Graptolites from the *Ludibundus* Beds (Middle Ordovician) of Tvären, Sweden

By

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ABSTRACT.—Graptolites have been isolated from limestone boulders derived from the bay of Tvären in Södermanland. Growth series are described for *Dicellograptus divaricatus* var. *salopiensis* ELLES & WOOD and *Climacograptus brevis* var. *mutabilis* nov. and the development of the proximal end in *Acanthograptus suecicus* (WIMAN) is determined from serial sections.

Contents

Preface

In the years prior to 1940, a considerable number of fossiliferous limestone boulders was collected from Tvären by members of the Swedish Geological Survey and an account of these specimens with their fauna was given by Dr. P. THORSLUND in 1940. The few graptolites mentioned had been identified by Dr. O. M. B. BULMAN and had been lying in Cambridge for some time before he suggested to me that I might undertake a detailed study of the material which promised to yield growth series of some forms.

In the summer of 1948, I was fortunately able to visit Sweden and I must express my deep thanks to the authorities in Stockholm and Uppsala who provided me with every facility for the study of HOLM's and WIMAN's type specimens and for further material from Tvären.

Throughout the work, Professor BULMAN has provided advice and helpful criticism on the many problems of morphology and taxonomy. To him and to Dr. VALDAR JAANUSSON who has guided this through the press, I must also express my sincere thanks.

Introduction

The material studied from Tvären consists of fragments of glacially transported boulders occurring on several islands in the Baltic, immediately south-east of the bay of Tvären on the coast of Södermanland, about 70 km S. of Stockholm.

The boulders, which include fossiliferous Ordovician rocks, were first noted in geological literature in 1927 by ASKLUND and WESTERGÅRD. From detailed studies of the boulder fan, ASKLUND concluded that the boulders came from solid beds in the bay and were transported south-east by ice from the mainland.

The bay is roughly triangular, bounded on two sides by the mainland, and on the Baltic side by numerous islands. The deepest part of the bay is slightly eccentric but the submarine contours between 20 m and 60 m are roughly circular. Glacial striae on the islands show that the general directions of ice movement was to the south-east from the mainland, and the boulders lie in a well defined fan whose apex is a point on the mainland immediately north of Tvären.

No similar beds or boulders are known in this area and there seems to be little doubt that the boulders of Ordovician rocks have come from Tvären where the beds are probably let down by faults forming a cauldron-like depression such as is suggested by the contours of the bay.

The limestone boulders are all fairly fossiliferous and have yielded numerous ostracods and brachiopods. The graptolites were only abundant in one boulder of a rather compact limestone, but occasional fragments were found in other boulders of a more highly crystalline limestone.

The shelly fauna has been studied in some detail by THORSLUND (1940) from whose paper the preceding information has been drawn.

The ostracods and brachiopods indicate that the Tvären limestones correspond to the lower part of the *Ludibundus* limestone as developed elsewhere in Sweden. The graptolites give very little evidence for correlation since the species have in most cases only been recorded from similar limestones in the Baltic area. The problems of correlation have already been discussed (JAANUSSON & STRACHAN, 1954) but further evidence is accumulating which may lead to some slight revision of the correlations given there.

Methods of Preparation of Material

The limestones are all fairly free from siliceous cement and were easily broken down to mud by treatment with dilute hydrochloric acid. The sludge was washed by decanting in various stages and much of the fine mud removed at the same time. The graptolites generally settled very quickly though a few floated and were picked off the surface with a pipette. When the mud had been largely washed away, the residue was examined in a petri dish under a low-power binocular microscope and the graptolites picked out with the pipette. Sponge spicules were very common in the residue and, in a few samples of highly crystalline limestone which were dissolved in dilute acetic acid, conodonts were also obtained. The majority of the conodonts belong to an apparently undescribed form which has also been found in abundance in the residue from the treatment of some *Ludibundus* limestone from Lockne in Jämtland.

The isolated graptolites were generally quite opaque and in some cases, e.g. the *Dicellograptus* and *Orthograptus uplandicus*, more or less crushed, but all the specimens of *Climacograptus brevis* var. *mutabilis* var. nov. were in full relief. Most of the specimens yielded to bleaching with concentrated nitric acid and potassium chlorate, the process being carried out in a watchglass and followed under the binocular microscope. The length of treatment required varied from ten minutes to about an hour, but no really satisfactory results were obtained when more than about half an hour of bleaching was required.

The specimens of *Dendrograptus* and *Acanthograptus* had already been isolated and no more were obtained in the further material treated. A few pieces of these dendroids were treated with the bleaching mixture but did not bleach at all well. In most cases, prolonged treatment was needed to make the specimens even partly translucent and such specimens generally dissolved in the clearing or mounting media. The same trouble has since been met again in dealing with some diplograptids and there appears to be some considerable chemical change on prolonging the bleaching process. The difficulty with the dendroids appears to be the presence of a thick cortical layer outside the fusellar layer which shows the growth lines.

Specimens of the dendroids were serially sectioned in an ordinary microtome since they could not be bleached, but only *Acanthograptus suecicus* yielded sections showing any internal structures. These, however, are remarkably well preserved and some details of the stolon system can be observed. A few fragments, similar to some of those figured by Kozłowski (1949) and placed in his orders *Tuboidea* and *Camaroidea*, have also been found but they are too small for any determinations of value to be made.

All the material described here belongs to the museum of the Palaeontological Institute of the University of Uppsala.

The illustrations have been mostly prepared by means of a camera lucida though attempts have been made to photograph some of the specimens. The difficulties in the photography are the reddish-brown colour of the specimens and the considerable depth of focus required at even moderate magnifications. Infra-red photography might solve the first difficulty and has been used with some success by KRAFT (1926) in his studies on diplograptids, but the second is a general difficulty in photographing small objects which are rarely sufficiently flat to lie within the depth of field of suitable microscope objectives. While the wash drawings are to a certain extent subjective and do not, for example, reproduce all the imperfections of the specimens, it is hoped that they give a sufficient idea of the specimens to enable the details of the structure to be grasped.

Systematic Palaeontology

Family *Dicranograptidae*

Genus *Dicellograptus*

Dicellograptus divaricatus var. *salopiensis* ELLES and WOOD

Pl. I, figs. 1–5, Pl. II, fig. 1, text-figs. 1, 2.

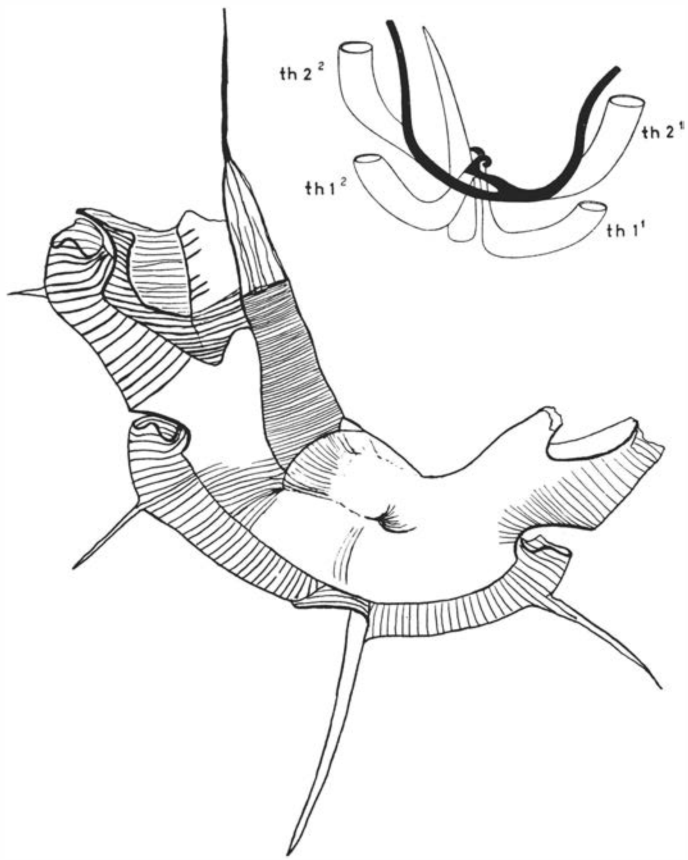
1904 *Dicellograptus divaricatus* var. *salopiensis* var. nov. — ELLES and WOOD, p. 145, pl. XX, figs. 7 a–e, text-fig. 89 a, b.

