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NEW OBSERVATIONS ON THE ANCORA SLEEVE AND THECAL MEMBRANES OF SILURIAN RETIOLITINAE (GRAPTOLITHINA)

Anna KOZŁOWSKA[1*], **Michael J. MELCHIN**[2] & **Alfred C. LENZ**[3]

[1] *Anna Kozłowska, Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warszawa, Poland; e-mail: akd@twarda.pan.pl*
[2] *Michael J. Melchin, Department of Earth and Environmental Sciences, St. Francis Xavier University, Antigonish, Nova Scotia, B2G 2W5, Canada; e-mail: mmelchin@stfx.ca*
[3] † *Alfred C. Lenz, Department of Earth Sciences, University of Western Ontario, London, Ontario N6A 5B7, Canada; e-mail: aclenz@uwo.ca*
** Corresponding author*

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Abstract: Typical Retiolitinae (Graptolithina) tubaria (an alternative term for rhabdosomes) are preserved as a network of lists, formed by bandages of cortical tissue, rarely with preserved fragments of thin membranes, which show evidence of a thin fusellar structure. This study focuses on some remarkable specimens, preserved with nearly complete cortical membranes of the ancora sleeve and metathecae. The studied three-dimensional material belongs to species of *Spinograptus* and *Cometograptus* from the upper Wenlock (Silurian) strata in Nunavut, Arctic Canada. The membranes of the ancora sleeve of *Spinograptus* were studied using infrared microscopy for the first time. Images of the membranes clearly show the arrangement of cortical bandages within the meshes of the networks, formed on the outside of the ancora sleeve in mature colonies. No traces of fusellar increments were observed in the ancora sleeve tissues. In addition, specimens of *Cometograptus* show traces of membranes in the thecal framework, again made of cortical bandages, with no trace of fusellar tissue connected to it. These new data expand our knowledge of the structure of retiolitine tubaria. During their evolution, the fuselli of the ancora sleeve became dominated by the cortical bandages, forming lists and extremely rare thin membranes.

Key words: Retiolitinae, Graptolithina, tubaria, ancora sleeve, membranes, infrared microscopy, Silurian.

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INTRODUCTION

Retiolitines are remarkable graptolites (Graptolithina), mostly preserved as a meshwork of rod-like lists, making up the thecal framework and ancora sleeve. The lists are built of cortical bandages, while the typical graptolite walls of the tubaria are formed by fusellae, covered by cortical bandages. The rod-like lists are more-or-less rounded in cross-section and were clearly built up concentrically, but all formed with original U-shaped seams, which may have been closed by later cortical overgrowth. Rarely, in some taxa, a series of equally spaced, curved increments can be observed within open seams, which are interpreted to be remnants of fusellar tissue (e.g., Bates and Kirk, 1992, fig. 75). Some specimens also show traces of preservation of continuous membranes on the thecal walls, and, rarely, on the ancora sleeve. Lenz and Thorsteinsson (1997) illustrated a single specimen of *Stomatograptus* with obvious fusellar layers attached to the thecal framework, but not on the lists of the ancora sleeve. This had been observed on flattened material decades earlier, for example, by Törnquist in *Retiolites* (Törnquist, 1890, fig. 2: 20–23) and Holm (1890, fig. 2: 7–9) in *Stomatograptus*.

Bates (1987a) and Bates and Kirk (e.g., 1986, 1992, 1997) provided detailed ultrastructural studies on very well-preserved uncompressed specimens of *Stomatograptus* and *Retiolites* from the Llandovery of Arctic Canada. On the basis of these and other studies, it was recognized that most retiolitines possessed two layers to their tubaria, the inner one corresponding to the thecal framework, a homologue of

the diplograptid ancestral tubarium, and outer ancora sleeve lists that were an extension of the ancora umbrella, a homologue of the petalolithine ancora and ancora umbrella. The outside ancora sleeve wall is made by a framework of lists, connected to the thecal walls at the lateral apertural lists, a structure which is unique among graptolites. There is no evidence of a fusellar covering of the ancora sleeve lists (Lenz *et al.* in Maletz, 2023b).

Many detailed studies of retiolitines have been published over the past decades, including Bouček and Münch (1944, 1952), Obut and Zaslavskaya (1976), Lenz and Melchin (1987a, b), Lenz (1994a, b), Kozłowska-Dawidziuk (1995, 1997, 2004), Lenz and Thorsteinsson (1997), Lenz and Kozłowska-Dawidziuk (2002a, b, 2004), Bates *et al*. (2005), Maletz (2010, 2022, 2023a), Kozłowska *et al*. (2013), and Melchin *et al*. (2017). The thecal and ancora sleeve membranes of the Retiolitinae are very poorly known, due to their rare and usually fragmentary state of preservation.

Although most of the observed membranes on retiolitines occur as part of the thecal framework, the remarkable exception among retiolitines is *Spinograptus*, the only post-*lundgreni* Biozone form to have continuous membranes on the ancora sleeve, and occasionally the sicula and thecal framework, studied mostly in uncompressed specimens using a scanning electron microscope (SEM; Lenz, 1994a, b; Kozłowska-Dawidziuk, 1997; Lenz and Thorsteinsson, 1997; Lenz and Kozłowska-Dawidziuk, 2002a, b; Bates *et al*., 2005).

The geographical distribution of species of *Spinograptus* with membranes from the upper Wenlock, the *praedeubeli-deubeli* and *ludensis* biozones (after the *lundgreni* event), is wide: Arctic Canada, Poland, and Uzbekistan (specimens shown to ACL and AK by the late Tania Koren'; Lenz, 1994a; Kozłowska-Dawidziuk, 1997; Lenz and Kozłowska-Dawidziuk, 2002a; Kozłowska *et al*., 2013). Isolated, uncompressed specimens of *Spinograptus* from Arctic Canada represent the best preserved retiolitines with continuous membranes of the ancora sleeve (Lenz, 1994a, b; Lenz and Thorsteinsson, 1997; Lenz and Kozłowska-Dawidziuk, 2002a).

One of the aims of this paper is to present new observations of the outside wall of the retiolitine tubarium, based on spectacularly well-preserved specimens of *Spinograptus* with a complete membrane of the ancora sleeve. Infrared microscopic observations of the new material show, for the first time, the arrangement and growth pattern of cortical bandages building the ancora sleeve membrane. They also reveal the absence of any evidence of fuselli remnants on the ancora sleeve lists. These new observations on this enigmatic structure, the ancora sleeve, may contribute to a better understanding of its mode of secretion, and life strategy, which is difficult to discern in the absence of extant representatives of the planktic graptolites. In addition, the present authors describe exceptionally preserved uncompressed specimens of *Cometograptus* that show membranes, in this case developed on the metathecal framework, built of cortical bandages, without any evidence of fusellar membranes.

Cortical bandages, forming lists, were composed of densely packed, originally collagenous, long and straight fibrils, running parallel to the length of the bandages (Kozłowska *et al*., 2024, fig. 2f). This is similar to the shape and arrangement of growth increments of *Cephalodiscus* and *Rhabdopleura* (Dilly, 1986; Gonzalez and Cameron, 2012) as well as to the connective tissues of vertebrates, e.g., ligaments and tendons. This provides the lists with maximum tensile strength and flexibility, giving them an advantage over the delicate fusellar tissue. This superior strategy allowed retiolitines to have a more effective free-floating lifestyle.

