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BENDIGONIAN GRAPTOLITES (HEMICHORDATA) OF VICTORIA

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Abstract

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Sixty graptolite species and subspecies are described mostly from the Bendigonian, but including a few involved in a proposed reclassification of the family Dichograptidae. Emphasis in choice of described species is placed upon those more or less endemic to Victorian sequences. Two new multiramous dichograptid genera are described: *Kellamograptus* and *Praegoniograptus*. The following new species are described: *Clonograptus erdtmanni*, *Orthodichograptus wilkinsoni*, *Tridensigraptus zhaoi* and *Zygograptus stewarti*. The genus *Clonograptus* is informally divided into two groups with differing thecal type; and the subfamily Dichograptinae is redefined and subdivided into the following sections: Anomalograpti (nov.); Dichograpti (Group A, emend. Group B, nov.); Temnograpti (emend.); Schizograpti (Group A, emend.; Group B, nov.); Pendeograpti (nov.); Tetragrapti (emend.); Mimograpti (nov.); Didymograpti (emend.). The scheme depends on the recognition of a proximal end template based upon the following modes, coupled with an appraisal of the branching type: clonograptid mode; dichograptid mode; tetragraptid mode; didymograptid mode. The subfamily Sigmagraptinae is redefined to include *Praegoniograptus* and to exclude *Laxograptus*. The following genera are redefined: *Clonograptus*, *Tetragraptus* (*Pendeograptus*), *Sigmagraptus*, *Goniograptus* and *Trichograptus*. Reconstructions are attempted for the first time of several of the giant dichograptids.

The general evolutionary framework of Bendigonian graptolite faunas is briefly described and several possible lineages are outlined, notably the *Goniograptus macer* to *Didymograptus gracilis* plexus; the *Clonograptus* to *Tetragraptus chapmani* line; and the possible *Adelograptus* to *Didymograptus adamantinus/perditus* line.

A study of the Pendeograpti results in *Pendeograptus pendens* and *P. fruticosus* being redescribed in terms of their detailed proximal development. The stratigraphic occurrences of these two are revised in such a fashion that the recognition of the Bendigonian Be1–Be4 subdivisions is enhanced.

The foregoing has resulted in necessary clarification of rhabdosomal terminology, and in a discussion of dichograptid branching patterns in multiramous genera and species.

Contents

Introduction

The Bengidonian (early Arenig) graptolite faunas represented a critical stage in the evolution of graptolites being the first very rich graptolite assemblage (Fig. 31) derived from an oceanic plankton. The Victorian localities, particularly around Bendigo, are probably the richest in the world for graptolites of this age and the preservation is in our view rather better than is conveyed in previous literature, although specimens have not so far been chemically isolated from the rock matrix. It is our long term intention to examine further the hydrodynamics of particularly the giant dichograptids but the present purpose is to document the diversity of Bendigonian graptolite faunas, concentrating on endemic forms, and to place them in an international setting. The research has posed a whole series of questions related to classification of the anisograptids and dichograptids. We have felt it incumbent on us to comment in preliminary fashion upon the Bendigonian stratigraphy, the evolution of some graptolites, and the mode of life and preservation of others. In the sphere of stratigraphy there is surely much more work to do although of course the Bendigonian is already more subdivided than is the Arenig in many parts of the world. But the potential for further fine subdivisions will increase as geologists continue to log temporary sections and to recollect others. In the palaeontological sphere it is possible that with a revision of several Scandinavian and North American faunas long overdue some of the apparently endemic Victorian forms might prove to be junior synonyms but we have been unable to confirm this. We have, in fact, concerned ourselves largely with full and proper descriptions of the Bendigonian graptolites and a small number of species from other horizons which tie in with them in some evolutionary or classificatory manner. These latter are listed in Table 1 along with Bendigonian species.

Most of the material described is housed in the collections of the Museum of Victoria in Melbourne. Specimen numbers are prefixed by P; where appropriate, numbers in brackets following the P numbers are the old numbers of the Geological Survey of Victoria (often these latter are the only numbers previously published). Specimens from other museum depositories are mentioned by institution as appro-

