

# A new type of graptolite synrhabdosome

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Three remarkable graptolite synrhabdosomes from the Lower Llandoveryan shales (revolutus Zone) on Bornholm are described and discussed. Two of the synrhabdosomes are composed of rhabdosomes of *Rhaphidograptus toernquisti* (Elles & Wood), the third includes climacograptid rhabdosomes that are not assigned to species. The synrhabdosomes are remarkable in that the stipes are attached by the virgellae. This is the reverse of the situation in previously known synrhabdosomes in which attachment is by the virgulae. The mode of formation of the synrhabdosomes is discussed, but for the present there remain many unexplained details of the development.

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During the author's study of the Silurian shales on Bornholm (Bjerreskov 1975) a few remarkable associations of graptolite rhabdosomes were found. The stipes are all from biserial graptoloids, and arranged in stellate aggregations, apparently attached to each other by their virgellae. Thus the arrangement is structurally completely different from earlier described stellate assemblages, in which a number of rhabdosomes are conjugated by their virgulae. Such assemblages are known as synrhabdosomes.

The synrhabdosomes originally pictured by Hall (1865) were composed of stipes of the biserial graptoloid *Lasiograptus*. Ruedemann (1895) described several synrhabdosomes, all composed of graptoloids of the biserial type, and a relation to the life cycle of the graptolites was suggested. Later Ruedemann (1947) described and figured a large number of synrhabdosomes, including specimens previously figured in 1895.

The synrhabdosomes described by Ruedemann in 1895 and 1947 are essentially composed of a number of rhabdosomes that are attached to a square plate by their virgulae. In some specimens the attachment plate is superimposed upon a number of ovate or circular discs that, apparently, commonly contain a great number of siculae. All development stages may be found within a synrhab-

dosome, including immature stages comprising no more than a single sicula. Ruedemann believed the central plate to represent a vesicle, possibly a floating organ, and introduced the term gonangia for the ovate discs.

Kozłowski (1948) compared the synrhabdosomes with formation of buds from the peduncle in *Cephalodiscus* (Pterobranchiata), in which a large number of new individuals is seen; these, however, do not remain in the mother zooid. *Cephalodiscus* itself shows no true colonial development. According to Kozłowski the synrhabdosomes were formed by similar processes, namely budding from the apical part of the original sicula, but in the synrhabdosomes, and unlike *Cephalodiscus* the individuals supposedly remained attached. Such siculae were referred to as pseudosiculae by Kozłowski. He further stated that the siculae in the synrhabdosomes could not be compared directly to sexually developed siculae in normal rhabdosomes, and that they may lack a differentiated prosicula. However, a thorough study of the pseudosiculae has not yet been undertaken.

Rickards, in the discussion following Kirk (1969), stated that synrhabdosomes without any central disc had an intermingling of the virgulae, in which the actual connection was made by extrathecal tissue. In 1975 he made a reconstruction of a synrhabdosome based

upon *Monograptus varians* Wood, where the virgulae (nemata) are joined by soft tissue and not by the virgulae themselves. The reconstruction is a consequence of his demonstration that the attachment by the nema (virgula) is an unlikely function of this organ. Following his theory the virgulae in the synrhabdosomes were joined by soft tissue secreted by the end of the virgulae, and only rarely do the virgulae remain tangled together after decay and the group of colonies became preserved together as synrhabdosomes. Rickards (1975) further stated that in spite of examination of many synrhabdosomes, he had not observed any float-like structures in the synrhabdosomes, but only tangled nemata (virgulae).

The structurally different graptolite aggregates described below are also referred to as synrhabdosomes, even though their mode of development deviates strongly from that of previously known aggregates.

### Provenance of the material

The present synrhabdosomes were found in a dark grey argillaceous shale rich in pyrite concretions. The shale is highly fossiliferous, but the fauna is restricted to graptolites. The exposure is situated at the rivulet Øleå, in the southern part of Bornholm, about 2 km north of the mouth (Bjerreskov 1975, loc. 2a). The samples were found in the bottom of the rivulet itself, and accordingly have not been affected by subaerial weathering.

