Graptolite nature of the Ordovician microfossil *Xenotheka*

PIOTR MIERZEJEWSKI

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Light microscopic, SEM and TEM investigations show that the periderm of the problematic Ordovician organic microfossil *Xenotheka klinostoma* Eisenack, 1937 is built of five layers: inner lining, endocortex, fusellum, ectocortex and outer lining. The outer lining is made of a previously unknown material named here verrucose fabric. The outer lining was presumably an adaptation which aided survival through periods of unfavourable conditions. The general morphology of the test as well as of the fusellar structure of the wall indicate that *Xenotheka* is an aberrant camaroid graptolite. This finding thus extends the upper stratigraphic limit of the order Camaroidea from the early Arenig to Llandeilo.

Key words: Graptolites, Camaroidea, organic microfossils, ultrastructure, Ordovician, Poland.

Piotr Mierzejewski [mierzejewski@post.pl], ul. Filtrowa 83 m. 49, PL-02-032 Warszawa, Poland.

Introduction

Xenotheka klinostoma Eisenack, 1937 is a distinctive sessile organic microfossil known from the Lower Ordovician beds of the Isle of Öland (Sweden) and from Ordovician glacial boulders (Eisenack 1937, 1970, 1971, 1976; Mierzejewski 1986). The species also occurs in the Ordovician of Estonia (personal information from the Late Dr Ralph Männil, 1985). ?*Xenotheka* sp. was mentioned from a Ludlow glacial boulder (Mierzejewski 1977). Several conflicting opinions about the affinity of *Xenotheka* have been published and its systematic position remained unclear. Eisenack (1937) noted its similarity to some sessile foraminifers. Cushman (1948) interpreted *Xenotheka* as a member of the Ammodiscidae, while Loeblich & Tappan (1964) assigned it to the Allogrommidae. Jansonius (1964) considered it to be a chitinozoan *incertae sedis*. Eisenack (1970, 1971) correctly suggested that it was related to the Graptolithina but referred it to the graptoblasts. He described the tiny *Xenotheka* 'Forsatz'

(appendix) as a homologue of a graptoblast filum (i.e. stolon fragment) and erreneously interpreted the 'Mündungsrohr' (tube of the test) as a graptoblast kryptopyle. When discussing the systematic position of *Xenotheka* myself, I concluded that it was not related to the graptoblasts (Mierzejewski 1986). I was of opinion that the type material of the species, figured by Eisenack (1937), looked like the sicula of a benthic graptolite illustrated by Kozlowski (1971: fig. 4) and questionably ascribed by him to the Crustoidea. I also found that the systematic position of *Xenotheka* was additionally complicated by the fact that the neotype of *X. klinostoma*, designated by Eisenack (1970: fig. 1), very closely resembled another Ordovician microfossil *Ascosyrinx tenuis* Kozłowski, 1967.

The primary aim of the present work was to study the fine structure of the *Xenotheka* periderm and to clarify the systematic position of *Xenotheka*.

The material studied in the present paper was etched in 10–15% acetic acid from limestone core samples taken at a depth of 473 m in the Krzyże 4 borehole (north-eastern Poland, region of Białowieża) and contains more than fifty specimens in an excellent state of preservation. The conodont evidence suggested a Llandeilo age (Dzik in Mierzejewski 1984a). The specimens were cleaned of mineral impurities by immersion in a 20% solution of hydrofluoric acid for 48 hours and studied with a Cambridge Stereoscan 180 at 30 kV. Several specimens were embedded in epoxy resin, cut by means of a L.K.B. Pyramitome or Ultratome and studied with a light microscope and a Tesla BS 500 TEM.

For terminology see Urbanek & Mierzejewski (1984).

The described material is deposited at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL).

Test structure of *Xenotheka*

External morphology. — The test of *X. klinostoma* is shaped more or less like an oval loaf of bread, with a inclined, peripherally situated cylindrical tube (Fig. 1). Opposite the tube, near the base of of test wall, there is often an opening (Fig. 1B–D, G), which in some cases is situated on a short process (Fig. 1D). The cylindrical tubes of all specimens studied are occluded (Figs 1E, 2A,C, 5A). Like the occluded tubes, the external surface of the test is always black, matt and verrucose. The base of the test (i.e. where it is attached to the substratum) takes the form of a flat or slightly concave irregular sole (Fig. 1B, C). A few specimens have two soles (Fig. 1D). The soles expand laterally and form thin basal membranes with irregular edges (Fig. 1D, E, see also Eisenack 1937: figs 21, 22 and 1970: figs 1, 2). There is variation in test length (0.48–0–90 mm) and width (0.30–0.45 mm), and in the inclination of the tubes (compare Fig. 1A, G). The tube ends are devoid of any processes.

Internal microstructure. — Under a light microscope thin longitudinal sections show that the wall of *X. klinostoma* is built of five layers: (1) inner lining, (2) endocortex, (3) fusellum i.e. fusellar layer, (4) ectocortex and (5) outer lining (Figs 2, 3).

(1) The inner lining is the most underdeveloped layer of the periderm. It appears structureless and opaque and is therefore easy to identify in thin sections (Fig. 2F). In

