TRIANGULATE MONOGRAPTIDS FROM THE MONOGRAPTUS GREGARIUS ZONE (LOWER LLANDOVERY) OF THE RHEIDOL GORGE (CARDIGANSHIRE)

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[Plates 19 to 23]

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A large collection of well-preserved specimens is used as a basis for a systematic study of *Monograptus 'triangulatus'* and its allies (Monograptids with non-overlapping triangular thecae, defined as Group VI in the *Monograph of British Graptolites*). Critical synonymies, diagnoses, descriptions and resemblances with other species are given, and three species and six varieties are new.

Particular attention is paid to two aspects of the work:

(1) The type of preservation and the changes undergone by thecae on compression. Many of the specimens are pyritized, in full relief, and from these, models were made of the shapes of uncompressed thecae which helped in interpreting the compressed ones. This enables revised descriptions of some species to be given.

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(2) The sequence of forms in the succession. Collection was made from definite narrow horizons and so tentative schemes of evolution could be drawn up. In this connexion some study has been made of *Monograptus revolutus* and related forms. There seems little doubt that *Rastrites longispinus* evolved from *Monograptus 'triangulatus'* and a form intermediate in both morphology and order of appearance has been found.

PART I

Introduction

This study of some Monograptid species having triangular thecae was carried out on abundant material, mainly collected from the Lower Llandovery rocks of the Rheidol Gorge, Pont-erwyd, near Aberystwyth. The geology of the Plynlimon and Pont-erwyd area was described by Jones (1909), and reference should be made to his work for a full description of the Rheidol Gorge section (pp. 483–91). The outcrop of the Monograptus gregarius zone shows a series of alternating blue-grey mudstones without fossils, and darker shales with pyritized graptolites. The present collection was made from the three lower fossiliferous bands of the M. gregarius zone (= Monograptus communis zone of Jones); these he named the Monograptus triangulatus var., M. triangulatus and Mesograptus magnus bands (localities F15, F16 and F17). In the present work the bands were subdivided into sections, mostly 6 in. each in thickness, and the horizons thus established within the bands are shown in figure 1.

The faunas collected from these horizons are given in table 1 and agree in the main with Jones's lists (1909, pp. 488-9), but subdivision of the bands has brought out two points of interest.

The basal horizon of the M. triangulatus var. band (T horizon)— the lowest fossiliferous part of the M. gregarius zone—shows a faunal assemblage much more like that of the beds below it (Monograptus cyphus zone) than that of the higher horizons of the same band (figure 1). In this T horizon, at most an inch thick, no specimens with triangular thecae were found; M. cyphus, however, a diagnostic fossil of the previous zone, is common here but very rare in the beds above and Monograptus sandersoni was found here but not above. There are also species such as Monograptus atavus, Monograptus revolutus and M. gregarius which are common to both zones. This horizon is succeeded by a few feet of unfossiliferous rock before graptolites typical of the M. gregarius zone occur (figure 1). Thus the boundary between the M. cyphus and M. gregarius zones can be identified with some certainty and occurs within Jones's M. triangulatus var. band, near the base, not at the layer of large calcareous nodules $6\frac{1}{2}$ ft. below the base as mentioned by him (p. 488).

Secondly, if my interpretation of the species is correct, in the Rheidol Gorge section the main abundance of what is here called *Monograptus separatus triangulatus* occurs below that of *M. separatus fimbriatus* (figure 1). However, the usually accepted subdivision of the zone is into three:

3. Monograptus argentus

- 3. Monograptus argenteus
- 2. Monograptus triangulatus
- 1. Monograptus fimbriatus

with M. triangulatus above M. fimbriatus. It is thus necessary to discuss further the history of the M. gregarius zone.

It was established by Charles Lapworth in his important paper on the Moffat region (1878), and included beds with M. cyphus and M. sandersoni near the base up to those with

Table 1.	The occurrence of graptolites in the M . Gregarius zone	
	of the Rheidol Gorge	

h	orizon	•••	T	S	R	\boldsymbol{Q}	P	0	N	M	\boldsymbol{L}	K	J	H	\boldsymbol{G}	\boldsymbol{F}	E	DE	D	C	AB	X
species																						
Climacograptus extrem	us		×				×					•				×		×		×		
C. hughesi			×					×								×						•
C. rectangularis								×						×					×		×	×
Rhaphidograptus toern	quisti							×		×	×			X	×	×	×	×	×	×	×	
Orthograptus bellulus	-			٠.									•	5	×	×				٠.		
Glyptograptus sinuatus	;							×				×	×	×	×			•.	×			
G. tamariscus			×					×		×			×		×	×			×		×	
G. tamariscus incertus													×		. ?							
Diplograptus magnus																						×
Petalograptus minor			•																			×
P. palmeus latus																						X
P. palmeus ovato-elong	atus									×	×											×
Petalograptus sp.								×														
Monograptus atavus			×	×			×	×	×		×		×		×	×	×	×	×	×	×	×
M. communis commun	is													×	×	X	×		×	×	×	×
M. communis rostratus						-							×	×	×	×			×	×	×	•
M. concinnus								×			×			5	• •	×	×	·		×		
M. cyphus			×		·								•	Ċ					Ċ	•		
M. cyphus var.								×			×		×						·			
Monograptus cf. gemn	natus of 1	Elles														×			Ċ	Ċ		
& Wood										•			•				•	•	•		•	•
M. gregarius			×				×	×	×		×	×	×	×	×	×	×	×	×	×	×	×
M. intermedius											•		×	×			•				X	
M. ? leptotheca									×		×						×					
M. pseudoplanus													5									×
M. revolutus B			×							•												•
M. revolutus C				×			×	×	×	×	×	×	×	X	×	×	×		×	×		×
M. revolutus D								×			×	×										
M. separatus separatus	5			×	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×	٠.	
M. separatus extremus									×	×	×	×										
M. separatus fimbriatu	ıs														×		×	×	×	×	×	×
M. separatus predecipi	ens			×			×	×		×	×											
M. separatus triangula	itus					×	×	×	×	×	×											
M. toernquisti toernqui	isti				×	×	×	×														
M. toernquisti elongati	ıs						×	×														
M. toernquisti brevis							×	×														
Monograptus sp. 1								×								X		×	×	×		
M. (Diversograptus) ?	capillari	s			•										×							
M. (?Diversograptus)	sanderson	$\imath i$	×											٠.								
Rastrites longispinus															×	×	×	×	×	×		
R. peregrinus																						×

Monograptus lobiferus, M. communis and Monograptus leptotheca at the top. Monograptus convolutus does not seem to have been found at all.

In 1888 Nicholson & Marr established in the Stockdale Shales of the Lake District the three zones:

- 3. M. convolutus
- 2. M. argenteus
- 1. M. fimbriatus

and showed their approximate equivalence to Lapworth's M. gregarius zone. Later papers treating various Welsh areas followed Nicholson & Marr in separating the M. convolutus zone from the beds below, the latter being termed M. fimbriatus or M. communis zone (e.g. H. Lapworth 1900; Elles 1909; Jones 1909).

In the Monograph of British Graptolites, part X (1914) Elles & Wood give the zones:

as equivalent to Lapworth's original *M. gregarius* zone. Thus these authors, presumably with Lapworth's assent, restricted the content of the term '*M. gregarius* zone' and gave the three subzones, bringing together the results from different areas.

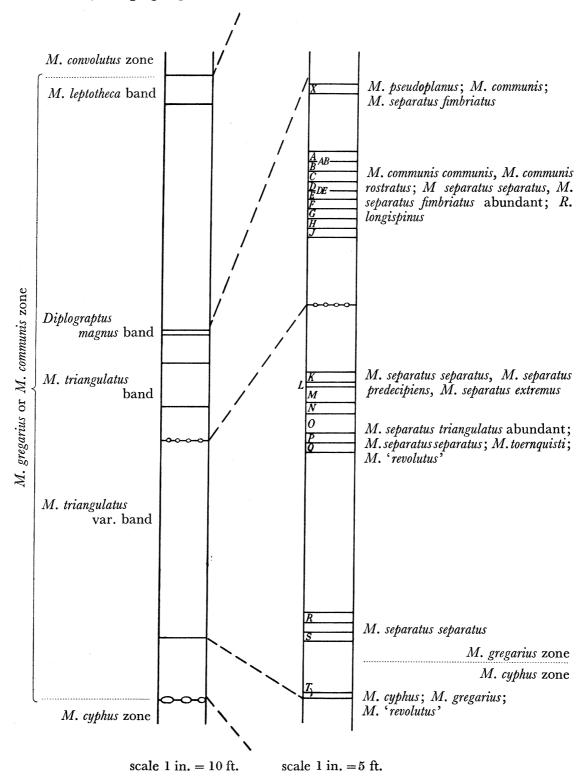


FIGURE 1. Vertical sections of the *M. gregarius* zone of the Rheidol Gorge, to show the subdivisions established and the occurrence of selected graptolites.

Study of the literature on the various regions shows that the *M. gregarius* zone (restricted) falls fairly clearly into two divisions. Of these the upper is generally characterized by *Diplograptus magnus* and *M. leptotheca*, and in the Rheidol Gorge section is represented by the *Diplograptus magnus* and *M. leptotheca* bands. The lower division usually contains *M. fimbriatus* and *M. triangulatus*, and in Rheidol is represented by the *M. triangulatus* var. and *M. triangulatus* bands.

In the Rheidol section, the lower division shows a sudden outburst fo *M. separatus triangulatus* about the middle, although specimens previously referable to '*M. triangulatus*' may occur throughout it. This is paralleled in the detailed sections given for other regions (e.g. Moffat—C. Lapworth 1878; Rhayader—H. Lapworth 1900; Conway—Elles 1909) in all of which special mention is made of a band where *M. triangulatus* is particularly abundant.

There is also, in the Rheidol Gorge, a sudden abundance of M. separatus fimbriatus (= 'M. fimbriatus') in the lower division, but this occurs above the M. separatus triangulatus outburst. Again, however, specimens previously referable to 'M. fimbriatus' occur throughout. In addition, Rastrites spp. are first seen in the M. triangulatus band in association with the M. separatus fimbriatus outburst, but do not occur below (figure 1). In the Scottish and Welsh areas mentioned above also, Rastrites seems to be confined to the upper part, above the outburst of M. separatus triangulatus.

The Skelgill (Westmorland) and Llanystwmdwy (near Criccieth, Caernarvonshire) sections appear to be exceptions to the general succession as outlined above. In Skelgill the *M. gregarius* zone of other regions is represented by the *M. fimbriatus* and *M. argenteus* zones, and these two divisions correspond roughly with the two divisions in other areas mentioned above. The species *M. triangulatus* is not common in the faunal lists given by Marr & Nicholson (1888), but there are two possibilities which would explain this difference:

- (a) The much smaller thickness shown at Skelgill (7 ft. in the *M. fimbriatus* zone compared with up to 60 to 70 ft. in Wales and possibly 15 ft. at Moffat), so that minor segregations would not be noticed unless collection is made inch by inch.
- (b) The base of the M. fimbriatus zone at Skelgill is everywhere faulted, and although Marr thought that not much was missing from the section, it may be that the horizon of abundant 'M. triangulatus' is faulted out.

The only account of the Llanystwmdwy rocks is that given by Fearnsides in his report of an excursion to the Portmadoc district (1912). The section is apparently very similar to that at Skelgill, although the base is somewhat uncertain. It is stated that 'the exposure begins some few feet below the zone of M. fimbriatus, but no fauna sufficient to determine the Dimorphograptus or Orthograptus modestus zone has yet been collected'. The M. fimbriatus and M. argenteus zones are each about 2 ft. thick and the M. fimbriatus zone in particular is rich in graptolites. Examination of Fearnsides's specimens in the Sedgwick Museum gave the following faunal lists (Monograptids only):

M. fimbriatus zone
M. atavus
M. 'revolutus'
M. separatus separatus
M. separatus triangulatus
M. separatus s.l.
? Monograptus toernquisti brevis

M. argenteus zone
M. atavus
M. 'revolutus'
M. argenteus
M. argenteus
M. separatus s.l. (one specimen)

The most interesting feature is that the 'M. fimbriatus' zone has no M. separatus fimbriatus, but M. separatus triangulatus is common. These rocks would therefore seem to represent a slightly lower horizon than the M. fimbriatus zone of Skelgill.

Whatever the relationship of the Skelgill and Llanystwmydwy sections with the others in Wales and Scotland previously discussed, the sequence described above from the Rheidol Gorge indicates that it would be misleading to retain the subdivision of the *M. gregarius* zone proposed by Elles & Wood. To transpose the two lower subdivisions would undoubtedly cause confusion, and it is perhaps more in accord with present knowledge to combine the two lower subzones, giving:

- 2. M. argenteus
- 1. M. triangulatus-M. fimbriatus

PRESERVATION

Types of preservation

Most of the specimens are preserved in pyrite. The best are in full relief, the material of the fossil consisting of three parts:

- (1) An internal mould of the skeleton of the colony in yellow pyrite, which may be smooth, showing traces of growth-lines as a series of parallel furrows, or of a rough granular appearance, or even with the surface broken by growths of cubic crystals.
- (2) Covering this, a thin brittle film of silvery or blackish material which also, if the conditions are suitable, shows growth-lines as grooves. This also is probably an internal mould, but very closely related to the original chitinous* wall of the theca.
- (3) A relatively thick layer of a greenish white waxy material which has been identified as a chlorite mineral of the pennine group.† This coats the thecae and also extends into subsequent cracks in the pyrite moulds. Thus it was apparently a later addition and shows only the general outline of the thecae from its outer surface. In preparing the fossils for examination it is flaked off with a needle where it still adheres to the specimen.

In other cases, particularly in specimens from the *Diplograptus magnus* band, the thecae are preserved in something less than full relief. These consist of a brittle silvery film which can show growth-lines as grooves and is comparable with layer 2 above. It often shows an irregular, folded surface, indicating that compression took place soon after the colony came to rest on the sea-floor and was probably due to the weight of later sediment. Within this is a powdery black material (?pyrite—cf. layer (1) above). An outer layer of chlorite ((3) above) is present on both sides of the compressed thecae, but the rock usually breaks so that the fossil and underlying chlorite remain on one piece, while a chlorite impression is seen on the counterpart. These chlorite impressions are also seen if the pyritic layer has flaked off.

The effects of primary compression

Compression which has taken place soon after deposition can substantially alter the appearance of a theca. Monograptids of the type under discussion, with non-overlapping

- * The term 'chitin' is employed throughout for convenience only and does not imply exact knowledge of the substance forming the graptolite rhabdosome.
 - † This determination was made by Dr J. M. Hancock, to whom I am grateful for the information.

thecae, may be considered as a series of open-ended tubes, the metathecae, free at one end and at the other opening into a 'common canal' tube which runs at right angles to the thecal tubes. When this structure is laterally compressed the height of the metathecal tubes is not appreciably altered, the main effect being to widen the common canal region and produce an apparently closer packing of the thecae (figure 2). This is well shown by the specimen figured on figure 54, plate 20, where the last five thecae are in relief and the earlier ones compressed; although normally a slight increase in width of theca is expected from one to the next, here there is a definite decrease between adjacent compressed and uncompressed thecae, the sixth and seventh seen.

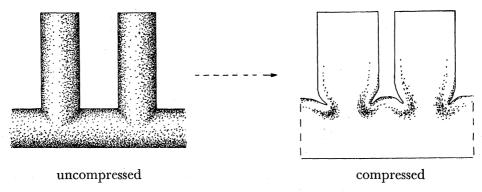


FIGURE 2. Diagram showing the effect of lateral compression on tubes at right angles.

In general, the thecae under discussion are triangular in side view, with a hooked apertural part, and in face view they widen gradually but markedly from the base. The hook is seen to be one of a pair of horns, while the central region of the aperture is more enrolled than the horns, forming a median dorsal lip (e.g. Monograptus separatus and its varieties, M. convolutus, M. toernquisti—see the figures of models of such thecae on plates 20 to 22.

Compression of this structure produces three main changes:

- (1) A closer packing effect.
- (2) An increase in breadth of the common canal.
- (3) A parallel-sided appearance of the thecae, because the apertural region which was the narrowest part in side view was also the broadest in face view.

These changes are most marked in thecae of the *M. separatus fimbriatus* type (see figure 51, plate 19), which widen quickly from the base and have no cylindrical common canal part to the theca. In compressed specimens the proximal and distal walls become almost parallel and the thecae appear close-set, even touching at the base. This feature is in large part responsible for the appearance usually thought typical of '*M. fimbriatus*' (see figure 47, plate 19) and can also give a 'fimbriatus' appearance to compressed thecae of *M. separatus separatus*. Each theca shows one or two ridges along its length, either on the central part or at the ventral and dorsal edges. These often represent the lateral parts, terminating in the horns, and their exact arrangement depends on the nature and amount of material inside the theca as it was compressed, and on the degree of post-mortem torsion, if any. Symmetrical compression is the more usual (figures 44, 47, plate 19), although there are a few clear cases where torsion has been involved. Then the aperture may face away from

(figures 48, 49, 63, plates 19 and 20), but occasionally towards, the observer (figure 46, plate 19).

With *M. separatus triangulatus* thecae the same changes are observed, but the close-packing effect is less marked since the original thecae were more slender, taller and wider-spaced. When compression was symmetrical there is, again, often a ridge along the centre of the theca, with proximal and distal bulges which give the 'leaf-like' appearance seen in figure 62, plate 20. With the enrolled part of the dorsal lip preserved, a 'beaked' appearance is produced (figure 61). Both these, but especially the latter, have been usually considered typical of *Monograptus* 'raitzhainiensis' since Elles & Wood's description (1913, p. 473).

In *Monograptus pseudoplanus* compressed thecae only are known, and again the folded surface indicates lateral broadening towards the aperture (figures 94, 96, plate 22). Thus a tentative model of the uncompressed theca has been reconstructed in the light of the facts noted above.

Closely related to these triangular thecae are the rastritiform ones, with transversely expanded apertures but a thecal segment consisting of two narrow cylinders at right angles, the common canal part and the metathecal tube. In the latter, the lateral widening is small relative to the height of the thecae. This kind occurs in Rastrites spp., and in the early thecae of M. separatus triangulatus and M. convolutus. Compression follows the same lines as described above for triangular thecae, but the change in shape is much less marked because of the cylindrical nature of the parts and their small diameter compared with the height of the thecae. Thus a compressed theca is still easily recognizable as rastritiform. In some cases a beaked appearance may be produced (figure 54, plate 20), but twisting occurs easily, especially with the really attenuated thecae, and the aperture may again face towards or away from the observer, giving a blunt-ended appearance. The effect of compression on the excavations between the thecae and on the common canal part is slight.

In the 'elongated' thecae (see later, p. 516 and figure 89, plate 22) of the proximal parts of *M. toernquisti* and *M. pseudoplanus* the effect of compression is slight. A very little broadening of the prothecal tube occurs, and the expansion is usually represented by a slight ridge on the metatheca which dies out towards the protheca (figure 94, plate 22).

In nearly all these cases there has been production of ridges and hollows along the length of the theca. This is often seen, and has been many times illustrated (see figure 13, p. 512) in completely compressed specimens now preserved as carbonaceous films or mere impressions in the rock. Presumably, then, these graptolites also were flattened soon after deposition.

Another interesting corollary is the 'phleoid' appearance of some *Rastrites* specimens, described as a separate species, *R. phleoides*, by Törnquist (1887, p. 490) and Přibyl (1942, p. 17). Elles & Wood (1914, p. 491) suggested that this was a preservational effect, and their idea is now strengthened; the phleoid appearance would be given by compression of a rastritiform theca with the horns prolonged into spines, the theca being twisted so that both projections are seen.

The thecae of *Monograptus spiralis* and *Monograptus planus* are also transversely expanded but differ from the forms already described in that the broadening is limited to the hooked apertural part and the main body of the theca is of a constant, fairly small width (figures 82, 92, plates 21 and 22). This part changes little in shape on compression. The apertural part

is very often twisted to one side, so that the aperture faces to the left or right and its dorsal margin is seen on the other side. When the rock breaks open the fossil adheres to it where the matrix penetrates the aperture so that the dorsal surface of the apertural region is nearly always seen. Thus the thecal aperture appears elongated and the height of the theca looks greater than it really is (compare the figures of *M. spiralis*, figures 81, 82, plate 21). The same effect is seen in *M. planus* (figures 92, 93, plate 22), but here the spines are shorter and the apparent change in shape is consequently less great.

Thecae which are not transversely expanded at all show little change on compression. Of the forms described here, the thecae of *M. communis* are the only such ones. The shape of the solid thecae can be seen from figures 100 and 101; and figure 106, plate 23, shows one theca in full relief and a number in half-relief. Here the folds in the thecal wall are indefinite and the only change is a certain broadening of the thecae, with sometimes a slight bulge on the ventral margin. If the hook is poorly preserved or exposed there may be variable appearances in the apertural region (figure 106, plate 23).

The effect of secondary compression

The mudstones and shales containing these fossils also show evidence of compression across the bedding planes, which is obviously a later feature, and although cleavage is not usually developed a lineation is always apparent, sometimes, at least, being caused by a series of minute ridges in a bedding plane surface which represents very small-scale folding. This later compression has had effects on the graptolites also. The main action has been to fracture the solid pyrite moulds, often at the thinnest and weakest places.

One variation created by this compression concerns the number of thecae per centimetre in the rhabdosome. This varies in the *M. separatus* group between 7 and 8 when the axis of the rhabdosome is parallel to the lineation of the rock and 14 and 15 when it is perpendicular. The high figure is largely due to compression, and in some specimens the rhabdosome can be seen to be buckled into 'anticlines and synclines' (figure 77, plate 21). More often the fossil is broken at the narrow common canal part of each thecal segment and the thecae are pushed over one another (figure 56, plate 20; figure 99, plate 23). Probably the average figure for uncompressed rhabdosomes is about 9 or 10 thecae per cm, as values such as this are common in rhabdosomes parallel to the lineation.

Another effect is seen particularly in the slender distal thecae of *M. separatus triangulatus* and *M. toernquisti*, where the pyrite mould is often broken across near the base, especially if the rhabdosome is at an angle to the lineation of the rock. Then the distal parts of the thecae may be bent backwards, exaggerating any backward-sloping appearance the thecae may have had (figures 38, 39, plate 19). The broader thecae (e.g. *M. communis*) are sometimes affected similarly, but the general result is less noticeable.

This compression has also affected the shape of the rhabdosome as a whole: if it is perpendicular to the lineation the curvature will appear greater than it really was; if the two are parallel it will appear less. It is interesting that in all cases seen here where the rhabdosome appears to be straight in the distal part, it lies parallel to the lineation, and thus may originally have had at least a slight amount of curvature.

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PART II

Descriptions of the species Genus MONOGRAPTUS Geinitz 1852

Monograptus separatus sp.nov.

(Plates 19, 20 and figures 67 to 70, plate 21)

- 1853 Monograpsus Becki Richter, p. 459 (pars), pl. XII, fig. 25, non figs. 23, 24.
- 1913 Monograptus triangulatus Elles & Wood, p. 471, text-fig. 327c (remaining figures under this heading are M. separatus separatus or M. separatus triangulatus).
- 1913 Monograptus raitzhainiensis Elles & Wood, p. 473, pl. XLVIII, fig. 3c, text-fig. 329 b (remaining figures under this heading are M. separatus separatus or M. separatus triangulatus).
- 1913 Monograptus communis var. rostratus Elles & Wood, p. 481 (pars), pl. XLIX, fig. 2a, non pl. XLIX, fig. 2b, text-fig. 337 (fig. 2c=M. separatus separatus).
- 1943 Demirastrites münchi Přibyl, p. 8, text-figs. 2A, B, D (fig. 2C = M. separatus separatus). (The above can only be referred to M. separatus s.l.)

Holotype. The specimen figured as figure 37, plate 19, from horizon D, M. triangulatus band, M. gregarius zone, Rheidol Gorge, Pont-erwyd, near Aberystwyth. Sedgwick Museum, SM. A 24438.

Paratypes are listed under separate varieties.

Number of specimens (including all varieties). About 600.

Horizon and localities.

M. gregarius zone, Rheidol Gorge

M. triangulatus var. band, horizons S, R, Q, P, O, N, M, L, K.

M. triangulatus band, horizons J, H, G, F, E, DE, D, C, AB.

Diplograptus magnus band, horizon X.

Material also seen from

Southern Uplands: Dobb's Linn, Moffat.

Lake District: Skelgill, Spengill Head, Gt. Rundale Beck.

Yorkshire: Hunterstye, near Austwick.

North Wales: Anglesey.

Central Wales: Rheidol Gorge, M. leptotheca

band, Abergwesyn.

Northern Ireland: Donaghadee, Pomeroy, Desertcreight, Co. Tyrone.

Diagnosis. Rhabdosome curved, proximal portion bent through 180° or more, but not spiral, distal part gently arched. Thecae on the convex side, with no overlap. The terminal part of each theca is bent over towards the proximal end, forming a hook as seen in side view; the aperture is transversely elongated.

Sicula small; first theca triangular, elongated in the direction parallel to the length of the sicula, with a small metathecal part; a variable number of the succeeding early thecae

(0 to 12) approach a *Rastrites*-like form in having dorsal and ventral walls parallel or subparallel in side view, and in being separated from one another by a prothecal portion of uniform width; these grade into triangular distal thecae, fairly well spaced and elongated in the direction perpendicular to the axis of the rhabdosome. Mature thecae 8 to 14 in 10 mm, 1·4 to 2·0 mm high, commonly 1·6 mm.

Description. The fish-hook curvature of the proximal part of the rhabdosome distinguishes this species from the spirally coiled M. convolutus group. The region of maximum curvature is often limited to two or three thecae and usually occurs between th 3 and th 7. The succeeding gentle curve of the distal part continues throughout the length of the rhabdosome in undistorted specimens. Fairly complete specimens may be about 30 mm long; the maximum seen is about 70 mm, in M. separatus triangulatus.

The sicula is generally less than 1.0 mm long and is about 0.1 mm across at the aperture. The first theca arises 0.1 to 0.35 mm from the aperture, and in the different varieties is from 0.6 to 1.0 mm long, thus extending beyond the tip of the sicula. It begins with a slowly widening protheca; near the tip of the sicula the rate of prothecal widening increases, initiating the triangular shape which is completed by the growth of the metatheca (figure 33, plate 19).

This general appearance of the sicula and first theca characterizes all varieties of this species. Differences which can be seen in the more extreme varieties consist mainly in slight changes of shape and measurement of the metatheca, not obvious because it is so small. This relative constancy contrasts with the considerably greater variation of succeeding thecae (th2 onwards) on which the varieties are in fact distinguished.

