ON *GLYPTOGRAPTUS DENTATUS* (BRONGNIART) AND SOME ALLIED SPECIES

by O. M. B. BULMAN

ABSTRACT. The original specimens of Brongniart's *Fucoides dentatus* can no longer be traced and must be assumed lost. It is therefore proposed that one of the originals of Hall's *Diplograptus pristiniformis* be taken as the neotype, and the species is defined with reference to this and redescribed. A new species believed related to *G. dentatus* is described from the Arenig rocks of Britain; *G. austrodentatus* Harris and Keble is redescribed; and four new varieties are recognized from Britain, Scandinavia, and North America. The relations of the *G. dentatus* and *G. austrodentatus* groups are discussed, and three other British species are described (two new and one new to Britain) which, though previously identified as *G. dentatus*, are here assigned to different genera.

THE earliest true diplograptids are of outstanding importance in graptolite phylogeny, and their sudden appearance has been described as one of the three major events in graptolite evolution. In North America and north-west Europe the majority of such forms have been referred to *Glyptograptus dentatus* (Brongniart); from Australia the species *G. austrodentatus* Harris and Keble has been described; and in China both these species have been recorded, together with *G. sinodentatus* Mu and Lee, and *G. curvithecatus* Mu and Lee.

The stratigraphical importance of the incoming of the diplograptids, as distinct from the much later 'Diplograptid Fauna' of Elles (1922, p. 194), was recognized by Harris and Thomas (1938, p. 66) and Bulman (1958, p. 162), but their use in detailed correlation is handicapped by a lack of exact knowledge of the material and of its stratigraphic range.

With the co-operation of several friends and colleagues, I have assembled representatives of as much of this early material as possible, and it is a great pleasure to acknowledge the ready and generous help I have received. Dr. D. J. McLaren (Canadian Geological Survey) arranged for the loan of the types of Hall's *D. pristiniformis* and placed at my disposal collections from the Levis Shales, and Dr. L. M. Cumming specially collected and sent material from Begin's Hill, Levis; Dr. D. E. Thomas (Department of Mines, Melbourne) sent a large collection of *G. austrodentatus*, and other specimens were collected and sent me by Dr. F. C. Beavis (University of Melbourne); Dr. D. E. Jackson sent specimens from the Yukon, and allowed me to draw upon his collection from the Skiddaw Slates; some sectionable specimens of *G. austrodentatus* were included in a collection from Marathon, Texas, sent some years ago by Professor C. O. Dunbar and Dr. W. N. Berry; Dr. Isles Strachan (Birmingham University), Mr. J. D. D. Smith (Geological Survey and Museum), Dr. H. W. Ball (Brit. Mus. (Nat. Hist.)), Mr. A. G. Brighton (Sedgwick Museum), and Professor T. S. Westoll (University of Newcastle) have assisted with the loan of material in their charge. Dr. D. Skevington has given me access to his observations on diplograptids from the Orthoceras Limestone; and Professor Pruvost and Professor Boureau kindly undertook the laborious, but unavailing, search for the types of *Fucoides dentatus* Brongniart. Finally, my assistant Mrs. C. M. Clarkson has rendered invaluable help in the sectioning of material, construction of wax models, photography, and the preparation of illustrations.

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Upon examination it becomes apparent that, though often badly preserved and sometimes distorted, a number of recognizably different species and varieties is present, and these appear to fall into two groups. These two groups are typified by *G. dentatus* and *G. austrodentatus*. They are also, it appears, represented by the two forms described (Bulman 1936) as *G. dentatus-teretiusculus* transient and *G. dentatus* respectively, from the Holm Collection in Stockholm. This Scandinavian material, augmented by recent preparations of Dr. D. Skevington, provides important information concerning the mode of development of the rhabdosome and the three-dimensional form of the thecae, which can be used in the interpretation of less well-preserved material from elsewhere.

The *G. dentatus* group centres around forms with a slender, somewhat pointed, proximal end; $th1^2$ has a dominantly upward direction of growth and the apertures of the first four thecae tend to be markedly alternating. The metathecal portion of the thecae has a glyptograptid curvature, with only an incipient geniculation situated low down on the metatheca, and the apertural rim may show a pair of very weakly developed lappets. *G. austrodentatus* contrasts with this in having a bluntly terminated rhabdosome, with $th1^1$ and $th1^2$ almost symmetrically disposed. The metathecal portion of the thecae has a more strongly marked geniculation situated midway along the metathecal length or even more distally, and the difference in metathecal form is very clearly shown by Skevington's preparations (cf. text-figs. 1*c*, 8*d*). The apertural margin in *G. austrodentatus* may possess a vertical or even somewhat introverted ventral lip.

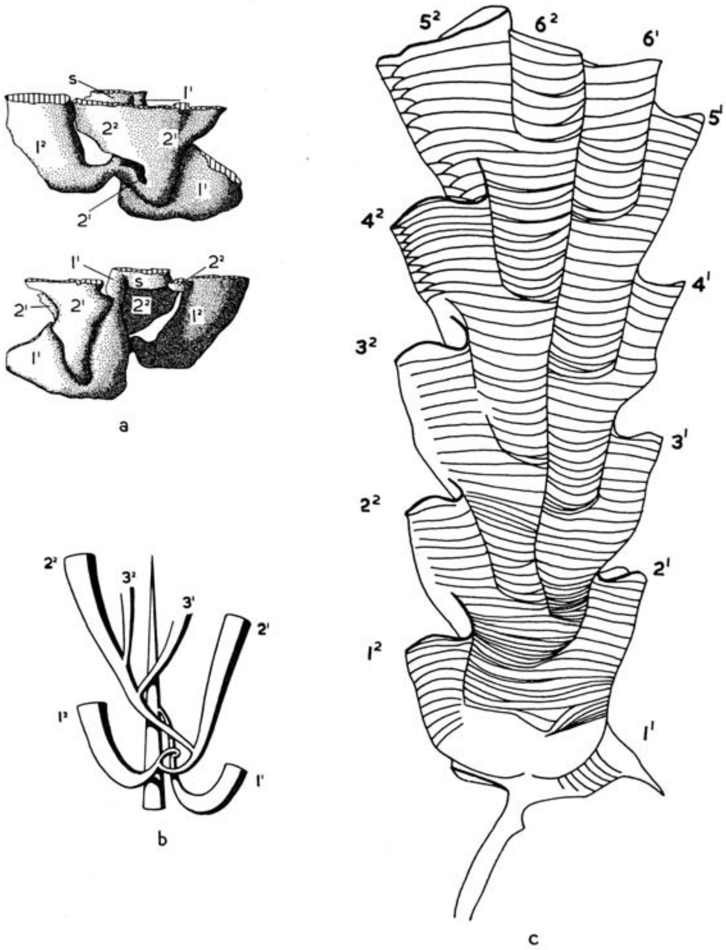
The possible relation of the variants and the interpretation of seeming intermediates is discussed below; and three British species are described which, though identified as *G. dentatus* in the past, are here assigned to different genera.

MODE OF DEVELOPMENT OF EARLY DIPLOGRAPTIDS

(*a*) *G. dentatus* group

Exact knowledge of the mode of development of the rhabdosome in this group derives from serial (microtome) sections of a specimen in the Holm Collection already described under the name *G. dentatus-teretiusculus* transient (Bulman 1936, pp. 57–61), supplemented by an excellent transparent proximal end of another specimen from Öland prepared and figured by Dr. D. Skevington.

It is unnecessary to repeat the description already published, but it was pointed out to me by Mrs. Clarkson that in constructing the original wax model I unwittingly exaggerated the vertical scale by about one-sixth, and she has prepared a corrected drawing depicting this model in true proportion (text-fig. 1*a*). The second theca, $th1^2$, originates comparatively low down on $th1^1$ and grows mainly across the sicula and upwards on the opposite side. $Th2^1$ has a slight initial downward growth before turning upwards. Dr. Skevington has kindly allowed me to reproduce (text-fig. 1*c*) his figure of his recent preparation (now in the Palaeontological Institute at Uppsala), the growth-lines of which conclusively demonstrate that (as hinted in Bulman 1936, p. 59) the dicalycal theca is $th2^2$. Nevertheless, it seems probable that members of the *dentatus* group from a lower stratigraphical level would have $th2^1$ dicalycal, and it would be impracticable (as regards shale material) to attempt any specific subdivision on this basis. Details are obscure in shale material, but development of this general type would account for and accord



TEXT-FIG. 1. *Glyptograptus dentatus* (Brongniart). *a*, Corrected drawing of wax model in the form of an internal cast of the thecal cavities of the proximal end made from 10 μ serial sections through specimen 419 (Holm Collection, Riksmuseum, Stockholm). Reverse (above) and obverse (below) aspect; only a small portion of the sicular cavity is shown where it communicates with th1^1; $\times 40$ approx. *b*, Thecal diagram. *c*, Specimen prepared from Orthoceras Limestone of Hällunden, Öland, by Dr. D. Skevington. Öl. 1232, Palaeontological Institute, Uppsala; $\times 35$ approx.

with the outline visible in shale material belonging to *G. dentatus*, *G. shelvensis*, and a considerable number of later Ordovician diplograptids.

(*b*) *G. austrodentatus* group

Development in this group is known from serial (microtome) sections and some early growth-stages of a form unfortunately described as *G. dentatus* from Öland (Bulman 1936, pp. 49–57), and incomplete or damaged serial sections (ground at $\frac{1}{40}$ mm. intervals) of two limestone specimens from Texas (text-fig. 3). Here again the original wax model was unintentionally distorted and is redrawn by Mrs. Clarkson along with the new Texas models in text-fig. 2.

Th1^2 arises relatively high up on th1^1 and grows initially upward to form a prominent hoodlike structure before turning downwards and ultimately outwards and upwards; and it therefore comes to trace a distinctive ∽-shaped course of growth. It gives rise to th2^1 at an early stage, and this theca also has a conspicuous downward element in its early portion and in fact presents a somewhat flattened replica of the same sinuous growth as th1^2. Th2^2 has also initially a downward direction of growth. Th1^1 and th1^2 are almost symmetrically disposed around the sicula, and there is even some degree of symmetry in the disposition of th2^1 and th2^2. The proximal end (when preserved in relief) commonly shows an inverted V-shaped swelling at the base of the median septum separating th2^1 and th2^2 (text-fig. 8*a*, *b*).

