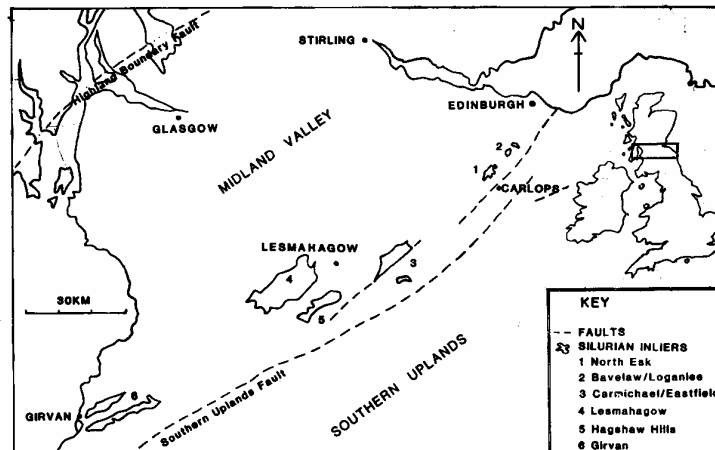


UPPER LLANDOVERY DENDROID GRAPTOLITES FROM THE PENTLAND HILLS, SCOTLAND

by ELIZABETH E. BULL

ABSTRACT. Well-preserved dendroids and graptoloids of Upper Llandovery, *Monoclimacis crenulata* Zone age are reported from the North Esk Inlier in the Pentland Hills, near Edinburgh, Scotland. The effects of palaeogeography and tectonics at the time of this zone are discussed, and a section on dendroid terminology is included. One new species *Dictyonema pentlandica* sp. nov. is described and ten other species (six of which have not been recorded from Britain before) are discussed. Emended diagnoses, based on material from the Pentland Hills, for the genus *Thallograptus* and most species are presented.

THE Pentland Hills near Edinburgh consist mainly of coarse clastic sediments and volcanics of early Devonian age. At certain points denudation has revealed the underlying Silurian rocks which form part of a chain of inliers of early Llandovery to late Wenlock age in the Midland Valley of Scotland (text-fig. 1). The North Esk Inlier, near Carlops, consists of a regressive sequence ranging from fully marine turbidites to terrestrial alluvial-fan deposits (Tipper 1976), and is the source of all the specimens discussed here (text-fig. 2). These beds are in places highly fossiliferous; extensive faunal lists were given by the UK Geological Survey (Peach and Horne 1899, pp. 589-606; later updated by Mykura and Smith 1962, p. 14). Major collections were made by the Survey and by enthusiastic amateurs (Haswell 1865; Henderson 1874, 1880; Henderson and Brown 1869); Laurie (1892, 1898, 1899) collected and described many specimens of eurypterid from a locality in the Gutterford Burn that has also yielded many graptolites. Graptolites were first described from the Pentland Hills by Lapworth (1874), from the Habbies Howe Inlier which is now known to be a further outcrop of the Reservoir Formation (Robertson 1985).

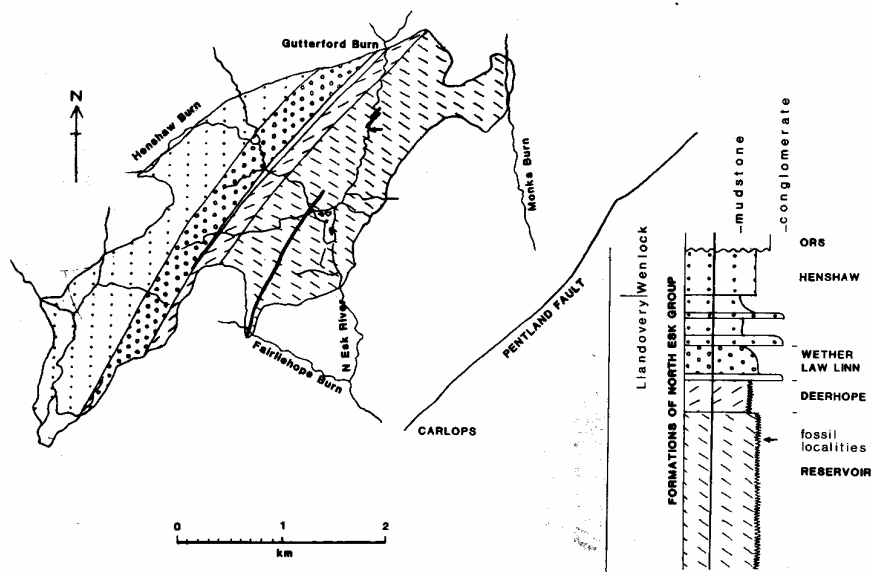


TEXT-FIG. 1. Location map showing the Silurian inliers discussed here, in the Midland Valley of Scotland.

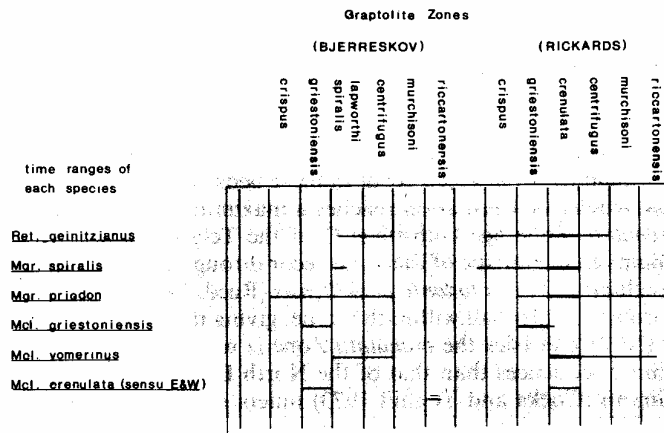
Interest in the area was rekindled by Lamont (1943, 1947, 1952, 1954, 1978), who illustrated many of the fossils (unfortunately with, at best, sparse descriptions) and was the first to suggest a late Llandovery age for the marine sequence, previously considered to be Wenlock. The stratigraphy was redefined by Tipper (1976) who described four formations in the North Esk Group (text-fig. 2). The Reservoir Formation is only sparsely fossiliferous, yielding rare graptolites, brachiopods, and trilobites throughout. Exposures along the Gutterford Burn, however, contain a diverse fauna, including eurypterids, starfish, and echinoids (Spencer 1914–1940; Brower 1975). The sediments and faunas of the overlying Deerhope Formation and highly fossiliferous Wether Law Linn Formation have been revised by Robertson (1985). The latter formation contains a shallow marine fauna which becomes progressively restricted towards the boundary with the succeeding Henshaw Formation (considered to be the Llandovery–Wenlock boundary). The Henshaw Formation is thought to be fluvial-terrestrial in origin (Tipper 1976). Robertson (1985) included an additional division, the Cock Rig Formation, between the Deerhope Formation and Wether Law Linn Formation.

Many of the fossil groups from the North Esk Inlier are poorly described, with some exceptions: the trilobites were comprehensively treated by Clarkson *et al.* (1977) and Clarkson and Howells (1981), the stylonoid eurypterids were studied by Waterston (1979), and the bivalves by Robertson (1985). Davidson's (1868) work on the brachiopods is greatly in need of revision. I describe here the graptolite fauna of the Reservoir Formation and sparse graptolite remains from the higher marine beds (Deerhope, Cock Rig, and Wether Law Linn formations), all of *Monoclimacis crenulata* Zone age.

The *crenulata* Zone assemblages given by two previous authors appear on text-fig. 3, which shows that in Britain most species, and especially *Monograptus spiralis*, have long time ranges—except for *Monoclimacis crenulata* itself, which is restricted to its zone. On Bornholm, however, Bjerreskov (1971) recorded '*Monograptus aff. crenulatus sensu Elles and Wood, 1911*', only from the *Monoclimacis griestoniensis* Zone and *Monograptus spiralis* only from the *spiralis* Zone (equivalent



TEXT-FIG. 2. Outcrop of the North Esk Inlier, Pentland Hills. The main fossiliferous localities are in the Reservoir Formation, just south of the dyke in the Gutterford Burn (arrowed), and in stream sections of the Wether Law Linn Formation.



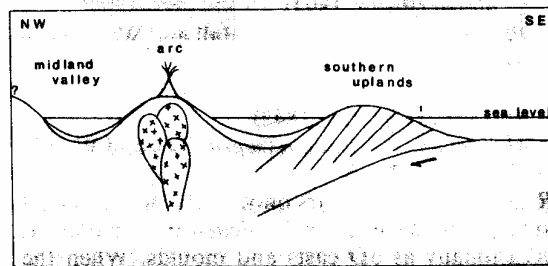
TEXT-FIG. 3. Time ranges of certain key late Llandovery graptoloids as given by Bjerreskov (1971) and Rickards (1976) for the east Baltic and Britain respectively.

in time to the lower *crenulata* Zone). Obviously some clarification of this broad zonal scheme is required, a process I hope to assist by recording the dendroids of the Pentland Hills.

Tectonic setting. Leggett *et al.* (1979) recognized the Southern Uplands of Scotland as an early Palaeozoic accretionary prism; the evolutionary history of the Midland Valley has been further described by Bluck (1983, 1984) (see text-fig. 4). The North Esk Group, a mainly regressive sequence, was deposited during late Llandovery times in an interarc basin (Bluck 1983). This partial isolation produced a relatively low faunal diversity, and possibly some unique faunal groups. The basin was probably a linear feature stretching from Northern Ireland in the south-west to the Baltic region in the north-east.

