# A Revision of Wiman's Dendroid and Tuboid Graptolites

By

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ABSTRACT.—The dendroid, and what are now recognised as tuboid, graptolites described by CARL WIMAN in a series of papers in this Bulletin between the years 1895 and 1901 are mostly preserved as microtome sections in the Palaeontological Institute at Uppsala.

Many of them retain traces at least of their detailed internal structure and can be re-interpreted in the light of present-day knowledge. From amongst this collection the following species are here described: —

Dendroidea: *Dendrograptus maximus* WIMAN, *D. oelandicus* WIMAN, *D. balticus* WIMAN, *Dendrograptus* sp. ( = Sp. no. 1 of WIMAN); *Dictyonema cavernosum* WIMAN, *D. peltatum* WIMAN; *Acanthograptus musciformis* (WIMAN), *A. impar* sp. nov.; *Coremagraptus formosus* (WIMAN).

Tuboidea: *Reticulograptus tuberosus* (WIMAN), *Galeograptus wennersteni* WIMAN and *Discograptus schmidti* WIMAN.

For these and all other WIMAN species, lectotypes have been chosen, and descriptions of two non-Scandinavian species *Reticulograptus thorsteinssoni* sp. nov. and *Galeograptus nicholasi* sp. nov. are included for comparison.

A new type of theca named the conotheca, possibly a modified autotheca, is described in *Reticulograptus* and *Discograptus* and reconstructions from serial sections of *Galeograptus wennersteni* have revealed a notable apertural modification of the basal autothecae.

## Contents

# Foreword

At the outbreak of the last war, Professor KOZLOWSKI had published (1938) a preliminary note recording the essentials of his discoveries concerning the stolonal structure and histology of the Dendroidea, but the full details could not be presented until 1949. During the war, confirmation of KOZLOWSKI's preliminary note was provided by the discovery of an exceedingly well-preserved portion of dendroid graptolite rhabdosome from Scotland, and in the uncertainties of the time it was thought desirable to publish an account of this (BULMAN 1942); more adequate description and illustrations were provided in 1944. It was suggested, moreover, that (1944, p. 4) in the light of these discoveries traces of comparable structures could be recognised in several of CARL WIMAN's published sections, and that (p. 5) "even in the absence of KOZLOWSKI's detailed results, covering a range of six genera and twelve species, we may assume with confidence that this basic stolon structure is universal amongst the Dendroidea".

When communications were re-established after the war and these publications reached Sweden, the late Professor G. SÄVE-SÖDERBERGH wrote to the senior author:—"Your remarks on the traces of a stolon system in WIMAN's sections made me quite interested to see how much might be preserved in his material. I have now looked through a few of his series, and I am glad to tell you that they confirm the general validity of your finds still more than is visible in WIMAN's figures. WIMAN has often omitted stolon sections in his figures (especially the text-figures); of course, it was difficult at that time to be sure what they did represent. ... Your interpretation of the series of *D. cavernosum*, figured by WIMAN 1897, pl. 1, 5–20, is also supported by data in the unfigured sections. It seems to me that the material is well worth being worked out."

Professor SÄVE-SÖDERBERGH's kindly interest in this led to the bulk of the WIMAN slide collection being sent to Cambridge in 1946. Intermittent work on these has been interrupted and postponed for a variety of reasons for nearly twenty years. The appointment of the junior author as Assistant in Research at the Sedgwick Museum at last provides an opportunity to remedy this neglect. In the interval, the long-awaited monograph by KOZLOWSKI has appeared (1949) and much additional information, largely a product of the

Warsaw school, has accumulated; but there are nevertheless several interesting features in the WIMAN material which merit publication.

During the period 1895–1901 CARL WIMAN described and figured twenty-one "dendroid" graptolites, including thirteen new species and three new genera. In one paper (1897) five species were left under open nomenclature (Species I–V), but Species III and V were later included with *Discograptus schmidti* and *Desmograptus? formosus* respectively. In his 1901 paper a further four graptolites were left under open nomenclature (Species VI–IX). In addition to this material, WIMAN had some isolated (unsectioned) rhabdosomes, and further sets of serial sections which he had not attempted to describe. In the present work we are giving an account of features of interest both in his described specimens and in his supplementary material.

In more recent years WIMAN's genera *Galeograptus* and *Discograptus* have been transferred from the Dendroidea to the Tuboidea. The species *Inocaulis suecicus* and *I. musciformis* are considered to belong to the genus *Acanthograptus*, whilst *Desmograptus? formosus* is now included in *Coremagraptus* BULMAN and a restoration of this was published in the *Treatise of Invertebrate Paleontology*, Part V, Fig. 11.

It has not proved possible to add anything to the existing descriptions of *Dictyonema rarum*, *D. flabelliforme*, and *Acanthograptus suecicus*. Of the species placed under open nomenclature by WIMAN the form "Species no. I" is described here as *Dendrograptus* sp. and we confirm WIMAN's attribution of Species III and V. The remaining six unnamed forms are largely in a poor state of preservation and no progress could be made with them. From WIMAN's supplementary collection a great deal of information has been obtained, and a new species, *Acanthograptus impar*, has been established. In the systematic section below fourteen species are described.

In the following systematic descriptions, the term "material" refers to slides (or specimens) sent to Cambridge; it does not usually include unsectioned specimens and is not a complete record of all material preserved at Uppsala. It has been shown by M. FLORKIN and his colleagues (e.g. FLORKIN, 1965, Bull. Acad. Belg. Cl. Sci., sér. 5, **51**, 156–169) that the graptolite skeleton contains no chitin, but that the substance is of a scleroproteic nature; the term sclerotized has therefore been used in place of "chitinized".

The senior author wishes to record his sincere appreciation of the generosity and forbearance of Professor G. SÄVE-SÖDERBERGH and subsequently of Professor PER THORSLUND, of the Palaeontological Institute of Uppsala, in furnishing him with the extended loan of this historic collection of slides. The conothecae here described in *Reticulograptus* and *Discograptus* have already been recognized and are still being investigated by Professor R. KOZLOWSKI, and we are grateful to him for his friendly discussions of this and other problems. The name conotheca has been proposed in consultation with Professor KOZLOWSKI. Dr. R. THORSTEINSSON has very generously provided us with further material of the genus *Reticulograptus* WIMAN, and we are indebted to Dr. D. J. MCLAREN, of the Canadian Geological Survey, for permission to describe the Canadian

species *R. thorsteinssoni* sp. nov. The serial sections of this species, and other sections of *Discograptus schmidti* and *Acanthograptus impar* were prepared with the assistance of Mr. W. WESTLEY at the Department of Zoology, Cambridge.

# Systematic descriptions

## Order *Dendroidea* NICHOLSON, 1872

## Family *Dendrograptidae* ROEMER, in FRECH, 1897

### Genus *Dendrograptus* HALL 1858

TYPE SPECIES. *Graptolithus hallianus* PROUT, 1851; subsequently designated HALL, 1862.

DIAGNOSIS. Generally robust, shrublike in habit, branching irregular, stipes unconnected, usually divergent, stem well developed, with basal attachment; autothecae denticulate, spined or with broad apertural processes, or to some extent tubular and isolate.

#### *Dendrograptus maximus* WIMAN 1901

Figs. 1–3

1901 *Dendrograptus? maximus* n. sp. WIMAN, pp. 187–188, pl. VIII, Figs. 4, 5, Text-fig. 6.

LECTOTYPE. The specimen figured by WIMAN (1901) as Text-fig. 6, and refigured here as Fig. 1, is here designated.

MATERIAL. A single specimen (G 91), the lectotype, preserved as a section series on slides (sections probably cut at 20 $\mu$).

HORIZON. From a silicified boulder of Upper Ordovician age at Öjle Myr, Gotland.

DESCRIPTION. The rhabdosome is known from some short fragments which show branching and lack dissepiments. One of the most characteristic features is the robust nature of the stipes. Thus, whilst the autothecae are not prominently denticulate, the dorso-ventral width measured at the autothecal aperture is about 1.3 mm. The lateral width varies from about 0.60–0.90 mm, and the thecal spacing is of the order of 8 in 10 mm.

The four slides (nos. G 91 *a–d*, partly figured on Fig. 1) are of a continuous series of sections. The cortical tissue is about 0.05 mm. thick and as preserved is often slightly separated from the fusellar tissue (see Fig. 1) which, by contrast, is extremely thin and often disrupted (see section 59, Fig. 1.). Stolons are present in the specimen but are not well preserved, probably in consequence of their extremely tenuous nature. A stolothecal stolon is seen in section 56, after $S^3$ has divided between sections 35 and 56 to produce a normal triad. The small bithecal tube of this triad is situated to the right of the stolothecal stolon in section 56. In subsequent sections (e.g. 67) the stolothecal stolon enlarges con-

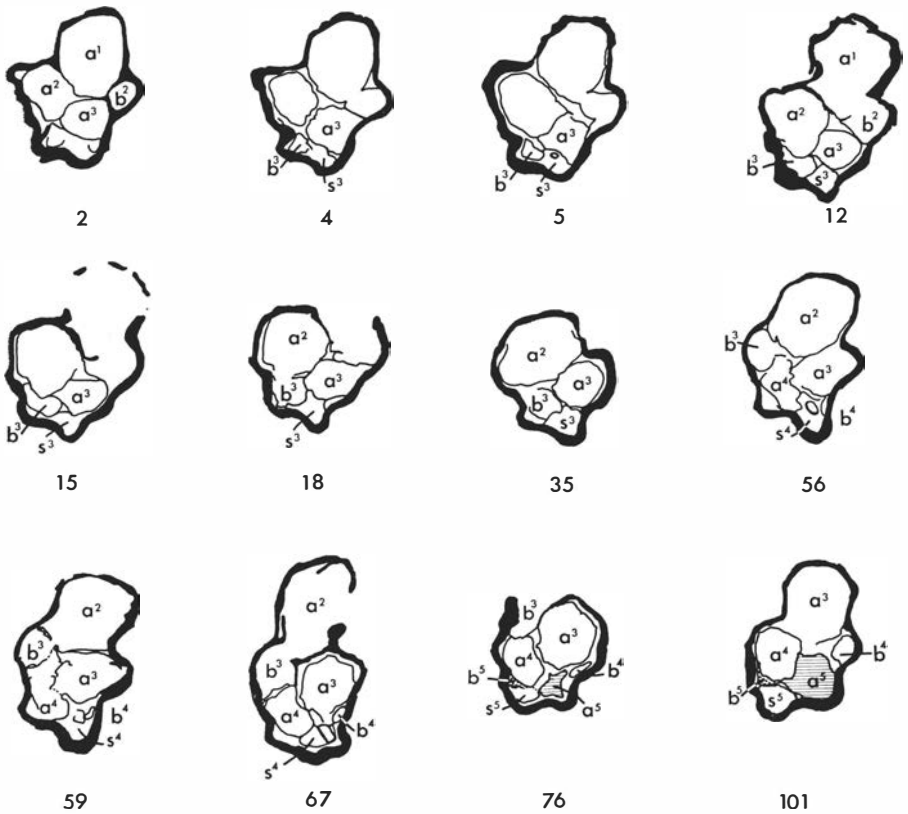
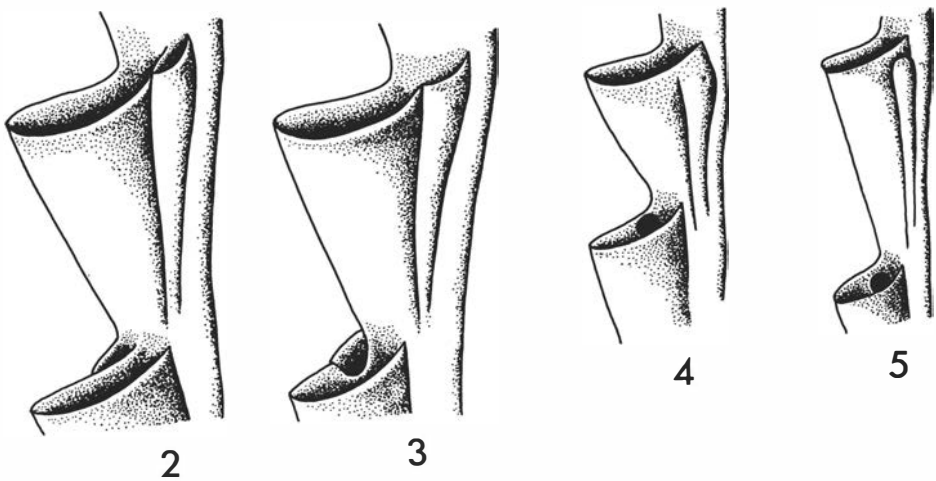



Fig. 1. *Dendrograptus maximus* WIMAN. Selected sections, probably at 20 $\mu$, of the lectotype. Sections 2–56 from slide no. G 91 *a*; sections 59–101 from slide no. G 91 *b*; *a*, autothecae, *b*, bithecae, *s*, stolothecae. × 18.

siderably and between sections 67 and 76 it again divides normally to produce a bitheca $b^5$ (stippled in sections 76 and 101), an autotheca $a^5$ (horizontal ruling in sections 76 and 101) and a stolotheca.

The bithecae are not very prominent externally. They are positioned laterally on the stipe and are a little more than 1.5 mm. in length. The bithecal aperture opens in close association with the aperture of the autotheca produced at the preceding node. Thus if bitheca $b^2$ (section 2, Fig. 1) is traced along the series it will be seen to open into the autothecal tube (sections 4, 5, 12), but the lateral wall of the bitheca continues long after the autotheca $a^1$ has ended (see sections 15, 18). A reconstruction of this association of autotheca and bitheca is shown in Fig. 3. The bitheca of the next generation $b^3$, can be traced more fully on the opposite side of the stipe (see section 2–76) and opens similarly.

However, the same specimen shows a slightly different relationship in which the bithecal and autothecal tubes remain distinct and open separately (reconstruction in Fig. 2). Another bitheca in the same series is intermediate and the bithecae in *D. maximus* probably vary between the two extremes.




Figs. 2–3. *Dendrograptus maximus* WIMAN. 2, reconstruction based on the lectotype illustrating bithecae which open at, or slightly above, the level of the autothecal aperture; 3, reconstruction based on the lectotype illustrating bithecae which open into the apertures of the autothecae. × 20. Fig. 4. *Dendrograptus oelandicus* WIMAN. Reconstruction based on the lectotype illustrating the typical relationship of autotheca and bitheca. × 20. Fig. 5. *Dendrograptus balticus* WIMAN. Reconstruction based on the lectotype of a portion of stipe illustrating the manner in which the bitheca opens into the autotheca. × 20.

The autothecae are approximately 3 mm. in length, are extremely prominent (being 0.5–0.6 mm. in diameter near the aperture), but are only slightly denticulate. The free ventral wall is inclined at 20–30° to the dorsal margin of the stipe.

A branching division is not exhibited by the section series, and nothing can be deduced from WIMAN's original figure, showing a branching stipe (1901, pl. VIII, Fig. 5). Dissepiments are absent.

REMARKS. *D. maximus* closely resembles *D. rigidus* BULMAN 1936 but differs in having far more widely spaced thecae (8 in 10 mm. compared with the 19–23 in 10 mm. given by BULMAN, and the 14–22 in 10 mm. given by SKEVINGTON (1963)) and a greater overall size. The thecae of *maximus* seem to be less denticulate, but the stipes have a greater average dorso-ventral width. From the interpretation of the section series given in Fig. 1, it would appear that in this species the stolotheca maintains a central position at successive nodes with bithecae and autothecae alternating, but the preservation is poor and none of the intermediate (unfigured) sections provide any additional information.

### *Dendrograptus oelandicus* WIMAN 1895

Figs. 4, 6

1895 *Dendrograptus? oelandicus* n.sp. WIMAN, pp. 293–296, pl. XII, Figs. 7, 8; pl. XIII, Figs. 1–11, 27; Text-figs. *a–f*. (p. 295).

1895 *Dictyonema peltatum* n.sp. WIMAN, pl. XIV, Figs. 9–14 (only)

1936 *Dendrograptus rigidus* n.sp BULMAN, pp. 16–23; Text-figs. 2–5; pl. 1, Figs. 27–35.
?1947 *Dendrograptus rigidus* n.sp. RUEDEMANN, p. 216; pl. 20, Figs. 19, 20.
1963 *Dendrograptus rigidus* BULMAN–SKEVINGTON, pp. 8–11, Figs. 4–9

LECTOTYPE (here selected). The specimen figured by WIMAN, 1895, pl. XIII, Figs. 1–6, now preserved as a section series (cut at 20–25 $\mu$) mounted on slide, no. G 831.

MATERIAL. Section series mounted on slides: the lectotype and the specimens figured by WIMAN 1895, pl. XIII, Figs. 7–11, 27, slides G 846–848; a further specimen figured WIMAN (1895, pl. XIV, Figs. 9–14) as *Dictyonema peltatum*, now preserved as serial sections (cut at 20–25 $\mu$) on slide no. G 818; an unfigured section series (cut at 25 $\mu$; slide no. G 822) labelled "*Dictyonema*", which except for a doubtful outgrowth (?dissepiment), is identical with *Dendrograptus oelandicus*.

HORIZON. WIMAN's slides are labelled "Asaphus kalk" (=grå Vaginatumkalk of HOLM) which is considered by BULMAN (1936) to be post *I. gibberulus* zone. SKEVINGTON (1963) assigns this to about the boundary of the *hirundo* and *bifidus* zones.

DESCRIPTION. The most complete specimen showing the form of the rhabdosome is that figured by WIMAN (1895, pl. XII, Fig. 8). This specimen exhibits seven branching points, of which the six most proximal ones are arranged in a roughly regular manner. The position of the seventh division, however, implies a somewhat irregular development. The stiff broad stipes diverge at varying low angles from each other and thereafter become subparallel. Branches occur at approximately 2–5 mm. intervals. The denticulate autothecae are a very prominent feature of the rhabdosome, and the free ventral walls are inclined to the dorsal margin at angles up to 40° or slightly more. The maximum dorso-ventral stipe width is about 0.7 to 0.8 mm. and the lateral width of the order of 0.4 mm. The thecal spacing is 16–22 in 10 mm., and the stipes are unconnected by dissepiments or anastomosis.

The section series reproduced as Fig. 6 retains a perfectly preserved stolon system. The fusellar tissue is robust and adheres closely to the cortical layer. A bithecal tube (stippled) is shown in section 77 (Fig. 6) and its development can be traced through the series. It opens into the autotheca produced at the preceding node a short distance below the autothecal aperture (sections 99–100, Fig. 6 and Fig. 4).

A stolothecal stolon is seen in the top right hand corner of sections 80 and 85. By section 88, that is just at the level of the autothecal aperture, it has divided to produce a normal triad of stolotheca, autotheca and bitheca. Sections 92 and 98 show the internal bitheca and stolotheca associated with the autothecal stolon, whilst section 99 cuts through the base of the autotheca. The stolothecal stolon again produces a normal division in section 106.

Branching divisions are displayed in the section series figured by WIMAN,

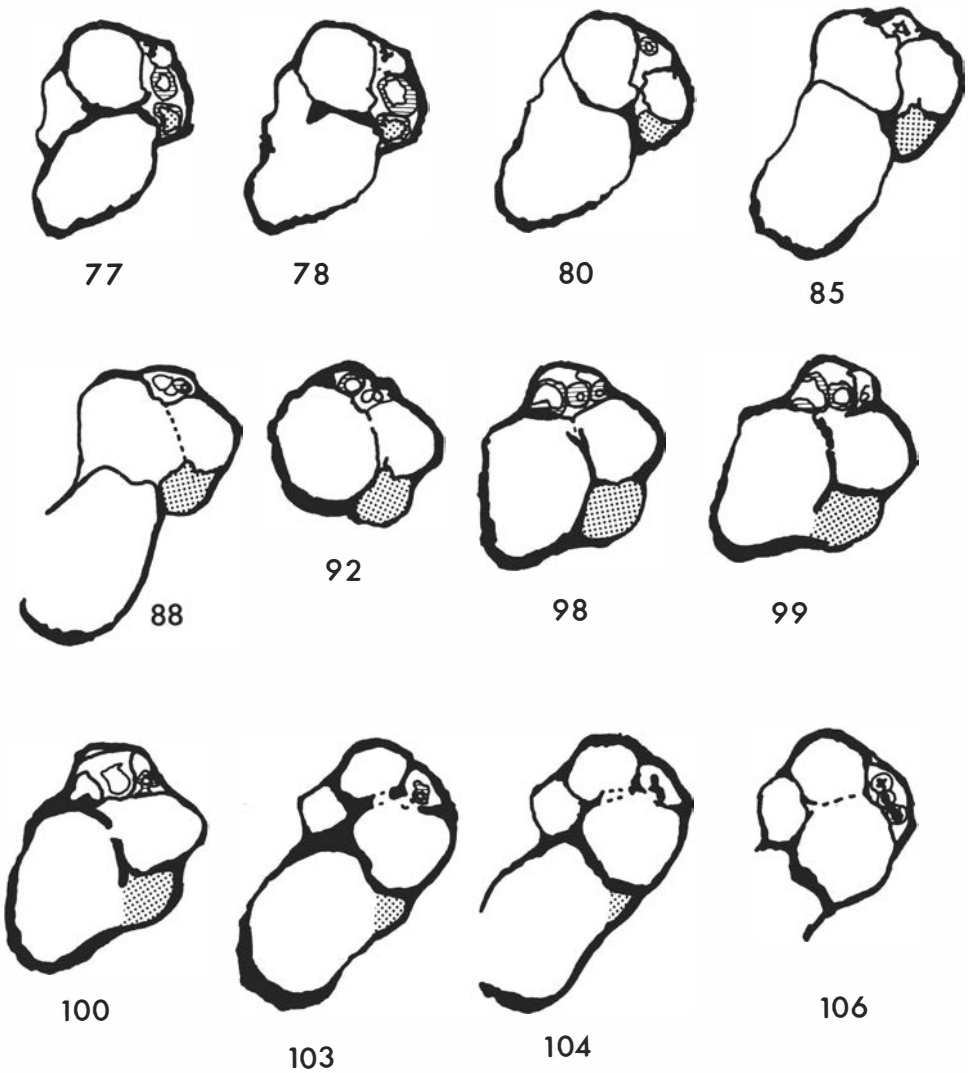



Fig. 6. *Dendrograptus oelandicus* WIMAN. Selected sections at 20–25 $\mu$ of the lectotype, slide no. G 831; sections 77, 78 and 99 also figured by WIMAN 1895 pl. XIII Figs. 1, 2, and 5 respectively; horizontal shading represents transparent tissue, and in some cases the thickness is depicted slightly exaggerated; full explanation in text. × 50.

(1895, p. 295) with the normal suppression of a bitheca; each branching node gives rise to two stolothecae and an autotheca.

The autothecal apertures usually begin to open on the side opposite to that at which the bitheca enters (see section 104, Fig. 6), but in some instances the ventral lip is continued as a denticle for about 0.13 mm above the general level of the aperture. Some of the figured thecae (e.g. WIMAN, 1895, pl. XII, Fig. 7)

appear to have more conspicuous denticles, but these are not in evidence in the sections.

REMARKS. The writers consider that the forms *D. oelandicus* WIMAN and *D. rigidus* BULMAN are conspecific. The Wiman specimens are a little narrower dorso-ventrally than the specimens described as *D. rigidus* by SKEVINGTON (1963), but these latter show rather more pronounced denticles than the material originally figured by BULMAN. Otherwise neither appears to differ significantly from WIMAN's species. The thecal spacing, autothecal and bithecal form, inclination of the free ventral margin of the autotheca, and general rhabdosomal features are all closely similar.

### *Dendrograptus balticus* WIMAN 1895

Figs. 5, 7 A

1895 *Dendrograptus? balticus* n.sp. WIMAN, pp. 296–298, pl. 10, Figs. 10, 11, Text-figs. 1–12, p. 296.

LECTOTYPE (here designated). The specimen figured by WIMAN 1895, p. 296, Text-figs. 6–12, and now preserved as serial sections (cut at 25 $\mu$) on slide no. B 311.

MATERIAL. The lectotype, and another section series preserved as slide no G 823.

HORIZON. Middle Ordovician; boulders from the South Bottnian area.

DESCRIPTION. The rhabdosome of *D. balticus* is known only from the original fragments figured by WIMAN (1895, pl. X, Figs. 10, 11). One of these (Fig. 11) shows relatively slender stipes, prominent autothecae, and irregular branching. The dorso-ventral stipe width is at the most 0.4 mm, and the thecal spacing approximately 10 in 10 mm. The serial sections, however, indicate that both the dorso-ventral stipe width and the lateral stipe width may reach 0.5 mm. At the level of the autothecal apertures the stipes are roughly circular in cross section. The free ventral walls of the autothecae are inclined to the dorsal stipe margin at approximately 20°. The bithecae, which open into the autothecal tube, are inconspicuous externally.

Fig. 7 A illustrates selected sections from the previously unfigured series (slide no. G 823). Section 7 shows an autotheca and a triad of smaller tubes comprising a bitheca (stippled), autotheca (adjacent to bitheca), and stolotheca. As the bithecal tube is traced through the series it increases in diameter and opens into the autothecal tube in section 25. Section 29 cuts the stipe at the upper limit of the bithecal tube. Shortly after this the autothecal aperture is formed, and it begins to open on the side opposite to that containing the bitheca. A reconstruction of the relationship between autotheca and bitheca is illustrated as Fig. 5 where it may be contrasted with *D. maximus* and *D. oelandicus*.

The autotheca in its proximal portion is not of much greater diameter than the bithecal tube produced at the same node, but once the bitheca has ended

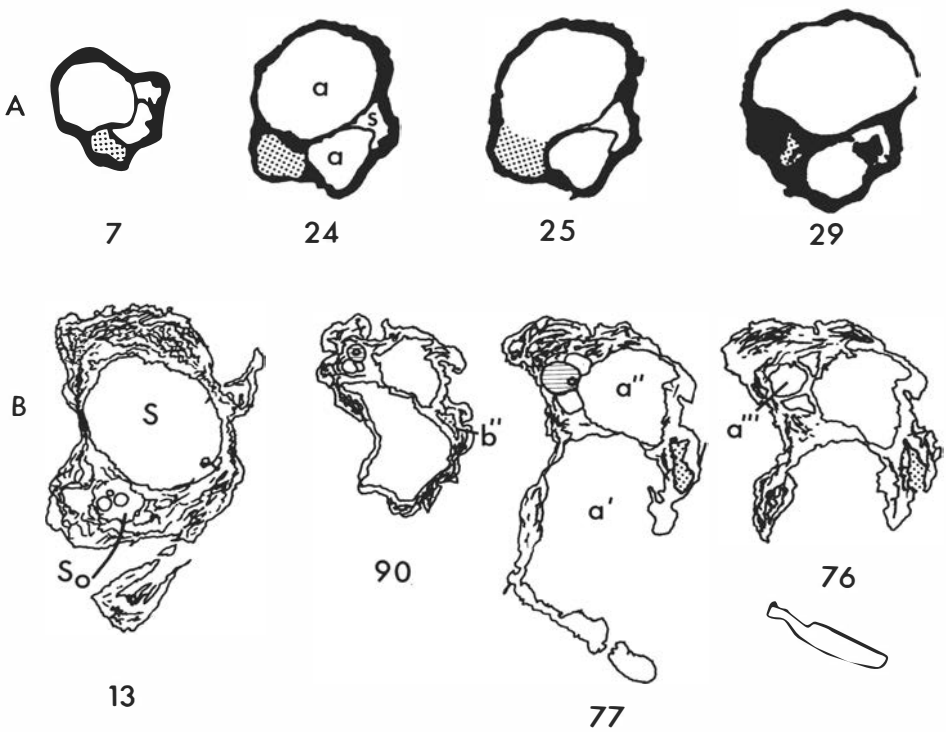



Fig. 7 A. *Dendrograptus balticus* WIMAN. Selected sections at 25 $\mu$ of slide no. B 311 illustrating the manner in which the bitheca (stippled) opens into the autotheca; *s*, stolotheca, *a*, autotheca. × 50.

