

Discovery of Pterobranchia (Graptolithoidea) in the Permian

PIOTR MIERZEJEWSKI and CYPRIAN KULICKI



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The fossil remains of a hemichordate exoskeleton, recognized as fragments of the stolons and their cyst-like swellings connected with the fusellar zooidal tubes, were derived by chemical isolations from Late Permian (Kazanian) mudstones of the Svalis Dome (central Barents Sea, Norway). These fossils, referred to as *Diplohydra szaniawskii* sp. nov., are the first undoubted representatives of the class Graptolithoidea found in Permian deposits. The genus *Diplohydra* Kozłowski, 1959, known previously only from the Ordovician and originally established as a thecate hydroid taxon, is reinterpreted as an aberrant member of the order Rhabdopleuroidea. This strange hemichordate, characterized by fusellar tubes distinctly narrower than stolon-like tubes and their swellings, reveals a certain degree of dimorphism in the stolon system. *D. szaniawskii* sp. nov. also displays some peculiar morphological features common to the Ordovician rhabdopleuroid genus *Rhabdopleurites* Kozłowski and the stolonoid genus *Stolonodendrum* Kozłowski.

Key words: Graptolithina, Pterobranchia, Rhabdopleuroidea, Permian, Norway, Barents Shelf.

Piotr Mierzejewski [mierzejewski@post.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland. Present address: ul. Filtrowa 83/49, PL-02-032 Warszawa, Poland;

Cyprian Kulicki [kulicki@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

A few years ago, contrary to the prevailing consensus among palaeontologists that the graptolites are an extinct group, Dilly (1993) suggested that the Recent pterobranch hemichordate *Cephalodiscus graptolitoides* Dilly, 1993 is probably classifiable as a living graptolite (for discussion see also: Rigby 1993; Svital 1993; Dilly 1994; Urbanek 1994a, b; Maletz and Erdtmann 1995). However, it is important to note that in the past, a similar conclusion was made by Beklemishev (1951, 1970) who proposed the class Graptolithoidea to embrace two diverse taxa: the extinct class Graptolithina (with the orders Stolonioidea, Camaroidea, Tuboidea, Dendroidea, and Graptoloidea), and the extant class Pterobranchia (with the orders Rhabdopleuroidea and Cephalodiscoidea). The most important common feature of the Graptolithoidea (with the exception of the enigmatic living *Atubaria* Sato, 1936) is the presence of an organic sclerotized exoskeleton composed of growth bands called fusellar increments or simply fuselli. As stated by Kozłowski (1947, 1949, 1966), fusellar tissue is not known in any other fossil or living animal (for summary of ultrastructural and biochemical study of this tissue see Armstrong et al. 1986; Urbanek 1986; Mierzejewski and Kulicki 2001). The presence of such a peculiar structural element makes the Graptolithoidea a very coherent group. It is remarkable that morphological differ-

ences between some living and fossil sessile Graptolithoidea are less pronounced than the differences between the sessile and the planktic orders within this class (Urbanek 1986). Beklemishev (1951, 1970), as pointed out by Urbanek (1986), erected the class Graptolithoidea, anticipating the results of future submicroscopic and molecular investigations and eliminated the actualistic bias in the recognition of the Graptolithina and the Pterobranchia as taxa of the same rank. Recent morphological and ultrastructural investigations by Urbanek and Dilly (2000) and Mierzejewski and Kulicki (2001) on the stolon system and periderm of the fossil and living Rhabdopleuroidea seem to support decisively Beklemishev's (1951, 1970) concept of the class Graptolithoidea. Similarly as Beklemishev (1951, 1970), we retain the names Pterobranchia and pterobranchs as common, non-taxonomic names given to cephalodiscids and rhabdopleurids, i.e., extant orders of the Graptolithoidea.