BIOSTRATIGRAPHY

The majority of the specimens described below were found in the Gutterford Burn section of the Reservoir Formation (text-fig. 2). This formation was interpreted by Tipper (1976) as originating from contourite or turbidite flow; further work has, in general terms, supported the turbidite model (Robertson 1985). Considered in the context of the whole sedimentary sequence the formation represents a prodelta sequence with a constant input of clastic material from a low grade sediment source, forming thin-bedded turbidites by currents lacking the strength to create significant sole



TEXT-FIG. 4. The tectonic picture in the late Llandovery (simplified after Bluck 1983, p. 130), showing the formation of an accretionary prism, which is now the Southern Uplands. The arc and fore-arc basin have not survived. The Midland Valley inliers were formed in an elongated interarc basin which occupied what is now the Midland Valley.

marks. The presence of *Ischadites* sp. (a calcareous alga) suggests formation in the photic zone at fairly shallow depth, although below storm-wave base.

The graptolites are found in two lithologies. First, in mudstones associated with either articulated eurypterids (Waterston 1979) or echinoids (Kier 1973), with their spines virtually undisturbed, and starfish (Spencer 1914–1940). Secondly, in winnowed bioclastic deposits (the 'Gutterford Limestone' Beds) which have evidently been transported, though not far nor for very long since well-preserved trilobites and other articulated fossils also occur in these beds.

The outcrop of the Reservoir Formation reaches a maximum thickness of 1500 m, all of which appears to be of *crenulata* Zone age (sub-stage C of the Telychian Stage: Cocks *et al.* 1970) as sparse graptolite remains characteristic of this zone occur throughout, together with other diagnostic forms such as the brachiopod *Eoplectodonta penkillensis* (Reed, 1917). The overlying Deerhope and Wether Law Linn formations also fall within this zone, giving it a total thickness of about 2000 m.

In other parts of the British Isles the *crenulata* Zone is represented by only a sparse graptolite fauna and much thinner sequences than that of the North Esk Inlier are found in the Carmichael (Rolfe 1960) and Girvan (Cocks and Toghill 1973) inliers of the Midland Valley, the Cross Fell Inlier (Burgess *et al.* 1970), the Howgill Fells (Rickards 1970), Northern Ireland (Rickards 1973), and recently in Kirkcudbrightshire (Kemp 1985; Kemp and White 1985).

The zone is much more clearly developed in Europe (Bouček 1953, 1957; Bjerreskov 1971), and attempts have been made to subdivide it. Bjerreskov noted the equivalence of the *crenulata* Zone to her *spiralis* Zone, and introduced a *Cyrtograptus lapworthi* Zone between it and the lowermost Wenlock *C. centrifugus* Zone. I consider her *lapworthi* Zone to equate with part of the *crenulata* Zone (text-fig. 3). Clarkson and Howells (1981) noted the similarity between the trilobites from the North Esk Inlier and those from the East Baltic; this has been confirmed by Howells (1982) and Ramsköld (1984).

Graptolite diversity in Scotland is generally lower in the west. Some forms, such as *Monograptus spiralis*, appear to show different time ranges across the region, relative to *Monoclimacis crenulata*, suggesting that one or more barriers to open access may have existed. At the south-west end of the Midland Valley conditions seem to have become more restricted with time. Cocks and Toghill (1973, p. 242) observed quite a thin *crenulata* Zone succession in the Girvan area, and hence inferred a short duration for the zone. This is unlikely, but the thin sequence does suggest that the consistently low graptolite faunal diversity in Britain is real and not caused by an increase in sedimentation rate.

More details about the *crenulata* Zone assemblage are emerging but, crucially, *M. crenulata* itself remains in need of revision. In the Pentland Hills, the dendroid species dealt with here outnumber the graptoloids, although *Monograptus priodon* is by far the most common graptolite. The current faunal list from the *crenulata* Zone of the North Esk Inlier is:

- Dictyonema pentlandica* sp. nov.
- Thallograptus* cf. *arborescens* Bouček, 1957
- T. inaequalis* Bouček, 1957
- Coremagraptus kalfusi* Bouček, 1957
- C. imperfectus* Kraft, 1982
- C. plexus* (Počta, 1894)
- Palaeodictyota pergracilis* (Hall and Whitfield, 1872)
- Retiolites geinitzianus geinitzianus* (Barrande, 1850)
- Monograptus priodon* (Bronn, 1835)
- M. spiralis* (Geinitz, 1842)
- Monoclimacis crenulata* (*sensu* Elles and Wood, 1911)

R. g. geinitzianus occurs only rarely throughout the succession, although it is more common in the lower beds. *Monograptus priodon* is common, usually as fragments preserved either flattened or occasionally as 3D casts and moulds. When the hooked part of the theca is missing, it can be

difficult to distinguish *M. priodon* from *Monoclimacis*; this may have caused confusion in the past as to the abundance of *M. crenulata*.

Monograptus spiralis is fairly common in the Reservoir Formation, and its coiled rhabdosomes are generally well preserved; the long thecal spines (Bulman 1932; Rickards *et al.* 1977, p. 73, fig. 37a), so rarely preserved, are present on some specimens. The zone fossil *Monoclimacis crenulata* is not common but the specimens available preserve its diagnostic features, e.g. sicula, apertural eversion, and genicular spines.

MORPHOLOGICAL TERMINOLOGY

The definitions of morphological terms given by Bulman (1970) are mostly followed here, but some terms applied to dendroids require further clarification; Ruedemann (1947, pp. 23–30) gave a historical review of terminology, later updated by Bouček (1957, pp. 17–25).

Branches. Two types of branching of the stipe are observed in dendroids: *dichotomous branching* (bifurcation) and *lateral branching*. In dichotomous branching the main stipe splits to form either two new main stipes that are usually continuous and go on to bifurcate again (e.g. *Dictyonema*), or two thinner branches that usually terminate rapidly (e.g. *Thallograptus*). Lateral branching was defined by Bulman (1970) as a 'division of the stipe in which branches diverge at an angle to parent stipe, which continues its original direction of growth'. Stipes formed in this way can be either the same thickness and rigidity as the main stipe, or thinner side branches; both types are observed in *Coremagraptus*. Ruedemann (1947) and Kraft (1982, 1984a) used the term 'monopodial branching' to describe how lateral branches form from only one side of the main stipe, but the term is redundant and its use should be abandoned. Genera of the family Acanthograptidae show both dichotomous and lateral branching.

Due to the particular type of preservation of material described in this paper, some of the internal structures of the dendroids can be seen, particularly in the acanthograptids *Coremagraptus*, *Thallograptus*, and *Palaeodictyota*, where the stipes consist of very many elongated tube-like thecae, up to 1 mm long (Bulman 1955, p. 22). When these form a lateral branch as a bundle of tubes, they are known as *twigs* (Bouček 1957, p. 87). The nature of these twigs is discussed below (p. 126).

Connection of branches. There are two ways in which the stipes connect or join: by *dissepiments* and by *anastomosis*. A dissepiment was defined by Bulman (1970, p. 22) as a 'strand of cortical periderm serving to connect adjacent branches in dendroid rhabdosome (especially in *Dictyonema*)'; his definition is followed here. The various types of dissepiment were discussed by Bouček (1957, p. 51). Bulman (1970, p. 23) defined anastomosis as 'temporary fusion, as of adjacent branches to form an ovoid mesh'. The term is used here only to refer to the approach and subsequent joining of two stipes or branches. Any later separation of the stipes is considered a distinct branching episode. When two adjacent stipes come together and anastomose, they then form a single stipe and have not been observed to maintain the separate character of the original stipes; where separate thecal bundles are described, I consider that these represent the superposition of one stipe upon another and not anastomosis.

Meshworks of stipes. Regular meshworks of stipes are formed by anastomosis or by formation of dissepiments. Variation in size and shape of the holes in the meshwork of most dendroids is taxonomically significant, so a consistent terminology is required. Bouček (1957, p. 2) suggested 'meshes' and 'fenestrulae' for the larger and smaller openings in the net respectively. The single term adopted here is *fenestellae*.

SYSTEMATIC PALAEOONTOLOGY

Localities. All specimens were found in the North Esk Inlier, Pentland Hills, Scotland and, unless otherwise stated, they originate from the 'Gutterford Limestone' bed locality in the Gutterford Burn (arrowed on text-fig. 2).

Repositories of specimens. RSM GY, Department of Geology, Royal Museum of Scotland, Chambers Street, Edinburgh; EDNCM, Grant Institute of Geology, King's Buildings, West Mains Road, Edinburgh; GSE, British Geological Survey, Murchison House, West Mains Road, Edinburgh.



TEXT-FIG. 5. *Dictyonema pentlandica* sp. nov. EDNCM 20237, conical proximal end; the rhabdosome is preserved gently folded and reaches a length of 200 mm; superimposed on this specimen are two fragments of *Coremagraptus imperfectus*, $\times 0.75$.

Class GRAPTOLITHINA Bronn, 1849
 Order DENDROIDEA Nicholson, 1872
 Family DENDROGRAPTIDAE Roemer in Frech, 1897
 Genus DICTYONEMA Hall, 1851
Dictyonema pentlandica sp. nov.

Plate 17; text-figs. 5-8

Diagnosis. Rhabdosome broadly conical, up to 400 mm axial length. Terminates proximally with a short stem, 5-10 mm long, either attached to a solid object or accompanied by fine root fibres. Some secondary thickening proximally. Stipes slender, 0.22 mm wide, 17-22 in 10 mm. Dissepiments regularly arranged and very thin, 0.06 mm, 11-13 in 10 mm. Autothecae not known; bithecae simple tubes extending alternately to either side of the stipe with aperture pointing distally, forming distinct swellings of the stipe, closely spaced, 28-30 in 10 mm.