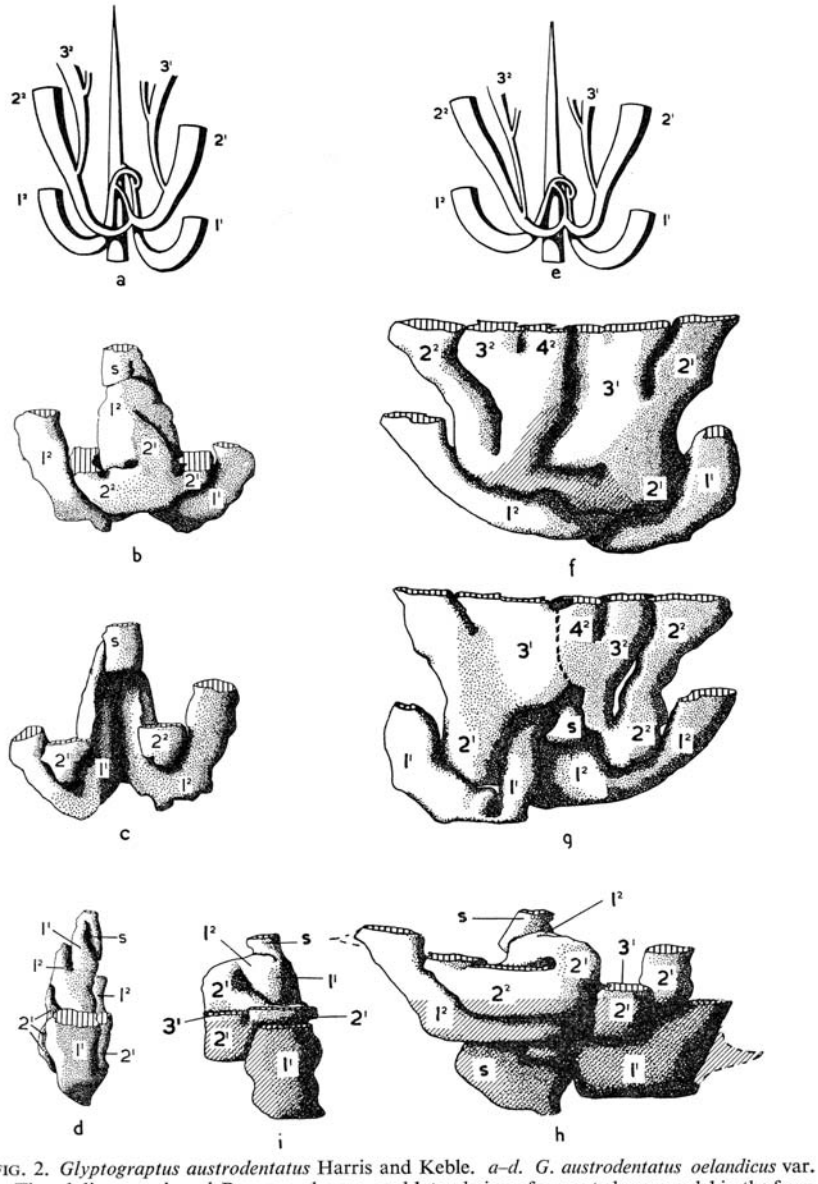
There is some variation in detail, but all three models agree in the main essentials—the ∽-shaped configuration of th1^2 with its conspicuous downwardly directed middle portion, and the initially downward growth of th2^1 and even th2^2. Such development is known to occur in *G. austrodentatus oelandicus* and *americanus* and would account for and accord with what is at present known of *G. austrodentatus austrodentatus* and *anglicus*. To judge from the configuration of the proximal end shown in Mu and Lee's figures (1958, text-fig. 9*e–g*) the same type of development characterizes *G. sinodentatus* and (1958, pl. 2, fig. 17) *G. curvithecatus* (as well as other forms mentioned below).

(*c*) Developmental relationships

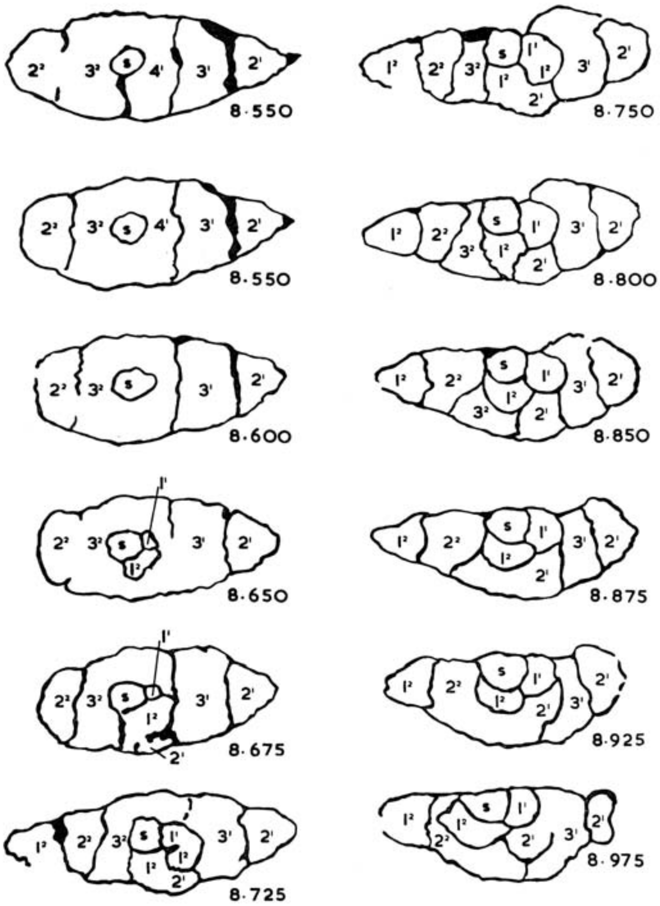
The recognition of these two types of proximal end side by side in what is probably the *I. gibberulus* Subzone of the *D. extensus* Zone (Shelve Church Beds, see p. 678) and their occurrence in a number of varietal forms at widely scattered localities in Europe, North America, Australia, and Asia, raises interesting possibilities concerning their relationship.

The emergence of the biserial glyptograptid rhabdosome is a most important evolutionary event, but these geographically distributed variants are not necessarily strictly contemporaneous nor confined to a narrow horizon; and the exact horizon is probably more reliably assessed by general faunal characteristics than by the mere occurrence of one or other of the *dentatus* or *austrodentatus* group of glyptograptids. Thus it seems probable that *G. austrodentatus anglicus* and *G. shelvensis* originate in the *I. gibberulus* Subzone (though both may also occur in the *D. hirundo* Zone); *G. austrodentatus oelandicus* is of upper *D. hirundo* Zone age; and *G. austrodentatus austrodentatus* probably lies somewhere between.

Secondly, it is (at present at least) impossible to deny that the *dentatus* and *austro-*



TEXT-FIG. 2. *Glyptograptus austrodentatus* Harris and Keble. *a–d. G. austrodentatus oelandicus* var. nov. *a*, Thecal diagram; *b, c, d*, Reverse, obverse, and lateral view of corrected wax-model in the form of an internal cast of the thecal cavities of the proximal end, made from $10\,\mu$ sections through specimen 1638 (Holm Collection, Riksmuseum, Stockholm); ×40 approx. *e–i. G. austrodentatus americanus* var. nov. *e*, Thecal diagram; *f, g*, Reverse and obverse views of wax model constructed from serial sections ground at $\frac{1}{40}$ mm. intervals through specimen SM A54407 (Marathon, Texas); *h, i*, Reverse and lateral views of wax model constructed from serial sections ground at $\frac{1}{40}$ mm. intervals through specimen SM A 53803 (Marathon, Texas); ×40 approx. Shaded areas indicate regions where crumbling of the encasing plaster resulted in complete or partial loss of sections. See also fig. 3.



TEXT-FIG. 3. *Glyptograptus austrodentatus americanus* var. nov. Selected sections from the series through specimen SM A53803 (Marathon, Texas), represented in the upper part of text-fig. 2 *h*, *i*. Conformation of the early parts of $th1^2$ and $th2^1$ is clearly shown and compares closely with microtome sections of *G. austrodentatus oelandicus* shown in Bulman 1936, text-fig. 21. × 32 approx.

dentatus groups may have evolved independently; and obviously independent scandent forms (including the cryptograptids, the scandent dichograptids, and probably also *Trigonograptus*) did indeed evolve independently at approximately the same period. Nevertheless, the dipleural rhabdosome form and generally similar thecal characters would seem to point to a monophyletic origin. This is supported also by the occurrence of forms apparently intermediate between *shelvensis* and *anglicus* in the Shelve Church

Beds. Some doubt is now thrown, however, upon my suggestion (Bulman 1936, p. 52) that the broader and narrower forms of what is here called *austrodentatus oelandicus* represent transients to *dentatus*, for it would now appear that the separation of the true *dentatus* type had already occurred. Having regard to the thecal changes as well as proximal-end changes involved in the separation of the *dentatus* and *austrodentatus* groups, it is unlikely that the process was operative over a long period of time. Until more accurate and detailed morphological (and stratigraphical) evidence is available, it it proposed as a working hypothesis to regard the true diplograptids as a monophyletic group, rapidly undergoing a primary division into two groups (*dentatus* and *austrodentatus*) each giving rise to a number of descendants in the *D. hirundo* and *D. bifidus* zones.

It is becoming apparent that the sequence of proximal-end development in diplograptids is more complicated than was originally supposed, and it is doubtful whether much is to be gained by any attempt to classify it into 'stages'. What has until now been called the '*dentatus* stage', with its atavistic features (in the strong downward component of $th1^2$ and $th2^1$, &c.) was originally conceived as having only a limited occurrence in 'the archaic diplograptid' of the lower Ordovician. Subsequent work on well-preserved material has added steadily to the number of species known to possess features of this development to a greater or lesser degree, and has extended its upward range certainly as high as the *G. teretiusculus* Zone. It is now suggested that the development of this whole group might be referred to under the more general term of the *streptoblastic type* of diplograptid development, in contrast to the *prosoblastic type* exemplified by the true *dentatus* and its descendants.

