Atlantic Geology

ATLANTIC GEOLOGY

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Willams, S. H. (1990). An Arenig graptolite from Bell Island, eastern Newfoundland - its biostratigraphic and paleogeographic significance. *Atlantic Geology*, *26*(1), 43–55.

Résumé de l'article

Un intervalle de siltites et de shales gris fence" au sein du Membre de Youngsters Gulch dans la Formation de Powers Steps (base du Groupe de Wabana) sur l'Oe Bell (Terre-Neuve orientale) a livr£ un assemblage monospecifique de graptolites appartenant au taxon Didymograptus (sensu lato) simulans Elks and Wood. Jusqu'a present, on n'avait document^ la presence de cette espece qu'en Grande-Bretagne et en Boheme, avec des representants possibles en Chine. Le tout corrobore la situation paleogeographique de Terre-Neuve durant l'Odovicien telle qu'admise courammenL La presence de D. (s.l.) simulans permet une correlation biostratigraphique exacte entre la Formation de Powers Steps et les unites equivalences en Amerique du Nord et en Europe. La formation date du dlbut ou du milieu de 1'Arenig, ce qui Iquivaut au Lit 11 du Groupe de Cow Head (Terre-Neuve occidentale), tune partk des zones ID. deflexus ou D. nitidus (Angleterre septentrionak),ainsiqu'k la portion inferieure de la Serie d* Arenig a Arennig Fawr (Pays de Galles septentrional).

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An Arenig graptolite from Bell Island, eastern Newfoundland - its biostratigraphic and paleogeographic significance

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An interval of dark grey silts and shales within the Youngsters Gulch Member of the Powers Steps Formation (basal Wabana Group) on Bell Island, eastern Newfoundland yields a monospecific graptolite assemblage consisting of *Didymograptus* (sensu lato) *simulans* Elles and Wood. This species has hitherto been recorded only from Great Britain and Bohemia, with possible specimens from China, thus lending support to the currently accepted paleogeographic reconstruction of Newfoundland in the Ordovician. The occurrence of *D.* (s.l.) *simulans* permits accurate biostratigraphic correlation of the Powers Steps Formation with equivalent North American and European sequences. The formation is of early/middle Arenig age, equivalent to Bed 11 of the Cow Head Group of western Newfoundland, to part of the *D. deflexus* or *D. nitidus* zones of northern England and to the lower part of the Arenig Series of Arennig Fawr, North Wales.

Un intervalle de siltites et de shales gris foncé au sein du Membre de Youngsters Gulch dans la Formation de Powers Steps (base du Groupe de Wabana) sur l'île Bell (Terre-Neuve orientale) a livré un assemblage monospécifique de graptolites appartenant au taxon *Didymograptus* (sensu lato) *simulans* Elles and Wood. Jusqu'à présent, on n'avait documenté la présence de cette espèce qu'en Grande-Bretagne et en Bohême, avec des représentants possibles en Chine. Le tout corrobore la situation paléogéographique de Terre-Neuve durant l'Ordovicien telle qu'admise couramment. La présence de *D.* (s.l.) *simulans* permet une corrélation biostratigraphique exacte entre la Formation de Powers Steps et les unités équivalentes en Amérique du Nord et en Europe. La formation date du début ou du milieu de l'Arenig, ce qui équivaut au Lit 11 du Groupe de Cow Head (Terre-Neuve occidentale), à une partie des zones à *D. deflexus* ou *D. nitidus* (Angleterre septentrionale), ainsi qu'à la portion inférieure de la Série d'Arenig à Arennig Fawr (Pays de Galles septentrional).

[Traduit par le journal]

INTRODUCTION

The stratigraphic succession of Bell Island, some 18 km west of St. John's, eastern Newfoundland (Fig. 1) comprises a gently dipping sequence of Ordovician deltaic and shallow marine siliciclastic and ironstone deposits, considered to have been formed when the Avalon Peninsula was part of a microcontinent "Avalonia", which was separate from Laurentia prior to the closure of Iapetus. The rich oolitic hematite of the Bell Island Group was an important source of iron ore during the earlier part of this century, mining operations having closed down in 1966. The first detailed description of the stratigraphy was published by Van Ingen in 1914, since which time a number of authors have discussed aspects of the sedimentology, stratigraphy and origin of the iron ore deposits. Ranger *et al.* (1984) proposed the lithostratigraphic classification currently in use; shoreline sediments assigned to the Upper Cambrian to Lower Ordovician Bell Island Group are overlain by somewhat deeper deltaic and shallow marine deposits of the Arenig Wabana Group on the north-western part of the island. Full details regarding stratigra-
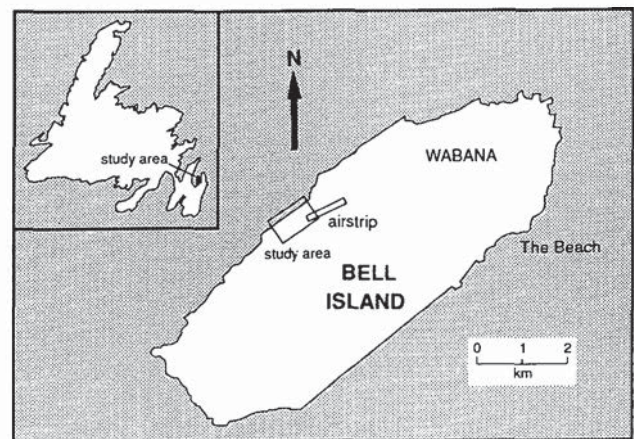

Fig. 1. Map of Bell Island and Newfoundland (inset), showing location of study area.

phy and depositional environments have been given recently by King *et al.* (1988) and Pickerill *et al.* (1988).

BIOSTRATIGRAPHY AND CORRELATION

Macrofossils are comparatively rare on Bell Island, although inarticulate brachiopods do occur sporadically throughout the less bioturbated intervals, together with occasional trilobites and cephalopods. The acritarch flora was discussed by Dean and Martin (1978), but other microfossils have yet to be studied. The strata are paleontologically best known for their rich ichnofauna which has been the basis for a number of taxonomic and paleoenvironmental studies during the past two decades (e.g., Seilacher and Crimes, 1969; Bergström, 1976; Pickerill and Fillion, 1983; Pickerill *et al.*, 1988).

Dean and Martin (1978, pp. 2-3) summarised published paleontological records up to the early 1970's, beginning with the pioneer studies by Billings (1872); they concluded that from these and from their own work based on trilobites and acritarchs that the Bell Island and Wabana groups were of early Ordovician age, ranging from Tremadoc to Arenig. Bergström (1976) came to a similar conclusion by incorporating ichnofaunal evidence; he considered that the Cambrian-Ordovician boundary might fall within the lower part of the Bell Island Group, although there was no unequivocal evidence for pre-Tremadoc fossils. Bergström (1976, p. 1631) furthermore stressed the geological and faunal similarities between strata on Bell Island and elsewhere on the Avalon Peninsula with those in the Mediterranean area, southern Britain and Bohemia. Pickerill and Fillion (1983) extended the use of ichnofossils on Bell Island for correlation, concluding that both the Cambrian-Ordovician and Tremadoc-Arenig boundaries fell within the Beach Formation of the Bell Island Group. They also discussed paleontological evidence for the strong link between European and Bell Island faunas, based both on invertebrate and ichnofaunal assemblages.

Graptolites are known from only one interval on Bell Island, in dark grey silty shales belonging to the Youngsters Gulch Member at the base of the Powers Steps Formation (Figs. 2, 3), the basal formation of the Wabana Group (Ranger, 1979; Ranger *et al.*, 1984; King *et al.*, 1988). The graptolites were first recorded by Van Ingen (1914, p. 138) as *Didymograptus nitidus*

(J. Hall); his specimens were identified at that time by Ruedemann (1947, p. 58), although later he (1947, p. 338, pl. 55, fig. 28; pl. 56, fig. 7) actually referred the material to *Didymograptus nicholsoni* Lapworth. Additional graptolites collected by Dean and Martin were identified by R.B. Rickards as "*Didymograptus* cf. *D. nitidus* (Hall) and *D.* cf. *D. v-deflexus* Harris" (Dean and Martin, 1978, p. 3), which he interpreted to indicate a level near the top of the Arenig *D. extensus* Zone of Britain.