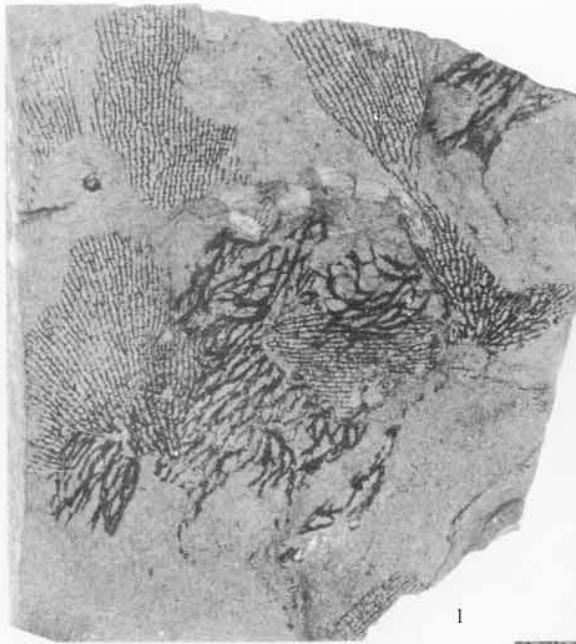
Type material. Holotype RSM GY.1985.30.1. Paratypes RSM GY.1985.29.4 and EDNCM 20237.

Other material. RSM GY.1980.51.5, 1985.29.1, 1985.29.2, 1985.30.2, 1897.32 and thirty-four unregistered specimens in 'Drawer 61' of RSM; and three unregistered EDNCM specimens.

Description. The rhabdosome grew as a broad cone but, due to the extremely large size of this species, it is not possible to tell how wide the cone became. It is commonly preserved with the walls forming broad undulating folds, and this may reflect the original form of the cone (text-figs. 5 and 6). The base of the cone is sometimes secondarily thickened, up to double the thickness of the normal stipe, and has a short stem (text-fig. 7A). No

EXPLANATION OF PLATE 17

Figs. 1-5. *Dictyonema pentlandica* sp. nov. Reservoir Formation, Gutterford Burn (see text-fig. 2); *crenulata* Zone, upper Llandovery. 1, RSM GY.1985.29.1, numerous fragments superimposed, associated with *Coremagraptus imperfectus* Kraft, 1982, $\times 0.5$. 2, RSM GY.1985.29.2, several rhabdosomes showing basal attachment and rejuvenation of meshwork, $\times 0.5$. 3, RSM GY.1985.30.1p, holotype, part of mesh showing an area of rejuvenation, $\times 3$. 4, RSM GY.1985.30.1, part of mesh where thecal structure is preserved; note that a pair of dissepiments is associated with each bifurcation, $\times 10$. 5, RSM GY.1985.29.4, showing secondary thickening of basal region and root fibres, $\times 1$.



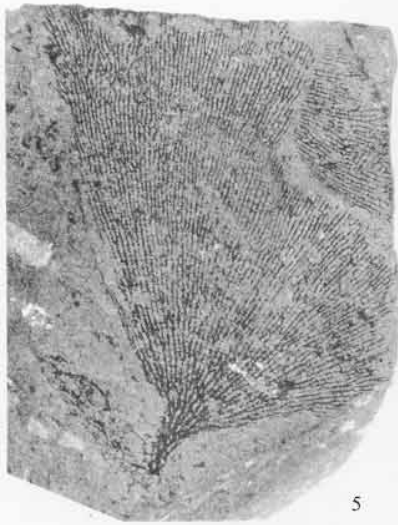
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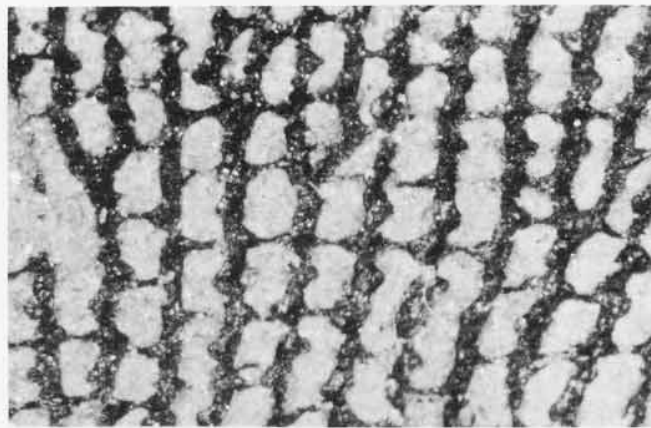
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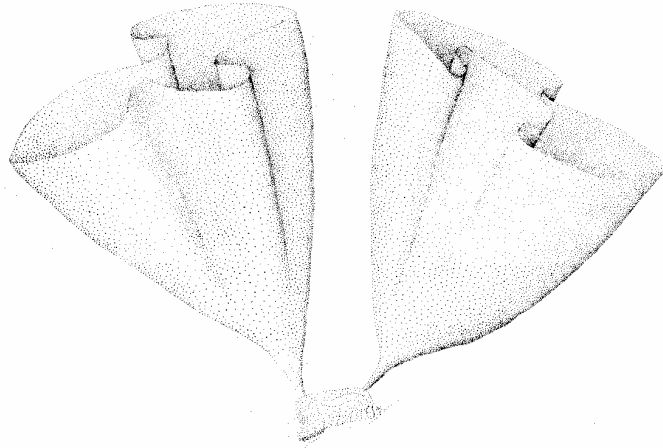
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BULL, *Dictyonema*, *Coremagraptus*

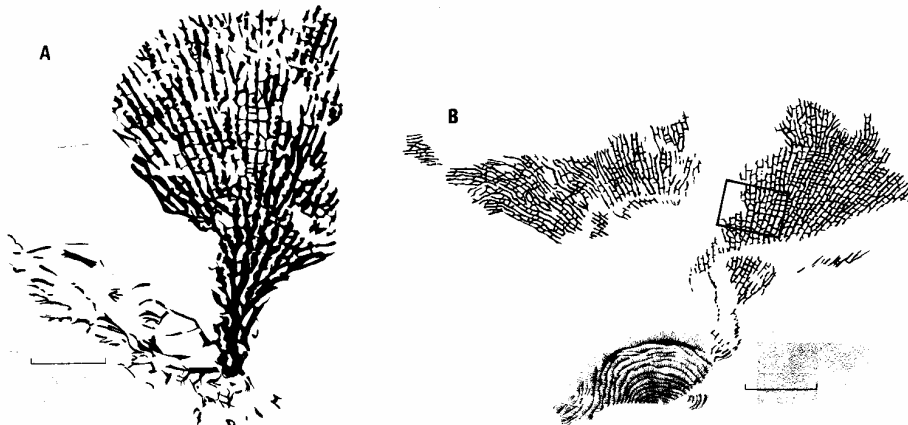
thecae were observed on the stem because of secondary thickening. This species is often found attached to shells (text-fig. 7B) such as *Leptaena* (which lived partially buried in the sediment) or less well-anchored forms, when the stem is accompanied by many small root fibres.

Autothecae are not seen, but the short, tubular bithecae give the rhabdosome a distinctive appearance, being preserved as regular swellings of the stipe (text-fig. 8A) which appear to be 'Type 1' bithecae of Bulman (1933), i.e. simple tubes emerging to the side of the main stipe with apertures pointing distally (see Chapman and Rickards 1982, p. 220).

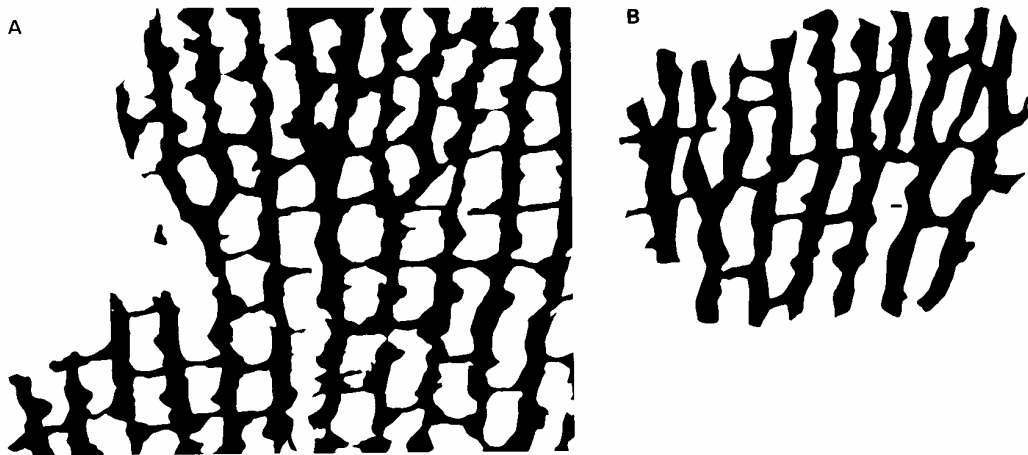
Stipes are straight and evenly spaced, bifurcating regularly every 6 mm; this interval does not become appreciably larger distally. Bifurcation is concentrated on certain stipes, while others are continuous, straight, and unbroken.



TEXT-FIG. 6. *Dictyonema pentlandica* sp. nov. Reconstruction showing the broad conical form; clusters lived attached by a short stem with root fibres to a solid object.



TEXT-FIG. 7. *Dictyonema pentlandica* sp. nov. Modes of attachment. A, RSM GY.1985.29.4, showing secondary thickening of stem and base region, and root fibres for securing stem within sediment. B, RSM GY.1985.30.1, attached to brachiopod shell securely anchored in the sediment (boxed area is shown on text-fig. 8A). Scale bars 10 mm.



