

Graptolites from the Ontikan Limestones (Ordovician) of Öland, Sweden

I: *Dendroidea*, *Tubeidea*, *Camaroidea*, and *Stolonoidea*

By

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ABSTRACT.—Remains of graptolites have been isolated from blocks of Ontikan (Lower Ordovician) limestone from the localities of Hälludden and Hagudden in the northern part of the island of Öland. A brief introductory section includes a description of the methods of isolation and preparation of this material, notes on terminology and an outline of the stratigraphy of the two localities.

The graptolites have been described in two parts; this paper contains the first part and deals with the eighteen species which are attributable to the orders *Dendroidea*, *Tubeidea*, *Camaroidea* and *Stolonoidea*. The thirteen species of dendroids include six—*Callograptus? perexilis*, *C.? perlongus*, *C.? sinuosus*, *Desmograptus separatus*, *Dictyonema variabile* and *Acanthograptus divergens*—which are new, whilst one has not been identified specifically; two new subgenera of the genus *Callograptus* are proposed. Each of the two tuboid species is accorded to a new genus—*Parvitubus* and *Multitubus*—and one of the species—*M. spinosus*—is new; two new monotypic families of the order *Tubeidea* are diagnosed. The two species attributed to the order *Camaroidea* belong to two genera. One new unnamed species is provisionally placed in the order *Stolonoidea*. A final section deals with general aspects of dendroid and tuboid morphology, phylogeny and taxonomy.

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Introduction

Towards the end of the last century, Dr. GERHARD HOLM, of the Swedish Geological Survey, was responsible for the preparation of a great deal of graptolitic material (numbering more than 3000 specimens) which he had isolated from Ordovician limestones of the Baltic area. Some members of this fauna were described by HOLM (1890, 1895), but a full description of the material was delayed until Dr. O. M. B. BULMAN's visits to Stockholm in the 1930's to study the HOLM Collection, which is housed in the Naturhistoriska Riksmuseet, Stockholm. The results of this work were embodied in a series of papers published in Sweden between 1932 and 1936: 'On the graptolites prepared by Holm, I-VII'. Of these papers, one entirely (VII, 1936), and four in part (I, 1932 *a*; IV, 1932 *b*; V, 1932 *c*; VI, 1934), dealt with material from the *glauconit-haltig, grå Vaginatum-kalk* of Hälludden, in northernmost Öland. This *Vaginatum* Limestone is part of the Orthoceratite Limestone (s.l.) sequence of the Baltic region.

Subsequent attempts to clear HOLM's material of enveloping carbonaceous matter have proved difficult, owing to the fact that the specimens were dry-mounted and are consequently somewhat brittle; also, it seems likely that the absence of traces of the chitinized stolonial system in sectioned dendroids from

the HOLM Collection (see, for example, BULMAN, 1936, Figs. 3, 4; pp. 19, 21, resp.) can be attributed to the type of mounting employed.

Furthermore, from a stratigraphical standpoint, the value of HOLM's material is marred by the lack of any indication of the levels from which the graptolite-bearing limestones were collected, rendering identifications useless for the purpose of detailed correlation.

During the summers of 1948–50, specimens of graptolitic limestone were collected from the cliff sections at Hälludden and Hagudden (JAANUSSON 1960*b*, fig. 2), in northernmost Öland, by Dr. MUTVEI and his co-workers (cf. JAANUSSON 1957, p. 81, footnote 1). The limestones were accurately fixed stratigraphically by reference to two horizons identifiable at both localities (for detailed descriptions of the cliff sections, see BOHLIN, 1949, pp. 532–539, 540–542, and Figs. 1–3, 5). This material was dispatched to Professor O. M. B. BULMAN, at Cambridge, and was subsequently entrusted to the writer, in 1958, for preparation and description.

In this paper, a short introductory section is followed by an account of the dendroids, tuboids, camaroids, and a possible stolonoid which have been recovered; a subsequent paper will deal with the graptoloids and their bearing on correlation.

It gives me great pleasure to record my gratitude to those who have assisted me in this work. Most notably, in this respect, my thanks are due to Professor O. M. B. BULMAN (Cambridge) for his constant supervision of this work in all its stages and for the facilities placed at my disposal in the Sedgwick Museum. In addition, I wish to thank Dr. ISLES STRACHAN (Birmingham) for much helpful criticism and useful discussion; Dr. HARRY MUTVEI (Stockholm) for handing over the material for description; Dr. VALDAR JAANUSSON (Uppsala) for notes on the stratigraphy of the graptolitic localities and for undertaking the task of guiding this paper through the press; Dr. ADAM URBANEK (Warsaw) for advice concerning the isolation and preparation of specimens; Mr. A. G. BRIGHTON (Cambridge) and the authorities of the Geological Survey of Canada for the loan of specimens; and the technical staffs of the Sedgwick Museum, Cambridge, and the Department of Geology, University College, London, for their invaluable assistance.

The work incorporated in this paper was carried out in the Sedgwick Museum, the University of Cambridge, during the tenure of a Studentship awarded by the Department of Scientific and Industrial Research, to whom I wish to express my gratitude.

Preparation and illustration of the material

The lithology of the Ordovician limestones of northern Öland has been fully investigated and described by JAANUSSON (in BOHLIN, 1955) and here it is sufficient to note that they are light to medium grey in colour, compact, and sometimes recrystallized; they carry a large amount of glauconite, and the limestone may be replaced by a glauconitic sandstone.

The limestones have yielded a large shelly fauna, including trilobites and nautiloids and less common bryozoans, gastropods, and brachiopods, whilst

in the process of isolating the graptolites, hydroids, chitinozoans and conodonts have been revealed.

The limestones of Hälludden and Hagudden are free of cementing silica and are readily broken down in dilute hydrochloric acid, or in acetic acid if a more gentle action is preferred. This treatment results in an accumulation of grey sludge, containing the graptolites and other chitinous remains, and abundant glauconite. Dr. URBANEK kindly suggested to me that if this stage of the treatment is carried out in a cylinder jar, it is subsequently possible to float off much of the finer sediment by agitating the sludge with a strong current of water; any chitinous matter coming to the top of the jar during these operations can be removed by pipette; the coarse material at the bottom of the jar can be further sorted by decanting in various stages. The final residue is examined under a microscope, a fraction at a time, and all chitinous remains are extracted—this is most easily accomplished by using a pipette.

Any specks of limestone adhering to the specimens, particularly in thecal apertures, can be removed by the strong effervescence produced in the reaction of hydrogen peroxide and sodium hydroxide. The length of time for which specimens are subjected to this treatment depends upon the amount of adherent material and the state of preservation, but usually one to two minutes is ample.

Whilst occasional specimens were recovered yellow and transparent, requiring no further treatment prior to dehydration and mounting, the majority of the isolated graptolites proved to be heavily carbonised. However, it was found possible to bleach most of these, to a greater or lesser degree, by immersion in a solution of conc. nitric acid and potassium chlorate (SCHULZE's solution). The time of immersion necessary to achieve transparency varies enormously, and is dependent upon the degree of carbonisation of the specimen. Usually, only a few minutes is necessary to render a sicular transparent, whilst early growth stages may require from 15 to 30 minutes; fragments of adult rhabdosome, heavily carbonised, have been immersed for up to two or three hours with scarcely any discernible change taking place.

Each stage of the treatment so far described is followed by a thorough washing of the specimens.

Dehydration in alcohol precedes transference of the specimens to the mounting medium—in this case *Euparal*; a thinner, *Euparal Essence*, is available as an intermediate stage in the process, if required. With *Euparal*, dehydration to absolute is not essential, whilst it is possible to transfer direct from the alcohol without the use of the thinner or of a preparation such as xylol; furthermore, *Euparal* has the advantage of not turning yellow with age. On the debit side, it takes several months to harden and is liable to contract in the process, so that the mounted specimens must be periodically checked and fresh *Euparal* added if necessary.

Large fragments of rhabdosome, either too large to be mounted wet, or too heavily carbonised to be bleached, can be mounted dry in tray-slides.

The material, on the whole, is poorly preserved. It is generally fragmentary and heavily carbonised, whilst some degree of squashing of the specimens, or wrinkling of the periderm, is universal. The several attempts made at serial-sectioning proved unrewarding and, in consequence, interpretation of morphology has been based largely on bleached specimens, and these, where necessary, have been illustrated by *camera lucida* drawings. It is difficult to get good photographs of mounted specimens.

All figured specimens and some additional material are housed in the Museum of the Palaeontological Institute, University of Uppsala, Sweden, and are numbered ÖI. 1041 to ÖI. 1164.

Terminology

Indiscriminate usage of the term *stipe width* in the literature has caused the appended dimensions to have little value in specific descriptions, unless the statement is amplified in some way. In view of the lack of suitable alternatives, it is proposed to retain this term but to qualify it with appropriate adjectives. Thus, *lateral stipe width* refers to the distance between the two lateral walls of a stipe, seen in dorsal or ventral aspect, whilst *dorso-ventral stipe width* has reference to measurements made between the dorsal and ventral stipe margins. In this latter case, it is necessary to indicate whether it is the *maximum* dorso-ventral width which is implied (from the dorsal margin to the distal tip of the ventral denticle, or to the ventral edge of the apertural margin of the theca if no denticle is developed), or the *minimum* dorso-ventral width, between the dorsal margin and the inner (or dorsal) edge of the thecal aperture.

The term *lappet* is used in a broader sense than is implied by the definition given in the Treatise (BULMAN, 1955, p. V 6); thus, projections—be they expanded, rounded or pointed—which are developed on the lateral margins of thecal apertures, are so named.

Introduction to stratigraphy

HOLM's (1895) *glauconithaltig, grå Vaginatum-kalk*, from Hälludden, is reported by JAANUSSON (1960a, p. 342) to be equivalent to the Langevoja, Hunderum and lowermost Valaste substages (formerly *Lepidurus*, *Expansus* and lowermost *Raniceps* Limestones) of the Ontikan (i.e. post-Tremadocian Lower Ordovician) limestone sequence in Öland. The graptolite fauna from Hälludden described by BULMAN (1936) is thought to have been derived largely from the Hunderumian and lowest Valastean.

The present graptolitic material is fixed stratigraphically by reference to two horizons identifiable both at Hälludden and at the neighbouring locality of Hagudden: a discontinuity surface (D) and an oolitic bed (O). The several levels from which material has been collected are listed below (and see also Tables 1a and 1b):