The subsequent thecae show a Rastrites-like form in the possession of the following characters: (a) initial prothecal part long, narrow, cylindrical (i.e. parallel-sided when seen in side view); (b) metatheca (i) of great height and small width in side view, (ii) with parallel dorsal and ventral walls (i.e. again cylindrical). The number of such thecae present in any form varies from 0 to 12, and the degree of Rastrites-likeness also varies. In general, in a variety which has a few rastritiform thecae these are only moderately Rastrites-like, whereas a variety with many shows the more extreme type. For details, see the diagnoses and descriptions of the separate varieties. In all cases they grade more or less imperceptibly into the distal triangular type.

The distal thecae show a good deal of variation within the limits of the general term 'triangular'. On the whole this runs parallel with the differences in the proximal end which determine the varieties; but, as is to be expected in a series of populations which are gradually changing, there are all grades of intermediate forms between the extremes. Thus it is usually impossible to assign a given distal fragment to anything other than 'M. separatus s.l.'.

The commonest type of theca, which may be regarded as central within the range of variation, is seen in side view as a triangle about 1.6 mm high and 0.8 mm across at its base (figures 3a, b). The dorsal and ventral walls are thus at an angle of about 30° to each other. This part is separated from the previous thecal segment by the early protheca, which widens slowly at first. Then its rate of widening increases and it merges into the main triangular part. The dorsal wall of the theca stands more or less perpendicular to the rhabdosome axis, or is slightly inclined towards the distal end.

This type is fairly common in M. separatus separatus and also in both M. separatus fimbriatus and M. separatus triangulatus. In both the latter, however, variations occur, affecting three main features: (a) height of the theca; (b) length of the initial prothecal part; (c) angle between the dorsal and ventral walls of the theca (which can be measured only approximately, because of the curvature of the walls). There are two extremes of thecal variation:

(1) When the height is small the protheca usually widens rapidly from the beginning so that the angle between the dorsal and ventral walls of the metatheca is greater than in the central type described above, and there is no slowly widening prothecal part (figure 3c). In side view the theca is therefore bluntly triangular with a 'fatter' appearance than the central form. The specimens of M. separatus separatus near M. separatus fimbriatus mostly approach this type, and it is common also in M. separatus fimbriatus itself.

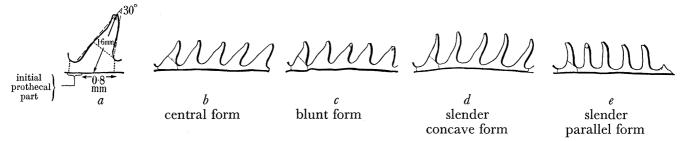


Figure 3. Distal thecae of M. separatus to show the variation in form. (Magn. $a \times 10$, rest $\times 5$ approx.)

(2) Where the thecae are of greater height the initial prothecal part widens slowly. The ventral wall may become concave in form (figure 3d), or may make a fairly distinct angle with the common canal (figure 3e), in which case the thecal walls are usually almost parallel. The thecae have a more slender and isolated appearance than in the central type: they occur in most of the specimens of M. separatus triangulatus seen.

The extreme type of theca seen in figure 3e does occur in M. separatus triangulatus (figure 56, plate 20), but it is typical of M. separatus extremus, where, as far as the distal thecae have been seen, they are of this form and about $2\cdot 0$ mm high.

Resemblances. The distal thecae of M. separatus are triangular with a height/length ratio of 1.5 to 2.0. This distinguishes them from (a) M. convolutus (Hisinger), where the ratio is usually more than 2, and (b) M. communis communis Lapworth, M. communis rostratus Elles & Wood, M. pseudoplanus sp.nov., M. spiralis (Geinitz), M. planus (Barrande) and Monograptus denticulatus Törnquist, where the height is not usually more than 1.5 times the length. The distal thecae of M. toernquisti sp.nov. are more difficult to distinguish; the thecae of M. toernquisti begin to bend forward to form the hook about half-way along the metatheca, whereas in M. separatus the hook is near the tip of the theca (figure 16, p. 516).

Monograptus separatus separatus var.nov.

(Figures 33 to 39, plate 19)

- ? 1852 Monograpsus triangulatus Geinitz, p. 47 (pars), pl. V, figs. 1, 2, non figs. 3-8.
- 1897 Monograptus triangulatus Perner, p. 14 (pars), text-fig. 12, ?non pl. 12, figs. 16, 30.
- 1912 Demirastrites pectinatus Eisel, p. 39 (pars), pl. III, figs. 16, 17, non figs. 18, 20.

- ? 1912 Demirastrites communis Eisel, p. 38 (pars), pl. III, fig. 19, non figs. 14, 15, 21.
- 1913 Monograptus decipiens Elles & Wood, p. 469 (pars), pl. XLVII, figs. 3c, d, textfig. 325c, non pl. XLVII, figs. 3a, b, e, text-figs. 325a, b.
- 1913 Monograptus triangulatus Elles & Wood p. 471 (pars), text-fig. 327a, ?pl. XLVII, figs. 4b, e, non pl. XLVII, figs. 4a, c, d, f, text-figs. 327b, c.
- 1913 Monograptus raitzhainiensis Elles & Wood, p. 473 (pars), pl. XLVIII, fig. 3b, non pl. XLVIII, figs. 3a, c, text-figs. 329a, b.
- 1913 Monograptus communis var. rostratus Elles & Wood, p. 481 (pars), pl. XLIX, fig. 2c, non pl. XLIX, figs. 2a, b, text-fig. 337.
- 1913 Monograptus fimbriatus Elles & Wood, p. 482, (pars), pl. XLVIII, fig. 4b, ?fig. 4c, non pl. XLVIII, figs. 4a, d, text-figs. 338a-d.
- ? 1933 Monograptus turriculatus var. dimorpha Sun, p. 41 (pars), pl. III, fig. 2a, non fig. 2b.
- ?1942 Demirastrites triangulatus triangulatus Přibyl & Münch, p. 3 (pars), text-fig. I, 3, non pl. I, figs. 1–5, text-figs. I, 1–2.
- ?1942 Demirastrites pectinatus Přibyl & Münch, p. 7 (pars), text-fig. I, 5, non pl. I, fig. 6, text-fig. I, 4.
- ?1943 Demirastrites münchi Přibyl, p. 8 (pars), text-fig. 2C, non text-figs. 2A, B, D.

Holotype. The specimen figured in figure 37, plate 19, from horizon D, M. triangulatus band, M. gregarius zone, Rheidol Gorge, Pont-erwyd, near Aberystwyth. SM. A24438.

Paratypes. SM. A24433-37, A24439 (figures 33 to 36, 38, 39, plate 19).

Number of specimens. About 200.

Horizon and localities.

M. gregarius zone, Rheidol Gorge M. triangulatus var. band, horizons S, R, Q, P, O, N, M, K

> M. triangulatus band, horizons J, H, G, F, E, DE, D, C.

Material also seen from

Southern Uplands: Dobb's Linn.

Lake District: Skelgill, Spengill Head.

Central Wales: Rheidol Gorge (Diplograptus magnus and M. leptotheca bands).

Northern Ireland: Donaghadee, Pomeroy.

Diagnosis. Shape of the rhabdosome, thecal apertures and sicula and first theca as described above (p. 494); thecae after the first—as few as two or as many as seven— Rastrites-like in form; subsequent thecae triangular.

Description. The sicula and first theca have been seen in only a few specimens, where they are not well preserved, so that the dimensions given are approximate. The sicula is small, 0.8 to 1.0 mm long and 0.1 to 0.15 mm broad at the aperture. The first theca arises 0.2 to 0.3 mm from the aperture of the sicula, and is about 0.75 mm long, extending beyond the tip of the sicula and reaching 0.25 to 0.3 mm in height.

The subsequent thecae approach a Rastrites-like form, the earlier ones more so than the later, so that the change to a triangular shape is gradual. The number involved varies from th 2 to 3 to th 2 to 8. Specimens can be graded on this basis, and it will be convenient to take three examples for purposes of description.

In what may be regarded as the central form (figures 34, 35, 37, plate 19) the thecae from th 2 to th 5 or th 6 are rastritiform, having a fairly long prothecal portion separating each. The metathecae are subparallel, not parallel in shape. From th 6 or th 7 onwards the thecae are triangular. The proximal thecae increase fairly regularly in height from one to the next, and an average height of 1.5 mm is reached at th 15. A further slow increase occurs, and the average value for distal thecae (th 20 onwards) is 1.6 mm.

The second group (figure 33, plate 19) includes those forms which are near to *M. separatus fimbriatus* in having fewer rastritiform thecae (th 2 to 3 to th 2 to 4 only). Again the metathecae are merely subparallel in shape, but have the isolate appearance due to a long, slowly-widening protheca. The range of thecal heights is similar to those of the previous example.

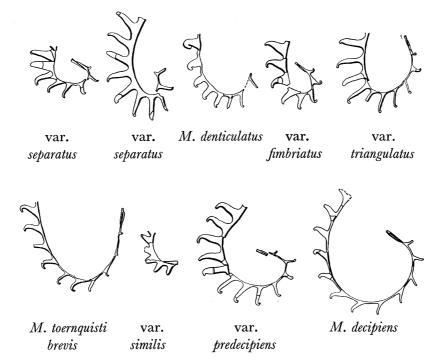


FIGURE 4. Resemblances among some proximal thecae. Magn. × 5 approx.

The third group shows variation towards M. separatus triangulatus. Here the thecae up to th 8 are rastritiform and the effect is more marked for two reasons (figures 36, 39, plate 19). First, the height of the thecae increases more rapidly in the first five or so thecae but then the rate of increase falls so that on an average the value of 1.5 mm is again reached at about th 15. Secondly, some of the early thecae may be truly parallel-sided and show a more distinct angle between the ventral wall and the common canal. When these cylindrical thecae occur, they are usually proximal to the subparallel ones. It is an unexpected feature that those of this group occurring at higher horizons have somewhat wider prothecal parts, and thus a wider common canal, than those from the lower (cf. figure 39 and figure 36, plate 19).

The distal thecae are triangular, usually of the 'central' type described above (p. 495). They number 8 to 14 in 10 mm and are between 1.4 and 1.8 mm high, commonly 1.6 mm.

Resemblances. It is impossible to identify this variety from distal fragments alone, for distinction of the varieties depends upon the nature of the proximal end. The nearest varieties are the two following:

M. separatus fimbriatus (Nicholson): M. separatus separatus may be distinguished by the presence of at least two rastritiform thecae (th 2 to 3) and by the greater height of those succeeding them in the region of maximum curvature of the rhabdosome (figure 4).

M. separatus triangulatus (Harkness). Specimens of M. separatus separatus near this may have thecae up to th8 rastritiform, but these, if they are parallel-shaped at all, are nevertheless of smaller height and more stocky in appearance than those of M. separatus triangulatus (figure 4).

M. separatus predecipiens var.nov. The proximal thecae of M. separatus separatus are stouter and have less attenuated common canal regions (figure 4).

M. denticulatus Törnquist. The first 4 or 5 thecae of the two species can easily be confused, but distally M. separatus separatus has no thecae with a parallel common canal region followed by a triangular metatheca, as has M. denticulatus. The distal thecae of M. separatus separatus are of greater height and less strongly hooked (figure 4).

Remarks. There has previously been considerable uncertainty about this species (see synonymy). The form seems to be fairly common and specimens have often been referred to various other species, usually to 'M. triangulatus' or 'M. fimbriatus'.

Monograptus separatus fimbriatus (Nicholson)

(Figures 5; and 40 to 51, plate 19)

- ? 1853 Monograpsus pectinatus Richter, p. 461 (pars), pl. XII, fig. 26, non fig. 27 (which = ? convolutus).
- ?1868 Graptolithus convolutus Carruthers, p. 127 (pars), non pl. V, figs. 1 a-c.
- 1868 Graptolites fimbriatus Nicholson, p. 536, pl. XX, fig. 5, ? figs. 3, 4.
- ? 1874 Monograptus fimbriatus Dairon, p. 183, pl. I, fig. 11.
- 1876c Monograptus convolutus var. fimbriatus, Lapworth, p. 5, pl. I, fig. 19.
- 1890 Monograptus convolutus Geinitz, p. 19 (pars), non pl. A, figs. 24, 25.
- ? 1897 Monograptus fimbriatus Perner, pl. XI, fig. 39, pl. XIII, figs. 21-23.
- ? 1897 Monograptus communis Perner, p. 15 (pars), pl. XI, figs. 18 a, b, non pl. XII figs. 5-9, 20, text-fig. 14.
- 1899 Monograptus fimbriatus Törnquist, p. 18, pl. III, fig. 24.
- ? 1899 Monograptus convolutus Var. pectinatus, Eisel, p. 55.
- 1912 Demirastrites pectinatus Eisel, p. 39 (pars), pl. III, figs. 18, 20, non pl. III, figs. 16, 17.
- Monograptus fimbriatus Elles & Wood, p. 482 (pars), pl. XLVIII, figs. 4a, d, text-figs. 338a, b, ?c, d, non pl. XLVIII, figs. 4b, c.
- 1913 Monograptus fimbriatus var. similis Elles & Wood, p. 483 (pars), pl. XLVIII, fig. 5d, non pl. XLVIII, figs. 5a, b, c, text-fig. 339.
- ? 1920 Monograptus fimbriatus Gortani, p. 46 (pars), pl. III, figs. 34, 35, non pl. III, fig. 33.
- ?1933 Monograptus turriculatus var. dimorpha Sun, p. 41, pl. VII, fig. 2b, non fig. 2a.
- ? 1942 Demirastrites pectinatus Přibyl & Münch, p. 7 (pars), pl. I, fig. 6, text-fig. I, 4, non text-fig. I, 5.

? non

1876 a Monograptus convolutus var. (b) fimbriatus Lapworth, p. 358, pl. XIII, figs. 4c, d. 1876 b Monograptus spiralis var. (a) fimbriatus Lapworth, p. 128, pl. V, fig. 17.

Type. The question of the type of this taxon is a complicated one, and a case is being presented to the International Council for Zoological Nomenclature which it is hoped will clarify the position. Provisionally the concept of *M. fimbriatus* has been related to a topotype (figured by Elles & Wood 1913, text-fig. 338a and here in figure 5), which is known to have been presented to Charles Lapworth by Nicholson and is now preserved at Birmingham University (Geology Department).

Number of specimens. About 230.



FIGURE 5. M. separatus fimbriatus, topotype. Skelgill. Magn. \times 5 approx.

Horizon and localities.

M. gregarius zone, Rheidol Gorge M. triangulatus band, horizons G, E, DE, D, C, AB.

Diplograptus magnus band, horizon X

Material also seen from Southern Uplands: Moffat.

Lake District: Skelgill, Spengill Head, Great

Rundale Beck.

Central Wales: Abergwesyn. Northern Ireland: Donaghadee.

Diagnosis. Shape of rhabdosome and form of the thecal apertures the same as described above (p. 494). Rastrites-like thecae absent from the proximal end, the early thecae being broadly triangular like the distal ones.

Description. As in other forms of M. separatus, the first theca is always elongated in the direction of the sicula. There are about a dozen specimens with the sicula and first theca well preserved. The sicula seems to be slightly longer than in M. separatus separatus, 0.8 to 1.15 mm, and is 0.1 to 0.15 mm broad at the aperture. The point at which the first theca arises ranges from 0.1 to 0.25 mm above the aperture of the sicula. This is noticeably less than the corresponding value in M. separatus separatus. Those specimens placed near M. separatus separatus on the evidence of the later proximal thecae show the higher values of 0.2 to 0.25 mm, whereas those which are most extreme specimens of M. separatus fimbriatus show values of 0.1 to 0.15 mm. The length of the first theca varies similarly. It ranges from 0.75 to 1.0 mm, the longer thecae occurring in the more extreme forms. Again, the height of the first theca is rather greater than in M. separatus separatus, 0.4 to 0.45 mm.

The subsequent thecae are triangular, even those from th 2 to th 8 appearing broad at their bases since the protheca widens rapidly throughout its length. The height of these proximal thecae is small, although certain specimens approach *M. separatus separatus* in the

subparallel form of th2 to 3 (figure 41, plate 19). The 'horns' of these early thecae are strongly curved but in the distal thecae this curvature becomes less.

The thecae increase in height regularly, as in *M. separatus separatus*, and the average height of the distal thecae is slightly less than 1.6 mm (range 1.4 to 1.8 mm). The variation in the distal thecae of this variety is shown in figure 6.

Resemblances. M. separatus separatus var.nov. The distal thecae alone are not easily distinguished, but those of M. separatus fimbriatus are often somewhat blunter in appearance (cf. figures 3b, 3c, 6). The proximal end shows no rastritiform thecae, and the early thecae are of small height and broad compared with the same thecae in near forms of M. separatus separatus (figure 4).

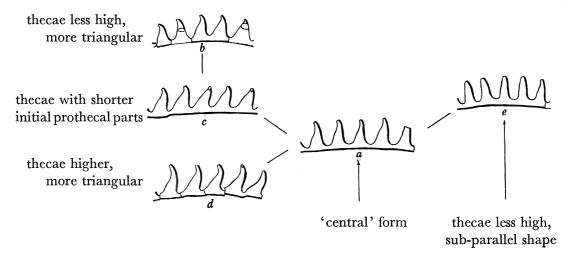


Figure 6. Variations in the distal thecae of M. separatus fimbriatus. Magn. \times 5 approx.

M. separatus similis (Elles & Wood): The two forms are closely similar except for the proximal end. In M. separatus fimbriatus the sicula extends only as far as th1. In M. separatus similis it is actually shorter, yet extends half-way along th2, since the thecae are very short (figure 4).

M. denticulatus Törnquist see p. 510.

Monograptus separatus similis (Elles & Wood) (Figure 7)

? 1876 a Monograptus convolutus var. (b) fimbriatus Lapworth, p. 358, pl. XIII, figs. 4c, d.

?1876b Monograptus spiralis var. fimbriatus Lapworth, p. 128, pl. V, fig. 17.

1913 Monograptus fimbriatus var. similis Elles & Wood, p. 483 (pars), pl. XLVIII, fig. 5c, text-fig. 339, ?pl. XLVIII, figs. 5a, b, non pl. XLVIII, fig. 5d. ?non

1942 Demirastrites pectinatus similis Přibyl & Münch, p. 8.

Lectotype. Přibyl & Münch (1942) chose as lectotype the specimen figured by Elles & Wood, 1913, pl. XLVIII, fig. 5a. Examination shows that this figure is slightly inaccurate, since the original specimen does not in fact show the sicula and can only be identified as ?similis. Application has been made to the ICZN to set aside the lectotype selection of Přibyl & Münch and in its place to designate as lectotype of similis the specimen illustrated

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by Elles & Wood as text-fig. 339 from the Birkhill Shales, Dobb's Linn. SM. A21479, figure 7 (Bulman 1957, p. 313).

Diagnosis. Like M. separatus fimbriatus except for the sicula and first few thecae. Sicula shorter, only 0.75 mm long, and extending to about the middle of th 2. The first theca particularly, and also the second and third, have shorter prothecae than in M. separatus fimbriatus, and th 1 is of greater height, about 0.55 mm.

Remarks. This variety has not been found in the Rheidol Gorge material, but is included here for the sake of completeness. Of the specimens described and figured as syntypes by Elles & Wood, only two showed the sicula, and can thus be accepted with certainty (see synonymy). The specimen figured by Elles & Wood on pl. XLVIII, fig. 5d, now has the sicula exposed and proves to be a specimen of M. separatus fimbriatus.



Figure 7. M. separatus similis, proposed lectotype. Dobb's Linn. SM. A21479. Magn. × 5 approx.

Monograptus separatus predecipiens var.nov.

(Figures 64 to 66, plate 20)

?1851 Rastrites triangulatus Harkness, p. 59 (pars), pl. I, figs. 3c, d, non figs. 3a, b.
?1913 Monograptus decipiens Elles & Wood, p. 469 (pars), text-fig. 325 b, non pl. XLVII, figs. 3a-e, text-fig. 325 a, c.

Holotype. The specimen figured on figure 66, from horizon L, top of M. triangulatus var. band, M. gregarius zone, Rheidol Gorge, Pont-erwyd, near Aberystwyth. SM. A24457.

Paratypes. SM. A24456, A24459 (figures 64, 65).

Number of specimens. About 35.

Horizon and localities.

M. gregarius zone, Rheidol Gorge M. triangulatus var. band, horizons S, P, O, M, L. Diagnosis. Th 2 to 7 to th 2 to 10 rastritiform, parallel shaped and with long narrow prothecal parts, of relatively small height, but the later ones fairly broad. Succeeding early thecae triangular but also of smaller height and greater breadth than in the typical form.

Description. A number of specimens show well-preserved siculae and first thecae. The sicula tends to be smaller than in the typical form, 0.95 mm long and 0.1 mm broad at the aperture. The first theca arises 0.1 to 0.3 mm from the aperture and is 0.6 to 0.9 mm long, often 0.8 mm. Its height is fairly great, 0.3 to 0.45 mm, and it is usually, as before, triangular in shape. Thecae 2 to 7 to 2 to 10 are definitely rastritiform, the early ones parallel and the later subparallel in shape. The increase in height from one theca to the next is less than in M. separatus triangulatus, and the height becomes more or less constant after about th 9 or th 10. Succeeding thecae are therefore only 1.2 to 1.4 mm in height, but

it should be noted that only proximal fragments up to th 12 have been recognized for certainty. The specimens differ from M. separatus separatus in that at least the first four thecae are much more rastritiform, with particularly long narrow common canal parts. The later Rastrites-like thecae are somewhat more stocky in appearance but still parallel or subparallel in form. In these respects, but not in height, they approach the form of corresponding thecae of M. separatus triangulatus.

Resemblances. M. decipiens Törnquist. The two forms are similar but M. separatus predecipiens has fewer rastritiform thecae. Th 3 to 9 have shorter common canal parts and are more stocky and broad in appearance (figure 4).

M. separatus separatus var.nov. See p. 499 and figure 4.

M. separatus triangulatus (Harkness). See p. 506 and figure 4.

MONOGRAPTUS SEPARATUS TRIANGULATUS (HARKNESS)

(Figures 52 to 63, plate 20)

- 1851 Rastrites triangulatus Harkness, p. 59 (pars), pl. I, figs. 3a, b, non 3c, d.
- 1852 Monograpsus triangulatus Geinitz, p. 47 (pars), pl. V, figs. 5-8, ?figs. 3, 4, non figs. 1, 2.
- ?1853 Monograpsus triangulatus Richter, p. 461.
- ? 1853 Monograpsus priodon Richter, p. 459, pl. XII, fig. 22.
- 1868 Graptolithus convolutus Carruthers, p. 127 (pars), non pl. V, figs. 1 a-c.
- ? 1868 Graptolites sedgwicki var. β triangulatus Nicholson, p. 535, pl. XIX, figs. 33, 34, pl. XX, figs. 1, 2.
- ? 1873 Graptolithus (Monograpsus) triangulatus Stache, p. 237.
 - 1874 Monograptus Sedgwickii (var. triangulatus) Dairon, p. 183, pl. I, fig. 11.
- 1876a Monograptus triangulatus Lapworth, p. 359, pl. XIII, figs. 5a, b.
- 1876 b Monograptus triangulatus Lapworth, p. 127, pl. V, fig. 14.
- 1876c Monograptus triangulatus Lapworth, p. 5, pl. I, fig. 2.
- 1890 Monograptus convolutus Geinitz, p. 19 (pars), non pl. A, figs. 24, 25.
- 1897 Monograptus triangulatus Frech, p. 649.
- ?1897 Monograptus triangulatus Perner, p. 14, pl. XII, figs. 16, 30, non text-fig. 12.
 - 1899 Monograptus triangulatus Törnquist, p. 19, pl. III, figs. 25–28, pl. IV, figs. 1, 2.
- 1899 Monograptus convolutus Var. triangulatus Eisel, p. 55.
- 1899 Monograptus convolutus Var. Raitzhainiensis Eisel, p. 55.
- 1907 Monograptus triangulatus Törnquist, p. 17.
- 1907 Monograptus triangulatus var. Raitzhainiensis Törnquist, p. 17, pl. III, figs. 2-4.
- ?1907 Monograptus triangulatus Vinassa de Regny, p. 179, pl. I, fig. 14.
- 1912 Demirastrites triangulatus Eisel, p. 36, pl. III, figs. 8-12, ? pl. III, figs. 6, 7, 13.
- 1912 Demirastrites communis Eisel, p. 38 (pars), pl. III, figs. 14, 15, 21, non fig. 19.
- 1913 Monograptus triangulatus Elles & Wood, p. 471 (pars), pl XLVII, figs. 4a, c, d, f, text-fig. 327b, non figs. 4b, e, text-figs. 327a, c.
- 1913 Monograptus triangulatus var. major Elles & Wood, p. 472 (pars), pl. XLVII, figs. 5a, b, text-fig. 328a, non pl. XLVII, figs. 5c, d, text-fig. 328b.
- 1913 Monograptus raitzhainiensis Elles & Wood, p. 473 (pars), pl. XLVIII, fig. 3a, text-fig. 329a, non pl. XLVIII, figs. 3b, c, text-fig. 329b.

- Demirastrites triangulatus Kirste, p. 212, pl. III, fig. 51. IQIQ
- Demirastrites pectinatus Kirste, p. 215, pl. III. fig. 54. 1919
- Demirastrites raitzhainiensis Kirste, p. 218. 91919
- Monograptus triangulatus Gortani, p. 42, pl. III, figs. 17, 18. 1920
- ?1920 Monograptus triangulatus var. maior Gortani, p. 43 (pars), pl. III, fig. 19, non figs. 20, 21.
- Monograptus triangulatus var. cirratus Gortani, p. 43 (pars), pl. III, fig. 23, non ?1920 figs. 22, 24.
- Monograptus raitzhainiensis Gortani, p. 44, pl. III, figs. 25-27. 1920
- Monograptus raitzhainiensis Sun, p. 39, pl. VI, fig. 5. ? 1933
- Demirastrites triangulatus triangulatus Přibyl & Münch, p. 3 (pars), pl. I, figs. 1-5, 1942 text-fig. I, 1, 2, non text-fig. I, 3.
- ? 1947 Monograptus cf. raitzhainiensis Ruedemann, p. 486 (pars), pl. 86, figs. 40, 41, non figs. 38, 39.