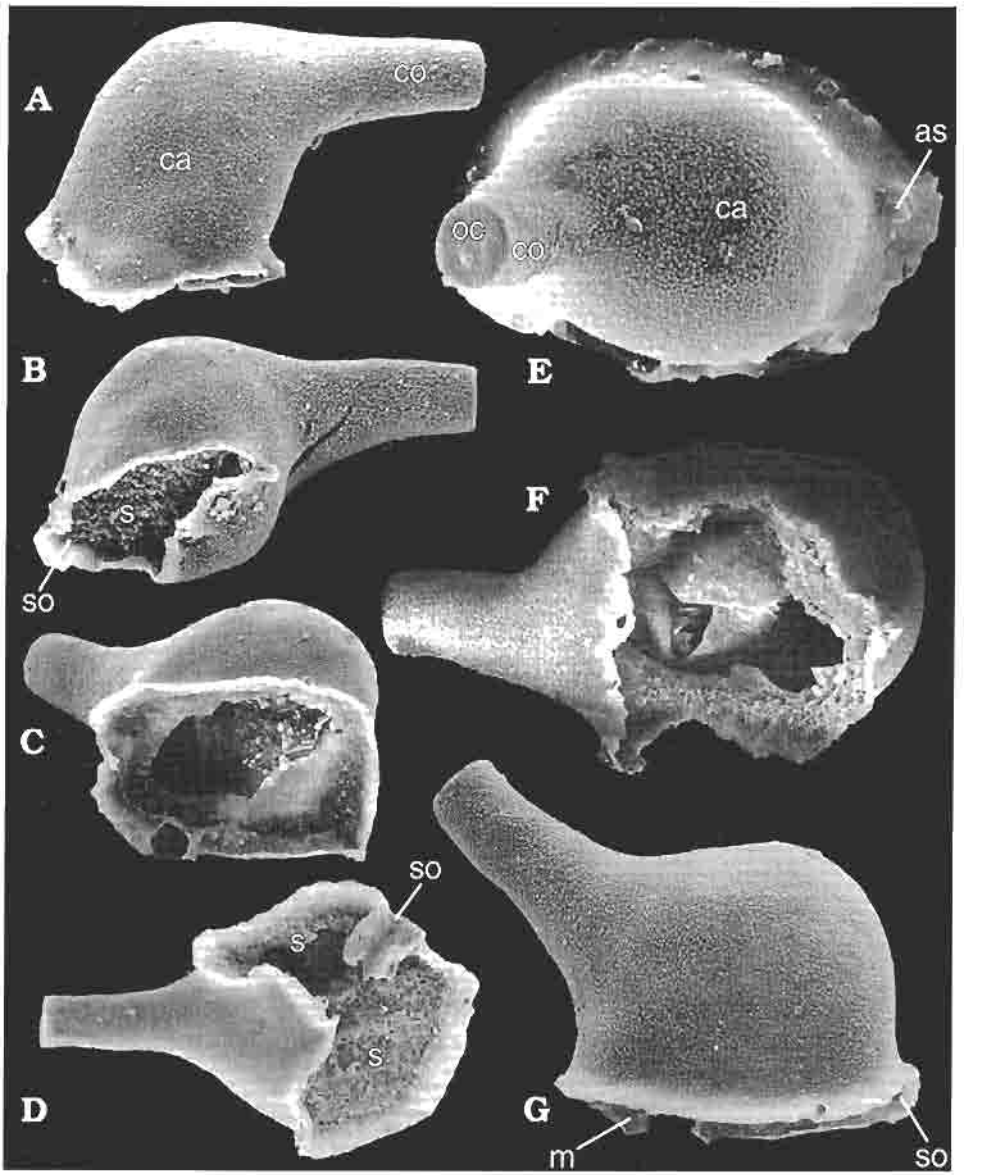

Fig. 1. *Xenotheka klinostoma* Eisenack, 1937; Llandeilo, borehole Krzyże 4, depth 473 m. SEM micrographs of autothecae. **A**, **B**. Lateral and dorso-lateral view; × 100 (ZPAL G/XXII/1). **C**. Dorso-lateral view of specimen with incomplete sole; × 100 (ZPAL G/XXII/2). **D**. Dorsal view of specimen with two soles; × 100 (ZPAL G/XXII/3). **E**. Ventral view; × 100 (ZPAL G/XXII /4). **F**. Dorsal view, × 130 (ZPAL G/ /5). **G**. Lateral view; × 130 (ZPAL G/XXII/6). Abbreviations: as, remains of autothecal stolon; ca, camara; co, collum; m, basal membrane; oc, occlusion of collum; s, sole; so, opening.

many cases the inner lining has broken away from the endocortex and fragments are displaced into the test cavity (Figs 2A–C, E, 3).

