# Autothecal morphs and dormancy in the camaroid graptolite *Xenotheka*

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The camaroid graptolite *Xenotheka klinostoma* Eisenack, 1937 is described from the lower Llanvirn limestones of Gilbergabrottet, northern Öland, Sweden. Two distinct autothecal morphs are recognized: (1) *normal morph* (described for the first time), i.e. an autotheca with an unsculptured outer surface, devoid of both an outer lining and autothecal occlusion, and inhabited by an active zooid; and (2) *sealed morph*, i.e. an autotheca coated and occluded, provided with a sculptured outer lining made of a unique verrucose fabric, and inhabited by an inactive or dormant zooid. In addition, the existence of a hypothetical (3) *unsealed morph* or re-opened autotheca, devoid of an autothecal occlusion but provided with an outer lining, and inhabited by a reactivated zooid, is predicted. The sealed morphs may represent an adaptation which allowed their inhabitants to survive adverse conditions. The outer lining of *Xenotheka* is compared with a peculiar outer membrane found in the modern hemichordate *Rhabdopleura*, from the intertidal zone of Fiji, and with camaroid extracamaral tissue.

Key words: Graptolithina, Camaroidea, microfossils, ultrastructure, dormancy, Ordovician, Sweden.

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## Introduction

At different times, the Ordovician benthic microfossil *Xenotheka* Eisenack, 1937 and its only species *X. klinostoma* Eisenack, 1937, has been placed among the foraminiferans, chitinozoans, graptoblasts, crustoid? siculae or problematica, and a consensus has never developed. Recently, this form has been assigned to the encrusting graptolite order Camaroidea and, in the absence of bithecae, within the family Cysticamaridae (Mierzejewski 2000a). The upper stratigraphic range of camaroid graptolites was thereby extended from the late Arenig to the Llandeilo. So far, *Xenotheka* has been reported from the Ordovician of Germany, Estonia, Sweden, and Poland (see Mierzejewski 2000a for references). Moreover, doubtful remains were identified by Mierzejewski (1978a) as ?*Xenotheka* sp., from an erratic boulder of Ludlow age found in northern Poland.

The periderm of studied *Xenotheka* autothecae is unique among graptolites in having a thin ornamented outer lining, constructed of a curious verrucose fabric (Mierzejewski 2000a). Verrucose fabric is typically composed of numerous tiny "verrucae" or nipples connected to an irregular net of thread-like elements of different thickness. Strikingly, the outer lining covers not only the periderm proper (comprising ectocortex, fusellar layer or fusellum, endocortex, and an inner lining) but it also occludes the autothecal aperture. This outer lining is presumably an adaptation which aided survival through periods of unfavourable or wholly adverse conditions.

The primary aim of this paper is to describe the discovery and significance of *Xenotheka* autothecae which lack an outer lining. Some problems concerning the morphology, dormancy and palaeoecology of *Xenotheka* are also discussed in comparison with other camaroid graptolites and the modern hemichordate *Rhabdopleura*.

The material studied originates from grey glauconitic limestones of Valaste age (lower Llanvirn) and was collected under the guidance of Dr. Svend Stouge in 1985 at a locality known as Gillbergabrottet 1 in northern Öland, Sweden. For detailed information on the location, lithology, fauna and biostratigraphy of the outcrop, see Bohlin (1949) and Grahn (1980). The *Xenotheka* material, along with numerous chitinozoans, scolecodonts, graptovermids and fragments of sessile graptolites, was extracted by dissolving the limestone in formic acid. All specimens studied under the SEM were coated with platinum or gold and examined using a Philips XL 20 and Cambridge Stereoscan 180. Numerous specimens of *X. klinostoma* from the Ordovician beds of Estonia, Öland, erratic boulders of glacial origin from Poland, and the Krzyże 4 borehole (northeastern Poland, Llandeilo) were used as comparative material. The material described was stored on a SEM stub and deposited in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL).