TEXT-FIG. 8. *Dictyonema pentlandica* sp. nov. RSM GY.1985.30.1. A, knobby appearance of stipe is caused by presence of large bithecae, $\times 10$. B, dissepiments associated with each bifurcation, $\times 10$.

Dissepiments are of constant length, perpendicular to the stipes, and often form continuous chains across the rhabdosome. Each point of bifurcation is directly associated with two dissepiments—one on either side of the zone of bifurcation (text-fig. 8B). The fenestellae formed by dissepiments and stipes are of fairly constant size (0.6×0.4 mm), and generally rectangular. When dissepiments grow from the swelling of a bitheca the fenestellae may become ovoid. Zones of mesh rejuvenation occur, similar to those described by Bulman (1950) for other species of *Dictyonema*, and are probably related to regrowth after damage (Pl. 17, fig. 3).

Discussion. This species shows considerable resemblance to both *D. delicatulum* Lapworth, 1881 (see Bouček 1957 and Kraft 1984b) and *D. elegans* Bulman, 1928. It is distinguished by: the very distinctive swollen or knotted appearance of the stipe, due to the thecal morphology; the large, very elongated nature of the rhabdosome; and the thinness of the stipes, which are slightly wider spaced ($17\text{--}22$ in 10 mm, rather than $22\text{--}23$ or $20\text{--}24$ respectively).

The general outline of the stipe, caused by the thecal type, closely resembles *D. geniculatum* Bulman, 1928, but is easily distinguished from it by the smaller size and spacing of the stipes. Kraft (1984a) noted the close similarity of *D. delicatulum* and *D. elegans*, particularly in poorly preserved specimens; he stressed that 'their stratigraphic distribution must be taken as the fundamental criterion', *D. delicatulum* being limited to lower Llandovery and *D. elegans* limited to Wenlock. Care should be taken in limiting dendroid faunas to particular stratigraphic horizons; it is uncertain at present whether these three species are stratigraphically useful, as *D. pentlandica* appears to be intermediate both structurally and temporally.

Family ACANTHOGRAPTIDAE Bulman, 1938

Included genera. I follow the classification of Bouček (1957; after Bulman 1938) and distinguish the genera *Acanthograptus* Spencer, 1878, *Thallograptus* Ruedemann, 1925, *Coremagraptus* Bulman, 1927, and *Palaeodictyota* Whitfield, 1902. Holland *et al.* (1967) referred only *Acanthograptus*, *Coremagraptus*, and *Palaeodictyota* to this family and assigned *Thallograptus* to the family Inocaulidae. The evidence presented below shows that *Thallograptus* is much more closely related to the Acanthograptidae.

Discussion. Bouček (1957, p. 86) grouped *Acanthograptus* and *Thallograptus* as forms with 'Rhabdosome composed of individual branches or completely ramified; branches mostly free, not uniting with each other'. Similarly, he grouped *Coremagraptus* and *Palaeodictyota* as forms with 'Rhabdosome infundibuliform, branches more or less flexuose and regularly united by anastomosis'. As I

consider *Acanthograptus* and *Palaeodictyota* to be the two morphological extremes of the family, no subfamilies (*sensu* Bouček) are defined here; since *Acanthograptus* is not found in the North Esk Inlier, it is only considered for the sake of completeness.

Acanthograptus is composed of relatively few tube-like thecae that regularly and continuously branch off from the main stipe in bundles of two autothecae and two bithecae to form very many small twigs, of approximately the same length, along the main stipes and usually ventrally or sub-ventrally. It is possible that all thecae terminate by turning away from the stipe and forming a twig, and that none terminate as pores on the surface of the branch. Bouček's diagrams (1957, e.g. fig. 37f) show some anastomosis of main stipes, but this is probably due to one branch being superimposed on another; indeed the lack of anastomosis seems characteristic of this genus.

Thallograptus is an intermediate form. Like *Acanthograptus*, a major distinguishing feature is the lack of anastomosis, but *Thallograptus* has much less regularity in the arrangement of its twig-like side branches. The main stipes maintain a constant thickness. They bifurcate and also form lateral branches, but the latter gradually become thinner, consisting of fewer and fewer thecae until only one or two remain (text-fig. 11C); this gives the rhabdosome a very spiny appearance (text-fig. 9B). In some species the thinning begins abruptly, giving the branch a swollen appearance (text-fig. 10B) at the base of the terminating twig.

Coremagraptus also has many side branches that thin as the constituent thecae successively reach their full length, although in this genus most thecae terminate together abruptly without one or two thecae becoming distally isolated. *Coremagraptus* shows quite frequent but not always very regular anastomosis. Sometimes two stipes are connected by a number of lateral branches from one joining with another. Side branches are increasingly less abundant in *Thallograptus* and *Coremagraptus*, and not all thecae terminate as discrete twigs (as in *Acanthograptus*). In both genera thecal apertures appear also as pores on the surface of the stipe (text-fig. 13).

Palaeodictyota is characterized by complete anastomosis, and represents the other morphological end member of the family. All thecae terminate within the stipe or as pores on its surface; none form twigs or discrete branches. The main stipes are fairly continuous and rarely bifurcate; the meshwork is formed by lateral branches joining other stipes, creating regular fenestellae with a distinctive and constant size and shape.

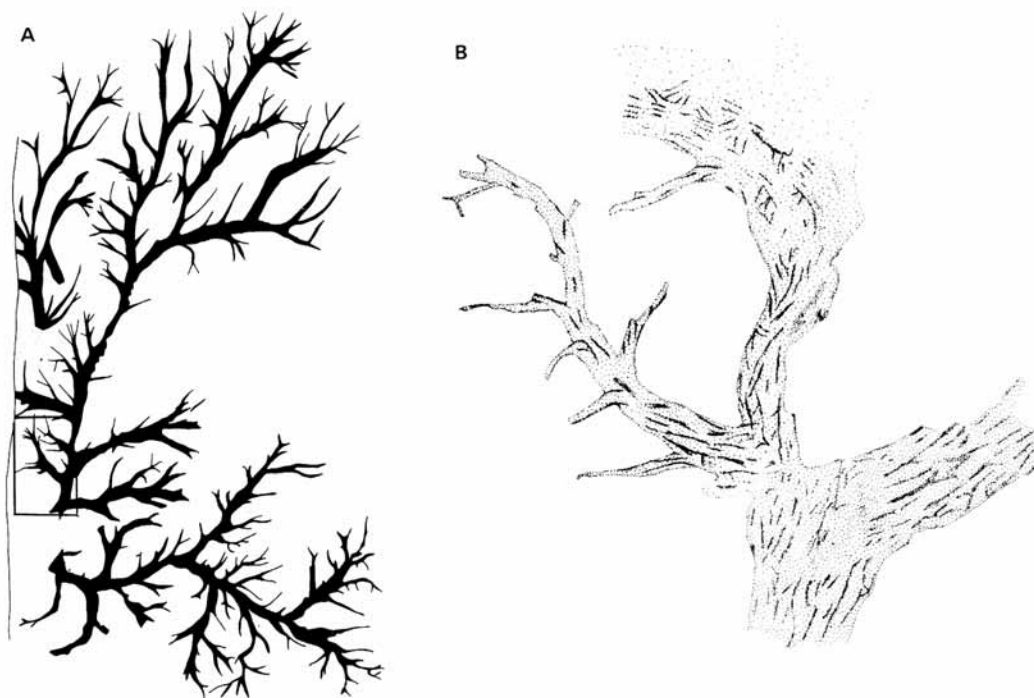
Genus THALLOGRAPTUS Ruedemann, 1925

Type species. *T. succulentus* (Ruedemann, 1904). Lower Ordovician of Deep Kill, New York and Point Levis, Quebec, Canada.

Emended diagnosis. Rhabdosome shrub-like, stipes bifurcating and forming lateral branches irregularly; branches discrete, no anastomosis; thecae tubular, adnate throughout their length, opening as pores on the surface; branches taper to a single theca distally.

Discussion. Ruedemann (1947) assigned *Thallograptus* to the family Inocaulidae, together with the genera *Inocaulis*, *Medusaegraptus*, and *Diplospirograptus*; I follow Bouček (1957, p. 88) in abandoning this classification. Neither the diagnosis by Bulman (1938) nor Ruedemann (1947, p. 230) adequately summarized all of the features of the genus. Ruedemann's reference to 'hair-like filaments' (see Bouček 1957, p. 97) appears either to be a misidentification or to refer to a different genus. Bouček (1957, pp. 97-98) discussed the lack of branch connection by cross-bars or anastomosis, and noted the intermediate nature of this genus between *Acanthograptus* and *Coremagraptus* without formally emending the diagnosis.

Thallograptus is recorded from both the Ordovician and Silurian. Bouček (1957) considered it to peak in numbers during the Ludlow, but it is now known to be common also in the Llandovery (Kraft 1982; this paper). Numerous species have been described (Bouček 1957; Ruedemann 1947; Kraft 1982, 1984a), and these are distinguished by thickness of stipe, length of branches, whether branches appear inflated before termination, angle of stipe, bifurcation, and branching.



TEXT-FIG. 9. *Thallograptus arborescens* Bouček. RSM GY.1985.28.2p. A, rhabdosome with well spaced, tapering branches, $\times 2$. B, enlargement of boxed area on A, showing preservation of thecal tubes and branches tapering to a single theca, $\times 25$.