The present study demonstrates the existence of a monospecific graptolitic assemblage in the Powers Steps Formation, belonging to *Didymograptus* (sensu lato) *simulans* Elles and Wood. *D.* (s.l.) *simulans* was first described by Elles and Wood (1901) from the Skiddaw Group at Barf and Randal Crag in the Lake District of northern England. In their description, Elles and Wood recorded its age merely as "Arenig (Middle Skiddaw Slates)", noting that "it has not yet been found associated with any other species". Since that time, *D.* (s.l.) *simulans* has been recorded from the *Schizograptus tardibrachiatus* Zone of Bohemia (Boucek, 1973) and from the *D. extensus* Zone at Arennig Fawr, North Wales (as "*D.* aff. *simulans*": Zalasiewicz, 1984a, 1984b, 1986), with possible examples from China (Mu *et al.*, 1979; see systematic section). Cooper and Fortey (1982, fig. 2) correlated the Bohemian *S. tardibrachiatus* Zone with the (misnamed) British *D. nitidus* Zone. Zalasiewicz (1984b, 1986) noted that the specimens from North Wales occurred in association with "*D.* aff. *deflexus* Elles and Wood", and were followed by strata yielding *Tetragraptus reclinatus* Elles and Wood, *Azygograptus* cf. *A. eivionicus* Elles and Wood, and *Didymograptus* cf. *D. praenuntius* Törnquist.

In their description of Arenig graptolites from the Cow Head Group of western Newfoundland, Williams and Stevens (1988) redescribed Elles and Wood's type material of *Pendeograptus pendens* for comparison with similar North American forms which they referred to *Pendeograptus* cf. *P. pendens*. The type material of *P. pendens* and *D.* (s.l.) *simulans* originated from Barf in the English Lake District, as did the types of *D. (Expansograptus) simulans*. Here they occur together with *A. eivionicus*, the latter of which A. Beckly (personal communication to Williams
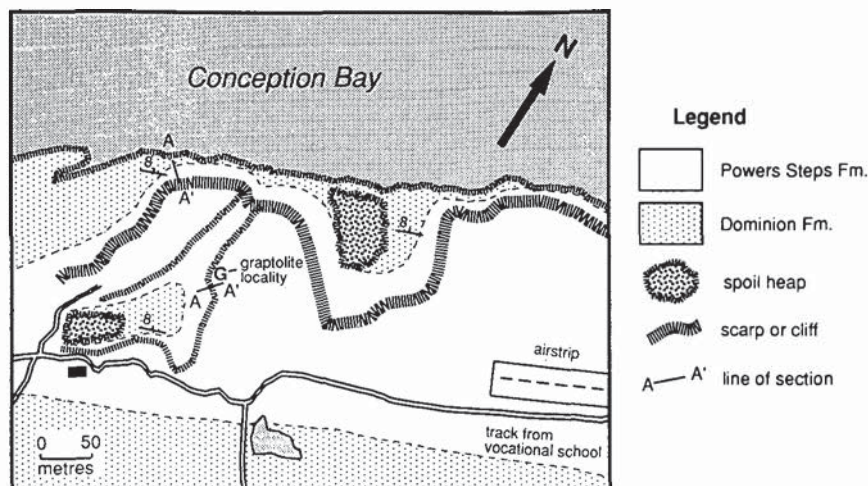

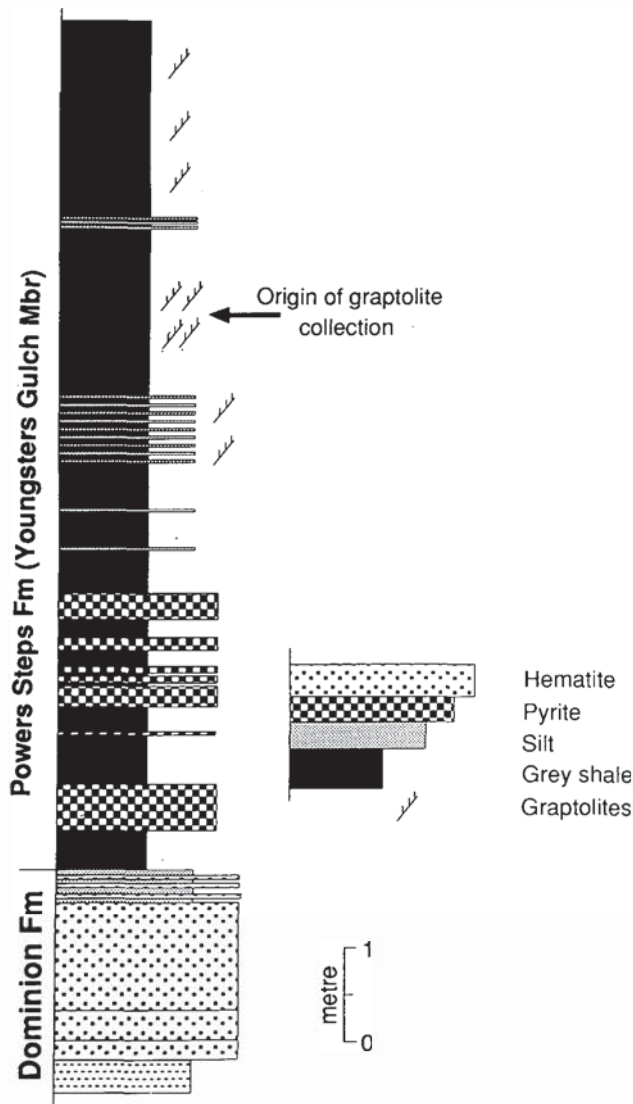Fig. 2. Geological sketch map of locality discussed in text.

Fig. 3. Composite measured section through top of Dominion Formation and basal Powers Steps Formation along lines A - A' indicated on Figure 2.

and Stevens) considered to be of early or middle Arenig age. Williams and Stevens (1988) thus concluded that *P. pendens* and *A. eivionicus* were probably characteristic of an interval equivalent to the *P. fruticosus* Zone of western Newfoundland (i.e., the lower part of Bed 11 of the Cow Head Group). *D.* (s.l.) *simulans* has also been found at Randal Crag in the Lake District (Zalasiewicz, 1986, fig. 3l and m), and thus ranges up into the later *Isograptus gibberulus* Zone in the Skiddaw Group. It is therefore possible that the assemblage from Barf is somewhat younger than concluded by Williams and Stevens (1988), and correlates with either the *D. bifidus* or *I. victoriae lunatus* Zone (upper part of Bed 11) of the Cow Head Group. Beckly (1988, p. 325) has also recorded *A. eivionicus* from the Aberdaron area of North Wales, in association with *D. praenuntius*, at a level well below an interval yielding an assemblage of unequivocal late Arenig age (equivalent to the *I. v. maximus* Zone of western Newfoundland), confirming an early or middle Arenig age for this species.

In summary, it is apparent that *D.* (s.l.) *simulans* is characteristic of the early/middle Arenig, equivalent to the *P. fruticosus* - *I. v. lunatus* zones of western Newfoundland and the *D. deflexus* - *I. gibberulus* zones of Great Britain. More precise correlation should be made possible in the future through ongoing studies on graptolite biostratigraphy in the Skiddaw Group by the British Geological Survey (e.g., Rushton, 1985).

Recent work seems to demonstrate that lateral species distribution of graptolites was more dependant on environmental control than geographic provincialism (cf. Finney and Skevington, 1979); *D.* (s.l.) *simulans* appears to be a good example, being apparently characteristic of relatively coarse-grained, siliciclastic sequences deposited in high-energy environments. Interestingly, it has not, however, been recorded from elsewhere in North America. This adds support to the hypothesis that the Avalon Zone of western Newfoundland was in relative proximity to parts of Europe during much of the Ordovician, and was separated from Laurentia, including most of North America, by the Iapetus Ocean (e.g., Seilacher and Crimes, 1969; Cawood *et al.*, 1988).

