 1858, species, has not been recognized in any planktic

FIG. 3. General shapes of graptolite colonies. *1a–b, Acanthograptus* sp. fragment, branching, Silurian (upper Wenlock), Canadian Arctic, ×21; *1b,* enlarged view of 1a, showing bitheca and autotheca, ×160 (Lenz & Kozłowska-Dawidziuk, 2001, pl. 1,12); *2, Pseudoglyptograptus barriei* ZALASIEWICZ & TUNNICLIFF, 1994, straight, biserial development, Silurian (middle Llandovery), Canadian Arctic, ×7 (Melchin, 1998, pl. 1, fig. 13); *3, Spirograptus guerichi* LOYDELL, ŠTORCH, & MELCHIN, 1993, narrow, conical spiral, Silurian (upper Llandovery), Sweden (Dalarna), ×12 (Loydell, Štorch, & Melchin, 1993, fig. 3B); *4, Spirograptus turriculatus* BARRANDE, 1850, narrow, conical spiral, Silurian (upper Llandovery), Czech Republic, ×2.4 (Loydell, Štorch, & Melchin, 1993, fig. 3A); *5, Cyrtograptus mehnerti* HUNDT, 1949, broad, low, conical spiral, Silurian (lower Wenlock, Sheinwoodian), Canadian Arctic, ×1.4 (Lenz & others, 2012, pl. 22, fig. 1); *6, Praegoniograptus clonograptoides* (Harris & Thomas, 1939), holotype, planar to umbrella shaped, Lower Ordovician, Victoria, Australia, ×1 (new); *7, Pristiograptus dubius* (SUESS, 1851), uniserial, Silurian (middle Wenlock), Canadian Arctic, ×9 (Lenz & others, 2012, pl. 11, fig. 8); *8, Sagenograptus macgillivrayi* (HALL, 1899), umbrella shaped, Ordovician (Tremadocian), Victoria, Australia ×1.1 (new); *9, Tetragraptus fruticosus* (HALL, 1865), pendent, bell shaped, Lower Ordovician (Floian), Canada (northern Yukon), ×3 (Jackson & Lenz, 2006, fig. 6D); *10, Rhabdinopora flabelliformis parabola* (BULMAN, 1954), cone shaped, Lower Ordovician (Tremadocian), Dayangcha, China, ×2.1 (new); *11a–b, Thallograptus* sp., bushy, stereopair, Silurian (Ludlow), Canada, ×16.5 (Lenz & Kozłowska-Dawidziuk, 2004, fig. 2,*12*); *12, Callograptus huckriedei* RICKARDS, HAMEDI, & WRIGHT, 2001, bushy, Lower Ordovician (Floian), Iran, ×7 (Rickards, Hamedi, & Wright, 2001, fig. 2D).

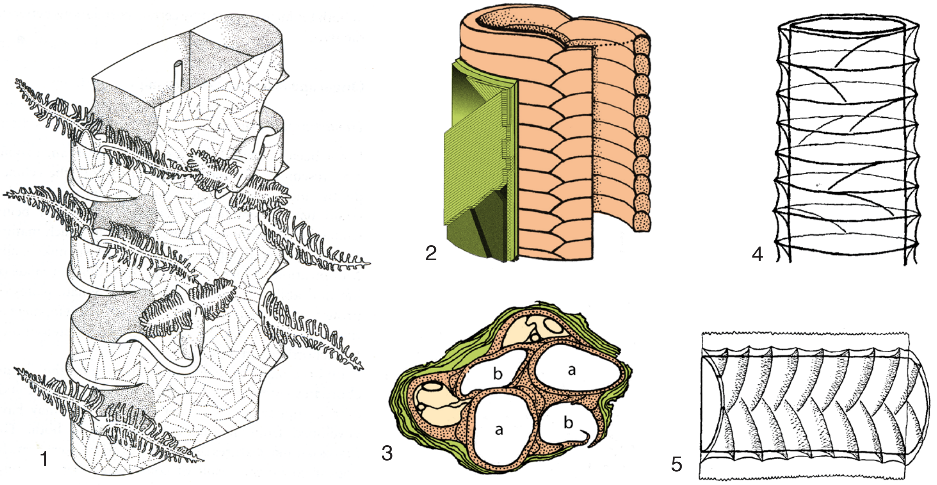

FIG. 4. Thecal construction in the Pterobranchia; illustrations of fusellar and cortical layers. *1,* Part of axonophoran colony with reconstructed zooids and cortical bandaged surface (adapted from Crowther & Rickards, 1977, fig. 3); *2,* zigzag fusellar structure and the outer crisscrossing cortical bandages (adapted from Bulman, 1970, fig. 5,*1,* and Kozłowski, 1938, fig. 2); *3,* cross section through stipe of dendroid showing autothecae (*a*), bithecae (*b*), fusellum and ectocortex (adapted from Bulman, 1955, fig. 6,*2*); *4–5, Rhabdopleura* sp.; *4,* portion of erect tube with fusellar full rings and irregular sutures; *5,* portion of creeping tube with fusellar half rings and zigzag sutures (Andres, 1977, fig. 4).

form. Thus, there are no bushy planktic colonies, as there are in benthic colonies (Fig. 3.11–3.12). Three-dimensional shapes are developed in coiled (Fig. 3.3–3.4) and cladial-bearing monograptids (Fig. 3.5) in the Silurian and Lower Devonian, but three-dimensional, spiral colonies are also present in Ordovician dicellograptids and dicranograptids.

THECAL WALL FORMATION

The tubes, or thecae, form housing structures for the individual members of the colony. They have a characteristic and simple construction in the form of fusellar half rings and full rings. The shape of these tubes may vary considerably and is used for taxonomic and phylogenetic interpretations. Isolated, erect tubes may be round in cross section, but creeping tubes are more often flattened on the ventral side. In complex colony structures, they may be shaped irregularly, depending on the attachment sides and connection between the tubes.

The two, basic constructional features of the thecae are the fusellum (fusellar layer) and the cortex (cortical layer) (Kozłowski, 1949). These two layers together (Fig. 4.2) have been termed the periderm in the past (Wiman, 1895), but it is now understood that these layers are formed by a special gland on the cephalic disc of the zooids and are not a dermal layer. As a result, the term periderm is inappropriate.

THE FUSELLUM

Each tube is secreted in individual, narrow increments, the fuselli (singular, fusellus). Numerous fuselli (collectively the fusellum of Kühne, 1955) are stacked one upon another with some lateral overlap (Fig. 4.2), forming a distally open tube for the individual housing of each zooid. Each fusellus possesses at least one oblique suture (Fig. 4.4), indicating the method of secretion as a strip of material around the circumference of the tube. The zooid of an extant pterobranch starts at one point and secretes the fusellus while moving its oral disc in a circle around the thecal aperture. In full fusellar rings, a single oblique suture defines the position at which the zooid started and finished the secretion of the individual fusellar ring. In fusellar half rings, two separate fuselli form a full ring of the thecal tube, producing a dorsal and a ventral suture (Fig. 4.2). The fuselli are, thus, growth segments laid down by the zooids in a highly regular and highly symmetrical fashion.

In early members of the Pterobranchia, the fuselli are full rings with irregularly placed sutures (Fig. 2.5, Fig. 4.4); during the evolution of the group, these sutures become more regular and are replaced by fusellar half rings (Fig. 4.5) with a much higher degree of symmetry. Regular fusellar half rings are laid down alternately right and left and produce the dorsal and ventral zigzag sutures of the tubes (Fig. 4.2,5). Full rings and half rings can, however, be found in the colonies of the extant *Rhabdopleura*. Creeping parts of *Rhabdopleura* colonies possess a distinct zigzag pattern on the dorsal side of the creeping tubes (Fig. 4.5), while erect tubes show fusellar full rings with a distinct collar structure (Fig. 4.4). The thickness of the fuselli (and, therefore, the fusellar layer) is usually uniform along the colony, but the height of the individual fuselli may vary considerably, depending on the position in the thecal tube and the ontogeny of the secreting zooid. Early fuselli of a theca are usually of a lesser height than distal or apertural fuselli (Walker, 1953), but a lesser height may also be seen at thecal apertures (Bates, 1987, pl. 1).

REDUCTION OF FUSELLAR THICKNESS

Fuselli possess an interior part made of fibrils and a thin, denser wall made of the same construction material (see discussion of ultrastructure below). The amount of material used to form the fuselli varies considerably among groups and a reduction in wall thickness and density is observable in a number of taxa. The Ordovician genera *Parisograptus* Chen & Zhang, 1996, and *Cryptograptus* Lapworth, 1880, show fairly thin thecal walls, visible often as translucent thecae with clearly observable fusellar structure, while associated graptolites on the same sedimentary surface show only thick, dark films of organic material (e.g., Williams & Stevens, 1988). In a further reduction of the fusellar wall material, it appears as if the taxa do not possess thecal walls at all, as the wall material is so thin that it rarely survives the fossilization process. The remains of thecal walls may be seen in ragged edges preserved, for example, in the cortical bandages of the retiolitids (e.g., Bates & Kirk, 1992, 1997). A considerable reduction may be present only in part of the colonies, but it can also affect the whole colony and may be counteracted by the development of secondary cortical covers. In stratigraphically younger taxa of the genus *Cryptograptus,* for example, the sicula and the first two thecae are so weakly sclerotized that they have not been found in isolated material. Some authors (e.g., Bulman, 1945; Maletz & Mitchell, 1996) have suggested that since cortical bandages on these structures have not been recognized in isolated material, they were never present.

Thin thecal walls, seldom preserved, and development of lists are traits in all Retiolitidae, most Lasiograptidae, some members of the Abrograptidae (Mu, 1958), and as an exception in other taxa. Thecal walls in retiolitids are rarely preserved, even though it can be shown from isolated material that they were originally present (Lenz, 1994, fig. 14,*3,7–9;* Lenz & Kozłowska-Dawidziuk, 2002, fig. 15) on both the thecal framework and ancora sleeve. Based on very rare preservation of thecal framework walls (Lenz & Thorsteinsson, 1997) as well as scars and shards in isolated material (Bates, 1987), it is clear that the thecal framework was composed of successive layers of fusellar bands. It is not clear, however, in what manner the ancora sleeve layer was constructed, since there appears to be no indication of fusellar laminae (see discussion of ancora sleeve below). In other,

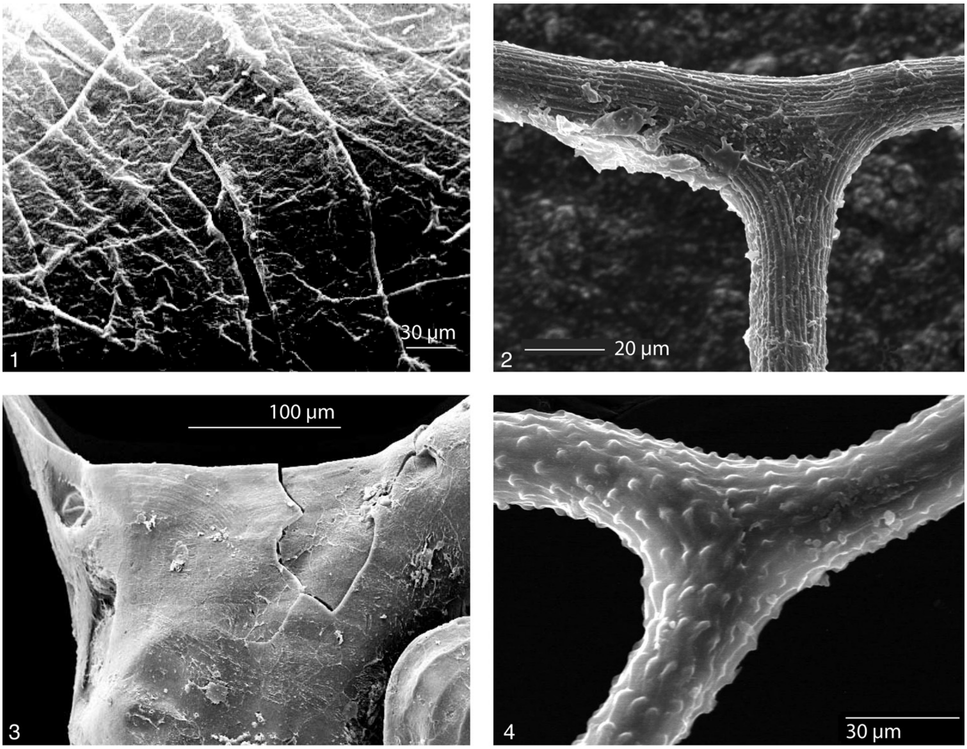

FIG. 5. Cortical bandages. *1, Rectograptus gracilis* (Roemer, 1861), bandages with distinct raised rims (new, courtesy of Piotr Mierzejewski); *2, Rotaretiolites* sp., showing cortical tissue of strong, parallel, ridgelike bandaging, Silurian (upper Telychian, Llandovery), Canadian Arctic (new); *3, Paramonoclimacis sidjachenkoi* (Obut & Sobolevskaya, 1965), Canadian Arctic, showing thin application of cortical material at growing end of colony (new); *4, Plectograptus macilentus* (Törnquist, 1887), pustulose surface of a plectograptine retiolitid, Silurian (Ludlow), glacial boulder, northern Germany (new).

unrelated groups (e.g., *Retiograptus* Hall, 1865; *Rectograptus* Přibyl, 1949), a reduction of the thickness and, ultimately, loss of thecal walls appears to have originated independently.

CORTEX

The cortex, cortical tissue, or cortical bandages are formed in extant pterobranchs in the same way as the fuselli, by the preoral lobe of the zooids. However, the cortical material differs considerably in the way in which it is laid down in the pterobranch colony. It can form thick masses of loose or spongy material around the individual tubes of a *Cephalodiscus* colony or thin layers of material surrounding and covering the surface of thecal tubes in planktic graptolites. In general, a differentiation of ectocortex and endocortex can be made (Crowther, 1981; Urbanek & Mierzejewski, 1984). Endocortex is made of cortical bandages laid down on the inside of the thecal tubes and is commonly found in some pterobranchs (Andres, 1977). It also is found in dendroids (e.g., *Dendrograptus*? sp. in Bates, 1997, pl. 4,*1*). Crowther (1981, pl. 16) indicated its presence even in monograptids. Ectocortex (Fig. 4.1–4.4) is much more generally distributed in the Pterobranchia and is found on the outside of colonies.

The cortex is often secreted in the form of distinct bands or bandages (Crowther & Rickards, 1977) on the outer surface of planktic graptolite colonies (Fig. 5), and

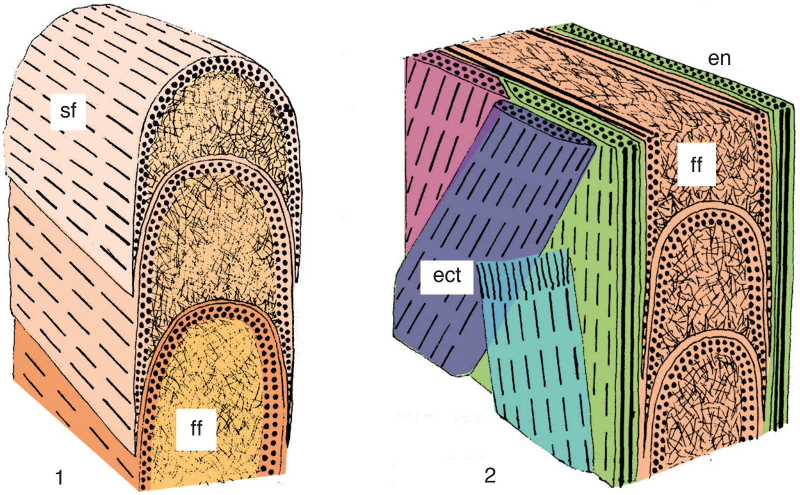

Fig. 6. Ultrastructure of the tubarium wall. *1,* Three stacked fuselli, showing sheet fabric (*sf*) and fusellar fabric (*ff*); *2,* tubarium wall structure with fuselli (*ff*), ectocortex (*ect*), and endocortex (*en*); ectocortex formed as separate bandages (adapted from Bates & Kirk, 1986, fig. 1).

is also present in similar form in benthic colonies (Bates & others, 2011). The precise development of the ectocortex and its distribution in the various groups of Paleozoic graptolites is little understood. Differences in the development are apparent, as some graptolites possess cortical bandages with distinct lateral ridges (Fig. 5.1). Cortical bandages can also be quite indistinct, as in many monograptids, and appear like faint brush strokes (Fig. 5.3). In the Silurian retiolitids, there are two kinds of ornamentation on the cortical bandage surfaces: linear striae and pustules (Fig. 5.2,4).

ULTRASTRUCTURE

Denis E. B. Bates

The ultrastructure of the fusellar tissue shows a complex secretion of the wall material. It can be differentiated into sheet fabric and fusellar fabric (Fig. 6). The details of this construction are visible only under the Scanning Electron Microscope (SEM) and Transmission Electron Microscope (TEM).

FUSELLI

Each fusellus starts with the deposition of a sheet of granular fabric on the head of the previous fusellus (Bates & Kirk, 1986; Bates & others, 1988). This is succeeded by a three-dimensional meshwork of fibrils, the fusellar fabric (Fig. 7.1–7.2). Generally, these have a random orientation, but variations may be noted. They may start with clumps of fibrils springing up from the base of the fusellus, rather like the roots of mangrove trees or trabeculae. They also tend to become denser towards the arch of the increment. Fibril diameter ranges from 20 nm to 70 nm, with a tendency to increase in diameter towards the bounding sheet of a fusellus. Clockwise spiral striae appear to be present in some taxa (Fig. 7.5,10).

Each arch is bounded by a sheet, which appears to be finely granular in form. This sheet may contain larger pustules, giving it a knobby surface (Fig. 7.6), the granular sheet fabric *sensu* Crowther and Rickards (1977). Oval vesicles are also characteristic of this bounding layer; they may be roofed over to give slight swellings, suggesting that there may be two layers to this bounding sheet, or they may appear as unroofed depressions (Fig. 7.6). Beneath the bounding sheet, there are usually fibrils intermingled with the fusellar fabric, parallel to one another and to the head of the incremental arch (Fig. 7.4).

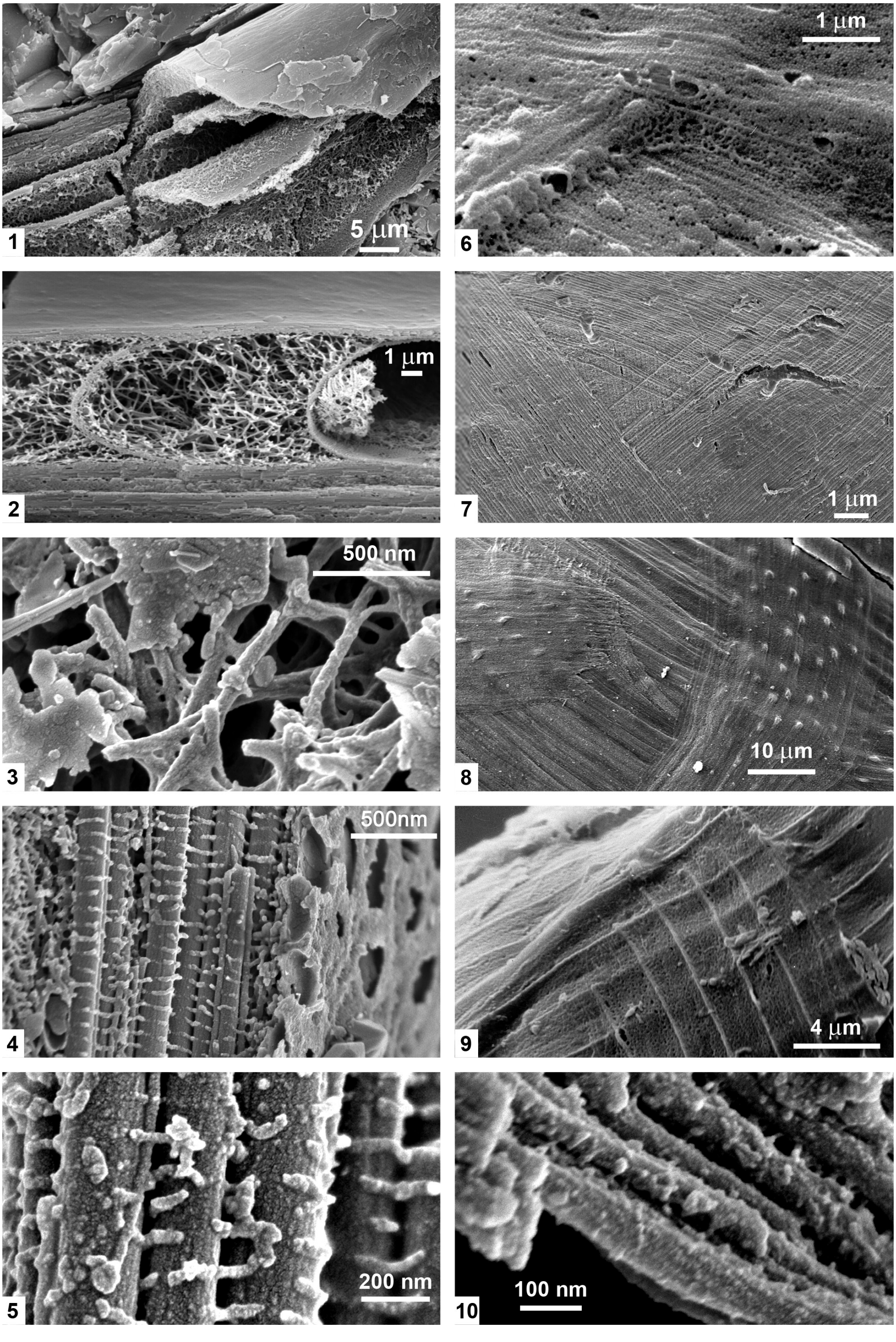

FIG. 7. *For explanation, see facing page.*

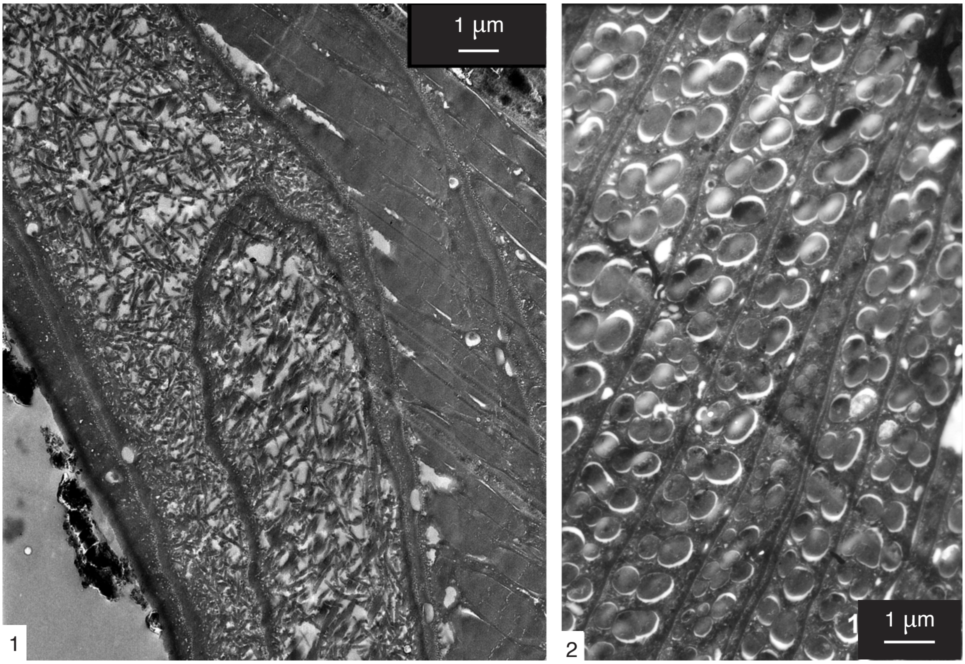

FIG. 8. TEM sections of tubarium wall construction. *1*, *Dendrograptus*? sp., two fuselli and bandages of the ectocortex, Gotland, Sweden; *2*, *Dendrograptus*? sp., cortical bandages, Gotland, Sweden (Bates, 1997, pl. 5).

