4. The Affinities of the Graptolites

By

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The graptolites are entirely Palaeozoic and mainly confined to Ordovician and Silurian deposits, but known already from higher Cambrian beds and surviving to the Carboniferous. Various attempts have been made to connect the group with small living colonial animals as the *Hydrozoa*, the *Polyzoa*, and the *Pterobranchia* (especially *Rhabdopleura*). Recently (KOZLOWSKI 1938, 1946, and 1949), relationship with the *Pterobranchia* has been considered definitely proved — a revival of an hypothesis put forth by ALLMAN in 1872 and further developed by SCHEPOTIEFF in 1905, but the arguments on which KOZLOWSKI bases his conclusions are partly different from SCHEPOTIEFF's. In his later papers BULMAN has adopted KOZLOWSKI's views and accordingly somewhat modified his own interpretation of certain structures in the graptolites.

At first view the *Pterobranchia* and the graptolites do not look very much alike. The former live in a system of tubes consisting of branching main tubes attached to stones, shells or even sandy bottom, and, at fairly regular intervals, of tubes containing the zooids which are connected within the main tubes by a system of stolons (the so called black stolon). The graptolites were not attached to the substratum in the same way, and their rhabdosomes are far more regular in the arrangement of the thecae. Traces of internal structures have been compared with the stolon in *Rhabdopleura*.

KOZLOWSKI's main argument appears to be the structure of the walls of the tubes or rhabdosomes which in both groups consist of half-rings (fuselles) of chitin or some similar substance piled on top of each other so that those on both sides meet along the middle of the tubes in a zig-zag-line (figs. 1 and 2). In *Rhabdopleura* the most regular arrangement of these fuselles is found in the walls of the main tubes and at the base of the living tubes. This structure is considered so unique that it can hardly have arisen independently in two unrelated groups: "Les tubes zoidaux libres de *Rhabdopleura* sont construits un peu différemment des thèques des Graptolithes, puisque leurs fusellus s'étendent sur la circonférence entière et chacun n'a qu'une seule suture oblique. De plus ces sutures obliques sont distribuées

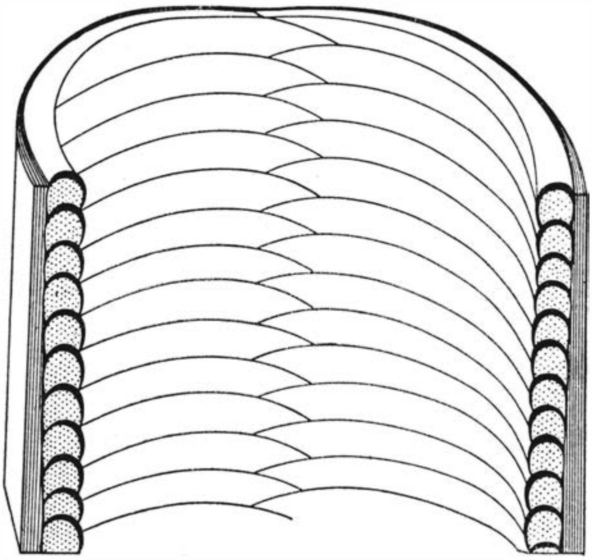

Fig. 1. Diagram showing the structure of the wall of the Dendroidean rhabdosome. From KOZLOWSKI. 1938.

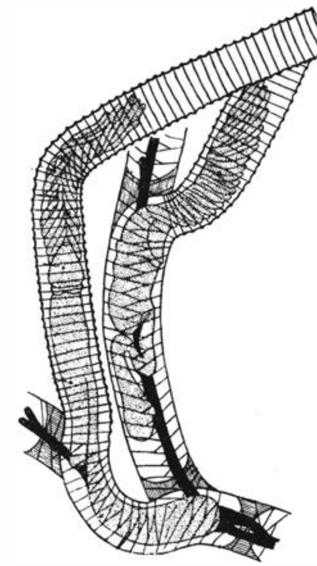

Fig. 2. *Rhabdopleura*. Part of a colony. From SCHEPOTIEFF.

irrégulièrement sur les faces des tubes zoidaux et n'arrivent pas par conséquent à constituer une ligne en zigzag" (KOZLOWSKI 1946, p. 101). "La manière de les construire est bien spéciale et aucun animal, vivant ou fossile, en dehors de ces deux groupes ne fait d'édifices chitineux semblables. Ce fait présente à mon avis une grande importance taxonomique, comparable à celle par exemple qu'ont les plumes pour caractériser la classe des Oiseaux. Il est très invraisemblable que la faculté de sécréter la chitine en forme des fusellus ait pu être acquise indépendamment dans deux groupes d'animaux sans liens de parenté, comme il est improbable que les plumes des oiseaux puissent être realisées par des animaux appartenant à des groupes génétiquement indépendants" (l. c. p. 102).

