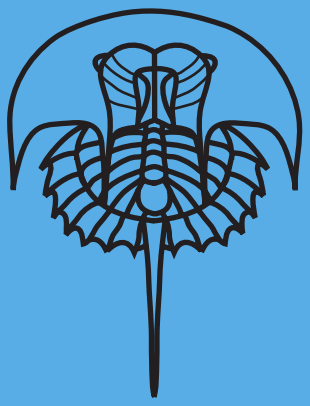

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PART V, REVISION 2, CHAPTER 12: GLOSSARY OF THE HEMICHORDATA

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PREFACE

The terminology of the Hemichordata used herein differs considerably from the terminology used in the previous versions of the "Graptolite *Treatise*" (Bulman, 1955, 1970), which were focused entirely on the fossil members of the Graptolithina and the few known tube-bearing extant and extinct Pterobranchia. Both classes were regarded as independent groups of the Hemichordata, but they are now included as a single taxon, the Pterobranchia, with the Graptolithina and the Cephalodiscida as two subclades (Mitchell & others, 2013). A number of terms had to be changed due to a better understanding of the construction of the graptolite tubarium and the phylogenetic relationships within the Pterobranchia, the main group of fossilized hemichordates, in an attempt to homogenize the terminology of these previously separated groups.

The term tubarium, for example, is reintroduced to the pterobranch terminology to describe the organic housing or domicile of all Pterobranchia, instead of using the term rhabdosome for the fossil Pterobranchia (Graptolithina in Bulman, 1955, 1970) and the coenecium for the extant members (Pterobranchia *sensu* Bulman, 1955, 1970). Lankester (1884) initially introduced the term tubarium to describe the housing of the extant Pterobranchia, as he considered the terms coenecium or zooecium inappropriate since they described the housing construction of bryozoans, to which the Pterobranchia were referred initially. Tubarium describes the housing construction of extant and extinct Pterobranchia more independently; it also describes it more precisely as being formed by glandular secretions and can easily be used for all members. It is therefore extended herein to include the homologous glandular constructions of the domiciles of fossil graptolite taxa.

Other terms, such as the periderm, have been eliminated due to constructional considerations. The term periderm, introduced by Wiman (1895), suggests a dermal construction of the tubarium, which is now known to be incorrect. The tubarium is formed from glands on the head shield of the zooids and is not a dermal construction as is the coenecium of a bryozoan. The tubarium can perhaps be compared with the formation of a hornet's nest, though a hornet's nest is largely constructed with foreign material. A comparison with hydrozoan colonies also falls short, as these are often covered by an organic exoskeleton, the perisarc (also identified as the periderm in Hyman, 1940, p. 400), which is secreted by the epidermis of the advancing stolon (e.g., Berking, 2006).

Early graptolite literature is written in a number of languages, including Chinese, Czech, English, French, German, Latin, Norwegian, Spanish, and Swedish. Thus, paleontological terms describing graptolite features were created in a variety of languages. Many terms originally proposed in other languages were translated into English before they became the standard,

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though a few kept their original form. Reference is given herein to the various terms translated from other languages to indicate the historical origin and evolution of the hemichordate terminology.

A number of papers were entirely dedicated to terminology (e.g., Törnquist, 1894; Wiman, 1893, 1896) or included chapters on terminology (e.g., Ruedemann, 1904; Jaanusson, 1960; Cooper & Fortey, 1982). However, I am not aware of any glossary for graptolite or pterobranch terminology, except for a German one (Kraatz, 1978), providing a compilation of graptolite terms in other languages than the English in the former versions of the Graptolite Treatise (Bulman, 1955, 1970). The German glossary (Kraatz, 1978) provides some translations of the terms of the English terminology, but no additional original terminology useful has been proposed and the terms are in general not included here.

References are provided for all morphological terms listed in this chapter, in case the terms were originally created for graptolites. The most recent revision is quoted and discussed in case of changes in use. General paleontological or biological terms not restricted to graptolites are not referenced. As modern taxa of the Enteropneusta are not included in the volume, and the anatomy of the soft-bodied organisms is not discussed, many terms related to the anatomy of these are not included herein, unless they are used in the various chapters dealing with taxonomy.

The precise terminology can have considerable effect on the taxonomic and evolutionary understanding of graptolite phylogenies and evolution. A good example is the use of the term virgella, long considered to be important for graptolite taxonomy and identified as a homologous character in all later graptoloids (Cooper & Fortey, 1982: Virgellina). However, as Bulman (1963b, p. 404) stated, "it is likely that the virgella spine has evolved more than once," a statement that was supported by the analysis of the dorsal and ventral virgellar spines by Maletz (2010). A differentiation of types of virgellar spines, therefore, is necessary for the understanding of graptolite taxonomy and evolution and should be reflected in the terminology.

General descriptive terms that have been used in the past to describe thecal form (dichograptid, glyptograptid, climacograptid) are not included herein and should not be used any more. These terms should be replaced by a more-precise constructional terminology. The climacograptid thecal style, for example, is based on a geniculate theca, but many apertural features in these thecae are not considered in this terminology (e.g., genicular additions, thecal apertural features, thecal overlap, local thickenings). Climacograptid thecae, in a very generalized sense, have been found in *Archiclimacograptus*, *Climacograptus*, *Amplexograptus*, *Monoclimacis*, *Pseudomonoclimacis* and other taxa and do not indicate a precisely defined term. These features are clearly developed independently in the listed genera.

Terms describing proximal development types (e.g., dichograptid, isograptid, diplograptid, and monograptid) are not included here as they are generalizations, initially used to describe the precise development of certain genera. They are now known to consist of numerous independently changing characters and are quite variable. Proximal development types, as long as they are used in graptolite taxonomy, are described in the individual chapters dealing with taxonomy.

Terms in bold type are recommended for use. Terms combining italic with nonbold type are not recommended for use.

MORPHOLOGICAL TERMS

abiesgraptid budding (Urbanek, 1963, p. 148). Mode of budding of thecal cladia in monograptids producing two daughter thecae symmetrically placed on either side of the mother theca and producing paired cladia.

abiesgraptid stage (Urbanek, 1963, p. 148). Stage of phylogenetic modifications in the development of a monograptid colony in which the procladium and the sicular cladium have acquired the ability to generate cladia.

aboral list (Bates, Kozłowska, & Lenz, 2005, p. 710). Thickened dorsal list at the base of the interthecal septum in axonophoran graptolites. Homologous with the transverse rod of the Retiolitidae.

adapertural plate (Urbanek, 1963, p. 147). The expanded base of the first theca of the second and subsequent sicular cladia in *Linograptus*, shaped as a subtriangular platform with the true thecal tubule rising on it.

anastomosis. A biological term used in pterobranch terminology to describe the temporary fusion of adjacent branches to form an ovoid mesh. Bulman (1945, p. 8) differentiated true anastomosis as a mere touching of stipes. Anastomosis including a thecal transfer is defined as pseudanastomosis by Rickards and Lane (1997, p. 173).

ancora, ancorae (Bouček & Münch, 1952, p. 4, fig. 1; Bates, Kozłowska, & Lenz, 2005, p. 706). Structure of four-branched lists formed at the end of the virgella in the Retiolitidae and some petalolithines. It includes the initial part of the ancora umbrella and the ancora sleeve.

ancora stage (Bouček & Münch, 1952, p. 4). Development of the ancora as the first stage in the growth of the ancora sleeve.

ancora sleeve (Bates, 1990, p. 719; Bates, Kozłowska, & Lenz, 2005, p. 706). Prolongation of the ancora umbrella of the Retiolitida to enclose the thecae on both the obverse and reverse sides of the tubarium, formed of a fusellar wall (usually not preserved) with bandaged lists secreted on one or both sides. Contact with the thecal framework is only along the lateral apertural rod (septal bar) portions of the apertural lists of the thecae.

ancora umbrella (Bates, Kozłowska, & Lenz, 2005, p. 706). Umbrella-shaped structure of lists developed from the ancora that comprises fusellar walls (not usually preserved), initially forking lists and subsequent spiral or polygonal lists, and, in some taxa, a circular rim with or without further looping lists.

angle of divergence (Herrmann, 1885, p. 43; Elles & Wood, 1901, p. 5, fig. 3); originally Divergenzwinkel (German). The angle between the ventral sides of the dorsal walls of the stipes, one of the features used to describe the tubarium shape.

annulus, annuli (Kozłowski, 1949, p. 55); originally bande annulaire (French). Internal bands on the sicula and early thecae of some monograptids, composed of fine, irregularly laminated cortical tissue forming thickened bands as secondary additions on the inside walls of siculae and thecae. Kraft (1926, p. 234) first misleadingly described this structure as Stillstandsgürtel (growth interruptions). Possible sicular annuli have also been described in dichograptids (Williams & Stevens, 1988).

Antisiculaseite (Wiman, 1895, p. 263; Holm, 1895, p. 436). Side of the graptoloid tubarium where the sicula is partly concealed by the crossing canal(s). See reverse.

antivirgellar spines. Spines opposite to the virgella of diplograptacean graptolites, usually paired, rarely single or multiple.

apertural apparatus (Kozłowski, 1962, fig. 3; Urbanek, 1966, p. 305); originally l'appareil apertural (French) of Kozłowski (1949, p. 28). All derivatives of the apertural segment of metatheca, which may consist of apertural lobe (or lobes), rostral processes, gorget, gular plate, and apertural lip.

apertural list (Lenz, 1994, p. 1345). List around the thecal apertures, originally described for Retiolitidae, but also useful for other graptolites. The term selvage has been used for the same feature.

apertural spine. Projection in form of a spine originating on the ventral or lateral margin of the thecal aperture, single or, less commonly, paired.

aperture. The opening of the thecal tubes. In the older literature (e.g., Barrande, 1850) the term orifice was used, but is now restricted to the secondary openings in the Retiolitidae; ostia (ostiae) is found in older literature for the apertures or openings of the housing of *Cephalodiscus.*

appendix (Bouček & Münch, 1952, p. 3). Reticulate tubular structure at distal end of the tubarium in the Plectograptinae, sometimes incorporating the nema, and interpreted as a terminal theca by Bates, Kozłowska, and Lenz (2005, p. 709).

apron (Loydell & Maletz, 2004, p. 69). Hoodlike growth over the central portion of the thecal aperture, formed from normal fuselli, generally covering the proximal and lateral apertural margins of the thecal aperture; present in some streptograptids (Monograptidae).

arienigraptid suture (Maletz & Mitchell, 1996, p. 642). Visible line of contact between the ventral walls of $th1^2$ and $th2^1$ on the reverse side in certain Isograptidae (*Arienigraptus*, *Pseudisograptus*).

arms. Paired extensions of the collar in pterobranch zooids (Fig. 1.2–1.3). Previously the term lophophore (see Lankester, 1884, p. 630) has been used for the arms of extant pterobranchs, but it is inappropriate as it suggests a homology to the Bryozoa.

aseptate. Biserial, dipleural tubarium lacking a median septum.

astogenetic patterns (Mitchell, 1987, p. 354). Sequence of budding at the initial dichotomy of the tubarium, giving rise to the first order stipes. See proximal development types.

astogeny. General biological term for the combined growth of individuals of a colonial organism; the growth of a graptolite colony describes the combined ontogenies of the zooids of a single colony (Urbanek, 1963, p. 148). See ontogeny.

auricula, auriculae (Kozłowski, 1962, p. 34). Expanded, earlike lateral lobes of highly modified thecae such as the cucullograptids (Monograptacea) and the Crustoidea.

autocortex (Urbanek & Towe, 1974, p. 13; Urbanek & Mierzejewski, 1984, p. 76). The individual cortical envelope of a theca, especially an autotheca. See ectocortex.

autotheca (Kozłowski, 1949, p. 24). The larger type of regularly developed graptolite thecae. Name proposed by Kozłowski (1949) in lieu of the term hydrotheca of earlier workers, which related the graptolites to the hydrozoans. See theca.

