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ULTRASTRUCTURE OF THE SICULA IN THE TUBOID GRAPTOLITE
KOZŁOWSKITUBUS ERRATICUS (KOZŁOWSKI, 1963)

Urbanek A.: Ultrastructure of the sicula in the tuboid graptolite *Kozłowskitubus erraticus* (Kozłowski, 1963). *Acta Palaeont. Polonica*, 24, 4, 493–503, December 24, 1979.

The sicula of *Kozłowskitubus erraticus* has been examined with TEM. The upper portion of prosicula is three-layered, the middle layer being a mesh. Its bottom consists of an attenuated, almost structureless membrane. The metasicula is made of strongly variable fuselli, built of fusellar and sheet fabric only (*Dictyonema* type of fuselli). The evidence available indicates that mesh fabric is the main component in all discophorous and in part of nematophorous prosiculæ (structural type "A"). Only some nematophorous prosiculæ are lacking the mesh component and therefore constitute structural type "B". The striking similarity of the sicula described with the embryonal vesicle of *Rhabdopleura* may not be evaluated until more becomes known on latter's ultrastructure.

Key words: Graptolites, ultrastructure, sicula.

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INTRODUCTION

The sicula of a tuboid graptolite *Kozłowskitubus erraticus* described by Kozłowski (1963) as *Dendrotubus erraticus*, reveals a striking similarity with the so-called embryonal vesicle of *Rhabdopleura compacta* Hincks (Stebbing 1970; Kozłowski 1971). Recent controversies about the affinities of graptolites and pterobranchs (see Urbanek 1976 a, 1978) made it necessary to examine the early stages of sessile graptolites and *Rhabdopleura* at the ultrastructural level, in the hope of finding clues to the phylogenetic evaluation of this similarity.

The present paper has been primarily conceived as a co-operative work with Professor P. N. Dilly (Department of Structural Biology St. George's Hospital Medical School, University of London). In June 1976 an ample material containing numerous early stages of *Rhabdopleura compacta* found near the Plymouth Laboratory was examined by Professor Dilly and the present author and fixed for future ultrastructural studies. At the same time first ultrathin sections of the sicula in *Koz-*

lowskitubus erraticus were preliminarily examined. This fossil material was supplied by the present author for a joint paper dealing with comparison of the detailed ultrastructure of early stages of the development of the colony in sessile graptolites and in *Rhabdopleura*.

A considerable delay in obtaining results on the *Rhabdopleura compacta* material induced the present author to publish his observations on the ultrastructure of *Kozłowskitubus erraticus* separately, in the hope that a future paper by Professor P. N. Dilly will provide additional information, necessary for comparison and drawing conclusions.

MATERIAL AND METHODS

The material of *Kozłowskitubus erraticus* siculae was kindly supplied by the late Professor R. Kozłowski from his rich collections of graptolites isolated from erratic boulders of Baltic origin. Two siculae were embedded in Epon 812 and used subsequently to obtain ultrathin sections with a Porter Blum Microtome provided with a diamond knife. They are numbered as specimen 1 and specimen 2 respectively.

Specimen 1 (pl. 13: 1) has been etched out of an erratic boulder numbered 0.446 from Ustka, Baltic Coast (Western Pomerania). The matrix of the boulder is a grey, medium-grained limestone and contains rich organic remains including, besides Tuboidea, algae, an unidentified monograptid, fragments of eurypterid skin (*Carcinosoma* sp.), pyritized Beyriichinae ostracodes and scolecodonts described by Kielan-Jaworowska (1966: 25). The age of the boulder is Silurian, most probably Lower Ludlow (Eltonian or Bringewoodian). Specimen 1 had a partly damaged metasicula and therefore supplied data concerning mainly the prosicula and its base.

Specimen 2 (pl. 13: 2—3) has been isolated from erratic boulder 0.91 found in Rewal, Baltic Coast (Western Pomerania). It represented a complete sicula with a long and slightly curved "neck" (metasicula) strongly resembling Kozłowski's specimen (1963: 1) reproduced in the present paper (fig. 1). The matrix of the boulder is fine-grained, light grey limestone and contains small fragments of tuboid graptolites, *Dendrograptus* sp. and scolecodonts. The boulder is probably Ordovician but the scarcity of the assemblage does not enable a safe determination of its age.

The bulk of Kozłowski's material has been obtained from the Baltic erratic boulders of Ordovician age, but it was later found that *Kozłowskitubus erraticus* occurs as well in Silurian drift material (unpublished data by Kozłowski). Recently Mierzejewski (1978) has arrived at an opinion that the species in question occurs in Middle Ordovician to Upper Silurian erratic boulders and "no difference was found between the Ordovician and Silurian forms".