The graptolites are mostly preserved in a flattened state, but well preserved relief or semi-relief specimens have also been found. Several cleavage planes, parallel to the original bedding planes, are densely covered by masses of graptolites. The rhabdosomes commonly show a parallel orientation, indicating that the stipes are current-orientated. No predominant current direction is evident, as the orientation of the rhabdosomes varies from one bedding plane to the next.

The following graptolite assemblage has been found at this locality: *Climacograptus rectangularis* (McCoy), *Pseudoclimacograptus hughesi* (Nicholson), *Glyptograptus sinuatus sinuatus* (Nicholson), *Rhaphidograptus toernquisti* (El-

les & Wood), *Monograptus cyphus* Lapworth?, *Monograptus sandersoni* Lapworth, *Monograptus incommodus* Törnquist, and *Monograptus revolutus* Kurck.

The fauna is indicative of the revolutus Zone in the Lower Llandoveryan (earlier named the Rastrites shale by Pedersen (1922)). The revolutus Zone is equivalent to the cyphus Zone in Britain (e.g. Hutt 1974). About 1 m above the levels containing the synrhabdosomes the graptolite fauna changes, as *Monograptus gregarius* Lapworth and *Monograptus triangulatus triangulatus* (Harkness) appear, indicating the transition to the gregarius Zone.

### Rhabdosomal structure

The material comprises two synrhabdosomes with a stellate arrangement of the attached rhabdosomes, and a further one that has suffered partial destruction before burial. These are the only more complete synrhabdosomes found in the rich graptolite material from this locality, but there are numerous samples with a few graptolite rhabdosomes positioned in such a way that their virgellae are almost in contact. Discs or vesicle-like structures are not present in any of the specimens and consequently there is no indication of the attachment of the virgellae to any such structure.

The best preserved synrhabdosome, MMH 13713 A, B (figs. 1, 2) comprises about 25 rhabdosomes that can be assigned to *Rhaphidograptus toernquisti*. The rhabdosomes are arranged in a fan-shape, all the stipes being orientated in a congruent manner, with their proximal parts (virgellae) at the slender part of the fan, the outer rhabdosomes forming an angle of 120° to each other. The fan arrangement has a radius of about 3 cm, and the rhabdosome length (the parts with the thecae) varies from 1.7–2.1 cm; the average length of the virgellae is about 1 cm. The rhabdosomes are preserved partly in relief.

The reference to *Rhaphidograptus* is based on the isolated sicula and the loss of th<sup>1</sup><sub>2</sub>. The width of th<sup>1</sup><sub>1</sub> is 0.5 mm, th<sup>5</sup><sub>1</sub>: 1.2 mm, th<sup>10</sup><sub>1</sub>: 1.4 mm and th<sup>15</sup><sub>1</sub>: 1.5 mm. The maximum distal width of the rhabdosomes is 1.6 mm. The median septa are straight and appear