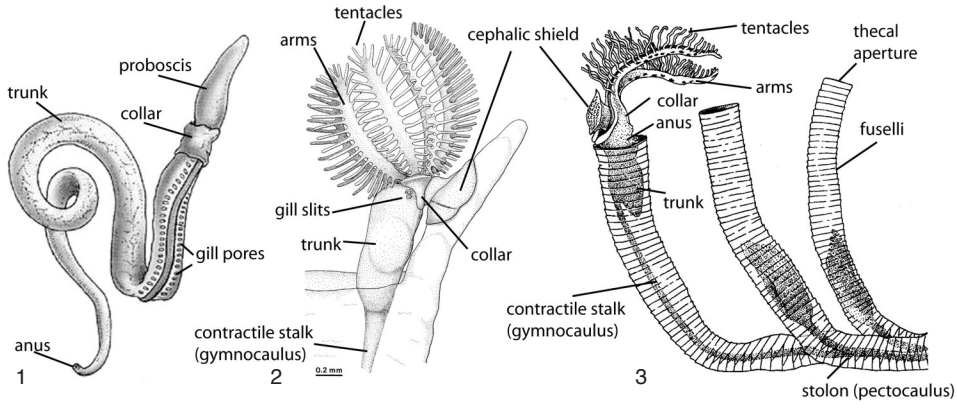

FIG. 1. Main parts of Enteropneusta (*1*) and Pterobranchia (*2–3*) anatomy. *1, Balanoglossus* sp.; *2, Cephalodiscus* sp. (adapted from Lester, 1985); *3, Rhabdopleura normanni* ALLMAN in NORMAN, 1869 (adapted from Schepotieff, 1907, pl. 22).

axial cord (SARS, 1872, p. 11). See pectocaulus.

axil (HOPKINSON, 1871, p. 20). Base of V-shaped bifurcation of dichotomously branched tubaria and especially the bifurcation of *Dicranograptus*, *Dicellograptus,* and *Oncograptus*.

axillary angle (ELLES & WOOD, 1904, p. 137). Angle between the dorsal sides of reclined stipes in uniserial and two-stiped reclined graptolites. See axil.

axonolipous (FRECH, 1897, p. 556). Term used in multiramous to pauciramous uniserial graptoloids. FRECH (1897) believed that the nema was lacking in these forms.

axonophorous (FRECH, 1897, p. 555). Term used in scandent biserial and uniserial graptoloids where the nema is enclosed in the tubarium or embedded in the dorsal wall of the stipes (see Axonophora).

bandages (CROWTHER & RICKARDS, 1977, p. 11). Parallel-sided deposits of aligned fibrils, usually covered by sheet fabric; mainly external (see Fig. 4); originally described as Chitinverdickungs-Bänder by KRAFT (1926, p. 231, pl. 7). See cortical bandages, cortex. KRAFT (1926, p. 231) described and illustrated the cortical bandages from isolated material, misinterpreting them as indications of the zooid anatomy (evidence of internal organs) due to his understanding of them being deposited on the inside of the sicula and thecae.

basal disc. Discoidal plate developed from apex of the sicula for attachment of dendroid graptolites.

basal membrane (KOZŁOWSKI, 1962, p. 10); originally membrane interthécale (French). Lower layer of the creeping tubes in encrusting graptolites and pterobranchs.

basal notch (URBANEK, 1963, p. 147). Incision in the margin of the ventral wall of the basal part of the first theca of the sicular cladia in *Neodiversograptus beklemiskhevi* and *Linograptus posthumus*.

biform (ELLES & WOOD, 1911, p. 361). Graptoloid tubarium with proximal and distal thecae of different form showing gradual or abrupt change along the length of the stipes of the tubarium; originally proposed for monograptids with at least two different types of thecae, but it can also be used for other graptolites with a thecal gradient.

bilateral symmetry. General biological term; symmetrical disposition of the stipes of the graptolite tubarium around the sicula. See also isograptid symmetry and maeandrograptid symmetry.

bipolar (URBANEK, 1963, p. 137; RICKARDS, 1973). Bilateral graptoloid tubarium formed as (1) a regeneration of a broken uniserial stipe through a pseudocladium or (2) a siculate monograptid with a sicular cladium; originally defined by URBANEK (1963, p. 137) exclusively for monograptids. ALBANI and others (2001, p. 390) identified janograptid "proximal ends" in dichograptids as regenerated uniserial stipes. The janograptid condition (genus *Janograptus*) in the Middle Ordovician is essentially an identical development to the bipolar regeneration with the formation of a pseudocladium in a monograptid.

biradiate (BULMAN, 1950, p. 68). Proximal development with two first-order stipes originating from the sicula through a single dicalycal theca; translated from bilateral (BULMAN, 1950, p. 68; see tri-radiate and quadri-radiate); revised by MALETZ (1992, p. 299). See triradiate, quadriradiate.

biserial. Scandent graptolitid tubarium with two series of thecae enclosing the nema; the thecal series can be arranged back to back (dipleural) (see Fig. 6.3) or side by side (monopleural) (see Fig. 6.4); also called duplex species by LAPWORTH (1873, p. 501) and diprionid in older literature. See uniserial, triserial, quadriserial.

bitheca, bithecae (HOLM, 1890, p. 10). Smaller type of regular graptolite theca, usually developed alternately on the right and left sides of the stipes (Fig. 2.3–2.5); corresponds to the gonangium, gonangia of early workers (see WIMAN, 1895, 1896).

black stolon (SCHEPOTIEFF, 1906, p. 465). The sclerotized, inflexible organic rod, usually embedded in the

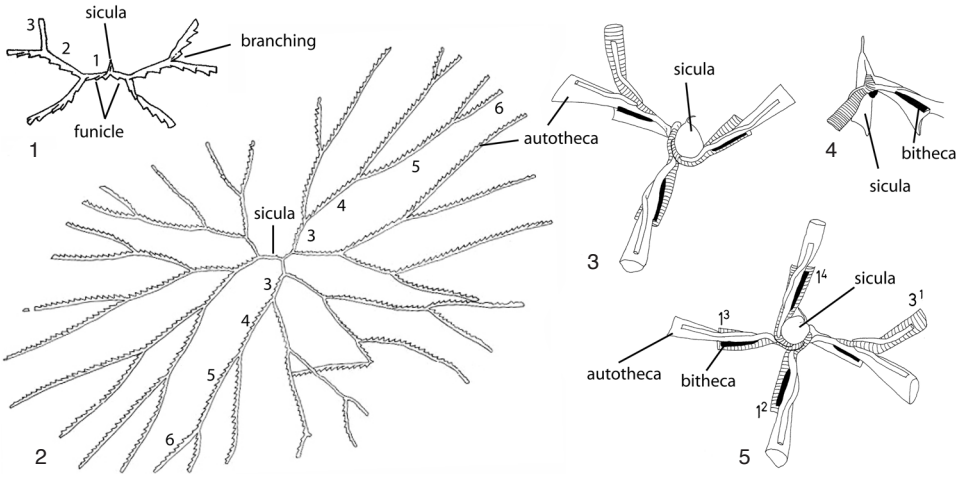

FIG. 2. Tubarium construction and terminology. *1–2,* Diagrams of *Clonograptus milesi* (HALL, 1861); numbers indicate the order of stipes (adapted from Lindholm & Maletz, 1989); *3–5,* succession of dicalycal thecae in quadriradiate to biradiate tubaria; dicalycal thecae are striped, bithecae are shown in black; *3,* tri-radiate *Anisograptus* RUEDEMANN, 1937; *4,* bi-radiate *Adelograptus* BULMAN, 1941; *5,* quadri-radiate *Staurograptus* EMMONS, 1855 (adapted from Maletz, 1992).

ventral wall of the mature tubes in the Pterobranchia (Fig. 1.3). See pectocaulus.

blastocrypt (URBANEK, MIERZEJEWSKI, & RICKARDS, 1986, p. 101). Secondary dark inner layer of the graptoblast.

blastotheca (URBANEK, MIERZEJEWSKI, & RICKARDS, 1986, p. 99). Terminal portion of a stolotheca and housed by a zooid that never functioned as an autozooid, being arrested in development of an early growth stage. See graptoblast, blastocrypt.

blastozooid (KOZŁOWSKI, 1971, p. 314). Term for the zooids of a graptolite colony formed through asexual budding.

branch. Single part of a branched graptolite tubarium (Fig. 2.1–2.2), sometimes used for the entire colony; in its strict sense it refers to the segment between dichotomies in multiramous forms (COOPER & FORTEY, 1982, p. 177). Earlier workers used the term frond (e.g., J. HALL, 1865). See stipe, which can be used interchangeably for branch.

branchial plumes (M'INTOSH, 1887, p. 10). Early term for the paired arms of pterobranch zooids; also branchial arms.

branching. Division of stipes. See dichotomous and cladial branching.

budding. Development of daughter zooids from the mother zooids in the Pterobranchia; also used for the branching of stipes.

budding individual (see BULMAN, 1932a, p. 26). Term used by earlier workers for the stolotheca or protheca.

calycle (J. HALL, 1865, p. 24). An early term for theca; see also denticle, cellule, cell, cup, and denticle (Zahn in German).

camara, camarae (KOZŁOWSKI, 1949, p. 170). Inflated proximal portion of autotheca in certain benthic, encrusting graptolites (camaroids, crustoids).

canaliculus, canaliculi (URBANEK, MIERZEJEWSKI, & RICKARDS, 1986, p. 103). System of parallel, fine canals perpendicular to the surface of the blastocrypt; first described but not named in URBANEK and RICKARDS (1974).

cauda, caudae (HUTT, 1974, p. 80). Parallel-sided, tube-shaped part of the prosicula, closed at the apex and provided with a spiral thread; identical to the nema prosiculae of KRAFT (1926, p. 222).

caulotheca (LANKESTER, 1884, p. 634). Thick, hard rim or cuticle formed on the gymnocaulus during transformation into the pectocaulus.

cell, cellule. Term used by earlier workers for theca (see BARRANDE, 1850, p. 5; J. HALL, 1865).

central disc (J. HALL, 1865, p. 20). Web of sclerotized tissue uniting the proximal ends of stipes in some graptoloid tubaria, mostly Dichograptidae; interpreted to be formed by addition of cortical bandages or cortex, but not known from isolated material.

cephalic disc, cephalic shield. The frontal part of the pterobranch zooid with the glands secreting the tubarium (Fig. 1.2–1.3); identical to the buccal disc or buccal shield of M'INTOSH (1887, p. 8), the buccal shield and praeoral lobe of LANKESTER (1884), the proboscis of HARMER (1905, p. 26).

cephalic plumes (M'INTOSH, 1887, p. 10; RIDEWOOD, 1907, p. 221). Early term for the arms of the pterobranch zooids; also termed branchial plumes, lophophor arms or branchial arms.