Both specimens (1, 2) were sectioned longitudinally to produce a number of sagittal sections, examined in London (St. George's Hospital Me-

dical School) with a Zeiss 9A electron microscope at 60 kV and in Warsaw (Institute of Zoology, Warsaw University) with a Tesla 100 B electron microscope also using 60 kV.

Acknowledgements

The present author wishes to express his gratitude to Mr. Ray Moss (Department of Structural Biology, St. George's Hospital Medical School, London) for his help in taking sections. He is also grateful to Mrs. G. Mierzejewska and Mr. P. Mierzejewski for their assistance during scoping in Warsaw, and to Miss L. Łuszczewska for taking light micrographs. The present author would also like to thank Professor P. N. Dilly for his friendly assistance throughout his visit to London and Plymouth. This visit was made possible by the scheme of exchange between the Royal Society of London and the Polish Academy of Sciences. Additional support to permit completion of the study was provided by a research project of the latter institution numbered II/6.

STRUCTURE OF THE SICULA IN KOZLOWSKITUBUS ERRATICUS

The light micromorphology of *Kozlowskitubus erraticus* has been described by Kozłowski (1963, 1971, see fig. 1). The prosicula is bottle-shaped and consists of a bulbous base, devoid of any traces of helical

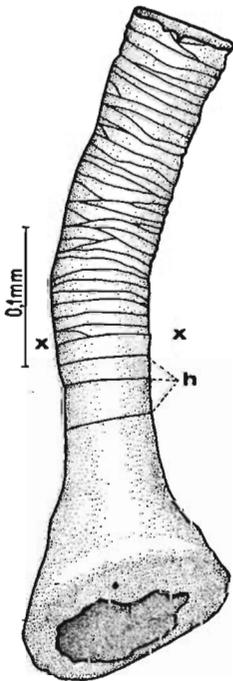


Fig. 1. A complete sicula of *Kozlowskitubus erraticus* with attachment membrane characteristically damaged (from Kozłowski 1963). *h* trace of helical line, *x-x* limit between the pro- and metasicula

line, and an ascending cylindrical upper part with a few whorls of a faint helical line. The metasicula features a long, cylindrical "neck" made of irregularly placed fusellar bands. The aperture of the metasicula is straight and devoid of apertural processes.

The boundary between the pro- and metasicula is obscure and somewhat difficult to recognise (comp. fig. 1, *x-x*). The marginal membrane which appears in later stages, was not developed in the specimen studied. A tubular cross-section seen at the base of the prosicula in specimen 1 (pl. 13: 1, *s*) may be ascribed to the prostolon.

Kozłowski (1963, 1971) has tentatively assigned the species in question to the genus *Dendrotubus* Kozłowski, emphasizing a number of differences with the typical representatives of that genus. Recently, Mierzejewski (1978) suggested that it should be placed in a new monotypical genus *Kozłowskitubus* Mierzejewski.

ULTRASTRUCTURE OF THE PROSICULA IN *KOZŁOWSKITUBUS ERRATICUS*

Ultrathin sections examined with a TEM reveal under lower magnification (pl. 14: 2—4) that the upper part of the prosicula consists of three components. These are: 1) a middle component, being the thickest of the three (some 3—4 μm) and formed by an irregular mesh of electron-dense fibrils, 2) a thinner dense layer (judging from the light micrographs it is situated on the outer surface), and 3) a thicker dense layer (which, judging from the light micrographs, is situated on the inner surface, comp. pl. 13: 3, inner dark band).

Seen at a higher magnification (pl. 14: 1—4; pl. 15: 1—2, *m*) the middle component shows details of fibrillar structure; the fibrils are frequently curved or sinuous, anastomosing or branching with rough surfaces often covered by granular bodies of variable electron density (pl. 15: 2—3, *b*). They produce an irregular and, as compared with the fusellar fabric, rather tightly packed network.

Both the thinner and thicker dense layers are made of condensed, almost homogeneous material, with inclusions of denser granular bodies. Within the thinner (dense) layer indistinct traces of layering may be recognized in places (pl. 14: 1, *o*). While the thinner dense layer is rather constant in width over longer stretches, the thicker (dense) layer changes in width producing irregular swellings toward the middle (pl. 14: 4; pl. 15: 1, *i*). At some places, however, it is relatively thin and even (pl. 16: 1—2, *i*). The fabric found in both dense layers of the prosicula, being composed of an almost homogeneous, medium electron-dense material, may tentatively be assigned to the "crassal fabric" as defined by Urbanek and Towe (1974: 4).