CORTICAL BANDAGES

Cortical bandages vary in dimensions and ornament, and also in the number of fabrics composing them. In a typical bandage the lowest layer is a thin sheet, again formed of a finely granular fabric. Occasionally, this is succeeded by random fibrils, especially where a bandage is laid down over an uneven surface (e.g., where it crosses the edge of a previous bandage). The bulk of the bandage is made of closely packed, parallel fibrils, the unit being from one to several fibrils thick, and varying in diameter from 80 nm to 400 nm (Fig. 7.4, Fig. 8.1). In most taxa, they have an ornament of striae that spiral clockwise (Fig. 7.5).

Interconnecting rods are smaller fibrils, which run perpendicular to the cortical fibrils of the cortex, observed in some genera. They are best developed in *Dictyonema*, where they are ~27 nm in diameter, and are regularly spaced at intervals of ~80 nm (Fig. 7.4–7.5).

The sheet layer covering the bandages is identical to that described above for the fuselli (Fig. 7.6). In some taxa, the edges

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Fig. 7. SEM photographs. *1,6, Geniculograptus typicalis* (HALL, 1865), Viola Springs Limestone, Upper Ordovician (Katian), Oklahoma, USA; *1,* fractured fuselli (new); *2, Desmograptus micronematodes* (SPENCER, 1884), fuselli, with thicker ectocortex below and thinner endocortex above, Racine Dolomite, Silurian (Wenlock), Illinois, USA (new); *3,10, Acanthograptus*? sp., erratic boulder, Middle Ordovician, Mochty, Poland; *3,* fusellar fibrils with spiral striae (new); *4–5, Dictyonema* sp., erratic boulder, Upper Ordovician, Orłowo, Poland; *4,* section through cortical unit with cortical fibrils and interconnecting rods, base of unit on the left, sheet fabric of surface with vesicles on the right (new); *5,* cortical fibrils with spiral striae (new); *6,* bandages with sheet fabric forming their surfaces, both roofed and unroofed vesicles are shown (new); *7, Cyrtograptus lundgreni* (TULLBERG, 1883), internal bandages, one fibril thick and without any sheet fabric, Kolka Borehole, Silurian (Wenlock), Latvia (new); *8, Gothograptus nassa* (WIMAN, 1895), bandages on genicular hood with pustules, Mulde Marl, Silurian (Wenlock) Gotland, Sweden (new); 9, *Reteograptus geinitzianus* (HALL, 1865), bandages with regularly spaced ridges, Athens Shale, Upper Ordovician (Sandbian), Alabama, USA (new); *10,* cortical fibrils with transverse ridges superimposed on the spiraling striae (new).

of the bandages are thickened (Crowther, 1981); in others the bandage is covered by a series of prominent, equally spaced ridges across the bandage (Fig. 7.9). So far, it has not been possible to determine whether these ridges are formed from parallel fibrils or from thickenings of the covering sheet layer. Some Silurian retiolitids have another type of bandage ornament, which bears a pattern of blunt tubercles or spines (Fig. 7.8). Internal bandaging (inner cortex) is much more rare. Commonly, internal bandages are much thinner (usually only one fibril thick) than external ones, and they lack the sheet covering (Fig. 7.7).

CHEMICAL COMPOSITION OF THE TUBARIUM

Pterobranch tubaria consist of organic material, as can easily be recognized from their brownish to black color and their reaction to tectonism within a rock, resulting in the surrounding pressure-shadow minerals (Underwood, 1992). Specimens weather out as dark films of material that may be attacked by bacteria and fungi in the laboratory. Early investigation suggested a material similar to chitin, but neither chitin nor cellulose was proven to be present (Foucart & others, 1965; Florkin, 1969). Instead, the presence of amino acids in three samples of Ordovician and Siluran age showed that they were composed of proteinaceous substances (e.g., Kozłowski, 1966). Towe and Urbanek (1972), Crowther and Rickards (1977), and Runnegar (1986), among others, interpreted the graptolite tubaria to be collagenous in composition, based largely on the observation of the banded fibrils in the cortical and fusellar material. The material of the fossil graptolite tubarium consists of an aliphatic polymer and does not contain any protein, even though the structure and analysis of the housing material of modern *Rhabdopleura* (Armstrong, Dilly, & Urbanek, 1984; Bustin, Link, & Goodarzi, 1989; Gupta, Briggs, & Pancost, 2006) indicated that the building material in fossil graptolites was originally collagen. Even the most recent investigation was unable to define the composition of the building material more precisely (Sewera, 2011).

ONTOGENY AND ASTOGENY

The Graptolithina show a complex pattern of sexual and asexual reproduction, the most conspicuous aspect of which is the asexual budding of the clonal, colonial zooids. Thus, the ontogenetic development of the individual zooids and their tubes needs to be differentiated from the astogenetic growth of the colony as a whole. The sexually produced founder zooid of the colony is usually easily differentiated from the later zooids. It inhabits (and produces) the sicula, the first theca of the colony.

A new benthic colony starts with the settling of a sexually produced larva and the secretion of the initial part of the sicula. In the extant *Rhabdopleura,* this is accomplished by a ciliated larva. The larva settles on a suitable surface and forms a cocoon or dome (Fig. 9.1–9.3), in which it morphs into the first zooid (Lester, 1988). In derived benthic graptolites (e.g., *Dendrograptus*), the larval stage included a prosicula as the housing for the sicular zooid (Kozłowski, 1971). The shape of the prosicula of benthic taxa varies considerably but it is known from only a very few species. In planktic graptolites, the prosicula always possesses a nema, inferred to indicate a planktic development and life mode.

SICULAR ONTOGENY

A sicula is present in all Graptolithina, but not in the Cephalodiscida. It represents the housing of the sexually produced founder zooid of the colony, comparable to the ancestrula of the Bryozoa. Its construction and the construction of the early thecal tubes can be regarded as the most important characters for a specific determination of graptolite taxa.

ATTACHMENT DISC AND NEMA

The attachment of the prosicula to the substrate in benthic encrusting and bushy dendroid forms is poorly known, as mostly

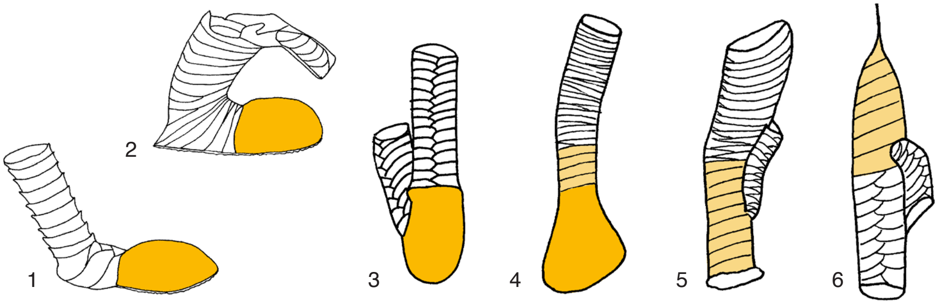

FIG. 9. Prosicular development and comparison with rhabdopleurid dome. *1, Rhabdopleura compacta* HINCKS, 1880, lateral view of juvenile with dome and initial (sicular) tube (adapted from Stebbing, 1970b, fig. 3); *2, Epigraptus* sp., juvenile with dome and initial tube (adapted from Kozłowski, 1971, fig. 1); *3, Rhabdopleura* sp., dorsal view of tubarium with initial part of first post-sicular tube (new); *4, Dendrotubus* sp., with distal helical line in the prosicula (adapted from Kozłowski, 1971, fig. 5); *5, Dendrograptus communis* KOZŁOWSKI, 1971, tubelike prosicula with helical line (adapted from Kozłowski, 1949, fig. 1); *6,* nematophorous sicula with helical line (adapted from Maletz, Steiner, & Fatka, 2005, fig. 2). *Darker color,* dome and possible equivalents; *lighter color,* prosicula with helical line.

only fragments are available and specimens in life orientation often possess considerable cortical overgrowth covering the initial attachment site. Erect, bushy taxa may possess a dendritic holdfast structure to anchor them to a substrate (e.g., *Dictyonema cavernosum* WIMAN, 1896). There is no credible evidence of any so-called root system in benthic graptolites extending into the sediment, and it has to be assumed that the attachment is invariably produced as cortical tissue by the zooids of the colony fixing the colony to a hard substrate. One extant species of *Rhabdopleura* is known to live in sandy areas and does not depend on attachment to a hard surface (e.g., bivalve shell, coral, or other organism) or hardground.

INITIAL PART OF THE COLONY

The initial part of the colony, represented by the prosicula or dome, shows a number of characters that help to identify its development and the phylogenetic relationships of taxa. The dome in modern *Rhabdopleura* (Fig. 9.1,3) is the only form of initial development known from modern pterobranchs, and it differs considerably from the prosicula of most graptolites. KOZŁOWSKI (1971) differentiated the discophorous sicula (Fig. 9.5) of the benthic taxa from the nematophorous sicula of the planktic forms (Fig. 9.6), based on the presence or absence of a free nema.

DOME AND PROSICULA

The prosiculae in *Rhabdopleura normani* and in *Rhabdopleura compacta* are known as the dome (Fig. 9.1,3). They are formed as a featureless membrane, encasing the developing or metamorphosing sicular zooid and are constructed by glands in the ventral epidermis of the larva (LESTER, 1988). In *Cephalodiscus* (*Orthoecus*) *densus* ANDERSSON, 1907, a possibly comparable structure, a cocoon is formed around developing larvae and is protected on the outside with sand grains (SCHIAPARELLI, CATTANEO-VIETTI, & MIERZEJEWSKI, 2004). The details of the construction of the dome or the cocoon are unclear. In *Rhabdopleura,* the sicular zooid produces a resorption foramen to hatch from the cocoon and starts to form the initial thecal tube (LESTER, 1988). The development of a dome in place of a prosicula has been documented for the Ordovician genus *Epigraptus* (KOZŁOWSKI, 1971; ANDRES, 1977) but is otherwise unknown in the Graptolithina (Fig. 9.2).

KOZŁOWSKI (1971) described the prosicula of the benthic *Dendrotubus* KOZŁOWSKI, 1949 (Fig. 9.4), as bottle-shaped, erect, with a helical line in the distal part, homologous to the helical line in the prosicula of planktic graptolites (Fig. 9.6). In contrast to the dome of the rhabdopleurids, the

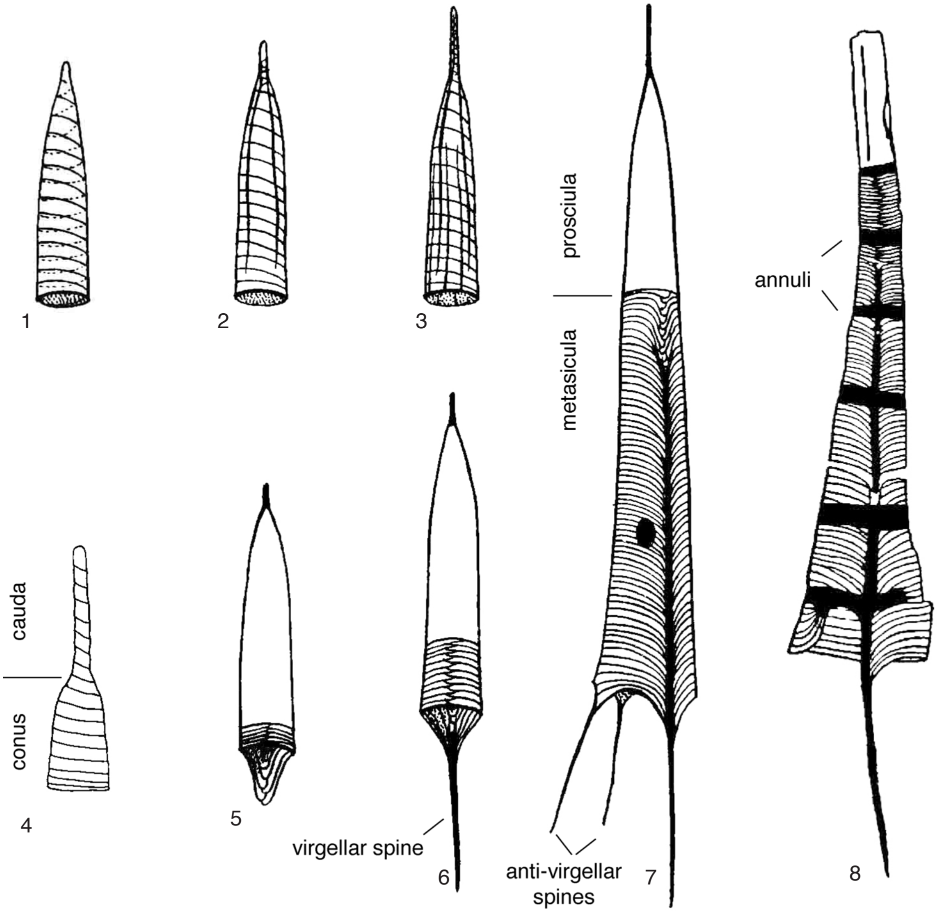

FIG. 10. Sicular development. *1,* Early prosicula with spiral line, cauda incomplete; *2,* prosicula with few longitudinal rods; *3,* mature prosicula with many longitudinal rods (*1–3* adapted from Bulman, 1955, fig. 36); *4,* conus and cauda differentiation in Anisograptidae (Hutt, 1974, fig. 1); *5,* early metasicula with few fusellar half rings and rutellum; *6,* development of virgellar spine in axonophorans; *7,* complete axonophoran sicula with paired antivirgellar spines and resorption foramen for th1[1] in metasicula (*5–7* adapted from Bulman, 1955, fig. 36); *8,* monograptid sicula with sinus stage and sicular annuli (adapted from Walker, 1953, fig. 1H).

prosicula of *Dendrotubus* is provided with a primary opening, an aperture through which the sicular zooid emerged and started to secrete the metasicular fuselli. This record represents the only evidence of a transition from the dome of the rhabdopleurids to the conical erect or nematophorous prosicula of the derived taxa. *Dendrograptus communis* KOZŁOWSKI, 1971 (Fig. 9.5) is the only benthic dendroid of which a tubelike sicula with attachment and typical helical line in the prosicula is known.

The nematophorous prosicula of the planktic Graptoloidea is known from many species, and its detailed development was described first by KRAFT (1926) for *Rectograptus gracilis* (ROEMER, 1861), even though WIMAN (1893a, 1893b, 1895) already described and illustrated many of the features from his isolated material. The prosicula is a conical structure with a distinct helical line, (Fig. 10.1–10.3) indicating its secretion as a continuous band of fusellar tissue, as is shown by unwound specimens

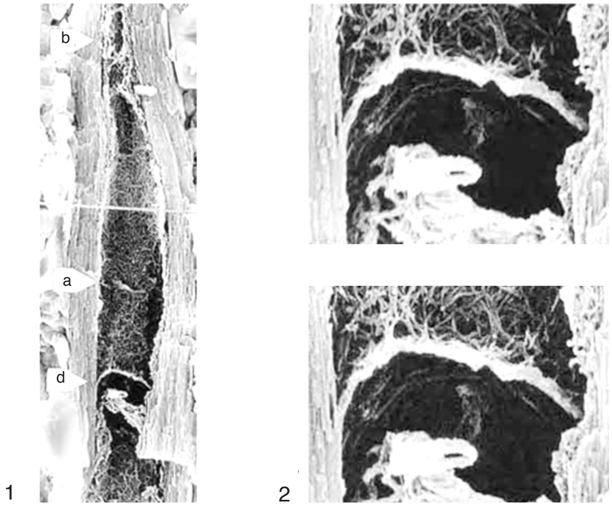

FIG. 11. SEM photograph of prosicular structure. *1*, Top of cauda, below diaphragm (*d*), proximal part of nema (*a*), wider part of nema, and beginning of narrow part of nema (*b*), ×950; *2*, stereopair (rotated vertically) showing diaphragm, ×1900 (adapted from Bates, 1996).

(KOZŁOWSKI, 1971). HUTT (1974) differentiated the prosicula into the conus and cauda (Fig. 10.4), based on the strong constriction at the tip of the conus. The cauda merges into the nema, but it still shows traces of the helical line, which is not present in the nema. The presence of the helical line can be interpreted to indicate that the conus and cauda were formed together from a juvenile zooid or larval stage. The helical line of the prosicula may be right- or left-handed, but there is no information on quantities and distribution of right- and left-handed specimens and the development in relation to right- and left-handed growth of the remainder of the colonies. A diaphragm (Fig. 11) has been recognized in the upper part of the conus of many species (KRAFT, 1926; HUTT, 1974; BATES, 1996; WILLIAMS & CLARKE, 1999).

In a second stage of development, in many species, the prosicula may add a number of longitudinal rods on the outside (Fig. 10.2–10.3). The longitudinal rods do not, in general, encroach onto the metasicula. Thus, they were formed at some later stage in the ontogenetic growth of the prosicula before the metasicular fuselli were added (KRAFT, 1926). In *Diplacanthograptus spiniferus* (RUEDEMANN, 1912) and a number of related Upper Ordovician taxa, one or two thickened strengthening rods remain of the prosicular construction, as the complete prosicula is not recognizable (or perhaps not preserved) in the fossil specimens. This is also occasionally seen in a number of Silurian (Llandovery) retiolitinids. The reason for the presence of the longitudinal rods is uncertain, but it may be noted that a number of early planktic forms lack the longitudinal rods, while they are very consistently present in later Ordovician taxa (WILLIAMS & CLARKE, 1999) and are still found in Silurian to Lower Devonian monograptids (JAEGER, 1991; URBANEK, 1997a).

THE METASICULA

The metasicula is invariably formed as a distally open tube from fusellar half rings that have a dorsal and ventral zigzag suture, but fuselli may be irregular in dendroid siculae (Fig. 9.4–9.5). It differs considerably from the prosicula in its development and is usually easily differentiated (Fig. 10). The fuselli may be more densely spaced in the proximal part and more widely spaced

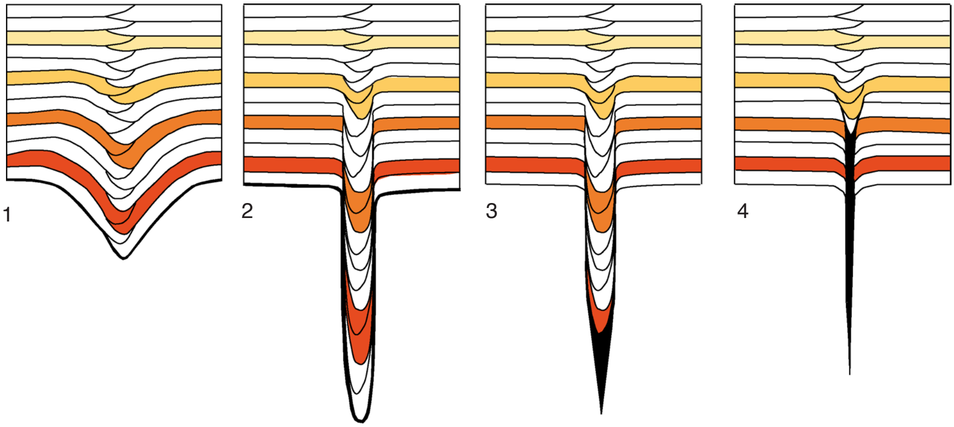

FIG. 12. The stages of development of the virgella: *1,* Rutellum; *2,* lamelliform rutellum; *3,* lanceolate virgella; *4,* virgella (adapted from Maletz, 2010, fig. 2).

close to the aperture. In early planktic forms, the differentiation is less prominent, as the helical line may be difficult to separate from the fuselli of the metasicula. KOZŁOWSKI (1954) stated that the zigzag sutures in a species of *Didymograptus* M'COY in SEDGWICK & M'COY, 1851–1855, s. str. (*Didymograptus artus* group) start only at some distance from the origin of the metasicula, and earlier fuselli are irregularly developed.

MALETZ (1992, 2010) used the origin of the first theca to define the ventral side of the sicula. The sicula is often adorned with a rutellum on this side, or with a spine, the ventral virgella (in most axonophorans). The rutellum is a rounded lip on the sicular aperture, formed by a downward extension and broadening of the fuselli at the ventral zigzag suture (Fig. 10.5). Its shape can be quite variable, and stongly elongated rutelli exist. The rutellum is usually broad and short, but it can be developed into a distinct spoonlike feature as in *Kinnegraptus* (SKOGLUND, 1961). A dorsal rutellum is present in some genera and species, especially in the monograptids (e.g., JAEGER, 1978, fig. 3; LENZ, 2013, fig. 9).

Beginning at the junction of the prosicula and metasicula in graptoloids, distinct, internal, thickened, parallel rings, known as sicular annuli (KOZŁOWSKI, 1949; Fig. 10.8), are present in many graptoloids. In many younger graptoloids, and commonly in the monograptids (such as those from the middle and upper Silurian; LENZ & KOZŁOWSKA-DAWIDZIUK, 1998), one or more annuli are formed on the inside walls of the metasicula (WALKER, 1953). Unlike the fusellar bands, the annuli are distinct, electron-dense, ringlike structures, lying parallel to each other but often at an oblique angle to the fusellar half rings on the dorsal and ventral sides of the sicula. The number and position of sicular annuli may be fixed in many upper Silurian taxa (URBANEK, 1997a). The function of annuli remains unknown, as does why they generally occur more frequently higher up the stratigraphic column. (URBANEK & others, 2012).

THE VIRGELLA

The metasicula may be provided with a virgella or virgellar spine (Fig. 10.6–10.8, 12), developing from a prominent rutellum on either the dorsal or ventral side (MALETZ, 2010). Its development can be differentiated into four stages (Fig. 12), often recognizable even in derived virgellate graptoloids. It starts with a rounded process, the rutellum, formed from the distal extension and widening of alternating fuselli on the ventral or dorsal side of the sicula. In a second stage, the rutellum is laterally restricted, and a thickened rim forms around it. At this stage, it is called a lamelliform rutellum (Fig. 12.2). In a third stage, a spine is added at the tip of the lamelliform rutellum, forming the lanceolate virgella (Fig. 12.3). A reduction of the lamelliform rutellum stage in the ontogeny of the virgella forms the true virgella (Fig. 12.4) in the last stage.

The virgella is now known to have originated independently in a number of early to Middle Ordovician graptoloids (MALETZ, 2010), as was suggested by BULMAN (1963). A dorsal and a ventral virgella are differentiated, based on the position on the sicula (MALETZ, 2010). The ventral virgella is found on the side of the origin of the first post-sicular theca. A dorsal virgella is on the opposite side of the origin of the first theca.

The sicular aperture can bear a number of further apertural modifications, other than the rutellum or the virgella (e.g., MITCHELL, 1987). A dorsal notch is present in many axonophorans, often associated with paired antivirgellar spines (e.g., in the Lasiograptidae). The Dicranograptidae possess lateral lobes and paired notches on the sides of the virgellar spine. The Monograptidae bear various apertural modifications and, while there are moderate variations within each pattern, many are species specific; for example, the tonguelike, ventrally curved, dorsal rutellum is a very common development among many single-stipe monograptids of the Lower Devonian (e.g., JAEGER, 1979; LENZ, 2013).

THE NEMA

The nema is a thin rod of material growing from the prosicula (cauda) in planktic graptolites, and the presence of a nema is, accordingly, regarded as evidence of a planktic life style (KOZŁOWSKI, 1971; RICKARDS, 1996). The nema of the Monograptidae has long been named the virgula, but it is now recognized to represent a modified type of nema, forming a leading rod on the dorsal side of the stipes of all monograptids (except those with a pseudovirgula), to which the thecae adhere (BULMAN, 1970; URBANEK & TOWE, 1975). Many biserial graptolites include the nema in the center of the colony, and this is often attached to an interthecal septum. However, the nema may also be off-center or even embedded in the obverse wall of the tubarium (see discussion of the median septum below). The distal end of the nema always grew in advance of the thecae in the development of the axonophoran colony.

