

# ORDOVICIAN GRAPTOLITES FROM THE GREAT PAXTON BOREHOLE, CAMBRIDGESHIRE

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**ABSTRACT.** The borehole penetrated beds with a lower Llanvirn fauna containing *Glyptograptus* cf. *denatus* (Brongniart), some other small and unidentified diplograptids, a *Paraulograptus?* sp., *Didymograptus pluto* sp. nov. (pendent), and a *Didymograptus* sp. (extensiform). The assemblage is quite different from others in Britain, but matches well with several from the Baltic and east European regions. *D. pluto* is described, with details of its proximal development, astogeny, and intrapopulation variation. Comparisons with *D. bifidus* (J. Hall) and *D. murchisoni* (Beck), which are species of quite different ages, show that convergent evolution strongly affected these pendent didymograptids. The different styles of proximal development (sicular shape, budding sequence) are the best means of unravelling these homeomorphies.

THE Llanvirn fauna of the Great Paxton borehole, 8 km south-west of Huntingdon in Cambridgeshire, England, is diverse and well preserved. It is of interest because it has the potential to provide clear evidence on the nature and development of the graptolites, trilobites, and brachiopods contained in the core. Additionally, as suggested in this paper and in Dewey *et al.* (1970), the sediments and the fauna were not related to deposits in the Welsh Basin or Skiddaw area of Britain, but were probably due to an extension of marine deposition eastwards from mainland Europe. Thus the fauna provides evidence bearing on the palaeogeography of the time.

Previous information on the fauna has been published by Stubblefield (1967) and Skevington (1973). In the former, only preliminary identifications of the graptolites and trilobites were listed. The more detailed account in Skevington (1973) attempted description of the fauna in terms of the existing taxonomy for pendent didymograptids. Unfortunately, that taxonomy was strictly typological, so that too-narrowly defined 'species' were distinguished within what is now known to be the intraspecific variation of a single pendent didymograptid species. The same study did not cover the highly important aspect of proximal development in the pendent species, and did not identify all the graptolite species in the core. The present paper gives attention to these problems and provides a full reassessment of the age and importance of the fauna.

## STRATIGRAPHY, AGE, AND PROVINCIAL RELATIONSHIPS

Stubblefield (1967) and Skevington (1973) have provided most of the necessary details of the location, stratigraphy, and palaeogeographical importance of the borehole. The Llanvirn shales young upwards through the core and are overlain unconformably by Liassic (Jurassic) strata. The top 0.5 m or so of Ordovician beds are bleached and deeply weathered; when unweathered they are grey, uncleaved shales and mudstones interbedded with pale micaceous sandstones and siltstones. The graptolite rhabdosomes are sometimes current-oriented parallel to the strike (150°; Skevington 1973). The core was discontinued after penetrating 27.7 m stratigraphic thickness of Llanvirn beds.

Skevington (1973) assigned the fauna to the upper Llanvirn *D. murchisoni* Zone, based largely on the identification of individuals in the fauna that could be matched in their stipe and thecal dimensions to the type specimens of *D. murchisoni* (Beck), *D. murchisoni* cf. *geminus* (Hisinger), *D. murchisoni speciosus* Ekström, *Glyptograptus* cf. *euglyphus* (Lapworth), and *Climacograptus pauperatus* Bulman. However, reidentification of all the material indicates that none of these forms is in fact present. Instead, the evidence now supports an early Llanvirn age assignment.

The several pendent didymograptid varieties identified by Skevington (1973) are now known to

belong to a single morphologically variable species—*D. pluto* sp. nov.—which is abundant throughout the core. Although outwardly this species shows a very close resemblance to the upper Llanvirn species *D. murchisoni* in the size and shape of its rhabdosome, it is quite different, particularly in its mode of proximal development. In this aspect, its most exact comparison is to the form described as '*Didymograptus* n. sp. b. aff. *D. minutus* Törnquist 1879' in Skevington (1965) from the very lowest beds of the lower Llanvirn '*D. bifidus* Zone' of Öland (Sweden). It is also similar in many of its dimensions to *D. pakrianus* Jaanusson (1960) from Pakri in Estonia, though there are some differences, and the proximal thecal development of *D. pakrianus* remains undescribed. *D. pluto* does not resemble any of the pendent species described from the Ordovician of Britain.

Further indications of an early Llanvirn age are derived from comparisons of the other species with some graptolite occurrences in the Baltic region and in Czechoslovakia. *Glyptograptus dentatus* is widespread in the lower Llanvirn (Bulman 1963; Skevington 1965, 1970) and the occurrence in the borehole of closely related material is suggestive of this level. Jaanusson (1960) recorded a form '*Didymograptus?* sp. C.' from the same beds as *D. pakrianus* at Pakri in Estonia, which is very nearly identical to the *Paraulograptus?* sp. now identified in the borehole. Although the graptolite fauna of the Pakri Beds has not in itself yielded a conclusive indication of age, the unit in which it occurs is regarded as early Llanvirn (Jaanusson 1960, p. 344, table 9). The genus *Paraulograptus* was first described from the lower Llanvirn *Corymbograptus retroflexus* Zone of Czechoslovakia (Bouček 1973). An extensiform didymograptid species closely comparable to such Arenig species as *D. formosus* Bulman (1936; Archer and Fortey 1974) also occurs in the borehole and lends further support to an early rather than late Llanvirn age. The unidentifiable diplograptids provide no further accurate age information.

From the above comments on correlation, it is clear that the fauna has strong provincial relationships with the Llanvirn faunas of the Baltic and east European regions. On the other hand, it is markedly different from the typical lower Llanvirn assemblages of Wales, Shropshire, and northern England. For instance, *D. artus* Elles and Wood, *D. nicholsoni*, and *G. dentatus* dominate those faunas but are absent or rare in the Great Paxton Borehole, where instead *D. pluto* and ?*Paraulograptus* sp. are dominant. Neither of these has previously been recorded in Britain.