Stipes 5 mm or more long, about 0.5 mm broad, diverging at a very variable angle from the sicula which is embedded in one stipe; thecae 12 in 10 mm, with introverted and introtorted apertures opening into and almost filling the rather deep excavations.

The sicula is about 1.5 mm long and has an apertural breadth of 0.2 mm. There is a very long virgella (up to 1 mm) but no apertural processes. The first two thecae are provided with long mesial spines which, however, are frequently broken. The whole sicula appears to be curved in the later stages of growth so that it is incorporated in one of the stipes.

Only a few specimens have been observed with more than 3 thecae and they are all so distorted that no reliable measure of the axial angle can be made. The sicula is always incorporated into the second stipe with th 2^2 and th 3^2 but the tip of the prosicula is generally free and prolonged into a short nema. The adult thecae are about 1.2 mm long and overlap for half their length. They narrow towards their apertures which grow distinctly inwards to open into deep excavations occupying about half the breadth of the stipe (text-fig. 2). The early thecae may bear a mesial spine.

The development of the rhabdosome can be followed in some detail as a growth series has been obtained. The prosicula is 0.4 mm long and 0.12 mm broad at its aperture. It shows the typical spiral line and two sizes of longi-

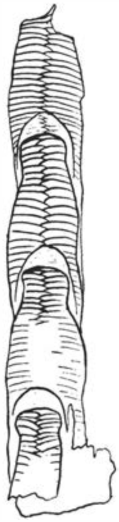


Text-fig. 1. *Dicellograptus divaricatus* var. *salopiensis* ELLES and WOOD. Partial restoration from several specimens. ×42. Tvären.

tudinal fibres, only the strong fibres reaching the apex (Pl. I, fig. 3). The stout virgella is initiated when the metasicula is about half grown, i.e. when 0.5 mm long. It develops very rapidly into a long process and the later growth lines are markedly bent aperturally on both sides of the virgella in the fully developed sicula (Pl. I, fig. 4, Pl. II, fig. 1).

The initial foramen is formed by resorption near the beginning of the virgella, i.e. relatively low down (Pl. II, fig. 1), and the initial bud grows across the head of the virgella and down towards the sicular aperture (Pl. I, fig. 5) for a short distance before developing a hood on the reverse side which is the first part of th 1^2. Th 1^1 continues growing down to the sicular aperture and then turns at right angles outwards for 0.5 mm before developing a spine and turning slightly upwards.

The sides of the aperture of th 1^1 are marked by a pair of lappets formed by two or three growth bands which do not extend round the inner edge of the aperture. The apertures of all the thecae appear to be free for a short



Text-fig. 2. *Dicellograptus divaricatus* var. *salopiensis* ELLES and WOOD. Fragment of stipe showing adult thecae. Approx. × 22. Tvären. T 287.

distance from the excavated portion of the next theca and the apertural portions of the thecae are thus free tubes, a condition not seen in adult diplograptids (text-fig. 1).

Th 1^2 develops by growing in an S-shaped manner from its initial foramen, first across on to the sicula (probably slightly upwards, though it cannot be definitely traced by growth lines), then down towards the sicular aperture (giving off the initial part of th 2^1) and finally swinging further across the sicula and extending freely at approximately right angles to the free virgella for about 0.5 mm, developing a spine similar to that on th 1^1. Its aperture is rather more introverted than that of th 1^1 owing to a broader development of the growth bands on the outer side of the theca. On the reverse side of the rhabdosome a small triangular portion of the sicula near the aperture is left uncovered between the lower parts of th 1^1 and th 1^2.

Just after th 1^2 has turned downwards towards the sicular aperture, a second hood is formed on its th 1^1 side. Owing to the prolonged bleaching required to render the specimens at all transparent, very few traces of growth lines have been left in this region of development and the growth of the third and fourth thecae cannot be followed in detail. This second hood grows outwards and downwards on its upper edge, the lower edge forming a pivot as is seen by the thickening of the edge. No trace has been seen of any flange growing up from th 1^1 to meet the downgrowing part of the hood and the formation of the two foramina for th 2^1 and th 2^2 cannot be seen. These two thecae however grow along the upper sides of the first two thecae from this point, the initial part of th 2^2 being considerably longer than that of th 2^1 (text-fig. 1). The two branches of the rhabdosome are developed by budding from these two thecae. The beginning of th 3^2 can be seen in one specimen (Pl. 1, fig. 2) but its exact relations to th 2^2 are obscure.

This mode of development is very similar to that of *Dicranograptus nicholsoni* HOPK. (BULMAN, 1944, p. 38). The sicular proportions are the same but the virgella arises much earlier in the *Dicranograptus* and the initial bud slightly earlier. The slight upward growth in the initial part of th 1^2 has been noted in *Dicranograptus nicholsoni* and also in some early diplograptids. The proximal end in *D. divaricatus* is much more compact than that of *Dicellograptus geniculatus* BULMAN, where the initial part of th 2^2 is also conspicuously longer than the corresponding part of th 2^1 (BULMAN, 1932, p. 19). The apertures of the first two thecae in these show considerable modification from the simple type which appears in many diplograptids (especially in th 1^1), e.g. *Diplograptus leptotheca* BULMAN, *Orthograptus apiculatus* (ELLES and WOOD), *Climacograptus bekkeri* ÖPIK, *C. orthoceratophilus* BULMAN, the last two showing well the difference between the simple first pair and the later climacograptid thecae.

In the form of thecae and the characteristic position of the sicula, this species is very close to *Dicellograptus divaricatus* HALL (ELLES, 1940, p. 429), but the stipes are narrower and the specimens thus fall within the variety *salopiensis*.

WHITTINGTON has recently described a similar type of development from the Ordovician of Oklahoma (WHITTINGTON, 1955). Although he refers his material to *Leptograptus*? sp. ind., the thecal form of his specimens is that characteristic of *Dicellograptus* and they have an open proximal end like that of *Dicellograptus geniculatus*.

Family Diplograptidae

Genus *Climacograptus*

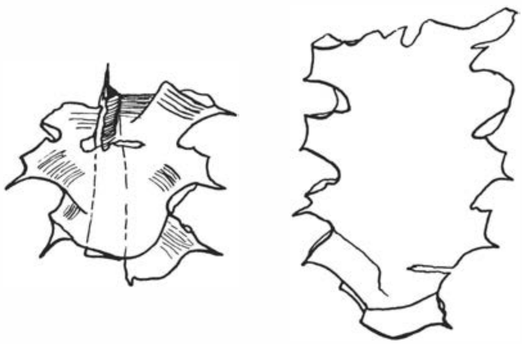
Climacograptus bekkeri (ÖPIK)

Text-figure 3.

1927 *Diplograptus bekkeri* n.sp. — ÖPIK, p. 28, pl. VI, figs. 1–15.
1932 *Climacograptus haljalensis* n.sp. — BULMAN, p. 10, pl. II, figs. 1–34, text-figs. 4–6.
1940 *Climacograptus bekkeri* (ÖPIK) — BULMAN, in THORSLUND, p. 114.