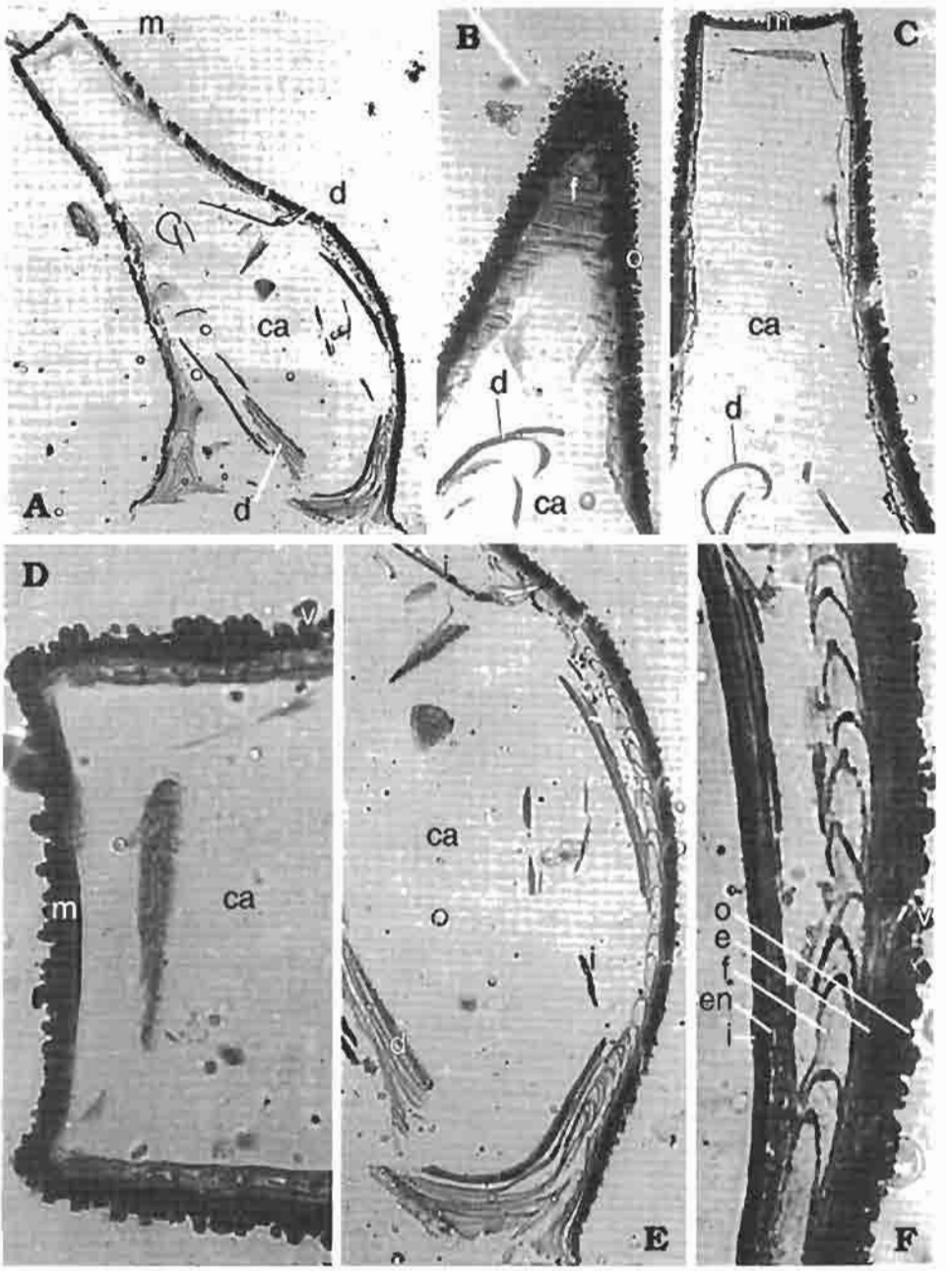

Fig. 2. *Xenotheka klinostoma* Eisenack, 1937. LM micrographs of thin sections through the autotheca (ZPAL G/ XXII/7). **A**. General view of longitudinal section; × 80. **B**. Oblique section of collum; × 150. **C**. Longitudanal section of collum; × 180. **D**. Portion of **C** enlarged to × 570. **E**. Longitudinal section through ventral wall of camara; × 160. **F**. Enlargment of the area outlined on **E**; × 530. Abbreviations: ca, cavity of autotheca; d, displaced fragments of periderm; e, ectocortex; en, endocortex; f, fusellar layer; i, inner lining; m, apertural membrane; o, outer layer; v, verruca.

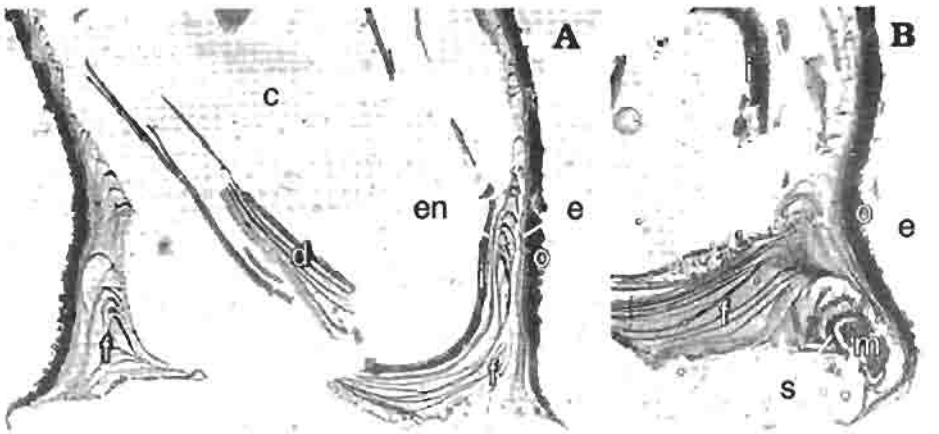

Fig. 3. *Xenotheka klinostoma* Eisenack, 1937. LM micrographs of thin sections (ZPAL G/ XXII/7). **A**. Arrangement of fuselli in proximal part of autotheca; × 160. **B**. Fragment of proximal part of autotheca with transversally sectioned autothecal stolon; × ca 100. Abbreviations: c, cavity of autotheca; d, displaced fragments of periderm; e, ectocortex; en, endocortex; f, fusellar layer; i, inner layer; m, material infilling stolon cavity; o, outer lining; s, stolonal sheath.

(2) The endocortex may be quite thick, semi-transparent, and is clearly distinguished from the neighbouring layers of the periderm by its lamination (Fig. 2F). It is built of strongly overlapping fuselli and is, therefore, dependent cortex.

(3) The fusellum is the most transparent layer of the periderm, and comprises fuselli displaying a strong, often symmetric, bilateral overlap of their limbs (Figs 2, 3). This layer is thickest near the base of the test and much thinner elsewhere (Figs 2A, E, 3).

(4) The ectocortex is identical to the endocortex, i.e: built of strongly overlapping fusellar limbs (Fig. 2E, F).

(5) The outer lining is thick and opaque (Figs 2, 3). Its outer surface is strongly verrucose. The outer lining covers the entire test apart from the sole, and occludes the tube apertures (Fig. 2A, C, D). Beneath the lining covering the aperture, a thin structureless pellicle is present (Fig. 2D).

Thin sections also show a peculiar micromorphological structure of the test. The above-mentioned small opening near the base of the test is surrounded by a thick ring-like structure made of an opaque material (Fig. 3B). The interior of the ring-like structure is partly infilled in an irregular way with concentrations of organic substance.

Organic matter of various shape and structure is commonly present inside the test cavities. It partially represents the remnants of the inner lining, endocortex and fusellum, suggesting a partial decomposition of the test wall. I cannot exclude the possibility that this is an artifact of preparation.

Ultrastructure. — All five layers of periderm recognized under the light microscope can be seen with the SEM (Figs 4, 5). Important new observations relate to the fine structure of the cortical layers (especially the ectocortex) and of the outer lining.