This streptoblastic type of development is best shown in the *austrodentatus* group of glyptograptids, but is well displayed also in *Lasiograptus hystrix* (Bulman 1936) and (with dicalycal $th2^2$) in *Gymnograptus retioloides* (Urbanek 1959). It appears also to be a characteristic of those climacograptids for which Přibyl (1947) proposed the name *Pseudoclimacograptus*, and combined with the septal features stressed by Přibyl and the thecal characters emphasized by Jaanusson (1960) may be held to justify the erection of this genus. *P. scharenbergi*, the genotype, has been shown to possess a modified version of this proximal end, and so may some other species at present included (Jaanusson 1960) but imperfectly known. It is, however, very well displayed in such geologically early species as *P. formosus* Mu and Lee, and *P. cumbrensis* sp. nov. The modifications seen in *P. scharenbergi* and the relationship postulated by Urbanek between *G. retioloides* and *G. linnarssoni* suggests that the prosoblastic type of proximal end does from time to time independently develop, and also that the dicalycal theca may be deferred to $th2^2$ even within the strictly streptoblastic type.

We arrive therefore at the supposition that the streptoblastic type of development characterizes perhaps the greater part of the early diplograptids, conservative as to their development but variable (in Arenig times) in thecal characters. From it is quickly derived the prosoblastic *G. dentatus* group, which appears to be ancestral to most of the later Ordovician glyptograptids, orthograptids, and climacograptids. From it also is derived, by thecal differentiation, the *Pseudoclimacograptus* group, and probably hallograptids and lasiograptids. Modification of the mode of development approaching or leading to a prosoblastic type may occur within any of these groups, but a fuller discussion of these relationships is outside the scope of this article.

THE HOLOTYPE OF *GLYPTOGRAPTUS DENTATUS*

The species now known as *Glyptograptus dentatus* was described (under the name *Fucoides dentatus*) by Brongniart in 1828 from 'le calcaire de transition, Pointe Levi près Québec dans le Canada (Coll. de M. Stockes)' and illustrated by four lithographed figures (pl. vi, figs. 9–12). In none of these is the proximal end represented, but the glyptograptid character of the thecae is clearly shown in the two enlarged figures, 11 and 12. The diagnosis reads: 'F. fronde membranaceâ, lineari (an simplici?), pinnatifido-dentatâ, enervi, dentibus triangularibus subacutis, apice obtuso'; and the relevant part of his description is contained in the first paragraph (p. 70): 'Nous ne connaissons que des fragmens de cette petite espèce de Fucoïde; ce sont des portions, longues de 2 centimètres environ, d'une fronde linéaire, d'une largeur très-uniforme et égale à peu près à 2 ou 3 millimètres. Ces frondes, qui paraissent minces et membraneuses, sont profondément dentées sur les bords et presque pinnatifides; les lobes ou dentelures sont triangulaires, très-réguliers, d'une forme aiguë, mais à pointe mousse.'

Apart from mention by Sternberg (1838) and Bronn (1849) I can find no further citation in the literature till 1865, when James Hall ('Graptolites of the Quebec Group') added a footnote to the description of his species *Diplograptus pristiniformis* (p. 110) suggesting that it was identical with *Fucoides dentatus*; and on p. 84 (footnotes) he writes of both *pristiniformis* and *bryonoides*: 'It is only since [Brongniart's] descriptions have been in print, and published references made to them, that I have discovered this identity, or I would have proposed to substitute the specific names of Brongniart [*dentatus* and *serra* respectively] for those given by me in 1857. I take the first opportunity of making the correction.' Hopkinson and Lapworth (1875) use the name *dentatus*, under which the species has always been described and recorded since.

A large number of Brongniart's types are preserved in the Muséum national d'Histoire naturelle in Paris; but a search for the *dentatus* originals has been unavailing, and they must presumably be regarded as lost. I am greatly indebted to Professor Pierre Pruvost and Professor Ed. Boureau for the trouble they have taken in trying to locate them.

Since Brongniart's originals can no longer be traced, it would seem natural to propose the selection of a neotype from among the material figured by James Hall. The specimens are probably from the same locality, and the identity has been accepted for nearly a century. I am most grateful to Dr. Digby McLaren, of the Canadian Geological Survey, for the loan of the specimens concerned.

Proposed neotype. Geol. Survey Canada 943 (Hall 1865, pl. 13, figs. 16, 17). Plate 96, fig. 1; text-fig. 4*a*.

Description. Rhabdosome length 2 cm., with 1 cm. of virgula preserved. Width 1·1 mm. at the level of $th1^1$, widening to 1·2 mm. at $th3^1$ and 1·5 mm. at 5 mm. length, reaching a maximum of 2·1 mm. Seven thecae occur in the first 5 mm., 10–11 in 10 mm. distally. Thecal overlap is not clearly shown, but seems to be slightly less than half at about 5 mm. from the proximal end and to increase distally. The shape of the ventral wall of the thecae (compressed) is smoothly but not uniformly curved, showing a stronger curvature just above the aperture of the preceding theca and becoming straighter distally; i.e. there is an incipient geniculum situated low down on the metatheca, and the extreme proximal part of the metatheca is slightly impressed. The aperture is denticulate, the apertural margin slightly inclined proximally inwards. The median septum is not visible; a stout virgula is, however, clearly impressed through the lateral periderm throughout the length of the rhabdosome. The sicula is not visible, but it possesses a stout virgella 2·5 mm. long which is apparently coated with some secondary cortical tissue.

Specimen 943a (Hall's fig. 15) has in my opinion been incorrectly drawn on Hall's plate and comprises not one but two separate but aligned rhabdosomes. The lower one (Plate 96, fig. 2) is complete proximally and attains a length of 3 cm. with a maximum breadth of 1·8–1·9 mm. The upper one is incomplete at the proximal end and is interrupted in the middle; the total length is 1·5 cm., with a maximum breadth of 1·9 mm. Thecae number about ten in 10 mm. distally, but preservation is too poor to admit the observation of much detail; they appear to be similar in all essentials to those of the proposed neotype.

Horizon. Subsequent work on the Levis Shales, particularly that of Raymond (1914), strongly suggests that the specimens must have come from the upper part of the Levis Shales, and probably from Raymond's Zone D_2; but nothing objective is known of the horizon and locality beyond Hall's statement 'Quebec Group; Point Levis' (and the same applies to Brongniart's specimens). No special significance attaches to the association which for the neotype comprises dichograptid stipes including a specimen of *Tetragraptus quadribrachiatus* (s.l.), and (on 943a) a figured dichograptid stipe labelled *Graptolithus denticulatus*.

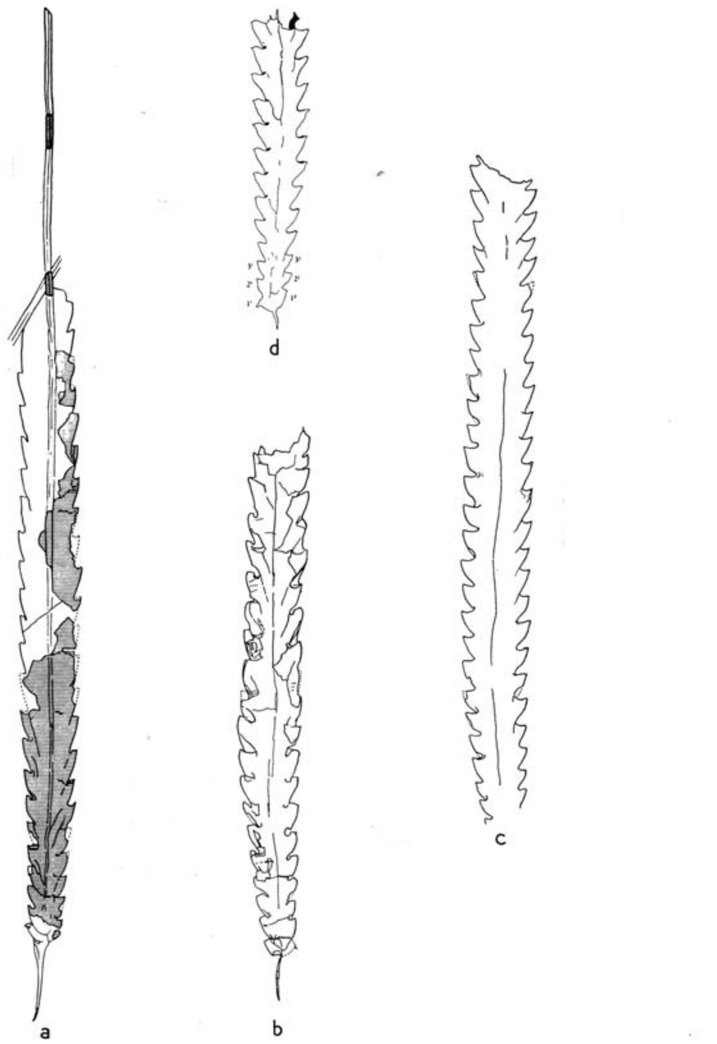
SYSTEMATIC DESCRIPTIONS

Glyptograptus dentatus (Brongniart)

Plate 96, figs. 1–5; text-figs. 1, 4

1828 *Fucoides dentatus* Brongniart, p. 70, pl. vi, figs. 9–12.
1838 *Sphaerococcites dentatus*; Sternberg, p. 29.
1848 *Fucoides dentatus*; Bronn, p. 505.
1848 *Sphaerococcites dentatus*; Bronn, p. 1162; 1849, p. 8.
1858 *Graptolithus pristiniformis* J. Hall, p. 133.
1865 *Diplograptus pristiniformis*; J. Hall, pp. 84 (footnote), 110, pl. 13, figs. 15–17.
1868 *Diplograptus pristiniformis*; Nicholson, p. 140, pl. 5, figs. 14, 15.
1875 *Diplograptus dentatus*; Hopkinson and Lapworth, p. 656, pl. xxxiv, figs. 5*a–h*, ? 5*i*, *k*.
1904 *Diplograptus dentatus*; Ruedemann, p. 719, pl. 17, figs. 10–13.
1907 *Diplograptus* (*Glyptograptus*) *dentatus*; Elles and Wood, p. 253, pl. xxxi, fig. 4*a–d*.
1907 *Diplograptus* (*Glyptograptus*) *dentatus appendiculatus*; Elles and Wood, p. 255, pl. xxxi, fig. 5.
1931 *Glyptograptus dentatus*; Bulman, p. 55, pl. 6, figs. 7–11, pl. 7, figs. 1, 2.
1936 *Glyptograptus dentatus/teretiusculus* transient; Bulman, p. 57, pl. 3, figs. 1–4, 8–11; pl. 4, figs. 1–3.
1947 *Glyptograptus dentatus*; Ruedemann, p. 404, pl. 69, figs. 1–8.

