Annales Societatis Geologorum Poloniae (2024), vol. 94: 205–223 https://doi.org/10.14241/asgp.2024.14

CORTICAL DEVELOPMENTS IN THE GRAPTOLITHINA (PTEROBRANCHIA) UNDER THE SCANNING ELECTRON MICROSCOPE – A REVIEW AND NEW CLUES

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Kozłowska, A., Bates, D. E. B. & Maletz, J., 2024. Cortical developments in the Graptolithina (Pterobranchia) under the scanning electron microscope – a review and new clues. *Annales Societatis Geologorum Poloniae*, 94: 205–223.

Abstract: The cortical bandages of the Graptolithina are involved in the construction of a number of structures of the tubaria. Cortical material differs from fusellar tissue in the type of fibrils and their arrangement. The fibrils of the bandages, forming the cortex, are densely packed, running parallel to the length of the bandage and creating strong and flexible material. Cortical tissue is present in all graptolites as a secondary development, overlying the fusellum and in some cases forming additional features. In the Retiolitinae, the main constructional role of the tubaria was taken over by a network of lists, made of cortical bandages, not the fusellum. Among the meshwork of cortical lists, there are thicker ones (clathrium), in various configurations, which possibly strengthened the tubaria. For example, the cortical structures are the sicular annuli, virga, virgella, nema, ancora umbrella and ancora sleeve of retiolitines. A scanning-electron-microscope study of the sicular annuli, specific for some monograptids, shows for the first time the ultrastructure of their cortical bandages. The details of thickened cortical construction may be useful for the interpretation of flattened material but also may provide a basis for misleading interpretations.

Key words: Paleozoic, Ordovician, Silurian, Pterobranchia, Graptolithina, tubarium, cortical structures, fusellum, sicular annuli.

Manuscript received 22 March 2024, accepted 8 July 2024

INTRODUCTION

The Paleozoic (mostly Cambrian to Early Devonian) graptolites, a special and unusual group of the Pterobranchia, known from a few benthic extant members, still leave numerous questions about their development and evolution to be investigated. Originating probably in the earliest Cambrian as inconspicuous benthic organisms, they bloomed in the Ordovician and Silurian as one of the most spectacular types of macroplankton (Maletz, 2017). Their tubaria (previously the rhabdosome), special housing constructions secreted from glands on the proboscis of the zooids, are preserved in many marine types of sedimentary rock as films of organic material and sometimes even in three dimensions (Fig. 1). Thus, the authors were able to compare these constructions with the tubaria of the few extant taxa in many details. From this information, the authors were able to recognize the highly variable tubarium development as being based on a few fundamental features, the fuselli forming the main construction, with the cortex largely secreted on the surface of the fuselli as a secondary development. Kozłowski (1938, fig. 2) illustrated the general formation of the thecal tubes from fusellar half-rings (Fig. 1), the main constructional units of the graptolite tubarium. Andres (1961, 1977, 1980) discussed a number of pterobranchs, both extant and extinct taxa, and compared their fusellar construction in some detail, showing that the construction of the extant *Rhabdopleura* and *Cephalodiscus* is identical to development in fossil graptolite taxa. Mitchell *et al.* (2013) finally identified the extant *Rhabdopleura* as a living graptolite and connected the fossil graptolites with the modern Pterobranchia.

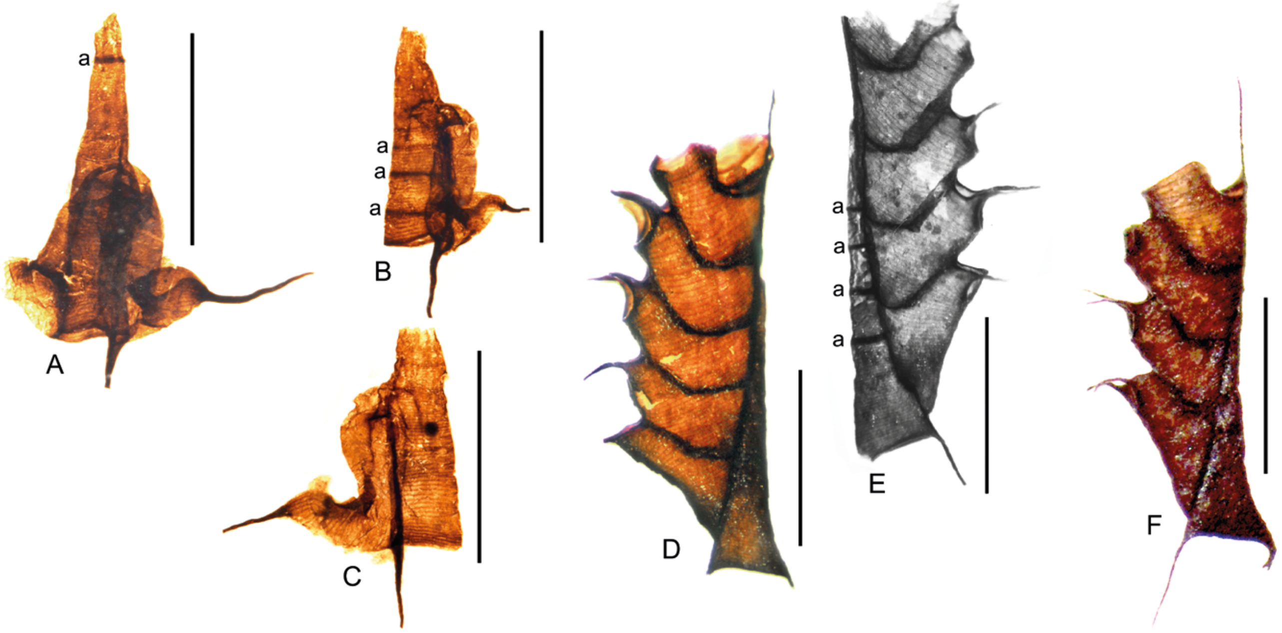

Fig. 1. Chemically isolated graptolite specimens. **A–C.** *Archiclimacograptus* sp., specimens showing fusellar construction, Newfoundland, Middle Ordovician, Canada; A – incomplete proximal end showing thickened rim around aperture of prosicula, GSC 143710; B – juvenile with at least three darker rings in metasicula, GSC 140112; C – juvenile without thickened rings inside, GSC 143711. **D–F.** *Saetograptus leintwardinensis* (Lapworth, 1880), glacial boulder, Nienhagen near Rostock, Mecklenburg-Vorpommern, Germany; D – specimen showing the thickened contact between the thecal wall and the interthecal septum, SMF 68294; E – specimen with four sicular annuli, SMF 68290; F – unbleached specimen, in which sicular annuli are not visible, SMF 75819. All scale bars are 1 mm; a indicates sicular annuli in A, B and E.

Kraft (1926, p. 231) first described the cortical bandages as „Chitinverdickungs-Bänder" (chitinous thickened bandages) for *Rectograptus gracilis*, but erroneously indicated that they are found on the inside of the sicula (the first theca of the colony). Such bandages (Fig. 2A, B) were already known to Holm in the late nineteenth century (see illustrations in Bulman, 1932a, pl. 3, fig. 7: *Diplacanthograptus spiniferus*). Crowther and Rickards (1977) and Crowther (1978, 1981) described for the first time in detail the cortical bandages on the outside (ectocortex) of a number of species and suggested their formation as the fundamental units of the cortex in all graptolites.

The most remarkable graptolite development is the network of cortical lists in the Retiolitinae, as described in numerous papers (e.g., Elles and Wood, 1908; Bates and Kirk, 1991; Kozłowska-Dawidziuk, 1995, 1997; Bates *et al.*, 2005; Lenz *et al.*, 2018). The tubarium construction of the group was established on the basis of excellently preserved, isolated, three-dimensional material, mostly from Arctic Canada and Poland (e.g., Lenz and Melchin, 1987; Lenz, 1993, Lenz *et al.*, 2012; Kozłowska *et al.*, 2019). Studies have confirmed that the cortical lists, made by successive layers of bandages, are laid down on the outer surface of the tubarium (ectocortex; Crowther, 1978) and the walls of the ancora sleeve (Bates and Kirk, 1984; Bates, 1990; Lenz *et al.*, 2018). The fusellar part of the two types of tubarium walls, the thecal and the outside wall, named the ancora umbrella and ancora sleeve, is extremely thin (Lenz, 1994) and not preserved in most specimens.

Many details of the secretion of the cortical bandages and the phylogenetic origin of this feature in the graptolites are still unknown. One may not only investigate the general shape of these housing constructions, but also minute details of the probably collagenous secretions with the transmission electron microscope (TEM; Towe and Urbanek, 1972; Urbanek and Towe, 1974; Crowther, 1981), where differences in the microstructural composition of the fuselli and the cortex are recognizable (Fig. 2E). In chemically isolated material, one also may recognize the individual cortical bandages (Fig. 2A, B) and even fibrils (Fig. 2F–H) of the secretions through use of the scanning electron microscope (SEM; Bates, 1997, 2003; Bates *et al.*, 2009). Thus, there is a fairly reasonable understanding of the general construction of the graptolite tubaria.

In this paper, the authors describe the phenomena resulting from the ability of graptolites to construct cortex material, forming various structures with numerous functions. Sicular rings are presented for the first time in SEM pictures.