So far the stratigraphic record gives little information on post-Carboniferous representatives of the Graptolithoidea; there are only a few discoveries of the extant genus *Rhabdopleura* Allman, 1869 in the Jurassic (Kulicki 1969, 1971) and Cretaceous (Kozłowski 1949, 1956; Kulicki and Mierzejewski in Mierzejewski 1986) of Poland, as well as in the Paleogene of Great Britain (Thomas and Davis 1949). In ad-

dition, some disputable remains of the living genus *Cephalodiscus* M'Intosh, 1882, from the Eocene were mentioned by Bulman (1970). An intriguing note by Deng Guogan (1985) concerning a dendroid graptolite assigned to the genus *Dictyonema* Hall, 1851 from China should be regarded as wholly erroneous (see Jaeger 1992).

The purpose of this paper is to describe a find of an undoubted Permian hemichordate remains representing the class Graptolithoidea. The specimens described here come from the wellcore sample P3 of the well named Dia 84-31 (Svalis Dome in the central Barents Sea, Norway) from a depth 10.18–10.40 m. They were found associated with a rich assemblage of various eunicid polychaete jaws, recently described by Nakrem et al. (2001). The age of this material, based on palynomorphs, has been estimated as Kazanian (Nilsson et al. 1996). The microfossils were extracted from the cherty mudstone matrix by standard chemical procedures using hydrofluoric acid and manual sorting of residues under the microscope. The dried material was platinum-coated and examined with a Philips scanning electron microscope XL 20. In the classification used here, the authors have adhered to the above mentioned proposal of Beklemishev (1951, 1970). All studied specimens are stored on SEM stubs and deposited in the collections of the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL).

General remarks

The stolon system of sessile graptolites displays a wide array of structural differentiation and is of great significance for phylogenetic studies (see for example: Kozłowski 1938, 1949, 1962; Bulman 1970; Urbanek 1986; Urbanek and Dilly 2000). As a rule, its fossils consist of fragments of a rather complicated structure composed of branched tubular elements called stolons, connected in some orders with various vesicular bodies, generally termed the stolon derivatives (cysts, graptoblasts, and cysts or capsules of the dormant buds). The stolons obtained by etching rocks with acids are usually well enough preserved for comparison in detail with contemporary forms, studies of fine morphological details (e.g., stolonial diaphragms), as well as the ultrastructure. The rhabdopleurid stolons and dormant bud capsules are more resistant to diagenetic agents than zooidal and stolonial tubes which are built up almost exclusively of the fusellar tissue. Undoubtedly, this is the reason why some of the material described by Kulicki (1969, 1971) of the Jurassic *Rhabdopleura kozłowskii* is represented only by dormant bud capsules (for observations on decomposition of Recent *Rhabdopleura* coenecium see Briggs et al. 1995 and Urbanek and Dilly 2000).

As was shown by Mierzejewski (1982, 1986), fossil remnants of rhabdopleurid, crustoid or dendroid stolon system are moderately common organic microfossils to be found in some marine deposits, especially of Ordovician

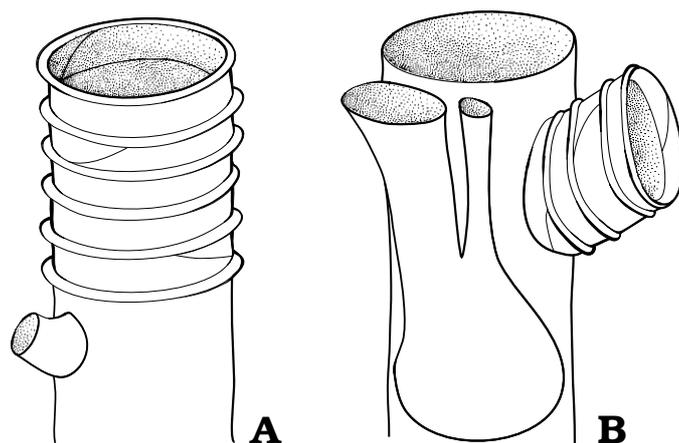


Fig. 1. Comparison of main structural elements of tubarium. A. *Rhabdopleurites primaevus* Kozłowski, 1967. B. *Diplohydra szaniawskii* sp. nov.