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# Morphological observations

The material consists of only two isolated autothecae; specimens A (length 670 µm) and B (length 980 µm). Both display the typical retort-like silhouette typical of *Xenotheka* (Fig. 1A$_1$, A$_2$, B$_1$). They are composed of two sharply differentiated parts: a bulb-shaped camara and a long, rather narrow collum, oriented more or less in parallel to the substrate (specimen A) or slightly bent upwards (specimen B). The camara adhering to the substrate is composed of a flat lower wall (also called the basal membrane or sole) and a convex upper wall. The lower wall appears structureless under the light microscope, but it is very rough and exhibits partially spongy or fibrous texture under the SEM. It extends laterally to form a marginal membrane, weak traces of which take the form of a protruding edge (Fig. 1A$_1$, A$_2$, B$_1$, B$_3$). The outline of the lower wall is subcircular (in specimen A) or oval and elongated (in specimen B, Fig. 1B$_3$). The proximal part of the camara is provided with a tiny opening for an autothecal stolon. There is a distinct difference between both specimens in the position of the opening: in specimen A its just above the attachment surface (Fig. 1A), whereas in specimen B it is distinctly higher, on the top of a subtrapezoidal flattened wall of the most proximal part of the autotheca (Fig. 1B). There is a strong similarity between this part of the camara and a blunt heel of a graptoblast, termed by Urbanek et al. (1986: 102, figs. 2C, 5C) as the talus. The stolonal opening of the autothecae contains a well-preserved, thick-walled vesicular diaphragm of the autothecal stolon. It is easy to see in specimen B; the outer surface of this diaphragm is remarkably smooth (Fig. 1B$_2$, B$_4$). The camara lateral walls bear no adpression traces of adjacent thecae.

The boundary between the camara and the collum is distinctly marked by a radical change in diameter. The collum length and diameter vary between 200–300 µm and 80–105 µm respectively. The aperture of the collum is open and devoid of any kind of apertural processes.

The condition of the periderm is good, except where a few cracks and holes betray its diagenetic history. In general, under the light microscope the periderm is black, very smooth and slightly lustrous. Only the distal part of the collum is dark brown, with indistinct traces of a fusellar structure. The attachment surface is also black and seems to be rough. Under the SEM, the periderm surface remains very smooth and featureless; it is almost enamel-like and covered only with a scattering of grains of sediment (Fig. 1A). This confirms that the outer surface of the periderm is a robust sheet fabric, which completely masks the underlying cortical fibril material. Thus, there is no indication of the true shape and extent of cortical units. In spite of their very good state of the preservation, the specimens examined show no trace of verrucose fabric or an outer lining. The proximal part of the camara of the specimen A displays parallel transverse lines, gently protruding over the surface, which correspond to the fusellar structure of the autotheca. No trace of a regular zig-zag suture

has been found. Only could one a characteristic oblique fusellar suture be observed (Fig. 1B$_2$). The height of fuselli width varies from 19–40 µm.

# Discussion

The autothecae of *X. klinostoma* described above match closely those from the Llandeilo of Poland (see Mierzejewski 2000a). They are of the same shape, dimensions and collum inclination, and equallly devoid of apertural processses. The stolonal vesicular diaphragm shown on SEM micrographs (Fig. 1A$_3$, B$_2$, B$_4$) was previously recognized under the light microscope and TEM as a stolonal sheath or ring-like structure (Mierzejewski 2000a: figs. 3A, 9). This structure closely resembles the vesicular diaphragms known in the camaroid *Bithecocamara* Kozłowski, 1949 as well as the crustoid *Urbanekicrusta* Mierzejewski, 1985 the tuboid *Kozlowskitubus* Mierzejewski, 1978 and the dendroids *Acanthograptus* Spencer, 1878 and *Koremagraptus* Bulman, 1927. However, the vesicular diaphragms of these graptolites always constitute one component of a heavily sclerotized stolon system. In contradistinction, the vesicular diaphragm of *Xenotheka* is the only known sclerotized fragment of the stolon system. The lack of stolonal vestiges connected with the vesicular diaphragms, as well as the absence of isolated stolon fragments from the residue of the etching process (see Mierzejewski 2000a) may suggest that *Xenotheka* lacked a well-sclerotized stolon system.

However, the autothecae of *Xenotheka* from Öland differ remarkably from the Polish and Estonian examples in their surface micromorphology: the periderm is smooth and devoid of that peculiar, distinctly ornamented outer lining of verrucose fabric, and their apertures are not sealed. There can be no doubt that the Öland specimens represent the expected "normal" (i.e. naked or uncoated) autothecae of *Xenotheka*.