Only three specimens of this species have been obtained from the limestone blocks so far and they are all flattened. Little can therefore be added to the detailed descriptions given by ÖPIK and BULMAN. BULMAN has noted (in THORSLUND, 1940, p. 114) that his species quoted above is synonymous with the earlier described species of ÖPIK. The characteristic thecal spines distinguished this species from other Ordovician climacograptids.

It should be noted that the first theca is of the simple curved form found in most diplograptids and that its spine is almost apertural in position. The second theca is intermediate in form between th 1^1 and the later thecae which



Text-fig. 3. *Climacograptus bekkeri* (Öpik). Two young specimens. Approx. × 15. Tvären. T 288 and T 289.

show the sharp curvature characteristic of climacograptids and have spines which are mesial in position.

Climacograptus brevis var. *mutabilis* nov.

Pl. I, figs. 6–10, Pl. II, figs. 2–4, text-figs. 4–8, 9 (A).

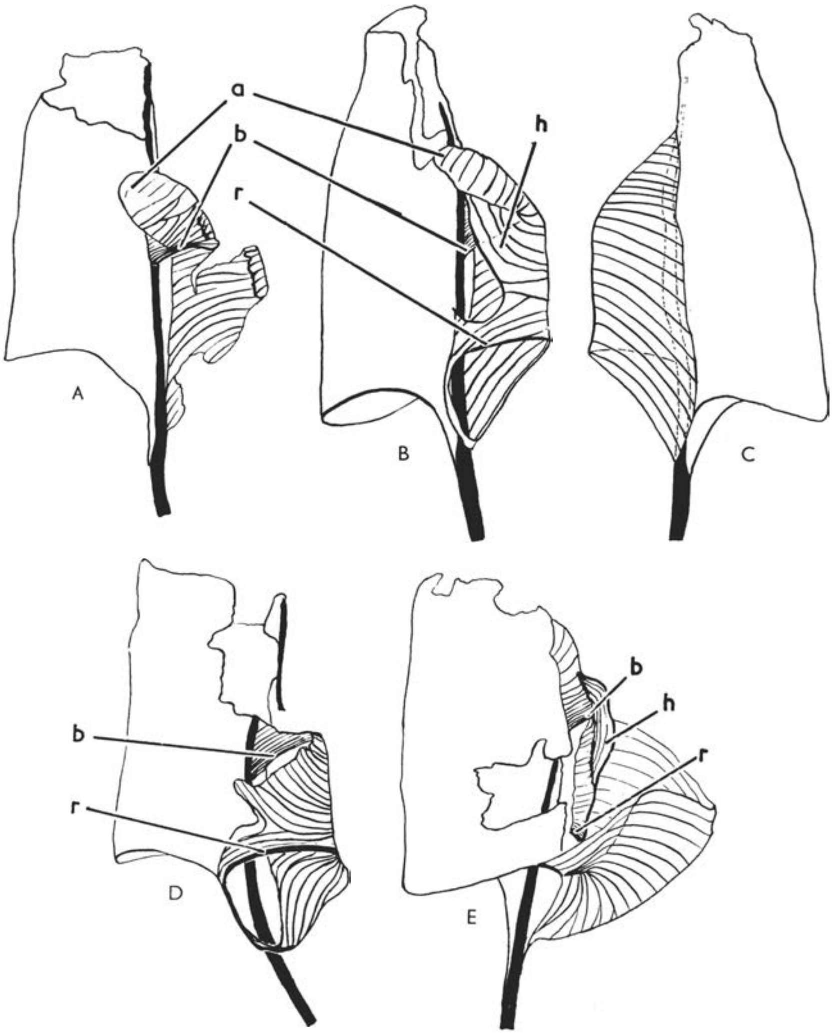
1940 *Climacograptus* aff. *kuckersianus* Holm MS, Wiman — Bulman, in Thorslund, p. 114.

Holotype is the specimen figured here as text-fig. 6. Rhabdosome up to 8 mm long and 1.5 mm broad, widening slowly throughout its length; thecae 14–15 in 10 mm, overlapping $\frac{1}{3}$ of their length; apertural excavations occupying $\frac{1}{4}$–$\frac{1}{3}$ of the length and about $\frac{1}{3}$ of the breadth of the rhabdosome; septum complete; virgula strong and wiry.

The sicula is 1.3–1.5 mm long, reaching to the level of the aperture of th 2^1, but as the prosicula passes gradually into the nema (later the virgula), its limits are difficult to determine exactly. The prosicula is about 0.3 mm long and has a breadth of 0.1 mm at its aperture. The virgella is developed in what appears to be the usual manner after about 0.3 mm of the metasicula has been formed (Pl. I, fig. 6) and is free for up to 0.5 mm at the sicular aperture where it is often thickened by material from th 1^1. The mouth of the sicula is even and without processes except for the virgellar side which is produced along the virgella (Pl. I, fig. 6).

The initial foramen is formed by resorption about halfway down the metasicula and probably before the growth of the sicula is complete, since in young specimens (e.g. Pl. I, fig. 6) it is nearer the aperture than in older ones.

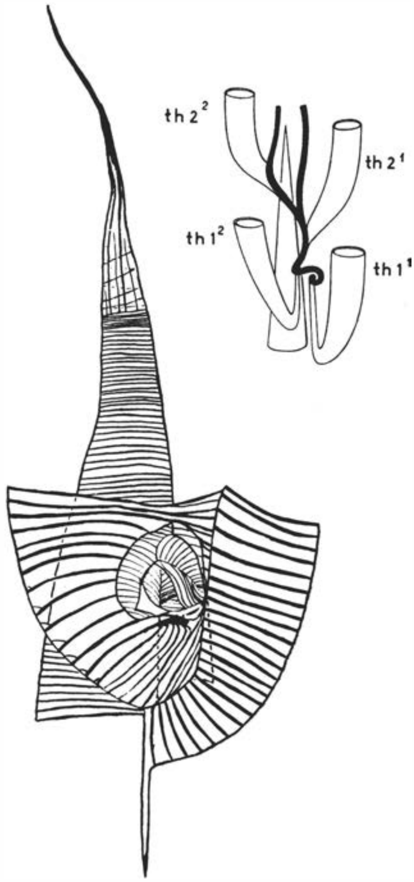
The initial bud grows across the virgella and down the sicula for a short distance before giving rise to the foramen for th 1^2. This is formed by the almost complete cessation of growth next the virgella, giving a thickened border (*b* in text-fig. 4), while growth continues on the outer edge so that a hood is formed. The upper edge of this hood grows across the initial bud, and slightly upwards, towards the virgella. The lower edge of the foramen is



Text-fig. 4. *Climacograptus brevis* var. *mutabilis* nov. Series of growth stages showing the development of th 1^1 and the initial part of th 1^2. Approx. × 100. *a*, initial bud. *b*, thickened border of initial bud. *h*, hood over foramen of th 1^2. *r*, selvedge formed at reflected part of th 1^1. Growth lines on sicula omitted; virgella shown solid black. A—T 290; B and C—T 302; D—T 291; F—T 292.

formed by a few growth bands which grow out from the virgella towards the hood and thus divide the opening into the two parts which develop into the first two thecae. These few growth bands are succeeded by the normal growth bands of th 1^1 continuing from the obverse side (text-fig. 4 D).