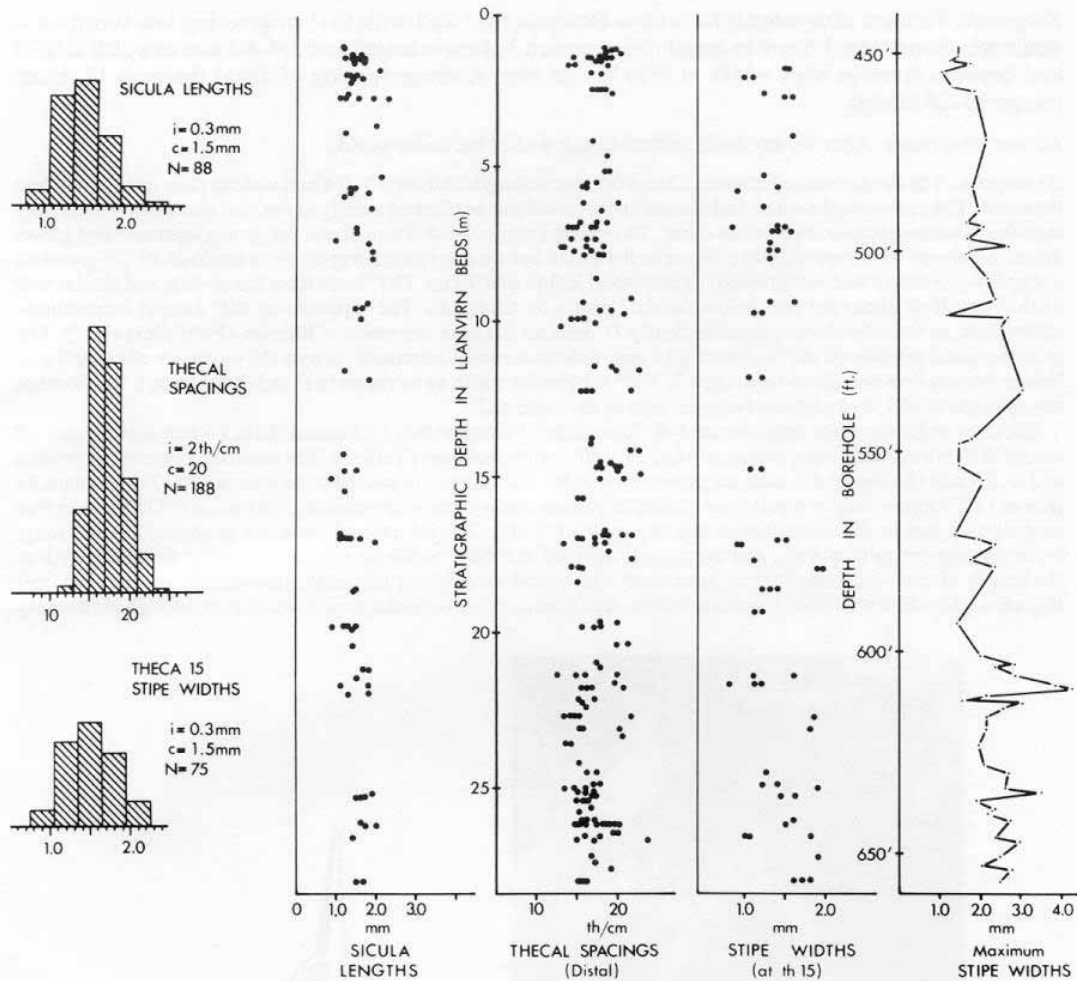
Thus the evidence suggests that the Cambridgeshire area in the Llanvirn was dominated by marine influences from mainland Europe, but was rather isolated from the faunas of Wales and neighbouring areas. Whether this was due to blocking by emergent areas or to large-scale facies control (? with the *D. pluto* fauna as a shallow water facies) is at present unknown.

#### SYSTEMATIC PALAEOLOGY

The morphological terms employed here are those of Bulman (1970). Several additional points need to be noted in connection with the biometric statistics. Measurements of sicula length were not taken from specimens with proximal cortical overgrowths. Proximal stipe divergence values were measured on dorsal margins of the stipes, directly adjacent to the sides of the siculae. Stipe widths were measured at 5-theca and not 5 mm intervals down the stipes, as has been more usual in past descriptions. This has been to ensure strictly homologous comparisons between those individuals and species with different thecal spacings. The characters 'distal stipe width' and 'stipe length' were measured on the full range of astogenetic growth stages and do not represent maximum values applicable only to the most mature stages of growth. Standard statistical parameters are abbreviated as: Mean ( $\bar{X}$ ), Sample size ( $N$ ), Maximum (max.), Minimum (min.), and Standard Deviation ( $\sigma$ ). The Variation Coefficient ( $V_c$ ) gives a dimensionless guide to the variability of a character and is the ratio  $S/\bar{X}$ . A rather more informal statistic reflecting the observed ranges of variation and which is employed in comparisons in a later section is termed the 'Range coefficient' ( $R_c$ ). It is equivalent to whichever is the larger of  $(X_{\max} - \bar{X})/\bar{X}$  and  $(\bar{X} - X_{\min})/\bar{X}$ .

Family DICHOGRAPTIDAE Lapworth, 1873  
Genus DIDYMOGRAPTUS M'Coy, 1851  
*Didymograptus pluto* sp. nov.

Text-figs. 2A, B, 3A-U, 4A-C



TEXT-FIG. 1. Biometric characters of *Didymograptus pluto* sp. nov. through the Great Paxton Borehole core. Depths down the borehole are recorded in feet below the surface (as originally logged), but a supplementary scale is also given to show the true (dip corrected) thicknesses in metres below the base of the overlying Jurassic. For the histograms  $N$  = number of measurements,  $i$  = class interval,  $c$  = centre point of one of the classes.