Two clearly distinct morphs of the autothecae in *X. klinostoma* can therefore be distinguished: (1) *normal morph* (i.e. a naked autotheca, with an unsculptured periderm and devoid of both an apertural occlusion and an outer lining); and (2) *sealed morph* (i.e. an autotheca with an ornamented outer lining) and an apertural occlusion, both made of the verrucose fabric. Clearly, the naked autothecae were inhabited by normal, active zooids, whereas the sealed autothecae were occupied by inactive zooids. According to the interpretation of the outer lining proposed by Mierzejewski (2000a), the coated autothecae should be regarded as an anatomical adaptation connected with diapause or dormancy (i.e. periods of arrested ontogenetic development in response to adverse environmental conditions). Such an interpretation implies the existence of a third, so far unknown post-dormant morph: an *unsealed morph* (i.e. re-opened or "uncorked" autotheca). This hypothetical autotheca would be covered with a continuous outer lining but lack the membrane sealing its aperture. Such a re-opened autotheca must have been occupied by a reactivated zooid which was able
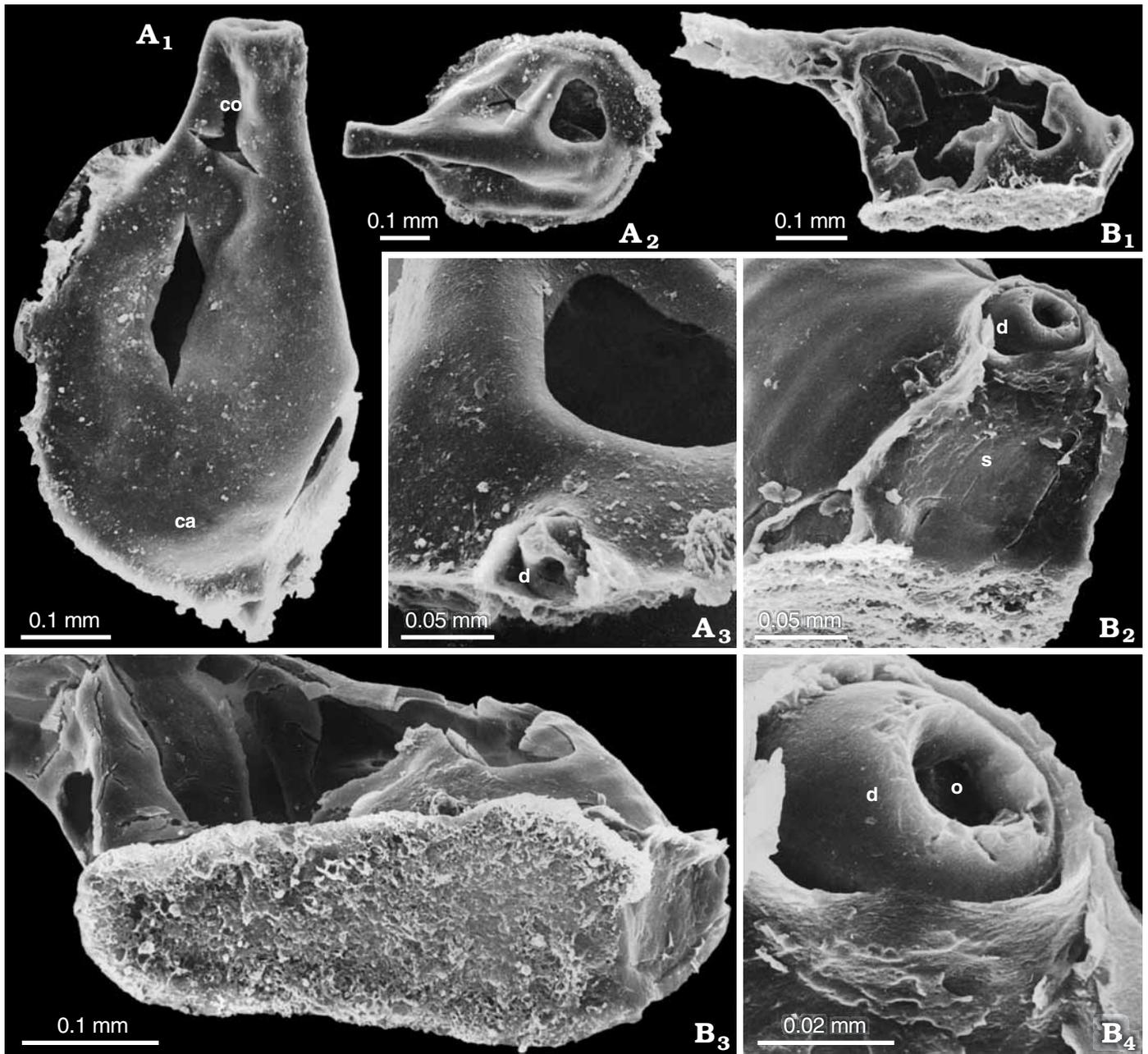
Fig. 1. *Xenotheka klinostoma* Eisenack, 1937; lower Llanvirn, Gilbergabrottet 1, Öland. Isolated autothecae, normal morph. **A**. Specimen ZPAL G.31/1 in lateral view ($A_1$), , upper ($A_2$)view, and proximal part of autotheca ($A_3$). **B**. Specimen ZPAL G.31/2 in lateral view ($B_1$), proximal part of autotheca ($B_2$), lower wall (attachment surface or sole) ($B_3$), and vesicular diaphragm ($B_4$). Abbreviations: a, attachment surface; d, vesicular diaphragm of autothecal stolon; a, autothecal aperture; ca, camara; co, collum; g, grains of sediment attached to periderm; m, remnants of marginal (basal) membrane; o, basal opening in camara wall filled with vesicular diaphragm; s, mould of the terminal portion of the parental stolotheca (?).