Thallograptus arborescens Bouček, 1957

Plate 18, figs. 1-4; text-figs. 9 and 10

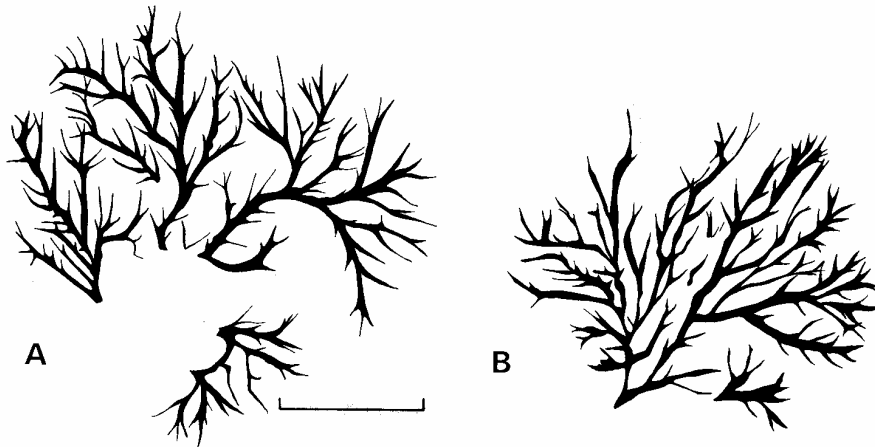
1957 *Thallograptus arborescens* Bouček, pp. 106-107, pl. 23, fig. 4.

Emended diagnosis. After Bouček (1957). Rhabdosome up to 30 mm wide, partially flabellate and shrub-like in form. Main branches approximately 1 mm thick, bifurcating regularly at 30-70°, thinning gradually to 0.5 mm, and nowhere perceptibly inflated. Lateral branching frequent, terminal branchlets 0.4-0.5 mm long, thinning to single theca, and separated by about 2 mm. Branches entirely free without anastomosis or dissepiments.

Material. RSM GY.1985.28.2-1985.28.4 and nine unregistered specimens all located in 'Drawer 62' of the RSM collections; GSE 14161 and two unregistered specimens; and EDNCM 1984.87.3-1984.87.5 and one unregistered specimen.

Description. RSM GY.1985.28.2 is undoubtedly *T. arborescens* and has terminating branchlets tapering from a maximum thickness of 0.2 mm to a single theca thickness (text-fig. 9B) of 0.04 mm, but exceptionally elongated up to 3 mm long. Branchlets curve out at progressively increasing angles from the stipe, which is not straight but changes course slightly at each branching episode. The mean angle of stipe bifurcation is 70°.

Other specimens examined, such as RSM GY.1985.28.3 and 1985.28.4 (text-fig. 10), GSE 14161 (Pl. 18, fig. 4), and EDNCM 1984.87.3-1984.87.5 (Pl. 18, figs. 1-3), are distinguished by a slight thickening at the base of some of the branchlets. All other dimensions are very similar to *T. arborescens* s.s., including main stipe



TEXT-FIG. 10. *Thallograptus arborescens* Bouček. A, RSM GY.1985.28.3p, showing some complete, well-preserved branches, sometimes superimposed. B, RSM GY.1985.28.4, specimen displaying branching pattern and apparent swelling of branch before end. Scale bar 10 mm.

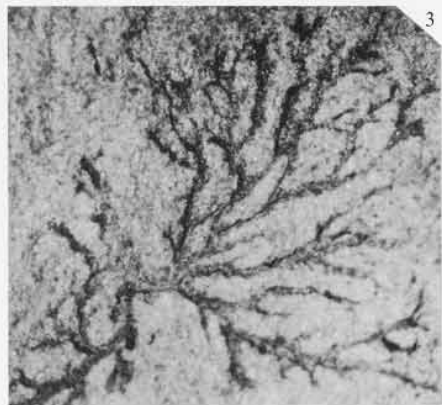
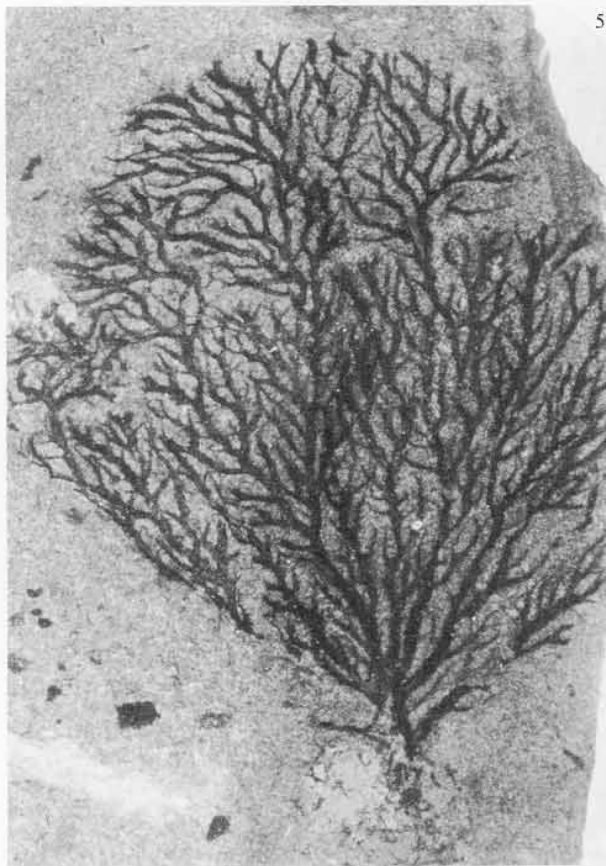
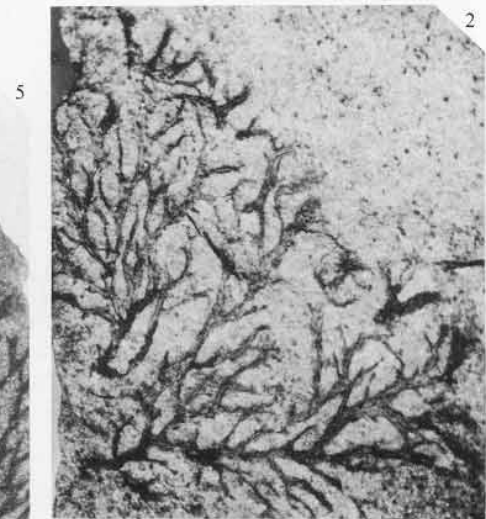
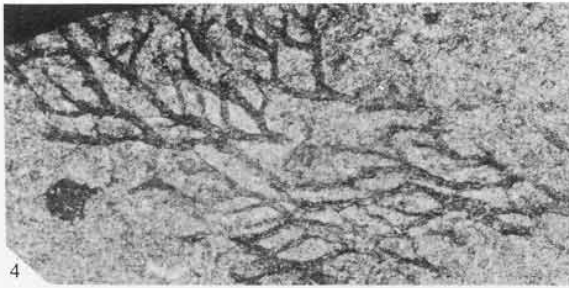
thickness of 0.6–0.8 mm, stipe divergence angle of 45–60°, and branchlets 1–2 mm apart and greater than 1.5 mm long; overall rhabdosome size up to 40 × 40 mm.

Discussion. Bouček noted only four specimens of this species (the holotype and three fragments), gave a diagnosis (emended here), and provided a clear figure (1957, pl. 23, fig. 4) from which it has been possible to identify the specimens figured here. All the present specimens are similar enough to be considered one species. Bouček noted that the branching pattern and lack of inflation of the branches made *T. arborescens* quite unmistakably distinct. Even allowing for a very slight inflation, this species is unlike any other.

Some of the specimens figured here bear previous identification labels. GSE 14161 carries a label by O. M. B. Bulman stating '*Koremagraptus* sp B'; his identification is undated (possibly 1957) and incorrect. Hardie identified RSM GY.1985.28.4 as *Callograptus* cf. *salteri* Hall, while Lamont identified RSM GY.1985.28.2 as *Calyptrigraptus digitatus* Lapworth, 1881. However, *T.* (= *Calyptrigraptus*) *digitatus*, as currently recognized, has a much smaller rhabdosome and thinner branches, despite the resemblance of RSM GY.1985.28.2 to one of Lapworth's figures.

EXPLANATION OF PLATE 18

- Figs. 1–4. *Thallograptus arborescens* Bouček, 1957. 1 and 4, Reservoir Formation, Gutterford Burn (see text-fig. 2); 2 and 3, Unit D of Tipper (1976), Wether Law Linn Formation; all *crenulata* Zone, upper Llandovery. 1, EDNCM 1984.87.3, branches show traces of thecal structure; fine lateral branches taper to a single theca, × 25. 2, EDNCM 1984.87.3, part of rhabdosome with regular branching, × 3. 3, EDNCM 1984.87.4, attached to a pebble and growing out in two directions, × 3. 4, GSE 14161, sparsely branched specimen, × 3.
- Figs. 5 and 6. *T. inaequalis* Bouček, 1957. Reservoir Formation, Gutterford Burn (see text-fig. 2); *crenulata* Zone, upper Llandovery. 5, RSM-GY.1985.28.10, compressed rhabdosome, × 1.5. 6, RSM GY.1985.28.9, distal portion of rhabdosome, × 2.



BULL, *Thallograptus*

Thallograptus inaequalis Bouček, 1957

Plate 18, figs. 5 and 6; text-figs. 11 and 12

1957 *Thallograptus inaequalis* Bouček, p. 107, text-fig. 47b; pl. 21, figs. 4 and 5.

Emended diagnosis. After Bouček 1957. Rhabdosome of medium to large size, composed of separate flabellately shrub-like stocks attached by individual stems to a central stem. Each stock composed of unequally ramifying main branches and thinner lateral branches, forming a dense network. Main branch width 0.7–0.8 mm. Lateral and terminal branches decrease in thickness from 0.5 to 0.2 mm. Branches rarely irregularly inflated. Nine to ten branches in 10 mm.