- cf. 1965 '*Didymograptus* n. sp. b. aff. *D. minutus* Törnquist, 1879' Skevington, p. 22, figs. 27-29.  
 1973 *Didymograptus acutus* Ekström, 1937; Skevington, p. 44, text-fig. 1a-c.  
 1973 *D. cf. acutus*; Skevington, p. 45, pl. 8, fig. 2; text-fig. 1d-g.  
 1973 *Didymograptus artus* Elles and Wood, 1901; Skevington, p. 46, text-fig. 2a-f.  
 1973 *D. cf. artus*; Skevington, p. 47, pl. 8, fig. 1; text-fig. 2g-j.  
 1973 *Didymograptus murchisoni* (Beck) 1839; Skevington, p. 47, pl. 8, figs. 3-5; text-fig. 3a.  
 1973 *D. murchisoni speciosus* Ekström, 1937; Skevington, p. 48, pl. 9, figs. 1-5; text-fig. 3b.  
 1973 *D. murchisoni cf. geminus* (Hisinger) 1840; Skevington, p. 49, pl. 8, fig. 6; text-fig. 3c.

*Holotype*. By8204 (text-fig. 3G herein and pl. 8, fig. 2 of Skevington 1973), from the 410 ft level of the borehole.

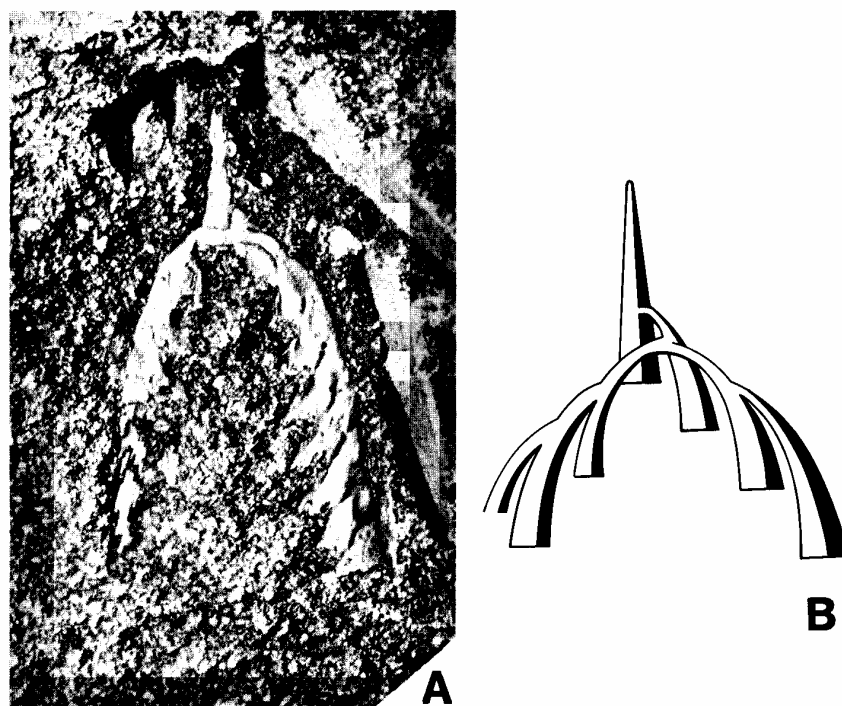
*Material*. Over 220 specimens (within the bracket of numbers By8110-9209; Institute of Geological Sciences, London); they included those described and figured by Skevington (1973).

**Diagnosis.** Pendent didymograptid with a dicalycal  $th1^2$  and with  $th1^1$  originating low down on a sicula which averages 1.5 mm in length. Stipes reach 3–4 cm in length and 2.0–4.3 mm in width at  $th30$  and beyond. Average stipe width at  $th10$  is 1.25 mm. Average spacing of distal thecae is 17 th/cm (range 13–23 th/cm).

**Derivation of name.** After the mythical ancient Greek god of the underworld.

**Description.** The siculae range between 2.3 and 0.9 mm in length and are 0.3–0.4 mm wide at their apertures when flattened. They are straight-sided and conical in form and are positioned axially in the rhabdosomes without any significant leaning to one stipe or the other.  $Th1^1$  buds from c. 0.4–0.5 mm above the sicular aperture and grows down, confluent with, but slightly oblique to the sicula before diverging abruptly at an angle of  $45^\circ$ . It grows to about 0.4–0.5 mm in width (flattened) over its total length of 0.7 mm.  $Th1^2$  buds from the reverse and sicular side of  $th1^1$  at a level about 0.3 mm below the  $th1^1$  origin on the sicula.  $Th2^1$  appears on  $th1^2$  almost immediately afterwards, so that the development is clearly *D. minutus* Stage in the sense of Bulman (1970) (text-fig. 2). The crossing canal portion of  $th1^2$  is about 0.13 mm wide and runs horizontally across the sicula for about 0.3 mm before turning downwards to form stipe 2.  $Th2^1$  is a similar width as it crosses  $th1^1$  to initiate stipe 1. The level of the aperture of  $th1^2$  lies midway between that of  $th1^1$  and  $th2^1$ .