METHODS AND MATERIAL

The isolated graptolites were recovered, following gentle dissolution of the host carbonate with about 20–30% HCl. A fine hairbrush or a pipette was used to pick and transfer specimens. The studied specimens are preserved either in glycerin, flattened on glass slides or mounted on SEM stubs. They are preserved in the collections of the following

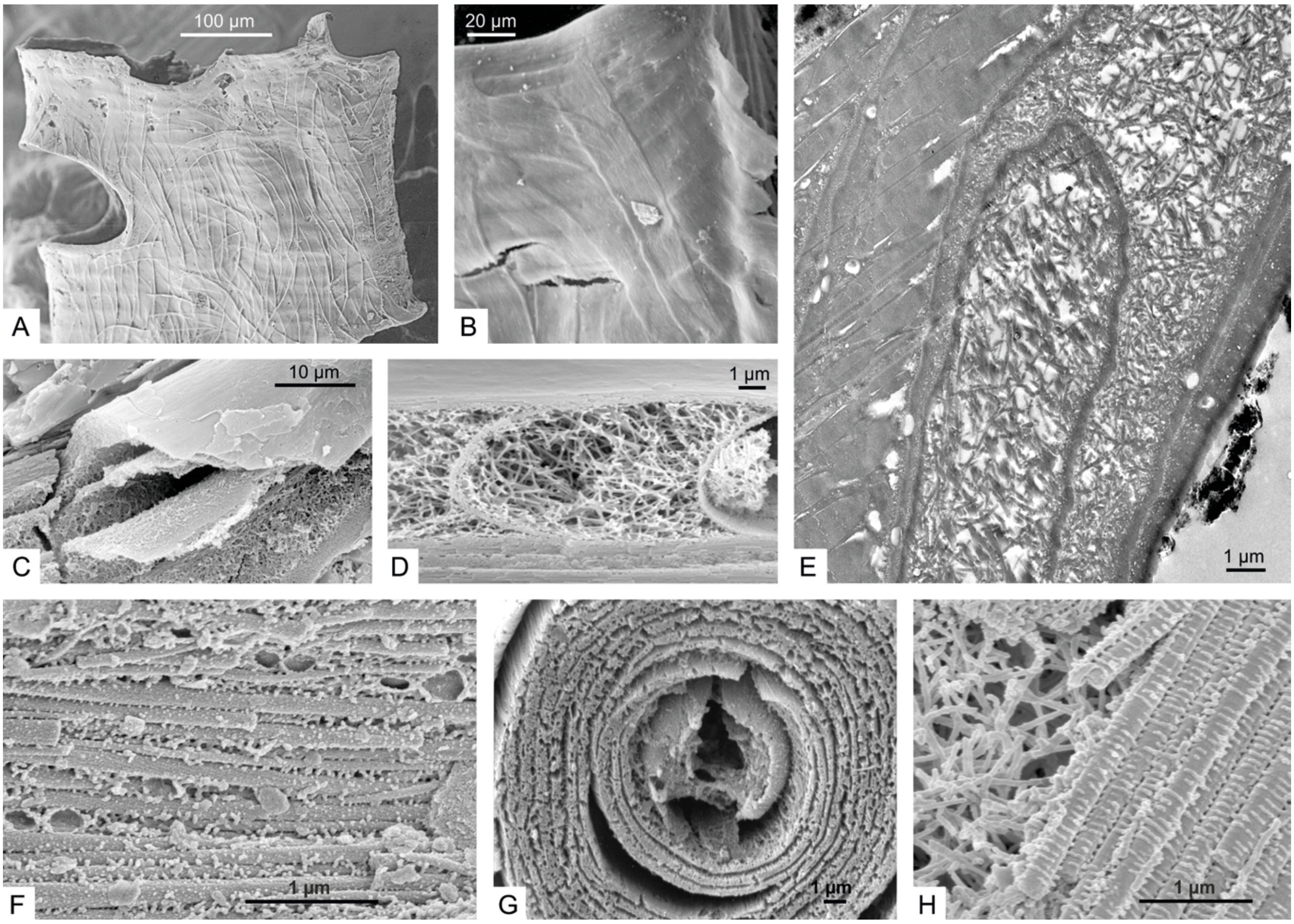

Fig. 2. SEM (A–D, F–H) and TEM (E) pictures of the graptolite cortical bandages and fusellum. **A.** *Diplacanthograptus spiniferus* (Ruedemann, 1908), distal end, showing fuselli and cortical bandages, USA, NMW 2019.34G.1034. **B.** *Geniculograptus typicalis* (Hall, 1865), high magnification of several cortical bandages on surface of fusellum, Upper Ordovician (Katian), USA, NMW 91.52G.726K (after Bates, 1987, pl. 1, fig, 2). **C.** *Geniculograptus typicalis* (Hall, 1865), fractured fuselli, decreasing in height towards the aperture, Upper Ordovician (Katian), USA, 91.52G.17E1 (after Bates, 1987, pl. 1, fig. 3). **D.** *Desmograptus micronematodes* (Spencer, 1884), fuselli with thicker ectocortex below and thinner endocortex above, Silurian, USA, FMNH PE60376 (after Saunders *et al*., 2009, pl. 1, fig. 1). **E.** *Dendrograptus* sp., two fuselli and cortical bandages (ectocortex to the left), Silurian, Sweden (after Bates, 1997, pl. 5, fig. 2). **F.** *Acanthograptus* sp. parallel cortical fibrils (right), crossed by cross-fibrils, Middle Ordovician (Viruan), Baltic erratic boulder 0.327, Poland (see Urbanek and Towe, 1974), NMW 2019.34G.1771A, photograph D. Bates. **G.** Unknown species, cross-section of the nema, looking towards the sicula, with many layers of parallel fibrils and damaged closure of fusellus in the centre, Upper Ordovician (Katian), Viola Springs Limestone, USA, NMW 91.52G.784B (after Bates, 1996, fig. 6A). **H.** *Acanthograptus* sp., spongy fusellar fabric (left) and parallel cortical fibrils (right) crossed by regular cross fibrils, Middle Ordovician (Viruan), Baltic erratic boulder 0.327, Mochty, Poland (see Urbanek and Towe, 1974), NMW 2019.34G.1771A, photograph D. E. B. Bates.

institutions: Field Museum, Chicago, Illinois, USA, (FMNH PE); Geological Survey of Canada, Ottawa, (GSC); Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland, (ZPAL); Museum für Naturkunde, Berlin, Germany, (MB.G.); National Museums and Galleries of Wales, Cardiff, UK, (NMW); Palaeontological Collections, Museum of Evolution, Uppsala University, Uppsala, Sweden, (PMU); and Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany, (SMF).

THE FUSELLUM

The fusellum is the basis of the graptolite tubarium, formed from the secretion of the zooid through glands on the cephalic shield. It consists of numerous half-rings or full rings, forming the tubarium (Fig. 1). The zooid encloses the edge of the current aperture and secretes a new fusellus, while slowly rotating around the opening (cf. Dilly, 1986). It takes several hours before *Rhabdopleura* has completed a single fusellus. The construction mode appears to be identical in *Cephalodiscus* (Dilly, 1988), but there is no clear differentiation of fusellar and cortical material in this genus (Gonzalez and Cameron, 2012).

Bates and Kirk (1986a, b) discussed the construction of the fuselli in some detail on the basis of SEM investigations. The differentiation of sheet fabric and fusellar fabric was recognized (Bates and Kirk, 1986a, fig. 1; Bates *et al*., 1988). Each fusellus is formed from three different layers, a sheet of granular fabric at the base, followed by a three-dimensional spongy meshwork of fibrils (the fusellar fabric) and a finely granular layer on top (Bates in Maletz *et al.*, 2016, figs 6, 7). These three layers must be formed by the zooids in one single step. The fibrils in the basal layer and the top layer are oriented parallel, but in the fusellar fabric in the centre of the fuselli they are randomly oriented and very loosely packed (Fig. 2D, H). These features have been investigated in a number of graptolites and can be regarded as a standard development. They are identical to the tubarium development in extant *Rhabdopleura* and *Cephalodiscus* (cf. Dilly, 1971, 1976; Andres, 1980). Harmer (1905, p. 10) discussed the „secondary lamella" in modern *Cephalodiscus*, now the cortex. Andres (1980, figs 2–7) illustrated the endo- and ectocortex in *Cephalodiscus*. Andres (1980, figs 15–17) also demonstrated the presence of the cortex in *Rhabdopleura*. Dilly (1976) described the ultrastructural development in the erect tubes of *Rhabdopleura compacta* and noted the smooth surface of the freshly formed rings, in contrast to the rough surface of older ones. The latter author described the rough surface as an effect of the secretion of additional material by the zooids, increasing the thickness of the tube walls. In his interpretation, the "scalloped edges" of the outer surface of the erect tubes are a secondary development (Dilly, 1976, fig. 4). This development may be regarded as cortical, but cortical bandages are not recognizable in the material.

The fusellum is clearly visible in many specimens, especially when the material is bleached (Fig. 1). According to Rigby and Sudbury (1995), the width of the fuselli is directly connected to the size of the zooids. This relationship can be suggested for fossil graptolites but can be verified only for extant *Rhabdopleura* and *Cephalodiscus* species.

The height of the individual fuselli is often small in the early part of the thecae and in most taxa, there are increases in height towards the thecal aperture (Fig. 1C, D). In *Cochlograptus veles* (Richter, 1871), the fuselli of the first theca ($th1^1$) are initially ca. 8–10 µm high and increase in height to about 35–40 µm in the metatheca, close to the aperture (Fig. 3G). In some cases, the height of the fuselli decreases towards the thecal aperture (Fig. 3C). Fuselli are visible in the distal part of a colony of *Arnheimograptus anacanthus* (Mitchell and Bergström, 1977; Fig. 3A) and measure about 20 µm in height. The colony clearly shows that the proximal end is more densely covered by cortical bandages and the fuselli are not visible. Towards the distal end, the fusellar construction becomes more visible, as it is not hidden beneath the cortical material. Even though no clear cortical bandages are visible in the specimens of *Hustedograptus* sp. (Fig. 3C, D) and *Archiclimacograptus* sp. (Fig. 3E, F), fusellar construction is only vaguely visible, even in the most distal parts of the colonies. A view of the colonies from the distal end shows the very thin and incompletely preserved internal tubarium walls (e.g., interthecal septa and median septum), in comparison with the thickened outer tubarium walls (Fig. 3D, F). Thickened genicular and apertural lists can also easily be seen in the material.

CORTEX DEVELOPMENT

The cortex is generally understood as a secondary development of the pterobranch tubarium, secreted on the surface of the fusellum (Figs 2A, B, 3). Kozłowski (1949, p. 41) introduced the term for the external secretion of material on the tubarium surface of graptolites, producing a secondary thickening of the thecal walls. This author assumed that secretion occurred beneath an epithelial evagination, which Urbanek (1976a) called the „perithecal membrane". Later, the possibility of TEM and SEM research arose and yielded new data on the fusellum. There were TEM investigations of the ultrastructure of well-preserved dendroids and graptoloids (Urbanek and Towe, 1974, 1975) and SEM and light-microscope studies of well-preserved cortical bandages on the outer (ectocortex) and inner surfaces (endocortex) of graptoloids (Crowther, 1978). As a result, the generally accepted manner of fusellum secretion is by cephalic shield of zooids, like that of modern Pterobranchia (*Rhabdopleura* and *Cephalodiscus*; e.g., Lester, 1985; Dilly, 1986).

The development of the cortex may include a number of additional features in Pterobranchia that are certainly secondary, thus secreted after the formation of the tubarium; these also may be developed independently in the various groups of graptolites and here are discussed separately. It is possible to differentiate between secretions extending the tubarium (e.g., apertural additions, nematularia, virgellaria) and surface secretions (bandages and sheets) on the basis of the position of their development, but not on the style of secretion. The rods and lists of cortical material invariably are formed from parallel-oriented, densely packed fibrils, overlain by a thin layer of sheet fabric (Bates, 1987) and represent the main constructional features of the Retiolitinae.