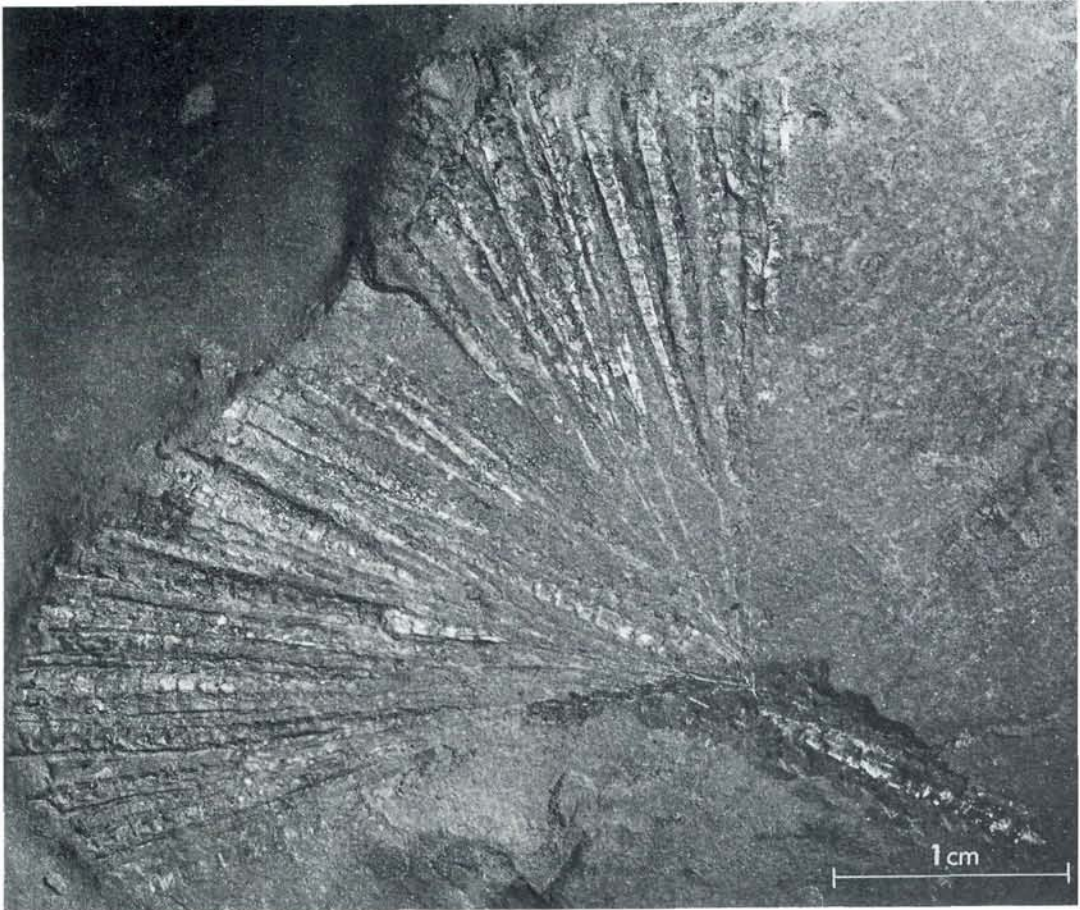


Fig. 1. Synrhabdosome of *Rhabidograptus toernquisti* (Elles & Wood). The *revolutus* Zone. MMH 13713 A.

to be complete. The thecae are strongly climacograptid and they number 12 per 10 mm in the proximal 10 mm. The virgellae are triangular in cross-section, and are twisted two-four times clock-wise as seen in distal view (see also Bjerreskov 1975: 43). The virgellae intermingle at their distal ends at about 1 cm from the siculae, but no attachment structures can be observed.

The other stellate synrhabdosome, MMH 13715 (fig. 3) is composed of radiating biserial graptolites that are apparently attached by their proximal ends near sicula. The synrhabdosome contains about 25 flattened rhabdosomes, all about 15 mm long; the longest rhabdosome is 2 cm. The rhabdosomes are 1.5–1.6 mm in distal width, and possibly 0.5 mm wide at the proximal ends. The thecae

number about 12 per 10 mm. The thecae appear to be of climacograptid type. The dimensions of the rhabdosomes are similar to those of the stipes in the synrhabdosomes described above, but as the proximal ends have not been identified with certainty, the rhabdosomes can be referred only tentatively to *R. toernquisti*.

In this case also the synrhabdosome is apparently without any attachment organs, but is distinct from the other synrhabdosomal structures recorded here by attachment very close to the siculae.

The third synrhabdosome, MMH 13714 (fig. 4) is somewhat broken, and 17 rhabdosomes are situated opposite each other in two groups, the stipes are possibly orientated approximately parallel to the current direction.