The stipe widths average approximately 0.7 mm at  $th1$ , 1.0 mm at  $th5$ , 1.25 mm at  $th10$ , 1.5 mm at  $th15$ , and 1.9 mm at  $th25$  but typically vary within a range of  $\pm 40\%$  of these means (Table 1). The usual maximum stipe widths of 2.0–3.0 mm (but up to 4.3 mm) are attained by  $th30$ . The thecae are spaced at an average of 17 th/cm distally (range 13–23 th/cm) but in most cases are slightly more closely spaced proximally.  $Th1$  has a 0.43 mm long free ventral wall, but in the distal thecae this may reach 0.7 mm. The intertheical septa are generally 2.0 mm long, 0.5 mm apart (when flattened), and are usually inclined at  $30$ – $50^\circ$  to the dorsal margins of the stipes. Growth in the length of each individual theca apparently continued throughout astogeny, particularly on the proximal thecae, so that stipe widths of 1.0 mm are often recorded at  $th1$ – $2$  on mature individuals even though in the early



TEXT-FIG. 2. *Didymograptus pluto* sp. nov. A, specimen By9055, preserved in partial relief, showing proximal development,  $\times 12$ . B, diagram of development.

stages this width is only 0.5–0.7 mm. The more mature individuals may also bear a proximal cortical membrane overgrowth over the siculae and early thecae (text-figs. 3a–d).

The stipe divergences are usually 80–110° proximally but tend to become sub-parallel distally (range: –10° to 70°).

*Discussion.* Table 1 and text-fig. 1 show that the entire collection of pendent didymograptids from the borehole represents successive populations of one slowly evolving species. The frequency distributions for the biometric characters are all unimodal. The amount of change in these characters through the core is negligible for almost all characters.

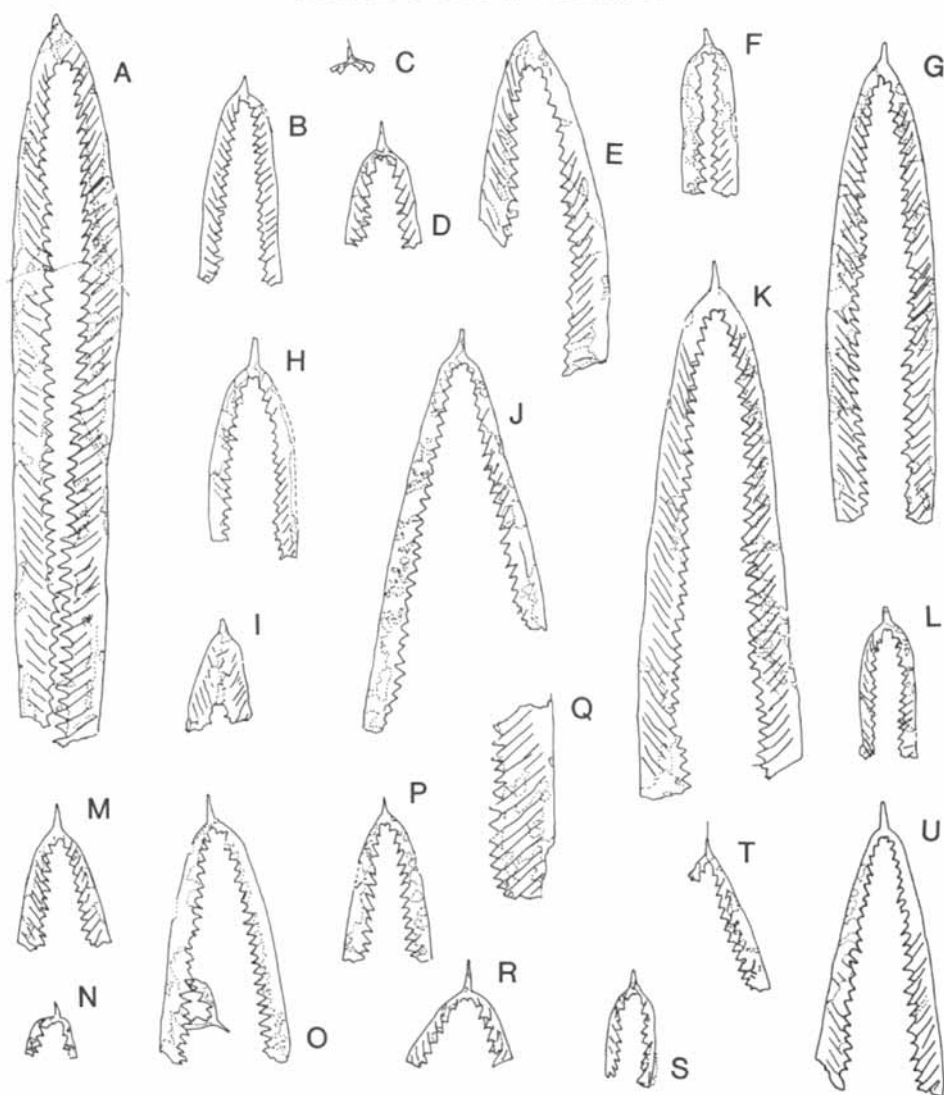
TABLE 1. Biometric statistics of *Didymograptus pluto*. All measurements in millimetres unless otherwise indicated.

Statistics:	<i>N</i>	$\bar{X}$	<i>S</i>	$V_c$ (%)	max.	min.	$R_c$ (%)
Characters:							
Sicula lengths	87	1.51	0.28	19	2.3	0.93	52
Theca 1 stipe widths	187	0.66	0.17	25	1.12	0.4	70
" 5 " "	178	1.01	0.19	19	1.84	0.6	82
" 10 " "	132	1.26	0.22	17	1.8	0.8	42
" 15 " "	74	1.49	0.28	19	2.05	0.9	39
" 20 " "	40	1.66	0.33	20	2.2	1.2	32
" 25 " "	13	1.79	0.18	10	2.4	1.5	34
Distal stipe widths	271	1.50	0.64	43	4.3	0.45	187
Proximal thecae/cm	154	18.6	2.04	11	23.8	12.8	31
Distal thecae/cm	188	17.2	2.2	13	22.7	13.2	32
Proximal stipe divergences	68	92.4°	22.5°	24	200°	35°	116
Distal stipe divergences	67	17.3°	28.6°	24	160°	–8°	825
Stipe lengths	132	12.3	9.8	80	43.0	3.0	250
Distal thecal inclinations	107	43.3°	8.5°	20	65°	10°	77

The exceptions are the distal and the 15 stipe widths, which both decrease upwards through the core. Two samples of ten specimens each show a difference in average distal widths of between 2.5 mm at the bottom of the core, and 1.6 mm at the top. The effect is certainly statistically significant, but it correlates with no other changes of morphology and is not regarded as important above the subspecies level. The fact that the size decreases upwards in *D. pluto* is important because it is in contrast to the usual observation of size increases in pendent didymograptid evolution. Unfortunately, it is not known whether the size decreases were directly the result of environmental changes upwards through the core, or whether they involved real (genetic-based) evolution within the species.