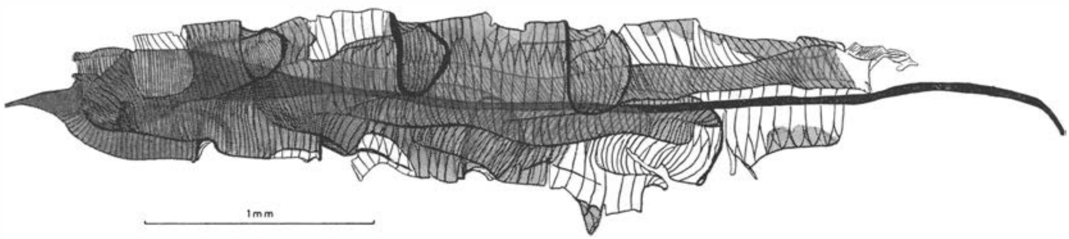
On the reverse side, the early part of th 1^1 ends at a thickened edge (*r* in text-fig. 4 D) where the theca is sharply reflexed. The upgrowing portion of th 1^1 on the reverse side has no direct contact with the earlier downgrowing part and completely encloses it. On the obverse side, the growth lines can



Text-fig. 5. *Climacograptus brevis* var. *mutabilis* nov. Reconstruction of proximal end partially dissected to show the initial bud and the bar between th 1¹ and th 1². × 50.

be seen to pivot on the point where the thickened edge "*r*" meets the outer thecal wall (Pl. I, fig. 10).

From its highest point, where the upper edge of the hood meets the sicular wall just below the initial foramen, the upper wall of th 1² appears to have grown downwards for a little before finally turning upwards and outwards. Between the sicular wall and the reverse wall of the rhabdosome there is a well-marked thickened bar which appears to be connected with the hood on its sicular side. It cannot be seen whether or not the hood is ever continuous down to this level (with the bar forming merely the thickened edge of the hood) but it is possible. In that case, th 2¹ would have to develop after th 1² had grown past the bar. The outer wall of th 1² is, however, entirely distinct from the hood. Its first few growth lines run across the angle of th 1¹ without interruption but the next two or three can be traced into the outer end of the bar in most specimens (text-fig. 7 A) and then on to the edge of th 1¹. In a few specimens (e.g. text-fig. 7 B), these growth lines cannot be traced into the bar which then appears to be attached to th 1¹



Text-fig. 6. *Climacograptus brevis* var. *mutabilis* nov. Largest isolated rhabdosome. Holotype. Tvären. × 30. T 293.

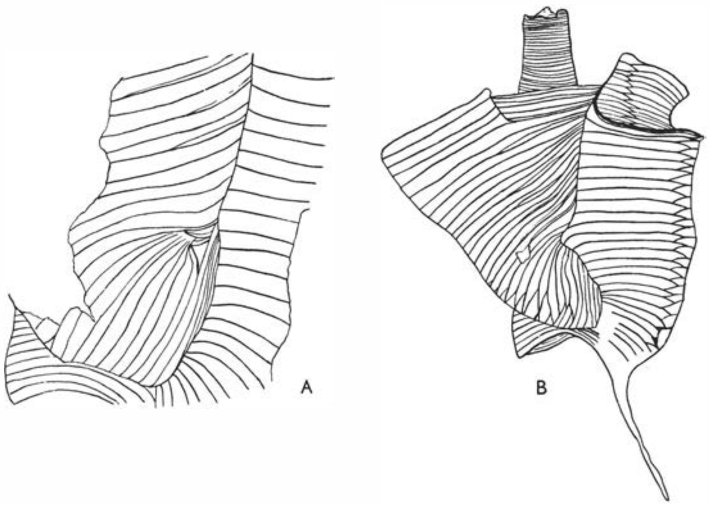
(see discussion below). At this stage, the growth lines near the bar are very close together while those at the ventral edge of th 1^2 are well spaced until the free ventral edge of the theca is nearly vertical. Continuous broad bands are then formed across the theca with some intercalated narrower ones at the inner margin above the bar indicating the development of the initial part of th 2^1. A second interpretation is therefore that the foramen for th 2^1 is between the observed part of the hood and the bar, which would then be formed between th 1^2 and th 2^1.

At the level of the first thecal aperture, the growth lines of th 2^1 become distinct from those of th 1^2 (text-fig. 7 B) and shortly afterwards those of the initial part of th 2^2 appear as intercalations.

Only a few specimens have been obtained which show satisfactorily the development of the later thecae. At the level of the second thecal aperture, the interthecal septum between th 2^1 and th 2^2 is formed and the growth lines beyond this are rather irregular for a short space before th 3^1 becomes distinct from th 2^2. At this point in one specimen (fig. 6), the median septum is initiated on the reverse side and a little above this, th 3^2 is developed. Later thecae are formed in linear series from these two which arise from th 2^2. Another specimen shows the beginning of the septum delayed still further as it arises between th 3^1 and th 3^2, the latter budding off just above the proximal end of the former.

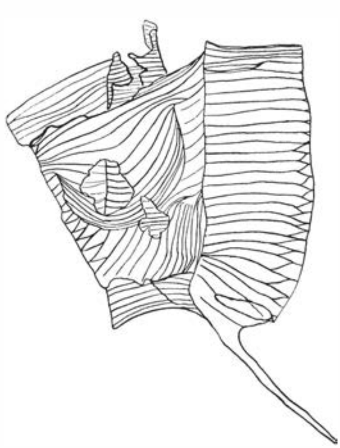
The median septum is marked by rather close but regular growth lines which tend to run diagonally instead of horizontally. The stout but flexible virgula connects the two parts of the septum so that the growth lines form an inverted V (text-fig. 6). The apertural margins are considerably thickened by secondary growth as are also the upper edges of the interthecal septa, which thus clearly delimit the margins of the excavations (text-fig. 6). The number of growth lines per theca decreases distally as has been noticed in other diplograptids but there is also apparently considerable variation in the number in the first theca alone, complete specimens having from 24 to 30 growth lines in the upgrowing portion of the theca.

The most interesting result from the examination of these specimens has been the discovery of the bar between the sicula and the outer thecal wall. As remarked above, no specimen shows the hood of the second thecal foramen



Text-fig. 7. *Climacograptus brevis* var. *mutabilis* nov. (A) Enlargement of part of Plate VI, fig. 5. × 120. T 286. (B) Young specimen showing th 1^1 and th 1^2, Approx. × 60. T 294. Tvären.

continuous with the bar although such a connection might easily be destroyed in preservation or the later preparation of the material. It seems unlikely, however, since several specimens show the hood at exactly the same stage as shown in text-fig. 4 B although th 1^2 may be complete. Text-fig. 7 A shows the disturbance in the growth lines of th 1^2 caused by the bar which must therefore have been formed after the start of the upward growth of th 1^2, unless the bar stood out as a free projection from the sicula which is unlikely. Text-fig. 7 B however shows another specimen in which the disturbance is confined to the development of a sinuous junction of th 1^1 and th 1^2 with apparently none of the growth bands of either theca forming part of the bar. In this case, it seems probable that the bar was complete after th 1^1 had passed that level and before th 1^2 had reached it. Most of the specimens available are too damaged for any reliable estimation of the relative growth



Text-fig. 8. *Climacograptus brevis* var. *mutabilis* nov. Young specimen showing regeneration of part of th 1^2. Approx. × 60. Tvären. T 295.

positions of the first two thecal apertures at any given stage to be made. There is also far too much variation in the growth lines of the early part of th 1^2 for conclusions to be based on only a few specimens. For example, while in text-fig. 7 B, the somewhat irregular growth bands of th 1^2 are formed of two parts with the typical zig-zag suture after the first six or seven, in text-figs. 7 A, 8, the growth bands are simple until the theca is free of the sicula. These two, however, also show growth lines running into the bar, and it is possible that the two phenomena are connected.