The ectocortex is built of several layers of fibrils arranged uniderectionally in particular layers (Fig. 4A, B). Neighbouring layers of fibrils run at oblique angles or per-

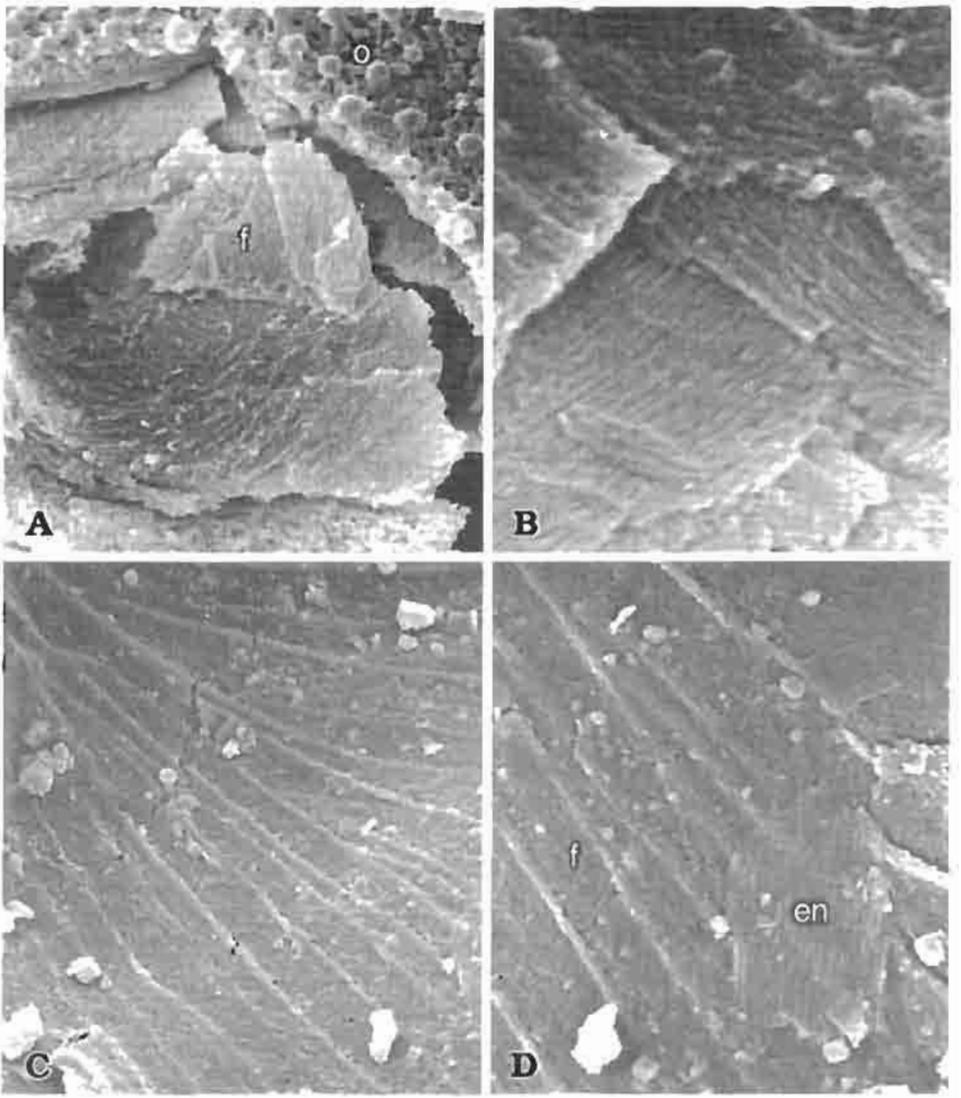

Fig. 4. *Xenotheka klinostoma* Eisenack, 1937; Llandeilo. SEM micrographs (ZPAL G/XXII/ 8). **A**. Obliquely fractured periderm of camara; × 450. **B**. Layers of fibrils in ectocortex; × 1600. **C**. Inner surface of fusellar layer; × 480. **D**. Patches of endocortex on inner surface of fusellar layer; × 600. Abbreviations: e, ectocortex; en, endocortex; f, fusellar layer; o, outer lining.

pendicular to each other, but the fibrils in individual layers show the same general orientation. The fibrils are straight and unbranched.

The endocortex is represented on SEM micrographs mainly by irregular patches (Fig. 4D). I interpret this phenomenon as a result of a *post mortem* partial decomposition of the periderm of the studied specimen (see also Fig. 3A).

The outer lining is built of a peculiar material named here verrucose fabric. It is composed of numerous tiny verrucae connected to an irregular net of thread-like ele-