to resume its normal life functions as environmental conditions improved. Obviously, if adverse conditions were long lasting, the zooid closed in a sealed autotheca presumably became subject to biological processes connected with ageing and leading directly to necrosis. It may be that the autotheca was sealed and unsealed more than once. There are ultrastructural observations that the outer autothecal surface was coated with the outer lining repeatedly within the lifespan of a colony. Some TEM transverse sections

through the outer lining show that it was sometimes at least double-layered (Mierzejewski 2000a: figs. 6A, 7A).

The phenomenon of diapause is poorly understood in graptolites. Only a few authors have dealt with this problem, and they focused almost exclusively on special dormant bodies called graptoblasts (e.g., Kozłowski 1962; Urbanek 1984; Urbanek et al. 1986; Crowther et al. 1987; Mitchell et al. 1993; Mierzejewski 2000b). Other forms of graptolite dormancy were described by Kozłowski (1949, 1962, 1971),

Bulman (1970), Urbanek (1986), and Mierzejewski (2001). Thecal occlusion seems to be the most common diapause adaptation among fossil graptolites and extant cephalodiscids. Bulman (1970: V17) defined occlusion as a "sealing of thecal aperture by sclerotized film". These structures have been recognized in the Graptoloidea (e.g., Urbanek 1958: 36), Dendroidea (e.g. Bulman 1933: 24; Kozłowski 1949: 43–44), Tuboidea (Mierzejewski 2001: 374, and herein Fig. 2A), but most often in the Camaroidea (Kozłowski 1949, 1971; Skevington 1963; Mierzejewski 2000a and herein; see also Urbanek 1984, 1986 for discussion). The abundant occlusion of autothecae is a striking morphological feature of some camaroid graptolite colonies.

It is commonly believed that the sealing of the autothecae in the Dendroidea and the Graptoloidea is related to the degeneration, atrophy or necrosis of zooids. On the other hand, Kozłowski (1949, 1971) compared the occluded autothecae of camaroid graptolites to the gonozooids or ovicells of extant cyclostomatous bryozoans. According to him, the camaroid autothecae were occupied by normal active zooids before their occlusion; after sealing their apertures with diaphragms, they degenerated in order to make space for their own eggs and embryos. He described and illustrated two types of occlusion in camaroid autothecae, dependent on their shape: (1) autothecae with a collum were occluded by irregular lamellae near the base of the collum (Kozłowski 1949: pl. 26: 8), and (2) autothecae devoid of a collum were occluded by diaphragms deposited directly over the apertures (Kozłowski 1949: pl. 26: 1, 1971: fig. 8). Additional forms of occlusion structures have since been observed (Mierzejewski, unpublished); for example, in an Ordovician dendroid-like camaroid (gen. et sp. nov. 1, Mierzejewski, Maletz, and Sudbury in preparation) the distinctly differentiated collum is occlluded by a thick, distinctly thimble-shaped "stoppers" inserted in the collum just beneath its aperture (Fig. 2B). The lack of continuity between the autothecal periderm and the "stopper" is remarkable. On the other hand, autothecae in the Tuboidea (closest relatives of the Camaroidea, see Kozłowski 1949; Skevington 1963; Mierzejewski 2001), are occluded by a thick diaphragm made of cortical tissue which merges directly into the thecal cortex (Fig. 2C).