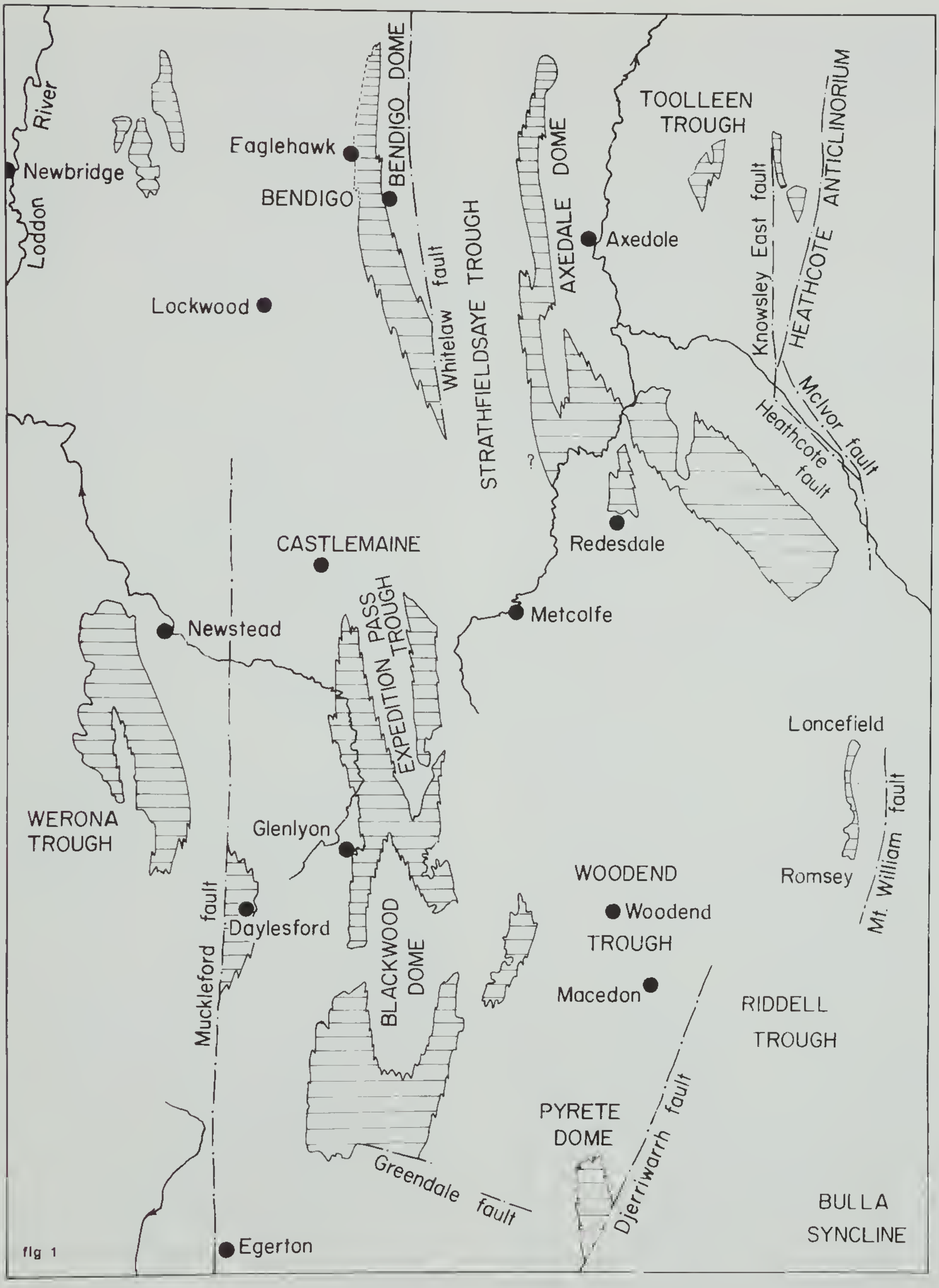


Figure 1. Locality map showing Bendigo and Central Victorian Goldfield region and general distribution of Bendigonian strata with position of some of the main localities mentioned in the text. With permission of the Department of Minerals and Energy.

priate. Always a scale bar of 1 mm or 5 cm is given with text-figures and an appropriate scale bar with the plates.

The selection of type species for existing genera follows Bulman (1970).

