

The stolon system in *Rhabdopleura compacta* (Hemichordata) and its phylogenetic implications

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Studies made with the light microscope on the stolon system of extant pterobranch hemichordate *Rhabdopleura compacta* Hincks, 1880 have revealed the presence of characteristic structures called herein diaphragm complexes. Each complex consists of the stolonial diaphragm proper and a thin-walled conical encasement, produced by a rapid inflation of the stolonial sheath around the diaphragm. Such structures have never been observed before either in the Recent or fossil Rhabdopleurida. However, both in their origin and in their relations to the stolon and to the zooidal tube, diaphragm complexes strongly resemble the internal portions of thecae as recognized in the sessile orders of the Graptolithina. The significance of the presence of these homologues of the enclosed initial portions of thecae in *Rhabdopleura compacta* for the understanding of the phylogenetic relationships between pterobranchs and graptolites is discussed.

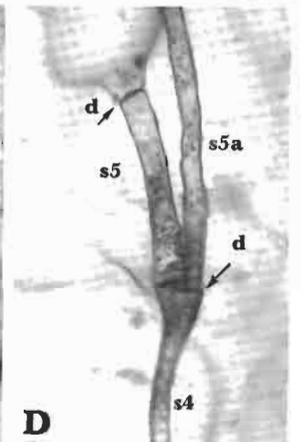
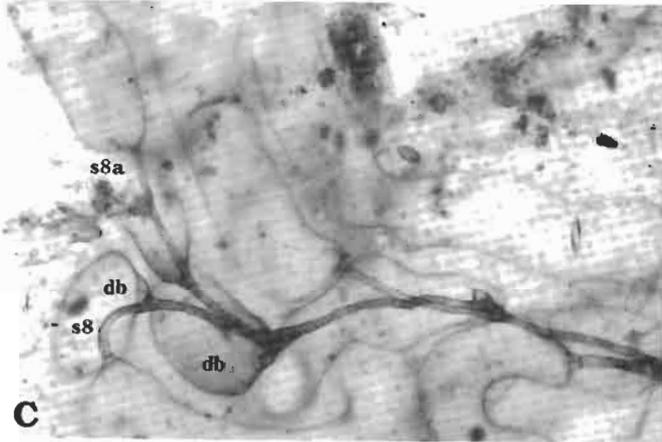
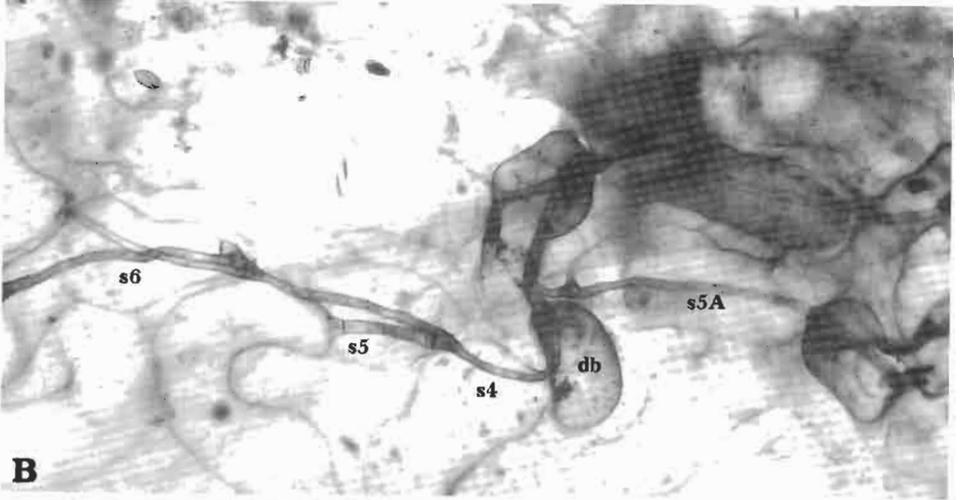
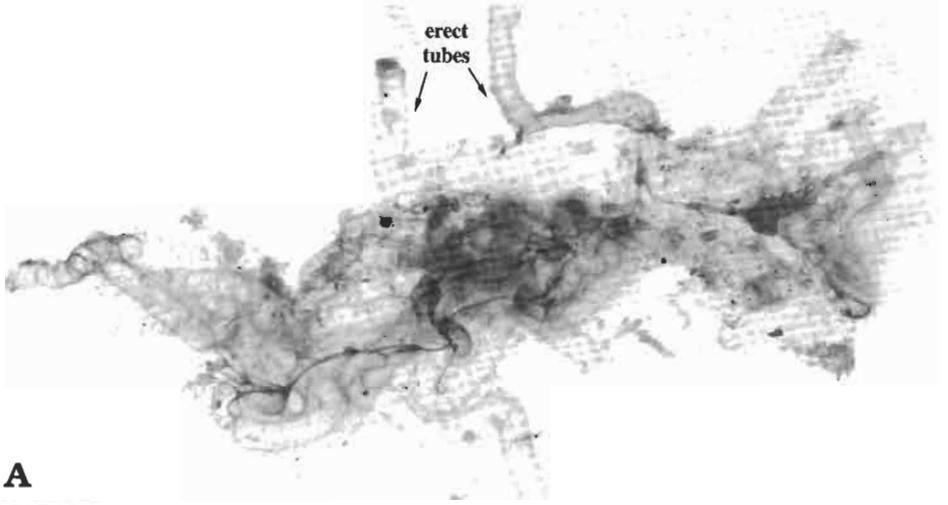
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Introduction

Rhabdopleura is a truly colonial hemichordate. Its colonies consist of a number of zooids joined together by stolons contained within tubes secreted by individual zooids. The tubes are composed of growth bands and reveal a characteristic microstructure (Figs. 1, 2) comparable with that in graptolites (known as fusellar structure). The stolon may be defined as a thread of soft tissue produced by the commonly called permanent terminal zooid, through an extension of its peduncle as the terminal zooid ad-



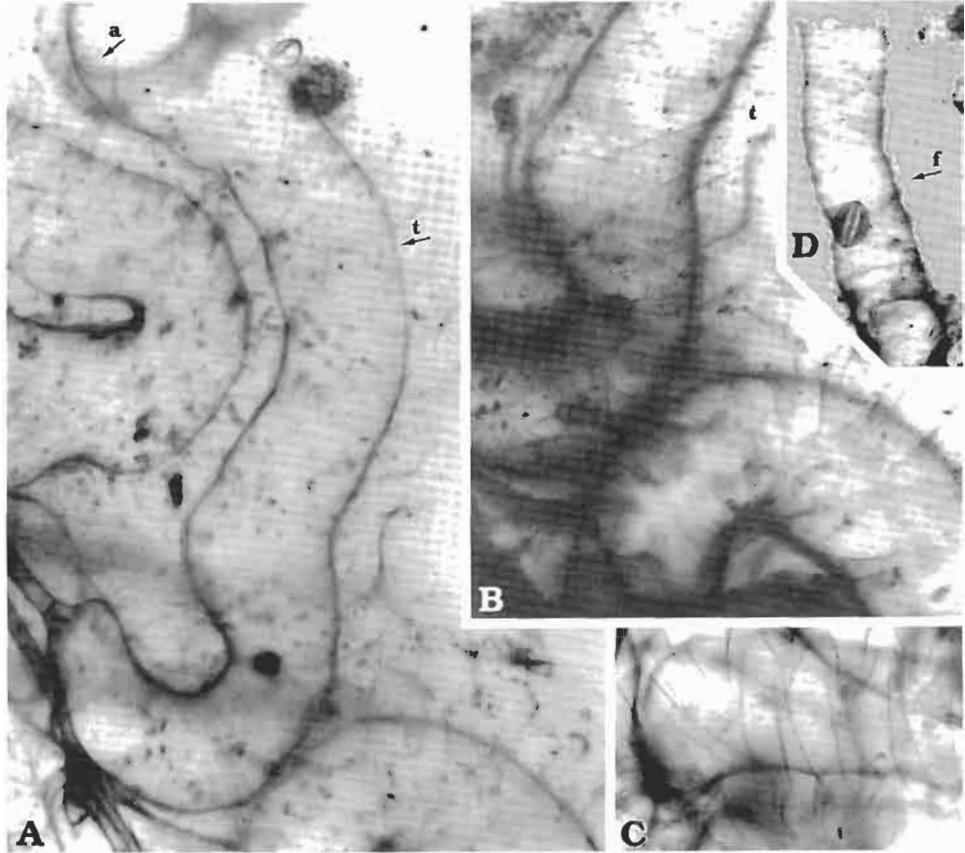


Fig. 2. *Rhabdopleura compacta*, structural details of fusellar zooidal tubes. **A.** A group of adnate zooidal tubes (**t**) with erected apertural part (**a**), $\times 150$. **B.** **C.** Fusellar structure of ventral wall with a zig-zag suture, $\times 150$. **D.** Erect portion of a tube with fuselli (**f**) visible, $\times 42$.

vances. In the early growth stage the stolon is naked ('gymnocaulus' in standard terminology), then it becomes sclerotized as the result of the secretion of black organic skeletal material around the thread (black stolon, 'pectocaulus' in standard terminology, Fig. 1B, C). However, before sclerotization, the stolon produces buds of regular feeding zooids. They form a chain of buds at different growth stages situated behind the terminal zooid. Next, each bud separates from its neighbour by secreting a transverse partition across the stolon bearing tube. Each chamber formed in this way becomes a basal part of an individual zooidal tube. Juvenile zooids sealed within such chambers form, by resorption, a circular pore in the upper wall of the tube. Emerging through it, they secrete an erect, free portion of the zooidal tube proper. Therefore the pattern of bud-

Fig. 1. *Rhabdopleura compacta*, main structural features of a tubarium. **A.** Overall view of a portion of colony composed of erect and adnate tubes, $\times 15$. **B.** **C.** Details of underlying stolon system seen in two overlapping views (particular segments of stolon are marked **s4–s8**, **s5A**, $\times 75$, see also explanatory drawing on Fig. 4. **D.** Bifurcation of stolon **s4** into **s5** and **s5a** and their diaphragms (**d**), $\times 150$.

ding of new zooids may be defined as monopodial. The entire skeleton of *Rhabdopleura* colony is hence composed of interconnected and sometimes irregularly tangled tubes and thus deserves the name of tubarium [the term introduced by Lankester (1884) and used by then by Schepotieff (1907b) and by Kozłowski (1949)]. Some of these tubes bear a stolon (ending with the permanently terminal zooid), and some are occupied by regular, feeding zooids attached by a contractile stalk (the peduncle) to the stolon. The main building material of the skeleton in *Rhabdopleura* is proteinaceous (Armstrong *et al.* 1984), although some observations suggest a biochemical difference between stolonial material and that of the tube wall proper.