DEPOSITIONAL ENVIRONMENT AND TAPHONOMY

Most graptolites from the Powers Steps Formation are preserved as flattened, carbonaceous films in dark grey silts and shales, which Pickerill *et al.* (1988) considered to be of prodeltaic origin. Although the preservation of graptolites in such marginal deposits is less common than in more distal facies, they are known from many other comparable shallow marine carbonate and siliciclastic sequences (e.g., Williams *et al.*, 1987). Perhaps of greater significance is the occurrence of 5-20 cm bands within the Youngsters Gulch Member of the Powers Steps Formation composed almost entirely of pyritized ooids and three-dimensional pyritized graptolite fragments (internal casts) cemented by a sparse dark grey, silty matrix.

Many of the Bell Island hematites are composed largely of oolitic hematite and chamosite. These are considered to have been precipitated as primary chamosite under somewhat reducing conditions in shallow lagoons, which then accumulated in a tidal flat and tidal or barrier bar environment, where they were oxidized to ferric hydroxide (goethite) and subsequently transformed to hematite (Pickerill *et al.*, 1988). The origin of the pyrite replacing both the ooids and graptolites has apparently not been studied, but presumably indicates reducing, sulphide-rich conditions as might be found in prodelta sedimentation. The presence of the detrital pyrite bands does, however, suggest early pyritization of graptolites within anoxic, fine-grained siliclastics followed by penecontemporaneous erosion and winnowing of the sediment to remove most of the mud and silt component. Pyritization of graptolites was probably an early diagenetic feature in most black shales where three-dimensional specimens occur, protecting them from flattening during compaction of the sediment. Proof that pyritization pre-dated lithification is, however, rare, making the occurrence within the Powers Steps Formation particularly important in understanding this kind of preservation.

SYSTEMATIC PALEONTOLOGY

Order **GRAPTOLOIDEA**
  Family DICHOGRAPTIDAE Lapworth, 1873
    Subfamily Dichograptinae Lapworth, 1873
      Genus *Didymograptus* M'Coy, 1851
        Subgenus *(Expansograptus)* Boucek and Pribyl, 1953

Type species (by original designation)

Graptolithus extensus J. Hall, 1858, p. 132.

Didymograptus (sensu lato) *simulans* Elles and Wood, 1901
Figs. 4A-T, 5A-G

1870	*Didymograpsus nitidus*, Hall sp.; Nicholson, pp. 342-343, fig. 3a-b.
1898	*Didymograptus nitidus* (Hall); Elles (*pars?*), pp. 499-502, fig. 19, (fig. 20?).
1901	*Didymograptus simulans*, sp. nov.; Elles and Wood, pp. 30-31, pl. 2, fig. 6a-b; fig. 19a-b.
?1934	*Didymograptus deflexus* Elles and Wood; Hsü, pp. 36-37, pl. 2, fig. 7a-c.
1947	*Didymograptus nicholsoni* Lapworth; Ruedemann (*pars?*), pp. 338-339, pl. 55, fig. 28; pl. 56, fig. 7 (*non* pl. 55, figs. 26-27?).
1973	*Expansograptus simulans* (Elles and Wood); Boucek, pp. 42-43, pl. 5, fig. 6; text-fig. 2a-e.
?1979	*Didymograptus inflexus* Chen et Xia (sp. nov.); Mu *et al.*, pp. 84-85, pl. 29, figs. 8-11.
?1979	*Didymograptus* cf. *inflexus* Chen et Xia (sp. nov.); Mu *et al.*, pl. 29, fig. 12.
?1979	*Didymograptus aequabilis* Chen et Xia (sp. nov.); Mu *et al.*, pp. 86-87, pl. 29, figs. 2-5 (non fig. 1).
?1979	*Didymograptus stratus* Chen et Xia (sp. nov.); Mu *et al.*, p. 90, pl. 31, figs. 14-17.
non 1979	*Didymograptus* cf. *simulans*; Mu *et al.*, pp. 102-203, pl. 35, fig. 30.
1984a	*Didymograptus* aff. *simulans* Elles and Wood; Zalasiewicz, fig. 7a-b (no description).
1984b	*Didymograptus* aff. *simulans* Elles and Wood; Zalasiewicz, p. 425, text-fig. 2a-d.
1986	*Didymograptus* aff. *simulans* Elles and Wood; Zalasiewicz, pp. 537-538, figs. 3a-j, 8a-b.
1987	*Didymograptus (Expansograptus) simulans* Elles and Wood; Fortey (*in* Fortey and Owens), fig. 124d (no description).

Type specimen

The holotype is SMA 17696 (housed in the Sedgwick Museum, University of Cambridge, U.K.), from lower or middle Arenig strata within the Skiddaw Group of Barf in the English Lake District (Strachan, 1971, p. 17). It has been figured previously by Elles and Wood (1901, pl. 2, fig. 6b; fig. 19a, c) and by Fortey (*in* Fortey and Owens, 1987, fig. 124d), and is refigured here (Fig. 5E).

Material and occurrence

Over one hundred specimens from the Youngsters Gulch Member of the Powers Steps Formation, Bell Island, 72 of which were used for statistical measurements.

Most are preserved as flattened, carbonaceous films, although a few specimens are pyritised in semi-relief. None are tectonically deformed. The type slab from Barf, northern England was employed for comparison, which contains five usable specimens. Although the enclosing sediment of the types has been affected by heavy shearing, the graptolites were originally preserved in semi-relief by pyritisation, and have not been too deformed by shearing. That pyrite has since largely rotted and disappeared, leaving the rhabdosomes preserved as internal moulds.

Diagnosis (revised)

Gently deflexed rhabdosome, with characteristically asymmetric proximal development reminiscent of pendent Llanvirn *Didymograpti*. Stipes reaching over 45 mm long, widening from 0.7-0.9 mm proximally to 0.9-1.3 mm in 10 mm, and attaining a maximum width of up to 1.5 mm distally. Sicula typically 1.4-1.6 mm long, curved throughout its length and inclined in its distal portion at a low angle to the axis of $th1^2$. Thecae curved, with simple apertures occupying 1/4-1/3 total stipe width, numbering 6-8 in 5 mm proximally, and decreasing to 5.5-7.5 in 10 mm distally.

Description

The stipes are long, straight and horizontal or slightly declined throughout most of their length, reaching over 45 mm in the longest rhabdosomes. They are proximally deflexed, stipes enclosing an initial angle which typically measures 100-130°, although it ranges from 60-155° in some specimens. Stipe width is extremely variable, both in the samples from Bell Island and in the type material. It typically increases from 0.7-0.9 mm at $th1^1$ to 0.8-1.2 mm in 5 mm and 0.9-1.3 mm in 10 mm. Stipe width subsequently increases slightly but continuously throughout development up to a maximum of 1.5 mm (but usually less). The distal growing tip, where reduction in stipe width occurs owing to incomplete thecal development, is only rarely preserved and where seen is only a few thecae long.

