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A combination of pseudovirgulae and lateral branching in a species of dichograptid

ABSTRACT: The development of *Sigmagraptus praecursor* Ruedemann is described in some detail from flattened and three dimensional material from Quebec. It is shown that early growth stages possess long pseudovirgulae developed from the dorso-lateral side of the apertures of $th1^1$ and $th1^2$, and along which the first pair of lateral branches grow in an upwards direction. Pseudovirgulae are lacking in later lateral branching. *Sigmagraptus praecursor* exhibits dichograptid development, $th1^2$ forming a single crossing canal and originating low down on $th1^1$ which probably has its origin on the prosicula. Pseudovirgulae and a combination of these with lateral branching has not been previously recorded in Ordovician graptolites: it is postulated that the pseudovirgulae may have assisted buoyancy, stability and orientation of the early growth stages.

INTRODUCTION

Much of the material used in this paper was collected by the staff and students at Laval University, Quebec, and by Dr J. Riva, Professor Fitz Osborne and M. Rene Bureau in particular. All the specimens are deposited in the collections of the Department of Geology at Laval. The Quebec specimens are undoubtedly *extensus* zone, Arenig in age, whilst the closely similar form recorded by Dewey & al. (1970) as *Sigmagraptus* aff. *praecursor* Ruedemann is from the same horizon in Western Eire. Ruedemann's originals from the Deep Kill section (bed 3) of New York are probably also *extensus* zone, Arenig and occur below strata yielding *Pseudotrigraptus ensiformis*, whilst the Australian and New Zealand recordings of *Sigmagraptus* spp. (see below) are from the Bendigonian and Chewtonian or approximately *extensus* zone Arenig.

Acknowledgements. I am indebted to Dr John Riva, Professor Fitz Osborne and Rene Bureau of Laval University, Quebec for a great deal of help in the field and laboratory. This research was also assisted by the grant of a moiety of the Tyrell Fund by the Geological Society of London. I should like to thank Professor O. M. B. Bulman and Dr Dennis Jackson for help with the manuscript.

SYSTEMATIC DESCRIPTION

Suborder *Didymograptina* Lapworth, 1880; emend. Bulman 1970

Family *Dichograptidae* Lapworth, 1873

(Section *Goniograpti*: multiramous forms)

Genus *SIGMAGRAPTUS* Ruedemann, 1904

Type species: Sigmagraptus praecursor Ruedemann, 1904, by original designation.

Diagnosis. — Rhabdosome with two zig zag main stipes with lateral branches off each theca of the main stipe, arranged alternately on both sides. Development dichograptid: *th1*¹ probably originates on prosicula; *th1*² originates low down on *th1*¹, near to sicular aperture and forms one crossing canal. Thecae long slender tubes with overlap up to almost half; thecae of main stipe longer than those of lateral branches.

Remarks. — *Sigmagraptus* is essentially a two stiped *Goniograptus* but differs in its mode of branching from the only *Goniograptus* known in any detail (Jaanusson 1965) in that it lacks an accessory theca and has each theca of the main stipes as a dicalycal theca. This means that "lateral branching" of *Sigmagraptus* is different from the "dichotomous branching" of *Goniograptus* (see discussion under "Remarks" of *S. praecursor* description).

Bulman (1970) considers the thecae of *Sigmagraptus* to have little overlap, but Ruedemann (1904) depicted overlap of almost $\frac{1}{2}$, and the present material confirms this (Fig. 3B) even though it is not clearly seen in flattened specimens.

The Quebec specimens are associated with *Didymograptus bifidus*, *D. extensus*, *D. nitidus*, *D. patulus*, *Phyllograptus*, species of *Tetragraptus*, including *T. serra*, *T. fruticosus*, and *Dichograptus octobrachiatus* in the C zone of the Levis shales, that is approximately *extensus* zone Arenig. Very few species have been recorded in the genus. Ross & Berry (1963) place *Bryograptus kirki* Ruedemann (1947) in *Sigmagraptus? kirki*, but the present writer agrees with Ruedemann. The following Australian species of *Sigmagraptus* have been recorded: *S. crinitus* (T. S. Hall), *S. laxus* (T. S. Hall), *S. yandooensis* Harris & Thomas.