The cortical membrane of the ancora sleeve may indicate the presence of some kind of soft tissue. A primary extrathecal mantle surrounding the colony, as suggested by Kozłowski (1949), Bates and Kirk (1987) and Bates (1987b), seemed unlikely to be consistent with the 'mortaring' model as in modern Pterobranchia (Crowther and Rickards, 1977). However, this constraint should not exclude the possible presence of some kind of extrathecal tissue, formed by mucus. The mucus secretion from the frontal glands of the tentacles was observed in *Rhabdopleura* and *Cephalodiscus* arms (Gilmour, 1979; Dilly, 1986). It is also possible that some other organisms, such as symbiotic microalgae, could have grown on the external mucus surface. This phenomenon is common among modern marine organisms.

The present authors follow the recent proposal that all of the Silurian "retiolitid taxa" that were traditionally assigned to the Retiolitidae should be assigned to the subfamily Retiolitinae (Melchin *et al*., 2011; Lenz *et al*. in Maletz, 2023b).

MATERIAL AND METHODS

The uncompressed specimens of *Spinograptus praerobustus* are from carbonate nodules from Abbot River, on Cornwallis Island, Nunavut (Arctic Canada), from the 23.3 m sample, *ludensis* Biozone, upper Wenlock (Lenz, 1994a). The collection contains dozens of isolated specimens, representing different growth stages. The *Cometograptus* material with thecal membranes is from the Rookery Creek section on Cornwallis Island, Nunavut (Arctic Canada), the RC1-02, 2 m sample, from the *lundgreni* Biozone, upper Wenlock (Lenz and Kozłowska, 2006).

The specimens studied were recovered following slow dissolution of the host carbonate in 5–20% HCl. A fine hairbrush was used to pick and transfer specimens to SEM stubs or plastic containers with glycerin. Visible light, infrared (IR) light and scanning (SEM) microscopy were used for specimen study. Figured specimens are housed in the Geological Survey of Canada and the Institute of Paleobiology, Polish Academy of Sciences.

Abbreviations: GSC – Geological Survey of Canada, ZPAL – Instytut Paleobiologii PAN im. Romana Kozłowskiego, IR – infrared microscopy, SEM – scanning electron microscope.

SPINOGRAPTUS WITH PRESERVED MEMBRANES

As noted above, *Spinograptus* is the only known retiolitine taxon with continuous membranes of the ancora sleeve as well as of most of the thecal walls. This is also

the only taxon among post-*lundgreni* Biozone retiolitines with well-preserved sicular and thecal walls. Such a state of preservation is in marked contrast with retiolitines, having tubaria composed only of a meshwork of lists. Specimens of *Spinograptus praerobustus* from Arctic Canada represent the best-known uncompressed forms with thecal (mostly metathecal) walls and continuous ancora sleeve membranes (Lenz, 1994a, b; Lenz and Thorsteinsson, 1997; Bates *et al*., 2005, fig. 2A, B). Visible light and infrared microscopes provided transmitted light images of the membranes (Figs 1, 3–6).

There is a significant difference in membrane development and appearance between astogenetically young and mature colonies (Fig. 1). The membranes of young colonies or of those at the growing distal ends of some colonies are thinner and more translucent than those of the proximal ends of more mature colonies (Fig. 1B, C), and in the young colonies the thin bandages of the ancora sleeve may be seen in transmitted, visible light (Fig. 1C1). The mature colonies have thick, more nearly opaque membranes, dark brown or black in colour with no structures visible in visible light microscopy (Fig. 1A).

The SEM images of juvenile and mature specimens of *Spinograptus praerobustus* show continuous membranes with a smooth surface (Fig. 2; e.g., Lenz, 1994a, b; Bates *et al*., 2005). The membrane covers the ancora sleeve lists and metathecal lists from the outside. The clathrial lists are clearly visible inside the mature tubarium with the thick membrane (Fig. 2A, E). Some delicate, small pustulose bandages are rarely visible on the membrane surface (Fig. 2C). The pustules are the micro-ornamentation on bandages, characteristic mainly of the post-*lundgreni* Biozone retiolitines, and are an important feature for retiolitine classification (Lenz and Melchin, 1997). Traces of fuselli, covered by a thick outer cortical membrane, are slightly visible on the first theca (Fig. 2B). The specimen with