The sicula is 1.2-1.9 mm long, with modal values of 1.4-1.6 mm probably reflecting the typical, undeformed dimension. It is gently curved throughout its length and inclined in its distal portion, where it runs at a low angle to the free ventral wall of $th1^2$ before opening into an aperture 0.3-0.4 mm wide. Although no isolated three-dimensional material is available for study, preservation in both flattened and pyritised specimens is sufficient to permit limited interpretation of proximal development. $Th1^1$ appears to have a prosicular origin on the rutellar margin, as found in most other dichograptids of equivalent Arenig age (see Williams and Stevens, 1988). It grows parallel to the sicular axis for about 0.8 mm before turning sharply out, after which it curves down until the aperture is reached. The free ventral wall of $th1^1$
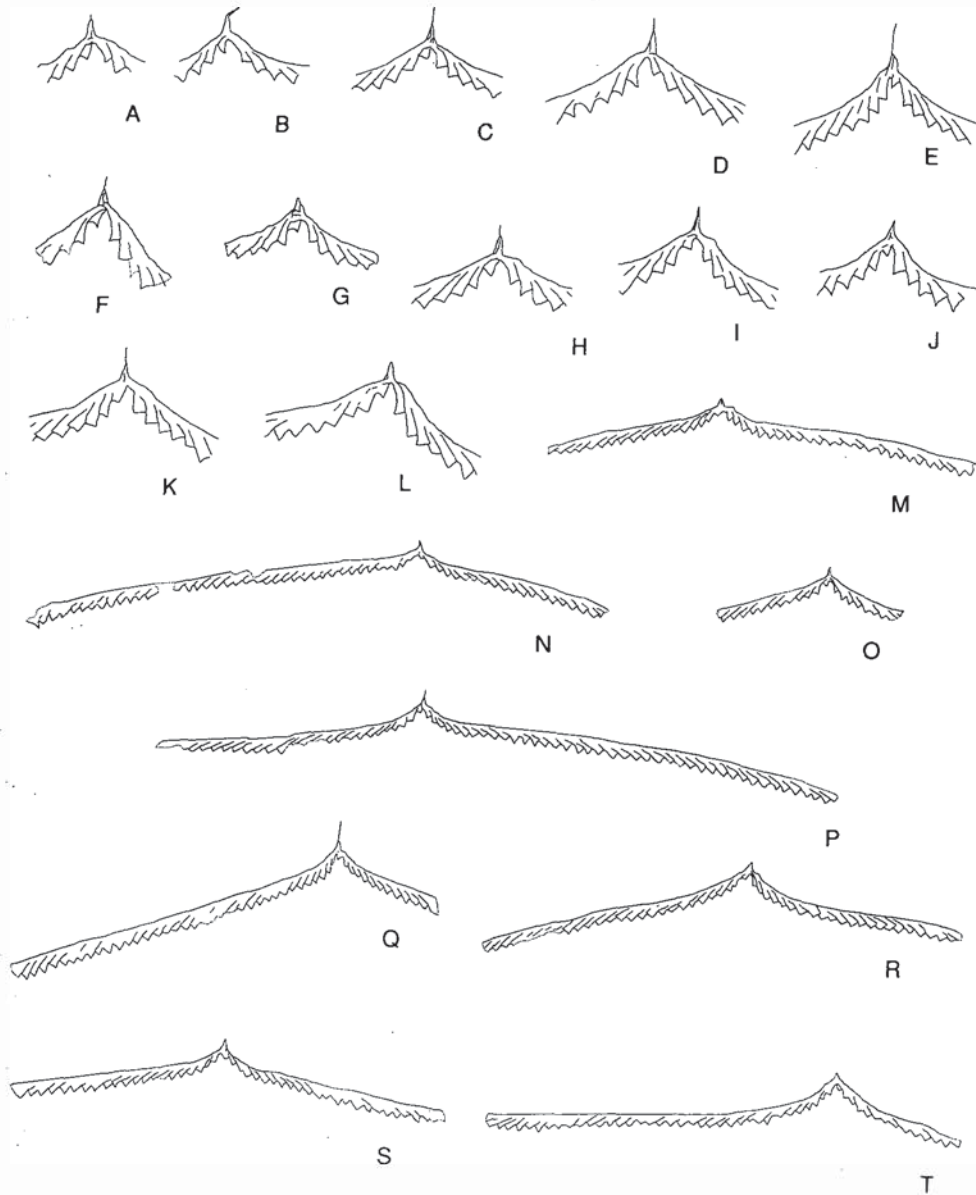
Fig. 4. *Didymograptus* (sensu lato) *simulans* Elles and Wood. From the basal Powers Steps Formation, Bell Island. A - L, x5, M - T, x2.5. (A) GSC 87509. (B) GSC 87510. (C, P) GSC 87511. (D) GSC 87512. (E, Q) GSC 87513. (F) GSC 87514. (G) GSC 87515. (H, M) GSC 87516. (I) GSC 87517. (J) GSC 87518. (K) GSC 87519. (L) GSC 87520. (N) GSC 87521. (O) GSC 87522. (R) GSC 87523. (S) GSC 87524. (T) GSC 87525.
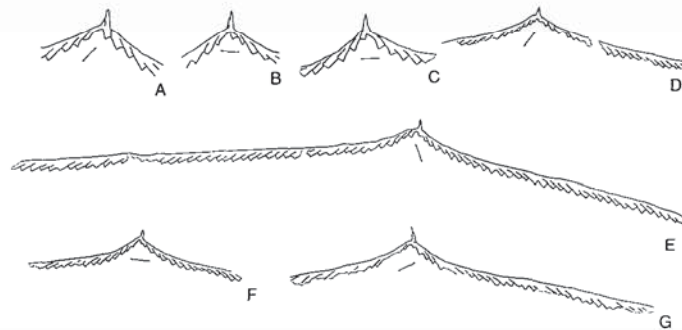
Fig. 5. *Didymograptus* (sensu lato) *simulans* Elles and Wood. Type material all on one slab, from the Skiddaw Group, Barf, northern England. Bars indicate direction of stretching lineation. A - C, x5, D - G, x2.5. (A) Apparently not catalogued. (B, F) SM A17698, figured by Fortey (in Fortey and Owens, 1987, fig. 124d). (C) SM A17697, figured by Elles and Wood (1901, text-fig. 19b). (D) SM A17700. (E) SM A17696, holotype, figured by Elles and Wood (1901, pl. 2, fig. 6b; text-fig. 19a, c). (G) SM A17695, figured by Elles and Wood (1901, pl. 2, fig. 6a).

is typically 0.8-1.0 mm long, while the rutellar margin of the sicula is free for 0.4-0.7 mm below its point of divergence. Th1^2 buds from th1^1 at its point of divergence from the sicula, growing across the reverse of the sicula before curving down to mirror the growth of th1^1. The aperture of th1^2 is normally reached at a level below that of th1^1, giving a marked asymmetrical appearance to the proximal region. The origin of th2^1 is unclear.

The form of the pendent proximal region is variable; this probably demonstrates variability in the living rhabdosome, although it has also been possibly affected by the attitude of stipes to bedding surfaces during burial and compaction (see below), the "tighter" appearance being related to oblique compaction. Thecae exhibit a distal concave curvature, having an initial low angle of inclination to the dorsal wall which increases throughout the length of each theca to a maximum 25-55° in proximal thecae and 20-45° distally. Thecal apertures are straight, occupying 1/4-1/3 total stipe width. Thecal density is 6-8 in 5 mm proximally, decreasing slightly to 5.5-7.5 in 5 mm distally. In some specimens the proximal dorsal stipe margin is somewhat irregular; it is unclear whether this indicates original prothecal folding, or is an artifact of deformation produced during compaction of the rhabdosome.

Remarks

The proximal development of *D*. (s.l.) *simulans* distinguishes it from almost all other deflexed and extensiform didymograptids; discussion here will, therefore, be restricted to those species to which the Bell Island material has been previously referred and to possible junior synonyms of *D*. (s.l.) *simulans*. Although it has a somewhat similar overall form, the proximal structure of *D*. (s.l.) *simulans* is very different from that of *D*. (*E.*) *nitidus* (J. Hall), recorded from the Powers Steps Formation by Van Ingen (1914). The latter species has recently been redescribed in detail by Williams and Stevens (1988), using both the type material from Levis, Quebec, and the rich fauna from the Cow Head Group, western Newfoundland. Although widely recorded in the literature, the diagnostic features of *D*. (*E.*) *nicholsoni* Lapworth, to which the Bell Island material was assigned by Ruedemann (1947), remain poorly understood, and the species is in need of thorough taxonomic revision. The specimens illustrated by Elles and Wood (1901, pl. 2, fig. 4a-c; fig. 16a-c) have a proximal appearance reminiscent of *D*. (s.l.) *simulans*, but are much narrower and lack the deflexed nature of the proximal end. The slender rhabdosome and gently inclined thecae with rather low thecal density of *D*. (*E.*) *nicholsoni* are more similar in appearance to sigmagraptines such as *Acrograptus gracilis* (Törnquist) than to typical dichograptids (see Cooper and Fortey, 1982, fig. 66; Williams and Stevens, 1988, fig. 79). Rickards (*in* Dean and Martin, 1978, p. 3) recorded *D*. (*E.*) *v-deflexus* Harris and *D*. (*E.*) cf. *nitidus; D*. (*E.*) *v-deflexus* has a similar overall form to *D*. (s.l.) *simulans*, but a proximal structure more like typical *Expansograptus* taxa.