<i>Hälludden</i>	<i>Hagudden</i>
+ 115 + 120D	
+ 38 + 43D	+ 25 + 30D
+ 23 + 26D	+ 20 + 45D
+ 18 + 22D	+ 20 + 25D
+ 10 + 30D	+ 10 + 15D
+ 5 + 8D	0 + 15D
~~~~~D	~~~~~D
- 76 - 82D	0 - 8D
- 100D	
- 110 - 113D	
- 113 - 116D	
- 118 - 120D	
- 135 - 140D	
-----O	-----O
- 84 - 92	- 83 - 86

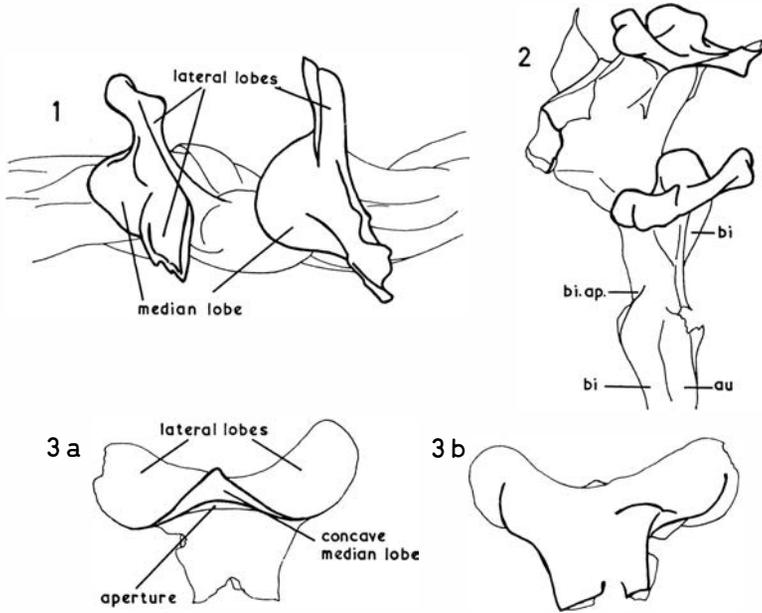
*Note:* The levels above D are designated as +D, and those between D and the upper surface of O as -D; the levels below the upper surface of O are designated as -, without any letter. Elevations are given in cm.

Faunal details given by BOHLIN (1949) and JAANUSSON (1957, 1960a and *in litt.*) show that those portions of the sequences which can be attributed, without doubt, to the respective substages are as follows.

<i>Substage</i>	<i>Hälludden</i>	<i>Hagudden</i>
Valaste	above +23D	above +142D
Hunderum	lower surface of O to +15D	lower surface of O to +63D
Langevoja	top of <i>Limbata</i> lstrn. to the base of O	top of <i>Limbata</i> lstrn. to the base of O

The range of the material collected at Hälludden (-84-92 to +115+120D) is thus from the upper part of the Langevojan to the lower Valasteian. At Hagudden, a more restricted vertical section was sampled (-83-86 to +20+45D) and this correlates with the uppermost Langevojan to the middle or upper Hunderumian.

The three substages represented at Hälludden and Hagudden are known to include the boundary between the graptolite zones of *Didymograptus hirundo* and *D. bifidus*, though the location of this boundary relative to the established substage divisions has yet to be determined with certainty. Discussion of this problem is reserved until the whole graptolite fauna of the present limestone material from Öland has been described.



Figs. 1-3: *Dendrograptus* cf. *D. cofeatus* KOZŁOWSKI. (1) Form of apertural processes in ventral aspect.  $\times 60$ ; Hälludden +23+26D; Öl. 1041. (2) Stipe division or dissepiment in ventral aspect.  $\times 35$ ; Hälludden +23+26D; Öl. 1042. (3) Free apertural portion of autotheca; (3 a) distal aspect, with aperture; (3 b) proximal aspect.  $\times 55$ ; Hälludden +23+26D; Öl. 1043. *ap*: aperture; *au*: autotheca; *bi*: bitheca.

## Systematic description

Order *Dendroidea* NICHOLSON, 1872

Family *Dendrograptidae* ROEMER, in FRECH, 1897

Genus *Dendrograptus* HALL, 1858

*Dendrograptus* cf. *D. cofeatus* KOZŁOWSKI, 1948

Figs. 1-3.

cf. 1948 *Dendrograptus cofeatus* KOZŁOWSKI, p. 120; Figs. 26-28; Pl. VII, figs. 1-6.

FIGURED MATERIAL.—Spec. Nos. Öl. 1041-Öl. 1043.

LOCALITY AND HORIZON.—Hälludden: +18+22D, +23+26D.

DESCRIPTION.—The material comprises several fragments of stipe, one of which (Fig. 2) appears to portray a single instance of stipe division; proximally to this is a section of unbranched stipe 7.0 mm in extent. Whilst lacking any appreciable overall curvature, the stipe fragments, in detail, are distinctly sinuous in thecal aspect.

The maximum dorso-ventral width of the stipes, recorded at the level of autothecal apertures, is 0.65-0.70 mm; the minimum width, 0.20-0.25 mm, is midway between two such apertures. Lateral stipe width is within the range 0.20-0.35 mm.

The autothecae are free aperturally for 0.15–0.17 mm; in this part of their length they are elliptical in cross-section, with the longitudinal dimension (0.17–0.20 mm) less than the transverse one (0.20–0.25 mm). The tri-lobed, ventral, apertural process can be as much as three times the lateral width of the autothecal aperture, whilst the length of the process, from origin to distal tip, ranges up to 0.25 mm (Fig. 1). The fragments of stipe recovered suggest the presence of 19–20 autothecae per cm.

In general, the bithecae are not readily discernible. However, in Ö1. 1042 (Fig. 2) two bithecae are present on the lateral part of the stipe, each opening below the aperture of the adjacent autotheca; the loss of the ventral process in the more proximal of the two autothecae makes it possible to observe the bi-thecal aperture in this case.

DISCUSSION.—Unlike *D. cofeatus*, bifurcation of the stipes does not take place at frequent intervals; it is not even certain that the single example noted in the description has been correctly interpreted, since it is possible that the feature present may be the base of a dissepiment, suggesting generic affinity of the fragments with *Callograptus* or *Dictyonema*, rather than with *Dendrograptus*. However, the preservation is such that no positive decision can be taken.

A slight difference noted in a comparison of the Öland material with *D. cofeatus* is the presence of concave curvature affecting the median lobe of the tri-lobed, ventral process; this feature is not clearly apparent in any of KOZŁOWSKI'S figured specimens. The effect is merely to deflect the distal tip of the lobe above the apertural margin of the dorsal wall (see Figs. 3 *a, b*), thus facilitating connection between the autothecal aperture and the exterior, along the mid-ventral line. In this respect, the autothecal processes show remarkably uniform development in the specimens available.

The observed morphological differences which exist between the present material and *D. cofeatus* could, perhaps, be explained in terms of derivation of the respective specimens from different parts of the rhabdosome. There still remains, however, a marked disparity in the age of the two sets of material (approximately *hirundo-bifidus* boundary and Tremadocian, resp.) and it has been thought wise to make only a provisional comparison of this Hälludden dendroid with *D. cofeatus*.

### *Dendrograptus rigidus* BULMAN, 1936

Figs. 4–9.

1936 *Dendrograptus rigidus* BULMAN, p. 16; Figs. 2–5; Pl. I, figs. 27–35.

1947 *Dendrograptus rigidus* RUEDEMANN, p. 216; Pl. 20, figs. 19–20.

FIGURED MATERIAL.—Spec. Nos. Ö1. 1045, Ö1. 1046*b*, Ö1. 1047*a*, Ö1. 1048, Ö1. 1049 *a, b*.

LOCALITY AND HORIZON.—Hälludden: +18 +22D, +23 +26D, +38 +43D; Hagudden: 0 +15D, +20 +25D, +25 +30D.



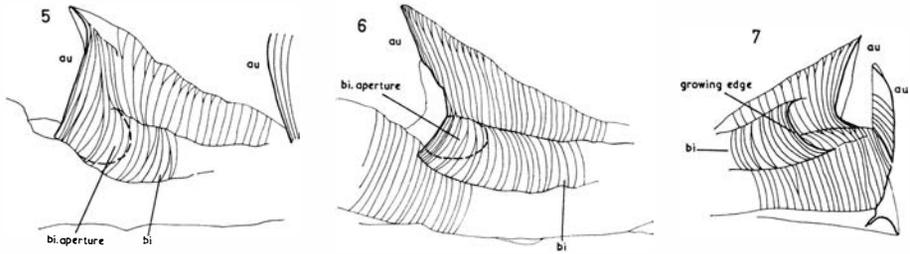
Fig. 4: *Dendrograptus rigidus* BULMAN. Two stipe fragments showing excessively developed autothecal denticles.  $\times 7.5$ ; Hagudden 0 + 15D; Öl. 1049.

DESCRIPTION.—A full description of this species was given by the author (BULMAN, 1936), and it is intended here only to note those features of special interest exhibited by the present Öland material.

Occasional large fragments of rhabdosome have been recovered, showing several orders of branching but with no apparent regularity. The angle of divergence of the stipes, following a division, does not exceed  $30^\circ$ , and is frequently appreciably less than this. In general, the interval between divisions increases distally.

The form of the autothecae, in lateral aspect, gives to the stipes a saw-tooth appearance: the free ventral wall of each autotheca is typically continued as a broad, roundly-terminated denticle, whilst the margin of the aperture is straight, or very slightly concave, and is approximately normal to the dorsal stipe wall. In several specimens from the 0 + 15D level at Hagudden, there is an exaggerated development of the autothecal denticles (Figs. 4 *a*, *b*); these latter frequently attain a length of 0.5 mm and may be as much as 0.66 mm in width, though most commonly this dimension is of the order of 0.33–0.37 mm; the lateral diameter of the autothecal apertures in these specimens averages 0.30 mm. In thecal (ventral) view, the denticle is often asymmetrical, being drawn out laterally more on one side than on the other. In those instances in which these apertural processes appear to have been preserved in an undisturbed state, an appreciable variation in attitude is noted, ranging from a direct continuation of the line of the free ventral wall, to a curved habit, in which they lie in the plane of the apertural margin, approximately normal to the dorsal wall of the stipe.

The inclination of the free ventral wall ranges from  $25^\circ$  to  $40^\circ$ . The maximum dorso-ventral stipe width, from the tip of the apertural denticle to the dorsal wall, varies from 0.75 mm to more than 1.0 mm; below autothecal apertures, the range is from 0.30 mm to 0.60 mm. The autothecae number from 14 to 22 in 10 mm. Owing to the fragmentary nature of the material, it is not possible to say if these measurements reflect the extent of the variation which can occur within a single colony or within the species as a whole.



Figs. 5-7: *Dendrograptus rigidus* BULMAN. (5) Bitheca opening into autothecal cavity behind aperture.  $\times 43$ ; Hälludden +23 +26D; ÖL. 1045. (6) Bitheca opening into autotheca at autothecal aperture.  $\times 42$ ; Hagudden +20 +25D; ÖL. 1046*b*. (7) Growing end of stipe.  $\times 42$ ; Hagudden +20 +25D; ÖL. 1046*b*. *au*: autotheca; *bi*: bitheca.

The bithecae lie on the lateral walls of the stipes and each opens into the cavity of the associated autotheca at, or just behind (i.e. proximally to), the aperture (Figs. 5, 6). Because of their position and form, the bithecae are scarcely evident externally, and where the periderm is extensively wrinkled they are generally completely obscured.

A stage in the growth of a bitheca and associated autotheca is illustrated in Fig. 7, in which it is seen that the autotheca develops a deep embayment in the dorso-lateral margin of the growing edge, on the side of origin of the bitheca; this embayment ultimately accommodates the aperture of this bitheca.

Abnormal development of the bithecae is of fairly common occurrence. Most usually, it involves the external opening of the bithecae, with a correspondingly greater prominence on the stipe.

No specimen of this species was completely cleared in SCHULZE's solution,

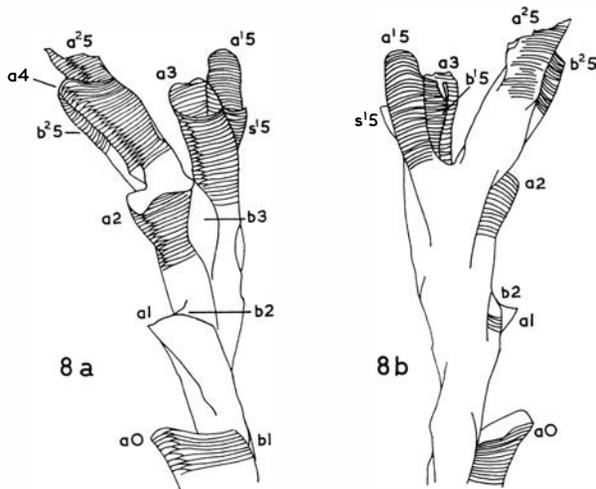


Fig. 8: *Dendrograptus rigidus* BULMAN. Stipe division; (8*a*) ventral aspect; (8*b*) dorsal aspect.  $\times 23$ ; Hälludden, horizon not known; ÖL. 1047*a*. *a*: autotheca; *b*: bitheca; *s*: stolotheca.



Fig. 9: *Dendrograptus rigidus* BULMAN. Fragment of rhabdosome with coiled structure growing from one stipe.  $\times 6$ ; Hagudden + 25 + 30D; ÖL. 1048.

but the balance of evidence culled from the better preserved material (Figs. 8 *a, b*) strongly suggests that stipe division involves the production of two stolothecae and one autotheca in place of a normal triad.

Coiled, tube-like outgrowths, which progressively increase in diameter with distance from their origins, are developed from the stipes of certain specimens from Hagudden (Fig. 9). When treated in SCHULZE's solution, fuselli are faintly discernible, indicating that the outgrowths are an integral part of the rhabdosome; where they contact adjacent stipes in the rhabdosome, the two are rigidly fused together; apart from the distal termination, which is invariably broken, the tubes have no opening to the exterior. ÖL. 1048 (Fig. 9) exhibits most clearly the form of these unusual structures and their relationship to the rest of the rhabdosome. In this specimen, two such structures are present, but one is broken shortly beyond its origin; the main outgrowth arises laterally on the stipe, like a branch, and its appearance is associated with a distinctly swollen zone on the stipe; the initial angle of divergence is slight, but strong coiling quickly asserts itself, directing the outgrowth away from the parent stipe—though it may again contact it in its subsequent course.

An abnormal process of the type just described does not invariably originate laterally, and development from the ventral stipe wall, in a position where one would normally expect an autotheca, has been observed. In such a case, there seems little doubt that the outgrowth has arisen by the indefinite extension of an autotheca.

Whatever the point of origin of these growths on the stipe—lateral, dorsal, or ventral—their form, a gradually expanding, coiled tube, is invariably the same. The fuselli of which they are composed indicate that they are an integral part of the rhabdosome; their most unusual feature is that they have been exactly reproduced several times.

REMARKS.—In his description of *Dendrograptus rigidus*, from the Ordovician of the United States, RUEDEMANN (1947) used a name pre-occupied by *D. rigidus* BULMAN, 1936; most fortunately, however, the species of RUEDEMANN and BULMAN appear to be conspecific.

### Genus *Callograptus* HALL, 1865

TYPE SPECIES.—*Callograptus elegans* HALL, 1865 (chosen by MILLER, 1889).

DISCUSSION.—To accommodate species of *Dictyonema* in which “the thecae are elongated and overlap so that in cross section several of them are found at the same place of the branch” (pp. 53–54), BOUČEK (1957) erected the subgenus *Dictyonema* (*Pseudodictyonema*). Thecal elongation in this case differs from that characteristic of the acanthograptids in that “the thecae are arranged in a vertical series above each other” (p. 54), rather than irregularly or in groups (twigs).

In respect of the genus *Callograptus*, which is of immediate concern, BOUČEK identifies two subgenera: *Callograptus* (*Callograptus*) and *Callograptus* (*Capillograptus*).

*C.* (*Callograptus*) accommodates the “typical callograpti with the thecae not running out into awns [autothecal denticles] and with the branches sporadically united by dissepiments” (p. 43). As “typical callograpti”, BOUČEK includes “the species of the group *C. salteri* HALL, fan-shaped or broadly infundibuliform, with a characteristically parallel growth of the branches, rarely united by dissepiments... [together with]... species of more irregular shapes, with flexuous stipes, farther apart and far more sparsely provided with dissepiments, which may equally well be referred to the genus *Dendrograptus*” (p. 42).

*C.* (*Capillograptus*) includes “the smaller species... [in which]... dissepiments are very sparse and fine, but mostly lacking. Long, hair-like awns grow from the ends of the autothecae” (p. 46).

From the above, it may be seen that BOUČEK incorporates in his subgenus *C.* (*Callograptus*) species in which the thecae retain the normal dendroid length, together with others (*C. salteri*, *C. hopkinsoni*) in which the thecae are elongate. Having used thecal length as a basis for the sub-division of *Dictyonema*, BOUČEK prefers to use the presence or absence of “awns” as a means of defining subgenera in *Callograptus*. In this respect, however, BOUČEK is inconsistent, for in outlining the phylogeny of the dendroids (1957, pp. 163–165), he reverts to length of theca as a character of significance: one of his basic phyletic stocks, involving elongation of the thecae, but without such structural complication of the stipes as is found in the acanthograptids, includes species of *C.* (*Callograptus*), whilst a second stock is comprised of the structurally simpler species of *C.* (*Callograptus*), along with *C.* (*Capillograptus*), in which the thecae retain the normal dendroid length. Thus, BOUČEK’s subgenus *C.* (*Callograptus*), according to his own interpretation of dendroid phylogeny, includes representatives of two of his lines of development.

It is generally agreed that thecal form is of fundamental significance in the elucidation of lines of descent in the Graptolithina, and it would seem likely that length of theca has greater value in this respect than does degree of development of apertural denticles on the autothecae. Thus, if the genus *Callograptus* is to be split into subgenera, it is suggested that thecal length is the more

natural basis upon which to attempt such a division. In this belief, and thereby conforming with BOUČEK's separation of the subgenus *Dictyonema* (*Pseudodictyonema*), it is proposed to identify two subgenera of *Callograptus*: *Callograptus* (*Callograptus*) BOUČEK, 1957, emend., and *Callograptus* (*Pseudocallograptus*) subgen. nov.

**Subgenus *Callograptus* (*Callograptus*) BOUČEK, 1957, emend.**

TYPE SPECIES.—*Callograptus elegans* HALL, 1865.

DIAGNOSIS.—Species of *Callograptus* in which the thecae retain the normal dendroid length.

REMARKS.—This is the typical subgenus of *Callograptus*, including all those species attributed by BOUČEK to *C.* (*Capillograptus*), together with those species of *C.* (*Callograptus*) BOUČEK having thecae of normal length.

Two species from Öland are provisionally included in this subgenus, the fragmentary nature of the material precluding a positive generic identification in either case.

***Callograptus* (*Callograptus*)? *perexilis* sp. nov.**

Figs. 10-19.

HOLOTYPE.—Spec. No. Öl. 1069 *a*; Fig. 10.

FIGURED MATERIAL.—Spec. Nos. Öl. 1060 *a*, Öl. 1061 *a*, Öl. 1062, Öl. 1063 *a*, Öl. 1064, Öl. 1065 *a*, Öl. 1066 *b*, Öl. 1067, Öl. 1068, Öl. 1069 *a*.

LOCALITY AND HORIZON.—Hälludden: -135-140D, -118-120D, -76-82D, +18+22D, +23+26D, +38+43D; Hagudden: 0-8D, 0+15D, +10+15D, +25+30D.

DIAGNOSIS.—Entire rhabdosome unknown. Stipes extremely tenuous and frequently bifurcating; angle of divergence moderate to large; stipes straight following division. Minimum dorso-ventral stipe width, below autothecal apertures, 0.08-0.15 mm. Autothecae long, slender, widening to aperture; inclined at 20° to 40°; with or without ventral denticle; typically isolate distally; 13-14 developed per cm. Bithecae laterally placed, opening in angle between free autothecal wall and rest of stipe; occasionally abnormally developed.

DESCRIPTION.—The form of the entire rhabdosome is not evident from the fragments recovered; it is composed of slender, branching stipes diverging generally at angles of 35°-40° (Fig. 10), though up to 60° has been recorded. The stipes are sporadically connected by dissepiments: thus, dissepiment bases are preserved in Öl. 1060 *a* (Fig. 11 *a*) and Öl. 1061 *a* (Fig. 12). In general, the fragments of stipe are stiff and straight following division (Fig. 10); the larger, unbranched fragments may show an appreciable dorsal concave curvature (Fig. 13); care must be taken, however, not to confuse preservational effects with original curvature, for the tenuous stipes were presumably readily flexed.