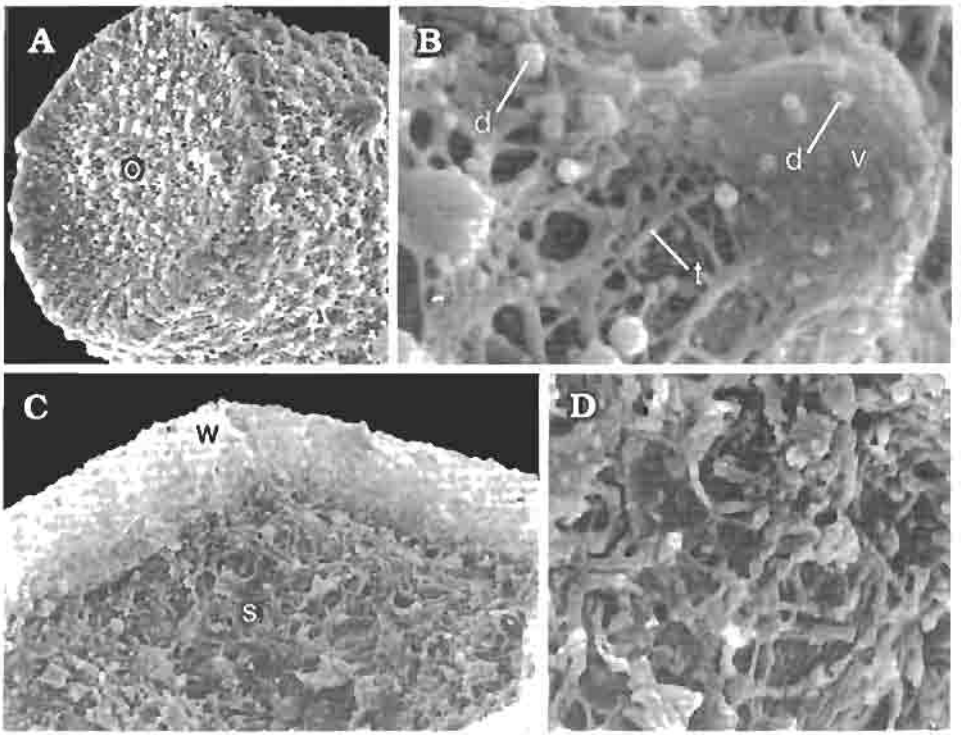

Fig. 5. *Xenotheka klinostoma* Eisenack, 1937. SEM micrographs. **A**. Distal end of collum with occluded aperture; × 430 (ZPAL G/XXII/6). **B**. Details of the outer lining surface; × 4500 (ZPAL G/XXII/8). **C**. Contact of the autothecal wall with sole: × 1800 (ZPAL G/XXII/3). **D**. Anastomosing fibrils and band-like thickenings of sole, enlargement of **C**: × 7800. Abbreviations: d, droplet; o, occluded aperture; s, sole; t, thread; v, verruca; w, wall of autotheca.

ments of different thickness (Figs 4A, 5A, B). The entire surface of verrucae and threads of the net is covered with irregularly distributed granules (Fig. 5B). Traces of the inner lining are rare because it has become separated from the endocortex (Fig. 1F). This disruption is a consequence of *post mortem* changes.

The fusellum is easy to identify due to the sharp boundaries of its component fuselli (Fig. 4C, D). No trace of regular zig-zag suture has been found. Fuselli may vary from 0.12 to 0.45 μm. The sole of *Xenotheka* is covered by an irregular net of numerous band-like thickenings (Fig. 5C, D).

Ultra-thin TEM sections through the proximal part of the test reveal some unexpected features. The boundaries between layers are not as sharp as they appear on LM and SEM micrographs. Moreover, in some cases there is no distinct difference in the fine structure of the fusellar layer and that of the cortex (both endocortex and ectocortex).

The inner lining is made of a crassal fabric (*sensu* Urbanek & Towe 1974: p. 4, i.e., an electron-dense and homogenous material revealing traces of layering), as it appears under the light microscope (Figs 6, 7C). On the other hand, layered parts of the lining may be regarded as an altered outermost part of the endocortex produced by a strong

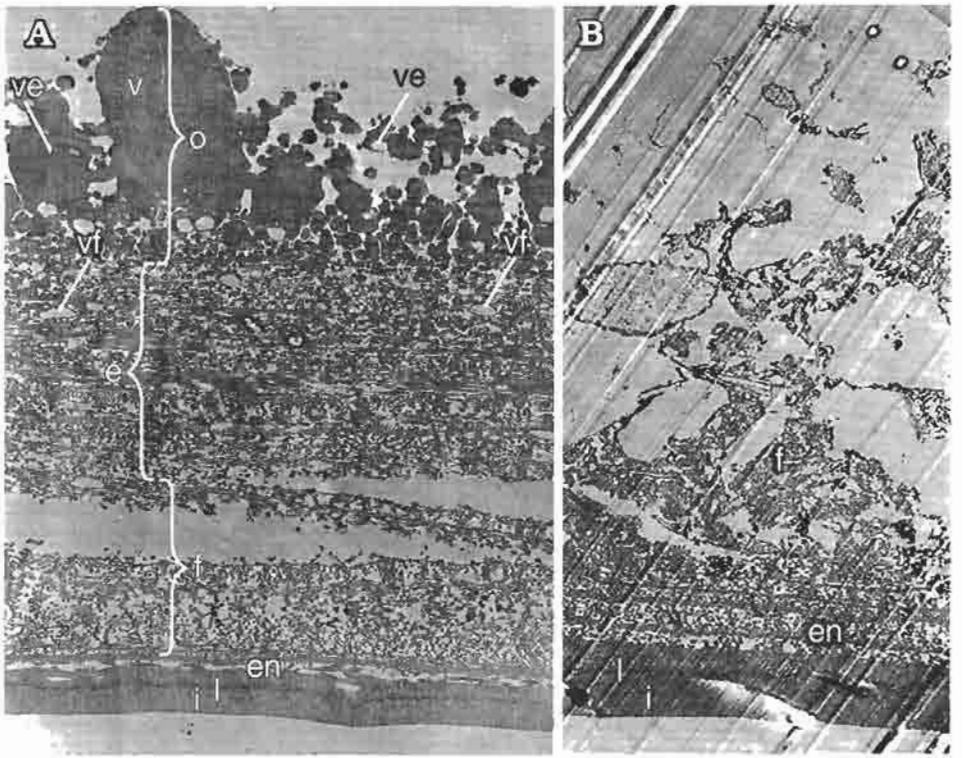

Fig. 6. *Xenotheka klinostoma* Eisenack, 1937. TEM micrographs. Transverse section through the autothecal periderm; × 2100. **B**. Disturbances in fusellar layer; × 4000. Abbreviations: e, ectocortex; en, endocortex; f, fusellar layer; i, inner lining; l, electron-dense line; v, verruca; ve, verruca vesicle; vf, interfibrillar vesicle.

condensations of the fibrillar material. In this situation, the electron-dense line in the inner lining may be interpreted as the proper boundary between the true lining and the transformed part of the endocortex.

The fusellar layer is composed of fuselli which may be compared to the *Dictyonema* type of Urbanek (1976). Each fusellus consists of an outer pellicle and a body (Fig. 8). The outer pellicle has the appearance of a distinct, electron-dense line. At higher magnification it is not quite homogenous but slightly granular. In the body of the fusellus, loosely packed fusellar fibrils do not differ essentially from the fibrils of some other graptolites but they do not always appear as solid cylinders without traces of internal structure. Many fibrils exhibit a large, distinct, translucent central core. These fibrils are very similar to the fusellar fibrils found in graptoblasts and recent cephalodiscids (see Mierzejewski 1984b: pls 15, 16). An incipient outer lamella is observed in the fuselli. Membranaceous vesicles are observed in contact with the outer lamella. In some cases one can observe disturbancs of unknown character in the fusellar layer (Fig. 6B).