Lectotype (Přibyl & Münch 1942, p. 4). The specimen figured by Harkness (1851) as Rastrites triangulatus, pl. I, fig. 3a (? and 3b), from Frenchland Burn, near Moffat, Dumfriesshire. Geological Survey and Museum, Geol. Soc. Coll. 6941. The specimens figured by Harkness to accompany his original description of R. triangulatus are not all the same; the one shown in his pl. I, fig. 3a, is what has come to be accepted as 'Monograptus triangulatus', and the original of this has been chosen as lectotype. The specimen is compressed, but shows the thecal characters reasonably well. The proximal part shows the fish-hook shape but is incomplete. The extreme proximal part shown on Harkness's figure is actually a fragment of another specimen, and the proximal end is not bent round into an almost complete circle as Harkness shows.

Number of specimens. About 120.

Horizon and localities.

M. gregarius zone, Rheidol Gorge

M. triangulatus var. band, horizons Q, P, O, N,

M, L.

Material also seen from

Southern Uplands: Moffat.

Lake District: Skelgill, Spengill Head. Yorkshire: Hunterstye near Austwick.

North Wales: Anglesey.

Central Wales: Rheidol Gorge (Diplograptus

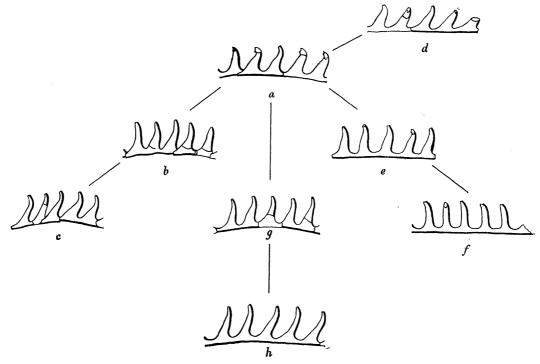
magnus band).

Northern Ireland: Donaghadee, Pomeroy, Desertcreight, Co. Tyrone.

Diagnosis. Th 2 to 8 to th 2 to 12 are rastritiform. Distal thecae of a slender triangular form.

Description. In this variety the sicula is well preserved in several specimens; it is rather small, 0.7 to 0.95 mm long and again 0.1 to 0.15 mm broad at the aperture. The first theca arises 0.2 to 0.35 mm from the aperture, as in M. separatus separatus, but the theca itself tends to be longer, 0.75 to 1.1 mm. It varies from 0.25 to 0.45 mm in height. In some specimens the theca is somewhat more slender than usual, approaching the Rastrites-like form of succeeding thecae.

The rastritiform character is more pronounced and affects more of the early thecae than in M. separatus separatus. Each theca is narrower in proportion to its height, and the parallel prothecal part of each thecal segment is also narrower. In addition, the thecae increase in height quite rapidly as far as th 7 or th 8, so that these early ones are higher than in M. separatus separatus. A height of 1.5 mm is reached at th 8 on the average. In the main bulk of the specimens the thecae after th 8 or th 9 are beginning to look less rastritiform since they have become relatively wider in side view than the previous ones; however, in some forms which are obviously tending towards M. separatus extremus the increase in height of the early thecae is greater than average so that th 7 and th 8 may be as much as 1.8 mm high and the rastritiform appearance may extend to th 10 to 12 (figure 55, plate 20).



Key a 'central' form

e sub-parallel thecae

b shorter initial prothecal part

f thecae almost parallel-sided

c thecae of greater height

g thecae of greater height, slender

d thecae of smaller height

h slender 'concave' form

FIGURE 8. Variation in the distal thecae of M. separatus triangulatus. Magn. × 5 approx.

After about th 8 the thecae usually increase very little in height or remain constant, the latter particularly in the more extreme forms mentioned above. All the distal thecae are triangular but slender in appearance, and range from 1·4 to 1·9 mm in height, the average being just over 1·6 mm (figure 8).

Resemblances. M. separatus separatus var.nov. This is one of the nearest forms. M. separatus triangulatus has a greater number of rastriform thecae (up to th12) and these are more slender and of somewhat greater height than the corresponding ones in M. separatus separatus (figure 4). Sometimes the distal thecae cannot be distinguished, but often those of M. separatus triangulatus are again somewhat higher and more slender in appearance (figures 3 and 8).

M. separatus predecipiens var.nov. The proximal ends have about the same number of rastritiform thecae, but in M. separatus predecipiens these are of smaller height and are separated by longer parallel common canal regions (figure 4).

M. separatus extremus var.nov. See p. 508 and figure 11.

M. convolutus (Hisinger). M. separatus triangulatus is distinguished by its fish-hook shaped rhabdosome, and its distal thecae, which are of smaller height (figure 9).





FIGURE 9. Resemblances between distal thecae. Magn. × 5 approx.

Remarks. The specimens here included under the name M. separatus triangulatus have often been separated as M. triangulatus and M. raitzhainiensis. The latter name was first given by Eisel (1899), without figures or description, but he later appeared to withdraw it by publishing a figure of 'Demirastrites triangulatus' and adding a note that this was previously named 'Var. Raitzhainiensis' by him (Eisel 1912, pl. III, figs. 6, 7, and legend). The specimen shows attenuated rastritiform proximal thecae in the region of maximum curvature of the rhabdosome, and squat small thecae distally. Its appearance is undoubtedly due to compression of the rock in a direction at right angles to the length of the specimen, causing the distal thecae to become smaller in height and the proximal ones to lie closer together, possibly also becoming of greater height. This opinion was held by Eisel himself, for in a paper on the preservation of graptolites (1908) he takes as one example M. triangulatus, and, giving a drawing essentially the same as the one in his 1899 paper, explains that the distal thecae 'normally pointed, are compressed on to the axis, blunt and broad' (p. 220). He states definitely that this is the 'Var. Raitzhainiensis' of his 1899 list.

Thus the first definitive description of raitzhainiensis was that given by Elles & Wood (1913, p. 473), and according to them, the difference between M. raitzhainiensis and M. triangulatus lay chiefly in the characteristic shape of the distal thecae of M. raitzhainiensis. Examination of their specimens shows that they are all compressed to some degree and are mostly in half-relief. This tends to make all the thecae look broader, but the distal triangular ones change in shape more than the proximal rastritiform ones and they appear wider and blunter. In this connexion, it is interesting that Elles & Wood mention a similarity between M. raitzhainiensis and M. fimbriatus distal thecae; for, as has been shown, the appearance usually thought typical of M. fimbriatus thecae is in large part due to the same type of preservation as is found in these 'M. raitzhainiensis' specimens, and the uncompressed thecae of the two types are similar in shape.

'M. raitzhainiensis' is accordingly included in the synonymy of M. separatus triangulatus.

 ${\it Monograptus \, separatus \, major \, (Elles \, \& \, Wood)}$

(Figure 10)

1913 Monograptus triangulatus var. major Elles & Wood, p. 472 (pars), pl. XLVII, fig. 5c, text-fig. 328b, ? pl. XLVII, fig. 5d, non pl. XLVII, figs. 5a, b, text-fig. 328a. ? 1920 Monograptus triangulatus var. cirratus Gortani, p. 43 (pars), pl. III, figs. 22, 24, non fig. 23.

non

1920 Monograptus triangulatus var. maior Gortani, p. 43, pl. III, figs. 19-21.

1942 Demirastrites triangulatus major Přibyl & Münch, p. 6.

Lectotype. Přibyl & Münch (1942) chose as lectotype the specimen figured by Elles & Wood, 1913, pl. XLVII, fig. 5a. Examination shows that this specimen is not referable to *M. separatus major*, but is a true *M. separatus triangulatus* Harkness. Application has been made to the ICZN to set aside the lectotype selection of Přibyl & Münch and in its place to designate as lectotype of *M. separatus major* the specimen illustrated by Elles & Wood as text-fig. 328b, from the *M. gregarius* zone (? *Diplograptus magnus* band), Rheidol Gorge, Pont-erwyd. GSM 26326 (figure 10) (Bulman 1957, p. 314).



FIGURE 10. M. separatus major, proposed lectotype, Rheidol Gorge. GSM. 26326. Magn. × 5 approx.

Horizon and localities.

M. gregarius zone, Rheidol Gorge

? Diplograptus magnus band.

Material also seen from

Southern Uplands: Moffat. Northern Ireland: Pomeroy.

Remarks. This variety was first described by Elles & Wood and its characteristic features were said to be: (1) Thecae longer than in M. triangulatus (i.e. higher)—(2) Thecae closer set than in M. triangulatus—7 to 12/cm. Of the specimens figured in the Monograph, three (pl. XLVII, figs. 5a, b, text-fig. 328a) appear to be little different from an ordinary M. separatus triangulatus, and their thecae do not exceed 2·0 mm in height. Pl. XLVII, fig. 5d, may possibly be different, but the thecae are only 2·05 mm high. The remaining two specimens (pl. XLVII, fig. 5c and text-fig. 328b) show thecae up to 2·25 mm high and these certainly cannot be referred to M. separatus triangulatus. As has been shown earlier, the number of thecae per centimetre is much affected by compression of the rocks and is probably of less significance.

Unfortunately the two specimens which may be *M. separatus major* are incomplete proximally, but the thecae become quite small in height towards the proximal end (figure 10). In the absence of any similar material in the present collection, the variety cannot be adequately defined. This lack of material is unexpected, because the two figured specimens come from the Rheidol Gorge locality and from the preservation and associated specimens of *Diplograptus magnus* it is fairly certain that the exact horizon is the *Diplograptus magnus* band.

Monograptus separatus extremus var.nov.

(Figures 67 to 70, plate 21)

?1913 Rastrites approximatus var. Geinitzi Elles & Wood, p. 492 (pars), pl. L, fig. 5b, text-fig. 347a, non pl. L, figs. 5a, c, d, text-fig. 347b.

?1920 Monograptus triangulatus var. maior Gortani, p. 43 (pars), pl. III, figs. 20, 21, non fig. 19.

Holotype. The specimen figured in figure 70, from horizon L, top of M. triangulatus var. band, M. gregarius zone, Rheidol Gorge, Pont-erwyd, near Aberystwyth. SM. A24479.

Paratypes. SM A24477, 78 (figures 68, 69), A24458, A24503.

Number of specimens. Ten.

Horizon and locality.

M. gregarius zone, Rheidol Gorge M. triangulatus var. band, horizons N, M, L, K. Diagnosis. Proximal thecae up to about th 12 very Rastrites-like, succeeding thecae broader and of smaller height, but parallel to subparallel in shape and not triangular.

Description. Only one specimen with a sicula is known with certainty (figure 69); another (SM. A24503) showing the sicula and three thecae is probably the same. The dimensions for the two specimens are as follows:

figured specimen (mm)	SM. A24503 (mm)				
0.7	0.9				
0.1	0.1				
0.1	0.225				
0.8	1.05				
(broken)	0.4				
	(mm) 0·7 0·1 0·1 0·8				

The sicula is much the same as in the other forms of this species, but the first theca arises fairly near the aperture and is more slender than usual as seen in the specimen SM. A 24503.

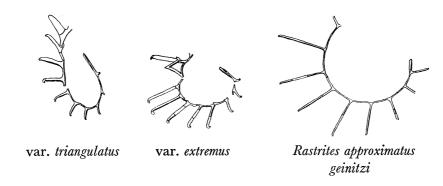


FIGURE 11. Resemblances among proximal thecae. Magn. × 5 approx.

The succeeding early thecae are more Rastrites-like than those of M. separatus or of M. separatus triangulatus, being even more attenuated in both prothecal and metathecal parts. The height of successive thecae increases rapidly by about 0.2 to 0.3 mm per theca so that the maximum height of 2.0 to 2.5 mm is reached between th9 and th12. The height thence gradually falls (compare M. separatus separatus and M. separatus triangulatus) to about 2.0 mm or slightly less. Distally the thecae become broader but remain almost cylindrical and are about 1.8 to 2.0 mm high.

Resemblances. M. separatus triangulatus (Harkness): M. separatus extremus may be distinguished by the greater number of rastritiform thecae at the proximal end, and also by the greater height of these thecae. They reach 2.0 mm or more and then the height decreases again, a feature not seen in M. separatus triangulatus (figure 11).

Rastrites approximatus geinitzi (Törnquist): The forms may be distinguished by the Rastriteslike first theca of R. approximatus geinitzi, and the much more slender thecae and common canal following this (figure 11). Proximal fragments of M. separatus extremus are, however, very like a Rastrites, and may have been confused with this or other species of the genus.

Remarks. The form is not common in the Rheidol Gorge section but is of importance as the precursor of a true Rastrites (see p. 529). It has been described as a Monograptus since the distal thecae are nearer to a M. separatus type than a Rastrites type. The common canal region is narrow, but not nearly so attenuated compared with the thickness of the metathecae as is found in the true Rastrites species, and this was a point stressed by Törnquist (1907, p. 4) for the distinction of the genera Monograptus and Rastrites. The difference between this form and Rastrites longispinus, its probable descendent, are much greater than those between it and M. separatus triangulatus, its immediate ancestor (cf. figures 68 to 70, plate 21 with figure 55, plate 20 and figure 71, plate 21).

Monograptus denticulatus Törnquist

(Figures 72, 73, plate 21)

1899 Monograptus denticulatus Törnquist, p. 18, pl. III, figs. 19–23.

Since this species and the three following have been studied in less detail than the foregoing ones, full critical synonymies are not appended. For M. denticulatus, a number of references will be found in Přibyl & Münch (1942).

Lectotype (Přibyl & Münch 1942, p. 8): the specimen figured by Törnquist (1899) on pl. III, fig. 19, from the zone of Diplograptus folium, Tomarp, Sweden (= M. convolutus zone in Britain). Specimen not seen.

Horizon and localities.

Material seen from M. convolutus zone Southern Uplands: Moffat.

Lake District: Skelgill.

Central Wales: R. Clywedog near Llanidloes.

Diagnosis. Rhabdosome fish-hook shaped, often short. Thecae on the convex side, without overlap. First 4 to 6 thecae rastritiform but of small height; distal thecae triangular but well spaced, height not exceeding 1.3 mm. The tips of the thecae are bent into a marked hook so that the aperture faces the dorsal side of the rhabdosome. The hook is transversely elongated.

Description. The sicula is small and slender. The first few thecae are parallel or subparallel in shape and well separated by long narrow prothecal regions. They are of small height, however, about 0.75 to 0.85 mm. Subsequent thecae gradually increase in width in side view, becoming more broadly triangular but still well spaced because of a thin, slowly widening protheca, which meets the ventral wall of the triangular part at a distinct angle. In later thecae this angle is less marked, and the protheca widens gradually, but the thecae still appear well spaced. There are 8 to 12 thecae in 10 mm.

The distal thecae do not seem to exceed a height of 1.3 mm, although the actual length of the metatheca is fairly great. Much of this is taken up in the hook, which is bent over so that the whole aperture faces dorsally. It is seen from the material preserved in half-relief that the aperture is transversely elongated to at least as great an extent as in the distal thecae of M. separatus (figures 72, 73, plate 21).

Resemblances. M. separatus separatus var.nov. and M. separatus fimbriatus (Nicholson). The two characteristic features of M. denticulatus are: (1) the small, well-hooked distal thecae; (2) the early thecae, after the first few, with narrow parallel common canal regions and broadly triangular metathecae. Both these distinguish it from the above forms (see p. 499 and figure 4).

M. communis Lapworth. The second feature mentioned above also provides a difference from M. communis. In the distal thecae the hook of M. denticulatus is more tightly enrolled so that the aperture faces towards the common canal; in M. communis it faces more towards the proximal end (figure 12).

M. pseudoplanus sp.nov. The hook of a M. denticulatus theca is larger and turns over further than in one of M. pseudoplanus; if the proximal ends are present M. denticulatus has rastritiform and triangular thecae, whereas those of M. pseudoplanus are elongated (figure 12).

proximal MARQ FRANT MARY

distal MARY MARY

FIGURE 12. Resemblances among proximal and distal thecae. Magn. × 5 approx.

Monograptus decipiens Törnquist

(Figures 74, 75, plate 21)

1899 Monograptus decipiens Törnquist, p. 20, pl. IV, figs. 9-14.

See Přibyl & Münch (1942) for references to this species.

Lectotype (Přibyl & Münch 1942, p. 12). The specimen figured by Törnquist (1899), pl. IV, fig. 10, from the zone of Diplograptus cometa, Tomarp, Sweden (= zone of M. convolutus in Britain). Specimen not seen.

Horizon and localities.

Material seen from M. gregarius zone: Central Wales: Llanbrynmair near Machynlleth.

M. convolutus zone: Lake District: Skelgill, Long Sleddale. North Wales: Criccieth.

M. pseudoplanus

Central Wales: R. Clywedog near Llanidloes, Pont-erwyd district.

Diagnosis. Rhabdosome spiral, fairly short; thecae on the convex side, without overlap, hooked and transversely elongated at the aperture. Sicula small. About the first eight thecae rastritiform but not of great height, separated by very long, slender prothecal parts. Distal thecae triangular with small hooks and of small height.

Description. The rhabdosome is relatively short and the loose spiral consists of no more than one or two whorls. In the specimen figured by Elles & Wood (text-fig. 325a), the sicula is small and slender, 0.85 mm long, with the first theca arising 0.15 mm from the aperture. The protheca is fairly long, as in M. separatus, extending beyond the tip of the

sicula, but here the metatheca also is fairly long, giving the whole theca a rastritiform appearance.

The early thecae are extremely slender, so that even though they are of small height, about 0.45 mm up to 1.0 mm, they appear very *Rastrites*-like. The increase in height from one to the next is usually small, sometimes almost negligible. The rastritiform appearance is enhanced by the prothecal common canal parts, which are extremely tenuous and at least as long or longer than the height of adjacent thecae (see Törnquist's figures, 1899).

About th 8 to 10, the shape becomes more triangular, since the protheca widens earlier, but there is still quite a long prothecal part at first. The distal thecae have a concave ventral wall in side view, with a slender apertural part. They are usually about 1.5 mm high (maximum seen 1.7 mm) and well spaced (10 thecae in 10 mm).

From specimens in half-relief it is evident that the thecae are transversely elongated at the aperture (figure 74, plate 21). They are well bent over to form the hook in the proximal ones, but less so in the distal ones, where the thecae are almost pointed in appearance.

Resemblances. M. planus (Barrande). The proximal parts are quite different, but the distal thecae are somewhat similar in proportions. Those of M. decipiens, however, have a smaller hook and there are no spines at the lateral margins of the aperture as in M. planus (figure 16).

M. separatus predecipiens var.nov. See p. 503 and figure 4.

Monograptus convolutus (Hisinger)

(Figures 13 and 76 to 78, plate 21)

1837 Prionotus convolutus Hisinger, p. 114, pl. XXXV, fig. 7.

See Přibyl & Münch (1942) for further references.

Holotype (Tullberg, 1882, explanation to pl. II, fig. 13). The specimen figured by Hisinger (1837) on pl. XXXV, fig. 7, and again by Tullberg (1882), on pl. II, fig. 13, from Furudal, Kopparberg, Sweden, from the zone of Diplograptus folium-Diplograptus cometa (= zone of M. convolutus in Britain). Specimen not seen.

Horizon and localities.

M. convolutus and M. sedgwicki zones: Southern Uplands: Moffat, Lockerbie.

Lake District: Skelgill, Long Sleddale.

North Wales: Criccieth.

Central Wales: Machynlleth, R. Clywedog

near Llanidloes.

Diagnosis. Rhabdosome spiral; thecae on the convex side, with no overlap. Thecae hooked and transversely elongated at the aperture.

Sicula small. First 8 to first 20 thecae Rastrites-like, gradually succeeded by distal thecae of a slender triangular form, usually 2.0 to 3.0 mm high.

Description. The spiral form of the rhabdosome is characteristic of the species, and even fairly short fragments show some dorsal curvature. Five whorls of the spiral are the maximum known. Most descriptions state that the extreme distal parts are merely arcuate or even straight. This is possible, since fragments with M. convolutus-like thecae are found

which are straight or only slightly bent, but no specimens have been figured showing both parts associated.

The sicula is not known with certainty, but a compressed specimen from Moffat which probably shows it is illustrated in figure 13. Unfortunately no more than the outline of the fossil can be seen, but it appears that the sicula is small and similar to that of *M. separatus*.

The rastritiform appearance of the early thecae commonly extends to the first 10 or 12 thecae seen. They are of small width in proportion to their height and have long narrow prothecal portions. They increase regularly in height from about 0.75 mm to about 2.0 mm.

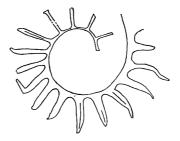


Figure 13. M. convolutus, proximal fragment possibly showing the sicula.

Moffat, SM. A21293. Magn. × 5 approx.

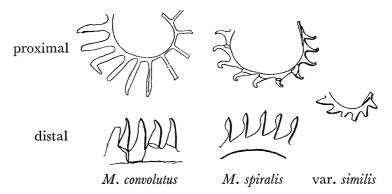


FIGURE 14. Resemblances among proximal and distal thecae. Magn. × 5 approx.

In one specimen however (figured in the *Monograph of British Graptolites*, pl. XLVII, fig. 1a), there is trace of at least twenty rastritiform thecae, reaching 4·0 mm in height. A number of similar specimens have been figured elsewhere (Carruthers 1868, pl. V, fig. 1a; Törnquist 1892, pl. III, fig. 6), and it may be that a detailed revision of the species would show that there was as much variation here as has been observed in 'M. triangulatus'.

In most cases, however, the characteristic form of the distal thecae is attained at about th 12. The protheca is triangular, widening steadily from the beginning and the metatheca is long, narrowing in side view but broadening laterally so that the aperture is about 1.0 mm across. The apertural region is gently curved, forming a slight hook. Distal thecae are usually 2.0 to 3.0 mm in height. In some specimens the height increases gradually along the rhabdosome to a maximum of 3.5 mm, and there are one or two fragments probably referable to this species (e.g. SM. A23802, A22626) which show thecae up to 4.0 mm in height. In all the forms, the height of the thecae means that they look to be close together, but they actually number 7 to 15 in 10 mm, according to the orientation of the specimen in relation to the compression of the rock.

Resemblances. M. separatus triangulatus (Harkness). The proximal thecae are usually of greater height in M. convolutus, as are also the distal thecae (figure 9). The spiral form of the rhabdosome is usually evident even in fragments and should serve to differentiate the two easily.

M. spiralis (Geinitz). Both show a spirally curved rhabdosome of several involutions, but quite different thecae; in M. convolutus they are at first Rastrites-like and then triangular, but always of greater height than length. In M. spiralis they are triangular throughout and normally about as long as high (figure 14).

MONOGRAPTUS SPIRALIS (GEINITZ)

(Figures 79 to 82, plate 21)

1842 Graptolithus spiralis Geinitz, p. 700, pl. X, figs. 26, 27.

A full critical synonymy will be found in Törnquist (1912), pp. 615-17.

Lectotype (Törnquist, 1912, p. 603). The specimen figured by Geinitz (1842) on pl. X, fig. 26; and in 1852 on pl. IV, fig. 32 as Monograpsus convolutus, from between Ronneburg and Paitzdorf, Thuringia. Specimen not seen.

Horizon and localities.

Material seen from *Monograptus crispus* zone: Crossfell region: Swindale Beck.

Rawthey Bridge,

near Sedbergh.

Diagnosis. Rhabdosome spiral, thecae on the convex side, without overlap. Sicula fairly long, usually extending to about the middle of the second theca. Thecae all similar in general form, triangular and about as long as high, with concave ventral margins and slender hooks at the transversely expanded apertures.

Description. The complete rhabdosome is fairly long, usually a spiral of three or four whorls. The spiral was probably not plane, but formed a shallow cone, for, although some specimens show a regular apparently plane spiral, in others the curvature is irregular, the whorls overlapping or the rhabdosome showing a sigmoidal form. Also relatively frequent instances occur of rhabdosomes showing in parts a dorsal or half-dorsal view, with the apertures of the thecae compressed beneath the part seen.

The sicula is 1·3 to 1·4 mm long and 0·15 to 0·2 mm broad at the aperture, and the first theca arises 0·2 to 0·3 mm above the aperture. The early thecae are short, so that the tip of the sicula extends as far as the middle of the second theca.

The first theca is 0.6 to 0.9 mm long and 0.5 to 0.75 mm high, and the common canal is about 0.1 mm wide in this region. The thecae increase gradually in dimensions along the rhabdosome but do not change their proportions of length and height to any great extent. Distal thecae preserved in relief are commonly about 1.4 mm. in height and number 9 to 14 in 10 mm. The common canal increases in width also, reaching 0.3 to 0.4 mm in the distal parts.

The thecae are the same shape throughout the rhabdosome, triangular, with a slightly concave proximal margin in side view. The apertures are well seen in Holm's reconstruction (see Bulman 1932, pl. 6, figs. 15, 16) which shows that as the hook begins the dorsal wall expands rapidly, producing lateral projections which are flattened curved membranes,

while the central part forms a dorsal lip overhanging the aperture (figure 82, plate 21). On compression this theca can give rise to a number of different appearances. The unusually thick common canal appears even wider when compressed and often measures about 0.8 mm, sometimes up to 1.0 mm, across (figure 81, plate 21). The other part mainly affected is the aperture. Bending or breaking seems often to have occurred where the main triangular part of the theca joined the fairly rigid lateral projections. Sometimes the apertural region is not preserved at all, and the theca appears as a blunt triangle with no hook. In other specimens the apertural region has tilted sideways so that one projection is pressed on to the metatheca, while the other is bent upwards and looks like a long tapering tip to the theca, making it appear of greater height than it really is (figure 81). Twisting of the hook combined with this effect produces a wide range of possible variation in the appearance (see the 8th theca of the specimen in figure 80).

Resemblances. M. separatus fimbriatus (Nicholson) and M. separatus similis (Elles & Wood). In all these the thecae are of the same form throughout the rhabdosome. Those of M. separatus fimbriatus and M. separatus similis are higher than long, while those of M. spiralis are nearly equal in length and height. The sicula in M. spiralis extends to th2, which provides a distinction from M. separatus fimbriatus, and it is longer and more slender than that of M. separatus similis (figure 14). The spiral form of the rhabdosome of M. spiralis should make its distinction easy.

M. convolutus (Hisinger). See p. 513 and figure 14.

Monograptus toernquisti sp.nov.

(Figures 15, 19 and figures 83 to 90, plate 22)

Holotype. The specimen figured in figure 84, from horizon O, M. triangulatus var. band, M. gregarius zone, Rheidol Gorge, Pont-erwyd, near Aberystwyth. SM A24480.

Paratypes are listed under separate varieties.

Number of specimens (including all varieties). About 50, mainly fragmentary. Horizon and localities.

M. gregarius zone, Rheidol Gorge M. triangulatus var. band, horizons R, Q, P, O. Material also seen from Lake District: Long Sleddale.