The pendent didymograptid taxa that were recognized in the same collection by Skevington (1965) were therefore morphotypes (see George 1971)—narrow, typologically defined, and conspecific varieties. Summed together they represent the normal range of intraspecific (genetic, astogenetic, environmental, and preservational) variations. Thus, the '*D. artus*' variety recognized by Skevington embraced the small (i.e. young) astogenetic growth stages of *D. pluto* that have high values of thecae/cm, while the form '*D. acutus*' represented the same, but with lower numbers of thecae/cm. The varieties '*D. murchisoni murchisoni*' and '*D. murchisoni speciosus*' referred to a similar variation in thecal spacings amongst the mature growth stages. Individuals in which the stipes widened very noticeably were assigned to '*D. murchisoni cf. geminus*'. All these and their accompanying 'cf.' varieties are now placed within the morphological range of *D. pluto*.

The proximal development of the species is shown clearly in two pyritized specimens (e.g. text-fig. 2) and in a few specimens at the top of the core, which were made semi-transparent by weathering prior to the Jurassic. It is comparable in nearly every way to the development of the '*Didymograptus*



TEXT-FIG. 3. *Didymograptus pluto* sp. nov., Great Paxton Borehole; representative sample of specimens showing the full width of the intraspecific variation, all  $\times 3.0$ . A, By8669; B, By9130; C, By8117; D, By9055; E, By8921; F, By8291; G, By8204; H, By8267; I, By8985; J, By8327; K, By9093; L, By8549; M, By8127; N, By8231; O, By8911; P, By8144; Q, By8911; R, By8224; S, By8211; T, By8198; U, By8205.

n. sp. b. aff. *D. minutus* Törnquist 1879' of Skevington (1965) and its synonym, the '*D. minutus* MUT. Holm' of Bulman (1936, 1970), which together should now be regarded as representing a small-sized subspecies of *D. pluto*. The similarities of basic developmental features and of dimensional aspects (like sicula length, crossing canal widths, thecal lengths, etc.) at the proximal ends means that at their early growth stages they are virtually indistinguishable.

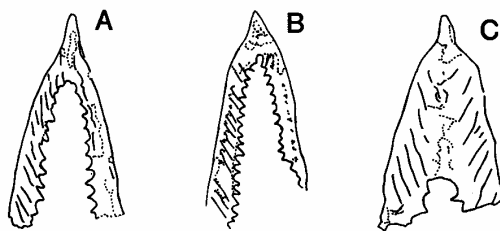
*D. pluto* is not closely related to the original *D. minutus* Törnquist from the Upper Arenig of Sweden. Skoglund (p. 25 in Skevington 1965) reported that the true *D. minutus* has a dicalycal th<sup>1</sup> and

Skevington (1965) noted that its sicula is different from that in his '*D. n. sp. b. aff. minutus* Törnquist 1879', which as noted above is identical to *D. pluto* at its proximal end.

*D. pluto* may be closely related to the following species:

(a) *D. pakrianus* Jaanusson, 1960 (lower Llanvirn of Estonia). This is very similar in its general dimensions and overall morphology (e.g. in the presence of proximal cortical overgrowths at maturity). The thecal spacings, however, range somewhat lower than in *D. pluto* (15.0–17.5 th/cm), and the rhabdosomes have a smaller size at full maturity. Unfortunately the proximal development of the species is unknown.

(b) *D. parindentus* Berry, 1960 (upper Arenig, Texas) resembles many of the younger growth stages of *D. pluto*, most markedly in overall shape and size, and in the shape and disposition of the sicula. The only described specimens of *D. parindentus* are flattened and the proximal development is unknown.



TEXT-FIG. 4. Proximal ends of mature growth stages of *Didymograptus pluto* sp. nov., illustrating the cortical overgrowths and thecal enlargement relative to young growth stages. A, By8922; B, By9181; C, By8985;  $\times 4$ .

Although certain specimens of *D. pluto* may be compared with collections of the following species on the basis of resemblances in a selection of characters, they are really quite different.

(a) *D. murchisoni* is similar in sicular size and rhabdosomal shape and size, and both develop proximal cortical overgrowths at maturity. *D. murchisoni*, however, has a wider thecal spacing (average 14.3 th/cm for topotypes) and  $th1^1$  is dicalycal (text-fig. 6B).

(b) *D. artus* Elles and Wood, 1901 also develops proximal overgrowths and has broadly similar thecal spacings (15–16 th/cm) but rarely reaches such great sizes as *D. pluto*. Like *D. murchisoni* it has a dicalycal  $th1^1$  (unpublished work by the author).