This structural pattern of the prosicula is modified at its base. Around the proximal bulbous part of the prosicula, seen on longitudinal sections

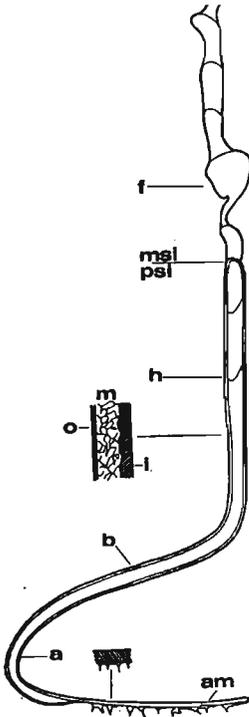


Fig. 2. Diagram showing minute details of structure of sicular wall in *Kozlowskitubus erraticus*. *a* angular bending of bulbous portion of the prosicula, *am* attachment membrane being probably an extension of inner dense layer of prosicular wall, *b* bulbous portion of prosicula, *f* fusellus, *h* traces of helical line (marked hypothetically, not recognized on sections), *msi/psi* boundary between the pro- and metasicula

in form of a genicular bending pl. 17: 3), the ultrastructure of the entire wall resembles that of the thicker dense component in the upper part of the prosicula. It is made of an almost structureless material, similar to that defined above as "crassal fabric" (pl. 17: 4). The wall of the bottom of the prosicula, with which it was attached to the substratum, is made of an almost homogenous material of low electron density. It is therefore less sharply defined (characteristically "nebulous"), with faint traces of certain fibrous structure (pl. 17: 2). On some micrographs showing the same basal part of the prosicula (around the bulbous swelling) some traces of layering may still be seen (pl. 17: 1), while the attenuated membrane of the bottom reveals parallel fibrils (pl. 16: 2). This may imply either a rather diversified mode of secretion close to the attached part of the prosicula, or different preservational states. The attachment membrane is most probably an extension of the inner dense layer (fig. 2, *am*).

Unfortunately, no reliable traces of a helical line were observed on ultrathin sections.

ULTRASTRUCTURE OF THE METASICULA

Studies with the light microscope revealed an irregular fusellar structure of the metasicula in *Kozlowskitubus erraticus* (Kozłowski 1963, 1971). Some fuselli form entire annuli devoid of an oblique suture, but the

majority are provided with a single oblique suture distributed randomly over the periphery without forming a zig-zag suture.

Longitudinal ultrathin sections studied with the TEM show a great variation in size, arrangement and form of fuselli (pl. 18: 1; pl. 20: 2; pl. 21: 3—4). There are sudden changes in these characters and in degree and form of overlap between the neighbouring fuselli (pl. 18: 1, f_1 — f_2 ; pl. 20: 2, 3). Some fuselli display differentiation into three, more or less distinct parts, namely the base, the trunk and the head (pl. 20: 2, pl. 21: 1, b , h , t ; comp. also Urbanek and Towe 1975: 17). The trunk, however, can not be distinguished as a separate part in a number of the fuselli examined. The base and head are made of a loose mesh of interconnected fusellar fibrils (pl. 19: 1, b , h), while their narrow trunks are composed of densely packed fibrils (pl. 21: 1, t). The fibrils have smooth surfaces but often produce tape-like widenings and form "web"-like structures at their points of junction (pl. 19: 1, w).

The fuselli are delineated and separated from each other by an electron-dense outer pellicle. This latter consists of a condensed fibrous material rather than a single sheet (pl. 20: 1; pl. 21: 2, p). The fuselli in *Kozłowskitubus erraticus* are devoid of an outer lamella and therefore in the classification proposed by Urbanek (1976b: 324—325) may be assigned to the *Dictyonema* type of fuselli. They have only the fusellar and sheet components and were secreted according to the formula: ph_1 — ph_2 (Urbanek 1976b).

