

## SOME UPPER TREMADOCIAN GRAPTOLITES FROM NORWAY

by NILS SPJELDNÆS

ABSTRACT. New material of Upper Tremadocian graptolites from the Oslo Region, preserved in full or half relief in pyrite, is described. *Bryograptus ramosus* Brøgger 1882 is shown to have distinct bithecae. '*Didymograptus kiaeri* Mønsen 1925 is also shown to have bithecae and is made the type of the new genus *Kiaerograptus*. *Adelograptus bulmani* sp. nov. is a peculiar species, which might have affinities both with the anisograptids and the leptograptids and might be intermediate between them. The presence of bithecae in some graptoloid-like forms in the Upper Tremadoc suggests that the presence of graptoloids in beds older than the Arenig might be questionable. The material present might indicate that a number of graptolite lineages are more complex than previously assumed, and that several lineages in the dichograptids and other graptoloid groups originated directly and independently from the dendroids.

BECAUSE of the bad state of preservation of the material, the details of the structure of most Upper Tremadocian graptolites are virtually unknown. The specimens are generally preserved as mineralized films, and only the number of branches, angle of bifurcation, and the gross outline of the thecae can be observed.

The author recently succeeded in finding some specimens of Upper Tremadocian graptolites from the Oslo Region which are preserved in full or half relief in pyrite. The specimens come from the *Ceratopyge* Shale (Zone 3 a $\beta$ ) and are found in the upper part of this formation, about 0.4–1.8 m. below the *Ceratopyge* Limestone (Zone 3 a $\gamma$ ), in two road sections at Slemmestad, about 20 km. SW. of Oslo.

The general stratigraphy, and an outline of the geology of the area is given by Stormer (in Høltedahl and Dons 1960, pp. 11–24, 45–47). One locality is about 300 m. ENE. of Stormer's locality 4 (loc. cit., text-fig. 25), and the second is along the same road, about 1½ km. to the SW. The horizon is rich in graptolites, but only a few of them are preserved in full relief.

Parts of the specimens preserved in full relief are sometimes distorted and swollen in a rather peculiar way which is interpreted as a result of the pyritization. The specimens were probably originally filled with, or replaced by, an iron-sulphide gel (possibly hydrotroilite or melnichovite); later the sulphide gel crystallized into pyrite, and the specimens became compressed by the diagenesis of the sediment. In the cases where the quantity of the gel was small, or where it was very rich in water, the specimens were compressed to mineral films. This is the usual preservation of the Tremadocian graptolites from the Oslo Region, and several other areas. In some few specimens, the sulphide content of the gel was sufficient to give an exact replica in massive pyrite of the specimens, or at least one in half relief. In some cases again the gel seems to have swollen, probably due to high osmotic pressure, and the fossils became swollen and distorted. This should be borne in mind when working with pyritized materials, as the process of fossilization may have caused quite considerable changes in the morphology of the specimens, and may make statistical, biometric work on such graptolites rather difficult.

In many specimens the pyrite has been oxidized, and the specimens are preserved as

casts partly filled with iron oxides. These specimens are studied on, and photographed from latex moulds. The moulds were made from latex emulsion stained with Indian ink and were whitened with ammonium chloride for photography.

The few specimens preserved in full relief reveal a number of details, not previously observed, especially the presence of bithecae in some specimens. In *Bryograptus ramosus* this was expected, even if it had not previously been possible to demonstrate their presence. It was more surprising to find bithecae in '*Didymograptus*' *kiaeri* Mønsen, which superficially looks like an extensiform didymograptid. Based on the early stratigraphic occurrence of this species, and some structural features (especially the long nema and the oblique sicula), the author suspected it was not an ordinary didymograptid. Bulman (1941, 1950) had also suggested that this species might be related to the Anisograptids, and this view has gained strong support from the material presented here.

A new genus, *Kiaerograptus*, is made to accommodate the two-branched, extensiform Anisograptids with distinct bithecae.

*Acknowledgements.* The author is deeply indebted to Professor O. M. B. Bulman, Cambridge, for advice and encouragement in preparation of this paper, and to Dr. Henningsmoen for having read the manuscript critically. The photographs were made by Faculty photographer B. Mauritz and the author.

*Bryograptus ramosus* Brøgger 1882

Plate 17, figs. 6-9; text-fig. 1

1882 *Bryograptus ramosus* Brøgger, p. 37, pl. 12, fig. 21.

1925 *Bryograptus ramosus* Brøgger; Mønsen, pp. 160-2, pl. 1, fig. 9, text-figs. 3a-c.

1954 *Bryograptus* cf. *ramosus* Brøgger; Bulman, p. 34, pl. 4, fig. 9.

*Description.* Some specimens presumably belonging to this species are preserved in full relief, and show distinct bithecae, situated alternately on both sides of the branches. Because of this pattern of budding, the apertures of the autothecae also occur alternately in two rows, instead of in one single row, which is usually the case in Graptoloid rhabdosomes.

The sicula is long, and needle-shaped, and the budding of the proximal part is easily seen in the best specimens (Pl. 17, fig. 8). The rhabdosome is initially rather elongate, and in at least one specimen (Pl. 17, fig. 7) there are definitely three primary branches.

EXPLANATION OF PLATE 17

All specimens belong to Paleontologisk Museum, Oslo, Norway. The specimens shown in figs. 3, 4, 7, 8, 9 are photographed from latex casts coloured with Indian ink and coated with ammonium chloride. The specimens shown in figs. 1 and 2 are coated with ammonium chloride, and the ones shown in figs. 5 and 6 are photographed by the maximum reflection method.