Revised diagnosis. Rhabdosome 2–3 cm. in length, widening gradually from a pointed proximal end furnished with conspicuous virgella. Width at $th1^1$ about 1 mm., increasing to 1·7 or 1·8 mm. at 10 mm., and attaining a maximum of 2·0–2·2 mm. Thecae 7–9 in the first 5 mm., 10–13 in 10 mm. distally, with glyptograptid curvature of the ventral wall of the metathecae, slightly impressed just above the aperture of the preceding theca; apertural margin slightly concave in profile view with very slightly developed lappets.



TEXT-FIG. 4. *Glyptograptus dentatus* (Brongniart). All figures ×5 approx. *a*, Proposed neotype, GSC 943, Point Levis, Quebec; figured by Hall 1865, pl. 13, figs. 16, 17. *b*, GSM 23073, *D. bifidus* Zone, Clynderwen Station, S. Wales; figured Elles and Wood, pl. 31, fig. 4*e* and text-fig. 174*b*. *c*, BMHN, Q1173, *D. bifidus* Zone, Ellergill, Milburn, Westmorland. *d*, Riksmuseum, Stockholm, 419 (Holm Collection), Orthoceras Limestone, Hälludden, Öland; figured Bulman 1936, text-fig. 22*b*.

Development prosoblastic, with dominantly upward growth of $th1^2$, the aperture of which is always at a higher level than that of $th1^1$. Median septum complete, practically straight.

Proposed neotype. Original of *Diplograptus pristiniformis* Hall, 1865, pl. 13, figs. 16, 17: CGS, no. 943: Levis Shales, Levis, Quebec. Here refigured as text-fig. 4*a* and Plate 96, fig. 1.

Description. The chief characteristics of this species are the gradual widening of the rhabdosome from a pointed proximal end, and the glyptograptid form of the thecae, the curvature being greatest near the base of the metatheca which becomes progressively straighter towards the aperture.

The form of the proximal end results from a mode of development originally described from serial sections of limestone material from Öland (see text-fig. 1*a*). The aperture of $th1^2$ lies well above that of $th1^1$, and at the proximal end the two series of thecal apertures are markedly alternate (a feature which may persist throughout the rhabdosome) and the whole proximal end tends to present a rather 'drawn-out' appearance in contrast to the truncated proximal end of the *austrodentatus* group of species. According to Skevington (MS.) the sicula has a length of only 1·3 mm. with an apertural width of 0·32 mm.: it is provided with a prominent virgella which may be 4 mm. or even more in length and sometimes shows secondary thickening. A subapertural spine is carried by $th1^1$ and a similar slender spine is usually visible on $th1^2$.

The form of the thecae is well seen in three-dimensional specimens from the Holm Collection (Bulman 1936) and in Skevington's figures (Plate 96, fig. 3, and text-fig. 1). The glyptograptid curvature is strongest low down on the wall of the metatheca, and in its distal (apertural) part the wall becomes nearly straight: on compression this may give the appearance of an incipient geniculation. There is a pair of rudimentary lappets on the apertural margin, produced (Skevington MS.) by uneven development of the final fusellus, and the apertural margin is concave in profile view, and straight (or very slightly concave) in true ventral view—a feature which may cause some variation in the appearance of the thecae on compression. The amount of overlap cannot be determined with any accuracy: in the proximal part of the rhabdosome it is rather less than one-half (Bulman 1936, fig. 32). According to Skevington's observations, the interthecal septum is apt to be incompletely developed even when it is indicated externally on the lateral walls of the rhabdosome. The median septum is here straight and originates between the bases of $th3^1$ and $th3^2$.

There is generally a well-developed virgula extending a centimetre or so beyond the distal end of the rhabdosome. Rarely this is expanded into an elongate vesicle, and such specimens were described by Elles and Wood (1907) under the name *G. dentatus appendiculatus*. It is doubtful whether this name is worth maintaining, particularly as a closely similar modification may occur in *G. shelvensis*. Synrhabdosomes have been figured by Bulman (1931) and Ruedemann (1947).

Occurrence. Widely distributed in the *D. bifidus* Zone—e.g. Canada—Zone D (? confined to D_2), Levis Shales, Quebec. *Britain—D. bifidus* Zone (South Wales, Shropshire, Lake District); ? *D. hirundo* Zone; ? *D. murchisoni* Zone. *Scandinavia*—Glaukonithåltig grå Vaginatumkalk, Öland (*D. hirundo*/*bifidus* Zone).

Glyptograptus shelvensis sp. nov.

Plates 97, figs. 1–3, 14; text-fig. 5

Diagnosis. Rhabdosome small, about $1\frac{1}{2}$ cm. long, widening gradually from less than 1 mm. (usually 0·8–0·9 mm.) at $th1^1$ to a maximum of 1·3–1·4 mm. (rarely 1·5 mm.). Thecae number about six in 5 mm. (maximum range 11–14 in 10 mm.). in more distal part of the rhabdosome, of the type of *G. dentatus*. Proximal end with virgella about 1 mm. in length, and delicate subapertural spines on $th1^1$ and $th1^2$; orientation of $th1^1$ and $th1^2$ and presumably mode of development as in *G. dentatus*.

Holotype. Sedg. Mus. Camb., A40788a, b (text-fig. 5*a*); Shelve Church Beds (upper part of *D. extensus* Zone), Shelve, Salop.

Description. The species resembles *G. dentatus* in the characters of the thecae and the general appearance of the proximal end, but differs in its smaller size and more parallel-sided rhabdosome.

The sicula is virtually unknown though one specimen (from Shelve) shows some indication of a sicula about 1·4 mm. in length. All the material is compressed and often slightly sheared, so that even thecal characters are not easy to determine; in the better preserved of the specimens, however, the thecae have an almost even glyptograptid curvature, with a slight indication of an incipient geniculation low on the metatheca as in *G. dentatus*. In place, however, of the incipient lappets of *G. dentatus* there seems to be a broad, low projection or 'lip' on the ventral portion of the edge of the aperture; in some preservations this may give an appearance of slight apertural 'isolation', but it is presumably due to the deposition of incomplete or uneven fuselli at the apertural margin.

The metathecal portion of $th1^2$ has a dominantly upward direction of growth and its aperture characteristically lies well above that of $th1^1$. Partly because of poor preservation and partly as a consequence of this orientation of $th1^2$, it is difficult to determine reliably the width of the rhabdosome at the level of the $th1^1$ aperture, but it appears to be always less than 1 mm. and may be as little as 0·75 mm. The mode of development is

EXPLANATION OF PLATE 96

Magnification ×5 approx., except where otherwise stated.

Figs. 1–5. *Glyptograptus dentatus* (Brongniart). 1, Proposed neotype, GSC 943 (figd. Hall 1865, pl. 13, figs. 16, 17). Quebec Group (probably D_2 of Raymond); Point Levis, Quebec. 2, GSC 943a (figd. Hall 1865, pl. 13, fig. 15), ×3 approx.; same locality. 3, Obverse (*a*) and reverse (*b*) view of rhabdosome in full relief, ×10 approx. Riksmuseum, Stockholm, Holm Collection 1280 (figd. Bulman 1936, pl. 3, figs. 1, 2). Vaginatumkalk (*D. hirundo/bifidus* Zone); Hälludden, Öland. 4, GSM 23073 (figd. Elles and Wood 1907, pl. xxxi, fig. 4*c*). *D. bifidus* Zone; Rhyd-y-behan Cottage, near Clynderwen, S. Wales. 5, GSM 23072 (figd. Elles and Wood 1907, pl. xxxi, fig. 4*b*). *D. bifidus* Zone; Gilfachwen near Clynderwen, S. Wales.

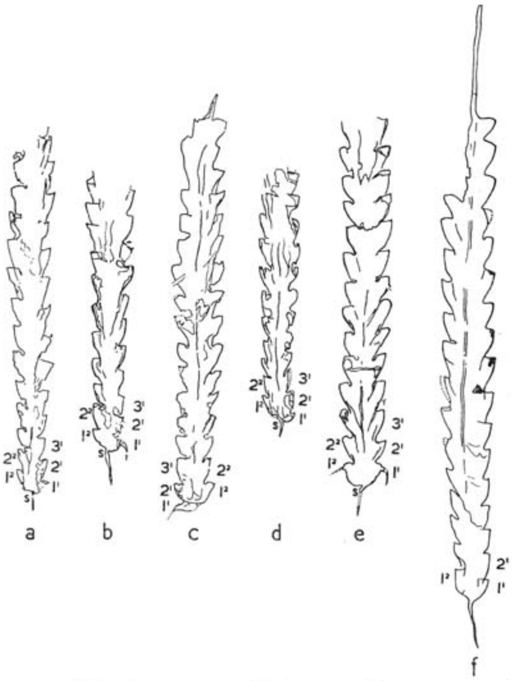
Fig. 6. *Climacograptus* cf. *biformis* Mu and Lee. GSM JR4141. Skiddaw Slates, ? *D. hirundo* Zone; NE. of Kirkland Church, Cumberland.

Figs. 7–8. *Pseudoclimacograptus cumbrensis* sp. nov. Skiddaw Slates, ? *D. hirundo* Zone; Bassenthwaite Sandbeds, Cumberland. 7, Holotype, SM A53044 (latex mould). 8, SM A18134 (latex mould) (distal part of rhabdosome).

Fig. 9. *Diplograptus ellesi* sp. nov. Holotype, BMNH, Q1174. *D. bifidus* Zone; Ellergill, near Milburn, Westmorland.

assumed to be generally similar to that of *G. dentatus*, but there is no evidence here that the dicalycal theca is other than th2^1.

The median septum, when recognizable, seems to be straight and complete at least from th2^2. Some specimens from the *D. hirundo* Zone (Skiddaw Slates) possess an expanded virgula as in '*G. dentatus appendiculatus*'.



TEXT-FIG. 5. *Glyptograptus shelvensis* sp. nov. All figures ×5 approx. *a–e*. Shelve Church Beds (? *I. gibberulus* Subzone), Shelve Church, Shropshire. *a*, SM A40788b, holotype. *b*, SM A40798. *c*, SM A40791b. *d*, SM A45891b. *e*, SM A40796, abnormal specimen in respect of th1^1 and th1^2. *f*, Skiddaw Slates (? *D. hirundo* Zone), Outerside, Cumberland; BMNH, Q1178.