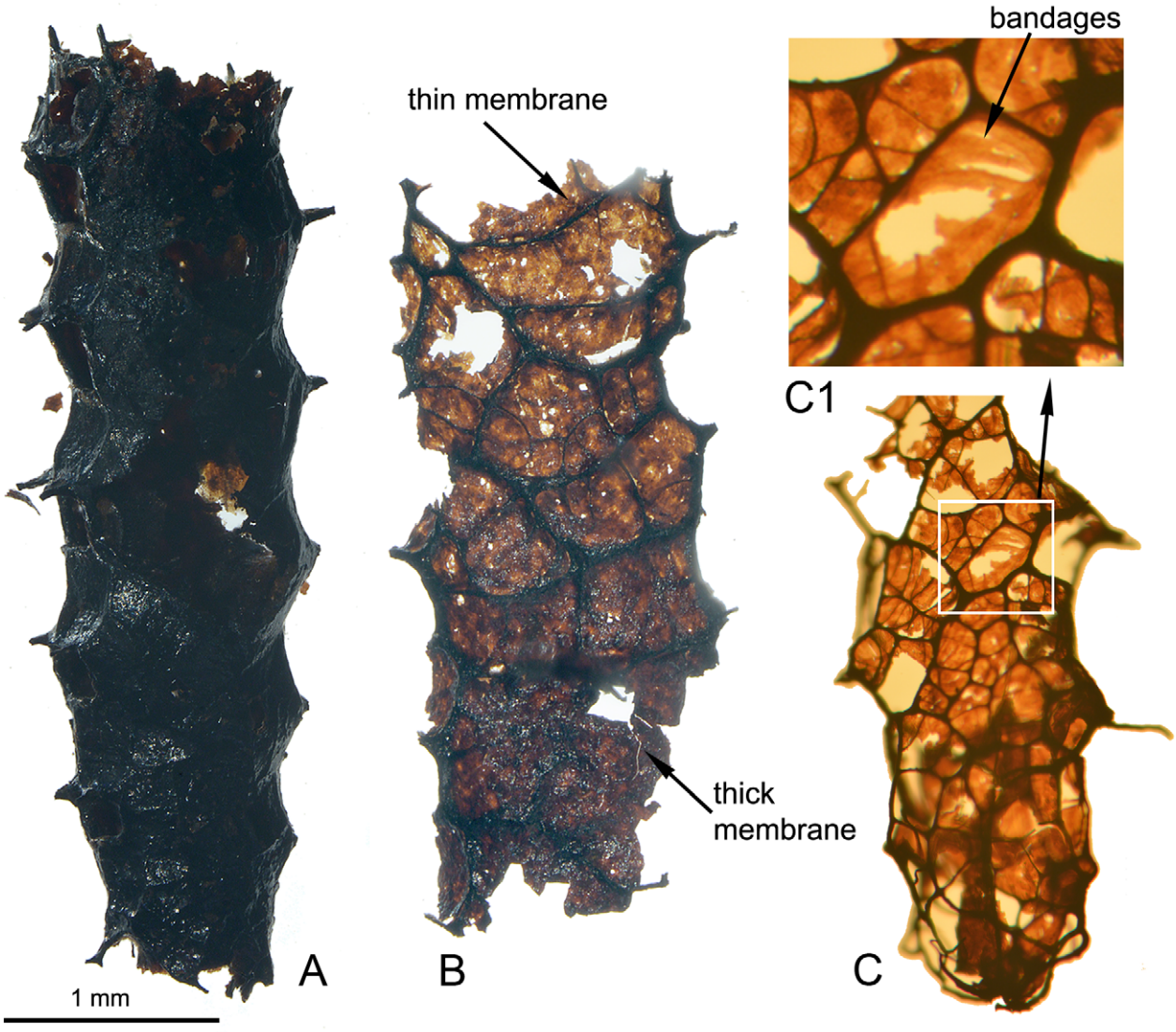


Fig. 1. Light microscope images of *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002a with membranes, Abbot River, 23.3 m, Cornwallis Island, Nunavut (Arctic Canada), ludensis Biozone (Lenz, 1994a); different stages of colony development. **A**. Mature tubarium with thick, almost opaque membranes, ZPAL G. 37/6. **B**. Fragment of less mature colony, lateral wall of ancora sleeve, ZPAL G. 37/7. **C**. Proximal part of juvenile colony with thin, transparent membrane, three pairs of thecae, well-preserved metasicula, reverse side, ZPAL G. 37/8. **C1**. Enlargement, showing bandages (arrow).

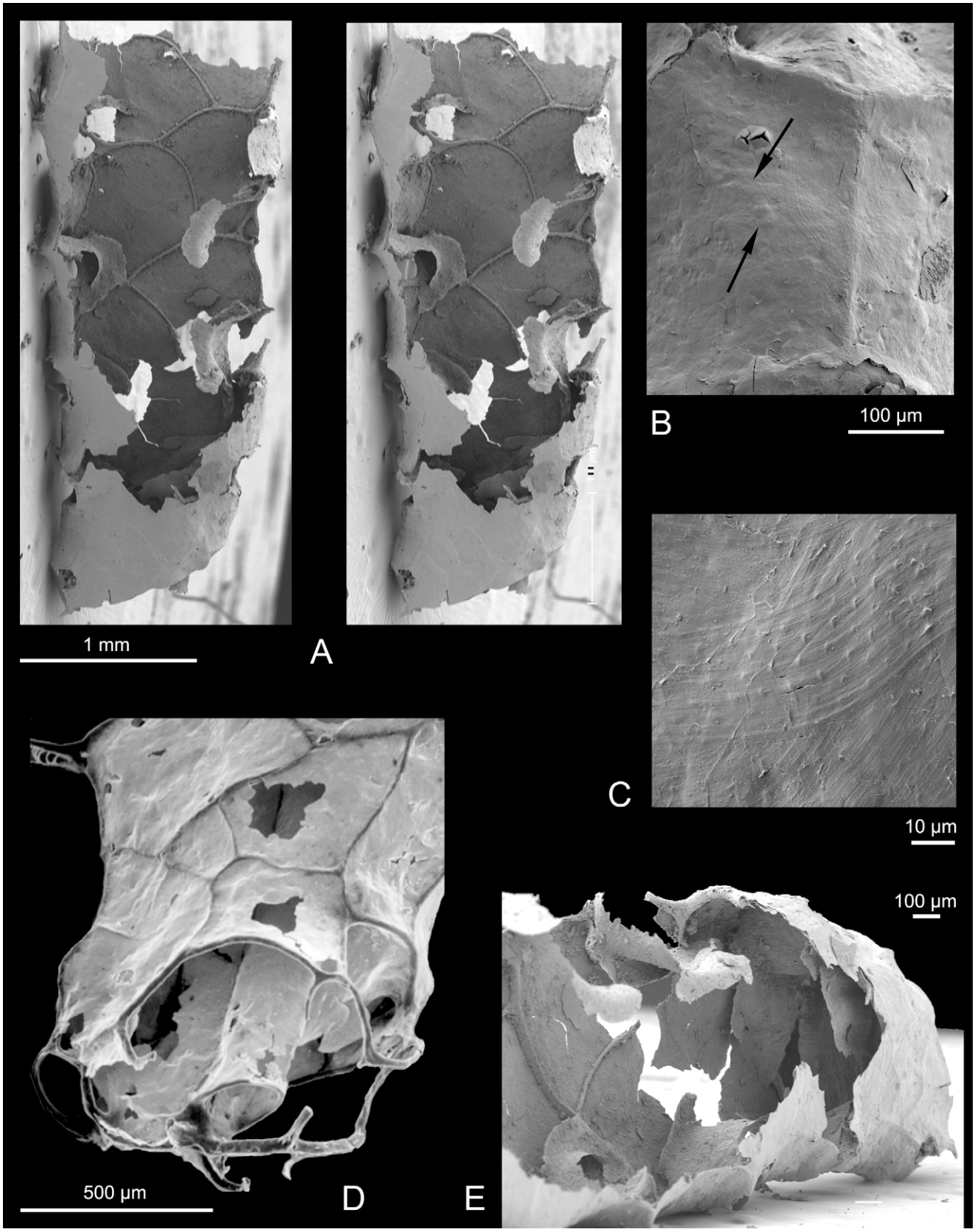


Fig. 2. SEM images of *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002a with thecal and ancora sleeve membranes, Abbot River, ABa3−98, 21 m, Cornwallis Island, Nunavut (Arctic Canada), *praedeubeli-deubeli* Biozone (Lenz and Kozłowska-Dawidziuk, 2002a). **A–C, E**. Tubarium of mature colony with thick membrane, showing ancora sleeve inside, ZPAL G. 37/9; A – stereopair, lateral side, showing interior of tubarium; B – exterior view of metatheca 11 with fuselli (arrows), covered by cortical membrane; C – enlargement, showing the membrane with thin bandages with small pustules; E – interior view. **D**. Proximal-lateral view of tubarium with thinner wall, showing metasicula and first thecae, specimen with thin membrane, obverse side, ZPAL G.37/1 (after Bates *et al*., 2005).