But if we consider the origin of the tubes, KOZLOWSKI's arguments lose much of their weight. There is no possible doubt (see DAWYDOFF 1948) that the tubes in *Rhabdopleura* are formed out of the secret from glands on the cephalic disc ("le produit de la secrétion des glandes du disque préoral" p. 461. "Die Substanz der Wohnröhren ist ein Ausscheidungsprodukt nicht nur der Drüsenpartie des Kopfschilds der Knospen oder Tiere, sondern wahrscheinlich auch aller Stellen der Körperoberfläche, wo die Epithelzellkerne mehrschichtig angeordnet sind. Letztere Stellen scheiden vermutlich die Substanz der kriechenden Röhren aus, während die der freien Wohnröhren wahrscheinlich nur das Produkt der Drüsenpartie des Kopfschilds ist". [SCHEPOTIEFF 1907 — Bd 24 — p. 224]). Thus the tubes are the same kind of structures as the tubes secreted by various kinds of worms and therefore of considerably less value as systematic characters than chitinous substances intimately connected with an epithelium reflecting in their structural details some physiological or histological properties of the underlying cells. The building of a tube from the secret from glands is an act of instinct, and the shape of the tube is strongly influenced by the surroundings. As regards *Rhabdopleura*, the main tubes are attached to the substratum, and after it has lost its power of producing buds, the stolon is imbedded in the lower part of the wall. When the fuselles are added to the main tubes the builder evidently starts at the bottom alternately on the right and the left side to secure the attachment of the tubes, and work towards the upper side; each half segment overlaps the preceding deposition of the opposite side and thus the zig-zag-line appears. That the free ends of the zooecia have another arrangement of its chitinous rings is quite natural as there is no contact surface interfering with the circling movements of the secreting disc.

Even if the rhabdosomes of the graptolites were formed in the same way (which they evidently are not) the similarity loses much of its value as a proof of close relationship as it is nothing so very remarkable that two animals build their tubes by adding sections on alternate sides.

KOZLOWSKI's careful study of the microscopical structure of the wall of the rhabdosomes in the graptolites has, however, revealed that there is a layer with lamellar structure outside the fusellar layer, and he points out that the external side of the rhabdosome must have had a coating of some soft tissue from which the lamellar layer was secerned. That an epithelium should grow out over a tube originally built of secret is, of course, out of question. The conclusion must be that also the fusellar layer in the graptolites was secerned from an epithelium. I shall come back to this question further on. But without knowing the microscopical structure of the rhabdosome one could fairly safely assume that it must have been formed on the surface or at the base of an epithelium as the thecae of the same rhabdosome are so like in their shape as if they were cast in the same mould and in more advanced forms rich in sharp angles and ornamental details, in many forms surrounding the apertures of the thecae in such a way that it is almost closed. In cases where the thecae of the same rhabdosome are dissimilar there is a gradual transition from more complicated forms to simpler ones, the same gradation occurring in all specimens of the same species. Further the thecae are placed at very regular intervals along the rhabdosome. Such structures must have arisen in constant contact with soft tissues; no animal, however skilful, can build with such precision.

Thus we have on one side a tube built of secret from the cephalic disc, with no other organic connection with the animal than the fact that the substance in the walls of the tubes was secreted by it (like cobwebs and honey-combs), on the other side a kind of cuticule or basal lamella — and no conclusion whatever can be based on a comparison between superficially similar structures of so entirely different origin.

The same applies to the virgella-like protrusion of the apertural border of the zooecia in *Cephalodiscus*. The way in which the buds in *Rhabdopleura* emerge from their chambers in the main tube (see below) must consequently also be only superficially similar to the budding from the sicula [in which, by the way, the structure of the wall may diverge around the aperture for the bud (BULMAN 1938, p. D 39, and KOZLOWSKI 1948, p. 80—83)], as the preserved wall of the sicula and that of the rhabdosome arising from it undoubtedly have the same origin.