and Silurian age. However, they were repeatedly misinterpreted for decades as remains of the “chitinous hydroids” or *incertae sedis* forms (e.g., Eisenack 1934, 1937; Kozłowski 1959; Skevington 1965). Such alleged “hydroid” genera as *Calyxhydra* Kozłowski, 1959, *Cylindrotheca* Eisenack 1934, *Kystodendron* Kozłowski, 1959, *Lagenohydra* Kozłowski, 1959, *Palaeotuba* Eisenack, 1934, and fossils described by Kozłowski (1959) as parataxonomic units *Gonothecae* Formae A, B, and C are simply rhabdopleurid stolons and dormant bud capsules. Finally, the fossils described herein are referred as to another fossil “chitinous hydroid” genus, namely *Diplohydra* Kozłowski, 1959. Earlier, Mierzejewski (1986) questioned the coelenterate nature of this enigmatic form and pointed out that *D. gonothecata* Kozłowski, 1959 and *D. solida* Kozłowski, 1959 display similarities in morphology to the rhabdopleurid genera *Kystodendron* Kozłowski, 1959 and *Rhabdopleurites* Kozłowski, 1967, respectively. In conclusion, however, he considered *Diplohydra* as a taxon of questionable affinities and was of the opinion that “highly fragmentary character of the type material and the lack of new ones makes any taxonomical decisions concerning this genus hazardous” (Mierzejewski 1986: 197).

The newly described form, *Diplohydra szaniawskii* sp. nov., in spite of its incomplete nature, provides distinctive features, especially in the presence of fusellar tubes, which fully justify its assignment to the Graptolithoidea. However, the morphological interpretation of this form is rather far from clear. This is mainly because of the peculiar and rather obscure interrelationships between its fusellar tubes and tubiform elements similar to the true stolon system of a rhabdopleurid tubarium. Almost all known sessile graptolites provided with a sclerotized stolon system, namely the Dendroidea, Crustoidea, Camaroidea, some Tuboidea, and Rhabdopleuroidea, have stolons made of nonfusellar material suddenly widening to the base of the fusellar element (theca or zooidal tube); for detailed de-

scriptions and figures of these structures refer to papers by Kozłowski (1949, 1962), Bulman (1970), Urbanek (1986) and Urbanek and Dilly (2000).

In contrast, *D. szaniawskii* sp. nov. displays an astonishing mode of connection between nonfusellar and fusellar elements of the skeleton: narrow fusellar zooidal tubes appear to be offshoots of distinctly broader (!) non-fusellar tubes (Figs. 1A, 2). Obviously, this unusual case raises some difficulties in the interpretation of the nature of these tubes because the supposition that the stolons were considerably wider than thecae would seem rather unlikely. Although present knowledge of morphology of *D. szaniawskii* sp. nov. morphology is inadequate for complete understanding, it does allow for some speculations on its systematic affinities.

Among the Graptolithoidea from the Ordovician of the Baltic region, there are two distinctive and unsatisfactorily known genera which may be useful for interpretation of *D. szaniawskii* sp. nov.: *Stolonodendrum* Kozłowski, 1949 and *Rhabdopleurites* Kozłowski, 1967. The former is the single member (excluding the problematic genus *Melanostrophus* Öpik, 1928) of the extinct order Stolonioidea, whereas the latter is a member of the extant order Rhabdopleuroidea. Both forms manifest similar morphology of branching and structure. As originally described by Kozłowski (1967, 1970), and restudied by Mierzejewski (1986), the stolonial tubes of *Rhabdopleurites primaevus* Kozłowski, 1967 have some parts showing no evidence of fusellar structure (see Andres 1977).

This unusual type of periderm, unknown in any other rhabdopleurids, differs essentially from the fusellar periderm in its ultrastructure because it is built of numerous closely packed thin membranes (Mierzejewski 1986: 179, pl. 27: 1). The boundary between nonfusellar and fusellar parts of these tubes, called, in Mierzejewski's terminology (1986: 172), partly nonfusellar stolonial tubes, is sharp and is strikingly similar to that between the nonfusellar prosicula and fusellar metasicula of the graptolites (Fig. 1B). On the surface of the nonfusellar parts of the stolonial tubes there are small projections with a central pore, most probably a structure connected with perforatory budding. On the other hand, the stolon in *Stolonodendrum* steadily broadens until its structureless wall passes abruptly into the fusellar structure of the theca proper (Kozłowski 1949).