Figs. 1-5 *Kiaerograptus kiaeri* (Mønsen). 1, Distal part of a branch showing bithecae, PMO 72833a;  $\times 13$ . 2, 3, Two proximal parts, PMO 72833b (2) and PMO 72834a;  $\times 10$ . 4, Specimen showing proximal part in somewhat oblique view, PMO 72834b;  $\times 10$ . 5, Lectotype, the specimen figured by Mønsen (1925, text-fig. 5, pl. 2, fig. 16), PMO 60212a;  $\times 4$ . Specimens 1-4 from Slemmestad, 20 km. SW. of Oslo; 5 is from Stensberggaten in Oslo; all from Zone 3 a $\beta$ .

Figs. 6-9. *Bryograptus ramosus* Brøgger. 6, Lectotype, a large rhabdosome from Zone 3 a $\beta$  at Vestfossen, Eiker (70 km. W. of Oslo). Probably the specimen figured by Brøgger (1882), pl. xii, figs. 21, 21a; PMO 72829;  $\times 2$ . 7, 8, Two proximal parts of young rhabdosomes, Zone 3 a $\beta$ , Slemmestad. 7, PMO 72831;  $\times 9$ . 8, PMO 72832;  $\times 7$ . 9, Fragments of two branches showing bithecae; Zone 3 a $\beta$  Slemmestad; PMO 72830;  $\times 20$ .

There are probably several different Bryograptids in the Upper Tremadocian of the Oslo Region. In the present material there are a number of different types, which vary as to size of the branches, and shape of rhabdosome. Monsen (1925, pp. 162-5, pl. 1, figs. 10-11, text-fig. 4a-b) described a new species from this horizon in Oslo, but my studies do not quite agree with the description given. The specimens discussed here as *B. ramosus* agree with the lectotype (Pl. 17, fig. 6) both in the thecal measurements, so far as they can be identified, and in the elongate rhabdosome with infrequent branching in the proximal part. Other specimens, including some of those referred to *B. ramosus* by Monsen (1925) have more frequent branching, and more rapidly expanding rhabdosomes.

It was anticipated by Bulman (1941, p. 106, 1954, p. 34) that this species had three primary branches, and therefore was a true *Bryograptus*. This is quite evident from the present material.

The real number of branches is known only in a few species of *Bryograptus*, and as far as the author knows bithecae have been recorded only in *B. ramosus*. It is possible that a number of the species now referred to *Bryograptus* do not have bithecae, and some might have only two primary branches.

#### KIAEROGRAPTUS gen. nov.

*Diagnosis.* Dendroid graptolite genus, probably referable to the family Anisograptidae. Sicula of graptoloid type, rhabdosome consisting of two branches of equal width, in one plane (extensiform type of branching). Distinct bithecae placed alternately on both sides of branches. Autothecae resembling the dichograptid type. Initial budding of dendroid type, except that the bithecae related to the early autothecae of each branch appear to be missing.

*Type species.* *Didymograptus kiaeri* Monsen 1925, from the Upper Tremadoc (Zone 3 a $\beta$ ) of the Oslo Region.

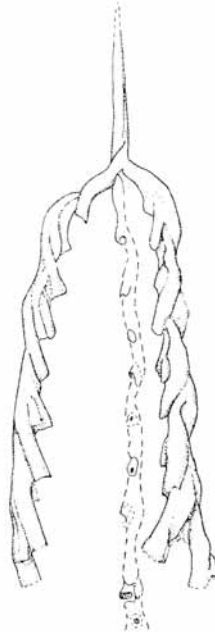
*Remarks.* The genus is at present monotypic, and its distribution is therefore identical with that of the type species. For discussion of affinities, see remarks on *K. kiaeri*.

#### *Kiaerograptus kiaeri* (Monsen 1925) comb. nov.

Plate 17, figs. 1-5; text-fig. 2

1925 *Didymograptus kiäri* Monsen, pp. 172-5, pl. 2, figs. 9-10, 12-14, 16, pl. 4, figs. 6-8, text-fig. 5a-c.

1925 *Didymograptus kiäri* var. *regularis* Monsen, pp. 175-6, pl. 2, figs. 11, 15.

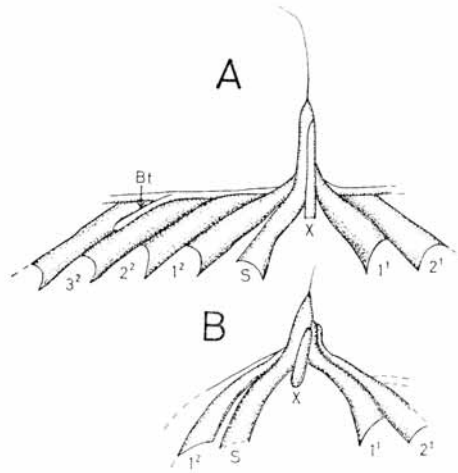


TEXT-FIG. 1. *Bryograptus ramosus* Brögger, from the Ceratopyge Shale, Zone 3 a $\beta$ , at Slemmestad, Oslo Region, Norway. A young rhabdosome in full relief, showing three primary branches, bithecae, and rather late secondary branching. The specimen is slightly distorted from excessive pyritization. PMO 72831;  $\times 13.5$ .