Diagnosis. Rhabdosome curved, more strongly proximally than distally, thecae on the convex side, without overlap. Sicula small; early thecae elongated, with a long narrow protheca and a small triangular hooked metatheca; giving place to broadly triangular distal thecae in which one-half to one-third of the length of the metatheca is bent slightly forwards as a hook. The aperture is transversely elongated.

Description. Most of the specimens are incomplete, but there are one or two good proximal fragments from which the form of the rhabdosome can be inferred. Proximally it is well curved, forming a broad arch or almost a spiral, with the maximum curvature extending over a fairly large number of thecae. The distal region is gently curved and a maximum length of 60 mm has been observed (figure 15), although most specimens are much shorter.

The sicula is small and slender. The early thecae consist of a long, narrow protheca which widens very slowly and a small triangular metatheca, so that the height/length ratio is about one-fifth. The number of these elongated thecae varies, but sooner or later the prothecae widen more rapidly and shorten in length. The metatheca is correspondingly

bigger and the height/length ratio becomes somewhat greater than 1. The usual proportions of distal thecae are attained at th7 to 12.

In the distal thecae the protheca widens steadily and fairly rapidly, while the metathecal part tapers towards the tip. It is at first inclined distally so that the theca seems to lean backwards, then about half-way along its length the direction of growth changes and

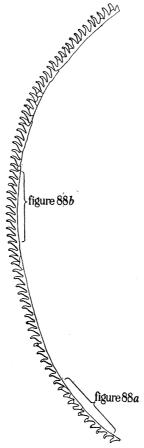


Figure 15. M. toernquisti, distal thecae. Horizon P, SM. A 24481. Magn. \times 2 approx. (Parts also illustrated in figure 88, plate 22.)

the last part of the metatheca bends forwards. In side view it terminates in a small aperture which faces ventrally. The metatheca broadens transversely as it tapers in side view, and the lateral parts are prolonged into a pair of horns. The central region of the aperture is slightly more enrolled.

The distal thecae are usually 1.4 to 1.6 mm high, although the maximum seen is 1.8 mm. Part of this is represented by the common canal, which is often from 0.3 to 0.5 mm wide in side view. The thecae number 9 to 14 in 10 mm.

Resemblances. Monograptus nobilis Törnquist. The distal thecae are different in shape, those of M. toernquisti being the larger and with hooks less definitely enrolled than in M. nobilis (figure 16).

M. planus (Barrande) and M. pseudoplanus sp.nov. These forms are similar to M. toernquisti in the early elongated thecae and the shape of the rhabdosome. However, the distal thecae are usually less than 1.5 mm high in M. planus and M. pseudoplanus and more than 1.5 mm in M. toernquisti (figure 16).

M. separatus sp.nov. and M. separatus triangulatus (Harkness). See p. 496.

Remarks. M. toernquisti is very near to M. nobilis Törnquist (1899, p. 20) in general form, but the different size and shape of the distal thecae means that the two forms must be regarded as distinct. M. nobilis has not so far been recorded from Britain, but the lectotype from Tomarp, Sweden, is figured in figure 91, plate 22 for comparison. It is in relief, but well embedded in the rock, so that the appearance of some of the more slender-looking distal thecae in the figure given is deceptive, for they are almost certainly slightly covered by matrix. Some of the better exposed ones, however, show indications of lateral broadening at the aperture, and there is no doubt that M. nobilis and M. toernquisti are closely related.

MM MM AM MAN MAN MIN

M. separatus

M. toernquisti

M. planus

M. decipiens

M. pseudoplanus

M. nobilis

FIGURE 16. Resemblances among distal thecae. Magn. × 5 approx.

Monograptus toernquisti toernquisti var.nov.

(Figure 84, plate 22)

Holotype. The specimen figured in figure 84, from horizon O, M. triangulatus var. band, M. gregarius zone, Rheidol Gorge, Pont-erwyd, near Aberystwyth, SM. A24480.

Number of specimens. About 35 (fragmentary).

Horizon and localities.

M. gregarius zone, Rheidol Gorge M. triangulatus var. band, horizons R, Q, P, O.

Material also seen from Lake District: Long Sleddale.

Diagnosis. First 5 or 6 thecae of the elongated type, gradually giving place to broadly triangular distal thecae.

Description. The sicula has not been seen in M. toernquisti toernquisti, but it was probably much the same as in the other varieties (see pp. 517 and 518).

The first theca seen consists of a narrow protheca $1\cdot0$ to $1\cdot2$ mm long, which widens very slowly. The metatheca is small and triangular so that the theca is only about $0\cdot2$ mm high. There are 5 or 6 of these elongated thecae, each successive one with a protheca widening slightly more rapidly than the one before, so that the metathecae are bigger, retaining the same triangular shape in side view. After this the prothecae also begin to shorten and eventually the height of the thecae becomes greater than the length. The usual proportions of distal thecae are attained about th 10, although the thecae here are somewhat smaller in size than later ones. The distal thecae are of the typical form described for M. toernquisti s.l.

Resemblances. Varieties of M. toernquisti sp.nov. The distinction depends on the number of proximal 'elongated' thecae (i.e. thecae about 4 to 6 times as long as high). M. toernquisti toernquisti has about five, whereas in M. toernquisti brevis there are only two (figure 17). M. toernquisti elongatus has six or seven and they are somewhat stouter in appearance owing to a slightly wider common canal (figure 17).

Monograptus toernquisti elongatus var.nov.

(Figures 85 to 87, plate 22)

Holotype. The specimen figured in figure 87 from horizon P, M. triangulatus var. band, M. gregarius zone, Rheidol Gorge, Pont-erwyd, near Aberystwyth. SM. A24484.

Paratypes. SM A24482, 83 (figures 85, 86).

Number of specimens. Seven.

Horizon and locality.

M. gregarius zone, Rheidol Gorge M. triangulatus var. band, horizons P, O.

Diagnosis. Usually 6 or 7 elongated thecae proximally; subsequent thecae, up to about th 12, longer than in the typical form. Distal thecae of the characteristic type.



M. toernquisti brevis M. toernquisti toernquisti

M. toernquisti elongatus

Figure 17. Resemblances among the proximal ends of M. toernquisti. Magn. \times 5 approx.

M. toernquisti elongatus

M. communis communis

FIGURE 18. Resemblances between sub-proximal thecae. Magn. × 5 approx.

Description. The sicula occurs in a number of fragments which are probably to be referred to this variety. It is small and slender, about 0.9 mm long and 0.15 mm across at the aperture. The first theca arises 0.2 to 0.25 mm from the aperture of the sicula and grows up it, widening very gradually. It is commonly 1.0 to 1.2 mm long and the sicula extends just over half-way along it. The metatheca is triangular, hooked and small, 0.2 mm high. The following thecae are similar, but somewhat stouter than in M. toernquisti toernquisti because the initial prothecae are slightly wider. After 6 or 7 thecae the prothecae shorten somewhat and widen rather more rapidly, so that by about th 12 or th 13 the usual proportions (height greater than length) of distal thecae are reached.

Resemblances. M. toernquisti toernquisti var.nov. See p. 516 and figure 17.

M. communis Lapworth. The intermediate thecae of M. toernquisti elongatus tend to have proportions similar to those of M. communis thecae. In M. toernquisti elongatus they are preceded by 6 to 7 long thecae, compared with 3 or less in M. communis, and are followed by distal thecae of height greater than length, whereas M. communis thecae are usually equilateral (figure 18).

Monograptus toernquisti brevis var.nov.

(Figure 19 and figure 83, plate 22)

Holotype. The specimen figured in figure 83, from horizon P, M. triangulatus var. band, M. gregarius zone, Rheidol Gorge, Pont-erwyd, near Aberystwyth. SM. A24485.

Paratype. SM. A24509.

Number of specimens. Eight.

Horizon and locality.

M. gregarius zone, Rheidol Gorge M. triangulatus var. band, horizons P, O.

Diagnosis. First 3 thecae elongated with a small metatheca. Next few with a fairly long slender metatheca, gradually succeeded by typical distal triangular ones.

Description. This variety is known only from two fairly complete proximal ends, of sicula and 11 thecae, and a few other fragments. The specimens are arched proximally with the maximum curvature over about th 3 to 6. The distal part of the rhabdosome was probably gently curved.

The sicula is slender, 0.85 mm long and 0.15 mm across at the aperture, and the first theca arises 0.2 mm from this. The first theca is 1.0 to 1.2 mm long, the sicula extending about half-way along it, and the metatheca is small. The theca is 0.25 mm high.



FIGURE 19. M. toernquisti brevis, distal thecae. P horizon. SM. A 24486. Magn. × 5 approx.

The main difference from *M. toernquisti toernquisti* lies in a quicker development of thecae with the usual proportions of distal triangular ones. The prothecae begin to shorten and the metathecae to lengthen about th 3 or th 4, but the prothecae still widen slowly. The metatheca consists of a long slender triangle, and the theca shows some similarity with the subparallel thecae of the *M. separatus* group. By th 7 or th 8 this effect is lost as the metathecae become wider in side view.

The thecae are all hooked, with a transversely expanded aperture and a pair of horns, as in *M. toernquisti toernquisti*. In the earlier thecae the hooks are marked, but form only at the tip of the theca. In the later ones the hook is less marked but the theca bends forwards rather earlier. There is only one distal fragment which may belong to this variety (figure 19), and this is unfortunately seen only as a median section of the rhabdosome. It shows the thecae hooked fairly near the tip, and the apertures facing proximally. It has thecae up to 1.4 mm in height and numbering 11 in 10 mm. If this distal fragment does not belong here and is allied rather with the *M. separatus* group it may be that the specimens seen are complete and the form was naturally very short.

Resemblances. Varieties of M. separatus sp.nov. The slender metathecae of th 4 to th 6 invite comparison with M. separatus triangulatus or M. separatus predecipiens. However, these thecae still show a triangular base, and are of smaller height. The three proximal elongated thecae are characteristic for M. toernquisti brevis (figure 4).

M. toernquisti toernquisti. See p. 516 and figure 17.

Monograptus communis Lapworth

(Figures 97 to 106, plate 23)

- 1876 a Monograptus convolutus var. (a) communis Lapworth, p. 358, pl. XIII, fig. 4b (fig. 4a is identifiable as M. communis communis).
- 1890 Monograptus convolutus Geinitz p. 19 (pars), non pl. A, figs. 24, 25.
- 1892 Monograptus convolutus var. communis Barrois, p. 117.
- ?1897 Monograptus communis Perner, p. 15 (pars), pl. XII, figs. 7-9, non pl. XI, figs. 18a, b, pl. XII, figs. 5, 6a, 6b (pl. XII, fig. 20, text-fig. 14 are M. communis communis).
- ? 1899 Monograptus convolutus var. communis Eisel, p. 55.
- ?1907 Monograptus communis Vinassa de Regny, p. 179.
- Monograptus communis Elles & Wood, p. 480 (pars), text-fig. 336b, ?pl. XLIX, figs. 1d, e, non pl. XLIX, fig. 1b (figs. 1a, c, text-fig. 336a are M. communis communis).
- 1913 Monograptus communis Dollé, p. 238, pl. X, figs. 5-7.
- ?1919 Demirastrites communis Kirste, p. 214 (pars), pl. III, fig. 53b, non fig. 53a.
- 1920 Monograptus communis Gortani, p. 45, pl. III, fig. 32 (fig. 31 is M. communis communis).
- 1945 Spirograptus communis communis Přibyl, p. 30, pl. VIII, figs. 2, 3, (fig. 1 is M. communis communis).
- ?1947 Monograptus communis Ruedemann, p. 477, pl. 86, figs. 42, 43. (The above can only be referred to communis s.l.)

non

1912 Demirastrites communis Eisel, p. 38, pl. III, figs. 14, 15, 19, 21.

Lectotype (Elles & Wood 1913, explanation of pl. XLIX, fig. 1a). The specimen figured by Lapworth (1876a) as Monograptus convolutus var. (a) communis, on pl. XIII, fig. 4a, from the Lower Birkhill Shales, Dobb's Linn, Moffat. Also figured by Elles & Wood (1913) as Monograptus communis, on pl. XLIX, fig. 1a. Lapworth's Collection, Department of Geology, Birmingham University.

Number of specimens (including all varieties). About 80.

Horizon and localities.

M. gregarius zone, Rheidol Gorge M. triangulatus band, horizons J, H, G, F, E, D, C, AB.

Diplograptus magnus band, horizon X.

Material also seen from

Southern Uplands: Moffat, Lockerbie, Galashiels.

Lake District: Skelgill.

Northern Ireland: Donaghadee, Pomeroy.

Central Wales: Pont-erwyd District (*M. convolutus* zone).

Diagnosis. Rhabdosome curved, proximal end through 180° or more, distal part gently curved. Thecae on the convex side, without overlap. Early thecae elongated, distal ones consisting of a roughly equilateral triangle. All the thecae hooked, the hook consisting of an almost cylindrical tube with no transverse expansion of the aperture.

Description. The rhabdosome is sometimes of considerable length and specimens up to 95 mm long have been seen, although the usual length is about 30 mm. The sudden curvature at the proximal end gives the 'fish-hook' appearance. It extends over about 4 or 5 thecae from th 3 or th 4 onwards. The succeeding part is gently curved and some of the longer specimens appear straight in the extreme distal regions.

The sicula is small and the first theca long and narrow, extending beyond it. Successive thecae become shorter and higher, eventually producing the more or less equilateral triangular shape of the distal thecae; the rate at which this process occurs is different in the two varieties.

The distal thecae are triangular in side view, the proximal wall sloping at an angle of about 40° to the axis of the rhabdosome, often slightly convex in outline. The distal wall formed by the metatheca stands more or less perpendicular to the axis. The apertural region is of constant width in side view, about 0.25 mm, from the point where it begins to curve over to form the hook, and the aperture faces proximally or half-ventrally.

Resemblances. M. separatus sp.nov. The distal thecae have a height/length ratio of 1:1, whereas in M. separatus this value is about 1.5:1. Also, the hook of M. communis is fairly wide in side view and of constant width throughout; in M. separatus the metatheca narrows continuously so that the aperture is narrow (see also p. 496 and figure 20).

M. toernquisti toernquisti var.nov. and M. toernquisti elongatus var.nov. See p. 517 and figure 18.

M. denticulatus Törnquist. See p. 510 and figure 12.

M. pseudoplanus sp.nov. See p. 524 and figure 12.

Monograptus communis communis Lapworth

(Figures 97 to 101, plate 23)

- 1876a Monograptus convolutus var. (a) communis Lapworth, p. 358 (pars), pl. XIII, fig. 4a, non fig. 4b.
- 1876 b Monograptus spiralis var. (b) communis Lapworth, p. 128, pl. V, fig. 16.
- 1876c Monograptus convolutus (communis) Lapworth, p. 5, pl. I, fig. 18.
- ? 1897 Monograptus communis Perner, p. 15 (pars), pl. XII, fig. 20, text-fig. 14, non pl. XI, figs. 18a, b, pl. XII, figs. 5, 6a, 6b, 7, 8, 9.
- 1913 Monograptus communis Elles & Wood, p. 480 (pars), pl. XLIX, figs. 1a, c, text-fig. 336a, non pl. XLIX, figs. 1b, d, e, text-fig. 336b.
- 1920 Monograptus communis Gortani, p. 45 (pars), pl. III, fig. 31, non fig. 32.
- ? 1933 Monograptus communis Sun, p. 40, pl. VI, fig. 6.
- 1945 Spirograptus communis communis Přibyl, p. 30 (pars), pl. VIII, fig. 1, non figs. 2, 3.

Lectotype (Elles & Wood 1913, explanation to pl. XLIX, fig. 1a). The specimen figured by Lapworth (1876a) as Monograptus convolutus var. (a) communis on pl. XIII, fig. 4a, from the Lower Birkhill Shales, Dobb's Linn, Moffat. Also figured by Elles & Wood (1913) as Monograptus communis on pl. XLIX, fig. 1a. Lapworth's Collection, Department of Geology, Birmingham University.

Number of specimens. About 50.

Horizon and localities.

M. gregarius zone, Rheidol Gorge

M. triangulatus band, horizons H, G, F, E, D, C, AB.

Diplograptus magnus band, horizon X.

Material also seen from

Southern Uplands: Moffat, Lockerbie, Galashiels.

Lake District: Skelgill.

Northern Ireland: Donaghadee, Pomeroy.

Central Wales: Pont-erwyd District (M. convolutus

zone).

Diagnosis. First theca with a long narrow protheca and a small triangular metatheca; successive ones becoming shorter and higher until the usual distal proportions of about 1:1 are reached between th10 and th15.

Description. The sicula is about 1.0 mm long and is 0.15 mm broad at the aperture. The first theca seems to arise about 0.3 mm from the aperture, and it is from 1.2 to 1.4 mm long extending well beyond the sicula tip. The protheca is narrow, increasing in width very slightly as it grows, and the metatheca is small, triangular and hooked in the same way as the later thecae; the theca is 0.2 mm in height.

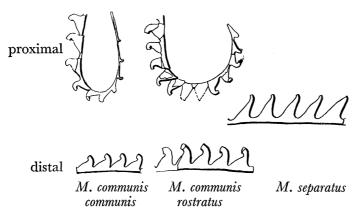


FIGURE 20. Resemblances among proximal and distal thecae. Magn. × 5 approx.

Successive prothecae widen more rapidly, the metatheca assuming greater importance as the thecae augment steadily in height. At first the increase is about 0·2 mm per theca, but it gradually falls off until by about th 15 it is very small. About here the thecae reach a fairly constant height of 1·3 to 1·4 mm. At the same time the early prothecae rapidly become shorter from one to the next until a minimum of about 0·6 mm is reached between th 4 and th 6. Then the length again increases to give the usual distal length of about 1·0 mm. The proportions of typical distal thecae are thus often reached about th 10.

In face view (figure 100b, plate 23) the distal thecae are of uniform width throughout, and the aperture is more or less circular in shape. Its dorsal margin is slightly concave in shape so that the convex edges of the lateral parts form a pair of rudimentary lappets (figures 100c, d). In one or two early thecae where the apertural region can be seen (figures 101c, d, plate 23) this feature is absent and the dorsal part appears entire.

Distal thecae are $1\cdot1$ to $1\cdot5$ mm high, usually $1\cdot3$ to $1\cdot4$ mm and they number 8 to 15 in 10 mm.

Resemblances. M. communis rostratus Elles & Wood. The two varieties are very similar and it may be impossible to distinguish the distal thecae, but usually those of M. communis

rostratus are slightly higher and somewhat shorter, producing a taller appearance (figure 20). In the proximal end, *M. communis communis* has 2 or 3 elongated thecae, whereas *M. communis rostratus* has only one; the thecae in the region of maximum curvature are of greater height but shorter in *M. communis rostratus*, and this is a characteristic difference. The curvature of the rhabdosome is often less abrupt in *M. communis rostratus* (figure 20).

MONOGRAPTUS COMMUNIS ROSTRATUS ELLES & WOOD

(Figures 102 to 105, plate 23 and figure 21)

- 1913 Monograptus communis var. rostratus Elles & Wood, p. 481 (pars), pl. XLIX, fig. 2b, text-fig. 337, non pl. XLIX, figs. 2a, c.
- 1913 Monograptus communis Elles & Wood, p. 480 (pars), pl. XLIX, fig. 1 b, non pl. XLIX, figs. 1 a, c, d, e, text-figs. 336 a, b.

1945 Spirograptus communis rostratus Přibyl, p. 31.



FIGURE 21. M. communis rostratus, distal thecae. C horizon. SM. A 24494. Magn. \times 2 approx.

Lectotype. Přibyl (1945) selected as lectotype the specimen figured by Elles & Wood, 1913, pl. XLIX, fig. 2a. Examination shows that this specimen is not referable to M. communis rostratus or even to M. communis, but is M. separatus sensu lato. Application has been made to the ICZN to set aside Přibyl's lectotype selection and to designate in its place the specimen illustrated by Elles & Wood as pl. XLIX, fig. 2b, and text-fig. 337, from the Lower Birkhill Shales, Dobb's Linn. Geological Survey of Scotland, 2630 (Bulman 1957, p. 314).

Number of specimens. About 30.

Horizon and localities.

M. gregarius zone, Rheidol Gorge M. triangulatus band, horizons J, H, G, F, D, C,

AB.

Material also seen from Southern Uplands: Moffat.

Lake District: Skelgill.

Diagnosis. Early thecae, except the first, all similar in length and increasing steadily in height, thus usually less elongated but higher than in the typical form. Distal thecae also of somewhat greater height than in the typical form.

Description. The sicula is not known with certainty but the fragment figured in figure 105 plate 23, may belong here. This sicula is 0.75 mm long and 0.1 mm broad at the aperture, with the first theca, 1.2 mm long, extending beyond the sicula. The theca is 0.2 mm high. The second theca is shorter, 0.8 to 0.9 mm, and thence as far as th 10 the prothecae shorten only very slightly, for the average there is 0.7 mm. However, the thecae increase in height by about 0.2 mm from one to the next, reaching 1.0 mm at th 10. After this the increase is more gradual.

The distal thecae (figure 21) are somewhat shorter and higher than those of M. communis communis, but otherwise similar. They range from 1.25 to 1.65 mm in height and the average is just over 1.4 mm. They number 8 to 14 in 10 mm.

Resemblances. M. communis communis Lapworth. See p. 521 and figure 20.

M. separatus sp.nov. The proportions of the distal thecae are rather similar in the two forms but the hook of M. communis rostratus is fairly wide in side view and of constant width throughout; in M. separatus the metatheca narrows continuously and the aperture is narrow (figure 20).

Monograptus pseudoplanus sp.nov.

(Figures 94 to 96, plate 22 and figure 22a)

Holotype. The specimen figured in figure 96 from horizon X, Diplograptus magnus band, M. gregarius zone, Rheidol Gorge, Pont-erwyd, near Aberystwyth, SM. A24497.

Paratypes. SM. A24495 (figure 94) A24496 (figure 22a).

Number of specimens. About 50.

Horizon and localities.

M. gregarius zone, Rheidol Gorge M. triangulatus band, horizon J.

Diplograptus magnus band, horizon X.

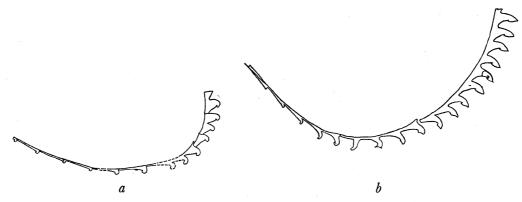


FIGURE 22. (a) M. pseudoplanus, proximal fragment. X horizon. SM. A 24496. Magn. × 5 approx. (b) M. planus, proximal end. Llanidloes, SM. A 23580. Magn. × 5 approx.

Diagnosis. Proximal rhabdosome broadly arched, distal part gently curved, thecae on the convex side, without overlap.

Early thecae elongated, with very small hooked metathecal parts. Distal thecae bluntly triangular, widening from the beginning of the protheca to the transversely expanded apertural region, which is hooked.

Description. The broadly arched form of the proximal part of the rhabdosome extends over 10 to 15 thecae, the first few thecae being almost straight and the distal part of the rhabdosome gently curved.

The sicula is unknown, but the earliest thecae seen are probably not far short of it (figure 22a). Here the protheca is slender and widens very slowly, but is often 1.0 to 1.2 mm long and may reach 1.6 mm. The metathecal part is insignificant, a small triangle 0.2 mm high with a tiny hook. The aperture is probably transversely expanded.

There are 5 or 6 of these elongated thecae, the most proximal being of the greatest length and smallest height. Subsequently the protheca shortens, reaching a minimum length of 0.6 to 0.7 mm between th 6 and th 12. At the same time it increases in width more rapidly in successive thecae. The metathecae, retaining the same triangular form, become bigger and the thecae increase in height to a constant value about th 15 to th 20.

There is considerable variation in the size of the distal thecae: the smallest are 0.8 mm long and 0.8 mm high (figure 94, plate 22); the largest are 1.0 mm long and 1.3 to 1.4 mm high (figure 96, plate 22). However, most specimens are intermediate, with thecae 1.1 to 1.2 mm high and numbering 10 to 15 in 10 mm.

Only compressed or half-relief specimens are known, but the latter give some idea of the shape of the solid theca. A suggested reconstruction is shown in figure 95, plate 22. The theca is of the general triangular type, widening laterally in the apertural region, which is prolonged into a pair of horns. The distinctive features are: (i) the proximal inclination of the dorsolateral parts of the theca, which gives it a 'leaning forward' appearance; and (ii) the well-hooked nature of the horns. An overhanging dorsal lip was almost certainly present in the central region of the aperture.

On compression, the thecal outline produced is very often like that shown in figure 94, plate 22, where the horn has formed a prominent ridge running diagonally across the theca. The part median to this has been flattened and gives the dorsal margin of the theca a rounded 'hunchback' appearance. It was probably at least as broad at the aperture as the theca is long. In most of the thecae preserved in this way the horn is broken and the dorsal lip is seen, looking like a small rounded lobe at the tip. This thecal outline is very common, and a trace of the oblique ridge can be seen even in many completely compressed specimens and those preserved only in chlorite.

Resemblances. M. planus (Barrande). Compressed specimens of M. pseudoplanus show the enrolled dorsal lip as a lobe at the tip of the theca, but the apertures of M. planus usually show their straight transversely expanded margin and small spines (figure 16).

M. communis Lapworth. The distal thecae of M. pseudoplanus are smaller and have a straight ventral margin inclined at a high angle to the axis of the rhabdosome, whereas in M. communis the ventral wall is convex and at a lower angle (figure 12). M. pseudoplanus has a greater number of proximal elongated thecae and quite different hooks.

M. denticulatus Törnquist. See p. 510 and figure 12.

M. toernquisti sp.nov. See p. 515 and figure 16.

MONOGRAPTUS PLANUS (BARRANDE)

(Figures 92, 93, plate 22 and figure 22b)

1850 Graptolithus proteus var. plana Barrande, p. 58, pl. 4, fig. 15.

This species has not been studied in detail and a full critical synonymy is not given. References will be found in Přibyl (1945, p. 33).

Holotype (Přibyl 1945, p. 34). The specimen figured by Barrande on pl. 4, fig. 15, as Graptolithus proteus var. plana, from the zone of Rastrites linnaei $(e\alpha_1)$, Zelkovice, Bohemia (= zone of Monograptus turriculatus in Britain). Specimen not seen.

Horizon and localities.

Material seen from Crossfell region: Hebblethwaite Gill near Sedbergh.

North Wales: Derwen. Central Wales: Llanidloes.