Chitinverdickungs-Bänder (German) KRAFT (1926, p. 231). See cortical bandages.

cladial branching (ELLES & WOOD, 1914, p. 505). Division of stipe where the branches originate from a thecal aperture or the sicular aperture. See dichotomous branching.

cladium, cladia (Elles & Wood, 1911, p. 505). Stipe developed from a mature thecal aperture through cladial branching. Urbanek (1963, p. 147) used the term cladium for any graptolite stipe, but it is suggested herein that the term be used in the restricted sense of Elles and Wood (1914), as it is generally used in the literature for a secondary branching from a thecal (or sicular) aperture. See procladium, metacladium, pseudocladium.

cladogeny (see Urbanek, 1963, p. 148). Describes (1) the growth of a colony or tubarium (rhabdosome) (Beklemishev, 1952) or (2) the branching of evolutionary lineages (Rensch, 1947).

clathrium, **clathria** (Bouček & Münch, 1952, p. 5; Bates, Kozłowska, & Lenz, 2005, p. 709). Skeletal framework of rods (lists) forming the preservable part of the retiolitid tubarium; supporting the reticulum or an attenuated fusellum. Included in this definition are lists of both the thecal framework and the ancora sleeve (Retiolitida). See reticulum.

clathriate. Possessing a clathrium.

coenoecium, coenoecia (Allman, 1856, p. 8). Describes the common dermal system of the Bryozoa [Polyzoa], consisting of ectocyst and endocyst; introduced for the tubarium of *Rhabdopleura* by Allman (in Norman, 1869, p. 312) and commonly used for extant Pterobranchia; equivalent to the terms rhabdosome and tubarium in the description of the Graptolithina.

collar. (1) Part of the pterobranch zooid on which the arms are positioned (Fig. 1.2–1.3), behind the cephalic shield; term originates from the homologization of the tripartite body development with the Enteropneusta *(Balanoglossus)* (Harmer, 1905, p. 30). (2) Externally protruding part of fusellar rings in erect fullrings of *Rhabdopleura* tubaria (Kulicki, 1969, p. 539). (3) Wide genicular rim or hood in *Lithuanograptus (=Metaclimacograptus)* described by Paskevicius (1976, p. 140); formed from microfusellar tissues (Maletz, 1997, p. 21). See fusellar collar.

collum, colla (Kozłowski, 1949, p. 170). Erect distal tubular portion of the autotheca in some early benthic graptolites (camaroids); not homologous to erect tubes of *Rhabdopleura.*

colony. Biological term to describe close associations of individuals of one species living together in some degree of interdependence; strictly, the members of a colony are in organic connection with each other. Term to describe the association of pterobranch individuals or zooids in constant organic contact with one other for mutual benefit and for secreting a common extracellular tubarium (Graptolithina). In a strict sense, this definition means that *Cephalodiscus* does not produce a colony, but an association of individuals, as these are not in a constant, life-long, organic contact, as are the zooids of *Rhabdopleura*.

columella (Cooper & Fortey, 1982, p. 282). Thickened column in the center of *Phyllograptus* colonies.

common canal (**Barrande, 1850, p. 5**; J. Hall, 1865, p. 23); originally canal commun (French). Continuous tubular cavity collectively formed by the prothecae of graptoloids connecting the individual thecae.

connecting canal (Törnquist, 1893, p. 5). Term used by earlier workers for the crossing canal.

connecting rod (Bates, Kozłowska, & Lenz, 2005, p. 709). Rod linking transverse rod and nema in Retiolitidae.

consecutive dichotomy (Cooper & Fortey, 1982, p. 176, fig. 6). Branching pattern in dichograptids in which only a single theca separates successive dichotomies, as in *Goniograptus.* See delayed dichotomy.

conotheca, conothecae (Bulman & Rickards, 1966, p. 50). Relatively large, conical theca with a small circular aperture; irregularly developed in tubaria of some tuboid graptolites.

contractile cord (Sars, 1872, p. 10). See gymnocaulus.

contractile stalk (Schepotieff, 1907, p. 199) The unsclerotized, contractile stalk of the pterobranch zooid; identical to the contractile cord of Sars (1872, p. 10), the funiculus of Allman (1869) and homologous to the pedicle or peduncle of *Cephalodiscus* (M'Intosh, 1887, p. 20). Originally kontraktiver Stiel (German). See gymnocaulus.

conus, coni (Hutt, 1974, p. 80). Distal, cone-shaped part of the prosicula, separated from the cauda by an internal diaphragm.

corona, coronae (Eisenack, 1951, p. 156; Bouček & Münch, 1952, p. 5). Initial proximal part of the ancora sleeve in the Retiolitida; Eisenack (1951) used the German term Kuppel, translated as corona by Bouček & Münch (1952). As used by Bouček & Münch (1952), it comprises the ancora, ancora umbrella, and lists to the base of the first thecal pair.

corona stage. See ancora umbrella.

cortex, cortical tissue (Kozłowski, 1949, p. 41–42). The outer layer of the graptolite housing construction, formed by slender, parallel-sided bandages (see Fig. 4); the cortex produces the secondary thickening of the tubarium walls; the secondary lamellae of Harmer (1905, p. 10) in extant Pterobranchia. See fusellum.

cortical bandages (Crowther & Rickards, 1977, p. 11). Formation of cortical layers from thin bandages, crisscrossing the fusellar construction of the tubarium, first described in detail by Crowther (1978, 1981). Kraft (1926, p. 231) described cortical bandages as Chitinverdickungs-Bänder (German) and misinterpreted them as internal features. Bulman (1932b, pl. 3, fig. 7–8: *Climacograptus diplacanthus*) illustrated cortical bandages in *Diplacantograptus spiniferus.* See cortex.

crassal fabric (Urbanek & Towe, 1974, p. 4). Electron dense and homogeneous material, sometimes with indistinct layering but usually lacking a pattern, producing a compact wall of considerable thickness forming the stolons.

crossing canal (Elles & Wood, 1901, p. 6). Proximal (prothecal or initial) portion of the primordial graptoloid thecae growing across the axis of the sicula on the reverse side of the sicula to develop fully on the opposite side. Earlier workers used the term connecting canal (see Törnquist, 1893, p. 5).

cryptopyle (Kozłowski, 1962, p. 19). Single or paired opening at the distal end of a graptoblast, opposite to the filum.

cryptoseptate, cryptoseptum (Urbanek, 1959, p. 290). Biserial tubaria in which the median septum is com-

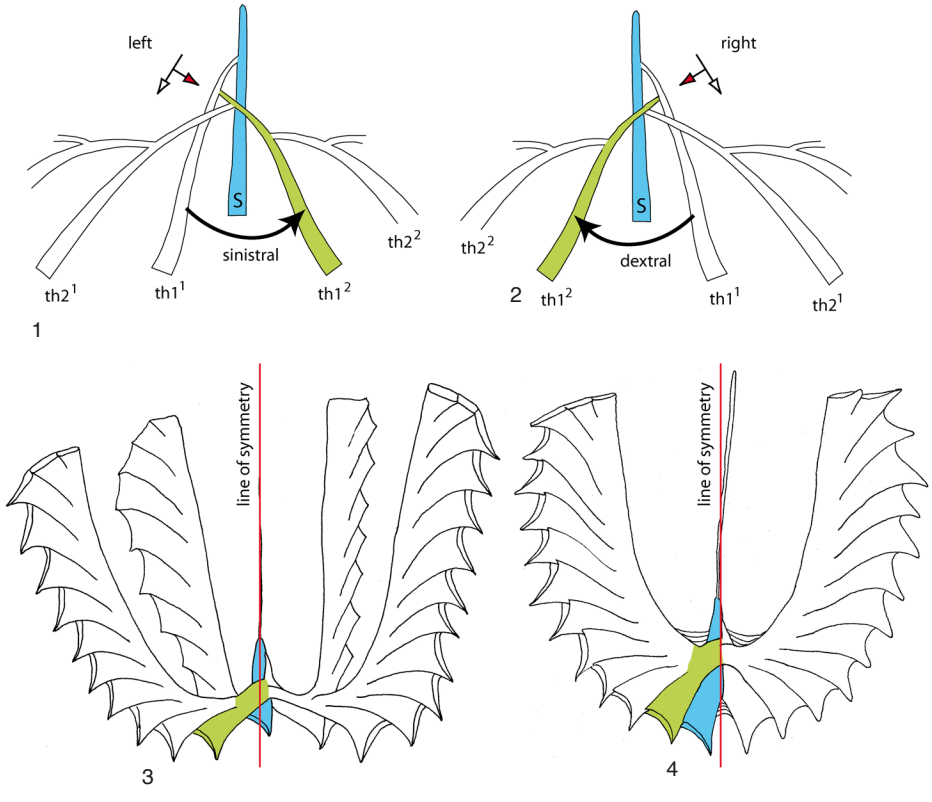

FIG. 3. Diagramatic depiction of sinistral *(1)* and dextral *(2)* development and maeandrograptid *(3)* and isograptid *(4)* symmetry, with the line of symmetry shown in red (sicula in *1–2* adapted from Toro & others, 2008, fig. 6; *3–4,* adapted from Maletz, 2011, fig. 2).

posed of cortical rods arranged as in septate forms, but lacking a fusellar septal membrane.

cupula, **cupulae** (LOYDELL & MALETZ, 2004, p. 68). Paired bulbous protuberances on the dorsal side of some monograptoid graptolites, flanking the nema. Cupulae are believed to represent prothecal folds at the base of the thecae. Cupulae occur in *Streptograptus* and related taxa (Monograptidae).

cyrtograptid budding (URBANEK, 1963, p. 148). Budding of a theca directly from the aperture of the mother theca. See cladial branching.

cyrtograptid stage (URBANEK, 1963, p. 148). Stage of phylogenetic modifications in the development of a colony, during which the process of astogeny produces a procladium and at least one thecal cladium that is generated by cyrtograptid budding. See cladial branching.

cyst, cysts. Common biological term. (1) Vesicles of varying size and shape occurring in autothecal cavities of crustoids. (2) Surface features in graptolites that may represent parasitic organisms.

declined (ELLES & WOOD, 1901, p. 5, fig. 3). Describes graptoloid tubaria with branches hanging below the sicula, subtending an angle of less than 180°, but not parallel to each other (pendent).

deflexed (ELLES & WOOD, 1901, p. 5, fig. 3). Similar to declined but with distal extremities of stipes tending to become horizontal.

delayed dichotomy (COOPER & FORTEY, 1982, p. 176, fig. 6). Branching pattern in dichograptids in which two or more thecae separate successive dichotomies after the first dichotomy, as, for example, in *Laxograptus*. See consecutive dichotomy.

dendroid, dendroidal. (1) Belonging to the order Dendroidea. (2) Descriptive term for tubarium growth showing irregular, bushy colony shapes in benthic graptolites.

denticle. Term used by earlier workers to describe the thecae of graptolites, and later by English workers for the ventral extension of the prosicula of dendroids along the zigzagging line of suture; considered imprecise by KOZŁOWSKI (1949, p. 20), who replaced it by the term languette. See rutellum.

denticulate. Pointed sicular and thecal apertures provided with a short spine or rutellum.

development type. See proximal development type.

dextral (Cooper & Fortey, 1982, p. 174). Clockwise direction of growth of tubarium (Fig. 3.2). See sinistral.

diad, diad budding (Kozłowski, 1949, p. 141). Mode of budding in pterobranchs resulting in two zooids at each nodal division, lacking regularity of thecal succession. See also triad budding.

diaphragm (Hutt, 1974, p. 80). Membrane stretching across the initial part of the prosicula and separating the conus from the cauda; identified first by Kraft (1926) as a membrane. See also stolonal diaphragm (Urbanek & Dilly, 2000).

diaphragm complex (Urbanek & Dilly, 2000, p. 214). Complex structure developed at the apex of the initial stolon of *Rhabdopleura* inside the mother theca.

dicalycal theca (Jaanusson, 1960, p. 303). Graptoloid theca giving rise to two daughter thecae, resulting in branching of multiramous graptolites. See monocalycal theca.

dichotomous branching. Stipe division where two branches diverge symmetrically from the parent stipe; see lateral branching, cladial branching. In a more restricted sense, also used for branching at the distal end of the graptolite.

dichotomy. Branching division with two stipes originating at the same point. The direction of growth of the parent stipe is abandoned, with the two stipes growing at identical angles away from it. See lateral branching.

dipleural (Jaanusson, 1960, p. 303). Biserial graptoloid tubaria in which two stipes are in back-to-back contact, resulting in two external lateral walls (Fig. 6.3). See monopleural.

diprionid. Early term for biserial (Barrande, 1850; Tullberg, 1883, p. 13).