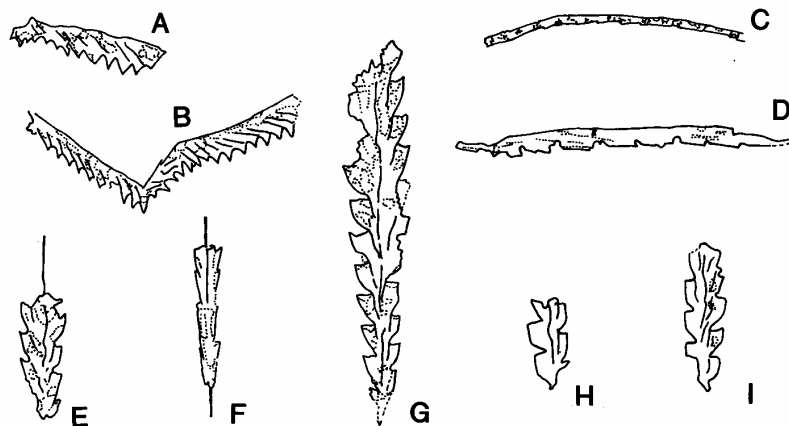
(c) *D. bifidus* (Hall)—as shown by collections from the type area of Quebec, Canada (e.g. SM A17307–8 Sedgwick Museum, Cambridge)—has similar stipe width and thecal spacing values to *D. pluto* and has a dicalycal  $th1^2$ . It differs in the rather short and squat shape of the sicula, and the high (probably prosicular) origin of  $th1^1$  from the sicula. Stipe divergences are significantly higher, especially proximally.

#### NOTES ON THE REMAINDER OF THE FAUNA

The extensiform didymograptid is a new discovery in the core. The material comprises just one proximal end and a distal stipe fragment (483 and 469 ft levels). It has a 1.3 mm long sicula with little supradorsal projection. In this it greatly resembles *D. cypselo* Archer and Fortey (1974). The thecae are spaced at 13.3 th/cm proximally but at 11 th/cm on the distal fragment, where the stipe width reaches 1.4 mm. The stipes are declined proximally and enclose about 160°. The material is too

limited for positive identification but a certain overall similarity to the form '*Expansograptus hudlicensis*' Bouček (1973) should be noted.

Little can be added to the description in Skevington (1973, text-figs. 3d-f) of the unusual fragile-stiped aulograptid that was labelled then as '*Didymograptus?* sp.' and '*Aulograptus?* sp.' These varieties represent preservational modes of the one species. The stipes are long, very thin, and apparently extensiform, though in the absence of specimens with a proximal end this is difficult to verify. The species is obviously closely related to the '*Didymograptus?* sp. C.' of Jaanusson (1960), as Skevington (1973) recognized. Bouček (1973) more recently described another similar form from Czechoslovakia as *Paraulograptus*. The type species, *P. expectatus* Bouček, has thin, fragile extensiform stipes with aulograptid thecae and obviously represents the same type of graptolite as the Great Paxton borehole species, which, accordingly, is now identified as '*Paraulograptus?* sp.' Imperfect material of *Paraulograptus* like this is distinguished from collections of *Aulograptus* by being thinner and by the length of the stipes. The more robust stipes of *Aulograptus* appear to have been less susceptible to fragmentation and collections always contain a large proportion of intact pendent rhabdosomes.



TEXT-FIG. 5. A, B, *Didymograptus* sp. (extensiform); A, By8282; B, By8237. C, D, *Paraulograptus?* sp.; C, By8174; D, By8567. E-F, H-I, diplograptids (unidentified); E, By8126; F, By8657; H, I, By9001. G, *Glyptograptus* cf. *dentatus* (Brongniart), By8122. All  $\times 8$  except A, which is  $\times 4$ .

Diplograptids occur sparsely through almost the entire length of the core at levels between 449 and 651 ft. However, few are identifiable. Most are fragmentary, preserved in subscalariform views, or are at too young a growth stage for effective identification (text-fig. 5F, H, I). One large specimen, though, is identified as *Glyptograptus* cf. *dentatus*. Its salient characters are: maximum length 9 mm; thecal spacings *c.* 10 th/cm proximally and 15 th/cm distally; maximum stipe width 1.6 mm (flattened). The proximal ends are strongly tapered and only 0.7 mm wide at th1. The sole ornamentation is a short virgella; the median septum is gently and sinuously curved. The thecae have quite convex profiles and wide apertural excavations. The intertheal septa are only short and simple and originate at a level above the previous thecal aperture. The differences between this form and *G. dentatus* proper include its closer thecal spacings, lack of apertural spines on th1<sup>1</sup>, and smaller overall size (though this may be an artefact of the small number of specimens available or of the local environment at the time of deposition). The form may be closely related to the *G. dentatus* recorded from Öland (Sweden) by Skevington (1965).



## DISCUSSION

*Intrapopulation variation.* Case studies of the intrapopulation variation in graptolite species have been rare. The Great Paxton borehole collection provides an excellent opportunity to illustrate this important phenomenon in a dichograptid graptolite.

The collection contains over 200 well-preserved individuals of *D. pluto* representing all stages of astogenetic growth. It has been pooled from a number of small collections of up to eleven specimens per 30 cm length of core. This pooling will have certain effects on the statistics and their interpretation. For instance, because of the changes in some values through the 25 m stratigraphical range, the variations shown in Table 1 are really intraspecific (rather than intrapopulation). This is not an important distinction for most characters (i.e. all except for the distal stipe width) because for most characters the upwards changes were negligible and the scatter of values in any one population is roughly equivalent to the scatter observed in the whole sample. Pooling will have the fortunate effect of smoothing out short-term (i.e. seasonal) variations in the species.

Table 1 sets out the primary biometric statistics for the collection. It shows that intrapopulation variations of the order of  $\pm 0.5$  mm in the sicula lengths, of  $\pm 4-5$  th/cm in the thecal spacings, of up to  $140^\circ$  in distal stipe divergences, and of up to 4 cm in stipe lengths occur, and should perhaps be expected more generally in didymograptid species.