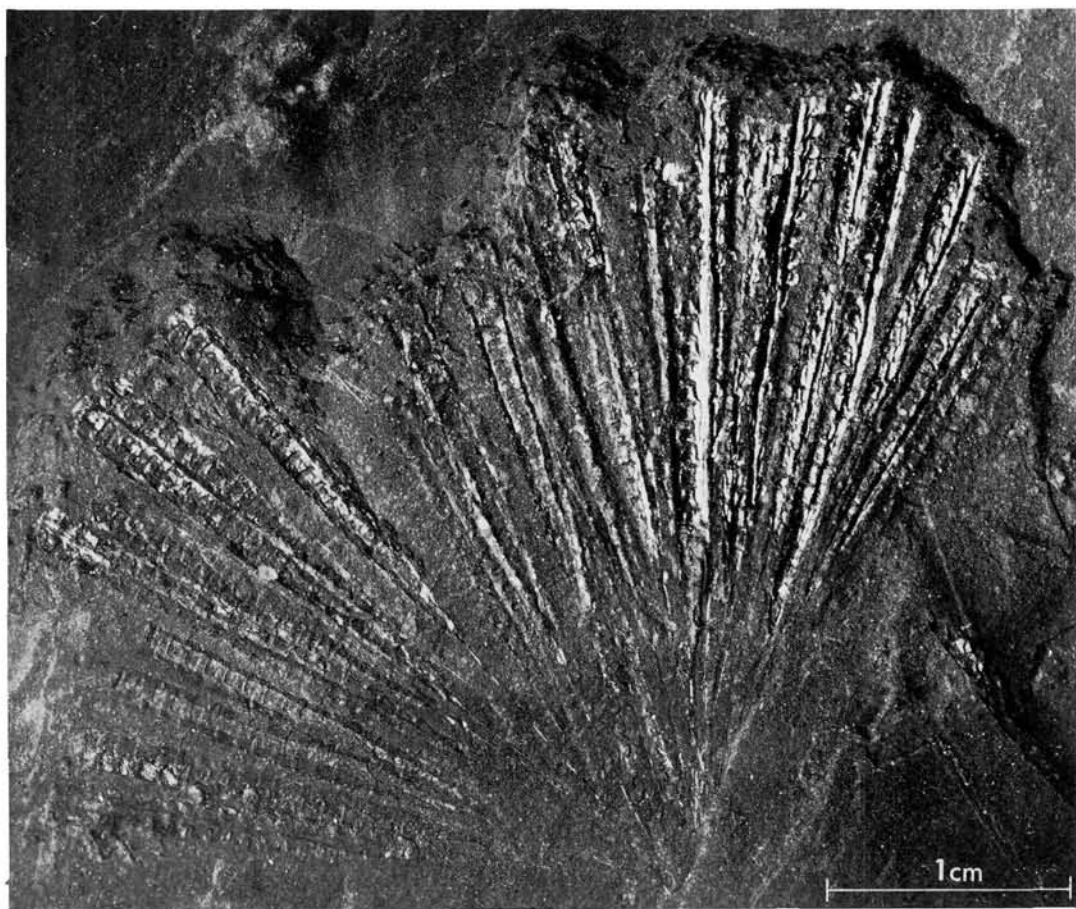


Fig. 2. Synrhabdosome of *Rhabdograptus toernquisti*. Counterpart of specimen shown in fig. 1. MMH 13713 B.

This synrhabdosome contains well preserved stipes of *R. toernquisti*, preserved partly in relief. In this case also, the rhabdosomes must have been joined together by their virgellae and, as in the two other synrhabdosomes, the stipes are nearly of the same length, here about 2 cm excluding the virgellae.

## Discussion

The available material does not permit any decisive conclusions to be reached concerning the formation of the new synrhabdosomes. The explanation that synrhabdosomes have an origin in a random attachment to seaweeds, the stipes later remained joined to each other, cannot be discounted, although a number of

arguments militate against a connection of graptolites and seaweeds (e.g. Kozłowski 1971). However, in the present case the circular-fan shape of the synrhabdosomes and especially the strict age grouping, as suggested by the equal stage of development of all the stipes in each synrhabdosome, seem to contradict a random arrangement and might suggest a connection with sexual reproduction.

Our knowledge of the development of previously known synrhabdosomes, namely the growth of the siculae with attachment and further development of the virgulae, does not provide an explanation of the origin of the present synrhabdosomes, in which the virgellae are attached. The present synrhabdosomes are apparently also distinguished from the previously described types by the nearly equal size of