Remarks. There appears to be some variation, particularly in the proximal end, which cannot be entirely attributed to preservation, but which is difficult to evaluate. One specimen (A40796, text-fig. 5*e*) has the general characters of *shelvensis*, but the initial thecae (1^1 and 1^2) are more or less symmetrical, and the thecae remain paired rather than alternate throughout the rhabdosome (as they are also in A40791, text-fig. 5*c*). Such variations suggest the occurrence of structural intermediates between *shelvensis* and *austrodentatus anglicus*. In general, however, the species is readily distinguishable from *austrodentatus anglicus* by its narrower rhabdosome, more pointed proximal end, type of theca, and smaller thecal number. In the collections from Shelve at the Sedgwick Museum, *shelvensis* outnumbers the others by about three to two.

The species is probably ancestral to *G. dentatus*, and some specimens from the *D. hirundo* Zone of the Skiddaw Slates appear to be transitional; but the relationship is difficult to substantiate.

There is some resemblance to Hsü's *G. dentatus intermedius*, but *G. shelvensis* lacks the peculiar basal spines of that species.

Occurrences. This is one of the characteristic fossils of the Shelve Church Beds, Shelve Church, Salop. According to Professor Whittard (in litt., 1962) the Shelve Church Beds occur some 500 feet below the base of the Hope Shales (*D. bifidus* Zone); the *D. hirundo* Zone, represented by the Tankerville Flags, is some 200 feet in thickness, and it is reasonable stratigraphically to assign the Shelve Church Beds to the upper part of the *D. extensus* Zone, probably equivalent to the *I. gibberulus* Subzone of the Skiddaw Slates (see Jackson 1962, p. 305). The species also occurs in the Skiddaw Slates in the *I. gibberulus* Subzone and in the overlying *D. hirundo* Zone; and in the upper part of the *G. dentatus* Zone (*T. ensiformis* Subzone) of the Arenig of Yukon (Jackson and Lenz 1962).

Glyptograptus austrodentatus Harris and Keble

Remarks. *G. austrodentatus* has proved to be a species of widespread occurrence represented in four continents by a number of slightly differing forms. Despite the poor preservation of much of the material, and the occurrence of some variation in any one

EXPLANATION OF PLATE 97

Magnification ×5 approx., unless otherwise stated.

Fig. 1. *Glyptograptus* cf. *shelvensis* sp. nov. SM A54388 Arenigian, Zone of *G. dentatus* (*T. ensiformis* Subzone); Road River, 2530, Yukon.

Figs. 2, 3, 14. *Glyptograptus shelvensis* sp. nov. 2, BMNH, Q1178. Skiddaw Slates (? *D. hirundo* Zone); Outerside, Cumberland. 3, SM A40784. Shelve Church Beds, *D. extensus* Zone (? *I. gibberulus* Subzone); Shelve Church, Shropshire. 14, BMNH, Q1176, Skiddaw Slates (? *D. hirundo* Zone); Outerside, Cumberland.

Fig. 4. *Glyptograptus austrodentatus anglicus* var. nov. SM A40786. Shelve Church Beds, *D. extensus* Zone (? *I. gibberulus* Subzone); Shelve Church, Shropshire.

Fig. 5. *G. austrodentatus mutabilis* var. nov. Holotype; SM A45906b. Shelve Church Beds, *D. extensus* Zone (? *I. gibberulus* Subzone); Shelve Church, Shropshire.

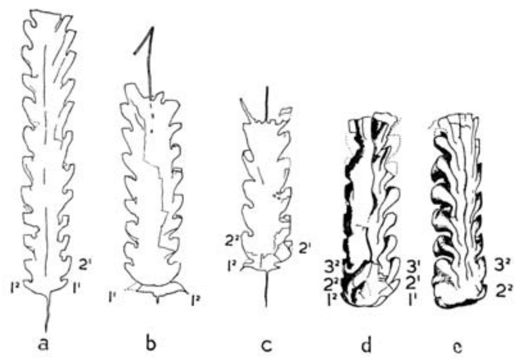
Figs. 6–9, 12, 15. *G. austrodentatus austrodentatus* Harris and Keble. 6, SM A51691. 7, SM A51692. 8, SM A51693. 9, SM A51689. All from Darriwil, D1 (zone of *G. austrodentatus*); loc. A310, parish of Sedgwick, Victoria, Australia. 12, SM A51698, ×10. Darriwil, D1 (zone of *G. austrodentatus*); loc. 2076, parish of Wellsford, Victoria, Australia. 15, Specimen sheared, but in high relief, showing form of thecae and interthecal septa. SM A51688 (latex mould), ×10. Darriwil, D1 (zone of *G. austrodentatus*); loc. A310, parish of Sedgwick, Victoria, Australia.

Figs. 10–11, 13. *G. austrodentatus* cf. *americanus* var. nov. 10, SM A54398. Arenigian, Zone of *G. dentatus* (*T. ensiformis* Subzone); Road River, 2540, Yukon. 11, SM A54405. Arenigian, Zone of *G. dentatus* (*I. caduceus* Subzone); Road River, 2565, Yukon. 13, SM A54406. Arenigian, Zone of *G. dentatus* (*I. caduceus* Subzone); Road River, 2580, Yukon.

Figs. 16–17. *G. austrodentatus oelandicus* var. nov.; Vaginatumkalk (*D. hirundo*/*bifidus* Zone); Hälludden, Öland. 16, Reverse (*a*) and obverse (*b*) view of rhabdosome in full relief. Riksmuseum, Stockholm, Holm Coll. 307 (figd. Bulman 1936, pl. 3, figs. 5, 6). 17, Reverse view in full relief, ×10. Holm Coll. 307 (figd. Bulman 1936, pl. 3, fig. 7).

Figs. 18–19. *G. austrodentatus americanus* var. nov. 18, SM A53803. Fort Pena formation, Zone 9 (*Hallograptus etheridgei*); 7 miles SW of Marathon, Texas. 19, GSC 8074, *Shumardia* limestone (D_1); Point Levis, Quebec.

area, these local forms seem to express genuine differences, to ignore which would be to extend unduly the range of variation in the species. There is evidence suggesting that these are not strictly contemporaneous, but it is not at present possible to recognize with certainty any distinctive chronological element in these variants, and their taxonomic status may be essentially that of geographical races. For convenience in terminology they are referred to as varieties.



TEXT-FIG. 6. *Glyptograptus austrodentatus austrodentatus* Harris and Keble. *a*, SM A51689. *b*, SM A51691. *c*, SM A51692. *d*, SM A51687, mould of proximal end in relief. *e*, SM A51688, latex cast of natural mould of proximal end in relief. All specimens from *G. austrodentatus* Zone (Darriwill, D1), loc. A310, Parish of Sedgwick, Victoria, Australia. ×5 approx.

Glyptograptus austrodentatus austrodentatus Harris and Keble

Plate 97, figs. 6–9, 12, 15; text-fig. 6

1932 *Diplograptus* (*Glyptograptus*) *austrodentatus* Harris and Keble, p. 39, pl. v, figs. 4, 5, text-figs. 1–4.

1935 *Diplograptus* (*Glyptograptus*) *austrodentatus*; Harris and Thomas, p. 295, fig. 3, nos. 1–5.

1938 *Glyptograptus austrodentatus*; Harris and Thomas, pl. 2, fig. 51.

1960 *Glyptograptus austrodentatus*; Thomas, pl. vi, fig. 85.

Revised diagnosis. Rhabdosome small, rarely exceeding 1 cm. in length, widening rapidly from an initial width of about 1·3 mm. at $th1^1$ to a maximum of 1·6–1·9 mm. (mainly 1·7–1·8 mm.) which is uniform over most of the rhabdosome. Thecae 6–6½ in 5 mm. distally, initially with a fairly pronounced geniculation one-third to halfway along the metatheca, becoming less prominent distally. Overlap nearly two-thirds. The first two thecae (1^1 and 1^2) are small, slender, almost symmetrically disposed with slender sub-apertural spines. Median septum complete, slightly undulating. Sicula 2–2·3 mm. long with slender virgella.

Lectotype. With the approval of Dr. D. E. Thomas I designate the original of Harris and Keble 1932, text-fig. 3 (specimen no. 31365, Geol. Surv. Vict.—cited in error as 3165).

Description. This is a well-characterized subspecies and amongst some thirty specimens sent me from Victoria there is very little variation that cannot be attributed to preservation.

Rhabdosomes rarely exceed 1 cm. in length and are almost parallel-sided throughout; the width at the first thecal pair is about 1·3 mm., and what is practically the maximum width is attained by the second thecal pair. In a few specimens the maximum width is as little as 1·45 mm. (? distortion) or as much as 1·9 mm., but the range is generally between 1·6 and 1·8 mm.

The form of the thecae is well shown in two specimens preserved as natural moulds in high relief. In profile view the wall of the metatheca is initially concave, becoming strongly convex about halfway along its length, and is very slightly introverted at the apertural end; this introversion appears to affect principally a vertical 'lip' of incomplete fuselli (see description of *G. shelvensis*). There seems to be some thickening at the sides of the aperture, and the ventral wall is somewhat flattened. A well-marked sinuous interthecal groove (text-fig. 6*d*, *e*) reveals a thecal overlap of three-fifths. In normal compressed rhabdosomes the interthecal groove is not seen, and the thecae show a fairly pronounced geniculation, becoming less pronounced distally and situated nearer the aperture of the theca.

Unfortunately the specimens preserved in relief provide no evidence of the mode of development of the rhabdosome, and flattened early growth stages cannot be interpreted in any detail. The symmetrical distribution of $th1^1$ and $th1^2$ suggests that development is of the streptoblastic type. The sicula is a little over 2 mm. in length and the apex extends to between the level of the third and fourth thecal pair.

Remarks. One specimen from loc. 2206 (parish of Wellsford) represents a form more like *G. shelvensis*; the proximal end is damaged, but $th1^2$ appears to open at the level of $th2^1$ (resulting in a much narrower proximal end) and the whole rhabdosome is narrower and the thecae more suggestive of *shelvensis*. Another specimen from loc. $\frac{LL}{22}$ (parish of Lancefield) shows a number of rhabdosomes which also differ in having a more pointed proximal end and seemingly more *dentatus*-like thecae, but the preservation is poor. The bulk of the material, however, conforms closely to the norm. As Harris and Keble observe, however, there is variation in thecal appearance as an effect of compression, and as pointed out above there is a slight progressive change in the thecae along a rhabdosome in the position where the 'geniculation' occurs on the metatheca and the extent to which it is developed.