Detailed qualitative and quantitative comparison of the specimens from Bell Island with the type material and that described from North Wales by Zalasiewicz (1986) clearly indicates that all three occurrences represent the same graptolite species (see statistical section below). Zalasiewicz (1986, p. 538) also briefly discussed several other described species from Scandinavia and China which he considered to be similar, and most of these are included in the synonymy listing of the present paper. Those specimens figured by Boucek (1973) as "*Expansograptus simulans*" are here considered to belong to that species, but *D. deflexus scanicus* Tjernvik from southern Sweden (Tjernvik, 1960, p. 217, fig. 3) appears to have more slender stipes with gently inclined thecae and a longer sicula, giving a proximal development reminiscent of *Pendeograptus* (as revised by Williams and Stevens, 1988). The figures of specimens from the Lower Yangtze Valley assigned to *D. deflexus* by Hsü (1934) are inadequate for positive identification, but most figured material of the new species *D. inflexus, D. stratus* and *D. aequabilis* described in Mu *et al*. (1979) appears similar to typical *D*. (s.l.) *simulans*. Their figured specimen referred to *D*. cf. *simulans*, however, has more robust stipes with steeply inclined thecae and does not belong to this species.

Generic assignment

Much has been written and discussed during the past few years concerning the importance of proximal structure in graptolite classification, as opposed to overall rhabdosome form. Although some details of early astogenetic development may be determined through examination of flattened material, unequivocal conclusions may only be drawn with the assistance of isolated, three-dimensional specimens. Cooper and Fortey (1982) were instrumental in beginning a complete revision of Lower Ordovician graptolite classification, including the genus *Didymograptus*. They recognised that the pendent forms of this genus, commonly referred to as "tuning-fork" graptolites, actually belonged to two unrelated lineages which evolved independently during the early/middle Arenig and the Llanvirn. They referred the early members, typified by *D. bifidus* (J. Hall) to the subgenus *Didymograptus (Didymograptellus)*; these were characterized by a prothecal origin of th1^1 and dicalycal th1^2. The Llanvirn taxa, typified by *D. murchisoni* (Beck), were assigned to *Didymograptus (Didymograptus)*, and characterized by a metathecal origin for th1^1 and dicalycal th1^1.

The overall deflexed rhabdosomal form of *D*. (s.l.) *simulans* is most similar to *Corymbograptus* (Obut and Sobolevskaya, 1964); the type species of this genus is, however, "*Didymograptus*" *v-fractus* Elles and Wood, which Williams and Stevens (1988, p. 17) considered related to, or synonymous with *Pendeograptus fruticosus* (J. Hall). The only other taxonomic group of horizontal or slightly deflexed, two-stiped dichograptids currently available is *Didymograptus (Expansograptus)*, the type specimen of which is *D*. (*E.*) *extensus* (J. Hall). Williams and Stevens (1988, p. 44) remarked that taxa currently assigned to the extensiform *Didymograpti* were in need of a similar kind of revision to the pendent *Didymograpti*, and that several distinct lineages were probably included within the subgenus as currently defined. The proximal development of *D*. (s.l.) *simulans* does not appear to be similar to that of *D*. (*E.*) *extensus*, (see description above) suggesting that the two are probably unrelated and should not be included within the same subgenus. Revision of this group is,

however, outside the scope of the present study; until such time that a revision is carried out, the Bell Island graptolites are best referred to *Didymograptus* (sensu lato).

STATISTICAL ANALYSIS OF ASSEMBLAGE

The abundant, monospecific assemblage of the Powers Steps Formation provides an unusually good opportunity to statistically test several hypotheses regarding interdependence of certain variables in graptolites, and the kind of rhabdosome growth exhibited. Although a few statistically-based graptolite studies have been published previously, notably Cooper (1973), it is rare to obtain statistically viable samples from a narrow stratigraphic interval, and the biometric study of graptolites has lagged far behind that of many other fossil invertebrate groups such as the brachiopods and trilobites. Another problem related to biometric analysis in graptolites was addressed by Fortey (1983), who recognised the interdependence of many geometric variables commonly used in species separation.

Measurements were made for 72 specimens from Bell Island, and 5 rhabdosomes on the type slab from England (Tables 1 and 2). Limited data were also taken from graphical plots of material from North Wales published by Zalasiewicz (1986, fig. 3). The 12 variables measured, together with their abbreviations on the tables, are as follows (also see Fig. 6 for explanation):

(a) Maximum stipe length [Stipe l]
(b) Proximal angle enclosed by stipes [Prox Ø] (this is equivalent to the "subsequent stipe divergence angle" of Zalasiewicz (1986))
(c) Length of sicula [Sic l]
(d) Stipe width at th1 [w @ th1]
(e) Stipe width 5 mm from sicula [w @ 5mm] (measured across the widest point of the stipe at the nearest thecal aperture to the 5 mm mark)
(f) Stipe width 10 mm from sicula [w @ 10mm] (measured across the widest point of the stipe at the nearest thecal aperture to the 10 mm mark)
(g) Stipe width 20 mm from sicula [w @ 20mm] (measured across the widest point of the stipe at the nearest thecal aperture to the 20 mm mark)
(h) Stipe width 30 mm from sicula [w @ 30mm] (measured across the widest point of the stipe at the nearest thecal aperture to the 30 mm mark)
(i) Proximal thecal density for 5 mm interval [Prox/5mm]
(j) Distal thecal density for 5 mm interval [Dist/5mm] (using the most distal 5 mm interval before the growing tip)
(k) Maximum thecal inclination to dorsal wall in proximal thecae [Prox thØ]
(l) Maximum thecal inclination to dorsal wall in distal thecae [Dist thØ] (using fully developed distal thecae before the growing tip)

The main reason for statistical study of this fauna was to test two hypotheses. First, were the variations in proximal angle, length of sicula and proximal thecal form (including stipe width, thecal density and inclination) inter-related and dependant on either original variation during life or post-mortem deformation? Secondly, did thecae continue to grow throughout astogeny as

demonstrated for several dichograptids by Williams and Stevens (1988), or did they attain their maximum length soon after budding?

With respect to overall rhabdosome form, the following situations would be expected:

(a) If the observed variation was due to original variation of the rhabdosome during life, little or no correlation between those variables mentioned may be expected.
(b) If the variation was due to twisting and distortion of the rhabdosome parallel to bedding during burial and compaction, some correlation between the variables might be expected.
(c) If variation was due to preservation of the rhabdosome in oblique orientation to bedding, a strong correlation would be expected between proximal angle, sicula length and proximal thecal form.

With reference to the plots given (Figs. 7 to 9), and by numerical analysis of the data, the following conclusions relating to the first problem may be drawn:

(1) (Fig. 7). Histograms of proximal angle, sicula length and width at th1 all display reasonably good normal distributions, as would be expected from a representative fossil assemblage.
(2) (Fig. 8). The bivariate plots of proximal angle against sicula length, proximal stipe width and proximal thecal inclination exhibit little correlation, either graphically or numerically, for the Bell Island material (correlation coefficients are 0.016, -0.074 and 0.262 respectively). This suggests that variation is due to options (a) or (b) above. It may, however, be significant that those rhabdosomes with atypical proximal angles (i.e., <100° and >130°) have shorter siculae, as would be expected if option (c) above was correct. I conclude that while most variation was related to variation in the living rhabdosome, anomalously short siculae were probably the product of oblique compaction.
(3) (Fig. 9). Plots of proximal angle against maximum stipe length suggests no correlation for the Bell Island specimens, but interestingly do seem to demonstrate an overall increase in angle with stipe length for the much smaller samples from both Arennig, North Wales and Barf, English Lake District, a phenomenon also observed by Zalasiewicz (1986, p. 538). Zalasiewicz postulated that this might represent a tendency for increased longevity amongst rhabdosomes with larger angles of stipe divergence, or alternatively a change in stipe attitude during astogeny. It is further possible that the variation might be due to adjustment as the stipes became oriented parallel to bedding during settling and subsequent sediment compaction, or even that the two British samples represent statistically invalid populations, and that the Bell Island distribution which shows no evident correlation is a more correct representation of the species.

