

A FLOATING ORGAN IN DICTYONEMA

BY

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1 PLATE, 4 FIGURES IN THE TEXT

The present paper deals with the find of an unusually well preserved specimen of the graptolite *Dictyonema flabelliforme* (EICHW.).

This graptolite is one of our better known fossils and is remarkable by its large horizontal distribution all through northern Europe and East, North America.

Several scientists have suggested that the *Dictyonema*-colonies were sessile forms attached to the bottom by root-like organs. Others have pointed out a pseudoplanktonic (GRABAU 1913) mode of life, i. e. the graptolite-colonies were attached to free floating objects. A planktonic mode of life has also been mentioned by some authors.

In December 1932 the author visited the *Dictyonema*-locality at Bygdøy sjøbad, Bygdøy, near Oslo. Looking at some shale-pieces I happened to pick out the specimen which is described in the following. The specimen belongs to the Paleontological Museum, Oslo (Cat. no. 33052). Probably other similar specimens can be collected later.

Dictyonema flabelliforme (EICHW.).

Pl. 1. Text fig. 1.

(A complete synonymy list published by BULMAN (1927, p. 12–13).

General description. The small specimen consists of a basal organ and the proximal portion of the rhabdosome. The longest stipe measures about 17 mm.

The basal organ has a well defined, symmetric outline. The dorsal border (orientation according to fig. 1) is transverse, straight or slightly concave. The lateral borders are well rounded. The

flattened surface is partly broken on the right side, a few faint ridges are indicated on the surface (fig. 1).

The rather straight ventral margin is produced into the basal branches of the rhabdosome. The two lateral branches are very distinct. A third branch has a rather oblique direction and belongs certainly to the other side of the funnel-shaped rhabdosome. The

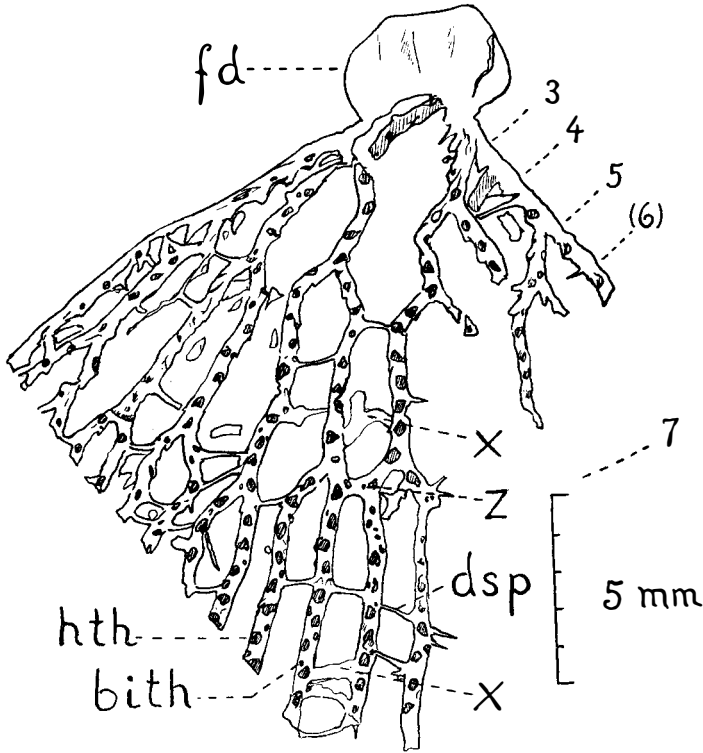


Fig. 1. *Dictyonema flabelliforme* (EICHW.). Drawing after specimen on Pl. 1. fd = basal organ. 3-7 = zones of branching. bith = bitheca. dsp = dissepiment. hth = hydrotheca. x = thin test between stipes. z = broad dissepiment with bitheca.

basal portion of this branch is connected with the disc, and the distal portion can not be connected with the remaining stipes preserved in a different layer. If we compare the three branches with structures found in sicula-specimens of *Dictyonema*, it is very probable that the branches represent three of the four branches from the second furcation. Fig. 3 indicates the hypothetical bifurcations inside the disc.