Fig. 10: *Callograptus* (*Callograptus*)? *perexilis* sp. nov. Holotype, in thecal aspect.  $\times 10.3$ ; Hälludden + 23 + 26D; Ö1. 1069 a.

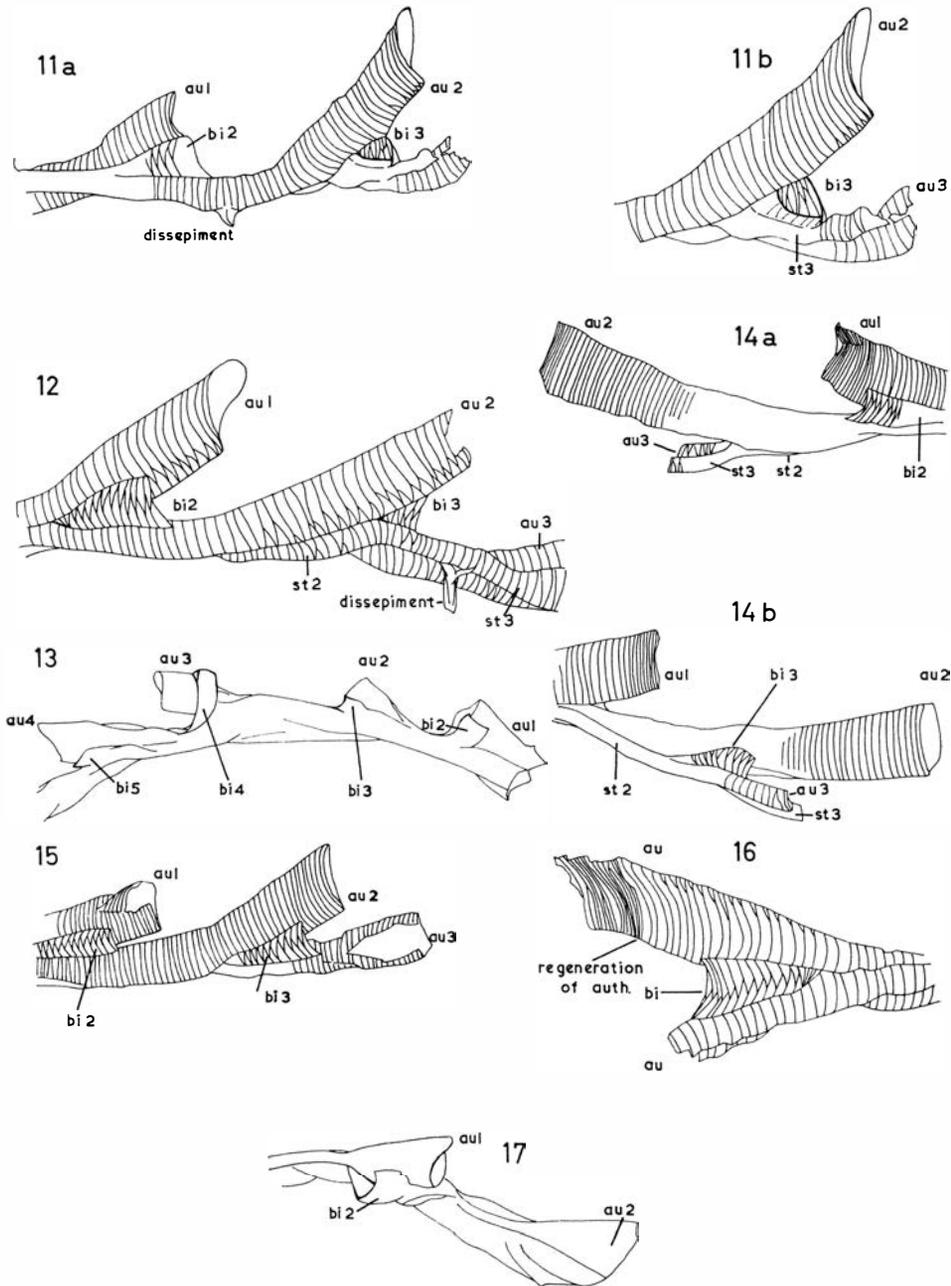
The minimum dorso-ventral width of the stipes, below autothecal apertures, ranges from 0.08 mm to 0.15 mm; lateral width does not exceed 0.25 mm.

The autothecae are long and slender and increase gradually in diameter towards the aperture; they are typically isolate distally. The inclination of the distal part of the theca to the dorsal stipe wall may vary from  $20^\circ$  to  $40^\circ$ , and the free ventral wall is accordingly either straight or with abrupt concave curvature (Figs. 11 *a, b*), in the two extreme cases. The apertural margin is rounded, 0.20–0.25 mm in diameter, and may be plain or with a blunt denticle developed from the ventral edge. To a certain extent, the presence of a denticle is correlated with a moderately inclined distal portion of the autotheca and a concave free ventral wall; conversely, the lack of a denticle usually accompanies a low angle of inclination.

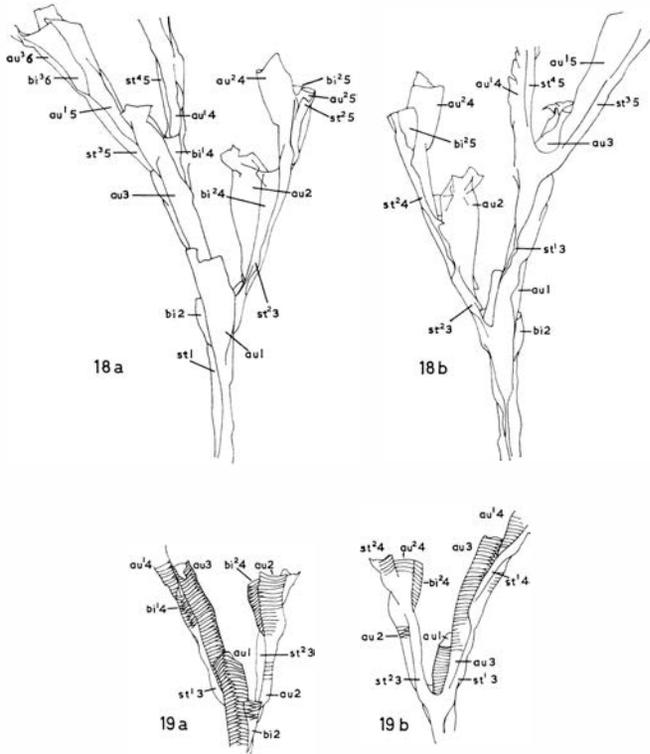
In Ö1. 1065 *a* (Fig. 16), the aperture of one autotheca was apparently damaged during life and an extension subsequently added at a slightly different orientation.

The larger stipe fragments suggest the presence of 13–14 autothecae per cm in the rhabdosome.

The bithecae lie dorso-laterally relative to the autothecae and typically open in the angle between the dorsal autothecal wall and the rest of the stipe (Figs. 12, 14 *a, b*), with the aperture directed distally on the side of origin of the bitheca. Occasionally, the bitheca may pass beneath the associated autotheca to open on the opposite side of the stipe, with the aperture directed laterally (*bi*₃ in Fig. 11 *b*); in one instance (Fig. 17), a bitheca (*bi*₂) passes beneath the associated autotheca (*aul*) and opens with the aperture facing proximally. In Ö1. 1062 (Fig. 13), two bithecae (*bi*₂, *bi*₄) have ventrally-directed apertures. Abnormal arrangement, in which consecutive bithecae open on the same side of the stipe, may be encountered (Figs. 13, 15).



Figs. 11–17: *Callograptus (Callograptus) ? perexilis* sp. nov. (11) Fragment of stipe in lateral aspect; (11a) complete specimen,  $\times 30$ ; (11b) distal end,  $\times 40$ . Hälludden – 135–140D; ÖL. 1060a. (12) Stipe fragment in lateral aspect.  $\times 43$ ; Hälludden – 118–120D; ÖL. 1061a. (13) Abnormally developed bithecae.  $\times 16$ ; Hälludden + 23 + 26D; ÖL. 1062. (14) Growing end of stipe; (14a, b) two lateral aspects.  $\times 22$ ; Hälludden + 23 + 26D; ÖL. 1063a. (15) Abnormally developed bithecae.  $\times 22$ ; Hälludden + 23 + 26D; ÖL. 1064. (16) Autothecal regeneration.  $\times 41$ ; Hälludden – 118–120D; ÖL. 1065a. (17) Recurved bitheca.  $\times 22$ ; Hälludden + 23 + 26D; ÖL. 1066b. au: autotheca; bi: bitheca; st: stolotheca.



Figs. 18–19: *Callograptus (Callograptus)? perexilis* sp. nov. (18) Two orders of stipe division separated by a single normal triad; (18a) ventral aspect; (18b) dorsal aspect.  $\times 19$ ; Hälludden +18+22D; ÖL. 1067. (19) Stipe division; (19a) ventral aspect; (19b) dorsal aspect.  $\times 28$ ; Hälludden +23+26D; ÖL. 1068. *au*: autotheca; *bi*: bitheca; *st*: stolothecca.

Several fragments of rhabdosome including stipe divisions were recovered and mounted, but interpretation of these is not readily obvious because of incomplete maceration. What is apparent, however, is the frequency with which division occurs, though no doubt some correlation exists between this and distance from the proximal end of the rhabdosome. It is possible for only a single autotheca to separate consecutive divisions; on the other hand, because of the length of the autothecae, the intervening distance in such cases is appreciable, and of the order of 1.15 mm.

The mode of branching can be deduced only from external evidence (Figs. 18a, b, 19a, b), but, in all instances, it has been possible to interpret the observed arrangement of thecae if it is assumed that, at the node bearing the division, two stolothecae and one autotheca replace the normal triad.

This species is characterised by the presence of extremely tenuous and generally straight stipes, combined with aperturally isolate autothecae and short, laterally-placed bithecae.

DISCUSSION.—The generic affinity of this species is doubtful. The stiff, divergent stipes favour inclusion within the genus *Dendrograptus*, whilst the isolated occurrence of dissepiments would suggest, rather, the genus *Callograptus*. In view of the intermediate characteristics of the latter genus (between *Dictyonema* and *Dendrograptus*), this species is provisionally placed within *Callograptus*, and is considered to be close to the *Dendrograptus* 'end' of that genus.

REMARKS.—Several of the fragments recovered were yellow and transparent, requiring no further treatment after isolation, apart from dehydration and mounting. This would suggest that the cortical layer, in such cases, was of much reduced, and presumably negligible, thickness. That this is not a characteristic feature of the species, however, is evidenced by the number of heavily carbonised specimens which exist; nor has it been possible to relate the material with reduced periderm to a particular level of occurrence in the limestone sequence.

DERIVATIO NOMINIS.—The specific name proposed has reference to the very slender nature of the stipes.

*Callograptus (Callograptus)? sinuosus* sp. nov.

Figs. 20-21.

HOLOTYPE.—Spec. No. Öl. 1080.

FIGURED MATERIAL.—Spec. Nos. Öl. 1078, Öl. 1079.

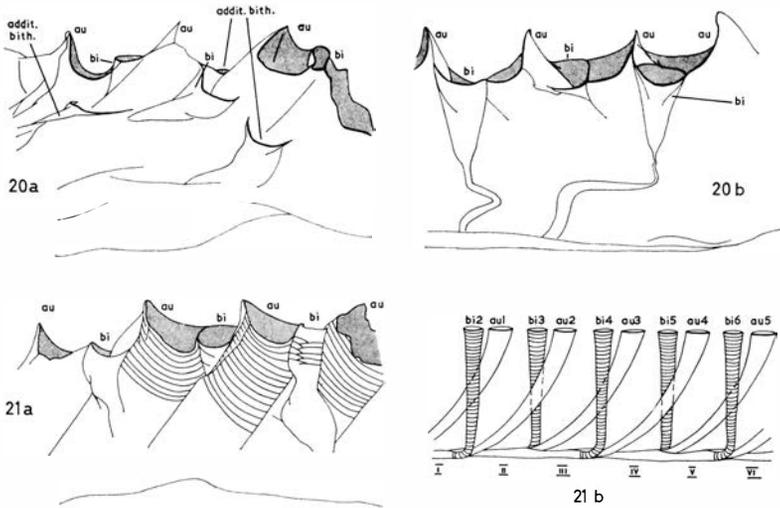
LOCALITY AND HORIZON.—Hälludden: -135-140D.

DIAGNOSIS.—Entire rhabdosome unknown. Stipes 1.85 mm in maximum dorso-ventral width; sub-parallel, bifurcating infrequently with small angle of divergence; rare anastomosis and dissepiments. Autothecae tubular, with restricted aperture; inclined at 50° and steepening aperturally; contact with rest of stipe complete but for short denticle; 14-16 developed per cm. Bithecae typically opening on ventral margin of stipe, between adjacent autothecal apertures and in line with these latter; following sinuous course initially and may be of greater length than autothecae.

DESCRIPTION.—The form of the entire rhabdosome is not known, but the fragments recovered suggest that it is composed of parallel to sub-parallel stipes, rarely anastomosing, and possibly linked by dissepiments. These latter cannot be identified with certainty, but short, flange-like outgrowths, occasionally encountered on the lateral walls of the stipes, are, perhaps, best interpreted as such.

Stipe division occurs at infrequent intervals, and one section of unbranched stipe measures almost 13 mm. The angle of divergence of the resultant stipes is small and parallelism is quickly achieved. Because of poor preservation, it was not possible to determine the disposition of the thecae at division.

The maximum dorso-ventral width of the stipes averages 1.85 mm, with a range of from 1.65 mm to 2.1 mm for this dimension.



Figs. 20–21: *Callograptus (Callograptus)? sinuosus* sp. nov. (20) Stipe fragment, two lateral aspects; (20a) distal termination of stipe; (20b) showing sinuous bithecae.  $\times 20$ ; Hälludden – 135–140D; ÖI. 1078. (21a) fusellar structure.  $\times 15$ ; Hälludden – 135–140D; ÖI. 1079; (21b) diagrammatic interpretation of thecal arrangement in the stipes. au: autotheca; bi: bitheca; I, etc.: stolothea I, etc.

The autothecae may be straight, with ventral angle of about  $50^\circ$  (Fig. 21a), or with ventral concave curvature, and thus being inclined at a higher angle distally than proximally. The autothecae are tubular in form, 1.75–2.0 mm in length, and three to four times as long as wide. The aperture is typically restricted; this is attributable to the positioning of bithecal apertures between adjacent autothecal apertures, at the ventral margin of the stipe (Fig. 21a). The apertural margin is concave and the ventral edge is provided with a distinct denticle, up to 0.2 mm in length; the denticle is normal, and the plane of the aperture approximately parallel, to the dorsal wall of the stipe (Figs. 20b, 21a).

The autothecae number 14–16 per cm; the overlap of adjacent autothecae is very great, and only a short portion of ventral wall—and this chiefly denticle—is free of contact with any other part of the stipe.

The bithecae typically open between adjacent autothecae, and in line with these latter, so that they are flanked proximally by the dorsal wall of one autotheca and distally by the ventral wall and denticle of the next following (which is the autotheca of the same generation as the bitheca). Variation in the position of the bithecal aperture is possible to the extent that the aperture may show a bias towards the side of origin of the bitheca, or it may lie below the ventral margin of the stipe.

Whilst the apertural portions are reasonably regular, however, neither the shapes nor the courses of the proximal parts of any two bithecae are identical (see Figs. 20b, 21a). The supposed structure of the stipes is diagrammatically

represented in Fig. 21 *b*, but it is idealised to the extent that the bithecae, because they frequently adopt a wandering course, may be much longer than the autothecae; in general, however, the growth of the bithecae is normal to the stipe length.

Apparently additional bithecae are occasionally developed (Fig. 20 *a*); they are laterally placed, and on opposite sides of the stipe to the normal bithecae; they open well below the ventral stipe margin.

Two features are distinctive of this species: the excessive dorso-ventral width of the stipes, and the form of the bithecae. The former can be attributed to the high angle of inclination of the autothecae, combined with their dimensions and abundance per cm. The bithecae, however, present certain anomalies, not the least of which is the relative conformity of their apertural portions as contrasted with the vagaries of their proximal parts.

DISCUSSION.—The generic affinity of the fragments included in this species is doubtful; the sub-parallel arrangement of the stipes, together with the occasional presence of what appear to be dissepiment bases, has suggested provisional inclusion within the genus *Callograptus*.

The possibility that this species might be more correctly placed in the order *Tubeidea*, family *Multitubidae* fam. nov. (see below, pp. 51–54), has not been overlooked; the presence of an apparently callograptid rhabdosome with uniformly spaced autothecae, but with bithecae which are clearly irregular in their proximal parts, suggests affinity with that family. The species is attributed to the *Dendroidea* (and provisionally to the genus *Callograptus*), however, on the evidence of the positioning of the bithecal apertures relative to the autothecae, which suggests that the thecae most probably originated in alternating triads.

REMARKS.—Collapse of the stipe structure, affecting all but the ventral margins of the stipes, is characteristic of all the specimens recovered, and is frequently accompanied by curling of the stipes about an axis parallel to their length. The quoted dorso-ventral width of the stipes is, therefore, something of an estimation, based on the least-affected specimens; furthermore, the structure of the stipes is uncertain and the affinity of the material, even at the order-level, is inconclusive.

DERIVATIO NOMINIS.—The specific name proposed has reference to the wandering courses adopted by the initial parts of the bithecae.

### Subgenus *Callograptus* (*Pseudocallograptus*) subgen. nov.

TYPE SPECIES.—*Callograptus salteri* HALL, 1865.

DIAGNOSIS.—Species of *Callograptus* in which the thecae are elongate, beyond the normal dendroid length, but which lack structural complication of the stipes such as is characteristic of the acanthograptids.

REMARKS.—This subgenus is proposed for those callograptids with elongate

thecae which were included by BOUČEK (1957) in his subgenus *Callograptus* (*Callograptus*).

Two species from Öland can be only provisionally attributed to this subgenus, owing to their fragmentary state of preservation. Each species shows elongation of the autothecae such that, whilst the normal association of autothecal and bithecal apertures is retained, in any given pair the autotheca is separated by two generations from the adjacent bitheca, instead of by one as in the typical dendroid structure. (A fuller explanation is given in the ensuing description of the two species.)

*Callograptus (Pseudocallograptus)?* cf. *C. (P.) salteri* HALL, 1865

Figs. 22–27.

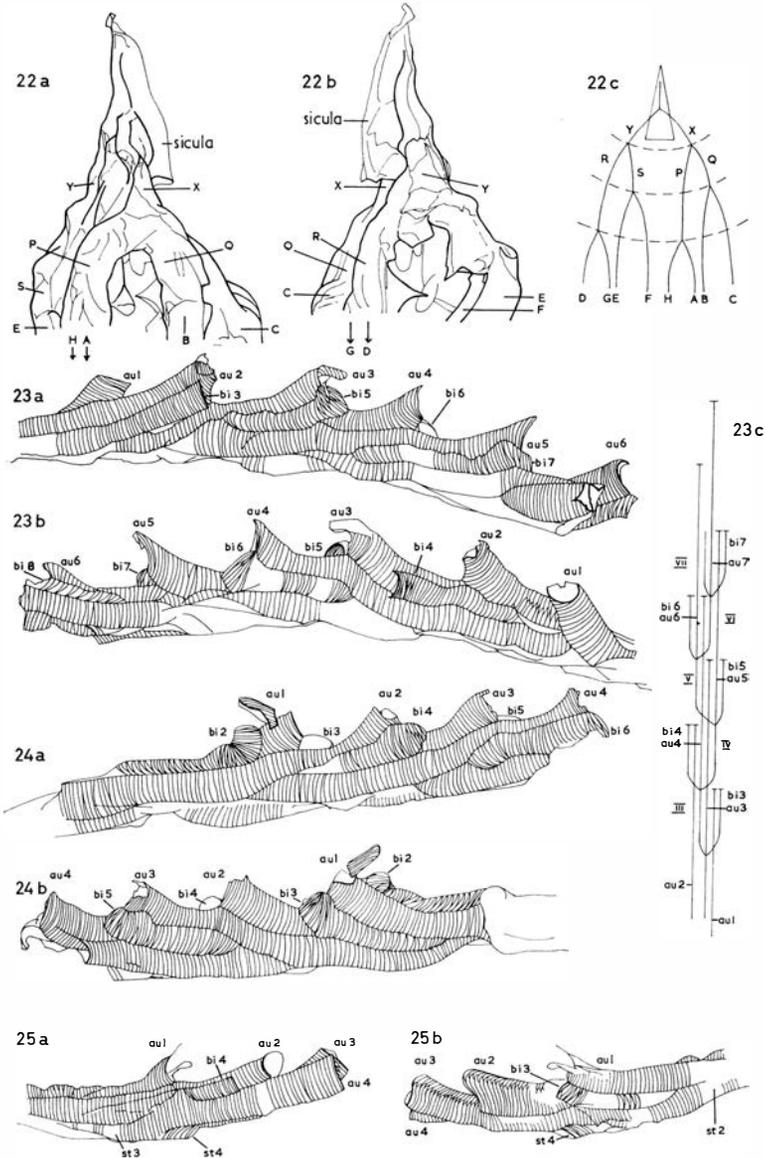
cf. 1934 *Callograptus salteri* BULMAN, p. 81; Figs. 39, 40; Pl. IX, figs. 1–7.

FIGURED MATERIAL.—Spec. Nos. Öl. 1082, Öl. 1083 *a*, Öl. 1084, Öl. 1085 *a*, Öl. 1086, Öl. 1087.

LOCALITY AND HORIZON.—Hälludden: +18 +22D, +23 +26D, +38 +43D; Hagudden: 0 +15D, +10 +15D, +20 +25D, +25 +30D.

DESCRIPTION.—The most distinctive feature of the structure of this species is the form of the autothecae, which are elongated to such an extent that the external origin of each is placed at the level along the stipe of the aperture of the autotheca produced three generations previously—instead of two, as in the normal dendroid stipe; moreover, this lengthening of the autothecae is achieved without disturbing the regular sequence of alternating triads which characterises the dendroid structure. One effect of autothecal elongation is increased width of the stipes in the dorso-ventral plane; also, in general, a cross section of a single stipe will reveal a stolotheca, a bitheca, and three autothecae (cf. 1 st., 1 bi., and 2 au. in a normal dendroid stipe). That the autothecae are of excessive length relative to the bithecae and stolothecae is clearly evident in Figs. 23 *a, b* and 24 *a, b*, whilst the stipe structure is diagrammatically illustrated in Fig. 23 *c*.

In form, the autothecae are tubular and are provided with a broad, flat and roundly-terminated apertural process which continues the line of the free ventral wall; the process may extend up to 0.25 mm beyond the aperture, but usually it is shorter than this, averaging 0.16 mm. The apertural margin is typically rounded (average diameter *c.* 0.25 mm), but may be transversely oval, as in Öl. 1086 (Fig. 26 *a*) which has a lateral diameter of the aperture of 0.3 mm and a dorso-ventral diameter of 0.22 mm. Occasionally, the aperture may be slightly restricted relative to the distal part of the autotheca. The free ventral wall may be gradually or abruptly concavely curved; in the latter case, the apertural region of the autotheca may be isolate (e.g. *auI*, Figs. 23 *a, b*). The position of the autothecal apertures alternates from side to side of the stipe, giving a slightly sinuous appearance in ventral (thecal) aspect (see Fig. 27); typically,



Figs. 22–25: *Callograptus* (*Pseudocallograptus*)? cf. *C. (P.) salteri* HALL. (22) Proximal end of rhabdosome; (22 *a, b*) two aspects of same.  $\times 14$ ; Hälludden + 23 + 26D; ÖI. 1082; (22 *c*) diagrammatic interpretation of proximal end. (23) Stipe fragment; (23 *a, b*) two lateral aspects.  $\times 18$ ; Hälludden + 18 + 22D; ÖI. 1083 *a*; (23 *c*) diagrammatic interpretation of stipe structure. (24) Stipe fragment; (24 *a, b*) two lateral aspects.  $\times 18$ ; Hälludden + 18 + 22D; ÖI. 1084. (25) Growing end of stipe; (25 *a, b*) two lateral aspects.  $\times 18$ ; Hälludden + 18 + 22D; ÖI. 1085 *a*. A, B, etc.: see text p. 22; *au*: autotheca; *bi*: bitheca; I, II, etc.: stolothecae I, II, etc.

14–16 autothecae are developed in 10 mm of stipe length, though as many as 17 and as few as 12 have been recorded in this distance.

At autothecal apertures, the maximum dorso-ventral width of the stipes is of the order of 0.74–0.82 mm; below such apertures, it lies within the limits 0.35–0.45 mm. Lateral stipe width averages 0.45 mm, but may be as little as 0.33 mm or as great as 0.74 mm.

The bithecae, in general, are of an exposed length equal to the distance between two autothecal apertures, so that, taking into account the increased autothecal length, a bitheca *bi*₅, for example, will open adjacent to the aperture of autotheca *au*₃ (Figs. 23 *a, b*). When normally developed (see *bi*₅ and *bi*₆, Figs. 23 *a, b*), each bitheca lies dorso-laterally to the adjacent autotheca and opens at the level of the autothecal aperture; the bithecal aperture is placed below that of the autotheca and is directed obliquely across the stipe, to the side opposite that on which the bitheca originates. The aperture itself may be placed on either side of the stipe, but most usually it is on the side of origin of the bitheca. The distal portion of each bitheca is typically inflated (Figs. 23, 24).

Departures from this normal type are frequent. Most usually, a slight increase in length occurs, causing the bithecal aperture to be placed well beyond (i.e. distally to) that of the autotheca with which it should be associated. This condition is evident in Figs. 23 *a, b*, in which *bi*₃, for example, has extended as far as the aperture of *au*₂, so that *au*₁ appears to lack an associated bitheca; again, the increased length of *bi*₄ in Fig. 23 *b* results in the presence of two bithecal apertures (*bi*₄ and *bi*₅) opening adjacent to the aperture of *au*₃. With increased length of the bitheca, the aperture is directed distally, rather than across the stipe.