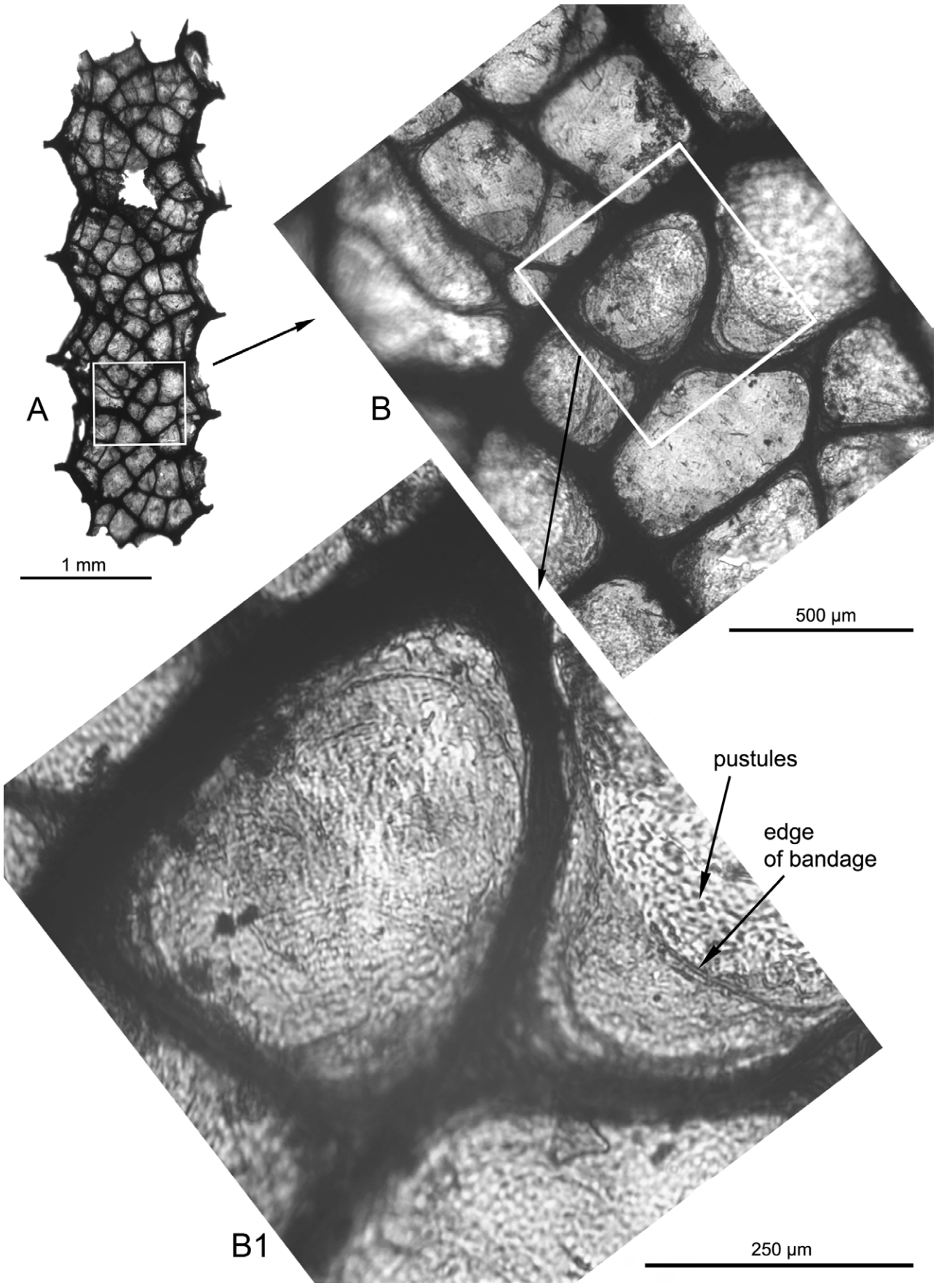


Fig. 3. Infrared microscope images of tubarium fragment of *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002a, showing ancora sleeve wall, GSC 145128, Abbot River, 23.3 m, Cornwallis Island, Nunavut (Arctic Canada), *ludensis* Biozone (Lenz, 1994a). **A**. Entire specimen. **B, B1**. Enlargements, showing meshes infilled by the membrane built on cortical bandages; B1 – pustules and thick edge of bandage, forming new list, marked by arrows.

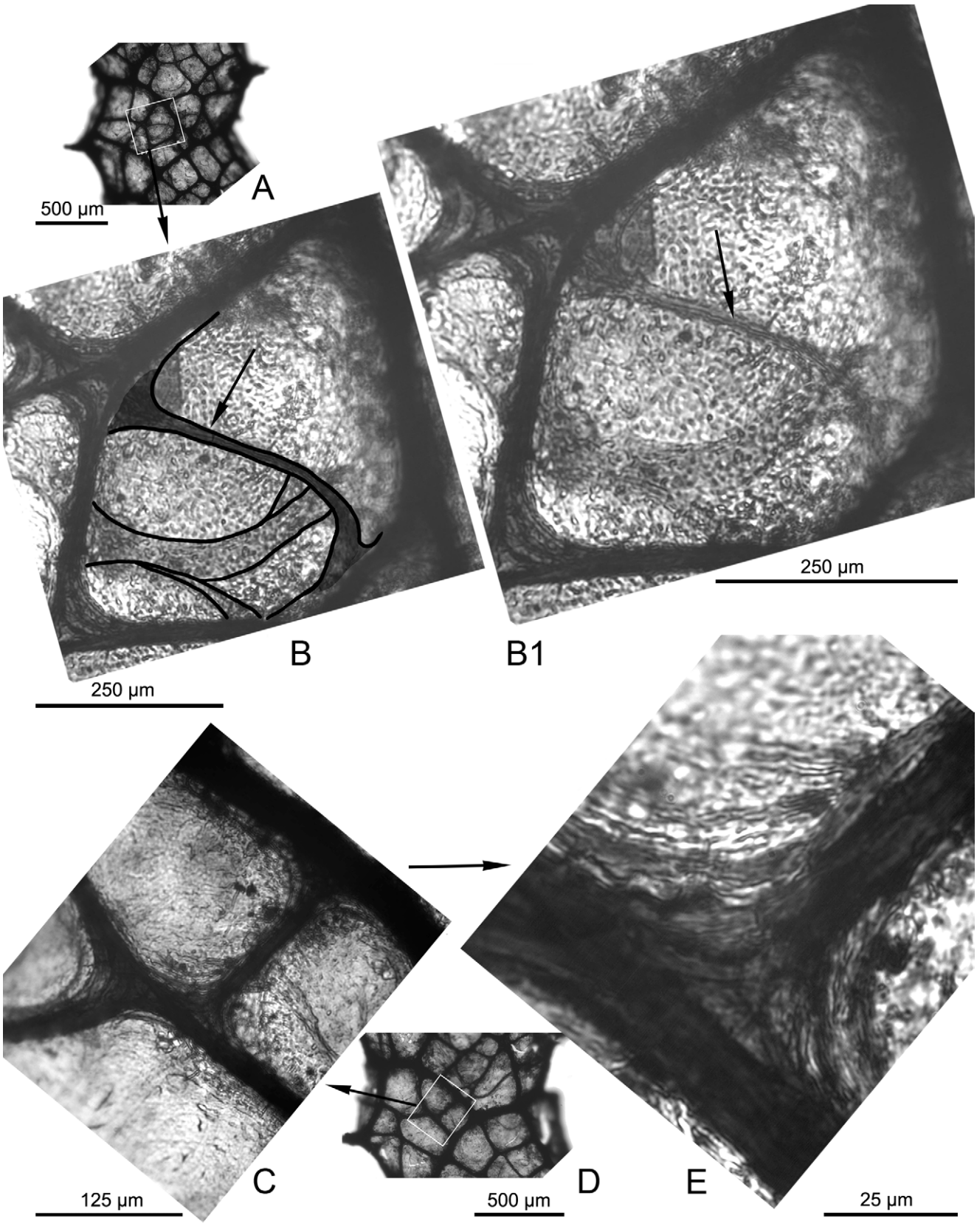


Fig. 4. Infrared microscope images of *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002a; GSC 145128, Abbot River, 23.3 m, Cornwallis Island, Nunavut (Arctic Canada), *ludensis* Biozone (Lenz, 1994a). **A**. Fragment of mesial part of tubarium. **B, B1**. Enlargements, showing ancora sleeve wall with meshes filled by the bending cortical bandages, bandages forming new list (arrowed). **C, E**. Enlargements of D. **D**. Fragment of mesial part of tubarium.