The Monograptidae incorporate the nema as a dorsal rod of their stipes, where it also extends beyond the growing end of the branches. The importance of the nema in monograptids can be inferred from the fact that colonies with cladial branching produce a secondary nema, or pseudovirgula, as (1) the leading rod for the cladial stipe from one of the lateral apertural spines in *Cyrtograptus* (THORSTEINSSON, 1955) and (2) as a separate new structure in the genus *Linograptus* (URBANEK, 1963) and possibly in others. A small number of strongly coiled Silurian monograptids over time abandoned the original nema, which was free at the isolated tip of the prosicula, and fabricated a pseudovirgula (Fig. 13) along which the stipe grew. This development was first recognized in *Cochlograptus veles* (RICHTER, 1871) by LOYDELL and CAVE (1994) and MALETZ (2001) and was later also found in the late Wenlock *Testograptus testis* (BARRANDE, 1850) by LENZ and MELCHIN (2008).

In retiolitid taxa without a fully preserved prosicula, the nema is connected to the virgella by the virga (BATES, KOZŁOWSKA, & LENZ, 2005), a list secreted on the surface of the prosicula. It has a flat or grooved inner surface and a convex outer one; in the absence of a preserved prosicula, the length of the virgal groove serves as a proxy for the site and length of the prosicula. Towards (or at) the apex of the prosicula, the virga changes into a full concentric construction, marking the beginning of the nema.

THE INITIAL FORAMEN

The genus *Rhabdopleura* has a resorption foramen, an opening for the emergence of the

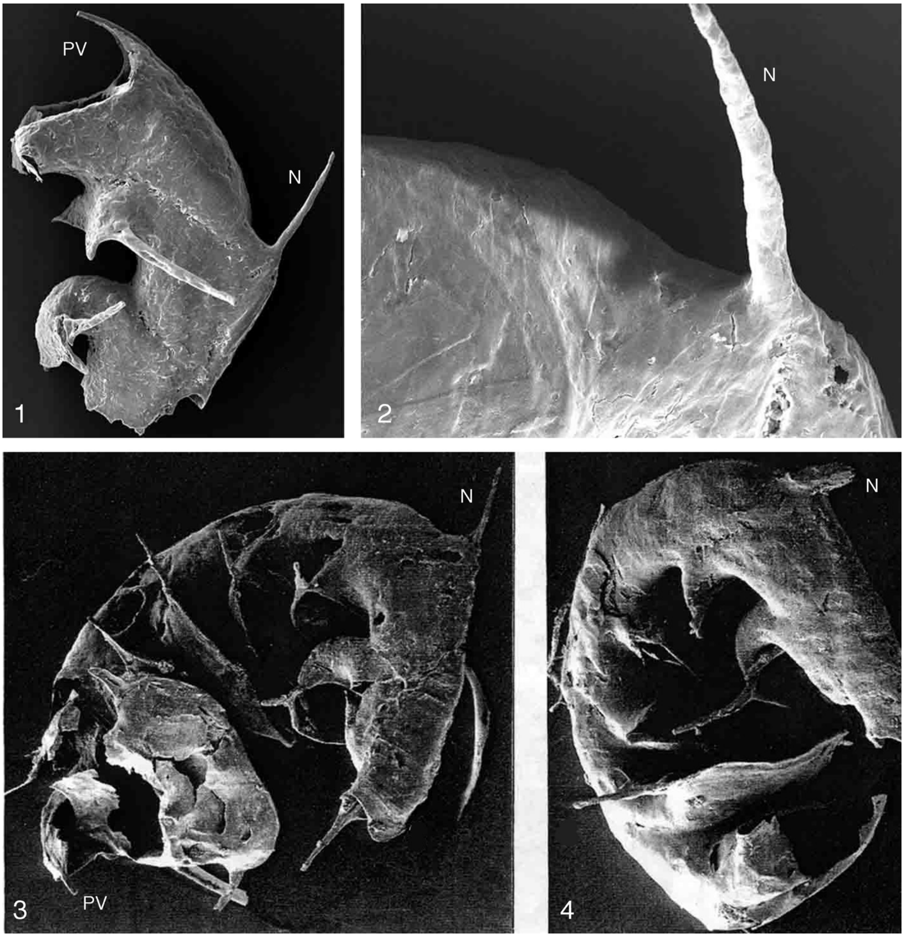

Fig. 13. SEM photographs of pseudovirgula. *1–2, Testograptus testis* (Barrande, 1850), Silurian (upper Wenlock), Canadian Arctic; *1,* tubarium fragment, ×35; *2,* enlargement of pseudovirgula, ×180 (Lenz & Melchin, 2008, fig. 4A1–4A2); *3–4, Cochlograptus veles* (Richter, 1871), Silurian (upper Llandovery), Dalarna, Sweden, complete specimen with well-developed pseudovirgula, ×40 (Maletz, 2001, fig. 3). *N*, nema, *PV*, pseudovirgula.

sicular zooid from the dome, and a second resorption foramen for the origin of the first post-sicular zooid (Stebbing, 1970a). All subsequent zooids resorb a foramen into their compartment of the tube of the growing branch. A constant terminal zooid shows a monopodial growth of the colony (Urbanek & Dilly, 2000). The derived taxa of the Graptolithina show a sympodial growth in which each new zooid represents the temporary terminal zooid (Urbanek, 1986).

The origin of the first post-sicular zooid is through a foramen in the sicula. The position and type of this foramen have considerable implications for the higher-level taxonomy of the graptoloids. Initially, it was a resorption foramen, known from a few benthic specimens and most early planktic taxa. It is positioned in the middle to upper (distal) part of the erect tubular prosicula in *Dendrograptus communis* (Kozłowski, 1971). Legrand (1964) and Hutt (1974) described the resorption foramen in the middle part of the conus in the upper Tremadocian *Adelograptus,* but it is unknown whether this position is typical of all Anisograptidae. A similar position can be

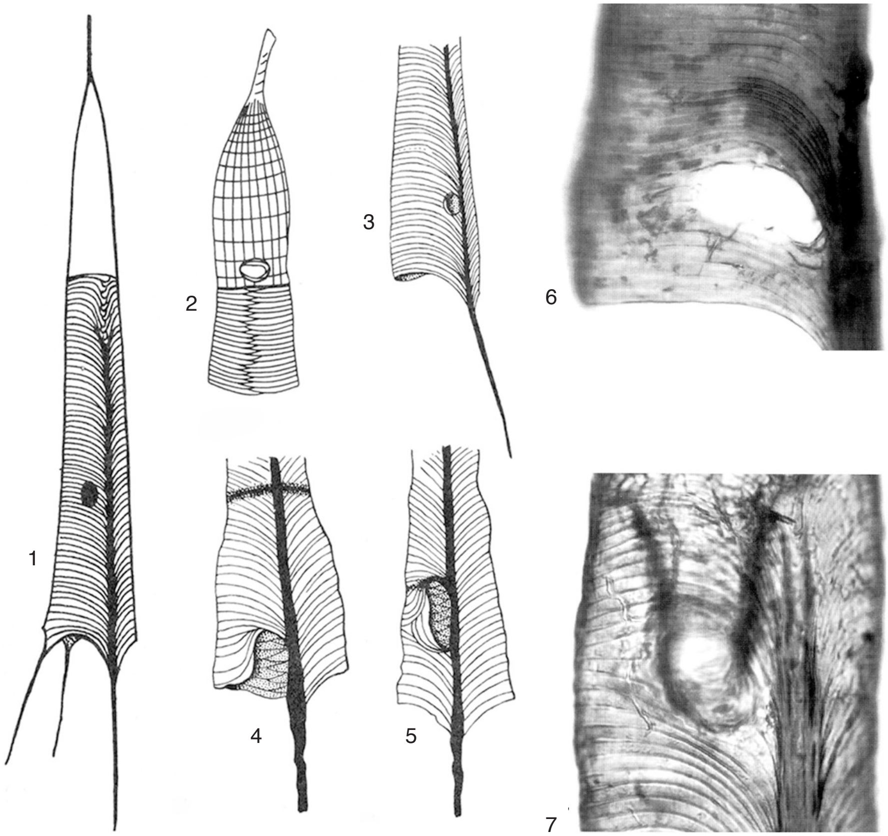

FIG. 14. Foramen development. *1, 3,* Resorption foramen in metasicula, typical of biserial graptolites; *2,* resorption foramen in lower part of prosicula as found in early dichograptids; *4–5,* sinus (*4*) and lacuna (*5*) stages, forming the primary opening for the first theca and developed only in monograptines; *6–7,* lenticular foramen in *Monograptus* sp. cf. *M. arciformis* CHEN & LIN, 1978, Silurian (lower Llandovery), ×270 (Dawson & Melchin, 2007, pl. 1).

seen in the basal Tremadocian *Rhabdinopora* (LEGRAND, 1974). The foramen is found in the middle part of the conical prosicula in species of the upper Floian *Didymograptellus* COOPER & FORTEY, 1982, but it is in the lowermost (distal) part of the prosicula in the closely related *Yutagraptus* RIVA, 1994, and *Xiphograptus* COOPER & FORTEY, 1982 (MALETZ, 2010). In most dichograptids, the origin of the first theca is in the lowermost part of the prosicula (WILLIAMS & STEVENS, 1988; WILLIAMS & CLARKE, 1999). The resorption foramen is found in the metasicula in the axonophorans (MITCHELL, 1987), mostly lying on the right side of the virgellar axis (Fig. 14.1), although sometimes the foramen is developed precisely along the virgellar axis, before the origin of the virgellar spine (LOXTON & others, 2011).

A change is seen in the Monograptidae (Fig. 14.4–14.7). The foramen in the monograptids has been considered in the past to be a primary foramen, left as an initial opening during the growth of the sicula through the sinus and lacuna stages (EISENACK, 1942). Isolated material shows that early monograptids—*Atavograptus* RICKARDS, 1974; *Pribylograptus* OBUT & SOBOLEVSKAYA, 1966; *Coronograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968; and *Lagarograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968—possess a resorption foramen (LUKASIK & MELCHIN, 1994, 1997). A

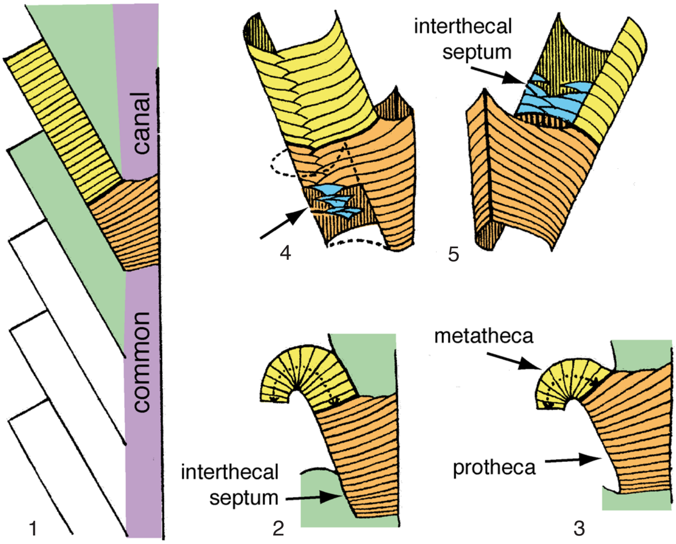

FIG. 15. Generalized shape and terminology of thecae. *1*, Lateral view of simple dichograptid (or pristiograptid) stipe with serially arranged thecae; *2–3*, lateral views of hooked thecae; *4*, oblique dorsal view showing development of interthecal septum; *5*, oblique ventral view showing development of interthecal septum (adapted from Bulman, 1955, fig. 30). *Purple,* common canal; *orange,* prothecae; *yellow,* metathecae; *blue,* interthecal septum.

modified resorption foramen with additional fusellar deflection is developed in a number of *Monograptus* s.l. species (MELCHIN & KOREN', 2001). DAWSON and MELCHIN (2007) recognized the lenticular foramen (Fig. 14.6–14.7) as the first primary type of foramen, in which an opening for the emergence of the first post-sicular zooid is left in the metasicula. The originally described primary foramen of the younger monograptids with its typical sinus and lacuna stages (Fig. 14.4–14.5) is widely distributed in the greater portion of the Silurian and Devonian monograptids.

THECAL ONTOGENIES

The thecae of the Graptolithina are simple tubes, formed by repetitive clonal constructions, either with identical constructional mode or following a gradual change along the stipes (URBANEK, 1973). Fairly abrupt changes in the morphology of the thecae along a stipe are seen in some species. The tubes in the Cephalodiscida, however, are formed as independent, not interconnected assemblages and are simple, round tubes when possessing an isolated aperture, sometimes provided with a distinct, perhaps ventral, rutellum, as seen in *Cephalodiscus* (*Idiothecia*) *nigrescens* HARMER, 1905. Even though modern pterobranchs, such as the extant *Rhabdopleura*, may possess separate male and female zooids, this differentiation is not expressed in the secretion of the housing tubes and interpretation is impossible from the fossil record.

The thecae, the housing structures for individual zooids, are the main building blocks of the graptolite colonies and define their construction and shapes. The individual thecae are interconnected through an opening in the Graptolithina, through which the next bud emerged to form its own thecal tube. The combined initial parts of the thecal tubes of a stipe are often called the common canal (Fig. 1, Fig. 15.1), to emphasize the interconnection of the clonal, colonial development of the colonies; its existence, in fact, provides the evidence for a truly colonial organism. The common canal can be quite variable in size, depending on the geometry of the tubes and the shape of the prothecal parts of the thecae.

The thecae generally show a distinct thecal overlap, the wall common to two overlapping thecae called an interthecal septum or internal septum (Fig. 15.5). The interthecal septum was secreted either by the first-formed thecal zooid or, in case of concurrent growth, as a combined effort of both thecal individuals (WALKER, 1953; URBANEK, 1958).

The degree of thecal overlap is quite variable and can reach high values (FORTEY, 1983). It is generally measured as a percentage of thecal length. Among the monograptids, a number of genera (e.g., *Campograptus* OBUT, 1949; *Rastrites* BARRANDE, 1850; and *Streptograptus* YIN, 1937) show little or no thecal overlap. Distally increasing thecal overlap is typical in many groups (e.g., *Didymograptellus* COOPER & FORTEY, 1982; *Expansograptus* BOUČEK & PŘIBYL, 1951; *Nicholsonograptus* BOUČEK & PŘIBYL, 1951; and certain monograptids including *Monograptus* s. str.) and often leads to extremely wide and robust distal stipes. Differences in the amount of thecal overlap can be used for taxonomic purposes, as in *Didymograptellus bifidus* (HALL,1865) by WILLIAMS and STEVENS (1988). (See discussion below of thecal gradients.)

The free ventral wall is the portion of the ventral theca margin that extends beyond the aperture of the preceding theca. The length of the free ventral thecal wall depends on the growth patterns of the thecae and is used for taxonomic differentiation in certain groups. It tends to be greater in thecae with low inclination.

The differentiation of the protheca and metatheca (Fig. 15) can be problematic, as a distinct break in the fusellar growth is not present in most thecae. The protheca may be recognized as the part of a theca before the insertion of an interthecal septum, but this varies from species to species. In taxa without an interthecal septum, the point at which the theca becomes a complete tube (for example, when the foramen of the daughter theca is closed) can be defined as the start of the metatheca (Fig. 15.3). This definition follows the distinction advocated in BULMAN (1955, 1970). MÜNCH (1938) discussed the common canal in monograptid thecae in some detail and suggested the terms semitubus, metatubus (protheca), and thecatubus (metatheca) to differentiate parts of the thecae, although these differ little from protheca and metatheca.

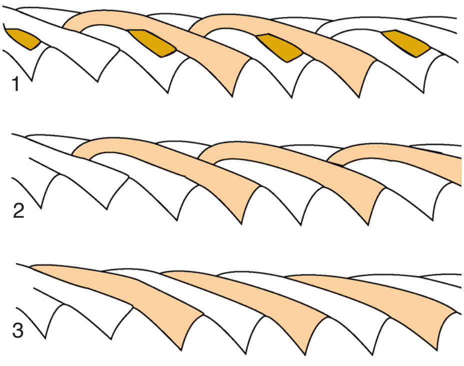

FIG. 16. Triad budding and plaited thecal overlap. *1,* Bithecate stipe in lateral view with lateral originating, alternating autothecae (*lighter color*) and bithecae (*darker color*), same construction would be seen on the other side of the stipe; *2,* non-bithecate stipe with plaited thecal overlap and lateral thecal origination; *3,* non-bithecate stipe with dorsal origins of autothecae (adapted from Lindholm, 1991, fig. 4).

AUTOTHECAE AND BITHECAE

Two main thecal types can be differentiated: the autothecae and the bithecae (COOPER & FORTEY, 1983). Many benthic graptoloids, and even a few early planktic forms, show this distinct differentiation of their thecal tubes, with larger tubes identified as autothecae and smaller ones as bithecae. The reason for this differentiation is unknown, although a sexual differentiation has been suggested (e.g., HUTT in PALMER & RICKARDS, 1991). Alternatively, KIRK (1973) suggested that the smaller bithecae may have housed cleaning individuals.

Autothecae and bithecae (Fig. 16) are arranged in a consistent and highly geometrical pattern in most bithecate colonies. Each autotheca is connected to a bitheca, except at branching points, where the bitheca is replaced by a second autotheca. Normally, the bithecae are found alternately on both sides of the stipes, but irregularities are common in some taxa. Several successive bithecae on one side of a stipe are found in *Kiaerograptus kiaeri* (MONSEN, 1925), for example (SPJELDNAES, 1963; LINDHOLM, 1991). Complex growth patterns of bithecae can be seen in many dendroid graptolites (e.g., BULMAN, 1955; RICKARDS & others, 2003).

A number of other thecal types have been described in the various benthic taxa. Conothecae, microthecae, and umbellate thecae occur in the Cyclograptidae BULMAN, 1938, while autothecae are modified into highly inflated camerae and erect columns in the Cysticamaridae BULMAN, 1955. The details are discussed in the various taxonomic chapters.

THECAL MORPHOLOGY AND MODIFICATIONS

The thecae of the Graptolithina are highly variable (Fig. 17), and the simple tubes of early benthic taxa are considerably modified in later forms. Structural modifications are here differentiated by their position on the thecae and their development. In the past, thecal types have been differentiated and named after their characteristic genera. Thus, dichograptid (Fig. 17.9), climacograptid (Fig. 17.11,15), diplograptid (Fig. 17.10), glyptograptid (Fig. 17.13), nemagraptid, leptograptid (Fig. 17.17), and other thecal types are commonly used in the descriptive terminology of graptoloid thecae (BULMAN, 1970). Initially, differences in the thecal shapes originate from the variation of widening of the thecae, which may be gradual and persistent (e.g., simple dichograptid), or in increments, producing bulges or cupulae (e.g., in *Pseudostreptograptus* LOYDELL, 1991, and *Streptograptus* YIN, 1937) on the dorsal sides of thecae (Fig. 17.4,8). In others, the thecae widen considerably from an initial width, and then continue parallel-sided (e.g., in climacograptids) or even decrease in width distally (e.g., *Dicranograptus* HALL, 1865, and some climacograptids).

Thecae with a sigmoidal ventral outline are often called glyptograptid thecae (Fig. 17.13). This sigmoidal shape of the ventral thecal side can be developed separately and independently in many different groups and, in an enhanced form, developed into a geniculum. The geniculum (Fig. 17.11,15) is a distinct angular feature on the ventral side of the theca and quite common in the biserial groups, as well as in some monograptids. It is often enhanced by hoodlike genicular flanges (Fig. 17.7,

FIG. 17. Thecal morphologies. *1, Proteograptus opimus* (LENZ & MELCHIN, 1991), Silurian (Wenlock, upper Sheinwoodian), Canadian Arctic, ×8.3 (Lenz & others, 2012, pl. 13); *2, Demirastrites triangulatus* (HARKNESS, 1851) Silurian (Llandovery), central Wales, ×6 (Palmer & Rickards, 1991, pl. 74); *3, Crinitograptus operculatus* (MÜNCH, 1938), Silurian (lower Ludlow), Canadian Arctic, ×72 (Lenz & Kozłowska-Dawidziuk, 2004, pl. 30); *4, Pseudostreptograptus williamsi* LOYDELL, 1991, Silurian (Llandovery, lower Telychian), Sweden, ×14 (Palmer & Rickards, 1991, pl. 76); *5, Monograptus priodon* (BRONN, 1849), Silurian (middle Wenlock), Canadian Arctic, ×7 (Lenz & others, 2012, pl. 8); *6, Okavites spiralis* (GEINITZ, 1842), Silurian (Llandovery, upper Telychian), Canadian Arctic, ×34 (new); *7, Papiliograptus papilio* LENZ & KOZŁOWSKA, 2002, Silurian (Wenlock, upper Homerian), Canadian Arctic, showing thecal geniculae with large, supragenicular hoods, ×8 (Lenz & Kozłowska-Dawidziuk, 2002, fig. 11); *8, Streptogaptus galeus* LENZ & KOZŁOWSKA, 2006, Silurian (Wenlock, lower Homerian), Canadian Arctic, ×90 (Lenz & Kozłowska, 2006, fig. 12); *9, Expansograptus abditus* WILLIAMS & STEVENS, 1988, Lower Ordovician (Floian), Newfoundland, Canada, with simple, tubelike thecae, cleared to show fusellar half rings, ×18 (Williams & Stevens, 1988, pl. 14); *10, Neodiplograptus sinuatus sinuatus* (NICHOLSON, 1869), Silurian (middle Llandovery), Canadian Arctic, with biform thecae, ×24 (Melchin, 1998, pl. 3); *11, Pseudoglyptograptus barriei* ZALASIEWICZ & TUNNICLIFF, 1994, Silurian (middle Llandovery), Canadian Arctic, with strong geniculae, ×6.5 (Melchin, 1998, pl. 1); *12, Chigraptus supinus* JACKSON & LENZ, 2003, Lower Ordovician (Tremadocian), Canada (northern Yukon), ×10 (Jackson & Lenz, 2003, fig. 6a); *13, Metaclimacograptus* sp., Silurian (middle Llandovery), Sweden, ×12 (Loydell & Maletz, 2009, pl. 3); *14, Lobograptus scanicus* (TULLBERG, 1883), Silurian (lower Ludlow), Canadian Arctic, with large, lobelike thecal lappets, ×28 (Lenz & Kozłowska-Dawidziuk, 2004, pl. 32); *15, Glyptograptus elegans* (s.l.) PACKHAM, 1962, Silurian (Llandovery), Canadian Arctic, ×21 (Melchin, 1998, pl. 5); *16, Paradelograptus kinnegraptoides* ERDTMANN, MALETZ, & GUTIÉRREZ-MARCO, 1987, Lower Ordovician (Floian), Canada (Yukon), ×10 (Jackson & Lenz, 2006, fig. 7n); 17, *Dicellograptus vagus* HADDING, 1913, Middle Ordovican (upper Darriwilian), Scania, Sweden, ×10 (new).