The largest fragment of rhabdosome recovered is a proximal end, with the sicula preserved (Öl. 1082, Figs. 22 *a–c*). Several orders of stipe division are included, which result in the development of a conical rhabdosome with autothecal apertures directed inwards. No attempt was made to clear this specimen; this, together with its wrinkled and damaged state, renders interpretation somewhat difficult. The sicula is tubular, though contracting slightly to the proximal end, with plain aperture, and is 1.64 mm in length; a stout nema, or slender, non-thecate stem, is given off proximally—insufficient is preserved to allow a positive identification. The initial bud (sicular stolotheca) appears close to the proximal end of the sicula and grows along the wall towards the aperture; approximately half-way along the sicula, branching begins with the development of the first thecal triad, giving the two stipes designated *X* and *Y* in Figs. 22 *a–c*. These latter extend to just beyond the level of the sicula aperture, where division again takes place, in both stipes, thus producing four (*P, Q, R* and *S*). At a further distance from the sicula approximately equal to the length of the first two stipes, *Q* and *S* divide to give *B, C* and *E, F*, resp.; after a similar interval, *R* and *P* produce *D, G* and *H, A*, resp. Thereafter, the interval between divisions becomes much greater. Several zones of bifurcation can thus

be recognised at the proximal end of the rhabdosome (Fig. 22 *c*); whether or not division is as regular distally is not known.

A single dissepiment is present in this specimen (Öl. 1082), linking the dorso-lateral parts of two adjacent stipes. No other fragment of rhabdosome carries any indisputable evidence of having borne a dissepiment.

From the number of specimens recovered exhibiting stipe division, it is probable that this was achieved at frequent intervals in the rhabdosome; in the proximal end specimen (Öl. 1082), there is correlation between this interval and position in the rhabdosome. In this same specimen, it is noted that, following division, the resultant stipes quickly converge and become parallel, or nearly so. In more distally situated examples, whilst the angle of divergence is small ( $20^\circ$  to  $30^\circ$ ), the branches remain straight and stiff, though rarely are more than two or three thecae preserved on each.

Stipe division is considered to involve essentially the production of two stolothecae and one autotheca in place of a normal triad, but it is complicated by the excessive length of the autothecae (see Figs. 26, 27), and, in view of this, three features are worthy of mention (thecal and stipe numbers used as examples have reference to text Fig. 26 *b*, in which division is assumed to occur at the third triad):

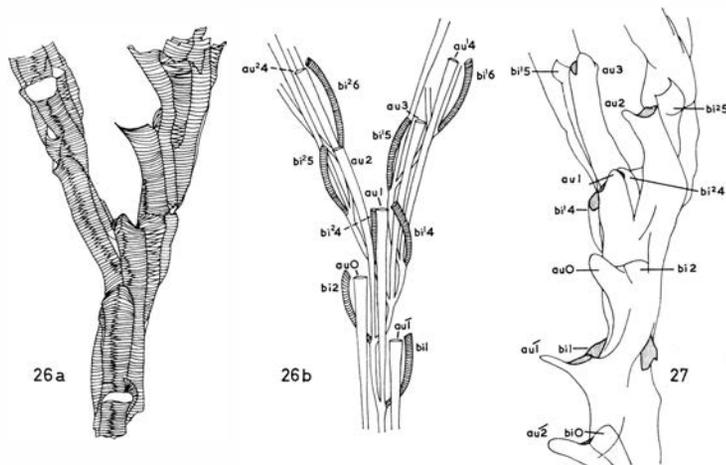
(I) Separation of the stipes is delayed for some distance after division of the stolon system occurs; one triad (the fourth) is developed in each stipe before they separate.

(II) Two bithecae ( $bi^1_4$ ,  $bi^2_4$ ) are associated with the aperture of the autotheca ( $au_1$ ) lying at the point of separation of the two stipes.

(III) Beyond the point of stolon division, one branch (stipe 2) contains two apertures ( $au_0$ ,  $au_2$ ), and the other (stipe 1), one ( $au_1$ ), of autothecae originating before the division. Beyond the point of separation of the stipes, only one stipe (No. 2) contains an autotheca ( $au_2$ ) of a generation preceding that at which division occurs (assuming, in this case, that the autotheca opening at the point of divergence— $au_1$ —is not included in either branch. In the normal dendroid arrangement, one branch contains the autotheca of the generation immediately preceding the division; the first autotheca of the other branch is the autotheca produced at the node bearing the division.)

The distinctive features of the material would thus appear to include the form of the rhabdosome, which is conical, with sub-parallel stipes and rare dissepiments; the presence of a sicula with nema or non-thecate stem; the excessive length of the autothecae, with consequent effect on the dorso-ventral width of the stipes, combined with the normal dendroid structure; the dorso-laterally placed bithecae, opening externally at the level of each autothecal aperture; and a mode of stipe division comparable with that present in dendroids of normal structure.

DISCUSSION.—Generic affinity is not conclusive, but inclusion within the genus *Callograptus* is suggested by the conical form of the rhabdosome, with



Figs. 26–27: *Callograptus* (*Pseudocallograptus*)? cf. *C. (P) salteri* HALL. (26 a) Stipe division in ventral aspect.  $\times 14$ ; Hälludden + 23 + 26D; Öl. 1086; (26 b) diagrammatic interpretation of same. (27) Stipe division in thecal aspect.  $\times 21$ ; Hälludden + 23 + 26D; Öl. 1087. *au*: autotheca; *bi*: bitheca.

parallel to sub-parallel stipes, at least proximally, and the presence of rare dissepiments. Distally, the stipes appear to diverge, as in *Dendrograptus*, but insufficient length of stipe is preserved beyond division to indicate whether or not this initial divergence is maintained, whilst the form of the rhabdosome does not accord with the irregular or bushy habit of *Dendrograptus*. The conical rhabdosome suggests affinity with *Dictyonema*, but attribution of the material to this genus is precluded by the rarity of dissepiments. Furthermore, whatever interpretation is placed on the structure developed from the proximal end of the sicula—suspensory nema or non-thecate stem—it will comply with the definition of *Callograptus*, for RUEDEMANN (1947) has described a specimen of *Callograptus salteri* in which the proximal end is developed as a sicula and nema, though a root and stem are considered characteristic of the genus.

Of the utmost importance in connection with the identification of the material at the specific level, is the existence, in the Arenigian of Shropshire and Wales, of species of *Callograptus*—*C. salteri* HALL and *C. hopkinsoni* BULMAN—in which parts of the rhabdosome are preserved in relief showing that, at a given level, a stipe is composed of numerous tubular thecae, suggesting that several successive generations of thecae are present, side by side. *C. hopkinsoni*, judging from the dorso-ventral width of the stipes and the number of thecae present at a given level, has a more complex structure than the Öland material; *C. salteri*, on the other hand, agrees with this latter in dorso-ventral stipe width as well as in autothecal abundance per cm. Furthermore, the autothecae, in both instances, are strongly denticulate and occasionally isolate (see BULMAN, 1934, p. 83; Fig. 40c). Provisionally, therefore, the present material is compared

with *C. salteri*; the positive identity of these must await greater knowledge of the structure of the latter.

REMARKS.—In the synonymy, only one record of the species *C. salteri* HALL is listed—that of BULMAN, 1934. This decision was taken because comparison is possible only with this author's material, which is partially in relief.

*Callograptus (Pseudocallograptus)? perlongus* sp. nov.

Figs. 28–30.

HOLOTYPE.—Spec. No. Öl. 1091 *a*; Fig. 28.

FIGURED MATERIAL.—Spec. Nos. Öl. 1091 *a, b*, Öl. 1092.

LOCALITY AND HORIZON.—Hälludden: +18 +22D, +23 +26D.

DIAGNOSIS.—Entire rhabdosome unknown. Stipes bifurcating, straight and ?sub-parallel; up to 1.0 mm in maximum dorso-ventral width. Autothecae elongate; robust and tubular with slightly restricted aperture; free ventral wall inclined at 30°; 14–16 developed per cm. Bithecae laterally placed, opening on side of origin with aperture directed ventrally and distally.

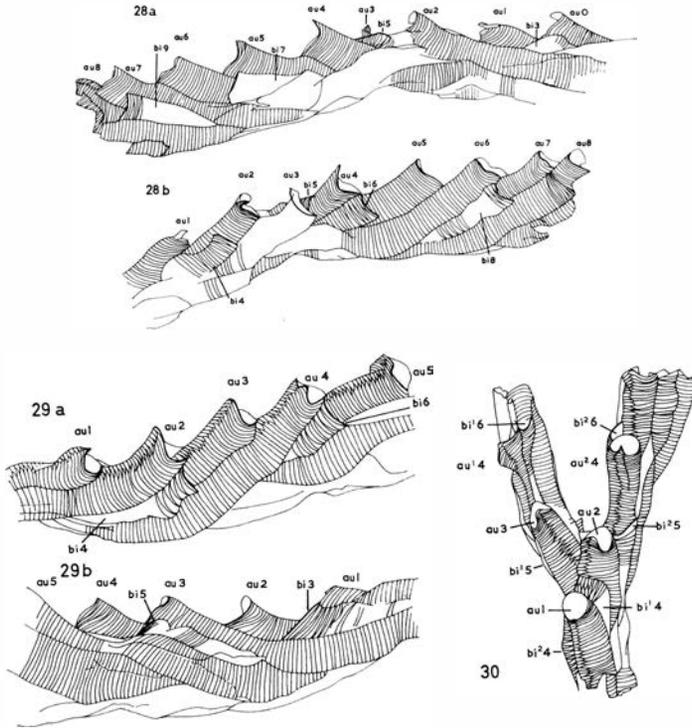
DESCRIPTION.—Although very little material is available for study (and what there is is fragmentary), the stipe structure appears to be identical with that of *Callograptus (Pseudocallograptus)?* cf. *C. (P.) salteri* (see text figs. 28 *a, b* and 29 *a, b*).

The largest single stipe fragment recovered—Öl. 1091 *a*, the holotype—includes nine autothecal apertures. The stipes do not appear to have been strongly curved, if at all; there is insufficient evidence to indicate whether or not the stipes become parallel or sub-parallel following bifurcation; dissepiments are completely lacking; and the form assumed by the rhabdosome is unknown.

At the level of autothecal apertures, a dorso-ventral stipe width of up to 1.0 mm is possible, whilst below the apertures, the range is from 0.55–0.75 mm. The lateral width of the stipes ranges from 0.35–0.72 mm.

The autothecae are tubular, though in ventral aspect they may appear globose (Fig. 30), due to slight restriction of the aperture. The distal part of each autotheca is inclined at *c.* 30° to the dorsal stipe wall, and is typically straight; the proportion of ventral wall which is free is very small, and the autothecae are never isolate aperturally. The apertural margin is rounded, whilst the plane of the aperture is straight or slightly concave; a short, roundly-terminated denticle is developed from the ventral edge. The autothecae are appreciably more robust than in *C. (P.)?* cf. *C. (P.) salteri*. Fourteen to sixteen autothecae are developed per cm; this relatively high number is achieved largely by the appreciable inclination of the distal part of each autotheca, but partly it is accounted for by the occasional off-setting of an autotheca to such an extent that it may be described as occupying a lateral position on the stipe (see *au3*, Figs. 28 *a, b*).

Each bitheca parallels the course of the distal part of the adjacent autotheca,



Figs. 28–30: *Callograptus (Pseudocallograptus)? perlongus* sp. nov. (28) Holotype: a fragment of stipe; (28 *a, b*) two lateral aspects.  $\times 12$ ; Hälludden + 23 + 26D; ÖL. 1091 *a*. (29) Stipe fragment; (29 *a, b*) two lateral aspects.  $\times 17$ ; Hälludden + 23 + 26D; ÖL. 1091 *b*. (30) Stipe division in thecal aspect.  $\times 14$ ; Hälludden + 23 + 26D; ÖL. 1092. *au*: autotheca; *bi*: bitheca.

though typically lying below this latter, in contact with the lateral wall of the next following autotheca (see Figs. 28 *a, b* and 29 *a, b*). The bithecal aperture is placed below (i.e. dorsally to) that of the adjacent autotheca, and is directed distally and ventrally.

Excessive lengthening of the bitheca has not been observed. Occasionally, however, a bitheca may open at the level of the ventral stipe margin, instead of below it; in general, the bithecae show little variation in the material available.

In the mode of stipe division (see Fig. 30), this species exhibits the same features as are portrayed by *C. (P.)?* cf. *C. (P.) salteri* (see p. 23).

DISCUSSION.—The material includes no indication of generic affinity and solely on the basis of its structural resemblance to *C. (P.)?* cf. *C. (P.) salteri*, it is provisionally placed within the genus *Callograptus*.

The characters which serve to distinguish this species from *C. (P.)?* cf. *C. (P.) salteri*—stipe dimensions, and the form of the autothecae and bithecae—also preclude comparison with *C. salteri* HALL. *C. hopkinsoni* BULMAN, though having equally robust stipes, differs in that this feature is achieved by the

presence of a greater number of thecae at a given level—rather than by more robust thecae, with greater inclination and overlap, as in the present species.

DERIVATIO NOMINIS.—The specific name proposed has reference to the excessive length of the autothecae, relative to the bithecae and stolothecae, as compared with the normal dendroid structure.

**Genus *Desmograptus* HOPKINSON, 1875**

*Desmograptus separatus* sp. nov.

Figs. 31–33.

HOLOTYPE.—Preserved in two parts as Specs. Nos. Öl. 1094, Öl. 1095.

FIGURED MATERIAL.—Spec. Nos. Öl. 1096, Öl. 1097 *b*, Öl. 1098 *b*.

LOCALITY AND HORIZON.—Hälludden: +5 +8D.

DIAGNOSIS.—Rhabdosome rooted, conical, apical angle *c.* 60°. Stipes anastomosing, lacunae varying in size, oval to rhombic in outline; average maximum dorso-ventral width of stipes 1.5 mm. Autothecae tubular, 0.25–0.3 mm in diameter; isolate distally; inclined at high angle to dorsal margin; slight ventral denticle; 14–16 developed per cm. Bithecae capriciously arranged and variable in form; frequently opening externally, on side of origin, with aperture directed proximally.

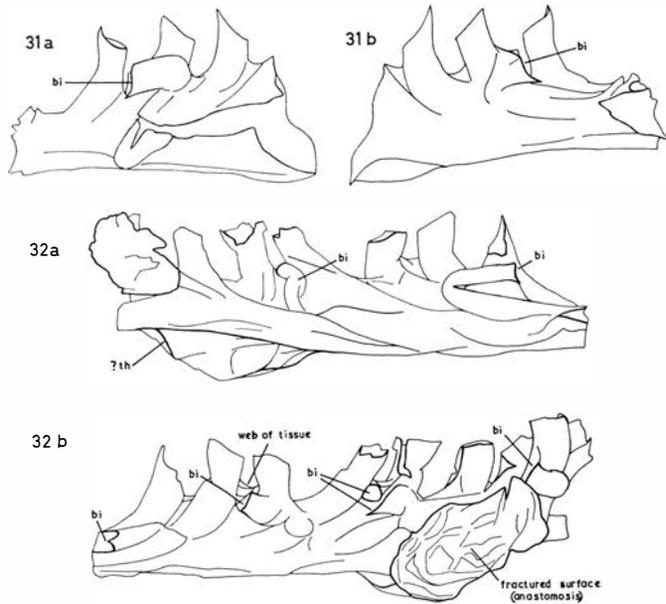
DESCRIPTION.—The funnel- or cone-shaped rhabdosome, with apical angle of approximately 60°, was attached by a branching root system and non-thecate stem. The two isolated fragments which together comprise the holotype each attains a length of 15.7 mm measured from the apex of the cone; a large portion of the rhabdosome retained in the limestone matrix has a maximum length of 17.0 mm, and a diameter of 11.5 mm at a distance of 10 mm from the apex of the cone.

The stipes are gently flexuous and anastomose at frequent intervals; the resulting lacunae are essentially ovoid in form, though the occasional development of angular curvature in the stipes can produce an acute rhombic outline. Proximally, the length/width ratio of the lacunae is 3.0–3.5:1; distally it ranges from 1.85–7.7:1.

Where anastomosis occurs, the stipes are united for a distance of 1.0–2.0 mm; in addition, adjacent stipes can be joined by dissepiments.

Lateral stipe width averages 0.5–0.6 mm; the dorso-ventral width, excluding the free, distal portions of the autothecae, may be as great as 1.0 mm, whilst the maximum width in this plane averages 1.5 mm.

The autothecae are tubular in form, with an apertural diameter of 0.25–0.30 mm; the distal portion, which is from 0.5–0.6 mm in extent, is inclined at a high angle to the dorsal margin, and is normal to it in the extreme case. A web of tissue may infill the angle between the free parts of two adjacent autothecae (Fig. 32*a*). Occlusion of an autothecal aperture with a layer of periderm has been observed.



Figs. 31–32: *Desmograptus separatus* sp. nov. (31) Stipe fragment; (31 *a, b*) two lateral aspects.  $\times 12$ ; Hälludden +5+8D; ÖI. 1097*b*. (32) Stipe fragment with evidence of anastomosis; (32 *a, b*) two lateral aspects.  $\times 11$ ; Hälludden +5+8D; ÖI. 1098*b*. *bi*: bitheca; *?th*: theca of uncertain type.

The number of autothecae per cm is variable throughout the rhabdosome; the average range for the several fragments which have been measured is 14–16 autothecae per cm.

The bithecae are irregularly developed with regard to both form and distribution, so that it is frequently impossible, in a fragment of stipe, to decide with which autotheca a bitheca should be associated. Commonly, a bitheca, in its distal part, is bent back upon itself, on the side of its origin, so that the aperture is directed proximally (Figs. 31 *a, b* and 32 *a, b*). On the other hand, a bitheca may undergo no proximal growth, but may parallel the course of the adjacent autotheca, on the lateral wall of the stipe, opening at the base of the free distal portion of the autotheca. Again, a bitheca may cross the ventral stipe margin to open on the side of the stipe opposite that on which it originates.

Capricious arrangement of bithecae may result in the presence of as many as three bithecal apertures at the same level along the stipe—though the correct number of bithecae, relative to the number of autothecae, occurs in a given length of stipe.

An isolated fragment of root is preserved as ÖI. 1096 (Fig. 33) and consists of a branching, filamentous system passing into a short length of thickened, non-thecate stem. A larger portion of the root is preserved in a fragment of limestone (ÖI. 1099); the stem is not visible, but the apex of the rhabdosome is

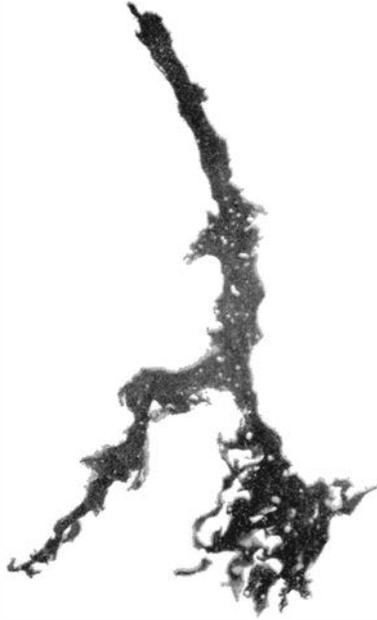


Fig. 33: *Desmograptus separatus* sp. nov. Part of root system.  $\times 7.5$ ; Hälludden +5+8D; Öl. 1096.

separated by a distance of 10 mm from the branching root structure. In this specimen, the root appears to be encased in a sheet of periderm, as though the branches are connected by webs of tissue; however, there is no trace of any such tissue in the isolated root fragment (Fig. 33).

The features distinctive of this species include the form of the autothecae, particularly the isolate distal portions; the variability of the bithecae in form and position on the stipes; and the dorso-ventral dimension of the stipes.

REMARKS.—All the specimens were derived from a single rhabdosome which collapsed in the process of isolation. Fortunately, the greater part of the original is preserved as two specimens, which together are designated as holotype. A part of the rhabdosome, including much of the root structure, is preserved in a fragment of limestone complementary to that from which the isolated material was obtained.

DERIVATIO NOMINIS.—The specific name has reference to the isolated distal portions of the autothecae.

*Desmograptus?* sp. *a*

Figs. 34 *a, b*.

FIGURED MATERIAL.—Spec. No. Öl. 1100.

LOCALITY AND HORIZON.—Hälludden: +23+26D.

DESCRIPTION.—The single fragment recovered is a portion of rhabdosome

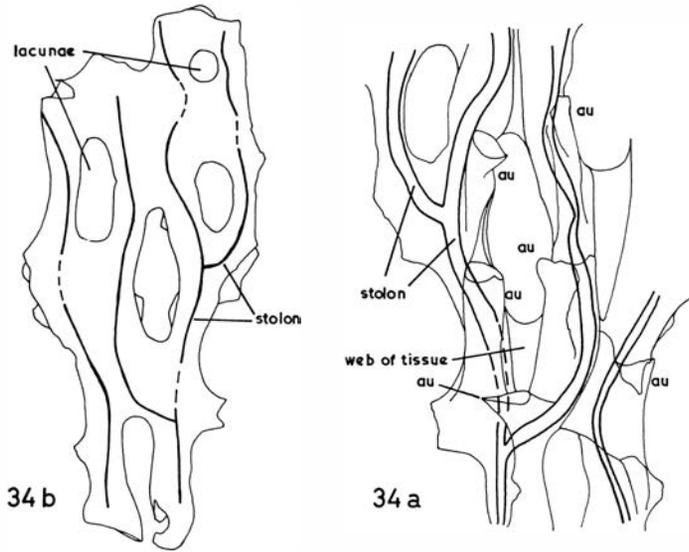


Fig. 34: *Desmograptus?* sp. *a*. Fragment of rhabdosome; (34 *a*) dorsal aspect showing 'stolon system',  $\times 14$ ; (34 *b*) ventral aspect of part of same showing stipe divisions,  $\times 17$ . Hälludden + 23 + 26D; Öf. 1100. *au*: autotheca.

6.0 mm in length and 2.25 mm in breadth; it comprises a bifurcating and anastomosing system of stipes.