Material. RSM GY.1985.28.5, 1985.28.7, 1985.28.9, and 1985.28.10, and GY.1897.32 from the Hardie Collection, all located in 'Drawer 62' of the RSM.

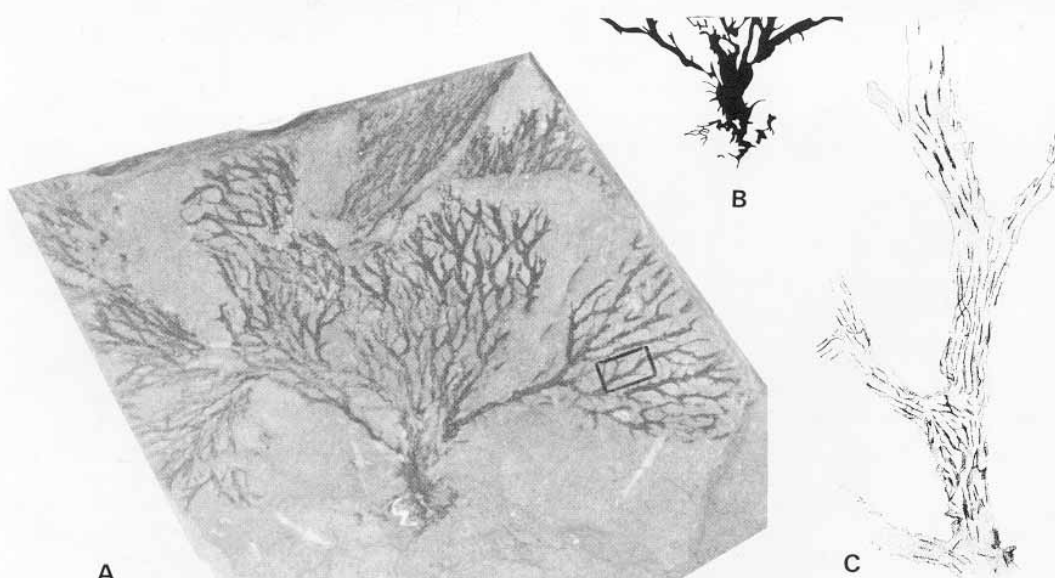
Description. The main central stem is sometimes attached to a shell (text-fig. 11B); secondary stems attach separate stocks to the central stem. Individual stocks number up to six per specimen and are preserved compressed above one another. Branches taper to a single thecal thickness (text-fig. 11C) and are not perceptibly inflated.

Discussion. Bouček (1957) suggested that specimens may differ due to the irregular growth of the branches. As each stock arises from an individual stem, they must have been vulnerable to displacement on deposition (text-fig. 11A), so producing a misleadingly irregular appearance.

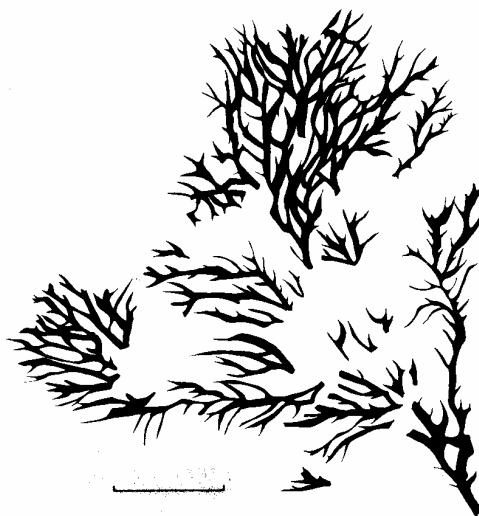
Genus COREMAGRAPTUS Bulman, 1927

Type species. *C. omniensis* Bulman, 1927. Upper Llandovery, Shropshire, England.

Description. The stipe consists of many generations of tightly packed, elongate thecae twisted into a rope-like form. Each theca is about 0.04 mm wide and average side branch width (preserved compressed) is 0.3 mm.



TEXT-FIG. 11. *Thallograptus inaequalis* Bouček. RSM GY.1985.28.7. A, at least six stocks attached to single stem, which is attached to a shell and associated with some root fibres (boxed area shown in C), $\times 1.5$. B, attachment area, $\times 1.5$. C, thecal structure, outline of thecal thickness, and thecal distribution are clear; branches taper to single theca, $\times 15$.



TEXT-FIG. 12. *Thallograptus inaequalis* Bouček. RSM GY.1985.28.5, single isolated stock. Branches appear to anastomose but were merely compressed and superimposed at deposition. Scale bar 10 mm.

Coremagraptus can develop quite large rhabdosomes, at least 130×70 mm. Anastomosis is common but irregular, and usually only the lateral branches are involved. Sometimes two stipes are united by unidirectional lateral branches from one stipe joining another. Numerous species of *Coremagraptus* have been described (Bulman 1927; Bouček 1957; Kraft 1982), the distinguishing features being thickness of stipe, degree of anastomosis, thickness, length, and abundance of lateral branches, and overall size.

Discussion. The nature of the thecae has been discussed at length (e.g. Bulman 1955, p. V27; Bouček 1957, pp. 87, 114). Thecae are not normally observed in unsectioned material, but specimens figured here are preserved as internal moulds, and thecal structure is discernible in the stipe walls. The ends of the side branches are detectably thinner, consisting of a smaller bundle of thecae than the main stipe (although considerably more than the three or four thecae mentioned in Bulman's original diagnosis). Where a pair of stipes are united by unidirectional lateral branches they act as one branch, and are quite often found superimposed on another pair.

Coremagraptus kalfusi Bouček, 1957

Plate 20, fig. 1

1931 *Callograptus* sp. Bouček, pl. 22, fig. 2a.

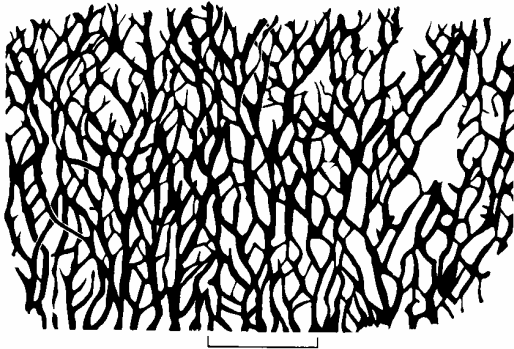
1957 *Coremagraptus kalfusi* Bouček, p. 124, text-fig. 57b; pl. 26, fig. 3.

Diagnosis. See Bouček (1957, p. 124).

Material. One specimen on RSM GY.1985.28.1. Only one other specimen is known, the holotype figured by Bouček (1957) from Lochkov, Bohemia.

Description. The specimen shows distinctive secondary thickening in the basal regions, up to three times normal stipe thickness of 0.4–0.6 mm. New stipes are formed by both bifurcation and lateral branches. Most main branches form dichotomously; most side branches form laterally. Six to seven side branches occur in 10 mm and the angle of bifurcation is $30\text{--}40^\circ$. Side branches reach a mean length of 1 mm before terminating and are more common proximally; they often have blunt ends, and it appears that all thecae ceased to grow when a certain length of branchlet had been attained. Anastomosis is more common distally with fenestellae of a fairly constant sized, elongated oval (2.7×1.0 mm). Overall rhabdosome size, 60×40 mm.

Discussion. This specimen and a specimen of *C. plexus* are on slab RSM GY.1985.28.1 which has been mislabelled '*Acanthograptus* cf. *multispinus* (Bassler)'. It is well preserved; such features as



TEXT-FIG. 13. *Coremagraptus imperfectus* Kraft. GSE 12093, showing unilateral anastomosis, the superimposing of neighbouring stipes, and the presence of short side branches. Scale bar 10 mm.

blunt branchlet ends are unlikely to be the product of damage to the colony during or after deposition.

Coremagraptus imperfectus Kraft, 1982

Plate 19; text-fig. 13

1982 *Coremagraptus imperfectus* Kraft, p. 90, pl. 11, fig. 1; pl. 12, fig. 2.

Emended diagnosis. After Kraft (1982, p. 90). Rhabdosome conical, of medium to large size, up to 120 × 70 mm. Stipes irregularly curved but continuous and 0.4–0.8 mm thick. Stipes occasionally bifurcating, lateral branching at 45–50° common, forming both new stipes and thinner branches. Six to nine stipes in 10 mm. Anastomosis frequent; other branches thin (thecae cease to form), terminate with rounded ends, and are up to 2 mm long. Fenestellae irregular ovoids pointed at each end, 1.0–1.5 mm wide and 2.5–5.0 mm long. Thecae tubular, adnate throughout their length with mean thickness of 0.08 mm.

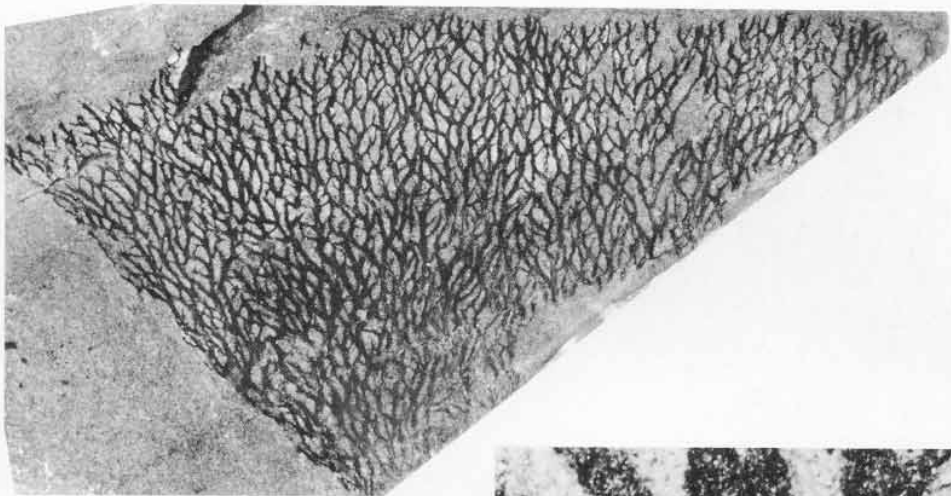
Material. RSM GY.1985.28.8, 1985.28.11 and eight unregistered specimens, all located in 'Drawer 62' of the RSM; GSE 12093 and its counterpart. One other specimen is known, the holotype figured by Kraft (1982) from the Zelkovic Formation, Hyskov, Czechoslovakia.