*Type data.* The lectotype, selected now by Monsen, *in museo*, is PMO 60212a, from Zone 3a $\beta$ , subzone b, at Stensberggaten in Oslo. The lectotype of *D. kiaeri regularis* is PMO 60219, from the same horizon and locality.

*Material.* In the present material there are more than 100 specimens most of which are compressed. About twenty-five specimens and fragments are preserved in relief, and seven of them show the proximal part in relief. The original types of Monsen, and about fifteen topotypes have also been used.

*Description.* The rhabdosome consists of two horizontal branches, up to more than 2.5 cm. long each. Because most of the specimens are fragmentary or too densely crowded, it is difficult to give exact measurements for the length of the branches. The branches are



TEXT-FIG. 2. *Kiaerograptus kiaeri* (Monsen) from the *Ceratopyge* Shale, Zone 3 a $\beta$ , at Slemmestad, Oslo Region, Norway. Somewhat diagrammatic drawings. A, Specimen in obverse view; about  $\times 14$ . B, Proximal part of a distorted specimen showing how both th<sup>1</sup> and th<sup>2</sup> (or rather the stolothecca from which th<sup>2</sup> buds) originates high up on the sicula; based on specimen PMO 72834b, Plate 17, fig. 4; about  $\times 14$ .

1.5 mm. wide. The autothecae are short, straight, and oblique with rather short overlap in the distal parts of the branches, and curved downwards with more overlap in the proximal parts. There are about 11 to 12 autothecae in 10 mm., and they are about 0.65 mm. in longer diameter. The bithecae are placed alternately on each side of the branches. They are somewhat irregularly cylindrical (about 0.3 mm. in diameter) and their apertures are higher up than those of the autothecae.

The sicula is long, and inclined, often considerably so. The inclination seems always to be towards the second (th<sup>2</sup>) branch, but since it is difficult to tell which side is the obverse in most of the compressed specimens, and there are few uncompressed ones, this cannot be stated without some reservation. The nema is long (more than 8 mm. in most specimens).

The budding of the initial part of this species differs considerably as could be expected, from that found in *Didymograptus*. Only specimens showing the obverse views of the

proximal part are well preserved, and all attempts to prepare the reverse side from them have been in vain. The reverse side is therefore known only from a distorted specimen (Pl. 17, fig. 4), and a fragmentary specimen (Pl. 17, fig. 3), where the left part of the proximal portion is broken away. Owing to this and the sources of error introduced by the preservation, the interpretation given must be regarded as tentative (cf. text-figs. 2a, b).

*Discussion.* The type of budding is more related to that found in the Dendroids, as described by Bulman (1936, text-figs. 24a, b) but it differs in that the first theca gives rise to two other primary thecae very high up on the sicula. One of them (X in text-fig. 2) is interpreted as the first bitheca, and the other as the first theca of the second branch. (In order to conform with Bulman's figure: the term X should be bi 1; first theca (1'), should be  $1^0+1^1+th1^1$ , &c. Since the present material does not allow such a delicate anatomic discrimination, the terminology has been somewhat simplified.)

Except for the first (X), bithecae are not found at the first thecae. Normally they do occur at the third or fourth autothecae on each branch. There are no specimens in which the first bithecae can be seen in both branches simultaneously because of the fragmentary nature of the specimens, but in the branches where this feature can be clearly observed, five specimens show the first bitheca after the third autotheca (such as in text-fig. 2a), and three specimens after the fourth theca. The number of observations of this kind is higher than the total of well-preserved proximal parts owing to the fact that the proximal part is compressed in a number of specimens where the branches are preserved in relief.

The sicula is long and conical, and where the branches originate it bends slightly towards the second branch. In this feature the distal part of the sicula resembles the distal part of the first thecae in *Didymograptus*, and the usual appearance of the specimen (Pl. 17, fig. 5) is at first glance puzzling, because the sicula resembles the first thecae, and the X resembles the sicula in externally similar Dichograptids. Other specimens (Pl. 17, fig. 4) reveal the three thecae originating from the proximal part of the sicula.

A certain amount of variation is found in this species, but it is difficult to discriminate between real variation, and changes due to different preservation. In some specimens the theca X is almost as long as the sicula, and especially in the small specimens there are distinct slits between the distal parts of the thecae (cf. Monsen 1925, pl. 2, figs. 15–16, text-fig. 5a). This is less well developed in old (large) specimens, and in the distal part of the branches.

*Remarks.* The only species referred to *Kiaerograptus* at present is the type species, but it possibly includes several species now referred to *Didymograptus*. Among the Tremadocian and Lower Arenigian didymograptids which might be suspected to have bithecae, many belong to the *geometricus*-type of branching, with two straight or slightly curved branches meeting at about  $120-150^\circ$  (*D. pritchardi* T. S. Hall, *D. taylori* T. S. Hall, *D. klotschichini* Obut 1961, and *Didymograptus* sp. of Bulman 1954, pl. 5, figs. 7–9). *D. primigenius* Bulman shows the increase in width of branches found in the *D. extensus* group, and might be a real graptoloid. More similar to *K. kiaeri* in rhabdosome shape are *D. abnormis* Hsü, *D. novus* Berry 1960 and *D. latus* T. S. Hall, the latter of which is found in Zone 3 b $\alpha$  (the basal Arenig) in the Oslo District.