The significance of the bar must at present be left open to question. Although not previously described, it can be seen in a few specimens of *Climacograptus brevis* figured by BULMAN from Laggan Burn and so is not peculiar to the Swedish specimens. In none of the Laggan Burn specimens, so far as can be seen from a preliminary examination, are the growth lines of th 1^2 affected and other specimens of *C. brevis* do not even show a sinuosity of the line between th 1^1 and th 1^2. If the bar is merely a strengthening device, its occurrence in this species might be accounted for by the fact that th 1^1 grows back sharply on the downgrowing initial bud. In all the other diplograptids so far described in detail, the space between the upgrowing th 1^1 and the sicula is filled with the wide hood of th 1^2 which serves to connect the two, while in *C. brevis* there is apparently no connection between the upgrowing th 1^1 and the reverse side of the sicula except the bar.

Text-fig. 8 shows an interesting example of regeneration of a damaged thecal wall. Th 1^2, when about half grown, has lost a semicircular piece of the wall which has then been replaced by a series of curving growth bands filling the gap. At the same time, th 1^1 appears to have added a few extra growth bands at its aperture.

The specimens described here were recorded as *Climacograptus* aff. *kuckersianus* HOLM by BULMAN (in THORSLUND 1940, p. 114) but the more detailed examination since has shown them to be closer to *Climacograptus brevis*. *C. kuckersianus* was first described by WIMAN (1895, p. 37, pl. ix, figs. 2, 3; pl. x, figs. 1–5) but his description is very meagre and the characters of the species must be derived from his figures which, however, only show the external appearance of the specimens. The septum appears earlier (at the level of the first thecal aperture) than in any of the Tvären specimens but that is probably of little significance since the Tvären material shows variation in the position of the septum and WÆRN (1948, p. 451) has shown that even in a continuously changing group of climacograptids, the position of the septum does not vary continuously, being, as it is, dependent on which theca is giving rise to the double series.

The apertural excavations are much narrower in *C. kuckersianus* than in the Tvären material and this appears to be the chief distinguishing feature. WIMAN's figure apparently shows some congestion of the growth lines in the initial part of th 1^2, probably due to the presence of the peculiar bar.

The Tvären specimens appear to be sufficiently close to *C. brevis* to be regarded as a variety of that species. They differ from the typical form in having a longer sicula (reaching the level of the aperture of th 2^1 and resembling *C. kuckersianus* while the sicula in *C. brevis brevis* only reaches the aperture of th 1^2) and in having the distal excavations rather sharper in outline. The varietal name *mutabilis* is given in consideration of the extreme variability in detail of the proximal end.

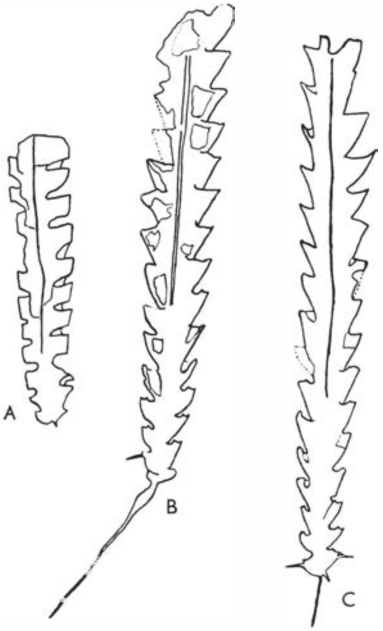
Genus *Orthograptus*

Orthograptus uplandicus (WIMAN)

Text-figs. 9 (B and C), 10.

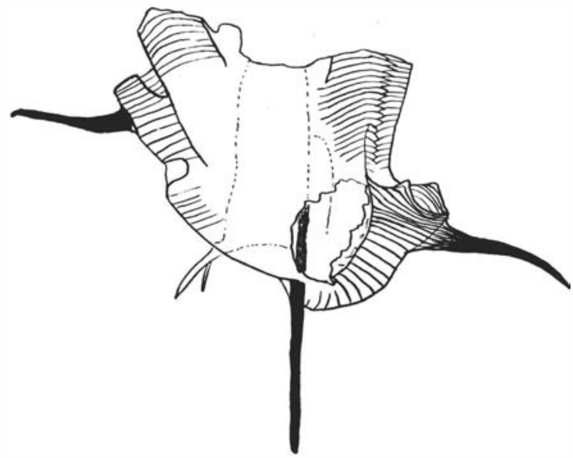
1895 *Diplograptus uplandicus* n. sp. — WIMAN, p. 36, pl. IX, fig. 1.
1940 *Diplograptus* (? *Glyptograptus*) *uplandicus* WIMAN — BULMAN, in THORSLUND, p. 114.

Rhabdosome up to 2 cm long and 2 mm broad increasing slowly throughout its length from an initial breadth of about 1 mm; thecae 11–12 in 10 mm, the proximal ones with distinct apertural lappets; virgella long, up to 5 mm; median septum beginning at the 7th thecal pair.



Text-fig. 9. (A) *Climacograptus* cf. *brevis* var. *mutabilis* nov. × 5. (B), (C) *Orthograptus uplandicus* (WIMAN). Reverse and obverse views. × 5. Tvären.

The sicula is 1.2–1.4 mm long (of which the prosicula forms a little more than a quarter), and has an apertural breadth of 0.3 mm. The virgella is very long even in the young growth stages and is formed in the usual way



Text-fig. 10. *Orthograptus uplandicus* (WIMAN). Broken proximal end of young specimen. × 40. Tvären. T 282.

when the metasicula is about 0.2 mm long. The sicular aperture bears a pair of processes 0.2 mm long on the side opposite the virgella. The initial bud arises about halfway down the metasicula and a little lower develops a hood forming the foramen of th 1^2.

The two basal thecae bear prominent apertural spines as well as the distinctive lappets but the later thecae only carry the lappets which become smaller distally and cannot be detected after the 8th or 9th thecal pairs. The distal part of the rhabdosome is definitely quadrangular in cross-section and the proximal thecae show only a slight curvature of the free ventral wall. The excavated appearance of many of the specimens in shale is probably due to the infilling of the apertures which are crescentic when viewed from above and the proximal parts of the free ventral walls are thus obscured.

The virgula is never prominent though it can be seen in the distal part of the rhabdosome when the specimen is damaged. The median septum appears to develop regularly between the 13th and 14th thecae but its structure cannot be determined.

Only a few specimens have been isolated from the limestone and these are all rather crushed. Nothing can therefore be said at present about the detailed development of the second and later thecae.

The quadrangular cross-section and the relatively straight thecae combine to place this species in *Orthograptus* rather than *Glyptograptus* while the apertural lappets and inclined apertures together with the stout virgella and basal spines indicate affinities with the group of *O. calcaratus* although it is rather smaller than the other species in that group. In isolated specimens a notable feature is that the first two thecae have modified apertural margins similar to those of the later thecae (text-fig. 10). In the majority of the diplograptids described in detail so far, the first pair of thecae are simple tubes with even apertures.

Family Acanthograptidae

Genus *Acanthograptus*

Acanthograptus suecicus (Wiman)

Plate II, figs. 5–11, text-figs. 11, 12.