The second problem may be solved by plotting stipe widths against maximum stipe length, and by qualitative observations of stipe expansion plots as used by Cooper and Fortey (1982) and Williams and Stevens (1988). Many dichograptids have rhabdosomes with characteristic, constant widths at specific points along the stipes, and these widths are often quoted as a diagnostic

Table 1. Statistical data for *Didymograptus (Expansograptus) simulans* from Bell Island (see Fig. 6 for explanation).

Stipe l /mm	Prox Ø /mm	Sic l /mm	w @ thl /mm	w @ 5mm /mm	w @ 10mm /mm	w @ 20mm /mm	w @ 30mm /mm	Prox/5mm	Dist/10mm	Prox thØ	Dist thØ
6.0	115	1.45	0.80	0.90	-	-	-	7.5	-	35	-
5.5	55	1.50	0.75	-	-	-	-	8.0	-	-	-
15.0	130	1.30	0.60	0.75	0.90	0.95	-	7.0	6.5	45	25
18.0	115	1.90	0.75	1.00	1.00	-	-	7.0	7.0	35	45
18.5	130	1.85	0.70	0.95	0.95	-	-	7.5	6.5	30	40
16.5	110	1.60	0.80	1.10	1.15	-	-	7.5	7.0	30	45
26.0	100	-	0.70	1.00	0.95	0.90	-	7.0	7.0	40	30
7.0	105	1.70	0.70	0.85	-	-	-	7.0	-	30	-
26.0	110	1.70	0.80	1.00	1.20	1.05	-	7.0	7.0	45	35
25.0	100	1.30	0.80	0.95	1.00	1.10	-	7.0	7.0	40	35
8.5	140	1.45	0.65	0.95	-	-	-	6.5	-	30	-
37.0	125	1.50	0.80	1.10	1.20	1.30	1.45	6.0	5.5	40	40
17.5	100	1.50	0.70	0.80	0.90	-	-	7.5	6.0	30	36
32.5	100	1.40	0.70	1.00	1.00	0.95	0.90	7.0	6.0	40	35
17.0	100	-	0.70	0.95	1.00	-	-	8.0	7.0	30	35
23.0	155	1.25	0.60	0.90	1.00	0.90	-	8.0	6.0	55	35
20.0	130	1.40	0.60	1.05	0.95	-	-	7.5	7.0	50	35
4.5	150	1.40	0.50	-	-	-	-	-	-	30	-
21.5	125	1.25	0.75	0.85	0.95	1.00	-	7.5	6.0	45	35
24.5	90	1.30	0.85	1.15	1.35	1.35	-	8.0	7.0	40	40
19.0	95	-	0.85	1.10	1.10	-	-	8.0	7.0	30	35
30.0	110	1.35	0.80	0.90	1.20	1.10	0.80	7.5	6.5	50	40
3.0	100	1.25	0.80	-	-	-	-	8.0	-	30	-
5.5	120	1.35	0.85	1.05	-	-	-	8.0	-	40	-
15.5	130	1.60	0.85	1.00	1.10	-	-	7.0	6.0	45	20
20.0	130	1.60	0.70	1.05	1.20	1.30	-	7.0	6.5	40	40
25.0	150	1.70	1.10	1.20	1.20	1.30	-	7.0	5.5	50	30
16.0	120	-	0.80	1.05	1.10	-	-	6.0	6.0	30	30
9.5	140	-	0.75	0.95	-	-	-	6.5	-	30	-
11.5	130	1.80	0.80	1.00	1.10	-	-	8.0	-	40	30
23.5	100	-	0.60	0.80	1.00	1.00	-	7.0	6.5	30	30
19.0	120	-	0.80	0.90	1.00	-	-	7.0	7.0	40	35
11.0	90	1.60	0.70	1.10	-	-	-	7.5	-	45	-
11.5	130	1.65	0.85	1.00	1.10	-	-	7.0	-	50	-
5.5	120	1.80	0.65	0.90	-	-	-	7.0	-	50	-
12.0	110	-	0.80	1.00	1.10	-	-	8.0	-	50	-
19.5	140	1.40	0.85	1.00	1.10	-	-	7.0	6.5	50	40
12.5	90	-	0.90	1.00	1.00	-	-	7.0	-	40	-
9.5	120	1.60	0.90	1.00	-	-	-	6.5	-	40	-
8.0	130	1.35	0.75	1.00	-	-	-	7.0	-	40	-
26.0	100	1.80	0.80	0.90	1.00	1.00	-	6.5	6.5	30	30
45.0	110	-	0.80	1.10	1.20	1.30	1.50	6.5	6.0	50	40
11.5	120	1.25	0.70	0.90	-	-	-	7.5	-	40	-
5.5	100	1.40	0.70	0.70	-	-	-	7.0	-	30	-
7.5	130	1.60	0.80	0.90	-	-	-	7.5	-	40	-
6.5	100	1.80	0.80	1.00	-	-	-	7.0	-	40	-
7.5	130	1.50	0.80	1.00	-	-	-	7.0	-	50	-
12.5	130	-	0.70	1.00	1.00	-	-	7.0	-	40	-
23.0	120	1.60	0.90	1.10	1.20	1.20	-	7.5	7.0	40	30
13.5	110	1.50	0.75	0.90	1.00	-	-	8.0	-	40	-
21.5	-	1.50	0.80	1.00	1.10	0.80	-	6.5	6.5	40	20
7.0	130	1.70	0.80	1.10	-	-	-	7.5	-	40	-
16.5	110	1.50	0.60	0.90	1.20	-	-	8.0	6.5	40	30
18.0	110	1.40	0.80	0.90	1.00	-	-	6.0	-	30	-
8.5	110	1.50	0.70	0.85	-	-	-	6.0	-	30	-
10.5	120	-	-	0.70	0.80	-	-	6.0	-	30	-
18.0	130	1.50	0.90	1.10	1.20	-	-	7.0	6.5	30	30
8.5	110	1.50	0.70	0.90	-	-	-	7.5	-	40	-
15.0	120	-	0.55	0.70	0.80	-	-	7.5	7.5	40	30
9.0	120	1.80	0.70	0.90	-	-	-	7.0	-	40	-
28.0	110	1.40	0.95	1.05	1.20	1.20	-	7.0	6.5	50	25
28.0	120	1.90	1.00	1.20	1.30	1.30	-	7.0	6.5	50	30
16.0	120	-	0.80	1.00	1.10	-	-	6.0	6.0	30	30
12.0	110	1.30	0.90	1.00	1.00	-	-	7.0	-	30	-
9.5	110	1.60	0.70	0.85	-	-	-	8.0	-	30	-
19.5	110	1.30	0.80	0.90	0.95	-	-	7.0	7.0	30	25
30.0	140	1.40	0.70	1.00	1.10	1.10	-	7.5	6.5	40	30
3.7	100	1.50	0.90	-	-	-	-	-	-	40	-
8.0	120	-	0.75	1.00	-	-	-	6.5	-	40	-
10.5	120	-	0.70	0.90	-	-	-	7.5	-	30	-
5.5	110	1.45	0.70	0.80	-	-	-	6.5	-	40	-
18.5	-	-	0.70	1.00	1.10	-	-	7.0	7.0	40	30

Table 2. Statistical data for *Didymograptus (Expansograptus) simulans* type material from Barf, northern England.