Sigmagraptus praecursor Ruedemann, 1904

(Figs 1—3)

1902. *Coenograptid* gen. nov. et sp. nov.; Ruedemann, p. 566.

1904. *Sigmagraptus praecursor* sp. nov.; Ruedemann, p. 702, Text-fig. 93; Pl. 5, Figs 13—14.

1915. *Sigmagraptus praecursor* Ruedemann; Bassler, pp. 1156—1159.

1947. *Sigmagraptus praecursor* Ruedemann; Ruedemann, p. 300, Pl. 49, Figs 17—20.

1970. *Sigmagraptus praecursor* Ruedemann; Bulman, p. v112, Fig. 77.5.

?1970. *Sigmagraptus* aff. *S. praecursor* Ruedemann; Dewey & al., p. 81.

Holotype: specimen figured by Ruedemann, 1904, Pl. 5, Figs 13—14 and again 1947, Pl. 49, Fig. 18.

Material. — About 200 specimens, many early growth stages, mostly flattened but not tectonically distorted, but some pyritized or in three dimensions in dolomitized mudstone.

Horizon. — C zone, Levis Shale, Ordovician, from various localities at Levis, Quebec; beds approximately coeval with the *extensus* zone of the Arenig strata in Great Britain.

Description. — The sicula is well seen in many specimens and has a length of 2.0–2.5 mm, usually nearer the latter figure, and an apertural diameter (flattened) of about 0.6 mm. A short portion of delicate nema is often preserved and on one specimen (Fig. 1H) this has a length of 1.5 mm when the sicula is only 1.8 mm grown. The prosicula has been only doubtfully seen in one specimen (Fig. 1I) and appears to be of the order of 0.5 mm in length. The virgella is a short (0.2–0.3 mm), broad process. Figure 1A also shows that when the sicula has reached a length of 1.8 mm, *th1¹* is 0.4 mm long and has its origin very high on the sicula, almost certainly on the prosicula. The high origin of *th1¹* is confirmed by the specimen illustrated in Fig. 1J, but normally the long slender prothecal portion of *th1¹* is exceedingly difficult to discern.

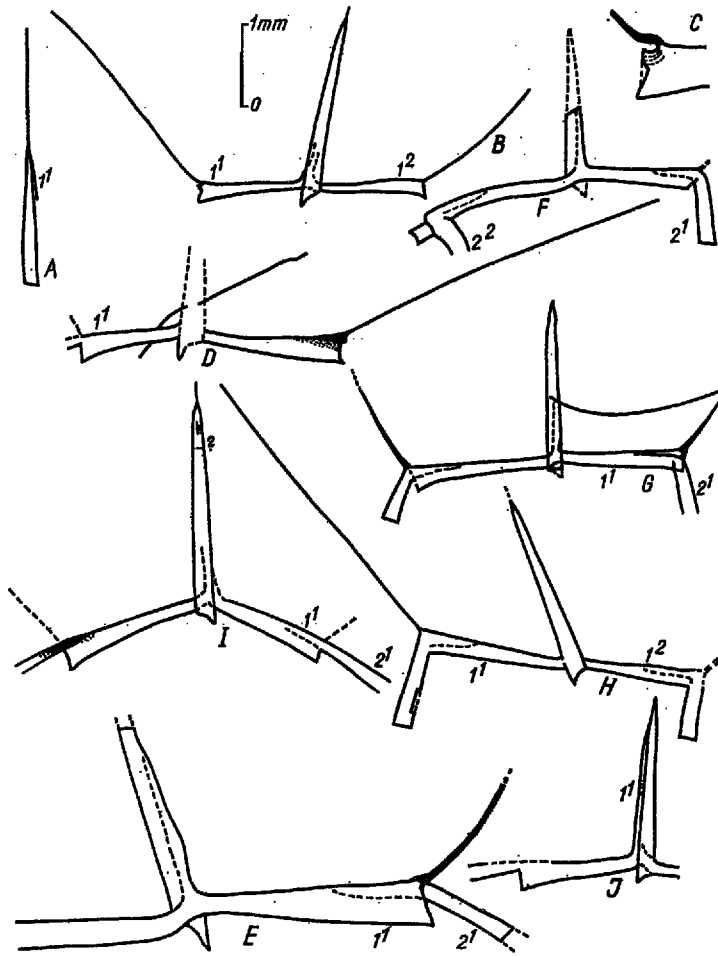
Th1¹ grows downwards on the virgella side of the sicula, perhaps for as much as 2.0 mm in some specimens, until it reaches the apertural region of the sicula. There it turns outwards and grows away from the sicula at an angle of about 90°, occasionally as much as 120° (Figs 1B, I). This free portion has a length of 1.2–1.4 mm, an initial diameter (flattened) of 0.1–0.15 mm and a slightly flared, denticulate apertural region up to 0.3 mm wide (Fig. 1D). In turning away from the sicula in such a manner *th1¹* leaves the virgella process free and clearly visible in most specimens (e.g. Fig. 1B).