Remains only the presence of a stolon in the two groups. The budding from the stolon in *Rhabdopleura* takes place in the following way (according to RAY-LANKESTER): there is an end bud which is so far advanced in its development that it is able to add fuselles around the terminal opening of the main tube, thus making this increase in length. Behind the end bud new individuals are budding from the stolon at irregular intervals but so that the bud nearest behind the end bud was the last one to appear and therefore the least developed. In its prolific portion the stolon has not yet formed the black (external) sheath characteristic of the older parts. Through intercalary growth the stolon stretches so that the buds become scattered inside the main tube and each bud becomes separated from its neighbour by a diaphragm of the same structure as the wall, i.e. pieced together of parts corresponding to the fuselles. When the bud is fully developed it pierces the wall of the main tube and builds its own tube in connection with its embryonic chamber. There is a certain disagreement between those who have studied *Rhabdopleura* as to the way in which the main tube grows; according to SCHEPOTIEFF its distal end is closed. This way of producing, along the sides of the stolon, a series of buds in all stages of development finally located in closed chambers of a secreted tube is so strange that very strong evidence is necessary before it can be ascribed to a fossil group like the graptolites in which all soft parts are unknown, and, moreover, the available evidence seems to indicate a very regular succession of terminal buds, at least in the graptoloidea reminding one of the sympodial branching among plants.

Fig. 3. Stolotheca of a Dendroid graptolite with the bases of the thecae budding from it. S Stolotheca, A Autotheca, B Bitheca. From BULMAN 1938.

Fig. 4. Diagram of the portion indicated by arrows in fig. 3, showing the possible relation of the epithelia to the chitinous substance secerned from them. Ectoderm black, entoderm red.

Fig. 5. Section through the rhabdosome of a Dendroid graptolite. From BULMAN 1938.

Fig. 6. Diagram of a Monograptid according to the interpretation attempted in the text. The tube at the 'back' of the rhabdosome containing the virgula marked only by the interspace between the epithelia and the virgular rod.