The best-known extant species are *Rhabdopleura normani* Allman, 1869 and *Rhabdopleura compacta* Hincks, 1880, which differ in minor morphological details. Fossil rhabdopleurids assigned to the genus are known as early as the Middle Cambrian. Some display a striking overall similarity to Recent representatives of the genus *Rhabdopleura* Allman, 1869, being even considered congeneric (Durman & Sennikov 1993). However, taking into account some structural details of the stolon system (see p. 7) we agree with Mierzejewski (1986) that the earliest representatives of true *Rhabdopleura* are known only from the Middle Jurassic (Bathonian).

Numerous recent studies on *Rhabdopleura compacta* reveal a number of important structural details, however, leaving the problem of the formation of successive zooidal tubes (the astogeny) still unresolved. Explaining this will be the main object of our paper.

Material and methods

Two fragments of *Rhabdopleura compacta* colonies were dredged off Stoke Point, Devon, England by Dr. A.R.D. Stebbing. The colonies were attached to the concave surfaces of dead shells of the bivalve *Glycimeris glycimeris*. The specimens were fixed in formol seawater for one week. Then they were processed for light microscopy by staining with Hemalum and Eosine and mounting in Canada balsam under a cover glass on three slides numbered X24297, X24298, X24299 respectively and housed at the Department of Anatomy, St George's Hospital Medical School, Cranmer Terrace, London. Photographs were taken with a Carl Zeiss 'Ultraphot' using the $\times 2.5$; $\times 4$; $\times 10$ objectives and different filters. Magnifications of figures are approximate.

Additional material used for comparative studies included thin sections through the rhabdosomes of the Ordovician dendroid graptolites *Acanthograptus* sp. and *Dendrograptus* sp. etched from their respective matrices by chemical treatment, embedded by standard procedures, sectioned with microtome or ultramicrotome and studied with an light microscopy.

Definition of the problem

Rhabdopleurid pterobranchs (Rhabdopleurida, Pterobranchia, Hemichordata) are considered to be direct ancestors of graptolites. This thesis is now well established and substantiated by a variety of evidence (summarized by Urbanek 1986). However, the initial inference was based on the unique fine structure of the skeleton, common to

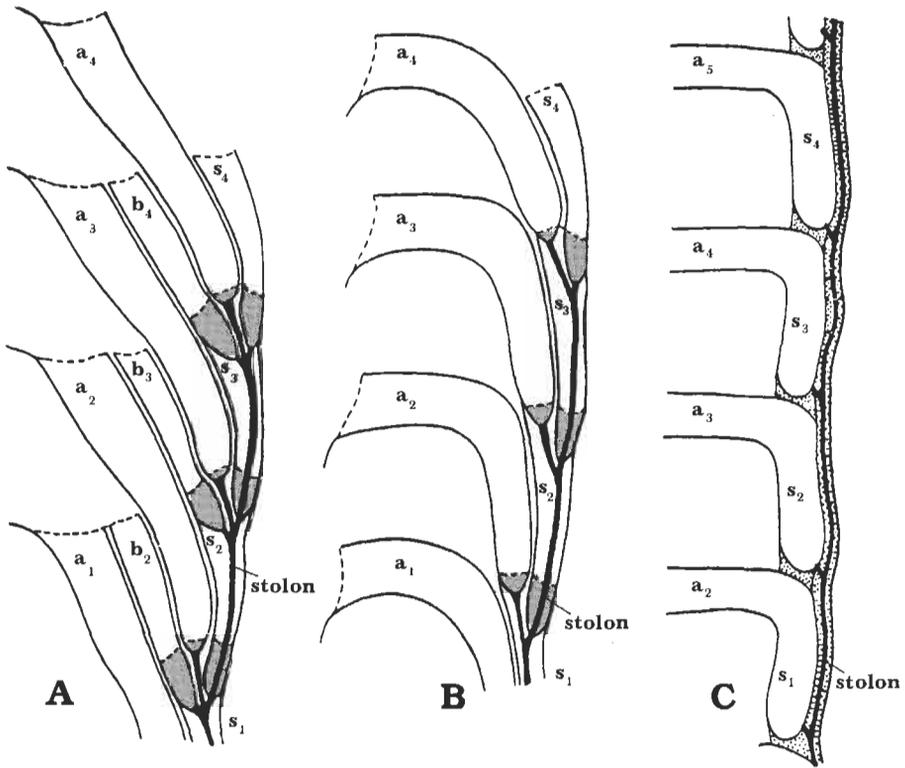


Fig. 3. Diagram showing the relation of the stolon to the thecae in dendroid graptolites (A – with, and B – without bithecae) and in *Rhabdopleura normani* (C). Internal portions of the thecae (shaded) are present in dendroids and lacking in *Rh. normani*. Abbreviations: a, autotheca; b, bitheca; s, stolotheca. After Kozłowski 1949, modified.

both the groups as well as on the specific features of the stolon system. The fact that no living group of animals, except for pterobranchs, possesses a sclerotized stolon ('schwarze Stolo', black stolon) was emphasized particularly by Schepotieff (1905). Kozłowski, in his classical studies (1938, 1947, 1949), revealed its striking similarity to the stolon system recognized by him in sessile orders of extinct graptolites (Graptolithina). Convincing evidence was presented that this essential similarity points to homology (Fig. 3). However, Kozłowski's studies supported by Bulman's data (1942, 1945, 1949), revealed also a remarkable difference in the morphogenetic behaviour of the stolons in the groups in question, namely the presence of the so-called 'internal portions' in the thecae of the sessile Graptolithina (Dendroidea, Tuboidea, Crustoidea). In these groups, the proximal, immature parts of their thecae are formed inside the parental tube (stolotheca after Kozłowski 1938) by an abrupt widening of the stolon, producing in this way an attenuated internal portion of the given theca, enclosed initially within the parental tube and only later merging with the external walls of the theca proper (Fig. 3A, B). In contrast, the data available at that time and based almost solely on the study of *Rhabdopleura normani* Allman, 1869, indicated that in rhabdopleurid pterobranchs new zooidal tubes were formed without any initial portion enclosed within the parental tube, zooids budding directly from the short peduncular

branches of the stolon. Therefore it was believed that the stolons in rhabdopleurid pterobranchs were devoid of any widened and attenuated portion comparable with the internal portion of the thecae in sessile graptolites (Fig. 3C). One could conclude that in spite of the remarkable overall similarity there existed an important difference in the morphogenetic role of the stolon between graptolites and pterobranchs. This conclusion follows from Kozłowski's reasoning (1949: p. 76, fig. 15) and his diagrams reproduced herein (Fig. 3). However, this considerable difference was rarely mentioned and, in fact, never evaluated. It was evidently believed that the internal portions produced by a sudden widening of the stolon were a late acquisition of the thecae in the Graptolithina (an autapomorphic character), which finds no equivalent among pterobranch structures.

The last conclusion is, however, untenable as a result of our present study on Recent *Rhabdopleura compacta* Hincks, 1880. The material presented herein clearly demonstrates that in this rhabdopleurid pterobranch the production of stolonial diaphragms is routinely associated with an abrupt widening of the stolonial sheath. Hence both diaphragm and the widening occur at the same level. The resulting structure termed by us the 'diaphragm complex' displays a striking resemblance to the internal portions of thecae in the sessile Graptolithina (compare Figs. 3A, B and 11B, shaded). In other words, the expanded stolonial sheath in *Rhabdopleura compacta* is homologous with the thin-walled enclosed initial portions of the thecae as seen in the Dendroidea, Tuboidea, and Crustoidea. Such structures have never been observed before either in Recent or fossil Rhabdopleurida. Our observations indicate that at least some rhabdopleurid pterobranchs display a budding pattern fully comparable with that recognized by Kozłowski in sessile orders of graptolites. Our observations contribute to a better understanding of the phylogenetic relationships between pterobranchs and graptolites as they shed a new light on the evolutionary changes associated with the origin of the early Graptolithina (see discussion below).

Stolons and diaphragms

Strongly sclerotized and pigmented (tanned) stolons in *Rhabdopleura compacta* may be seen easily through the tube walls and traced along considerable length (Fig. 1B, C). They display a fairly stable width (20 μm), with only few constrictions or swellings. This makes *Rhabdopleura compacta* different from some fossil rhabdopleuroids which like Ordovician *Rhabdopleurites* (see Kozłowski 1967) reveal strongly variable width of stolons. In contrast to Recent *Rhabdopleura normani*, *Rhabdopleura compacta* has its stolons not embedded in the lower wall of the zooidal tube but lying free within the zooidal tubes, well above that wall. Consequently, they are rounded in section and exhibit a smooth surface, without vesicular swellings around the diaphragms, so characteristic of some rhabdopleurids (e.g., *Rhabdopleura kozłowskii* of Bathonian, Kulicki 1969) and of some Graptolithina (see below).

A detailed analysis of the stolon and its derivatives (such as dormant buds, and diaphragms, or diaphragm complexes) in a portion of the tubarium is shown in Fig. 4A, B. Both figures overlap in the area of stolon trifurcation (arrowed and marked by an asterisk) One of the stolon branches thus produced (Fig. 4A, 5As) makes a detour (a 'U'

turn) and grows alongside the previous tube, displaying a distinct thigmophilic behaviour of the zooid. The other branch (Fig. 4B, s4) forms successive segments of a longer stolonal tube (s4–s8a) with a number of bifurcations (dichotomous branchings) of the stolon. One of the branches extends the stolon, while the other leads to the corresponding zooidal tube (t). Stolonal tubes are partitioned by the transverse septa (ts) into chambers, housing usually two but rarely only a single branch of the stolon (Fig. 4B, s5, s5a). While dichotomic splitting of the stolon is a regular process, its trifurcation seems rare and involves a special shape of the corresponding stolonal tube called herein the trifurcation tube (Fig. 4A, B, tt). Zooidal tubes are frequently coiled and superimposed over the lower ones (e.g., the tube related to s8 on Fig. 4B). Some zooidal tubes seem empty probably as a result of the necrosis of corresponding zooids (e.g., tubes related to s3 and s4) but have their connection with the stolon preserved being potentially capable of regeneration from the stolon (rejuvenation), a process suggested by some observations (Stebbing 1970).