Mierzejewski (1986) was of the opinion that other parts of *Stolonodendrum* colonies had been most probably described as the isolated erect parts of autothecae of the tuboid graptolite *Conitubus siculoides* Kozłowski, 1949. Moreover, he found that colonies of *Stolonodendrum* are strikingly similar to colonies of *Rhabdopleurites* and recalled the earlier opinion of Urbanek (in Kuźnicki and Urbanek 1967) that there are no marked differences in the morphology of two orders, the Stolonioidea and the Rhabdopleuroidea. Finally, Mierzejewski (1986: 176) did not exclude the possibility that *Stolonodendrum* and *Rhabdopleurites* may represent the same rhabdopleurid family Rhabdopleuritidae. These comparisons and considerations enable the suggestion that *D. szaniawskii* sp. nov. is related to both of these discussed genera.

Systematic paleontology

Class Graptolithoidea Lapworth, 1875

(in Hopkinson and Lapworth 1875)

sensu Beklemishev, 1951

Order Rhabdopleuroidea Beklemishev, 1951

Family unknown

Genus *Diplohydra* Kozłowski, 1959

Type species: *Diplohydra longithecata* Kozłowski, 1959.

Emended diagnosis.—Stolon system devoid of diaphragms, peduncular stolons and true capsules of the dormant buds. Major stolon with irregularly arranged lateral offshoots. Lateral offshoots form diads composed of the two daughter stolons. As a rule, one of the daughter stolons is strongly inflated and, sometimes, forms an imperfect composite cyst.

Species assigned.—*Diplohydra longithecata* Kozłowski, 1959, *D. micropedunculata* Kozłowski, 1959, *D. solida* Kozłowski, 1959, *D. gonothecata* Kozłowski, 1959, *D. szaniawskii* sp. nov.

Remarks.—The genus *Diplohydra* was erected by Kozłowski (1959) on the basis of chemically isolated material from Ordovician erratic boulders of Baltic origin, occurring in the glacial (Pleistocene) deposits of central and northern Poland. Originally, it was interpreted as a representative of the hydrozoan coelenterate order Hydroida. Later, Kozłowski's species of *Diplohydra*, with the exception for *D. gonothecata*, were recorded from the Ontikan Limestones (lower Ordovician) of Öland (Sweden) by Skevington (1965). Mierzejewski (1986) questioned both the hydroid nature of *Diplohydra* and congeneric character of the four species. All material described here agrees with the original description of *Diplohydra*, as stated by Kozłowski (1959: 240): "Les espèces groupées dans ce genre sont caractérisées par la présence, le long des rameaux, des thèques de deux catégories, groupées par paires et communiquant entre elles de différente manière." At present, it is clear that the alleged thecae of two categories should be reinterpreted as stolons, some of which are inflated and similar to capsules of the dormant buds. It is of interest to note that Kozłowski (1959: fig. 20B₂) discovered a "glomérule chitineux" in the "gonotheca" of *D. gonothecata* which strikingly resembles clusters of minute spherules observed in cysts of Rhabdopleurida and Camaroidea (Mierzejewski 1986, 2000), as well as in graptoblasts (Crowther et al. 1987). According to Mierzejewski (1986, 2000), this material appears to correspond to yolk material known from the dormant bud capsules in living *Rhabdopleura*.

The large stratigraphic gap between the Ordovician species of *Diplohydra* and Permian *D. szaniawskii* sp. nov. might argue against congenerity of these forms. However, the Rhabdopleuroidea are undoubtedly a very conservative group. For example, the extant genus *Rhabdopleura* is known from the Jurassic (Kulicki 1969, 1971) and some fos-