discophorous (Kozłowski, 1971, p. 314). Possessing a sicula with an attachment disc, but lacking a free nema; taken as indication of a benthic life style. See nematophorous.

discoidal preservation. Disclike view of the (multiramous) tubarium with the sicula roughly perpendicular to the stratification. See lateral preservation.

dissepiment. Strand of cortical tissue connecting adjacent branches or stipes in graptolite tubaria. Harmer (1905, p. 16) discusses numerous bridges connecting adjacent branches in *Cephalodiscus dodecalophus*. These may be constructionally homologous to the dissepiments in the Graptolithina. In botany, the term is used differently to denote a partition dividing an organ into chambers.

distal. Last-formed part of tubarium, stipe, or theca; farthest from the point of origin.

distal lobe (Loydell & Maletz, 2004, p. 69). Rounded or elongated, broadly triangular processes on the lateral apertural margins of streptograptids (Monograptidae).

diversograptid budding (Urbanek, 1963, p. 148). The budding of a theca directly from the aperture of sicula, producing only one sicular cladium and not capable of producing more cladia; synonymous with cladial branching.

diversograptid stage (Urbanek, 1963, p. 148). Stage of phylogenetic modifications in the development of a colony, in which astogeny results in the formation of a bipolar tubarium consisting of a procladium and sicular cladium and also of the thecal cladia budding from them.

dormant buds (Stebbing, 1970, p. 210). Large closed, vesicular bodies; interpreted as enclosing hibernating zooids, and also identified as sterile buds by Schepotieff (1907, p. 198: sterile Knospen). See hybernacula, statoblast.

dorsal. Term denoting the side of the stipe opposite to the thecal apertures, or a comparable side of the thecal aperture; not necessarily related to direction of growth, but presumably to the dorsal side of the zooids.

ectocortex (Crowther, 1981, p. 13; Urbanek & Mierzejewski, 1984, p. 76). The cortical material deposited on the outer surface of the thecal walls or, generally, on the outer surface of the tubarium. Urbanek and Towe (1974) differentiated the ectocortex into autocortex and rhabdocortex. See endocortex.

end bulbs (M'Intosh, 1887, p. 11). Bulbous structures at the tips of the arms of *Cephalodiscus* zooids. M'Intosh (1887, p. 11) described the end bulbs as glandular, but Harmer (1905, p. 39) stated that there is no evidence for a function of the end bulbs.

endocortex (Urbanek & Mierzejewski, 1984, p. 76). The cortical material deposited on the inner surface of the thecal walls or, generally, within the cavities of the tubarium. See ectocortex.

eucortex (Urbanek & Mierzejewski, 1984, p. 76). The secondary component made of the typical cortical tissue, including sheets, well-defined straight, parallel, fibrils and some ground substance.

everted. Outward-facing thecal aperture.

exoskeleton. Term often used for the coenecium or tubarium (rhabdosome) of graptolites. The graptolite tubarium is not an exoskeleton, but a housing structure or domicile, secreted by the organism. See tubarium.

extensiform (Elles & Wood, 1901, p. 5, fig. 3). Term denoting stipes growing more or less horizontally away from the vertical sicula.

external orifice (Barrande, 1850, p. 6). Term used by Barrande for the thecal aperture.

extroverted. Thecae turned back upon themselves by the exaggerated growth of the dorsal margin of the aperture.

fibrils, fibrillar structure (Dilly, 1971, p. 502). Ultrastructural features of the graptolite fusellum; the fine elements forming the collageneous material of the graptolite and pterobranch fusellum. The term fibrils was also used for the surface patterns of cortical bandages in the Retiolitinae by Bates and Kirk (1978, pl. 4), now described as longitudinal striations (Lenz & Melchin, 1987a, p. 162).

filum, fila (Kozłowski, 1949, p. 207). Remains of the stolon in graptoblasts.

finite. Graptolite tubarium with limited growth, forming terminal thecae of reduced size or special shape; found in some Retiolitidae, but also in the Axonophora, such as the genera *Brevigraptus* and *Corynoides.*

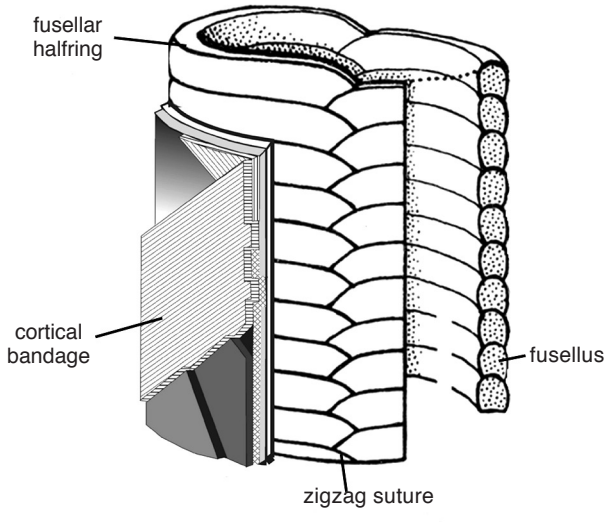

FIG. 4. Formation of the tubarium through fuselli and cortex (adapted from Crowther, 1981).

flabellate. Fan-shaped tubarium form with stipes spreading out in a single plane; used for benthic graptolites.

float. A membrane at the proximal or distal end of a tubarium that is interpreted as supporting a stable orientation of the tubarium in the water column or as a float or flotation device. See **nematularium.**

foramen, foramina. (1) Opening in the sicula for the development of the bud of th1[1]. (2) Opening in retiolitid colonies, not to be confused with thecal apertures. See primary porus, resorption foramen.

fornical foramen (COOPER & FORTEY, 1982, p. 180). The wide openings between thecal series in *Phyllograptus,* representing the remains of the median septum between the four scandent thecal series.

fornix (COOPER & FORTEY, 1982, p. 180). The arched strut standing in place of the median septum in the axial region of the quadriserial *Phyllograptus.*

free ventral wall. The portion of the ventral thecal margin that extends beyond the aperture of the preceeding theca.

frond. Term used by earlier workers (e.g., J. HALL, 1865) for the stipes of graptolites.

funicle (from the Latin funiculus, funiculi) (J. HALL, 1865, p. 19; LINDHOLM & MALETZ, 1989, p. 713). The combined first-order stipes in the multiramous graptoloids (Fig. 2.1). Originally proposed by J. HALL (1865) for non-thecate intial parts of dichograptids connecting thecate stipes. It is now known that thecae are present throughout the proximal area in graptolite colonies, but that they may be obscured by secondary overgrowth.

fusellar collar. Externally protruding part of fusellar ring in erect fullrings of *Rhabdopleura* tubaria (KULICKI, 1969, p. 539); called ribs, Rippen, or Kragen in ANDRES (1977, p. 57). See collar.

fusellar tissue (KOZŁOWSKI, 1949, p. 20, 40–41). Inner organic layer of the tubarium, generally composed of alternating L and R bands of fuselli. See fusellum.

fusellum, fusella (KÜHNE, 1955, p. 363; URBANEK & TOWE, 1974, p. 4; URBANEK & MIERZEJEWSKI, 1984, p. 74). Primary skeletal material of graptolites and pterobranchs, formed from fuselli. See cortex.

fusellus, fuselli (KOZŁOWSKI, 1949, p. 20). Individual halfrings or fullrings of scleroproteic material secreted by the cephalic disc of the graptolite and pterobranch zooids and forming the tubarium (Fig. 4) and laid down sequentially. Fuselli were first described as Querrunzeln by RICHTER (1871, p. 233), who stated that they form a zigzag suture on the dorsal and ventral sides of the cells; recognized as growth lines by LAPWORTH (1873). HARMER (1905, p. 10) identified fuselli as the primary lamellae in extant Pterobranchia. See growth lines.

geniculum (JAANUSSON, 1960, p. 304). Angular bend in the upward ventral direction of growth of the graptoloid theca. It may be adorned with a thickened rim, spines, or other genicular processes.

genicular process (JAANUSSON, 1960; BATES, KOZŁOWSKA, & LENZ, 2005, p. 709). Processes formed at the geniculum of a graptolite theca.

glossograptid bulge (MALETZ & MITCHELL, 1996, p. 643). Conspicuous proximal bulge formed by a variable number of proximal thecae growing in a spiral pattern and covering the sicula and th1[1] on both the obverse and reverse sides of the Glossograptidae; first illustrated from isolated material by WHITTINGTON and RICKARDS (1969).

gonangium, gonangia. Term used by earlier workers for the bithecae (e.g., WIMAN, 1895, 1896). RUEDEMANN (1895) also used the term to describe the oval disk to which *synrhabdosomes* are attached.

graptoblast (Kozłowski, 1949, p. 206). Ovoid-shaped chambers present in crustoids; interpreted as rejuvenated zooidal chambers by Urbanek & Mierzejewski (1984) and Mierzejewski (2000).

graptolite. General term for the tubaria of the Graptolithina; derived from the genus *Graptolithus* Linnaeus, 1735; originally interpreted as inorganic markings by Linnaeus (1735).

grapto-gonophore (Nicholson, 1866, p. 489). Fossils identified as ovarian vesicles or grapto-gonophores, but representing various non-graptolitic taxa (Page & others, 2009).

growth lines. Expression of the fusellar structure (see fuselli) on the surface of the graptolite tubarium; first described by Barrande (1850, p. 8: striae), but not recognized as such. Lapworth (1873) was the first to describe the striae on the surface of many graptolites as growth lines. Richter (1871, p. 233) described growth lines of graptolites with the term Querrunzeln and remarked that they form a zigzag suture (Zickzacknaht) on the upper and lower side of the thecae (Zellen, cells).

gymnocaulus (Lankester, 1884, p. 629). The unsclerotized, contractile stalk of the pterobranch zooid (Fig. 1.2–1.3); identical to the contractile cord of Sars (1872, p. 10), the funiculus of Allman (1869) and homologous to the pedicle or peduncle of *Cephalodiscus* (M'Intosh, 1887, p. 20). The previous definition in Bulman (1970, p. 10), "Unsclerotized stolon situated behind the terminal bud in *Rhabdopleura* from which the zooids proliferate," relates only to the terminal bud in *Rhabdopleura* and not to the individual gymnocauli of the zooids; thus, it does not convey the original meaning of Lankester (1884). The term is also used for the homologous unsclerotized stolon in graptolites (Hutt, 1974, p. 81).

heart-shaped axial cavity (Xiao & Chen, 1990, 1994). Cavity enclosed by the two reclined and subsequently scandent stipes in *Proncograptus*, *Procardiograptus,* and *Diceratograptus.*

helical line (Kozłowski, 1949, p. 56); originally ligne hélicoïdale (French). See also spiral thread or spiral line. Identical to the Schraubenlinie of Kraft (1926).

helicotheca (Kozłowski, 1949, p. 163); originally hélicothèque (French). Type of autotheca in Tuboidea with coiled initial part.

Höckerchen (Eisenack, 1951, fig. 11). See pustules.

horizontal. Graptoloid tubarium with stipes growing at a right angle to the axis of the sicula. See extensiform.

hybernacula (Lankester, 1884, p. 639). Large, closed, vesicular bodies; interpreted as enclosing hibernating zooids, also identified as statoblasts (Lankester, 1884, p. 639) and sterile buds by Schepotieff (1907, p. 198: sterile Knospen). See dormant buds.

hydrorhabd (Frech, 1897, p. 549). See tubarium.

hydrosome. Term used by earlier workers for the graptolite tubarium, suggesting a relationship to the Hydrozoa. Ruedemann (1895, p. 224) used the term for synrhabdosomes.

hydrotheca (e.g.,Nicholson & Marr, 1895, p. 529). Term used by earlier workers for the autothecae of the Dendroidea and other benthic graptolite groups and for the thecae of the Graptoloidea, suggesting a relationship to the Hydrozoa.

hypoblastic (Legrand, 1987, p. 61). Term for a certain proximal development type.

infragenicular wall (Jaanusson, 1960, p. 304). Thecal wall between the geniculum and the preceeding theca in geniculate graptolites.

initial bud. Outgrowth formed by the first post-sicular zooid through a foramen in the sicular wall, producing the first theca of the tubarium.

initial foramen. Opening for the first post-sicular zooid of a graptolite colony.