The presence of a diaphragm either in the middle or at the end of the stolon (stolonal diaphragm, Figs. 1D, 4B, d) is a remarkable feature of *Rhabdopleura compacta*. The diaphragm is formed due to an incomplete septation of the stolonal lumen by skeletal material, the resulting septum being provided with a central pore. The latter produces constriction of the cellular content of the stolon but enables continuity of the soft tissues across the diaphragm (Figs. 6D, 7D). The role of diaphragms in pterobranchs is unknown, however, an analogy with ligatures of the stolon as applied in regeneration experiments on many hydrozoans comes immediately to mind. Such ligatures ensure a relative physiological isolation of a given portion of the stolon from the rest of the colony, and increases the individuality of its tissues. This might result in a local differentiation of the tissues towards a new zooid or otherwise. Multiple diaphragms (diaphragms produced immediately one after another) and characteristic of some species of the genus are rare in *Rhabdopleura compacta* (Fig. 7E).

In general, although characteristic of Recent rhabdopleurans, diaphragms seem to appear rather late in their phylogeny. The majority of early Palaeozoic rhabdopleurids are devoid of diaphragms or, at least, diaphragms were not recognized in their stolons. The earliest *Rhabdopleura* with well-developed diaphragms is of Bathonian age (Kulicki 1969, 1971), while in *Kystodendron*, representing the central group of Ordovician Rhabdopleuridae, both major stolons and peduncular stolons have no diaphragms (Mierzejewski 1986: p. 182). Diaphragms, however, were recognized by Kozłowski (1956: fig. 24D₂) inside the so-called terminal stolons of their composite dormant buds (see below). Peduncular stolons display instead distinct constrictions, which probably replace diaphragms functionally. However, distinct diaphragms, frequently vesicular, were recognized in many Ordovician Graptolithina such as the Dendroidea, Tuboidea and Crustoidea. Therefore diaphragms are another disparate feature displaying mosaicism in the course of phylogeny.

The lumen of the sclerotized sheath of the stolon is filled with the cellular content (Fig. 6D). According to Schepotieff (1907a) soft tissues of the stolon like those in the contractile stalk (the peduncle) of the zooid, correspond to the body wall of the zooid and are made of ectodermal and mesodermal derivatives. More recent studies of the cellular content of the black stolon in *Rhabdopleura compacta* have revealed the presence of blood vessels and possible nerve fibres (Dilly 1975: figs. 12, 13).

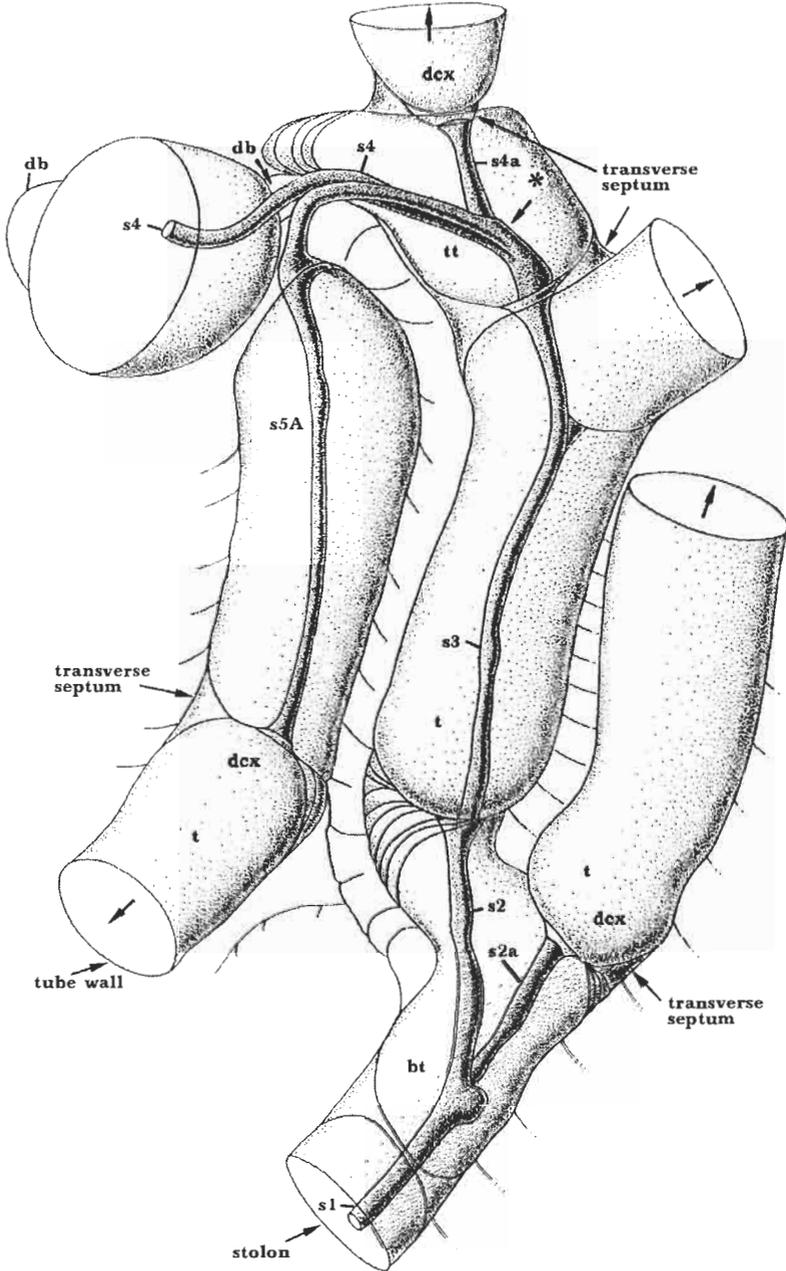
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Fig. 4. **A, B.** Explanatory drawings of overlapping portions of the tubarium in *Rhabdopleura compacta* to show details of stolons (s) and their derivatives: dormant buds (db) and diaphragm complexes (dcx), while zooidal tubes (t) are only outlined. Other abbreviations: **bt**, bifurcating tube; **tt**, trifurcating tube; **d**, diaphragm. **A.** A more proximal part showing trifurcation of the stolon (at the point marked by an asterisk and arrowed) as well as an 'U' turn of one of the branches of stolon (s5A). **B.** A more distal part showing stolon system from the point of trifurcation (marked as above) onwards (branches s4, s4a-s8, s8a). Further explanations in text.

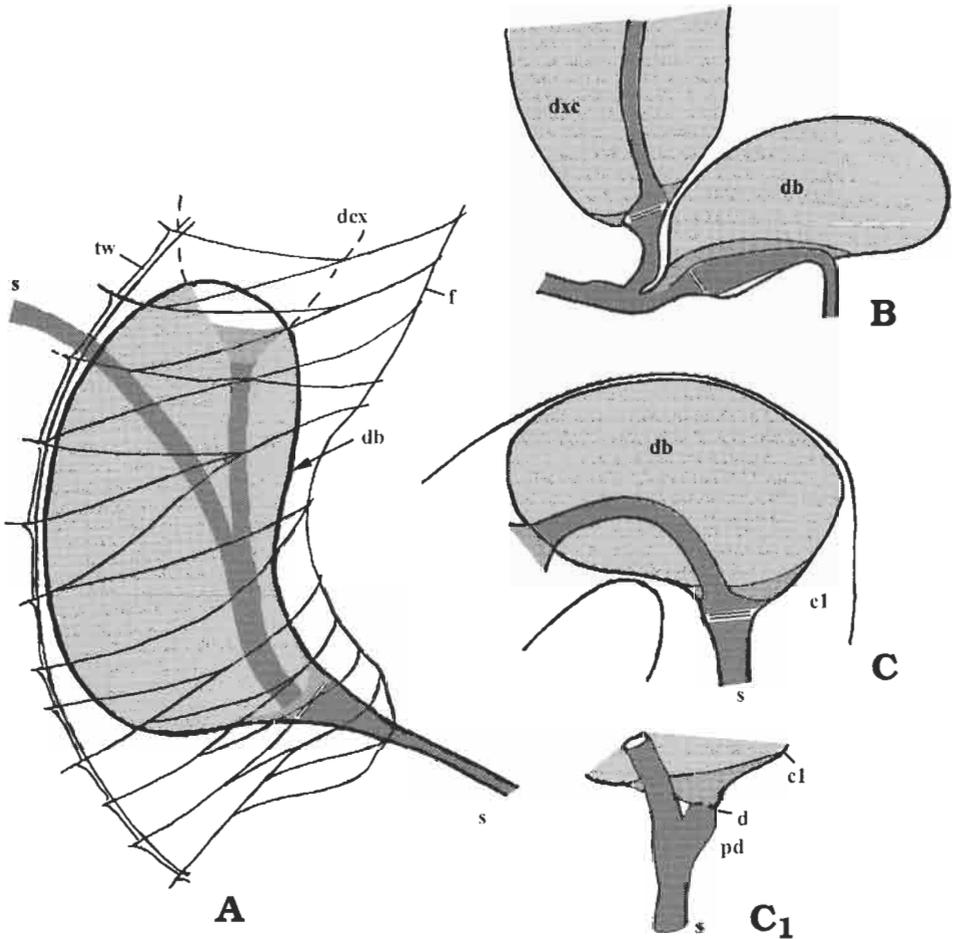


Fig. 5. Outline drawings of the dormant buds in *Rhabdopleura compacta*. **A**. A dormant bud (**db**) seen through the zooidal tube wall (**tw**) with fuselli (**f**) producing the ventral zigzag suture. **B**. Stolon (**s**) with associated dormant bud (**db**) and diaphragm complex (**dxc**). **C**, **C**₁. Stolon with an adnate dormant bud as well as the generalized relation between stolon (**s**), shortened peduncular stolon (**pd**), its diaphragm (**d**), collar (**cl**) and the dormant bud proper (**db**). Stolons are strongly shaded, collars and their equivalents – medium, and dormant buds and their equivalents – weakly shaded.

Capsules of the dormant buds and diaphragm complexes associated with the terminal portions of the growing stolon are specialized stolon derivatives and are discussed below.