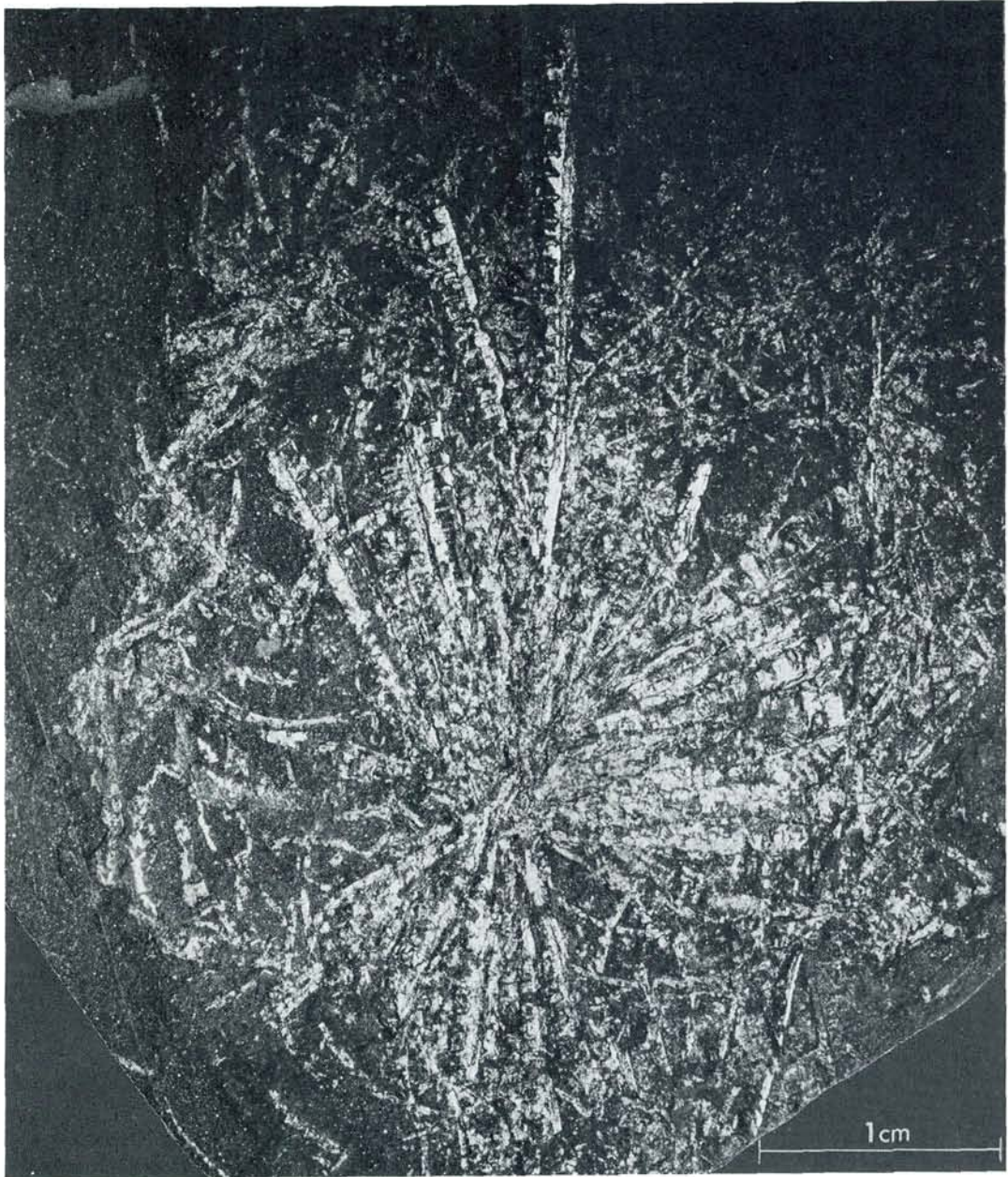


Fig. 3. Synrhabdosome composed of indeterminate climacograptid graptolites, possibly *R. toernquisti*. MMH 13715.

all the attached stipes. There do not appear to be earlier observations of *Rhaphidograptus* forming synrhabdosomes.

A budding of many new siculae from an initial sicula may explain the development of the present synrhabdosomes, as Kozłowski (1948) suggested for the previously described

but structurally different synrhabdosomes. Among the graptoloids only a few structures have been shown to be developed from the sicula and the virgella. In the *Linograptinae* a cladial growth with thecae from the aperture of the sicula has been described (e.g. Urbanek 1963). However, budding from a sicula with



Fig. 4. Somewhat broken synrhabdosome of *R. toernquisti*. The *revolutus* Zone. MMH 13714.

formation of a rather large number of new siculae (at least 25) instead of thecae has not been demonstrated. In the linograptids there is a development of a virgellarium (Urbanek 1963 = a central disc, Teller 1964) at the tip of virgella. This structure may have been connected with buoyancy (Urbanek 1963), but with the presently known morphology a similar structure does not seem able to develop and support synrhabdosomes comprising about 25 individual rhabdosomes. Accordingly the author prefers not to correlate the above described synrhabdosomes with any of the structures described by Urbanek.