Under the TEM there is no distinct boundary between the fuselli and the ecto- and endocortex (Fig. 6A). They are built of long fibrils arranged in layers, subparallel within a given layer and with the fibrils of adjoining layers set oblique to each other. It should be noted that the fibrils are of the same diameter as the fusellar fibrils. Some

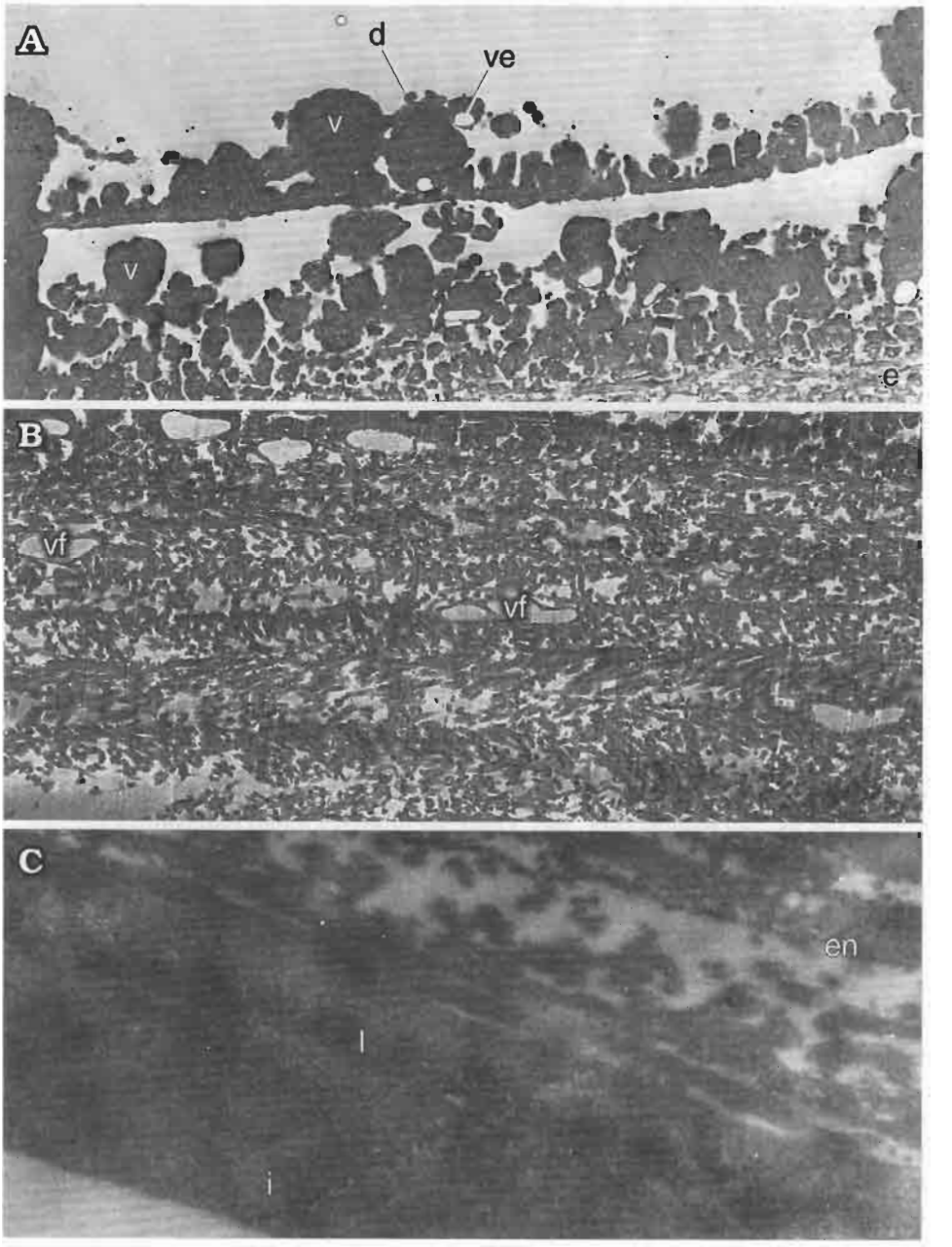

Fig. 7. *Xenotheka klinostoma* Eisenack, 1937. Transverse section through the outer lining; × 3200. **B**. Structural features of the ectocortex, × 3200. **C**. Transverse section through the inner lining; × ca 9000. Abbreviations: d, droplet; e, ectocortex; en, endocortex; i, inner lining; l, electron-dense line; v, verruca; ve, verruca vesicle; vf, interfibrillar vesicle.