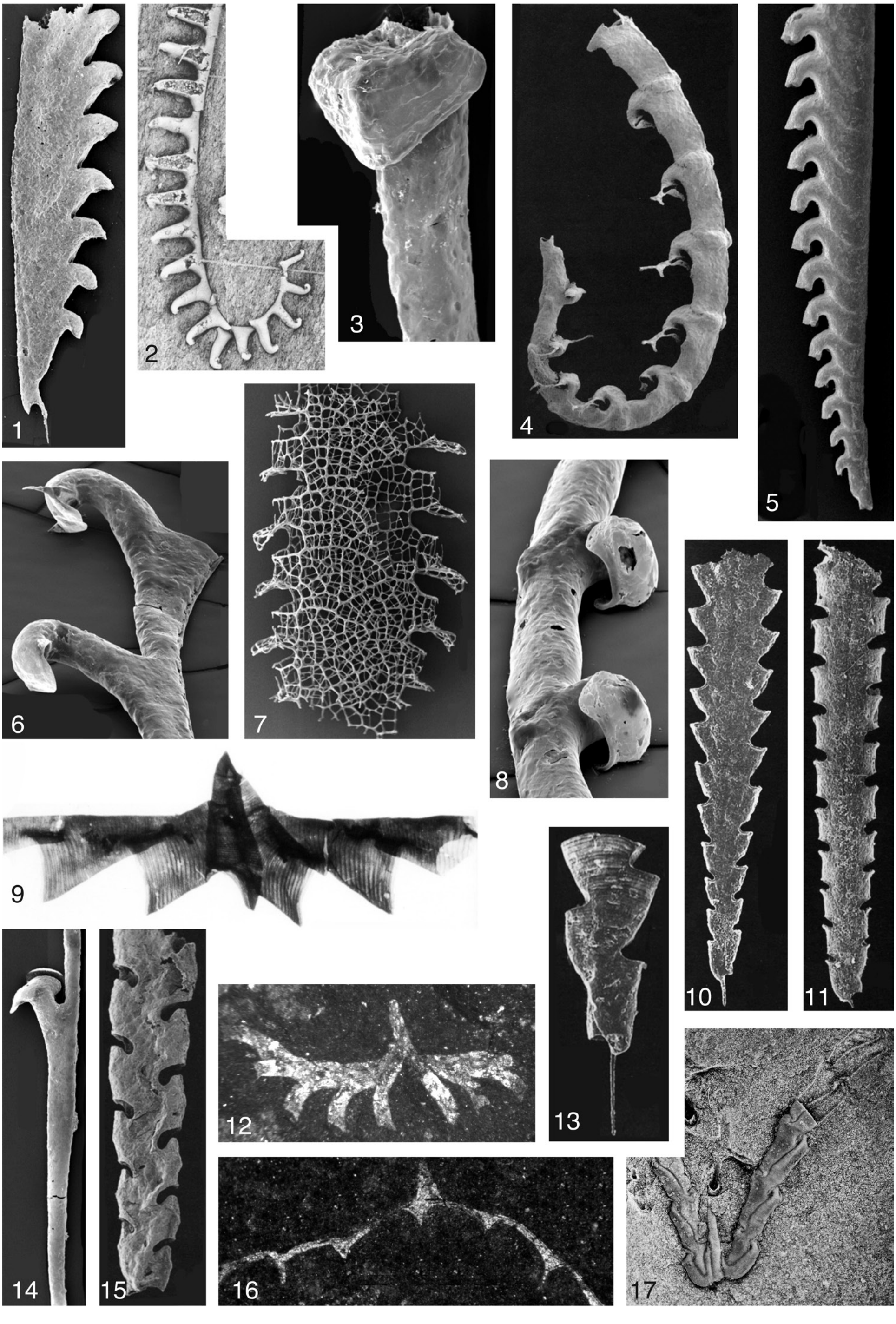

FIG 17. *For explanation, see facing page.*

Fig. 18.2), but spines, lobed additions, and other enhancements may be present. The geniculum can also be rounded, but it invariably involves an abrupt change in inclination of the ventral thecal wall. Geniculate thecae are common in graptolites of all groups, from the dichograptids (*Aulograptus* SKEVINGTON, 1965) to axonophorans (*Climacograptus* HALL, 1865; *Archiclimacograptus* MITCHELL, 1987; *Dicellograptus* HOPKINSON, 1871; Fig. 17.17), to monograptids (*Monoclimacis* FRECH, 1897), and retiolitinids (Fig. 17.7). The geniculum in all these graptolites is structurally homologous, but evolutionarily analogous, as is evidenced by its independent origination in many groups.

Thecae with a distinct recurved thecal aperture are often called hooked thecae. The thecal hook is formed from an isolated metatheca with continuous fuselli. A typical example is *Monograptus priodon* BRONN, 1849 (Fig. 17.5), in which the distal metathecae form an open hook. A lateral or transverse widening of the thecal apertures can be associated with this thecal development, but restricted apertures may also be present. Hooked thecae may or may not show thecal overlap or even astogenetic variation in this character, for example, *Stimulograptus* PŘIBYL & ŠTORCH, 1983 and *Monograptus.* A special case of the hooked thecal aperture is identified as lobate (BULMAN, 1970), in which the metatheca grows back on itself, for example, *Campograptus lobiferus* (M'COY, 1850) and *Lapworthograptus* BOUČEK & PŘIBYL, 1952. Hooked thecae are most common in the Monograptidae, and more numerous and varying elaborations are found in these forms than in any other group.

A thecal development that may appear very similar to the hooked thecae has been identified as hooded thecae (BULMAN, 1970). In this form, a thecal hood covers the thecal aperture (Fig. 17.3). The thecal hood is formed either as an extension of the dorsal wall of the theca or as a secondary, sometimes genicular addition to the thecal aperture. It is not comparable in development to the hooked theca, in which the development is completely formed by the dorsal and ventral thecal walls. Hooded and hooked thecae are very difficult to differentiate in flattened material. Isolated specimens showing fusellar structure may be needed to recognize the precise development.

The thecae of the monograptids show the greatest variety—simple tubes, smoothly hooked (Fig. 17.5), tall, scarcely overlapping, elongated, distally hooked (Fig. 17.2,4), bi- or multiform, or complex proximally to simpler distally (Fig. 17.1). They may have large thecal hoods that obscure the thecal aperture (Fig. 17.3), strongly hooked theca (sometimes with torsion), and/or various kinds of spines (Fig. 17.6), or have lobate and asymmetrical lappets (Fig. 17.14). On the other hand, thecae with fairly complex or unusual features were already present in a few Tremadocian and Floian taxa, such as *Paradelograptus* ERDTMANN, MALETZ, & GUTIÉRREZ-MARCO, 1987 (Fig. 17.16); *Psigraptus* JACKSON, 1967; and *Chigraptus* JACKSON & LENZ, 1999 (Fig. 17.12).

Thecal isolation is common in many graptolites. In the benthic Cyclograptidae and Acanthograptidae, the typical thecal tubes possess isolated apertures, but thecal overlap is present on the stipes. An isolation of thecal apertures can be seen in many planktic graptoloids. The metathecae can be completely or only partially isolated. In taxa with complete metathecal isolation, there is no thecal overlap and, accordingly, no interthecal septum is present (Fig. 17.2).

Partial isolation can be found in benthic taxa and also in many planktic forms. Partial isolation of the metatheca has been described in the Tremadocian genera *Chigraptus* (Fig. 17.12) and *Kiaerograptus* and is common in Silurian monograptids with thecal hooks (e.g., *Monograptus*, *Streptograptus*). Completely isolated metathecae are present in *Rastrites* BARRANDE, 1850; *Demirastrites* EISEL, 1912; *Lituigraptus* NI, 1978; and a number of other monograptid genera, in which a gradual change in thecal shape often is also present. The term triangulate has been used frequently for the thecal shapes in this group (Fig. 17.2; SUDBURY, 1958).

The orientation of the thecal aperture ranges from introverted through perpendicular to everted, unless hooks modify the apertural orientation. This orientation can also be affected by apertural modifications, which are common in graptolites and often used for identification of both species and genera. Apertural modifications are highly variable and often difficult to interpret in flattened material. Even the number and orientation of spines and flanges often cannot be identified correctly without isolated, three-dimensionally preserved specimens. Apertural modifications are defined independently of the orientation of the aperture and may include a wide variety of spines (Fig. 17.4,6), lobes, shelves, and selvages. These can be defined by their position on the theca as dorsal, ventral, or lateral.

Prothecal folds and intrathecal folds, termed recumbent folds by COOPER and NI (1986), are features related to the origin of the thecae in some Sinograptina and in the axonophorans and have not been recognized in benthic graptolites. Thecal folding is indicated through a change in growth direction of a thecal tube. The theca is generally growing back on itself, forming a conspicuous bending of the tube. The growth direction is taken to differentiate prothecal and intrathecal folds (Fig. 18). The development of a prothecal fold is formed around the base of an interthecal septum (Fig. 18.1), while in intrathecal folds, a secondary bar or septum is formed from the dorsal side of the stipe (Fig. 18.2). The details of the development of prothecal and intrathecal folds are not known from isolated material.

Prothecal folds have been used to define the Sinograptidae (MU, 1957) but are now known to be present in a number of independent groups of planktic graptoloids. The earliest example includes the dichograptid *Cymatograptus undulatus* (TÖRNQUIST, 1901) from the lower Floian of Scandinavia (JAANUSSON, 1965), but bithecate taxa with apparent prothecal folding have been described also. Prothecal folds in the upper Tremadocian *Cymatograptus lauzonensis* ERDTMANN, 1966, now *Kiaerograptus lauzonensis* (see MALETZ & EGENHOFF, 2001), are enhanced by the presence of bithecae with lateral thecal origins, the plaited thecal overlap of LINDHOLM (1991).

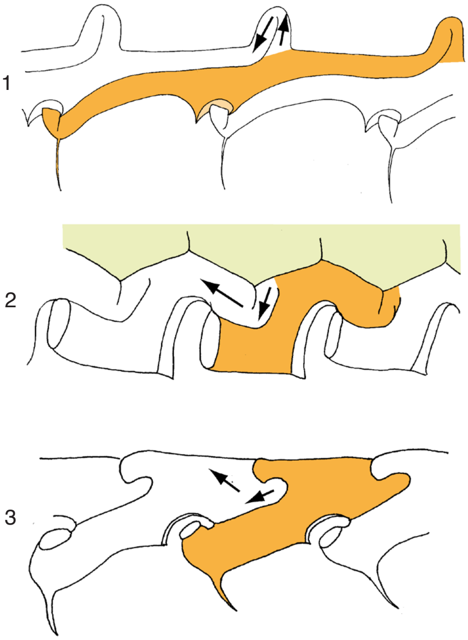

FIG. 18. Diagrams of prothecal and intrathecal folds. *1, Holmograptus* sp., pronounced prothecal fold; *2, Haddingograptus* sp., intrathecal folds with bar originating from median septum, *3, Dicellograptus* sp., intrathecal fold in relief specimen without fusellar structure; all reconstructions adapted from relief material (new). Second thecal series indicated by *darker color.*

SERIALITY OF THECAE

The zooids of *Rhabdopleura* bud from each other in a sequential manner, forming a serial succession. However, the secreted tubes of the individual zooids branch irregularly from this succession to both sides of the main axis (Fig. 1.2). The erect tubes in *Rhabdopleura normani,* for example, may originate on the left and right side of the central axis (Fig. 1.2), showing no apparent regular organization (LANKESTER, 1884). Due to the clonal development of the colonies and the constructional mode of new tubes, a distinct regularity was easily evolved and is found in most derived graptolites. Irregularities are most pronounced in benthic encrusting colonies, probably recalling the original unordered development of the *Rhabdopleura* colonies. The Cyclograptidae retain some of the disorganization of their thecal tubes but develop a distinct internal regularity, fostered by their underlying budding system. The thecal tubes in these forms are round, with isolated apertures. A differentiation into a dorsal and ventral side is visible only through the presence of the zigzag sutures of the regularly organized fusellar half rings of the tubes.

Most dendroids and graptoloids developed a highly precise seriality of their thecal arrangements in which all thecal apertures on the stipe are precisely oriented in the same direction (Fig. 1.1, Fig. 15.1, Fig. 16). This arrangement has been retained by all planktic taxa, including the Silurian to Lower Devonian monograptids (Fig. 17). The ventral rutellum and the development of thecae without complete apertural isolation are found already in such dendroid graptolites as *Dendrograptus* and *Dictyonema* (Wiman, 1896; Bulman, 1933). This differentiation of the dorsal and ventral sides of the thecal tubes is developed in all derived pterobranchs with serially arranged thecae.

THECAL GRADIENTS

Thecal gradients or astogenetic variation of thecae is an aspect of many planktic graptolites and has been studied in some detail (e.g., Bulman, 1963; Urbanek, 1973). Minor gradual change in size of thecae is most commonly observed in graptolites, especially in the dichograptids, often associated with a distally increasing thecal overlap (see Cooper & Fortey, 1982; Williams & Stevens, 1988). Biform or multiform colonies are common in many axonophorans (biserials and monograptids), showing different thecal styles at the proximal and distal ends (Fig. 19). Changes can be fairly gradual and include minor structural modifications of the apertures, but taxa with dramatic changes along the stipes are not uncommon, such as in *Paramonoclimacis sidjachenkoi* (Obut & Sobolevskaya, 1965) and *Monograptus limatulus* Törnquist, 1892, in which stipe fragments could easily be referred to different genera. The modifications may be precisely located, and a distinct change may be found at a certain theca along the length of the colony (Fig. 19), but they can also be more variable.

THE WIMAN RULE AND TRIAD BUDDING MODEL

The Wiman rule originally described the interconnection of three thecal types and the branching of the thecal tubes, which is the external expression of the internal stolon system (Kozłowski, 1949). Initially, triad budding was understood as a branching in triads from a stolotheca, in which the stolotheca does not possess an apertural opening, but is accompanied by a new autotheca and a bitheca. Kirk and Bates (in Kirk 1969), and Bulman (1970, p. 26) recognized the stolotheca as the "immature basal portion of the succeding autotheca." Thus, a separate stolothecal zooid does not exist, and the stolotheca and succeeding autotheca are now regarded as a single unit, the autotheca (Cooper & Fortey, 1983).

In a typical triad, each autotheca produces a new autotheca and a new bitheca (Fig. 20.1), effectively eliminating the need of the term stolotheca. The Wiman rule, in its revised meaning, essentially states that at each branching point a new autotheca is formed on one side of the stipe, while on the other side, a bitheca is developed at the same point. The development produces bithecae and autothecae, alternately, on the left and right side of the stipes (Fig. 16.1, Fig. 20). All thecal origins are lateral in these taxa, forming a structure that was termed plaited thecal overlap (Fig. 16.1) by Lindholm (1991), including taxa in which bithecae are absent (Fig. 16.2).

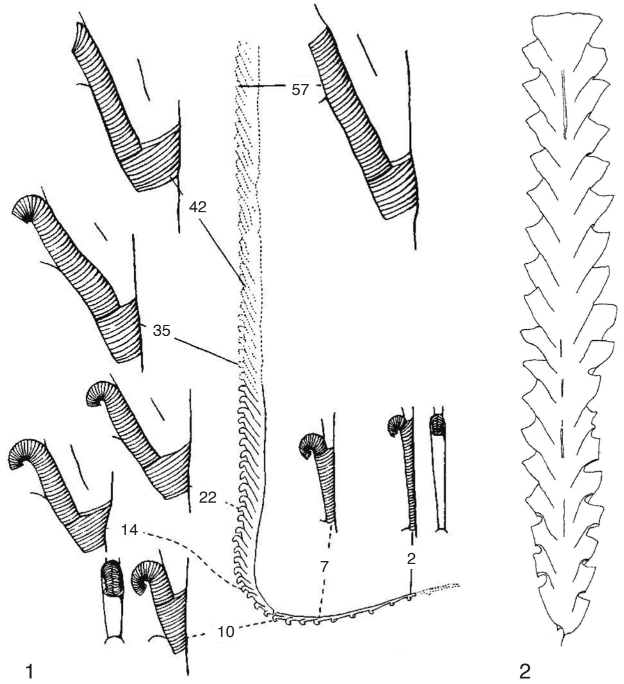

FIG. 19. Thecal gradients. *1, Pernerograptus argenteus* (NICHOLSON, 1869), thecal modifications along the stipes of a specimen; *numbers* indicate position of thecae along stipe (Bulman, 1955, fig. 29); *2, Neodiplograptus apographon* (ŠTORCH, 1983), thecal gradient (Loydell, 2007, fig. 10D).

The number of bithecae of the planktic graptoloids became fewer over time, apparently in all lineages. By the end of the Tremadocian, they are scarce and are completely absent during the Floian. The details of these changes are still unclear, but a number of separately evolving lineages may have lost their bithecae and the plaited thecal overlap independently (FORTEY & COOPER, 1986; LINDHOLM, 1991). In derived graptoloids, the thecal origins are on the dorsal side of the stipes, even though lateral thecal origins from a dicalycal theca can still be found at branching points.

THE DICALYCAL THECA

The structural details of the branching in graptolite colonies is known from specimens preserved in full relief and from isolated specimens. Dichotomous branching is invariably related to the presence of a dicalycal theca (Fig. 20), a theca that produces two autothecae instead of an autotheca and a bitheca (MALETZ, 1992). In forms with triad budding, branching is achieved through the replacement of a bitheca with an autotheca at one of the triads. A bitheca, therefore, is missing at the branching point (Fig. 20.1–20.2). The previous autotheca curves distinctly in the direction of one of the new stipes, and the first new autotheca of this stipe grows along its back. The second theca produced by the dicalycal theca bends directly away to form the second stipe (Fig. 20.2).

Successive dicalycal thecae are present in early planktic graptolites (e.g., *Staurograptus* EMMONS, 1855; *Rhabdinopora* EICHWALD, 1855), but apparently a dicalycal theca can produce only one further dicalycal theca and one normal autotheca (MALETZ, 1992). In younger graptoloids, dicalycal thecae are separated by at least one normal monocalycal theca and, thus, are not successive.

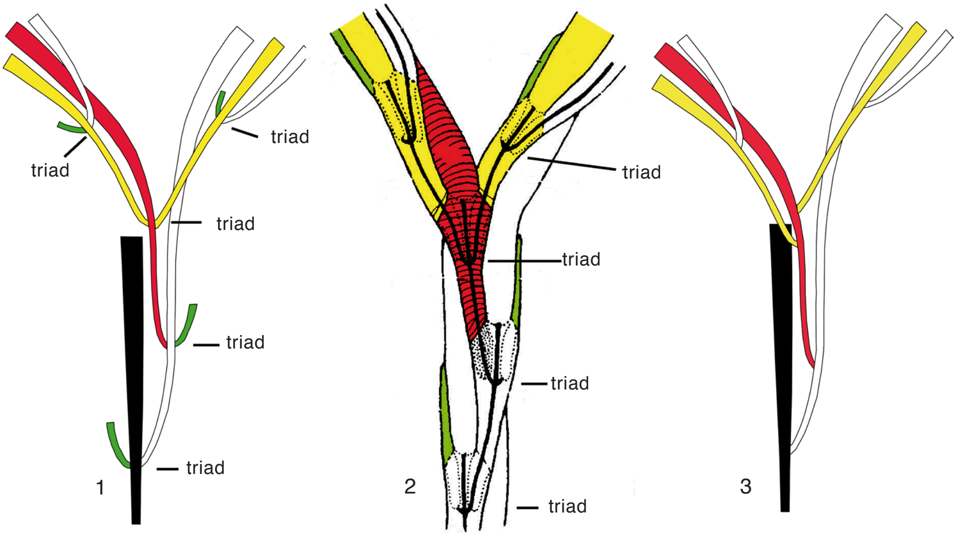

FIG. 20. Triad budding and dicalycal theca. *1,* Diagram of bithecate taxon showing the triad budding system (adapted from Cooper & Fortey, 1983, fig. 7); *2,* branching division of *Rhabdinopora flabelliformis* (EICHWALD, 1855), also showing the internal stolon system (adapted from Bulman, 1970, fig. 13.1); *3,* thecal diagram of non-bithecate form; note that the two daughter thecae originate at different levels on the dicalycal theca (adapted from Cooper & Fortey, 1983, fig. 7). *Red,* dicalycal thecae; *yellow,* derived autothecae; *green,* bithecae.

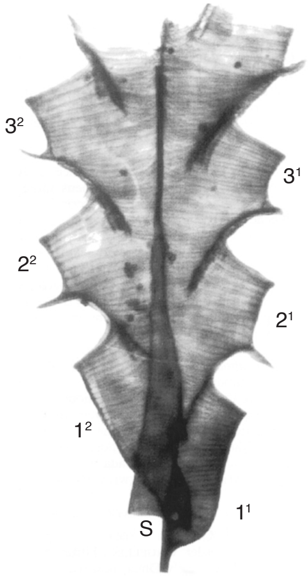

FIG. 21. Theace labeling procedure on the scandent biserial *Paraclimacograptus exquisitus* RICKARDS, 1970; ×52; *S,* sicula (adapted from Russell, Melchin, & Koren', 2000).

In graptolithines without triad budding, the development differs slightly, but follows the same general rules described by MALETZ (1992). The main difference is that in non-bithecate taxa, autothecae can produce only a single new theca (an autotheca), while a dicalycal theca retains the ability to produce two new autothecae (Fig. 20.3). Another difference can be seen in the origination of the daughter thecae, which are not paired any more, but originate at different levels on the mother theca (Fig. 20.3).

THECAL NOTATION

Thecal notation was introduced by ELLES (1897) for biserial colonies and was adopted and modified by BULMAN (1970). Its modern use is discussed by COOPER and FORTEY (1982) and is followed herein. It is easy for two-stiped colonies, in which the thecae of thecal series 1 (the primordial series of ELLES, 1897) are labeled $th1^1$, $th2^1$, $th3^1$, etc., and the thecae of thecal series 2 are labeled $th1^2$, $th2^2$, $th3^2$, etc. (Fig. 21). The

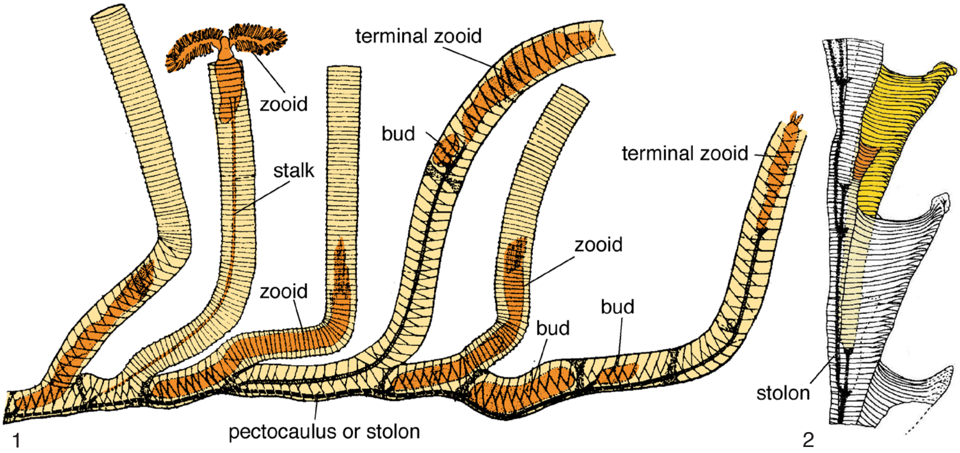

FIG. 22. The stolon system. *1,* Pectocaulus (stolon) in *Rhabdopleura* (adapted from Kozłowski, 1949, fig. 11, and Schepotieff, 1907, pl. 22); *2,* stolon system (*black*) in stipe fragment of *Adelograptus tenellus* (LINNARSSON, 1871) (adapted from HUTT, 1974, fig. 8).

thecal notation is a bit more complicated in taxa with a higher number of stipes, but it is rarely used. COOPER and FORTEY (1982, 1983) provided a useful system for such taxa and compared it with the system of BULMAN (1970). The system used by LEGRAND (1964) is not supported here.

THE STOLON SYSTEM

An important aspect of the Graptolithina is the stolon system (Fig. 20.2, Fig. 22.1), which connects the individual zooids in the extant *Rhabdopleura* (URBANEK & DILLY, 2000), and is also known from fossil graptolites (e.g., KOZLOWSKI, 1949; HUTT, 1974; BATES & URBANEK, 2002; SAUNDERS & others, 2009). The stolon system, which is not secreted by the cephalic shield, may represent the only preservable part of the actual organisms, the zooids. In the Cephalodiscida, the new zooids originate from the base of the zooidal stalk (originally called the peduncle or contractile stalk) and separate when mature. In the Graptolithina, a stolon system is developed connecting the individual zooids for life as a true colony (LANKESTER, 1884; SCHEPOTIEFF, 1906). The zooidal stalk attaches the zooid to the stolon, the sclerotized and inflexible strand of organic matter connecting all zooids with each other (Fig. 22). Details of the stolon system are difficult to obtain and are unknown from most planktic graptoloids.