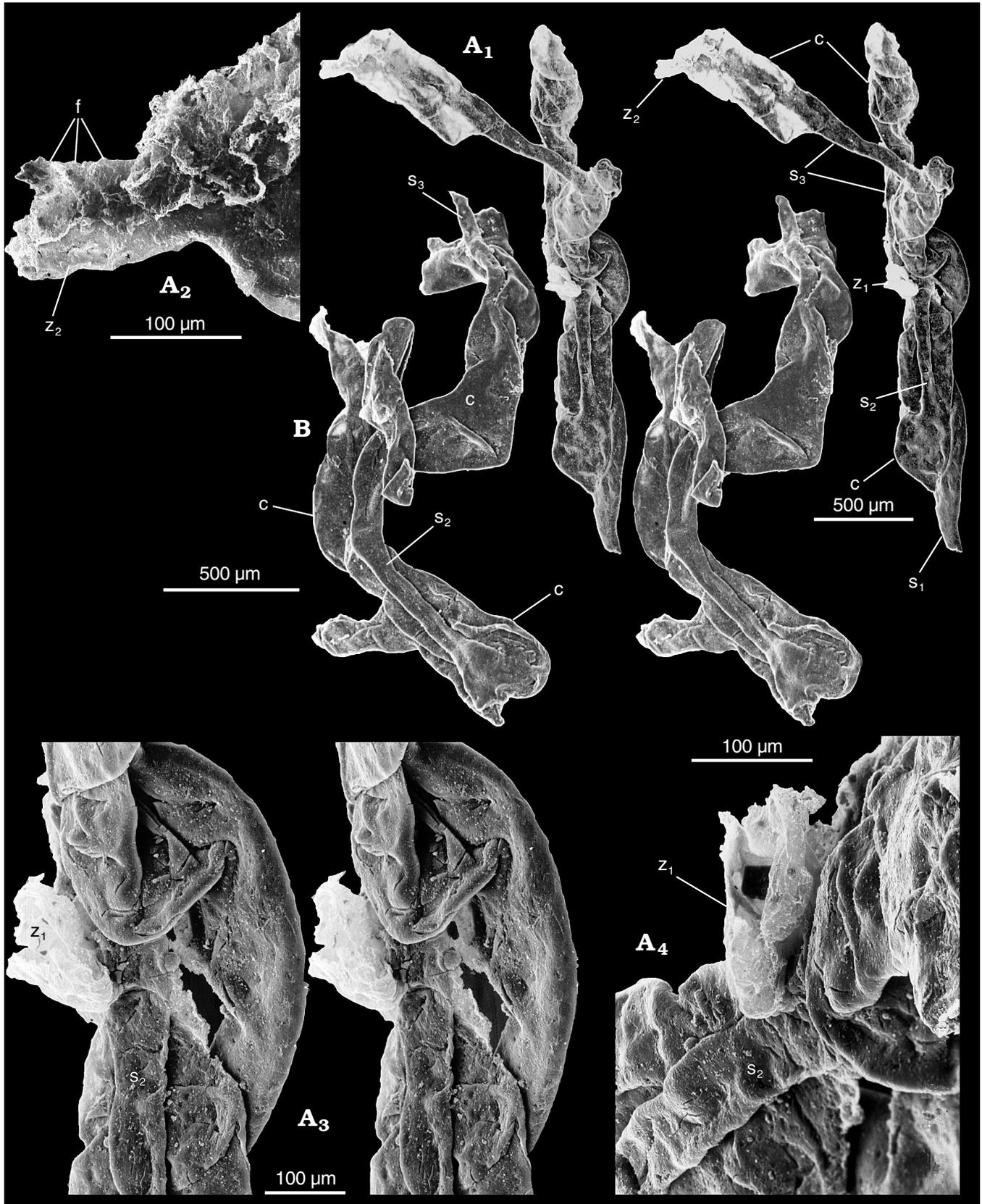


Fig. 2. *Diplohydra szaniawskii* sp. nov. Upper Permian (Kazanian), borecore sample P3 of the well Dia 84-31 (10.18–10.40 m) from the Svalis Dome (central Barents Sea, Norway). SEM micrographs. **A.** Holotype (ZPAL Pb.0/1): entire specimen (A₁), enlargements (A₂–A₄); A₁, A₃ stereopairs. **B.** Branched stolons with swellings (ZPAL Pb.0/2); stereopair. Abbreviations: c, cyst-like swelling of the stolon (imperfect cyst of the dormant bud); f, fusellar increments; s₁, s₂, s₃, stolons; z₁, z₂, fusellar zooidal tubes.