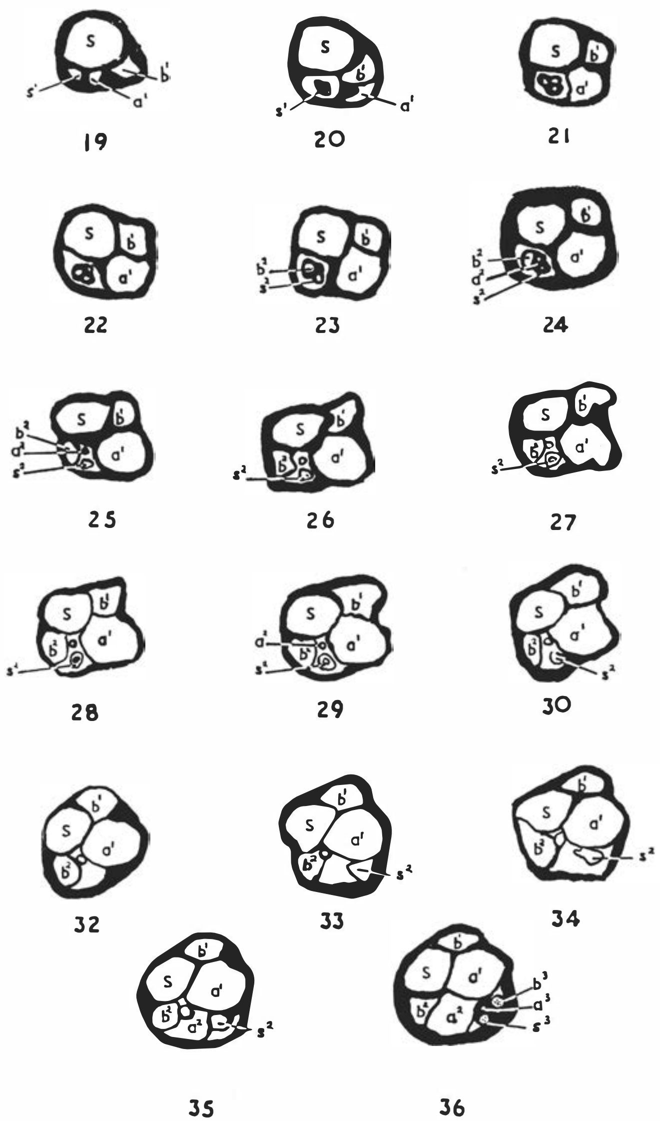
1937 *Acanthograptus suecicus* (Wiman) — Bulman, p. 182, text-figs. 1, 2 (with full synonymy).

The structure and affinities of this species have been fully dealt with by Bulman in the paper quoted above, but some further details are now available owing to a re-interpretation of some of his sections in the light of later work by Kozłowski (1938, 1947, 1949) and Bulman (1942, 1944) on the internal structures in dendroids. The specimen showing the proximal end and disc of attachment mentioned by Bulman (1937, p. 183) has been serially sectioned and it is now possible to give some details of the initial development of the rhabdosome.

The serial sections were cut at intervals of 8 μ and show throughout a thick development of cortical tissue round the thecae themselves. This secondary tissue shows very little signs of structure apart from an irregular layering in some parts of the sections and in general appears to be somewhat gelatinous in nature. The first twenty or so sections are apparently through the basal disc which is composed of cortical tissue. There is no sign of the sicula in the first five sections and it appears first at one side of the disc as preserved in the sections (see Pl. II, fig. 8).

The total length of the sicula is unknown. It can be traced in the sections for 0.4 mm and, judging from its appearance before sectioning, was probably not more than 0.6 mm when complete. Its diameter is 0.1 mm for most of its length and there is no apparent widening from its apex to its aperture. In the first section showing the sicula, the initial bud is present outside the sicula and appears to have divided already to form the first triad (Pl. II, fig. 8). Throughout the next fifteen sections the sicula and bud become surrounded by the secondary tissue while the bud grows across the sicula, its position relative to the sicula as seen in section swinging round about 90°. It is probable that the triad is at this stage still inside the first stolotheca but no definite stolothecal wall can be seen. The triad consists of a stolotheca and a bitheca with a small but distinct autothecal stolon between them (Pl. II, fig. 9).

Section 19 (text-fig. 11) shows the first autotheca developing from its stolon while the stolotheca of the same triad is filled with the developing stolon of the next triad. In sections 20–22, the autotheca widens rapidly to its full size which is equal to that of the sicula, and in section 22 the second triad



Text-fig. 11. *Acanthograptus suecicus* (WIMAN). Part of section series through the proximal end of the rhabdosome. T 278. Section interval 8 μ. $\times$ 100. Periderm shown black; for detailed structure see Pl. II. S: sicula. a^1, a^2, a^3: autothecae of successive generations. s^1, s^2, s^3: stolothecae. b^1, b^2, b^3: bithecae.

is clearly seen within the stolotheca. The triad at this stage consists of three thick-walled tubes, two approximately equal in size with the much smaller third one between them and slightly towards the inner side. In section 25, the two larger stolons have enlarged considerably to form the bitheca and stolotheca, the former being the larger and having a clear lumen while the stolotheca shows the continuing stolon in its centre (better shown in section 27).

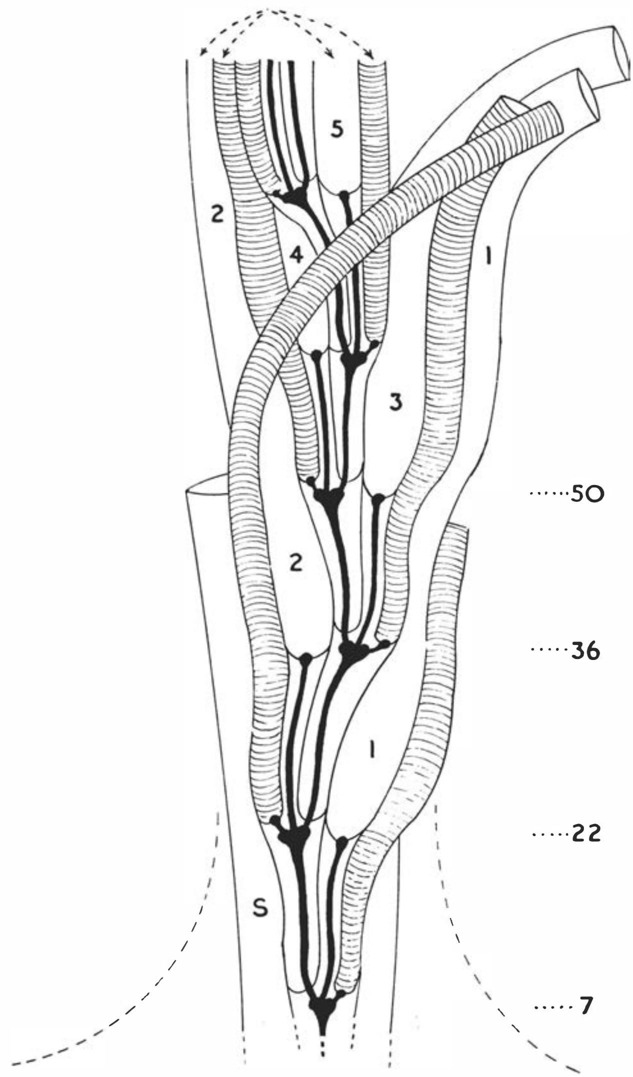
The small autothecal stolon is very well shown in sections 30–34. It is probable that the large space in these sections between the bitheca and the stolotheca of the same triad is really the base of the autotheca which has developed a pouch-like process proximal to the end of the autothecal stolon which can still be seen in section 35.

Section 36 shows the third triad in the lumen of the second stolotheca, with an appearance comparable to that seen in section 22. A feature which appears to be of regular occurrence is the presence of granules in the thecal stolons just below the points where they open out into the thecae. In the later sections the cortical tissue becomes much reduced in quantity though there remains quite a thick covering round the thecae which are compacted into a roughly cylindrical form (Pl. II, fig. 7). The triad divisions take place regularly and at the same levels at which the autothecal stolons of the previous triad widen rapidly to form the true autothecae. This relationship may not hold for the more distal part of the rhabdosome examined by BULMAN where the triad divisions are also slightly less frequent, numbering 8 in 170 sections as opposed to 4 in the first 50 sections at the proximal end, all the sections being nominally 8 μ thick.