COLONIAL ASTOGENY

OBVERSE AND REVERSE SIDE

The two sides of the graptolite colonies may differ considerably in their appearance, especially when the proximal development on the reverse side of the tubarium is complex. This is clearly seen in all Graptoloidea, except for the single-stiped Monograptidae. The initial portions of the first thecae, the crossing canals, grow across the sicula and cover it in part on one side of the tubarium. This side is generally identified as the reverse side. The only part of the sicula visible on the reverse side of a biserial colony is the aperture and the virgella (Fig. 23.5), but on the obverse side, at least part of the sicula is visible (Fig. 23.6). In nonbiserial taxa, the complete sicula is visible on the obverse side (Fig. 23.2). The genera *Pseudisograptus* (Fig. 23.1) and *Arienigraptus* cover a larger part of the sicula on the reverse side of the colony, where the complex construction of the manubrium takes place.

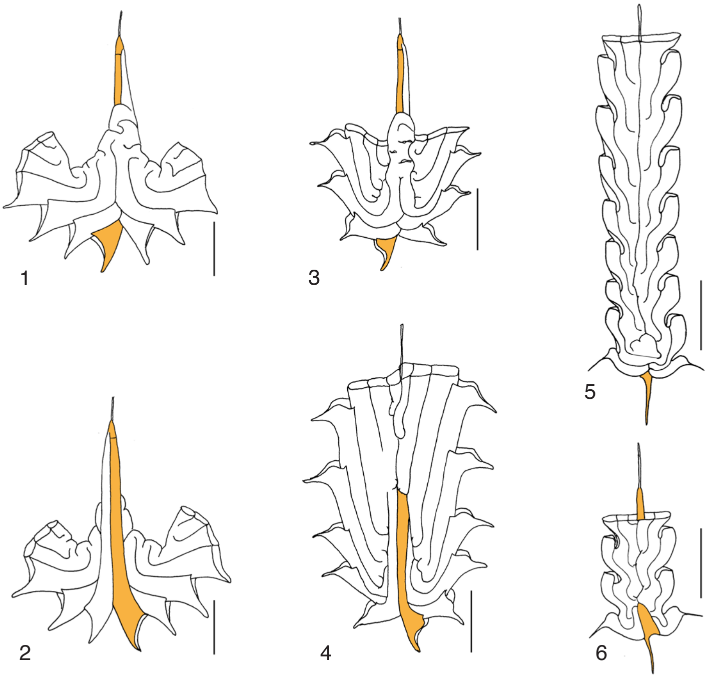

FIG. 23. Obverse and reverse sides of colonies. *1–2, Pseudisograptus bellulus* COOPER & NI, 1986, in reverse (*1*) and obverse (*2*) views; *3–4, Exigraptus uniformis* MU in MU & others, 1979, reverse (*3*) and obverse (*4*) views; *5–6, Levisograptus austrodentatus* (HARRIS & KEBLE, 1932) reverse (*5*) and obverse (*6*) views; sicula shown in color to highlight the differences of obverse and reverse sides, scale bars, 1 mm (new).

DEXTRAL AND SINISTRAL DEVELOPMENT

The proximal geometry, structure, and development types of the major groups of the Graptoloidea were redefined by COOPER and FORTEY (1982, 1983), and dextral and sinistral developments were differentiated (Fig 24). Dextral and sinistral growth types have been illustrated from various anisograptid and dichograptid specimens, but the frequency of the dextral and sinistral development types is unknown, due to the very limited number of specimens available. The dextral and sinistral development of the proximal end may not be connected to the dextral and sinistral development of the helical line of the prosicula. Most authors (e.g., BULMAN, 1936; LEGRAND, 1964; HUTT, 1974) agree that the proximal development in anisograptids can be either dextral or sinistral. SPJELDNAES (1963) discussed the dextral and sinistral development of the late Tremadocian genera *Bryograptus* LAPWORTH, 1880; *Kiaerograptus* SPJELDNAES, 1963; and *Ancoragraptus* JACKSON & LENZ, 2003, in some detail and provided illustrations of both types in his relief specimens from the uppermost Alum Shale Formation of Norway. TORO and MALETZ (2008) described dextral and sinistral specimens of *Cymatograptus bidextro* TORO & MALETZ, 2008, from the middle Floian of Argentina, the youngest-known taxon in which dextral and sinistral development is present. The dextral development is the standard in younger graptoloids and a sinistral development is extremely rare (COOPER & FORTEY, 1983).

THE PROXIMAL DEVELOPMENT

STEBBING (1970a) described the early astogeny of extant *Rhabdopleura compacta* zooids and the tubarium structure. The sicular zooid buds a new zooid from the base of the zooidal stalk, then forms a septum

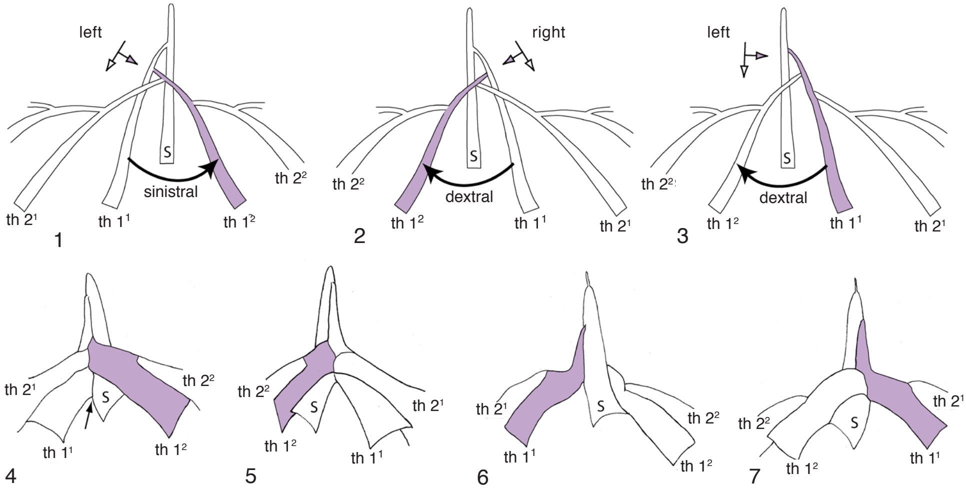

FIG. 24. Dextral and sinistral development and the proximal development types in Dichograptacea (with thecal notation). *1–3,* Thecal diagrams; *1,* isograptid-type, sinistral development; *2,* isograptid-type development, dextral; *3,* artus-type development, dextral; *4–7,* reconstructions of proximal developments; *4–5,* isograptid-type development in *Cymatograptus* sp., sinistral (*4*) and dextral (*5*) style; *6–7,* dextral, artus-type development in *Cymatograptus bidextro* TORO & MALETZ, 2008, obverse (*6*) and reverse (*7*) views (Toro & Maletz, 2008, fig. 6).

to separate a part of the dome as an initial housing for the first zooid. The first zooid subsequently resorbs a foramen into its part of the dome and starts secreting fuselli and a new tube alongside the tube produced by the founder zooid.

The development is similar in species with an erect or planktic prosicula. However, the zooids construct a tube much smaller than the initial tube of the first post-sicular zooid of *Rhabdopleura*. Growth is initially in the direction of the sicular aperture, and is related to a considerable widening of the tubes and an increasingly regular development of the fuselli. This initial growth pattern is seen in all graptoloids, including normalograptids, except the monograptids in which the first theca emerged and always grew in a direction opposite to that of the sicular aperture.

The most important aspect of the next step in the astogeny of the graptolite colony (other than uniserial taxa) is branching, and especially the branching of the Early Ordovician forms, as it defined the shape of the emerging colony. Branching was accomplished by the development of a branching division, expressed as a dicalycal theca in the tubarium.

The proximal development has been the focus of numerous investigations, which provided the basis for the main taxonomic interpretations and classification of the graptoloids. ELLES (1922) differentiated four types of proximal development: the dichograptid, leptograptid, diplograptid, and monograptid types. This early concept was elaborated upon by a number of people, and more than thirty different proximal development types and subtypes are now differentiated (e.g., MITCHELL, 1987, 1994; MELCHIN, 1998; MELCHIN & others, 2011).

The earliest proximal development type is called the isograptid type (COOPER & FORTEY, 1983), with a first dicalycal theca at th1^2 (Fig. 25.1). The artus-type development (Fig. 25.2) differs mainly in the change to a first dicalycal theca at th1^1. It is interesting, however, to mention that almost all nonaxonophoran graptoloids show the isograptid-type development no matter what thecal style or stipe orientation the colonies possess. The only difference from the artus-type development is the position of the dicalycal

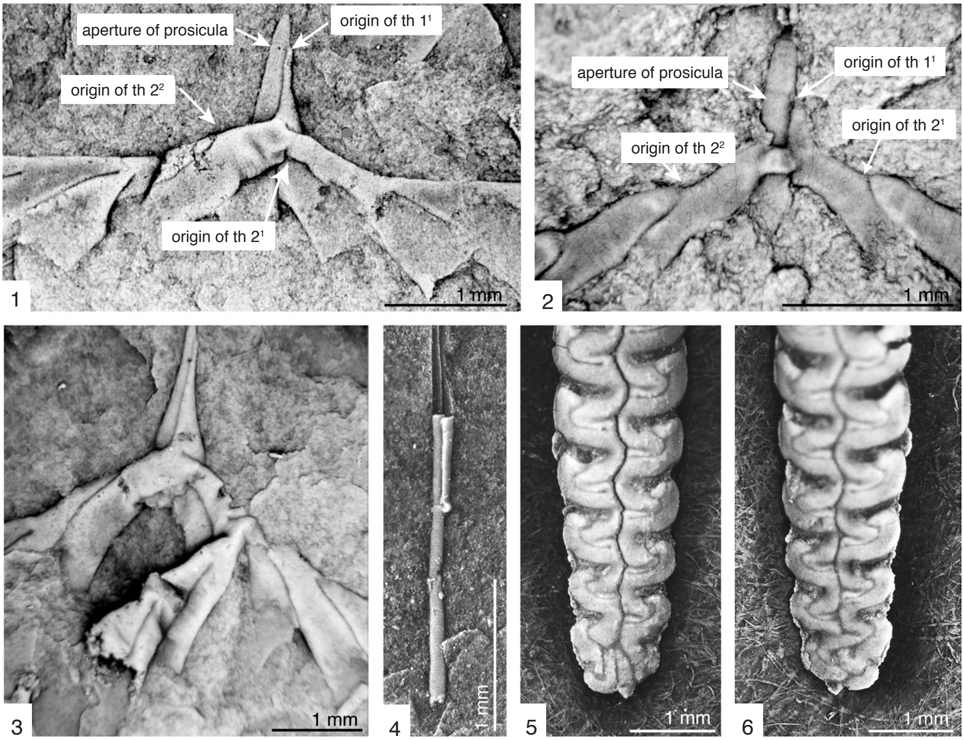

FIG. 25. Proximal development types. *1, Expansograptus holmi* (Törnquist, 1901), reverse side, isograptid-type development, latex cast (adapted from Toro & Maletz, 2008, fig. 5); *2, Cymatograptus bidextro* Toro & Maletz, 2008, reverse side, artus-type development (adapted from Toro & Maletz, 2008, fig. 5); *3, Tetragraptus amii* Elles & Wood, 1902, reverse side, isograptid-type development, latex cast; *4, Huttagraptus* sp., pattern M astogeny, early monograptid development with long sicula; *5, Archiclimacograptus* sp., obverse side; *6, Archiclimacograptus* sp., reverse side, pattern C astogeny (*3–6,* new).

theca (Cooper & Fortey, 1983). A finer differentiation of the proximal development types of the Dichograptina could otherwise easily lead to another plethora of proximal development types.

The majority of the described proximal development types are from the axonophorans with their complex, proximal-end structure. These types basically define the position of the initial dicalycal theca and the development of the crossing canals, but often include numerous independent characters of the sicula and thecae (Fig. 26). Cooper and Fortey (1983) differentiated the proximal-end construction into the proximal development type and the proximal structure, but this distinction was not adopted by axonophoran taxonomists.

Following Mitchell (1987), Melchin and Mitchell (1991), Melchin (1998), and Melchin and others (2011) defined a number of proximal development types in the axonophorans. These were based on increasingly smaller differences in the construction of the graptolite colonies. The main characters of these proximal developent patterns include the position of the dicalycal theca, the origin and growth direction of the primordial thecae, and the placement of the insertion of the median septum. Some of these patterns originated independently several times during the evolution of the axonophorans (Maletz, 2011b).

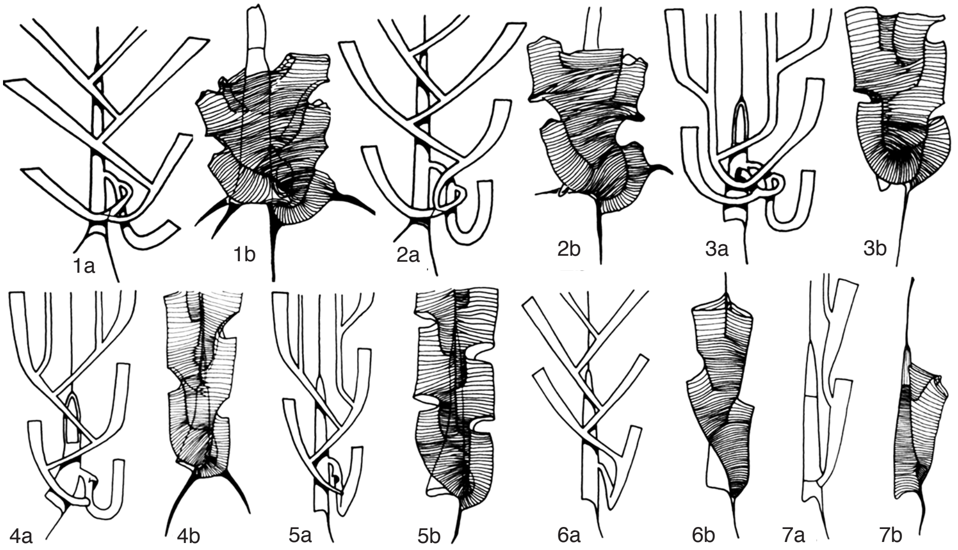

FIG. 26. Proximal development and proximal structure in axonophorans. *1a–b, Amplexograptus maxwelli* (Decker, 1935), pattern G; *2a–b, Anticostia lata* (Elles & Wood, 1906), pattern K; *3a–b, Styracograptus tubuliferus* (Lapworth, 1876), pattern D; *4a–b, Diplacanthograptus spiniferus* (Ruedemann, 1912), pattern E; *5a–b, Normalograptus kuckersianus* (Wiman, 1895), pattern H; *6a–b, Glyptograptus tamariscus* (Nicholson, 1868), pattern I; *7a–b, Pristiograptus* sp., pattern M (all adapted from Melchin & Mitchell, 1991, fig. 1–2).

The proximal development patterns are not known for many graptolites; chemically isolated or, at least, relief specimens as well as growth series of juveniles are needed to establish the development. The interpretation of the proximal development types is difficult or impossible for flattened material (see also discussion in Mitchell, 1987).

CONTINUED THECAL GROWTH

The number of thecae simultaneously growing at the tip of a stipe depends considerably on the length, overlap, and inclination of the thecae and is difficult to estimate. In slender sigmagraptines, a single theca may be growing at any time. However, in wide-stiped dichograptids, as well as in biserial colonies, a variable number of thecae may simultaneously grow at the tip of the stipe. Williams and Stevens (1988) demonstrated the continued thecal growth in the growth series of *Didymograptellus bifidus* (Hall, 1865); *Expansograptus nitidus* (Hall, 1865); and *Expansograptus pennatulus* (Hall, 1865) from western Newfoundland. They concluded that, especially in *E. pennatulus*, numerous thecae continued growing intermittently during the astogeny of the colony, leading to a continuous widening of the stipes for quite some time and a considerable changing of the tubarium shape during late-stage astogeny into the gerontomorph colony (Fig. 27).

THE MEDIAN SEPTUM

The development of the median septum in biserial axonophoran graptolites varies depending on the taxonomic group. The median septum is essentially the shared wall separating the two thecal series and is visible as the line separating the two thecal series in relief material (Fig. 28.1–28.2). There is little information on the detailed construction of the median septum in most graptolites, but some general information is available. Bulman (1970) commented on the fact that there is no evidence that the median septum comprises more than a single layer of fuselli, following the description of Urbanek

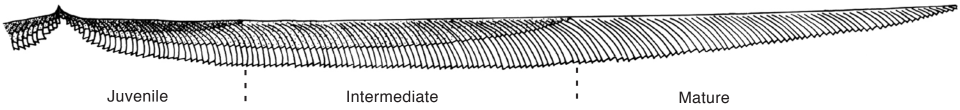

FIG. 27. Astogeny and thecal growth in *Expansograptus pennatulus* (HALL, 1865) showing continuing, but periodic, lengthening of early-formed thecae as the tubarium lengthens and matures (Williams & Stevens, 1988, fig. 44).

(1959) of the median septum of *Urbanekograptus retioloides* WIMAN, 1895, as a single-layered feature with numerous intercalating fuselli. Rare specimens of biserial graptolites can separate and rejoin the two thecal series temporarily as in *Cardiograptus amplus* HSÜ, 1947 (HAN & CHEN, 1994), suggesting that the median septum may be formed from two separate fusellar layers. The median septum can be complete (Fig. 28.1) or incomplete, and may begin at some distance from the proximal end (Fig. 28.3). URBANEK (1959) introduced the term cryptoseptate for *Gymnograptus linnarssoni* (MOBERG, 1896), in which the nema is attached to the tubarium walls by rods (adapertural ring) but lack a fusellar sheet.

The median septum may be present on one side of the tubarium only, usually the obverse side, but not on the reverse side in many Silurian taxa: e. g., *Cephalograptus* HOPKINSON, 1869; *Petalolithus* SUESS, 1851 (BATES & KIRK, 1992, fig. 41). The embedded nema and base of the partial median septum appear always to be attached to the obverse wall in axonophorans (see a number of examples in MELCHIN, 1998).

A median septum may be lacking completely (Fig. 28.5) in unistipular taxa in which the thecal origins are developed alternately, (e.g., *Amplexograptus* ELLES & WOOD, 1907; *Gymnograptus* BULMAN, 1953; and *Anticostia* STEWART & MITCHELL, 1997)—or intermittently, as in *Skanegraptus* MALETZ, 2011b. A number of taxa delay the dicalycal theca and produce a unistipular proximal part without a median septum and a bistipular distal part of the colony with a delayed insertion of the median septum (Fig. 28.3).

A median septum is also present in tri- and quadriserial taxa (*Phyllograptus* HALL, 1858; *Pseudophyllograptus* COOPER & FORTEY, 1982; *Pseudotrigonograptus* MU & LEE, 1958), where it is formed in a complex way through the dorsal sides of three or four connected thecal rows. In *Phyllograptus,* the dorsal thecal walls are largely lacking and the structure is represented only by the columnella supported by a complex network of struts and horizontal perforated plates (COOPER & FORTEY, 1982).

The monopleural taxa of the Glossograptidae do not possess a median septum. The two thecal series are attached laterally to each other and appear to have a double layer of fusellum, which is visible in relief specimens.

BRANCHING

Benthic and many planktic graptolites are able to produce multiramous colonies due to the branching of stipes in a number of different ways (Fig. 29). Theoretically, the number of stipes in pterobranch colonies is unlimited, and some benthic colonies are more than 50 cm in diameter and contain thousands of zooids on numerous branches. Planktic species (e. g., *Paratemnograptus magnificus* PRITCHARD, 1892), may have diameters of up to 100 cm. The longest monograptid has been measured at 1.45 m long and is still incompletely preserved (LOYDELL & LOVERIDGE, 2001). The exact development and differentiation of the stipes is often impossible to recognize, especially in flattened material, but the main features have been identified from chemically isolated specimens and can be referred to two structural types, dichotomous and cladial branching.

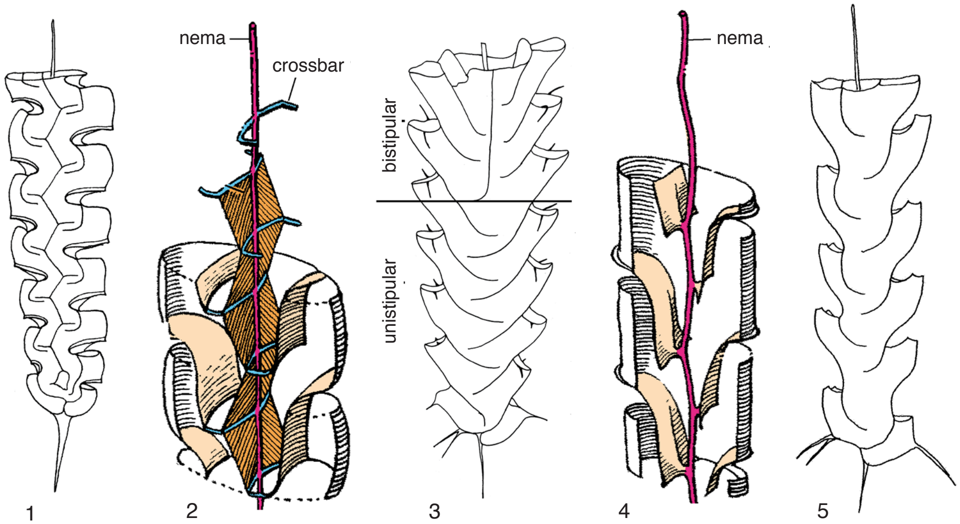

FIG. 28. Median septum. *1, Haddingograptus oliveri* (BOUČEK, 1973), bistipular colony with complete, strongly zigzag median septum, reverse view; *2,* the complete median septum (adapted from Bulman, 1955, fig. 34); *3, Orthograptus quadrimucronatus* (HALL, 1865), reverse view, showing unistipular and bistipular parts of colony; *4,* tubarium without median septum, nema connected centrally to interthecal septa (adapted from Bulman, 1955, fig. 34); *5, Anticostia macgregorae* (STEWART & MITCHELL, 1997), reverse view, unistipular colony with alternating thecae (reconstructions in *1, 3, 5,* from Maletz, 2014). *Dark brown,* median septum; *light brown,* interthecal septa.

DICHOTOMOUS BRANCHING

Branching in earlier pterobranchs is entirely and invariably developed at the tips of the stipes, the growing end, where new thecae are added to the colony (Fig. 29.1). This type of branching is identified as dichotomous branching, even though in some taxa, branching appears to be based on a lateral origination of the new stipes (Fig. 29.3). A secondary, later branching from an older part of the stipes cannot be produced by these colonies. The details of the branching structure are only recognizable in well-preserved, isolated material or in relief specimens.

In dichotomus branching, the two resulting stipes diverge at identical angles from the path of the previous branching division (Fig. 29.1, Fig. 30); thus, the original direction of the prebranching stipe is not continued (e.g., in *Adelograptus* BULMAN, 1941; *Clonograptus* NICHOLSON, 1873). In some species, one of the resulting stipes follows the original direction, while the second stipe grows at a distinct angle (e.g., *Schizograptus* NICHOLSON, 1876; *Trichograptus* NICHOLSON, 1876). In this development, it appears as if the second stipe is produced differently and has a lateral origin (Fig. 29.3). Relief specimens show that this lateral branching is only an apparent difference: the construction of both the lateral and the dichotomous branching divisions is structurally identical. It is, however, observable that lateral branches often start growing later, after the main stipe has already achieved a certain length. (Fig. 29.3).