Where anastomosis occurs, adjacent stipes are in contact for distances of the order of 1.0–2.0 mm. The lacunae are predominantly oval in outline; the largest has a length of 1.25 mm and a maximum width of 0.45 mm—which is only slightly greater than the lateral width of the stipes (0.4 mm).

Bifurcation is most readily evidenced by the course of what appears to be a carbonised stolon system (Figs. 34 *a, b*), comprised of branching, parallel, or near-parallel, sided tubes; nodes of trifurcation, however, are entirely wanting. Anastomosis tends to mask division of the stipes, but the course of this 'stolon system' shows the presence of two stipes at the proximal end of the specimen and four at the distal end, indicating two orders of dichotomy and showing, furthermore, that this division is restricted to one of the original stipes (Fig. 34 *a*).

There is no positive evidence of bithecae in the specimen, though it is possible that they may lie below the autothecae, each opening into the cavity of these latter through the dorso-lateral autothecal wall.

Only two autothecae are developed in a distance of 2 mm in the specimen, suggesting 10 per cm. The proximal portion of each autotheca lies in the plane of the stipes, but the distal end is appreciably inclined and may be isolate. A pointed, ventral, apertural denticle is developed, lying in the plane of the aperture.

DISCUSSION.—The specimen has the rhabdosomal features characteristic of the genus *Desmograptus*, but on two accounts its dendroid affinities must be

questioned: the lack of evidence of trifurcation of the 'stolon system', and the possible absence of bithecae. Consequently, its attribution to *Desmograptus* is only provisional.

REMARKS.—A specific name has not been proposed in view of the uncertainties concerning affinity, the poor state of preservation, and the recovery of only a single, fragmentary specimen.

**Genus *Dictyonema* HALL, 1851**

***Dictyonema cotyledon* BULMAN, 1934**

Figs. 35-40.

1934 *Dictyonema cotyledon* BULMAN, p. 11, Figs. 2-5; Pl. 4, figs. 1-10.

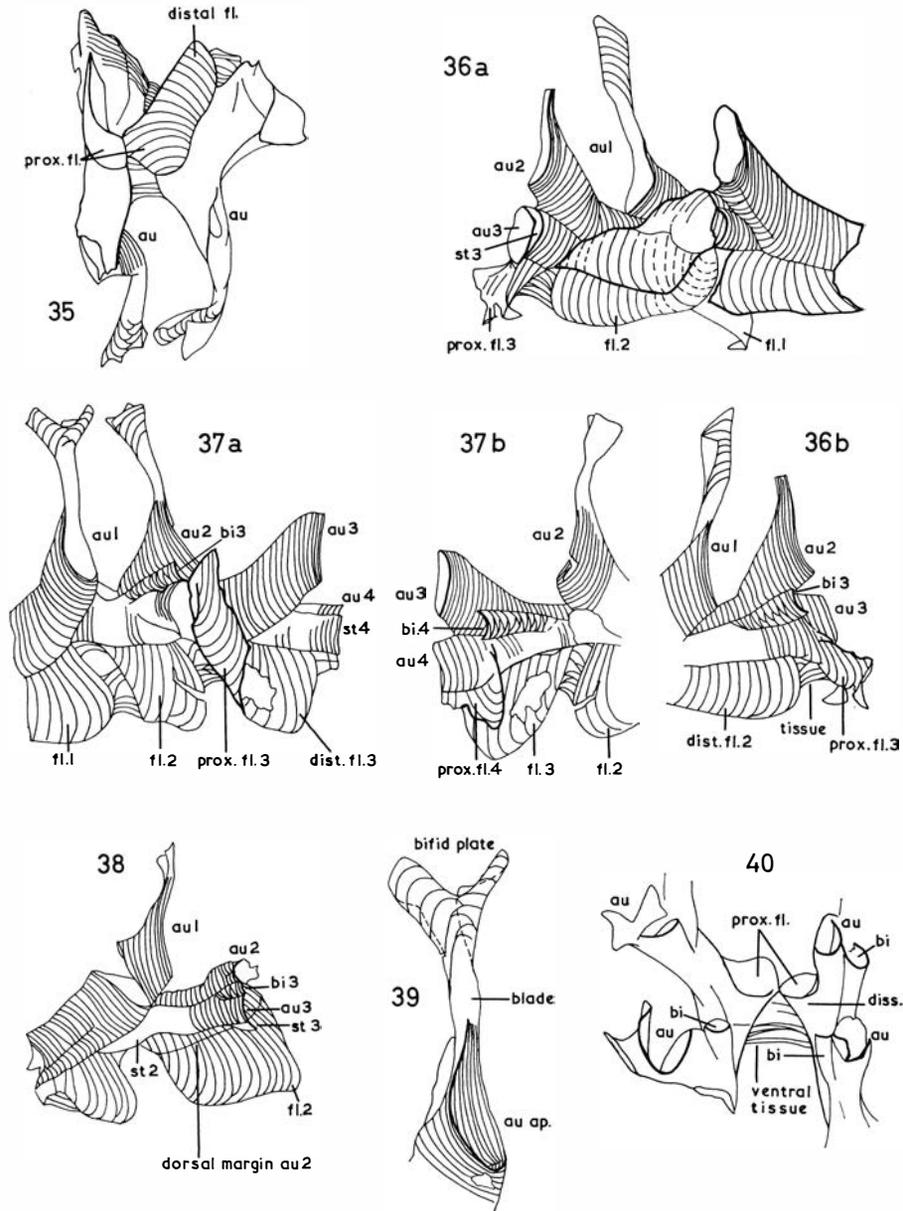
FIGURED MATERIAL.—Spec. Nos. Öl. 1101 *b*, Öl. 1102 *a, b*, Öl. 1103 *b*, Öl. 1104.

LOCALITY AND HORIZON.—Hälludden: +18+22D, +23+26D; Hagudden: 0+15D, +20+25D.

DIAGNOSIS (amended).—Entire rhabdosome unknown, possibly small, rooted; mesh fairly regularly constructed, consisting of stipes with zig-zag flexure united by dissepiments at two autotheca (1 mm) intervals, giving a honeycomb appearance which is further enhanced by the development of a dorsal flange system comprising short, web-like components of fusellar tissue, each of which is associated with an autotheca and approximately corresponds in position and length with the free part of that theca. Stipes slender; lateral width 0.01-0.25 mm; dorso-ventral width, including autothecal apertural process and flange, 1.25 mm; excluding these, 0.4 mm. Autothecae slightly isolate, with long apertural spine terminating in bifid plate; 20 autothecae developed per cm. Bithecae typically occupy dorso-lateral position on stipe, opening on side of origin with aperture facing distally.

DESCRIPTION.—Öl. 1104 gives evidence of the form and structure of the rhabdosome, but provides no indication of its overall shape. The stipes are slender and rigidly flexed in zig-zag fashion. Lateral stipe width does not exceed 0.25 mm, whilst the interspaces, at their widest, are two to three times this measurement. Dissepiments are produced at intervals of two autothecae (i.e. every 0.75-1.0 mm), giving a mesh-like rhabdosome having a fair degree of regularity. A distinctive feature of the stipes is the presence of a flange system on the dorsal margin, comprised of web-like components each of which is associated with an autotheca and approximately corresponds in position and length with the free part of that theca. Widely spaced growth lines are evident in many instances; each component is composed of only a single layer of fusellar material.

The form and origin of the flange sections deserves a detailed consideration. Each section is L-shaped (Fig. 35), with rounded angle; distally, it is aligned roughly parallel to the length of the stipe, but proximally, an abrupt, though rounded, curvature causes the structure to be directed transversely across the



Figs. 35–40: *Dictyonema cotyledon* BULMAN. (35) Fragment of rhabdosome in dorsal aspect to show structure of flange.  $\times 35$ ; Hälludden + 23 + 26D; ÖL. 1101 b. (36) Growing end of stipe; (36 a) complete specimen showing early stage in flange development,  $\times 35$ ; (36 b) reverse of latter, growing tip only,  $\times 35$ . Hälludden + 23 + 26D; ÖL. 1102 a. (37) Growing end of stipe; (37 a) complete specimen,  $\times 35$ ; (37 b) reverse of latter, growing tip only,  $\times 35$ . Hälludden + 23 + 26D; ÖL. 1102 b. (38) Fragment of rhabdosome without connecting tissue between adjacent flange sections.  $\times 35$ ; Hälludden + 23 + 26D; ÖL. 1103 b. (39) Autothecal apertural process.  $\times 65$ ; Hälludden + 23 + 26D; ÖL. 1102 b. (40) Fragment of rhabdosome to show composite nature of dissepiments.  $\times 35$ ; Hälludden + 23 + 26D; ÖL. 1104. au: autotheca; bi: bitheca; dist: distal part of; fl: flange; prox.: proximal part of; st: stolothea.

stipe and to project outwards from it on one side. The proximal ends of alternate components are curved outwards on the same side of the stipe and are continued onto the dorsal surfaces of the dissepiments (which are situated at two autotheca intervals and where the zig-zag flexures of adjacent stipes are at their closest proximity). The combined effect of the presence of dissepiments, the zig-zag nature of the stipe flexure, and the existence of the dorsal flange system, is to produce, on the dorsal surface of the rhabdosome, a honeycomb-like structure, composed of hexagonal cells.

Each component of the flange system is associated with an autotheca. The component originates at approximately the level along the stipe of the aperture of the autotheca (say  $a_2$ —Figs. 36 *a, b*, 37 *a, b*) of the preceding generation, but apart from this coincidence, there is no relationship between the two. A section through the stipe at this level would reveal the apertures of  $a_2$  and the associated bitheca ( $b_3$ ), the proximal part of  $a_3$ , the stolotheca  $s_3$  and the initial part of the flange component associated with  $a_3$ . The component originates on the dorso-lateral wall of  $a_3$ , on the side of the stipe which contains  $b_3$ . Growth of the flange section from the point of origin is in three primary directions: outwards from the stipe on the side of origin; downwards, or dorsally; and across the stipe, beneath the dorsal edge of  $a_3$ . This mode of growth is achieved by the formation of semi-circular growth bands arranged in concentric fashion about the origin (Figs. 35, 36 *b*).

The direction of growth of  $a_3$ , following the appearance of the flange section, undergoes a marked change, producing a sharp flexure in the stipe. The change in growth is always away from the side of the stipe on which the flange originates—and as the flange appears alternately to right and left, a zig-zag flexuring is produced in the stipe. The course followed by the initial part of the flange component lies obliquely to the new direction of growth of  $a_3$ ; on reaching the side of the stipe opposite to its origin, the component is curved to assume parallelism with the length of  $a_3$  (Fig. 37 *a, b*). At first, it appears to be produced by a dorsal continuation of the wall separating  $a_3$  and  $s_3$  and, later, the wall dividing  $a_3$  and  $b_4$ ; thus, the distal part of the flange component would appear to be a direct dorsal continuation of that lateral wall of  $a_3$  which is on the side of the stipe opposite to the origin of the flange (in Fig. 38, flange 2 is clearly a dorsal continuation of the wall of  $a_2$ ). At approximately the stage when the change in direction of growth of the flange section occurs, this structure has usually achieved its maximum outward extension from the stipe on the side of its origin; consequently, the degree of curvature of the growth bands progressively decreases until, in the main (or distal) part, they are appreciably curved only where they pass into the free (or dorsal) edge of the structure.

The flange components are quite discrete structures and there is no evidence that they are “supported on short spines which are developed from the back of the stipe at the level of every [auto-] theca” (BULMAN, 1934, p. 13). Adjacent sections (on the same stipe) may be joined, however, by a web of tissue infilling

the gap between the distal extremity of one and that part of the wall of the next following where the change in the direction of growth occurs (Figs. 36 *a, b*, 37 *a, b*); this tissue is not invariably developed, however (Fig. 38). The function of the flange is not known.

The dorso-ventral stipe width, including the flange and the autothecal apertural process, averages 1.25 mm, though it may be as great as 1.5 mm; without the process, it is 0.85 mm, of which the flange accounts for approximately one half.

The autothecae are tubular and may be distally isolate; an average number of 20 is present in 10 mm. The prominent apertural process assumes the form of a spine-like structure, directed normal to the stipe length, terminating in a curled, bifid plate (Fig. 39). The total length of the process averages 0.4 mm. In detail, the ventral margin of the autothecal aperture is extended as a narrow blade whose edges are first curled round in a distal direction, retaining the form of the ventral part of the apertural margin. Before the terminal plate is reached, however, the direction of curling is reversed, so that the edges of the blade and the plate face proximally. Growth lines, where discernible, indicate that the plate is produced by a widening of the blade, and its bifid form by a restriction of growth along the line of the zig-zag suture.

The bithecae occupy a dorso-lateral position on the stipe, relative to the autothecae, and open on the side of their origin with the aperture facing distally.

Opposed conical outgrowths, from the autothecae of adjacent stipes, join at their apices to produce dissepiments. In its basic form, the dissepiment is, at its mid-point, extremely fine and thread-like, but it increases in diameter towards the stipes which it unites. As explained above, the proximal parts of adjacent flange components extend out from the stipes towards each other, along the dorsal walls of the dissepiments. In addition, a web-like tissue infills the gap between the lateral walls of the adjacent stipes and the ventral wall of the dissepiment. Each dissepiment is, therefore, a composite structure, built up of a connecting rod, the dorsally-situated proximal parts of two flange sections, and a ventral tissue (Fig. 40); the overall effect is to produce a vertically-set partition, normal to the elongation of the stipes. It has not been possible to determine the extent to which these several structures are dependent upon one another with regard to relative order of formation, though it seems likely that the growth of the dissepiment proper and the flanges must be closely associated, whilst the ventral tissue is in the nature of a subsequent infilling.

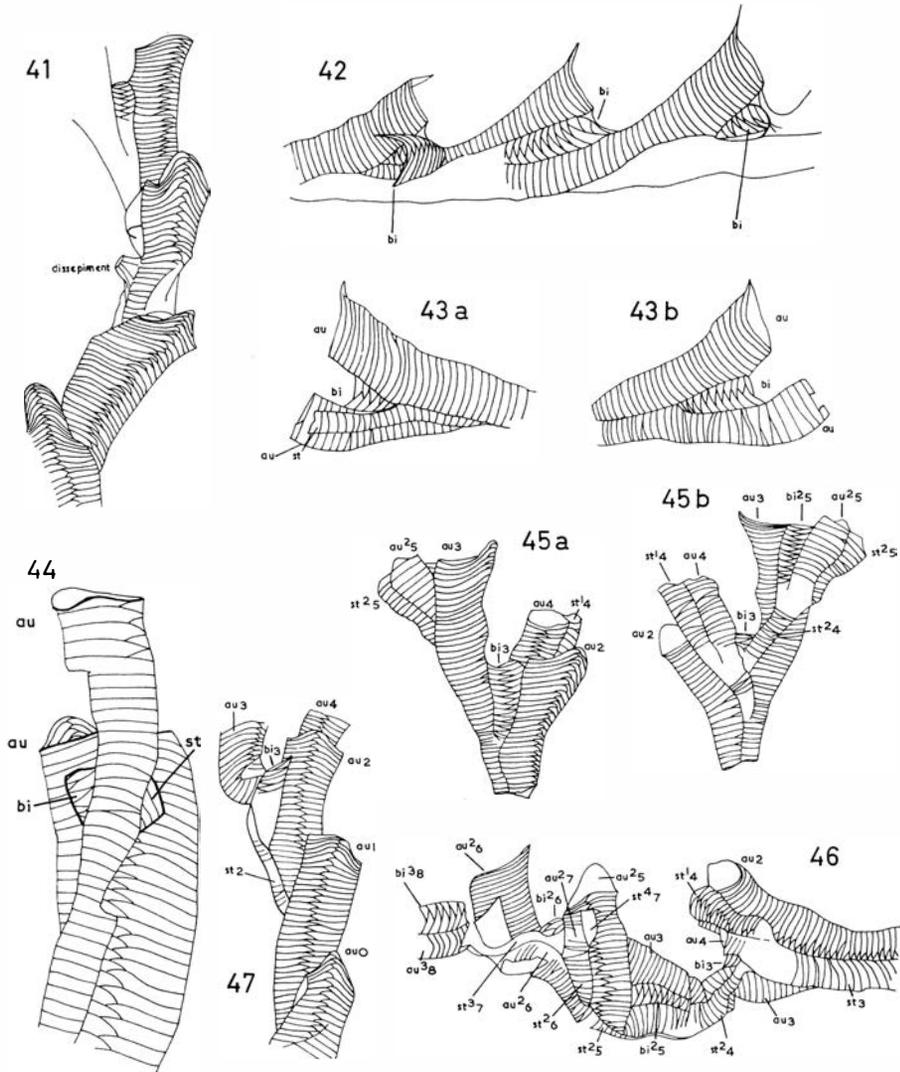
*Dictyonema* cf. *D. holmi* BULMAN, 1934

Figs. 41-47.

cf. 1934 *Dictyonema holmi* p. 25, Fig. 12; Pl. 8, figs. 1-14.

FIGURED MATERIAL.—Spec. Nos. Öl. 1105 *a*, Öl. 1106, Öl. 1107 *b, c*, Öl. 1108 *b*, Öl. 1109 *b*, Öl. 1110 *b*.

LOCALITY AND HORIZON.—Hälludden: +23 +26D.



Figs. 41–47: *Dictyonema* cf. *D. holmi* BULMAN. (41) Fragment of rhabdosome with dissepiment base, ventral aspect.  $\times 36$ ; Hälludden +23 +26D; ÖL. 1105 a. (42) Fragment of stipe with recurved bithecae, lateral aspect.  $\times 36$ ; Hälludden +23 +26D; ÖL. 1106. (43) Growing end of stipe; (43 a, b) two lateral aspects.  $\times 36$ ; Hälludden +23 +26D; ÖL. 1107 c. (44) Growing end of stipe, dorsal aspect.  $\times 86$ ; Hälludden +23 +26D; ÖL. 1108 b. (45) Stipe division; (45 a) ventral aspect; (45 b) dorsal aspect.  $\times 36$ ; Hälludden +23 +26D; ÖL. 1107 b. (46) Two orders of stipe division separated by two normal triads.  $\times 35$ ; Hälludden +23 +26D; ÖL. 1109 b. (47) Stipe division in ventral aspect, note lateral curvature of autothecae.  $\times 36$ ; Hälludden +23 +26D; ÖL. 1110 b. au: autotheca; bi: bitheca; st: stolotheca.

DESCRIPTION.—The form of the complete rhabdosome is not known. It is composed of stipes which are generally straight, though occasional slight curvature is possible; stronger flexuring, as in ÖL. 1109 b (Fig. 46), is most

probably the result of distortion. Dissepiments are only developed infrequently (Fig. 41).

Dorso-ventral stipe width at autothecal apertures, but discounting the slight apertural processes, is from 0.41–0.47 mm; below the apertures, an average width of 0.18 mm, with a range of from 0.15–0.21 mm, is recorded.

The autothecae are tubular, with straight, free ventral wall inclined at 30°–35° to the dorsal stipe margin; distal isolation is possible, though usually it is masked by the position of the bithecae (Fig. 42). In ventral aspect, the autothecae are seen to exhibit distinct lateral curvature throughout their length (Fig. 47). The apertural margin is rounded, with average diameter 0.21 mm; the ventral edge is provided with a sharply-terminated denticle. A range of from 14–24 autothecae per cm was obtained from the several fragments measured, but it must be noted that these fragments seldom show more than two or three autothecal apertures. The most commonly occurring figure was 17 autothecae per cm.

The bithecae are prominently displayed externally (Figs. 42, 43 *a, b*). Each lies initially in a dorso-lateral position relative to the associated autotheca, but the apertural part passes beneath the dorsal autothecal wall to open on the opposite side of the stipe, with the aperture typically directed normal to the stipe length. Occasionally, continued growth has permitted the aperture to face proximally, so that the bitheca concerned is doubled back upon itself (Fig. 42).

Abnormality in bithecal development is confined to variation in the extent to which the apertural portion of each bitheca crosses the stipe.

Several branched fragments have been recovered, frequently showing division at intervals of only one or two autothecae (Fig. 46). The mode of branching—judged from external evidence—involves the production of two stolothecae and one autotheca in place of a normal triad (Figs. 45 *b*, 46). The stipes generally remain straight for a short distance beyond the point of separation.

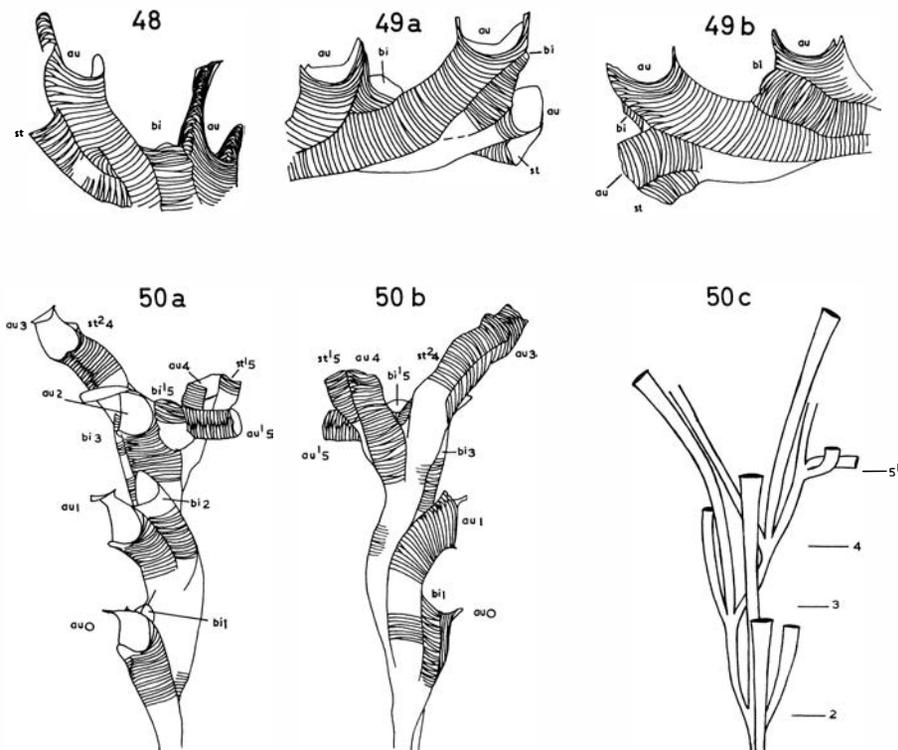
The characteristic features of the material are thus: the slender form of the stipes, with tubular denticled autothecae numbering approximately 17 per cm; bithecae which pass beneath the autothecae to open on the side opposite their origin; and the occasional presence of dissepiments.

DISCUSSION.—The material described above can be compared with *Dictyonema holmi* BULMAN, from the HOLM collection.

Agreement is noted in respect of the form and dimensions of the autothecae; the number of autothecae per cm (16); the type of bitheca developed (including occasional slight abnormalities); and the irregular spacing of the dissepiments.

There is, however, a marked disparity in stratigraphic occurrence. The Öland material has been recovered from the base of the *bifidus* zone (+23 to +26D at Hälludden) whilst *D. holmi* occurs at levels (stages D and F1 in the Estonian succession) which can be correlated with the *wilsoni* to *anceps* (?) zones of the British sequence.

It is unlikely, but not impossible, that a single dendroid species ranged



Figs. 48–50: *Dictyonema rhinanthiforme* BULMAN. (48) Growing end of stipe.  $\times 35$ ; Hälludden, horizon not known; ÖL. 1113. (49) Stipe fragment; (49a, b) two lateral aspects.  $\times 36$ ; Hälludden, horizon not given; ÖL. 1114a. (50) Stipe division; (50a) ventral aspect; (50b) dorsal aspect.  $\times 25$ ; Hälludden, horizon not known; ÖL. 1115b; (50c) diagrammatic interpretation of Fig. 50a. *au*: autotheca; *bi*: bitheca; *st*: stolotheca; 2, 3, etc.: successive triads (Fig. 50c).

throughout the greater part of the Ordovician. Larger fragments of rhabdosome, or even a whole rhabdosome, may be necessary to bring out points of difference, but in the absence of more complete specimens the material under consideration is compared with *D. holmi* to emphasize their similarity.

*Dictyonema rhinanthiforme* BULMAN, 1934

Figs. 48–50.

1934 *Dictyonema rhinanthiforme* BULMAN, p. 16; Fig. 6; Pl. 4, figs. 11–13.

FIGURED MATERIAL.—Spec. Nos. ÖL. 1113, ÖL. 1114a, ÖL. 1115b.

LOCALITY AND HORIZON.—Hälludden: horizon not known.

DESCRIPTION.—The material recovered agrees essentially with the author's description of the species, but provides additional information relating to the mode of stipe division (Figs. 50a–c) and the growing end of a stipe (Fig. 48), together with details of growth lines (Figs. 48–50).

Stipe division involves the production of two stolothecae and one autotheca in place of a normal triad. In *Öl. 1115 b* (Figs. 50 *a-c*), slight irregularity is noted due to the appearance, on the right-hand stipe (in ventral aspect), of a normal triad—5¹, Fig. 50 *c*—almost on top of the triad supporting the division. In the normal triad, autotheca *a*¹₅ is directed laterally relative to the elongation of the stipe, whilst bitheca *b*¹₅ grows over the ventral wall of *a*¹₅ to open close to the origin of this autotheca.