Initialteil (Wiman, 1895, p. 263). See prosicula.

internal orifice (Barrande, 1850, p. 7). Primary opening in the mother theca from which the daughter theca originates.

interpleural list (Lenz, 1993, p. 12). Medially placed ventral list connecting the upper apertural list of one theca with the lower apertural list of the succeeding thecal aperture of a retiolitid tubarium (synonym of the mid-ventral list).

interthecal septum (Törnquist, 1893). Membrane separating the overlapping thecal cavities in graptoloids. It comprises the dorsal wall of a theca and part of the ventral wall of the succeeding theca.

introverted. Inward-facing thecal aperture resulting from the exaggerated growth of the ventral wall of the thecae; usually accompanied by the sigmoidal curvature of the thecal axis.

introtorted. Refers to the change in direction of growth of the metatheca toward, rather than away from, the dorsal stipe margin, as in *Dicranograptus.*

isograptid arch (Cooper & Fortey, 1982, p. 180). The arch formed by the ventral walls of the dicalycal theca and its first daughter theca. The structure helps distinguish development types in dichograptids; in species with artus-type proximal development, there is a single thecal aperture showing beneath the arch (that of the sicula), whereas in isograptid-type proximal development, there are two apertures showing beneath the arch (those of the sicula and $th1^1$).

isograptid suture (Maletz, 1994, p. 28). Line of contact between the sicula and $th1^1$, which is visible in reverse view below the isograptid arch in many dichograptids. It gives a measure of the position of the crossing canals on the sicula.

isograptid symmetry (Cooper, 1973, p. 56; Cooper & Fortey, 1982, p. 180). Sicula and $th1^1$ forming a symmetrical pair (Fig. 3.4). See maeandrograptid symmetry.

keroblastic (Legrand, 1987, p. 61). Term for a certain proximal development type in Llandovery axonophorans.

Kuppel (Eisenack, 1951, p. 156). See corona.

labia, labiae (Lenz & Kozłowska Dwidziuk, 2004, p. 17). Thickened apertual lip with distinctive paired structures in Retiolitidae (*Neogothograptus*).

lacinia (Elles & Wood, 1908, p. 319; revised by Bates, 1990, p. 717). A three-dimensional network of unseamed lists, thickened by concentric growth of bandages. The lists are attached to ventral apertural spines, to paired obverse and reverse spines branching from the nema, and also to the virgella and paired

dorsal sicular apertural spines. A lacinia is present in the Archiretiolitidae and in *Paraglossograptus* (Glossograptidae). Originally termed marginal meshes by Lapworth (in Hopkinson & Lapworth, 1875, p. 641).

lacuna stage (Eisenack, 1942, p. 31); originally Lacuna-Stadium (German). Second stage in the development of the initial foramen of the growth of the first theca in the Monograptacea. The primary foramen is surrounded by fusellar growth bands. See sinus stage, porus stage.

Längsverstärkungsleisten (Kraft, 1926, p. 224). See longitudinal ridges, longitudinal strengthening rods.

languette (Kozłowski, 1949, p. 20, 22, and 33). The apertural ventral and dorsal terminal extensions of the thecae in dendroid graptolites along the zigzag suture line of the fuselli. It replaced the less-precise denticle of English workers, which had been originally used for the thecae of graptolites. Kozłowski (1949, p. 22) differentiates a dorsal languette and a ventral languette. The ventral languette is homologous to the rutellum of Williams and Stevens (1988).

lappet. Rounded lateral apertural processes of thecae or the sicula; mistakenly also used for ventral apertural lappets, now called rutelli.

lateral apertural rod (Bates, Kozłowska, & Lenz, 2005, p. 709). The part of the apertural list in Retiolitidae that connects with the lists of the ancora sleeve.

lateral branching. A special case of dichotomous branching in which one of the stipes diverges at an angle to the parent stipe, which continues its original direction of growth (e.g., *Holograptus*).

lateral preservation. (1) Tubarium showing only one side (see discoidal preservation). (2) Lateral preservation in stipes indicated by the typical sawtooth appearance, showing thecal rutelli.

lateral proximal orifices (Bates, Kozłowska, & Lenz, 2005, p. 720). Openings on the lateral wall between the rim of the ancora umbrella and base of ancora sleeve.

left-handed (origin of thecae) (Stubblefield, 1929, p. 274; revised by Cooper & Fortey, 1982, p. 173). Refers to thecae originating on the (biologically) left side of the theca when seen from the dorsal side.

lenticular porus (Dawson & Melchin, 2007, p. 91). An opening for the emergence of the first post-sicular zooid, which is left in the metasicula. A number of pre-porus fuselli are deflected proximally around the subsequently forming th1 bud and continue their path in a distal direction onto the virgellar spine. One or two truncated or incompletely formed fuselli may be present. The post-porus fuselli are deflected in the opposite direction, but resume their original direction close to the virgellar spine, forming a lenticular primary opening for the th1 bud. See primary porus, resorption foramen.

linea (Lapworth, 1897, p. 251). See nema.

linograptid budding (Urbanek, 1963, p. 148). Term used to denote multiple sicular cladia.

linograptid stage (Urbanek, 1963, p. 148). A stage of phylogenetic modification in the development of a colony, in which a procladium and numerous sicular cladia are produced in astogeny; restricted to the genus *Linograptus.*

list, lists (revised by Bates, Kozłowska, & Lenz, 2005, p. 709). Skeletal rod in Retiolitidae that strengthens the fusellar walls with localized cortical bandages.

longitudinal ridges, longitudinal strengthening rods (Kraft, 1926, p. 224); originally Längsverstärkungsleisten (German). Cortical ridges on the outside of the prosicula, formed before the growth of the metasicula.

lophophore (Lankester, 1884, p. 630). Paired arms or groups of arms in the zooids of pterobranchs, provided with ciliated tentacles and situated adjacent to the mouth of the zooid; originally lophophor arms or branchial arms (Lankester, 1884, p. 630), but also branchial or cephalic plumes (M'Intosh, 1887, p. 10; Ridewood, 1907, p. 221). A lophophore is typically present in Brachiopoda, Bryozoa, and Phoronida; thus, the term should not be used for the Pterobranchia. See arms.

maeandrograptid symmetry (Cooper, 1973, p. 56; Cooper & Ni, 1986, p. 316). Used to describe $th1^1$ and $th1^2$ forming a symmetrical pair on both sides of the sicula (Fig. 3.3). See isograptid symmetry.

manubrium (Cooper, 1973, p. 54; Maletz & Mitchell, 1996, p. 642). A complex and prominently shouldered structure on the reverse side of arienigraptid graptolites (Isograptidae), which is formed by the strong downward growth of the initial part of $th1^2$ and $th2^1$ and their descendant thecae. It always involves the formation of an arienigraptid suture. The sicula and the early thecae extend downward at least as far as their descendant thecae.

manubrium shoulders (Cooper & Ni, 1986, p. 315). Dorsal margin of the manubrium, from the origin of the stipes at the sicula to the sharp dorsal flexure in the dorsal stipe margin.

manubriate (Cooper, 1973, p. 56). Tubaria having a manubrium.

marginal meshes (Lapworth in Hopkinson & Lapworth, 1875, p. 641). See lacinia.

median plane (Cooper & Fortey, 1982, p. 178, fig. 8). The plane of symmetry of branching tubaria, containing the tubarium midline and the two first-order stipes.

median septum. Membrane in quadriserial, triserial, and biserial dipleural graptoloids, separating the thecal series, originating at various levels in the tubarium. In some biserial dipleural forms, a partial median septum occurs on the obverse side only.

mesial. (1) The middle part of the tubarium. (2) The middle part of the free ventral wall (supragenicular wall) of a theca.

metacladium (Urbanek, 1963, p. 147). Thecal or sicular cladium as opposed to *procladium* or main stipe. See cladium.

metasicula (Kraft, 1926, p. 225). Distal part of sicula composed of fusellar growth bands or fuselli; named the Aperturalteil by Wiman (LOVE 1895). See prosicula.

metatheca. Distal part of the graptoloid theca. See protheca.

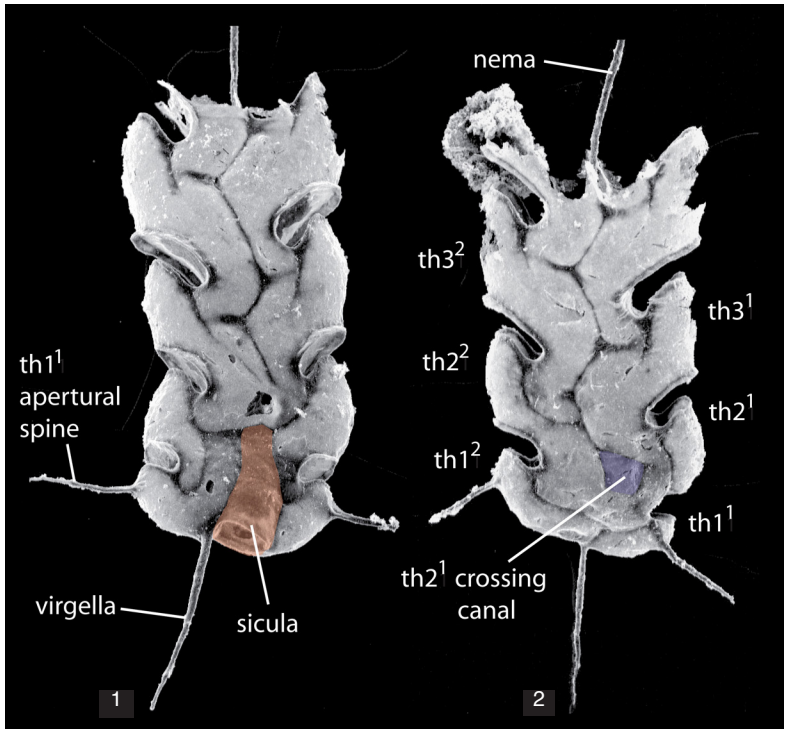

FIG. 5. SEM photos of *Archiclimacograptus* sp. (western Newfoundland) illustrating obverse *(1)* and reverse *(2)* views of a biserial, dipleural tubarium, with thecal notation (new).

microfusellar tissue (URBANEK, 1970, p. 194). Fusellar substance composed of extremely fine and somewhat irregular growth bands.

microtheca (KOZŁOWSKI, 1949, p. 163); originally microthèque (French). Type of autotheca occurring in Tuboidea, characterized by a narrow terminal portion and differently oriented apertures.

mid-ventral list (BATES, KOZŁOWSKA, & LENZ, 2005, p. 709). Centrally placed longitudinal list running from the transverse rod or from the genicular list to the thecal lip (Retiolitidae). Identical to interpleural list of LENZ (1993, p.12).

monocalycal theca (JAANUSSON, 1960, p. 303). Graptoloid theca giving rise to only one subsequent thecae. See dicalycal theca.

monofusellar tissue (URBANEK, 1958, p. 19). Fusellar substance deposited in single and not alternating series of growth bands, forming full fusellar rings (e.g., the erect tubes of *Rhabdopleura*) or in lateral lobes of thecal apertures.

monograptid budding (URBANEK, 1963, p. 148). Subapertural, nonperforational budding of theca from an initial, primary opening, subaperturally placed in relation to the definite aperture of the respective mother theca. Synonymous with cladial branching.