Th1² seems to originate low down on *th1¹* just before the latter leaves the sicula (Fig. 1E, F). It grows away from *th1¹* at a high angle (110–120°), and slightly downwards, thereafter growing away from the sicula at about 90° at the apertural lip of the sicula on the anti-virgella side. In consequence *th1²* reaches somewhat lower than *th1¹* and can easily be recognized because of this even in poorly preserved specimens. There is, therefore, only one crossing canal and the development is of dichograptid type. In most cases, in reverse view (Fig. 1F), *th1²* grows across the front of the sicula, but in a few specimens (Fig. 1J) the opposite seems to be the case. In the specimen shown in Fig. 1J *th1²* apparently grows across the front (as drawn) and its course is indicated by dashed lines: this specimen is also one of a few with little indication of a zig-zag growth of the main stipe, so that it is just possible that it represents another species. *Th1²* has an unusually variable free ventral wall of 1.20–1.75 mm length, and a total length of up to 1.95 mm. Like *th1¹*, *th1²* has a denticulate aperture, often with a thickened lip, but the denticulation is almost certainly a result of flattening (see below under description of cladia).

The writer has no growth stages *between* the completion of *1¹* and *1²*, but very shortly after they are fully grown each develops a long, very slender, dorso-lateral apertural spine (Fig. 1B, D, E, G, H etc.). These spines may be up to 4.0 mm in length and are directed upwards at approximately 40–50° to the direction of growth of each of the first two theca, so that the rhabdosome as a whole at this stage has the appearance of the latter *W* (Fig. 1B). The spines are certainly apertural in origin (Fig. 1C), and in Fig. 2A the spine on *1¹* is circular in cross section at the position of the small kink (arrowed) and rather spatulate at its tip. Subsequently the first two lateral branches of the rhabdosome grow along the spines and the latter are thus best regarded as pseudovirgulae, albeit at present unique amongst Ordovician graptolite species.

Following development of the pseudovirgulae *th2¹* and *2²* arise from *th1¹* and *1²* respectively, and usually form a sharp angle with their parent theca (Fig. 1E, H).

and Fig. 2A). The growth of 2^1 (Fig. 1E) is downwards from $th1^1$ at an angle of some $30-40^\circ$ from the latter's line of growth; occasionally the angle may be much as 90° (Fig. 1F, H) and less commonly may continue in the same line as the parent theca (Fig. 1I and Fig. 2C). Thecae $1^1, 2^1, 3^1$ et seq. form one of the two main stipes (Fig. 2D) and thecae $1^2, 2^2, 3^2$ et seq. form the other; in the commonest situation, each theca of the main stipe is at an angle of some $30-40^\circ$ to the theca preceding and the one following (Fig. 2E) so that each main stipe has a pronounced zig-zag appearance. At the angular bends are lateral branches directed alternately upwards and downwards (Fig. 2E, and see below). Figure 1E depicts not only the angular change in growth of the main stipe at the aperture of $th1^1$, but the position of $th2^1$