Occurrence. The best material used in the above description was from loc. A310, parish of Sedgwick, allotment 2, section 11. The subspecies characterizes a well-marked zone (D1) at the base of the Darriwilian in Victoria.

Glyptograptus austrodentatus var. *anglicus* var. nov.

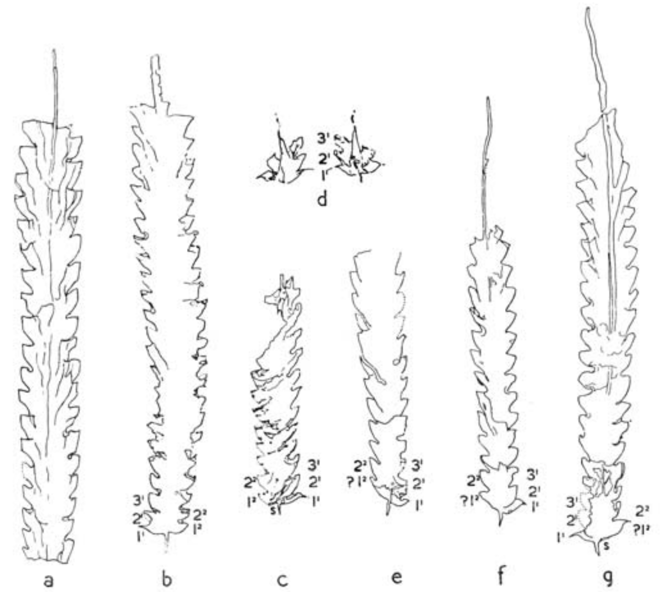
Plate 97, fig. 4; text-fig. 7*a–d*

Diagnosis. Rhabdosome small, 1–1½ cm. long, widening from an initial width of about 1·2 mm. (1·1–1·3 mm.) at the level of $th1^1$ aperture to a maximum of about 1·7 mm. (1·6–1·8 mm.). Thecae numbering 7–7½ in 5 mm. (maximum range 13–17 in 10 mm.) in the more distal part of the rhabdosome, of the type of *G. austrodentatus*. Sicula 1·4 mm. in length, the apex extending to the level of the third thecal pair with conspicuous virgella; $th1^1$ and $th1^2$ symmetrically disposed, with delicate subapertural spines.

Holotype. SM A53381 (text-fig. 7*b*): Shelve Church Beds, Shelve, Shropshire.

Description. This variety resembles *G. austrodentatus* in the characters of the thecae, with an incipient geniculation about halfway along the metatheca, and the blunt proximal end with $th1^1$ and $th1^2$ almost symmetrically disposed; differences are enumerated below.

The sicula is known from an early growth stage (text-fig. 7*d*) where it is seen to be only 1·4 mm. in length and to extend to the level of the third thecal pair. It is provided



TEXT-FIG. 7. *a*, *Glyptograptus austrodentatus* cf. *anglicus*. Skiddaw Slates (? *D. hirundo* Zone), NW. of Lingside, Cumberland, SM A18162. *b–d*, *G. austrodentatus anglicus* var. nov. *b*, Holotype, SM A53381. *c*, SM A45892. *d*, Early growth stage (and counterpart), SM A40789a and b. *e–g*, *Glyptograptus austrodentatus mutabilis* var. nov. *e*, SM A40799. *f*, Holotype, SM A45906a. *g*, SM A40786. *b–g*, Shelve Church Beds (? *I. gibberulus* Subzone), Shelve Church, Shropshire. All figures ×5 approx.

with a conspicuous virgella which may show some secondary cortical thickening. The thecae number 14–16 in 10 mm. (exceptionally 13 or more than 16); they show a pronounced glyptograptid curvature due to the presence of a slight geniculation about halfway along the metatheca; the infragenicular portion is concave (in some preservations strongly so) and the supragenicular portion more gently curved and slightly inclined outwards. A slight ventral apertural 'lip' (similar to that described in *G. shelvensis*) appears to be present, but there is no introversion.

The visible portions of $th1^1$ and $th1^2$ are more or less symmetrically developed and it is inferred that the mode of development of the rhabdosome is of the streptoblastic type. The resulting square-cut termination of the rhabdosome is a conspicuous feature.

It differs from *austrodentatus austrodentatus* in the possession of more numerous thecae; the possession of a smaller sicula, with a more pronounced virgella; and a less conspicuous difference in size between the thecae of the first and second thecal pairs. The *austrodentatus* thecae typically show a slight but distinct introversion, which is lacking in *anglicus*.

Occurrence. The variety occurs most abundantly in the *I. gibberulus* Subzone (p. 678) of the Shelve Church Beds in Shropshire. Poorly preserved specimens, which appear to be referable to this form, occur in Skiddaw Slates in the *D. hirundo* Zone, but have not so far been noted from undoubted *I. gibberulus* Subzone there.

Glyptograptus austrodentatus var. *mutabilis* var. nov.

Plate 97, fig. 5; text-fig. 7*e–g*

Diagnosis. Rhabdosome rarely exceeding 1 cm. in length, with an almost uniform breadth of 1·5–1·7 mm. (1·0–1·2 mm. at $th1^1$). Thecae 14–15 (rarely 13) in 10 mm., resembling in general character those of var. *anglicus*. Proximal end asymmetric, with $th1^2$ upwardly directed and opening near the level of the aperture of $th2^1$.

Holotype. SM A45906a, b (Plate 97, fig. 5; text-fig. 7*f*).

Remarks. This form differs from *anglicus* in possessing a somewhat more slender rhabdosome, rather fewer thecae in 10 mm., and principally in the character of the proximal end, which is not so bluntly truncated and approximates in appearance to that of the prosoblastic group. It would seem to be transitional between the two large groups, but since details of the proximal end are unknown it is included in the *austrodentatus* group because of the characters of the thecae and the greater breadth of the rhabdosome at the proximal end.

Occurrence. This form occurs not infrequently in the Shelve Church Beds (*I. gibberulus* Subzone), Shropshire.

Glyptograptus austrodentatus var. *oelandicus* var. nov.

Plate 97, figs. 16, 17; text-figs. 2*a–d*, 8

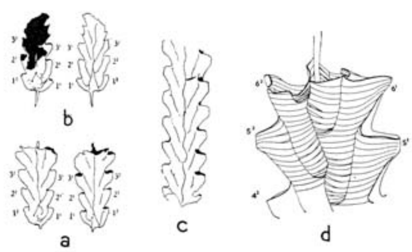
1936 *G. dentatus*; Bulman p. 49, pl. 3, figs. 5–7, 12–13, 14–21, and pl. 4, figs. 4–6, text-figs. 18–21.

Diagnosis. Rhabdosome 1 cm. or more in length, widening from an initial width of about 1 mm. at $th1^1$ to a maximum of about 1·8 mm. Eight thecae occur in the first 5 mm. of the rhabdosome length, but distally number about 14–15 in 10 mm. Thecae with pronounced sigmoid curvature, the geniculation situated about midway on the metatheca proximally; and about two-thirds along the metatheca distally; overlap rather more than one-half proximally, half distally. Median septum undulating, markedly so at the proximal end. Sicula 1·3–1·8 mm. in length, with prominent virgella; development pronouncedly streptoblastic in type, with 'truncated' proximal end and subsymmetrical disposition of $th1^1$ and $th1^2$.

Holotype. *G. dentatus* Bulman 1936, pl. 3, figs. 5–7 (Holm Collection, no. 307, Riksmuseum, Stockholm); Glaukonithåltig grå Vaginatumkalk, Hällunden, Öland. Here reproduced as Plate 97, figs. 16, 17.

Description. The variety has been described in Bulman (1936, pp. 49–57) and the mode of development described on pp. 5–6 and shown in text-fig. 2 is based on an excellent series of microtome sections and an incomplete series of growth stages.

The form of the thecae in undistorted three-dimensional material is best seen in one of Dr. Skevington's transparencies on which text-fig. 8*d* is based. As in *G. dentatus*, the interthecal septum is sometimes not developed, or is extremely short, even though its course is indicated externally on the lateral walls of the rhabdosome.



TEXT-FIG. 8. *Glyptograptus austrodentatus oelandicus* var. nov. *a*, Reverse and obverse views of specimen 1647. *b*, Reverse and obverse views of specimen 1646. *c*, Distal portion of rhabdosome, specimen 1641. All specimens from Orthoceras Limestone, Hälludden, Öland, Holm Collection, Riksmuseum, Stockholm; from Bulman 1936, text-figs. 19 and 18a. $\times 5$ approx. *d*, Distal end of rhabdosome showing form of thecae and growth-lines. Hälludden, Öland; D. Skevington prep. (Palaeontological Institute, Uppsala, Öl. 1230). $\times 15$ approx.

Remarks. In the original description (1936, p. 52) reference was made to the existence of broad and narrow forms, the narrow forms having a more pointed proximal end, rather less overlap, and a more distally sited geniculum. It may be that these narrower forms have a similar relation to typical var. *oelandicus* that the forms here described as var. *mutabilis* bear to var. *anglicus*, but it seems unlikely that they represent real transients to *G. dentatus* at this rather high horizon when the *dentatus* type had already been differentiated.

The variety differs from *austrodentatus* in having a less 'truncated' proximal end, a less parallel-sided rhabdosome, and more numerous thecae. $Th1^1$ and $th1^2$ are not so symmetrically disposed, and the thecae are more alternating and lack any ventral apertural 'lip'.

From var. *anglicus* it differs principally in its rather more pointed proximal end, less symmetrically disposed basal thecae, and in lacking the vertical apertural 'lip'.

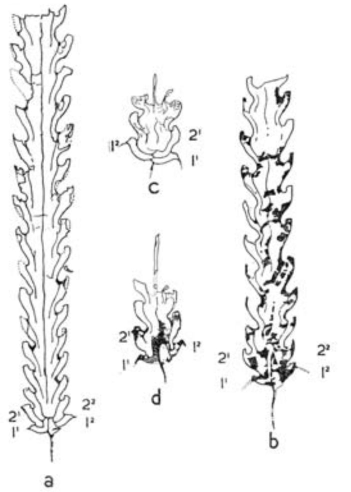
Occurrence. Glaukonithåltig grå Vaginatumkalk, Öland (*D. hirundo/bifidus* Zone).