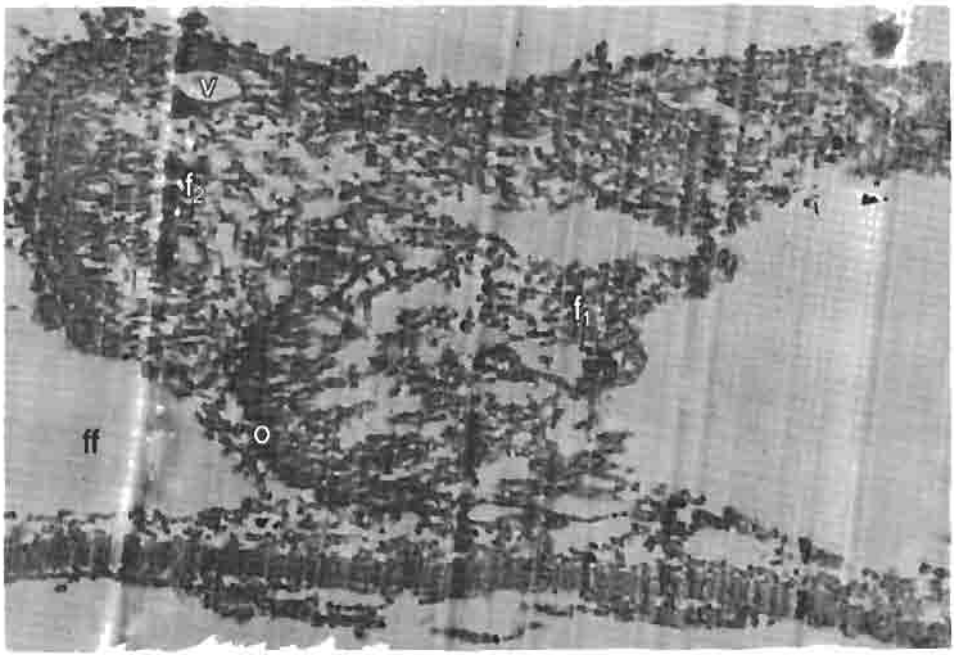

Fig. 8. *Xenotheka klinostoma* Eisenack, 1937; Llandeilo. TEM micrograph of longitudinal section through heads of two successive fuselli; × 8500. Abbreviations: f_1–f_2, successive fuselli; ff, base of following fusellus; o, outer lamella; v, fusellar vesicle.

elongated interfibrillar vesicles occur between particular layers of cortical fabric; each vesicle has its own pellicle (Fig. 7B). These are probably either remnants of $1c_1$-sheet fabric (*sensu* Urbanek & Towe 1974: p. 4) or an incipient sheet fabric. Generally, there is a lack of distinct sheet fabric in the cortex. It is worth mentioning that Dr R.B. Rickards in his review of this paper wrote as follows: "Description of this fabric as 'remnants of $1c_1$-sheet fabric' implies that *Xenotheka* is phylogenetically derived from an organism that possessed a more fully developed sheet fabric. Yet no evidence is presented for this interpretation. Could it not also be that this is an incipient stage of development in the sheet fabric and a primitive condition rather than a derived condition ?".

The outer lining is built up of a completely homogenous material (Figs 6A, 7A), named above as verrucose fabric. Some TEM micrographs show a specific 'lamination' of this material but this is only an artefact, formed during the cutting of ultra-thin sections. There is no sharp boundary between the outermost part of the ectocortex and the innermost part of the outer lining (Fig. 7A). This feature is caused by the lack of delimiting sheet fabric to the ectocortex. The boundary is almost certainly marked by the outermost alignment of interfibrillar vesicles. Nevertheless, it should be stated that some similar isolated vesicles are found within what is unquestionable outer lining material.

The thick ring-like structure that surrounds a small opening near the base of *Xenotheka* is interpreted as the proximal part of an autothecal stolon (Fig. 9). It is made of crassal fabric with distinct traces of a laminar structure in some areas. The inner cav-

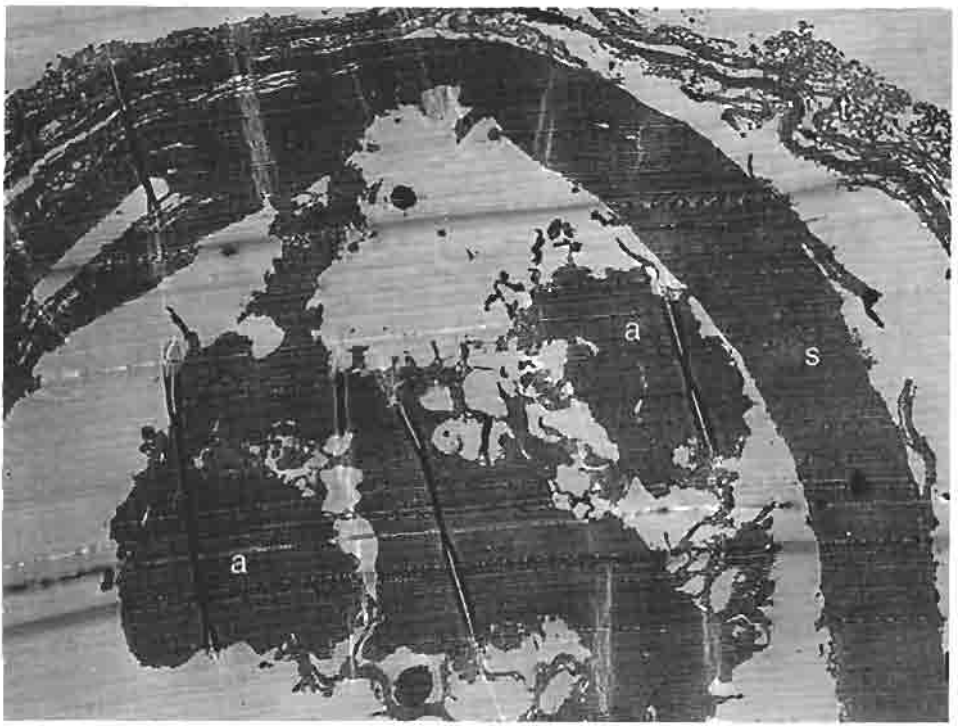

Fig. 9. *Xenotheka klinostoma* Eisenack, 1937. TEM micrograph through the autothecal stolon sheath penetrating the autothecal wall; × 2800. Abbreviations: a, accumulation of an organic material in stolonal sheath cavity; s, stolonal sheath; t, tissue connecting stolonal sheath with autothecal wall.

ity of the structure contains accumulations of an homogenous organic matter incorporating irregular vesicles and fissueres.

Affinities of *Xenotheka*

The results of the light and electron microscopic investigations help to clarify the systematic position of of *Xenotheka* Eisenack, 1937. It is certainly an encrusting graptolite, and its periderm is fully comparable with that of most other graptolites. Only the outer lining of verrucose fabric is unknown in the Graptolithina (and in the Pterobranchia). It is worth noting that outer lining of unusual structure has been also found in the periderm of *Pterobranchites antiquus* Kozłowski, 1967 (Mierzejewski 1984a).