However, the formation of the present synrhabdosomes must have been different from the development of the previously described synrhabdosomes but is possibly connected with sexual reproduction as supposed for the normal synrhabdosomes (Rickards 1975).

A possible explanation may be that a number of siculae develop within an attachment structure, most likely extrathecal tissue, in such a manner that the initial parts of the siculae (?prosiculae) were not attached, as must have been the case in the earlier described synrhabdosomes (fig. 5). The soft tissue may have been secreted by the siculae themselves. In the next stage the budding and formation of

the rhabdosomes took place, and the siculae and thecae were released from the original tissue. This could have happened simultaneously with a growth of the virgellae in such a way that the extreme distal parts remained attached.

This theory cannot as yet be verified, and until more informative material has been found crucial details in the development of these "reversed" synrhabdosomes must remain unexplained.

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### Dansk sammendrag

Der beskrives en ny type synrhabdosomer (sammenheftede graptolitkolonier). Det foreliggende materiale er fra Bornholm og henføres til *revolutus* Zonen i Nedre Llandoveryen. To synrhabdosomer er sammensat af *Rhaphidograptus toernquisti* rhabdosomer, det tredje af en climacograptid form, som ikke er artsbestemt.

De foreliggende eksemplarer er bemærkelsesværdige ved at graptolitkolonierne har været sammenheftede ved deres virgellae, og ikke som tidligere beskrevne synrhabdosomer ved deres virgulae. Forskellige muligheder for genesen af synrhabdosomerne diskuteres, og der opstilles en hypotetisk model. Mange detaljer i udviklingen af synrhabdosomerne kan dog ikke forklares, før der foreligger et mere informativt materiale.

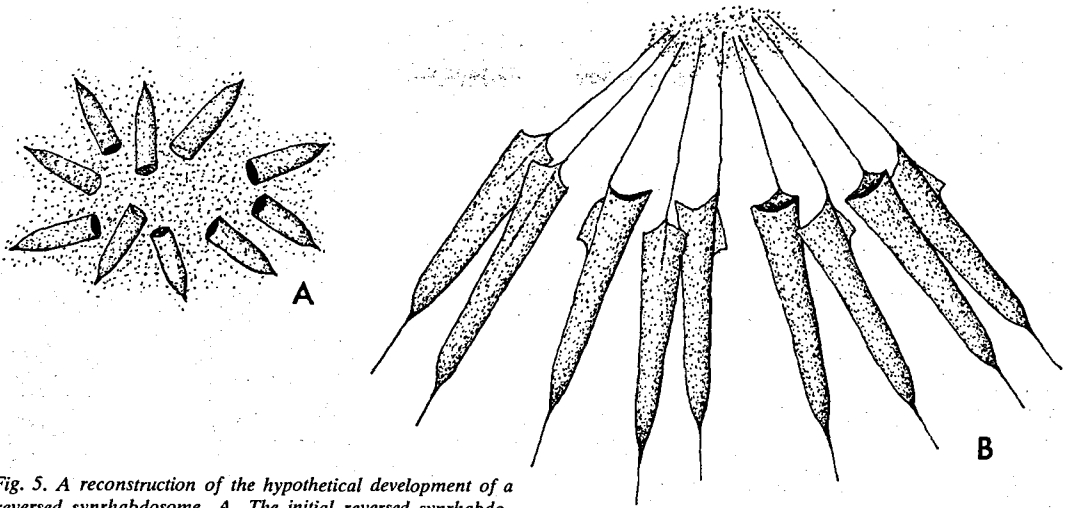


Fig. 5. A reconstruction of the hypothetical development of a reversed synrhabdosome. A. The initial reversed synrhabdosome with prosciculae, joined by soft tissue (stippled). B. A later growth stage, some of the siculae having the first theca. The virgellae are developed and remain connected by the soft tissue.

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