The left-hand stipe in *Öl. 1115 b* clearly illustrates two features of dendroid growth: firstly, that the stolotheca is the proximal part of the autotheca of the next generation and, secondly, that, in a single generation, the bitheca and stolotheca originate as buds back along the autotheca, defining the point at which, for ease of description, the stolotheca is considered to give rise to the autotheca of the next generation. Thus, in Figs. 50 *a-c*, bitheca *b*²₅, which will open at the aperture of *a*₃, and stolotheca *s*²₅, have not yet appeared, although stolotheca *s*²₄ has extended as far as the aperture of *a*₃, and the more proximal portion of the specimen shows that the bitheca is produced some distance before the aperture of the adjacent autotheca is reached.

REMARKS.—The horizon from which the limestone fragment containing this species was collected, is not known, though the included fauna suggests derivation from either the +18+22D level or the +23+26D level at Hälludden.

*Dictyonema variabile* sp. nov.

Figs. 51-59.

HOLOTYPE.—Spec. No. *Öl. 1116*; Fig. 51.

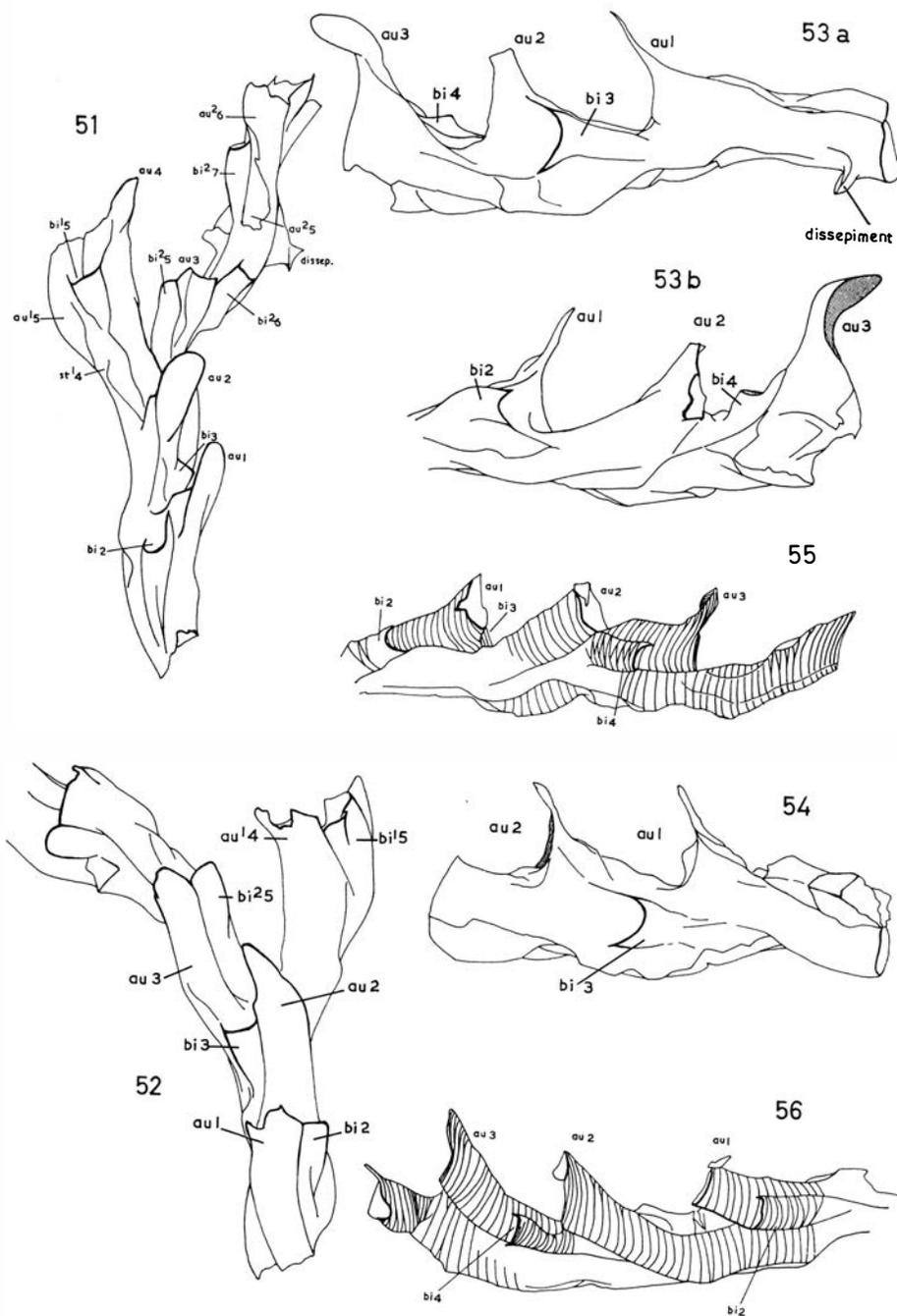
FIGURED MATERIAL.—Spec. Nos. *Öl. 1116-Öl. 1121, Öl. 1122 a, Öl. 1123, Öl. 1124.*

LOCALITY AND HORIZON.—Hälludden: -135-140D.

DIAGNOSIS.—Entire rhabdosome unknown. Stipes frequently branching, with low angle of divergence; occasional dissepiments present. Stipes typically sinuous in thecal aspect; dorsal margin undulating; maximum dorso-ventral width 1.1-1.2 mm. Autothecae tubular, with prominent, ventral, apertural processes; 9-11 developed per cm. Bithecae variable in form, but typically short and laterally positioned on stipe; aperture faces distally, on side of bithecal origin.

DESCRIPTION.—The shape of the rhabdosome is unknown, though its structure is reasonably clear. The several specimens exhibiting stipe division suggest that branching may have taken place at frequent intervals, whilst occasional flange- or rod-like outgrowths, from the dorsal or dorso-lateral parts of the stipes, are presumably dissepiments (Figs. 51, 53 *a*). In thecal aspect (Figs. 51, 52), the stipes are typically sinuous, resulting from lateral curvature of the autothecae, and, in addition, the stipes may be flexed dorsally, ventrally or laterally.

Lateral stipe width is variable, reaching a maximum (0.55-0.7 mm) at or



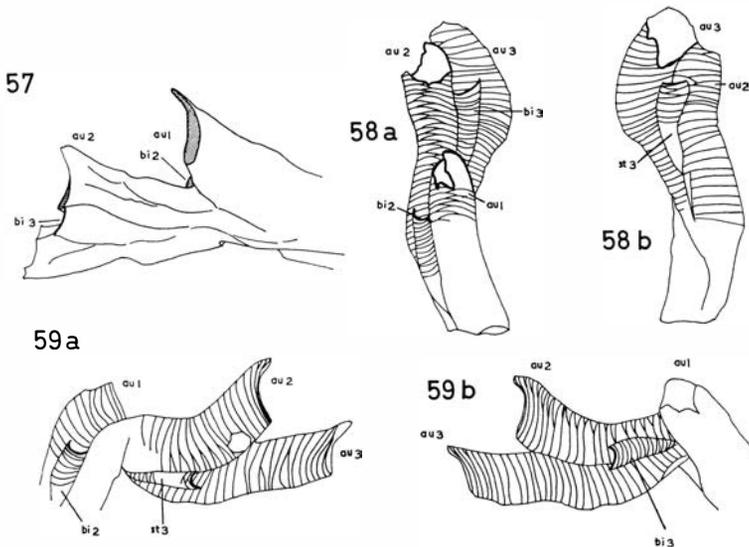
Figs. 51–56: *Dictyonema variabile* sp. nov. (51) Holotype, ventral aspect.  $\times 20$ ; Hälludden – 135–140D; ÖL. 1116. (52) Stipe division, ventral aspect.  $\times 13$ ; Hälludden – 135–140D; ÖL. 1117. (53) Stipe fragment; (53a, b) two lateral aspects, note variation in form of bithecae.  $\times 18$ ; Hälludden – 135–140D; ÖL. 1118. (54) Stipe fragment in lateral aspect;  $\times 18$ ; Hälludden – 135–140D; ÖL. 1119. (55) Growing end of stipe.  $\times 20$ ; Hälludden – 135–140D; ÖL. 1120. (56) Growing end of stipe.  $\times 20$ ; Hälludden – 135–140D; ÖL. 1121. au: autotheca; bi: bitheca; dissep.: dissepiment; st: stolotheca.

about the level of autothecal apertures, and a minimum (0.4–0.5 mm) just distally to these. The presence of long, apertural processes on the autothecae results in a maximum dorso-ventral stipe width of 1.1–1.2 mm; discounting the processes, a width of from 0.8–0.95 mm is recorded at the level of the autothecal apertures, whilst below the apertures a width of 0.3–0.45 mm is to be expected. The variation possible in the dorso-ventral width at a given level is due not so much to position in the rhabdosome, but rather to the undulating nature of the dorsal stipe margin (Figs. 54, 55).

A well-developed apertural process is characteristic of the autotheca, taking the form of a broad, roundly-terminated blade of variable length: the maximum recorded length is 0.46 mm, but 0.40 mm is a more common measurement, whilst much shorter processes, of 0.25–0.30 mm, are of frequent occurrence. The apertural process continues the concave curvature of the free ventral wall which, in *Öl. 1121* (Fig. 56), for example, is sufficient to isolate the distal end of the autotheca.

The larger rhabdosomal fragments recovered, with three to four autothecae preserved, suggest the presence of about 10 autothecae per cm, with a range of from 9–11.

Slight restriction of the apertural margin is possible, as in *Öl. 1122 a* (Fig. 57). Secondary chitin has been laid down along one lateral edge—the left in thecal aspect—of the apertural margin of autotheca *au1* in *Öl. 1119* (Fig. 54); this additional tissue has not followed the contour of the margin, but has taken the



Figs. 57–59: *Dictyonema variabile* sp. nov. (57) Stipe fragment with distally isolate autothecae.  $\times 20$ ; Hälludden – 135–140D; *Öl. 1122 a*. (58) Stipe fragment; (58 a) ventral aspect; (58 b) dorsal aspect.  $\times 18$ ; Hälludden – 135–140D; *Öl. 1123*. (59) Stipe fragment; (59 a, b) two lateral aspects.  $\times 21$ ; Hälludden – 135–140D; *Öl. 1124*. *au*: autotheca; *bi*: bitheca; *st*: stolotheca.

form of a distinct lappet, directed distally. Rarely, the complete occlusion of an autothecal aperture has been observed.

Typically, as in ÖL. 1123 (Fig. 58 *a*), the bithecae lie high on the lateral part of the stipe and open on the side of their origin, some distance behind the aperture of the adjacent autotheca. In ventral aspect, they are seen to lie at a slight angle to the elongation of the stipes.

Many variations of this general type are possible, based on the position of the bithecal aperture relative to that of the adjacent autotheca. Thus, in ÖL. 1119 (Fig. 54), the aperture of bitheca *bi*₃ is placed almost as far back along the stipe as the aperture of the preceding autotheca (*aur*), whilst in ÖL. 1117 (Fig. 52), each bitheca opens at the level along the stipe of the associated autotheca. In ÖL. 1118 (Figs. 53 *a, b*), in which three bithecae are preserved (*bi*₂–*bi*₄), *bi*₂ originates high on the lateral part of the stipe, but aperturally it is directed obliquely down towards the dorsal margin; *bi*₃ is of the 'normal' type, opening well behind the aperture of the associated autotheca; *bi*₄ is directed ventrally and is provided with a prominent lip or denticle on the distal rim.

This species is distinguished by the prominent apertural denticles on the autothecae, the presence of relatively few autothecae per cm, and the variation possible in the form of the bithecae.

DERIVATIO NOMINIS.—The specific name proposed has reference to the variation which exists in the form of the bithecae.

### Family *Acanthograptidae* BULMAN, 1938

DIAGNOSIS.—Rhabdosome shrub-like or cyathiform, with rigid, bifurcating or more or less flexuous, anastomosing branches composed of numerous elongate thecae (BULMAN, 1938).

RANGE.—?Upper Cambrian, Lower Ordovician to Middle Devonian.

DISCUSSION.—The characteristic features of this family may be summarized as follows:

(a) Thecae tubular and elongate, so that thecae of several generations are present at any level along the stipe; in *Acanthograptus*, a regular variation in length of theca occurs.

(b) The theca may open on all sides of the stipes; in *Acanthograptus*, the association of thecae in groups (twigs), each composed of two autothecae and two bithecae, is characteristic. The twigs may be placed on any side of the stipes.

(c) As a consequence of (a) and (b), stipe structure is complex.

BOUČEK (1957) has pointed out two possible explanations for the long duration of the acanthograptid structure: the persistence of a conservative, but highly specialised, line of development, or periodic differentiation and development from those stocks in which the thecae had retained the normal dendroid length and arrangement in the stipes.

The former suggestion seems to account better for the structure of *Acanthograptus*, in which there is, as exemplified by the species *A. czarnockii* KOZŁOWSKI, *A. succicus* (WIMAN), *A. musciformis* (WIMAN) and *A. divergens* sp. nov. (see below, p. 43), thecal elongation accompanied by regular variation in thecal length and the grouping of thecae into twigs. This association of characteristics would seem to be a feature so specialized as to involve a single phyletic line.

*Coremagraptus*, on the other hand, whilst having elongate thecae and some tendency to grouping, does not appear to show the same regular variation in thecal length noted in *Acanthograptus*. Such a structure could more easily have arisen repeatedly from those species of *Callograptus*, *Desmograptus*, *Dictyonema* and *Reticulograptus* in which the thecae show some elongation beyond the normal dendroid length, but without loss of the typical arrangement (see above, pp. 19–27; BOUČEK 1957; BULMAN 1927–34, 1934).

From the above, it would seem that there are sufficient grounds for placing *Acanthograptus* and *Coremagraptus* in separate families. Furthermore, the writer is in agreement with BOUČEK (1957) in considering that certain species at present attributed to the genus *Acanthograptus*, but in which the stipe structure appears to be simpler or less regular, may prove to belong to a distinct genus.

### Genus *Acanthograptus* SPENCER, 1878

#### *Acanthograptus divergens* sp. nov.

Figs. 60, 61.

HOLOTYPE.—Spec. No. Öl. 1129; Fig. 60.

FIGURED MATERIAL.—Spec. Nos. Öl. 1129, Öl. 1132.

LOCALITY AND HORIZON.—Hälludden: +10 + 30D, +18 + 22D, +23 + 26D, +38 + 43D; Hagudden: 0 + 15D, +10 + 15D, +20 + 45D, +25 + 30D.

DIAGNOSIS.—Rhabdosome ?dendrograptid, with rigid, infrequently-branching stipes, diverging at low to moderate angles (20°–45°). Autothecae tubular, increasing slightly in diameter to aperture, which may or may not carry a ventral denticle; isolate distally to varying extent; ?alternately long and short in length. Bithecae never isolate, opening on all sides of stipe. ?Structure comparable with that of *A. succicus*, but no apparent twig formation.

DESCRIPTION.—The rhabdosome appears to have been constructed on the dendrograptid pattern, with generally stiff and straight stipes bifurcating at infrequent intervals (Fig. 60); no specimen includes more than one order of dichotomy, and the longest fragment of unbranched stipe measures 11 mm. The angle of divergence of the branches resulting from division is generally of the order of 30° to 45°, but may be as low as 20°.

The autothecae are tubular, expanding slightly towards the aperture. This latter is circular to oval in outline; in the former case, the average diameter

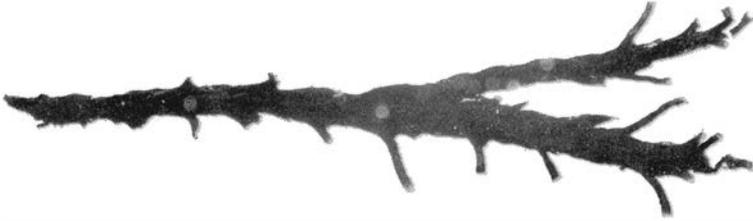


Fig. 60: *Acanthograptus divergens* sp. nov. Holotype: fragment of rhabdosome.  $\times 10.3$ ; Hälludden +23+26D; Öl. 1129.

is 0.12 mm, whilst in the latter, the minor diameter (either dorso-ventral or lateral) ranges from 0.08–0.12 mm, and the major from 0.10 mm to 0.15 mm. The apertural margin may be diversified by a slight denticle on the ventral edge, but this is not invariably developed and, when present, is scarcely discernible.

The distal portion of each autotheca is typically isolate, though the extent to which this is developed is extremely variable, ranging from as little as 0.4 mm to a maximum of almost 1.0 mm. The autothecae themselves are possibly of two lengths, with the shorter thecae approximately half the length of the longer (this is discussed further in the section dealing with the structure of the stipes).

The length of the bithecae is uncertain, but it is possible that they may also be of two lengths, though much more nearly equal than in the case of the autothecae. They are typically confined to the stipe, but may extend along the free distal portions of the autothecae, though they are never themselves isolate. The shape of the aperture is variable from circular to semi-circular; in the former case, the diameter ranges from 0.04 mm to 0.06 mm.

THE STRUCTURE OF THE STIPES.—A fragment of stipe was serially-sectioned, but proved to be of insufficient length to give any indication of the structure, the interpretation of which has been based almost entirely upon the association and distribution of the autothecae in a single growing end specimen—Öl. 1132 (Figs. 61 *a, b*)—viewed in the light of the known structure of *A. suecicus* (WIMAN), as elucidated by BULMAN (1937).

Distinct twigs, each comprised of two autothecae and two bithecae, arising from the stipes as in *A. suecicus*, are not clearly evident in this specimen, nor, indeed, in any of the recovered material—rather, the autothecae open independently. In spite of this fact, however, it is suggested that a grouping of the thecae such as is present in *A. suecicus* does exist, but a true twig arrangement is not achieved because the two autothecae in each group diverge so markedly from the point at which each becomes free of contact with the rest of the stipe, that their apertures are placed on opposite sides of the stipe.

The diagrammatic interpretation of Öl. 1132 (Fig. 61 *b*) agrees with the structure of *A. suecicus* to the extent that the autothecae are alternately long and short; the difference lies in the separation of the two autothecae in each group

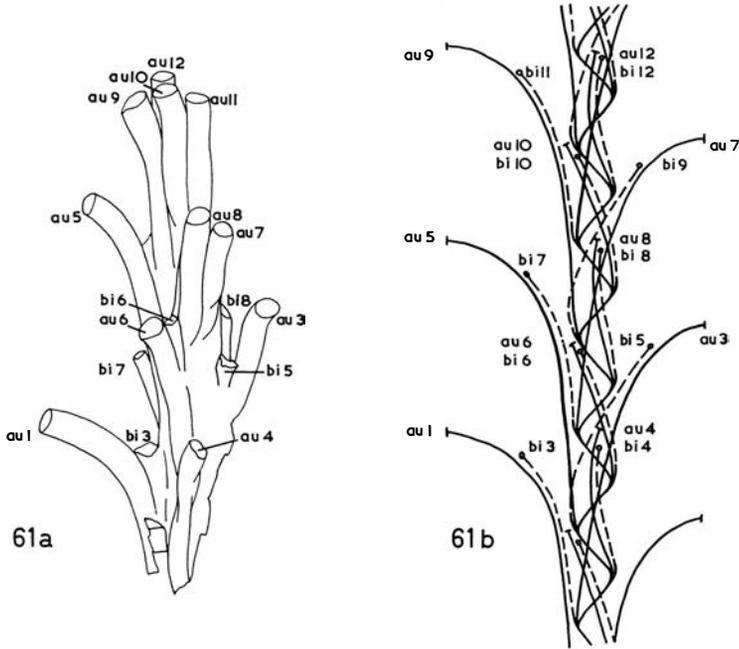


Fig. 61: *Acanthograptus divergens* sp. nov. Growing end of stipe; (61a) thecal aspect.  $\times 24$ ; Hagudden + 20 + 45D; Ö. 1132; (61b) suggested interpretation of the latter. au: autotheca; bi: bitheca.

in the former compared with their close association in the latter. Thus, in Ö. 1132, the twigs, if they existed, would be composed, in part, of *au*1 and *au*4, *au*3 and *au*6, *au*5 and *au*8, *au*7 and *au*10, and *au*9 and *au*12. According to this interpretation, the laterally placed autothecae (*au*1, *au*3, *au*5, etc.) are approximately twice the length of those situated ventrally or ventro-laterally (*au*4, *au*6, etc.), and consecutive generations give alternately long and short autothecae.

The length of the bithecae is not clear, but it is assumed—as in *A. suecicus*—that they are also of two lengths, though these are much more nearly equal than in the case of the autothecae; a generation giving a long autotheca is considered also to give a long bitheca, and *vice versa*. If this is the case, then *bi*3 will be associated with *au*1 and *bi*4 with *au*4; similarly, *bi*5 will open adjacent to *au*3, and *bi*6 to *au*6. Thus, the ‘twigs’ now comprise *au*1, *au*4, *bi*3 and *bi*4, *au*3, *au*6, *bi*5 and *bi*6, etc., as in *A. suecicus*; the two autothecae in each ‘twig’ are separated by two generations, and the two bithecae belong to consecutive generations with the younger of the two the same age as the younger autotheca.

The interpretation outlined above is based on several assumptions—most notably concerning the lengths of the autothecae and bithecae—and it finds its only support in the distribution of the free distal portions of the autothecae,

which, in any case, it was designed to fit! Better preservation, with the possibility of obtaining an appreciable length of sectionable rhabdosome, alone will verify the truth of these suggestions.

Whether or not other arrangements of thecae occur within the acanthograptid material recovered is not known, but if the position of autothecal apertures along the stipe is a reflection of the structure, then the degree of probability is high. Possibly, two or more species have been confused or, alternatively, an identical structure might be masked by slight variation in thecal length.

DISCUSSION.—To date, only three species of *Acanthograptus* have been described from isolated material: *A. suecicus* (WIMAN), *A. musciformis* (WIMAN), and *A. czarnockii* KOZŁOWSKI; comparison is possible only with these.

In *A. musciformis*, the autothecae are divergent, as in the Öland species, but more individuals appear to be present at a given level along the stipe, whilst externally a greater degree of regularity is evident in their arrangement.

*A. czarnockii* is the earliest of the three species of *Acanthograptus* which have been described in the isolated state. The autothecae in this species possess distinct ventral denticles, whilst those in the Öland species are scarcely discernible; furthermore, the dimensions of the thecal apertures in this latter do not approach those of *A. czarnockii*.

In ÖL. 1132 (Figs. 61 *a, b*), the arrangement of the autothecae has been explained in terms of the known structure of *A. suecicus*, from the Middle Ordovician limestones of Sweden—the fact that this is possible suggests some affinity between the two. The lack of any clear evidence of twig structure externally possibly indicates that the Öland species is an earlier, less regular, ancestor of *A. suecicus*.

DERIVATIO NOMINIS.—The specific name proposed has reference to the divergent nature of the isolate portions of the autothecae.

### Order *Tuboidea* KOZŁOWSKI, 1938

Two new families of the order *Tuboidea* are proposed; each is represented, at the present, by a single, monotypic genus: *Parvitubus* gen. nov. and *Multi-tubus* gen. nov. In stipe structure (in so far as this can be determined from the external arrangement of the thecae), both families stand closer to the *Dendroidea* than does either the *Tubidendridae* or the *Idiotubidae*. Departure from the regular, dendroid, stolonial system of alternating triads is reflected only in, and is possibly limited to, the bithecae.

In the general form of the rhabdosome, *Parvitubus* can be compared with the *Idiotubidae*, but the basal thecorhiza characteristic of the latter is replaced by a mass of structureless tissue in the former. Furthermore, in stipe structure, *Parvitubus* is clearly distinct, for not only are the stipes composed of autothecae, bithecae and stolothecae, but these appear to be produced in regular triads,