Bendigonian stratigraphy

It has long been recognised that the Bendigonian can readily be divided into four successive subdivisons based upon faunal changes, Be1–Be4, the last being the latest. Largely this has been a result of research over many years by T.S. Hall and by W.J. Harris and D.E. Thomas, and supplemented more recently by collections made by officers of the Mines Department (Geological Survey of Victoria). Most of the material collected by Hall, Harris and Thomas is now held by the Museum of Victoria, and officers of both departments have been responsible for much accurate curating of the collections. Although our own stratigraphic notes lean heavily on the earlier results of Harris and Thomas (e.g. 1938b) and, indeed, to a considerable extent confirm them, we have incorporated in Table 1 not only our own findings but those of several modern workers who have given us access to unpublished stratigraphic or locality information, most notably O.P. Singleton, F. VandenBerg and I. Stewart. We have also reexamined the Harris and Thomas faunal lists for a large number of localities in the Bendigo region. They had over 2 600 Ordovician graptolite localities in the vicinity of Bendigo alone. Of this number more than 500 are referable to the Bendigonian. Not all the faunas have been fully worked out but most of the information gaps are in the Chewtonian, Yapeenian and Castlemainian, not the Bendigonian.

From this we gained a little more insight into the work of Harris and Thomas and in particular which criteria they used in practice for distinguishing Be1–Be4. In addition to examining these Bendigonian faunal association records we have examined the many trays of Bendigonian graptolites in the Museum of Victoria. During this last exercise we recorded the species occurrences on well over 1000 graptolite slabs from numerous localities and from Be1–Be4. The results are plotted in Table 2. It should perhaps be emphasised that at least half the slabs studied were "as collected" and had not been sorted.

The stratigraphic ground rules established by the above workers have been incorporated in numerous papers dealing with international correlation (e.g. T.S. Hall, 1899; Harris and Keble, 1932; Thomas, 1960a) and have also been summarised by several modern workers (e.g. Dewey et al., 1970; Cooper, 1979; Webby et al., 1981; Cas and VandenBerg, 1988). Beavis (1976) published a range chart of the species most crucial to international correlation, then the most up to date opinion since Thomas (1960a); and also a family distribution diagram based upon the data in Thomas (1960a). In his chart (Beavis, 1976: Table 3.1) there is little distinction between Be1 and Be2, except that the upper part of Be2 lacks *T. approximatus*. His ranges agree with those of Thomas who recorded *T. approximatus* from the lower part of Be2. However, in our examination of the collections (Table 2), the records, and the literature we can find no evidence that this species occurs higher than Be1. This is confirmed by O.P. Singleton (pers. comm.) from his own researches and by Webby et al. (1981) and by Cas and VandenBerg (1988). Even Beavis (1976: 26) stated when writing of the occurrence of *T. fruticosus* and *T. approximatus* "... but in Be2 the latter is absent". On the evidence we agree with this statement but not the range chart. Beavis also stated (1976: 26) that "the anisograptids are restricted to the lowest zones of the Ordovician sequence – the Lancefieldian" yet his chart (fig. 31, second page) shows them ranging into Be1, and our own research (Table 1) has them ranging into Be2. Thomas (1960a) had *Clonograptus* sp. ranging as high as the Darriwilian although he regarded that group as belonging to the Dichograptidae not the Anisograptidae. Beavis (1976) distinguished Be2 from Be3 in that *T. fruticosus* (3 branched) appears half way up the latter division (again agreeing with Thomas' 1960a range). Thomas himself, in the above mentioned Mines Department unpublished records, commonly used an association *T. fruticosus* 3 and 4 branched as an indication of Be3. However, our own observations show that the 3-branched forms appear rarely in Be2 and are fairly common throughout Be3. Webby et al. (1981) did not record 3-branched forms from Be2, and nor did Cas and VandenBerg (1988). Again, Singleton's independent observations (pers. comm.) confirm that *T. fruticosus* occurs throughout Be3. We have no records of 4-branched forms from Be3, thus giving a very clear distinction of Be2 and Be3 in terms of this species at least. But it should be noted that Webby et al. (1981) and Cas and VandenBerg (1988) recorded these from both Be3 and Be4, though the former paper noted that they are rare (1976: 3). As far as we can tell this is the only important inconsistency in Thomas' ranges. Where independent evidence exists in the faunal lists or in the Museum of Victoria collections an association of 3- and 4-branched *T. fruticosus* indicates Be2, not Be3. Clearly this matter will be resolved by field work in the future.

It is our opinion that in terms of what may be described as more or less cosmopolitan species the following distinctions of Be1–Be4 may be regarded as workable (but see also Webby et al. 1981: 3 and Fig. 2):

1. Be1 is typified by an association of *T. approximatus* and *T. fruticosus* (4-branched).
2. Be2 is characterised by an association of *T. pendens* and *T. fruticosus* (4-branched). *T. approximatus* is absent and *T. fruticosus* (3-branched) does occur but is not common.
3. Be3 still has *T. pendens* fairly common, *T. fruticosus* (3 branched) with rare *T. fruticosus* (2-branched: which incidentally we do not regard as synonymous with *D. vfractus* as was suggested by Thomas (1960b)). It should be noted that an association of a limited number of specimens of *T. pendens* and *T. fruticosus* (3-branched) would not in itself be enough to distinguish Be2 from Be3. Sufficient specimens would be needed to show that *T. fruticosus* (4-branched) were absent.
4. Be4 has an abundance of *T. fruticosus* (3-branched) in association still with *T. pendens* (Now less common).