The variations can also be expressed in terms of Variation Coefficients—useful parameters for comparing between species and characters (Simpson *et al.* 1960). For most characters they lie in the range 10–30% (e.g. for thecal spacings, sicula lengths, and stipe widths beyond th5). In such cases the low variability is usually confirmed by the small total ranges, and the 'Range coefficients' are seen to measure about 25–40% of the mean values. Characters with this low type of variability will be the most useful in species diagnosis. Basic features of the proximal development have a very low variability (are virtually constant) and will also be highly useful.

In contrast, characters like th1, th5, and maximum stipe widths, the stipe divergences and stipe lengths have very large amounts of variation indeed ( $V_e \geq 20-80\%$ ,  $R_e \geq 30-200\%$ ). They must be of little value in discriminating between species.

Intrapopulation variations in graptolites stem from a variety of causes which act unequally on the characters. Included amongst the causes are natural genetic variations within the gene pool, astogenetic growth, environmental (ecophenotypic) effects imposed during life, and preservational vagaries. The intrapopulation variations shown by *D. pluto* (Table 1) are an illustration. The characters with the smallest degrees of variation, such as the thecal spacings, sicula lengths, and stipe widths beyond th5, probably had their variations determined largely by genetic processes. Because rhabdosomes cannot undergo changes in length during diagenetic compression, thecal spacings and sicula lengths are immune from preservational variations, except perhaps for breakages prior to burial.

Most other characters have strong superimposed preservational variations. The very great change in overall size from the sicula stage up to the th50 stage in *D. pluto* accounts for the observed wide variations in stipe lengths and maximum stipe widths. Cortical thickening and continued growth of the thecae at the proximal end during astogeny probably accounts for the relatively high variabilities observed in the th1 and th5 stipe widths. A preservational phenomenon that will strongly affect the stipe widths beyond th5 and the thecal inclinations is the flattening of the stipes when they are caught in a variety of orientations from profile to scalariform during burial. This will induce wide variations in stipe widths and thecal inclinations. Finally, the chance factors involved when rhabdosomes settle into the sediment will strongly affect the measurements of the distal stipe divergences.

*Morphotypes.* Similar variations to those found in *D. pluto* are predicted to occur in the majority of species-collections of pendent didymograptids and other dichograptids. Thus, it is of no use describing collections of these graptolites in terms of morphotypes with very constricted ranges of variation (fractions of the real intrapopulation variation). Such taxa—like those in Skevington (1973)—will have no natural genetic or phylogenetic significance.

It is instructive to look at the narrowness of the variation that has been allowed in morphotypes, in comparison to actual intrapopulation variations. This can now be done in the case of the morphotypes of Skevington (1973), which are covered by the ranges of variation in *D. pluto*. Obviously the morphotypes constitute narrow and artificial divisions of the real species.

	Skevington morphotypes	<i>D. pluto</i> collection
Thecae/cm	± 2-3	± 4.0-5.8
Stipe widths	± 0.3-0.5 mm	± 0.7-1.2 mm
Max. stipe widths	c. 1.5 mm	c. 4.0 mm
Distal stipe divergences	± 20-30°	-25°-+140°
Stipe lengths	c. 12 mm	c. 40 mm

Unfortunately the use of narrow morphotypes is traditional in pendent didymograptid systematics. Many well-known taxa in Elles and Wood (1901-18), Bulman (1931), Ekström (1937), Decker (1944), Ruedemann (1947), Lemon and Cranswick (1956), Berry (1964, 1970), and Bouček (1973) are morphotypes that have been identified only by comparisons with one or a few type specimens. While the taxa of these papers may be familiar, in fact the characteristics of their populations are almost completely unknown. A conversion to population-defined units will be required before much progress can be expected in understanding the stratigraphical record of the pendent didymograptids.

*Evolution and biostratigraphy.* It is a widely held belief that the pendent didymograptid group was highly conservative in its evolution (Bulman 1958, p. 116; Bergström and Cooper 1973, p. 335). This view is incorrect. The faunas at separate levels do appear superficially the same in terms of stipe dimensions and thecal spacings, but this was probably due to convergent evolution producing repeated homeomorphs in stipe and thecal dimensions. In contrast, styles of proximal thecal development appear to be characteristic of separate groups of species which have restricted stratigraphical ranges (see below). This feature, and the complexity of the patterns of proximal development (which makes it unlikely that they were affected by convergent evolution), both suggest that the proximal end structure of these graptolites can be used very effectively in outlining the true lines of descent in the group.

Here the principle is used to illustrate the convergences that affected *D. pluto*, *D. purchisoni*, and also *D. bifidus*.

First, it is observed that the three species have very different modes of proximal development. Given the importance of this character for taxonomy within the group, this suggests that all three were not closely related—in spite of their similarities (convergences) in thecal and stipe dimensions.

The developmental characters (see text-figs. 2 and 6) are as follows:

(a) *D. bifidus* has a high point of origin (? from prosicula) for th1<sup>1</sup> from the sicula, th1<sup>2</sup> is dicalycal, and the sicula is usually short, inflated, and paired to some extent with the th1<sup>1</sup>.

(b) *D. pluto* has a low origin for th1<sup>1</sup> from a long, straight-sided, and isolated (unpaired) sicula; th1<sup>2</sup> is dicalycal.