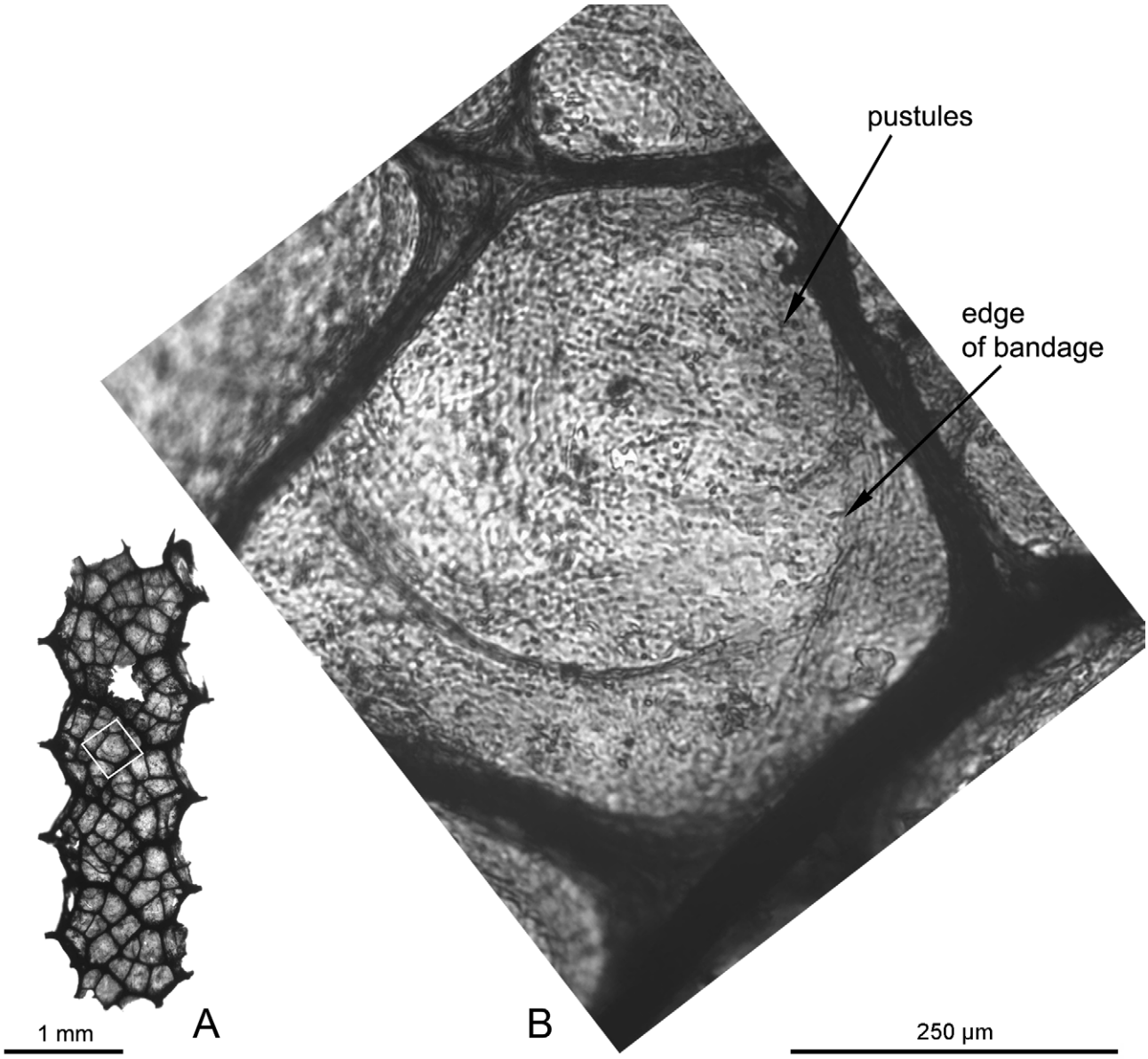


Fig. 5. Infrared microscope images of *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002a; fragment of mesial part of tubarium, GSC 145128, Abbot River, 23.3 m, Cornwallis Island, Nunavut (Arctic Canada), *ludensis* Biozone (after Lenz, 1994a). **A**. Whole specimen. **B**. Enlargement, showing reticular mesh of the ancora sleeve infilled by the membrane built on overlapping, bent cortical bandages (arrow). Note the edges of bandages.

a proximal end (Fig. 2D) has a thin membrane of the sicula and the two first thecae. It represents a young stage of colony growth. The thecal framework preservation is fragmentary, representing mostly the metathecal part (Fig. 2A). The specimens of *Spinograptus praerobustus* with the most nearly complete thecal walls inside the ancora sleeve were described by Lenz (1994b, fig. 2.2, specimen GSC 104665).

The infrared microscope (IR) allows one to obtain clear, transparent images of membranes (Melchin and Anderson, 1998). The membranes of *Spinograptus praerobustus* are translucent with clearly visible stronger clathrium lists and thinner lists forming reticulum meshes (Figs 3–6). The space between the ancora sleeve lists is filled by the membrane, built of pustulose cortical bandages. The arrangement of the bandages inside some of the meshes shows that they fill each mesh independently since they bend along the list margins (Figs 3B, B1, 4B, B1, 5B).

In most IR images, it is difficult to distinguish individual bandages, but their edges are usually clearly visible (Figs 3–5). The membranes in places consist of several overlapping layers of bandages, creating a thicker membrane. In some places inside the reticular mesh, the bandages form thicker margins, which appear to create a new thin list, dividing the mesh into two smaller segments (Figs 3B, B1, 4B, B1).

The infrared microscope images of the specimen, illustrated in Figure 6, show details of the partly preserved proximal part of a tubarium up to the third pair of thecae with a well-preserved inner membrane, representing a fragment