*D. norvegicus* Mosen (1925, pp. 176–7, pl. 2, figs. 6–7; pl. 4, figs. 4–5; text-fig. 6) is another Tremadocian species, from the same horizon as *K. kiaeri*. Like *Tetraraptus kolderupi* Mosen it is found only at the type locality in Oslo (Stensberggaten), which is also the type locality for *Triograptus osloensis* Mosen. All these three species have the same size and shape of the sicula, the same width of the branches, and the same type and size of thecae. The latter are easily identified, being widely conical, and apparently loosely connected. In the type material there are, besides several hundred branch fragments, about ninety-five good specimens of *Triograptus osloensis*, five to six of *D. norvegicus*, and two to three of *T. kolderupi*. It is impossible to separate these three species on branch fragments only, but very easy to discriminate between them and all other graptolites in the same horizon.

This might indicate either that they all belong to one species with a somewhat erratic mode of branching, or that they belonged to a very rapidly developing lineage. The latter was the view held by Mosen (1925, p. 171). The presence of specimens with abnormal budding in *Triograptus osloensis*, such as the specimen figured by Mosen (1925, pl. 3, fig. 7), where the third branch might not be primary, but seems to bud from the second theca in one of the other branches, might suggest the former hypothesis. It is also possible that the peculiar thecal structure made the branches brittle, and *D. norvegicus* may only be specimens of *T. osloensis* from which one branch has been broken off. This problem will, however, have to be studied in more detail on better material, and at present it may only be concluded that the three species in question evidently form a closely related, and possibly isolated, group.

Mosen (1925, pp. 175–6, pl. 2, figs. 11, 15) distinguished a separate variety of *K. kiaeri* (*regularis*). After studying the type material, and the new material described here, the author is inclined to regard the specimens referred to this variety as falling within the normal limits of variation of *K. kiaeri*.

In spite of having only two primary branches, this genus seems to fit conveniently into the family Anisograptidae. This family is somewhat heterogeneous, embracing all few-branched dendroids, even if their number of primary branches is unknown, or less than three. The asymmetrical sicular part of *K. kiaeri* suggests that it might have developed

## EXPLANATION OF PLATE 18

All specimens belong to Paleontologisk Museum, Oslo, Norway. The specimens shown in figs. 2, 8, and 9 are photographed from latex casts coated with ammonium chloride. The other specimens are photographed directly, without coating.

Figs. 1–10. *Adelograptus? bulmani* sp. nov. 1, Proximal parts of two specimens, the upper one a left-handed specimen in obverse view, and the lower one a right-handed specimen in reverse view (text-fig. 3A is based on the lower specimen); PMO 72835b–c;  $\times 13$ . 2, Distal branch showing 'Leptograptoid' thecae; PMO 72836c;  $\times 6$ . 3, Proximal part, 'right' specimen, reverse view; PMO 72835g;  $\times 13$ . 4, Proximal part, 'left' specimen, reverse view; PMO 72835h;  $\times 13$ . 5, Proximal part, 'right' specimen, obverse view; PMO 72835i;  $\times 13$ . 6, Proximal part, 'right' specimen, obverse view, having only the first bitheca and th<sup>1</sup>; PMO 72835e;  $\times 13$ . 7, Proximal part, 'right' specimen, obverse view showing the small th<sup>2</sup>; PMO 72835d;  $\times 25$ . 8, Proximal part, 'right' specimen, reverse view, with a constriction of the proximal part of the sicula (prosicula?); PMO 72836a;  $\times 21$ . 9, Proximal part, 'right' specimen, obverse view, showing sicula, first bitheca and th<sup>1</sup>. The peculiar fringes on the aperture of the sicula might be due to pyritization; PMO 72836b;  $\times 21$ . 10, Proximal part of two adult specimens; the upper one a 'left', and the lower, the holotype, a 'right'; PMO 72835f and PMO 72835a (holotype);  $\times 25$ .

from originally three-branched forms, and the genus is therefore, at least provisionally, referred to the Anisograptidae.

*Adelograptus? bulmani* sp. nov.

Plate 18, figs. 1-8; text-figs. 3, 4

*Type data.* The holotype is PMO 72835a, a rhabdosome with five thecae preserved in half relief in pyrite. It is from the upper part of the *Ceratopyge* Shale (Zone 3 a $\beta$ ) in a road section in Bodalen, about 1.5 km. WSW. of Slømmestad, in the Oslo District, Norway. On the same slab as the holotype there are several other specimens of this species in various stages of development, some of which are figured in this paper. They are preserved in pyrite, in half or full relief.

*Material.* About fifty specimens, mostly proximal parts, preserved on two small shale slabs from the type locality.

*Diagnosis.* Species probably referable to *Adelograptus*, having the system of initial budding and general shape of rhabdosome found in that genus. The sicula is very long, and the long, overlapping thecae have almost leptograptoid apertures. Only two branches have been observed; if further branching occurs, it is irregular and in the distal parts of the rhabdosome. No bitheca except the first one has definitely been ascertained. Left- and right-handed forms occur.

*Description.* The rhabdosome is small, consisting of two horizontal to slightly reclined branches. In most of the specimens in which the sicula is preserved, the branches are short, three or four thecae on each as a maximum. There are a few specimens with longer branches, up to six thecae.