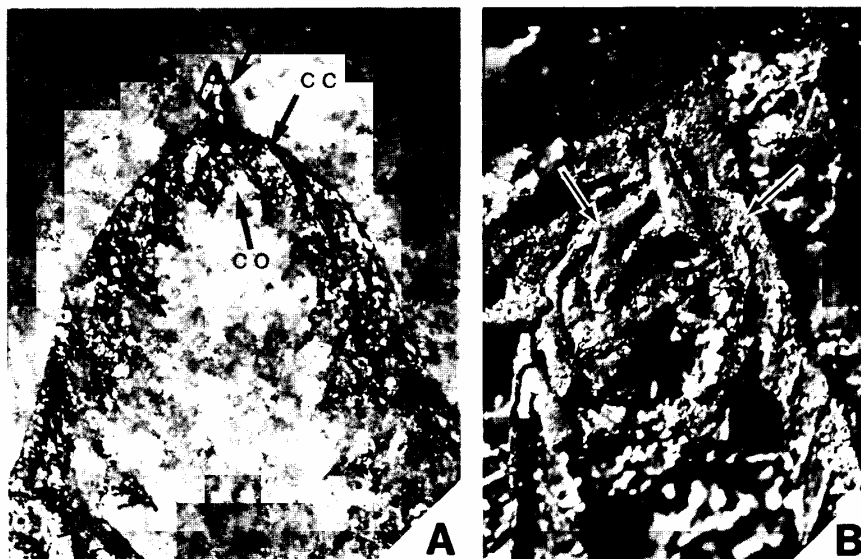
(c) *D. purchisoni* has a low origin for th1<sup>1</sup> from a long and isolated (unpaired) sicula, and th1<sup>1</sup> is dicalycal.

Work in progress by the author indicates that each species represents one of three major subdivisions of the pendent didymograptid group. The subdivisions may have been related or derived independently from other dichograptids, but in any case they have a clear pattern of stratigraphic occurrence:

Group (a) lower to upper Arenig; the *D. bifidus* from Quebec is lower Arenig and occurs with *Tetragraptus fruticosus* (Hall).

Group (b) ?upper Arenig to lower Llanvirn; *D. pluto* is lower Llanvirn.

Group (c) upper Arenig to upper Llanvirn; *D. purchisoni* is upper Llanvirn.



TEXT-FIG. 6. A, *Didymograptus bifidus* (J. Hall), lower Arenig, 'Point Levis, Quebec', Canada; SM A13703-8, preserved in partial relief, showing proximal development; note crossing canal (CC) leading to  $th2^1$  passing reverse side of  $th1^1$ , and slight cortical overgrowth (CO) between the sicula and  $th1^1$ ;  $th1^1$  originates at the level marked 'TO'. B, *Didymograptus murchisoni* (Beck), upper Llanvirn, Abereiddi Bay, Dyfed, Wales; SM A24630, preserved undeformed and in full relief inside a pyrite nodule; arrows point to origins of  $th1^2$ , and  $th2^1$  (note traces of interthecal septa). Both  $\times 12$ .

These ranges support the arguments which maintain modes of proximal development as the prime means of separating lines of descent in the pendent didymograptid group. Thecal, stipe, and general rhabdosomal dimensions are of no use for this purpose as they suffered repeated instances of evolutionary convergence. This, and a reliance on such dimensions in the identification of species, are what have made the biostratigraphy of the group so difficult.

The extent of convergence in rhabdosomal form that can be shown by unrelated species of different ages is illustrated in Table 2. This shows that for *D. bifidus*, *D. pluto*, and *D. murchisoni*, ranges of intrapopulation variation in stipe width, stipe length, stipe divergence, thecal spacing, and even sicula length overlap enormously. This is a clear case of homeomorphy (convergence) between unrelated and age-separated species.

The result of this overlap is that rhabdosomes looking very much like typical *D. murchisoni* are found commonly in collections of *D. pluto* (cf. pl. 3, figs. 1-3 in Elles and Wood (1901-18) with text-figs. 3A, G, K herein). It was precisely this convergence in general form which permitted Skevington (1973) to misidentify some individuals of *D. pluto* with *D. murchisoni*—in spite of the great differences at the proximal ends.

The convergences between *D. Pluto* and *D. bifidus* are at the stage of the younger rhabdosomes and are concerned more with thecal spacings. Thus, a morphotype which has been confused and identified in collections of both species is '*D. artus*' (e.g. Skevington 1973; Berry 1970). The real *D. artus* is a lower Llanvirn species and is different from *D. bifidus* and *D. pluto* in—amongst other things—its proximal development. Reports of a very long stratigraphical duration (Arenig-Llanvirn) for *D. artus* are wrong and are based on the identification of homeomorphs similar in their

TABLE 2. Comparison of the biometric characters of *Didymograptus bifidus*, *D. pluto*, and *D. murchisoni*. All measurements are in millimetres unless otherwise stated. Details of collections of *D. bifidus* and *D. murchisoni* are from unpublished work by the author.

Species:	<i>D. bifidus</i> (Hall)	<i>D. pluto</i> sp. nov.	<i>D. murchisoni</i> (Beck)
Horizon:	Lower Arenig	Lower Llanvirn	Upper Llanvirn
Material:	SM A13707-8	By8110-9209	GSM 6820 b
Number of specimens	8	220	35
Sicula lengths	1.3-1.7	0.93-2.3	1.4-1.7
Theca 10 stipe widths	1.9-2.5	0.8-1.8	1.3-2.0
Distal stipe widths	2.1-3.7	1.5-4.3	2.0-3.4
Distal thecae/cm	14.3-16.6	12.8-23.8	12.5-16.7
Proximal stipe divergences	99°-122°	35°-116°	72°-119°
Distal stipe divergences	39°-50°	-8°-160°	-10°-13°
Maximum stipe length	30	43	4
Localities	'Point Levis, Quebec, Canada.'	Great Paxton Borehole, Cambridgeshire. (Topotypes)	Gelli Hill, Builth Wells, Wales. (Type-slab)

stipe and thecal dimensions to the holotype specimen of '*D. artus*' in a range of faunas at different levels.

#### CONCLUSIONS

Phylogenetic and biostratigraphical studies of pendent didymograptid faunas are likely to fail or err badly unless (1) diagnostic characters of the species are determined with reference to their intraspecific variation, and (2) attention is given to the styles of proximal development. In cases where this is not practised, confusion will develop between unrelated homeomorphs of different ages and artificial taxa (morphotype varieties) will be diagnosed on characters of exceptionally wide intrapopulation variability.

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