Dormant buds

Rhabdopleurid colonies reveal the presence of spherical or ovoid (bean-shaped) bodies, connected with the stolon and enclosed in pigmented peridermal capsules (Fig. 5, **db**). They are considered to be an overwintering device common to pterobranchs and to some

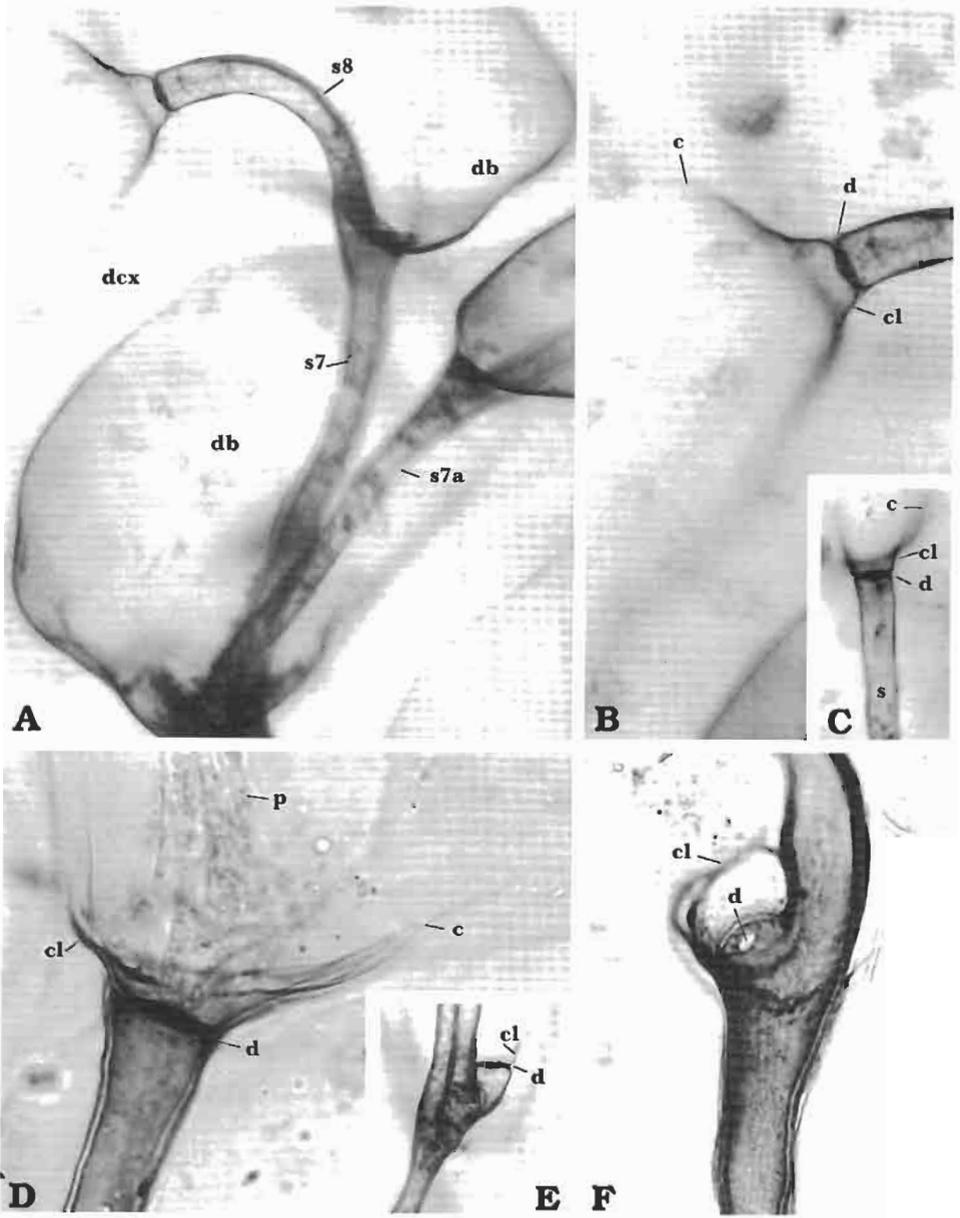


Fig. 6. *Rhabdopleura compacta*, diaphragm complexes as stolon derivatives. A. Stolon system with dormant buds (db) and a diaphragm complex (dcx). B, C. Diaphragm (d), collar (cl) and cone (c) as structural elements of the complete diaphragm complex. D. Continuation of soft tissues across the diaphragm. E, F. Incompletely preserved diaphragm complexes made of diaphragm (d) with its central pore (visible in F) and the collar (cl).

sessile graptolites. They were observed by Lankester (1884) who called them 'hybernacula', and by Schepotieff (1907b) who called them 'sterile Knospen' (sterile buds). He

was convinced that they did not develop into zooids like normal buds. However, Stebbing (1970) provided evidence that this is certainly untrue for *Rhabdopleura compacta*, where dormant buds are capable of developing into zooids. Stebbing introduced the term 'dormant buds', which more adequately describes the function of these bodies. This term is being used by subsequent students (Dilly 1975; Durman & Sennikov 1993), although some workers describe them as 'cysts' (Kozłowski 1956, 'les kystes'), while Kulicki (1971) uses term 'cysts of dormant buds' for dormant bud capsules.

Capsules of the dormant buds are among the most resistant parts of the rhabdopleurid tubarium, and they might be quite common locally in fossil sediments (Kozłowski 1956 for the Danian, and Kulicki 1969 for the Bathonian). A massive storage of tissues and yolk within the heavily sclerotized membrane has an obvious and rather universal adaptive significance, however encapsulated dormant buds appeared in rhabdopleurid phylogeny probably with a certain time lag and not in all lineages. Their presence in the Middle Cambrian '*Rhabdopleura*' *obuti* is possible, however, the dark ovoid bodies, which were observed within the tubarium and resemble dormant buds may be also interpreted either as preservational features or (probably less convincingly) as traces of fossilized zooids (Durman & Sennikov 1993).

While Ordovician *Rhabdopleurites* and *Rhabdopleuroides* lack encapsulated dormant buds, coeval *Kystodendron* reveals both conventional dormant buds as well as composite or multiple dormant buds capsules (Mierzejewski 1986). This latter type of dormant buds was first observed by Kozłowski (1956) in the Danian *Rhabdopleura*. Their morphological significance is discussed below (p. 18). Among the Graptolithina, possible dormant buds were recognized within the autothecae of the Crustoidea as blackish vesicles connected with the stolon (other vesicular bodies unrelated to the stolon may represent remnants of degenerating zooids). A different and specialized kind of dormant bodies recognized also in the Crustoidea called graptoblasts have a functional analogue in the hibernacula or dormant zoecia of certain bryozoans and might be compared morphologically with the resting terminal portions of the stolon tubes in rhabdopleurid pterobranchs (Urbanek 1983).

The fragments of *Rhabdopleura compacta* under study colonies reveal numerous dormant bud capsules, seen as semi-transparent, light-brown bodies (Fig. 1B, C, db). Many of them look emptied and are somewhat flattened, while in some a remnant of cellular content may be seen. The relation between the dormant bud capsule and the underlying stolon is well observed in certain cases (Figs. 5C, 6A). The dormant bud capsules are connected with the main branch of the stolon by a shortened peduncular branch, forming what looks like a heel, which is probably provided with a single diaphragm (Fig. 5C, C₁, d). The presence of the latter was established with certainty only in a few cases, probably because as a rule the diaphragm is obliterated. In rhabdopleurans, the peduncular stolon is attached either to the proximal or the lower surface of the dormant bud capsule. The situation recognized in *Rhabdopleura compacta* is intermediate and is fairly similar to that observed in the Danian *Rhabdopleura vistulae* (Mierzejewski 1986: pl. 25: 5, 6). The most proximal portion of the capsule is dark pigmented, resembling thus by its position the dark pigmented collar (cl) in the standard diaphragm complex as described above. The remaining portion of the capsule may be compared with the cone (c) as defined above. As observed by Stebbing (1970: p. 210), 'secretion of the capsule proceeds from the

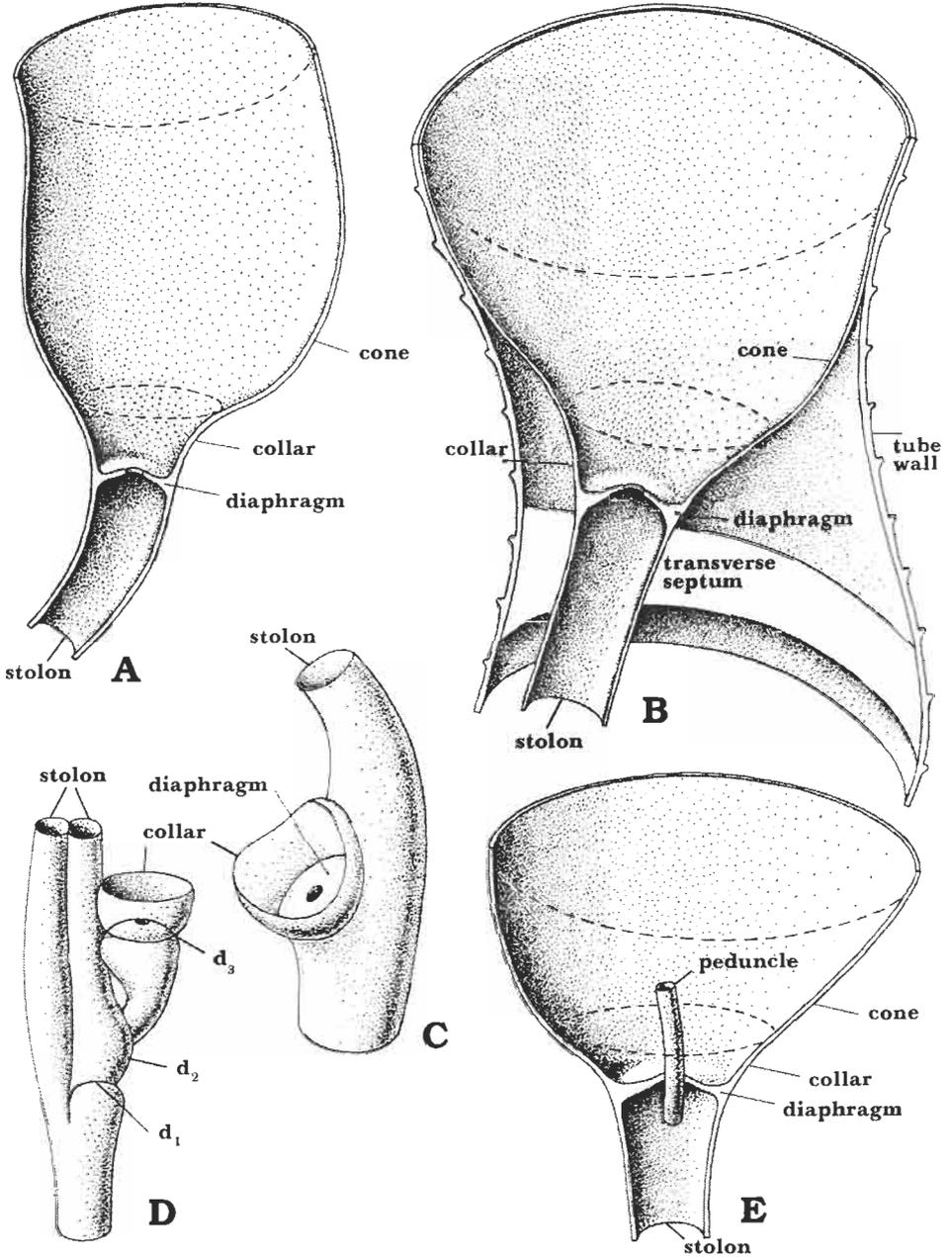


Fig. 7. Diagram showing structural elements of the diaphragm complex in *Rhabdopleura compacta*. A. Optical cross-section through the diaphragm complex showing its relation to the stolon, transverse septum and the zooidal tube wall. B. Another example of the complex; made of diaphragm, collar and the cone. C. Incomplete diaphragm complex with preserved collar and exposed diaphragm provided with a central pore. D. Rare case of multiple diaphragms (d_1 - d_3) related to the branching of the stolon. E. Direct observation provides evidence for the continuation of soft tissues between stolon and the contractile peduncle of the zooid across the diaphragm and through its pore.