Diagnosis. Rhabdosome broadly arched proximally, gently curved distally, thecae on the convex side, without overlap.

Early thecae elongated with a small triangular hooked metatheca, giving place to triangular distal thecae about as long as high, with hooks which are slightly transversely expanded and have a pair of small lateral spines.

Description. The sicula has been seen in one specimen (figure 22b) and is slender, 1.4 mm long and 0.15 mm broad at the aperture (compressed). The first theca arises 0.15 mm from the aperture, and is 1.3 mm long, the tip of the sicula being level with the metathecal part.

The early thecae consist of a long slowly widening protheca, up to 1.45 mm in length, and a small triangular hooked metatheca whose dorsal wall is inclined towards the distal end so that the theca appears to lean backwards. Subsequent prothecae become slightly shorter and widen more rapidly; the metathecae increase in size until the thecae are equilateral in side view at th 8 to th 10. The distal thecae are commonly 1.0 to 1.2 mm high and number 10 to 12 in 10 mm. The theca remains fairly narrow from side to side until the hook begins to form. Then it widens so that the aperture is oval in shape, with a straight dorsal margin and a pair of short dorsolateral spines. On compression this expanded part is often tilted sideways so that one spine points upwards and the theca appears of greater height than it really is (figure 93, plate 22).

Resemblances. M. pseudoplanus sp.nov. See p. 524 and figure 16.

M. decipiens Törnquist. See p. 511 and figure 16.

M. toernquisti sp.nov. See p. 515 and figure 16.

Genus RASTRITES Barrande 1850

RASTRITES LONGISPINUS (PERNER)

(Figure 71, plate 21 and figure 23)

1897 Rastrites peregrinus A var. longispinus Perner, p. 9, pl. 13, figs. 32, 35, text-fig. 7.

The species has not been studied in detail so a critical synonymy is not given. For further references, see Přibyl (1942), p. 6.

Lectotype (Přibyl 1942, p. 7). The specimen figured by Perner (1897) as Rastrites peregrinus A var. longispinus, on text-fig. 7, from Kosov, Bohemia. Specimen not seen.

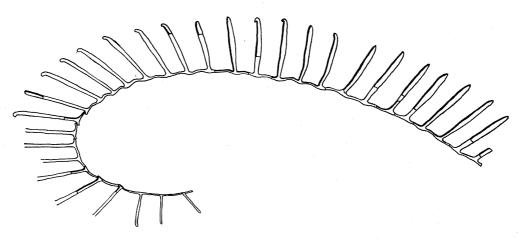


FIGURE 23. Rastrites longispinus. G horizon, SM. A 24498. Magn. \times 5 approx.

Number of specimens. Sixteen. Horizon and locality.

M. gregarius zone, Rheidol Gorge M. triangulatus band, horizons G, F, E, DE, D, C. Remarks. Most of the Rheidol Gorge specimens consist of chlorite impressions only, but one fairly complete example is pyritized (figure 23 and figure 71, plate 21). Here the thecal hooks are well preserved and the distal thecae reach 3.5 mm in height. The specimen is thus on the small side according to Elles & Wood (1914, p. 489) who give a range of 3.0 to 5.0 mm for the thecae. However, it corresponds closely with one figured by these authors as R. longispinus (pl. L, fig. 2g and text-fig. 344b) which also came from the Rheidol Gorge section. The other fragments in the present collection are similar.

distal thecae height/length ratio			KEY TO THE SPECIES	
1·5 or less	early thecae	elongated rastritiform equilateral	about six elongated theacae less than five elongated thecae —	{ M. pseudoplanus \ M. planus { M. communis communis \ M. communis rostratus M. denticulatus { M. spiralis \ M. communis rostratus
	(elongated	 .	M. toernquisti and all varieties
1.5–2.0	ly thecae	rastritiform	fish-hook shaped rhabdosome	M. separatus separatus M. separatus predecipiens M. separatus triangulatus
			spiral rhabdosome	M. decipiens
	early	equilateral	——	{ M. separatus fimbriatus { M. separatus similis
2·0 or more	habdo- some	fish-hook shape		M. separatus major M . separatus extremus
	hal so	spiral	·	M. convolutus

PART III

EVOLUTION

Introduction

Of the Monograptids described above, some are truly biform in the sense used by Elles & Wood (1911, p. 361), for example *M. separatus triangulatus*, while others are uniform in having thecae of the same shape the whole length of the rhabdosome. In some of the latter all the thecae have the same proportions and they are really uniform, e.g. *M. spiralis*, whereas in others the proximal and distal thecae may be of such different proportions (e.g. *M. toernquisti*) that there is as much difference between them as between the two types of, say, *M. separatus triangulatus* thecae.

There is, therefore, in most of the forms a change in the type of theca along the rhab-dosome. The distal thecae are more often preserved and usually attain a constant form over a considerable length of the colony. They are thus the most useful for subdivision of a large group like the whole of the Monograptids (see, for example, Elles & Wood 1911, pp. 360-1), but the result provides only a key, perhaps also putting out a few pointers towards a fuller evolutionary picture. For this the proximal end must be considered as well.

All the forms to be primarily considered here show triangular distal thecae without overlap. An attempt at subdivision which gives precedence to the form of the distal thecae results in the following grouping:

1. Forms with transversely expanded triangular thecae with a dorsal lip and a pair of horns

M. separatus (all varieties)

M. convolutus

M. denticulatus

M. decipiens

M. toernquisti (all varieties)

M. pseudoplanus

2. Forms with triangular thecae which are transversely expanded but different from those in group 1 above (and also different from each other):

M. spiralis

M. planus

3. Forms with triangular thecae which are not transversely expanded at the aperture:

M. communis (both varieties)

4. Form with Rastrites-like distal thecae:

R. longispinus.

Thus there is really one big group (no. 1) and a number of remaining forms which would seem at first to have no obvious grouping or relationship. However, within this big group, further division can be made if the nature of the proximal end is also considered, and this gives:

1 A. Those with at least some rastritiform thecae at the proximal end:

M. separatus (most varieties)

M. convolutus

M. denticulatus

M. decipiens

1B. Those with axially elongated thecae:

M. toernquisti (all varieties)

M. pseudoplanus

1 C. Those with triangular thecae of the same general proportions throughout the rhabdosome:

M. separatus fimbriatus

M. separatus similis

It can then be seen that, considering their proximal ends, the species *M. spiralis*, *M. planus*, *M. communis communis* and *M. communis rostratus* would also fit into these groups, supplementing groups B and C, and the remaining form, *R. longispinus*, is obviously nearest to group A. The result is a far more satisfactory grouping. This then might provide a more suitable basis for the classification of these forms, and for a discussion of their evolution, in spite of the difference in the distal thecae.

The grouping then provisionally adopted is as follows:

A. Forms with at least a few rastritiform thecae at the proximal end, usually passing into distal triangular ones:

M. separatus separatus

M. separatus predecipiens

M. separatus triangulatus

M. separatus major

M. separatus extremus

M. convolutus

M. decipiens

M. denticulatus

R. longispinus

B. Forms with axially elongated thecae at the proximal end, giving place to triangular distal thecae:

M. toernquisti toernquisti

M. toernquisti elongatus

M. toernquisti brevis

M. communis communis

M. communis rostratus

M. pseudoplanus

M. planus

C. Forms with thecae which are triangular in shape the whole length of the rhabdosome:

M. separatus fimbriatus

M. separatus similis

M. spiralis

(M. delicatulus)

In this grouping then, precedence is given to the general nature of the proximal end. It is suggested that the members of group A are more closely related to one another than they are to the members of group B, and vice versa, and that the forms in group C may fit into one or both of the other groups. This hypothesis provides a more reasonable picture of the evolution than can otherwise be constructed, and in which certain definite trends can be seen to operate.

Evolution in group A and related forms

Group A. M. separatus separatus, M. separatus predecipiens, M. separatus triangulatus, M. separatus major, M. separatus extremus, M. denticulatus, M. decipiens, M. convolutus, R. longispinus.

Related forms. M. separatus fimbriatus, M. separatus similis, M. spiralis, M. delicatulus.

In the Rheidol section group A forms are the most common, and with the fine stratigraphical subdivisions employed it has been possible to establish some probable lines of evolution. Table 2 shows the numbers and percentages of the more important species found at each horizon.

horizon	species	Monograptus separatus fimbriatus	M. separatus separatus	M. separatus predecipiens	M. separatus triangulatus	M. separatus extremus	Rastrites longispinus
A– E		230	22	-		-	12
$F\!\!-\!\!J$		87 %	9 % 65				$\frac{4\%}{4}$
K-L		1 %	93 %	26		8	6 % —
M-N		i	10 % 4	68 % 5	22	$rac{22\%}{2}$	
O– Q		, 	12%	$^{16\%}_{4}$	$\frac{66\%}{95}$	6 % —	
R-S			$\frac{5\%}{110}$	4 % 1 1 %	91 %		

Table 2. Analysis of numbers of group A forms collected

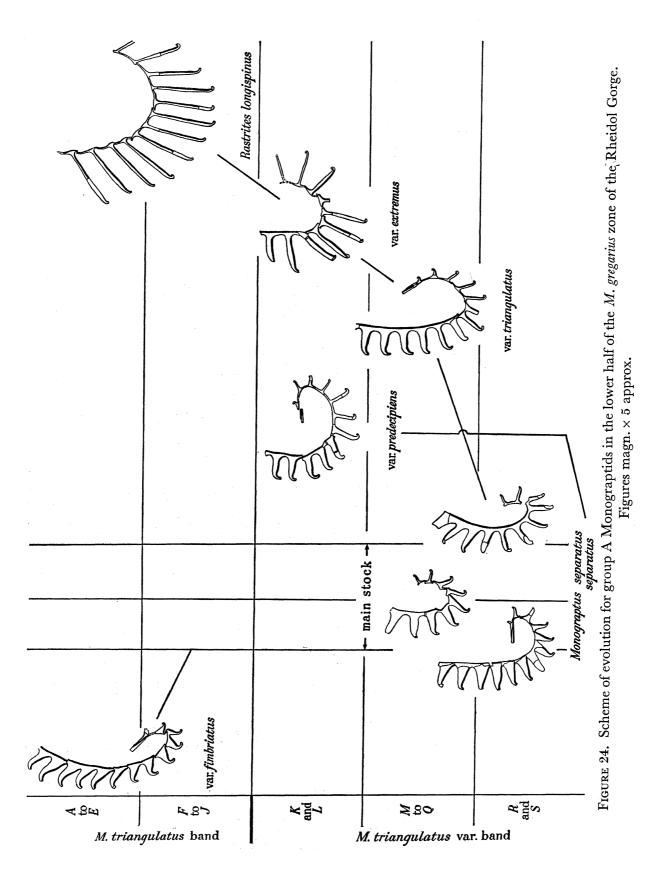
The important features are:

- (1) The persistence of M. separatus separatus throughout the section.
- (2) The first occurrence of M. separatus triangulatus at horizon Q, and of M. separatus fimbriatus at horizon G, and the sudden abundance of each soon after its appearance.
- (3) The presence of Rastrites longispinus in the section F-J and above, but not below this. The lines of evolution which these facts suggest are shown in figure 24. The persistent main stock is Monograptus separatus separatus, showing all gradations between its extremes of variation; in general it has but few rastritiform proximal thecae, while the distal ones are triangular.

One probable line of evolution extends from this form through *M. separatus triangulatus* and *M. separatus extremus* to *Rastrites longispinus*, implying a change from a biform Monograptid to a uniform one by way of more extreme biform types. These forms are each different from their ancestor in two ways: (a) in having a greater number of rastritiform thecae, and these thecae being more rastritiform; (b) in a slight degree of modification of the distal thecae in the same 'rastritiform' direction; so that, although the alteration is most marked at the proximal end, each stage really shows a modification acting on the whole rhabdosome, rather than a simple progression of a new character from the proximal to the distal end.

The final stage, from M. separatus extremus to Rastrites longispinus shows the greatest difference between ancestor and descendant; the much larger stratigraphical gap between the main horizons of the two (about five times the thickness of rocks between those of M. separatus triangulatus and M. separatus extremus) may account for the lack of intermediate forms.

A second line of evolution occurs higher in the section, where *M. separatus separatus* is believed to give rise to *M. separatus fimbriatus*. Here rastritiform characters of the earlier thecae are lost and they are all triangular. Again the biform *M. separatus separatus* has produced a uniform type, but the evolution has been in the 'opposite' direction—the proximal thecae have lost their distinctive characters and have come to resemble the distal thecae. It seems certain that *M. separatus fimbriatus* is not present in the lower beds, and its sudden importance at the top of the *M. triangulatus* band confirms the impression that it is a new form.



The third line of evolution—perhaps of less importance than the other two—is that leading from M. separatus separatus to M. separatus predecipiens. This runs parallel to the M. separatus triangulatus-Rastrites line, the same processes occurring but at different rates, so that the early thecae become more Rastrites-like by their slenderness and their long narrow common canals, but only slightly by their increase in height. These forms are always rare and are best seen about the top of the M. triangulatus var. band. Fragments which may belong here are found at the lowest horizons, so that the form probably became distinct from M. separatus separatus at an early stage. The two forms may have had completely distinct ancestries, but it seems unlikely considering their close similarity.

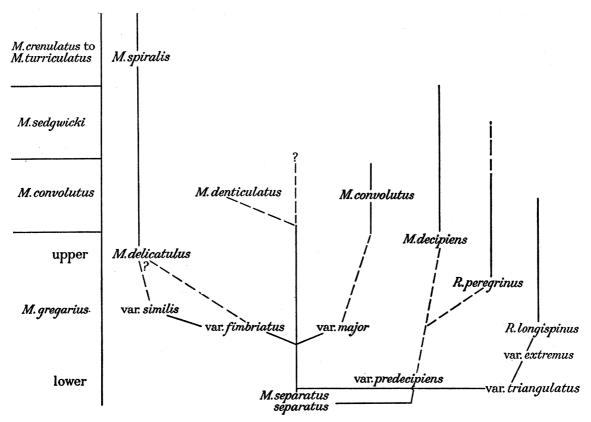


FIGURE 25. Some suggested lines of evolution in group A and related forms.

Throughout these changes the form of the thecal apertures has remained remarkably constant—transversely expanded and consisting of a pair of horns separated by a median dorsal lip.

For the remaining members of this group the stratigraphy and variation is known in much less detail. However, it is possible to see comparable changes and in some cases to extend and amplify the evolutionary lines (figure 25).

Two forms apparently fairly close to the M. separatus triangulatus-Rastrites line are M. separatus major and M. convolutus. M. separatus major is not well known, but seems to occur in the upper part of the M. gregarius zone (see pp. 507 and 542), so that it could have arisen either from M. separatus triangulatus or M. separatus extremus, or independently from M. separatus separatus. The small size of its proximal thecae favours the latter view. The tall distal thecae suggest that M. separatus major might be ancestral to M. convolutus. A new

factor introduced here, of course, is the spiral form of the rhabdosome, and this can be regarded as a prolongation of the strong curvature of the proximal end in *M. separatus*. Thus there is possibly a separate line of evolution, beginning somewhat later than the *M. separatus triangulatus-Rastrites* line, showing the same trends acting at different relative rates.

M. decipiens is said to occur rarely at the top of the M. gregarius zone and becomes more common in the succeeding M. convolutus and M. sedgwicki zones. Its relatively low thecae and long common canal parts invite comparison with M. separatus predecipiens, and it is likely that the latter was a stage in the evolution of the true M. decipiens. Rastrites peregrinus, which was found in the Diplograptus magnus band, may also be related, since it too has low thecae and long common canals and could be an offshoot from the M. separatus predecipiens-M. decipiens line.

M. denticulatus occurs in the M. convolutus zone and has proximal thecae very like those of M. separatus separatus, but the distal thecae are smaller and more strongly hooked. Possibly, then, M. denticulatus is a direct offshoot from the main stock, supposing this persisted to at least the base of the M. convolutus zone.

Closely connected with the *M. separatus fimbriatus* line of evolution are *M. separatus similis*, *M. spiralis* and *M. delicatulus*, all these having triangular thecae throughout the rhabdosome. It is probable that *M. separatus similis*, occurring in the *M. gregarius* zone, although at what exact horizon is unknown, is a derivative of *M. separatus fimbriatus*. The two forms are very similar, but the first few thecae of *M. separatus similis* are more triangular and have shorter prothecae than those of *M. separatus fimbriatus*. This is a change which had already begun in the production of *M. separatus fimbriatus* from *M. separatus separatus*.

Either of these forms could have given rise to M. spiralis, which occurs at a high horizon—the zones of M. turriculatus to M. crenulatus. A characteristic feature is the extreme shortness of the prothecae at the proximal end, so that the sicula extends at least half-way up the second theca. This can readily be seen as a further development of the short prothecae begun in M. separatus similis. The spiral form of the rhabdosome in M. spiralis is a development paralleled by that of M. convolutus, and it is interesting that this seems to occur independently of the type of variation seen in the proximal thecae. In this case there is at present a considerable gap of some 2 to $2\frac{1}{2}$ zones between the possible ancestor and descendant. However, a form described by Elles & Wood (1913), M. delicatulus, may be important here. Its given range is rare throughout the M. gregarius and M. convolutus zones, and it is a spiral form. Unfortunately the sicula is unknown and all specimens are compressed and badly preserved, but as far as can be seen it has all triangular thecae which probably had some transverse expansion of the aperture. Thus it could provide a link between M. separatus fimbriatus or M. separatus similis and M. spiralis.

The origin of the group A forms

It has been suggested above that all the species and varieties so far discussed are derived in one way or another from M. separatus separatus, but the evidence assembled throws no light whatever on the origin of this form itself. In the Rheidol Gorge section, M. separatus occurs at the very base of the M. gregarius zone and is underlain by a few feet of unfossiliferous rock before the half-inch band (horizon T) mentioned in the stratigraphical section

(see p. 486) occurs, with a fauna allied to that of the *M. cyphus* zone. The Monograptids found here were: *M. cyphus*, *M. gregarius*, *M. revolutus*, *M. atavus* and *M. sandersoni*. In addition, other forms which were recorded from the *M. cyphus* zone in Britain by Elles & Wood include Diplograptidae, Dimorphograptidae, *Monograptus acinaces*, *Monograptus concinnus*, *Monograptus incommodus*, and *Monograptus difformis*. Among these the only forms showing any tendency to a hooked type of theca are *M. revolutus* and its varieties and *M. difformis*. However, both these have elongated proximal thecae, and, as will be shown in the next section, are much more likely to be connected with the group B forms. All the other *M. cyphus* zone forms show straight overlapping thecae.

Evolution in group B and related forms

Group B. M. toernquisti toernquisti, M. toernquisti elongatus, M. toernquisti brevis, M. communis communis, M. communis rostratus and M. pseudoplanus.

Related forms. M. revolutus and vars. austerus and praecursor, M. argenteus, and var. cygneus, M. difformis, M. limatulus and M. planus.

These forms are on the whole less common than those of group A, as can be seen from table 3. It shows that M. toernquisti and its varieties are the lowest members found, at horizons P and O. Complete specimens are not common, but distal fragments occur in fair abundance. At the base of the M. triangulatus band M. communis communis and M. communis rostratus appear and both are fairly abundant throughout the band. Badly preserved fragments have also been found in the Diplograptus magnus band and the species is recorded by Elles & Wood from the M. convolutus zone. The main constituent of the fauna in the Diplograptus magnus band, however, is the form described as M. pseudoplanus.

species Monograptus M. toernquisti M. toernquisti M. communis M. communis M. pseudotoernquisti horizon toern quistielongatus communis rostratus planus brevis X50 96%20 30 A–E60 % 40% F–J20 10 67 %33%K-N7 8 35 O-Q70% 14 % 16 % R–S

Table 3. Analysis of numbers of group B forms collected

The related forms (except *M. planus*) have not been described in full above, but a preliminary survey of some variations in the species *M. revolutus* has been made on material collected mainly from the Rheidol Gorge. These are illustrated in figures 26 and 27, and the principal characteristics and the horizons of occurrence are summarized in table 4 (p. 536), together with those of closely related forms.

The form named M. revolutus A (figure 26a) is a composite reconstruction from two specimens figured in the Monograph of British Graptolites as M. revolutus and known definitely to come from the M. cyphus zone of the Rheidol Gorge. It is very similar to a

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specimen seen from Kurck's (1882) original locality for *M. revolutus*, the *M. cyphus* zone of Bollerup, Sweden, and its significant features are:

- (1) Long narrow proximal thecae, with a small overlap, which increases slowly as the rhabdosome widens gently.
 - (2) About 25 hooked thecae.
 - (3) Distal straight thecae inclined at an angle of about 15° to the axis of the rhabdosome.

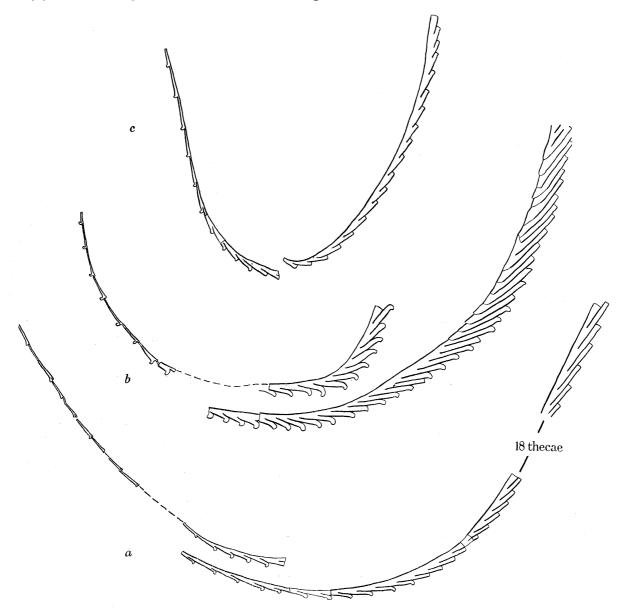


Figure 26. Some variations in *M. revolutus* forms from the *M. cyphus* and *M. gregarius* zones of the Rheidol Gorge. (a) *M. revolutus* A; (b) *M. revolutus* B; (c) *M. revolutus* C. Magn. × 5 approx.

Next in the sequence is M. revolutus B (figure 26b), which occurs only in horizon T. This shows:

(1) Early thecae elongated but without overlap. Overlap begins after about 10 thecae and increases quickly as the rhabdosome widens rapidly. It reaches one-half at 7 or 8 thecae after its inception.

- (2) At least 30 hooked thecae.
- (3) Distal thecae at an angle of about 20 to 25° to the axis, overlapping four-fifths.

In addition the rhabdosome is unusually broad from side to side and many of the hooked thecae have a tapering metathecal part. A few thecae of *M. revolutus* B were isolated from the matrix and are figured in figure 107, plate 23, where the presence of a pair of rudimentary

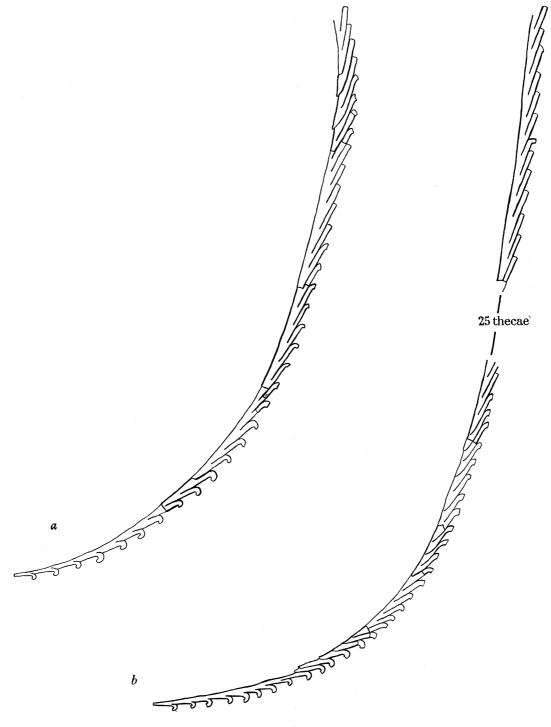


FIGURE 27. Forms of M. revolutus from the M. gregarius zone of the Rheidol Gorge.

(a) M. revolutus D; (b) M. revolutus var. praecursor. Magn. \times 5 approx.

horns can be seen at the apertures of the thecae. This suggests some affinity with the transversely expanded thecae seen, for example, in M. toernquisti or even M. separatus.

- M. revolutus D (figure 27a) appears next and is abundant at horizon O, although fragments are known also at horizons K, L, G, and C. This shows:
- (1) Elongated early thecae without overlap—this begins after about 10 thecae and reaches one-half at 10 to 15 thecae after this. Thus overlap increases at a rate intermediate between those of *M. revolutus* A and B. The rhabdosome also widens at an intermediate rate.
 - (2) Hooked thecae about 40 in number, probably cylindrical in form.
 - (3) Distal straight thecae at an angle of about 20° to the axis.

Table 4. M. Revolutus and related forms, horizons of occurrence and some important characters

character	overlap begins at about theca:	number of thecae with overlap up to ½	number of hooked thecae	angle of inclination of distal straight thecae	maximum width of rhabdo- some (in mm)	zone of occurrence
M. revolutus A	1	$\boldsymbol{22}$	25	15°	0.85	M. cyphus
M. revolutus B	10	7–8	32	2025°	1.4	lower half of M . gregarius horizon T
M. revolutus C	5	15–20	10	1015°	0.7	lower half of M . gregarius horizons $S-A$, X
M. revolutus D	12	14	42	15–20°	1.1	lower half of \hat{M} . gregarius horizons $O-C$
M. revolutus praecursor, type	10	10–15	40	20°	0.9	Plower half of M . gregarius horizons $A-J$
M. argenteus	6 seen	3	30	30°	1.7	upper half of M. gregarius
M. argenteus cygneus	6 seen	7–8	30	20°	1.1	upper half of M. gregarius to top of M. convolutus
$oldsymbol{M}.$ $oldsymbol{limatulus}$	5 seen	11	10	20°	0.7	M. convolutus, M. sedgwicki

This form is closely similar to the type of M. revolutus var. praecursor, designated and figured by Elles & Wood (1911, p. 386), which also came from the Rheidol Gorge, from the M. triangulatus or M. triangulatus var. bands. There is a specimen of M. separatus fimbriatus on the same slab as the type of M. revolutus praecursor, so it seems fairly certain that it actually came from the M. triangulatus band, i.e. horizons A to J.

A final form is M. revolutus C (figure 26c) which has elongated, slightly hooked thecae without overlap at the proximal end. However, soon after overlap begins the hooks become reduced and are represented by merely a slight expansion of the dorsal lip. This is finally lost and the thecae become straight. The overlap is always small. This form occurs almost throughout the section, from horizon O to A.