monograptid stage (URBANEK, 1963, p. 148). Stage of phylogenetic modification in the development of a colony, in which the process of astogeny produces only a procladium by monograptid budding.

monopleural (JAANUSSON, 1960, p. 303). Biserial graptoloid tubarium in which two stipes are in contact laterally (Fig. 6.4), each stipe having only one lateral external wall (Glossograptidae). See dipleural.

monopodial growth. Type of colonial growth with permanent terminal zooid behind which new zooids arise as the stem elongates; known exclusively in *Rhabdopleura*. See sympodial growth.

monoprogressive branching (COOPER & FORTEY, 1982, p. 177, fig. 6). Branching pattern in which only one of the two daughter stipes formed at a dichotomy divides again, with the other daughter stipe remaining unbranched, as in *Goniograptus*, after the first dichotomy. See progressive branching.

multiramous. Having numerous branches or many branches.

nema, nemata, or **nemas** (LAPWORTH, 1897, p. 251). Filiform process or extension at the apex of the prosicula (Fig. 5.1–5.2); originally defined by LAPWORTH (1897) as the flexuous primordial filiform process from which the sicula is suspended. The secretion of the nema starts at the tip of the cauda. The nema may be free (Dichograptina), incorporated in the tubarium (Diplograptina, Glossograptina), or fully visible on the dorsal side of the stipe (Monograptidae). The nema in the Diplograptina and Monograptidae

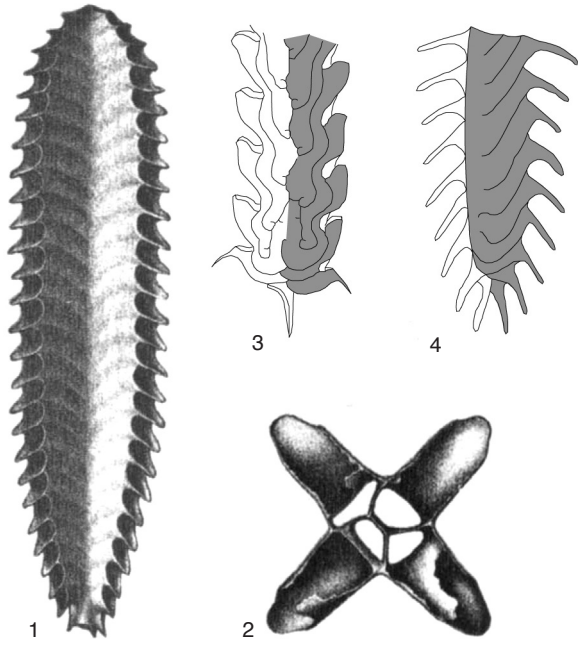

FIG. 6. Biserial and quadriserial tubaria. *1–2,* Quadriserial colony of *Pseudophyllograptus* sp. in lateral view and cross section (adapted from Holm, 1895, pl. 14); *3,* biserial, dipleural tubarium in *Levisograptus austrodentatus; 4,* biserial, monopleural tubarium of *Glossograptus* sp. (Maletz, Carlucci, & Mitchell, 2009).

is commonly called the virgula. RICHTER (1850, p. 201) mistook the nema as a siphon, based on the belief that graptolites are related to nautiloids. See pseudovirgula.

nema prosiculae (KRAFT, 1926, p. 225). See cauda.

nemacaulus (RUEDEMANN, 1904, p. 487). Term proposed by RUEDEMANN (1904) in lieu of nema.

nematophorous (KOZŁOWSKI, 1971, p. 314). The possession of a free nema in the graptolite sicula, which is taken as indication of a planktic life style. See discophorous.

nematularium (MÜLLER, 1975, p. 330; BATES, KOZŁOWSKA, & LENZ, 2005, p. 709: for retiolitids). Distal development of a vane or spiral structure of the nema.

nozzle (LOYDELL & MALETZ, 2004, p. 69). The elongated arch on the dorsal side of the thecal aperture in streptograptids (*Streptograptus, Pseudostreptograptus, Mediograptus*).

obverse (TÖRNQUIST, 1893, p. 3). Refers to the side of the graptoloid tubarium on which the sicula is most completely visible and the crossing canals are covered (Fig. 5.1); similar to Siculaseite of (WIMAN, 1895) and others. See reverse.

occlusion. Sealing of the thecal aperture by sclerotized film, possibly made up of cortical material.

ontogeny. General biological term for the growth of organisms, used herein for the growth of an individual, a zooid; previously used by KOZŁOWSKI (1971, p. 314) only to describe the ontogeny of the sicular zooid, but it is applicable to all derived zooids. The combined ontogenies of all zooids of a colony represent the astogeny of the colony. See astogeny.

oozooid (KOZŁOWSKI, 1971, p. 314). Term for the sicular zooid.

order (of branching) or **order of stipes.** Successive divisions of dichotomous branches (Fig. 2.1–2.2) or successive generations of cladia. MALETZ (1992, p. 298) preferred to use the term 1st to nth order of stipes in the Dichograptina instead of the terms primary and secondary stipes.

orifice (BATES, KOZŁOWSKA, & LENZ, 2005, p. 709). An opening of the tubarium that is partially or entirely rimmed by lists of the ancora sleeve in Retiolitidae. Includes thecal orifices, proximal ventral orifices, proximal lateral orifices, and stomata. The term was used by earlier workers for thecal apertures (e.g., BARRANDE, 1850: internal and external orifices).

ostia, ostiae. Term used in earlier graptolite literature for thecal apertures.

outer ancora (BATES, KOZŁOWSKA, & LENZ, 2005, p. 710). Structure formed by lists on the outside of the ancora umbrella in some Retiolitidae.

outer lamella (URBANEK & TOWE, 1974, p. 5). Fabric of parallel fibrils in a fusellus immediately beneath the bounding pellicle of sheet fabric.

pachythecae (KOZŁOWSKI, 1970, p. 405). Large thecae in *Acanthograptus* with amorphous wall structure and no fuselli; interpreted as possibly parasitic in origin, like the tubothecae.

paracortex (Urbanek & Mierzejewski, 1984, p. 76). Secondary component of cortex made by multiple deposition of sheets separated by an intersheet material, lacking well-defined, individualized cortical fibrils; produced by a tightly packed, condensed meshwork of fibrous material.

parasicula (VandenBerg, 1990, p. 40). Tubular downgrowth of the sicular aperture in biserial graptolites. The term parasicula was first introduced by Eisenack (1938, p. 156) for the misinterpreted metasicula of a dendroid graptolite, later identified as *Epigraptus bidens* (Eisenack, 1941).

paratheca, parathecae (Mitchell, Chen, & Finney, 2007, p. 1123). Tubular outgrowths from the thecal apertures in the proximal part of some biserial graptolites (*Appendispinograptus*).

pauciramous. Planktic pterobranch colony consisting of few branches.

pedicle (M'Intosh, 1887, p. 20). Thin, flexible, cylindrical stalk at the rear end of the *Cephalodiscus* zooids, provided with a sucker for attachment; new buds originate from the base of the pedicle; term borrowed from the terminology of the Brachiopoda. See gymnocaulus.

pectocaulus (Lankester, 1884, p. 634). The sclerotized, inflexible black stolon, usually embedded in the ventral wall of mature tubes in the Pterobranchia (Fig. 1.3); identical to the axial cord of Sars (1872, p. 11) and the chitinous rod of Allman (1869). The stolon is presumably free in the tubarium of planktic graptolites, **but is rarely found in the fossil record.** The terms pectocaulus and stolon can be used interchangeably, but the latter is more widely distributed.

peduncle (M'Intosh, 1887, p. 6). Thin, flexible, cylindrical stalk at the rear end of the *Cephalodiscus* zooids, provided with a sucker for attachment; new buds originate from the base of the pedicle; M'Intosh (1887) used both pedicle and peduncle for the gymnocaulus of *Cephalodiscus*. The term is homologous to the gymnocaulus of *Rhabdopleura* and should not be used. See gymnocaulus. Term also used for pelecypods.

pendent (Elles & Wood, 1901, p. 5, fig. 3; Cooper, 1973, p. 52, text-fig. 5). Denotes a downward direction of growth of stipes or of thecae when the tubarium is oriented so that the apex of the sicula points vertically upwards.

pericalycal (Bulman, 1968, p. 214; Maletz & Mitchell, 1996, p. 643). Taxa with an isograpid- or artus-type development, with the enclosure of the obverse side of the sicula by $th2^2$ (or $th1^2$ in some derived species), with resulting initial monopleural growth of the two thecal series such that the tubarium acquires a secondary rotational symmetry normal to the plane of isograptid symmetry. See platycalycal.

periderm (Wiman, 1895, p. 263). Scleroproteic substance forming the tubarium of the Pterobranchia, composed of an inner layer of alternating fusellar bands (fuselli) showing growth lines and an outer (cortical) layer of finely laminated tissue from thin bandages. The term should not be used any more, as the name suggests a dermal origin, which is incorrect (Mitchell, Chen, & Finney, 2013, p. 51). As there is no definite replacement term, the „material can simply be referred to as tubarium or wall material depending on the specific context" (Mitchell & others 2013, p. 51).

plaited overlap, plaited arrangement (Cooper & Ni, 1986, p. 314; Lindholm, 1991, p. 289; Maletz & Mitchell, 1996, p. 642). (1) Parallel growth and overlap of several thecae, as in the manubrium of pseudisograptids. (2) The overlapping of thecae in bithecate and nonbithecate tubaria with lateral thecal origins (Lindholm, 1991). Both constructional features are developed independently but show similar results in their typical development of multiple parallel-oriented thecae.

platform (Loydell & Maletz, 2004, p. 69). Smooth concavity, usually with a distinct genicular rim, in which the coiled metatheca with its aperture sits. Common to streptograptids but occurring also in other monograptids.

platycalycal (Bulman, 1968, p. 214; Maletz & Mitchell, 1996, p. 643). Descriptive term used in biserial graptolites (Axonophora) to denote a concentration of budding on the reverse side of the tubarium with a largely free sicula on the obverse side. It largely describes a dipleural development. See *pericalycal*.

pleural disk (Finney, 1985, p. 361). Paired disk structures growing from the pleural list of the thecae in a non-retiolitid axonophoran in a horizontal to subhorizontal fashion. Known only in *Dicaulograptus cumdiscus.*

pleural list (Bates, Kozłowska, & Lenz, 2005, p. 710). Side lists; lateral longitudinal lists of the ancora sleeve, connected to successive lateral apertural rods (septal bars). The pleural lists in *Dicaulograptus cumdiscus* (Finney, 1985) are thecal lists and not homologous to the pleural lists of the Retiolitidae.

plumes. See arms.

polymorphic. Pterobranch colony comprising more than one kind of zooid or tubarium with more than one type of theca (autothecae, bithecae) or gradational thecal developments along the stipes, as in many monograptids.

polypary (Scharenberg, 1851, p. 5); originally polypenartige Geschöpfe (German for polyp-like organisms). Term used by earlier workers for the tubarium (see Elles & Wood, 1903, p. 26).

polypide (Sars, 1872, p. 8). Early term for pterobranch zooid, suggesting a bryozoan relationship.

polypidum (Harkness, 1851, p. 60). Old term for tubarium.

polyzoarium (Sars, 1874, p. 24). Old term for the tubarium of *Rhabdopleura.*

porus stage (Eisenack, 1942, p. 29); originally *Porus-Stadium* (German). First stage in the development of the initial foramen for the growth of the first theca in many graptolites, except for derived monograptids. A hole is formed in the ventral side of the sicula for the emergence of the first post-sicular zooid. See sinus stage, lacuna stage.

post-coronal orifices (Lenz, 1993, p. 12). Openings in the ancora sleeve above the ancora umbrella in the Retiolitida; they can be described as ventral orifices.