point where the bud is attached to the stolon towards its distal end, so that the capsule remain open-ended for some time'. Such an open-ended capsule displays an essential similarity to the standard diaphragm complex, especially when the capsule of the dormant bud is tightly adpressed to the internal surface of the zooidal tube. Similar close contact has been observed in some Recent and fossil Rhabdopleurida, e.g., in Recent *Rhabdopleura normani* and in Jurassic *R. kozlowskii*. This is evidenced by the presence of 'costulation', that is imprints of fusellar growth bands (visible on the inner surface of the zooidal tube proper) on the black crust of the dormant bud, frequently showing also a zig-zag suture (Kulicki 1971: fig. 6). In this case the black crust of the capsule behaves like the lining of the standard diaphragm complex. In *Rhabdopleura compacta* the dormant bud capsule is usually added to the inner wall of the zooidal tube, while gaps between the capsule and the tube wall are rather rare (Dilly 1975: p. 393, fig. 11). But even in the case when the dormant bud capsule is separated by a space from the adjacent walls of the zooidal tube, a striking similarity to the diaphragm complex remains and in fact the dormant bud may be considered a closed diaphragm complex. As diaphragm complexes are skeletal structures clearly related to the early growth stages of the budding new zooids to be only later replaced by the zooidal tube proper dormant buds may be considered arrested buds whose skeletal coat was made permanent. Hence, the origin of a dormant bud may be understood as a suppression of the zooidal tube morphogenesis at an early growth stage. This interpretation resembles to some degree Lankester's (1884) opinion that dormant buds (his 'hybernacula') originate from normal buds by the arrest of their growth. Moreover, from the morphogenetic point of view, both structures appear through a rapid widening (inflation) of the stolonal sheath (see discussion below).

The diaphragm complex

The material studied clearly demonstrates that *Rhabdopleura compacta* routinely produces along with simple diaphragms (see above) those associated with an abrupt widening of the stolonal sheath, called here diaphragm complexes (Figs. 6, 7, dcx). As the widening of the stolonal sheath and the diaphragm occur at the same level, each such complex is composed of (1) the diaphragm proper (d), being the septation inside the sclerotized stolonal sheath, with usually a somewhat convex upper (distal) surface provided with a central pore, and (2) a collar (cl), a semiconical, thick-walled, well pigmented (tanned) band of skeletal material, which derives directly from the stolonal sheath at the diaphragm level and surrounds it. Each collar extends into a thin-walled, pale and rather inconspicuous (3) cone (c) being the basal portion of a new zooidal tube enclosed within the parental one. The wall of the cone adheres tightly to the inner surface of the parental zooidal tube producing in this way a sort of lining. The entire diaphragm complex is made of the same material as the stolonal sheath, which is denser than the fusellar material of the zooidal tube proper – therefore the lining produced by the cone may be traced on optical sections of the parental tube wall over considerable distances (Fig. 8A, F).

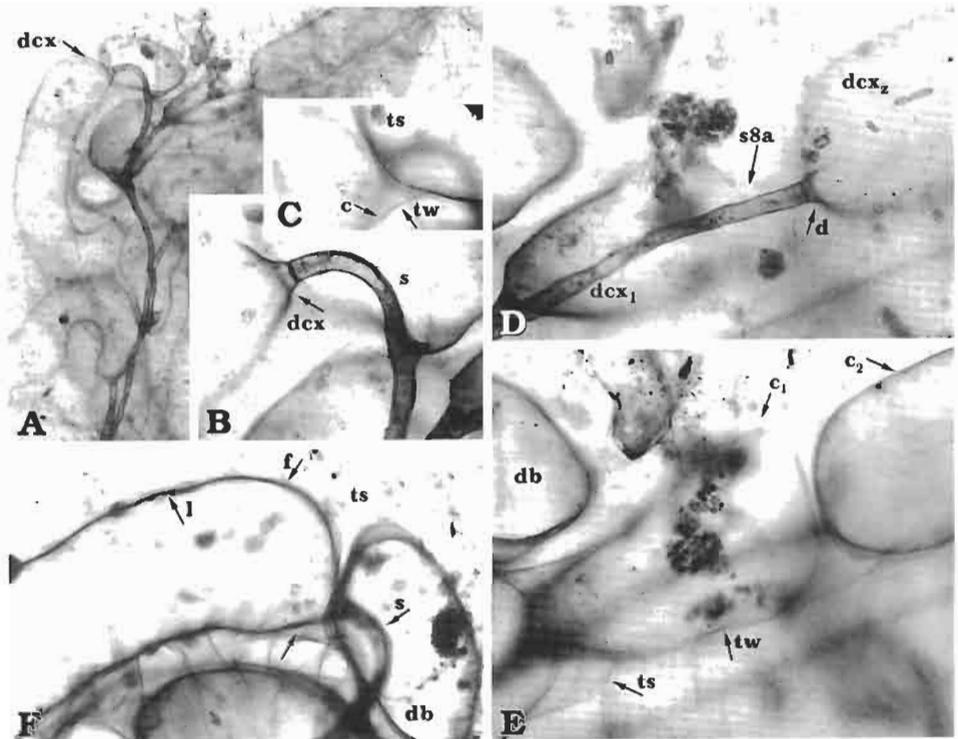


Fig. 8. *Rhabdopleura compacta*, relation of the diaphragm complex to the zooidal tube wall **A**. Transparent zooidal tubes and internal stolon system with diaphragm complex (**dcx**), $\times 40$. **B**, **C**. Details of **A** showing: origin of a diaphragm complex (**dcx**) by means of inflation of stolon (**B**, arrowed) and free space (**C**, arrowed) between the cone and the fusellar wall of the zooidal tube, $\times 400$. **D**, **E**. A stolon segment (**s8a**) with two successive diaphragm complexes (**dcx**₁, **dcx**₂) seen in optical section (**D**) and from outside (**E**) to reveal two successive cones (**c**₁, **c**₂) inside a common thecal wall (**tw**), $\times 125$. **F**. Optical section through a zooidal wall showing an outer, translucent fusellar layer (**f**) and an opaque lining (**l**) produced by the cone of the adjacent diaphragm complex. Free space between the cone and the tube wall arrowed, $\times 100$. Other abbreviations: **c**, cone; **db**, dormant bud; **s**, stolon; **ts**, transverse septum; **tw**, tube wall.

Diaphragm complexes may be seen in different views, the most instructive being the lateral one, providing an optical cross section through the entire structure (Figs. 6A, B, 7A, B). A diagrammatical view of the entire structure is shown in Fig. 7A, B. They reveal different aspects of diaphragm complexes summarized above. The diaphragm proper and its central pore is best seen on specimens with a damaged cone, exposing the collar with the diaphragm inside (Figs. 6E, 7C, d). The soft tissues of the stolon (so-called gymnocaulus) are constricted by the diaphragm as seen in Figs. 6D, 7D, and continue either as the peduncle (**p**) of the zooid proper or as the next segment of the stolon (Fig. 8D, E). Diaphragm complexes are distinct features which most probably were observed by earlier students but were misunderstood, for instance what was observed by Briggs *et al.* (1995: p. 17, fig 2C) and interpreted as 'the stolon with a series of swellings along its length which represents immature zooids' is most probably a series of diaphragm complexes.

Relation of the diaphragm complexes to the zooidal tube wall

Direct observations reveal that most of the diaphragm complexes are associated with the transverse partitions inside the zooidal tube (Figs. 7A, 8A, F, ts). The stolon passes through such partitions excentrically, shifted to the lower wall of the zooidal tube and produces the diaphragm and the collar immediately over the distal surface of the partition. The attenuated material of the cone merges after a short distance with the wall of the zooidal tube and adheres to its inner surface producing a kind of lining (l) seen beneath the semi-transparent fusellar layer (f) of the zooidal tube proper. This opaque lining may be traced on optical sections observed in transmitted light (Fig. 8, f, l) over a distance of 6–7 fuselli, but other evidence may suggest even longer distances of several fuselli. The same relations were revealed on diaphragm complexes seen in lateral view inside the zooidal tubes (Fig. 8D, E, dxc). Occasionally some free space may be seen between the cone (c) of the diaphragm complex and the tube wall proper (tw), indicating an independent origin of these two structural elements of the tubarium and their secondary merging (Fig. 8C).

In some cases, the lining produced by a given diaphragm complex may almost immediately be followed by another lining related to the next diaphragm complex (Fig. 8D, E, dxc₁–dxc₂), which strongly resembles the sequence of events observed within the dendroid stolothecae (compare Fig. 3A, B, s₁–s₄). Such frequent production of diaphragm complexes might, at least theoretically, result in the accumulation of linings produced by a number of diaphragm complexes situated along a given stolon tube. Whether these observations shed some light on the origin of the heavily laminated secondary deposit described by Kulicki (1971) inside the zooidal tubes of Jurassic *Rhabdopleura kozłowskii* is, however, uncertain.