The rhabdosome forms a wide cone. The diverging angle is 90° — 100° . The cone might have been broken and flattened out. The outer branch on the right side is preserved in a slightly deeper level than the central stipes. One branch in the fourth furcation zone (hatched in fig. 1) has a downward direction suggesting the connection with the other side of the cone. The stipes show a regular bifurcation in certain zones. The zones of branching (BULMAN 1927 p. 26) are indicated on fig. 1. The first observable branching zone (3) lies 1 mm from the disc. The next three: 2, 4.5—5 and 9.5 mm from the disc. The zone marked (6) is irregular, not present in the other branches. The distances between each branching are considerably smaller than those stated by BULMAN (1927 p. 26) as an average in *D. flabelliforme*. The stipes has an average breadth of 0.5 mm.

As seen on pl. 1 the stipes show rows of black spots indicating the thecæ. In the black spots the test is broken revealing the cavities or theca. Several authors have shown that the thecæ opens on the inside of the cone-shaped colony. In the specimen present, the surface of the stipes represent the outside. The openings must therefore represent the broken outer walls of the thecæ. The structure of the thecæ of *Dictyonema* was first worked out by WIMAN (1895) in the Silurian form *D. rarum*. The structure of *D. flabelliforme* has been described lately by BULMAN (1925 and 1927). In his last paper BULMAN mentions three types of individuals: hydrothecæ, bithecæ and budding individuals. He says (1927 p. 14): "in the opinion of the writer, the existence of this budding individual as a separate entity be open to question".

On pl. 1 and fig. 1 the large openings certainly represent the hydrothecæ (hth). Along the lateral margins, smaller openings are present which indicate the bithecæ (bith). The alternating position on each side of the stipe is shown by BULMAN (1925 p. 61). The position is the same in the present specimen. In two neighbour stipes the bithecæ have a corresponding position, the most common position according to BULMAN. The outer branch on the left side shows the thecæ in lateral view. The edges of the thecæ are not well exposed. The dissepiments (dsp fig. 1) have mostly the usual shape of transverse threads connecting the stipes. In some cases the dissepiments are very broad and looks as if they consisted of a very thin test (x fig. 1). Those structures may have been destroyed in most

specimens of *D. flabelliforme*¹. Earlier illustrations, as far as I have found out, show only the thread-shaped dissepiments BULMAN (1927, pl. 1, fig. 4) figures a broad dissepiment with one bitheca. The same structure was mentioned by WESTERGAARD (1909 p. 58). In the present specimen a broad distinct dissepiment has one bitheca indicated (z fig. 1). This dissepiment seems to be different from the thin tests (x fig. 1).

Dimensions.

Breadth of disc = 4.5 mm, length = 2.2 mm. Average breadth of stipes = 0.5 mm.

Number of hydrothecæ in 10 mm..... 15

Number of stipes in 10 mm..... 8

The number of dissepiments vary too much to give any data.

Remarks.

In his fine monograph of the British Dendroid Graptolites, BULMAN (1927, 1928 b) discusses the many varieties of *Dictyonema flabelliforme*. The diagnosis of *D. f. forma typica*, in general agrees with the present form. The broad cone may indicate *D. f. anglica* BULMAN, which is not much different from the *forma typica*. The var. *sociale* (SALTER) and var. *norvegica* (KJERULF) differ in numbers of stipes and thecæ from the present form. BRØGGER (1882 p. 32) gave a very good description of the Norwegian forms of *Dictyonema*. His description and illustrations of *D. f. forma typica* correspond in general with the present form. Unfortunately little is preserved of the more mature part of the present specimen. Preliminarily, until more material is obtained, the form may be referred to as *Dictyonema flabelliforme* (EICHW.) without a closer determination.

The basal organ.

A very large number of specimens of *Dictyonema flabelliforme* has been examined by the various authors. The European paleontologists found the rhabdosome always originating in a distinct sicula.

MATTHEW (1895, pl. 49) found in a few canadian specimens of a Devonian *Dictyonema* a root-like basal organ connected with the rhabdosome. WIMAN (1897) described apparently very typical root-like

¹ The delicate nature of the structures perhaps corresponds to the test of the basal organ. They may have served as floating organs.

structures in the Silurian form *Dictyonema cavernosum*. RUEDEMANN. in his excellent monograph of the graptolites of New York (1904, pl. 1, fig. 10) figures a young individual of *D. flabelliforme* with a long nema ending in a sub-circular "primary disc" (fig. 2 a). RUEDEMANN (1908 p. 159) also mentions root-like structures in *Dictyonema*. HAHN (1912 p. 148) has specially described and discussed the basal organs of the early *Dictyonema*. Some of his figures are redrawn in