COMPARISON AND PRELIMINARY CONCLUSIONS CONCERNING THE ULTRASTRUCTURE OF THE SICULAE IN GRAPTOLITES

Kozłowski (1971: 314) has distinguished two fundamental morphological types of siculae, i.e.: the discophorous sicula (the siculae of sessile graptolites provided with a basal disc) and the nematophorous sicula (the siculae of free-living graptolites marked by the presence of a nema). These names denote two contrasting morphological types of graptolite colonies. Our extremely limited knowledge of the ultrastructure of graptolite colonies does not permit us to present an analogous classification based on submicroscopic features. The ultrastructure of only three graptoloid prosiculae have been described so far, namely: *Orthograptus gracilis* (Romer) (by Wetzel 1958), *Didymograptus* sp. and *Pristiograptus dubius* (Suess) (by Urbanek and Towe 1975). Only the latter two are described in detail. They both represent the nematophorous type in terms of a morphoecological classification but display striking differences in their ultrastructural organization. *Didymograptus* has a prosicula composed of 1) the middle component (being a loose mesh of interconnected fibrils) as well as 2) the outer and 3) inner components with

a cortical appearance (structural type "A"). *Pristiograptus* reveals a much simpler pattern with its prosicula made of a cortical-like inner component covered by a compact layered fabric. This fabric is similar to the material within the central part of the adjacent virgula. Thus a mesh fabric is lacking in *Pristiograptus* (structural type "B").

The evolutionary and stratigraphic position of *Didymograptus* might imply that the structure of its prosicula is primary (ancestral) while that in *Pristiograptus* sp. is of a derived character. This assumption is corroborated by the recognition of mesh fabric as the main component of the prosicula in *Kozlowskitubus erraticus*. The same is indicated by finding a mesh component within the wall of the prosicula in a dendroid sicula (unpublished). This mesh is covered on both sides by cortical derivatives with a characteristically loose packing of fibrils. These observations suggest that discophorous prosiculae display structural type "A".

The homology between the middle components of *Kozlowskitubus* (discophorous sicula of a sessile graptolite) and *Didymograptus* (nematophorous sicula of a free-living graptolite) seems safe. The latter has preserved ancestral ultrastructural features in spite of the new adaptations acquired at the morphological level of organization. This fact appears to be responsible for a certain incongruence between the morphological and ultrastructural classification of graptolite siculae as indicated on Table 1.

Table 1

Comparison of structural classification of siculae

morphoecological classification (Kozłowski 1971)	ultrastructural classification
I. discophorous type	type "A"
II. nematophorous type	type "B"

The metasacula of *Kozlowskitubus erraticus* is composed of *Dictyonema* type fuselli (without an outer lamella). This may indicate that those simple fuselli preceded phylogenetically the more advanced *Acanthograptus* type, although certainly more data are needed to substantiate this working hypothesis (Urbanek 1976b).

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ULTRASTRUKTURA SIKULI GRAPTOLITA TUBOIDOWEGO
KOZŁOWSKITUBUS ERRATICUS (KOZŁOWSKI, 1963)

Streszczenie

Współczesne kontrowersje wokół pochodzenia i stanowiska systematycznego graptolitów (por. Urbanek 1976a, 1978) wymagają zbadania sikuli *Kozłowskitubus erraticus*, która wykazuje uderzające podobieństwo do pęcherzyka embrionalnego *Rhabdopleura compacta* (Stebbins 1970; Kozłowski 1971).

Sikula wspomnianego graptolita, zbadana na skrawkach ultracienkich za pomocą transmisyjnego mikroskopu elektronowego, wykazała, że prosikula jest tu trójwarstwowa, przy czym środkowa warstwa ma budowę gąbczastą. Podstawa prosikuli ma ściankę złożoną ze scieniałej, prawie bezstrukturalnej błony. Natomiast metasikula składa się z fuzelusów bardzo zmiennych pod względem kształtu i wielkości. Fu-

zelusy te zbudowane są jedynie z tworzywa fuzelarnego i błonki zewnętrznej (typ fuzellusów *Dictyonema*, Urbanek 1976b).

Istniejące dane świadczą o tym, że prawdopodobnie u wszystkich dyskofoforycznych i części nematoforycznych prosikul warstwa gąbczasta jest głównym składnikiem ściany (typ strukturalny "A"). Tylko pewne nematoforyczne prosikule są pozbawione tej warstwy i stanowią typ strukturalny "B".

Uderzające podobieństwo morfologiczne opisanej sikuli do pęcherzyka embrionalnego *Rhabdopleura* będzie mogło być ocenione po poznaniu ultrastruktury tego ostatniego.

АДАМ УРБАНЕК

УЛЬТРАСТРУКТУРА СИКУЛЫ ТУБОИДНОГО ГРАПТОЛИТА
KOZLOWSKITUBUS ERRATICUS (KOZŁOWSKI, 1963)

Резюме

В свете современных разногласий по поводу происхождения и систематического положения граптолитов (ср. Urbanek 1976a, 1978) особое значение приобретает изучение сикулы *Kozlowskitubus erraticus*, которая характеризуется необычайным сходством с эмбриональным пузырьком *Rhabdopleura compacta* (Stebbins 1970; Kozłowski 1971).