Urbanek (1966, p. 306) introduced the term microfusellar tissue for late-stage additions at the apertures of some monograptids. He described them as „very narrow and densely crowded stripes". Urbanek (1976b) discussed in some detail microfusellar development and illustrated his findings in TEM sections. This author clearly described the transition from „normal" fusellar development with a core of fusellar fabric, surrounded by sheet fabric, to the variable development of microfuselli with a thin core of fusellar fabric and others completely without this. He then identified lateral overlapping fuselli, bearing a „dependent cortex" (Urbanek, 1976b, fig. 1), actually representing the thinning side of the fuselli, in which no fusellar fabric is left. Thus, he indirectly suggested that the cortex is just the sheet fabric secreted by the graptolite zooid, an interpretation that the present authors accept. Thus, the microfusellar additions of Urbanek (1966, 1970, 1976b) can and should easily be understood as cortical additions to the tubaria (independent cortex of Urbanek, 1976b) and the term microfusellar should not be used any more.

Cortical additions are present in many monograptids (e.g., *Bohemograptus*, *Heisograptus*, *Neocucullograptus*), but also as genicular hoods in retiolitines (e.g., *nassa* hoods in *Gothograptus* and *Neogothograptus*: Bates *et al.*, 2011; Kozłowska, 2015; Kozłowska *et al.*, 2019; Maletz, 2023b). Urbanek (1970, p. 170) introduced the term

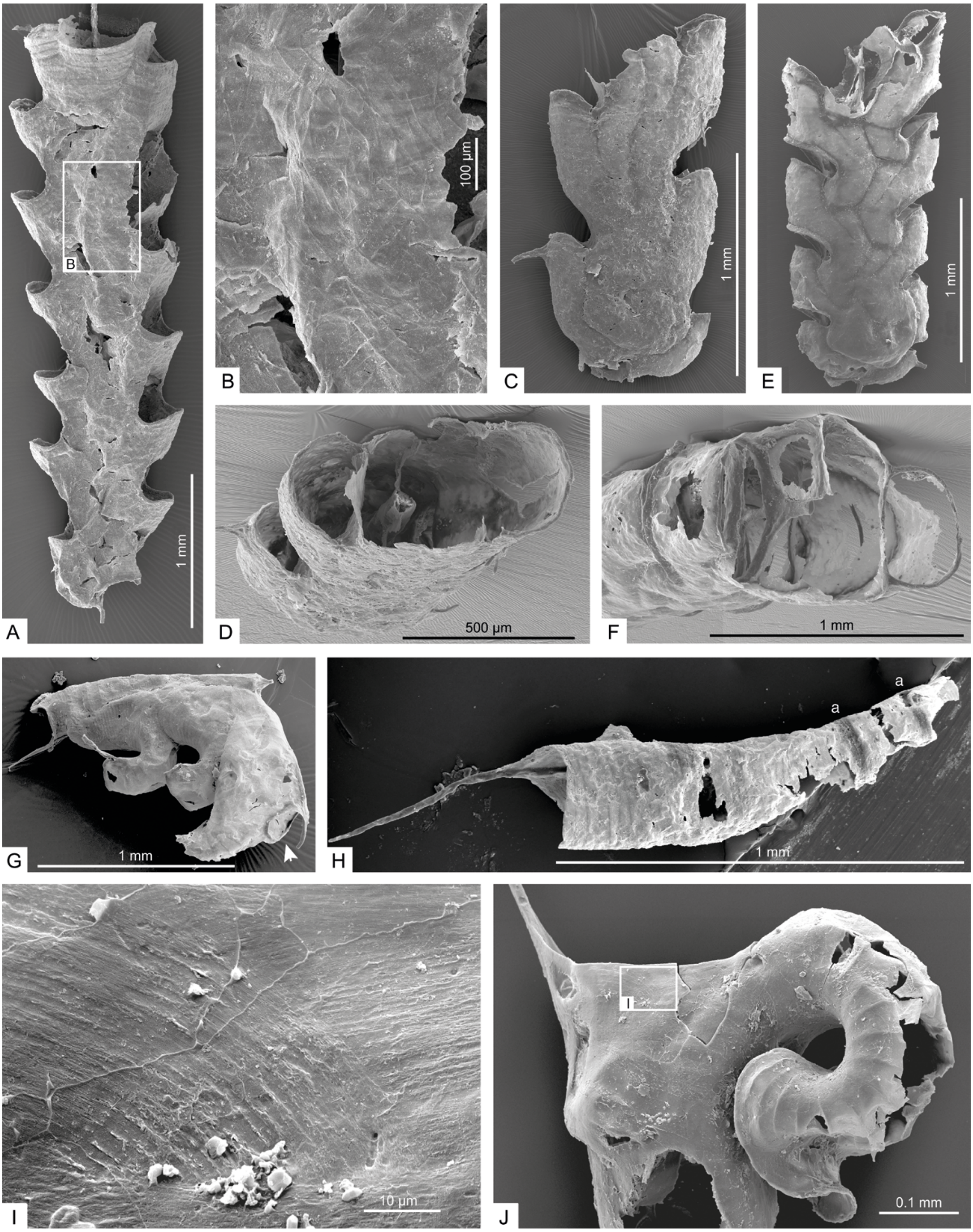

Fig. 3. SEM photos of specimens showing fusellar and cortical development. **A, B.** *Arnheimograptus anacanthus* (Mitchell & Bergström, 1977), obverse view; A – showing fuselli in distal part and B – cortical bandages with thickened rims in detail; Ohio, USA, SMF 75833 (see Maletz, 2019, fig. 10.5). **C, D.** *Hustedograptus* sp.; C – reverse view; D – distal view showing thickened thecal walls, thin interthecal septa and median septum, Newfoundland, Canada, SMF 106335. **E, F.** *Archiclimacograptus* sp.; E – reverse view with partially translucent walls showing thecal thickenings; F – view of distal end, showing thickened thecal rims, geniculae and only partially preserved thin thecal walls with fuselli, Newfoundland, Canada, SMF 106336. **G.** *Cochlograptus veles* (Richter, 1871), specimen showing thickened rim at base of new theca (white arrow), Dalarna, Sweden, PMU 31876 (after Maletz, 2020b, fig. 4A). **H.** Monograptid indet, sicula, showing fusellar growth and two sicular annuli, lateral view, glacial erratic boulder, Jarosławiec 46, Poland, ZPAL G. 75/2. **I, J.** *Paramonoclimacis sidjachenkoi* showing cortical bandages with fine parallel strokes near growing end; I – enlargement; J – whole specimen; Cornwallis Island, Canada, GSC 140091 (see Maletz *et al.*, 2019, fig. 8D). a – sicular annuli in H.

pseudomicrofusellar for more irregularly developed secondary additions in monograptids, a term that just represents cortical additions to the tubaria, with the incorporation of a variable amount of fusellar fabric (see also Kozłowska and Urbanek, 2013). Other cortical additions are the sicular annuli shown on Figures 3H and 4.

Cortical thickening of membranes

The excessive thickening of cortical layers, as described by Bates *et al.* (2011), is found all over the surface of many tubaria, often forming thick covers, especially in some dendroid graptolites. This type of cortex, described as an ectocortex, is present in numerous taxa, from benthic dendroids to dichograptids, diplograptids and monograptids. This seems to be a general, normal development in these taxa. In the thick cortical covers, individual cortical bandages often are not recognizable.

Bates *et al.* (2011, p. 212) stated that „thickening of the cortex has been recorded in various groups of graptolites, so is very unlikely to be a diagnostic feature for any taxonomic level". There is hardly any detailed information on this development and its precise construction available, as the investigation looked largely at cross-sections (Urbanek and Towe, 1974, p. 12). Thus, the development from precisely formed bandages is uncertain and it may also represent irregularly secreted material, as has been documented for *Cephalodiscus* (Gonzalez and Cameron, 2012). Ridewood (1918) described the tubarium of *Cephalodiscus* (*Orthoecus*) *solidus* Andersson, 1907 with its tubes encased in a „common coenoecial substance" (possibly a representation of excessive ectocortex material), keeping the individual thecal tubes together. There is no information of the presence of distinct cortical bandages in this construction that may include foreign material, like sand grains, diatoms and other materials. Gonzalez and Cameron (2012) described a continuum of fusellar and cortical development for *Cephalodiscus*, but no bandaging, indicating the style of secretion.

Parallel-sided elongated secretions (Fig. 2A, B) are widely distributed in the graptolites and are invariably regarded as cortical bandages now (cf. Kraft, 1926; Urbanek and Towe, 1974, 1975; Crowther and Rickards, 1977). They are described as distinct parallel-sided features on the outside of the tubaria (ectocortex of Crowther, 1981). Urbanek and Towe (1974) earlier differentiated autocortex and rhabdocortex in specimens of *Dictyonema* sp.

The cortex in the graptoloids is generally composed of closely packed fibrils, running parallel to the length of the bandage (Figs 2F–H, 3I, J). The bandages are either randomly placed over the surface of the fusellum to give a fairly even cortex covering or are concentrated along certain paths to form strong lists that are developed to extreme in the Retiolitinae (Bates, 1987, fig. 5). Cortical bandages were first illustrated from Gerhard Holms' material of *Diplacanthograptus spiniferus* by Bulman (1932a, pl. 3, fig. 7; *Climacograptus diplacanthus*). Cortical bandages are not secreted randomly on the surface of the fuselli, but show a distinct orientation (Maletz, 2020a), generally from the proximal to the distal parts of the thecae. Crowther (1981) provided the best illustrations of cortical bandages from a large variety of taxa, showing that bandages often radiate from thickened thecal apertures.

The width of the cortical bandages is about 30–40 µm in *Cochlograptus veles* (Fig. 3G). The width of the cortical bandages of 35–50 µm can be shown also for *Arnheimograptus anacanthus* (Fig. 3B). The bandages of this species show thickened lateral rims and thus are easily recognized. In other taxa, a clear differentiation of bandages is not possible, especially where the edges are tapering (Crowther, 1981, fig. 10C) but a parallel arrangement of fibrils is often recognizable (Fig. 3I). Crowther (1981) discussed the intra- and interspecific variation of the width of the cortical bandages in some detail. The latter found a maximum width of nearly 100 µm for bandages in *Orthograptus apiculatus* (Elles and Wood, 1907). The minimal width of bandages in other taxa starts at less than 10 µm (see Crowther, 1981, fig. 2: *Normalograptus brevis* (Elles and Wood, 1906). The length of the cortical bandages is quite variable and has not been measured in detail for most taxa. Crowther (1981, pl. 13, figs 6, 7) illustrated an example with a rounded termination of a cortical bandage in *Paraclimacograptus innotatus* (Nicholson, 1869) and cortical bandages of regular width in *Geniculograptus typicalis* (*Climacograptus typicalis* in Crowther, 1978, pl. 22, fig. 2).

Bandages in an abnormal specimen of *Diplacanthograptus spiniferus*, illustrated by Bates (1994), are perhaps worthy of mention here: normal bandages 21 µm wide with squarish ends and thickened sides; abnormal ones 40 µm wide with rounded ends and no side thickening.