A tentative scheme of evolution for these forms and the ones with triangular thecae associated with them is shown in figure 28. It seems probable that the ancestor was M. revolutus A, since it was the earliest form to occur and all its thecae show overlap. The hooks are small and affect few thecae, but so far as can be seen are more or less cylindrical. If so, M. revolutus D and M. revolutus praecursor could be direct descendants of the earlier M. revolutus, in a slowly evolving main stock. The changes may be summarized:

- (1) Loss of overlap in the initial thecae, but a greater rate of increase in it distally, coupled with a higher inclination of the distal thecae so that the rhabdosome is broader.
 - (2) Increase in size and number of hooks.

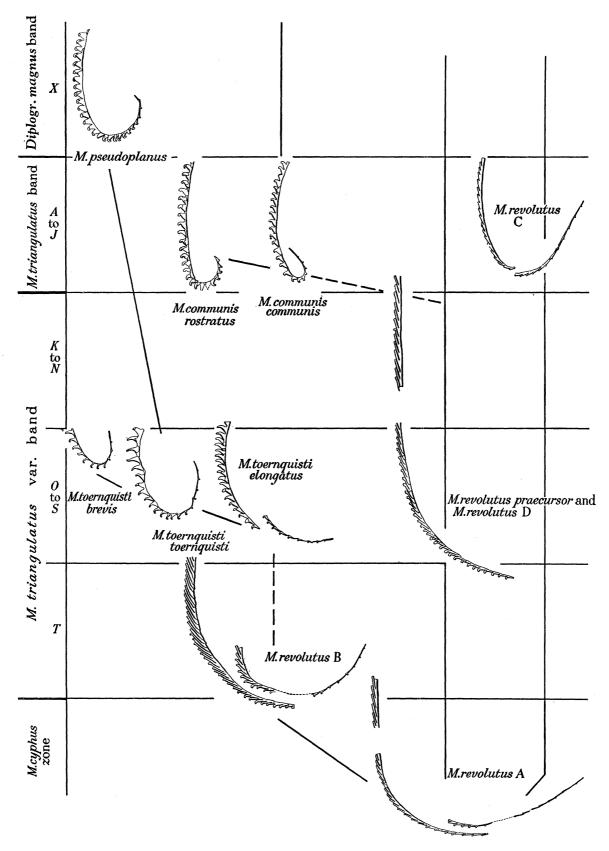


Figure 28. Scheme of evolution for group B Monograptids and forms of M. revolutus in the M. gregarius zone of the Rheidol Gorge. Figures magn. × 2 approx.

M. revolutus B is regarded as a sudden offshoot from this main stock at horizon T. Here somewhat similar changes have occurred, but at a faster rate, so that M. revolutus B has distal thecae overlapping more and a rhabdosome widening earlier than M. revolutus D, but a smaller number of hooked thecae. A new feature is the tendency for transverse broadening of the thecae and the formation of horns at the aperture.

Next in the succession is *M. toernquisti*, all forms of which have the transversely expanded type of aperture. Possibilities here are either that it arose directly from the main *M. revolutus–M. revolutus praecursor* stock, the apertures becoming modified and overlap being lost, or that it arose from the main stock through *M. revolutus* B. The type of aperture and the high inclination of *M. revolutus* B thecae favour the latter interpretation.

Although the varieties of *M. toernquisti* described above are few numerically they are interesting in possibly forming a series continuing the general trend of evolution. *M. toernquisti toernquisti* occupies the central position of the three. *M. toernquisti elongatus* is nearer to the main stock in its slowly widening rhabdosome, which attains the characters of the distal thecae only slowly, while in *M. toernquisti brevis* only 2 or 3 thecae show real elongation. Thus these varieties show respectively less and more extreme divergence from the ancestor than the typical form.

M. communis communis and M. communis rostratus appear next in the sequence, in the M. triangulatus band, and here M. communis communis has a few elongated thecae while M. communis rostratus has only one or two. If significance is attached to the cylindrical character of the apertures, it would seem likely that M. communis was a direct offshoot from the main stock, with again, loss of overlap, more rapid widening of the prothecae and a reduction in the number of elongated proximal thecae as the main changes. The first product would be M. communis communis, and further development along the same lines could lead to M. communis rostratus, where the prothecae widen even more rapidly than in M. communis communis and there are virtually no elongated thecae.

M. pseudoplanus occurs at the top of the section, in the Diplograptus magnus band, and its 5 or 6 elongated proximal thecae and transversely expanded apertures would suggest a derivation from M. toernquisti toernquisti. Alternatively, it could be argued that the almost total lack of forms of this sort at the top of the M. triangulatus var. band and throughout the M. triangulatus band suggests a separate origin from the main stock. However, there is one specimen of M. pseudoplanus from horizon J, which is intermediate in time between the two.

M. revolutus C occurs from horizon O to horizon A and remains constant throughout. It probably arose from M. revolutus A at an early stage. Its reduced number of hooks and limited overlap may indicate a retrogressive stock, or they might even suggest a separate ancestry from a form with straight thecae.

The dominant trends which can be seen in these series are as follows:

- (1) Loss of overlap in the proximal or in all the thecae.
- (2) Increase in the angle of inclination of the thecae to the rhabdosome, accompanied by either (a) increase in the amount of overlap, or (b) complete loss of overlap.
- (3) Reduction in the number of proximal elongated thecae in forms where all overlap is first lost.
 - (4) Hooked thecae spread further along the rhabdosome.

- (5) Increased dorsal curvature of the rhabdosome.
- (6) A tendency in some cases for the thecae to become transversely expanded at the aperture.

An interesting feature of the forms showing overlap is the relation between it, the curvature of the rhabdosome, and the hooked thecae. All the colonies are dorsally curved, with the greatest curvature in the region where overlap begins and increases to about one-half. When the overlap reaches a half and more the thecal hooks begin to decrease and the distal straighter part begins. The more rapidly the overlap increases the shorter is the region of maximum curvature, and the greater the curvature of any one theca in this part.

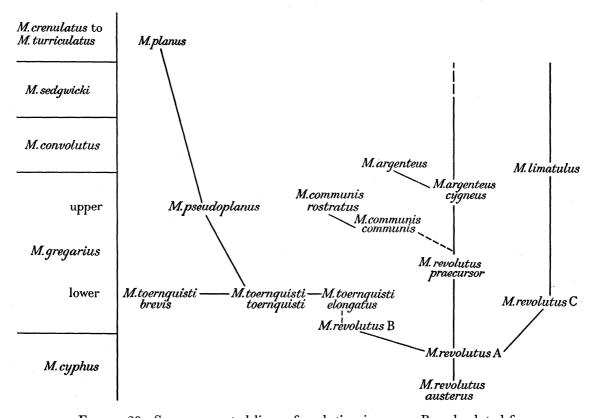


FIGURE 29. Some suggested lines of evolution in group B and related forms.

This is paralleled in the forms without overlap, with all hooked thecae, by the region where the thecae are changing from the proximal to the distal type, and the curvature here is usually fairly marked.

A number of other species may also have a place in the general scheme and can be mentioned here, although they are not described above (figure 29).

M. revolutus var. austerus was described by Törnquist (1899, p. 12) and Elles & Wood (1911, p. 385) as a form showing less curvature than the typical form, and, indeed, the specimens figured here from the Monograph of British Graptolites may really belong to this variety. Since one tendency throughout the group is an increase in curvature, it may be that M. revolutus austerus is the most primitive member of the stock.

M. difformis is a rare species described by Törnquist from Tomarp, Sweden (1899, p. 13) and recorded by Elles & Wood from Britain, including the Rheidol Gorge. Unfortunately

this is not represented in the present collection, and its exact horizon remains unknown. The proximal curvature is fairly strong; here the thecae are at first elongated and then of a shorter but higher triangular shape, still without overlap. After the region of maximum curvature, overlap begins and the thecal hooks diminish until the distal thecae become straight. This appearance makes M. difformis a likely intermediate between M. revolutus and one of the forms lacking overlap, possibly M. toernquisti since the shape of the early thecae in the two forms is similar.

Both M. argenteus and the variety cygneus occur in the upper part of the M. gregarius zone and are near to M. revolutus. M. argenteus s.str. has early elongated thecae without overlap, but when overlap begins it increases rapidly and in this part the rhabdosome bends suddenly through about a right angle. The distal part has a straight axis with the thecae inclined at about 30° to it and the hooked thecae are replaced by straight ones after about 35 thecae. M. argentus cygneus is more slender than M. argenteus, 'the thecae are inclined at a lower angle, and are more distant' (Elles & Wood 1911, p. 389). The siculae of the two forms are unknown, but it is likely that there are fewer elongated proximal thecae in M. argenteus than in M. argenteus cygneus. This variety thus bears a similar relation to M. argenteus as does M. revolutus A or M. revolutus D to M. revolutus B, and it may be tentatively suggested that M. argenteus cygneus continues the M. revolutus-M. revolutus praecursor main stock while M. argenteus is an offshoot from this. It may be noted that M. argenteus cygneus is of widespread occurrence, while M. argenteus is restricted to the Lake District and Llanystwmdwy; M. argenteus cygneus extends from the upper half of the M. gregarius zone to the top of the M. convolutus zone, whereas M. argenteus is found only at the top of the M. gregarius zone.

M. limatulus occurs in the M. convolutus and M. sedgwicki zones and its few, slightly hooked, elongated proximal thecae, followed by straight ones with overlap up to half only, suggest a derivation from M. revolutus C.

M. planus, a form with no overlapping thecae, is found in the zones of M. turriculatus to M. crenulatus and its six elongated thecae suggest a parallel with M. toernquisti and M. pseudoplanus. It could be a derivative of M. pseudoplanus; the transverse expansion seen in the latter is more limited to the apertural region in M. planus and the overlapping dorsal lip is lost, the horns of M. pseudoplanus being reduced to a pair of small spine-like projections.

The origin of the group B forms

Again, the evidence presented above throws no light on the origin of the ancestral species, *M. revolutus*. It is generally considered to be derived from *M. cyphus*, since the distal thecae of both are similar and both are dorsally curved species. If this is so, the change in the proximal end would be considerable; hooked thecae must have developed, the sicula must have become much shorter and smaller, and the early thecae more slender than they are in *M. cyphus*. The considerable overlap and the characters of the distal thecae seem to eliminate all other Monograptids occurring in the *M. cyphus* zone, except perhaps *M. atavus*, which has slender proximal thecae with only a small overlap.

Evolution from some pre-existing Monograptid seems, however, more plausible than a direct mutation from one or other of the biserial forms.

Conclusion

As explained above, the characters of the proximal thecae have been considered the most important in forming these two groups. The main effect of an alternative view would be to put *M. toernquisti* and *M. pseudoplanus* with the *M. separatus* forms (group A). Further subdivision on a basis of the proximal ends gives *M. toernquisti* and *M. pseudoplanus* maintaining the same relationship to one another but originating from *M. separatus*. Then difficulty arises in the case of *M. revolutus* B, which surely cannot be separated from the other *M. revolutus* forms, and yet has transversely expanded hooked thecae with apertures very similar to the *M. toernquisti* and *M. separatus* types. Thus in any case, similar thecal characters appear to have arisen in two groups.

In both the groups an important change which occurred in several lines of evolution is the loss of overlap. It has usually been thought that this was from species with much overlap, through those with little, to those with none. However, the process is more complicated in detail. The dorsal wall of a non-overlapping theca is always inclined at a high angle to the axis of the rhabdosome and this also applies nearly always to the ventral wall. In forms which show any overlap at all, a high angle of inclination is inseparable from a large amount of overlap. It may be then, that the non-overlapping forms were produced from the overlapping, through those with much overlap, and a high angle of inclination, such as M. revolutus B and M. argenteus.

An increase in the angle of inclination of the thecae is a trend seen in the whole of the Monograptid fauna, whether the overlap is lost as in M. communis and M. lobiferus, or retained as in M. chimaera and M. colonus. It is also seen in some Diplograptids, particularly in the genus Petalograptus.

In the Monograptids this trend may be connected with the development of curvature in the rhabdosome: many dorsally curved forms have non-overlapping thecae, and the latter feature is necessary if a high angle of inclination is to be combined with dorsal curvature. The majority of ventrally curved forms has overlapping thecae, and the high angle of inclination again connects the two features.

In the schemes discussed above perhaps the most strongly supported line of evolution is that from M. separatus separatus through M. separatus triangulatus to Rastrites longispinus. The idea that 'M. triangulatus' gave rise to R. longispinus has been accepted among British and Swedish workers for many years, and was included by Dr Elles in her paper (1922, p. 197, table opp. p. 200) where 'M. raitzhainiensis' was suggested as the M. triangulatus ancestor. It was thought that these forms with early rastritiform and later triangular thecae were likely to be 'preceded by a form of Monograptus, as yet unrecognized, in which all the thecae were triangular in shape' (Bulman 1933, p. 318). Challinor (1945) suggested that 'M. fimbriatus' might fill this place, and attempted to establish the gradual statistical predominance of 'M. triangulatus' over 'M. fimbriatus—M. raitzhainiensis', on material collected from known horizons in the M. triangulatus and M. triangulatus var. bands of the Rheidol Gorge. In this work the type of preservation was considered, but less was known about its effects, or about the original form of the thecae. Although I have not been able to examine the specimens concerned, Challinor's text-figures show nothing which would not fit in with the interpretation presented here except for the specimen referred to

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M. triangulatus major, text-fig. 16, p. 103, from the M. triangulatus band—no M. triangulatus major occurs in the present collection.

Opposition to this theory has come from Czechoslovakian authors, in particular Přibyl & Münch (1942). They maintain that M. separatus triangulatus and its allies (the genus Demirastrites Eisel 1912) are intermediate between Rastrites and Monograptus, particularly the species of the genus Spirograptus Gürich 1908 (M. communis, M. spiralis, etc.). They continue: 'with regard to the stratigraphy, Demirastrites appears contemporaneously with the genus Rastrites. The first representatives of both genera occur together in the zone of D. pectinatus (= fimbriatus)'* (p. 1). Later, writing of the evolution, 'In reality the development in both genera, Rastrites and Demirastrites, is quite independent and parallel. It is already known that the oldest representatives of both genera usually appear contemporaneously and together. We are, however, quite convinced that both genera have grown out from a common ancestral type which is as yet, unfortunately, unknown' (p. 2).

Some comments on these views are desirable. In the first place, the occurrence of two forms in the same zone is not necessarily disproof of the production of one from the other. Many examples are known where the ancestor persists together with its descendant into the later beds.

Secondly, since no details of the stratigraphy of the collecting localities are given, it is difficult to know how well established is the Bohemian succession of zones. Marr's paper on the Silurian of Bohemia (1880) showed the discontinuous nature of the outcrops and the intense faulting which has occurred in the region; if the horizons have been fixed on a basis of Eisel's work in Germany (1899, 1902) and the succession established by Elles & Wood in the *Monograph* (1901–18), there may have been some confusion here. The zones used by Přibyl & Münch in this part of the succession seem to be:

- 3. Demirastrites convolutus
- 2. Demirastrites triangulatus
- 1. Demirastrites pectinatus (= fimbriatus)

and it is stated more than once that Rastrites occurs with D. pectinatus in the lowest zone. Evidence is here presented, however, that in Britain the main abundance of M. separatus fimbriatus is above the prolific horizon of M. separatus triangulatus; and it may be suggested that Přibyl & Münch's two lower zones should be reversed or at least combined. In Britain also, Rastrites spp. are common in the same beds as 'M. fimbriatus'.

In addition, Marr stated that the lowest zone was never completely exposed in one continuous section (p. 604), and in places its base was concealed or faulted (p. 596). Both these conditions would make the actual succession of forms difficult to perceive.

Throughout, two main features of the graptolite rhabdosome have been considered: (a) the form of the proximal thecae; (b) the type of distal theca, especially the nature of the aperture. The thesis put forward here has been that the first of these is of greater importance in showing relationships between forms than is the second, and indeed that a similar type of distal theca can be found in not very closely related forms.

^{*} This extract and the following one are quoted in translation.

Appendix. The measurement of thecal size in monograptids without overlap

In descriptions of graptolites two of the measurements usually given are the number of thecae per centimetre and the breadth of the rhabdosome. This usually applies to the distal portion only, however. In these forms the proximal end is of much importance, and measurements have been made here also. As the rhabdosome is often strongly curved, separate thecae have been measured; the *length* is the distance from the narrowest part of the rhabdosome proximal to the theca to the corresponding narrowest part distal to the theca, measured parallel to the dorsal margin of the rhabdosome. The *height* is the maximum width from the dorsal to the ventral margin of the theca and equals the breadth of the rhabdosome as given by other authors (figure 30).

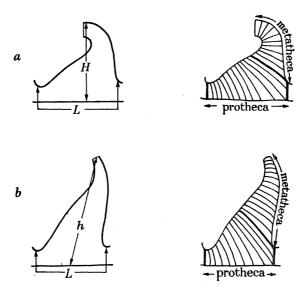


Figure 30. Measurements of Monograptid thecae without overlap.

(a) M. communis; (b) M. separatus.

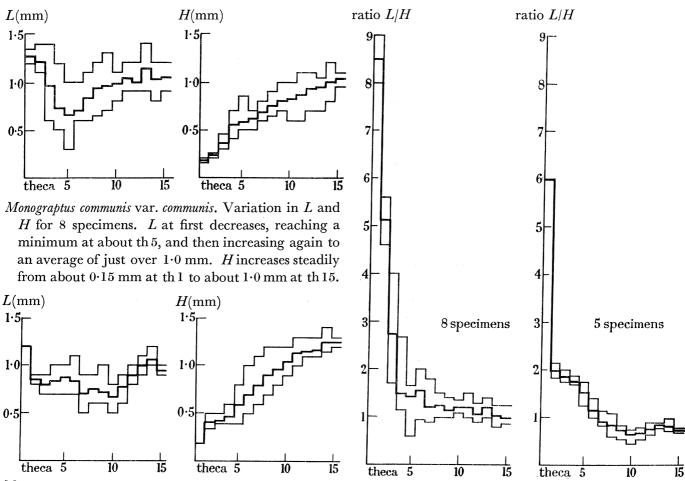
In these thecae with no overlap, these quantities correspond fairly closely with more fundamental parts (figure 30). The length is the same as the length of the protheca; the height gives a measure of the size of the metatheca, where the length cannot easily be measured because of the curve of the hook. Attempts have been made to give some quantitative expression to the amount of 'hooking' of these thecae, e.g. Elles & Wood (1913), descriptions of lobed and hooked forms; Waterlot (1945, p. 88, footnote and text-fig. 433), but the ratios are difficult to use as they depend on measurement of curved lines; the quantities must either be measured on a drawing or merely estimated by eye. The dimensions of length and height described above were employed as something easily and rapidly measured, either on a camera lucida drawing or on the fossil itself, using a Brinnell magnifier.

Measurements were made on the two most abundant groups—the 'communis' forms (M. communis communis and M. communis rostratus) and the 'separatus' forms (M. separatus and the varieties). It must be stressed that the statistics obtained were not used as a means of differentiating one variety from another; they illustrate certain aspects of the differences

between them but do not by any means give the whole picture. In each group the treatment has varied slightly with the exact shapes of thecae concerned.

In the M. communis forms, the length (L) is measured as described, parallel to the axis of the rhabdosome, and the height, designated H, is taken perpendicular to this. The graphs and explanations (figure 31) show measurements made on the first fifteen thecae and illustrate the differences between M. communis communis and M. communis rostratus. The ratio L/H intensifies these differences and is also shown.

In the M. separatus forms the attenuated early prothecae readily break on compression and so often the true length cannot be measured accurately. Thus only the height of the thecae is dealt with. It is shown as 'h' and is measured parallel to the dorsal and ventral walls in rastritiform thecae, or on a line along the centre of the theca in triangular ones



Monograptus communis var. rostratus. Variation in L and H for 5 specimens. L again decreases, but more gradually, the minimum occurring at th 10. H increases somewhat more rapidly, thus attaining an average of 1.25 mm at th 15.

Monograptus communis var. communis. The ratio is at first high, but drops rapidly as far as theca 4. After this the fall is gradual, the value reaching 1.0 at th 15.

M. communis var. rostratus. Here the ratio for th 1 is less and it decreases as far as th 10. Then there is a slight rise, but the value remains below 1.0.

Figure 31. Graphs showing measurements made on specimens of *M. communis*.

——, minimum and maximum values; ——, mean value.

(figure 30). This is because the metathecal and prothecal tubes of rastritiform thecae are not always at right angles, and measurement perpendicular to the axis of the rhabdosome would then give a misleading result.

The graphs and explanations (figure 32) show the results for *M. separatus* and its varieties and *Rastrites longispinus*, in the first fifteen thecae; again this illustrates only one aspect of the differences and takes no account of the rastritiform or triangular shape of the thecae. This one aspect, the increase in height of the thecae, is well shown, however, by the graphs for the forms in the *Rastrites* line of evolution.

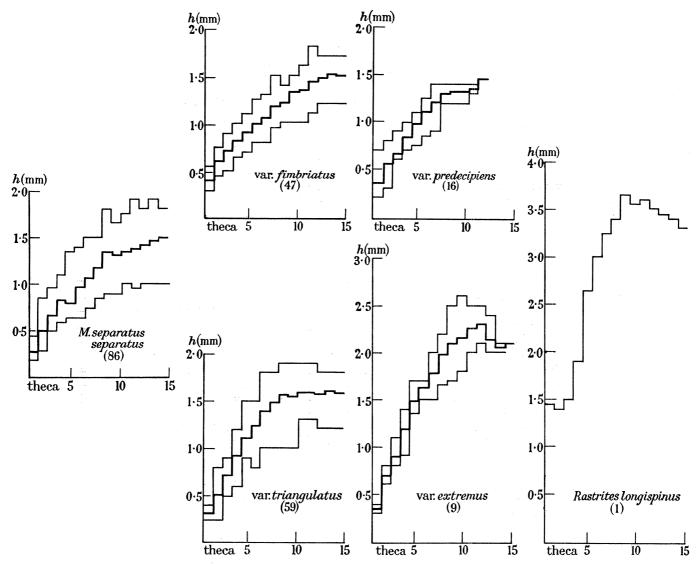


FIGURE 32. Variation in height in the first 15 thecae of M. separatus varieties and Rastrites longispinus. The diagrams of M. separatus separatus, M. separatus triangulatus, M. separatus extremus and Rastrites longispinus illustrate the line of evolution. In M. separatus separatus an average height of 1.5 mm is reached at th 15. The same height is attained by about th 10 in M. separatus triangulatus and by about th 5 in M. separatus extremus. In M. separatus triangulatus the average height of succeeding thecae is 1.6 mm but in M. separatus extremus an increase continues to a maximum of 2.25 mm. In the Rastrites the earliest thecae seen are about 1.5 mm long and successive ones reach 3.5 mm or more. —, minimum and maximum values; —, mean values. The numbers in brackets on the graphs show the number of specimens of each.

KEY TO SPECIMENS ILLUSTRATED ON TEXT-FIGURES

	KEY TO SPECIME	NS ILLUSTRATED ON	TEXT-FIGURES	
				+ if drawing
		museum		laterally
figure	name	number	horizon	reversed
3a, b	var. separatus	SM. A24439	0	+
c	var. fimbriatus	24452	\underline{C}	+
d	var. triangulatus	$\begin{array}{c} 24475 \\ 24474 \end{array}$	P	
	var. triangulatus	24474	0	
	var. separatus	$24433 \\ 24437$	$rac{E}{G}$	- -
	var. separatus denticulatus	21418a	convolutus z. Skelgill	+ +
	var. fimbriatus	24445	D Skeight	+
	var. triangulatus	24460	o	+
	var. brevis	24485	P	+
	var. similis	21479	Dobb's Linn	_
	var. predecipiens decipiens	$\begin{array}{c} 24456 \\ \text{GSM.} \ 26316 \end{array}$	L Pont-erwyd district	+ +
6 a	var. fimbriatus	SM. A 24454	D	- T
$\stackrel{ou}{b}$	vai. jimoriaius	24452	$\stackrel{oldsymbol{D}}{C}$	+
$\stackrel{\circ}{c}$		24443	$\stackrel{\circ}{AB}$	÷
d		24453	$oldsymbol{C}$	
e		24455	D	_
8 a	var. triangulatus	$24471\mathrm{b}$	N	
\boldsymbol{b}		24472	0	+
d		$24468 \\ 24469$	M = M	+ +
u e		$\begin{array}{c} 24403 \\ 24473 \end{array}$	O	-
$\overset{\circ}{f}$		24474	$\overset{\circ}{o}$	
g		24460	o	+
		$\boldsymbol{24475}$	P	
9	var. triangulatus	24460	0	+
	convolutus	23535	R. Clywedog	_
11	var. extremus	24478a	L	
	var. triangulatus var. geinitzi	$\begin{array}{c} 24465 \\ ext{GSM. } 26902 \end{array}$	Q Pont-erwyd distri	+
12	denticulatus, prox. & distal	SM. A21418a	convolutus z. Skelgill	+
12	var. communis, prox.	24488	C	<u> </u>
	distal	24489a	\overline{AB}	+
	pseudoplanus	24495a	X	+
14	convolutus, prox.	21293	Moffat	+
	distal	23831	convolutus z. Skelgill	-
	spiralis, prox. distal	$\begin{array}{c} 24499 \\ 21987 \end{array}$	crispus z. Swindale crispus z. Swindale	
	var. similis	21479	Dobb's Linn	
16	separatus	24439	D	+
10	toernquisti	24481	$\stackrel{oldsymbol{ u}}{P}$	
	planus	23580	Llanidloes	+
	decipiens	GSM. 26315	Pont-erwyd	
	pseudoplanus nobilis	SM. A 24495a LO. 1505	X triang. z. Tomarp	+
1.77		SM. A24485	P	
17	var. brevis var. toernquisti	24480	0	+
	var. elongatus	24482 & 3	$\stackrel{\smile}{P}$	
18	var. elongatus	24482	P	
	var. communis	24487	\overline{C}	_
20	var. communis, prox.	24487	\boldsymbol{C}	
	distal	24489 a	AB	+
	var. rostratus, prox.	24493	C	
	distal separatus	$24492 \\ 24439$	D O	+ +
	soparavas	4 110 0	9	, pr

	KEY TO SPECIMENS	S ILLUSTRATED ON TE	EXT-FIGURES (cont.)	
				+ if drawing
		museum		laterally
figure	name	number	horizon	reversed
24	var. separatus	SM. A 24433	\boldsymbol{E}	
	var. separatus	24436	H	+
	var. separatus	24437	\boldsymbol{G}	+
	var. fimbriatus	24446	\overline{C}	+
	var. predecipiens	24457	$\stackrel{L}{O}$	+
	var. triangulatus	24460	\boldsymbol{O}	+
	var. extremus	24479	$oldsymbol{L}$,	
	R. longispinus	$24498\mathrm{b}$	G	+
26 a	revolutus A, prox.	GSM. 49926a	cyphus z.	+
	distal	Pg1015	cyphus z.	
\boldsymbol{b}	revolutus B, prox.	SM. A 24504	$reve{T}$	+
	distal	24505	T	_
c	revolutus C, prox.	24506	$oldsymbol{F}$	
	distal	$\boldsymbol{24507}$	$oldsymbol{E}$	_
27 a	revolutus D	24508	0	
b	var. praecursor	GSM. Pg867	?triang. band.	_
28	revolutus A, prox.	GSM. 49926a	cyphus z.	-
	distal	Pg1015	cyphus z.	+
	revolutus B, prox.	$\mathbf{SM.A2\breve{4}504}$	$ar{T}$	
	distal	24505	T	+
	revolutus C, prox.	24506	$oldsymbol{F}$	+
	distal	24507	$oldsymbol{E}$	+
	var. praecursor	GSM. Pg867	?triang. band.	+
	var. toernquisti	$\mathbf{SM.A}2\bar{4}480$	o	-
	var. elongatus, prox.	24483	P	_
	distal	24482	\boldsymbol{P}	
	var. brevis	24485	\boldsymbol{P}	+
	var. communis	24487	C	
	var. rostratus	24493	C X	
	pseudoplanus	24497	X	

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Descriptions of plates 19 to 23

(All figures magnified $\times 7.5$ except where shown on the plates.)