The distances between branching divisions can be quite variable and increase distally along the colony in most species (Fig. 29.1). This progressive branching includes a highly variable number of thecae of each stipe division, and irregularities are common. A more regular type of branching is shown by the monoprogressive branching in *Goniograptus* M'COY, 1876 (Fig. 29.2) and a few other genera, in which branching is

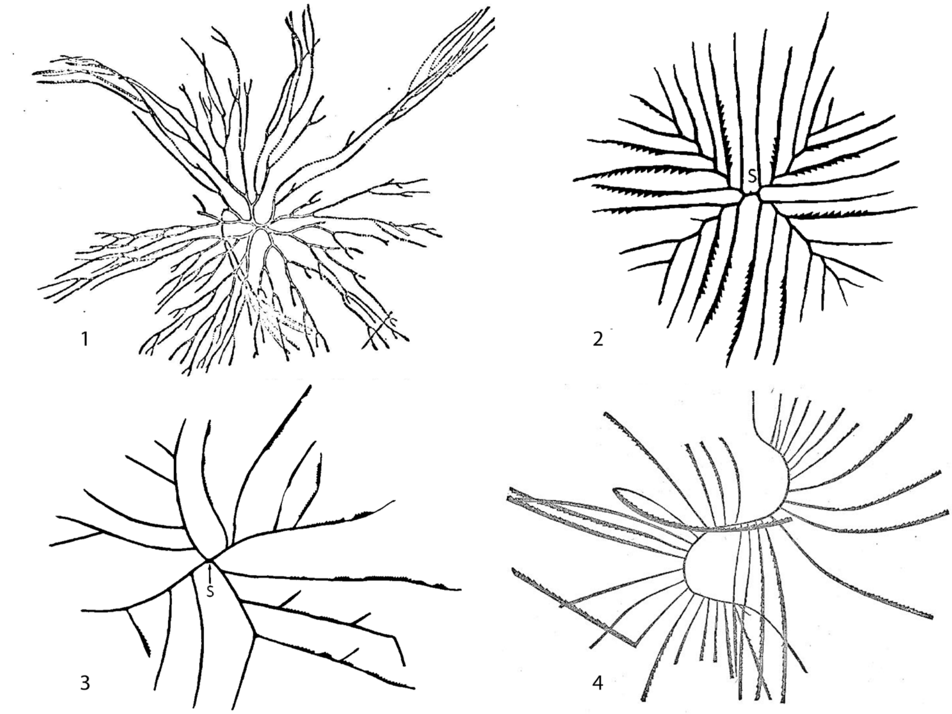

Fig. 29. Branching styles in multiramous colonies. *1, Clonograptus flexilis* (Hall, 1858), showing progressive dichotomous branching (Hall, 1865, fig. 8); *2, Goniograptus* sp., monoprogressive branching with four main stipes forming a zigzag line, *S*, sicula (Bulman 1970, fig. 77.1); *3, Schizograptus* sp., dichotomous lateral branching from four second-order stipes, *S*, sicula (Bulman, 1970, fig. 80.1); *4, Nemagraptus gracilis* (Hall, 1847), reconstruction, cladial branching at regular intervals on one side of the two main stipes (Hall, 1859, fig. 10).

regularly developed after one or two thecae. The main stipe in these genera displays a distinct zigzag shape, with branches originating alternately on both sides, resulting in fewer distal branches. This type of branching is also present in a few benthic graptolites (e.g., *Ptilograptus* Hall, 1865).

CLADIAL BRANCHING

Cladial branching (Fig. 31) represents a special type of branching, which is quite different from the normal dichotomous branching at the tip of the colonies, but its precise construction is often impossible to recognize in flattened specimens (see *Nemagraptus*, Fig. 29.4). Cladial branching is secondarily produced by mature zooids, and branches originate from the aperture of its mother theca, not from the dorsal side of the stipe as in dichotomous branching.

Cladial branching is recognized when a thecal tube develops at the apertural opening of a previously formed theca and at some distance proximally from the growing end of the main stipe. At first, small flanges of fusellar material, attached to the thecal aperture, are produced by the daughter zooid of the mother thecae and subsequently develop into a thecal tube. The thecal shape may be identical to that of its mother theca, but can also be quite different. Cladial branching is best known from *Cyrtograptus* (see Thorsteinsson, 1955) (Fig. 31.1,4) but is also known in taxa such as *Linograptus* Frech, 1897; *Diversograptus* Manck, 1923; and *Neodiversograptus* Urbanek, 1963 (Fig. 31.2–31.3).

Theoretically, cladial branching may be present at any place in the colony, but it is usually restricted to certain positions in most genera and species. In the genus

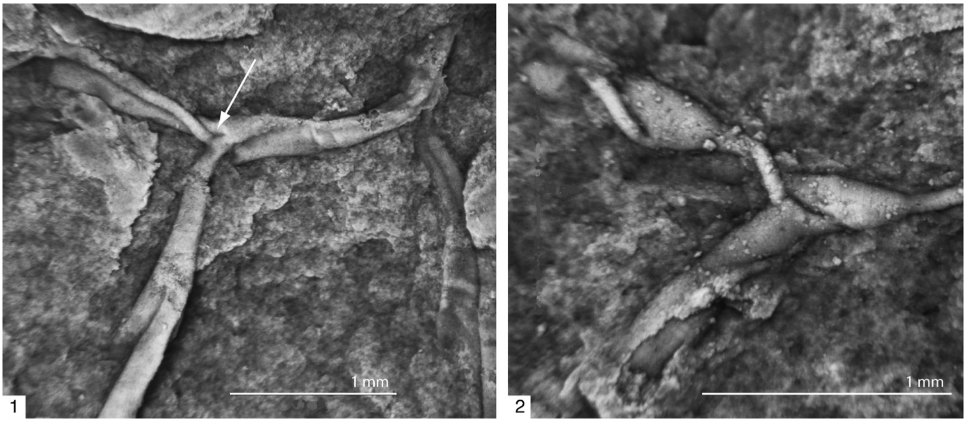

FIG. 30. Dichotomous branching. *1, Trichograptus dilaceratus* (HERRMANN, 1885), Lower Ordovician (lower Floian), DI 858, slightly curved main stipe with lateral branch growing downwards in photo, note lateral origin of theca at branching point (*arrow*), latex cast; *2,* indeterminate dichograptid on slab with GSC 123 228 (Jackson & Lenz, 2003, fig. 9m), Lower Ordovician (upper Tremadocian), showing thin prothecae and strongly widening metathecae, all thecae originate laterally, latex cast (new).

Cyrtograptus CARRUTHERS in MURCHISON, 1867, thecae produce cladial branching at regular distances, and the position of cladia can be important for the taxonomic identification of various species. Paired cladial branches and multiple cladial branches occur in a small number of Ordovician to Lower Devonian genera and species (e.g., *Amphigraptus* LAPWORTH, 1873; *Tangyagraptus* MU, 1963; *Abiesgraptus* HUNDT, 1935; *Linograptus* FRECH, 1897). Single and multiple cladial branches appear also at the sicular aperture in upper Silurian and lower Devonian monograptids (Fig. 31.2–31.3). Numerous cladia may be developed at the sicular aperture in *Linograptus* (URBANEK, 1963).

The oldest known cladial branching is documented from the Middle Ordovician (Darriwilian) genus *Pterograptus* (SKWARKO, 1974; MALETZ, 1994). Cladial branching occurs in *Nemagraptus* and other dicranograptids (*Amphigraptus*, *Tangyagraptus*) but is most commonly developed in the Silurian to Lower Devonian monograptids (*Abiesgraptus, Cyrtograptus*, *Diversograptus*, *Linograptus*, *Sinodiversograptus* MU & CHEN, 1962). The cladial branching appears to have originated independently numerous times throughout the evolution of the graptolites. Cladial branching in the monograptid genera invariably involves the development of a secondary nema along which the cladial branches grow. Such a structure is not present in the cladia of Ordovician dichograptids and dicranograptids. Thus, Ordovician and Silurian taxa adopted a fundamentally different approach to the construction of cladia.

STIPE ORIENTATION

The colony shapes in planktic graptolites are quite variable, based on the development of the stipes. Generally, the orientation of the stipes is considered in relation to the sicula, although ELLES (1922, fig. 42) proposed the nema as the main defining character for the orientation of the colonies. In the standard orientation of the sicula with the aperture downward and the free nema directed upwards, the stipe orientation is defined as pendent to scandent and all variations between (Fig. 32). This orientation may not represent the orientation of the living graptolite colonies, since very little can be known for certain about the orientation of graptolite colonies in the water column. The colony shapes of many graptolite species vary quite considerably, but the general stipe orientation usually can easily be recognized.

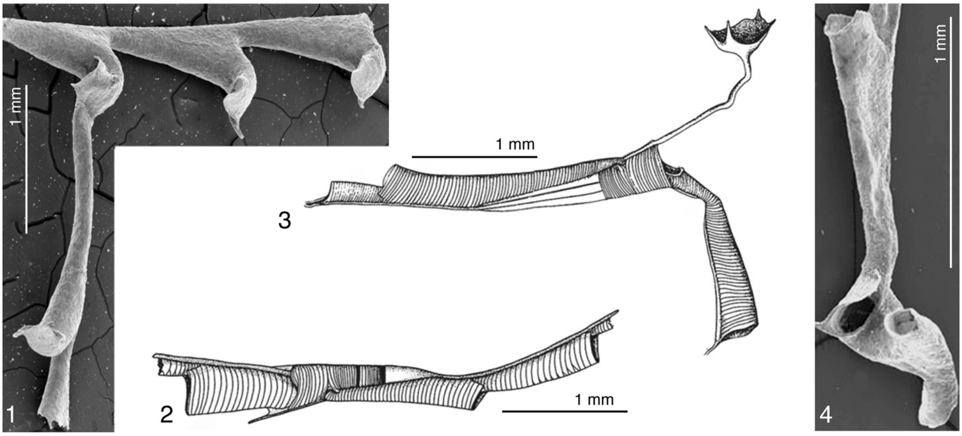

FIG. 31. Cladial branching in *Cyrtograptus*, *Linograptus,* and *Neodiversograptus. 1, Cyrtograptus perneri* BOUČEK, 1933, fragment with thecal cladium, Silurian (Wenlock, upper Sheinwoodian), Canadian Arctic (new); *2, Neodiversograptus nilssoni* (BARRANDE, 1850), specimen with wide, sicular cladium, Silurian (Ludlow, lower Gorstian) (Urbanek, 1997b, fig. 2B); *3, Linograptus posthumus* (RICHTER, 1875), reconstruction showing sicular cladium and idealized virgellarium attached to virgella, upper Silurian (Urbanek, 1997b, fig. 5D); *4, Cyrtograptus radians* BOUCEK, 1933, fragment with thecal cladium, Silurian (Wenlock, lower Homerian), Canadian Arctic (Lenz & Kozłowska, 2006, fig. 16.2).

During the burial process, the highly flexible tubarium was commonly distorted, especially the longer, more mature stipes.

Scandent graptoloids can be constructed in two fundamentally different ways (JAANUSSON, 1960). These colonies usually have two or four stipes connected to each other. In biserial axonophoran colonies, the two stipes are connected back-to-back, a condition identified as scandent (Fig. 32) and dipleural (Fig. 33.1). Four-stiped scandent taxa include the Lower to Middle Ordovician genera *Phyllograptus, Pseudophyllograptus,* and *Pseudotrigonograptus,* in which the colony has a cross-shaped cross section (Fig. 33.5–33.6).Three-stiped scandent taxa are extremely rare. The only example known from well-preserved material is *Pseudotrigonograptus minor* MU & LEE, 1958 (FORTEY, 1971), a phyllograptid graptoloid.

The stipes are connected along their lateral margins in the glossograptids (e.g., *Glossograptus, Cryptograptus*), enclosing the sicula and the initial growth of the proximal thecae. This development is identified as a monopleural arrangement (Fig. 33.1–33.2). In monopleural colonies, the proximal structure is difficult to ascertain, as the details are only visible in juvenile specimens. Mature specimens encase the proximal structure by the later growth of the stipes and completely cover them. Partially monopleural development is found in a few taxa, most notably in *Kalpinograptus* JIAO, 1977 (Fig. 33.3), in which the proximal end is monopleural, but distally the stipes separate from each other; the outline of the genus is very similar to a typical reclined isograptid. The tubarium structure in taxa with a monopleural development appears to be identical on both sides, whereas in dipleural taxa the structure is different on the obverse and reverse sides.

STIPE CONNECTIONS

Pterobranch colonies are formed from a highly flexible material, and the interference of individual stipes might be common when overlapping. However, the stipes in multiramous erect and planktic colonies tend to keep a precisely defined, minimum distance between them. This distance might be a function of avoiding unintended interaction and competition during feeding and, thus, be defined by the size of the zooids and the feeding range of their arms (STARCHER & MCGHEE Jr., 2003). Computer modeling by

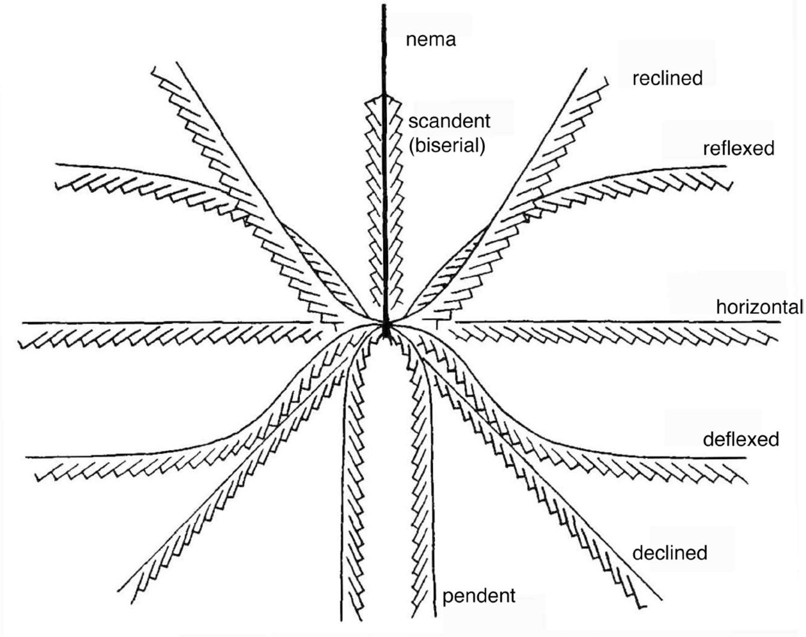

FIG. 32. Diagram illustrating the orientation of graptolite stipes to the nema and the terminology (Bulman, 1970, fig. 38).

FORTEY and BELL (1987) added support to the proposal that the various stipe configurations in multiramous forms were designed for maximum feeding efficiency of stipes and minimum interference with their neighbors.

Dissepiments are the easiest, although uncommon, way of giving rigidity to the tubarium and keeping stipes from overlapping or interfering with each other. Dissepiments are thin bands of fusellar and cortical tissue connecting adjacent stipes (URBANEK & MIERZEJEWSKI, 2009). Dissepiments are developed in erect, benthic dendroid colonies (*Dictyonema* HALL, 1851; *Ptiograptus* RUEDEMANN, 1908) and can be found in a few early planktic forms (*Rhabdinopora* EICHWALD, 1855; *Staurograptus* EMMONS, 1855; and *Sagenograptus* OBUT & SOBOLEVSKAYA, 1962) (Fig. 34.1). They appear to grow from two adjacent stipes, perhaps as a joint work of zooids from each stipe, and meet in the middle, where they are often thinner. Dissepiments can be distributed irregularly along the stipes, depending on the need for separation. In many dissepimentous species, however, they form a highly regular mesh of stipe connections and the density of dissepiments has been used to identify taxa, especially within the genus *Rhabdinopora* (COOPER & others, 1998). This often highly regular meshwork is reminiscent of colony development in some bryozoans (e.g., *Fenestella*), and these taxa may easily be confused if the construction material is not considered in fossil specimens. The bryozoans do not produce an organic housing; instead, they form their housing structures, the zooecium, as a calcified cuticle (LANKESTER, 1884).

HARMER (1905) discussed numerous bridges connecting adjacent branches in *Cephalodiscus dodecalophus* M'INTOSH, 1887. These bridges are structurally homologous to the dissepiments of benthic and planktic graptolites. *Cephalodiscus dodecalophus*, even though not a colonial pterobranch, forms branched, erect structures in a way similar to that of an erect colonial pterobranch.

ZALASIEWICZ (1993) described a rare occurrence of structures resembling dissepiments in *Spirograptus turriculatus* (BARRANDE,

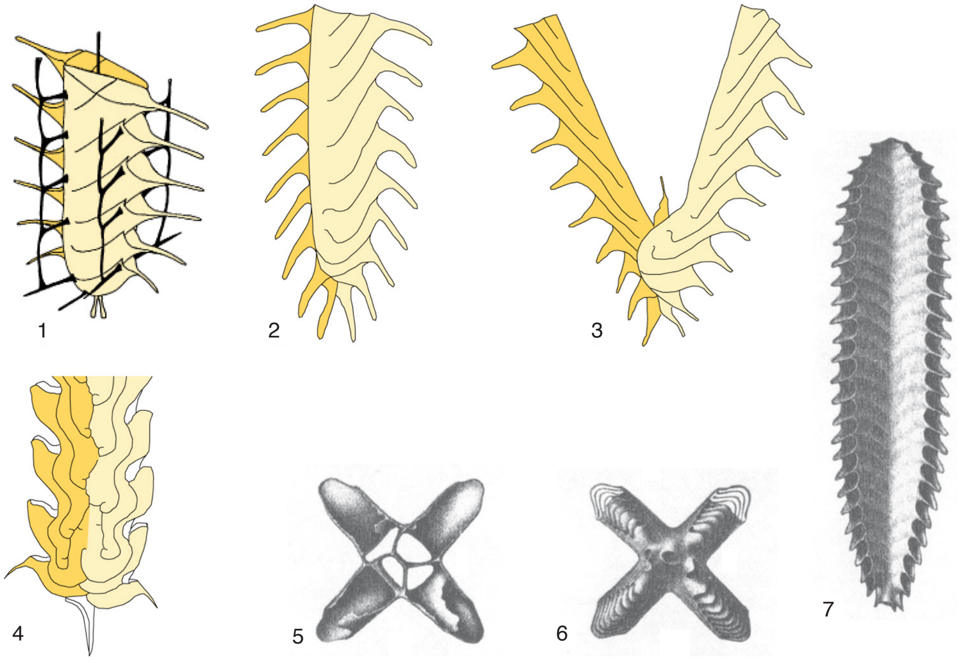

FIG. 33. Monopleural and dipleural development. *1, Paraglossograptus* sp., reconstruction of colony showing monopleural arrangement and development of lacinia from lateral apertural spines (new); *2, Glossograptus* sp., monopleural; *3, Kalpinograptus* sp., with initially monopleural and distally two-stiped colony; *4, Levisograptus austrodentatus* (Harris & Keble, 1932) dipleural, reverse view, (*1–4*) left and right sides in different colors (*2–4* adapted from Maletz, Carlucci, & Mitchell, 2009, fig. 5); *5–7, Pseudophyllograptus* sp., quadriserial colony, cross sections (*5–6*) and lateral view (*7*) (Holm, 1895, pl. 13).

1850), which formed as outgrowths from apertural thecal spines that connected to the dorsal side of the underlying stipe. These developments should not be designated dissepiments, as their construction is based on previously secreted and subsequently elongated spines, and, are not independently developed features. However, they served the same (presumed) purpose of keeping the stipes separate and not overlapping.

Anastomosis includes the transfer of individual thecae or groups of thecae from one stipe to another or the temporary connection of two adjacent stipes (Fig. 34.2–34.3). It is found in the tubarium of a few, erect, benthic pterobranch genera, such as *Desmograptus* (Fig. 34.3); *Koremagraptus* Bulman, 1927; or *Palaeodictyota* Whitfield, 1902 (Fig. 34.2). This feature is not well understood. Bulman (1945) described anastomosis in *Koremagraptus kozlowskii* Bulman, 1945, from the Upper Ordovician of Britain, based on isolated, bleached material. Rickards and Lane (1997) differentiated pseudanastomosis as anastomosis with transfer of thecae, from anastomosis as temporary connection of stipes without thecal transfer.

EXTRATHECAL DEVELOPMENTS

Many different extracolonial features can be recognized in the graptolites, especially in the planktic forms. They are differentiated herein, based upon their position in the colony and precise development.

NEMATULARIA

A short nema is present in most early (Tremadocian) planktic graptoloids, including the branched nemal tufts of some early *Rhabdinopora* specimens (Lin, 1988;

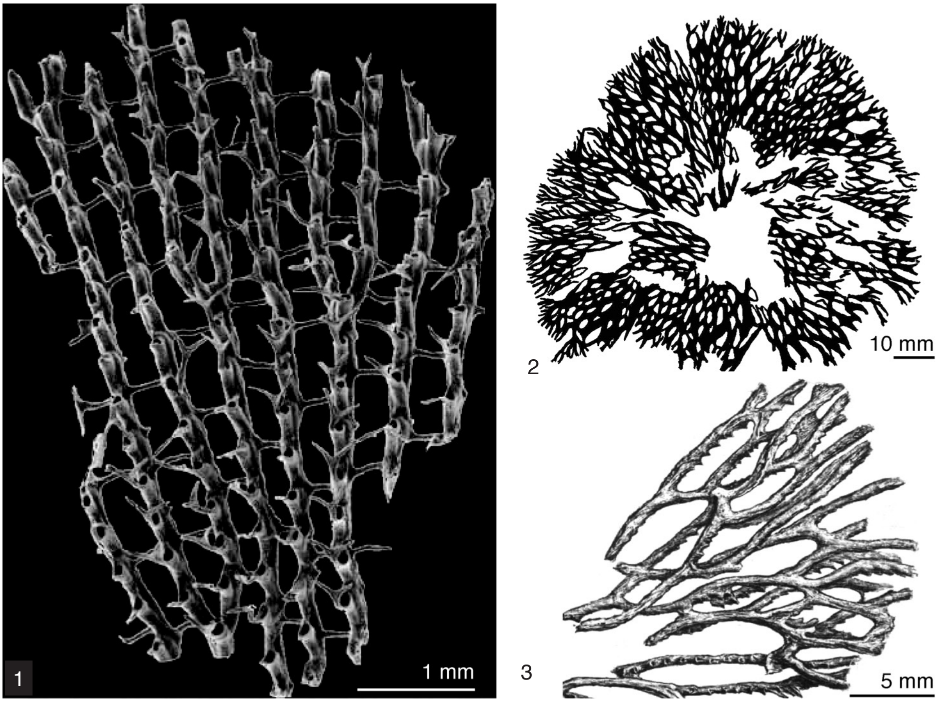

Fig. 34. Dissepiments and anastomosis. *1, Dictyonema* sp. cf. *Dictyonema cervicorne* Holm, 1890, colony fragment showing well-developed dissepiments, Ordovician, glacial boulder, Poland (Urbanek & Mierzejewski, 2009, fig. 3); *2, Palaeodictyota anastomotica* (Ringueberg, 1888), showing anastomizing stipes, upper Silurian (Bulman, 1970, fig. 21,*3*); *3, Desmograptus idoneus* Bulman, 1933, fragment showing anastomosis with thecal transfer (Bulman, 1933, pl. 4,*18)*.

Fig. 35.9). Although the nema is usually short, a long nema and a considerable development of nematularia (Fig. 35) can be found in the Lower Ordovician (Floian) species (e.g., *Pendeograptus* Bouček & Přibyl, 1951; *Kinnegraptus* Skoglund, 1961; *Isograptus* Moberg, 1892; and *Pseudisograptus* Beavis, 1972). The nema is incorporated into the colonies of the axonophorans and evolved into the long, slender nemata typical of these taxa, often bearing nematularia at the tip (Fig. 35.10). The nema is either incorporated into the ventral thecal walls of the biserial colonies and connected to the thickened lists around the thecal origins, or may be free inside unistipular tubaria with their alternating thecal origins. It generally extends far beyond the distal end of many axonophoran colonies (Fig. 35).