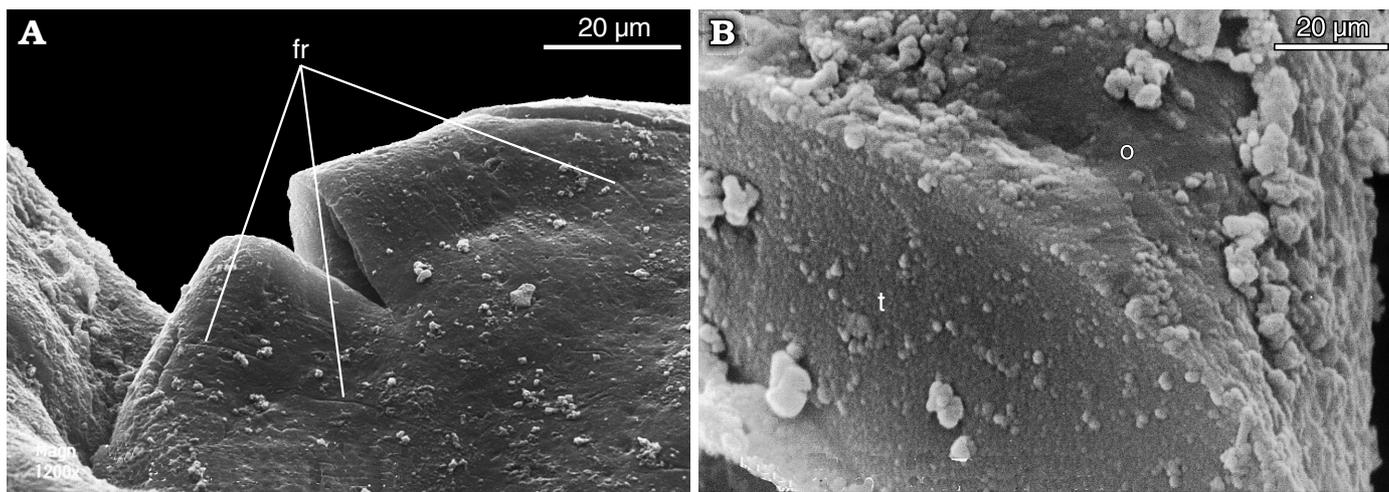


Fig. 3. *Diplohydra szaniawskii* sp. nov. Upper Permian (Kazanian), sample P3 of the well Dia 84-31 (10.18–10.40 m) from the Svalis Dome (central Barents Sea, Norway). SEM micrographs. Fine structure of the stolon system (ZPAL Pb.0/1). **A**. Outer surface of the cyst-like swelling. **B**. Broken stolonal sheath. Abbreviations: fr, furrow (impression of the cortical fibrils?); o, outer surface of the stolonal sheath; t, area of the transversally broken stolonal sheath.

sils disputably attributed to this taxon were described from the Middle Cambrian (Durman and Sennikov 1993), Silurian (Mierzejewski 1977; Rickards *et al.* 1984) and Carboniferous (Mortelmans 1955).

The fragmentary condition of our material does not permit a closer determination of the systematic position of this form. The family membership is unknown since it differs widely from other rhabdopleurids. Moreover, it is hardly possible to determine the nature of its resemblance to *Rhabdopleurites* and *Stolonodendrum*. In our opinion, it seems reasonable that *Diplohydra* represents an unknown evolutionary line of the order Rhabdopleuroidea. A fact of great interest is that stolonal diads do show a certain degree of dimorphism, a feature unknown in other fossil and living rhabdopleurids. Unfortunately, the interpretation of this phenomenon remains obscure.

Distribution.—Poland and Sweden, Ordovician; Norway (Barents shelf), Upper Permian.

Diplohydra szaniawskii sp. nov.

Figs. 2, 3.

Holotype: The specimen figured in Fig. 2A1–A4 (ZPAL Pb.0/1).