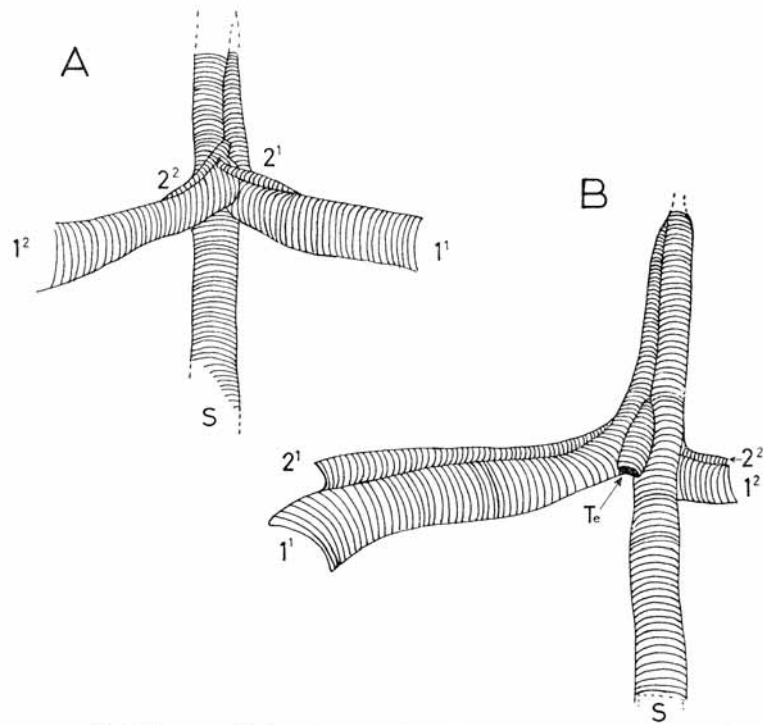
The thecae are long, gradually tapering and with a considerable overlap. Three thecae are observed in a cross-section of a branch. The thecae occur alternately on both sides of the branch, and cross in their initial part, just after budding. The apertures of the first thecae on each branch are curved slightly down, but subsequently are directed distally. In the specimens preserved in half relief, most of the thecae seem to be of the dichograptid type, or intermediate between this and the leptograptoid. Among the specimens preserved in full relief, there are some branch fragments, presumably belonging to this species, which appear to be more like the leptograptoid type of thecae (Pl. 18, fig. 2).

The proximal part is preserved in an astonishing number of the specimens, in fact most of the material seems to consist of immature specimens, showing the sicula, and only some few thecae (text-figs. 3-4). In some specimens (Pl. 18, fig. 8) a well-defined prosicula-like structure is seen. This feature is not consistently found, and might be due to the capricious effects of the pyritization. The sicula is long and narrowly conical, almost cylindrical. The first theca (1<sup>1</sup>) buds from the proximal part of the metasicula, follows it until about half-way down, and turns at right angles to the sicula. The proximal part of the first theca is irregularly cylindrical. It is also remarkable in budding alternately from the right (normal) and left side of the sicula. The 'left' specimens are fewer in number than the normal ones, but because of the difficulty in determining this feature with absolute certainty, no exact ratio between the two forms can be given. It appears to be about 1:3 or 1:4.

Subsequent budding seems to be somewhat different in the 'left' and normal specimens, but because of the lack of 'left' material preserved in reverse view (only two specimens) this could not be definitely stated with the present material.

In addition to these thecae there is a special one, which buds from  $1^1$ , before the origin of  $2^1$ , and is interpreted as the first bitheca.

In the branches, bithecae have not been observed. This does not exclude their presence, because a number of the specimens are broken at the critical points (Pl. 18, fig. 7), and in



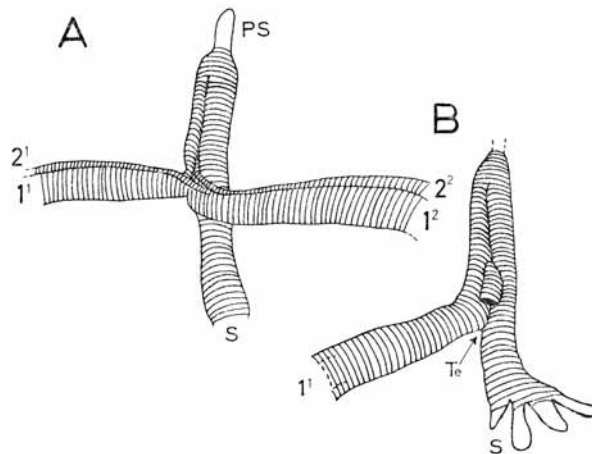
TEXT-FIG. 3. *Adelograptus? bulmani* sp. nov. from the *Ceratopyge* Shale, Zone 3 a $\beta$  at Slemmestad, Oslo Region, Norway. A, Proximal part of a 'right' specimen (drawing based on specimen PMO 72835b, Plate 18, fig. 1); about  $\times 30$ . B, An obverse view (drawing based on specimen PMO 72835d, Plate 18, fig. 7); about  $\times 30$ . S, sicula; Te, first bitheca.

others diffuse swellings of the branches are observed both where bithecae are to be expected, and in other places. These swellings are in most cases probably due to preservation (pyritization), but might in some cases be due to bithecae. Such suspect structures are generally found in the more distal parts of the branches, but have occasionally also been observed in connexion with the early thecae (cf. the extreme left part of the lower specimen in Pl. 18, fig. 7). The first bitheca is always large and distinct, and if other bithecae are present, they must be considerably smaller and less developed.