A number of extracolonial features are connected to the nema at the distal end of the colonies. These features have been called Schwimmblase (Dacqué, 1923; Münch 1938), floating device (Müller & Schauer, 1969: Schwebeapparat), or buoyancy mechanism (Bulman, 1970), and were termed—more neutrally—the nematularium by Müller (1975). Nematularia have been suggested to be gas-filled chambers used as flotation devices (e.g., Hundt, 1939; Bouček & Přibyl, 1941). However, recent studies have convincingly demonstrated that nematularia are solid, planar structures formed of successive layers of fusellar tissue (Urbanek, Koren', & Mierzejewski, 1982; Mitchell & Carle, 1986). Examples include two isolated, three-dimensional nematularia associated with *Normalograptus brevis* (Elles & Wood, 1906) in which one of the nematularia is clearly a solid, three-vaned structure (Bulman, 1947, pl. 9,*14–15*). In addition, a few three-dimensionally

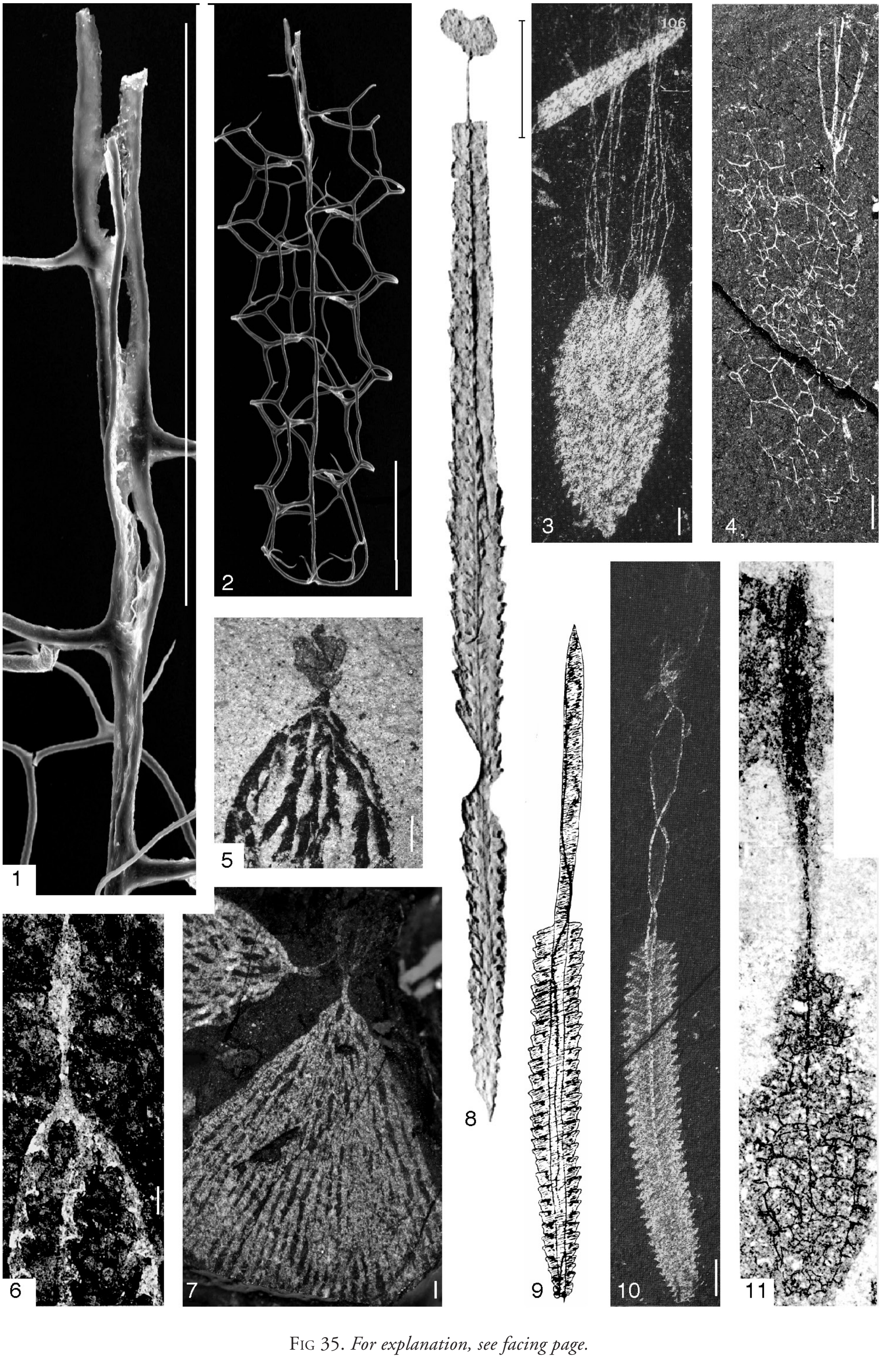

FIG 35. *For explanation, see facing page.*

preserved, two-vaned, paddle-shaped, and three-vaned nematularia—all retaining original shapes and all solid—have been discovered in Silurian retiolitids from the Canadian Arctic (Lenz & Kozłowska-Dawidziuk, 2001) and shown in Figure 35.1 and 35.2.

Størmer (1933) described a proximal organ in *Rhabdinopora flabelliformis* (Eichwald, 1840) and interpreted it as a possible disclike floating device. Harris and Keble (1928) described a similar structure in *R. scitulum*, although the nematularium appears to be a bundle of fibers (Fig. 35.7). Possible small nematularia are present in the Lower Ordovician species—the upper Tremadocian anisograptids (e.g., *Kiaerograptus*? *peelensis* Jackson, 1974) and the Floian dichograptid *Pendeograptus fruticosus* (Hall, 1858) (Jackson & Lenz, 2006; Fig. 35.6). However, nematularia are more common in Middle Ordovician to Silurian axonophorans. Slender, long, and slightly spiraled nematularia are present in the Dapingian isograptids (Moberg, 1892) and are found to be typical for the Middle Ordovician glossograptid *Cryptograptus* Lapworth, 1880, identified as *Tonograptus* by Williams, (1992).

In many taxa, the nema broadens distally, gradually or abruptly, into a prominent nematularium that ranges from a slim to broad band that may be flat (Fig. 35.9), helically spiraled (Fig. 35.10–35.11), or three vaned, disclike, or heart shaped (Fig. 35.8) or may be developed as multipronged structures distal to the growing end of the tubarium (Fig. 35.3–35.4). The nema may be recognizable in the center of the structure or reach only to the base of the nematularium.

Generally, nematularia are partially or completely external to the main body of the tubarium, but some band-shaped, paddle-shaped, two- or three-vaned nematularia, or multifurcating, thickened rods originate well within the (mature) tubarium and continue distal of the main tubarium, as, for example, *Cystograptus* Hundt, 1942; Jones & Rickards, 1967 (Fig. 35.9). This is particularly evident among the retiolitids, though also present in a number of other biserial graptoloids. As is well known in *Cystograptus vesiculosus* (Nicholson, 1868) and *Archiclimacograptus decoratus* (Harris & Thomas, 1935), the nematularia may have been constructed at the growing tip of the nema, far beyond the advancing zooidal tubes and overgrown during the later astogeny of the colonies (Fig. 35.8–35.9).

Finney (1985) summarized the evidence for small, hollow spheres that are attached to the siculae or nemata of some planktonic dendroids and graptoloids, particularly during the very early life stage of the colony. From the relatively poor preservation, however, it is unclear whether these features are a normal feature of juvenile graptolite colonies or an artifact of preservation. They may, perhaps, even be acritarchs or other palynomorphs accidentally attached to the colonies.

Fig. 35. Nematularia and other extraneous structures. *1–2, Paraplectograptus* sp., Silurian (upper Wenlock), glacial boulder, Germany; *1,* enlargement showing triradiate cross section of nematularium, ×85; *2,* showing internal nematularium, ×20 (new); *3, Dischidograptus regius* (Hundt, 1957), showing branched structures distally, Silurian (Llandovery), Germany, ×1.8 (Palmer & Rickards, 1991, fig. 106, as *Petalograptus ovatoscopularus* Schauer, 1971); *4, Eiseligraptus eisenacki* (Hundt, 1951), with multifurcated nematularium, Silurian (upper Llandovery), Hohenleuben, Germany, ×3 (new); *5, Rhabdinopora flabelliformis parabola*? (Bulman, 1954), showing lobate nematularium, Dayangcha, China (new); *6, Pendeograptus fruticosus* (Hall, 1858), showing ovate nema structure, Lower Ordovician (Floian), Canada (northern Yukon), ×4.5 (Jackson & Lenz, 2006,); *7, Rhabdinopora scitulum* (Harris & Keble, 1928), showing proximal end with tuft-like bundle of fibers, Lower Ordovician (Tremadocian), Victoria, Australia, ×3.2 (new); *8, Archiclimacograptus decoratus* (Harris & Thomas, 1935), with heart-shaped nematularium, Upper Ordovician, Nevada, USA, ×2.2 (Ross & Berry, 1963)**;** *9, Cystograptus vesiculosus* (Nicholson, 1868), with long nematularium, Silurian (Llandovery), Germany, ×3 (Schauer, 1971); *10, Parapetalolithus* sp., with a strongly spiraled nematularium, Silurian (Llandovery), Germany, ×2.5 (Palmer & Rickards, 1991, fig. 38); *11, Plectograptus*? *karlsteinensis* Kozłowska-Dawidziuk, Lenz, & Štorch, 2001, with spiraled nematularium, upper Silurian (Wenlock, upper Homerian), Czech Republic, ×4.5 (Kozłowska-Dawidziuk, Lenz, & Štorch, 2001).

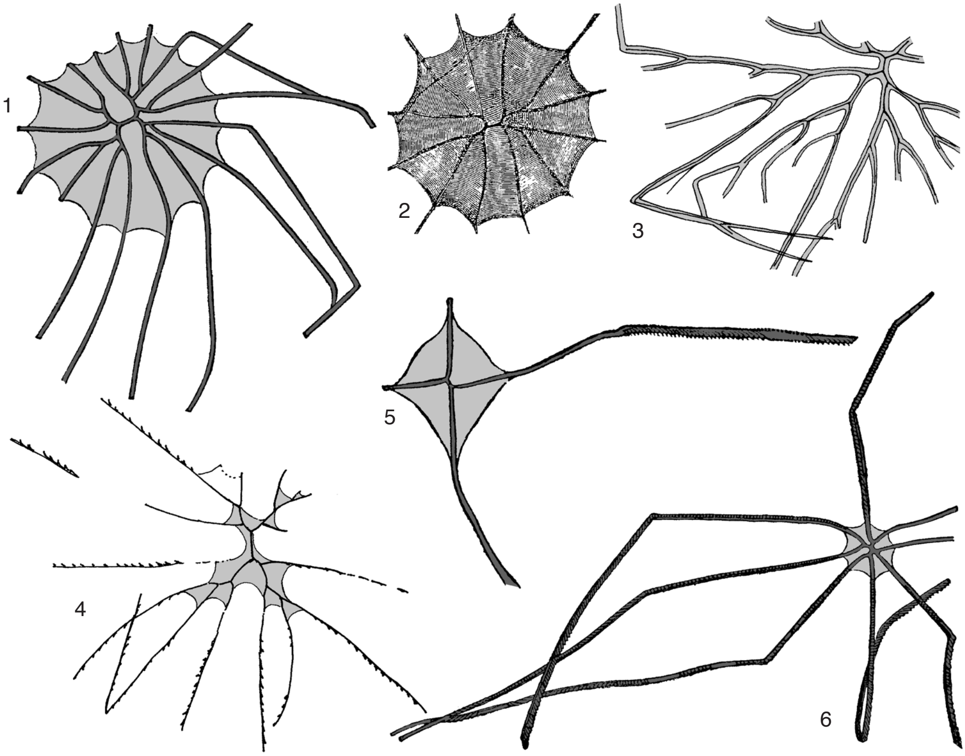

Fig. 36. Proximal webs or membranes. *1, Loganograptus logani* (Hall, 1865), extensive membrane development, ×0.75 (adapted from Hall, 1865, fig. 6); *2, Loganograptus kjerulfi* (Herrmann, 1885), proximal membrane, ×0.5 (Herrmann, 1885, fig. 10); *3, Adelograptus tenellus* (Linnarsson, 1871) showing extreme thickening of stipes, particularly in proximal regions, ×1 (adapted from Westergård, 1909, pl. 4,*8*); *4, Goniograptus palmatus* Harris & Keble, 1932, membranes between some of the branching divisions, ×0.75 (adapted from Harris & Keble, 1932, pl. 6, fig. 5); *5, Tetragraptus headi* Hall, 1865, proximal membrane, ×0.33 (adapted from Hall, 1865, fig. 4); *6, Dichograptus octobrachiatus* (Hall, 1858), ×0.33 (adapted from Hall, 1865, fig. 4).

PROXIMAL WEBS

Web structures are common in certain groups of graptolites, especially in multiramous Lower to Middle Ordovician dichograptids (Fig. 36). Ruedemann (1947) illustrated numerous dichograptids with web structures. They have been described from shale material, but are unknown from isolated specimens. Therefore, their construction is poorly understood. In a number of genera (e.g., *Dichograptus* Salter, 1863; *Loganograptus* Hall, 1868; and *Tetragraptus* Salter, 1863), these webs appear to be formed from fusellar material, as growth lines are sometimes recognizable (Fig. 36.2). They connect adjacent stipes and appear to start at the proximal end and grow outwards as thin membranes, but they are lacking in juvenile specimens. It is unclear whether they cover or engulf the thecae, however. Jaanusson (1960) described the pendent didymograptid *Didymograptus pakrianus* Jaanusson, 1960, with a considerable overgrowth of the proximal end, forming a large communal cavity for the proximal thecae.

A distinct, apparent, lateral thickening of the proximal stipes of the colonies is found in numerous multiramous Lower to Middle Ordovican dichograptids, such as *Adelograptus* Bulman, 1941 (Fig. 36.3); *Clonograptus* Nicholson, 1873; and *Stellatograptus* Erdtmann, 1967). Details of this development are uncertain, as isolated

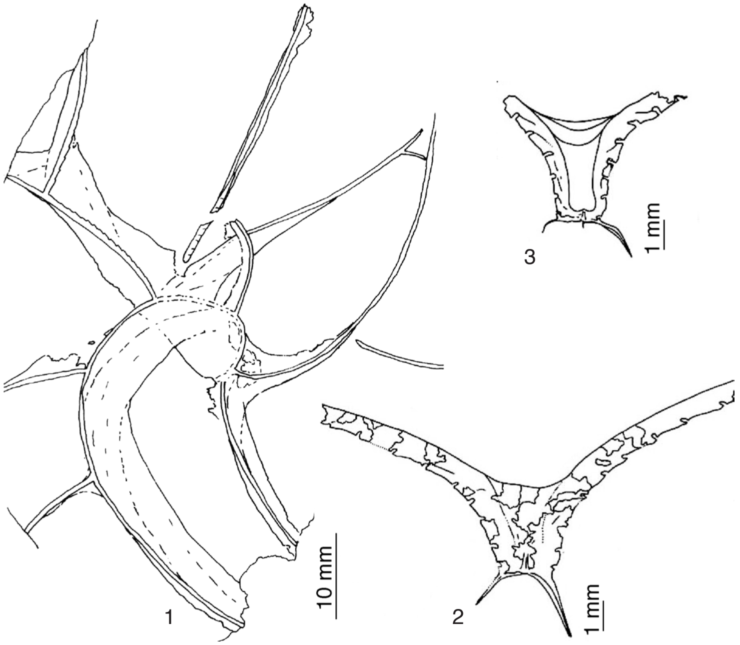

FIG. 37. Proximal membranes. *1, Cyrtograptus murchisoni* CARRUTHERS in MURCHISON, 1867, with remnants of thin, multilayered membranes, mostly in the proximal region, Silurian (lowermost Wenlock), UK (adapted from Underwood, 1995, fig. 2c); *2–3, Dicellograptus turgidus* MU, 1963, showing proximal membrane closing reclined stipes of proximal end, Upper Ordovician, Vinini Formation, Nevada, USA (Štorch & others, 2011, fig. 10).

material is not available and specimens are flattened. In juvenile specimens of the same species, the stipes are much more slender and thecal apertures can be recognized. These stipe modifications could be interpreted as lateral web structures, similar to the proximal webs of other forms, but alternatively they could represent actual thickening of the stipes, which appears to be common in many dendroid graptolites as a gerontic feature.

Proximal webs may be found in the axils of Upper Ordovician *Dicellograptus*, where they cover and obscure the sicula (Fig. 37.2–37.3). In outline, these specimens may resemble more closely specimens of *Dicranograptus* HALL, 1865, with a short, wide, biserial proximal end, as, for example, in *Dicellograptus moffatensis* CARRUTHERS, 1859 (CARRUTHERS, 1858); and *Dicellograptus ornatus* ELLES & WOOD, 1904 (WILLIAMS, 1982).

Proximal webs and membrane-like features are extremely rare in monograptids. MOBERG (1893) described *Monograptus pala* MOBERG, 1893, with an apparent large, rounded proximal membrane. As MOBERG's illustrated specimens show the thecae in scalariform view (Fig. 38.8), a more precise identification is impossible and details of the membrane are not available.

A single *Cyrtograptus* specimen with an extensive proximal membrane has been discovered in the Canadian Arctic (LENZ, 1974). In this specimen, the membrane partly covers the thecal apertures of the proximal end of the specimen. It is, in part, a double membrane that extends along the initial spiral part of the colony. UNDERWOOD (1995) illustrated a similar and more completely preserved membrane in a flattened specimen of *Cyrtograptus murchisoni* CARRUTHERS in MURCHISON, 1867 (Fig. 37.1).

Bladderlike structures, or sacs, are developed in a few Ordovician axonophorans, most typically shown in *Archiclimacograptus*

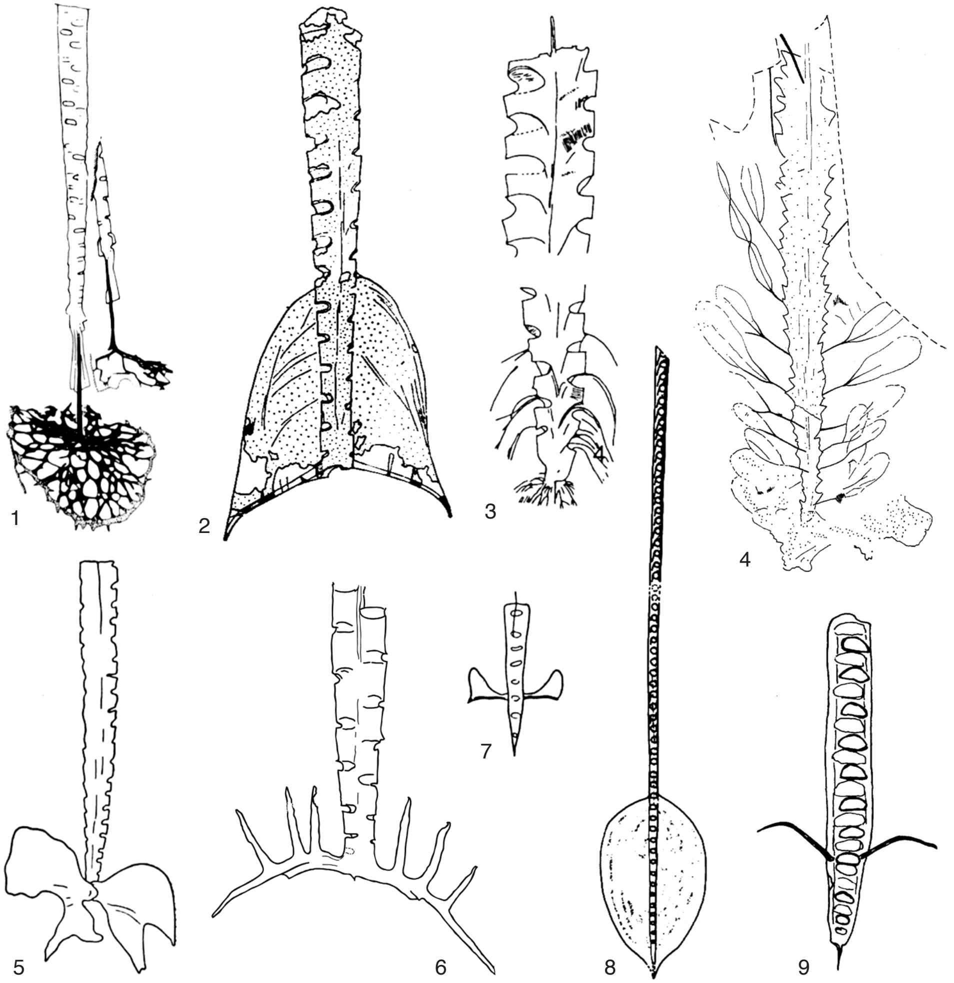

FIG. 38. Scopulae and other extraneous proximal structures. *1, Climacograptus*? *baragwanathi* HALL, 1906, Upper Ordovician (Katian), Australia (VandenBerg & Cooper, 1992, fig. 9D); *2, Climacograptus bicornis* (HALL, 1847), with large proximal membranes, Upper Ordovician (Sandbian), New York, USA (Riva, 1976, fig. 6N); *3, Comograptus comatus* OBUT & SOBOLEVEKAYA in OBUT & others, 1968, Silurian (Llandovery), Norilsk region, Siberia, Russia (Koren' & Rickards, 1996, fig. 6G); *4, Dittograptus* sp., specimen with numerous scopulae, Silurian, Thuringia, Germany (Müller, 1977, fig. 11); *5, Climacograptus*? *papilio* MU, 1963, with proximal membranes, Upper Ordovician, China (Mu, 1963, fig. 11); *6, Appendispinograptus venustus* (HSÜ, 1959) showing development of complex parathecae, Wufeng Formation, southwestern China (Mitchell, Chen, & Finney, 2007, fig. 1.4); *7, Climacograptus ensiformis* MU & ZHANG in MU, 1963, Upper Ordovician, China (Mu, 1963, fig. 12); *8, Monograptus pala* MOBERG, 1893, with large proximal membranes (Bulman, 1970, fig. 70.15); *9, Climacograptus*? *uncinatus* KEBLE & HARRIS, 1934, Upper Ordovician, Vinini Formation, Nevada, USA, (Carter, 1972, fig. 2l).

bursifer (ELLES & WOOD, 1906) (ELLES & WOOD, 1906, pl. 27,*6*). A possibly similar development is known from the Llandovery *Glyptograptus auritus* (BJERRESKOV, 1975). It is unclear whether they represent membranes or three-dimensional features. Proximal webs are also constructed in mature specimens of a number of climacograptids, where they grow upwards from the dosal side of the proximal spines in *Climacograptus bicornis* (HALL, 1847) (Fig. 38.2) and may reach the fourth or fifth thecal pair (RIVA, 1976, fig.

6). *Climacograptus papilio* MU, 1963 (Fig. 38.7) may also construct considerable webs based on the proximal spines, but they are not attached to the sides of the colony.

SCOPULAE AND OTHER LATERAL AND PROXIMAL NEMAL DEVELOPMENTS

Scopulae are special developments on the sides of axonophoran colonies and form paddle-like structures (Fig. 38.4). The scopulae may originate from the nema, but the development is unclear for most taxa. Scopulae are usually bladelike with a thickened rim around a thin fusellar membrane (BATES, 1987; BATES & KIRK, 1991). They are most common in the Upper Ordovician Lasiograptidae, but analogous features may be found in a few Silurian normalograptids (e.g., *Dittograptus* OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968; see KOREN' & RICKARDS, 1996).

The paired lateral spines of *Climacograptus*? *uncinatus* KEBLE & HARRIS, 1934 (Fig. 38.9), are based on the nema, and form at an early stage in the development of the colony (CARTER, 1972). After only a few millimeters of growth of the colony, the nema splits into two rods that grow subhorizontally outwards. The nema stops growing, and the colony grows across this point unchallenged and without the production of a new nema. MU (1963) described a similar development from the poorly known *Climacograptus ensiformis* (Fig. 38.7), but in this material a nema apparently continues through the colony.

VIRGELLARIA

In *Linograptus posthumus* (RICHTER, 1875), the virgellarium, a construction formed from the tip of the virgella, may represent the typical development of a virgella-related feature. Unfortunately, the details of its development are uncertain, as the isolated specimens do not show the remains of the fusellar structure. The virgellarium is formed of a membrane with four petals, ending in fingerlike or umbrella-like outgrowths (URBANEK, 1963, 1997b) (Fig. 31.3). MÜLLER (1977) illustrated a number of virgellar features as virgellaria and suggested a detailed terminology of these features, but details are extremely rare. Virgellar extensions are limited to the extremely long virgellar spines in a number of biserial taxa (e.g., *Archiclimacograptus* MITCHELL, 1987; *Orthograptus* LAPWORTH, 1873). Bifurcation of the virgella, as in *Normalograptus bifurcatus* LOYDELL, 2007, appears to be extremely rare (LOYDELL, 2007), and has not been found in other taxa. The development of the ancora umbrella and ancora sleeve in the Retiolitidae also belongs to the modifications of the virgella.