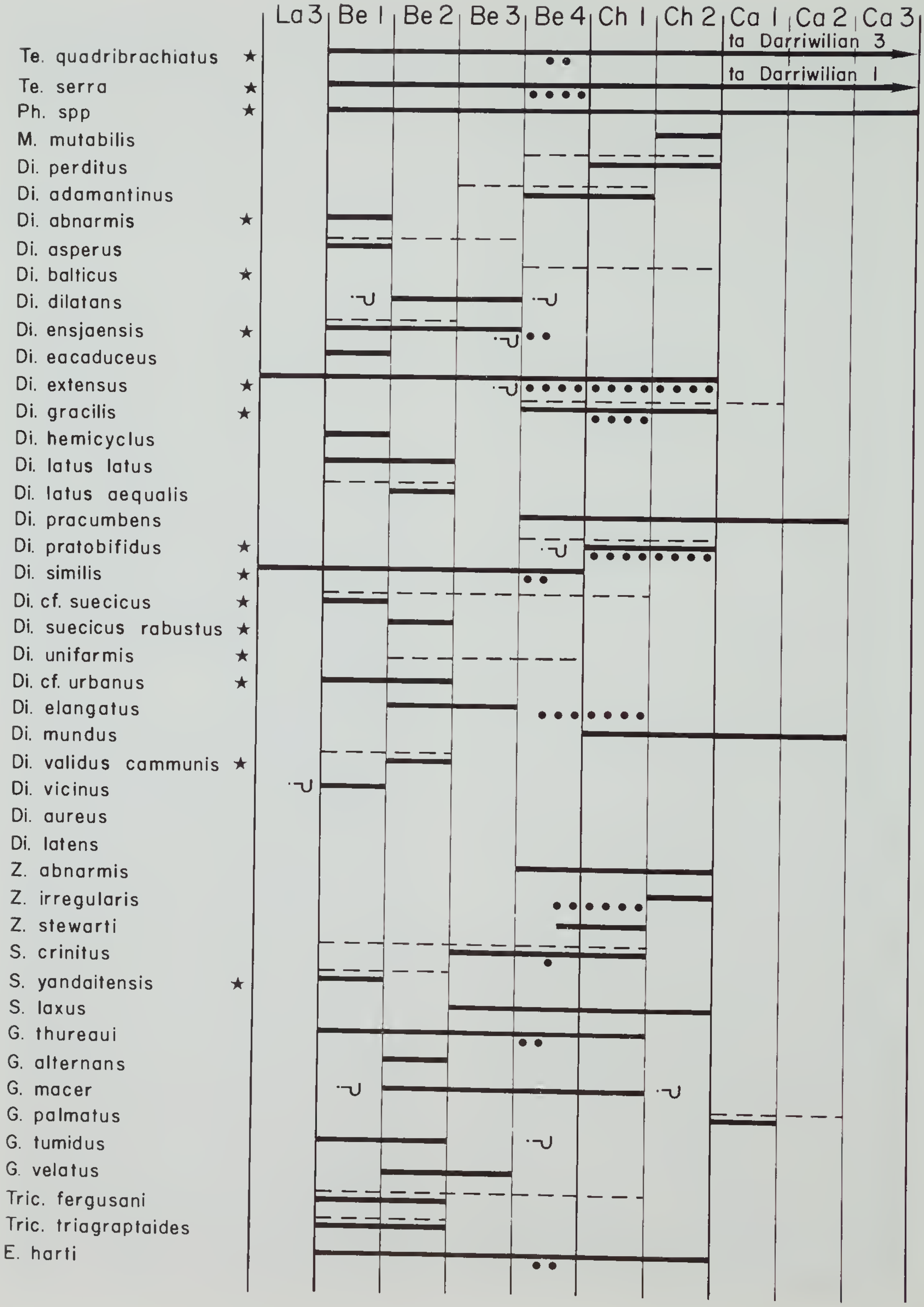
However, this consideration of the faunal differences of Be1–Be4 in terms of internationally valuable species is in one sense rather a negative approach. It will be clear from Tables 1 and 2 that a number of endemic species are extremely important in distinguishing Be1–Be4 in Victoria. For example *Pseudobryograptus crassus* and *T. acclinans* are fairly common in Be1 but occur no higher. Similarly several clonograptids occur in Be2 (*C. ramulosus*, *C. trochograptoides*) and not in Be1, and vice versa. As always Be3 is the least distinguished but *S. laxus* appears here, as does *D. deflexus*, and *T. bryonoides* with *T. fruticosus* (2-branched). Be4 has, in addition to the above mentioned, *Praegoniograptus timidus* (in profusion at some localities according to Harris and Thomas (1939)), orthodichograptids (rare), *D. adamantinus*, *D. gracilis*, *D. procumbens*, *Zygograptus abnormis*, and *Z. stewarti*. Table 2 also emphasises several other important facets of the distribution of Bendigonian graptolites. It is immediately clear that the Pendeograpti and Tetragrapti dominate the faunas, particularly the former. In our examination c Harris' Mines Department (Geological Survey of Victoria) records we found that 98.5% of Bendigo Bendigonian localities have *T. fruticosus* present making it very useful in stratigraphy when the above mentioned evolutionary changes are related to numbers of specimens. The Didymograptini are almost as important numerically. In contrast the multiramous anisograptids and dichograptids are a relatively small element of the whole fauna (often recorded as 5 specimens or less on Table 2). This is in accord with general evolutionary trends, discussed below, towards rapid phasing out of multistiped species.