The first bitheca cannot be definitely traced at the level of the sicular opening but it is probable that it opens beside the sicula, apparently the usual arrangement in dendroids. Unfortunately the sections beyond this level are rather broken for about 15 sections and it is impossible to trace the thecae definitely through the gap.

The stolons are generally only preserved for a short distance at a time though the autothecal stolons are very prominent. Occasional traces of the stolothecal stolon can be found throughout its length and the triad divisions are usually easily seen. The alternation of the relative positions of the stolo- and bithecae in succeeding triads appears to be an essential part of the division.

KOZŁOWSKI has figured stages in the initial development of the dendroid colony (1947, fig. 3) and these show several points which can be deduced from the serial sections described here. The first triad division takes place as soon as the initial stolon appears outside the sicula and the development of the autotheca is conspicuously delayed. Though his siculae are considerably longer than those of *A. suecicus*, there appears to be little room for more than two triad divisions before the sicular aperture. In his 1949 paper (p. 139), KOZŁOWSKI describes the proximal end of what is probably a rhabdosome developed from a stolon since while having the outward appearance of a young individual, it has no sicula. In this specimen of *Acanthograptus czarnockii* KOZŁOWSKI, the stolon present at the base produces a triad at 560 μ from the base and a second triad after another 250 μ. These are both however much longer than the stolons in *A. suecicus* which are only 120 μ long at the proximal end and about 170 μ long in the distal parts of the



Text-fig. 12. *Acanthograptus suecicus.* Diagrammatic reconstruction (after BULMAN) of proximal end showing first thecal grouping (au 1, 3; bi 2, 3) and probable second group (au 2, 5; bi 4, 5). Vertical scale × 200 approx.

rhabdosome. Unfortunately the length of the stolon can only be determined in a few favourable cases and at present cannot be used in classification though it may be of considerable systematic importance.

Text-fig. 12 is redrawn from a diagram by BULMAN which shows the thecal grouping beyond the stage shown in the reconstruction (Pl. II, fig. 6). Owing to the break in the section series the grouping of the thecae in the first twig cannot be definitely proved but the diagram shows how the characteristic grouping of *Acanthograptus* can be attained from the proximal end. KOZŁOWSKI has claimed (1949, p. 139–140) that in *A. czarnockii* the autothecae are separated by sometimes one and sometimes two generations. BULMAN's re-examination of *A. suecicus* suggested that there were regularly two generations between the autothecae of a twig and in WIMAN's table (1895, p. 65) it is quite possible that there is another generation between his thecae b and b_1 as his section series does not show the origin of his theca b. KOZŁOWSKI's specimen of *A. czarnockii* (KOZŁOWSKI, 1949, text-fig. 37 A) shows the same grouping except for his third twig, but that is at the growing point of his specimen and there is no need to assume that the visible grouping is the final one (i.e. III–a4, a6, b6) and that autotheca 7 could not develop in time to make the normal grouping of a4, a7, b6, b7.

Family Dendrograptidae

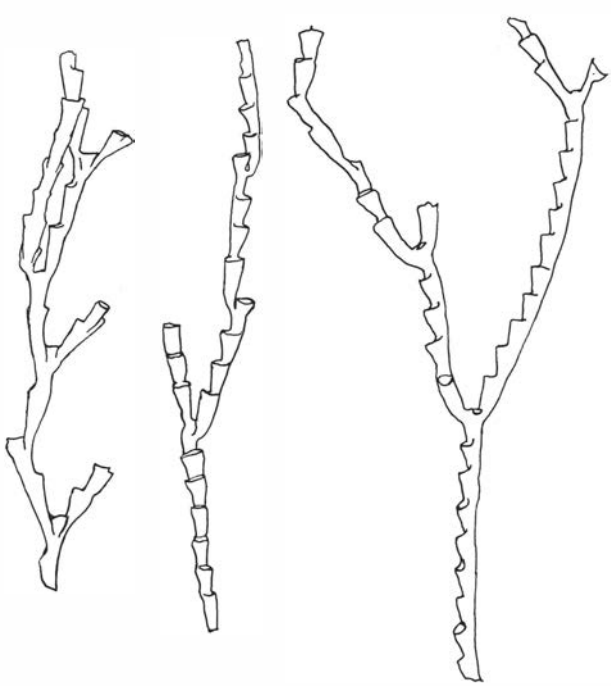
Genus *Dendrograptus*

Dendrograptus sp.

Text-fig. 13.

1928 *Temnograptus* sp. — ÖPIK, p. 38, pl. III, fig. 20.

A large number of fragments probably referable to this genus have been obtained from the limestone blocks. The branching is only by dichotomy but appears to be rather irregular. Some specimens show branching every



Text-fig. 13. *Dendrograptus* sp. × 5. Tvären. T 284, T 280, and T 279.

two to four thecae while others may have ten or more thecae before dividing. Up to fifth order branches have been found in spite of the fragmentary nature of the material.

The stipes have a breadth of about 0.5 mm and the longest isolated piece is 2 cm long. The thecae are simple and number 11–12 in 10 mm. Bithecae have been observed but no details of the internal structure are available as serial sections show that very little is preserved beyond the outer walls of the rhabdosome. Some of the specimens show considerable secondary thickening and probably represent the more proximal parts of the rhabdosome. The thecal apertures are very obscure in most of these. In the distal parts of the rhabdosome, however, the bithecae appear to open into the autothecal cavity just below its opening. The evidence of the serial sections is not inconsistent with this interpretation which has been described by BULMAN for *Dendrograptus rigidus* (1936, p. 18).

The specimens are certainly not referable to the type species of *Temnograptus* in which the branching is much more widely spaced and the thecae are fewer per cm. *Dendrograptus rigidus* is probably the closest form but has about twice as many thecae per cm though its size and branching are very similar to those of the material from Tvären.

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Explanation of Plates

Plate I

Dicellograptus divaricatus var. *salopiensis* Elles and Wood.

1. Growth stage with early development of th 2^2. × 50. T 301.
2. Late growth stage with beginning of th 3^2. × 22. T 298.
3. Early sicula. × 80. T 296.
4. Later sicula with virgella. × 80. T 297.
5. Complete sicula with initial bud. × 45. T 300.

Climacograptus brevis var. *mutabilis* nov.

6. Metasicula with virgella and initial foramen. × 50. T 305.
7. Metasicula with initial bud and foramen of th 1^2. × 50. T 302.
8. Slightly later stage than that on Pl. II, fig. 4 showing the bar between th 1^1 and th 1^2, and the beginning of the outer wall of th 1^2. × 50. T 304.

9–10. Reverse and obverse views of stage with three thecae. × 50. T 286.

Plate II

Dicellograptus divaricatus var. *salopiensis* Elles and Wood.