Fig. 7 B. *Dendrograptus* sp. Selected sections from a series at 20 $\mu$ cut through a basal disc (section 13 slide no. G 785*a*) and a separate series at 20 $\mu$ through a more distal part of stipe (sections 90–76 slide no. G 784); *s*, sicula, *a*, autotheca; thin tissue is shown in horizontal shading; *so*, first triad of stolons, bitheca, *b''*, is stippled. × 60.

(in association with the preceding autotheca) the autothecal tube expands to a transversely elliptical cross section. The stipe as a whole maintains an approximately circular cross section.

The stolon system is not well displayed in either section series, but traces of stolons are present in some sections, and the development of the thecal tubes themselves can always be followed with relative ease since any particular section through the stipe never cuts more than four tubes.

REMARKS. The roughly circular cross section of the stipes in the region of the autothecal apertures may be contrasted with the cross section in a like position in such species as *D. maximus* and *D. oelandicus*. On the other hand the relationship between the bithecal and autothecal apertures of *D. balticus* is clearly of the same general type as in *maximus* and *oelandicus*. A final aspect which serves to distinguish *D. balticus* from many species is that any particular section through the stipe never cuts more than four thecal tubes. In *D. maximus* and *D. oelandicus* (described above) as many as 6 may be cut in a single section.

### *Dendrograptus* sp.

Fig. 7 B

1897 Species no. I WIMAN, pp. 355–6; pl. XI, Figs. 2, 3 & 15–25.

MATERIAL. A section series (cut at 20 $\mu$) of a basal disc now preserved on slides nos. G 785 *a–b*, partly figured by WIMAN 1897 (pl. XI, Fig. 25) refigured in part as Fig. 7 B (section 13) in this work; a section series (cut at 20 $\mu$) of a more distal portion of stipe partly figured by WIMAN 1897 (pl. XI, Figs. 15–24) and cut from the specimen figured on the same plate as Figs. 2, 3; (slide no. G 784).

HORIZON. Upper Ordovician, Öjle Myr, Gotland.

DESCRIPTION. The full form of the rhabdosome cannot be deduced from such small fragments, but the sicula and early thecal tubes appear to have been embedded in a basal disc (see Fig. 7 B, section 13), and neither the proximal nor the distal fragment shows traces of dissepiments. Although deposited in approximately concentric layers, the cortical tissue has a peculiar "spongy" appearance both in the basal disc region and on the distal fragment where it has been more sparingly deposited. Occasional outgrowths of "spongy" cortical tissue can be seen (Fig. 7 B, section 90).

The selected sections 90, 77 and 76 (Fig. 7 B) illustrate the development of the thecal tubes in the more distal fragment. Section 90 shows an inconspicuous bithecal tube *b″*, (stippled) to the right of the autotheca produced at the preceding node. The early portion of autotheca *a″* is seen between the bitheca, *b″*, and the stolotheca, within which the stolon has divided to produce three daughter stolons. Autotheca, *a′*, and bitheca, *b″*, open in sections 77 and 76 respectively, by which time they have considerably increased their dimensions. The dorso-ventral stipe width at the level of the autothecal aperture is 0.7–0.9 mm. Other autothecae than *a′* in the same series show that the distal part of the free ventral wall is extended into a denticle of rather variable shape (see also WIMAN 1897, pl. XI, Figs. 2, 3). The thecal spacing is 16–17 in 10 mm.

The bithecae are of relatively small diameter, and externally must be quite inconspicuous. The bitheca figured in sections 90, 77 and 76 opens at about the same level as the autotheca *a′*, but the same section series shows that the bithecal tube is quite variable and in fact more commonly opens considerably earlier than the autotheca produced from the preceding node (see for example WIMAN 1897, pl. XI, Figs. 21–24).

REMARKS. Despite their differences in age, WIMAN's species no. I bears a considerable resemblance to the Tremadocian species *D. communis* KOZLOWSKI, as may be seen on comparing WIMAN's Figs. 2 & 3 (pl. XI) with the specimens depicted by Kozlowski as Fig. 1 *a* (pl. VI). In each case the autothecal denticle is of the same irregular type, whilst the general dimensions such as dorso-ventral stipe width, angle of inclination of the free ventral margin and thecal

spacing are almost identical. Bithecae of the type described here occur in *D. communis* although in this latter species the bithecae show greater variation in form.

## Genus *Dictyonema* HALL, 1851

TYPE SPECIES. *Gorgonia? retiformis* HALL, 1843; subsequently designated MILLER 1889.

DIAGNOSIS. Conical, varying from cylindrical to almost discoidal, with thecate or non-thecate stem, or rarely attached by nema; branching dichotomous, usually rather regular, stipes straight, sub-parallel or parallel, united by transverse dissepiments, anastomosis rare or absent; autothecae denticulate, commonly spined, rarely tubular and isolate.

### *Dictyonema cavernosum* WIMAN, 1896

Figs. 8–16

1896b *Dictyonema cavernosum* n.sp. WIMAN, pp. 2–12, pl. 1, Figs. 1–20.
1897 *Dictyonema cavernosum* WIMAN–WIMAN, pp. 352–355, pl. XI, Figs. 1, 6–11, pl. XII, Figs. 15–19, 25.
1901 *Dictyonema cavernosum* WIMAN–WIMAN, p. 187, pl. VIII, Fig. 2.
1927 *Dictyonema cavernosum* WIMAN–BULMAN, p. 10, Text-fig. 4 B.
1938 *Dictyonema cavernosum* WIMAN–BULMAN, p. D 10, Fig. 9*f;* p. D 11, Fig. 10.
1955 *Dictyonema cavernosum* WIMAN–BULMAN, p. V 30, Fig. 14. 1.

LECTOTYPE.—The specimen figured by WIMAN, 1896*b*, pl. 1. Figs. 1, 5–20, now preserved as serial sections mounted on slides nos. G 778 and G 779 is here designated as lectotype.

MATERIAL.—Several specimens preserved as serial sections (cut at 20 $\mu$) including the lectotype; the specimen figured by WIMAN 1897, pl. XI, Figs. 1, 6–11 and pl. XII, Figs. 15–19 (slides nos. G 782 and 783) the specimen figured by WIMAN 1896*b* as Text-figs. 2 and 3 (slide no. G 780); the specimen figured by WIMAN 1896*b* as Text-fig. 4 (slide no. G 781); an unfigured series labelled *Dictyonema recessatum?* (slide no. G 824); and four further unfigured slides (slide nos. G 825–828).

HORIZON.—Upper Ordovician; from silicified boulders, Gotland.

DESCRIPTION.—The rhabdosome is conical with a well developed basal disc. Whilst all the specimens which were available to us are preserved as serial sections, the general form of the rhabdosome is beautifully shown in WIMAN's figures (1896*b*, pl. 1, Fig. 1 and Text-fig. 1; 1897, pl. XI, Fig. 1). Individual stipes have their maximum lateral width (about 0.3 mm) at the level of the bithecal apertures which are inflated in the same manner as *Dictyonema cervicorne* HOLM, though to a lesser degree. Indeed, it will be shown below that the bithecae of *D. cavernosum* are very similar in their whole construction to those of *D. cervicorne*, though the rhabdosome of *D. cavernosum* has a more

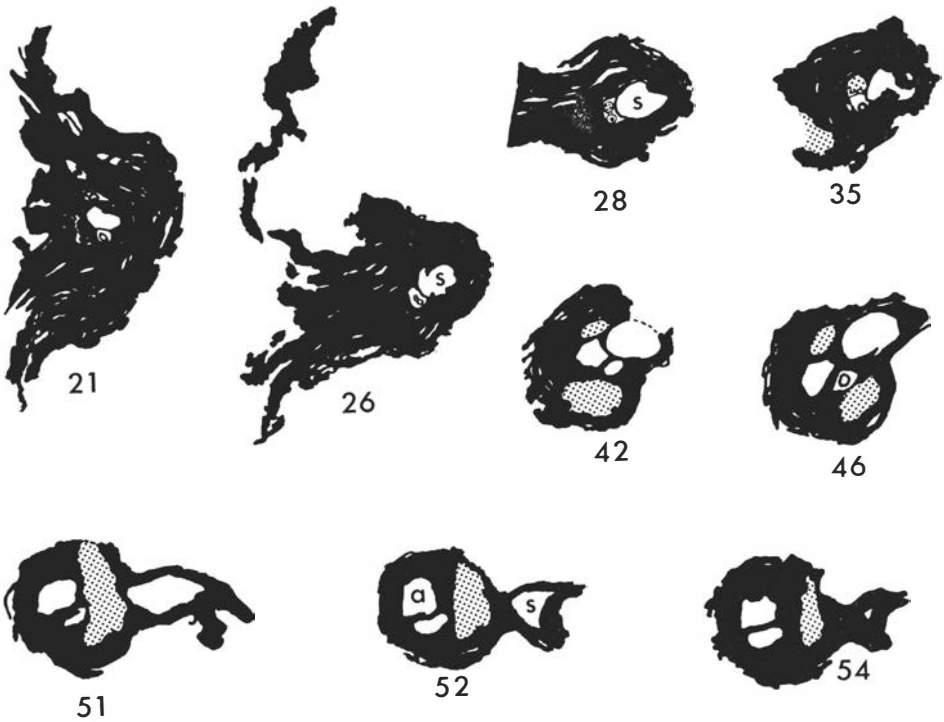



Fig. 8. *Dictyonema cavernosum* WIMAN. Selected sections of the lectotype cut at 20 $\mu$ (slide no. G 778; originally figured by WIMAN 1896 pl. 1 Figs. 5–20) *s*, sicula; first bitheca of rhabdosome is stippled. ×45.

regular meshwork of stipes and dissepiments, and the dissepiments themselves are simpler. The thecal spacing is 16–20 per cm.

Fig. 8 illustrates selected sections through the proximal end from a series cut at 20 $\mu$ and figured by WIMAN, 1896*b*, pl. 1, Figs. 5–20. A simplified reconstruction from the same series was prepared by BULMAN (1955, Fig. 14. 1), and a slightly modified reconstruction is figured here as Fig. 9. Section 21 shows the sicula and initial bud, which contains one stolon, enclosed in the thick cortical tissue of the basal disc; prior to the formation of the initial bud the sections are too badly preserved to interpret. The initial bud, with its contained stolon, grows along the side of the sicula for 0.1 mm before the first node and triad of a stolon is seen (section 26). The base of the first bithecal tube of the colony is seen in section 28, and the bithecal stolon is, therefore, approximately 0.04 mm in length (sections at 20 $\mu$ intervals). Section 28 also shows the autothecal stolon in a central position between the first bitheca and the stolotheca with its contained stolon. As is shown by later sections in the series, the open tube illustrated in section 35 (stippled) is the apertural region of bitheca *1*, which is sharply hook-shaped with its aperture facing towards the proximal end of the rhabdosome (Fig. 9). This mode of development of bitheca *1* proves that much of the cortical

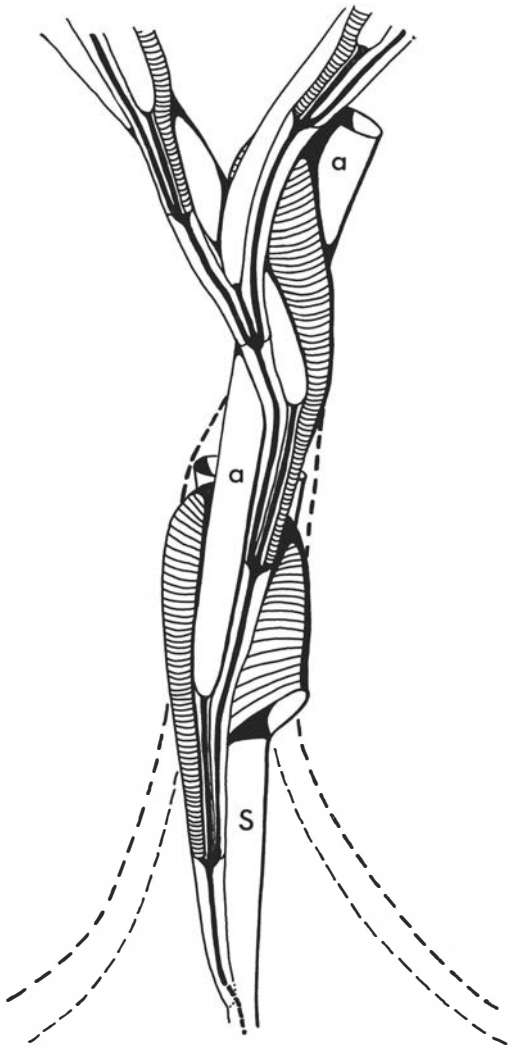



Fig. 9. *Dictyonema cavernosum* WIMAN. Reconstruction of the lectotype *s* = sicula; *a* = first autotheca; bithecae shaded; autothecae white; stolons heavy black lines; fine dashed line indicates extent of early tissue forming basal disc; heavy dashed line indicates the extent of late-formed cortical tissue which closes the sicular aperture. × 50 approx.

tissue of the basal disc was deposited quite early in the development of the rhabdosome, before the apertural region of bitheca *1* was formed. That later deposition of skeletal tissue took place is indicated by the closing of the sicula in what would normally be its apertural region (sections 52 and 54).

The further development of the rhabdosome, which involves the production of a branching division of two stolothecal stolons and one autothecal stolon is illustrated in Fig. 9. One of these two stolotheca and the autotheca, together with the first autotheca *a* and second bitheca, forms the right-hand branch,

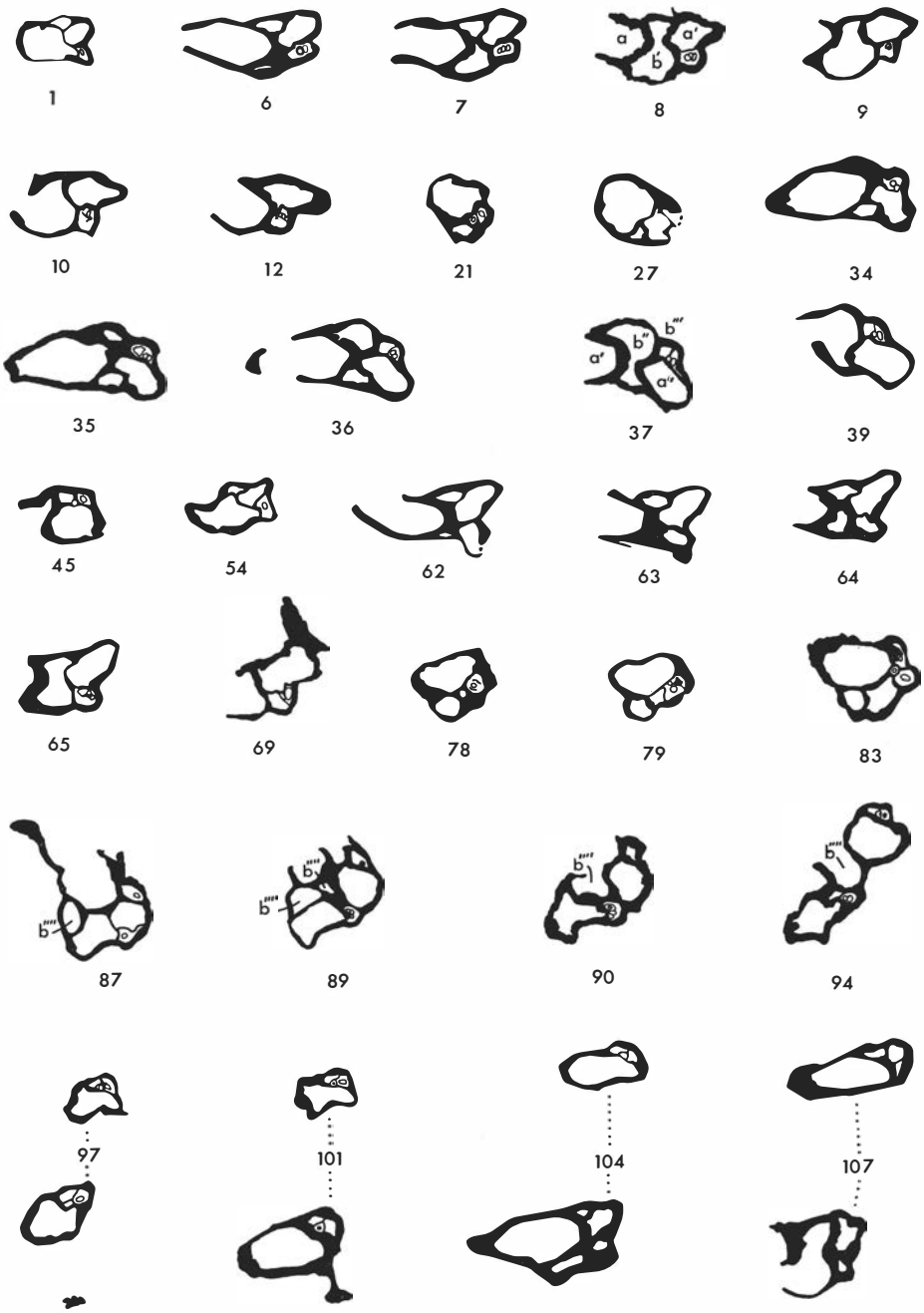



Fig. 10. *Dictyonema cavernosum* WIMAN. Selected sections cut at 20 $\mu$ of the specimen preserved on slide no. G 780; originally figured by WIMAN 1896 Text-Figs. 2, 3; *a*, autothecae, *b*, bithecae; full explanation in text. × 50.

whilst the beginning of the left-hand branch is composed of the other stolotheca and the second autotheca.

Unlike the first bithecal aperture, the second does not face proximally, but opens just above autotheca *1*. Its morphology will be described in more detail below where it is compared with later bithecae.

Figures 10 & 11 illustrate, respectively, selected sections from a series also figured by WIMAN (1896*b*, Text-figs. 2, 3), and a reconstruction from these sections. These sections represent a more distal portion of the stipe than those figured by WIMAN, and include the development of several autothecae. The stolon system is well displayed and a branching division can be traced.

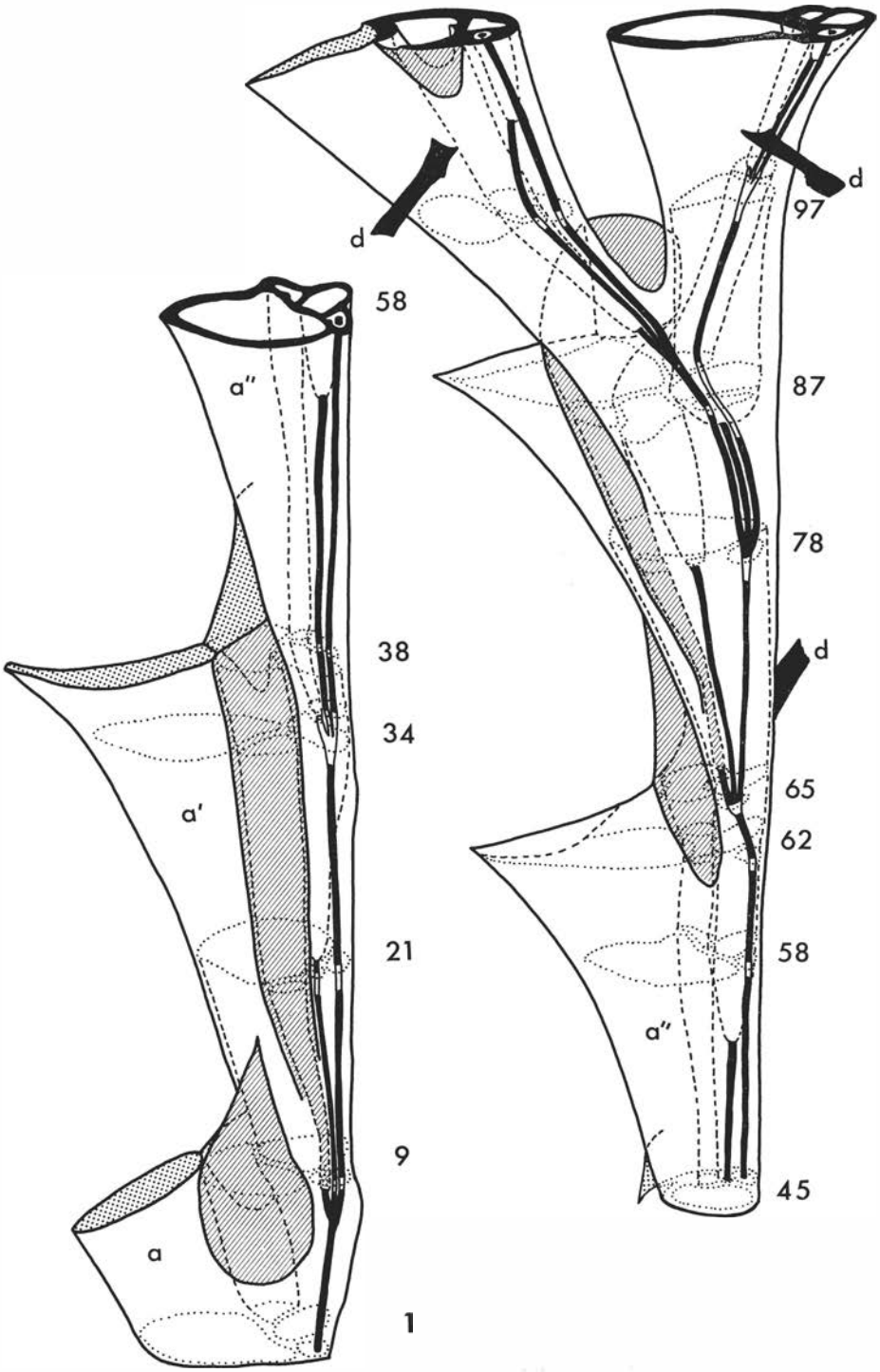
Section 8 (Fig. 10) shows a bitheca, *b'*, separating the apertural region of an autotheca, *a*, from the second autotheca of this series, *a'*, and a stolotheca. The stolotheca contains three stolons. If the bitheca is traced through the earlier sections 1, 6 and 7 it can be seen to grow firstly along one (upper) side of the stipe (section 1), and is then also seen as an elongate cavity on the opposite (lower) side (section 6). The two portions of the bithecal tube connect in section 8. Finally the bitheca opens (sections 10, 12) half facing the side upon which it originated (see also Figs. 11 & 12 B), and above the autothecal aperture. It is probable that the narrower bithecal cavity in the lower part of section 6 was secreted by soft parts which were able to operate some distance in front of the already-deposited skeletal layers, since there is no connection between the two cavities until section 8.

The next bitheca to be formed on this part of the rhabdosome (labelled *b''* in section 37) is developed in exactly the same way as *b'* except that it originated on the opposite side of the stipe. Again the aperture half faces the side upon which the bitheca originated. This type of bitheca, characterized by pronounced inflation of the apertural region, is illustrated in Fig. 12 B, and may be contrasted with the first bitheca of a *D. cavernosum* rhabdosome (Figs. 9 & 12 A); it must, however, be regarded as typical of the more distal bithecae. In succeeding paragraphs the first bitheca is termed "type 1" and the typical distal bithecae are termed "type 2".

The section series (Fig. 10 and reconstruction, Fig. 11) may be of a somewhat damaged portion of the stipe since the actual apertural margins of both the autothecae do not seem to be completely developed. Fig. 13 is a drawing of two fragments of stipe originally figured by WIMAN (1896*b*, pl. 1, Figs. 3, 4) and in which the shape of the thecal apertures is clearly displayed.

A third type of bitheca, being a slight modification of the typical distal

Fig. 11. *Dictyonema cavernosum* WIMAN. Portion of stipe reconstructed from the section series (slide no. G 780) illustrated in Fig. 10, a, autothecae (labelled as in Fig. 10); bithecae shaded; *d*, dissepiments; coarse stipple indicates apertures; stolons in solid black except where they pass the level of selected sections (1–97), which are indicated by fine dotted lines; course of thecae is shown by broken lines where the tubes are invisible either externally, or in this lateral view. × 100.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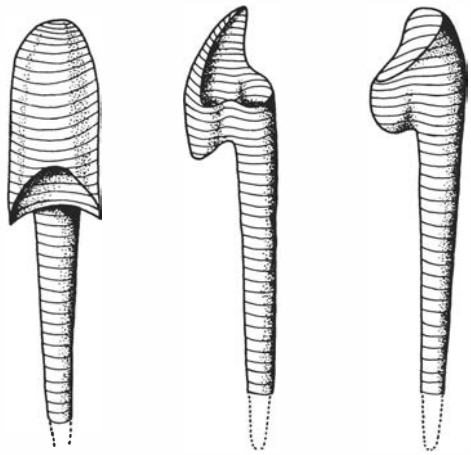
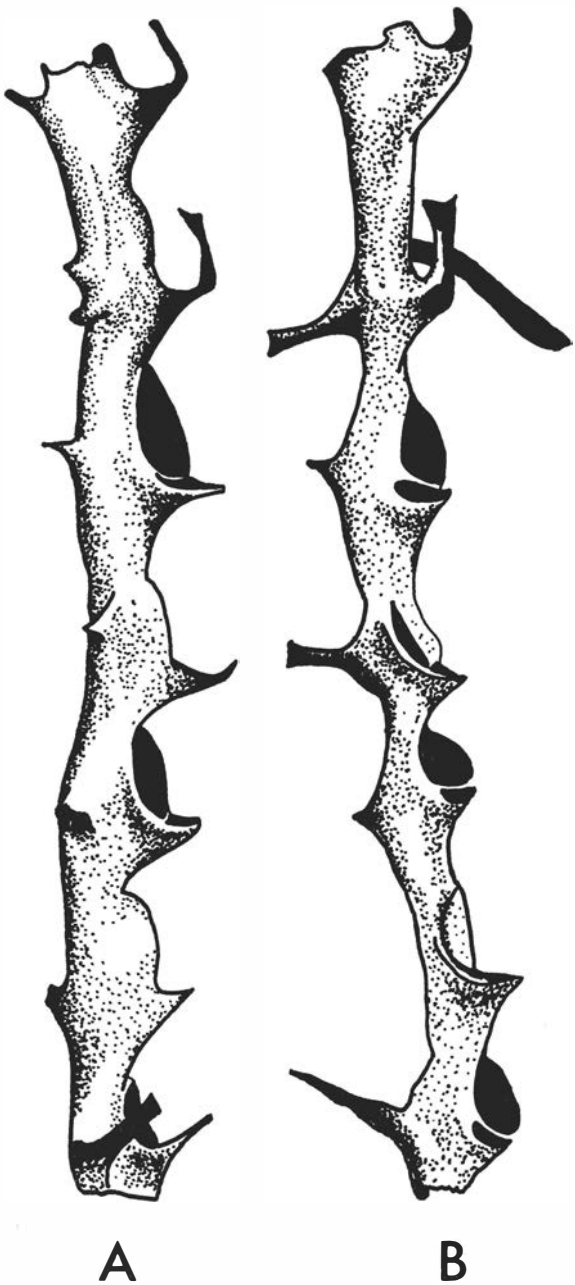



Fig. 12. *Dictyonema cavernosum* WIMAN. Reconstructions of the bithecae; *A*, the first bitheca of the rhabdosome (type 1); *B*, a typical distal bitheca from a normal portion of stipe (type 2); *C*, a bitheca (type 3) situated at a branching point on the stipe (see also Fig. 11); thin black lines are contour lines, not growth lines. × 50 approx.

type, is found at a branching point of a stipe. In this the bithecal tube *b'''* again pushes its way between the preceding autotheca and the rest of the stipe (section 87, 89, Fig. 10), but it opens facing *away* from its side of origin (sections 90, 94 and Figs. 10 and 13 C). The second bitheca of the *cavernosum* rhabdosome (Fig. 9), also occurring in the region of a branching point, is intermediate between the above described types 2 and 3 in that its aperture, like that of type 3, half faces the side of its origin (see WIMAN 1896*b*, pl. 1, Figs. 14, 20). Here, however, the bitheca continues a short distance along one of the branches before opening, and is, therefore, also intermediate between types 2 and 3 in its position with relation to a branching point. The similarity between the bithecae of *D. cavernosum* and *D. cervicorne* is strikingly illustrated by comparing Figs. 12 B, C with BULMAN's figures of the latter species (1933, Fig. 17). The short bithecal stolon of *D. cavernosum* never exceeds 0.05 mm.