Bates and Kirk (1992) stated that the tubaria of the Retiolitinae are largely represented by a network of thickened lists made of cortical bandages (Fig. 5F–H). These lists are laid down on the surface of the lateral ancora sleeve walls (Fig. 5G), derived from distal extension of the ancora umbrella (Bates *et al.*, 2011; Lenz *et al.*, 2018). Older forms (e.g., *Pseudoretiolites*, *Stomatograptus*) show finely striated bandages with parallel ridges or smooth as in other graptolites (Figs 2B, 6J). Bandages with pustules (Kozłowska *et al.*, 2009, fig. $6B_2$; Fig. 5H) are a unique feature for all the Retiolitinae appearing after the *lundgreni* event, e.g., in *Holoretiolites* and Plectograptus (Kozłowska-Dawidziuk, 2004, fig. 1), but originated already in the mid Telychian (see Maletz, 2022b, fig. 8).

Nematularia and virgellaria

The nema developed various types of nematularia as distal extensions of the tubarium (Kozłowski, 1971, fig. 11). Nematularia are widely distributed in graptolites and all investigated cases indicate a fusellar to entirely cortical bandage secretion with thickenings around the edges. It is unclear if the nematularia represent a monophyletic development, as these delicate features are infrequently preserved in the fossil record.

The nematularia and virgellaria of the graptolites may be identified as cortical developments, as they represent secondary secretions on the finished thecal tubes or the nema/virgella. Urbanek *et al.* (1982, fig. 5) discussed the fine structure of the nematularium of *Cystograptus vesi-*

culosus from sections, showing cortical (in their term: microfusellar) construction. Maletz *et al.* (2017, fig. 3.14B–D) illustrated the heart-shaped vesicle of *Archiclimacograptus decoratus* from western Newfoundland, showing very fine „growth lines", suggesting a „microfusellar" (= cortical) addition. The nematularium of *Paraplectograptus hermanni* is secreted as a thin (?fusellar) membrane with a thickened cortical rim (Maletz, 2023a, fig. 4h, i), but fusellar construction of the membrane cannot be verified. It may represent a combination of fusellar and cortical secretions. The nematularium of *Orthoretiolites hami* is formed from a membrane of fusellar or cortical development with thickened rims of cortical bandaging.

Thickened lists of the sicula

Several independently formed thickened lists can be found on the sicula, including longitudinal lists (Fig. 4G–I) and sicular annuli or rings (Fig. 4A–F). They were formed on the prosicula and metasicula membranes during different stages of sicular ontogeny.

The longitudinal lists (Fig. 4G–I) on the outside of the prosicula (cf. Kraft, 1926; Bates, 1996; Maletz *et al.*, 2014), formed before growth of the metasicula started, are the first-formed and phylogenetically, probably the oldest secondary features on the graptolite tubarium. According to Urbanek (1958), they consist of thin bands of thickened material, stretching across the surface from the apex of the prosicula and often extending to the region of the apertural border. They do not encroach onto the metasicula (Fig. 4G, H), but secondary cortical lists may cover them and reach onto the metasicula (Fig. 4I). Williams and Clarke (1999) described paired ridges for late Tremadocian to early Floian anisograptids and dichograptids, and single ridges for younger dichograptids, but it is uncertain whether these features are precursors of the longitudinal lists of the axonophorans.

Several longitudinal lists are fused together at the tip of the prosicula and end or merge with the nema (Kraft, 1926, pl. 6: *Rectograptus*; Walker, 1953a: *Amplexograptus*, fig. 3F). The cortical bandages, reaching from the prosicula onto the nema, are well developed in a specimen of *Paraplectograptus* (see Lenz, 1993, pl. 13, fig. 9), showing four longitudinal lists/rods, the only remnants of the prosicula. One of these rods eventually may become the virga, the list secreted on the surface of the prosicula, connecting virgella and nema, specific only to retiolitines (Bates and Kirk, 1992).

In some climacograptids, the prosicula appears to be reduced (Fig. 4I) and is preserved as a single or two thickened longitudinal lists, connecting the metasicula to the nema (see Maletz, 2020a: *Diplacanthograptus*). Crowther (1981, fig. 30) illustrated a juvenile sicula of *Diplacanthograptus spiniferus* under the name *Orthoretiolites hami robustus* Skevington, 1960 (see Williams and Clarke, 1999, pl. 3, figs 10–12: as *Climacograptus spiniferus*).

The sicular annuli (Figs 3H, 4A–F) can be understood as surface features, found on the inside of the sicula. They were first noted by Kraft (1926) and described in detail by Kozłowski (1949) and Urbanek (1958) in a number of monograptid genera. The connection to the darker rings in Ordovician dichograptids (Williams and Stevens, 1988) and in some specimens of the genus *Archiclimacograptus* (Fig. 1B) is uncertain.

Walker (1953b, fig. 1F) illustrated sicular annuli in a section, showing that they are formed from successive thin layers, identifiable as cortical bandages. It is not entirely clear when they first appear in the fossil record, but a thickened ring at the thecal origins (Fig. 3G) is already present in some specimens of *Cochlograptus veles* (see Lenz and Melchin, 2008, fig. 2D) in the mid-Telychian (Llandovery, Silurian).

Some post-*lundgreni* extinction-interval monograptids in the upper Homerian (Wenlock, Silurian) bear variable numbers of sicular annuli, including *Colonograptus praedeubeli*, *Bohemograptus bohemicus* and *Lobograptus progenitor* (Lenz and Kozłowska-Dawidziuk, 1998). These structures are more common in Ludlow monograptids. They were described for 21 species by Urbanek (1958, 1963, 1966, 1970, 1997), Lenz and Kozłowska-Dawidziuk (1998) and Whittingham *et al.* (2022) but are clearly more widely distributed. Urbanek *et al.* (2012) noticed a different number of sicular rings (annuli) in two *Pristiograptus dubius* group species from Poland. In the Gorstian group, the sicular rings vary in number (up to 8 rings) and in their position on the sicula. During the Ludfordian, *Pristiograptus* displayed a uniform occurrence of three rings, occupying a consistent position on the sicula: the first situated on the boundary between the prosicula and metasicula, the second located at about 1/3 of the length of the metasicula, and the third ring found close to the primary notch area. Urbanek (1997, p. 117) discussed the late Silurian (late Ludfordian) restructuring of the sicula, on the basis of the reduction of the number of sicular annuli. This author regarded the phenomenon of progressive biostratigraphical change in number and placement of the sicular annuli as a directional (anagenetic) trend.

The incompletely preserved metasicula of a monograptid, probably of *Saetograptus chimaera*, shows three sicular annuli (Fig. 4A–F). The delicate metasicular wall is damaged and is preserved better, where it is reinforced by the virgella and the sicular annuli. The head of each fusellus of the metasicula is particularly prominent internally, where it occurs as a narrow ridge (Fig. 4E, F). An "X-ray" effect also accentuates the heads, where the electron beams pass through the thecal walls (Fig. 4B, C). The three sicular annuli are about 200 µm apart and have a width of about 30 µm and a thickness of 2–3 µm. They form robust rings, largely parallel to the fuselli, but do not sweep forwards with the fuselli at the virgella as was noted by some authors (e.g., Walker, 1953b; Urbanek, 1958). Annulus three is formed by few bandages and is only visible as a dark band on the interior on the sicula (Fig. 4A, B) and again as an X-ray effect in the exterior view. Thus, the zooid has barely started to secrete this feature. All sicular annuli have finely striated surfaces. The striations running parallel along the length of the annulus (Fig. 4E, F) presumably represent the fibrils of the cortical tissue. As internal bandages, they probably lack a sheet surface, unlike most external bandages (e.g., Crowther, 1981, pl. 19). The edges of the bandages and therefore the width of these cannot be recognized in the material.

The virgella, as a dorsal or ventral spine on the aperture of the sicula, evolved several times independently in the Graptolithina (Maletz, 2010). It is formed by the distal extension of the fuselli at one of the zigzag sutures and represents a thickening (and probably strengthening) in this region of the sicula. This is clearly demonstrated by the two dark lines along the lanceolate virgella in early axonophorans (Maletz, 2010, fig. 5), representing parts of the