Stipe l /mm	Prox Ø	Sic l /mm	w @ th1 /mm	w @ 5mm /mm	w @ 10mm /mm	w @ 20mm /mm	w @ 30mm /mm	Prox/5mm	Dist/10mm	Prox thØ	Dist thØ
15.4	111	1.60	0.55	0.80	0.95	-	-	6.5	6.5	26	33
40.3	130	1.50	0.70	0.88	1.05	1.20	1.30	6.5	5.5	35	30
3.6	111	1.42	0.55	-	-	-	-	6.5	-	29	-
10.7	111	1.50	0.45	0.85	0.70	-	-	7.0	-	27	30
24.5	119	1.83	0.70	0.80	1.00	1.15	-	-	6.0	30	26
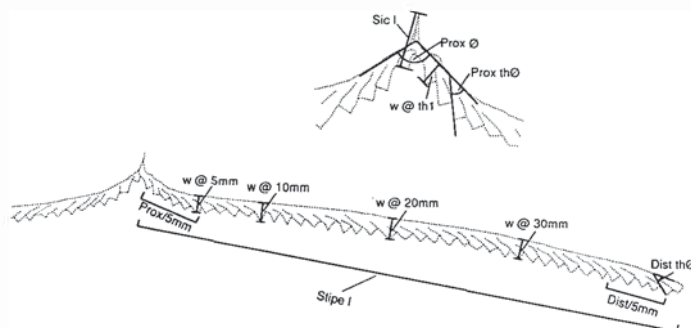
Fig. 6. Modified drawings of *Didymograptus (Expansograptus) simulans*, illustrating parameters measured for statistical analysis.
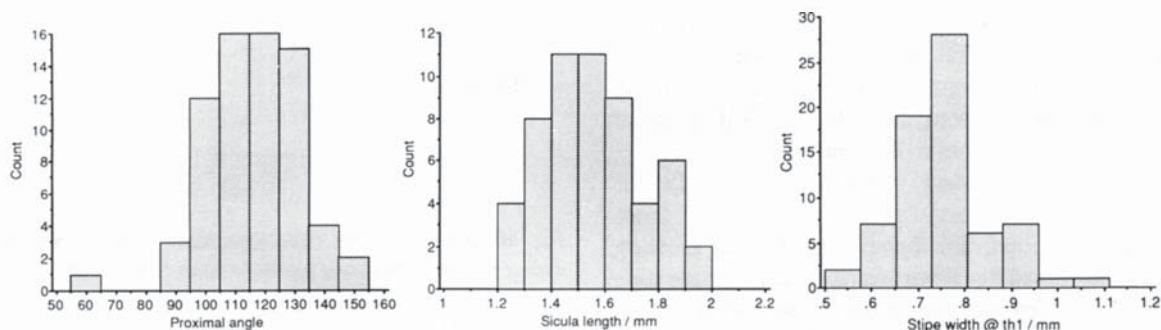
Fig. 7. Frequency distribution plots for proximal angle, sicula length and proximal stipe width of *Didymograptus (Expansograptus) simulans* from Bell Island.
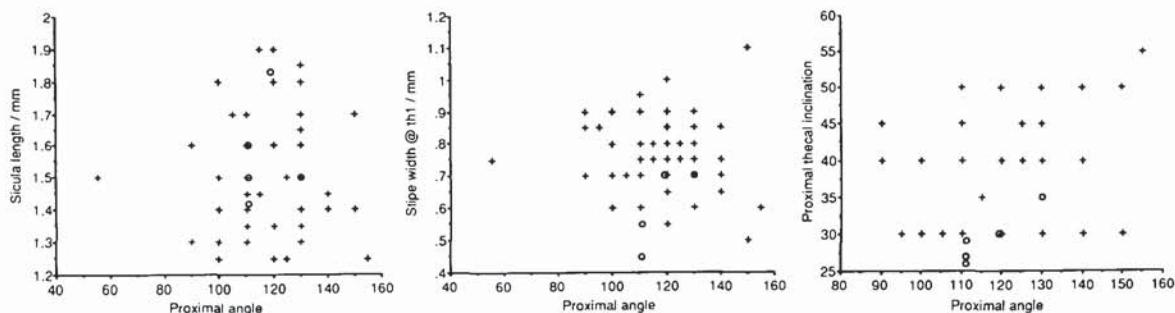
Fig. 8. Bivariate plots of proximal angle against sicula length, proximal stipe width, and proximal thecal inclination. Crosses indicate Bell Island specimens, open circles are for type material from Barf, northern England.
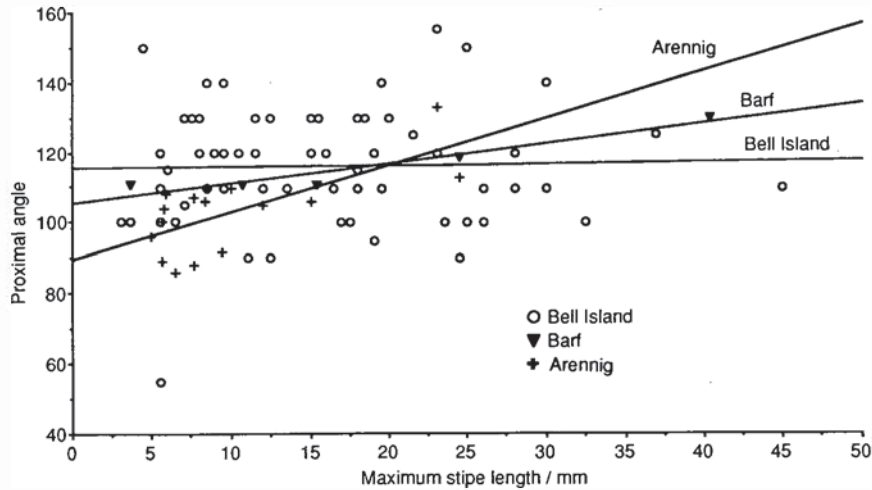
Fig. 9. Bivariate plots of proximal angle against maximum stipe length for specimens of *Didymograptus* (sensu lato) *simulans* from Bell Island, Barf and Arennig.

taxonomic feature. Williams and Stevens (1988) found, however, that in some dichograptids thecae continued to grow throughout astogeny, resulting in mature rhabdosomes with wider stipes than juvenile specimens of the same species. The two growth strategies may be distinguished by plotting stipe widths at specified positions along the stipe (e.g., at 5 mm, 10 mm, 20 mm, etc.) against maximum stipe length. If thecal growth ceased early after initial formation, the plots for each position will fall on a horizontal line (e.g., *Xiphograptus svalbardensis* (Archer and Fortey): see Williams and Stevens, 1988, text-fig. 48). If thecal growth was continuous, the plots will fall on a sloping line (e.g., *Didymograptus (Expansograptus) pennatulus* (J. Hall): see Williams and Stevens, 1988, text-fig. 43). Furthermore, those with more continuous growth are characterized by long growing tips on the stipes (the most distal portion of the stipe where stipe width decreases away from the sicula due to incomplete thecal development), whereas those where full development is attained rapidly have only short growing tips.

Stipe expansion plots (Fig. 10) and scatter plots of stipe widths against maximum stipe length for *D.* (s.l.) *simulans* from Bell Island (Figs. 11, 12) demonstrate little correlation at first glance, except for the plot of stipe width at 30 mm against maximum stipe length (Fig. 12), suggesting that full thecal development was attained rapidly throughout most of the rhabdosome. Computer-generated regressions, however, suggest more continuous growth for the samples from both Bell Island (Figs. 11, 12) and Barf (Fig. 13), an observation also made qualitatively by Zalasiewicz (1986, p. 538), with a pattern similar to that documented by Williams and Stevens (1988, text-fig. 43) for *Didymograptus (Didymograptellus) bifidus* (J. Hall) from western Newfoundland. It therefore appears that thecal growth continued for a period of time after initial budding, although not to the extent found in *D. (E.) pennatulus*. Comparative plots of proximal stipe width against maximum stipe length for the samples from Bell Island, Arennig and Barf (Fig. 14) indicate different regression values for each, suggesting that thecal growth continued for a longer period of astogeny in *D.* (s.l.) *simulans* from Barf than in the Arennig population, while growth was
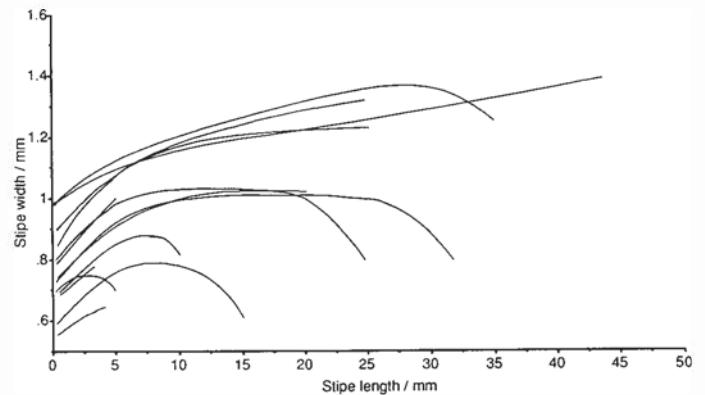