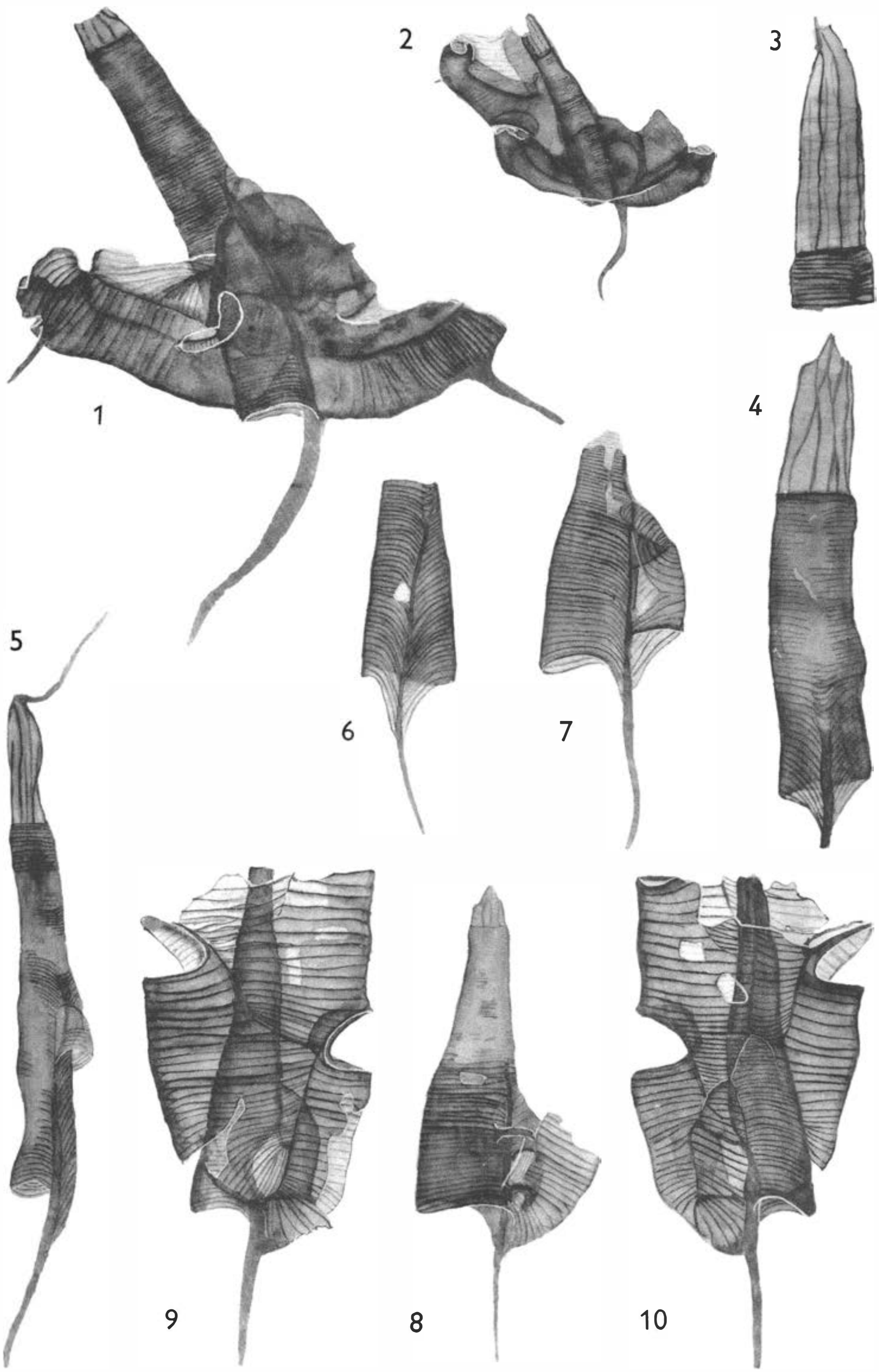
1. Broken sicula showing virgella and initial foramen. × 45. T 299.

Climacograptus brevis var. *mutabilis* nov.

2. Adult thecae in relief. × 17. T 285.
3. Young specimen, compressed. × 17. T 283.
4. Complete sicula with developing th 1^1. × 50. T 303.

Acanthograptus suecicus (Wiman).

5. Photograph of proximal end of specimen before sectioning. × 4.75.
6. Restoration from sections of the internal casts of the thecae of the proximal end. × 175.
7. Serial section no. 36. × 75.
8. Serial section no. 7. × 75.
9. Serial section no. 19. × 75.
10. Serial section no. 22. × 75.
11. Drawing of proximal end before sectioning. × 22.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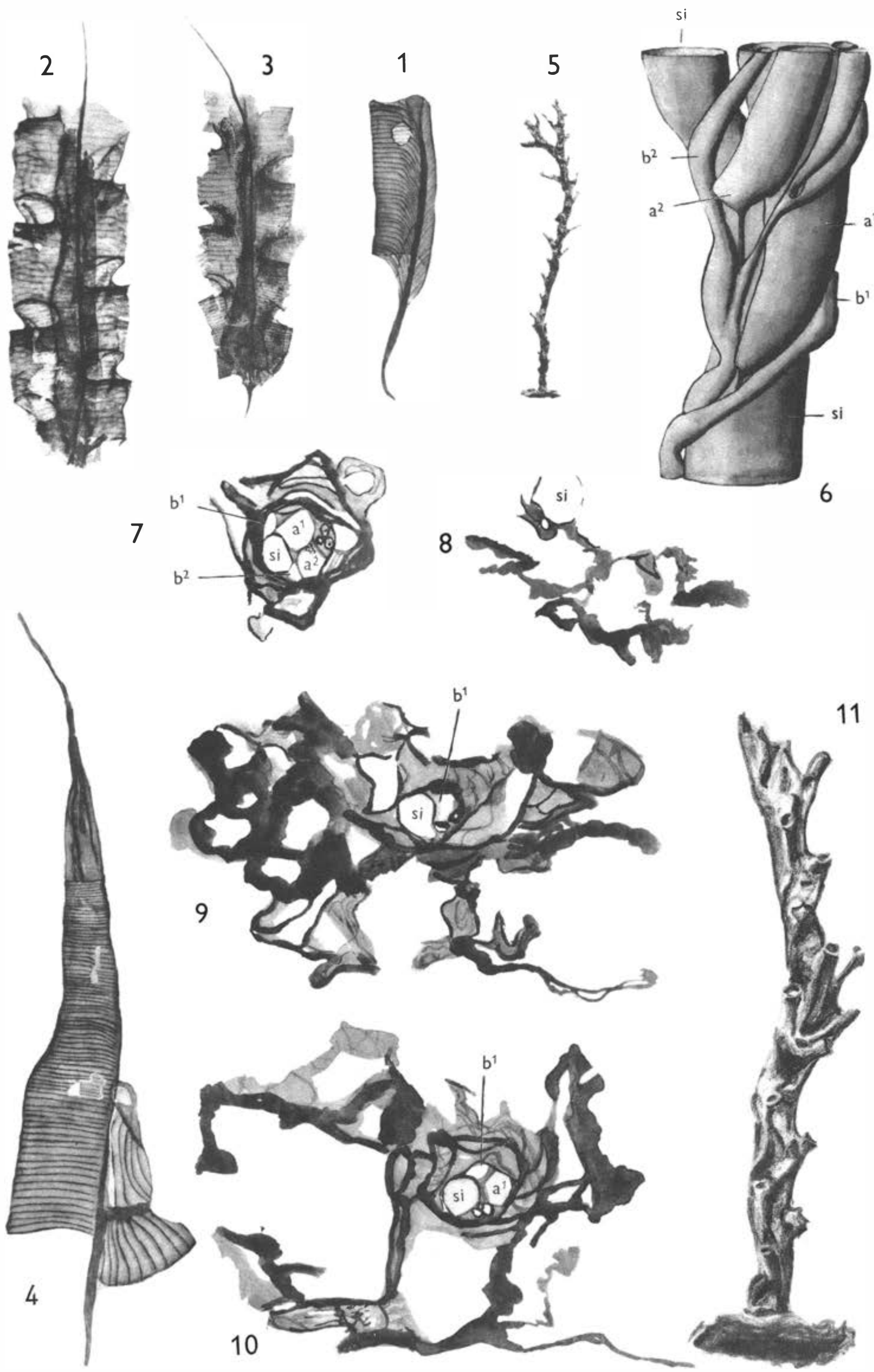
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