differing from those of the *Dendroidea* only in that they are non-alternating, the bithecae being confined to one side of the stipe.

The rhabdosome in *Multitubus* is probably dendroid in form, comparable with that of *Callograptus* but lacking evident dissepiments. The stipes, again, are composed of autothecae, bithecae and stolothecae, but the bithecae, in a given length of stipe, are approximately twice as numerous as the autothecae, suggesting a less regular, or, at least, a more complex, structure than in *Parvitubus*.

KOZŁOWSKI (1948, pp. 107–108) has outlined the possible genetic relationship between the *Tubeidea* and the *Dendroidea*, but concludes that any decision on the subject cannot be other than hypothetical in view of our relatively scant knowledge of the *Tubeidea*. Thus, the astogeny of the tuboid rhabdosome is completely unknown and, whilst the earliest representatives of this order are Tremadocian in age, the structure is by then so distinct from that of the dendroids that it is almost certain that the *Tubeidea*, like the *Dendroidea*, had their origin in the Cambrian.

KOZŁOWSKI tentatively suggests (see diagram, 1948, p. 109) that the two orders arose from a common ancestral stock, rather than that one is an off-shoot from the other (as the graptoloids are from the dendroids).

With regard to this problem of the relationship between the dendroids and the tuboids, the present material from Öland is of especial interest: whilst clearly, from a chronological point of view, this material cannot be considered as phylogenetically intermediate between the two orders, morphologically it undoubtedly is. Although rhabdosomal form is most probably an adaptation to environment, it is of interest to note that in *Multitubus* the rhabdosome is possibly dendroid (cf. the *Tubidendridae*) and in *Parvitubus* it is encrusting (cf. the *Idiotubidae*), and in a morphological sense, *Multitubus* and *Parvitubus* can be considered transitional between the *Dendroidea* and the *Tubidendridae* and *Idiotubidae*, respectively. *Multitubus* and *Tubidendrum* have retained a dendroid rhabdosome, but the detailed stipe structure shows two stages of increasing complexity and irregularity; *Parvitubus* has adopted the rhabdosomal form of the *Idiotubidae*, but has retained a structure only slightly removed from that of the *Dendroidea*.

It is concluded that the existence of *Multitubus* and *Parvitubus* favours a relationship between the tuboids and dendroids comparable with that between the dendroids and graptoloids, but if the transition was from the tuboid to the dendroid structure, or *vice versa*, is not known.

### Family *Parvitubidae* fam. nov.

TYPE GENUS.—*Parvitubus* gen. nov.

DIAGNOSIS.—Rhabdosome encrusting, ?discoidal; stipes erect, unbranched, composed of autothecae, bithecae and stolothecae. Autothecae long, straight

and tubular, uniformly disposed along ventral margin; bithecae also long and tubular, regularly developed but restricted to one side of stipe; stolothecae dorsal in position. Stipe structure uncertain, but uniform spacing of autothecae and bithecae suggests origin from regularly-spaced, non-alternating triads.

REMARKS.—This family is represented, at the present, by the single, monotypic genus *Parvitubus* gen. nov.

### Genus *Parvitubus* gen. nov.

TYPE SPECIES.—*Azyograptus?* *oelandicus* BULMAN, 1936.

DIAGNOSIS.—As for family.

REMARKS.—The diagnosis of the type genus, and hence of the family, is necessarily provisional, since little is known concerning the internal arrangement and origin of the thecae.

By comparison with such idiotubid genera as *Discograptus* WIMAN, *Galeograptus* WIMAN, and *Cyclograptus* SPENCER, the general form of the rhabdosome is thought to be discoidal, comprising a basal encrustation from which arise simple (i.e. unbranched) stipes. In contradistinction to all genera within the family *Idiotubidae*, these stipes are composed of autothecae, bithecae and stolothecae, whilst the thecae do not appear to participate in the basal root structure, which cannot, therefore, be equated exactly with the idiotubid thecorhiza.

The arrangement of thecae along the stipes is more regular than in the *Tubidendridae*, but, as in the *Tubidendridae* and in some dendroids, the stipes, at any given level, comprise thecae of several generations. The autothecae in *Parvitubus* are not spirally coiled, nor are they dimorphic.

DERIVATIO NOMINIS.—The name proposed for the type genus has reference to the fact that, in stipe structure, it is very little removed from the *Dendroidea*.

### *Parvitubus oelandicus* (BULMAN, 1936)

Figs. 62–72.

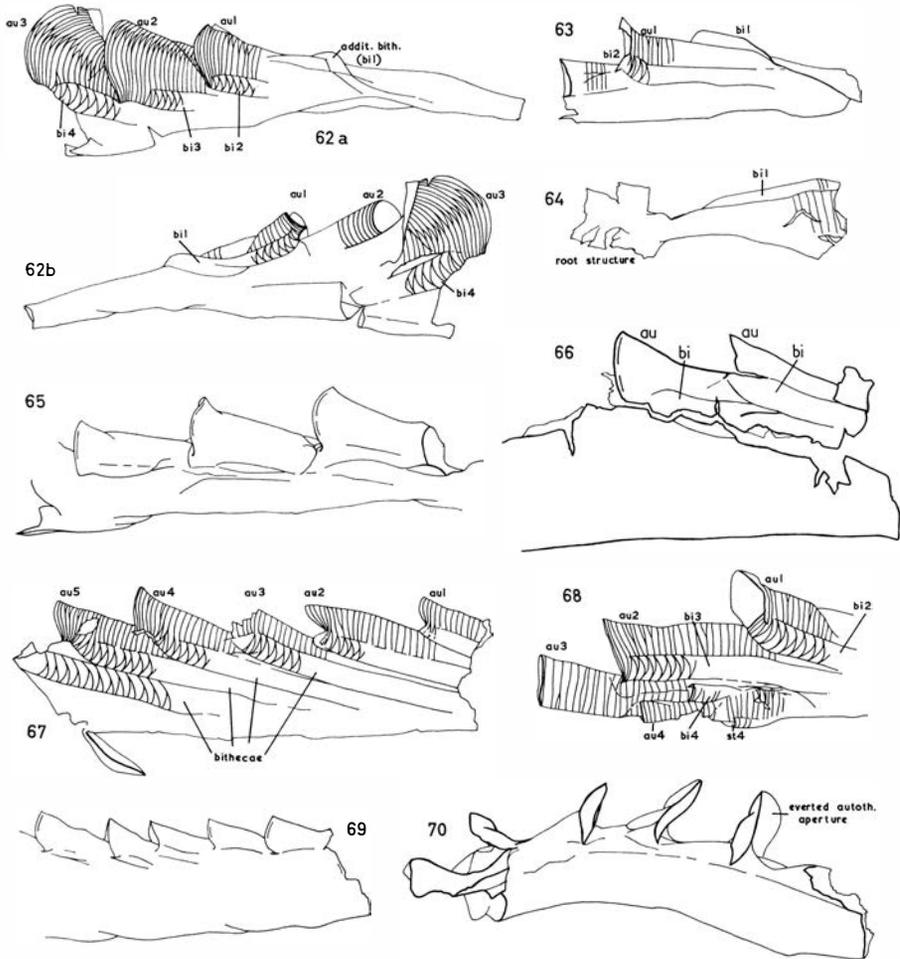
1936 *Azyograptus oelandicus* BULMAN, p. 46; Fig. 17; Pl. 2, figs. 16–29.

HOLOTYPE.—Spec. No. 1306: BULMAN, 1936, Pl. 2, figs. 23, 24, 28, 29.

FIGURED MATERIAL.—Spec. Nos. Öl. 1141 *a*, Öl. 1142, Öl. 1143 *b*, Öl. 1144, Öl. 1145 *a*, Öl. 1146, Öl. 1147 *b*, Öl. 1148–Öl. 1151.

LOCALITY AND HORIZON.—Hälludden: –135–140D, –118–120D, +18+22D, +23+26D; Hagudden: 0–8D, 0+15D, +10+15D.

DIAGNOSIS (amended).—Rhabdosome ?discoidal, comprising several stipes rising independently from a rooted structure. Stipes straight, or with slight dorsal curvature; never branched; at least 15 mm in length; uniform maximum dorso-ventral width of c. 1.5 mm. Autothecae 10–12 per cm; long, straight and tubular, with everted apertural margins and overlapping at least 0.66.



Figs. 62–70. *Parviturus oelandicus* (BULMAN). (62) Proximal stipe fragment; (62 *a, b*) two lateral aspects.  $\times 12$ ; Hälludden +23+26D; Öl. 1141 *a*. (63) Proximal stipe fragment, lateral aspect.  $\times 17$ ; Hälludden –118–120D; Öl. 1142. (64) Proximal end with fragment of basal root structure.  $\times 18$ ; Hagudden 0–8D; Öl. 1143 *b*. (65) Stipe fragment in lateral aspect;  $\times 17$ ; Hälludden –118–120D; Öl. 1144. (66) Stipe fragment in lateral aspect.  $\times 10.7$ ; Hälludden +18+22D; Öl. 1145 *a*. (67) Partially cleared stipe fragment.  $\times 12$ ; Hälludden +23+26D; Öl. 1146. (68) Growing end of stipe in lateral aspect.  $\times 22$ ; Hälludden –118–120D; Öl. 1147 *b*. (69) Stipe fragment in lateral aspect.  $\times 11$ ; Hälludden –135–140D; Öl. 1148. (70) Stipe fragment with strongly everted autothecal apertures.  $\times 17$ ; Hagudden +10+15D; Öl. 1149. *au*: autotheca; *bi*: bitheca.

One bitheca developed in association with each autotheca, but occurring only on left side of stipe (in thecal aspect), and opening into autothecal cavity just behind aperture. An additional bitheca may be associated with the first autotheca. Budding involves the production of ?regularly-spaced, non-alternating triads.

DESCRIPTION.—The material recovered comprises several fragments of

unbranched stipe of the type described by BULMAN (1936) from the HOLM collection, and provisionally attributed by him to the genus *Azygograptus* (*A.?* *oelandicus*).

The author's description includes the observation that the proximal end in this species is always ragged and is evidently broken, most specimens ending in an open tube, and it was concluded that the material represents an *Azygograptus* in which the entire sicula is in every case broken away. Similar, broken proximal ends are found in the present material and, in all cases except one, the stipe terminates (or originates) in a narrow, broken tube (see Figs. 62 *a, b*, 63). In the one excepted instance (Fig. 64), the proximal tube has attached to itself fragments of tissue which are best regarded as part of a basal root structure. This latter apparently consists only of structureless tissue and thus differs greatly from the encrusting thecorhiza of the *Idiotubidae*.

It is concluded that the entire rhabdosome in this species is most probably discoidal, with a basal root system from which the unbranched stipes arise independently, simulating the rhabdosomal form of the idiotubid genus *Discograptus*.

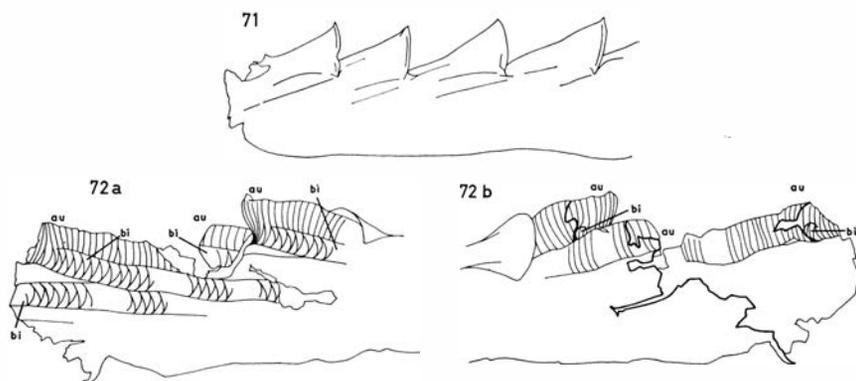
In addition to the single root fragment, the material includes sections of stipe of varying lengths, the longest measuring just over 15 mm. The stipes are typically straight, but may show slight dorsal concave curvature.

Dorso-ventral stipe width is usually constant throughout the extent of a given fragment of stipe, excepting where this is a proximal end. The majority of specimens have an average maximum width in this plane of 1.5 mm, with a range of from 1.3–1.75 mm. A few fragments fall well outside these limits: thus, specimens from the -118-120D level do not exceed 0.9 mm in width (Fig. 65), whilst those from the +18+22D level have a stipe width greater by almost 1.0 mm than that of any other specimen included within this species (Fig. 66).

In the whole range of material available, irrespective of stipe width, the autothecae and bithecae have a uniformly low angle of inclination to the dorsal margin, of the order of 10°–20°; consequently, the number of thecae encountered in a fragment of stipe at a given level is largely a function of the dorso-ventral width of that fragment; furthermore, by implication, the lengths of the autothecae and bithecae, assuming they originate at the dorsal margin of the stipe, is also dependent on this dimension. One growing end of a stipe has been recovered (Fig. 68), and if the thecae have been correctly identified (see below), each autotheca originates as far back along the stipe as the aperture of the autotheca produced three generations previously—and this specimen is a narrow-stiped form.

The excessive length of the autothecae in no way detracts from their regular disposition along the stipe.

The autothecae are tubular in form, and the apertural margin is characteristically everted; in most cases, eversion is slight (Figs. 65, 67, 71), but in the extreme case the margin is drawn out into a wide rim encircling the aperture (Fig. 70).



Figs. 71–72: *Parvitubus oelandicus* (BULMAN). (71) Stipe fragment in lateral aspect.  $\times 11$ ; Hälludden – 135–140D; ÖL. 1150. (72) Stipe fragment; (72 a, b) two lateral aspects.  $\times 17$ ; Hälludden – 135–140D; ÖL. 1151. au: autotheca; bi: bitheca.

The plane of the apertural margin is normal to the stipe length; the height of the aperture may account for as much as 0.5–0.33 the dorso-ventral width of the stipe.

The autothecae average 10–12 per cm, though the range is from 8–15. Abundance is not dependent upon stipe width.

A bitheca is developed in association with each autotheca (Figs. 62 a, b, 63, 65, 67, 72 a, b), but all occur on the same side of the stipe—the left in thecal aspect, facing distally—and are not alternating as in the *Dendroidea*. They lie dorso-laterally to the autothecae and open into the autothecal cavity just behind the aperture; they are scarcely evident externally and any swelling likely to be present where each opens into an autotheca is effectively masked by the eversion of the autothecal aperture.

An additional bitheca may be associated with the first autotheca (Figs. 62 a, b, 63, 64). This bitheca originates, presumably, in the root system, or at least at the base of the stipe. Growth of this bitheca is firstly along the left side of the stipe, but later it may cross the ventral margin onto the right-hand side (Figs. 62 a, b) and open into the cavity of the first autotheca, which then has two associated bithecae.

The bithecae, like the autothecae, are of excessive length and low inclination, and extend back (i.e. proximally) until their origin at the dorsal margin of the stipe. In the single growing end specimen recovered (Fig. 68), two-fold division, giving an autotheca and a stolotheca, can be identified, but the immature bitheca (*bi*₄) also present appears to originate slightly distally to the *au*₄–*st*₄ diad, and it is uncertain whether this should be interpreted as a slightly abnormal triad, or as two closely associated diads. In view of the regular occurrence of both autothecae and bithecae throughout the stipe, the suggestion is favoured that the three immature thecae (*au*₄, *st*₄, *bi*₄) observed in ÖL. 1147 b (Fig. 68)

are the product of a single trifurcation. In this case, the bitheca is two-thirds the length of the autotheca produced at the same node, and opens into the cavity of the autotheca of the preceding generation.

DISCUSSION.—To what extent variation in dorso-ventral stipe width (and hence in the number of thecae to be encountered at a given level along the stipe) should be regarded as a basis for varietal, or even specific, distinction cannot be stated until a complete rhabdosome is forthcoming. For the present, the uniformity of autothecal and bithecal form in the available material is considered sufficient reason for the erection of a single, undifferentiated species.

REMARKS.—The uncertain generic affinity of this species, when first described, stemmed from the state of preservation of the material—which was isolated, but not cleared, and which consisted only of single stipe fragments. It is only when rendered transparent that the regularly-arranged bithecae can be observed on the stipe, for they lie flush with the lateral wall and open into the autothecae.

### Family *Multitubidae* fam. nov.

TYPE GENUS.—*Multitubus* gen. nov.

DIAGNOSIS.—Entire rhabdosome unknown; essentially dendroid in appearance, recalling the genus *Callograptus*, but lacking evident dissepiments; stipes straight, sub-parallel and bifurcating. Autothecae regularly arranged along ventral margins. Bithecae numerous, capriciously arranged on all sides of stipe. Stipe structure uncertain.

REMARKS.—This family is represented, at the present, by the single, monotypic genus *Multitubus* gen. nov.

### Genus *Multitubus* gen. nov.

TYPE SPECIES.—*Multitubus spinosus* sp. nov.

DIAGNOSIS.—As for family.

REMARKS.—In the suggested form of the rhabdosome and the arrangement of the autothecae, the genus *Multitubus* can be compared with a typical dendroid, and it is only the bithecae which indicate departure from the regular structure of that order.

The regularity of autothecal arrangement, together with the presence of only one type of autotheca and the suggestion that the stipes are too slender to possess a very complex structure at a given level—all favour the conclusion that *Multitubus* cannot be placed alongside *Tubidendrum* in the *Tubidendridae*.

Furthermore, a presumably dendroid rhabdosome, with stipes comprised of autothecae, bithecae and stolothecae, precludes comparison with the *Idiotubidae*.

Comparison with *Parvitubus* reveals a similar, regular arrangement of autothecae and the presence of all three thecal types in the stipes, but there is a

difference in rhabdosomal form, whilst the relatively greater number of bithecae compared with autothecae, in *Multitubus*, suggests a less regular structure.

DERIVATIO NOMINIS.—The name proposed for the type genus has reference to the greater number of bithecae, compared with the number of autothecae, in a given length of stipe.

*Multitubus spinosus* sp. nov.

Figs. 73, 74.

HOLOTYPE.—Spec. No. Öl. 1155; Figs. 73 *a, b*.

FIGURED MATERIAL.—Spec. Nos. Öl. 1155, Öl. 1156.

LOCALITY AND HORIZON.—Hälludden: +115 +120D.

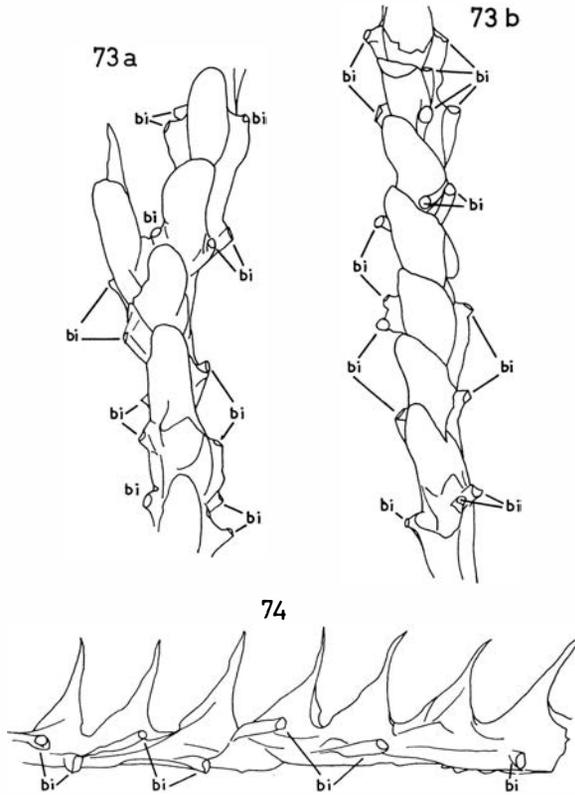
DIAGNOSIS.—Rhabdosome recalling that of *Callograptus*, but without dissepiments. Stipes straight, sub-parallel, bifurcating at large intervals. Autothecae regularly arranged along ventral margin; provided with prominent apertural denticles; numbering 15–17 per cm. Bithecae approximately twice as numerous as autothecae, capriciously arranged on stipe; spinose and isolate distally. Structure of stipes uncertain, but uniform spacing of autothecal apertures suggests some degree of regularity.

DESCRIPTION.—The form of the entire rhabdosome is not known, though it is considered to be basically dendroid in appearance, with straight, bifurcating stipes and regularly-positioned autothecae.

The most distinctive feature of the species concerns the form and abundance of the bithecae. In a given length of stipe, the bithecae are approximately twice as numerous as the autothecae (Figs. 73 *a, b*; 74); thus, in Öl. 1155 (Figs. 73 *a, b*), in the space of 16 autothecal apertures, there are 34 bithecae visible, and more may be present, hidden from view by the large apertural denticles on the autothecae. The distribution of the bithecae along the stipes is capricious; they may occur in clusters of two or more, or be distributed singly, and though most abundant on the lateral walls of the stipes, they may open also on the ventral and dorsal walls. The nearest approach which the bithecae achieve to a definite pattern is seen in Fig. 74, where there is a tendency to a regular positioning of bithecal apertures alternately ventral and dorsal along one side of the stipe; a study of the material as a whole, however, suggests that any such arrangement is coincidental.

The bithecae are tubular in form and aperturally isolate, having the appearance of hollow, spinose outgrowths from the stipe (Figs. 73 *a, b*; 74); the average apertural diameter is 0.12 mm.

The autothecae are characterised by an excessively-developed apertural process, taking the form of a long, flattened blade, narrowing distally but roundly-terminated (Figs. 73 *a, b*; 74); it may extend up to 0.4 mm beyond the autothecal aperture. The average inclination of the ventral autothecal wall is 45°, but the process is usually much more steeply inclined. The autothecae are never isolate distally.



Figs. 73-74: *Multitubus spinosus* sp. nov. (73 a, b) parts of holotype in ventral aspect.  $\times 18$ ; Hälludden + 115 + 120D; Öl. 1155. (74) Stipe fragment showing spinose bithecae.  $\times 18$ ; Hälludden + 115 + 120D; Öl. 1156. *bi*: bitheca.