Fig. 10. Representative stipe expansion plots for specimens of *Didymograptus* (sensu lato) *simulans* from Bell Island.
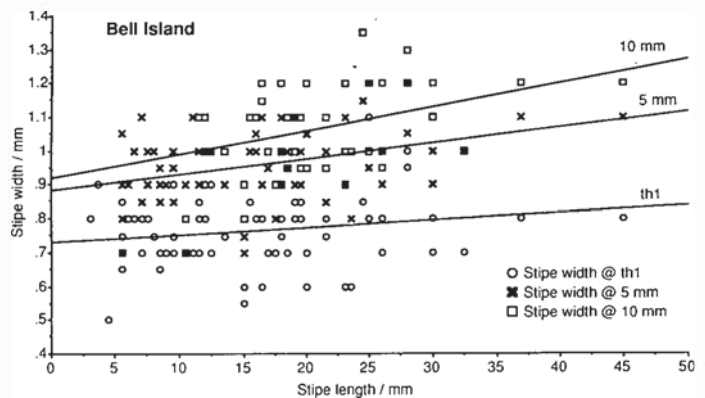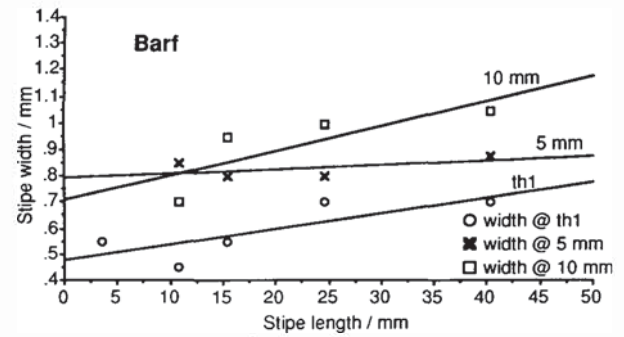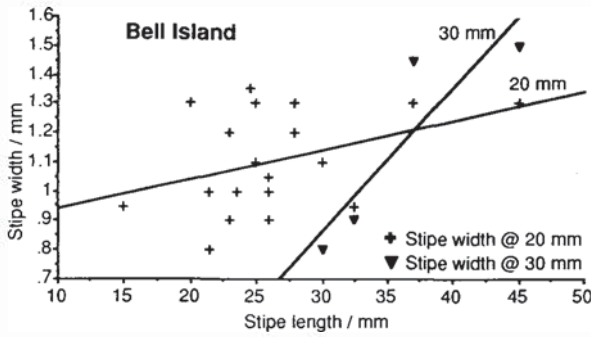

Fig. 11. Bivariate plots of stipe widths at th1, 5 mm and 10 mm from sicula against maximum stipe length for Bell Island specimens of *Didymograptus* (sensu lato) *simulans* (n.b. regression lines are computer-generated).

completed more rapidly than either of these in rhabdosomes from Bell Island. Similar intraspecific variation for populations of *D. (D.) bifidus* from different localities was noted by Williams and Stevens (1988, text-fig. 30); this phenomenon may perhaps have been due to environmental controls such as food supply rather than to genetic variation.

Although plots of sicula length against stipe widths at th1, 5 mm and 10 mm exhibit little definite relationship (Fig. 15), there does appear to be a slight visual correlation between increasing sicula length and stipe width (correlation coefficients are 0.186, 0.254 and 0.224 respectively), suggesting that those rhabdosomes with wider stipes also have longer siculae and adding support to a pattern of more continuous thecal growth.

Fig. 12. Bivariate plots of stipe widths at 20 mm and 30 mm from sicula against maximum stipe length for Bell Island specimens *Didymograptus* (sensu lato) *simulans* (n.b. regression lines are computer-generated).

Fig. 13. Bivariate plot of stipe widths at th1, 5 mm and 10 mm from sicula against maximum stipe length for material of *Didymograptus* (sensu lato) *simulans* from Barf (n.b. regression lines are computer-generated).
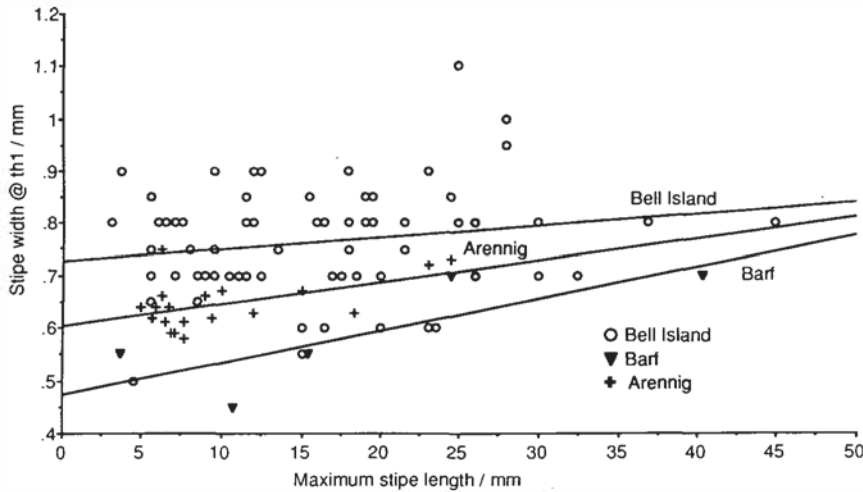

Fig. 14. Comparison of bivariate plots of stipe widths at th1 against maximum stipe length for specimens of *Didymograptus* (sensu lato) *simulans* from Barf, Arennig and Bell Island (n.b. regression lines are computer-generated).
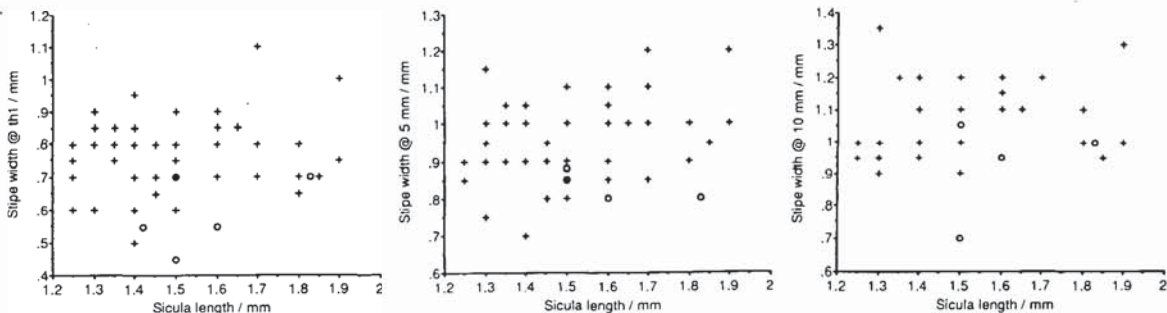

Fig. 15. Bivariate plots of sicula length against proximal stipe width, stipe width at 5 mm, and stipe width at 10 mm from the sicula for *Didymograptus* (sensu lato) *simulans*. Crosses indicate Bell Island specimens, open circles are for type material from Barf, northern England.

of the final manuscript. Kelly Brophy helped input most of the statistical data and drew many of the graptolite specimens. Fieldwork for the project was funded through an NSERC Operating Grant, whilst all graphics and statistics were generated on a Macintosh II and laser printer purchased with an NSERC Minor Equipment grant.

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