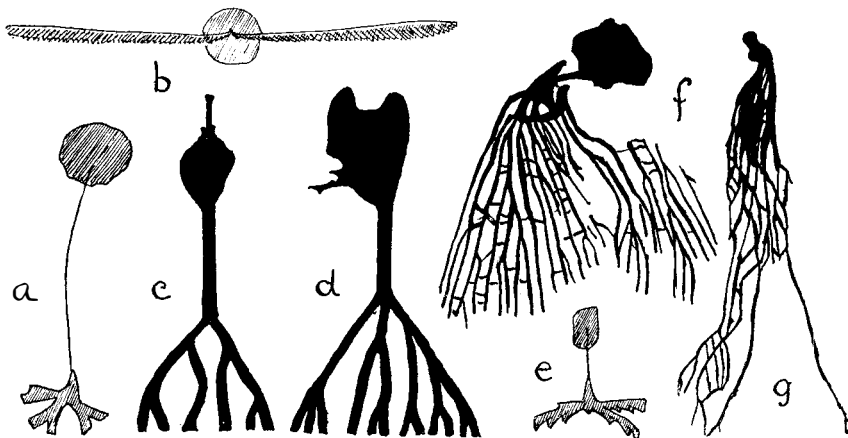


Fig. 2. Basal organs in graptolites.

- a = *Dictyonema flabelliforme* (after RUEDEMANN 1904, pl. 1, fig. 10).
 b = *Didymograptus patulus* (loc. cit. pl. 13 fig. 9).
 c = *Dictyonema flabelliforme*, var. *ruedemanni* (after HAHN 1912, pl. 21, fig. 4 d).
 d = *D. f.* var. *acadia* m. f. *ruedemanni* (loc. cit. pl. 21, fig. 3 b).
 e = *Staurograptus dichotomus* (loc. cit. pl. 2, fig. 17).
 f = *Dictyonema flabelliforme*, var. *leroyense* (loc. cit. pl. 20). A Devonian form.
 g = *Desmograptus cancellatus* (loc. cit. pl. 20).

fig. 2 c, d. The specimens fig. 2 c and d have the basal organs connected with strong "stems". The basal organ has a symmetric outline in c and looks as if it was broken on the left side in d.

In *Dictyonema flabelliforme* var. *leroyense* and *Desmograptus cancellatus* (fig. 2 f, g) no distinct "stem" is traceable. The basal organ seems to have partly covered the proximal portion of the rhabdosome. In the specimen of *D. f. leroyense* (fig. 2 f) the basal organ has probably broken off from the rhabdosome, a transverse broad ring indicates the connecting line. The *Desmograptus* form has a rather small basal organ, but in the proximal portion of the

colony the spaces between the stipes are filled with apparently the same membran as that forming the basal organ.

A large number of European specimens have been examined without showing any trace of basal organs. WESTERGAARD (1909 p. 58) have examined nearly a hundred specimens with well preserved sicula, but found no traces of other organs. One specimen showed a bifurcation of the point of the sicula, but the structure was probably accidental.

Our knowledge of the European *Dictyonema* is much advanced through the extensive studies of the British forms by Dr. BULMAN. BULMAN (1928 a) discusses the root-like structures of the dendroid graptolites. He separates two types of "stems" between the basal organ and the rhabdosome: one type corresponding to the nema, and another formed by the budding individuals and thus representing part of rhabdosome. BULMAN assumes that the development of the stem varied very much within one species.

The Norwegian specimen, above described, resembles to a large extent those figured by HAHN (1912) (fig. 2 f, g). In both cases we have a basal organ partly covering the proximal portion of the rhabdosome. The outline with the attachment of the initial stipes is more symmetric in the Norwegian specimen.

Explanation of the basal organ.

WIMAN assumed after the structures found in the Silurian species that the colonies were attached by root-like organs to the sea-bottom, forming meadows in the deeper regions.

RUEDEMANN (1904, p. 515), discusses the basal structures in connection with the habit of life of *Dictyonema flabelliforme*. He does not come to a conclusion wheter the form was benthonic, pseudo-planktonic or planktonic. He mentions a planktonic mode of life as a possibility, especially for the younger stages in which he discovered a primary disc attached to a long nema.

HAHN (1912) studying specially the basal organs found a great resemblance between the basal attachment organs of Gorgonias and the basal organs of *Dictyonema*. He assumed that the basal organs represented root-like structures.

BULMAN (1928 b p. 32) says about *Dictyonema* that through the upper Ordovician a more truly sessile habit seems to have been

acquired. Regarding the Silurian forms, he says (p. 47) that they might have been attached to objects on the seabottom or alternatively to floating objects.