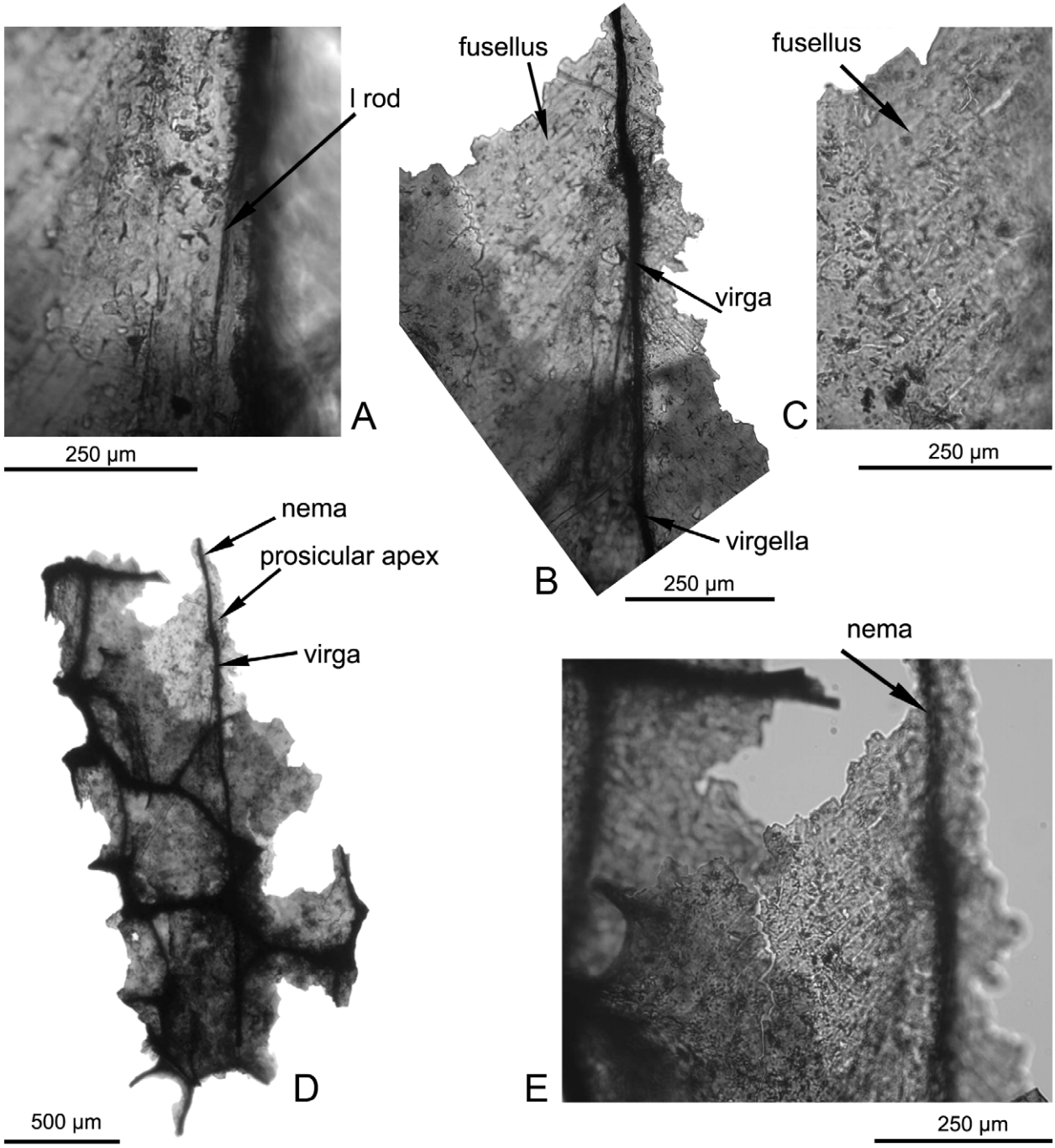


Fig. 6. Infrared microscope images of *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002a; partly preserved proximal part of the tubarium; GSC l45129, Abbot River, 23.3 m, Cornwallis Island, Nunavut (Arctic Canada), *ludensis* Biozone (Lenz, l994a). **A**. Fragment of prosicula, enlargement. **B**. Whole prosicula along virga (arrow). **C, E**. Enlargements of first thecal membrane, showing diagonal fuselli. **D**. Whole specimen.

of the thecal wall, prosicula and metasicula. The fusellar membrane, shown in Figure 6B, C, E, represents the wall of the first thecae. The beginning of the nema starts from the prosicular apex, at the level of the characteristic bending of the virga (Fig. 6B). The virga then becomes distinctly straight, corresponding to the prosicula with a length of approximately 600 µm. The longitudinal rods of the prosicula are visible about 200 µm below the prosicular apex (Fig. 6A). The edge of the prosicular rim is not clearly visible, but the characteristic curvature of the virga indicates the transition from the prosicula to the metasicula (Fig. 6B).

COMETOGRAPTUS WITH METATHECAL MEMBRANES

Well-preserved uncompressed specimens of *Cometograptus apsis* Lenz and Kozłowska-Dawidziuk, 2001 have membranes on the metathecae between the lip and pleural lists (Fig. 7). The inside surface of the membrane is smooth (Fig. 7C). There is a continuation of the bandages of the lists onto the metathecal membrane, i.e., they form a continuous surface. The membrane, however, is not complete and has some empty spaces, not filled by bandages (Fig. 7B, E, G, I).