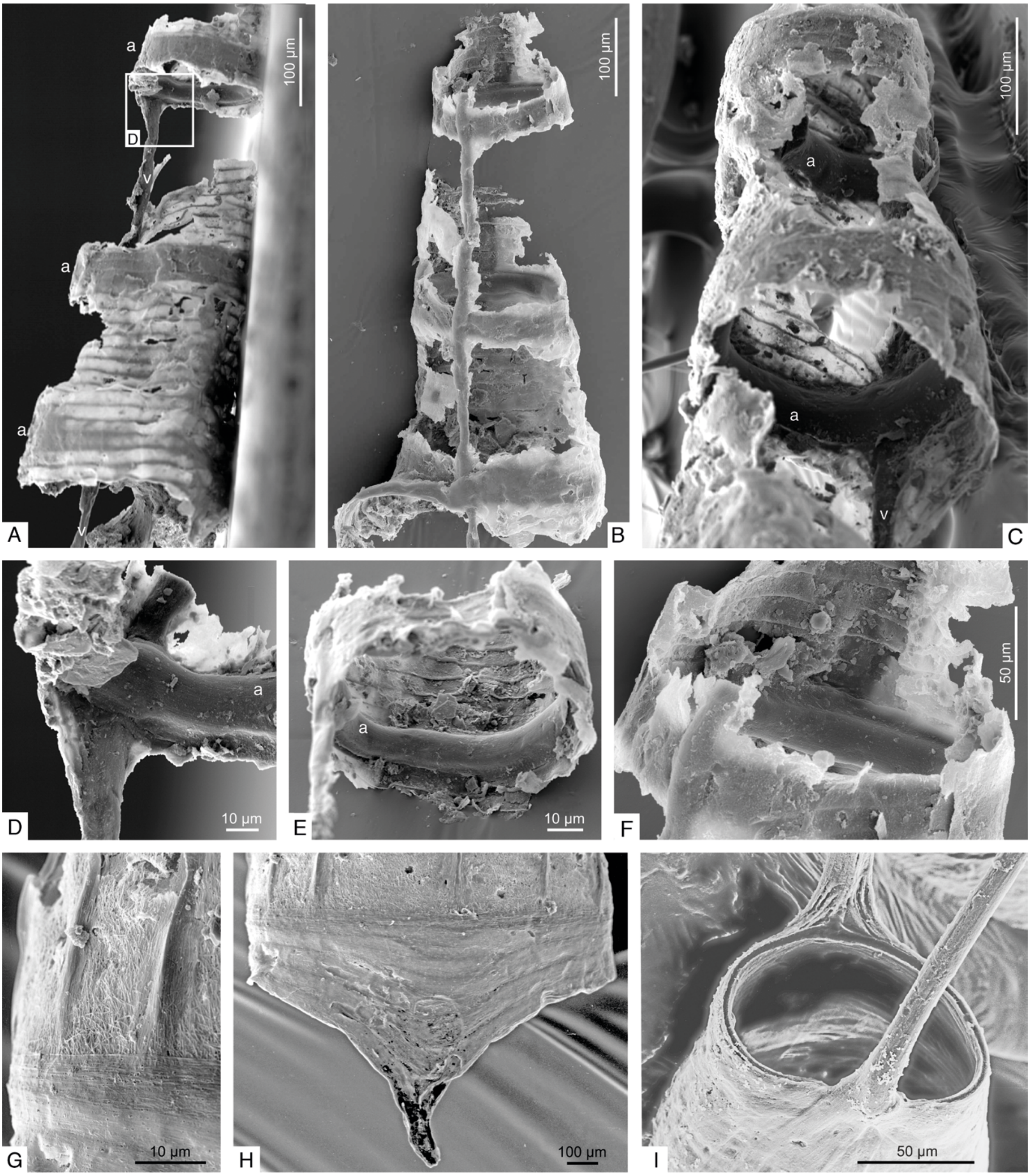

Fig. 4. Internal thickenings in the sicula with annuli, SEM (A, C, D, G–I) and BSE (B, E, F) photos. **A–F.** Partial metasicula of a monograptid with three annuli, glacial erratic boulder from Jarosławiec 46, Poland, ZPAL G. 75/1; A – lateral view; B – ventral view; C – second annulus, dorsal view inside metasicula; D – annulus crossing virgella on inside of metasicula; E – close-up of first annulus in broken piece; F – internal view of the first annulus. **G, H.** Sicula indet, showing boundary between prosicula and metasicula with longitudinal lists, Viola Springs Limestone, USA, NMW 91.52G.765. **I.** *Diplacanthograptus spiniferus* (Ruedemann, 1908), attachment of two longitudinal lists to metasicula, furrow indicates lack of prosicula, note the secondary cortical bandages. Viola Springs Limestone, USA, NMW 2019.34G.686A. a – sicular annulus, v – virgella.

fuselli, in which the fusellar fabric is lost and only the denser sheet fabric is found.

The virgella in some monograptids has a secondary internal list, formed from cortical bandaging, running along it, thickening it in a similar manner to the sicular annuli (Fig. 4B–D). It is called here the virgellar list and is considered to be a secondary feature, not involved in the construction of the virgella, and does not represent the virgella itself. The vaguely recognizable striations on the surface (Fig. 4D) indicate a secretion by the sicular zooid as in the sicular annuli (Fig. 4F). This development has not been recognized in older, Ordovician to early Silurian graptoloids. Urbanek (1997, fig. 9) illustrated the thickened list along the virgella from a number of late Silurian monograptids and identified it with the virgella. This longitudinal list inside the sicula starts approximately at the point, where the secretion of the virgella begins and the fuselli bend forwards, as is seen in *Pristiograptus dubius* and *Saetograptus chimaera* (cf. Walker 1953b).A connection to the sicular annuli is not seen in this material. In younger monograptids from the Ludfordian (Ludlow) and Pridoli, the virgellar list usually starts at the second sicular annulus (cf. Urbanek 1997, fig. 9: *Wolynograptus acer*, *Skalograptus lochkovensis*).

In the present material from the Gorstian (Ludlow), the virgellar list is overlain by the sicular annuli (Fig. 4D) and thus was formed earlier; no further thickening occurred, once the sicular annuli started to develop.

The genus *Formosograptus* shows two sicular annuli and a longitudinal list along the virgella, apparently on the outside of the sicula (cf. illustration in Urbanek, 1997, fig. 20B$_2$). However, the entire development also may represent internal thickenings, overlain by a very thin fusellum, and partial flattening of the material, but the description by Urbanek (1997) is unclear here.

Thickened apertural rims and genicular processes

In many graptoloids, but especially visible in many Monograptidae (cf. *Pristiograptus*: Urbanek, 1997; Urbanek *et al*., 2012), are thickened rims of the apertures (Fig. 3G). Apertural thickening may be a standard in many graptolites, as can be seen in the thickened apertural rims in axonophorans (see Fig. 3C–F). It appears to be rare in Lower to Middle Ordovician dichograptids and sinograptids, however (see Maletz, 2022a).

These rims were formed from secondary cortical secretions of the zooids in the form of bandages, as are other thickening features in the graptolite tubaria and a gradual increase in thickness towards the proximal end and the sicular aperture can be seen (cf. Urbanek, 1997, pl. 19: *Pseudomonoclimacis latilobus*). The youngest thecal apertures do not show any thickening of the rim. Extreme thickening on the inside of the thecal aperture has been recognized in sections of *Normalograptus scalaris* (Hisinger, 1837) by Loydell and Maletz (2009, fig. 2), but verification of this being due to the secretion of cortical bandages was not possible.

The apertural rims may in other taxa be thickened only in part. Thus, only the thecal lip, the ventral part of the ancora sleeve orifice, is thickened considerably in some retiolitines. Horizontally expanded apertural lips with paired labiate structures are characteristic, especially of *Neogothograptus purus labiatus* (Lenz and Kozłowska-Dawidziuk, 2004, pl. 4, figs 4, 6, 7, pl. 5: 2–5) and *Gothograptus kozlowskii* (Kozłowska *et al*., 2019, fig. 17A).

Genicular processes are usually built by cortical tissue and in some cases of thin fusellar membranes. The most typical genicular processes and the thickest are formed in the retiolitines, e.g., in *Gothograptus nassa*, and are named the *nassa* hood (Kozłowska *et al*., 2019, fig. 1), formed by densely packed parallel bandages. During astogeny, the hoods are covered by irregularly running bandages, as is typical of the fusellar membrane. This additional layer makes them thick and massive. This type of genicular structure is located close to the apertures of thecae, almost covering them, as in *Gothograptus nassa* (Kozłowska *et al*., 2019, fig. 3). More complex processes occur in *Gothograptus auriculatus*, which has additional lateral lobes, named auricles, especially well-developed in mature specimens (Kozłowska *et al*., 2019, fig. 13A).

Transverse lists

The thickened list, surrounding the base of each new theca in many graptolites (cf. Fig. 5A, D), has been identified by a number of terms. In the biserial axonophorans, it was identified as a combination of the cross bar and the aboral list (see Maletz *et al*., 2019, fig. 5.2), where the aboral list represents the base of the interthecal septum (Fig. 5A). In the Retiolitinae (Fig. 5D), this list is identified as the transverse rod or transverse list (Lenz *et al*., 2018, fig. 9.2). It is here suggested that the term aboral list be abandoned and the term transverse list used be consistently for all graptolites.

The thickened proximal part of the interthecal septum, the transverse list, is clearly shown in a cross-section of *Geniculograptus typicalis* (Fig. 6E, F), where a concentric layering is present before the layers sweep forwards, as the interthecal septum grows. It appears to have formed first as a rod-like structure, perhaps as a spine or pair of spines, internal to the growing tubarium. It is not possible from the material available to determine whether two spines, growing towards one another, meet and join. Note that the list is thickened more on its proximal side. The junctions of the transverse list with the thecal walls are commonly thickened, so that the list has a dumbbell shape (Fig. 6E, F). This shape can also be seen in the Late Ordovician *Styracograptus* and *Appendispinograptus* specimens illustrated in Wang *et al*. (2020, figs 3L, 4E), unistipular (aseptate) taxa, in which the transverse list is connected to the nema by a short list (Fig. 5C). This development is, however, somewhat different from the development in bistipular tubaria (Fig. 5A, B), in which a connection of the transverse list to the nema does not exist.

Transverse lists are common in the older retiolitines from the pre-*lundgreni* event (e.g., *Retiolites* (Fig. 5D), *Stomatograptus, Paraplectograptus*, *Cometograptus*). They are of similar thickness to the other clathrial lists (strong lists of both thecal and ancora sleeves) of their tubaria. The transverse lists are reduced or lacking in younger retiolitines, where the main clathrial lists may be stronger.

In retiolitines, however, the transverse lists are the only representation of the interthecal septum, as there is no thecal overlap and an interthecal septum or membrane is not present. The basal retiolitids, the Petalolithinae, still have an interthecal septum (Lenz *et al*., 2018). An extremely long interthecal septum can be found between the very long thecal tubes in *Cephalograptus* and an interthecal septum may be present in *Hercograptus*. The evolutionary loss of the interthecal septum in the Retiolitinae cannot be followed in the fossil record, as these membranes are extremely delicate and rarely have been recognized. Another problem is the lack of information on the fusellar construction in the Retiolitinae.

The nema-virga-virgella complex

The virgella-virga-nema complex forms an elongated feature inside the retiolitine tubarium and can easily be compared to the development of the nema and virgella in other axonophorans. The nema is known as a basic structure along the tubaria in the monograptids,but has its origin in the basal