Glyptograptus austrodentatus var. *americanus* var. nov.

Plate 97, figs. 18, 19; text-figs. 2*e–i*, 3, 9

1960 *Glyptograptus* cf. *austrodentatus*; Berry, p. 87, pl. 13, fig. 2, 3.

Diagnosis. Rhabdosome 1–1¼ cm. long, widening from an initial width of about 1·3 mm. at $th1^1$ to a maximum of 1·6–1·9 mm. Thecae numbering 5–6 in 5 mm. in more distal part of the rhabdosome, of the general type of *G. austrodentatus*, but with a prominent ventral apertural 'lip' (as in *G. shelvensis*), overlapping one-half proximally and somewhat more distally. Median septum complete, slightly or conspicuously undulating; proximal end with th1^1 and th1^2 subsymmetrically disposed, a prominent virgella, and delicate subapertural spines on th1^1 and th1^2.



TEXT-FIG. 9. *Glyptograptus austrodentatus americanus* var. nov. *a*, SM A53803, Marathon, Texas, obverse view of specimen before sectioning of proximal end. *b*, SM A23025a. *c*, SM A23024. *d*, SM A53801. *b–d*, From Shumardia Limestone (?), Point Levis, Quebec (T. C. Nicholas Coll.). All figures ×5 approx.

Holotype. G. cf. *austrodentatus*; Berry 1960, pl. 13, fig. 2, 3; Fort Pena formation, Marathon (XPM 20334).

Description. This variety differs from the typical form in its slightly larger rhabdosome, larger and fewer thecae, and more prominently developed ventral apertural 'lip'. The initial thecae, th1^1 and th1^2, tend to be relatively larger and less conspicuously symmetrical in their disposition than in *austrodentatus*, though the development is of streptoblastic type.

The development is known from an imperfect section series from the limestone material of Marathon, Texas. Crumbling of the encasing plaster resulted in the loss of nearly all sections below the level of the origin of th2^1, but the restoration shown in text-fig. 2 reveals a sufficiently close approximation to the Holm material from Öland. The initially upward growth and hood formation of th1^2, and the downward growth of the initial part of th2^1 are well displayed here and in the section series, text-fig. 3.

Occurrence. Two specimens used for sectioning, from the Fort Pena formation of Marathon, Texas.

Three specimens (two of immature rhabdosomes) from Levis, Quebec (T. C. Nicholas Coll., Sedgwick Museum). There is some doubt as to the horizons of these, but they are probably from the lower portion (D_1) of the *dentatus* Zone, and additional specimens from the Shumardia limestone (D_1) of Begins Hill have been collected by Dr. Cumming.

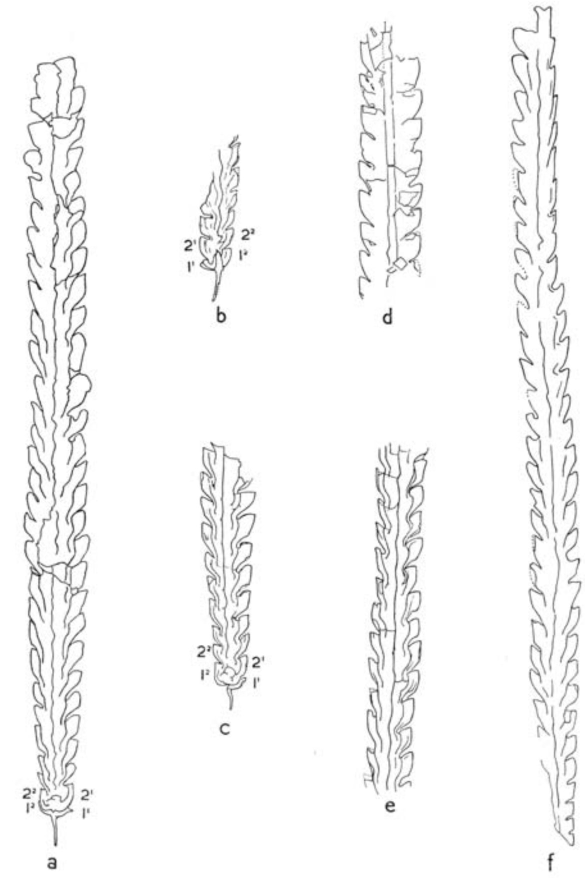
The *austrodentatus* from the Yukon (*T. ensiformis* and *I. gibberulus* Subzones of Jackson and Lenz 1962) seems most nearly related to this variety, but the rhabdosome is more slender and the apertural lip of the thecae is not so conspicuously shown.

A form possibly related to this has recently been described by Blake (1962) as *G. dentatus*, from what is probably the *D. hirundo* Zone of the Trondheim area.

Pseudoclimacograptus cumbrensis sp. nov.

Plate 96, figs. 7, 8; text-fig. 10

Diagnosis. Rhabdosome $2\frac{1}{2}$–3 cm. in length, widening from 1·2 or 1·3 mm. at th1^1 to a maximum of 1·8–2·0 mm., parallel-sided for the greater part of its length. Thecae 7 in the first 5 mm., 11–12 in 10 mm. distally, of climacograptid type but lacking pro-



TEXT-FIG. 10. *Pseudoclimacograptus cumbrensis* sp. nov. *a*, Holotype, latex cast of natural mould, SM A53044. *b*, Proximal end, obverse, latex cast of SM A18139. *c*, Proximal end, reverse, latex cast of SM A18133. *d*, Distal thecae, flattened, latex cast of SM A53041. *e*, Distal thecae in partial relief, latex cast of SM A18134. *f*, SM A18134. All specimens from Skiddaw Slates (? *D. hirundo* Zone), Bassenthwaite Sandbeds, Cumberland. ×5 approx.

nouncedly angular geniculation, and with gently convex supragenicular ventral wall; length about 2·2 mm., overlapping two-thirds. Development of streptoblastic type, giving a blunt proximal end (with strong virgella), but with thecal apertures alternating.

Holotype. SM A53044. Plate 97, fig. 7, text-fig. 10*a*; Skiddaw Slates, Bassenthwaite Sandbeds, Cumberland.

Description. This species shows considerable resemblance to *Ps. formosus* Mu and Lee in its thecal characters, but is an altogether larger rhabdosome.

Many specimens are preserved as natural moulds in strong relief and are best studied as latex casts.

The development is of streptoblastic type, and an inverted V-shaped swelling at the base of the median septum, separating the initial portions of $th3^1$ and $th3^2$, reveals that there must be an important downward-growing portion of $th2^1$. $Th1^1$ and $th1^2$ are not, however, symmetrically developed, and the thecae are in the main alternating throughout the rhabdosome. Mature thecae are over 2 mm. in length and overlap for two-thirds of their length. When undistorted, they are seen to be strongly sinuous; but the geniculation is not sharply angular and in some preservations (especially when completely flattened) may appear almost glyptograptid. The aperture is slightly introverted, producing what is in effect a slight ventral apertural lip, but it is doubtful whether this is due to the formation of any incomplete fuselli (cf. Jaanusson's figure, 1960, pl. iv, fig. 5, of *Ps. angulatus sebyensis*).

The median septum is somewhat undulating proximally, becoming straight distally. A stout virgula may project distally, and there is a strong virgella about 1 mm. in length.

Remarks. The species differs from Keller's *Pseudoclimacograptus romanovskyi* (probably *G. teretiusculus* zone) in its much greater thecal overlap, and probably (though this is difficult to determine from Keller's figures) in the characters of the proximal end. Hsü (1959) has described a variety of that species from, probably, Llanvirn strata under the name *sinicus*, but this is characterized by prominent basal spines on $th1^1$ and $th1^2$ and a gradually widening rhabdosome. In thecal characters and the nature of the proximal end, it comes nearest to Mu and Lee's *Ps. formosus*, from a comparable horizon, but the rhabdosome is two or three times as long and nearly twice as broad.

Occurrence. Skiddaw Slates—probably *D. hirundo* Zone—at Bassenthwaite Sandbeds, Cumberland. It is represented in Dr. Jackson's collections at Newcastle from the *D. hirundo* Zone of Ling How and Halls Fell.

Climacograptus cf. *biformis* Mu and Lee

Plate 96, fig. 6; text-fig. 11*a*

Cf. *Climacograptus biformis* Mu and Lee, 1958, p. 423, pl. v, figs. 1–5.

Remarks. This form is known from a single immature specimen and its counterpart (GSM, JR4140, 4141) from the Skiddaw Slates (? *D. hirundo* Zone) near Kirkland Church, Cumberland. It agrees in general character and in all dimensions with Mu and Lee's species from the *A. confertus* Zone (? = *bifidus*) of the Ningku Shale, except in possessing rather more numerous thecae (about 7 in 5 mm. compared with 11–12 in 10 mm. in the proximal region of *biformis*). The distal thecae of *Cl. biformis* become glyptograptid (hence the specific name) and there is a strong suggestion of this in the Skiddaw specimen, which was in fact originally identified as *G. dentatus*.

The proximal end suggests derivation from the *dentatus* group and this would appear to be the earliest true climacograptid. Its generic position in relation to *Diplograptus* s. str. is, however, somewhat uncertain.

Diplograptus ellesi sp. nov.

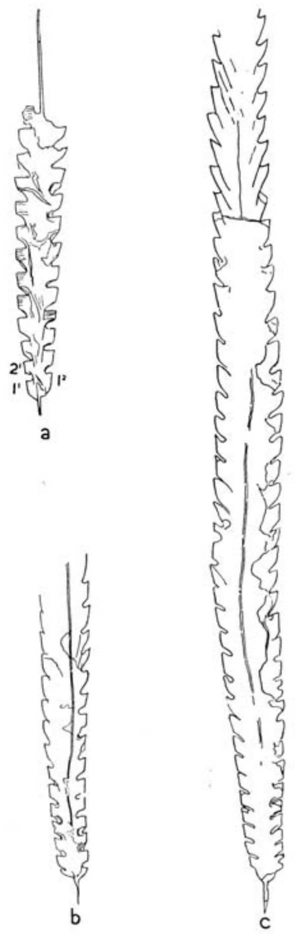
Plate 96, fig. 9; text-fig. 11*b*, *c*

Diagnosis. Mature rhabdosome about 3 cm. in length, widening from an initial width of 0·8–0·9 mm. at $th1^1$ to a maximum of 2·0–2·1 mm., thereafter typically narrowing again to about 1·8 mm. Thecae 7–8 in the first 5 mm., 12–13 in 10 mm. distally, overlapping about two-thirds their length; those at the proximal end are of amplexograptid type, with apertural excavations about one quarter the rhabdosome width and one-third the length of the free ventral wall; becoming glyptograptid distally. Periderm somewhat attenuated. There is a strong wiry virgula, commonly projecting well beyond the distal extremity, but the median septum is invisible. Virgella conspicuous.