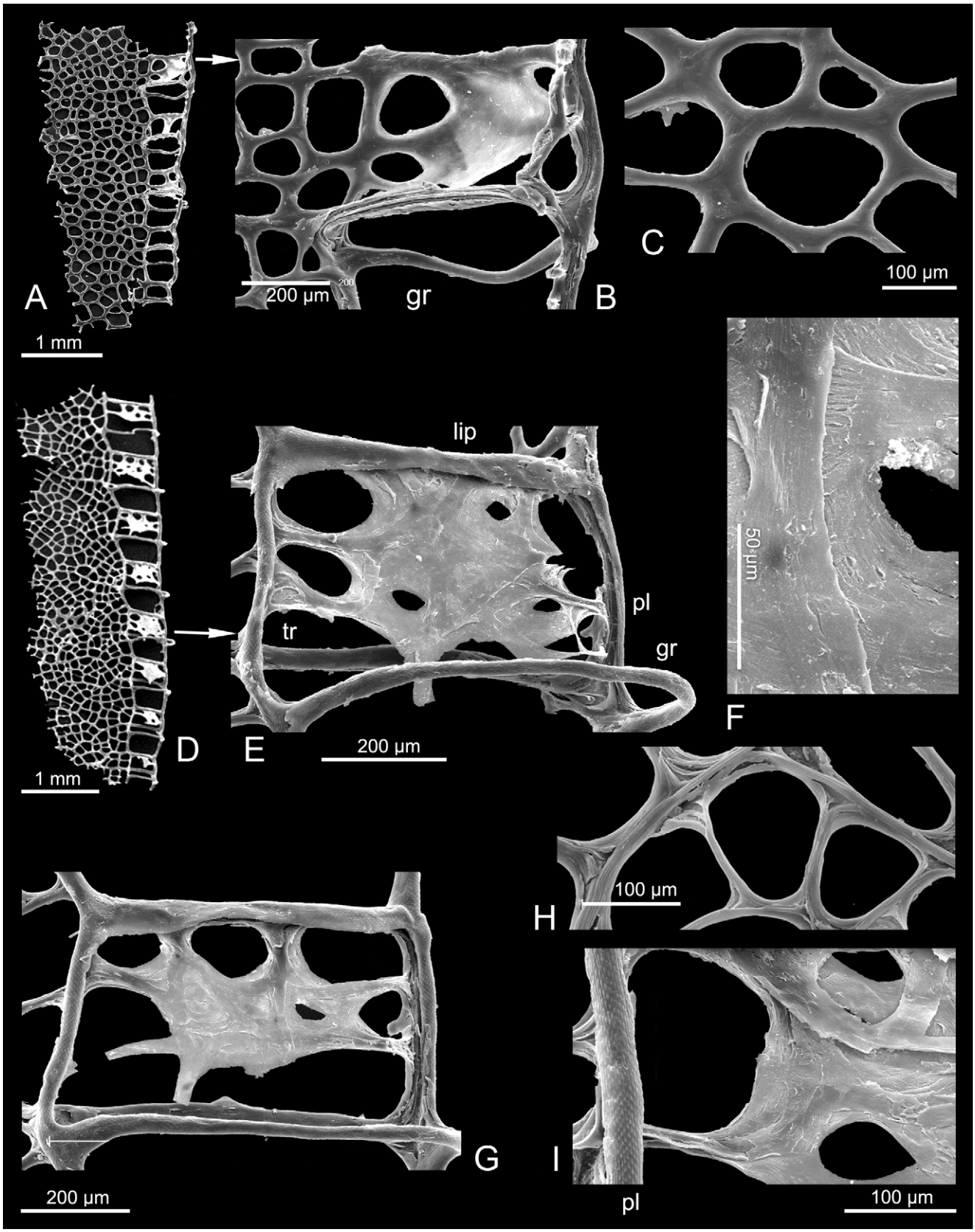


Fig. 7. Two fragments of two specimens of *Cometograptus apsis* Lenz and Kozłowska-Dawidziuk, 2001 from Rookery Creek, RC1-02, 2 m, Cornwallis Island, Nunavut (Arctic Canada), *lundgreni* Biozone (Lenz and Kozłowska, 2006). **A–C**. Fragment of specimen, GSC 145130, lateral side of ancora sleeve and ventral wall, view from the inside; B – enlargement of metathecae, with membrane preserved; C – smooth surface of ancora sleeve lists. **D–I**. Fragment of specimen, GSC 145131, view from the outside; D – whole specimen, lateral side of ancora sleeve and ventral wall; E – exterior view of metatheca with cortical membrane; F – enlargement of membrane, showing layers of bandages with well-preserved fibrils; G – metatheca with membrane; H – exterior view of the ancora sleeve lists with seams; I – fragment of metatheca, showing bandages; gr – genicular rod, incr – increment, lar – lateral apertural rod, pl – pleural list, tr – transverse rod.

The bandages of the membranes are clearly visible, lying one on top of the other (Fig. 7E, F, I). Along the pleural lists are clearly visible deep seams, with some fusellar increments inside them (Fig. 7G), but there is no evidence of extension of those increments outside of the seams and no indication that the cortical bandages of the membrane were ever in contact with the increments or any fusellar tissue.

The ancora sleeve of *Cometograptus apsis* is characterized by the smooth surface of the lists on the inside (Fig. 7C) and seams on the lists occur on the outside of the tubarium (Fig. 7I; Lenz and Kozłowska-Dawidziuk, 2001, 2006; Kozłowska-Dawidziuk, 2004; Lenz *et al*., in Maletz, 2023b). The ancora sleeve lists show no traces of membranes or increments (Fig. 7I). These observations show that both the metathecal bandages and the lists of the ancora sleeve of *Cometograptus apsis* were secreted from the inside of the tubarium (Fig. 7B, C). The bandages of the ancora sleeve and the metatheca are smooth, whereas the bandages of the lip, genicular rod and pleural lists have distinctive pustules (Fig. 7I).

SUMMARY AND CONCLUSIONS

The preserved membranes on the ancora sleeve of the uncompressed specimens of *Spinograptus* from Arctic Canada are built of cortical bandages with pustules. New IR studies show that bandages progressively filled the space inside the ancora sleeve meshes. Initially, they are mostly arranged around the margins of the lists; subsequent bandages fill in the mesh opening with a more irregular pattern that gradually makes the membrane thicker. These cortical membranes occur on the outside surfaces of the ancora sleeve, whereas the ancora sleeve lists in *Spinograptus* have their seams on the inside surface (e.g., Lenz *et al*., in Maletz, 2023b). In mature colonies, the bandages form a smooth membrane covering the outside of the whole ancora sleeve of the tubarium. It is significant that there are no traces of the fuselli on the membranes of the ancora sleeve in *Spinograptus*. This contrasts with the membranes that occur on the thecal framework in this genus, which show clear fusellar increments (see Fig. 6 and Lenz and Thorsteinsson, 1997) that are overlain with cortical bandages (Fig. 2B, C). This pattern of membrane development further contrasts with that observed in specimens of *Cometograptus*, which show membranes made of cortical bandages, with no evidence of fusellar tissue on preserved membranes at all on the ancora sleeve, either fusellar or cortical. There is only one fusellar increment, preserved on metatheca (Fig. 7G). Therefore, this mode of membrane growth and the lack of fusellar traces on the ancora sleeve suggest that it was formed without a fusellar layer.

It could be argued that the lack of evidence for fusellar tissue, preserved in contact with the membranes made of cortical bandages described here, may simply be the result of the fusellar membranes being too thin to be preserved. However, the fact that both the ancora sleeve cortical and thecal fusellar membranes are preserved in specimens of *Spinograptus*, suggests that if fusellar membranes had also been present on the ancora sleeve, they would also have been preserved. In addition, previous studies have suggested that when fusellar membranes have been present, the fusellar increments forming those membranes emerged from the seams within the lists (e.g., Bates and Kirk, 1992). Moreover, if all of the cortical membranes observed in the present specimens were deposited directly on top of an existing fusellar wall, as seen in non-retiolitine graptolite groups (and in the metathecal framework membranes of our specimens of *Spinograptus*), one would predict that in retiolitines the cortical membranes would have grown from the very edges of the seams, where the fusellar membranes would have emerged.

However, there is no observed evidence of fuselli or contact between the cortical bandages and fuselli in the ancora sleeve membrane within the seams of lists, except in the metathecal walls of *Spinograptus* where both fuselli and cortical layers occur. This study is the first to show that membranes preserving only cortical tissue can form in retiolitine graptolites.

The observed phenomenon of loss of fusellar tissue in retiolitines possibly is related to the reorganization of tissues that make up the tubarium. The cause of this is unknown, as it took place 425–440 Ma. It is most likely that the dominance of strong and flexible cortical tissue may be due to a more effective strategy of gaining greater resistance to the dynamic conditions of the marine environment. The reduction of fuselli seems to be an advanced adaptation, using a minimum amount of structural material to maximize tubarium strength.

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REFERENCES

Bates, D. E. B., 1987a. The construction of graptolite rhabdosomes in the light of ultrastructural studies. *Indian Journal of Geology*, 59: 1–28.

Bates, D. E. B., 1987b. The density of graptoloid skeletal tissue, and its implication for the volume and density of the soft tissue. *Lethaia*, 20: 149–156.

Bates, D. E. B. & Kirk, N. H., 1986. Mode of secretion of graptolite periderm, in normal and retiolite graptolites. In: Hughes, C. P. & Rickards, R. B. (eds), *Palaeoecology and Biostratigraphy of Graptolites*. *Geological Society Special Publication*, 20: 221–236.

Bates, D. E. B. & Kirk, N. H., 1987. The role of extrathecal tissue in the construction and functioning of some Ordovician and Silurian retiolitid graptolites. *Bulletin of the Geological Society of Denmark*, 35: 85–102.

Bates, D. E. B. & Kirk, N. H., 1992. The ultrastructure, mode of construction and functioning of a number of Llandovery ancorate diplograptid and retiolitid graptolites. *Modern Geology*, 17: 1–270.