GRABAU (1929 p. 2) discussing the habits of the graptolites leaves it has an unsolved question whether *Dictyonema* was a benthonic or epiplanktonic form. The same opinion was shared by Lapworth (WALTHER 1897).

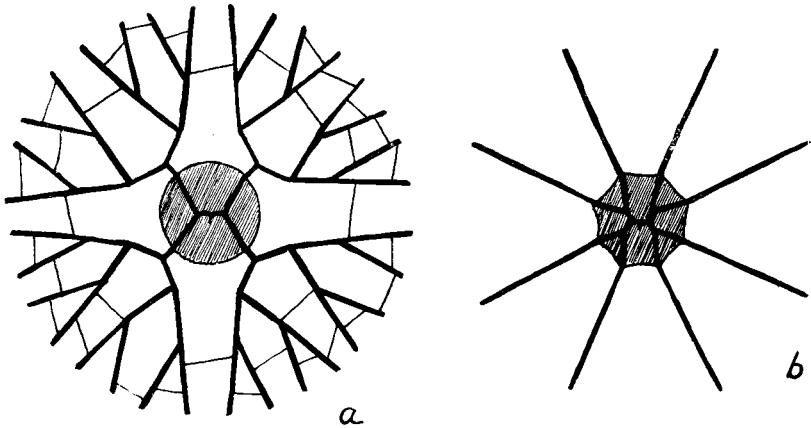


Fig. 3.

- a = Hypothetical ventral projection of the specimen on Pl. 1 of *Dictyonema flabelliforme*. Diagrammatic outline of rhabdosome.
 b = *Dichograptus*. Diagrammatic outline after figures by RUEDEMANN (1904, pl. 8).

STUBBLEFIELD (1929) made an important discovery in showing that some of the early members of the graptolitoidea had bithecæ besides the ordinary hydrothecæ. *Dictyonema* of the order dendroidea is hence related to the early graptolitoidea. Basal organs have been found in several of the lower Ordovician forms. RUEDEMANN (1904) described a primary disc in a number of species. Two of his figures are redrawn in fig. 2 b, c. *Didymograptus* (2 b) has a circular disc connected with the sicula without any longer nema. In *Stau-rograptus* (2 e) a short nema is present between the disc and the sicula. The nema seems to be characteristic for the young individuals. In *Dichograptus* (fig. 3 b) a larger central disc is preserved in many cases. The disc is stretched out between the branches of the rhabdosome. The proximal portion of the stipes including the

sicula, is visible within the disc. It is important to notice the disc only is preserved in a certain number of individuals. The delicate integument was easily destroyed. RUEDEMANN (1904, p. 622) also describes a similar central disc in specimens of *Goniograptus*, a branched form resembling *Dictyonema*, but instead of being cone-shaped as *Dictyonema* the colony was expanded and therefore lacking the dissepiments.

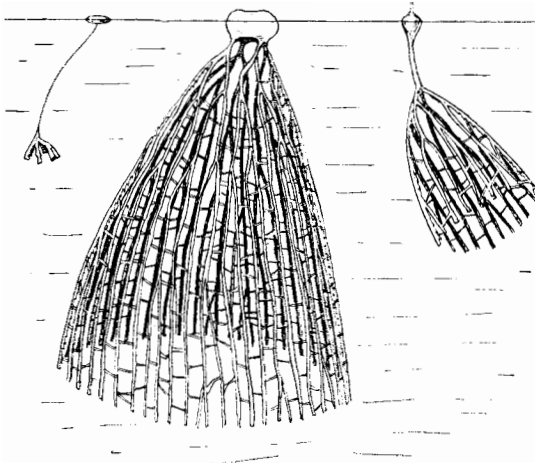


Fig. 4. Floating specimens of *Dictyonema flabelliforme* (EICHW.). Reconstruction. The development of the floating organ and the "stem" seem to vary considerably.

It is very likely to expect a similar central disc in the mature specimens of *Dictyonema*. Fig. 3 a indicates a structure comparable with that in *Dichograptus*.

The cone-shaped larger colonies of *Dictyonema* are always exposed in lateral view.

The central disc, if present, would also be preserved in lateral projection. The basal organs found in some American specimens (fig. 2, f, g) and the described Norwegian specimen fully correspond to those present in *Dichograptus* and *Goniograptus*. RUEDEMANN (1904, p. 596) says about the "root-like" structures in *Dictyonema flabelliforme* and the central disc of *Dichograptus*: "It is proper to conclude that we have in Dictyonemas a case entirely homologous to that observed in the Dichograptidae".