Исследование ультратонких срезов сикулы данного граптолита с помощью трансмиссионного электронного микроскопа показало, что её просикула состоит из трёх слоев, причем срединный слой имеет губчатое строение. Стенка основания просикулы состоит из истонченной почти бесструктурной плёнки. Метасикула, в свою очередь, складывается из фюзеллюсов, отличающихся большой изменчивостью по форме и величине. Фюзеллюсы состоят исключительно из фюзеллярного материала и наружной оболочки (тип фюзеллюсов у *Dictyonema*, Urbanek 1976).

Полученные данные свидетельствуют о том, что главным строительным материалом стенок у всех дискофорных и части нематофорных просикул является, по видимому, губчатый слой (структурный тип „А”). Только у некоторых нематофорных просикул этот слой отсутствует, и они относятся к структурному типу „В”.

Объяснение разительного морфологического сходства между указанной сиколой и эмбриональным пузырьком *Rhabdopleura* станет возможным лишь в результате ультраструктурных исследований последнего.

EXPLANATION OF THE PLATES 13—21

Plate 13

Light microscopic features of the sicula in *Kozlowskitubus erraticus*

1. Specimen 1, $\times 375$.
2. 3. Specimen 2, $\times 115$ and $\times 600$ respectively.
b attenuated base of prosicula, *m* metasicula, *p* prosicula, *s* prostolon, *w* upper wall of prosicula.

Plate 14

Ultrastructure of the upper wall of the prosicula in *Kozlowskitubus erraticus* (specimen 1) as seen with the TEM on longitudinal sections (1—4).

i inner dense layer, *m* middle component, *o* outer component.

Plate 15

Ultrastructural details of the upper portion of the prosicular wall in *Kozlowskitubus erraticus*, specimen 1, as seen with the TEM on longitudinal sections (1—2). Note the uneven thickness of the inner dense layer (*i*) and granular bodies (*b*) within the fibrous material of the middle component (*m*).

b granular bodies, *i* inner dense layer, *m* middle component, *o* outer component.

Plate 16

Ultrastructural details of the upper portion of the prosicular wall in *Kozlowskitubus erraticus*, specimen 1, (1, 3) and fibrils recognized within the attenuated bottom portion of the prosicula (2). Note the reduction of thickness of the dense layer on micrographs 1 and 3.

i inner dense layer, *m* middle component, *o* outer dense layer.

Plate 17

Structural features of the lower portion of the prosicular wall in *Kozlowskitubus erraticus* as seen with the TEM on longitudinal sections.

1. Wall of the prosicula base.
2. Attenuated portion of the prosicula base.
- 3-4. Structure of the bulbous part of the prosicula at the genicular bending (3) and ultrastructural details of the recognized material (4).

Plate 18

Ultrastructure of the metasicula in *Kozlowskitubus erraticus* as seen with the TEM on longitudinal sections.

1. A group of successive fuselli (f_1 — f_3) showing great variation in size, arrangement and form.
- 2-3. Details of f_2 and f_3 visible on fig. 1.

Plate 19

Ultrastructural details of the fusellar tissue in *Kozlowskitubus erraticus* as seen with the TEM on longitudinal sections through the metasicula.

1. Details of the boundary between f_1 — f_2 on pl. 18:1.
2. Details of the specimen seen on pl. 20:2.
b base of a fusellus, h head of a fusellus, f coarse fusellar fabric, p outer pellicle, w web-like structures between fusellar fibrils.

Plate 20

Ultrastructural details of fusellar tissue in *Kozlowskitubus erraticus* as seen with TEM on longitudinal sections through metasicula.

1. Fragment of a fusellus with loose network of fibrils and a strong outer pellicle.
2. Diminutive fusellus situated between two larger ones.
3. Strong overlap of adjacent fuselli.
b basis of fusellus, f fusellar fibrils, h head of fusellus, p outer pellicle, t trunk of fusellus

Plate 21

Fuselli and fusellar wall of the metasicula in *Kozlowskitubus erraticus* as seen on longitudinal sections.

- 1-2. TEM micrographs showing fusellus and details of its ultrastructural fabric.
 - 3-4. Light micrographs showing a capricious variation in the size and shape of fuselli ($\times 600$).
b base of fusellus, f fibrils of the fusellar fabric, h head of fusellus, p outer pellicle, t trunk of fusellus.
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