Bates, D. E. B. & Kirk, N. H., 1997. The ultrastructure, construction and functioning of the genera *Stomatograptus* and *Retiolites*, with an appendix on the incremental construction of the rhabdosome in *Petalolithus*, and its comparison with that of the thecal framework in *Retiolites* and in *Stomatograptus*. *University of Wales, Aberystwyth, Publication*, 10: 1–168.

Bates, D. E. B., Kozłowska, A. & Lenz, A. C., 2005. Silurian retiolitid graptolites: morphology and evolution. *Acta Palaeontologica Polonica*, 50: 705–720.

Bouček, B. & Münch, A., 1944. Die Retiolitien des mitteleuropäischen Llandovery und unteren Wenlock. *Mitteilungen der tschechischen Akademie der Wissenschaften*, 51: 1–53.

Bouček, B. & Münch, A., 1952. Retioliti středoevropského svrchního wenloku a ludlowu. *Sborník Ústředního Ústavu geologického, oddíl paleontologický*, 19: 1–151. [In Czech.]

Crowther, P. R. & Rickards, R. B., 1977. Cortical bandages and the graptolite zooid. *Geologica et Palaeontologica*, 11: 9–46.

Dilly, P. N., 1986. Modern pterobranchs: observations on their behaviour and tube building. *Geological Society Special Publication*, 20: 261–269.

Gilmour, T. H. J., 1979. Feeding in pterobranch hemichordates and the evolution of gill slits. *Canadian Journal of Zoology,* 57: 1136–1142.

Gonzalez, P. & Cameron, C. B., 2012. Ultrastructure of the coenecium of Cephalodiscus (Hemichordata: Pterobranchia). *Canadian Journal of Zoology*, 90: 1261–1269.

Holm, G., 1890. Gotlands graptoliter. *Svenska Vetenskaps-Akademiens handlingar*, 16: 1–34.

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

Kozłowska, A., Dobrowolska, K. & Bates, D. E. B., 2013. A new type of colony in Silurian (upper Wenlock) retiolitid graptolite *Spinograptus* from Poland. *Acta Palaeontologica Polonica,* 58: 85–92.

Kozłowska-Dawidziuk, A., 1995. Silurian retiolitids of the East European Platform. *Acta Palaeontologica Polonica*, 40: 261–326.

Kozłowska-Dawidziuk, A., 1997. Retiolitid graptolite *Spinograptus* from Poland and its membrane structures. *Acta Palaeontologica Polonica*, 42: 391–412.

Kozłowska-Dawidziuk, A., 2004. Evolution of retiolitid graptolites - a synopsis. *Acta Palaeontologica Polonica*, 49: 505–518.

Kozłowski, R., 1949. Les Graptolithes et quelques nouveaux groupes d'animaux du Trémadoc de la Pologne. *Palaeontologia Polonica,* 3: 1–235.

Lenz, A. C., 1994a. Uppermost Wenlock and lower Ludlow plectograptine graptolites, Arctic Islands, Canada: new isolated material. *Journal of Paleontology,* 68: 1344–1349.

Lenz, A. C., 1994b. A sclerotized retiolitid, and its bearing on the origin and evolution of Silurian retiolitid graptolites. *Journal of Paleontology*, 68: 851–860.

Lenz, A. C. & Kozłowska-Dawidziuk, A., 2001. Upper Wenlock (Silurian) graptolites of Arctic Canada: pre-extinction, *lundgreni* Biozone fauna. *Palaeontographica Canadiana*, 20: 1–61.

Lenz, A. C. & Kozłowska-Dawidziuk, A., 2002a. Upper Homerian (Upper Wenlock, Silurian) graptolites from Arctic Canada. *Journal of Paleontology*, 76: 321–346.

Lenz, A. C. & Kozłowska-Dawidziuk, A., 2002b. Late Wenlock and early Ludlow graptolite extinction, evolution and diversification: a reassessment. *Special Papers in Paleontology,* 67: 171–183.

Lenz, A. C. & Kozłowska-Dawidziuk, A., 2004. *Ludlow and Pridoli (Upper Silurian) Graptolites from the Arctic Islands, Canada*. NRC Research Press, Ottawa, Ontario, Canada, 141 pp.

Lenz, A. C. & Kozłowska, A., 2006. Graptolites from the *lundgreni* Biozone (lower Homerian: Silurian) Arctic Islands, Canada: new species and supplementary material. *Journal of Paleontology*, 80: 616–637.

Lenz, A. C. & Melchin, M. J., 1987a. Silurian retiolitids from the Cape Phillips Formation, Arctic Islands, Canada. *Bulletin of the Geological Society of Denmark*, 35: 161–170.

Lenz, A. C. & Melchin, M. J., 1987b. Peridermal and interthecal tissue in Silurian retiolitid graptolites: with examples from Sweden and Arctic Canada. *Lethaia*, 20: 353–359.

Lenz, A. C. & Melchin, M. J., 1997. Phylogenetic analysis of the Silurian Retiolitidae. *Lethaia,* 29: 301–309.

Lenz, A. C. & Thorsteinsson, R., 1997. Fusellar banding in Silurian retiolitid graptolites. *Journal of Paleontology*, 71: 917–920.

Maletz, J., 2010. Retiolitid graptolites from the collection of Herman Jaeger II: *Cometograptus*, *Spinograptus*, *Plectograptus*. *Paläontologische Zeitschrift*, 84: 501–522.

Maletz, J., 2022. Tubarium construction in the Retiolitinae (Graptolithina, Axonophora). *Earth-Science Reviews*, 232: 1–20.

Maletz, J., 2023a. Retiolitid graptolites from the collection of Hermann Jaeger III. *Paraplectograptus, Gothograptus* and their relatives. *Paläontologische Zeitschrift*, 97: 323–352.

Maletz, J., 2023b. *Treatise on Invertebrate Paleontology, Part V, Hemichordata, Second Revision, Including Enteropneusta, Pterobranchia (Graptolithina)*. University of Kansas Paleontological Institute, Lawrence, Kansas, U.S.A. xxx + 548 pp., 310 figs.

Melchin, M. J. & Anderson, A. J., 1998. Infrared video microscopy for the study of graptolites and other organic-walled fossils. *Journal of Paleontology*, 72: 397–400.

Melchin, M. J., Lenz, A. C. & Kozłowska, A., 2017. Retiolitine graptolites from the Aeronian and lower Telychian (Llandovery, Silurian) of Arctic Canada. *Journal of Paleontology*, 91: 116–145.

Melchin, M. J., Mitchell, C. E., Naczk-Cameron, A., Fan, J. X. & Loxton, J., 2011. Phylogeny and adaptive radiation of the Neograptina (Graptoloida) during the Hirnantian extinction and Silurian recovery. *Proceedings of the Yorkshire Geological Society*, 58: 1–30.

Obut, A. M. & Zaslavskaya, N. M., 1976. New data on the early stages of Retiolitidae development. In: Kaljo, D. & Koren', T. N. (eds), *Graptolites and Stratigraphy*. Academy of Sciences of Estonian SSR, Institute of Geology, Tallinn, pp. 119–127. [English version of Obut, A. M. & Zaslavskaya, N. M., 1974].

Törnquist, S. L., 1890. Undersökningar över Siljansområdet graptoliter. *Lunds Universitet Årsskrift*, 26: 1–33.