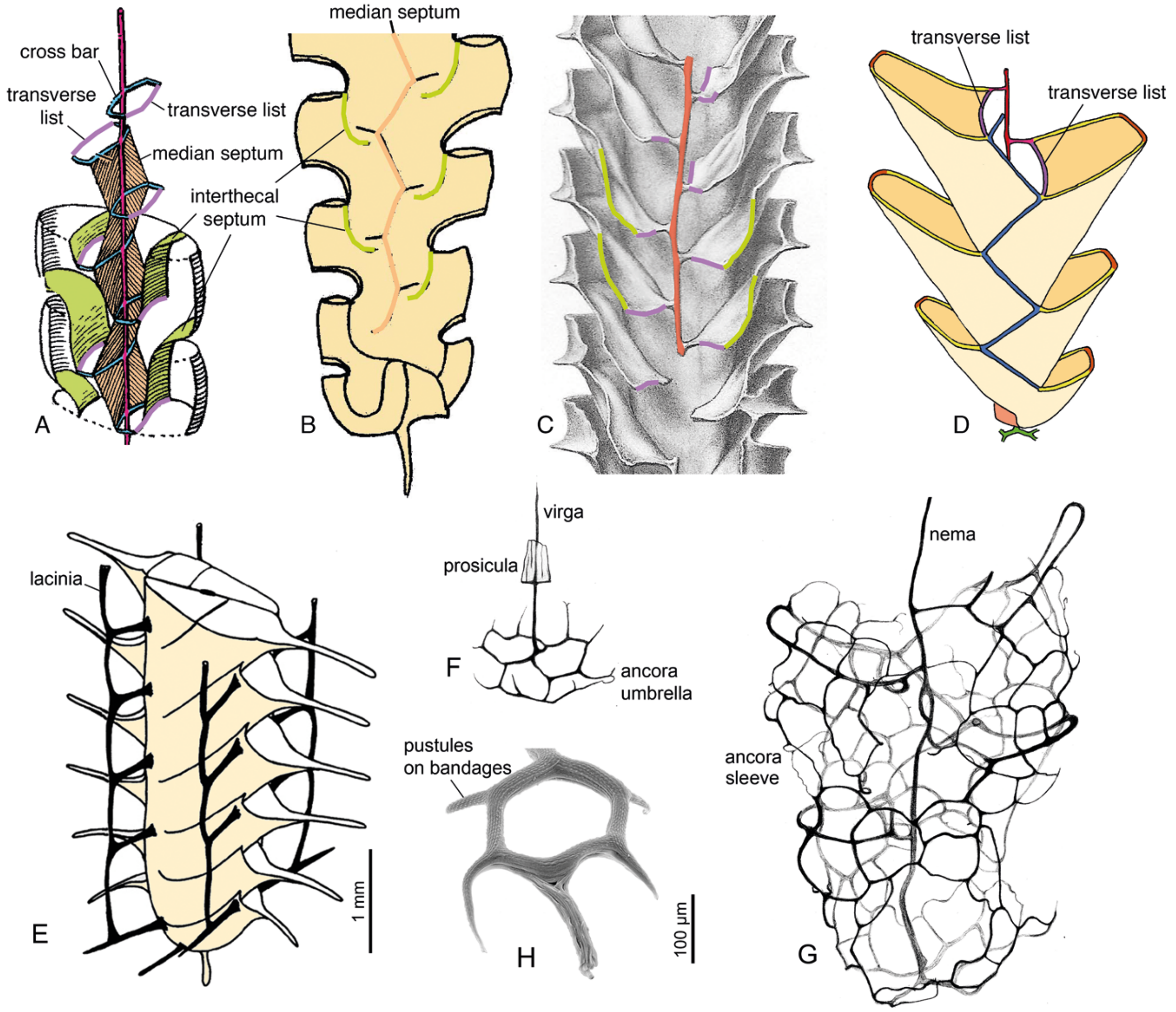

Fig. 5. Homologies of thecal lists (A–D), tubarium with lacinia (E) and tubaria of retiolitines (F–H). **A.** Thecal development in biserial, bistipular colony, showing interthecal septa and median septum in colour (based on Bulman, 1955, fig. 34.2). **B.** *Haddingograptus eurystoma*, obverse view showing external traces or impressions of median septum and interthecal septa in bistipular tubarium (after Maletz, 1997, fig. 29A). **C.** *Geniculograptus typicalis*, distal fragment, showing nema (red) connection by short lists to middle of transverse list (pink) in a biserial, unistipular tubarium (after Bulman, 1932b, pl. 5, fig. 40a). **D.** *Retiolites geinitzianus*, reverse view, showing thecal style, ancora sleeve omitted (after Maletz, 2022b, fig. 1F). **E.** *Paraglossograptus proteus*, thecal wall and lacinia (based on Maletz and Zhang, 2023, fig. 216.6). **F. G.** Drawings of *Retiolites geinitzianus* specimens, Zawada 1 core, Poland, 1621.7–1628.0 m, I–II; F – ancora umbrella stage of colony development, ZPAL G. 75/7; G – tubarium represented by cortical lists network of ancora sleeve, obverse view, ZPAL G. 75/8, (A. Kozłowska drawings, not scaled). **H.** *Plectodinemagraptus gracilis*, ZPAL G. XVI/1409, Mielnik IG 1 core, Poland, depth 946 m, *hemiaversus*/*aversus* Biozone, ventral orifice, view from the outside, showing bandages with pustules (after Kozłowska and Bates, 2014, fig. 3.5).

Ordovician (the „nematophorous" graptolites: Kozłowski, 1971, p. 314). It is incorporated into the tubarium in biserial graptolites but can be found on the dorsal side in monograptids. It grows from the tip of the prosicula (cauda), having a concentric construction with a rounded ridge near the dorsal side of the tubarium in somewhat obliquely preserved specimens, and may be thickened considerably. The virgella developed as an extension of the fuselli at the zigzag suture

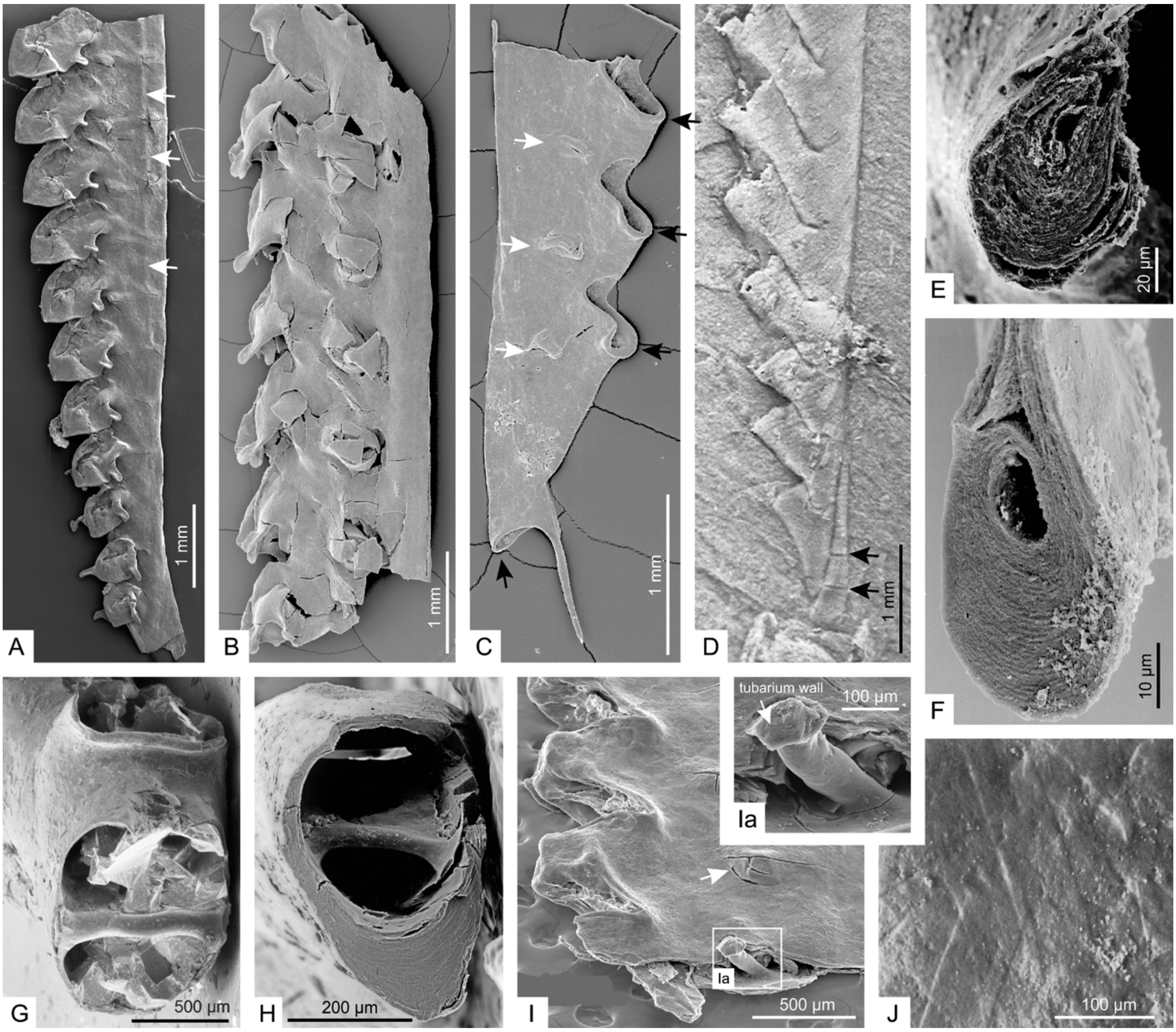

Fig. 6. Deformation of graptolites showing thickenings. **A.** *Monograptus flemingii elegans* Elles in Boswell and Double, 1940, general view of mature specimen with ridges and fractures becoming more prominent distally; white arrows indicate nema, Bartoszyce IG 1 core, 1712.7 m, Poland, *Cyrtograptus lundgreni* Biozone, ZPAL G. 75/3. **B.** *Monograptus flemingii compactus* Elles and Wood, 1911, portion of stipe with prominent fractured bulges marking the transverse lists, Bartoszyce IG 1 core, 1679.8 m, Poland, *Cyrtograptus lundgreni* Biozone, ZPAL G. 75/3. **C.** *Colonograptus praedeubeli* (Jaeger in Barca and Jaeger, 1990), proximal end with three thecae showing thickened apertural rims (black arrows) and pressed through transverse lists (white arrows), note also thickened sicular apertural rim, Bartoszyce IG 1 core 1646.8 m, ZPAL G. 75/4, Poland. **D.** *Colonograptus praedeubeli* (Jaeger, 1990), arrows indicate sicular annuli, Pojo, Cochabamba, Bolivia, (see Maletz *et al*., 2002, fig. 2B). **E.** *Geniculograptus typicalis* (Hall, 1865), aboral list with apparently empty core, extending distally, note the thickening on the proximal side, Viola Springs Limestone, Rayford, USA, NMW 2019.34G.467. **F.** *Geniculograptus typicalis* (Hall, 1865), cross-section through aboral list and interthecal septum, the fusellar core of the initial spine appears to be empty, and following the extension of the septum the list becomes greatly thickened on the proximal side, Viola Springs Limestone, Oklahoma, USA, NMW 2019.34G.801B. **G.** *Monograptus priodon*, transverse list, with a dumbbell shape, is about 55 µm thick, compared to a thecal wall thickness of about 8 µm, NMW 2019.34G.1548B (specimen destroyed on stub), Cape Phillips Formation, Cornwallis Island, Canada. **H.** *Amphigraptus* sp., dumbbell-shaped aboral list with thinner interthecal septum, Viola Springs Limestone, USA, NMW 91.52G.394F. **I, Ia.** *Monograptus* sp., fragment with bulges marking the transverse lists (arrow), *Cyrtograptus lundgreni* Biozone, Bartoszyce IG-1 core, 1679.8 m, Poland, ZPAL G. 75/6; Ia – enlargement of transverse rod (arrow) coming out of the tubarium wall. **J.** Superposed cortical bandages of ectocortex of *Climacograptus typicalis* (after Crowther, 1978, pl. 22, fig. 2), not to scale.

along the ventral wall of the aperture of the sicula. A thickening of the virgella through an internal list can be seen in some monograptids, but rarely has been recognized.

The virgella and nema are connected in most retiolitines by the virga, but other axonophorans do not show any direct connection of both features. The virga is formed secondarily from bandages, deposited on the prosicular wall from the apex to the virgella, as a prominent, modified longitudinal list. It shows a flattish inner side and a convex outer side.