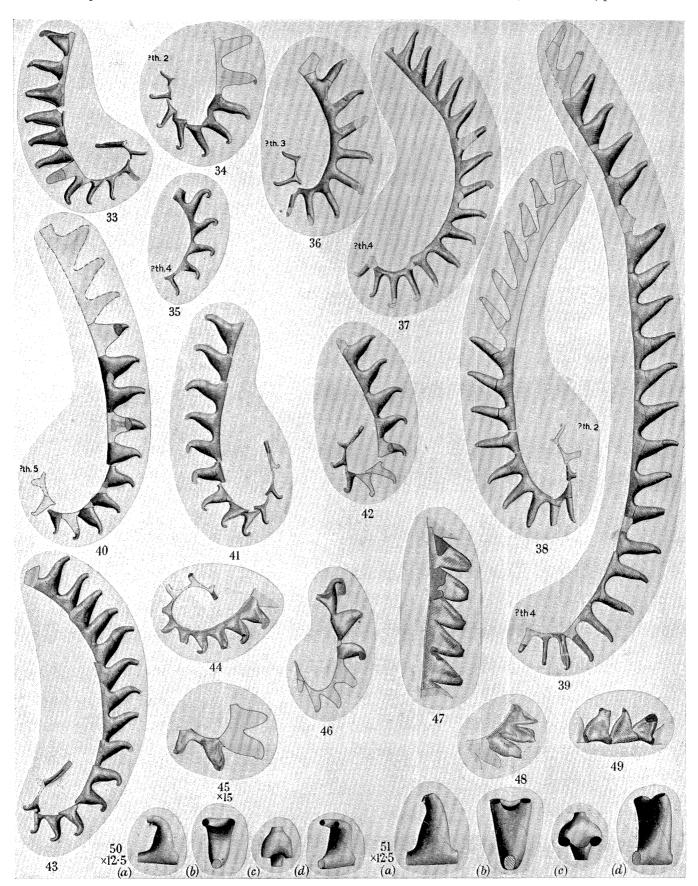
PLATE 19

Monograptus separatus separatus var.nov.

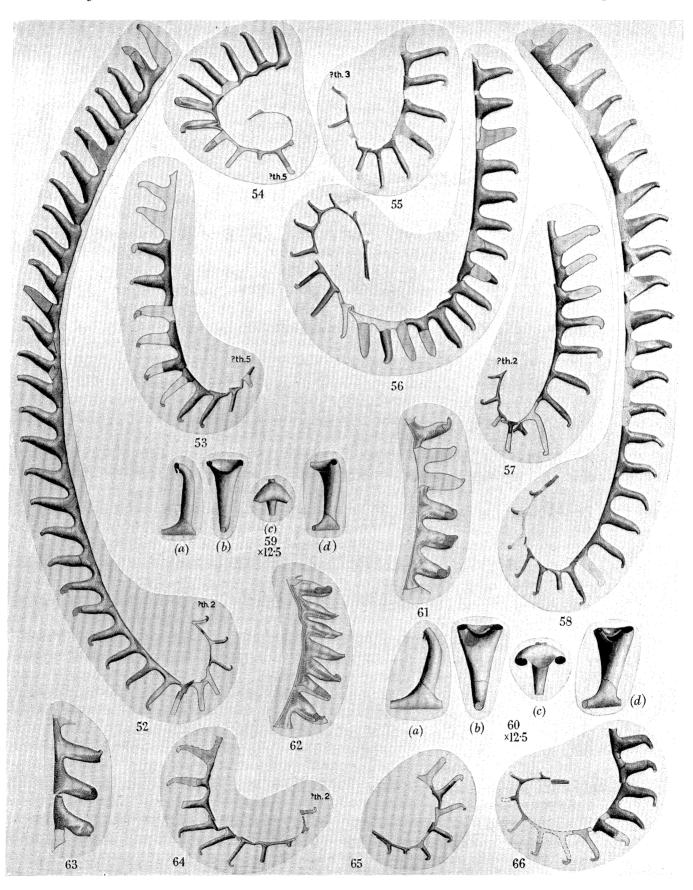
- Figure 33. Paratype, near M. separatus fimbriatus, slightly compressed. E horizon, Rheidol Gorge. SM. A 24433.
- FIGURE 34. Proximal fragment, paratype. H horizon, Rheidol Gorge. SM. A 24436.
- FIGURE 35. Proximal fragment, paratype rather near M. separatus fimbriatus. D horizon, Rheidol Gorge. SM. A 24435.
- FIGURE 36. Paratype from G horizon, Rheidol Gorge. SM. A 24437.
- Figure 37. Holotype, about central within the range of variation permitted and fairly complete. D horizon, Rheidol Gorge. SM. A 24438.
- Figure 38. Paratype, longer specimen in full relief and mounted on a slide. C horizon, Rheidol Gorge. SM. A24434a.
- Figure 39. Paratype, nearer M. separatus triangulatus in the characters of the proximal thecae. O horizon, Rheidol Gorge. SM. A24439.

Monograptus separatus fimbriatus (Nicholson)

- FIGURE 40. Extreme variant with small distal thecae. AB horizon, Rheidol Gorge. SM. A24443.
- FIGURE 41. Specimen showing sicula, from C horizon, Rheidol Gorge. SM. A 24444.
- FIGURE 42. Fragment with sicula. D horizon, Rheidol Gorge. SM. A 24445.
- Figure 43. Fairly complete specimen with taller distal thecae. C horizon, Rheidol Gorge. SM. A24446.
- FIGURE 44. Proximal fragment with part of the sicula, compressed and showing the ridges extending diagonally across each theca. X horizon, Rheidol Gorge. SM. A24447.
- FIGURE 45. Few proximal thecae preserved in half-relief. The apertural region of the second theca is compressed so that the right horn is seen as a ridge at the dorsal margin. X horizon, Rheidol Gorge. SM. A 24449. (Magn. × 15 approx.)
- FIGURE 46. Fragment from Skelgill. The last theca seen is in almost full relief and the hook of the right horn is well seen, while the central part and the left horn are bent forwards and seen, compressed, proximal to the right horn. *M. fimbriatus* zone, Skelgill. SM. A 21459.
- Figure 47. Distal thecae of specimen in half-relief, showing ridges at both margins of each theca, which give the typical 'fimbriatus' appearance. X horizon, Rheidol Gorge. SM. A24450.
- Figure 48. Part of a compressed specimen. The third theca seen is twisted so that the aperture faces away from the observer, and the ridges formed by both horns can be seen. X horizon, Rheidol Gorge. SM. A 24448.
- Figure 49. Few thecae of a specimen in almost full relief. The first theca is again twisted away from the observer, as above; the third one is broken across and shows the triangular cross-section formed on part-compression. From the *M. fimbriatus* zone, Lower Footbridge, Skelgill. SM. A 24501.
- FIGURE 50. Figures of a model of one proximal theca. (Magn. \times 12·5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- Figure 51. Figures of a model of a distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.



(Facing p.550)



Monograptus separatus triangulatus (Harkness)

- FIGURE 52. Long specimen, fairly complete. Phorizon, Rheidol Gorge. SM. A 24464.
- FIGURE 53. Specimen in relief from O horizon, Rheidol Gorge. SM. A24461.
- FIGURE 54. Fragment with the last five thecae in full relief and the earlier ones compressed. The compressed thecae are broader in side view than the uncompressed ones, even although proximal to them. N horizon, Rheidol Gorge. SM. A 24470.
- FIGURE 55. Specimen near M. separatus extremus. O horizon, Rheidol Gorge. SM. A 24463.
- FIGURE 56. Specimen with proximal part of the rhabdosome curved more than usual, and somewhat parallel-sided distal thecae following this. Q horizon, Rheidol Gorge. SM. A 24465.
- FIGURE 57. Specimen rather approaching M. separatus extremus. O horizon, Rheidol Gorge. SM. A24462.
- FIGURE 58. Long specimen with sicula well shown. O horizon, Rheidol Gorge. SM. A24460.
- Figure 59. Figures of a model of one proximal theca. (Magn. \times 12·5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 60. Figures of a model of one distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 61. Part of a compressed specimen. The first and last thecae show the beaked appearance usually thought typical of 'raitzhainiensis' thecae. M horizon, Rheidol Gorge. SM. A 24467.
- Figure 62. Part of a specimen with the distal thecae showing the 'leaf-like' appearance which can be produced on compression. M horizon, Rheidol Gorge. SM. A 24466.
- FIGURE 63. Three distal thecae, partly compressed. The first one shows the hook of the left horn and there is an expansion behind it caused by compression of the dorsal lip. From the Stockdale Shales, Mealy Gill, Coniston, Lake District. SM. A23469.

Monograptus separatus predecipiens var.nov.

- FIGURE 64. Paratype, fairly complete specimen showing the long prothecal regions of the early thecae. L horizon, Rheidol Gorge. SM. A 24459.
- FIGURE 65. Paratype, proximal fragment with sicula. L horizon, Rheidol Gorge. SM. A24456.
- FIGURE 66. Holotype, with sicula and in relief. L horizon, Rheidol Gorge. SM. A 24457b, with additions from A 24457a.

Monograptus separatus extremus var.nov.

- FIGURE 67. Figures of a model of one proximal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 68. Paratype from K horizon, Rheidol Gorge. SM. A 24477 a, with additions from A 24477 b.
- FIGURE 69. Paratype showing the sicula and the rastritiform thecae of the proximal end. L horizon, Rheidol Gorge. SM. A24478a, with additions from A24478b.
- Figure 70. Holotype, showing rastritiform proximal thecae and distal ones becoming broader. L horizon, Rheidol Gorge. SM. A 24479.

Rastrites longispinus (Perner)

FIGURE 71. Part of specimen in full relief, figured in full in figure 23. G horizon, Rheidol Gorge. SM. A 24498 b.

Monograptus denticulatus Törnquist

- FIGURE 72. Figures of a model of one distal theca, reconstructed from the evidence of the specimen in figure 73. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 73. Fairly complete specimen, slightly compressed. M. convolutus zone, Skelgill, Lake District. SM. A21418a.

Monograptus decipiens Törnquist

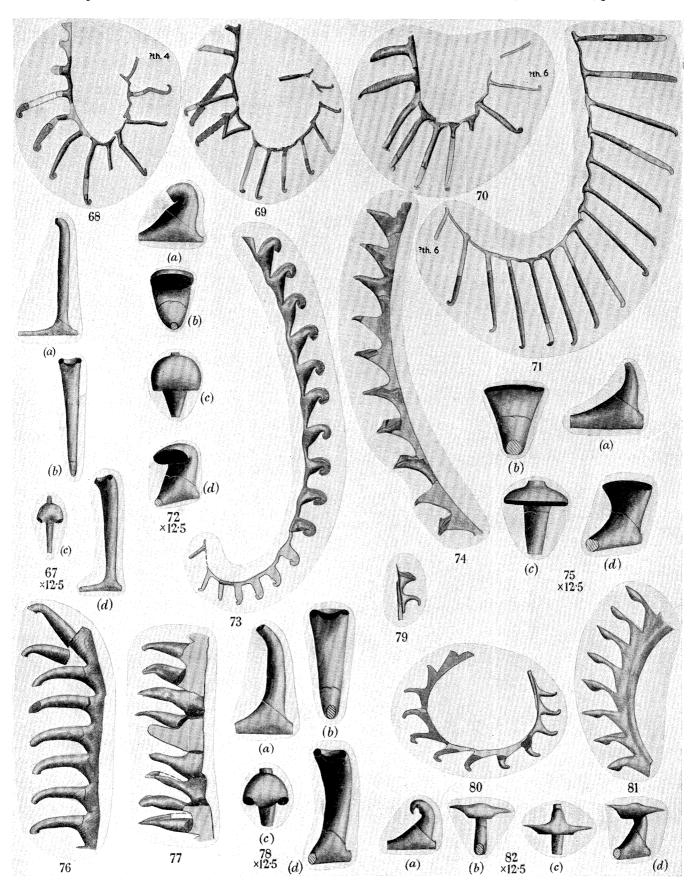
- FIGURE 74. Distal thecae, partly compressed. The first, third and fourth thecae show well the 'dorsal bulge' due to compression of a transversely expanded theca. Part of a specimen from the Pont-erwyd district. GSM. 26315.
- FIGURE 75. Figures of a model reconstruction of the distal theca. (Magn. \times 12·5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

Monograptus convolutus (Hisinger)

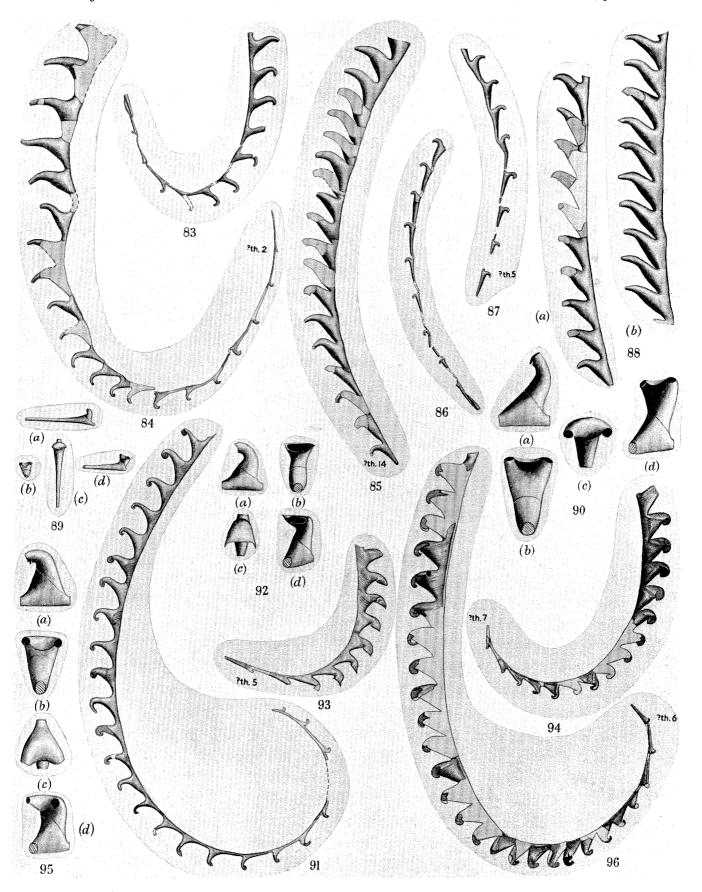
- FIGURE 76. Distal thecae in full relief. Part of a specimen from R. Clywedog, near Llanidloes. SM. A 23535.
- FIGURE 77. Distal thecae in half-relief. Part of a specimen from the M. convolutus zone, Skelgill, Lake District. SM. A 23831.
- FIGURE 78. Figures of a model of one distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

Monograptus spiralis (Geinitz)

- FIGURE 79. Fragment showing the sicula and first theca. M. crispus zone, Swindale, Knock. SM. A 24500.
- FIGURE 80. Larger fragment, partly in relief. The later thecae show some of the different appearances of the apertural region when the theca is compressed. *M. crispus* zone, Swindale, Knock. SM. A 24499.
- FIGURE 81. Distal thecae, compressed, and with the apertural regions tilted so that the right side is compressed on to the main body of the theca and the left projects away from it as a pointed tip to the theca. The aperture faces away from the observer and the bulge near the tip of the theca represents the dorsal lip of the theca. *M. crispus* zone, Swindale, Knock. SM. A21987.
- Figure 82. Figures of a model of one theca, showing the transverse expansion of the dorsal lip. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.



 $(Facing\ p.\ 552)$



Monograptus toernquisti brevis var.nov.

FIGURE 83. Holotype, with sicula, the most complete specimen seen. P horizon, Rheidol Gorge. SM. A 24485.

Monograptus toernquisti toernquisti var.nov.

Figure 84. Holotype. Some of the distal thecae are probably somewhat distorted. O horizon, Rheidol Gorge. SM A 24480.

Monograptus toernquisti elongatus var.nov.

- Figure 85. Paratype, a fairly long specimen showing the intermediate and distal thecae. P horizon, Rheidol Gorge. SM. A 24482.
- FIGURE 86. Paratype, a proximal fragment showing the sicula and early elongated thecae beginning to give place to the intermediate ones. *P* horizon, Rheidol Gorge. SM. A 24483.
- FIGURE 87. Holotype, showing the early elongated and the intermediate thecae which are characteristic for the variety. P horizon, Rheidol Gorge. SM. A 24484.

Monograptus toernquisti sp.nov.

- Figure 88. Parts of a long specimen showing the distal thecae only, and figured in full on figure 15. P horizon, Rheidol Gorge. SM. A 24481. a, proximal part; b, distal part.
- FIGURE 89. Figures of a model of one proximal elongated theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 90. Figures of a model of one distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

Monograptus nobilis Törnquist

FIGURE 91. Lectotype, in relief in pyrite. Zone of M. triangulatus, Tomarp, Sweden. Palaeontological Institute, Lund, LO 1505.

Monograptus planus (Barrande)

- FIGURE 92. Figures of a model of one distal theca, reconstructed from the evidence of the compressed thecae. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 93. Specimen in half-relief in pyrite, from the *M. crenulatus* zone, Tach Wood, near Llanidloes. SM. A 23581.

Monograptus pseudoplanus sp.nov.

- FIGURE 94. Paratype, small specimen in half-relief. X horizon, Rheidol Gorge. SM. A 24495a.
- Figure 95. Figures of a model of a distal theca, reconstructed from knowledge of the compressed thecae. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 96. Holotype, in half-relief in pyrite in parts and the rest in chlorite. X horizon, Rheidoi Gorge. SM. A 24497.

Monograptus communis communis Lapworth

- FIGURE 97. Good specimen with sicula. C horizon, Rheidol Gorge. SM. A 24487.
- FIGURE 98. Smaller specimen. C horizon, Rheidol Gorge. SM. A 24488.
- FIGURE 99. Long specimen from AB horizon, Rheidol Gorge. SM. A 24489 a.
- FIGURE 100. Figures of a model of a distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 101. Figures of a model of one proximal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

Monograptus communis rostratus Elles & Wood

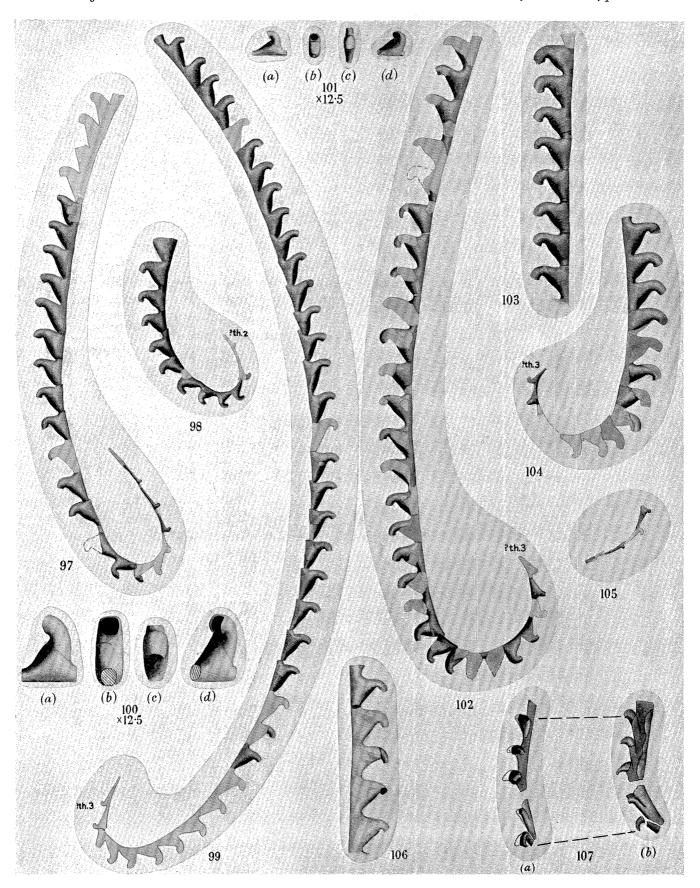
- FIGURE 102. Long specimen, characteristic of the species. C horizon, Rheidol Gorge. SM. A 24493.
- Figure 103. Distal thecae, part of a specimen figured in full in figure 21, showing growth lines well. C horizon, Rheidol Gorge. SM. A 24494.
- FIGURE 104. Specimen showing the tall thecae near the curve of the rhabdosome. D horizon, Rheidol Gorge. SM. A 24492.
- FIGURE 105. Proximal fragment, possibly M. communis rostratus, showing the sicula and first three thecae. G horizon, Rheidol Gorge. SM. A 24491.

Monograptus communis Lapworth

FIGURE 106. Few distal thecae, the last one in relief but the rest compressed, showing the slight changes in shape on compression. G horizon, Rheidol Gorge. SM. A24490.

Monograptus revolutus Kurck B

FIGURE 107. A few of the later hooked thecae, showing overlap less than half, etched out and mounted on a slide. T horizon, Rheidol Gorge. SM. A 24502. a, half ventral view, showing the transverse expansion of the distal parts of the thecae, and the formation of horns at the aperture. The part embedded in the balsam on the slide is reconstructed in outline; b, the same in side view.



(Facing p.554)

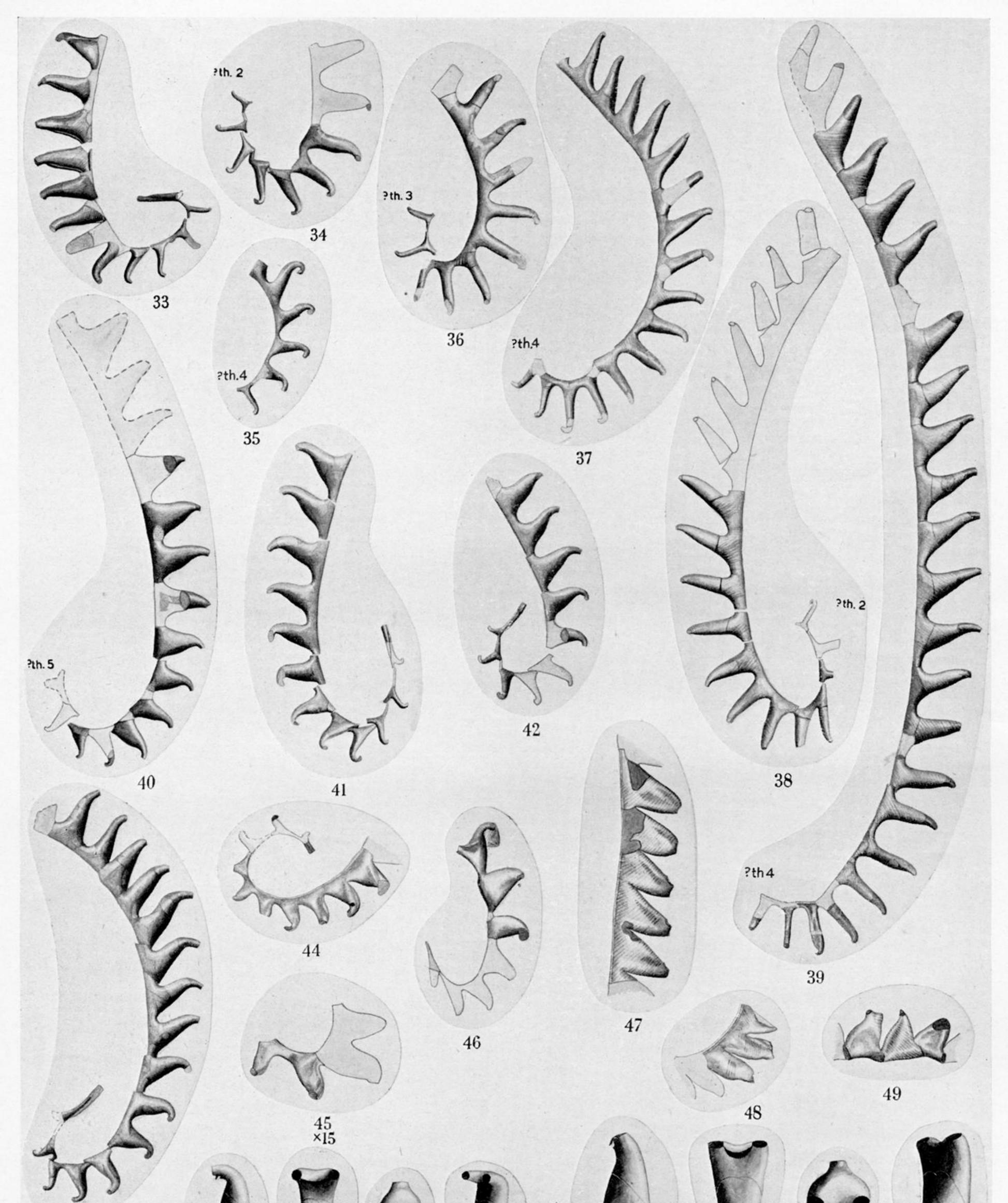


PLATE 19

(a)

(6)

(c)

(a)

Monograptus separatus separatus var.nov.