with respect to this aperture and its pseudovirgula. Such a relationship implies some degree of overlap between $th1^1$ and 2^1 (shown by the dashed line) and this is confirmed in other specimens (Fig. 1G and Fig. 2A) where $th2^1$ clearly originates about 0.5–0.7 mm below the aperture of $th1^1$ and on the dorsal side of that theca. At the aperture itself $th2^1$ turns sharply downwards and away from the pseudovirgula (Fig. 1E, G and Fig. 2A). Figure 1C is an enlargement of the base of the pseudo-

virgella shown in Fig. 1B: there is a slight bend near the base of the spine and an associated embayment in the apertural margin of $th1^1$ with a suggestion of growth lines (dashed). It is not considered that these represent the origin of the lateral branch, but rather that they show the origin of the spine itself from the fusellar tissue of the thecal tube. The preservation is not good, however, and small portions of periderm may be missing along the apertural lip, which is not strongly thickened, an interpretation perhaps supported by the specimen depicted in Fig. 2A.

Figure 1F, H illustrate the further development of $th2^1$ and 2^2 . In Fig. 1I and 1J $th2^1$ and 2^2 are seen developing in a straight line with $th1^1$ and 1^2 , whilst Fig. 2A is of the more usual situation and also confirms that several main stipe thecae develop before the first lateral branch. The writer has seen up to 3 main stipe thecae of the first series and up to 2 of the second completed before lateral branch development (e.g. Fig. 2A). Regrettably there are few growth stages showing the growth of thecae along the pseudovirgulae (Fig. 2B). This last specimen has three completed thecae on the first lateral branch of the first thecal series and approximately 0.5 mm of pseudovirgula projecting beyond them. On the same specimen one and a half thecae are developed on the first lateral branch of the second series but the pseudovirgula is not preserved. Both main stipes are broken after the first thecae and first lateral branch. It is fairly common to find lateral branch fragments with a pronounced dark rod along the dorsal wall (Fig. 3A, C) which certainly represents the pseudovirgula. These fragments are presumably of the first pair of lateral branches: that they are often longer than three thecae indicates that the pseudovirgulae must grow with the branches.

Initial lateral branch development is difficult to understand. It is certain that th^n of the main stipe gives rise to th^{n+1} of the main stipe by a dorsal bud some