Relation of the diaphragm complex to the zooid

Tubes occupied by normal feeding zooids are frequently coiled, the most distal portion being usually erect (Figs. 1A, 2D). The portion of the zooidal tube situated beyond the last transverse partition (and at the same time the last diaphragm complex associated with it) is much longer than the body of a contracted zooid. The zooid is attached by a contractile stalk, the peduncle, to the stolon, through the pore within the last diaphragm. Although constricted by the diaphragm, the continuity of soft tissues between the stolon (s) and the contractile stalk (p) is obvious (Fig. 9A, B). When the zooid is strongly contracted (probably because of the unfavourable conditions) its metasome fills the space of the last diaphragm complex and its peduncle is coiled beneath the trunk segment (Fig. 9B, p). It is easy to see that the diaphragm complex produces a sort of encasement for the contracted adult zooid. During the earlier growth stages, the diaphragm complex also serves as a protective shell for the bud.

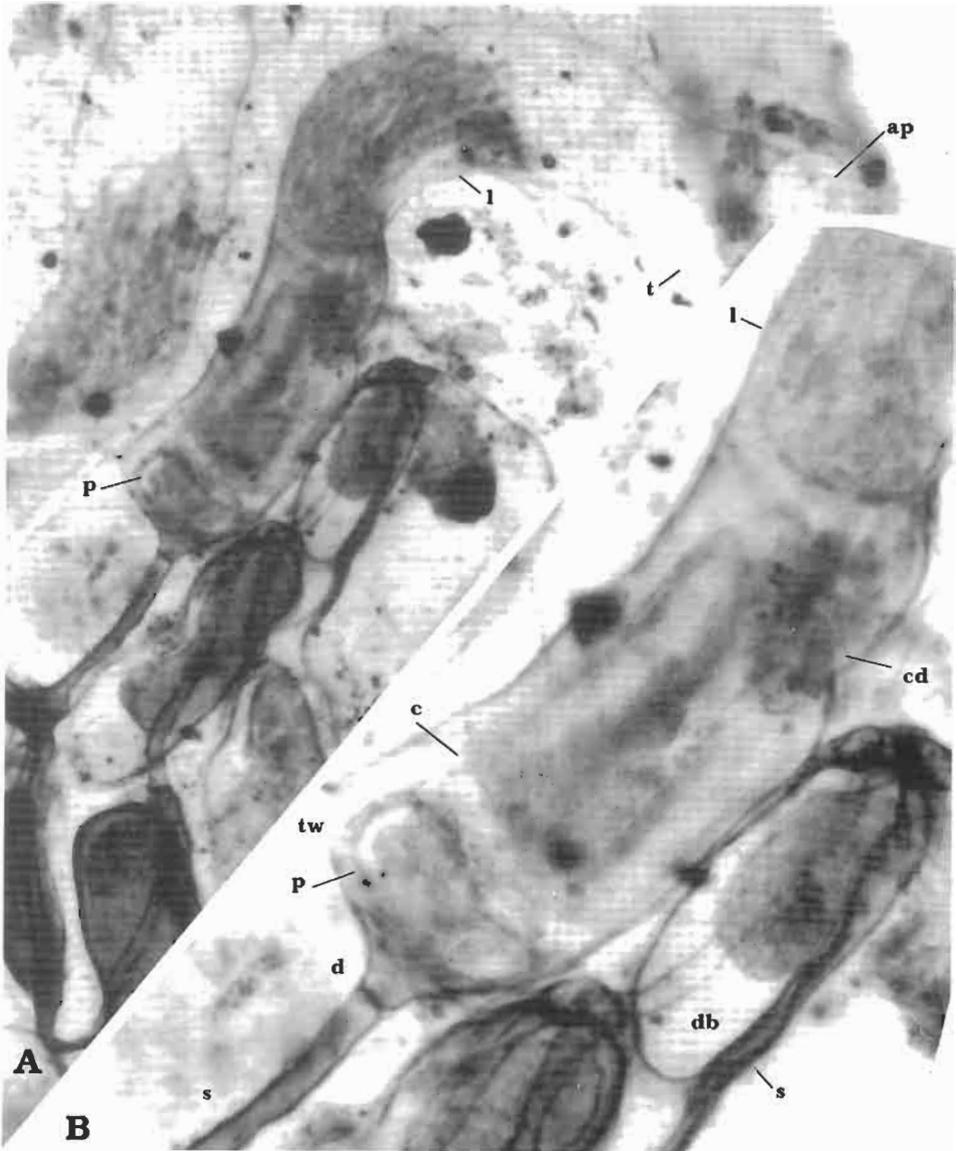


Fig. 9. *Rhabdopleura compacta*, the terminal diaphragm complex situated at the base of an erect portion of the zooidal tube (t) with contracted zooid. A. Zooidal tube with contracted zooid and its diaphragm complex, $\times 75$. B. Details of A showing contracted zooid inside the terminal diaphragm complex, $\times 200$. Abbreviations: ap, aperture of the zooidal tube; c, conus of the diaphragm complex; cd, cephalic shield; d, diaphragm; db, dormant bud; l, lophophore; p, coiled peduncle; s, stolon; t, zooidal tube; tw, tube wall.

Comparison with other rhabdopleurids

As the diaphragm complex reveals an essential similarity to dormant bud capsules (see Fig. 10A, B), one could conclude that rhabdopleurid colonies are equipped with a uni-

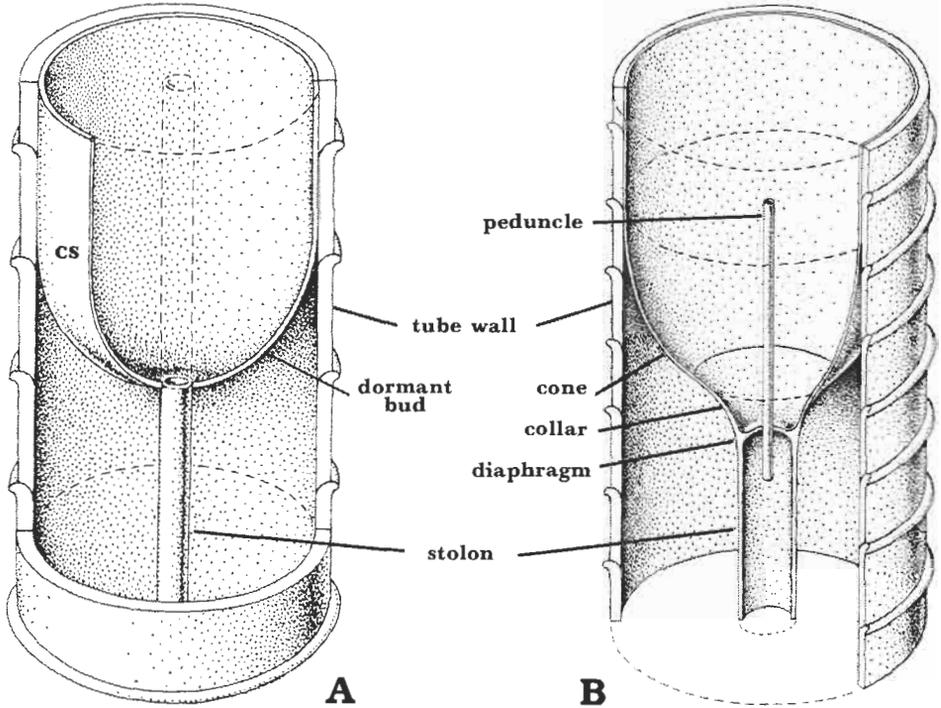


Fig. 10. A, B. Comparison of main structural elements of the dormant bud capsule (A, cs) and the diaphragm complex (B), seen on the cross-sections through their proximal parts. Note that both structures reveal the same relation to the stolon proper and to the zooidal tube wall as both originated through rapid inflation of the peridermal sheath of the stolon and form peridermal membranes which are adnate to the inner surface of the zooidal tube wall.

versal structural adaptation enabling an easy shift from an active life to a semidormant or dormant life stage protected by membranous derivatives of the stolon and *vice versa*. The growing zooid passes the stage of a semi-encapsulated bud and in case of need may retreat to its protective encasement represented by the last diaphragm complex. The dormant bud may be transformed, under certain circumstances, into the normal bud, displaying active feeding. Therefore, one may conclude that soft tissues of the stolon and its peridermal sheath as well as of buds (both dormant and zooidal) form a single anatomical and adaptive complex, called herein the **stoloblast** (from Latin *stolon*, *stolo*, branch or sucker and Greek *blastos*, bud). This system is largely independent of the surrounding fusellar tubes and differentiates, due to, simple elementary processes, which include branching (mostly dichotomous), incomplete septation (formation of diaphragms), and inflation of the stolonal sheath. This last process led to the formation of dormant bud capsules, diaphragm complexes in pterobranchs and internal parts of the thecae in graptolites. The ability of the narrow tubular sheath to abrupt widening is best visualized in multiple or composite dormant buds seen in Danian *Rhabdopleura vistulae* as well as in some species of Ordovician *Kystodendron* (Kozłowski 1956; Mierzejewski 1986). Dormant bud capsules are arranged in tandem series (like beads) on a single branch of the stolon, each bud being provided with a proxi-

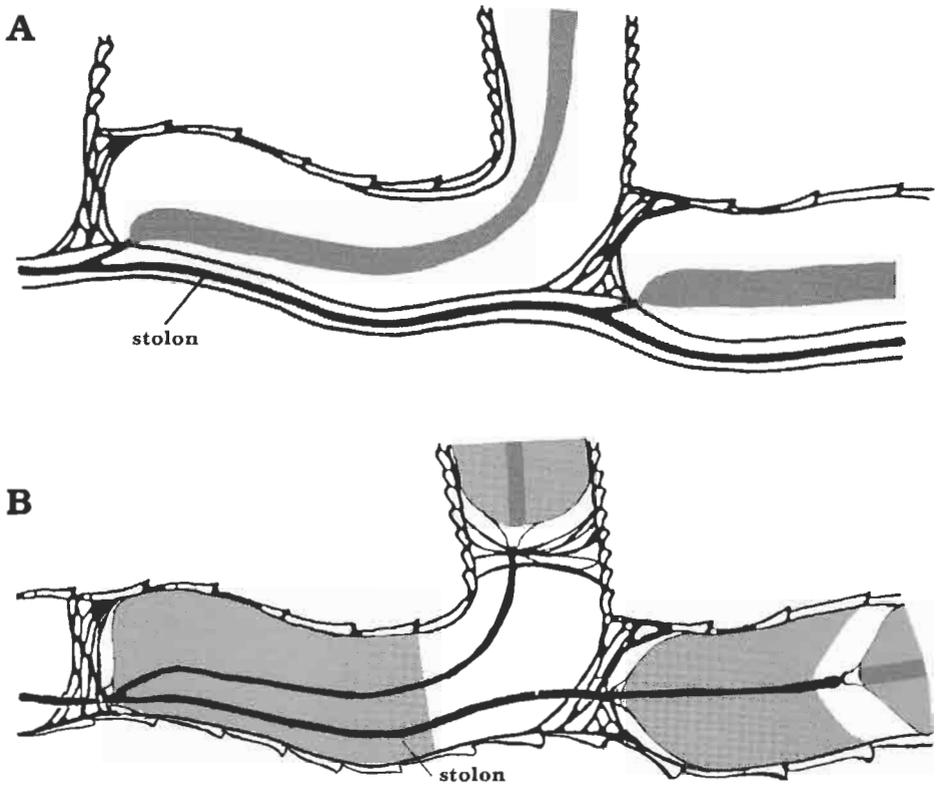


Fig. 11. Comparison of structural features of tubarium. **A.** *Rhabdopleura normani*. **B.** *Rhabdopleura compacta*. Homologues of internal portions of thecae are shaded. More explanations in text (**A**, after Schepotieff 1970 from Bulman 1970, modified; **B** original).