International correlation of the Bendigonian

The most recent correlations of Be1–Be4, with which we readily concur, are those of Beavis (1976), Cooper (1979), Cooper and Fortey (1982), Dewey et al. (1970), Jackson (1964), Skevington (1968) and Webby et al. (1981). The Bendigonian is essentially Arenig in age, the base of Be1 corresponding roughly to midway up the *approximatus* Zone as far as the latter is recognised internationally: the distinction between La3 and Be1 suggests that the *approximatus* Zone elsewhere may be capable of further useful subdivision. Be3 and Be4 correspond approximately to the *D. deflexus* Zone and in fact the eponymous species appears at the base of Be3 (Table 2) in Victoria, which the present writers confirm.

What is of interest is a comparison we have made of the Spitsbergen species occurrences of Cooper and Fortey (1982) with those in Victoria (Tables 1 and 2), both being within the Pacific Faunal Province. Of the 61 species or subspecies so far recorded from the equivalents of the Bendigonian to Castlemainian in Spitsbergen only 25 are common to Spitsbergen and Victoria, in which latter region we can list 110 species or subspecies. Comparing the Bendigonian alone there are perhaps 19 or 20 forms common to both areas, but if Be1 and 2 are excluded (probably absent in Spitsbergen) there are 32 species in the Spitsbergen list and 31 in the Victorian rocks. Of these 17 are common to both regions. However, the common element could be slightly greater because exact correlation of the two regions may not yet have been achieved. Our revision of the Victorian sequence does note that, accepting the Cooper and Fortey correlation, several species occur later in Spitsbergen than in Victoria, possibly suggesting that V_1 in Spitsbergen may go down into Be2 time.

Nevertheless it is of note that intermediate correlation is effected by a relatively small number of cosmopolitan species such at *T. fruticosus*,


La 3
Be 1
Be 2
Be 3
Be 4
Ch 1
Ch 2
Ca 1
Ca 2
Ca 3
to Darriwilian 3
to Darriwilian 1
Te. quadribrachiatus ★
Te. serra ★
Ph. spp ★
M. mutabilis
Di. perditus
Di. adamantinus
Di. abnarmis ★
Di. asperus
Di. balticus ★
Di. dilatans
Di. ensjaensis ★
Di. eacaduceus
Di. extensus ★
Di. gracilis ★
Di. hemicyclus
Di. latus latus
Di. latus aequalis
Di. pracumbens
Di. pratobifidus ★
Di. similis ★
Di. cf. suecicus ★
Di. suecicus rabustus ★
Di. unifarmis ★
Di. cf. urbanus ★
Di. elangatus
Di. mundus
Di. validus communis ★
Di. vicinus
Di. aureus
Di. latens
Z. abnarmis
Z. irregularis
Z. stewarti
S. crinitus
S. yandaitensis ★
S. laxus
G. thureaui
G. alternans
G. macer
G. palmatus
G. tumidus
G. velatus
Tric. fergusani
Tric. triagraptaides
E. harti