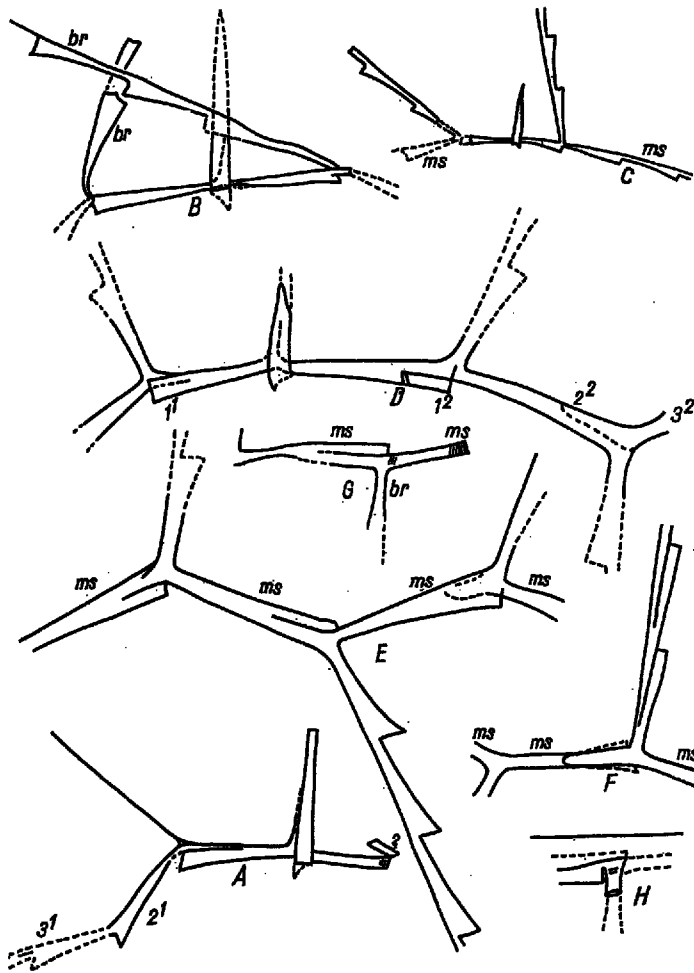
Fig. 1

Sigmagraptus praecursor Ruedemann, 1904

- A — sicula and early growth of $th1^1$ with long nema preserved; Lauzon County, R. Bureau Colln., same slab as E & H
- B — pseudovirgulae developed but $th2^1$ and 2^2 not yet started, obverse view; section 100, Lauzon County, R. Bureau & J. Riva Colln.
- C — enlargement of base of spine of $th1^1$ of B
- D — early growth stage with part of $th2^1$ developed; black area near aperture of $th1^2$ is early overlapping growth of $th2^2$; same locality as B, slab now labelled R. B. R. 2; *D. extensus*, *D. nitidus* on same slab
- E — showing growth of $th2^1$ and long adpressed portion of $th1^1$; same slab as A and H
- F — $th2^2$ slightly less well developed than $th2^1$, pseudovirgulae probably broken off; Lauzon County, R. Bureau Colln.
- G — $th2^1$ has thin periderm, is more advanced than $th2^2$, and growth stage is about the same as F
- H — some growth stage as F and G, but showing full development of pseudovirgula from aperture of $th1^1$; same slab as A
- I — junction of prosicula and metasaccula possibly preserved; early growth of $th2^2$ very blackened; pseudovirgulae broken; locality N 200, Lauzon County, J. Riva & R. Bureau Colln. Suggested course of $th1^1$ & 1^2 across front of sicula — dashed line
- J — origin of $th1^1$; apparent growth across front of sicula (as drawn) is indicated by dashed lines; specimen pyritized and immediately adjacent to specimen depicted in D

All figures are $\times 15$ except C & E, which are $\times 30$.

0.5—0.7 mm below the aperture of n (Fig. 2E). The origin of th^{n+1} is sometimes seen as a distinct lump (Fig. 2F). There is usually a sharp change in the angle of growth as th^{n+1} leaves the apertural region of th^n (Fig. 2E) and the lateral branch appears to arise at this point on th^{n+1} and to grow away at a high angle to the parent stipe (Fig. 2E, F). Although there are few growth lines on the material to hand, some three dimensional specimens (Fig. 2G, H) strongly suggest that this is the correct interpretation of the origin of the first theca of the lateral branch. Figure 2G shows the high angle the branch makes with the parent stipe, but when this part of the specimen was lifted clear of the rock with a fine needle the relationship seen in Fig. 2H was apparent. The last figure is drawn laterally reversed for ease of comparison with Fig. 2G and it demonstrates almost conclusively the budding of the



first theca of the branch from th^{n+1} in the region of the aperture of th^n . Thus each main stipe theca is dicalycal and gives rise to a lateral branch at 0.5—0.7 mm from its origin and to the next main stipe theca some 0.5—0.7 mm before its aperture. In such material in the rocks the true orientation of the various parts of the rhabdosome with respect to each other is not always clear, but if the main stipe thecae of the second series all have the same dorso-ventral orientation (whilst changing their

direction of growth slightly) then the lateral branches are budded off alternately to the left and upwards and to the right and downwards (Fig. 2D, E). Those of the first series bud off to the right and upwards and to the left and downwards (Fig. 1E and Fig. 2A).

No pseudovirgulae have been observed in connection with lateral branches following the first pair and, bearing in mind the number of specimens available, it seems likely that they are restricted to the first pair. This is supported by the fact that later branches do not seem to have a solid black rod along their dorsal margins whilst the few possible growing ends are quite bluntly terminated projecting forwards only a little in the dorsal region.