The plane of the aperture is normal to the stipe length; the margin is elliptical in outline, with lateral diameter 0.31-0.38 mm and dorso-ventral diameter 0.35-0.41 mm.

The autothecae number 15-17 per cm. They are perfectly aligned along the stipes with no irregularity in development.

In Öl. 1155 (the holotype), two orders of stipe division are preserved; the angle of divergence is small ( $c.15^\circ$ ) and the resulting stipes quickly assume parallelism. The measured distance between the two divisions is 8.75 mm. Apart from the lateral curvature which follows branching, the stipes are typically straight and stiff. The maximum dorso-ventral width, including the apertural denticle, is of the order of 1.0-1.1 mm; the minimum dorso-ventral width is 0.3-0.4 mm. Lateral stipe width averages 0.45 mm.

The structure of the stipes is very imperfectly known, and the interpretations forwarded are based solely on external evidence. Any such interpretation must account for the uniform spacing of the autothecae and the relatively greater

abundance and capricious arrangement of the bithecae, compared with the autothecae. Possibly, triads are developed at regular intervals, each giving an autotheca, a stolotheca and a bitheca, whilst stolotheca-bitheca diads are inserted irregularly between the triads. Alternatively, triads may not be developed at all, only diads, as in *Tubidendrum*; this would involve uniformly-spaced autotheca-stolotheca diads, with randomly interspersed stolotheca-bitheca diads.

Whatever the correct interpretation of the observed thecal arrangement, the stipe structure is clearly more complex and less regular than in *Parvitubus*, whilst in comparison with *Tubidendrum*, the reverse holds true.

DISCUSSION.—It is considered that the hollow, spine-like, slender structures on the stipes have been correctly identified as bithecae. It is most unlikely that they are dissepiment bases, for example, since they are equally well developed on all sides of the stipes and frequently two or more occur at the same level. If identified as spines, their form and distribution, considered together, are without parallel in the *Graptolithina*, whilst such an interpretation requires bithecae to be absent in this species, for no other structures are present which could be recognised as such.

DERIVATIO NOMINIS.—The specific name proposed has reference to the spinose form of the bithecae.

### Order *Camaroidea* KOZŁOWSKI, 1938

#### Family *Cysticamaridae* BULMAN, 1955

##### Genus *Cysticamara* KOZŁOWSKI, 1948

##### *Cysticamara accollis* KOZŁOWSKI, 1948

Fig. 75.

1948 *Cysticamara accollis* KOZŁOWSKI, p. 183; Pl. III, figs. 3–5; Pl. XXVI, fig. 1; Pl. XXVIII, figs. 1, 2; Pl. XXIX, figs. 1–17.

FIGURED MATERIAL.—Spec. No. ÖL. 1158 (preserved in glycerine).

LOCALITY AND HORIZON.—Hälludden: – 118 – 120D.

DESCRIPTION.—The recovered fragment of *C. accollis* is several times larger than KOZŁOWSKI's holotype (1948, spec. No. 193).

Over a large area of rhabdosome, the apertures of the camarae show some degree of regularity in their arrangement, forming a series of sub-parallel rows (Fig. 75 *a*); such a pattern is present also in KOZŁOWSKI's holotype, but, because of the small size of this latter, it is not so noticeable. In unpublished and undated photographs of this species, taken by HOLM, the alignment of the apertures is at an angle of 35°–40° to an edge of the rhabdosome, so that the apertural arrangement evidently does not reflect the trend of the growing edge of the colony.

The camaral apertures are more prominently displayed than in the Polish material, each being situated at the apex of a conical structure, which might

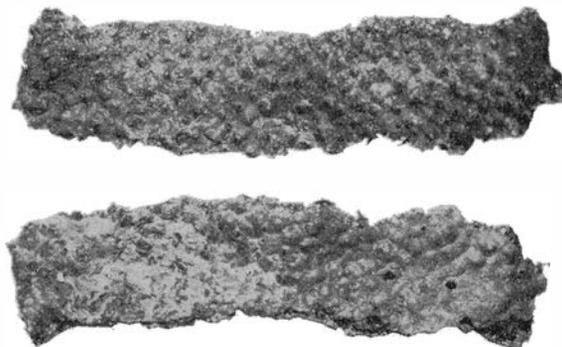


Fig. 75: *Cysticamara accollis* KOZŁOWSKI. Fragment of rhabdosome; the upper figure in ventral (thecal) aspect; the lower figure in dorsal aspect.  $\times 5$ ; Hälludden - 118-120D; Öl. 1158.

properly be described as a rudimentary collum. Extensive deposition of secondary chitin around the apertures, together with occasional occlusion, has been noted.

The specimen proved not to section particularly well, and the sections, where decipherable, do little more than confirm KOZŁOWSKI'S conclusions that the stolons bud irregularly, that they are encased in extra-camaral tissue rather than stolothecae, and that, whilst some stolons give rise to camarae, others die out in the extra-camaral tissue. An additional feature observed was that the stolons may occur on the lower surface of the colony, as well as on the upper surface and between the camarae.

### Genus *Graptocamara* KOZŁOWSKI, 1948

#### *Graptocamara hyperlinguata* KOZŁOWSKI, 1948

Figs. 76, 77.

1948 *Graptocamara hyperlinguata* KOZŁOWSKI, p. 187; Fig. 59; Pl. XXX, figs. 3-6.

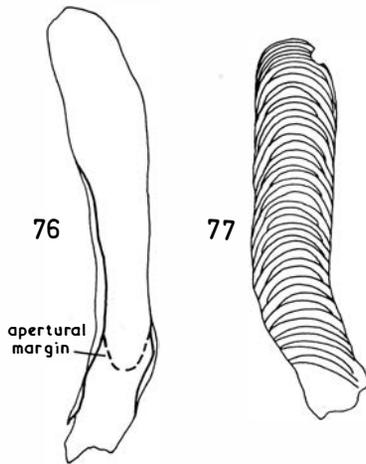
FIGURED MATERIAL.—Spec. Nos. Öl. 1159 *c, d*.

LOCALITY AND HORIZON.—Hagudden: o + 15D.

DESCRIPTION.—The material recovered comprises specimens of the collum and of the apertural part of the camara, though the aperture itself is in no case preserved in its entirety.

The maximum length of a collum is 1.65 mm; proximally, the width is 0.25-0.28 mm and distally, 0.40 mm. The spinose type of collum noted by KOZŁOWSKI (see 1948, p. 188, Fig. 51 A, B) is not represented in the Hagudden material; on the contrary, the collum increases in width distally and is roundly-terminated (cf. 1948, p. 188, Fig. 59 C). The sickle-shaped (*lame de faucille*) fuselli on the ventral wall of the collum are clearly in evidence in Öl. 1159 *d* (Fig. 77).

In Öl. 1159 *c* (Fig. 76), sufficient of the camara is preserved to permit the course of the apertural margin to be approximately deduced.



Figs. 76–77: *Graptocamara hyperlinguata* KOZŁOWSKI. (76) Apertural process (collum) of the camara, broken line denotes probable margin of camaral aperture.  $\times 25$ ; Hagudden 0 + 15D; ÖI. 1159 c. (77) Apertural process (collum) showing growth lines.  $\times 25$ ; Hagudden 0 + 15D; ÖI. 1159 d.

## Order *Stolonoidea* KOZŁOWSKI, 1938

### ?*Stolonoidea* gen. et sp. indet.

Figs. 78–81.

FIGURED MATERIAL.—Spec. Nos. ÖI. 1160, ÖI. 1161, ÖI. 1162 a, ÖI. 1163.

LOCALITY AND HORIZON.—Hälludden: +23 +26D.

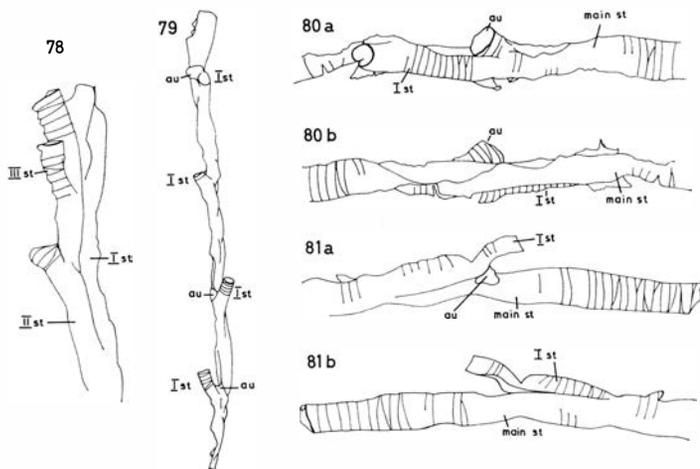
DESCRIPTION.—A number of fragments, presumably all derived from the same rhabdosome, portray an unusual structure which appears to approach most closely that of the *Stolonoidea*; obvious differences exist, however, and the attribution of the material to that order is necessarily provisional.

The rhabdosome is comprised of a single main tube bearing lateral branches and, by comparison with the stolonoid structure, these are interpreted as stolothecae (see Fig. 79). The lateral, or branch, stolothecae may arise on any side of the main stolotheca; also, the stolothecal fuselli are completely encircling, and hence it is assumed that the rhabdosome was erect and not encrusting.

The longest single length of main stolotheca recovered (ÖI. 1160) measures 25.2 mm; the diameter ranges from 0.10–0.18 mm. This main stem is typically flexed at the point of separation of each branch, but otherwise it is not normally curved in any way.

The fuselli forming the walls of the stolothecae (Figs. 80 a, b, 81 a, b) are complete rings, with the two ends joining at an oblique suture; these latter are not regularly arranged along any one side of the stolotheca.

Branch stolothecae originate some distance back along the main stolotheca from the point at which actual separation is achieved (Figs. 80 a, b, 81 a, b);



Figs. 78–81: ?*Stolonoidea* gen. et sp. indet. (78) Part of specimen to show orders of branching.  $\times 62$ ; Hälludden + 23 + 26D; ÖL. 1160. (79) Main stolonotheca with lateral branches and autothecae.  $\times 26$ ; Hälludden + 23 + 26D; ÖL. 1161. (80) Partially cleared specimen showing complete fuselli; (80 a, b) two lateral aspects.  $\times 42$ ; Hälludden + 23 + 26D; ÖL. 1162a. (81) Partially cleared specimen; (81 a, b) two lateral aspects.  $\times 42$ ; Hälludden + 23 + 26D; ÖL. 1163. au: autotheca; st: stolonotheca; I st, etc.: first order stolonotheca, etc.

they are appreciably more slender than the adjacent part of the parent stolonotheca. The angle of divergence is of the order of  $25^{\circ}$ – $30^{\circ}$ . Branch stolonothecae may themselves give rise to branches, acting in the same capacity as the main stolonotheca; a third generation of branching is preserved in ÖL. 1160 (Fig. 78).

An opening may be present in the wall of the parent stolonotheca, situated in the angle between this latter and the branch stolonotheca (Figs. 79–81). By analogy with the stolonoid structure, such openings are identified as autothecal apertures. The aperture may be merely a hole in the wall of the stolonotheca (Fig. 81 a), or the autotheca may extend out for a short distance from the parent stolonotheca (Fig. 80 a, b), and in this latter case, fusellar structure is discernible.

The autothecae are quite subordinate features of the rhabdosome, and no confusion should arise in distinguishing them from branch stolonothecae.

DISCUSSION.—The structure of the present material has been interpreted in the light of the known structure of the *Stolonoidea*; this has permitted the identification of an erect rhabdosome comprising a branching system of stolonothecae and relatively insignificant autothecae—but an exaggerated development of stolons (the essential characteristic of the order *Stolonoidea*) has no counterpart in the Öland material, in which a stolonial system of any kind is entirely wanting. Such is also true, however, of almost all the material in which one would expect a stolonial system to be developed, and is presumably a preservational feature; even so, the dimensions of the stolonothecae in the present material are such that stolons of the magnitude characteristic of the *Stolonoidea* could not be accommodated.

The type species of the genus *Melanostrophus* ÖPIK—*M. fokini* ÖPIK, 1930—has affinity with the present material in that the skeleton is composed of free, rounded tubes showing a fusellar structure (EISENACK, 1936). These tubes characteristically occur in complex, felted associations; branching of individual tubes, as in the present species, has not been observed.

EISENACK has noted circular to oval, smooth-margined openings in the walls of the tubes of *M. fokini*; these, he suggests, served for connection between adjacent tubes rather than as thecae. Their presence is of interest in view of the similar openings, identified as autothecae, found in the Öland species (see above). A decision concerning the true function of these openings in both

Table 1a. A List of the Species found at Hälludden and a Tabular Summary of their Distribution

Fauna	Levels from which collections made												
	- 84 - 92	- 135 - 140D	- 118 - 120D	- 113 - 116D	- 110 - 113D	- 100D	- 76 - 82D	+ 5 + 8D	+ 10 + 30D	+ 18 + 22D	+ 23 + 26D	+ 38 + 43D	+ 115 + 120D
DENDROIDEA													
<i>Dendrograptus</i> cf. <i>cofeatus</i> KOZŁOWSKI										×	×		
<i>D. rigidus</i> BULMAN										×	×	×	
<i>Callograptus?</i> <i>perexilis</i> sp. nov.		×	×				×			×	×	×	
<i>C.?</i> <i>sinuosus</i> sp. nov.		×											
<i>C.?</i> cf. <i>salteri</i> HALL										×	×	×	
<i>C.?</i> <i>perlongus</i> sp. nov.										×	×		
<i>Desmograptus separatus</i> sp. nov.								×					
<i>Desmograptus?</i> sp. indet. a											×		
<i>Dictyonema cotyledon</i> BULMAN										×	×	×	
<i>D.</i> cf. <i>holmi</i> BULMAN											×	×	
<i>D. rhinanthiforme</i> BULMAN										×	×	×	
<i>D. variabile</i> sp. nov.		×											
<i>Acanthograptus divergens</i> sp. nov.									×	×	×	×	
TUBOIDEA													
<i>Parvitubus oelandicus</i> (BULMAN)		×	×							×	×		
<i>Multitubus spinosus</i> sp. nov.													×
CAMAROIDEA													
<i>Cysticamara accollis</i> KOZŁOWSKI			×										
STOLONOIDEA													
? <i>Stolonoidea</i> gen. et sp. indet.											×		

Table 1b. A List of the Species found at Hagudden and a Tabular Summary of their Distribution

Fauna	Levels from which collections made						
	- 83 - 86	0 - 8D	0 + 15D	+ 10 + 15D	+ 20 + 25D	+ 20 + 45D	+ 35 + 30D
DENDROIDEA							
<i>Dendrograptus rigidus</i> BULMAN			×		×		×
<i>Callograptus?</i> <i>perexilis</i> sp. nov.		×	×	×			×
<i>C.?</i> cf. <i>salteri</i> HALL			×	×	×		×
<i>Dictyonema cotyledon</i> BULMAN			×		×		
<i>Acanthograptus divergens</i> sp. nov.			×	×		×	×
TUBOIDEA							
<i>Parvitubus oelandicus</i> (BULMAN)		×	×	×			
CAMAROIDEA							
<i>Graptocamara hyperlinguata</i> KOZŁOWSKI			×				

species—as thecae, as a means of connection between adjacent tubes, or as passageways for the stolons—must await the recovery of material with a preserved stolonial system, assuming that one should be developed.

KOZŁOWSKI has suggested that *Melanostrophus* is possibly a stolonoid (BULMAN, 1944, p. 18), and BULMAN (1955) includes the genus, provisionally, in that order. With regard to the Öland species, it has been decided not to propose a name until the structure is known in greater detail and hence its affinities are more certain; in the meantime, it is doubtfully included in the order *Stolonoidea*.

## Aspects of dendroid and tuboid morphology, phylogeny and taxonomy

1. BRANCHING IN THE DENDROID RHABDOSOME.—It has been noted elsewhere that fragments of rhabdosome recovered from the Ontikan limestones did not section sufficiently well to reveal any details of internal structure. From external evidence alone, however, it has proved possible to account for the observed arrangement of autothecal and bithecal apertures at the incidence of stipe division in a dendroid rhabdosome if it is assumed that, at the node bearing the division, a bitheca is suppressed in favour of a stolotheca.

The special characteristics of stipe division in those species of *Callograptus?* in which the autothecae are elongated beyond the normal dendroid length have

been listed above (see p. 23), but it is worthy of emphasis that the production of two stolothecae and one autotheca in place of a normal triad, combined with slight adjustments in thecal length, will account for all the features observed.

2. DENDROIDS WITH ELONGATE THECAE.—*Callograptus?* cf. *C. salteri* and *Callograptus?* *perlongus* are comparable with certain species of *Dictyonema*, *Desmograptus* and *Reticulograptus* to the extent that the autothecae show some elongation beyond the normal dendroid length whilst still retaining the typical arrangement of thecae in the stipes. From such a basis, the stipe structure characteristic of the genus *Coremagraptus* is readily derivable by continued lengthening of the thecae (relative to the spacing of the nodes) and a loss of their regular arrangement; furthermore, the nature of these changes is such that the *Coremagraptus* structure could well have arisen repeatedly from those species of *Callograptus*, *Dictyonema*, etc. with elongate thecae, and particularly is this so if it is believed that the form assumed by the rhabdosome is primarily an adaptation to environment.

The structure of *Acanthograptus*, involving as it does a regular variation in thecal length and a grouping of thecae into twigs, would seem to be so highly specialized as to imply a single line of development. It seems possible, therefore, that thecal elongation is a characteristic of more than one phyletic line and, if this is the case, to use this feature as a primary taxobasis in the family *Acanthograptidae* is unnatural.

3. SUBGENERA OF THE GENUS CALLOGRAPTUS HALL.—BOUČEK (1957) recognised two subgenera of *Callograptus* on the basis of the degree of development of apertural denticles on the autothecae. A revised classification of the genus at the subgeneric level is proposed using thecal length as the primary taxobasis, and thereby conforming with BOUČEK's objective in defining the subgenus *Dictyonema* (*Pseudictyonema*).

The two subgenera of *Callograptus* proposed are:

*Callograptus* (*Callograptus*) BOUČEK, 1957, emend. [= *Callograptus* (*Callograptus*) BOUČEK, 1957, *pars* + *Callograptus* (*Capillograptus*) BOUČEK, 1957].

*Callograptus* (*Pseudocallograptus*) subgen. nov. [= *Callograptus* (*Callograptus*) BOUČEK, 1957, *pars*].

4. PARVITUBIDAE FAM. NOV. AND MULTITUBIDAE FAM. NOV.—Two new families (*Parvitubidae* fam. nov. and *Multitubidae* fam. nov.) of the order *Tubeidea* KOZŁOWSKI are proposed; each is represented, at the present, by a single, monotypic genus: *Parvitubus* gen. nov. and *Multitubus* gen. nov., respectively. In stipe structure, both families probably stand closer to the *Dendroidea* than does either the *Tubidendridae* or the *Idiotubidae*. Departure from the regular, dendroid, stolonial system of alternating triads appears to be restricted to the bithecal origins. In *Parvitubus* (type species: *Azygograptus?* *oelandicus* BULMAN, 1936), the bithecae are regularly produced but are confined to one side of the stipe; in *Multitubus* (type species: *Multitubus spinosus* sp. nov.), the bithecae

open, and presumably also originate, capriciously on the stipe and, in a given length of stipe, are approximately twice as numerous as the autothecae.

5. THE RELATIONSHIP OF THE TUBOIDS AND DENDROIDS.—The recovery of graptolites apparently morphologically intermediate between the *Tubeidea* and the *Dendroidea* suggests that the relationship between these two orders may be otherwise than was implied by KOZŁOWSKI (1948): rather than the derivation of both from a common ancestral stock, one would seem to be an offshoot from the other. At the present, there is no evidence to indicate whether the tuboids preceded the dendroids, or *vice versa*.

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