Autothecal occlusion in *Xenotheka* differs sharply from all other known camaroid and other graptolites: it is made of a unique material, the verrucose fabric, and it spreads across the entire outer surface of the autotheca (Fig. 2A and Mierzejewski 2000a: figs. 1E, 2A, C, 5A). Previously, I had supposed that the outer lining of *Xenotheka* was secreted in "the form of an organic emulsion rising into the water, which subsided to the rhabdosome, covering the surface, occluding the thecal aperture, and then hardening" (Mierzejewski 2000a: 82). Crucial support for this interpretation would be provided by biological models of similar processes in fossil or modern hemichordates, and I think the key to understanding the process can be found in Dilly and Ryland's (1985) investigations of modern *Rhabdopleura*. This "living fossil", regarded by Beklemishev (1951, 1970) and Mierzejewski and Kulicki

(2001, 2002) as a member of the hemichordate class Graptolithoidea, is the best biological model for studies on the skeletal tissues of fossil graptolites. According to Dilly and Ryland (1985), the coenecium of their *Rhabdopleura* was distinctly linear, forming a typical runner-type colony, overgrowing and penetrating the undersides of coral boulders in the intertidal zone of Fiji. The zooids of this form exhibited a unique mode of tube building, with its horizontal tubes "contained within an irregular membrane that lined the cavity from which the horizontal tube arose" (Dilly and Ryland 1985: 616). Presumably, the enclosing "bag" was constructed by the zooids "plastering" a layer of secreted material across the substrate surrounding the fissure in which the tube was found. Remarkably, in many cases the coenecium components were tightly overgrown by the coral mass, implying a rather close contact between the periderm proper and the peculiar surrounding membrane.

The morphology and fine structure of the rhabdopleuran skeleton are well known (see Urbanek and Dilly 2000; Mierzejewski and Kulicki 2001 for references) but nothing similar to this outer membrane has ever been previously reported. The unusual anatomical structure of the colonies from Fiji is connected directly with its unusual habitat: *Rhabdopleura* is normally found so far usually at moderate depth, in relative cold waters, but has never before been found in the intertidal zone of warm waters. In this situation it seems clear that its secretion of an outer membrane may be a physiological response to these peculiar environmental conditions. I regard the secretion of this peculiar structure as very useful and instructive in the present discussion.