mal peduncular stolon as well as by a terminal one (which passes eventually into the peduncular stolon of the nearest distally placed dormant bud). The presence of intermediate structures being vesicular swellings of the stolon rather than true 'cysts' illustrates a different degree of inflation as defined above (compare Kozłowski 1956: pl. 3: 12–14 and Mierzejewski 1986: pl. 25: 1, 2). In the light of these observations, the tissue content of the dormant bud is a homologue of the soft stolon and at the same time a homologue of the contractile stalk of the zooid (Fig. 10A, marked by discontinuous lines). But the diaphragm complexes of *Rhabdopleura compacta* and the internal portions of the thecae in the sessile Graptolithina also are caused by the inflation of the stoloblast. Inflation provided a solution of a common adaptive task, namely the creation of a protective layer around the sensitive tissues and ensured a multiple utilization of peridermal material in the stolonal sheath. Moreover, it seems that the inflation of the stoloblast was most probably invented by Rhabdopleurida and inherited as a morphogenetic mechanism by the Graptolithina.

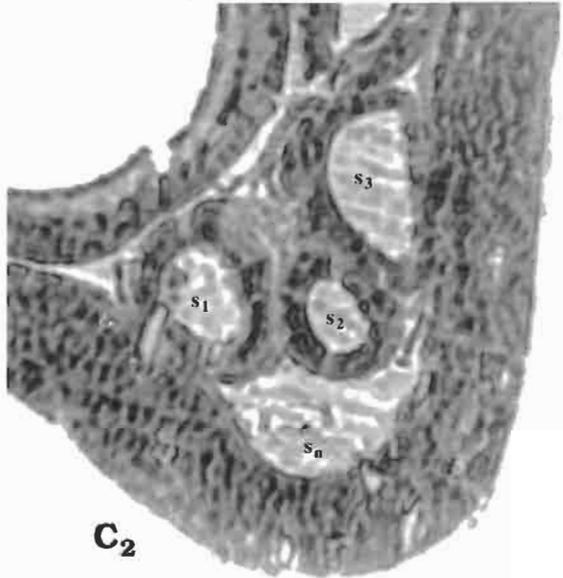
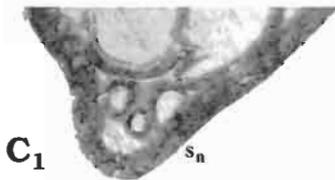
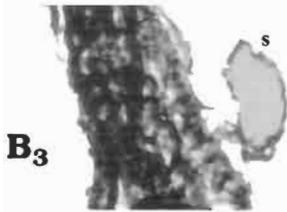
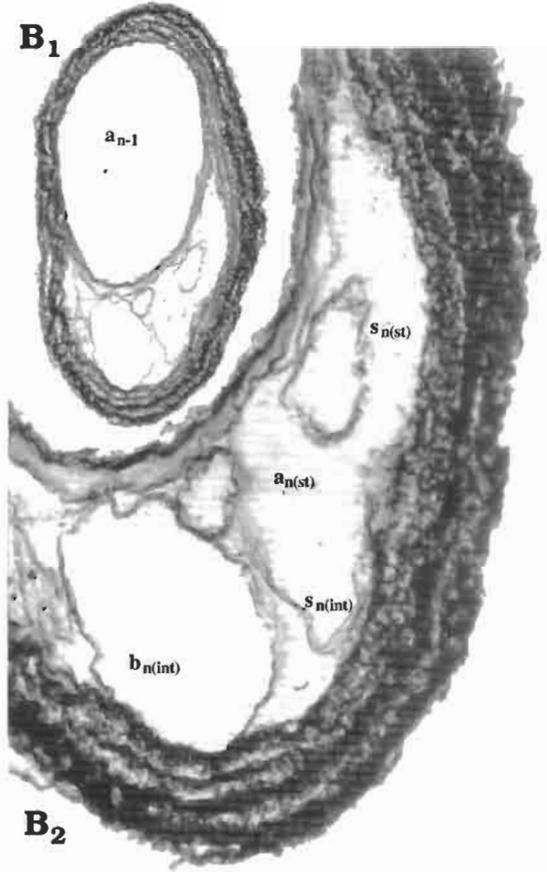
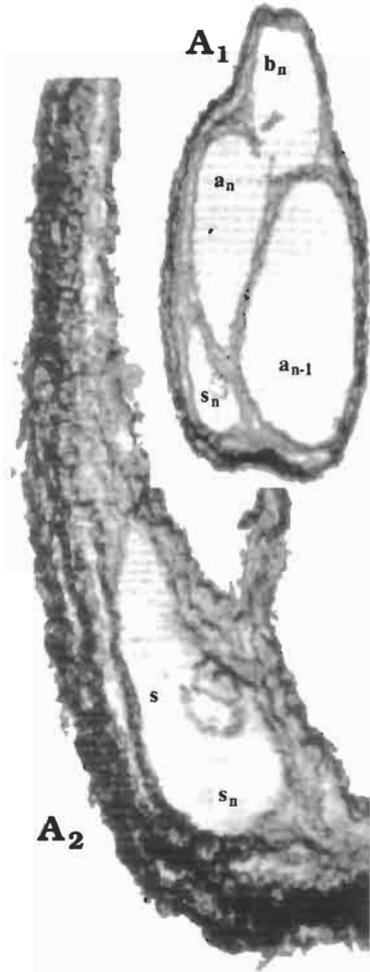
At the moment, homologues of the internal portions of the thecae have been recognized among rhabdopleurids only in *Rhabdopleura compacta*. Therefore, the anatomical situation in this latter species differs distinctly from that recognized in *Rhabdo-*

pleura normani (compare Fig. 11A, B). While in the *Rh. normani* stolon is embedded in the lower wall of the zooidal tube and produces only short peduncular stolons to which contractile stalk (peduncle) is immediately attached (Fig. 11A), the lateral branches in *Rh. compacta* are much longer, ending with a diaphragm complex situated at the base of the erect portion of the tube (Fig. 11B). The cone of the diaphragm complex forms a sort of lining within the zooidal tube (shaded area on diagram, Fig. 11B). It is obvious that *Rhabdopleura compacta* approached more closely the anatomical situation recognized in the sessile orders of the Graptolithina (Figs. 11B). Most probably, the fossil rhabdopleurid ancestors of graptolites displayed an anatomical structure similar to that recognized in the Recent *Rhabdopleura compacta*. Moreover, it is possible that the structural details of the stolon system described herein are not unique and are also present in some other species of the group, but have not been detected yet. After all, the peculiar structure of stolon system in *Rhabdopleura compacta* escaped the attention of zoologists for quite a long time.

Comparison with Graptolithina

The stolon system of rhabdopleurid pterobranchs, unique among extant invertebrates, may be best compared with that in the sessile orders of fossil Graptolithina, the dendroids (Dendroidea) being the best known group. A comparison with dendroid graptolites is possible only after having taken into account certain specific features of their organization, which obscure the otherwise striking similarity. Here belongs i.a. the differentiation of zooidal tubes called in graptolites the thecae, into three categories, namely into auto-, bi-, and stolothecae. This thecal trimorphism may be best explained (Kozłowski 1947, 1949) as a manifestation of a strong sexual dimorphism (which in pterobranchs is quite insignificant). This explains the differentiation into larger autothecae housing female zooids and smaller bithecae occupied by males. On the other hand, the difference between the autothecae and the stolothecae are explained as a difference between the immature (juvenile and proximal) and mature (distal) portion of the same individual. In the Dendroidea and Crustoidea, thecae appear by regular budding in triads (in Tuboidea and Camaroidea, in diads), composed in each generation of an autotheca, a bitheca and a stolotheca. The autotheca always occupies a cen-

Fig. 12. Stolons and their derivatives in Dendroidea as seen with LM in transmitted light on selected microtome sections through the stipe. **A₁, A₂**. *Dendrograptus* sp., showing a triade of thecae (**b_n, a_n, s_n**) as well as the aperture of an autotheca (**a_{n-1}**) of the preceding triade. Note the presence of stolon (**s**) within **s_n**, × 180, × 520, respectively. **B₁, B₂**. *Dendrograptus* sp. aperture of an autotheca (**a_{n-1}**) and a stolotheca (**s_{n-1}**) containing internal part of a bitheca of the following triade (**b_{n(int)}**) as well as internal portion of a stolotheca (**s_{n(int)}**) with its own segment of stolon (**s_{n(st)}**). Note that autotheca **a_n** is represented at this level by its stolon: **a_{n(st)}**, × 165, × 520 respectively. **B₃**. *Dendrograptus* sp., stolon (**s**) within a stolotheca, × 520. **C₁, C₂**. *Acanthograptus* sp. a stolotheca (**s_n**) sectioned just above the nodal point of the stolon system to reveal a triad of stolons, with **s₂** being the autothecal stolon, while **s₁** and **s₃** correspond to lateral thecae (either to bitheca or stolotheca), × 120, × 232, respectively. Further explanations in text. **A, B**. Isolated by chemical treatment from the Upper Tremadoc cherts of Wysoczki, Holy Cross Mountains; **C** by the same technique from the erratic boulder of Middle Ordovician (Viruan) age, numbered O.327 and collected in Mochty, Valley of Vistula River, Central Poland.