The branching of the rhabdosome is also difficult to ascertain. In *A. hunnebergensis* the second-order branching generally takes place after the second or third thecae. A great



number of specimens of *A. ? bulmani* with short branches do not show any second-order branching. This indicates that if second-order branching was present, it took place after the fifth theca, or by lateral budding in branches longer than five theca. None of the longer branch fragments ascribed to this species show branching, but in the same beds there is what is believed to be another species of *Adelograptus* which differs from *bulmani* in having somewhat thinner branches, and shorter, more conical sicula. This species, which is less well preserved than the material of *bulmani*, shows second-order branching rather regularly at the fourth or fifth thecae. Unless the preservation is very good, it might be difficult to discriminate between distal branches of these two species.



TEXT-FIG. 4. *Adelograptus? bulmani* sp. nov. from the *Ceratopyge* Shale, Zone 3 a $\beta$ , at Slemmestad, Oslo Region, Norway. A, The proximal part of a 'left' specimen in reverse view (drawing based on specimen PMO 72836a, Plate 18, fig. 8); about  $\times$  30. B, Proximal part of 'right' specimen in obverse view (drawing based on specimen PMO 72836b, Plate 18, fig. 9); about  $\times$  30. PS, prosicula; S, sicula; Te, first bitheca.

*Remarks.* The affinities of this species are somewhat obscure. It superficially resembles a primitive Leptograptid in the thecal budding in the proximal part, in the direction of the thecae (except the first ones), and in the general shape of the rhabdosome. It differs from the later Leptograptids in the almost cylindrical metasicula, which is regarded as a dendroid feature (Kozłowski 1960), in having the primary branches diverging near the middle of the metasicula instead of near the aperture, in the presence of the first bitheca, and in the existence of 'left' and 'right' forms.

There is a suggestion (text-fig. 4) that th<sup>2</sup><sub>2</sub> arises from th<sup>1</sup><sub>1</sub> and, if this should prove to be correct the type of development, differs fundamentally from any of the types described by Bulman (1955, p. V56).

A closer examination of the initial and distal budding suggests that it is closely related to that in *Adelograptus* (cf. Stubblefield 1929, text-figs. 2, 4, 6, and especially Bulman 1941, text-fig. 1) except that the bithecae (other than the first one), are apparently missing.

It is possible to imagine a development of the leptograptoid type of budding directly from that found in this species, but until intermediate forms are found and much more detailed studies are made, this hypothesis could not be seriously considered. If, however, the distal bithecae really are missing in *A.?* *bulmani*, it might represent a transitional form between the Dendroids and Graptoloids such as *Kiaerograptus*. As mentioned above, it is difficult to show this and other important anatomical features beyond doubt, and the species is therefore, with some doubt, left in *Adelograptus* for the time being. There can be little doubt that it is a descendant of one of the typical representatives of that genus.

#### GENERAL REMARKS

The presence of bithecae in virtually all upper Tremadocian species which are sufficiently well preserved to show this feature clearly, might indicate that there were few if any graptoloid graptolites before the Arenig. Most Tremadocian graptolites could either be referred to the dendroids, or they are preserved only as mineralized films, and their alleged graptoloid affinities are based only on their astogenic resemblance to various Dichograptids. The discovery of a two-branched, extensiform dendroid indicate that such criteria might not be valid in all cases, and in order to prove that species belong to the graptoloids, more evidence than number of branches and angle of branching is necessary. It is possible that the widening of the stipes characteristic of the didymograptids of the *extensus*-group, which is less prominent in *Kiaerograptus kiaeri*, might be useful in specimens where the presence or absence of bithecae could not be ascertained. It is still possible that there were some graptoloid graptolites in the Tremadoc, but they were certainly fewer than hitherto supposed, and the remaining records must be carefully checked before they can be definitely accepted as graptoloids.

It is also possible that a number of species in the lower Arenig now parading as dichograptids really are few-branched dendroids, only that the bithecae are overlooked because of the state of preservation of the material. Such species might be suspected in the *Bryograptus-Tetragraptus fruticosus-Didymograptus protobifidus* lineage, and in didymograptids of the *geometricus* type, because their constant angle of branching (120–150°) might indicate that they are descendants of three-branched forms. *Didymograptus latus* T. S. Hall, which was shown by Thomas (1961, p. 9) to be as highly developed as the later *D. hirundo*, might also belong to an entirely different group, perhaps that of *Kiaerograptus kiaeri*, or might be one of its descendants. Both have, in contrast to the *extensus*-group, long nemas and branches of uniform width.

The presence of bithecae in *K. kiaeri* has also some phylogenetic significance, showing that the tendency to branch-reduction went as far as two-branched forms in the dendroid graptolites. It also gives support to Bulman's (1954a, p. 208; 1958, p. 161) view that the transition between the dendroids and graptoloids was a gradual one, taking part in several lineages independently. This transition was not necessarily contemporaneous in all lineages, but seems to have taken place frequently about the Tremadoc–Arenig boundary.

*K. kiaeri* is an intermediate species between the Dendroidea and the Graptoloidea. The autothecae, the general shape of the sicula, and the absence of bithecae at the first autothecae are graptoloid features, whereas the initial budding and the bithecae at the distant parts of the branches are dendroid ones.