Annuli in Retiolitinae

The appendix is a terminal, distally oriented tube, the tip of the retiolitine tubarium, indicating the finite growth of the colonies in the *Gothograptus* lineage (Kozłowska *et al*., 2019). Annuli inside the appendix are seen in *Gothograptus kozlowskii* as well as in *Neogothograptus balticus* and *N. eximinassa* (Fig. 7C, D, G). They have a smooth surface without the pustules, typical of the bandages in *Gothograptus* and *Neogothograptus*. Thus, they are constructionally more similar to the sicular annuli of the monograptids.

The genus *Gothograptus*, regarded as the ancestor of the lineage, has the nema attached to the lateral wall of the tubarium (Fig. 7E, F, H). The annuli in *Gothograptus kozlowskii* are prominent, connected to the nema. In *Neogothograptus*, the nema is free, therefore not attached to the thecal wall and the appendix. The appendix annuli of *Neogothograptus balticus* and *N. eximinassa* are developed as full rings (Fig. 7A–D, G), and thus, differ from those in *Gothograptus* where they are attached to the nema (Fig. 7F).

The cortical lists outside of the thecal wall

An ancora sleeve is characteristic of the retiolitines, the group of graptolites that is unique in possessing an additional lateral wall, the ancora sleeve. It is derived from distal extension of the virgellar ancora (Bates *et al*., 2005) and forms a meshwork of cortical lists outside the thecal wall. The meshwork is built by strong (clathrium) and thin (reticulum) lists of varied configurations in different lineages (e.g., Kozłowska-Dawidziuk, 2004).

The thin fusellar wall of retiolitines is preserved only exceptionally (e.g., Lenz and Melchin, 1987), and their tubaria are supported by strong lists, formed exclusively from bandages, deposited outside of the fusellar wall. Therefore, mostly the rod-like bandaged lists of the thecal wall and the ancora sleeve wall are preserved. These lists are characterised by the presence of seams, meaning traces

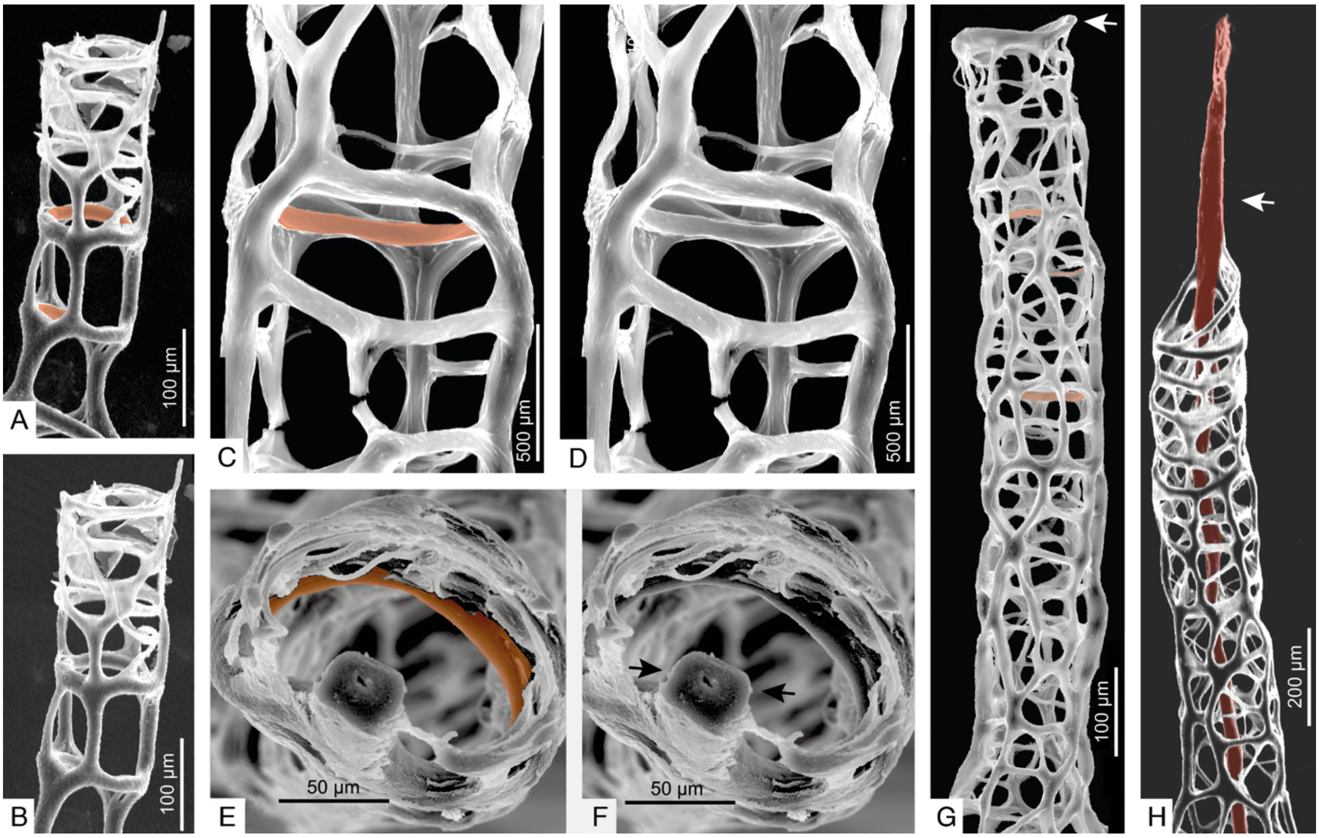

Fig. 7. Annuli in the Retiolitinae. **A, B.** *Neogothograptus balticus* (Eisenack, 1951), JM 56/4, MB.G. 1082, showing possibly annuli in appendix (complete specimen in Maletz, 2008, fig. 7G). **C, D.** *Neogothograptus eximinassa* Maletz, 2008, JM 61/15, MB.G. 1123, annulus in appendix? (complete specimen in Maletz 2008, fig. 8G). **E, F.** *Gothograptus kozlowskii* Kozłowska-Dawidziuk, 1990, holotype, ZPAL G.XIII/43, view into appendix showing annulus on reverse side, arrows indicate nema (complete specimen in Kozłowska *et al*., 2019, fig. 18). **G.** *Neogothograptus eximinassa* Maletz, 2008, JM 61/01, MB.G. 1123, note thickened rim of appendix (complete specimen in Maletz, 2008, fig. 8H). **H.** *Gothograptus berolinensis* Maletz, 2023a, JM84/05, note attachment of nema (in red; arrow) to appendix (complete specimen in Maletz 2023a, fig. 10A). Annuli indicated in red in (A, C, E, G); nema in red in (H).

of the unpreserved fusellar wall (Bates, 1987, 1990, fig. 7; Kozłowska-Dawidziuk, 1997, fig. 9C, D). The surface ornamentation of bandages can be finely striated, with parallel ridges, or pustules that are unique to the retiolitines (see details in, e.g., Bates *et al.*, 2005; Fig. 5H).

The lacinia

The lacinia is the three-dimensional network of unseamed lists, surrounding the thecae (Fig. 5E). This is analogical to the retiolitine ancora sleeve, built of lists with seams (Bates and Kirk, 1991), since the lacinia lists do not grow by extension of the ancora of the virgella. Bates and Kirk (1992) documented the cortical origin of the spines and lacinia meshwork of the Ordovician Lasiograptidae, differing fundamentally from the construction of the Silurian retiolitine graptolites.

The lacinia is present in the Ordovician graptolites: Lasiograptidae and in Glossograptidae (*Paraglossograptus*) (Elles and Wood, 1908, p. 319; revised by Bates, 1990, p. 717; Fig. 5E). The lacinia lists are attached to thecal and sicular apertural spines, to the nema, as well as to the virgella (Maletz *et al.*, 2016). The fusellar tissue of the thecal wall of Lasiograptidae tubaria is reduced, and frequently only thin lists with seams are preserved, indicating their origination on the fusellar surfaces of the thecae, in contrast to the unseamed lacinial lists. In some Lasiograptidae, the lists form a complex meshwork structure around the entire colony. In early lasiograptids, the thecal fusellum is more complete, so the difference from the encasing lacinia is easily recognizable. Bates and Kirk (1992) described the development of several Lasiograptidae genera (*Orthoretiolites*, *Pipiograptus*, *Phormograptus*) from the Viola Springs Limestone in some detail and established the constructional elements of their tubaria.

Patagium

The patagium is a specific, basically cortical structure, known in *Bohemograptus papilio* (Kozłowska and Urbanek, 2013). It is a paired latero-dorsal addition, located in the proximal part of the tubarium, built by the main cortical rods dividing repeatedly into irregular thinner lists. Some remnants of delicate membranes are spread between the lists. It looks like a pair of wings, projecting horizontally from the tubarium (Kozłowska and Urbanek, 2013, figs 4, 5).

DIAGENETIC FLATTENING AND TECTONIC DEFORMATION

Numerous examples can be provided to show the cortical thickening of membranes, lists and other features in the Graptoloidea. These have a considerable impact on the preservation and interpretation of the graptolite specimens in rocks, both in relief material and as flattened films. Distortions may easily lead to the misidentification of graptolite species (cf. Richter, 1853; Eisel, 1908; Maletz, 2020b). They also help us to identify certain constructional details, not seen from the outside in relief specimens and in flattened material, not only found in shales, but also in chemically isolated specimens.

Rickards (1968, fig. 1) described the thickened base of the interthecal septum and the thickened ventral apertural lip of *Monoclimacis*? *galaensis* (Lapworth, 1876). However, there is some thickening along the junction of the two, structurally like the fillet weld between two steel plates. Compaction of the specimens enhances the differences in resistance of the thickened lists to the thin membranes of the tubaria. This results in subdued oblique ridges on the surface of the flattened material (Fig. 6A). The flattening of the tubaria may also produce cracks or fractures in the fusellum (Fig. 6B, C) and can lead to the thickened lists producing fractures in the fusellum or even punching holes into the fusellum, as can be seen in specimens of *Monograptus* sp. (Fig. 6I, Ia).

The shape and orientation of the transverse list has distinctive results, where the material is flattened. If the list is approximately vertical before flattening, it can resist the pressure better than the thecal walls, causing cracking and penetration of the lateral walls of the thecae (Fig. 6I). If the list is not vertical, it can appear in profile, showing the course of the list, with one or both ends bulging more through the surface of the lateral wall (Fig. 6B, C). The transverse lists are slightly concave distally and mark the beginnings of the second and third thecae in this specimen.

Radzevičius (2003) and Urbanek *et al.* (2012) illustrated the variability of the presence/absence of thickened apertural lists in the genus *Pristiograptus* and their importance for the discrimination of taxa. The latter authors illustrated a large number of full relief to completely flattened specimens and demonstrated the possibility of recognizing internal features like thickened transverse lists, apertural lists and sicular annuli in their material.