It is possible that the outer membrane of *Rhabdopleura* is comparable with the outer lining of *Xenotheka*. This in turn suggests that *Xenotheka* may have inhabited a similar environment to *Rhabdopleura* from Fiji, i.e. rocky shorelines in the intertidal zone. Such zone is commonly bored by various bioeroders (e.g., bivalves, sponges, and various "worms"). Some autothecae of *Xenotheka* possess two distinct attachment surfaces or curiously irregular soles which indicate that they encrusted with irregular sufaces (see Mierzejewski 2000a: 72, fig. 1D). In such an environment the most common adversity was a periodic lack of water, connected with sea-level change. It is of interest to note that crustoid graptolites could apparently overgrow a firm substrate in very shallow water and that some of them were pioneering encrusters (Mitchell et al. 1993; see Mierzejewski 2000b). Crustoids routinely produced graptoblasts as a means of resisting environmental changes which threatened the survival of the colony. Secretion of an outer lining by the camaroid *Xenotheka* was probably another kind of diapause adaptation for surviving periods of unfavorable conditions. It seems possible that *Xenotheka* secreted a membrane of gel-like material which covered the surfaces of surrounding holes and fissures. As the tide turned, this material settled down onto the rhabdosome and stuck to the periderm forming the outer lining and, simultaneously, occluding the autothecae. Presumably, this served to keep the organism alive and *Xenotheka* was able to
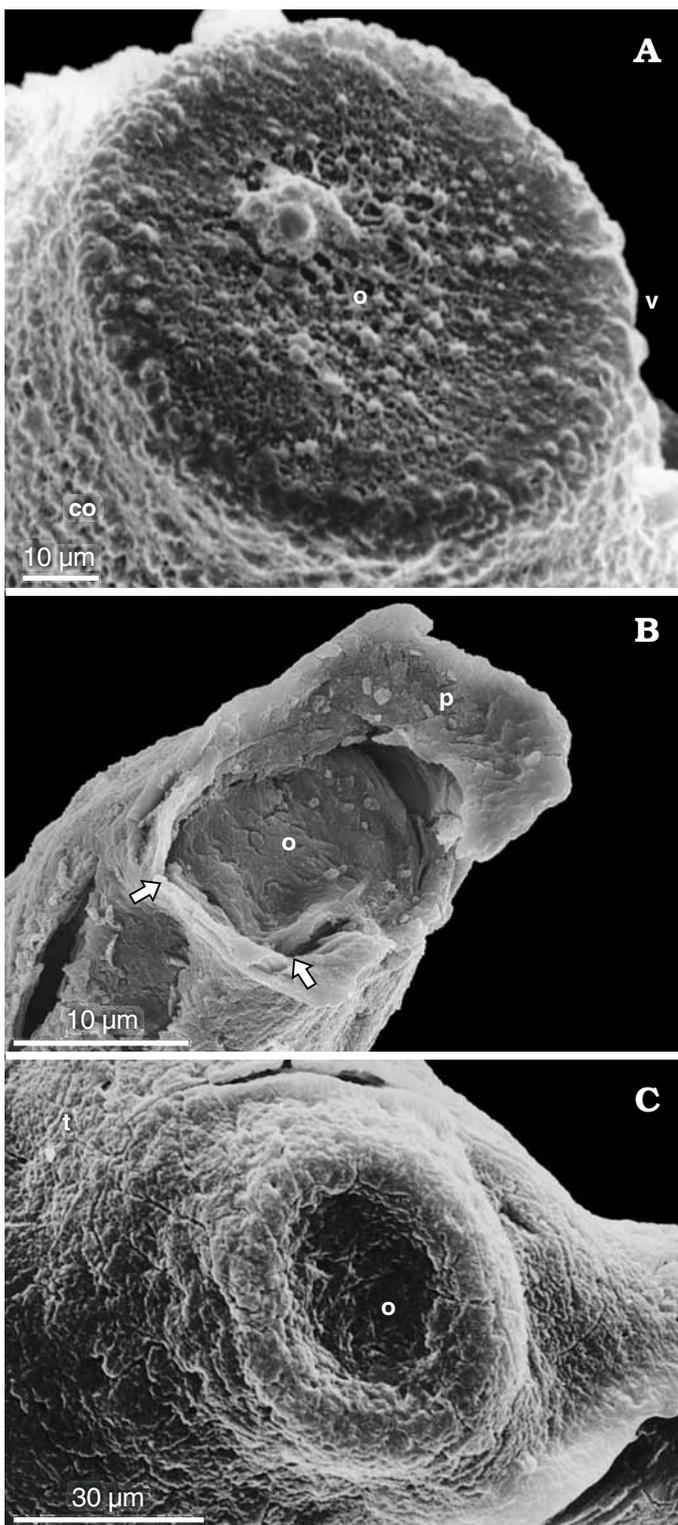
Fig. 2. Sealing of the thecal aperture (occlusion) in some sessile graptolites. SEM micrographs. **A**. *Xenotheka klinostoma* Eisenack, 1937; ZPAL G.12/4, Llandeilo, borehole Krzyże 4 (Poland), depth 473 m. Distal part of autotheca. **B**. Camaroid gen. et sp. nov. 1; ZPAL G.31/4, Ordovician erratic boulder, northern Poland. Distal part of autotheca. **C**. *Epigraptus kozlowskii* Mierzejewski, 1978 (Tuboidea); ZPAL G.31/3, Lower Ordovician (Kunda Stage, Aluoja Substage), Sukhrumägi in Tallinn, Estonia. Bitheca on the thecorhiza surface. Explanations: c, camara; co, collum; o, occlusion; p, apertural process; t, thecorhiza; v, verruca of verrucose fabric. Arrow shows discontinuity between autothecal wall and occlusion.

withstand unfavourable influences when it would otherwise perish. The "droplet" character of the lining (Mierzejewski 2000a), as well its indistinct and irregular layering, are consistent with such an hypothesis.