The autothecae of the *cavernosum* rhabdosome are rather less conspicuous than the swollen bithecae. The autothecal apertures bear a sharp denticle or short spine which may bifurcate distally as in *D. cervicorne*, but this is not usually shown (see Fig. 13 and WIMAN 1896*b*, pl. 1, Figs. 3, 4, Text-fig. 1). There is some variation in the length of the autothecal stolon. Thus on the section series (slide no. G 780; Figs. 10 and 11) the autothecal stolons produced at the first, third and fifth nodes persist through 14 sections and are, therefore, approximately 0.28 mm in length. The autothecal stolon produced at the second node in the series is, however, considerably longer at 0.44 mm, while that produced at the fourth node (the branching node) is only 0.14 mm long,




Figs. 13 A–B. *Dictyonema cavernosum* WIMAN. Two typical portions of stipe showing the conspicuous bithecal apertures, relatively inconspicuous autothecal apertures, autothecal spines, and dissepiments; originally figured by WIMAN 1896, pl. 1 Figs. 3, 4. ×45.

and that produced at the last node illustrated (Fig. 11, right hand branch) is of similar length.

A certain amount of variation is also shown in the distance between nodes. The usual figure is from 0.5 mm to 0.6 mm, but the distance between the 3rd and 4th nodes, and again between the 4th and 5th nodes, is about half this value. Away from the branching portions of a stipe the nodes are situated at about the level of the autothecal aperture.

Dissepiments are preserved in section series (slides no. G 780; Figs. 10 and 11) where they appear as relatively thin, oblique rods connected with the cortical layer of the autothecae. The original figures of WIMAN suggest some irregularity in the form and arrangement of the dissepiments, although his specimen in Text-fig. 1 (1896*b*) does have a more regular development of rods in places. There is clearly not so much irregularity as is exhibited by the dissepiments of *D. cervicorne* HOLM.

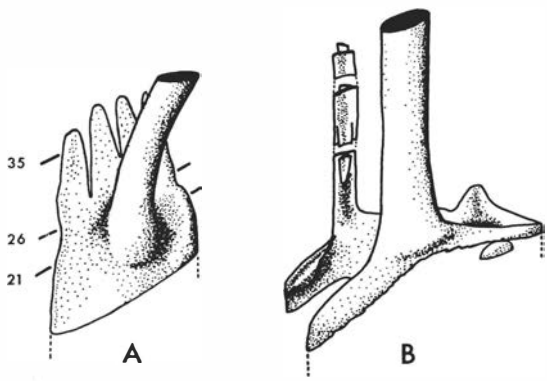
The section series (slide no. G 781), partly figured by WIMAN (1896*b*, Text-fig. 4) confirms the above interpretation of slide no. G 780. Thus a branching division is shown in which the bitheca from the preceding node follows one of the branches for a short distance and is intermediate between types 2 and 3 above. Prior to the branching division the normal distal (type 2) bitheca is found. The stolothecal stolon preceding the branching divisions is very short.

That the basal disc is highly variable in form is clearly indicated by WIMAN's original figures (1896*b*, pl. 1, Fig. 1; 1897, pl. XI, Fig. 1; 1901, pl. VIII, Fig. 2). Two of these figures each show the development of a single rhabdosome from a basal disc, but the third (1897) purports to illustrate the growth of two rhabdosomes from a single root system of branching hollow threads.

The section series figured by WIMAN (1897, pl. 12, Figs. 15–19) was prepared from the specimen figured on pl. XI as Fig. 1*b*. It shows that the development of rhabdosome 1*b* is quite normal and identical with that of the lectotype. The basal root structure is extremely irregular, but part of the series cuts through the robust tube connecting "a" and "b" on WIMAN's pl. XI, Fig. 1. There is no evidence that this tube carries a stolon, or that it has anything to do with the *origin* of the rhabdosome 1*b*, or is other than part of the attachment structure.

There is no evidence to suggest that the object lettered "a" in Fig. 1 (pl. XI) is a second rhabdosome. It consists of a tubular structure, considerably damaged, which opens downwards as well as upwards. At least four slender tubes (of stolonal proportions) connect with the main tube and three of these open into it. One in particular continues to form a thickened ridge along the length of "a". There is some evidence in later sections of smaller tubes within the main tube "a", but the preservation is so poor that interpretation of them cannot be attempted.

The unfigured series (slide no. G 824) is also of a basal disc (see Figs. 14 B and 15). It can be seen from the reconstruction that the rhabdosome develops as a relatively robust stem, (the details of which are given in Fig. 15 and are




Figs. 14 A–B. *Dictyonema cavernosum* WIMAN. *A*, Diagrammatic reconstruction of the basal "disc" structure of the lectotype (section series on slide no. G 778; see Fig. 8). × 15 approx. *B*, diagrammatic reconstruction of the basal "disc" structure exhibited by a previously unfigured section series (slide no. G 824); see also Figs. 15, 16; the stipe structure, comprising sicula and first triad covered by thick cortical tissue (Fig. 15), is not shown in either *A* or *B*. Nos. 21, 26, and 35 indicate the approximate levels of the sections in Fig. 8. × 15.

described below) associated with minor plates consisting, apparently, of the same material as that forming the cortical layer. They show no structural details other than an indication of the concentric layers of normal cortical tissue. One such plate continues to grow distally for a considerable distance parallel to the main stem. One of the specimens figured by WIMAN shows a very similar type of structure (1901, pl. VIII, Fig. 2). Such structures are best interpreted as basal skeletal material enveloping some small irregular object.

The basal disc of the lectotype (Fig. 14 A) is different again and conforms more closely to the usual concept of a disc of attachment. However, it does not resemble very closely the original figure of the (unsectioned) lectotype (1896*b*, pl. 1, Fig. 1). It is possible that in the preparation of the sections the basal disc was partly destroyed.

The section series (slide no. G 824) which permits reconstruction of the unusual basal attachment (Fig. 14 B), also exhibits an abnormal development of the most proximal thecae (Figs. 15, 16). Sections 7, 8 and 11 (Fig. 15) illustrate the separation of the first stolothecal tube, and contained stolon, from the sicula. The first node (see Fig. 16) gives rise to a triad of bithecal stolon, autothecal stolon, and stolothecal stolon. The first bitheca (*b'* on Fig. 16 and stippled on Fig. 15), unlike that of the lectotype, grows directly upwards between the sicula and the other thecal tubes, and ends facing distally; the bithecal aperture becomes closed with secondary tissue (sections 48–62, Fig. 15) a short distance below the sicular aperture (which is also closed by secondary deposits; see sections 60, 62).

The autotheca produced at the first node (*a'* in Fig. 15, fine stipple in Fig. 16) develops in a normal manner for some distance (section 32, Fig. 15) but then ends in a position adjacent to the second node of the rhabdosome (Fig. 16;

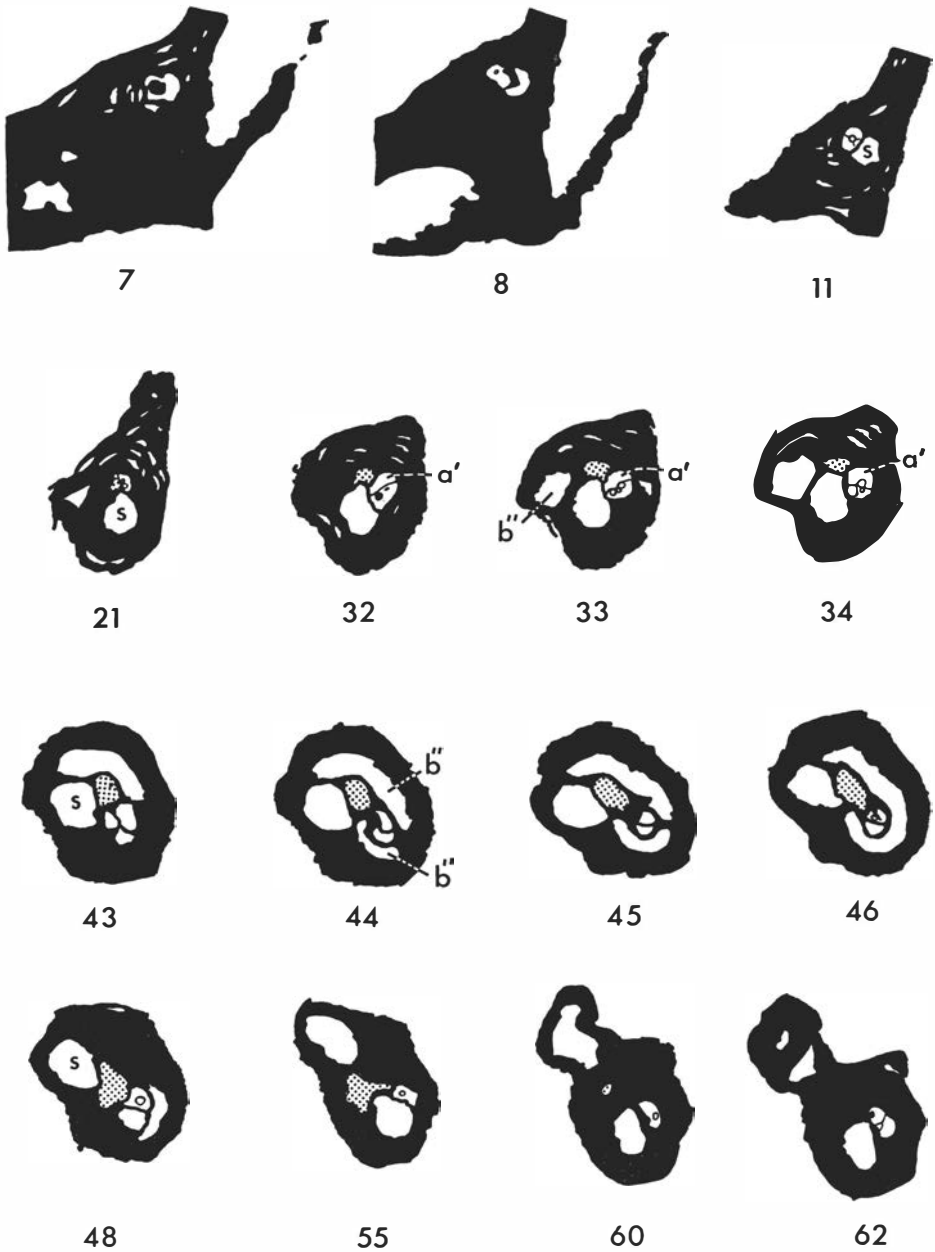



Fig. 15. *Dictyonema cavernosum* WIMAN. Selected sections at 20 $\mu$ of a previously unfigured specimen (slide no. G 824) illustrating an abnormal development of the proximal end; full explanation in text; *S*, sicula; *b*, bitheca; first bitheca of rhabdosome is stippled; *a'*, first autotheca. (In Fig. 16, all bithecae are shaded.) $\times$ 50 approx.

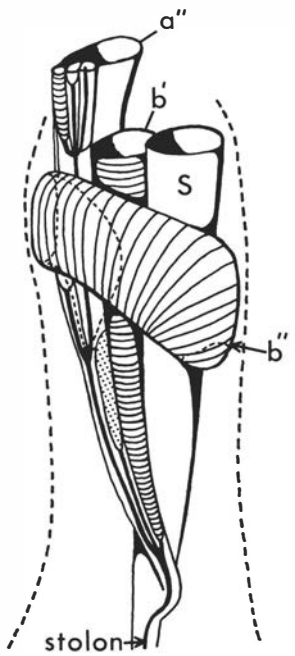



Fig. 16. *Dictyonema cavernosum* WIMAN. Reconstruction of the abnormal proximal end from the section series of slide no. G 824 (see also Fig. 15); *S* = sicula; bithecae shaded; *a* = autotheca; abnormal first autotheca is stippled; course of bitheca *b''*, where unseen, is indicated by a fine broken line; coarse broken line indicates extent of cortical tissue which closes the aperture of *b'* and partly closes the aperture of S. × 50.

sections 33, 34, Fig. 15), and is apparently crowded out upwards by the thecal tubes developing from this second node between sections 34 and 43, (Fig. 15).

It would seem, therefore, that neither the bitheca nor the autotheca resulting from the first division of the stolon reach normally complete development. The second node produces a normal autotheca (*a''* in Fig. 16), but the bitheca (labelled *b''* in Figs. 15 and 16) develops in a similar manner to that of bitheca *1* in the lectotype, except that it is unable to separate the sicular aperture from the rest of the stipe, since this position is already occupied by the malformed first bitheca. Bitheca *2*, therefore, grows round the dorsal side of the stipe and ultimately opens adpressed to the sicula on the ventral side. Its aperture again is closed by secondary deposits (see sections 32, 33, Fig. 15).

The third node is located slightly below the level of the sicular aperture, and the rhabdosome develops quite normally from this point. In the lectotype the *second* node is found just below the sicular aperture (Fig. 9).

REMARKS.—RUEDEMANN (1947) suggested that *D. cavernosum* belonged to his genus *Airograptus*. This genus, however, has been rejected by BULMAN (1955) on the grounds that there is no evidence that the stipes are connected by thecal spines. Although the autothecal spines of *cavernosum* may be long when fully

preserved, there is certainly nothing to suggest that these connect adjacent stipes.

It would seem from the evidence afforded by the abnormal proximal end, that the hook-shaped first bitheca of the *D. cavernosum* rhabdosome has some special significance, at least during the early stages of rhabdosomal development. Having failed to produce a normal first triad, the bitheca of the second node simulates the first bitheca of a normal rhabdosome.

### *Dictyonema peltatum* WIMAN, 1895

Figs. 17–19

1895 *Dictyonema peltatum* n.sp. WIMAN, pp. 286–291; pl. X, Figs. 12, 15; pl. XII, Figs. 3–5 (*non* 1, 2); pl. XIV, Figs. 15–22 (*non* 9–14, 23–29), Text-figs. *a–g* (p. 289).
1896a *Dictyonema peltatum* WIMAN–WIMAN, p. 244.
1897 *Dictyonema peltatum* WIMAN–FRECH, p. 575; Figs. 142, 144.
1901 *Dictyonema peltatum* WIMAN–WIMAN, pp. 186–187; pl. VIII, Fig. 10.
1933 *Dictyonema peltatum* WIMAN–BULMAN, pp. 31–32; pl. 3, Figs. 17–19.
1938 *Dictyonema peltatum* WIMAN–BULMAN, p. D 5, Fig. 6*b*; p. D 8, Fig. 8*b*.
1955 *Dictyonema peltatum* WIMAN–BULMAN, p. V 25, Fig. 9. 3; p. V 26, Fig. 10. 2.

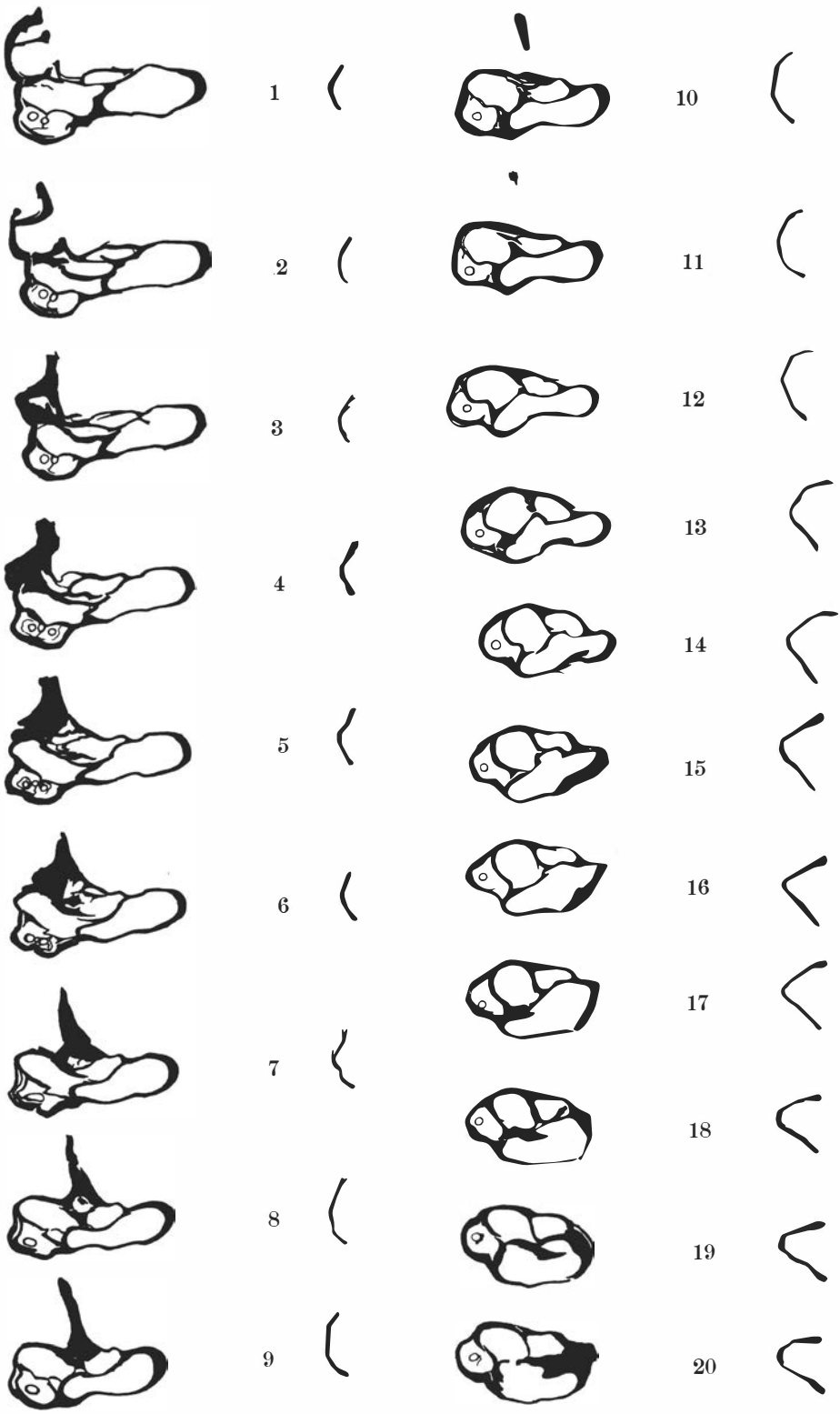
LECTOTYPE (here designated).—The specimen figured by WIMAN (1895) as Figs. 15–18, plate XIV, now preserved as serial sections (at 20–25 $\mu$) on slide no. G 817.

MATERIAL.—The lectotype; the specimen figured by WIMAN (1895) as Figs. 19–22, plate XIV now preserved as serial sections (at 20 $\mu$) on slide no. G 818; the specimen figured WIMAN (1895) as Text-figs. on p. 289 now preserved as serial sections (cut at 20 $\mu$) on slide no. G 808; two further slides (nos. G 829 and G 830) of serial sections (cut at 20 $\mu$) prepared, but unfigured, by WIMAN; two slides (nos. G 805 and G 832, cut at 20–25 $\mu$ and 20–30 $\mu$) showing branching divisions with both longitudinal and transverse sections, unfigured by WIMAN. All the above specimens were isolated from a flint boulder (no. 4), Visby. From another flint boulder (no. 5, labelled Gotland) WIMAN isolated another specimen and prepared a section series (slide no. G 833; probably cut at 20 $\mu$) which he did not figure. This series is figured here as Figs. 17–18.

HORIZON.—Recorded as Upper Ordovician, Öjle Myr, Gotland.

DESCRIPTION.—The general form of the rhabdosome is best displayed by the specimens illustrated by WIMAN (1895, pl. XII, Fig. 3; 1901, pl. VIII, Fig. 10) and by BULMAN (1933, pl. 3, Fig. 17). It can be seen to consist of a delicate meshwork defined by slightly sinuous stipes and slender connecting dissepiments. The stipe width is approximately $\frac{1}{4}$ mm–$\frac{1}{3}$ mm above the autothecal apertures but at the autothecal apertures themselves the dorso-ventral width may be as

Figs. 17, 18. *Dictyonema peltatum* Wiman. Continuous section series, previously unfigured, (slide no. G 833) prepared by WIMAN; full explanation in text; transparent tissue stippled. × 40.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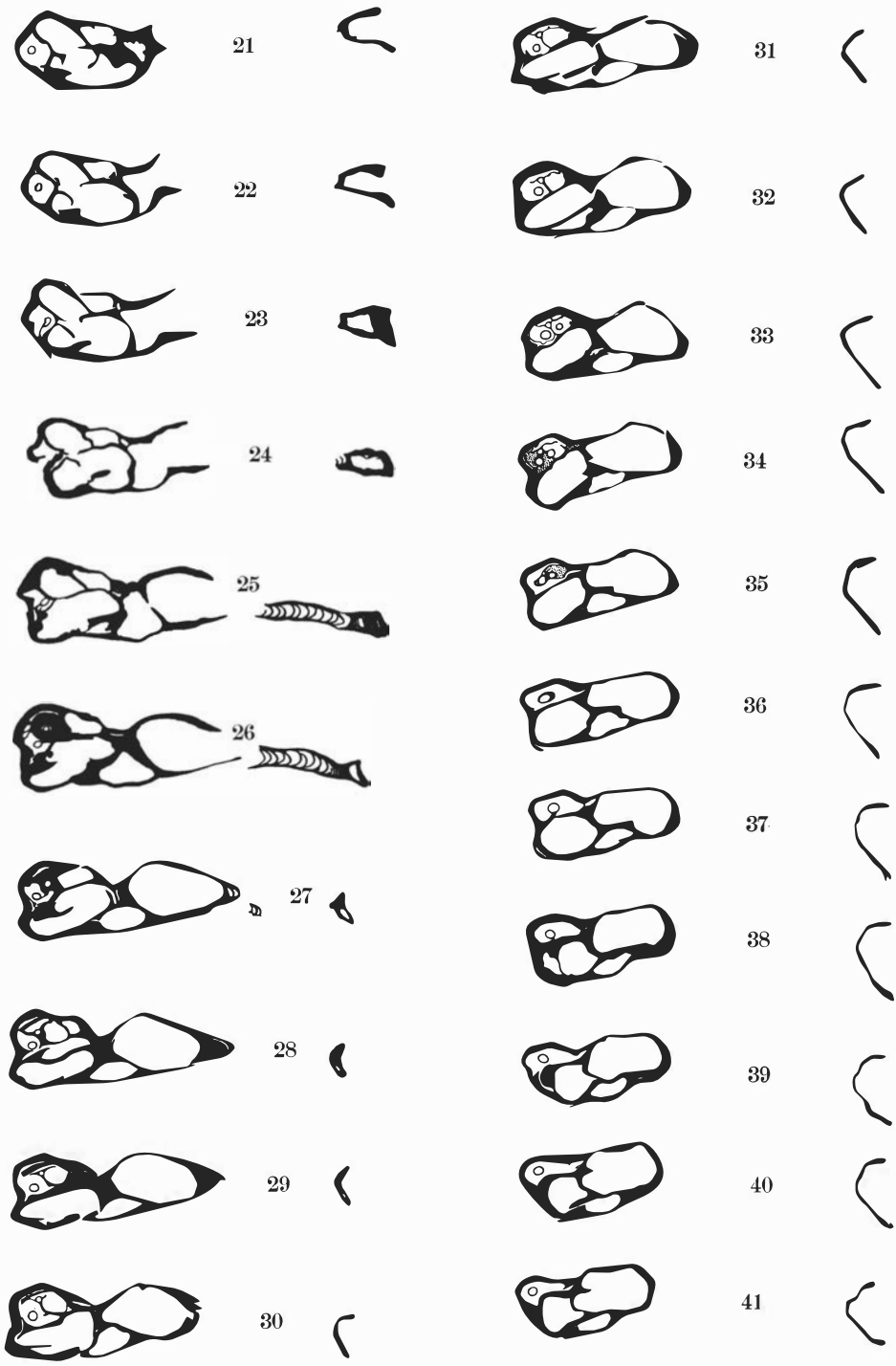



Fig. 18

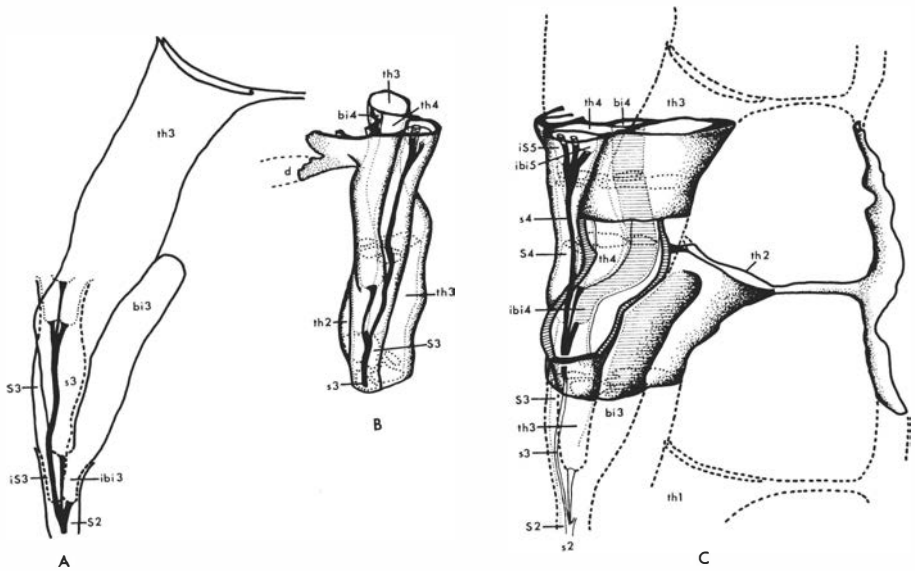



Fig. 19. *Dictyonema peltatum* WIMAN. Reconstruction based on the section series illustrated in Figures 17 and 18 (slide no. G 833); *A*, restoration showing stolon system and triads; *B*, dorsal view of portion of stipe; *C*, lateral view of portion of stipe with front wall partly cut away; *s*, stolons; *S*, stolothecae; *iS*, internal stolothecae; *bi*, bithecae; *ibi*, internal bithecae; *th*, autothecae; *d*, dissepiments.

much as 0.8 mm (excluding apertural processes). The distance between stipes is from 0.75 mm to 1.0 mm. Dissepiments are common and irregularly spaced (see BULMAN 1933, pl. 3, Fig. 17) at approximately 10–14 in 10 mm.

The bithecae are almost invisible externally. On the other hand the autothecae are very conspicuous with pronounced autothecal processes, consisting of long spines terminating in sub-discoidal, plate-like structures. These plate-like terminations may fuse, thus connecting adjacent autothecae on the same stipe, but there is no evidence to suggest that these processes connect adjacent stipes. The thecal spacing is usually 14–18 in 10 mm though the specimen figured by WIMAN (1901) as Fig. 10, plate VIII has about 20 in 10 mm.