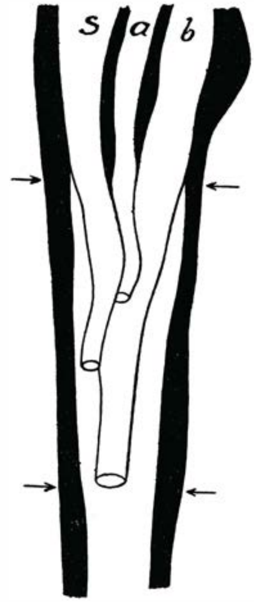

Fig. 3

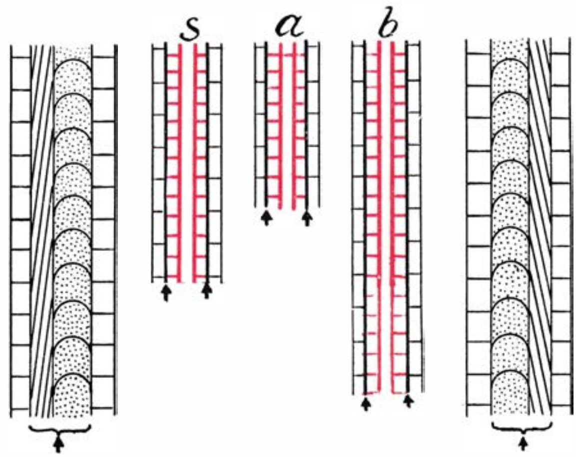

Fig. 4

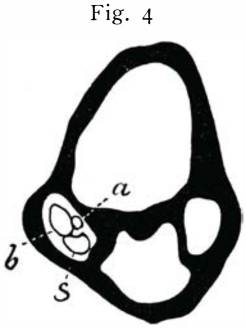

Fig. 5

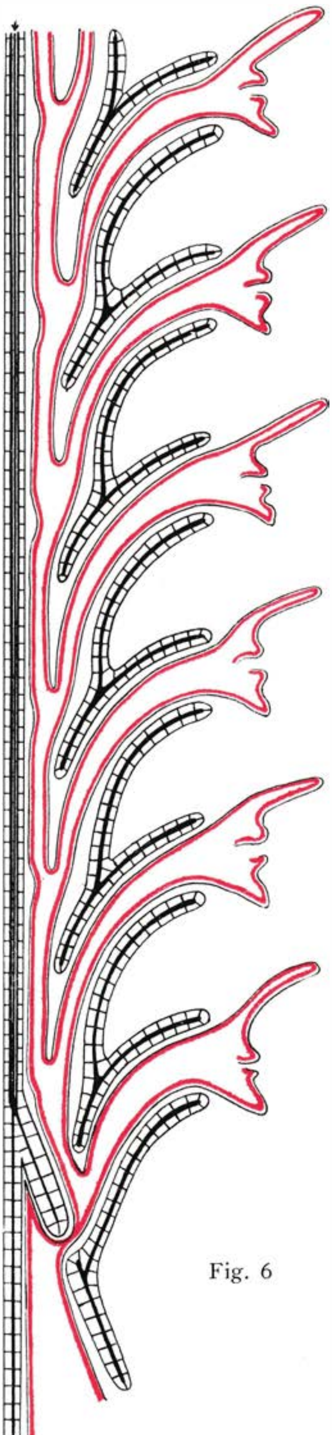

Fig. 6

The resemblance between the graptolites and the *Pterobranchia* is altogether superficial, at least as far as our present knowledge of the groups goes. WIMAN considered the graptolites as systematically separate from all known living and fossil forms, thus, arisen from unknown ancestors and extinct without descendants, a standpoint which is negative, it is true, but, without knowledge of the soft anatomy of the graptolites, the only really sound one, if it is modified to say that lacking the said knowledge, we are deprived of the possibility to connect the graptolites with any special branch of the existing zoological system. And why could there not have existed during the Palaeozoic a group of animals which is now extinct?!

It is possible, however, that some more information about the soft parts can be gained from a study of the structure of the chitinous walls of the rhabdosome and the base of the thecae preserved in the interior of the rhabdosomes of the dendroid graptolites.

KOZLOWSKI states that the cortical layer of the rhabdosome indicates the presence of external soft tissues in the living colony. According to his figure (1938, fig. 2; fig. 1 in the present paper) this layer is composed of lamellae overlapping upwards and only an external epithelium can have produced this type of overlapping. The internal fusellar layer is here presumed not to have been produced by the same epithelium as it is of a quite different structure, but to be the product of an internal epithelium. If so, the entire wall of the rhabdosome was formed between two epithelia and it would be comparable to the "Stützlamelle" (Mesogloea) in the Hydrozoa. To suppose the wall to be a kind of cuticule secerned from the free surface of the epithelium is for many reasons impossible: An external position of this epithelium would involve the presence of an epithelial fold of which the part producing the cuticule would have been the internal layer, the outer layer not being registered by any preserved structures, — further, the inner layer must either have produced both the cortical layer and (externally to this!) the fusellar layer, or only the cortical layer; in the latter case the cortical layer would be in secondary contact with the fusellar layer which was a cuticular product of another epithelium! I cannot think of any reasonable way to fit in a cuticule in the structure of the wall and therefore assume that the wall was a product secerned from the bases of two adjoining layers of epithelial cells. But the internal of these layers can hardly have been the entoderm as there are chitinous tubes within the cavity of the rhabdosome (fig. 3). I do not know the microscopical structure of the wall of these tubes; it is certain, however, that the tubes must have enclosed the entoderm as some of them are connected with the autothecae which were evidently nutritorial. The chitinous membrane was probably not a cuticule secerned by the entoderm towards the lumen of the theca (the lumen in the interior of the stolon in *Rhabdopleura* can, however, be filled with chitinous substance); it may be an ectodermal cuticule, but it may also — and perhaps more likely — have been formed between two layers of cells (like the wall of the rhabdosome).

The colonies of the graptolites would then have consisted of two systems of double-walled epithelial tubes within each other, the internal one consisting of entoderm and ectoderm, the external one of two ectodermal layers, i.e. the ectoderm presumably formed a fold growing up as a protective tube around the internal slenderer system of tubes. In the Dendroidea the two systems join at the nodes where the buds expand to form autothecae and bithecae. In the Graptoloidea the rhabdosomes show no restrictions or ridges at which the zooides could have been attached, and if the structures are interpreted (maybe *in absurdum*) according to what has been put forth above, one would arrive at a groundplan for the graptolites as in fig. 6. If the chitinous wall is correctly interpreted as a highly differentiated mesogloea there is no place for a mesoderm in the organization of the living animal, and if so the graptolites would be a peculiarly specialized group of coelenterates.

Fig. 6 is not intended to be a reconstruction of a graptolite, but it is only a way to sum up the above discussion. A quite different interpretation of the observed structures may be possible.

A study of the microscopical structure of the wall of the rhabdosome at different points, as for instance where two thecae have a common wall or where the edge of one theca abuts against the wall of a neighbouring one, may disclose further facts of importance for the understanding of the nature of the graptolites.

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