The recognition of two (or even three?) autothecal morphs in *Xenotheka* broadens our knowledge of graptolite polymorphy (the frame of reference for all such studies was established by Kozłowski 1949, and has been well reviewed by Urbanek 1986). The autothecae of *Xenotheka* are, in my opinion, the first example of seasonal or periodic morphs within a single species. This phenomenon has not previously been recognized in graptolites but is common among other invertebrates. The dimorphism of *Xenotheka* represents a new variety of the secondary specialization of autothecal zooids which also manifests itself as tuboid microthecae and conothecae, crustoid graptoblasts, and the occluded autothecae of camaroids and tuboids (see Urbanek 1986 for discussion).

The shape of a complete rhabdosome of *X. klinostoma* is unknown, as is its early growth and mode of development. I have studied nearly 100 specimens of this graptolite from Poland, Estonia, Sweden and in glacial boulders, all of which were isolated autothecae. Yet in spite of their beautiful state of preservation, two or more joined autothecae have never been found. Moreover, no other components of the *Xenotheka* rhabdosome, such as stolons, stolothecae or bithecae, are known. A short process with an opening containing the vesicular diaphragm (Fig. 1A$_3$, B$_2$, B$_4$) is the only trace of its stolon system. The periderm of *Xenotheka* is usually well preserved and was evidently highly resistant to diagenetic influences. The outer surface of the periderm bears no traces of adjoining structures and is uniformly coated with the outer lining. All these observations suggest how the *Xenotheka* rhabdosome might be reconstructed. It was probably a rather large, irregularly spreading runner-type colony, attached to the substrate and possibly penetrating it. The mode of branching is unknown, but was presumably dichotomous at irregular intervals. The rhabdosome was composed of autothecae linked by naked stolons (i.e. devoid of sclerotized stolonal sheaths). This may be deduced from the lack of stolonal sheaths connected with autothecae, and the smooth surface of the vesicular diaphragm in the proximal part of each autotheca (Fig. 1B$_2$, B$_4$). However, it may be that the autothecae were sometimes accompanied by vestigial stolothecae, as suggested by the talus-like structure in specimen B (p. 94, Fig. 1B$_1$, B$_3$).

The lack of joined autothecae and their imprints on the periderm show that the autothecae were very loosely dispersed. The rhabdosome was devoid of bithecae; its components were not embedded in the extracamaral tissue. Thus, *Xenotheka* resembles a colony of the modern *Rhabdopleura* from Fiji (discussed above) in both the distribution of its thecae and its naked stolons. According to Dilly and Ryland's (1985) observations, their hemichordate formed a very loose and linear (i.e. runner-type) colony, branching coenecium which encrusted and penetrated the coral mass, with naked stolons (previously unknown in *Rhabdopleura*)

connecting the zooids together. This striking similarity between the reconstructed rhabdosome of *Xenotheka* and the *Rhabdopleura* coenecium from Fiji reflects morphological plasticity under varying ecological conditions within the Hemichordata.

The outer irregular membrane of *Rhabdopleura*, the outer lining of *Xenotheka* and the extracamaral tissue of some Camaroidea likely represent similar forms of hemichordate responses to unfavourable environmental conditions, connected in some degree with the phenomenon of diapause. These structures may represent not only a strong functional analogy but also an interesting example of essential homology. It is possible that the secretion of outer membranes or extracamaral tissue should be interpreted as a colonial response provoked by overgrowing encrusters.

# Conclusions

- *Xenotheka klinostoma* is represented by at least two distinct autothecal morphs, i.e. normal and sealed, corresponding to active (pre-dormant) and inactive (dormant) stages of the zooid life. The succeeding (hypothetical) morph, containing a reactivated zooid in the post-dormant stage, awaits discovery.
- *X. klinostoma* may be categorized as a cryptic encruster, inhabiting undersides and vacated borings in the intertidal zone, forming runner-type colonies with completely naked stolons.
- The outer lining of *X. klinostoma*, the outer irregular membrane of some modern *Rhabdopleura*, and the extracamaral tissue of the Camaroidea may be equivalent structures, and can be interpreted as responses to similar environmental signals.

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