I propose that *Xenotheka* is a representative of the camaroid graptolites (Camaroidea) and I interpret its tests as isolated autothecae. Autothecae of the Camaroidea are strongly differentiated into two parts: an inflated proximal part (camara) and a distal tube (collum). At the proximal extremity of the camara there is a small opening for an autothecal stolon. The same elements are easy to recognize in *Xenotheka*. Thus, I interpret the *Xenotheka* test (Eisenack's 'Hülle') as a camara and Eisenack's 'Fortsatz' (ap-

pendix) as a part of the autothecal stolon. Another important feature of the Camaroidea is that occlusion of the autothecae is very common (Kozłowski 1949).

Comparison between the periderm of *Xenotheka* and that of other camaroids is not easy. The first investigations of the microstructure of camaroid periderm were undertaken by Kozłowski (1949). He found that the wall of camaroid autothecae was built of two layers, fusellar and cortical. He additionally observed that in many cases the proximal parts of autothecae were partially embedded in a peculiar material, an extracamaral tissue that formed a sort of a sheath. The periderm of *Tubicamara coriacea* Kozłowski, 1949 has been studied in detail under LM, SEM and TEM by Urbanek & Mierzejewski (1991). Its periderm is three layered, comprising an inner lining, fusellar layer and ectocortex. It is worth noting that the outer surface periderm of the *T. coriacea* is often rough because of numerous irregularly scattered tubercles. However, the resemblance of this surface to the verrucose fabric of the outer lining of *Xenotheka* is only superficial. The periderm of *Tubicamara* was recovered from cherts with hydrofluoric acid and its sculptured surface results from partial corrosion. Urbanek & Mierzejewski (1991) observed other alterations of peridermal tissues due to fossilization and suggested that the inner lining of *Tubicamara* was nothing but an altered endocortex. This makes comparison of the fine structure of *Xenotheka* and *Tubicamara* difficult.

The curious outer lining of verrucose fabric is especially interesting. The function of this lining was to occlude the apertures of autothecae as well as to cover the rhabdosome. This was presumably an adaptation which enabled the organism to survive periods of adverse conditions. Perhaps the zooids were able to resume their normal life functions when conditions improved.

The recognition of this new verrucose fabric considerably complicates previous views on how the periderm was secreted. The relationship between the outer lining of verrucose fabric to the other peridermal components is rather problematic. The organization of the outer lining, its uniform distribution across the autothecae and its occlusion of the autothecal apertures cannot be accounted for by any previously suggested mode of secretion (for example see Urbanek 1976, 1986; Crowther 1978, 1981). Undoubtedly the outer lining was formed secondarily with respect to the secretion of fusellar and cortical tissues. In my opinion, the outer lining material in *Xenotheka* was secreted by a special organ that is unknown in other graptolites. This most likely took the form of an organic emulsion rising into the water, which subsided to the rhabdosome, covering the surface, occluding the thecal apertures, and then hardening. The 'droplet' character of the verrucose fabric is consistent with such an hypothesis.

Several dozen *Xenotheka* autothecae from Krzyże 4 were studied. All have an identical outer lining and all have their apertures occluded. They may have originated from a single colony which disintegrated during the processing of the core sample. The colony may have been built of loosely dispersed autothecae, connected by a stolonal system and a thin basal membrane. As there is no evidence of bithecae in *Xenotheka* I allocate this genus tentatively to the family Cysticamaridae Kozłowski, 1949.

The recognition of the systematic position of *Xenotheka* extends the upper stratigraphic range of camaroid graptolites from the late Arenig to the Llandeilo.

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Ordowicka mikroskamieniałość *Xenotheka* jest graptolitem

PIOTR MIERZEJEWSKI

Streszczenie

Tematem pracy jest mikrostruktura, ultrastruktura oraz stanowisko systematyczne zagadkowej mikroskamieniałości organicznej *Xenotheka klinostoma* Eisenack, 1937. Gatunek ten, znany z ordowiku obszaru bałtyckiego, opisywany był w przeszłości jako należący do Foraminifera (Allogrommidae bądź Ammodiscidae), Chitinozoa *incertae sedis*, Graptoblasti lub jako skamieniałość o nieznanym stanowisku systematycznym.

Badania przeprowadzono na kilkudziesięciu doskonale zachowanych okazach, pochodzących z landeilu wiercenia Krzyże 4 (głębokość 473 m). Zastosowano metodę mikrotomowych skrawków seryjnych dla mikroskopii świetlnej oraz standardowe metody transmisyjnej i skaningowej mikroskopii elektronowej. Uzyskane wyniki pozwoliły na jednoznaczne wykazanie, iż ścianki *X. klinostoma* mają budowę typową dla wielu graptolitów, a mianowicie zbudowane są z warstwy fuzelarnej, pokrytej od zewnątrz i od wewnątrz warstwami korteksu (tzw. ektokorteks i endokorteks), określanego mianem korteksu zależnego. Najbardziej wewnętrzną warstwę ścianki tworzy cienka, homogeniczna wyściółka, pokrywająca endokorteks. Z kolei ektokorteks pokryty jest od zewnątrz niezwykłym, zupełnie nieznanym dotąd u graptolitów tworzywem ultrastrukturalnym, dla którego wprowadzono nazwę tworzywa brodawkowatego („verrucose fabric").

Badane mikroskamieniałości rozpoznano jako izolowane autotęki graptolitów inkrustujących z rzędu Camaroidea. Rząd ten, ustanowiony przez Romana Kozłowskiego (1949), znany był dotąd niemal wyłącznie na podstawie materiałów pochodzących ze słynnego stanowiska w Wysoczkach (górny tremadok Gór Świętokrzyskich). Rozpoznanie przynależności systematycznej rodzaju *Xenotheka* Eisenack, 1937 podnosi górną granicę stratygraficzną występowania Camaroidea z dolnego arenigu do landeilu, a niepewne znalezisko tej formy było sygnalizowane nawet z ludlowu.

Wszystkie zbadane autoteki mają apertury okludowane cienką diafragmą utworzoną z tworzywa brodawkowatego. Okluzja autotek jest wśród Camaroidea zjawiskiem nagminnym, lecz diafragmy występują z reguły wewnątrz autotek, między „collum" a „camara".