Thecal spacing on the branches is usually of the order of 8 in 10 mm although a few specimens have been observed with as few as 5 in 10 mm (Fig. 3A, C). Thecal overlap on flattened specimens is difficult to see but it is clear from pyritized material (Fig. 3B) that overlap involves about half the ventral wall of each theca. It is also clear from such specimens that the thecal apertures of the lateral branch thecae (and probably also the main stipe thecae) are relatively simple. The apparently denticulate nature is almost certainly introduced during flattening of the stipes, as is the increased dorso-ventral width: whilst flattened branch fragments one up 0.4 mm wide, those in relief are about 0.25–0.3 mm. With such a relatively high thecal overlap the first theca of each lateral branch must be shorter than subsequent thecae, which is the opposite of the situation usually obtaining in cladia-bearing graptolite species. Most lateral branch thecae have a length of 1.5–1.7 mm, except the first which may be only 1.2 mm long. Main stipe thecae, except *th1¹* and *1²* have a total length of the order of 2.6 mm and a free ventral wall of up to 2.0 mm.

Some bedding planes have specimens almost certainly referable to *S. praecursor* in which the first pair of lateral branches is pendant from the main stipes and the following pair reclined. The writer has obtained none with pendant pseudovirgulae, and where pendant first and second branches are observed all the specimens

Fig. 2

Sigmagraptus praecursor Ruedemann, 1904

- A — further growth of first series main stipe just before first lateral branch; Lauzon County, Colln. R. Bureau
- B — first pair of lateral branches (*br*) growing along pseudovirgula; first branch ahead of second in development; second pseudovirgula not preserved and thecae of main stipe broken after *1¹* and *1²*; same slab as Fig. 1E. Suggested course of *th1¹* in front of sicula indicates by dashed lines
- C — as B, but with main stipes (*ms*) preserved and lacking the usual zig-zag structure; same slab as Fig. 1D
- D — showing development of main stipe zig-zag and lateral branches; same locality as Fig. 1D, labelled R. B. R. 2.
- E — more distal thecae of zig-zag, and growth of lateral branches; locality N 200, Lauzon County, J. R. and R. Bureau Colln.; *ms*, main stipe theca
- F — formation of lateral branch from main stipe theca (*ms*); Trans-Canada Highway, chainage figure 463 00, Lévis, specimens in dolomitic rock; pendant, horizontal and reclined didymograptids at same locality and on same slab
- G & H — development of lateral branch from high angle bud; Lauzon County, R. Bureau Colln.; *ms*, main stipe thecae; *br*, lateral branch

All figures are $\times 15$ except C, which is $\times 5$

on that bedding plane are the same. In other respects they are indistinguishable from "normal" specimens of *S. praecursor*.

Remarks. — The Quebec material closely resembles the originals described by Ruedemann (1904) particularly in the shape of the rhabdosome, the length of the internodes with one lateral branch to each main stipe theca, the lateral branch thecal spacing and the dorso-ventral width of the stipes. Thecal overlap is about the same in both cases. Early growth stages and development and the nature of the sticula were not described by Ruedemann.

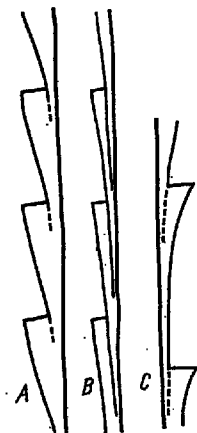


Fig. 3

Sigmagraptus praecursor Ruedemann, 1904

A & B — thecae of lateral branches, latter in pyrite in relief; same slabs as Fig. 2F

C — unusually widely spaced thecae possibly of a lateral branch or of distal extremity of a main stipe, apertural lip thickened; locality N 200, Lauzon County, J. Riva and R. Bureau Colln.