The section series depicted on Fig. 17, 18 and reconstructed as Fig. 19, is of a portion of stipe in which the stolon system is particularly well shown. Sections 41–36 (Fig. 18) show a stolothecal stolon centrally situated in a stolothecal tube (top left in each section). In section 35 it splits into three stolons. The most slender of these stolons, which moves into a dorsolateral position on the stipe by section 33, eventually gives rise to an autothecal tube in section 25. The most dorsal stolon of the triad is a stolothecal stolon and forms the second node of this series in section 6 (Fig. 17). The ventral stolon of the first triad forms a bithecal tube in section 32, which can then be traced throughout the remainder of the illustrated sections. The distal development of another bithecal tube is shown in sections 41–21. In section 26 it begins to push its way between the

autothecal aperture and the rest of the stipe, and in section 25 reaches the opposite lateral wall of the stipe. Immediately following this (section 24–21) it opens into the autothecal tube. It is much more usual, however, for the bitheca to open into the autotheca without pushing through to the opposite side of the stipe.

The large autothecal tube of section 41 increases in size until section 29 when it begins to develop a spine from the free ventral margin. The form of this spine, and its connection with the ventral fused plate structure, is shown in sections 27–25. It is clear that the spine is formed by a ventral extension of the fusellar layer, and some indication of the zig-zag suture is discernible in section 26. Other sections show that the autothecal aperture tends to be very slightly isolate.

The fused ventral process is convex towards the dorsal side of the stipe (sometimes sharply so, see sections 22–18) and is continuous throughout the series. An oblique dissepiment joins the stipe in sections 11–1.

Two of the sections series (slides no. G 808 and G 805; one partly figured by WIMAN, 1895, Text-figs. *a–g*, p. 289) each show a branching division. This is achieved in the normal way by the suppression of the bitheca and the production of two stolothecal stolons and one autothecal stolon at one of the nodes. Immediately below the branch the stipe is approximately circular in cross section, in contrast to the rest of the stipe which is always elliptical with the long axis of the ellipse lying in the dorso-ventral plane.

A further series (slide no. G 805) of longitudinal sections shows the only instance of anastomosis recorded in the case of *D. peltatum*. There is of course no internal communication between the two stipes.

REMARKS.—Of WIMAN's original figures, some were subsequently referred to other species: thus Figs. 1 and 2 (plate XII 1895) and Figs. 23–29 (plate XIV 1895) were later included in the synonymy of *Discograptus schmidti* WIMAN (see WIMAN, 1901, p. 191).

The section series (slide no. G 818) partly illustrated as Figs. 9–14 (plate XIV 1895) seems to be indistinguishable from *Dendrograptus oelandicus* WIMAN (described above), and is here included in the synonymy of that species.

### *Dictyonema rarum* WIMAN

?1861 *Dictyonema flabelliforme* ROEMER, p. 32, pl. v. Fig. 4.
1895 *Dictyonema rarum* n.sp. WIMAN, pp. 283–6, Text-figs. *a–m.* (p. 284), pl. XII, Figs. 6, 10, pl. XIII, Figs. 12–26, 28.
?1897 *Dictyonema Sadewitzense* F. ROEM. nov. nom. –ROEMER, pp. 573–4.
1901 *Dictyonema rarum* WIMAN–WIMAN, p. 187.
1938 *Dictyonema rarum* WIMAN–BULMAN, p. D 2, Fig. 2, p. D 3, Fig. 3*c*, p. D 5, Fig. 6*d*.
1955 *Dictyonema rarum* WIMAN–BULMAN, p. V 26, Fig. 10: 4.

LECTOTYPE.—The specimen figured by WIMAN (1895) as Text-figs. *a–m* (p. 284), and pl. XIII, Figs. 12–26.

## Family *Acanthograptidae* BULMAN, 1938

### Genus *Acanthograptus* SPENCER, 1878

TYPE SPECIES.—*A. granti* SPENCER 1878.

AMENDED DIAGNOSIS.—Robust dendroid composed of rather stout divergent branches bifurcating irregularly; very rarely anastomosing; thecae elongate tubular, usually isolate distally to give spinous appearance to branch; grouping of two autothecae and two bithecae in "twigs" is characteristic.

REMARKS.—The species *A. musciformis* (WIMAN), described below, shows some features reminiscent of the genus *Coremagraptus*, namely tendency to anastomosis (albeit locally) and a complex and probably irregular, internal structure. On the other hand the stipes exhibit a typical acanthograptid grouping of two bithecae and two autothecae, and on this character may be strongly contrasted with *Coremagraptus* in which the formation of twigs is capricious and their composition inconstant. The regular grouping of thecae into twigs is probably of more value than anastomosis as a biocharacter for distinguishing *Acanthograptus* and *Coremagraptus*.

#### *Acanthograptus suecicus* (WIMAN)

1895 *Ptilograptus suecicus* n.sp. WIMAN, p. 301 and Text-Fig., pl. XII, Figs. 11 & 13
1896a *Ptilograptus suecicus* WIMAN–WIMAN, p. 246, Figs. 18, 19.
1901 *Inocaulis suecica* WIMAN, p. 191.
1908 *Acanthograptus suecicus* (WIMAN)–RUEDEMANN, p. 192.
1937 *Acanthograptus suecicus* (WIMAN)–BULMAN, pp. 182–188, Text-figs. 1,2.
1959 *Acanthograptus suecicus* (WIMAN)–STRACHAN, pp. 62–66, Text-figs. 11,12, pl. 11, Figs. 5–11.

LECTOTYPE.—The specimen figured by WIMAN (1895) as Text-figures A–N, p. 301.

#### *Acanthograptus musciformis* (WIMAN)

Figs. 20–22

1901 *Inocaulis musciformis* n.sp. WIMAN, p. 191, pl. VIII, Figs. 6, 7; pl. VII, Figs. 19–21.

LECTOTYPE (here designated). The specimen figured by WIMAN (1901) on pl. VII as Figs. 19–21, a section series cut at 20 $\mu$ mounted on slides nos. G 74*a* and G 74*b*.

MATERIAL.—The lectotype; an unfigured section series (slide no. B 319) and numerous incomplete specimens isolated from the matrix.

HORIZON.—Upper Ordovician; Öjle Myr, Gotland.

DESCRIPTION.—The rhabdosome is composed of stiff, robust stipes which bifurcate at irregular intervals. After bifurcation the stipes diverge at varying angles and may become subparallel at less than 1 mm apart. Anastomosis is not uncommon, but is extremely irregular: several specimens though long do not

exhibit this feature. The stipes have an average lateral width of 0.40 mm. Others, clearly of a compound nature with several stolonal chains, have a lateral width of up to 1 mm. Each stipe has a distinct dorsal side upon which few thecae open (see below). Twigs are usually composed of two diverging autothecae, and are directed alternately to the right and left. The typical thecal grouping in *A. musciformis* is built up of two autothecae and two bithecae, but the bithecae open at stipe level, not on the twig. One of the two bithecae has its aperture between the points where the isolated portions of the autothecal pair diverge from the stipe, whilst the second may be found at various positions on the stipe.

The autothecae are long slender tubes which expand very slightly near their apertures to approximately 0.10 mm. When fully preserved the apertures have a rounded ventral denticle from 0.05–0.10 mm long. The isolate portion of the autothecal tube is of the order of 0.5–0.7 mm in length, but occasionally examples may be as long as one millimetre. The twigs are usually composed of two divergent autothecae (more rarely of two autothecae and one of the bithecae) and grow out from the stipe at high angles (up to 70°). The two autothecae in the twig may remain together for a short distance but finally diverge at angles up to 40°. In many instances the isolate portion of one autotheca is shorter than that of the other.

The number of twigs in any given length of stipe seems to depend upon the complexity of that particular portion of stipe. Some stolothecal divisions in the lectotype result in two stolothecal stolons and one autothecal stolon (see Fig. 21) although such a division is not related to the production of a branch and in consequence a branch may comprise two, three or even more stolonal chains. Moreover these stolonal chains are not independent of each other and a twig may be composed of thecae which result from several. Thus in Fig. 21 the fifth thecal group (autothecae 15 and 21, and bithecae 25 and 28) draws its individuals from more than two lines of development. It has not proved possible to detect any recurrent pattern of internal structure as a basis of the thecal groups. This may be a consequence of the short length of sectioned stipe available, but it is more probable that in such a compound stipe the internal regularities seen in simpler species of *Acanthograptus* (such as *A. suecicus* (WIMAN)) are to some extent lost. Nevertheless it should be noted that the formation of outwardly identical thecal groups and twigs is adhered to. In Fig. 21 only bitheca 16 does not seem to fit into the scheme, although it may have strayed from the first grouping which is incomplete. Of those groups (5, 6 and 7) which are seen in their entirety, each has a relatively long and a short autotheca, whilst groups 3 and 5 each have a long and a short bitheca; group 7 on the other hand has two short bithecae. In terms of absolute length, however, neither the autothecae nor the bithecae can be divided into two groups. The autothecae in Fig. 21 range from 0.66 mm (th 34) to 1.4 mm, (th 21), whilst the bithecae may be as short as 0.40 mm (bi 16) or longer than 1 mm (bi 25).

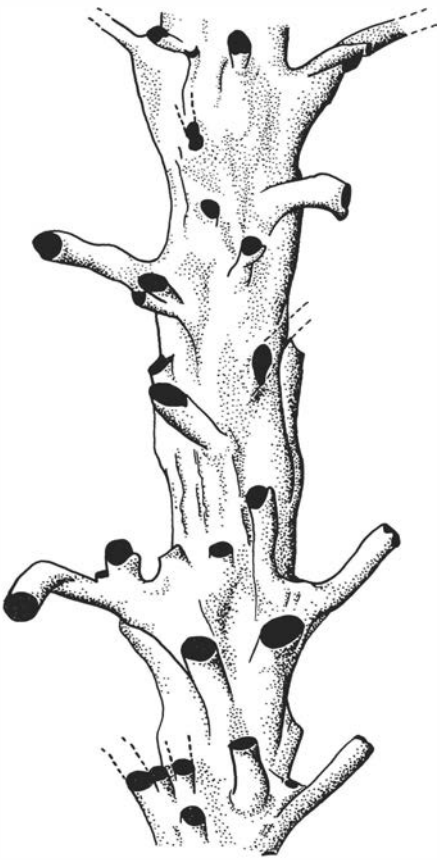


Fig. 20

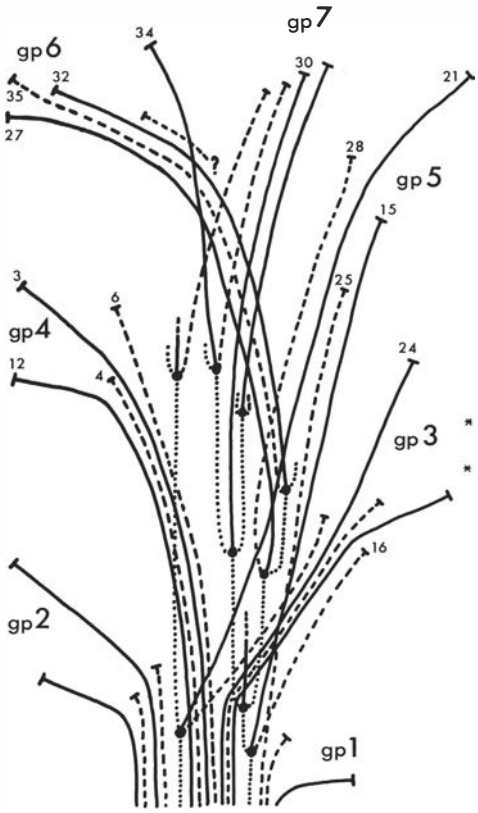



Fig. 21

Figs. 20–21. *Acanthograptus musciformis* (WIMAN) 20. Camera lucida drawing of portion of stipe, ventral view; broken lines indicate probable extensions of damaged autothecae; specimen no. G 846, × 40.—21. Diagram showing the thecal composition of a portion of sectioned stipe (lectotype; slide no. G 74); asterisks indicate the portion of stipe illustrated in Fig. 22, the thecae being numbered in the same way; thecal numbers (16, 24 etc.) do not indicate the orders of origin of thecae; gp. 1–7, thecal groupings of two autothecae (solid lines) and two bithecae (broken lines); stolothecae are represented by dotted lines and nodes are indicated by a black spot. × 60 approx.

The bithecae may be distinguished from the autothecae by their short stolons, and by the smaller diameter of the thecal tube which never exceeds 0.06 mm even in the apertural region. The bithecal apertures are simple, inconspicuous and generally closely adpressed to the stipe. Very occasionally a bitheca will grow for some distance along a twig, where it is situated between two non-divergent autothecae (see Fig. 22, bitheca 25). It is more usual, however, for one of the two bithecae in the twig grouping to open on the stipe between the two autothecae, at the point where the latter begin to diverge. The second bitheca opens in any position on the stipe, but at approximately the same level.

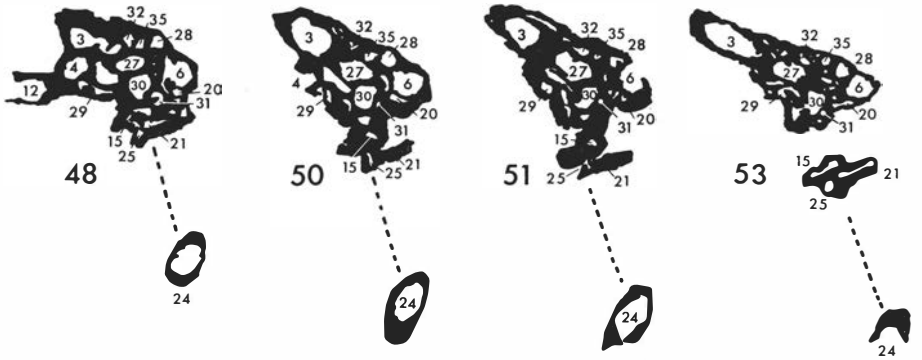



Fig. 22. *Acanthograptus musciformis* (WIMAN). Selected sections of the lectotype (sections 48 and 50 from slide no. G 74*a*, sections 51 and 53 from slide no. G 74*b*); thecae not numbered in order of origin, but as Fig. 21. The series shows a twig (group 5) in which the autothecae (15 and 21) do not diverge, and in which the bitheca (25) is part of the twig. × 50.

Anastomosis is not a regular feature and long portions of stipe show a typically dendroid aspect. In some places, however, it is quite common and seems to be of several grades of complexity. Thus adjacent stipes may be in contact for a short distance only, or remain in contact for a considerable distance. Simpler connections between stipes are made between the long isolate portions of the autothecae. The autothecae from adjacent stipes may touch, or an autothecal tube from one stipe may cross over completely to an adjacent stipe. This latter kind of anastomosis may be an accidental feature reflecting the wide divergence of the autothecae in the twigs.

REMARKS.—The striking thecal grouping and twig formation of *musciformis* places the species in the genus *Acanthograptus*.

*A. musciformis* differs from *A. suecicus* in the complex nature of the stipe, and in having autothecae which diverge strongly in their isolate portions. In those portions of stipe where the autothecae do not diverge (Fig. 22; and groups 5 and 7 in Fig. 21) *musciformis* may be distinguished from *suecicus* in having a greater number of thecal tubes (including more than one stolotheca) in any cross section of the stipe.

Externally *A. musciformis* is similar to the L. Ordovician *A. divergens* SKEVINGTON in that both possess "twigs" consisting of a pair of divergent autothecae, and a thecal grouping of two autothecae and two bithecae. The nature and dimensions of the autothecae and bithecae also appear to be very similar. However the internal structure as interpreted by SKEVINGTON (1963, pp. 43–45) is clearly much simpler than *musciformis* although he does suggest (op. cit., p. 45) that the structure might possibly be complicated.

### *Acanthograptus impar* sp. nov.

Figs. 23–25

HOLOTYPE.—The specimen illustrated in Fig. 24, preserved as serial sections cut at 10 $\mu$ on slide series G 835.


Fig. 23. *Acanthograptus impar* sp. nov. Camera lucida drawing of isolated specimen (no. G 847) prepared by WIMAN, showing narrow isolate autothecae and bithecae of two sizes opening on the stipe; full explanation in text; *A*, dorsal view; *B*, ventral view. ×40.

MATERIAL.—The holotype and three well preserved fragmentary specimens isolated from the matrix.

DERIVATION OF NAME.—*impar*, Lat., unequal, odd; refers to nature of thecal grouping in different parts of the stipe.

HORIZONS AND LOCALITIES. Upper Ordovician; Öjle Myr, Gotland.

DESCRIPTION.—The available portions of stipe suggest that the species possesses an essentially dendroid rhabdosome. One of the specimens has first order branches which diverge at low angles from the parent-stipe and become

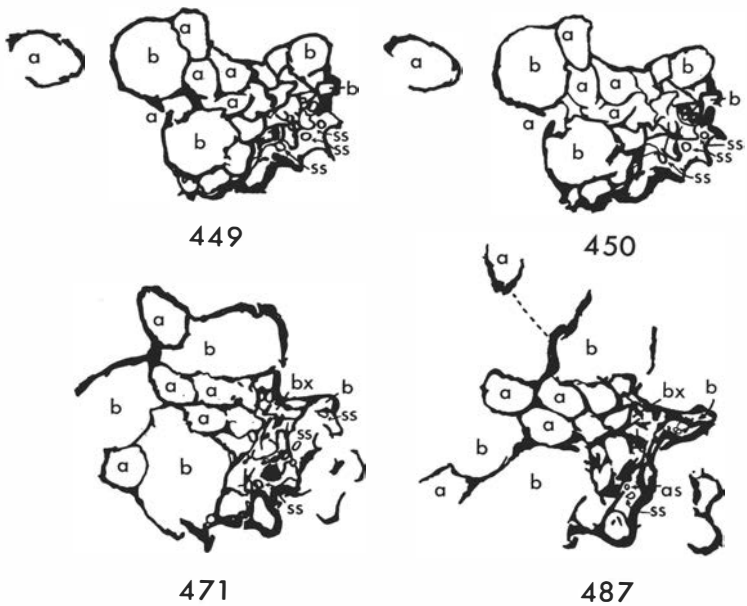



Fig. 24. *Acanthograptus impar* sp. nov. Selected sections of the holotype (slide no. G 835); *a*, autothecae; *b*, bithecae; *bx*, bitheca produced at node in section 450; *ss*, stolothecal stolon; *as*, autothecal stolon. ×65.

subparallel distally, whilst in another specimen the branches diverge at 40°. The stipes are robust, stiff, and have a maximum overall lateral width of 1.8 mm. Excluding the isolate parts of the thecae, however, the lateral width rarely reaches 1 mm and may be as little as 0.5 mm. The thecae are rather loosely arranged in groups, which, in the more compound portions of stipe, are composed of two autothecae and two bithecae. The thecal groups open alternately to left and right (Fig. 23 B), and there is a distinct dorsal surface to the stipe upon which relatively few thecae open (Fig. 23 A) and where no thecae have isolate portions.

The stolothecae are situated dorsally and are relatively large tubes often reaching a diameter of 0.07 mm, whilst the stolothecal stolons are strongly sclerotized and can be easily traced from section to section. Whereas the stolothecal stolons have a diameter of 0.026 mm, swelling to 0.04 mm immediately prior to a node, the autothecal stolons never exceed 0.01 mm and are often of the order of 0.007 mm. The proximal and distal limits of each stolothecal stolon possess structures closely similar to the *diaphragmes vésiculaires* described by KOZLOWSKI (1963) in the tuboid *Dendrotubus erraticus* and the dendroid *Dendrograptus* sp. These vesicular structures are illustrated diagrammatically in Fig. 25. It will be seen that the vesicle separating the two stolothecal stolons is very similar to that at the base of the bitheca. On the other hand the base of the autothecal stolon appears to be of simpler construction. It is also of interest

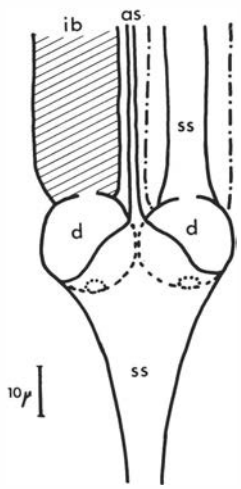



Fig. 25. *Acanthograptus impar* sp. nov. Diagrammatic reconstruction of a normal node; *ss*, stolothecal stolon; *as*, autothecal stolon; *ib*, internal bitheca (shaded); *d*, *diaphragmes vésiculaires;* dot/dash line indicates position of internal stolotheca.

that the bithecal stolon is represented wholly by the vesicular portion. The distal extremity of the autothecal stolon also appears to have a vesicular diaphragm, but its exact form cannot be ascertained.

Fig. 25 represents the normal division of the stolothecal stolon, which produces a normal triad of bithecal stolon, autothecal stolon, and stolothecal stolon. Other divisions result in two stolothecal stolons and an autothecal stolon (i.e. suppression of bitheca); it is this type which causes the stipe to become compound since the production of two stolothecae at a node is not necessarily related to the branching of the stipe. Any cross section of the stipe may cut through as many as 30–35 thecal tubes of which as many as five may be stolothecae. On the other hand the most simple parts of the stipes probably have only a single line of development, and far fewer individuals.

All the specimens available have a peculiar crumpling of the dorsal side of the stipe (Fig. 24) and whilst it is possible to recognise the *origins* of the bithecae and autothecae, it has proved impossible to trace any thecal tube from its beginnings to its apertural region. Fig. 23 illustrates the three types of thecal apertures found in *A. impar:*

a. small denticulate apertures of the thecae with long, narrow isolate portions,

b. small simple apertures of the narrow thecae closely adpressed to the stipe,

c. large simple apertures usually found near the base of a twig, and never isolate.

The presence of apertural denticles on those thecae with long, isolate portions suggest that they are autothecae, whilst the small inconspicuous thecae are almost certainly bithecae. Those thecae with large apertures cannot be autothecae since the stipe would then have more bithecae than autothecae, and,

as bithecae are suppressed at some nodes, the reverse should be true. Furthermore the thecae with large simple apertures are only broad tubes in the last 0.2–0.4 mm of their total length. Internally they rapidly become quite inconspicuous (see tube *bx* in Fig. 24) and it seems most probable that they represent bithecae which perhaps owe their large apertures to their position of opening on the stipe (i.e. at the base of a twig composed of two divergent autothecae). *A. impar* would then be similar to *A. musciformis* and *A. suecicus* in having the bithecae opening in two distinct positions, namely at the base of a twig, and closely adpressed to the stipe in any other position.

Some of the secondary stipes are clearly of a more simple structure initially than the specimens illustrated in Figs. 23 and 24. One branch has a lateral width of approximately 0.5 mm and the groups each consist of one of the narrow thecae with a long isolated portion, and one of the large thecae which opens near the base of the twig. After a few millimetres, however, the stipe clearly becomes compound and the grouping reverts to the more common association of two autothecae and two bithecae.

REMARKS.—The general aspect of the stipe is distinctly acanthograptid, but it is clear that the typical thecal grouping of simpler species of *Acanthograptus* is not maintained in the complex compound stipes. It is natural that there should be differing numbers of autothecae and bithecae when the latter are suppressed (without branching taking place) and this in itself might be sufficient to break down the regular grouping. Like *A. musciformis*, *A. impar* must be regarded as having some features resembling *Coremagraptus*, but the fact that thecal groups and twigs are still formed suggests reference to *Acanthograptus*. It can be imagined, however, that in stipes only a little more complex, and involving anastomosis, the thecal grouping and twig structure could lose all regularity.

## Genus *Coremagraptus* BULMAN 1927

TYPE SPECIES.—*Coremagraptus onniensis* BULMAN 1927.

AMENDED DIAGNOSIS. Rhabdosome conical or flabellate; branches complex, particularly in those species from younger stratigraphical levels; branches and twigs anastomosing irregularly; thecae very long, tubular, and usually adnate for much of their length.

REMARKS.—The genus was founded for a Lower Silurian species combining "the form of stipe and thecal structure of the *Inocaulis-Acanthograptus* group with the habit of the *Dictyonema-Desmograptus* group" (BULMAN 1927, p. 345); and it was then suggested (p. 345) that "Species no. V" of WIMAN 1897 (= *Desmograptus? formosus* WIMAN 1901) probably belonged to the new genus. Other species which have been added since include *C. fibratus* BULMAN 1927 (Lyckholmer Kalk), *C. kozlowskii* BULMAN 1944 (Balclatchie Beds) and a considerable number of species described by BOUČEK from the Silurian of Bohemia. Of these, only *C. kozlowskii* and *C. formosus* are known in detail from microtome

sections, the remainder being preserved in varying degrees of imperfection in shales and shaly limestone.

The very elongate tubular thecae, adnate for most of their length, place the genus in the Acanthograptidae, although, as has already been pointed out (BULMAN 1944, p. 8) "the thecae in their arrangement lack the beautiful regularity of alternating pairs of long and short autothecae and bithecae associated with the twig formation of *Acanthograptus*". SKEVINGTON (1963, p. 42) suggests that these differences indicate separate origins for *Acanthograptus* and *Coremagraptus* and considers that there are grounds for placing the two genera in different families.

Apart from the above characters the distinctive features of *Coremagraptus* are the presence of branchlets and twigs, and the anastomosis of twigs and branches.

BOUČEK (1957) included in *Coremagraptus* a number of species with flabellate rhabdosomes. The same writer also noted a tendency for the younger (Wenlock, and especially Ludlow) species to develop even more complex branches. This increase in complexity is strikingly illustrated by comparison of the section series of *C. kozlowskii* with that of *C. formosus* described herein.

### *Coremagraptus formosus* (WIMAN)

Figs. 26–29

1897 Species no. V. WIMAN, pp. 361–365; pl. 11, Fig. 5, pl. 14, Figs. 1–31.
1901 *Desmograptus? formosus* n.sp. WIMAN, pp. 188–9; pl. 8, Fig. 21, Text-fig. 7.
1927 Species no. V of WIMAN–BULMAN, p. 345.
1944 *Desmograptus? formosus* WIMAN–BULMAN, p. 8.
1955 *Koremagraptus sp.* BULMAN, pp. V 26 & V 27, Text-fig. 11: 2.
1957 *C. (?) formosus* (WIM.)–BOUČEK, pp. 114 & 115.

LECTOTYPE.—Specimen figured by WIMAN, (1897), pl. 14, Figs. 1–31 as species number V, and now preserved as serial sections mounted on slides, nos. G 796–804.

MATERIAL.—The slides of the lectotype; a further series of ten slides cut at 20 $\mu$ (G 852) from which much of the present information is drawn, and a single slide of a section series partly figured by WIMAN (1901) as Text-fig. 7, and pl. 8, Fig. 21. The last-mentioned section series is of a pyritized, poorly preserved specimen near the proximal end of the rhabdosome. It is useful only in the way it illustrates the general rhabdosomal characters of branching, twig formation and anastomosis.

HORIZON.—Upper Ordovician; Öjle Myr, Gotland.