During my stay in the New York State Museum in Albany, Dr. R. RUEDEMANN very kindly showed me his fine models of graptos-

lites. In an "aquarium" he has the graptolite colonies hanging down from a pneumatocyst floating on the surface. The found structures in *Dictyonema flabelliforme* seem to suggest a similar mode of life. The floating disc found in the Norwegian specimen (fig. 1 fd and pl. 1) shows no impressions of the branches of the rhabdosome. This fact indicates that the basal organ was not a flat disc, but a vesicular body. In the expanded forms as *Dichograptus* the dorsal and ventral surface of the bladder is squeezed together. In this case it is interesting to notice one specimen of *Goniograptus* figured by RUEDEMANN (1904, pl. 7, fig. 9). This specimen, which is laterally compressed, has ". . . a proximal, apparently baglike appendage". This structure certainly represents the vesicular body, laterally compressed. RUEDEMANN made a separation between the primary disc attached by a thin nema, and the secondary disc formed after the proximal thecæ. Both LAPWORTH (WALTER 1897 p. 253), RUEDEMANN (1904 p. 597) and BULMAN (1928 a) agrees however, on the assumption that the development of a thin nema, a stem, or a membrane covering the initial portion of the rhabdosome might occur in the same species.

Returning now to the figures reproduced from HAHN (1912). We find that the "root-like" organs, attached by a stem to the cone-shaped rhabdosome (fig. 2 c, d) very likely represent a pneumatocyst. The symmetric outline of fig. 2 c, speaks in favour for this assumption. The broken margin of fig. 2 d, might be explained as a bursted bladder.

Regarding the Silurian forms, some specimens of *Dictyonema cavernosum* (WIMAN 1897) certainly looks as if they were attached to some objects by their long stolons. In that case we must remember that several specimens might have been mutually connected. Some parts of the modified nema or proximal rhabdosome might have been developed as bladders. Some of the root-like structures might be explained as bursted pneumatocysts where only the more solid part of the delicate membran is preserved. If the Silurian dendroids grew attached to other objects it is strange that no attached specimen is described.

Conclusion.

Hundreds of examined specimens of *Dictyonema flabelliforme* show the cone-shape rhabdosome originating in a free sicula. No basal organ is found. In a few American specimens, and the one

Norwegian described above, a basal organ is preserved. The found structures correspond closely with those found among the earlier graptolitoidea. The "central disc" in *Dichograptus* is only preserved in a certain number of specimens, a fact indicating that the basal organ consisted of a delicate membrane. The laterally compressed specimens of *Dictyonema* give the impression that the basal organ formed a vesicular body and not a flat disc.

The found structures show that the basal organ of some species of *Dictyonema*, probably represents a floating organ (Pneumatocyst) and not root-like structures.

The structure of the pneumatocyst varies to a large extent. We do not know whether it was always present, but the absence in most preserved specimens, is certainly due to the delicate nature of the membrane.

The presence of a pneumatocyst in *Dictyonema flabelliforme* signifies that these graptolites were planktonic forms. The pneumatocyst probably floated on the surface of the sea with the cone-shaped rhabdosome hanging down. The rich phytoplankton in the surface layers would give sufficient nourishment for the large graptolite colonies. Fig. 4 gives an idea of the probable habit of life of *Dictyonema flabelliforme*.

The assumption of a planktonic mode of life of *D. flabelliforme* explains very well the wide horizontal distribution of this form. East American specimens can hardly be separated from those found in the northern part of Europe. GRABAU (1929 p. 7) shows that the slightly younger graptolite faunas, represented by species of *Dichograptus*, *Goniograptus*, *Phyllograptus*, *Tetragraptus*, *Didymograptus*, and others, had an even larger distribution. The same species are found in western Europe, eastern North America, Australia and China.

HAHN (1912, p. 152) and BULMAN (1927 p. 27—28) among others, describes cases in which several specimen of *Dictyonema* are arranged around a common centre. HAHN found two specimens attached to the same disc or basal organ. These facts indicate that many specimens might have been connected by a common pneumatocyst and thus forming a large colony of the kind found by RUEDEMANN in *Diplograptus*.

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Dictyonema flabelliforme (EICHW.).

4,5 ×. Specimen showing basal organ. Dictyonema-shale, Bygdøy Sjøbad, Bygdøy, near Oslo. Aut. coll. Belongs to Pal. Mus. Oslo, cat. no. 33 052. Photographed in alcohol. Photograph not retouched.