The flattening features in graptolites have been interpreted in different ways in the past. Haberfelner (1933) interpreted the thickened transverse lists in monograptids as muscle scars, following the ideas of Ulrich and Ruedemann (1931) in their interpretation of biserial graptolites, but Obut (1947) preferred to identify them as carbonized gonads. Urbanek (1958, p. 18) recognized the thickened list at the base of the interthecal septum in his microtome sections. Flattening of the tubaria produced the protuberances, distortions and fractures visible in numerous monograptid specimens (Urbanek 1997, p. 91).

Considerable thickening of the thecal membranes in biserial graptolites can be seen in *Normalograptus scalaris* (see Maletz, 2003; Loydell and Maletz, 2009). Mature specimens of this species show a thick cover of cortical material on the thin fusellum, leaving only the slit-like thecal apertures openings free. The median septum, interthecal septa (Fig. 5A, B) and other features are not visible on the outside, but some details may be revealed, due to compression of the specimens (cf. Loydell and Maletz, 2009, pl. 1). The internal membranes, the interthecal septa and the median septum, are not thickened (see Maletz, 2003). These internal walls are also often not preserved in isolated biserial graptolites, preserved in full relief. A quite differently preserved taxon associated with this species is *Korenograptus nikolayevi* (Obut, 1965), with a fairly thin fusellum and little cortical cover, except around the thecal apertures (see Loydell and

Maletz, 2009, fig. 3), showing a nearly complete flattening of the colony. Thus, even if the tubarium shape is quite similar in both taxa, the amount of cortical cover is very different and may not be produced to stabilize the tubarium and protect it from collapse.

FUNCTION OF THICKENING FEATURES

Many features of graptolites are enhanced through preservational aspects, especially through diagenetic flattening, metamorphic coalification of the tubaria and bleaching of the rock through weathering. Through coalification, graptolite tubaria are more easily visible on the surface of black shale layers, as they gain a silvery shine of the organic material. Therefore, details appear and tiny species, otherwise difficult to recognize, will be found on the shale surfaces. The material reacts similarly to thermal heating with carbonization, as does plant material (see Maletz, 2020b).

Diagenetic and tectonic modifications are quite important for the identification of graptolites, but the modifications may distort specimens and make details difficult to recognize and thus may lead to misidentification and misinterpretation. Thickened lists within the tubaria may be less compressed than the thin membranes and form externally visible features (Fig. 6). All the mentioned features, showing thickening of membranes and lists, easily could be interpreted as strengthening features for the tubarium, but this interpretation appears to be simplified if looked at in detail. This cortical thickening is commonly concentrated at certain features only and may be lacking in other, closely related taxa (cf. *Pristiograptus*: Urbanek *et al*., 2012).

Zalasiewicz *et al*. (2013) illustrated „hourglass" bodies in flattened specimens of *Dicranograptus* aff. *ramosus* from the Upper Ordovician of southern Scotland and interpreted them as the remnants of a stolon system. In view of the appearance of the transverse lists illustrated here, it seems more likely that they are transverse lists. As can be seen in their figure 3, the remains are shattered, with the thecal walls broken into small fragments, while the hourglass structures (the transverse lists), being thicker, have resisted disintegration much better. It may be noted that, on the left-hand stipe, the lists gradually change position from proximal to distal, perhaps owing to original torsion of the stipe (cf. Maletz, 2020b, fig. 3A).

Sicular annuli in monograptids first appeared widely in the Wenlock and become more common in the Ludlow. They are observed first above the *Cyrtograptus lundgreni* Biozone of the upper Homerian (Urbanek *et al*., 2012) with the onset of the post-lundgreni diversification of monograptid faunas. During the Gorstian, the number of sicular annuli is quite variable and up to 8 annuli have been counted (Lenz and Kozłowska-Dawidziuk, 1998). The Ludfordian and Pridoli monograptids show fewer and more tightly controlled positions of the sicular annuli. Porębska (1984) described the Pridoli to Early Devonian monograptids from the Bardo Mountains and indicated a maximum of two or three sicular annuli in all described species in her illustrations. This may indicate that a strengthening is not the reason for the presence of the annuli, especially considering that earlier monograptids – even species included in the same genus (e.g., in *Pristiograptus*) – do not show sicular annuli (Urbanek *et al*., 2012, fig. 1).

Whittingham *et al*. (2022) suggested that the origin of the sicular annuli represents the „product of the effects of sea level change cascading through changes in primary productivity". The authors indicated that there is a positive correlation between the presence of annuli and high-stand conditions of sea level, when there was higher phytoplankton diversity and productivity. The siculae without annuli occurred during the regressive parts of sea level cycles. Thus, they considered an ecological controlled feature (more food = more annuli) but were unable to find a mechanism that would explain the formation of the annuli. Whittingham *et al*. (2022, p. 35) also suggested that sicular annuli are unique to tropical regions, citing the lack of sicular annuli from the Bolivian material of Maletz *et al*. (2002). This is, however, based on the preservation of the material, as can be seen in the recognition of sicular annuli in *Saetograptus argentinus* by Lopez (2022, fig. 4.3) and in a specimen of *Colonograptus praedeubeli* from Bolivia (Fig. 6D; drawing in Maletz *et al*., 2002, fig. 2B).

It is clear from the detailed and precise work of Urbanek (1997), however, that the presence and position of the sicular annuli is taxonomically controlled. It may be based on the differentiation of ontogenetic changes in the growth patterns of the sicular zooid, but as nothing is known about the anatomy of the zooids, this may be impossible to verify. Rigby and Sudbury (1995) suggested that graptolite zooids had three stages in their ontogeny, of which only the first one is seen in the secretion of the tubarium. The feeding and reproductive stages do not leave any evidence in the fossil record. It may be possible that forms with sicular annuli have added ontogenetic stages, expressed in these annuli as the only palaeontological evidence.

Thickened thecal lists produce considerable modification, where the specimens are flattened, and thus easily could be interpreted as the result of maintaining the shape of the graptolite tubarium, especially when the delicate development of some of the retiolitines is taken into account. Retiolitine graptolites with their meshwork of lists can easily be compressed, especially in shales, but may keep a full three-dimensional shape in limestones, owing to early cementation of the material and the lack of compaction. Chemically isolated specimens, preserved in three dimensions, often deform under stress when handled, but spring back to their original shape, when the stress is no longer applied. Thus, they are still elastic, even after hundreds of millions of years of being embedded within the rocks.

Others, however, are quite fragile and even lifting them with a fine brush for transport may break them. Thus, the organic material, of which the graptolite tubaria are secreted, can under the right conditions be flexible and behave as do the tubaria of extant species. Under other conditions, the material is more strongly affected, presumably by diagenesis and tectonics, and is fragile. Flattened specimens, freed from the surrounding rocks, stay flat and attempts to manipulate them may easily result in their breakage or destruction.

The taxonomy of the retiolitines shows that a dense meshwork of cortical lists is produced in some taxa, but not in other, closely related ones. The genus *Neogothograptus* may serve as an example (cf. Kozłowska *et al.*, 2009; Kozłowska, 2015; Maletz, 2023b). Taxa with a very dense reticulum formed by thin lists (*Gothograptus reticulatus*) and others with only a few strong clathrial lists (*Neogothograptus melchini*) can be seen. Also, the astogeny of these taxa shows that the fine reticulum is constructed long after the main lists of clathrium of the specimens are secreted. The astogeny of *Neogothograptus eximinassa* (Maletz, 2023b, fig. 4) indicates that the tubarium may be completely formed when very few reticular lists are present and are only when the tubarium reached its final size are the majority of the reticular lists secreted. The reticulum is, thus, a late-stage development and not necessary for stabilization purposes. The fusellum and the ancora sleeve membranes were extremely thin in all these species and were not preserved in the fossil record. These membranes already may have been destroyed during the lifetimes of the specimens, while the reticular lists remain. The lack of reticulate bandages on the surface of the fusellum and ancora sleeve in immature specimens apparently did not affect the life of these colonies, indicating that there was no need to strengthen the membranes. Thus, it is necessary to look for other reasons to explain the dense reticulum in the retiolitines.

A new aspect of the retiolitines that has been recognized during this research is the presence of features, similar to the sicular annuli of the monograptids. A number of retiolitines, especially of the genera *Gothograptus* and *Neogothograptus*, appear to show internal bandaging in the appendix that may represent annuli (Fig. 7). In these taxa, the reticulum is formed on the outside of the tubarium membrane (e.g., Kozłowska-Dawidziuk, 2004, fig. 1), showing pustulose bandages with seams on the inside.

Specimens of *Neogothograptus balticus* clearly show thickened lists, formed from smooth cortical bandages on the inside of the appendix in an identical fashion to the sicular annuli of the monograptids (Fig. 7A, B). An identical construction was found in *Neogothograptus eximinassa* (Fig. 7C, D, G). In this species, the aperture of the appendix is distinctly thickened (Fig. 7G), indicating the end of the growth period of the colony. Both species do not show any indication of the presence of a nema in the appendix. A single specimen of *Gothograptus kozlowskii* was found, in which an annulus can be seen in the appendix. The view from the distal end into the growing appendix shows a single annulus on the reverse side and the thickened nema on the obverse side (Fig. 7E, F). Also, in this specimen the surface of the annulus is smooth and does not show a pustulose surface of the reticulum. It appears that the annulus is only present on the reverse side of the appendix and does not reach the nema that is incorporated into the obverse side (Fig. 7E, F).

CONCLUSIONS

The cortical material of graptolites is made up of bandages, invariably formed of parallel-oriented, densely packed fibrils, overlain by a thin layer of sheet fabric, creating strong and flexible material.

The rods and lists of the cortical material represent the main, strong constructional features of the Retiolitinae. They exhibit variable amounts of cortical bandages, organized in particular meshwork patterns that form on the outside, the ancora sleeve. They are much thicker and denser in mature tubaria in many taxa, indicating that they were not needed to support the colonies and stabilize their shapes. However, having very thin fusellar membranes, most probably the network of lists was used to support the colonies.

The cortical thickening of the tubarium membranes to strengthen the tubaria is unlikely for planktic graptolites, as many taxa are known that do not exhibit much associated cortical development, yet others from the same environment have an extensive cortex. Thus, a different function needs to be sought.

Thickenings at thecal apertures are most likely related to the movements of zooids in and out of the thecae. During these movements they secreted the cortical bandages and thickened the thecal lips more strongly than in other parts of the tubaria. Thickening of thecal apertures, however, does not occur in all graptolites.

As cortical overgrowth covers numerous details in the tubarium construction of the Graptolithina. The tectonic compression and flattening of colonies enhances differences in list thickness and allows the interpretation of internal features, otherwise not readily visible.

ACKNOWLEDGEMENTS

We would like to thank reviewers David Loydell and Jan Zalasiewicz for helpful comments that improved this manuscript. Anna Kozłowska thanks to Paweł Bącal from Institute of Paleobiology PAS for taking photos of specimens with sicular annuli under the BSE microscope.

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