DESCRIPTION.—The general form of the rhabdosome was well figured by WIMAN (1897, pl. 11, Fig. 5 and 1901, pl. 8, Fig. 21) and it can be seen to be conical, with a relatively robust proximal region, and a distal meshwork composed of numerous, irregularly-anastomosing, branches, branchlets and twigs. The great variation in thickness of the main branches and the irregular nature

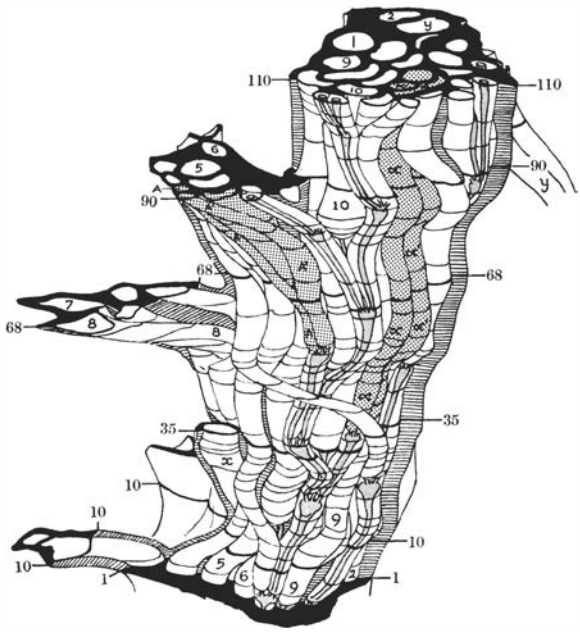
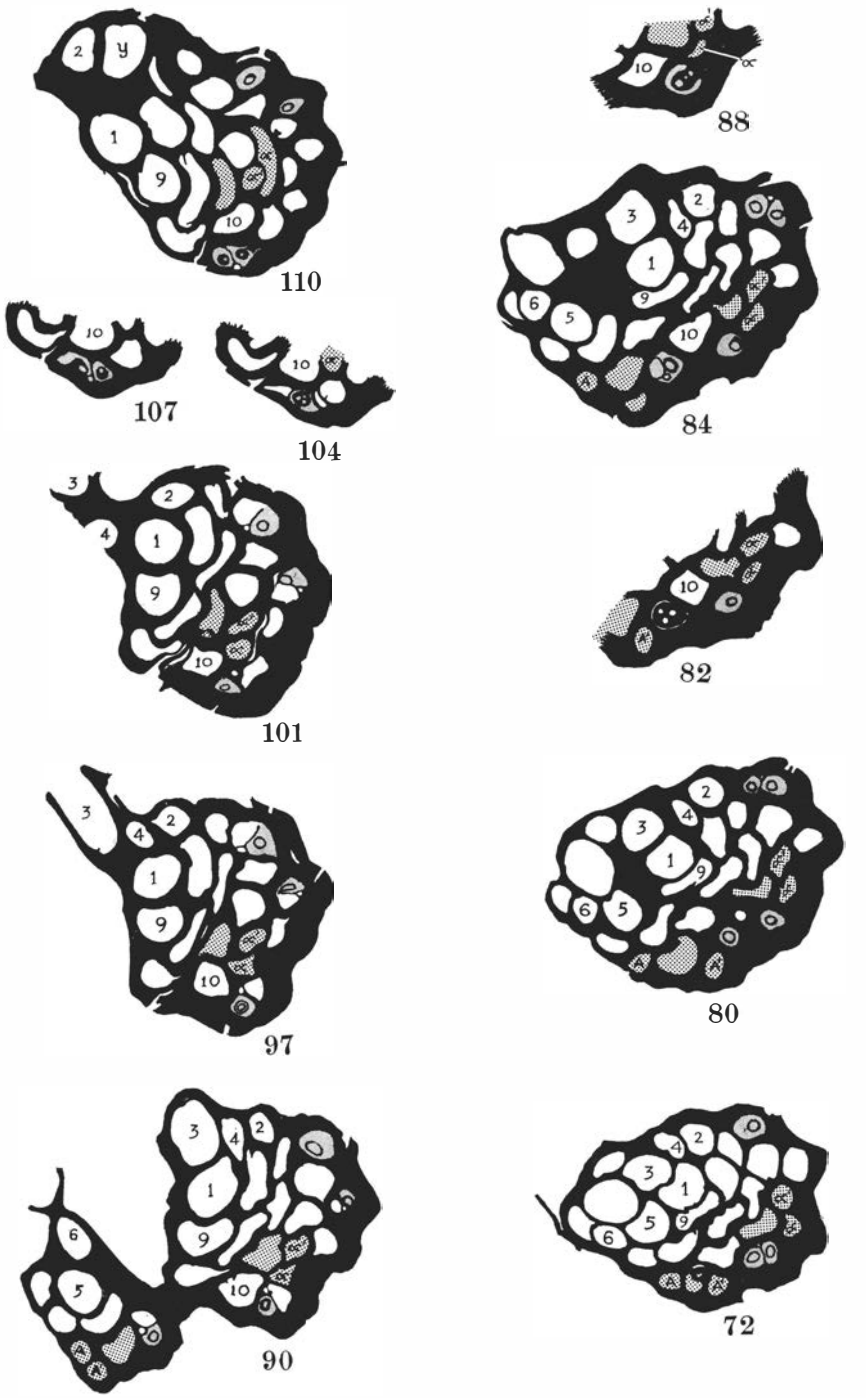



Fig. 26. Portion of a branch of *Coremagraptus formosus* (WIMAN), reconstructed from slides g and h of the section series G 852. Bithecae mentioned in text are stippled; some of the autothecae are numbered in order to facilitate study of the reconstruction; the numbers 1, 10, 35 etc. refer to the appropriate sections of the slide series. ×65 approx.

of the meshwork is pronounced. On average the branches are rather less than 1 mm broad, approximately oval in cross section, and at any one level are composed of about twenty thecal tubes. More rarely, preceding a stipe division, the branches have 30–35 thecal tubes. In the section series illustrated (G 852, Figs. 27–29) the portion of branch maintains an average of some 20 thecal tubes without suffering any major division or anastomosis. Of these individuals there are not usually more than 2 or 3 stolothecae. The branchlets and twigs are composed of lesser numbers of individuals, and the latter may be defined as relatively small groups of thecae which do not include a stolotheca. Twigs are usually composed of 4–6 thecal individuals, but the number is not so regular as in *Acanthograptus*. Because they lack stolothecae, a limit is imposed upon their development.

The autothecae and bithecae mostly open in twigs, but occasionally open separately either flush with the surface of a branch (see *x* section 35, Figs. 26 and 28), or extending free for a considerable length. Individual thecal tubes are probably of the order of 4 mm long. For example, those numbered 1 and 2 (Figs. 27–29) can be traced through the entire series of sections figured, which means, (since the sections are at 20 $\mu$ intervals), that although incomplete they are at least 2.2 mm long. The average diameter of the thecal tubes is 0.08 mm; and the maximum diameter, at the thecal aperture, is 0.15 mm.




Figs. 27–29. Selected sections from slides g and h of the slide series G 852 cut at 20 $\mu$. Full explanation in text. $\times 65$ approx.

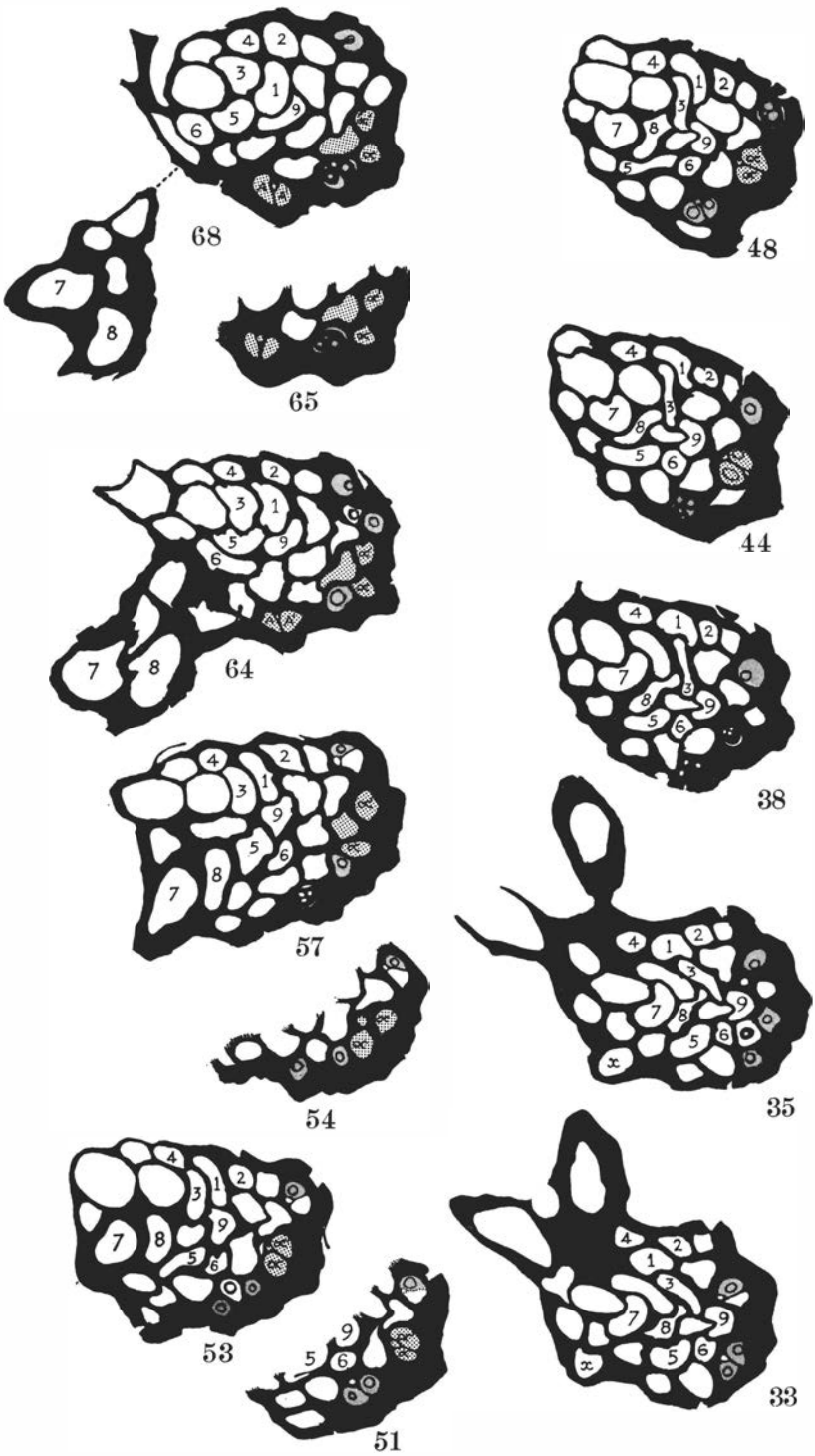



Fig. 28

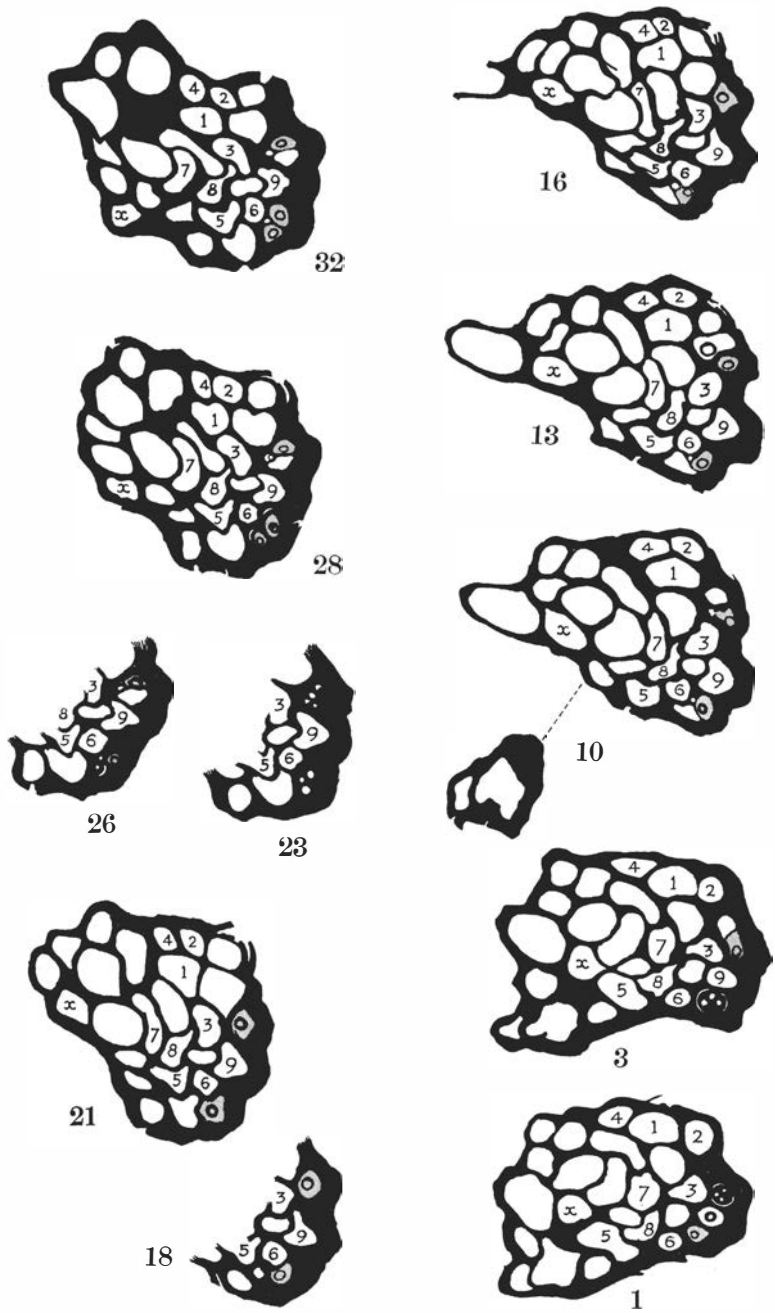



Fig. 29

The stolothecae have an average length of about 0.5 mm, but some are quite long and others short (see Fig. 26), whilst all show varying degrees of flexuosity.

The stolon system is well illustrated in this section series (G 852). A stolothecal stolon is shown, for example, immediately to the right of autotheca 6 (Fig. 29, section 1): it occupies the centre of the stolothecal tube. In the next section (3) it has divided to form three stolons which are symmetrically disposed in a thickened node. Like the parent stolon they are circular in cross section. Of these stolons, the bithecal stolon is very short, and section 10 cuts through the bithecal tube, which is already approaching its normal width. By contrast the top of the autothecal stolon is not reached until section 21. The autothecal stolon is traceable from section 3 to 18 and a slight increase in diameter is apparent in the last three sections which are immediately prior to the base of the autothecal tube. The third stolon in section 3 gives rise to a stolothecal stolon and tube of average length. The stolon division clearly follows the WIMAN rule and gives rise to an autothecal stolon, a bithecal stolon and another stolothecal stolon.

The next division (sections 21–28) is of different type, in which the bitheca is suppressed and one autothecal stolon and two stolothecal stolons are produced, although as has already been pointed out (BULMAN 1955, p. V 27), this does not seem to be immediately related to the bifurcation of the stipe. In sections 23 and 26 the stolon walls at the node point are so thick that they fill, or almost fill, the stolothecal tube. The autothecal stolon is not visible in section 28 but can be detected again in section 32, and thereafter until section 35 (Fig. 28). Section 38 cuts through the autothecal tube which is already of considerable diameter. In this section also, the two stolothecal stolons of the former triad divide once again, and whilst in one division the bitheca is suppressed (producing two stolotheca and an autotheca), in the other (the upper node on section 38) it seems that the stolotheca is suppressed, resulting in an autothecal stolon and what can only be interpreted as two bithecae. This triad of bithecae (labelled $\alpha$ and $\alpha'$) and autotheca is stippled in section 38 and, throughout the remainder of the section series.

The other node illustrated in section 38, which produces two stolothecae and an autotheca, again shows one line of development which results in a "dead end" owing to suppression of the stolotheca at a subsequent division (sections 54, 57, and 64, et seq., bithecae labelled $A$ and $A^1$; the triad is again stippled). The triad is last seen in section 90 (Fig. 27) where it forms part of a minor branch association of thecal tubes.

A normal division involving suppression of a bitheca and the production of two stolothecae and an autotheca is seen in section 68 and the following sections. One line of development becomes involved in the branchlet (last shown in section 90; Fig. 27) whilst the other continues to develop producing two further normal triads in the main branch.

Anastomosis is common and irregular and takes place between branches,

branchlets, and twigs. For example a twig may anastomose with an adjacent branch. Thus theca *y* of section 110 is the distal theca of a twig originating from the adjacent branch in section 73 (not figured), which includes four thecae to section 82, three to section 96, two to section 98, and only the terminal theca uniting with the figured stipe (Fig. 26). WIMAN reports (p. 362) that a twig may be composed of thecae from adjacent branches, three from one and one from the other. Clearly there is considerable variation in the composition of the thecal twigs.

As will be seen from WIMAN's pl. 11, Fig. 5 (a portion of rhabdosome x3), anastomosis of branches does occur but is not frequent, and most of the anastomosis is between twigs or between twig and branch. The section series does not show any good examples of main branch anastomosis, to illustrate interchange of thecae and stolothecae under these conditions.

One of WIMAN's figured series (series sp.V, slides G 798–801) shows anastomosis and subsequent separation of a minor branch, but this may be abnormal. Here a branch consisting of eight thecae and a stolotheca anastomoses (slide G 799) with an adjacent branch composed of fifteen thecae, and subsequently separates with the transfer of three thecae to smaller branch. This may be related to the failure of the stolothecae of the smaller branch, which appears to undergo abnormal division into two bithecae, but preservation is poor and the stipe is damaged.

There is as yet no proof of the transfer of stolothecae during anastomosis, but since a complex branch may include three or four stolothecae this is certainly possible.

REMARKS.—It is clear that *Coremagraptus* contrasts with *Acanthograptus* in the regularity of its development. A triad of stolons produced at a node may conform to the WIMAN rule, or give rise to a branching division, but the latter does not necessarily give rise immediately to a branch. An additional irregularity is the not infrequent suppression of stolothecae. However, the triad division of each stolon places the genus securely in the Dendroidea.

## Order *Tuboidea* KOZLOWSKI, 1938

## Family *Tubidendridae* KOZLOWSKI, 1949

AMENDED DIAGNOSIS.—Rhabdosome erect, ?flabellate; stipes dividing irregularly and anastomosing or united by single thecae, comprising at any given level numerous thecae of several generations; stolothecae more or less embedded in stipe, variable in length, with no regular budding rhythm; autothecae may be spirally coiled in middle portion, dimorphic in one genus, one form (microthecae) with narrow contracted apertural portion; conothecae present in one genus; bithecae with stolons of variable length, from long to short; stolon system well developed and sometimes highly sclerotized.

REMARKS.—It is considered that WIMAN's genus *Reticulograptus* should be placed with *Tubidendrum* in the *Tubidendridae*. The regularity, externally, of the

autothecae of *Reticulograptus* suggest that this genus is closer to the Dendroidea than *Tubidendrum*, and the same feature led SKEVINGTON (1963) to erect the new family Multitubidae for his genus *Multitubus* (=*Reticulograptus*).

## Genus *Reticulograptus* WIMAN 1901

(=*Multitubus* SKEVINGTON 1963)

TYPE SPECIES.—*Dictyonema tuberosum* WIMAN 1895.

AMENDED DIAGNOSIS.—General form of entire rhabdosome unknown, but essentially dendroid, probably lacking true dissepiments, anastomosis common in one species; autothecae regularly arranged externally, but with autothecal stolons and thecal tubes of variable length; conothecae irregularly developed; bithecae may be twice as numerous as autothecae, capriciously arranged on all sides of stipe, bithecal stolons of variable length; stolothecae relatively inconspicuous, but three or more occur at any one level in even quite slender portions of stipe, variable in length with no regular budding rhythm.

REMARKS.—*Reticulograptus* has hitherto been placed in the Dendroidea, but the stolon system and thecal structures revealed by WIMAN's serial sections of the genotype show it to be a tuboid closely related to *Tubidendrum* KOZLOWSKI. It differs from this latter genus in having, externally, a regular arrangement of autothecae, whilst the autothecae do not show spiral coiling in the middle portions.

The tuboid *Multitubus* SKEVINGTON 1963 is congeneric with *Reticulograptus*. Both have a regular external arrangement of autothecae, and in each case the number of capriciously arranged bithecae is about twice the number of autothecae, whilst dissepiments are absent. Anastomosis has not been recorded in *Multitubus spinosus* SKEVINGTON.

### *Reticulograptus tuberosus* (WIMAN 1895)

Figs. 30–35 A, C

1895 *Dictyonema tuberosum* n.sp. WIMAN, pp. 291–2; pl. XII, Figs. 9, 12; pl. XIV, Figs. 1–8.

?1895 *Dendrograptus? bottnicus* n.sp. WIMAN, pp. 298–301; pl. XII, Fig. 14; pl. XV, Figs. 1–36.

1897 *Dictyonema? tuberosum* WIMAN–WIMAN, pp. 359–60; pl. XII, Figs. 20–24.

1901 *Reticulograptus tuberosus* WIMAN–WIMAN, p. 189.

LECTOTYPE (here designated).—The specimen figured by WIMAN (1895) as Figs. 1–2 and 4–8 (*non* 3), pl. XIV, now preserved as serial sections (cut at 15 $\mu$ and 9 $\mu$) on slides nos. G 813, G 811, G 815, G 814.

MATERIAL.—The lectotype; a section series (slide no. G 812; cut at 15 $\mu$) figured by WIMAN (1895, pl. XIV, Fig. 3); a section series labelled "Ser. II, *Dictyonema* sp. 1" (slide no. G 836; cut at 15 $\mu$); two slides (nos. G 837, G 838)

of sections cut at 25 $\mu$, labelled "*Dictyonema tuberosum* W."; four slides (nos. G 839 to G 842) of sections cut at 15 $\mu$ labelled "*Dictyonema tuberosum*". All the above material is from siliceous boulder no. 1, Visby.

A section series on eight slides (no. G 795; cut at 20 $\mu$, labelled "Ser. V, *Dictyonema tuberosum*") of the specimen figured by WIMAN (1897, pl. XII, Figs. 20–24); a previously unfigured section series on fourteen slides (no. G 843) labelled "Ser. II", locality unknown, probably cut at 20 $\mu$.

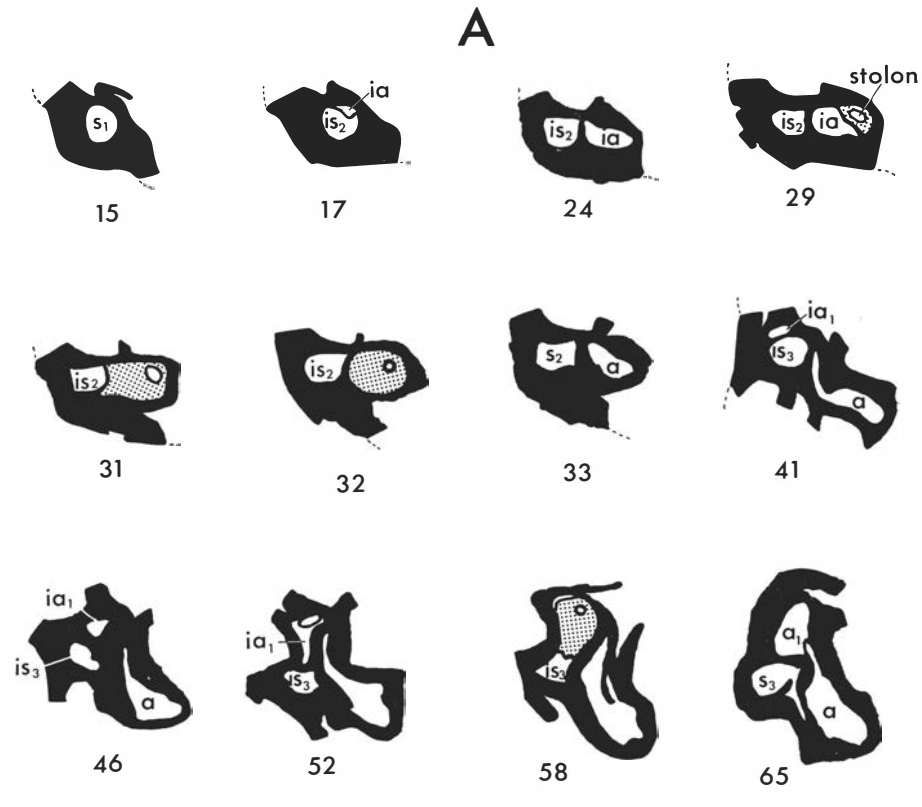
The specimen figured by WIMAN 1895, pl. XII, Fig. 9.

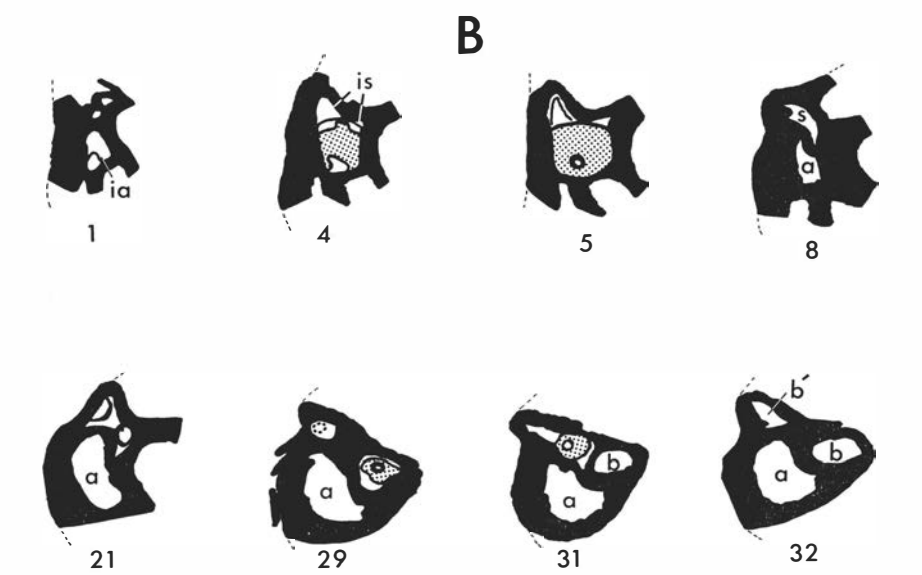
HORIZON.—Upper Ordovician; from silicified boulders, Gotland.

DESCRIPTION.—The general rhabdosomal characters are not yet completely known, but a large fragment of rhabdosome figured by WIMAN (1895, pl. XII, Fig. 9) shows the irregular meshwork resulting from complex anastomosis of the stipes. It is not possible to determine whether the rhabdosome is conical or flabellate. Several slender, dissepiment-like rods are also seen connecting stipes but it will be shown below that these are merely the most simple instances of anastomosis exhibited by the species. The lateral stipe width varies from about 0.25 mm to as much as 1.5 mm at complex anastomosis points, whilst the maximum dorso-ventral stipe width only varies between 0.40 and 0.70 mm. The autothecal spacing is 16–22 in 10 mm; but in any particular length of stipe there may be up to twice as many bithecae. Thus 34 bithecae are associated with 18 autothecae on one portion of the lectotype. The number of bithecae opening in the vicinity of an autothecal aperture varies from 0 to 4. Transverse sections of the stipes may reveal the presence of a quite variable number of thecal tubes. Except where adjacent stipes anastomose, however, there are not usually more than fifteen tubes, of which as many as three may be stolothecae.

The stolothecae are relatively inconspicuous tubes with a diameter of approximately 0.04 mm. Fig. 30 A depicts two diad divisions (15–33, 33–65) which produce, in each case, a stolotheca and an autotheca. A typical stolothecal tube *S1*, with no traces of a contained stolon, is seen in section 15. Sections 17 and 24 show this stolothecal tube dividing into two tubes $is_2$ and *ia* of roughly equal size (section 24). At a slightly later stage (section 29) a stolon is seen close to the wall of *ia* and by section 33 this has given rise to an autothecal tube *a*. The tube *ia* is the internal autothecal tube of autotheca *a*, and the contained stolon is the autothecal stolon. (In Figs. 30 and 35 the cavities labelled $is_1$ and $is_2$ refer to that portion of the stolothecal tube considered to be homologous with the internal stolothecae as defined in the dendroids). The stolotheca, $S_2$, then divides in an identical manner to produce the internal stolothecal tube, $is_3$, an internal autotheca, $ia_1$, and finally (section 65) the autotheca $a_1$. The autothecal stolon of $a_1$ can be seen at the margin of $ia_1$ in section 52.