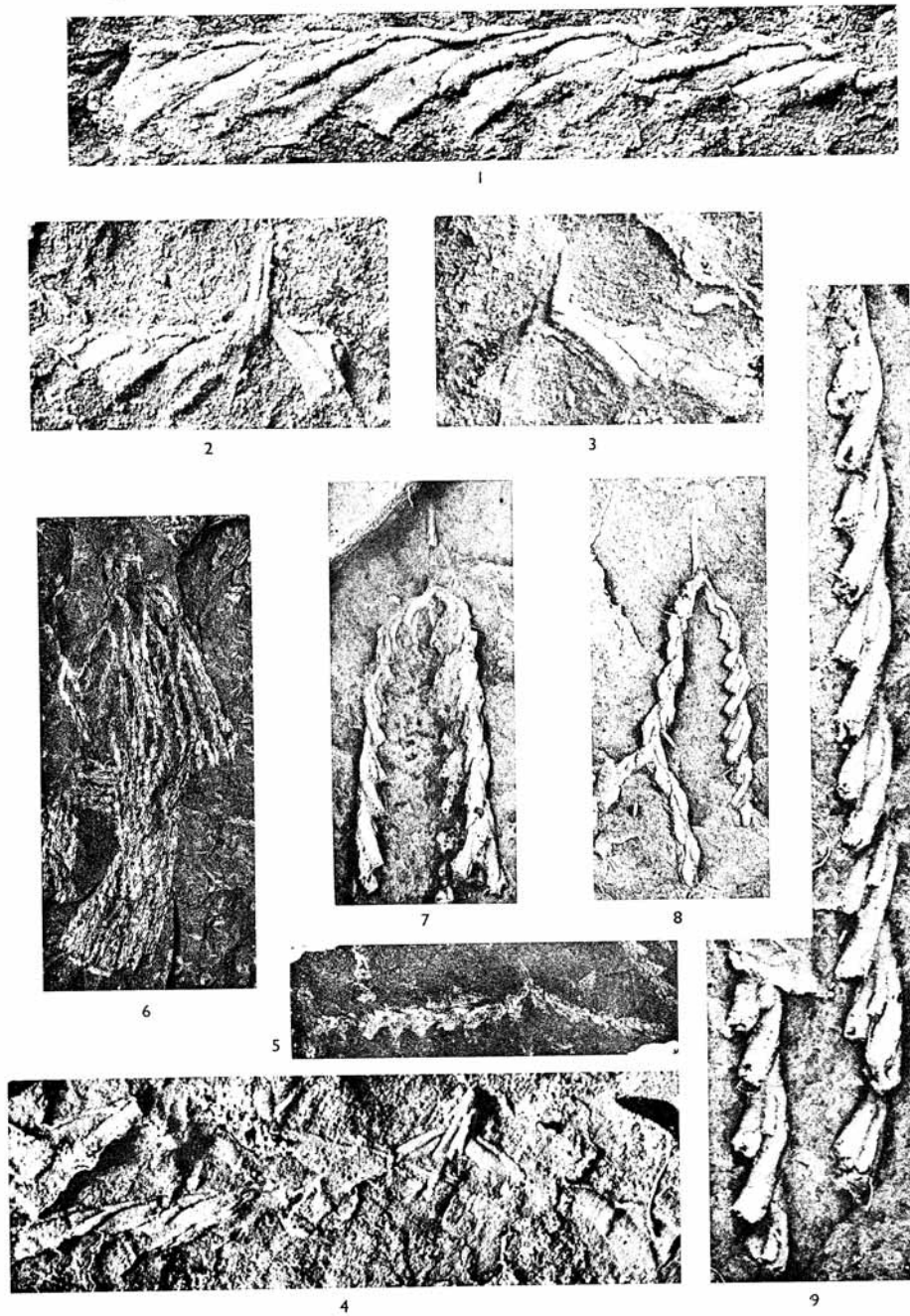
Urbanek (1960) in a recent paper discussed the evolutionary changes in graptolite colonies. He drew attention to the well-known fact that in Monograptids new thecal types are often introduced in the proximal part of the colonies. This might also be the case with *K. kiaeri*, where the new type of thecae (without bithecae) is found in the proximal part of the branches. If more complete material had been present, it might have been possible to follow the development from a purely dendroid two-branched form through types like *K. kiaeri* to extensiform graptolites without bithecae, such as in the evolutionary lineages referred to by Urbanek, but in this case from one order to another. This might indicate that studies on thecal variation might be of considerable phylogenetic importance in the Dendroids and Dichograptids also.