Discussion. Kraft's original figured specimen is incompletely preserved but is unmistakably conspecific with the material described here. Both have long sections of stipe between each branching or anastomosing episode, and both show a tendency for the lateral branches of one stipe to arise in one direction. These may then join (anastomose) with another stipe that is not at that point producing any branches, so that a 'step-ladder' appears, which is often free to move independently and can be found superimposed over other stipes (text-fig. 13).

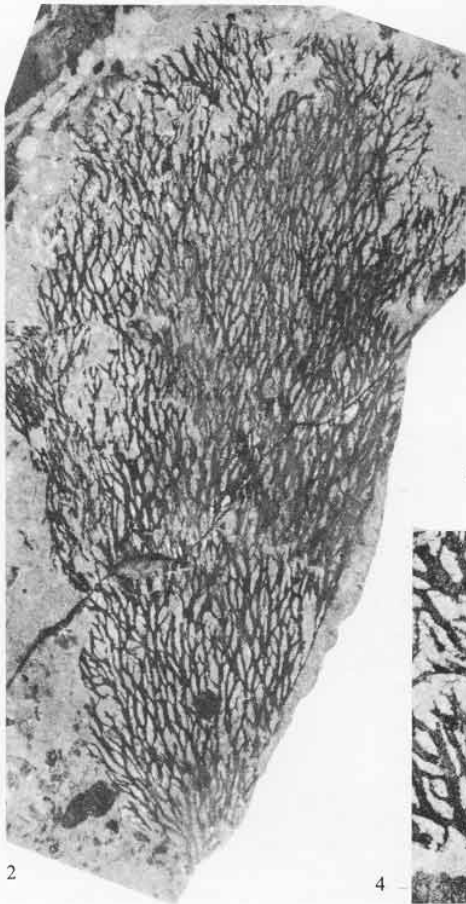
C. imperfectus is fairly similar to *C. spectabilis* Bouček, 1957 (a common species of *Coremagraptus* from the Lochkov beds of Lejskov, Czechoslovakia). *C. spectabilis* has much stouter, thicker stipes, which do not thin towards the ends of the branches, and *C. imperfectus* does not show secondary thickening. Hence *C. spectabilis* is not an adult form of *C. imperfectus*.

EXPLANATION OF PLATE 19

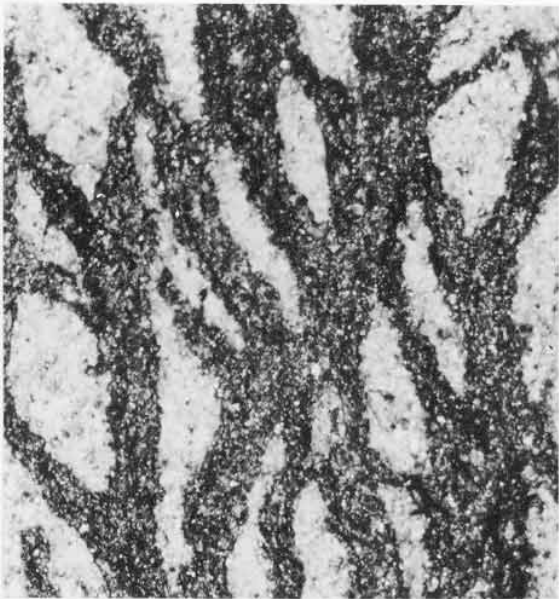
Figs. 1–4. *Coremagraptus imperfectus* Kraft, 1982. Reservoir Formation, Gutterford Burn (see text-fig. 2); *crenulata* Zone, upper Llandovery. 1, RSM GY.1985.28.8, distal region of large, fan-shaped rhabdosome, × 1. 2, RSM GY.1985.28.11, sheared, incomplete fragment, × 1. 3, GSE 12093, showing anastomosis, side branches, and traces of thecal structure, × 10. 4, GSE 12093, showing anastomosis and many terminating side branches, × 2.5.



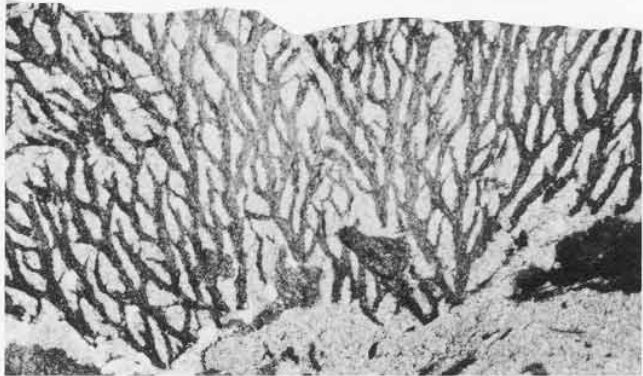
1



2

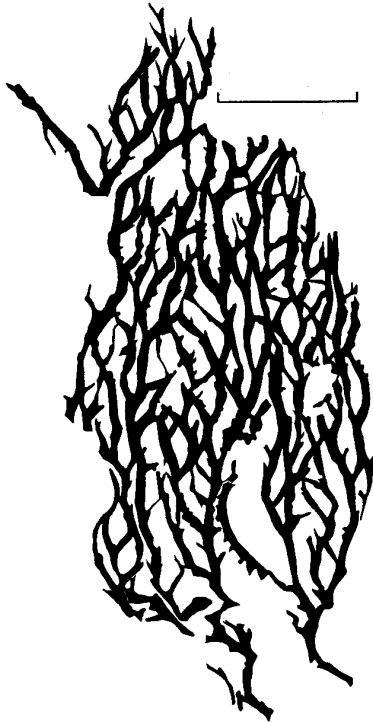


3



4

BULL, *Coremagraptus*



TEXT-FIG. 14. *Coremagraptus plexus* Počta. RSM GY.1985.28.1p, showing regular anastomosis and many short side branches, associated with a short section of *Monograptus spiralis* Geinitz. Scale bar 10 mm.

Coremagraptus plexus (Počta, 1894)

Text-fig. 14

1894 *Desmograptus plexus* Počta, pp. 188-189, pl. 5, figs. 1 and 2 (*non* figs. 3 and 4).

1894 *Desmograptus textorius* Počta, pl. 4, fig. 9 (*non* fig. 8, 8a).

1957 *Coremagraptus plexus* (Počta); Bouček, pp. 117-119, text-fig. 54a-d; pl. 27, figs. 2 and 3; pl. 28, fig. 1; pl. 33, fig. 3.

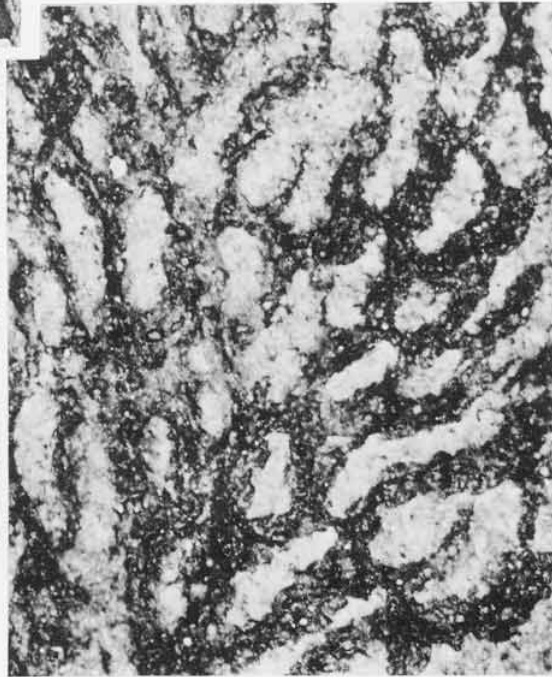
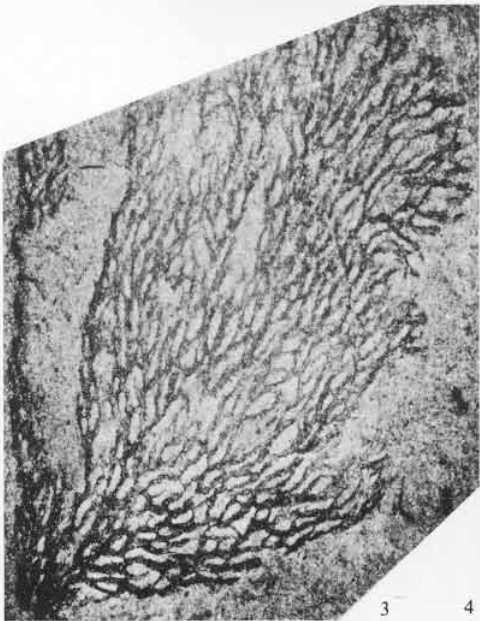
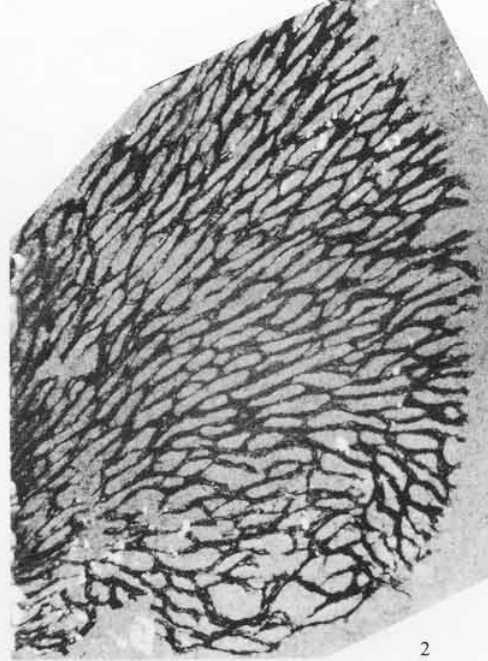
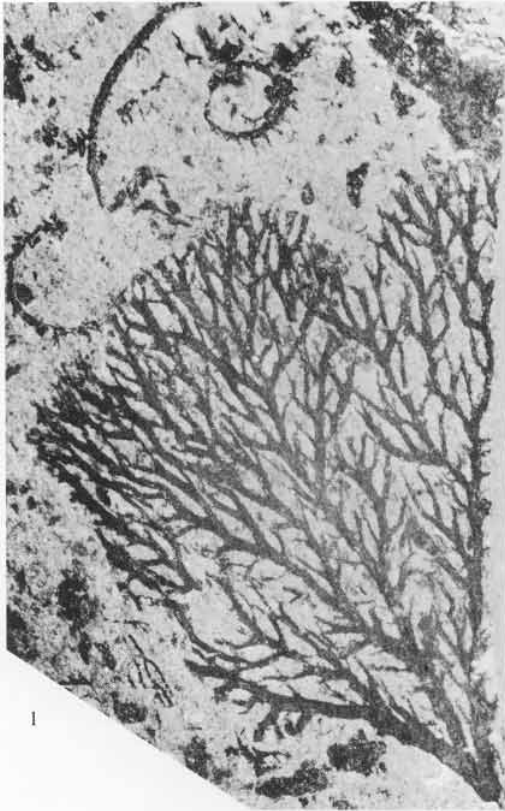
Material. One well-preserved specimen, RSM GY.1985.28.1, a fragment of a larger form.