ANCORA SLEEVE

The ancora sleeve is a special development in the Retiolitidae. It consists of a secondary membrane surrounding the tubarium and its original thecal construction. Usually, the ancora sleeve is preserved as a more or less regularly developed system of lists, the reticulum, which developed from the distal extension and development of the virgellar structure, the ancora umbrella. It is composed of seamed lists made up of cortical tissue and enlarged by concentric layering. This combination of the ancora sleeve forming the outer wall and the thecal framework forming the inner wall is unique among the graptolites. While it is clear that the thecal framework was formed by the laying down of a succession of thin fusellar sheets, the origin of the sheets in the ancora sleeve is unclear (e.g., BATES, 1987; BATES & KIRK, 1992). In the vast majority of specimens, the fusellar layer is too thin to be preserved in the fossil record. It is most commonly recognized through the presence of fusellar shards (Fig. 39.6) in the seams of the list structures (BATES & KIRK, 1992) and, especially the very rare, complete preservation of fusellar sheet layers (LENZ, 1994; LENZ & THORSTEINSSON, 1997).

As the lacinia in the Lasiograptidae is developed quite differently from the clathrium and reticulum (ancora sleeve) of the Retiolitidae, they may be treated as analogs rather than homologs. Whereas the lacinia lists of the lasiograptids and glossograptids are without

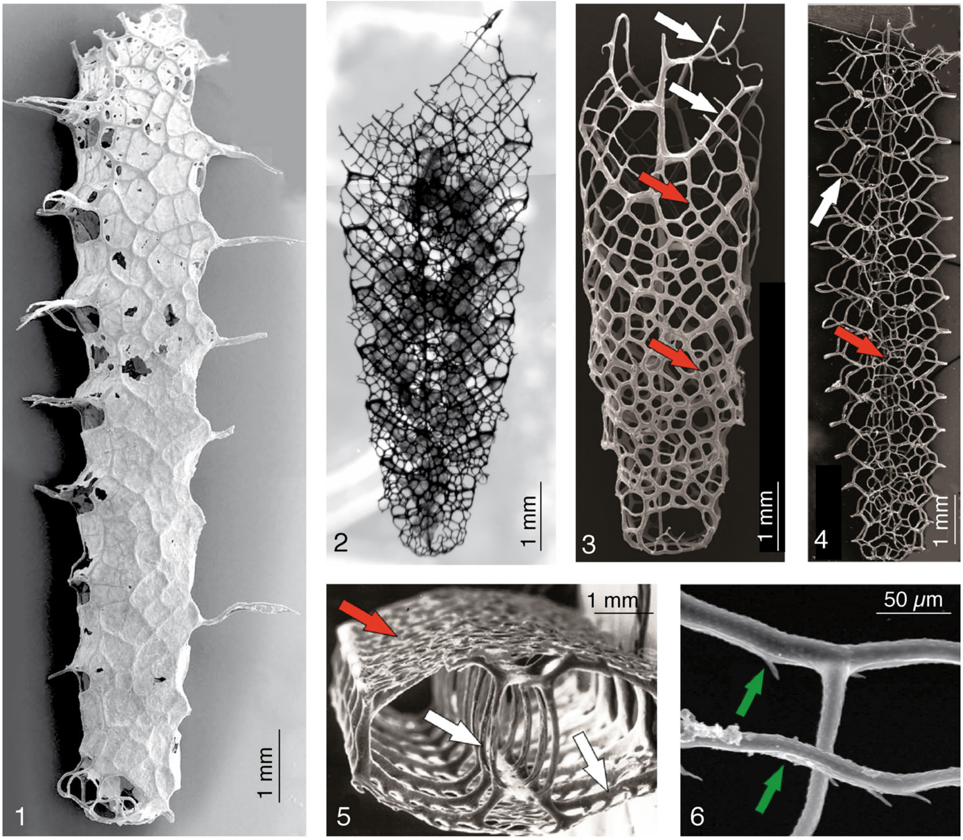

FIG. 39. Clathrium and reticulum. *1, Spinograptus clathrospinosus* (EISENACK, 1951), with preserved ancora sleeve membranes (Lenz & Kozłowska-Dawidziuk, 2002, fig. 14,*7*); *2, Retiolites geinitzianus* BARRANDE, 1850, showing partial preservation of thecae (Maletz, 2008, fig. 1a); *3, Retiolites* sp., longitudinal view, SEM photograph (new); *4, Pseudoplectograptus simplex* KOZŁOWSKA-DAWIDZIUK, 1995, (Lenz & others, 2012, pl. 2); *5, Retiolites* sp., cross section (new); *6, Paraplectograptus eiseli* (MANCK, 1917), enlarged view, showing seams and remains of fuselli in the thecal framework lists (new). *White arrows,* clathrium (*3–4*); *red arrows,* reticulum (*3–5*); *green arrows*, remains of fuselli (*6*).

list seams, both the clathrial lists (generally the equivalent of the thecal framework; Fig. 39, *white arrows*) and the reticulum (the finer meshwork, mainly related to the ancora sleeve; Fig. 39, *red arrows*) invariably bear seams that were probably occupied by very thin fusellar bands. Only in the seams of the thecal framework lists are fusellar shards observed (Fig. 39.6), whereas the seams of the ancora sleeve are apparently devoid of fusellar shards.

LACINIA

The lacinia is typically a development of a meshwork of rods originating as thecal spines with a concentric core and producing a complex, three-dimensional, meshwork structure around the entire colony in some Lasiograptidae (Fig. 40.1–40.2). The spines and bars are formed from fusellar material, often covered and thickened by cortical overgrowth (BATES & KIRK, 1991). At the same time, the fusellar structure of the archiretiolitid colonies is reduced, and often only thin bars remain outlining the thecal framework (Fig. 40.1). These lists show the distinct seams, indicating their origination on the fusellar surfaces of the thecae (BATES & KIRK, 1991). In early lasiograptids, the fusellum is more complete, and the differ-

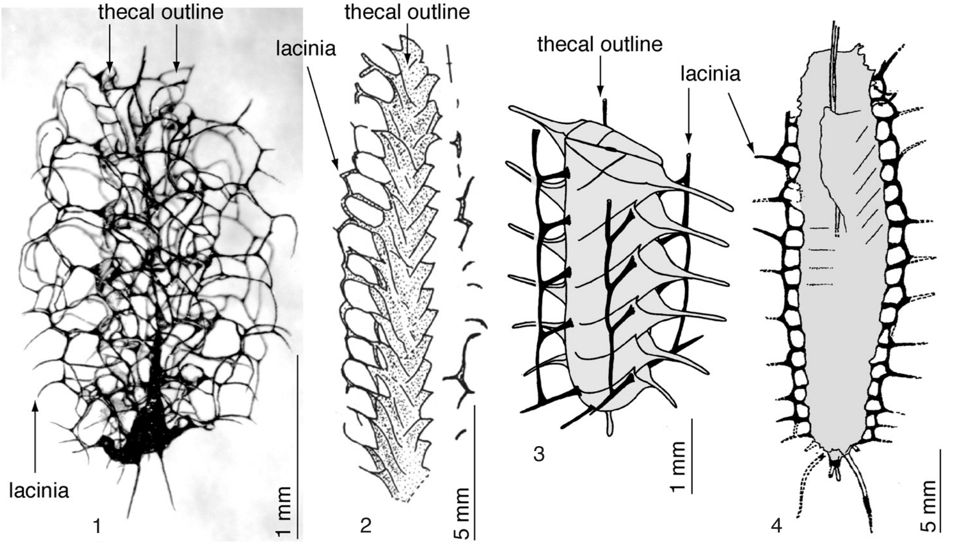

FIG. 40. The Lacinia. *1, Pipiograptus* sp., specimen showing a vague thecal outline and the extensive lacinia, sicula, and first theca completely sclerotized, Viola Limestone, Oklahoma, USA (new, photograph provided by Daniel Goldman); *2, Neurograptus margaritatus* (LAPWORTH, 1876), specimen with sclerotized tubarium and lacinia (Williams & Bruton, 1983, fig. 24a); *3, Paraglossograptus* sp., reconstruction showing lacinia (new); *4, Paraglossograptus tentaculatus* (HALL, 1865), GSC 950b, syntype showing lacinia development and connection to lateral apertural thecal spines (adapted from Rickards, 1972, fig. 1a).

ence from the encasing lacinia is easily recognizable (Fig. 40.2).

A small amount of lacinia is seen to develop in the Glossograptidae. Species of the genus *Paraglossograptus* MU in MU & others, 1962, possess lateral thecal spines that are interconnected with vertical bars. Four ladderlike structures are formed in *P. proteus* (HARRIS & THOMAS, 1935) (WHITTINGTON & RICKARDS, 1969), but a more complex meshwork can be found in *P. tentaculatus* (HALL, 1865) (Fig. 40.3–40.4). This type of a lacinia is not homologous to the lacinia in the Lasiograptidae. Details of its construction are not available.

LATE-STAGE AND GERONTIC MODIFICATIONS

A number of late-stage and gerontic modifications can be observed in the colonies, often considerably changing the colony shape and easily leading to misidentifications. They appear in large, supposedly mature tubaria and have never been found in juveniles. These features include the excessive development of cortical tissues in many benthic and a few planktic graptolites but also the resorption of structural details in mature colonies. The parasicula and parathecae or the strongly elongated proximal thecal spines of certain biserial graptolites may also be examples of gerontic development. The elongation of proximal spines and the virgella, though common in many biserial graptolites, does not add any new features to the tubaria and, thus, is not considered here.

PARASICULA AND PARATHECAE

A colony feature first introduced in some early biserials is the parasicula (VANDENBERG, 1990), an apertural elongation of the sicula that forms a tube of various lengths, as illustrated by BULMAN (1947) in *Pseudoclimacograptus scharenbergi* (ELLES & WOOD, 1906). Based on the observations by LOXTON and others (2011) of an isolated specimen of *Appendispinograptus supernus* (ELLES & WOOD, 1906), the parasicula is

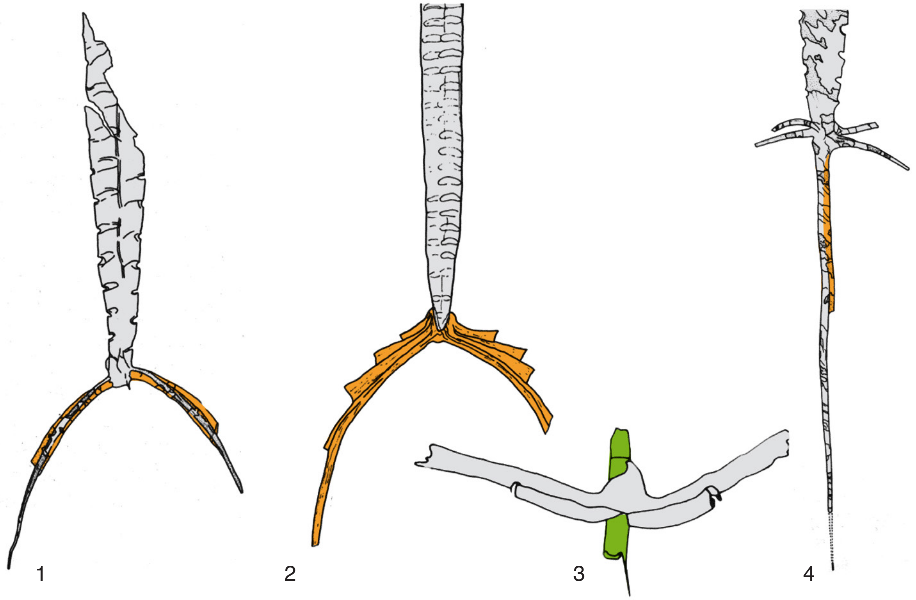

Fig. 41. Parasicula and parathecae. *1–2, Appendispinograptus longispinus* (Hall, 1902); *1,* with at least one pair of parathecae; *2,* mature tubarium with multiples of parathecae and long spine pairs (adapted from Riva, 1974, fig. 4d); *3, Nemagraptus gracilis* (Hall, 1847), with sicula proximal region extending well below thecal level, and moderately long virgella (adapted from Finney, 1985, fig. 12–11); *4, Climacograptus hastatus* (Hall, 1902) with multiples of spines, a very long virgella, and long parasicula (Riva & Ketner, 1989, fig. 9b). *Brown,* parasiculae and parathecae; *green,* sicula in *Nemagraptus.*

composed of narrow fuselli. The parasicular tube grows along the elongating virgella and may twist around it. A number of climacograptid species develop the parasicula as a species-specific character. Mitchell, Chen, and Finney (2007) recognized similar tubular extensions of the proximal thecal pairs and termed them parathecae (Fig. 38.6, Fig. 41). Mitchell, Chen, and Finney (2007) and, more extensively, VandenBerg (1990) described the development of parasiculae and parathecae in a number of species of *Appendispinograptus* Li & Li, 1985 (Fig. 41.1–41.2,4). The parasiculae and parathecae originated as tubular outgrowths along the virgella and the proximal thecae, respectively. These structures, in some species, progressively grew into very long and robust spinelike structures as the colony matured. The earliest parasicula known is from the lower Darriwilian in the genus *Archiclimacograptus* Mitchell, 1987 (Maletz, 1997).

A number of Lower Ordovician anisograptids (especially the Tremadocian genera *Ancoragraptus* and *Chigraptus*), certain Middle Ordovician sigmagraptines (*Perissograptus* Williams & Stevens, 1988; *Maeandrograptus* Moberg, 1892), and Middle to Upper Ordovician nemagraptids such as *Nemagraptus gracilis* (Hall, 1847), possess a long, free portion of the apertural part of the sicula that extends well below the lowest level of the thecae (Fig. 41.3). These bear some resemblance to the parasiculae of Ordovician biserials. However, in these taxa, the siculae are completely formed before the development of the stipes, and the free, projecting parts are not a late-stage addition to the colonies. These are not homologous constructions so should not be identified as parasiculae.

Other basal structures, which are probably progressively enlarged as the tubarium matured, include the large meshwork in

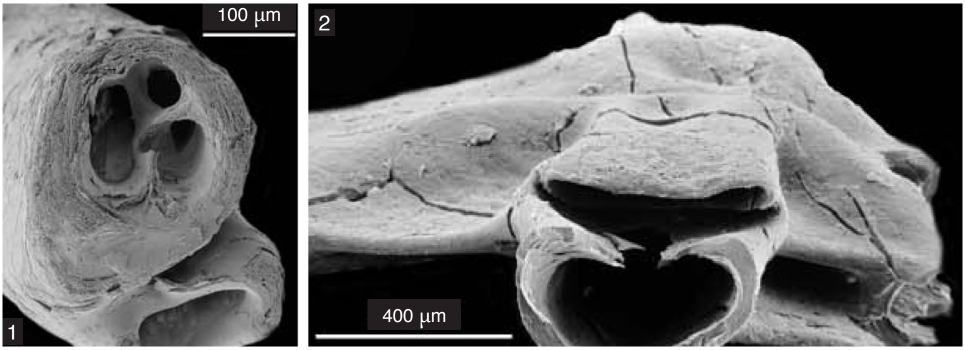

FIG. 42. Cortical overgrowth. *1, Dendrograptus* sp., broken end of stipe showing thecal cavities and excessive cortex development; *2, Amphigraptus* sp., view into thecal opening with thick cortical cover (Bates & others, 2011).

Climacograptus? *baragwanathi* HALL, 1906 (Fig. 38.1); this is apparently an extension of the virgella and, thus, may be constructionally comparable to the ancora sleeve of the retiolitids. Another example of progressive proximal development is the numerous spines at the sicula and the early thecae in *Comograptus comatus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968 (Fig. 38.3). The development of the bulbous construction at the proximal end of *Climacograptus wilsoni* LAPWORTH, 1876 (WILLIAMS, 1994) appears to start from a short parasicula, but details are unknown. The round shape seen in most specimens suggests a vesicle of some kind.

CORTICAL OVERGROWTH

A thick cover of cortical tissue (Fig. 42) can cover important structural details in dendroid graptolites and is occasionally found in planktic taxa (BATES & others, 2011). Cortical overgrowth can be excessive in certain taxa and can completely occlude thecal apertures. In general, the cortical overgrowth is more pronounced in the proximal regions of the colonies and, thus, can be regarded as a late-stage or gerontomorph addition, but its secretion may start early in the astogeny of the graptolite colony. The thecal development and form are completely obliterated in extreme cases, and only a vague outline of the colony shape remains. Therefore, the cortical overgrowth may influence considerably the appearance of the graptolites and provide problems for taxonomic identifications.

RESORPTION

Large parts of the siculae are lacking in mature stages of the colonies of a few species of planktic graptolites. This has been interpreted as a resorption of part or even all of the sicula or other parts of the colonies. One of the most impressive examples was represented by the lack of a visible sicula in the genus *Janograptus* TULLBERG, 1880. However, ALBANI and others, 2001, showed that isolated specimens from the Table Head Group of western Newfoundland are actually regenerated stipes of extensiform dichograptids and the genus *Janograptus* is based on regeneration of stipes, a feature that becomes common only in narrow Silurian monograptids (see discussion of regeneration and pseudocladia below).

A clear effect of resorption is the lack of a visible supradorsal part of the sicula in *Dicellograptus jonstrupi* HADDING, 1915, and related Upper Ordovician taxa (WILLIAMS, 1982). Juveniles invariably show a complete sicula prominently exposed in the axil of the colony (Fig. 43.1), but the sicula is no longer visible in mature specimens (Fig. 43.2); moreover, the axil may show a slight bump in the horizontal, proximal part of

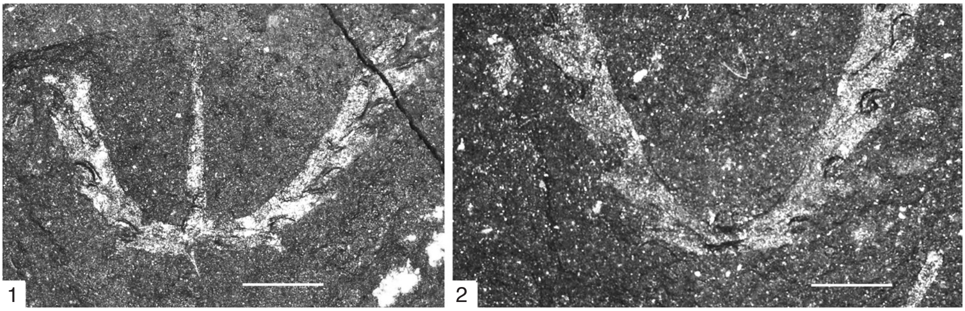

FIG. 43. Resorption in *Dicellograptus jonstrupi* HADDING, 1915, Risebaeck, Bornholm, Denmark. *1,* LO 2689t, juvenile; *2,* LO 2690t, mature specimen, scale bars, 1 mm (new).

the stipes only. Resorption of the apex of the sicula has also been seen in *Pleurograptus lui* MU, 1950, from the Upper Ordovician of Nevada (ŠTORCH & others, 2011).

REGENERATION

Graptolite colonies, like all colonial organisms, possess a considerable capacity for regeneration of their damaged tissues and secreted housing structures (Fig. 44). Even though the regeneration of the soft tissue in fossil specimens cannot be seen, the tubaria often show considerable evidence of this capacity (KRAFT, 1926; BULMAN, 1932; EISENACK, 1941b; URBANEK, 1958; RIGBY, 1994). In isolated material, damage and

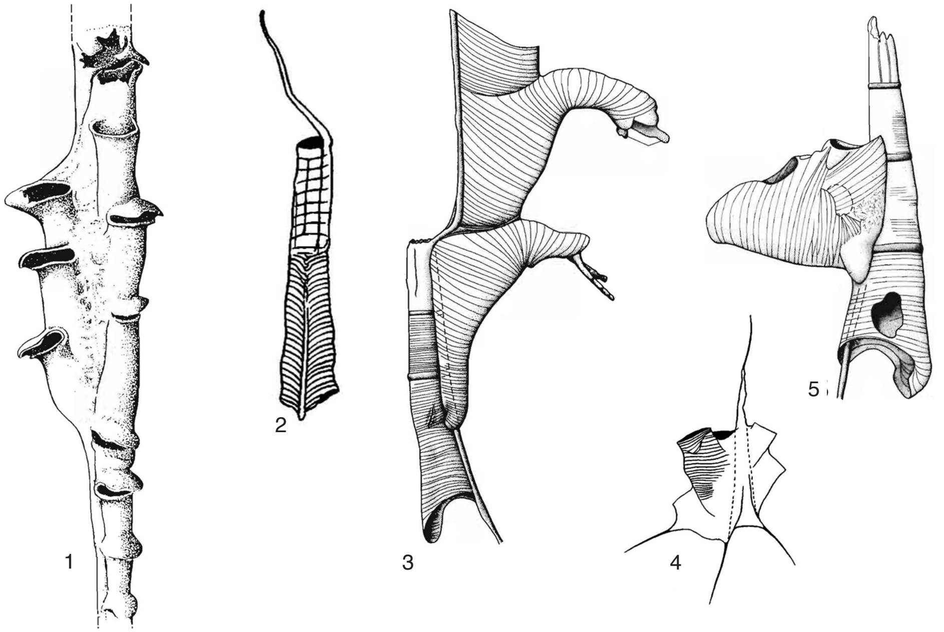

FIG. 44. Malformation and regeneration. *1, Slovinograptus balticus* (TELLER, 1966), abnormal development from uniserial to biserial, upper Silurian, Poland (Urbanek, 1997a, fig. 10); *2, Rectograptus gracilis* (ROEMER, 1861), most proximal portion of prosicula missing (Bulman, 1970, fig. 47); *3, Uncinatograptus spineus* (TSEGELNIUK, 1976), damage to proximal part of sicula and subsequent offset regeneration, upper Silurian, Poland (Urbanek, 1997a, fig. 12); *4, Rectograptus gracilis* (ROEMER, 1861), regeneration of th2^1 (Bulman, 1970, fig. 47); *5, Neocolonograptus lochkovensis* (PŘIBYL, 1940), regeneration of th1 (Urbanek, 1997a, fig. 11).

repair can be seen through unconformities of fusellar structures. Repair is commonly seen in juvenile siculae. Many have experienced damage; regeneration of nemata and partly missing prosiculae are common. When damage occurred at a growing end of a colony (e.g., through breakage of part of the stipe), the zooids were able to regenerate and start secreting new fuselli without changing the design of the colony. If the damage occurred in older parts of the colonies, cortical tissue was used to repair the tubarium, but normal fusellar tissue was no longer developed. The repaired section was instead formed of a structureless film of material (BULMAN, 1970).

Malformation is also often visible in graptolites. Biserials can lack the second stipe as demonstrated from a specimen of *Dicaulograptus hystrix* (BULMAN, 1932), in which the second stipe is abandoned after a single theca, while the first stipe continued to grow a number of thecae (BULMAN, 1932b, pl. 9, fig. 9). Others develop a third stipe, as described in *Orthoretiolites hami* WHITTINGTON, 1954 (BATES & KIRK, 1991). MALETZ (2003) described an isolated specimen of *Normalograptus scalaris* (HISINGER, 1837) with a typical biserial proximal end and a distal portion lacking a second stipe. In this specimen, a thick covering of cortical material covers the ventral and lateral sides of the uniserial part. The dorsal part does not show a cortical cover and is broken, suggesting a genetically determined control of the deposition of cortical material. Malformation can also be seen in the accidental development of a partly biserial monograptid that was described by URBANEK (1997a) from isolated material (Fig. 44.1).

A special case of regeneration is the development of pseudocladia (URBANEK, 1963), seen in some species of *Diversograptus* and *Linograptus*. Broken stipe fragments of many monograptids are able to regenerate a complete second stipe as a pseudocladium, producing a bipolar colony without a sicula. RICKARDS (1973) illustrated a number of Silurian monograptid taxa from shale material, showing bipolar colonies without the presence of a sicula, but isolated specimens are extemely rare and usually fragmentary.

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