## REFERENCES

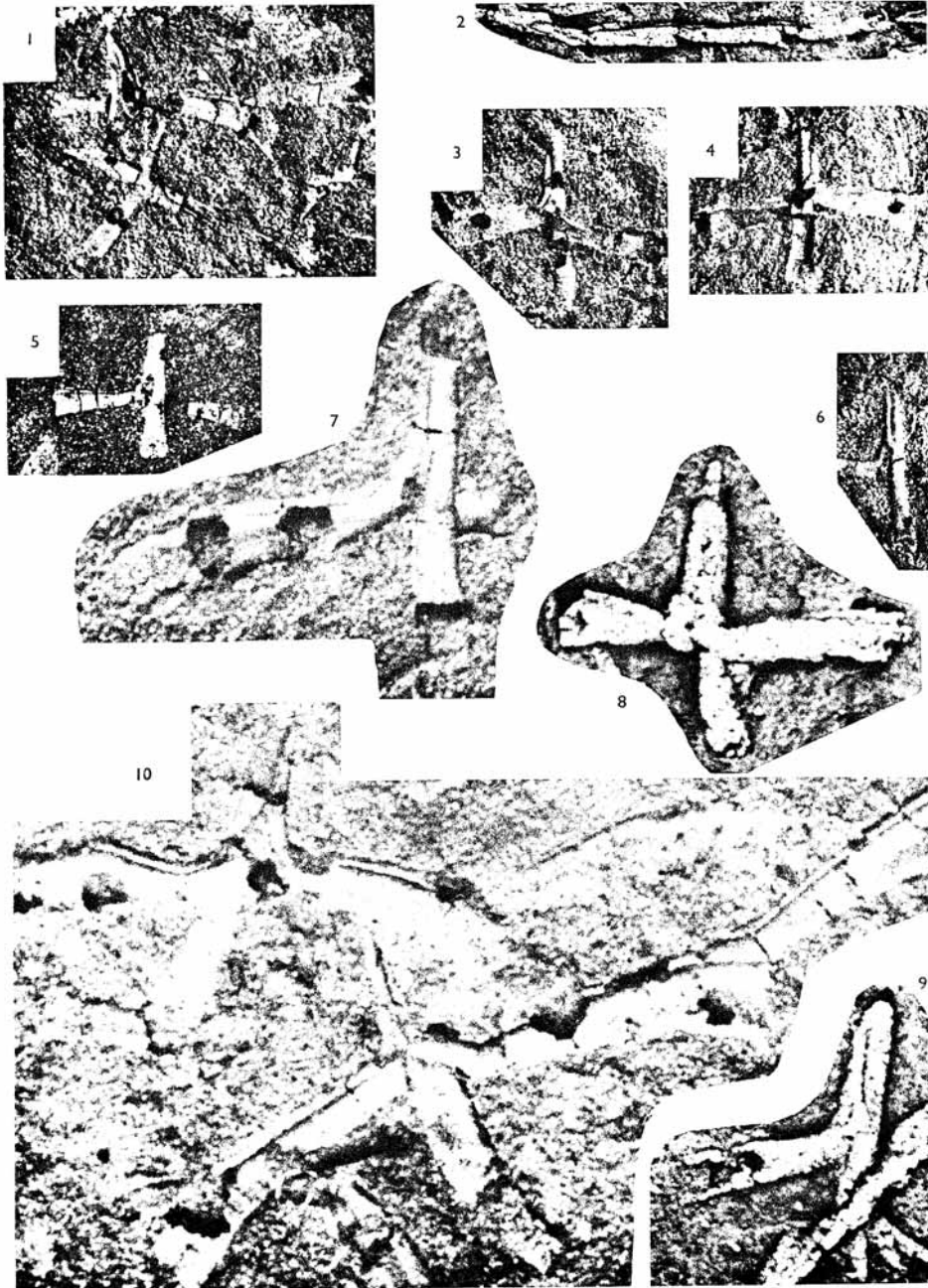
- BROGGER, W. C. 1882. *Die Silurischen Etagen 2 und 3 im Kristianiagebiet und auf Eker*. viii+376 pp., 12 pl. Christiania (Oslo).
- BULMAN, O. M. B. 1936. On the Graptolites prepared by Holm. Part. VII. The Graptolite fauna of the Lower *Orthoceras* Limestone of Hälludden, Öland, and its bearing on the evolution of the Lower Ordovician Graptolites. *Arkiv f. Zool.* **28A**, 17, 107 pp.
- 1941. Some Dichograptids of the Tremadocian and Lower Ordovician. *Ann. Mag. Nat. Hist.*, ser. 11, **7**, 100–21, pl. 2.
- 1950. Graptolites from the *Dictyonema* shales of Quebec. *Quart. Journ. Geol. Soc. London*, **106**, 63–99, pl. 4–8.
- 1954. The Graptolite fauna of the *Dictyonema* shales of the Oslo Region. *Norsk Geol. Tidsskr.* **33**, 1–40, pl. 1–8.
- 1954. Status of invertebrate paleontology: Graptolithina. *Bull. Mus. Comp. Zool.* **112**, 201–15.
- 1955. Graptolithina. In MOORE, R. C. ed.: *Treatise on Invertebrate Paleontology, Part V*, 101 pp.
- 1958. The sequence of Graptolite faunas. *Palaentology*, **1**, 159–73.
- HOLTEDAHL, O. and DONS, J. A. 1957. Geological guide to Oslo District. *Skrifter Vidensk. Akad. Oslo*, I, Mat.-Nat. Kl. 1957, **3**, 86 pp.
- KOZŁOWSKI, R. 1960. *Calyxdendrum graptoloides* n. gen. n. sp., a Graptolite intermediate between the Dendroidea and the Graptoloidea. *Acta Paleont. Polonica*, **5**, 107–25.
- MONSEN, A. 1925. Über eine neue Ordovicische Graptolitenfauna. *Norsk Geol. Tidsskr.* **8**, 147–87. 4 pl.
- STUBBLEFIELD, C. J. 1929. Notes on some early British Graptolites. *Geol. Mag.* **66**, 268–85.
- THOMAS, D. E. 1960. The zonal distribution of Australian Graptolites. *Journ. Proc. Roy. Soc. New South Wales*, **94**, 1–58, 15 pl.
- URBANÉK, A. 1960. An attempt at biological interpretation of evolutionary changes in Graptolite colonies. *Acta Paleont. Polonica*, **5**, 127–234, 3 pl.

NILS SPJELDNE  
 Institutt for Geologi,  
 Blindern, Oslo,  
 Norway

Manuscript received 30 March 1962



SPJELDNÆS, Upper Tremadocian graptolites



SPJELDNÆS, Upper Tremadocian graptolites