preoral lobe (Lankester, 1884, p. 625). Anterior glandular lobe or disc in the zooids of the pterobranchs secreting the tubarium. See also cephalic shield.

primary lamellae (Harmer, 1905, p. 10). Term introduced for the fuselli of extant Pterobranchia.

primary porus (Eisenack 1942, p. 31). Pores left as an initial opening during the growth of the sicula through the sinus and lacuna stages. See resorption foramen.

primary stipe. Monsen (1925, p. 160) already differentiated between primary and secondary stipes (Hauptzweige and Nebenzweige). The term was to describe the stipes originating from the sicula. See order of stipes.

primordial astogeny (Mitchell, 1987, p. 354). The initial part of a graptolite colony exhibiting specialized ontogenies with thecae determining the proximal development type. Synonymous with proximal development type.

primordial series (of thecae) (Elles, 1897, p. 189). The thecal series starting with $th1^1$ in a biserial dipleural colony. See *second series*.

primordial thecae (Holm, 1895, p. 437; Mitchell, 1987, p. 354). The initial thecae of a graptolite colony exhibiting specialized ontogenies. See primordial astogeny.

proboscis. Term for the head part of enteropneusts (Fig.1.1), homologous to the cephalic shield of the pterobranchs (Fig. 1.2–1.3). Generally used as a biological term for the tubular feeding and sucking organs of invertebrates, but also for the trunk of elephants.

procladium (Urbanek, 1963, p. 147; Bulman, 1970). Term proposed for main stipe of cladia-bearing tubarium, with normal cladia being distinguished as metacladia. The term procladium could in theory be used for any graptoloid stipe, but the name would imply a cladial origin which is misleading. See cladium.

progressive branching (Cooper & Fortey, 1982, p. 177, fig. 6). Branching pattern in which each of the two new branches formed at a dichotomy divide again, as in *Clonograptus, Etagraptus*, forming a multiramous colony; see monoprogressive branching.

prosicula (Kraft, 1926, p. 222). The initial part of sicula, secreted as a cone with faintly marked spiral thread to which longitudinal fibers are added; called the Initialteil by Wiman (1895).

prosicular ring (Bates & Kirk, 1992, p. 57). The sclerotized remains of the prosicula, preserved as a ring defining the prosicular aperture in many Retiolitidae.

prosoblastic (Bulman, 1963a, p. 671; Mitchell, 1987, p. 354). Type of diplograptid proximal development in which $th2^1$, and ultimately $th1^2$, grow upward and forward from their origin; $th1^2$ is roughly J-shaped with a downward-growing initial part. See streptoblastic.

protheca. Initial part of graptoloid theca before differentiation of succeeding theca (insertion of the median septum). A general definition does not exist and the term is used in various connections.

prothecal fold (Mu, 1957, p. 412 [English text]). Inverted U-shaped curvature of part of protheca (usually initial portion) giving a nodded appearance to the dorsal margin of the stipe.

proximal. First-formed part of the tubarium, nearest to the point of origin of the colony, the sicula.

proximal development type (Elles, 1922, p. 170; Cooper & Fortey, 1982, p. 171; Mitchell, 1987, p. 354). Initial budding sequence of the tubarium. Proximal development types are commonly used to identify evolutionary relationships within the graptolites. Individual types are variably named and are not listed here. See astogenetic patterns.

proximal structure (Cooper & Fortey, 1982, p. 173). The proximal structure refers to the orientation, attitude, and arrangement of proximal thecae.

pseudanastomosis (Rickards & Lane, 1997, p. 173). Temporary fusion of adjacent branches to form an ovoid mesh including the transfer of thecae between stipes. See anastomosis.

pseudocladium (Urbanek, 1963, p. 147). The regenerated stipe of a bipolar tubarium lacking a sicula. A pseudocladium is a regenerated stipe and not formed through cladial branching; thus, the term is inappropriate. See cladium.

pseudocortex (Urbanek & Mierzejewski, 1984, p. 76). Secondary component of cortical tissue produced by accumulation of sheets with an extremely scarce and poorly defined intersheet material devoid of any fibrous elements.

pseudopericalycal (Cooper & Ni, 1986, p. 317). Term used to describe the proximal development in glossograptids. See pericalycal.

pseudovirgula (Urbanek, 1963, p. 147). Dorsal rod in the cladia of some Monograptidae, originating as a thecal or sicular apertural spines. Term used by Loydell & Cave (1994) for a secondary nema in *Cochlograptus veles*. See virgula.

pustule, pustules (Bates, Kozłowska, & Lenz, 2005, p. 710). Regular protuberances on the sheet fabric bounding bandages of lists in Plectograptinae (Retiolitidae); first recognized by Eisenack (1951, fig. 11: Höckerchen).

quadriradiate (Bulman, 1950, p. 68). Proximal development with four first-order stipes originating from the sicula through three successive dicalycal thecae (Fig. 2.5); originally quadri-radiate" in Bulman (1950, p. 68) and revised by Maletz (1992, p. 303); see biradiate, triradiate.

quadriserial. Scandent graptoloid tubarium composed of four rows of thecae in back-to-back contact as in *Phyllograptus* (Fig. 6.1–6.2). See biserial, monoserial.

Querrunzeln (Richter, 1871, p. 233). Richter (1871) erroneously described growth lines of graptolites with this term and remarked that they form a zigzag suture (*Zickzacknaht*) on the upper and lower side of the thecae (Zellen). See growth lines, fuselli.

radicle (J. Hall, 1865, p. 19). Term used by earlier workers to identify the point of origin of the stipes or the "initial point" in graptolite tubaria; vague reference to the unrecognized sicula in dichograptids.

reclined (Elles & Wood, 1901, p. 5, fig. 3). Graptoloid tubarium with branches growing upward, subtending an angle of less than 180° between their dorsal sides.

reflexed (Elles & Wood, 1901, p. 5, fig. 3). Graptoloid tubarium with branches growing upward, similar to reclined, but with distal extremities of the stipes tending to be horizontal.

regenerative virgula (Urbanek, 1963, p. 147). Thickened cortical fiber, secondarily formed as an axis of the pseudocladium (regenerated stipe), as the result of regeneration in the Monograptidae. This feature is a secondarily grown nema.

resorption foramen (Kozłowski, 1949, p. 22); originally bourgonnement perforant (French). Opening in the sicula, formed by resorption by the initial bud of the first theca (th1[1] zooid). Kozłowski (1949, p. 23) called the primary opening for later thecae the bourgonnement apertural. See porus.

reticulum, reticula (Bouček & Münch, 1952, p. 5; Bates, Kozłowska, & Lenz, 2005, p. 710). Delicate irregular network of secondary lists on the ancora sleeve and the thecal wall of the Retiolitidae.

retroverted. Thecal apertures facing proximally as the result of the hooked or reflexed shape of the metatheca, following excessive growth of the dorsal wall of the theca.

reverse (Törnquist, 1893, p. 3). Side of the graptoloid tubarium in which the sicula is partly concealed by the crossing canal(s); Antisiculaseite of Wiman (1895, p. 263), Holm (1895, p. 436), and others.

rhabdocortex (Urbanek & Towe, 1974, p. 13; Urbanek & Mierzejewski, 1984, p. 76). The common cortical envelope of a tubarium or of a group of thecae. See ectocortex.

rhabdosome (Törnquist, 1890, p. 5). Housing or domicile of graptolites; hydrosome, polypary, polypier, polypariet, and stock (listed in Ruedemann, 1904, p. 483) are comparable terms used in earlier literature (e.g., Tullberg, 1883: *hydrosoma*). See tubarium.

rhabdosome midline (Cooper & Fortey, 1982, p. 178, fig. 8). The primary axis of symmetry of the tubarium, which passes medially through the tubarium, from top to bottom (Fig. 3.3–3.4). See tubarium midline.

right-handed (origin of thecae) (Stubblefield, 1929, p. 274; revised by Cooper & Fortey, 1982, p. 173). Origin on the (biologically) right side of the sicula or later theca when seen from dorsal side of the stipe.

root, roots. Irregular branching structure made from cortical tissue, developed from apex of the sicula and serving for the attachment of benthic graptolites. The term is not recommended as the anchoring construction is not a root system (as in modern plants), but a development for firm attachment on a surface only.

rutellum, rutella (Williams & Stevens, 1988, p. 20; Maletz & Mitchell, 1996, p. 644). Rounded, ventral, outward apertural elaboration on graptolite thecae. Initially intended for the sicula only. Homologous with the languette of the Dendroidea.

saccoid (Elles & Wood, 1914, p. 505). "Sac-like expansion" forming the initial part of the cladial thecae in *Cyrtograptus*.

scalariform. Preservational view presenting ventral (thecal) aspect of the graptoloid tubarium, mostly used for biserial taxa, but applicable also for other graptolites.

scandent (Elles & Wood, 1901, p. 5, fig. 3). Graptoloid tubarium with stipes growing erect distally and enclosing or including the nema.

Schraubenlinie (Kraft, 1926, p. 222). German term translated as helical line, spiral thread or spiral line; identical to ligne hélicoïdale of Kozłowski (1949, p. 56).

sclerotized. Hardening of the tubarium walls after the secretion of scleroproteic substances by zooid(s).

scopulae (Elles & Wood, 1908, p. 319; referred to Hopkinson & Lapworth, 1875). Peculiar ramifying fibrous development from edges of median septum (in lasiograptids); identified as reproductive processes in J. Hall (1865).

seam (Bates & Kirk, 1978, p. 429). Feature in retiolitid graptolites indicating the presence of unpreserved fusellar walls.

secondary lamella (Harmer, 1905, p. 10). Early term for the cortical tissue in extant Pterobranchia.

secondary lists (Lenz, 1994, p. 1345). Synonymous with reticulum.

secondary stipes. See order of stipes, primary stipes.

second series (of thecae). (Elles, 1897, p. 189). The thecal series starting with th1[2] in a biserial, dipleural colony. See primordial series.

selvage. Thickened margin or rim, especially of the aperture of thecae with cortical bandages.

septal bar (Bates & Kirk, 1978, p. 437). Synonymous with lateral apertural rod.

septum. Membrane separating thecal series or thecae. See interthecal septum; median septum.

sheet fabric (Urbanek & Towe, 1974, p. 4). Electron-dense, homogeneous, or very densely reticulated pellicle delimiting particular fuselli or layers.

sicula (Lapworth, 1873, p. 501). Housing of the initial zooid of a graptolite colony (Fig. 2.4, 5.1), formed by the prosicula and metasicula. Richter (1871, p. 236) first recognized the role of the sicula and described it as the foot (Fuss in German) or attachment (Haftorgan) in *Monograptus priodon*; radicle and initial part are similar terms used in earlier literature.

sicular bitheca (Bulman, 1927, p. 18; Stubblefield, 1929, p. 272). First bitheca of graptolite colony, associated with the sicula and visible on the obverse side of the proximal end.

sicula side (Siculaseite) (Holm, 1895, p. 436; Wiman, 1895, p. 263). Side of the graptoloid tubarium in which the sicula is usually partly visible and the crossing canals are covered. See obverse.

sigmoidal structure (Lenz, 1993, p. 12, pl. 18,5). Solidly sclerotized, sigmoidally curved, bladelike mid-ventral structure in some Retiolitidae, running from the transverse rod to the genicular list.

sinistral (Cooper & Fortey 1982, p. 174). Anticlockwise growth direction of proximal thecae (Fig. 3.1). See dextral.

sinus stage (Eisenack, 1942, p. 31); originally Sinus-Stadium (German). First stage in the development of the initial foramen for the growth of the first theca in monograptids. A deep notch is formed at the ventral side of the temporal aperture of the sicula. See lacuna stage, porus stage.

solid axis (Barrande, 1850, p. 4; J. Hall, 1865, p. 21); originally axe solide (French). Term used by earlier workers for the virgella and nema of the graptolite tubarium.

spinoreticuli (Lenz, 1993, p. 15). Reticular lappets of fusellar material attached to the genicular lists at the upper apertural lists of some Retiolitidae, common in *Spinograptus, Agastograptus;* can be branched or replaced by simple spines.

spiral thread or **spiral line** (Kraft, 1926, p. 222); originally Schraubenlinie (German). Spiral line of single fusellus forming the prosicula; also ligne hélicoïdale of Kozłowski (1949, p. 56). See helical line.

stalk (Fowler, 1904, p. 25). General term for gymnocaulus and pectocaulus in Pterobranchia (Fig. 1.2–1.3).

statoblast. Large, closed vesicular bodies, interpreted as enclosing hibernating zooids; also identified as sterile buds by Schepotieff (1907, p. 198). Allman (1869, p. 61) described what appear to be arrested buds that have not burst through the wall of the axial tubarian chamber as statoblasts. Statoblasts were originally described for bryozoans (Polyzoa) by Allman (1856, p. 37). See dormant buds.

sterile buds (Schepotieff, 1907, p. 198); originally sterile Knospen (German). Large, closed vesicular bodies, interpreted as enclosing hibernating zooids; see dormant buds, hybernacula (Schepotieff, 1907, p. 200).