A similar series is illustrated in Fig. 30 B, but in this case the two diad divisions produce firstly an autotheca *a* and stolotheca *S*, and secondly two bithecae *b* and *b'* which ends this particular stolon line. Section 1 shows the autothecal


A
s1
15
ia
is2
17
is2
ia
24
stolon
is2
ia
29
is2
31
is2
32
s2
a
33
ia1
is3
a
41
ia1
is3
a
46
ia1
is3
52
is2
58
a1
s3
a
65


B
ia
1
is
4
5
s
a
8
a
21
a
29
a
b
31
b'
a
b
32

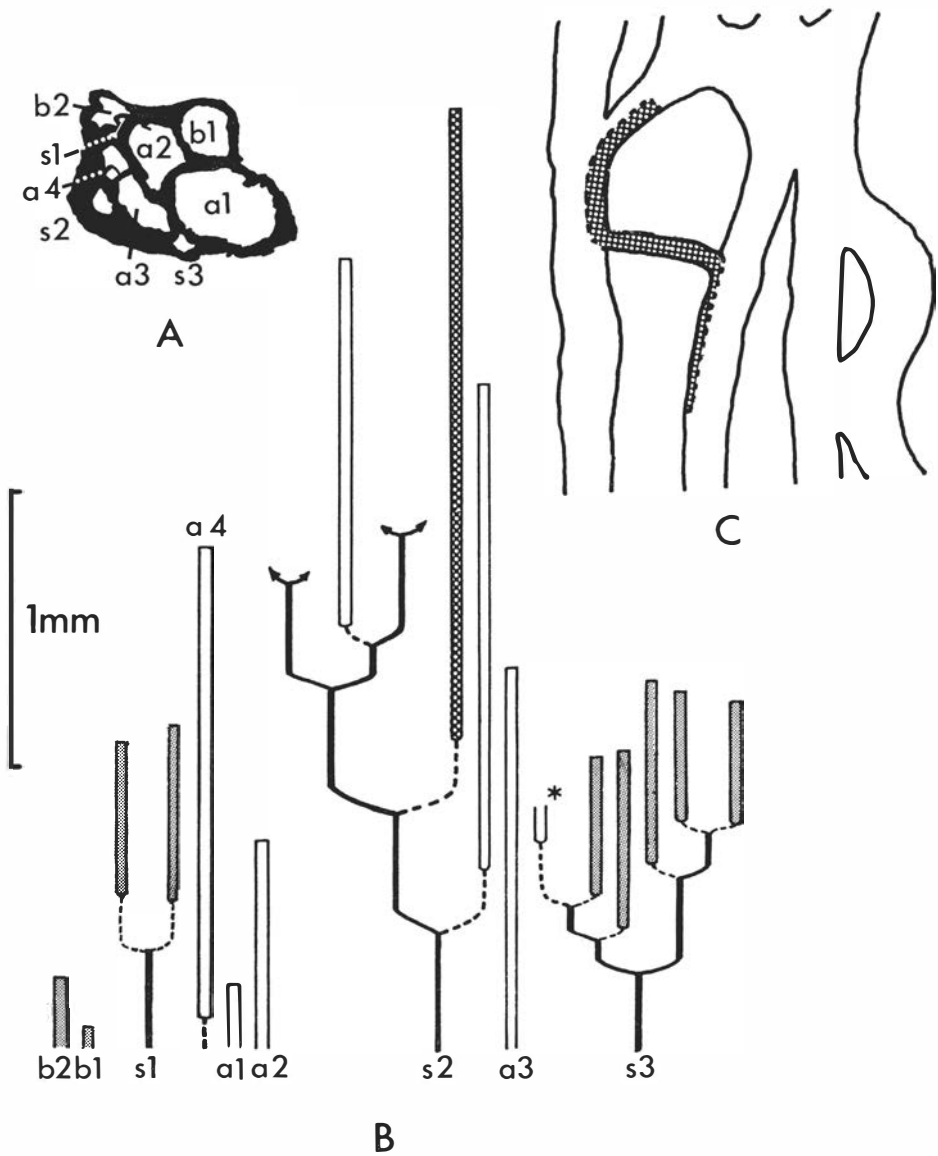



Fig. 31. *Reticulograptus tuberosus* (WIMAN). *A*, section 1 of slide no. G 843 *a*, ×60; *a*, autothecae; *b*, bithecae; *s*, stolothecae. *B*, thecal composition diagram of portion of stipe development distal to section 1, slide no. G 843 *a; b*, bithecae (fine stipple); *a*, autothecae (white); *s*, stolothecae (heavy black lines); coarse stipple indicates an autotheca which transfers to an adjacent stipe; asterisk indicates an autotheca which transfers at a later stage; autothecal stolons are heavy broken lines; bithecal stolons, finer broken lines. The lettering of *A* & *B* is for the purpose of these diagrams only. *C*, simplified reconstruction of portion of rhabdosome involving the stipe illustrated in *B;* heavy stipple shows the position of the transferring autotheca. ×17.5.

Fig. 30. *Reticulograptus tuberosus* (WIMAN). Portions of selected sections from slide no. G 843; (section 1–33 slide no. G 843 *a;* section 41–65 slide no. G 843 *b*) illustrating diad division of the stolothecae; full explanation in text; *s*, stolothecae; *is*, internal stolothecae; *a* ,autothecae; *ia*, internal autothecae; *b*, bithecae; stipple indicates semi-transparent tissue; broken lines indicate position of stipe margin. ×90.

stolon at the margin of the internal autotheca *ia*. The internal stolotheca *is* is so crushed that it appears in sections 1–5 as two tubes; but it contains no stolon. The stolotheca *S* again divides in sections 21–32 to produce two bitheca *b* and *b'*. At the level of section 21, stolotheca *S* has divided into two tubes each containing a bithecal stolon at the margin. One of these stolons results in the bitheca *b* (section 31), and the other in bitheca *b'* (section 32).

A closely similar diad division has been observed in *Reticulograptus thorsteinssoni*, but in this species there are no internal autothecal or bithecal tubes. The autothecal and bithecal stolons lie at the margins of the stolothecae (see Figs. 37 A–C) which, as in *R. tuberosus*, do not contain sclerotized stolons.

The absence of stolons within the stolothecae cannot readily be explained on grounds of poor preservation since the autothecal and bithecal stolons are almost invariably preserved. It is probable that the stolothecal stolons were not sclerotized. The fact that the autothecal and bithecal stolons lie at the margins of the internal autothecae and bithecae (*R. tuberosus*), and at the margins of the stolothecae (*Reticulograptus thorsteinssoni*) suggests that the stolothecal stolons lay close to the side of the stolothecal tube, unless they were of such large diameter as completely to fill the stolothecal tube.

The diad divisions of the stolon in *R. tuberosus* result in any pair of thecae except two autothecae. Thus the associations *ab*, *as*, *bb*, *bs* and *ss* may all occur, and are all present in the portion of stipe represented in Fig. 31 B. Quite commonly three stolothecal tubes may be found in a single transverse section of a stipe. Usually the stolothecae are in a dorsal or lateral position (Figs. 31 A; 32 A, B; 33, section 37), but more rarely they are embedded within the stipe (Fig. 33, section 47; Fig. 34). The distance between nodes is quite variable (Fig. 31 B), and in some instances the stolothecae may be only 0.1 mm in length.

The autothecae of *R. tuberosus* have isolated apertural regions facing ventrally (see WIMAN 1895, pl. XII, Fig. 12; Fig. 32 A, B herein), and often a short spine is developed from both the ventral and dorsal extremities of the aperture. In the serial sections the autothecae are conspicuous by reason of their relatively large diameter, which reaches 0.2 mm in contrast to the bithecal tubes which are usually less than half this size. As may be seen in Fig. 31 B the autothecal stolons are of variable length. Thus whilst they are usually longer than the bithecal stolons, the third autotheca produced from the $S_2$ line of development has a stolon which is almost as short as the normal bithecal stolons (see $S_3$ line of development, Fig. 31 B).

Like the autothecal stolons, the autothecal tubes vary considerably in length. The second autotheca on the $S_2$ line of development (Fig. 31 B) is over 2 mm long, which is about twice the length of the next autotheca on the same line. In view of this considerable variation in length shown by both the autothecae and the autothecal stolons it is the more remarkable that the autothecal apertures are spaced so regularly along the stipe. In Fig. 31 B the autothecal apertures are placed at approximately half millimetre intervals.

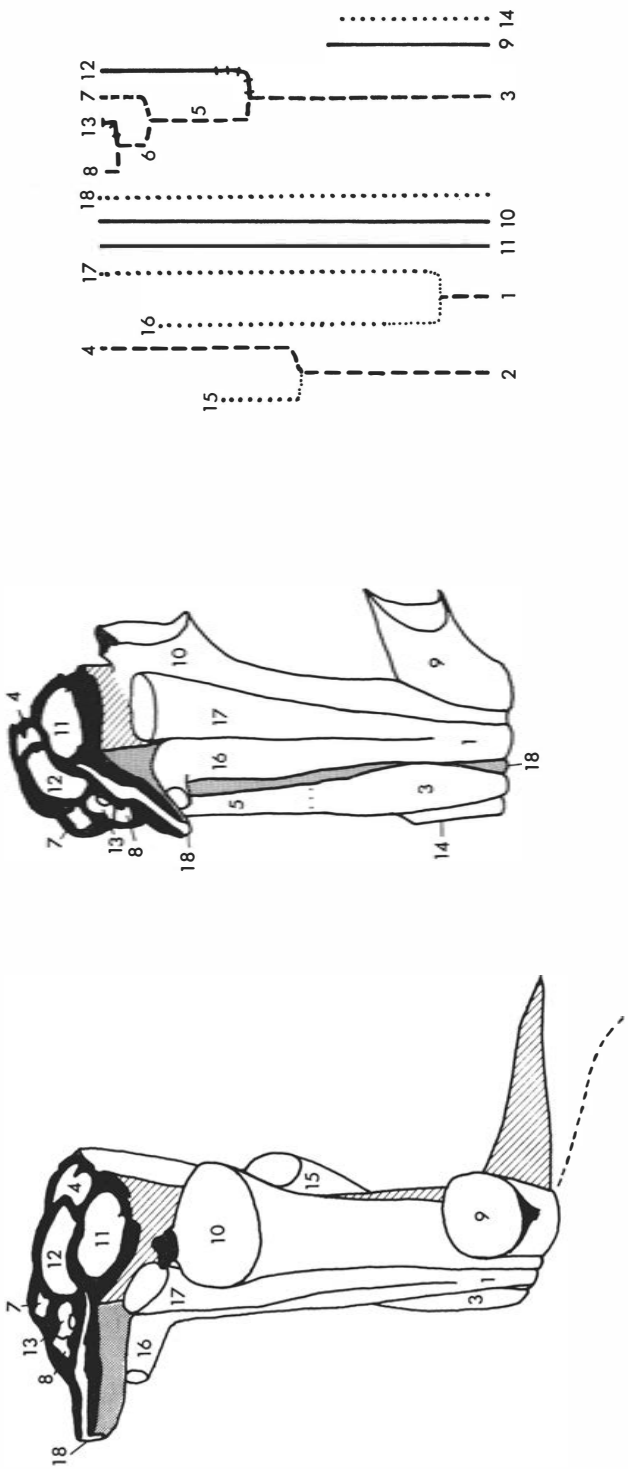



Fig. 32. *Reticulograptus tuberosus* (WIMAN). *A, B*, reconstruction of portion of lectotype (slide no. G 814) respectively in ventral and lateral views. ×60. *C*, diagram of thecal composition of the portion of stipe illustrated in *A* & *B*; theca numbers as in *A* & *B*: stolothecae 1–8; autothecae 9–13; ithecae 14–18; autothecal stolons are thick broken lines; bithecal stolons are fine dotted lines.

The bithecae are narrower and about twice as numerous as the autothecae. In length they vary from rather less than 0.5 mm to more than 0.6 mm (Fig. 31 B), but occasionally specimens are less than a quarter of a millimetre long (no. 15 in Figs. 32 A–C). The bithecal stolons are mostly quite short as, for example, those produced from $S_3$ (Fig. 31 B), but occasionally they may be almost as long as the average autothecal stolons (e.g. bithecae produced from $S_1$ line of development Fig. 31 B). Clusters of bithecae are produced at irregular intervals along the stipes; and it can be seen from Fig. 31 B that no fewer than seven bithecae open between the levels of the autothecal apertures $a_2$ and $a_3$. By contrast a particular autothecal aperture may have no bithecal apertures in the immediate vicinity. Fig. 32 illustrates a short portion of stipe in which one bitheca (14) opens at the level of autotheca 9, on the opposite side of the stipe, whilst four bithecae (15–18) open in the vicinity of autotheca 10. This figure also shows the two common modes of opening exhibited by the bithecae. They may be inconspicuous, with their apertures more or less adpressed to the stipe as in 14, 15 and 17, or they may have isolate apertures like 18 which would confer a "spiny" appearance to that portion of the stipe. Transverse sections show that the bithecal tubes are usually clustered round the autothecal tubes (Fig. 33, section 37) and may be positioned dorsally, ventrally, or laterally, and may also open in any of these positions.

Anastomosis is commonly exhibited by the specimens examined, but no dissepiments have been found. The most simple type of anastomosis involves the transfer of a single autotheca or bitheca from one stipe to another. In Fig. 31 B the long autotheca (coarse stipple) crosses from one stipe to the adjacent stipe. It eventually opens part way along a more complicated branch leading back to the first stipe. A simplified reconstruction is given in Fig. 31 C. Simple thecal connections of this type are effected approximately at right angles to the general direction of stipe growth and bear a superficial resemblance to true dissepiments: indeed in flattened specimens they could be quite indistinguishable from dissepiments.

Fig. 33 further illustrates the transfer of an autotheca (stippled) from one stipe to another. Beyond section 47, the bitheca (horizontal shading) crosses to the lower stipe. More complicated transfers of thecae during anastomosis have been observed, for example:

a. a "pair" (autotheca and bitheca) making the crossing; or the autotheca crossing completely whilst the bitheca opens half way across.

b. a "pair" (autotheca and bitheca) crossing at the same time as a similar "pair" crosses in the opposite direction.

c. yet more complicated transfers in which both autothecae and bithecae may open half way across.

No instances of anastomosis have been observed involving stolothecae.

Thecae of a rather puzzling type, here called *conothecae*, occur at irregular

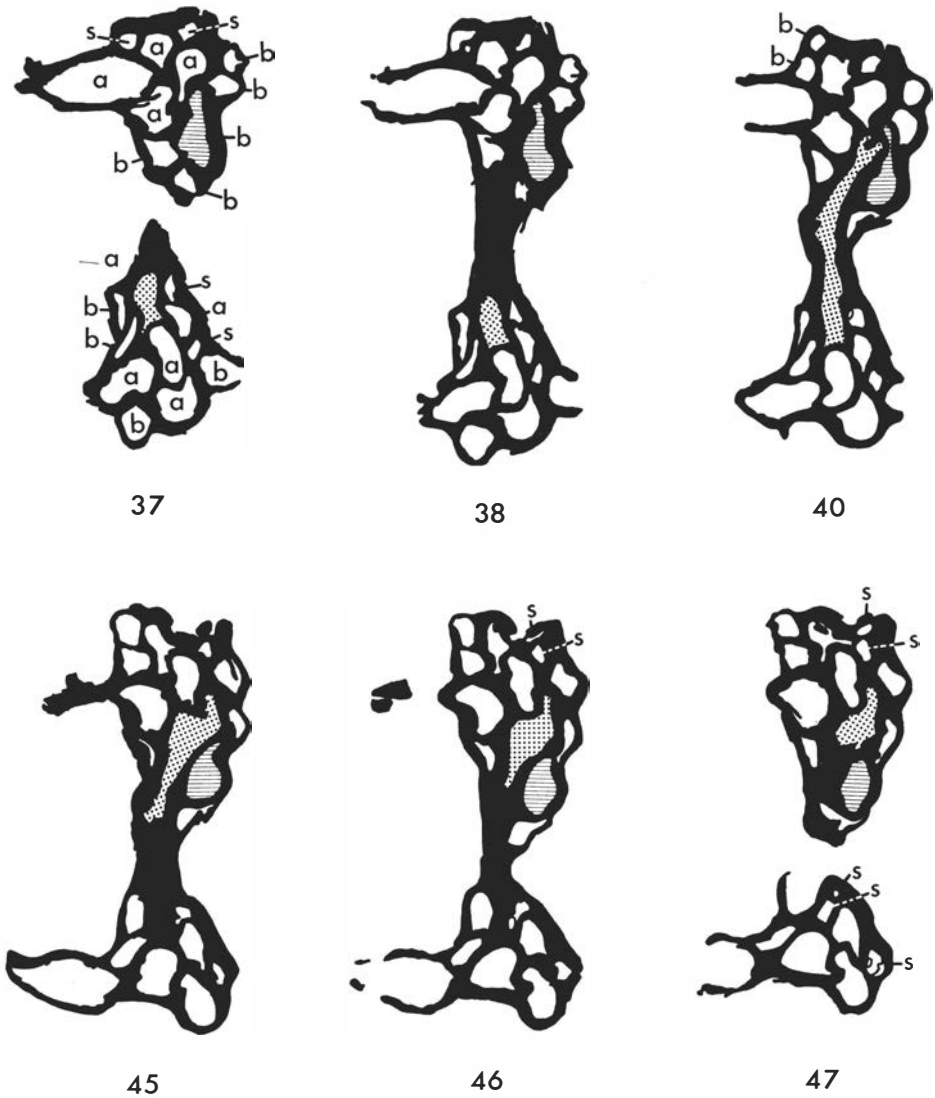



Fig. 33. *Reticulograptus tuberosus* (WIMAN). Selected sections from slide no. G 795 illustrating anastomosis of stipes; full explanation in text; *s*, stolothecae; *a*, autothecae; *b*, bithecae. × 50.

and widely spaced intervals along the stipes. Their form and origin is illustrated in Fig. 34. The stolotheca *S* (section 234) divides between section 234 and 240 to produce a bitheca (*b* in section 240) and a tube of smaller diameter *ic* which eventually joins with the conothecal cavity *c* in sections 244 to 248. The junction of *ic* and *c* is difficult to depict because of the rather thick sections, but it involves an inverted U-bend on the part of *ic* and probably also the presence of "basal" tissue of the thecal tube *c*. The narrow tube *ic* is the internal portion of

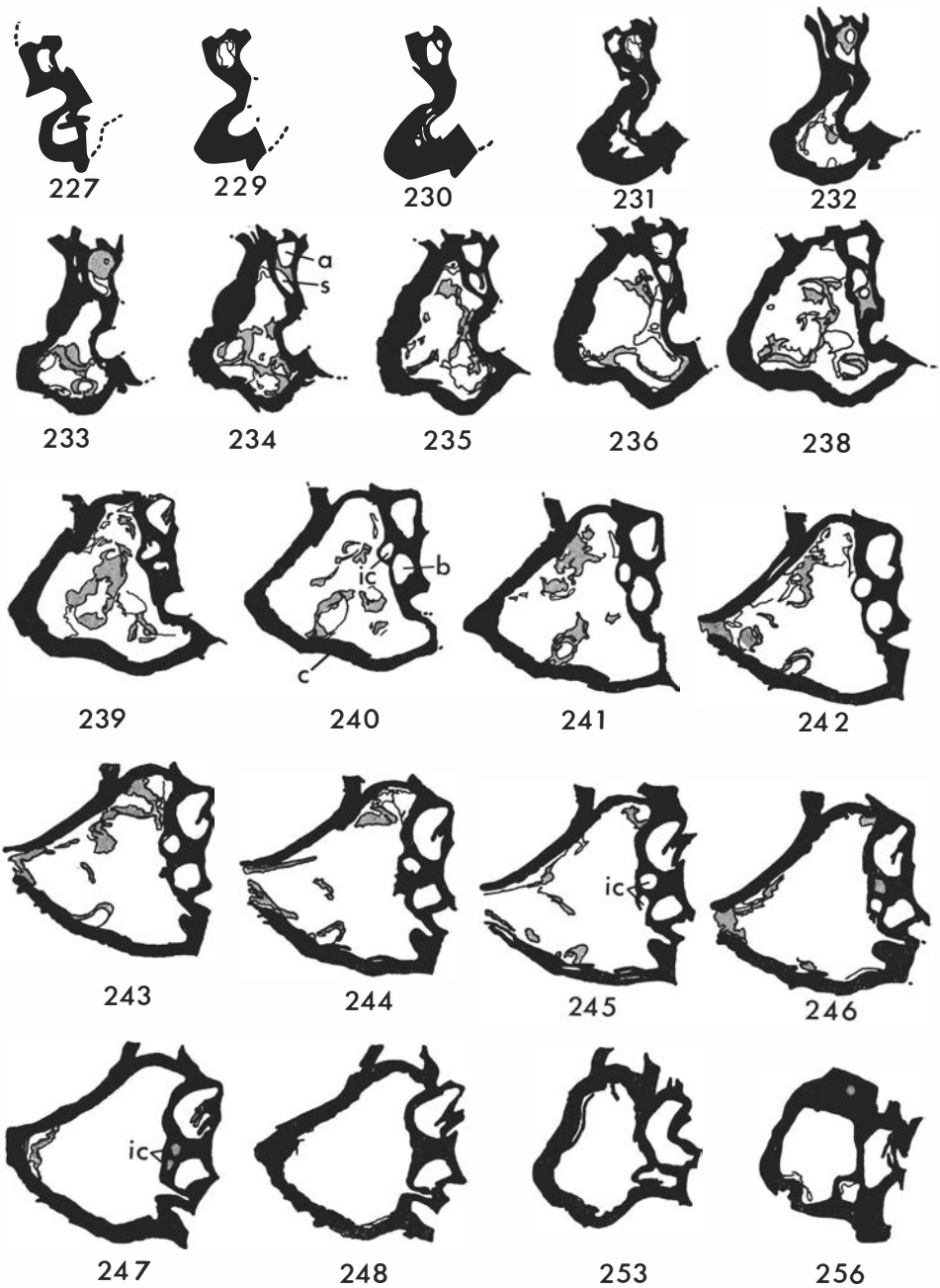



Fig. 34. *Reticulograptus tuberosus* (WIMAN). Portions of selected sections (slide no. G 843) illustrating the development of a conotheca; full explanation in text; *a*, autotheca; *s*, stolotheca; *b*, bitheca; *ic*, internal conotheca; *c*, conotheca; fine stippled indicates semi-transparent non-fusellar tissue. × 50.

the theca *c*. The length of *ic* is about 0.2 mm compared to the much shorter internal bithecal tube produced from stolotheca *s*. The conical form of *c* is well shown by the series, and its aperture can be seen in section 242 to 247. Several of these conothecae have been available for study in serial sections and they each show the same type of connection involving a tube of small diameter and the large conical body. But only the section series of Fig. 34 shows the presence within the conical tube, albeit vaguely, of a loosely coiled (?spirally coiled) thin-walled tube (the transparent walls of this tube are shown in very fine stipple). No growth lines have been detected on this tube. In the same section series another conical theca contains a small fragment of transparent tube which exhibits a closed, rounded end. Again there are no traces of fusellar structure. Reconstructions of these thecae are shown in Figs. 35 B and C.

This interpretation of the structure of the conothecae is confirmed by examination of similar thecae on *Reticulograptus thorsteinssoni*. Here, however, the connection of the narrow internal portion with the robust conical portion is much clearer since the internal thecal tube does not have the distal U-bend of *R. tuberosus*. Fig. 36 shows two such conical thecae positioned laterally on the stipe. The distal limit of the internal tube *ica* and its immediate connection with *ca* is well displayed in sections 333–337; and an identical connection in the case of *cb* is seen in sections 332 to 337. The apertures of both *ca* and *cb* are visible in section 348. Neither in *R. tuberosus* nor in *R. thorsteinssoni* does the narrow internal conothecal tube contain a sclerotized stolon, although a thecal base and connecting pore are usually seen separating the internal tube from the conical part.

All the instances of stolothecal division involving the production of a conotheca mark the end of that particular line of development, for the other theca produced is invariably a bitheca.

REMARKS.—Conothecae have also been detected in the tuboid species *Discograptus schmidti* WIMAN (see below), and Professor Kozlowski has kindly shown us what are apparently the same kind of thecae on specimens belonging to the tuboid genus *Idiotubus* KOZLOWSKI. We are not aware of the occurrence of these conical thecae in genera outside the Tuboidea.

The conical thecae share some features in common with the microthecae described by KOZLOWSKI (1949) in the genus *Tubidendrum*. Thus they are relatively uncommon, irregularly spaced on the stipes, have a constricted apertural portion, and have a swollen middle part. Microthecae were regarded as abnormal autothecae by KOZLOWSKI. Since the internal portion of the conotheca is longer than the internal portion of the bitheca associated with it (see for example Fig. 35 B) it is possible that the conical thecae are also modified autothecae. The conical thecae are distinct from microthecae, however, in that the swollen middle parts do not show spiral coiling and are not embedded in the stipe. The fact that the microthecae are deeply embedded in the stipe may be a reflection of the more complex compound stipe structure of *Tubidendrum*, and

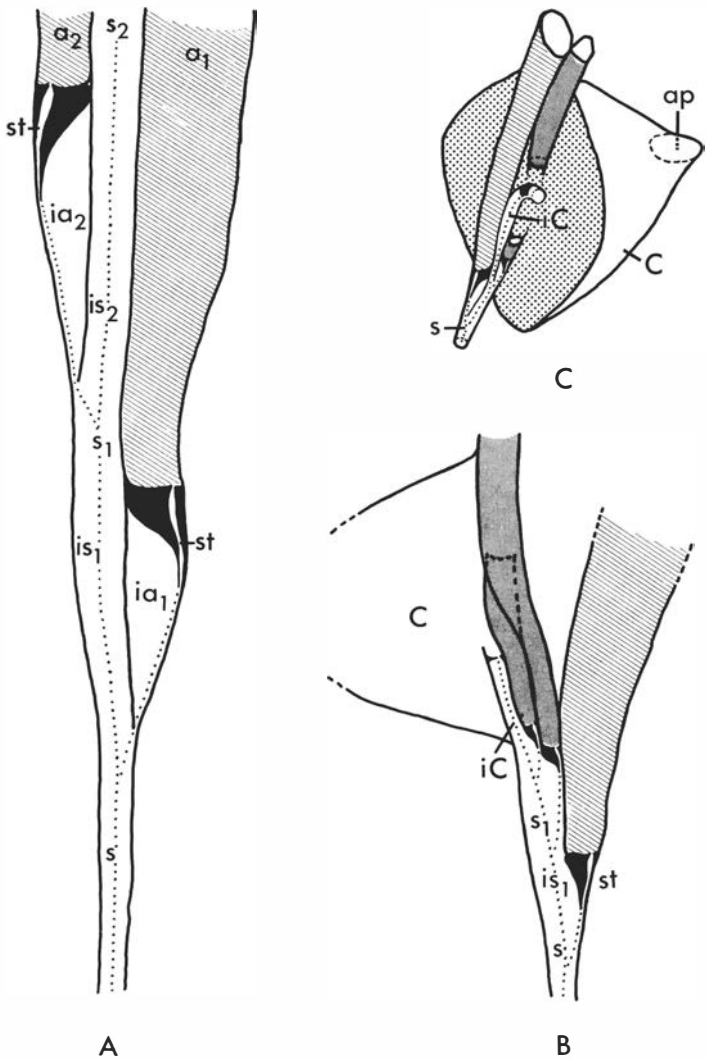



Fig. 35. A, *Reticulograptus tuberosus* (WIMAN). Diagrammatic reconstruction illustrating diad division of the stolotheca; based on the section series depicted in Fig. 30 A (slide no. G 843); *s*, stolotheca; *a*, autotheca; *is*, internal stolotheca; *ia*, internal autotheca; *st*, autothecal stolon; solid black is the thick stolon wall of non-fusellar tissue; labelling is for the purpose of this diagram only; ×90. *B*, *Reticulograptus thorsteinssoni* sp. nov. Diagrammatic reconstruction of a line of development resulting in a conotheca, based on the series illustrated in Fig. 36; full explanation in text; *s*, stolotheca; *is*, internal stolotheca; *st*, stolon; *ic*, internal conotheca; *c*, conotheca; bithecae finely stippled; autotheca shaded; ×90. *C*, *Reticulograptus tuberosus* (WIMAN). Diagrammatic reconstruction of a line of development resulting in a conotheca based on the series depicted in Fig. 34; *s*, stolotheca; *ic*, internal conotheca; *c*, conotheca; *ap*, conothecal aperture; labelled for the purpose of this diagram only; in *A*, *B*, & *C* the suggested course of unsclerotized stolons is indicated by dotted lines. ×40.

the spiral coiling (exhibited by both the microthecae and autothecae in *Tubidendrum*) may be a generic characteristic.