Holotype. BMNH, Q1174. Plate 96, fig. 9, text-fig. 11*c*. Skiddaw Slates (*D. bifidus* Zone), Ellergill, near Milburn, Westmorland.

Description. The full-grown rhabdosome is some 3 cm. in length, widening steadily from a narrow but rounded proximal end (0·8–0·9 mm. at the level of the aperture of $th1^1$) to a maximum of 2·0–2·1 mm. Typically it narrows again slightly towards the distal end (1·7–1·8 mm.) giving it a distinctive, slightly fusiform shape. The periderm is evidently somewhat attenuated, so that shale specimens, strongly compressed, show traces of a wiry virgula throughout the length of the rhabdosome. No definite traces of a median septum have been discerned, but its presence is probable. The proximal end possesses a stout virgella with some indication of secondary cortical thickening.

The initial thecae appear to be small and are relatively inconspicuous; details of development are unknown. The proximal thecae are of amplexograptid type, with rounded and only slightly inclined apertural excavations, which are about one quarter the rhabdosome width and about one-third the length of the free ventral wall, and may show a slight selvage. The supragenicular wall is almost parallel to the rhabdosome axis and the apertural margins are gently concave in true profile. Distally the thecae become glyptograptid in character and have an overlap of nearly two-thirds. In much of the material, the transition from one type to the other occurs well within the first centimetre of rhabdosome length in the region of the twelfth thecal pair; but in



TEXT-FIG. 11. *a*, *Climacograptus* cf. *biformis* Mu and Lee, Skiddaw Slates (? *D. hirundo* Zone), Kirkland Church, Cumberland; GSM, JR4141. *b*, *c*, *Diplograptus ellesi* sp. nov., *D. bifidus* Zone, Ellergill, Milburn, Westmorland. *b*, SM A18129. *c*, Holotype, BMNH, Q1174. ×5 approx.

one specimen the amplexograptid thecae persist distally to about the eighteenth thecal pair.

Remarks. In general character this species resembles *D. decoratus* Harris and Keble. No specimen has yet been observed, however, with the distinctive heart-shaped vesicle at the distal termination of the virgula, all the dimensions of the rhabdosome are considerably smaller, and the thecae are more closely spaced. It may prove to be only varietally distinct; but to record it here under the name *decoratus* might lead to insecure stratigraphical correlations.

Occurrence. Skiddaw Slates—*D. bifidus* Zone; Ellergill and Thornship Beck, near Shap, Westmorland.

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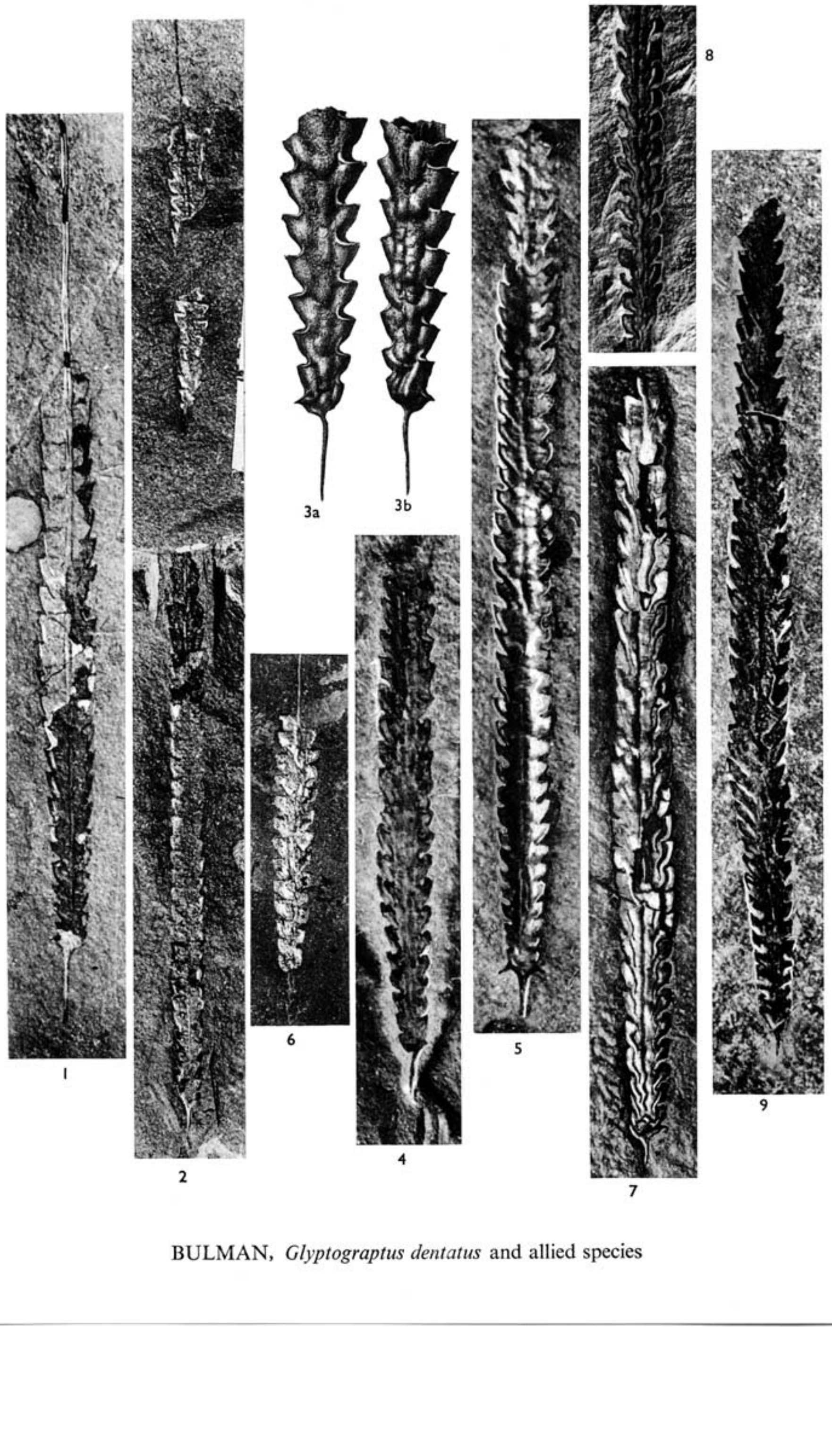
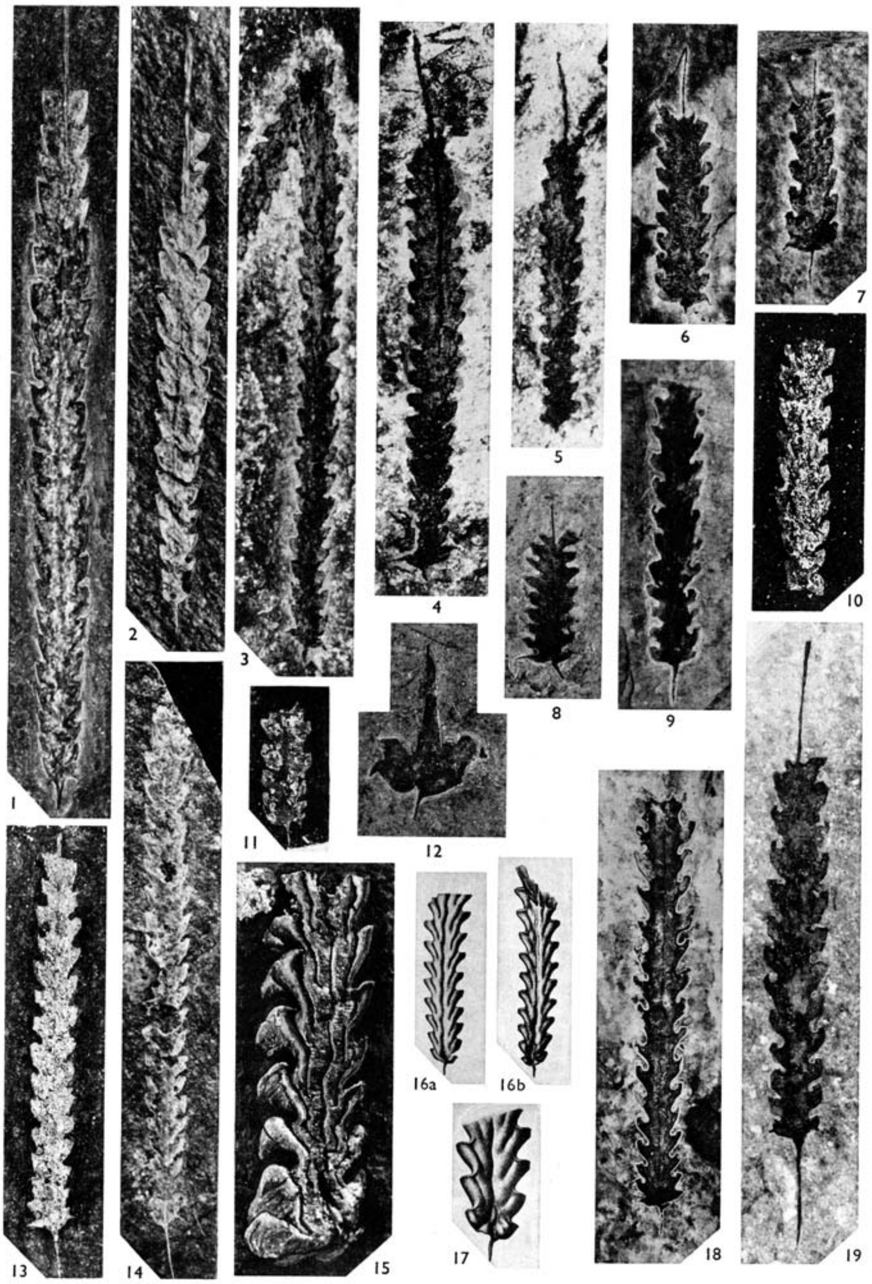


BULMAN, *Glyptograptus dentatus* and allied species



BULMAN, *Glyptograptus*