Type locality and type stratum: The boring Dia 84-31 in Svalis Dome (central Barents Sea, Norway), depth 10.18–10.40 m, Kazanian (uppermost Permian).

Derivation of the name: Named in honour of the discoverer, Professor Hubert Szaniawski.

Diagnosis.—A species with the stolon system composed of stolons and their broad and long subcylindrical or slightly irregular swellings. The swellings as imperfect dormant bud cysts closed or ending with terminal stolons. Fusellar zooidal tubes minute, distinctly narrower than stolons and their swellings.

Material.—Three specimens (ZPAL Pb.0/1-3), all etched from matrix.

Description.—General form of the colony unknown, but presumably linear. The holotype is an irregularly curved bundle of stolons 3.41 mm long, connected with two fusellar zooidal tubes (Fig. 2A₁). Stolons, having a thickness of about 65–115 µm, are provided with large (600–750 µm long and 210–250 µm wide) subcylindrical or slightly irregular cyst-like swellings. Cyst-like swellings may be interpreted as imperfect conventional and composite cysts of dormant buds. Two fusellar tubes 135–145 µm long and ca. 90 µm wide, grow out at a high angle from the stolon proper (tube z₁) and the cyst-like swelling of the stolon (tube z₂). Fusellar tubes show no trace of apertural or thecal modification such as widenings or apertural processes that would indicate their true nature. Fusellar growth increments are hardly visible and are spaced at about 58 per mm. The other specimen lacks fusellar tubes and is composed of branched stolons with cyst-like swellings (Fig. 2B).

Remarks.—Despite incomplete preservation, the holotype and the second specimen are sufficiently large fragments of coenecia for revealing diagnostic characteristics. However, more information may be provided if more and better preserved material becomes available. Its general features correspond well to those of other species assigned to the genus. The species here described shows a particularly striking similarity to *D. gonothecata* but differs in its remarkably greater dimensions. So far, *D. szaniawski* sp. nov. is the only known species of *Diplohydra* found with remnants of fusellar elements. However, the nature of the fusellar tubes is not clearly understood, and whether they represent stolonal tubes, or zooidal tubes is a problem that is difficult to solve. It should be kept in mind that the fusellar tubes of the Rhabdopleuroidea are fairly undiagnostic (see Mierzejewski 1986), although the form under consideration is a single rhabdopleurid species provided with these elements narrower than nonfusellar tubes.

Occurrence.—Upper Permian (Kazanian), Norway (Barents Shelf).

Fine structure of *Diplohydra szaniawskii* sp. nov.

As observed under a light microscope, all elements of the examined specimens appear to be made of jet black, opaque and matt material. Stolons and capsules of the dormant buds are distinctly thick-walled, whereas the walls of the fusellar tubes look membranous and reveal weak traces of very fine, narrow fusellar increments.

Under SEM examination the stolons and dormant bud capsules appear almost completely flattened, wrinkled and cracked (Fig. 3). The outer surfaces of these elements are rough and irregularly pitted, most likely as a result of their diagenetic history. However, peculiar striations are observed on the outer surface of the capsule illustrated on Fig. 4A. These striations are made of numerous long, straight and parallel shallow furrows. There is a strong similarity between this structure and that of the dormant bud capsule of the Jurassic *Rhabdopleura kozłowski* Kulicki, 1969 (see Mierzejewski and Kulicki 2001: fig. 9). The observed furrows should be interpreted as impressions of very long and thick endocortical fibrils underlying the inner surface of fusellar tubes. Such endocortical fibrils have recently been observed in the zooidal tubes of the living *Rhabdopleura normani* Allman, 1869 (Kulicki and Mierzejewski, unpublished results). The walls of the stolons and cyst-like swellings are built of the same organic material and seem to be completely structureless in fractured surfaces, sometimes with possible traces of weak concentric layering (Fig. 3B), as were described by Mierzejewski (1986) in the Ordovician rhabdopleurids *Kystodendron longicarpus* (Kozłowski) and *K. subtilis* (Kozłowski). The fine structure of the zooidal tubes was described in detail in our previous paper (Mierzejewski and Kulicki 2001).

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