Description. This species is distinguished by the presence of many short processes on the stipe walls, or very many short side branches 0.2-0.4 mm long. These appear to be bundles of thecae turning away from the stipe together when they have nearly reached total length; this feature is very much more common in *C. pseudoplexus* Bouček, 1957, but the present specimen is from a much older horizon.

EXPLANATION OF PLATE 20

Fig. 1. *Coremagraptus kalfusi* Bouček, 1957. Reservoir Formation, Gutterford Burn (see text-fig. 2); *crenulata* Zone, upper Llandovery. RSM GY.1985.28.1, showing basal secondary thickening, a distal increase in anastomosis, and branches abruptly truncated; associated with *Monograptus spiralis* Geinitz, 1842, $\times 2$.

Figs. 2-4. *Palaeodictyota pergracilis* Hall and Whitfield, 1872. Location as fig. 1. 2, GSE 14163, showing shape of fenestellae and distortion of mesh, $\times 3$. 3, GSE 14164, $\times 3$. 4, showing thecal structure and thecae terminating as pores on the surface of stipes, $\times 10$.



BULL, *Coremagraptus*, *Palaeodictyota*

The specimen figured (text-fig. 14) is on the same mislabelled slab as a specimen of *C. kalfusi* (see above). It is a broken fragment but still quite large (20 × 50 mm). Most branches form through bifurcation of others. Anastomosis is quite common, although some branches were superimposed during compression to appear anastomosed.

Genus PALAEOICTYOTA Whitfield, 1902

Type species. *P. anastomtica* (Ringueberg, 1888) from Ordovician and Silurian of New York, Ontario, and Kentucky, figured by Ruedemann (1947, p. 269).

Diagnosis. 'Rhabdosome of anastomosing branches composed of numerous tubular thecae which are adnate throughout their length and open as pores on the surface of the branches' (Bulman 1938).

Discussion. Bulman's diagnosis is short but adequate, and requires only certain points to be emphasized. The presence of tubular thecae, a characteristic of the Acanthograptidae, distinguishes *Palaeodictyota* from the otherwise morphologically similar *Desmograptus*. *Palaeodictyota* represents an 'end-member' of the Family Acanthograptidae (see above), being characterized by complete anastomosis with no branches terminating separately, except at the outer edge of the rhabdosome. Ruedemann (1947) separated this genus from the Acanthograptidae and referred it to 'Dendroidea incertae sedis'.

Occurrence. Most common in the Wenlock to upper Ludlow of Bohemia; recorded from Ordovician to uppermost Silurian rocks.

Palaeodictyota pergracilis (Hall and Whitfield, 1872)

Plate 20, figs. 2-4; text-figs. 15 and 16

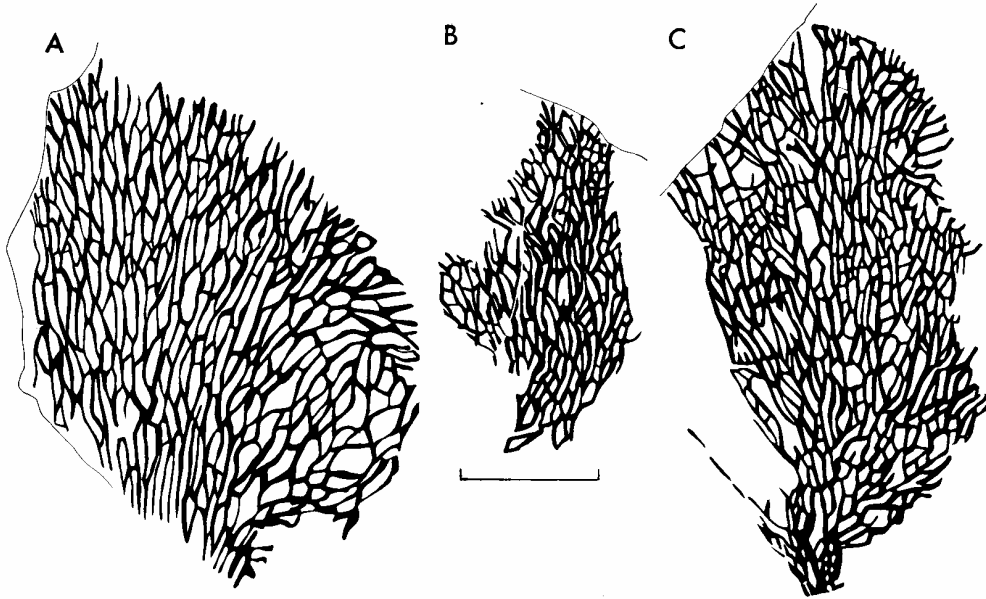
- 1872 *Dictyonema pergracile* Hall and Whitfield, p. 181, figured.
See Ruedemann (1947, p. 272) for 1888-1896 synonymy.
1908 *Desmograptus pergracilis* Ruedemann, p. 2.
1915 *Desmograptus pergracilis* Bassler, p. 403.
1947 *Palaeodictyota pergracilis* (Hall and Whitfield); Ruedemann, p. 272, pl. 23, fig. 10; pl. 30, figs. 10 and 11.

Emended diagnosis. Rhabdosome of medium to small size, 30 × 40 mm, narrowly conical, extending from a short stem. Branches thin and continuous, 0.2-0.5 mm. Bifurcation rare, lateral branching common. Anastomosis complete, branches do not terminate separately. Branches of constant thickness, forming a flexible meshwork with sixteen to eighteen stipes in 10 mm. Fenestellae rounded rectangular, 1.7-4.0 mm long by 0.3-1.6 mm wide. Thecae tubular, adnate throughout, opening as pores on stipe surface.

Material. GSE 14163-14165, and 12040; unregistered RSM specimens in 'Drawer 62' of the museum.

Description. Stem about 3 mm wide and 4 mm long, with stipes branching out from it (text-fig. 15). Branches usually remain straight but are pulled around fenestellae as if it were more important for the fenestellae to maintain a constant shape. The meshwork is also prone to being preserved stretched out at the edges, or compressed (text-fig. 15). Branching and anastomosis follows no regular pattern. Branches maintain a remarkably constant thickness. Thecae open as pores on the surface (text-fig. 16) but the openings are not seen in profile.

Discussion. This species is very similar in general morphology to *P. undulatum* (Počta, 1894) (see Bouček 1957, p. 131), but is distinguished by its much finer branches (less than 0.5 mm, compared with over 1.0 mm). *P. raymondi* Ruedemann, 1947, has similar meshwork dimensions but a much smaller rhabdosome. *P. raymondi* also encompasses extreme variation in mesh shape and size, and shows some secondary thickening, which is not seen in *P. pergracilis*. GSE 14164 and GSE 12040 were identified on specimen labels by O. M. B. Bulman as *Koremagraptus* sp. A (undated).



TEXT-FIG. 15. *Palaeodictyota pergracilis* Hall and Whitfield. A, GSE 14163, showing the mesh stretched at one edge but continuous elsewhere. B, GSE 14165, specimen greatly compressed on deposition, causing mesh to close up. C, GSE 12040, showing usual distribution of mesh, extending from stem region. Scale bar 10 mm.



TEXT-FIG. 16. Thecal structure of *Palaeodictyota pergracilis* Hall and Whitfield. GSE 14163, showing thecae terminating as pores on surface of stipes, $\times 15$.

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