tral position, while bi- and stolothecae usually alternate right- and left-handedly. Termed the Wiman rule, this regular pattern of budding in dendroid graptolites is considered to be a characteristic feature of the order, although crustoids share the same plan. This course of events is reflected by the underlying stolon system, strongly sclerotized and capable of preservation. The stolon system may be directly observed on strongly bleached fragments of dendroid stipes (transparencies). However, crustoids offer exceptional opportunities to study the anatomy of their heavily sclerotized stolon system, which becomes exposed due to the destruction of the membranous lower walls of their encrusting colonies (Kozłowski 1962: fig. 18B). Much of our knowledge on the stolon system of sessile graptolites comes from microtome sections (Fig. 12). Stolons (*s*) are always enclosed within tubular stolothecae (Fig. 12A₁, A₂, S_n), each stolothecha carrying a section of the stolon, which branches in regular intervals, producing in the middle of its length three stolons (a triad of thecal stolons, Fig. 12C₁, C₂, s₁–s₃). Each of these stolons inside the parental stolothecha, widens abruptly to produce a thin-walled proximal or internal portion of a given theca (Fig. 12B₁, B₂, b_{n(int)}, S_{n(int)}). The autothecal stolon is the longest while its internal portion is the most shallow (Fig. 12B₂, a_{n(st)}). Internal portions of a given triade eventually emerge from their parental stolothecha, each autotheca being a direct extension of the parental stolothecha and displaying concordance of their fusellar systems (Fig. 3A). The bitheca and the stolothecha of the next generation are situated laterally and display a more or less distinct discordance with the fusellar system of their parental stolothecha.

Assuming the lack of sexual dimorphism (and therefore the elimination of bithecae) as an acquisition attained by sessile graptolites, the construction of the dendroid stipe may be reduced to a state strongly comparable with that of the tubarium in the rhabdopleurid pterobranchs. Such a mental experiment was conducted by Kozłowski (1949; see also Fig. 3B herein). He suggested that the stolonal tube of *Rhabdopleura* was a homologue of the stolothecha in the sessile Graptolithina, while the data presented above indicate that the diaphragm complexes in *Rhabdopleura compacta* are homologous to the internal portions of the thecae recognized in sessile orders of the Graptolithina. As described by Kozłowski (1938, 1948) and Bulman (1944), the internal portions of thecae are produced through a sudden widening of a given branch of the stolon, precisely at the level where the stolon shows a constriction or a diaphragm, forming around the stolon a roughly conical and thin-walled projection, which is enclosed within the parental theca. Diaphragms are situated at the point of origin of the three thecal stolons (in Dendroidea) or where the thecal stolons join the bases of respective thecae (in Crustoidea and in some Tuboidea). In many cases, diaphragms are associated with globular swellings, producing the so-called vesicular diaphragms. This structural plan was best studied in Dendroidea, but is tenable for the remaining sessile orders of the Graptolithina (with the exception of Camaroidea, where internal portions of autothecae are lacking).

Hence, the diaphragm complex of *Rhabdopleura compacta* reveals an essential similarity to the internal portion of the theca as described in sessile graptolites. This similarity is exhibited by (1) the relation to the stolon (both appear through a sudden widening of the stolon (inflation) at a precise level related to the position of the diaphragm in the stolon, and both share its specific structure), as well as by (2) the relationship to the wall of the theca (= zooidal tube), both structures being enclosed in the

parental tube (= theca) and eventually merging with its inner surface. Being the derivatives of the stolon, both diaphragm complexes and initial portions of the thecae display a specific structure and probably also a specific chemical composition. Kozłowski (1949) described the sheath of a stolon and the internal portion of thecae in dendroids as composed of a thin structureless membrane. Later studies with TEM recognized a specific 'crassal fabric' within these structures (Urbanek & Towe 1974). There is no doubt that the stolon and stolonal derivatives differ both structurally and chemically from ordinary thecal walls made of regular fusellar and cortical tissue. An indirect evidence for chemical difference is implied by Bulman's (1944) studies, who by over-maceration prepared the stolons and associated internal portions of thecae out of *Koremagraptus* rhabdosomes. They reveal a striking similarity to the stolon system in *Rhabdopleura compacta* and associated diaphragm complexes. The stolonal material is more resistant to decomposition than the thecal one, both in sessile graptolites and in extant rhabdopleurid colonies. The latter show frequently peripheral portions of colonies made of decomposed zooidal tubes with their stolon system preserved. The same seems to follow from taphonomic observations on the decay of the skeletal material in extant *Rhabdopleura* (Briggs *et al.* 1995).

Phylogenetic significance of homologous features

The present study has revealed that *Rhabdopleura compacta* shares more anatomical characters with the Graptolithina than do some other extant species referred to this genus (e.g., *Rhabdopleura normani*). Thus the question arises whether (1) this reflects merely the fact that Rhabdopleurida (and *Rhabdopleura* in particular) are in general closely related to the Graptolithina, or whether (2) some extant species of this genus are more closely related to the Graptolithina than the others.

The classical view would consider such characters as the presence or absence of the internal portions of the thecae as key features speaking for a direct relationship between their bearers. Generally, it was believed that the key features of a new group (in our instance the Graptolithina) are assembled in a linear and progressive manner, a view evidently related to the obsolete orthogenetic understanding of evolutionary change. More recent investigations on fossil transitional groups show, however, that key characters can arise independently in different clades (or lineages) within such groups. Such cases were referred by de Beer (1971) to the category of 'latent homology'. The independent origin of homological features in closely related transitional taxa was observed by many palaeontologists, most notably by Tatarinov (1976) in his penetrating studies on the evolution of mammal-like reptiles. Most recently, Tatarinov (personal information) has elevated this pattern of evolution to a generalized concept of 'discontinuous homology'.

Tatarinov's observations and conclusions are finding more and more support in recent phylogenetic analyses based on fossil material. Thus, early tetrapods display characters of some later lineages, producing what Clack (1998: p. 66) called 'melange of crown group characters', and Shubin (1998: p. 12) says in this context that "new features are often 'cut and pasted' on different groups at different time".

We believe that this remarkable pattern of expression of some features, observed by many palaeontologists and taxonomists finds its best and most general explanation in the 'underlying synapomorphy' concept as advanced by Saether (1979, 1983) and developed by Sluys (1989). This concept explains the repeated appearance of homologous features in different but closely related lineages as a striking feature of evolution within monophyletic groups. The resulting parallelism is an expression of the common apomorphic tendencies caused by largely the same evolutionary potential, in turn, an effect of the proximity of the common ancestry. A remarkable feature of the underlying synapomorphy is mosaicism in the expression of homologous characters. They may appear in the representatives of some clades being absent from the others. A number of genetic factors (such as epistasy, differences in the genetic background, etc.) and epigenetic factors (developmental constraints, switch genes) as well as selective forces may be responsible for blocking the expression or re-activation of corresponding genes. Therefore, in the light of the underlying synapomorphy concept all species belonging to a monophyletic group have the potential ability to develop certain homologous structures but only some express this ability. This concept fits the fossil record and the pattern of parallel evolution observed in it (Urbanek 1998) and may be applied to our case of *Rhabdopleura compacta*. One should assume that the common ancestor of rhabdopleurids acquired, by a corresponding mutation, the ability to produce homologues of the internal portions of the thecae. This potential ability and at the same time an apomorphic tendency characteristic of the group is, however, expressed only in some species, being silent in most of them. Hence the presence of homologues of the internal portions of the thecae may be safely interpreted as evidence of close relations between the two groups in question. Therefore our answer to the question risen is in favour of the first alternative: most reasonably we should consider *Rhabdopleura* a monophyletic group, generally closely related to the Graptolithina and therefore exhibiting certain apomorphic tendencies expressed in a mosaic presence of some homological features characteristic of graptolites. They are expressed in some extant (and possibly also fossil) species, while lacking in some others. However, the former are not necessarily more closely related to the descendants than the latter. This should be especially true in the case of such extant species as *Rhabdopleura compacta*.

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Stolony *Rhabdopleura compacta* (półstrunowce, pióroskrzelne) i ich znaczenie filogenetyczne

ADAM URBANEK I P. NOEL DILLY

Streszczenie

Duże podobieństwo stolonów współczesnych i kopalnych rhabdopleurydów (Pterobranchia, Rhabdopleurida) oraz osiadłych rzędów kopalnych graptolitów (zwłaszcza Dendroidea i Crustoidea), jest jednym z argumentów przemawiających za bliskim pokrewieństwem obu grup. Badania Kozłowskiego (1949) wykazały, że przy dużym ogólnym podobieństwie stolonów rhabdopleurydów i stolonów Graptolithina występuje także znamienne różnica: podczas gdy u graptolitów występują tzw. części wewnętrzne tek, u pióroskrzelnych nie stwierdzono ich występowania. Nasze badania przeprowadzone na materiale *Rhabdopleura compacta* Hincks, 1880 zebrany w przybrzeżnych wodach Kanału La Manche w okolicy portu Plymouth (Anglia), wykazały jednak u tego gatunku obecność struktur homologicznych z częściami wewnętrznymi tek graptolitów. Struktury te nazwane przez nas kompleksami diafragmowymi, składają się z właściwej diafragmy (tj. przegrody w stolonie opatrzonej centralnym otworem), oraz stożkowatej osłonki powstałej przez raptowne rozszerzenie (inflację) stolonu. W ten sam sposób powstają wewnętrzne części tek u przedstawicieli osiadłych rzędów graptolitów.

Badania nasze wykazały także głębokie podobieństwo między budową osłonek perydermalnych pączków przetrwalnikowych i kompleksów diafragmowych u *Rhabdopleura* oraz wewnętrznych części tek u Graptolithina. Te pochodne stolonu wraz z samym stolonem można określić jako stoloblast, tj. część szkieletu kolonii całkowicie odrębną od mających strukturę fuzellarną rurek zooidalnych. Sporadyczne występowanie u pewnych rhabdopleurydów struktur homologicznych z częściami wewnętrznymi tek u przedstawicieli osiadłych rzędów graptolitów jest jeszcze jednym dowodem przemawiającym za bezpośrednim związkiem rodowym obu tych grup. Wysuwamy przypuszczenie, że to sporadyczne występowanie bardzo swoistej cechy morfologicznej jest przejawem ukrytej homologii, lub też mówiąc inaczej – ukrytej synapomorfii, wyrażającej się istnieniem wspólnych tendencji apomorficznych u Rhabdopleurida i Graptolithina.