All figures are $\times 15$

Although the side branches of *S. praecursor* are technically lateral branches, their development is very similar to the dichotomous branching described by Skelvington (1965) in the case of dichograptid sp. A, except that in the former each main stipe theca is dicalycal and not merely the one involved in the branching. Dichograptid sp. A is shown diagrammatically by Bulman (1970, Fig. 64d); in this figure if the thecal aperture of th_n is brought back to the point where $th_{(n+2)^a}$ arises from $th_{(n+1)}$ then the situation is very close to that in *S. praecursor*. $Th_{(n+2)^a}$ would have to be shortened, and each "main stipe" theca be dicalycal, before the exact *praecursor* situation was obtained. The similarity is such that it raises the whole question of the distinction between dichotomous branching and lateral branching.

Perhaps a closer comparison of branching can be made between *S. praecursor* and *Goniograptus* sp. (Jaanusson 1965). The two genera have similar rhabdosomal plans, *Goniograptus* having four zig-zag stipes and *Sigmagraptus* two. But the dichotomous branching in Jaanusson's material (the only ones known in any detail) involve an accessory theca interposed between each of the dicalycal main stipe theca. It is a strangely complex arrangement because if the accessory theca is (hypothetically) removed (see Jaanusson 1965, Fig. 4) and the succeeding two thecae brought back to the preceding main stipe theca, then the development is exactly that in *S. praecursor* as described herein.

The branching in *Goniograptus* sp. could be described either as dichotomous or lateral, and that in *S. praecursor* as lateral branching, but the latter is so close to the clearly dichotomous divisions in dichograptid sp. A that the distinction seems some what forced to the present writer.

At the distal extremities of the main stipes in Ruedemann's original specimens there is a number of thecae developed with no lateral branches. It is possible that the widely spaced thecae mentioned above (Fig. 3C) are in reality from this part

of the rhabdosome: on the other hand some of these appear to have a black rod along the dorsal side of the stipe.

It remains to comment upon the function of the pair of pseudovirgellae. That they are not necessary for lateral branch growth is strongly suggested by the probable absence of them on later branches. Therefore their main function must have been during the early growth of the colony (Fig. 1B, D, E etc.). Naturally the long sicula, thecae and spines disposed in a letter W arrangement would facilitate buoyancy and consequent transport by currents, and if the spines were solid rods unconnected with much thickness of living tissue the rhabdosome might well have drifted with the prosicula downwards and spines pendant. However, since the spines and nema were coated by a relatively extensive sheet of extrathecal tissue this may have provided buoyancy in the form of vacuolated tissue and the rhabdosome could have drifted prosicula upwards: perhaps supporting this contention is that those rhabdosomes with pendant first pair of lateral branches (which would tend to keep the prosicula upwards) apparently lack pseudovirgulae. Subsequent development of the colonies is complex and clearly the necessity for pseudovirgulae, and even a nema is lost. On present knowledge one can only suggest that the mode of life changed in some manner, perhaps slightly, from the early to the late growth stages.

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R. B. RICKARDS

**POWIĄZANIE PSEUDOVIRGULI Z LATERALNYM ODGAŁĘZIENIEM
U GATUNKU DICHOGRAPTIDÓW**

(Streszczenie)

Na podstawie materiału spłaszczonego oraz zachowanego w reliefie pochodzącego z Quebecu (Kanada) podano opis i niektóre szczegóły rozwoju *Sigmagraptus praecursor* Ruedemann. Wykazano, że wczesne stadia wzrostu kolonii posiadają długą pseudovirgulę, rozwijającą się po stronie dorso-lateralnej apertur $th1^1$ i $th1^2$, wzdłuż której wzrasta w górę pierwsza para lateralnych odgałęzień. *Sigmagraptus praecursor* Ruedemann wykazuje rozwój dichograptidowy; $th1^2$ tworzy pojedynczy kanał i rozwija się z $th1^1$, która bierze prawdopodobnie swój początek od prosiculi. Pseudovirgula i jej powiązanie z lateralnym odgałęzieniem nie była dotychczas znana wśród ordowickich graptolitów. Sugeruje się, że pseudovirgula mogła być pomocna przy stateczności, stabilności i orientacji wczesnych stadiów wzrostu kolonii.

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