The nature of these individuals is obscure. A distinctive feature of *R. thorsteinssoni*, *R. tuberosus* and *D. schmidti* is that despite considerable irregularities in length of stolon and thecal tube, the autothecal apertures are spaced along the stipe with remarkable regularity, and it is possible that the conothecae are in some way related to the suppression of superfluous autothecae. The imperfectly-preserved tissue contained in the conothecae of *R. tuberosus* recalls at first sight the spheroidal eggs and embryos recognised by KOZLOWSKI (1949, pp. 97, 98) in the autothecae of *Cysticamara accollis* and *Tubidendrum bulmani*, but it appears here to be the remains of some loosely coiled tubular structure.

### *Reticulograptus thorsteinssoni* sp. nov.

Figs. 35 B, 36, 37, 38, 39

HOLOTYPE.—The specimen illustrated here as Figs. 36, 37 and 39, preserved as a section series cut at 10 $\mu$ on six slides nos. GSC 20321 *a–f*.

MATERIAL. The holotype and fifteen other well preserved, isolated fragments of stipe, nos. GSC 20322–20332, and SM. A52536–9.

DERIVATION OF NAME.—After Dr. R. THORSTEINSSON who kindly provided the above material.

HORIZON AND LOCALITY.—Cape Phillip Formation, Wenlock Series, Silurian; North coast of Cornwallis Island, Canadian Arctic.

DESCRIPTION.—The complete rhabdosome is unknown, but sufficiently large fragments of stipe are preserved to demonstrate the essentially dendroid aspect. Anastomosis between the subparallel stipes is fairly common, resulting in a characteristic rectangular meshwork, but dissepiments are absent. The lateral stipe width varies between 0.3 and 0.4 mm, whilst the maximum dorso-ventral stipe width (excluding spines) is approximately 0.7 mm. The autothecal spacing is 15 in 10 mm. Bithecae are usually twice as numerous as the autothecae but are irregularly spaced. Some thirty conothecae have been detected on the fifteen specimens, and most are positioned laterally on the stipes.

The stolothecae are inconspicuous oval tubes with a diameter of not more than 0.08 mm. They are usually positioned dorsally or laterally on the stipe (Fig. 36, section 332; Fig. 39, section 484), but less commonly may be deeply embedded within the stipe as, for example, immediately prior to the production of a conotheca (stolotheca *S9* in Fig. 39, sections 449–455). There is considerable variation in the length of individual stolothecae. Thus in Fig. 39, $S_2$ is first seen in section 441 and does not give rise to other thecae until section 476 where the stolon of bitheca $b_6$ occurs at the margin of the tube. In contrast with this, $S_3$, also originating in section 441, divides in section 457 where the autothecal stolon of $a_4$ can be detected. $S_2$ is 0.35 mm long, and $S_3$ less than half this. It may be noted that in *R. thorsteinssoni* the autothecal and bithecal stolons

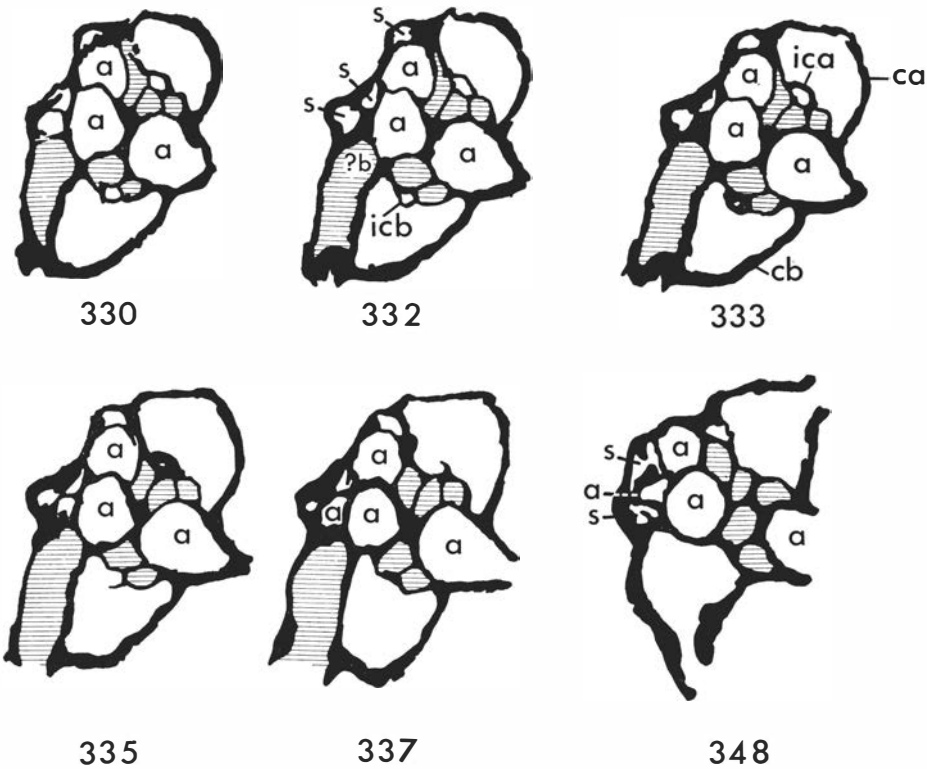



Fig. 36. *Reticulograptus thorsteinssoni* sp. nov. Selected sections cut at 10 $\mu$ from the holotype slide no. G.S.C 20321*d* illustrating the form of the conotheca; *s*, stolothecae; *a*, autothecae; bithecae shaded; *ica*, *icb*, internal conothecae; *ca*, *cb*, conothecae. × 60.

are not contained in internal tubes (cf. Figs. 35 A and 35 B) and it is therefore impossible to distinguish the internal autothecae and internal bithecae recognisable in *R. tuberosus* (Fig. 35 A). Figs. 37 A–C further illustrate the above feature. Section 301 (Fig. 37 A) depicts a stolothecal tube which gives rise to a bitheca *b* in sections 310–312. The bithecal stolon has its maximum diameter in section 310, whilst section 311 shows a minute pore in the thecal base which connects the stolon to the bithecal tube. In a very similar manner the stolotheca *S* in Fig. 37 B results in the autotheca *a* and the stolotheca $S_1$. That portion of the tube labelled $S_1$ in sections 303–306 must be approximately equivalent to the internal stolothecal tube of the dendroids. In those parts of the stipe where the stolotheca divides more than once in a short distance, as it does when a conotheca is produced, it becomes impossible to distinguish any "internal" part to the stolotheca (see Fig. 35 B). As in *R. tuberosus* the production of a conotheca marks the end of that particular line of development.

The autothecae are long tubes with distinctive isolate apertures (Figs. 38 A–B). Of the specimens available only a few show the autothecal apertures un-

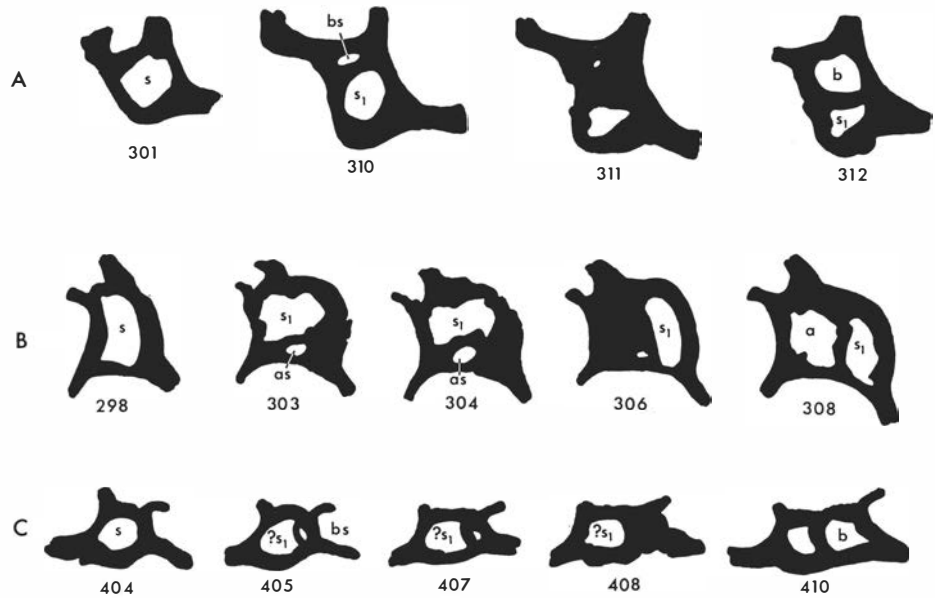



Fig. 37. *Reticulograptus thorsteinssoni* sp. nov. Portions of selected sections at 10 $\mu$ of the holotype illustrating diad division of the stolotheca, × 112; *A*, *B* slide no. G.S.C 20321*d*; *C* slide no. G.S.C. 20321*e*; full explanation in text; *s*, stolotheca; *as* autothecal stolon; *bs*, bithecal stolon.

damaged, and in these instances the dorsal margin projects as a spine which may be as much as half a millimetre in length. The ventral margin is drawn out into a shorter spine, whilst the apertural region as a whole faces ventrally. The autothecal tubes are circular in section (Fig. 39) and have a maximum diameter of 0.20 mm. One of the most distinctive features of the stipes is the regular spacing of the autothecal apertures (Figs. 38 A–B). As in *R. tuberosus* there is a considerable variation in length of the autothecal stolon, though it is usually longer than the bithecal stolon (Fig. 35 B), and the length of the autothecal tube also varies. In spite of this the autothecal apertures are spaced with remarkable constancy at 15 in 10 mm. The autothecae $a_1$ and $a_2$ of Fig. 39 are respectively 1.54 mm and 1.70 mm in length, but other autothecae may be somewhat longer or shorter, particularly where they are involved in branching or anastomosis.

The bithecae are usually about twice as numerous as the autothecae, are arranged very irregularly, and may open in almost any position on the stipe. Fig. 38 A depicts a short length of stipe in which there are rather more bithecae than is usual. Thus 23 bithecae open in association with only 6 autothecae. The majority of bithecae have small, inconspicuous apertures, which are closely adpressed to the stipe walls. Occasionally bithecae have relatively large apertures (e.g. the most distal bitheca on Fig. 38 A). Many open on the lateral walls of the stipe, but some are found on the free ventral autothecal walls, and yet others on the isolated part of the dorsal autothecal wall (see Fig. 38 for all these

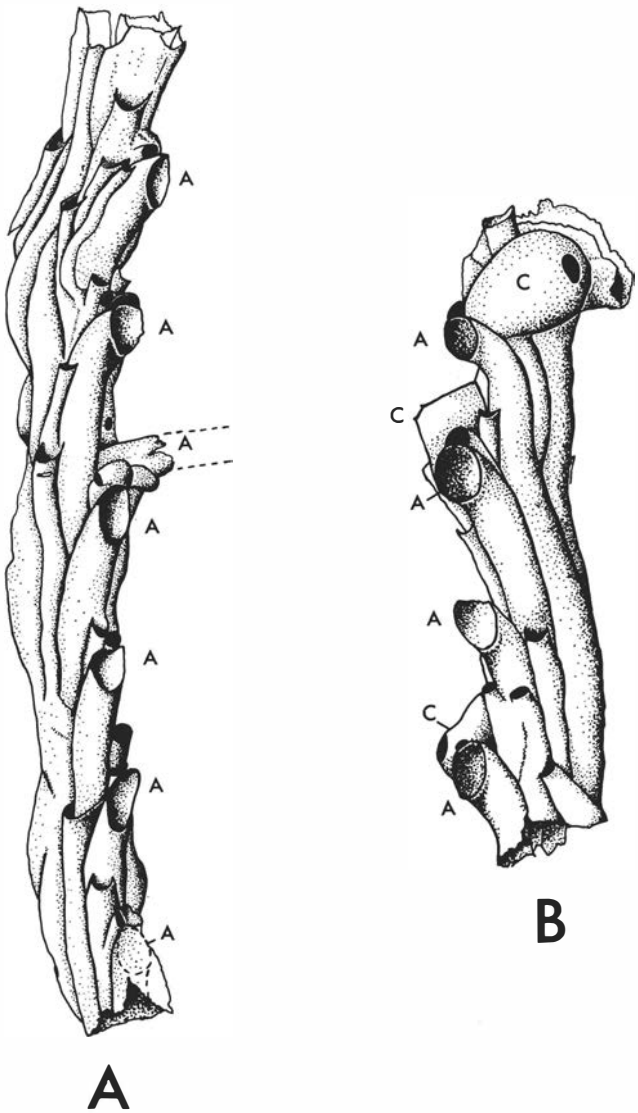



Fig. 38. *Reticulograptus thorsteinssoni* sp. nov. Camera lucida drawings illustrating: *A*, portion of stipe with large number of bithecae associated with six autothecal apertures (*A*); *B*, portion of stipe with conothecae (*C*) and four autothecal apertures (*A*). *A* & *B* are fragments of the same specimen, no. G.S.C. 20322. × 40.

types). Less commonly the bithecal apertures are situated dorsally. The length of the bithecal tube is quite variable. In Fig. 39 the bitheca $b_4$ has a length of only 0.35 mm, i.e., one fifth of the length of the average autotheca; others may be almost 1 mm long, but the average length is approximately half a millimetre.

Anastomosis in *R. thorsteinssoni* usually involves the simple transfer of an autotheca from one stipe to another. Since the thecal tube concerned grows out

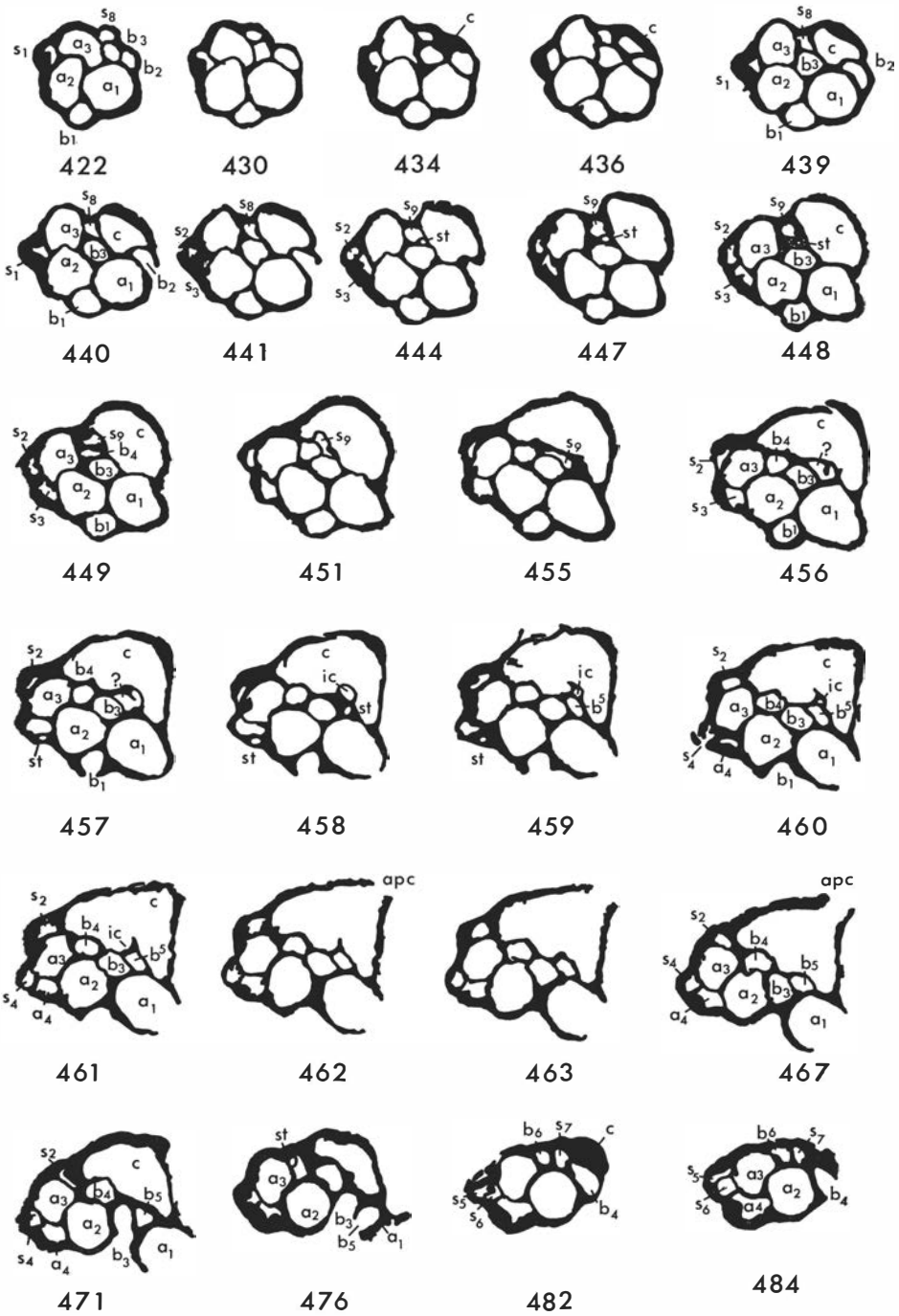



Fig. 39. *Reticulograptus thorsteinssoni* sp. nov. Selected sections at 10 $\mu$ of the holotype slide no. G.S.C. 20321 *e;* full explanation in text; *s*, stolothecae; *a*, autothecae; *b*, bithecae; *c*, conotheca; *ic*, internal conotheca; *st*, stolon. × 50.

from the stipe almost at right angles, the resultant meshwork is rectangular, and in flattened specimens such thecal transfers might easily be confused with dissepiments and produce an appearance similar to *Dictyonema*. The third autotheca from the distal end of the stipe in Fig. 38 A is in the process of transfer to an adjacent stipe. More complicated anastomosis is less common, but where observed it is noticeable that the junctions are not at right angles and resemble more closely the normal type of anastomosis.

Conothecae are fairly common, and are usually positioned laterally on the stipe or, occasionally, at the point where an autotheca leaves the stipe for an adjacent one. The conical portion is about half a millimetre in diameter at the base, and has a height of approximately 0.25–0.50 mm. Each internal conothecal tube has a diameter similar to the bithecae, but a length of only 0.05–0.10 mm. The junction of the internal and external part is clearly shown in Fig. 36. The internal conothecae *ica* and *icb* are without stolons, but each exhibits a thecal base and connecting pore in sections 335 and 333 respectively. The conotheca then swells rapidly to form the conical part. The conothecal apertures are small, oval in shape (as in Fig. 35 C), and are situated at the end of a short neck (Fig. 36 section 348 and Fig. 39 section 467); a reconstruction of a conotheca is illustrated in Fig. 35 B. The production of a conotheca (always in conjunction with a bitheca as in *R. tuberosus*) marks the end of a line of development.

REMARKS.—*R. thorsteinssoni* is clearly very close to the Ordovician species *R. tuberosus*. It differs in having a predominantly rectangular meshwork. The general proportions of the stipes, autothecal spacing, type of autothecae, and number of bithecae are similar in both species, but *thorsteinssoni* lacks the distinctive internal autothecal and bithecal tubes that are found in *tuberosus*, whilst the stolothecae are shorter. The distal extremity of the internal conotheca of *thorsteinssoni* lacks the characteristic terminal bend of *tuberosus*.

## Family *Idiotubidae* KOZLOWSKI, 1949

### Genus *Galeograptus* WIMAN, 1901

TYPE SPECIES.—*G. wennersteni* WIMAN 1901.

AMENDED DIAGNOSIS.—Rhabdosome discoidal, erect portions of autothecae associated in comparatively few (6–10) peripheral branches bifurcating usually once near mid-length; bitheca extending along branches; stolons probably not sclerotized.

REMARKS.—*Galeograptus* is much smaller than *Cyclograptus* which has 20–30 peripheral stipes and a large basal disc.

#### *Galeograptus wennersteni* WIMAN, 1901

Figs. 40–42

1901 *Galeograptus wennersteni* n.g. et n.sp. WIMAN, pp. 189–191; pl. VIII, Figs. 8 & 9; Text-figs. 7, 8 (p. 190), *non* Fig. 7 (p. 188).

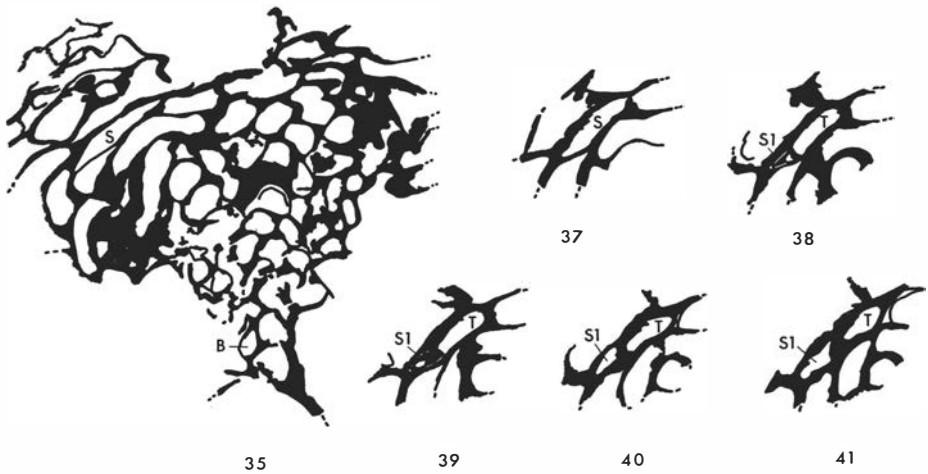



Fig. 40. *Galeograptus wennersteni* WIMAN. Portions of selected sections of the lectotype (slide no. G 93) illustrating the structure of the base of a stipe (section 35) and diad division of the stolotheca (sections 35–41); *S*, stolotheca; *B*, bitheca; *T*, indeterminate theca. × 60.

LECTOTYPE (here designated).—The specimen figured by WIMAN (1901) as Text-figs. 7 and 8 (p. 190), and pl. VIII, Fig. 8, now preserved as serial sections, slides no. G 93 *a–r*. Section intervals not known.

MATERIAL.—The lectotype only.

HORIZON AND LOCALITY.—Upper Ordovician; Öjle Myr, Gotland.

DESCRIPTION.—The rhabdosome is discoidal, about 1.5–2.0 mm. in diameter proximally, widening steadily to 5 mm distally. Ten peripheral stipes, each composed of bundles of autothecae and bithecae grow upwards from the thecorhiza for a distance of about 4 mm. The overall height of the rhabdosome, including the thecorhiza, is a little over 6 mm.

Above the basal disc individual stipes have a lateral width of approximately 1 mm, a dorso-ventral width up to 1.2 mm, and are roughly triangular in cross section. Clusters of thecal tubes, later to become separate stipes, are recognisable in the thecorhiza 0.20 mm above the base of the rhabdosome. At 0.70 mm above the base, and still within the thecorhiza, the clusters are more clearly defined and are composed of at least 35 thecal tubes (e.g. Fig. 40, section 35). Although clearly defined the stipes are connected dorso-laterally by thecal tubes (probably stolothecae; see below), and ventrally by the apertural processes of the autothecae (to be described below).

Arising from the thecorhiza, stipes decrease gradually in thickness as more and more thecae open with their apertures facing the inside of the ring of stipes. The stipes usually bifurcate near mid-length, and immediately after the division consist of about 10–15 thecal tubes. Some stipe divisions, however, occur immediately above the thecorhiza and others more distally, so that the position of branching cannot be regarded as a regular feature.

Fig. 40 illustrates the diad division of a stolotheca *S* to produce a further stolotheca *S1* and a thecal tube *T*, the nature of which cannot be ascertained. Sections 35 and 37 show the undivided stolothecal tube *S* in a dorsal position on the stipe. In sections 38 and 39 the stolotheca has given rise to a thecal tube *T* and a tube of small diameter *S1* with relatively thick walls. This latter tube expands in sections 40 and 41, whilst in later sections (unfigured) it divides again to produce a stolotheca and an unidentifiable theca. Stolons have not been recognised in any of the sections and may not have been sclerotized.

The diminutive thecal tube *B* in section 35 (Fig. 40) opens some sections later without any apertural expansion or ornamentation and is presumably a bitheca. Thecal tubes of similar small diameter to *B* are common on all the stipes and occur throughout the lengths of the stipes. These bithecae are usually positioned laterally and open unobtrusively in the same position. The thecae of large diameter, which are positioned ventrally on the stipe for some distance below their apertures, are certainly autothecae. They are produced initially near the dorsal side of the stipe and then migrate slowly, more or less deeply embedded in the stipe, to a ventral position prior to opening. The apertural regions of the autothecae are considerably expanded, and, in the proximal parts of the stipes, have complex apertural modifications.

Fig. 41 illustrates selected sections of the lectotype showing the development of the apertural regions of the most proximal autothecae. The umbrella-shaped apertural modifications of these thecae are reconstructed in Fig. 42. In sections 104 and 109 (Fig. 41) the autotheca *B* can be seen growing through the gap left by the distal extremity of the preceding autotheca *A* (the position of *A* relative to *B* is shown by a dotted line in Fig. 42 A). Autotheca *A* ends between sections 109 and 112, and at the same time autotheca *B* expands considerably as it nears its aperture. The aperture first appears in section 115, whilst the connection of the autothecal tube with the umbrella-shaped apertural modification is seen in section 114. Further development of the aperture of *B* is shown in sections 124–130, the most distal parts remaining in sections 129 and 130 leaving a gap through which grows the next autothecal tube *C*. The apertural modification of *C* is marked by a dotted line in Figs. 41 (sections 115–130) and 42. It can be seen from Fig. 42 that the apertural modifications of successive thecae form an "umbrella" over the preceding autothecal apertures. This kind of aperture is found on the first 7–9 most proximal autothecae of each stipe, but thereafter the autothecae, although expanding towards their apertures, are provided only with moderately long dorsal and ventral flanges (see WIMAN 1901, pl. VIII, Figs. 8, 9). The change from one type of autothecal aperture to the other is abrupt. Thus theca *D* (Fig. 41 sections 128–130) is of the distal type, contrasting sharply with theca *C* (Fig. 42 A). In all other respects, and in their position on the stipe, these distal thecae agree with the earlier more strongly modified autothecae, and like them are of greater diameter than the inconspicuous, laterally-positioned bithecae.