Stillstandsgürtel (Kraft, 1926, p. 234). See annulus.

stipe (Jaanusson, 1960, p. 303; Bulman, 1970, p. 11). Single branch of a branched graptolite tubarium (Fig. 2.1–2.2), sometimes used for the entire colony (in monograptids); in its strict sense it refers to the segment between successive dichotomies in multiramous forms (Cooper & Fortey, 1982, p. 177). Earlier workers used the term frond (e.g., J. Hall, 1865). See branch, which is used interchangeably for stipe.

stoloblast (Urbanek & Dilly, 2000, p. 218). The soft tissues of the stolon and its organic sheath, including the buds in Rhabdopleuridae.

stolon (Schepotieff, 1906, p. 514); originally black stolon (schwarzer Stolo in German). Thin, sclerotized sheath surrounding the unsclerotized thread of soft tissue, from which pterobranch buds originate (Fig. 1.3); identical to the pectocaulus of Lankester (1884, p. 634).

stolotheca (Kozłowski, 1949, p. 24; Cooper & Fortey, 1983, p. 212). Originally one of the three principal types of thecae in dendroid graptolites (autotheca, bitheca, stolotheca); according to Cooper and Fortey (1983, p. 212), stolotheca and autotheca form a single continuous unit, the autotheca.

stoma, stomata (Bates, Kozłowska, & Lenz, 2005, p. 710). Lateral (obverse and reverse) orifices in the ancora sleeve, sometimes bounded by a chimneylike reticular wall in Retiolitidae.

strengthening rods, longitudinal strengthening rods (Kraft, 1926, p. 224); originally Längsverstärkungsleisten (German). Cortical ridges on the outer side of the prosicula, formed before the growth of the metasicula. See also longitudinal ridges.

streptoblastic (Bulman, 1963a, p. 671; Mitchell, 1987, p. 354). Type of diplograptid development in which $th1^2$, $th2^1$, and even $th2^2$ grow essentially downwards, with $th1^2$ being S-shaped and growing initially upwards from its origin. See prosoblastic.

supradorsal (Cooper, 1973, p. 52, fig. 5) In horizontal and reclined dichograptids, that portion of the sicula and theca 1^1 that projects above the line of the dorsal margin of the diverging stipes.

supragenicular wall (Jaanusson, 1960, p. 304). Thecal wall above the geniculum.

suture. Boundary between fuselli (**zigzag suture**) or in cases between thecae (arienigraptid suture).

sympodial growth. Type of colonial growth in which each zooid is in turn terminal zooid of its branch. See monopodial growth.

synrhabdosome (Ruedemann, 1904, p. 483; Gutierrez-Marco & Lenz, 1998). Originally defined as a colony of colonies, but now interpreted as an association of graptoloid tubaria, normally of one species (with rare exceptions), attached distally by their long, thin nemata to a particle or enmeshed in a tangle of thin nemata; rarely are tubaria of a synrhabdosome attached by the virgellae. Ruedemann (1895, p. 224) used the term hydrosome for the synrhabdosomes and the term rhabdosome for single tubaria.

taeniocortex (Urbanek & Mierzejewska, 1978, p. 639). A secondary component produced by the accumulation of well-defined, ribbonlike units, bundles of cortical fibrils, or made of a different material and sealed by a sheet or free of it.

terminal theca. Last theca developed in a finite tubarium, often reduced in size. See appendix.

test (Barrande, 1850). Term used by earlier workers for the tubarium of graptolites.

theca, thecae (Lapworth, 1873, p. 502). Sclerotized tube or housing of the individual zooids of a graptolite colony. Lapworth (1873) identified the theca as a chamber in which the organism sits. The term cell or cellule was often used in the earlier literature (see Elles & Wood, 1902, p. XVII).

thecal aperture. Distal opening of the thecae; earlier workers used the term orifice, which is now restricted to the openings in the ancora sleeve of the Retiolitidae (Bates, Kozłowska, & Lenz, 2005, p. 709).

thecal framework (Bates, 1990, p. 717; Bates, Kozłowska, & Lenz, 2005, p. 710). Regular network of lists, of thecal origin (i.e., excluding the lists of the ancora sleeve) in retiolitids. It comprises the nema, virga, virgella, transverse rods, lateral apertural rods, lips, and connecting rods. It is part of the clathrium of the Retiolitidae.

thecal gradient. Change in thecal style along a stipe.

thecal notation (Elles, 1897, p. 189–190). Scheme used in the naming of thecae (Fig. 5.2), which was introduced by Elles (1897) and revised most recently by Cooper and Fortey (1982, p. 175–175).

thecorhiza (Kozłowski, 1949, p. 141); originally thécorhize (French). Encrusting basal disc in Tuboidea, composed principally of prothecae, from which metathecae and bithecae arise singly, in clusters, or as branches.

transverse rod (Bates, Kozłowska, & Lenz, 2005, p. 710). List at the base of a thecal wall, bearing a seam that marks the attachment to it of the fusellum of the wall. Homologous with the aboral list of non-retiolitid graptoloids, but as the retiolitids have no interthecal septum, the tranverse rod forms the distal part of the thecal aperture.

triad (budding) (Kozłowski, 1949, p. 23). Process of budding resulting in regularly alternating triads of autothecae and bithecae; one autotheca and one bitheca originate on alternate sides from a mother-autotheca. See Wiman rule (Kozłowski, 1949, p. 17: règle de Wiman).

triradiate (Bulman, 1950, p. 68). Proximal development with three first-order stipes originating from the sicula through two successive dicalycal thecae; originally tri-radiate (Bulman, 1950, p. 68); revised by Maletz (1992, p. 303). See biradiate, quadri-radiate.

triserial. Stipes or tubaria bearing three rows of serially arranged thecae, arranged back to back. See uniserial, biserial, quadriserial.

tubarium (Lankester, 1884, p. 624). Dwelling or housing of the Pterobranchia, secreted from a glandular region on the cephalic shield of the pterobranch zooid; originally proposed for *Rhabdopleura* Allman as a replacement for the inappropriate term coenoecium. Sars (1874) introduced the term polyzoarium for the genus *Rhabdopleura.* The term rhabdosome has long been used for the tubarium of extinct graptolite taxa (see Bulman, 1955, 1970). Mitchell and others (2013) reintroduced the term tubarium for extinct and extant Pterobranchia.

tubarium midline (Cooper & Fortey, 1982, p. 178, fig. 8: rhabdosome midline). The primary axis of symmetry of the tubarium, which passes medially through the tubarium from top to bottom (Fig. 3.3–3.4). The tubarium is normally oriented, for descriptive purposes, with the sicula vertical, apex uppermost, and the tubarium midline vertical. In biserial graptolites, the midline lies along the median septum and the nema.

tubotheca (Kozłowski, 1970, p. 394). Tubular structures, not showing fuselli, on the tubaria of some Cyclograptidea and Dendroidea; interpreted as the tubes of other animals living in association with graptolite colonies.

twig (Wiman, 1895, p. 301); originally Zweig (German). Compound branches in some dendroid graptolites (acanthograptids). Wiman (1895) differentiated between *Ast* (branch or stipe) and *Zweig* (twig).

two thecae repeat distance, 2TRD (Howe, 1983, p. 635). Measuring unit for the thecal spacing, used most commonly for Monograptidae, but more recently introduced to diplograptid and dichograptid graptolites.

umbellate theca (Bulman, 1970, p. 12). Type of autotheca in some Cyclographidae, characterized by enlarged, reflexed, umbrella-shaped hood extending back over the aperture of preceeding autotheca; initially called "umbrella-like" thecae (Bulman & Rickards, 1966, p. 62).

uniserial. Stipes or tubaria bearing a single row of serially arranged thecae. See biserial, triserial, quadriserial.

ventral (Kozłowski, 1949, p. 22). (1) The side of the metasicula giving rise to the rutellum and on which th1[1] originates (see Maletz, 1992). (2) Side of the stipe on which the thecal apertures are located; not necessarily related to position of growth of tubarium, but assumed to be related to ventral side of the zooid.

vesicular diaphragm (Urbanek & Dilly, 2000, p. 222). Globular swelling on main stolon coinciding with the nodes or points of origin of daughter stolons in *Rhabdopleura.*

virga (Bates & Kirk, 1992, p. 57; Bates, Kozłowska, & Lenz, 2005, p. 710). List formed of cortical bandages laid down on the outer surface of the prosicula, which connects the nema and the virgella in Retiolitidae.

virgella, virgellae (Törnquist, 1897, p. 4; Kozłowski, 1949, p. 54, fig. 7F and footnote 2). Structure formed by the growth of the fuselli on the metasicula extending distally from the sicular aperture to form a spine (Fig. 5.1); first described correctly by Kozłowski (1949); called the mouth-spine by Wiman (1896, p. 188). Maletz (2010) described the evolutionary development and differentiated dorsal and ventral virgellae.

virgellarium (Urbanek, 1963, 175). Umbrella-shaped structure developed at the tip of the virgella in linograptids (Monograptidae); also used to describe other secondary secretions related to the virgella.

virgellar tape (Chen, 1986, p. 127 [English text]). Structure on the virgella, poorly defined, unclear.

virgula (Wiman, 1896, p. 188). Term originally proposed for a hollow rod extending from the prosicula. Wiman (1896, fig. 2, 5) used the term even for the part of the virgella incorporated into the sicula in his illustrations of monograptids and diplograptids (including retiolitids). The virgula is the older term and is often used for the nema in monograptids but not for dichograptids (see Rickards, 1996). Synonymous to nema. See pseudovirgula.

web structure. See membrane.

Wiman rule (Kozłowski, 1949, p. 17); originally règle de Wiman (French). Process of budding resulting in regularly alternating triads of autotheca, bitheca, and stolotheca. See triad budding.

zig-zag list structure (Bates, Kozłowska, & Lenz, 2005, p. 710). The zigzag structure is made of clathrial lists (Retiolitidae), reverse mid-dorsal lists of the thecal framework (Retiolitinae), or ancora sleeve lists (Plectograptinae).

zigzag suture (Richter, 1871, p. 233; Kraft, 1926, p. 227); originally Zickzacknaht, Zick-Zacknacht, Wechselzeilennaht (German). Regular connection of the fusellar halfrings on the dorsal and ventral sides of the thecae (Fig. 4).

zooecium, zooecia (Harmer, 1905, p. 10). The individual housing tubes of *Cephalodiscus* zooids; term adopted from Bryozoa terminology. See tubarium.

zooid. Soft-bodied individual inhabiting the theca or the tubarium (thecal zooid, sicular zooid).

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