- FIGURE 33. Paratype, near M. separatus fimbriatus, slightly compressed. E horizon, Rheidol Gorge. SM. A 24433.
- FIGURE 34. Proximal fragment, paratype. H horizon, Rheidol Gorge. SM. A 24436.

(a)

- Figure 35. Proximal fragment, paratype rather near M. separatus fimbriatus. D horizon, Rheidol Gorge. SM. A 24435.
- FIGURE 36. Paratype from G horizon, Rheidol Gorge. SM. A 24437.

(c)

(a) (b)

- FIGURE 37. Holotype, about central within the range of variation permitted and fairly complete.

 D horizon, Rheidol Gorge. SM. A 24438.
- Figure 38. Paratype, longer specimen in full relief and mounted on a slide. C horizon, Rheidol Gorge. SM. A24434a.
- Figure 39. Paratype, nearer M. separatus triangulatus in the characters of the proximal thecae.

 O horizon, Rheidol Gorge. SM. A 24439.

Monograptus separatus fimbriatus (Nicholson)

- FIGURE 40. Extreme variant with small distal thecae. AB horizon, Rheidol Gorge. SM. A 24443.
- FIGURE 41. Specimen showing sicula, from C horizon, Rheidol Gorge. SM. A 24444.
- Figure 42. Fragment with sicula. D horizon, Rheidol Gorge. SM. A 24445.
- Figure 43. Fairly complete specimen with taller distal thecae. C horizon, Rheidol Gorge, SM. A 24446.
- Figure 44. Proximal fragment with part of the sicula, compressed and showing the ridges extending diagonally across each theca. X horizon, Rheidol Gorge. SM. A 24447.
- FIGURE 45. Few proximal thecae preserved in half-relief. The apertural region of the second theca is compressed so that the right horn is seen as a ridge at the dorsal margin. X horizon, Rheidol Gorge. SM. A24449. (Magn. × 15 approx.)
- Figure 46. Fragment from Skelgill. The last theca seen is in almost full relief and the hook of the right horn is well seen, while the central part and the left horn are bent forwards and seen, compressed, proximal to the right horn. *M. fimbriatus* zone, Skelgill. SM. A 21459.
- Figure 47. Distal thecae of specimen in half-relief, showing ridges at both margins of each theca, which give the typical 'fimbriatus' appearance. X horizon, Rheidol Gorge. SM. A 24450.
- FIGURE 48. Part of a compressed specimen. The third theca seen is twisted so that the aperture faces away from the observer, and the ridges formed by both horns can be seen. X horizon, Rheidol Gorge. SM. A24448.
- Gorge. SM. A 24448.

 Figure 49. Few thecae of a specimen in almost full relief. The first theca is again twisted away from the observer, as above; the third one is broken across and shows the triangular cross-section formed on part-compression. From the M. fimbriatus zone, Lower Footbridge, Skelgill. SM.
- A 24501.

 FIGURE 50. Figures of a model of one proximal theca. (Magn. × 12.5 approx.) a, lateral view;
- b, face view; c, ventral view; d, half-side view.

 Figure 51. Figures of a model of a distal theca. (Magn. × 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

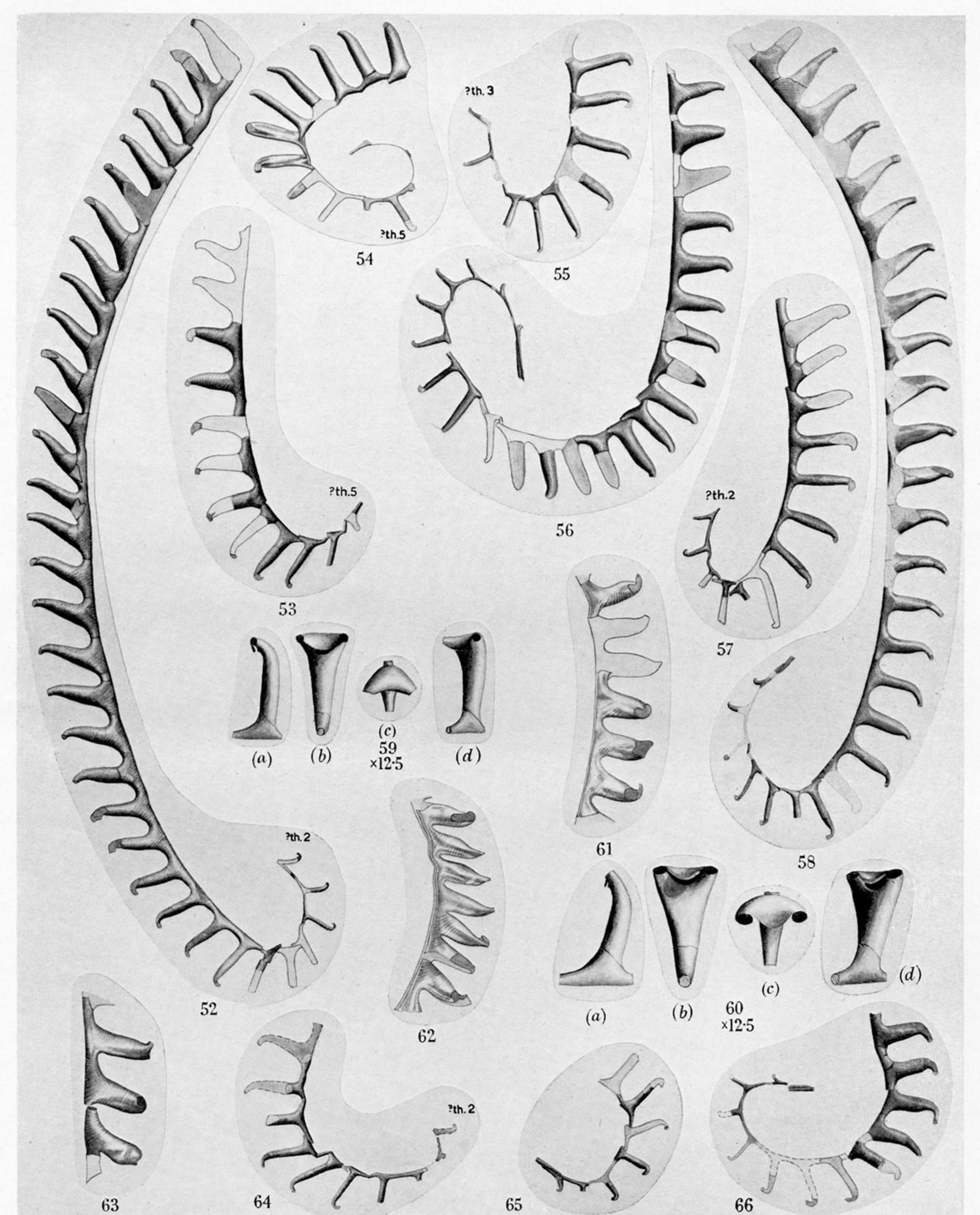


PLATE 20

Monograptus separatus triangulatus (Harkness)

- FIGURE 52. Long specimen, fairly complete. Phorizon, Rheidol Gorge. SM. A 24464.
- FIGURE 53. Specimen in relief from O horizon, Rheidol Gorge. SM. A 24461.
- FIGURE 54. Fragment with the last five thecae in full relief and the earlier ones compressed. The compressed thecae are broader in side view than the uncompressed ones, even although proximal to them. N horizon, Rheidol Gorge. SM. A24470.
- FIGURE 55. Specimen near M. separatus extremus. O horizon, Rheidol Gorge. SM. A 24463.
- FIGURE 56. Specimen with proximal part of the rhabdosome curved more than usual, and somewhat parallel-sided distal thecae following this. Q horizon, Rheidol Gorge. SM. A 24465.
- FIGURE 57. Specimen rather approaching M. separatus extremus. O horizon, Rheidol Gorge. SM. A 24462.
- FIGURE 58. Long specimen with sicula well shown. O horizon, Rheidol Gorge. SM. A24460.
- FIGURE 59. Figures of a model of one proximal theca. (Magn. × 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 60. Figures of a model of one distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 61. Part of a compressed specimen. The first and last thecae show the beaked appearance usually thought typical of 'raitzhainiensis' thecae. M horizon, Rheidol Gorge. SM. A 24467.
- FIGURE 62. Part of a specimen with the distal thecae showing the 'leaf-like' appearance which can be produced on compression. M horizon, Rheidol Gorge. SM. A 24466.
- FIGURE 63. Three distal thecae, partly compressed. The first one shows the hook of the left horn and there is an expansion behind it caused by compression of the dorsal lip. From the Stockdale Shales, Mealy Gill, Coniston, Lake District. SM. A 23469.

Monograptus separatus predecipiens var.nov.

- Figure 64. Paratype, fairly complete specimen showing the long prothecal regions of the early thecae. L horizon, Rheidol Gorge. SM. A 24459.
- FIGURE 65. Paratype, proximal fragment with sicula. L horizon, Rheidol Gorge. SM. A 24456.
- Figure 66. Holotype, with sicula and in relief. L horizon, Rheidol Gorge. SM. A 24457b, with additions from A 24457a.

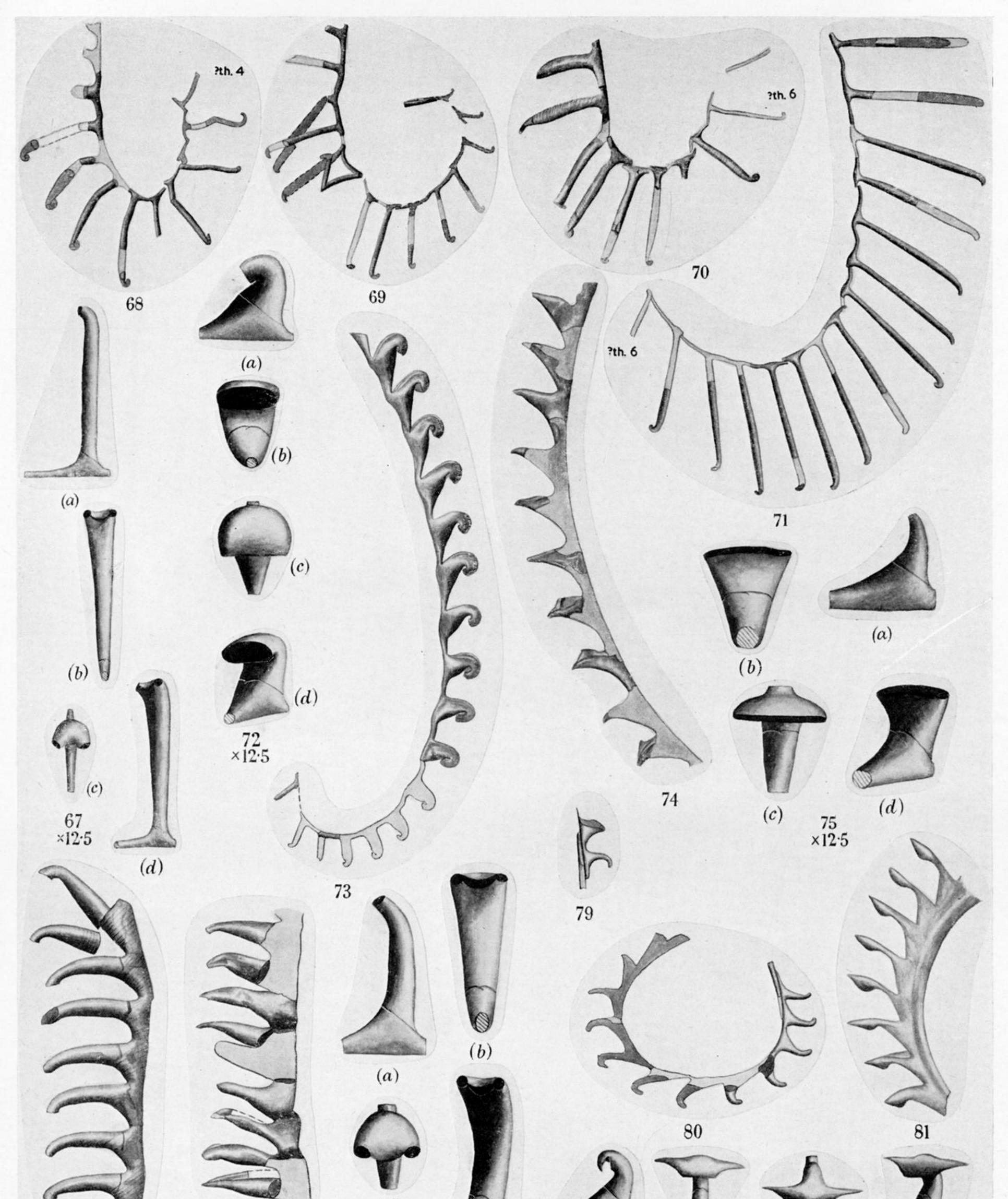


PLATE 21

Monograptus separatus extremus var.nov.

FIGURE 67. Figures of a model of one proximal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

FIGURE 68. Paratype from K horizon, Rheidol Gorge. SM. A 24477a, with additions from A 24477b.

FIGURE 69. Paratype showing the sicula and the rastritiform thecae of the proximal end. L horizon, Rheidol Gorge. SM. A24478a, with additions from A24478b.

Figure 70. Holotype, showing rastritiform proximal thecae and distal ones becoming broader. L horizon, Rheidol Gorge. SM. A 24479.

Rastrites longispinus (Perner)

Figure 71. Part of specimen in full relief, figured in full in figure 23. G horizon, Rheidol Gorge. SM. A 24498b.

Monograptus denticulatus Törnquist

FIGURE 72. Figures of a model of one distal theca, reconstructed from the evidence of the specimen in figure 73. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

FIGURE 73. Fairly complete specimen, slightly compressed. M. convolutus zone, Skelgill, Lake District. SM. A21418a.

Monograptus decipiens Törnquist

FIGURE 74. Distal thecae, partly compressed. The first, third and fourth thecae show well the 'dorsal bulge' due to compression of a transversely expanded theca. Part of a specimen from the Pont-erwyd district. GSM. 26315.

FIGURE 75. Figures of a model reconstruction of the distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

Monograptus convolutus (Hisinger)

FIGURE 76. Distal thecae in full relief. Part of a specimen from R. Clywedog, near Llanidloes. SM. A 23535.

Figure 77. Distal thecae in half-relief. Part of a specimen from the M. convolutus zone, Skelgill, Lake District. SM. A 23831.

FIGURE 78. Figures of a model of one distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

Monograptus spiralis (Geinitz)

FIGURE 79. Fragment showing the sicula and first theca. M. crispus zone, Swindale, Knock.

SM. A 24500.

Figure 80. Larger fragment, partly in relief. The later thecae show some of the different appearances

of the apertural region when the theca is compressed. M. crispus zone, Swindale, Knock. SM. A 24499.

Figure 81. Distal thecae, compressed, and with the apertural regions tilted so that the right side is

compressed on to the main body of the theca and the left projects away from it as a pointed tip to the theca. The aperture faces away from the observer and the bulge near the tip of the theca represents the dorsal lip of the theca. M. crispus zone, Swindale, Knock. SM. A21987.

FIGURE 82. Figures of a model of one theca, showing the transverse expansion of the dorsal lip. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

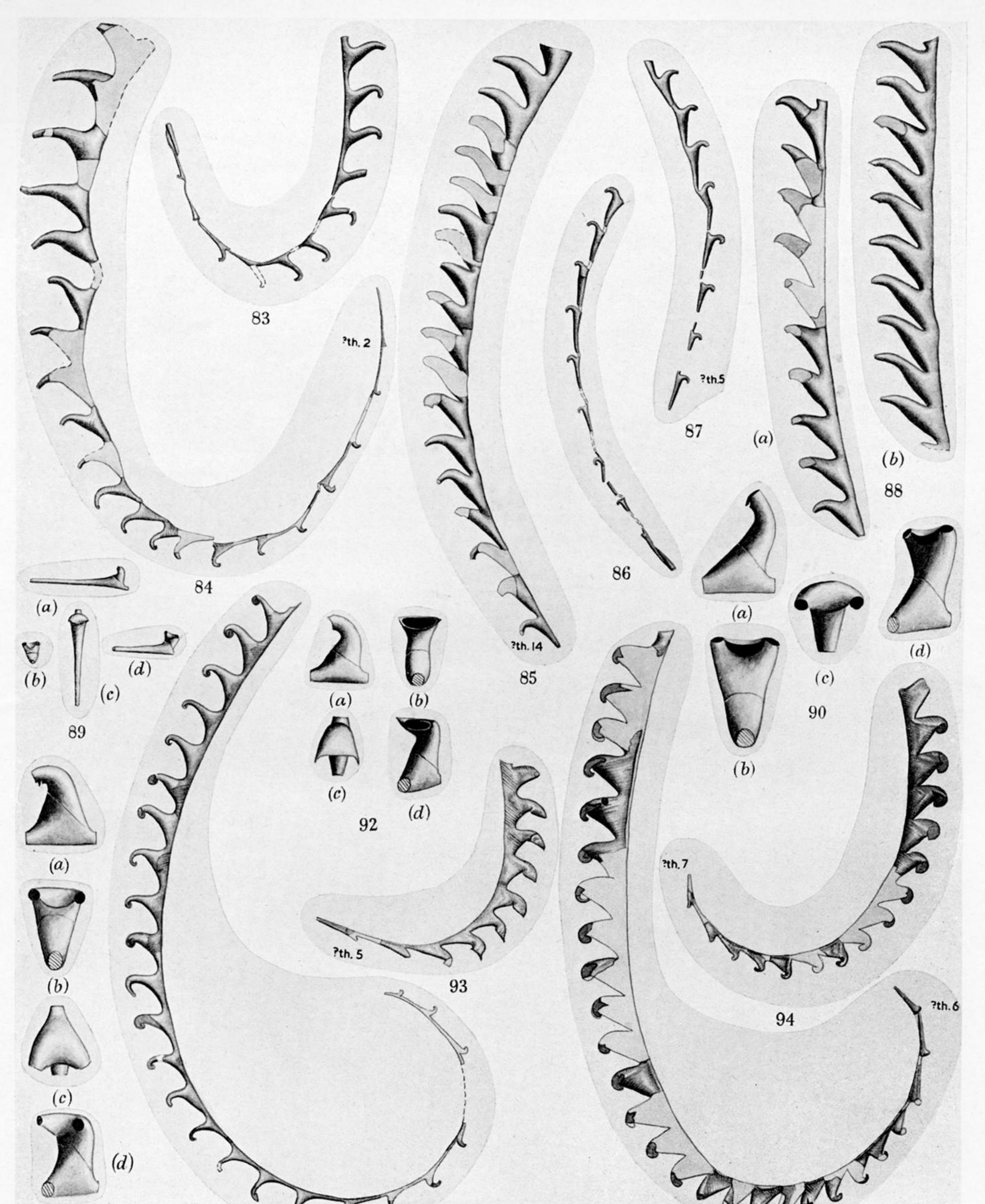


PLATE 22

Monograptus toernquisti brevis var.nov.

FIGURE 83. Holotype, with sicula, the most complete specimen seen. P horizon, Rheidol Gorge. SM. A 24485.

Monograptus toernquisti toernquisti var.nov.

FIGURE 84. Holotype. Some of the distal thecae are probably somewhat distorted. O horizon, Rheidol Gorge. SM A 24480.

Monograptus toernquisti elongatus var.nov.

- FIGURE 85. Paratype, a fairly long specimen showing the intermediate and distal thecae. P horizon, Rheidol Gorge. SM. A 24482.
- FIGURE 86. Paratype, a proximal fragment showing the sicula and early elongated thecae beginning to give place to the intermediate ones. P horizon, Rheidol Gorge. SM. A 24483.
- FIGURE 87. Holotype, showing the early elongated and the intermediate thecae which are characteristic for the variety. P horizon, Rheidol Gorge. SM. A 24484.

Monograptus toernquisti sp.nov.

- FIGURE 88. Parts of a long specimen showing the distal thecae only, and figured in full on figure 15.

 P horizon, Rheidol Gorge. SM. A 24481. a, proximal part; b, distal part.
- FIGURE 89. Figures of a model of one proximal elongated theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 90. Figures of a model of one distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

Monograptus nobilis Törnquist

Figure 91. Lectotype, in relief in pyrite. Zone of M. triangulatus, Tomarp, Sweden. Palaeontological Institute, Lund, LO 1505.

Monograptus planus (Barrande)

- FIGURE 92. Figures of a model of one distal theca, reconstructed from the evidence of the compressed thecae. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 93. Specimen in half-relief in pyrite, from the M. crenulatus zone, Tach Wood, near Llanidloes. SM. A 23581.

Monograptus pseudoplanus sp.nov.

- Figure 94. Paratype, small specimen in half-relief. X horizon, Rheidol Gorge. SM. A 24495a.
- FIGURE 95. Figures of a model of a distal theca, reconstructed from knowledge of the compressed thecae. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 96. Holotype, in half-relief in pyrite in parts and the rest in chlorite. X horizon, Rheidoi Gorge. SM. A 24497.

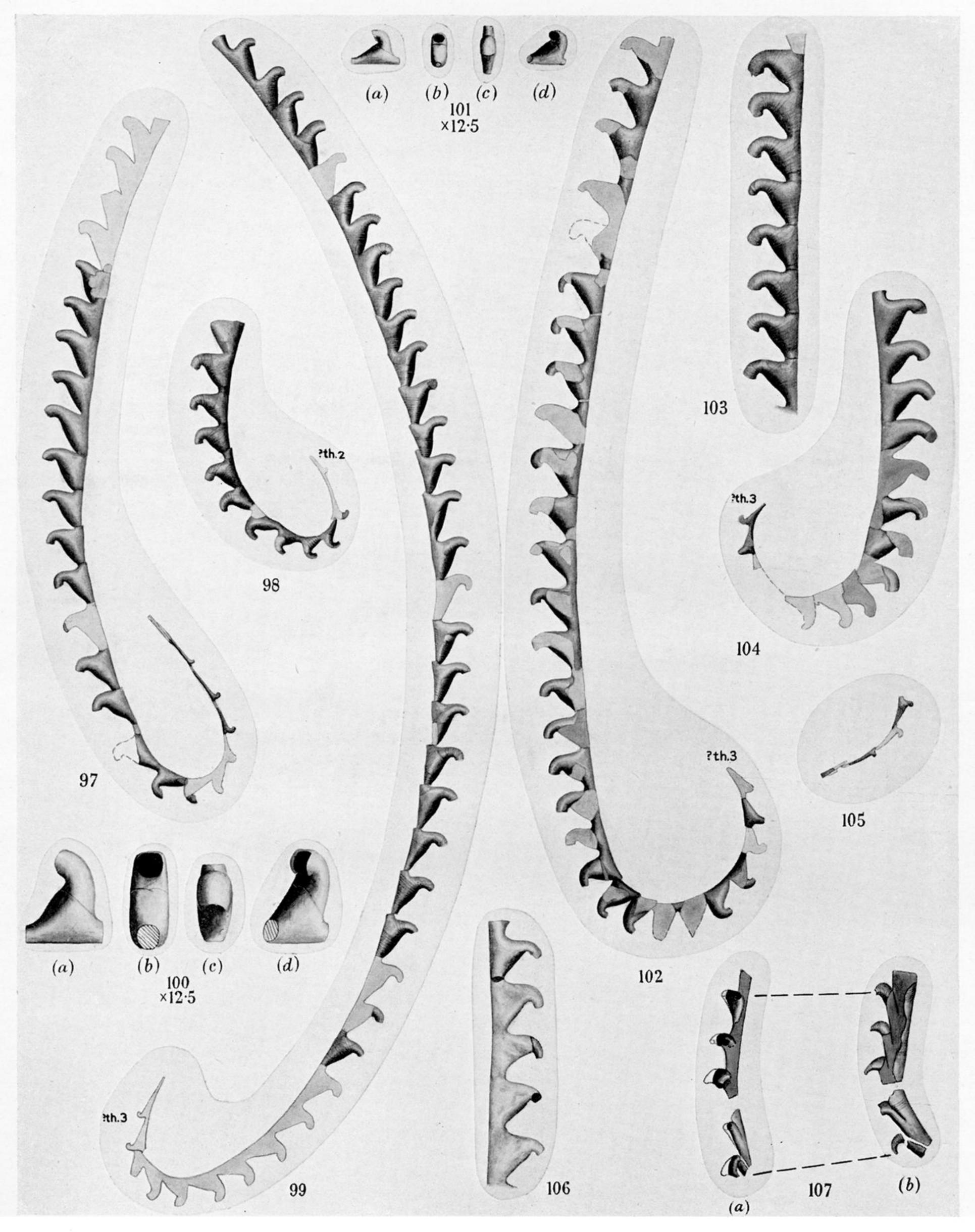


PLATE 23

Monograptus communis communis Lapworth

- Figure 97. Good specimen with sicula. C horizon, Rheidol Gorge. SM. A 24487.
- FIGURE 98. Smaller specimen. C horizon, Rheidol Gorge. SM. A 24488.
- FIGURE 99. Long specimen from AB horizon, Rheidol Gorge. SM. A 24489a.
- Figure 100. Figures of a model of a distal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.
- FIGURE 101. Figures of a model of one proximal theca. (Magn. \times 12.5 approx.) a, lateral view; b, face view; c, ventral view; d, half-side view.

Monograptus communis rostratus Elles & Wood

- Figure 102. Long specimen, characteristic of the species. C horizon, Rheidol Gorge. SM. A 24493.
- FIGURE 103. Distal thecae, part of a specimen figured in full in figure 21, showing growth lines well. C horizon, Rheidol Gorge. SM. A 24494.
- Figure 104. Specimen showing the tall thecae near the curve of the rhabdosome. D horizon, Rheidol Gorge. SM. A 24492.
- Figure 105. Proximal fragment, possibly M. communis rostratus, showing the sicula and first three thecae. G horizon, Rheidol Gorge. SM. A 24491.

Monograptus communis Lapworth

FIGURE 106. Few distal thecae, the last one in relief but the rest compressed, showing the slight changes in shape on compression. G horizon, Rheidol Gorge. SM. A 24490.

Monograptus revolutus Kurck B

FIGURE 107. A few of the later hooked thecae, showing overlap less than half, etched out and mounted on a slide. T horizon, Rheidol Gorge. SM. A 24502. a, half ventral view, showing the transverse expansion of the distal parts of the thecae, and the formation of horns at the aperture. The part embedded in the balsam on the slide is reconstructed in outline; b, the same in side

view.