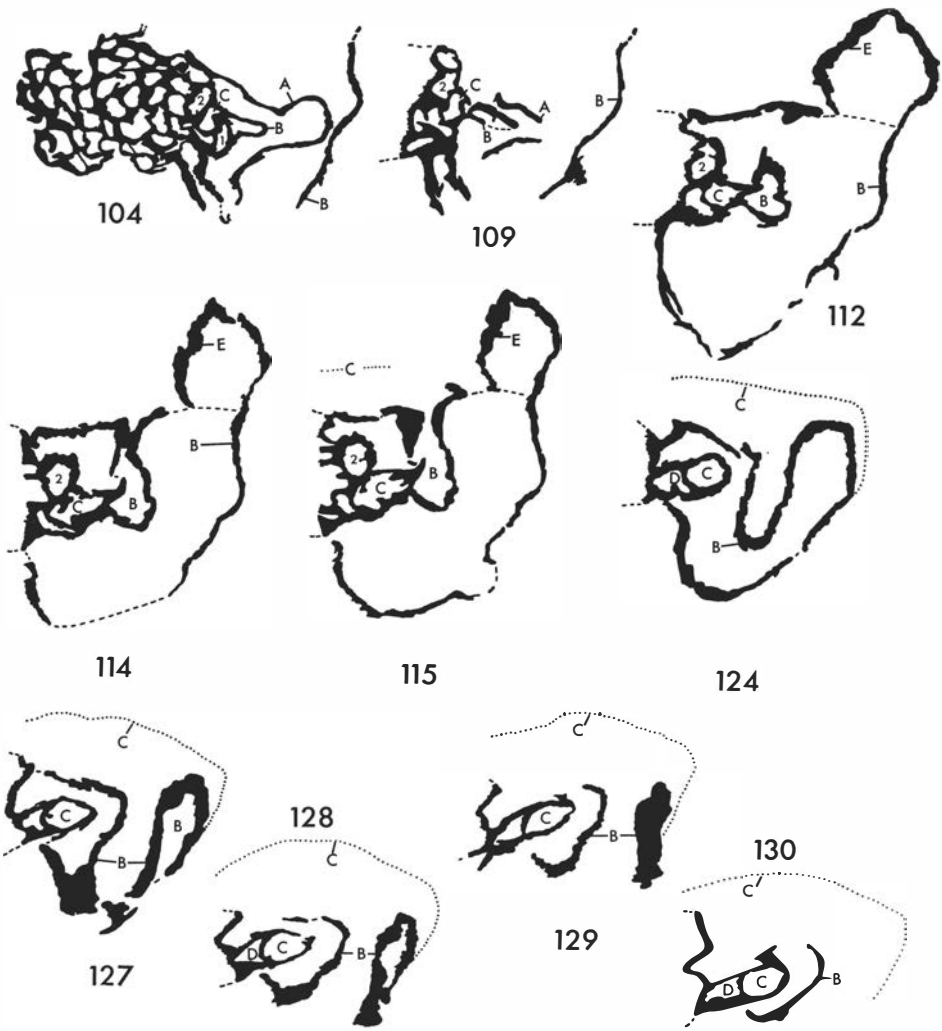



Fig. 41. *Galeograptus wennersteni* WIMAN. Portions of selected sections of the lectotype (slide no. G 93) illustrating the umbrella-shaped apertural modifications of the autothecae (*A–D*); 1, 2 are bithecae; *E* is part of an autotheca from another stipe; full explanation in text. × 30.

The autothecal "umbrella-shaped" apertural modifications are in contact laterally with similar structures from adjacent stipes, and ventrally with those produced from stipes on the opposite side of the rhabdosome. Therefore, when viewed from above, the cavity between the ring of stipes (in the proximal region) will be entirely filled by the autothecal apertures and apertural tissue. The degree of interference between adjacent complex autothecal apertures increases proximally where the stipes become closer together. In this region the preservation of the specimen does not permit detailed description, but the autothecal modifications seem to be basically the same as those depicted in Figs. 41 and 42.

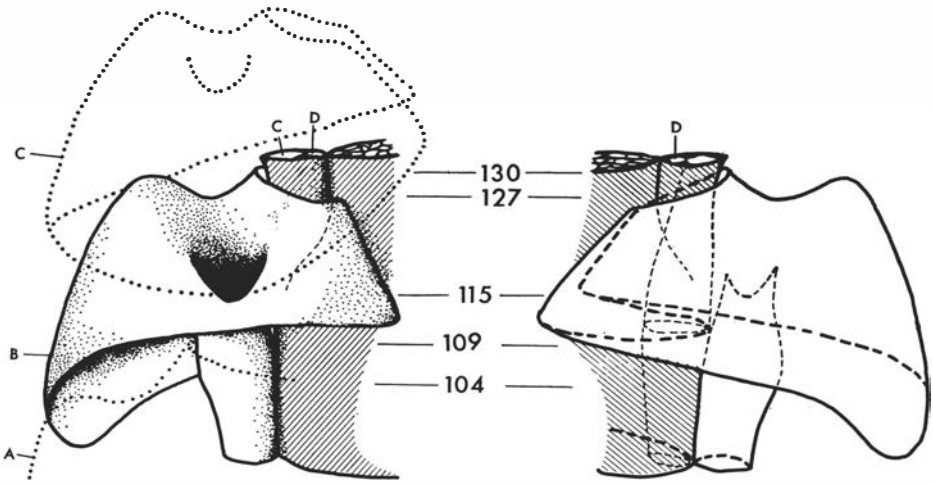



Fig. 42. *Galeograptus wennersteni* WIMAN. Reconstruction of umbrella-shaped apertural modifications of proximal autothecae; notation as in Fig. 41; full explanation in text; nos. indicate position of sections depicted in Fig. 41. × 50.

The upper limit of the complex autothecae coincides approximately with the level above which stolothecae cannot be detected, and the portion of rhabdosome below this level may be regarded as the thecorhiza. The "umbrella-shaped" thecae are presumably represented by the arcuate structures in WIMAN's Fig. 8 (pl. VIII).

Figs. 41 and 42 also demonstrate the asymmetry of the aperture of the proximal autothecae. The apertures of *A*, *B* and *C* (Fig. 42 A) all face anticlockwise round the ring of stipes. Whilst all the complex autothecal apertures on one stipe face the same way, the apertures on another stipe may face clockwise. It is not possible to determine whether there is any marked asymmetry in the simpler autothecal apertures.

### *Galeograptus nicholasi* sp. nov.

Figs. 43 A, B

HOLOTYPE.—Specimen no. S.M. A 52535*a–b*, a transfer preparation of a specimen in relief.

MATERIAL.—The holotype only; collected by Mr. T. C. NICHOLAS on a Sedgwick Club excursion to Shropshire in 1953.

HORIZON AND LOCALITY.—Buildwas Beds (Wenlock Series, ?zone of *C. linnarssoni*) River Severn, Buildwas, Shropshire.

DESCRIPTION.—The rhabdosome is discoidal and approximately 2 mm in diameter in the region of the basal disc. Flattening of the specimen has taken


Fig. 43. *Galeograptus nicholasi* sp. nov. *A*, composite drawing of holotype, a transfer preparation on two slides (nos. SM A 52535*a–b*); dotted lines indicate position, prior to preparation, of the fragment illustrated as *B* (SM A52535*b*); broken lines indicate outline of stipes where barely discernible. × 10.

place whilst the rhabdosome was in an upright position so that the stipes now lie more or less in the bedding plane and radiate from the basal disc. The overall diameter of the rhabdosome is 10 mm. Each of the six primary stipes has a total length of not more than 4 mm. The stipe development is somewhat irregular and asymmetrical: the point of bifurcation being at varying distances from the basal disc; three of them exhibit a further division of one of the branches (Fig. 43).

In the proximal regions, close to the basal disc, the stipes are approximately 1 mm wide (partially flattened) and are composed of not less than ten (and probably about 20) thecal tubes. Away from the basal disc the stipes become less complicated as some thecal tubes terminate, and the distal extremity of each stipe may be composed of as few as 1–3 thecae. The distal narrowing of the stipes gives them a distinctive thorn-like aspect.

Details of the thecal tubes cannot be ascertained but it is at least clear that many thecae extend throughout the length of the stipe, thus suggesting that stolothecae do not occur on the upright parts of the stipes. Individual tubes have a maximum diameter of 0.1 mm and the apertural regions seem to be slightly isolate and unornamented. Growth lines can be detected in places.

The long narrow thecae which make up the stipes are presumably autothecae, although two types of thecae cannot be detected on the rhabdosome. In the penultimate stage of preparation of the specimen the upper surface of the thecorhiza was largely destroyed, but it is known that numerous thecae open immediately above the thecorhiza (remains can be seen in Fig. 43 A), and these may have been bithecae.

REMARKS.—*G. nicholasi* is not unlike *G. wennersteni* in terms of general form and rhabdosome size. Thus both species have a basal disc of the same general dimensions, stipes of approximately the same length, and apparently similar modes of stipe division. *G. wennersteni*, however, has ten primary stipes which are probably composed of more thecae than in *G. nicholasi*. Nor can the "umbrella-shaped" autothecae of *G. wennersteni* be detected in *G. nicholasi*.

## Genus *Discograptus* WIMAN 1901

TYPE SPECIES.—*Discograptus schmidti* WIMAN 1901.

AMENDED DIAGNOSIS.—Rhabdosome discoidal, erect portions of autothecae in more or less regular radially arranged groups on upper surface; bithecae and conothecae confined to thecorhiza; sicula not unlike that in *Dendrotubus*, inconspicuous, centrally situated in disc, apex (presumed prosicula) encrusting.

### *Discograptus schmidti* WIMAN, 1901

Figs. 44–46

1895 *Dictyonema peltatum* n.sp. WIMAN, pl. XII, Figs. 1 & 2, pl. XIV, Figs. 23–29.
1897 Species no. 3. WIMAN, pp. 358–9, pl. XI, Fig. 4, pl. XIII, Figs. 1–11.
1901 *Discograptus schmidti* n.g. et n.sp. WIMAN, pp. 191–2, pl. VIII, Figs. 1 & 18.

LECTOTYPE (here designated).—The specimen figured by WIMAN 1897, pl. XI, Fig. 4 and pl. XIII, Figs. 1–11, now preserved as a section series cut at 20 $\mu$, slide no. G 786.

MATERIAL.—The lectotype; the specimen figured by WIMAN 1901, pl. VIII, Fig. 1, preserved as a section series, slide no. G 76; the specimen figured by WIMAN 1895, pl. XIV, Figs. 23–27 now preserved as a section series cut at 25 $\mu$, slide no. G 806; the specimen figured by WIMAN 1895, pl. XII, Figs. 1 and 2 and pl. XIV, Figs. 28 and 29, now preserved as a section series cut at 25 $\mu$ slide no. G 807; an unfigured section series prepared by WIMAN, slide no. G 89; five slides prepared by the writers from two specimens originally isolated by WIMAN, cut at 8 $\mu$ (slides G 844) and 10 $\mu$ (slides G 845); several complete specimens (unsectioned) isolated by WIMAN, and numerous fragments of disc and stipes.

HORIZON.—Upper Ordovician; from silicified boulders, Gotland.

DESCRIPTION.—Most of the rhabdosomes have a basal disc with a diameter of 1–2 mm, but occasional specimens attain a diameter of 4 mm, whilst the one figured by WIMAN (1901, pl. VIII, Fig. 18) is fully 6 mm in diameter. The thecorhiza is about 0.5 mm thick, and the stipes project above the thecorhiza for a distance of 4 mm at the most.

The stipes are arranged in a roughly radial manner about the centre of the disc, where a short, upright, but inconspicuous tube can usually be detected. This latter tube has a greater diameter than the bithecae, but unlike the autothecae has no adnate portion. This tube is unique in the rhabdosome, and since the whole colony appears to develop from this point it is reasonable to conclude that it is the sicula. The sicula projects above the thecorhiza for about 0.2–0.3 mm, and has a diameter near its aperture of 0.1 mm. As it is traced down into the thecorhiza (see "58" in Figs. 44 and 45, sections 15–7) the sicula maintains its diameter until 0.05 mm from the base of the rhabdosome when it suddenly expands in the manner of the sicula of *Dendrotubus erraticus* (KOZLOWSKI 1963) to approximately 0.15–0.20 mm (section 5, Fig. 44). The overall length of the sicula is about 0.5 mm. A distinction cannot be made between prosicula and metasicula but the attached portion presumably represents, in part, the prosicula. The sicular aperture is furnished with at least one spine which may bifurcate in the same way as the ventral autothecal process (see below). There is a suggestion in some specimens of a *pair* of bifurcating spines on opposite sides of the aperture, and in this respect it differs from the autothecal apertures, which have a bifurcating ventral spine, and a robust, plate-like dorsal process which only rarely shows a tendency to divide.

Unfortunately the exact nature of the origin of the first stolotheca and the early stolothecal divisions cannot be clearly seen. Of the numerous later stolothecae which can be traced, none show traces of stolons, and it seems very likely that the stolons are not sclerotized. In the absence of contained stolons, the stolothecae are recognised by their ability to give rise to other thecal types, but each stolothecal division results in two thecae only. In general the stolothecal

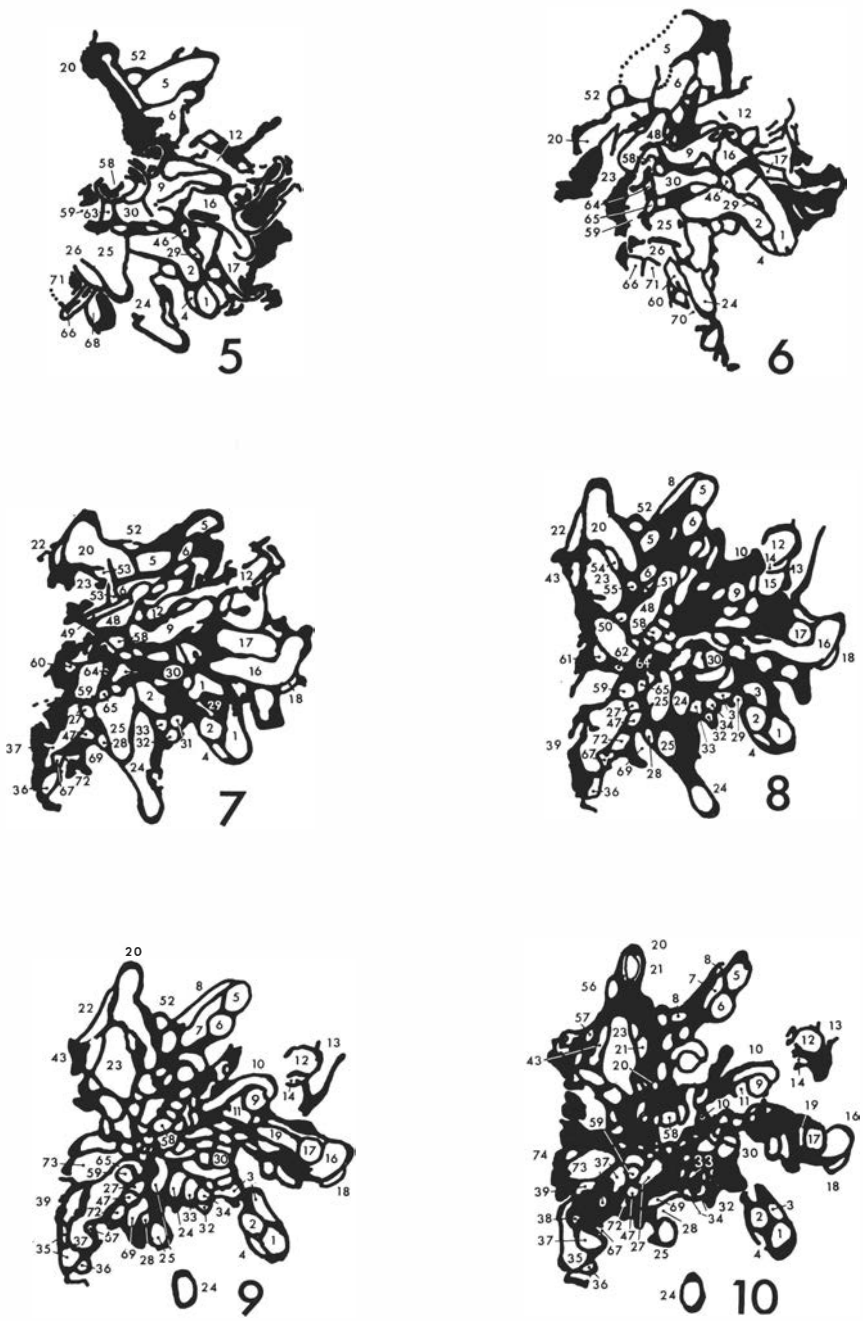



Fig. 44. *Discograptus schmidti* WIMAN. Selected sections from the lectotype (slide no. G 786); full explanation in text; numbering of thecal tubes does not indicate order of origin. ×25.

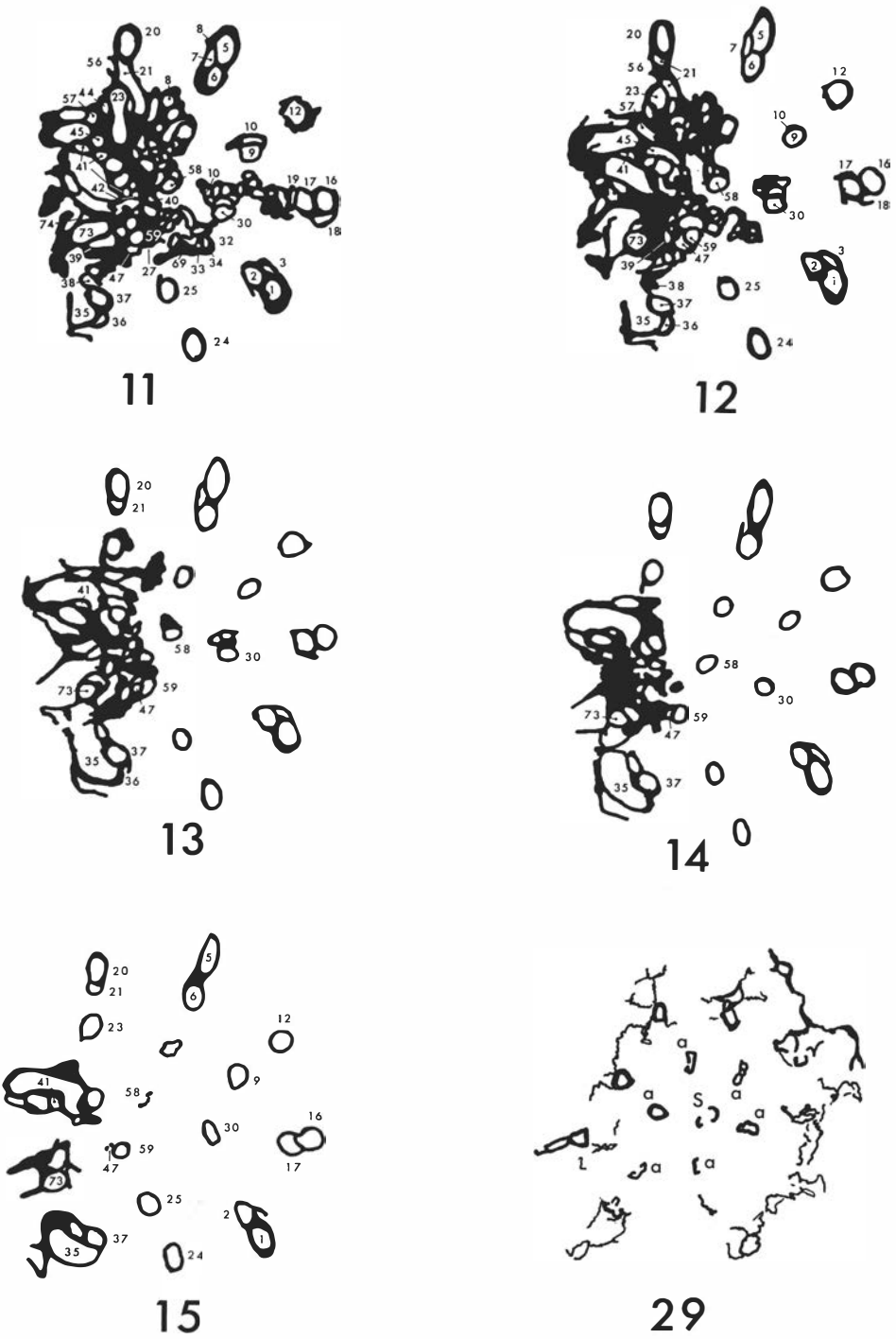



Fig. 45. *Discograptus schmidti* WIMAN. Sections 11–15 are selected from the lectotype (slide no. G 786); 58 is the sicula; full explanation in text; numbering of thecal tubes does not indicate order of origin; section 29 from a section series prepared by the writers (slide no. G 844); *s*, sicula, *a*, autothecae. × 25.

tubes are inconspicuous, but have variable dimensions. Some for example have encrusting portions which, with the adnate parts of the autothecae and some bithecae, help to form the encrusting base of the rhabdosome. In such examples the stolothecal tubes have dimensions only a little less than the adnate portions of the autothecae. For example the stolothecae 26, 66, 68 and 71 (sections 5, 6, Fig. 44) are nearly comparable with the autothecae 24 and 25 which occur nearby in the thecorhiza. On the other hand stolotheca 63 (section 5, Fig. 44) is a much smaller tube which gives rise to the thecae 64 and 65 (section 6). Both these latter are stolothecae and have diameters typical of the majority of such thecae. Stolotheca 64 cannot be traced very far, but 65 eventually divides again to produce a further stolotheca and the autotheca 37 (section 9, Fig. 44). Since the adnate portion of autotheca 37 is well-established in section 7 (Fig. 44) and since the connection with the stolotheca 65 is not made until section 9 (that is immediately below the top of the adnate portion of autotheca 37; see section 10), the development of this autotheca must be very similar to the autothecae of some bithecocamarids (see BULMAN 1955, p. 142, Fig. 26). However, it is far from certain that the "inner ring" of autothecae (e.g. 59, 30, 9, Figs. 44, 45) originated in this way and, indeed, it seems more probable that they are connected with the early stolothecae close to the basal tissue of the rhabdosome. It is even likely that in such a complex thecorhiza as in *D. schmidti*, the thecal morphology—particularly of the proximal parts of each theca—is a little variable.

The autothecae are prominent both in their erect and adnate parts, and have a diameter of 0.2 mm. The proximal regions of each thecal tube are encrusting for less than half a millimetre in the case of the inner autothecae, and rather more than this for the outer autothecae. There is a progressive increase in overall autothecal length from the first-formed to the later autothecae. The earliest autothecae are found in a ring of five stipes, each of which is situated about 0.4 mm from the sicula. Each stipe in this "inner ring" is composed of a single autotheca in association with one or more bithecae which usually open near the base of the stipe (see autotheca 30 in section 13, Fig. 45; 59 in section 15; 9 in section 11).

Autothecae in the outer stipe may be quite long. Thus Figs. 46 A and B depict two stipes each composed of five autothecae; the last autotheca in both is fully 3.5 mm in length in its erect part and its total length will, therefore, be more than 4 mm. By contrast autothecae of the "inner ring" may be less than 1 mm.

The autothecal apertures are most distinctive and have the ventral margin extended into a long bifurcating spine (Figs. 46 A, B). The dorsal margin is also furnished with a stout process which, although sometimes showing a slight tendency to bifurcate, is more usually lamelliform and shorter than the ventral process (Fig. 46 A). The autothecae are spaced at about 20 in 10 mm.

The bithecae in *D. schmidti* are about twice as numerous as the autothecae,

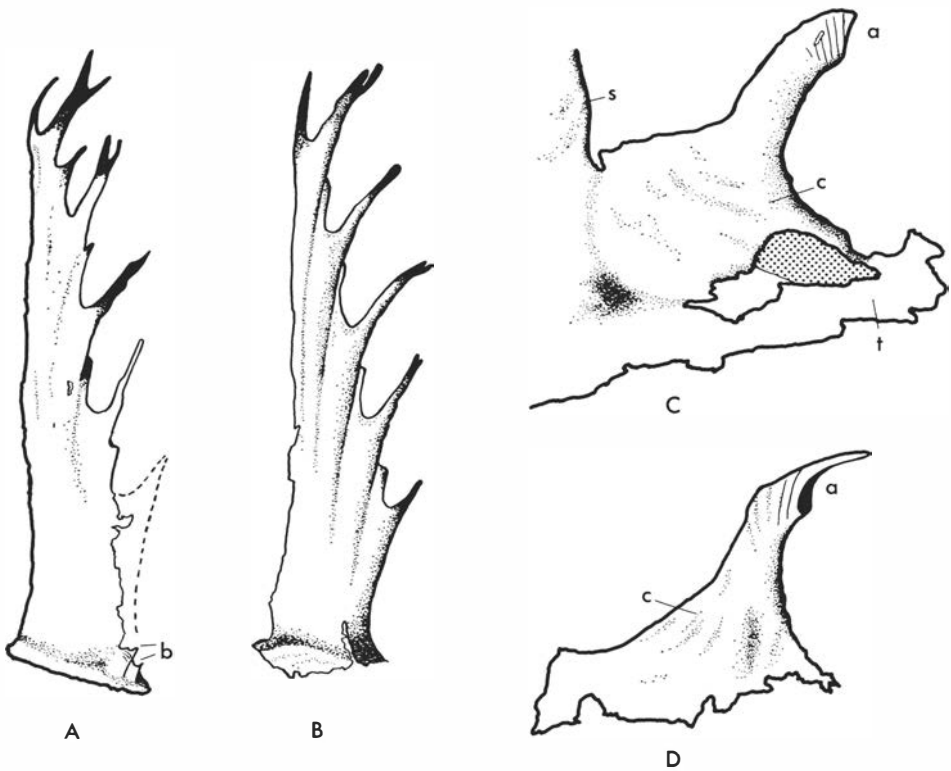



Fig. 46. *Discograptus schmidti* WIMAN. *A*, *B*, fragmentary specimens (respectively G 848 & G 849) showing stipes, autothecae with spined apertures, and attached fragments of thecorhiza with bitheca (*b*) ×40. *C*, *D*, fragmentary portions of thecorhiza each with a specimen of conotheca *c*; *s*, base of stipe; *a*, conothecal aperture; *C* is specimen no. G 850; *D* is specimen no. G 851. ×90.

and when the rhabdosome is viewed from above their sinuous course on the thecorhiza is most characteristic. Some of the bithecae open with their apertural region slightly isolated from the top of the thecorhiza, but the majority terminate inconspicuously near the base of the stipes, adpressed to the thecorhiza or the base of the stipe. It is often difficult to see the bithecal apertures even under high power. The apertures are unadorned by spines, and show no expansion, whilst the bithecal tubes rarely exceed 0.05 mm in diameter. Some bithecae persist along the stipes for a considerable distance (e.g. bithecae 3, 18, 10, 7, 21, Figs. 44, 45), but in other respects closely resemble the more proximal bithecae.

A few examples of conothecae (Figs. 46 C, D) closely resembling those described on *Reticulograptus* have been found. These occur only on the thecorhiza and project distally. The broad base of the cone may be half a millimetre in diameter, and the apertural region elongated and restricted. The tube near the aperture has a diameter of less than 0.1 mm. Unfortunately few of the sections are cut through these thecae, and of those that are, none is well enough

preserved to enable a detailed description to be given. It seems possible however, that the cone is connected by a narrow tube to the rest of the thecorhiza. The sections which show the conothecae are quite thick and it is possible in places to make out growth lines in the oblique walls. These show quite clearly that the cone consists of a single tube, broad at its base, and narrowing towards its apex where the aperture is situated.

REMARKS.—As in *Reticulograptus* it seems remarkable that the autothecae should be so regularly spaced upon the stipes (see Figs. 46 A, B), particularly when it is considered that all the autothecae in *D. schmidti* originate in the thecorhiza. The significance of the conothecae in general is discussed under *Reticulograptus tuberosus.*

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