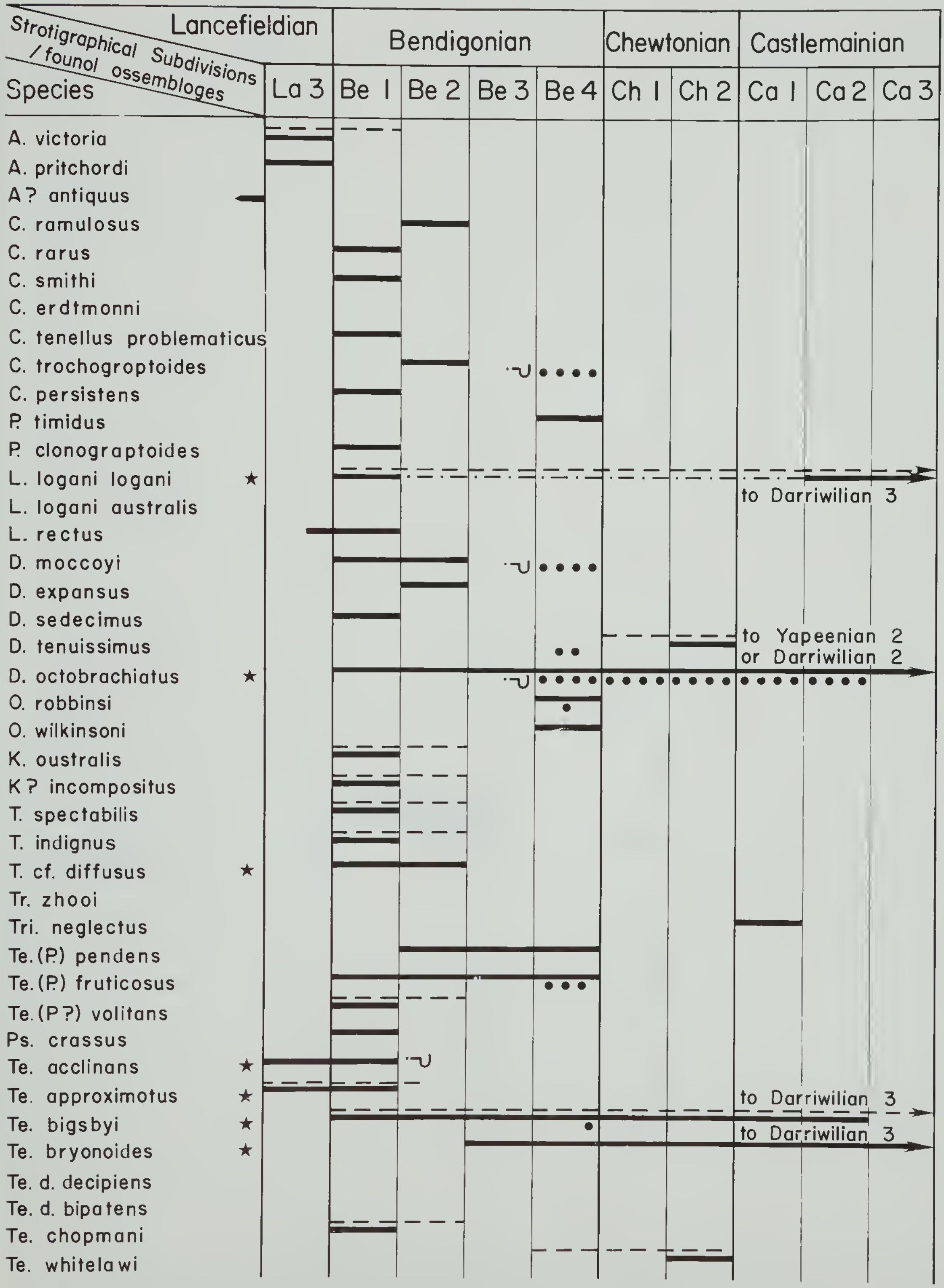


Table 1. Ranges of Bendigonian graptolites, and some others described in this paper, based upon Thomas (1960) and other papers, our own observations, and further corrected from two manuscript revisions of the Thomas paper by O.P. Singleton (pers. comm.) and one manuscript revision by VandenBerg (pers. comm.). Those species marked with an asterisk are more cosmopolitan species not described in this paper, but which are valuable in international correlation. Dashed lines indicate Thomas (1960) ranges where these disagree with current views. Dotted lines give the approximate position of species described by Cooper and Fortey (1982) which are common to Spitsbergen and Victoria.

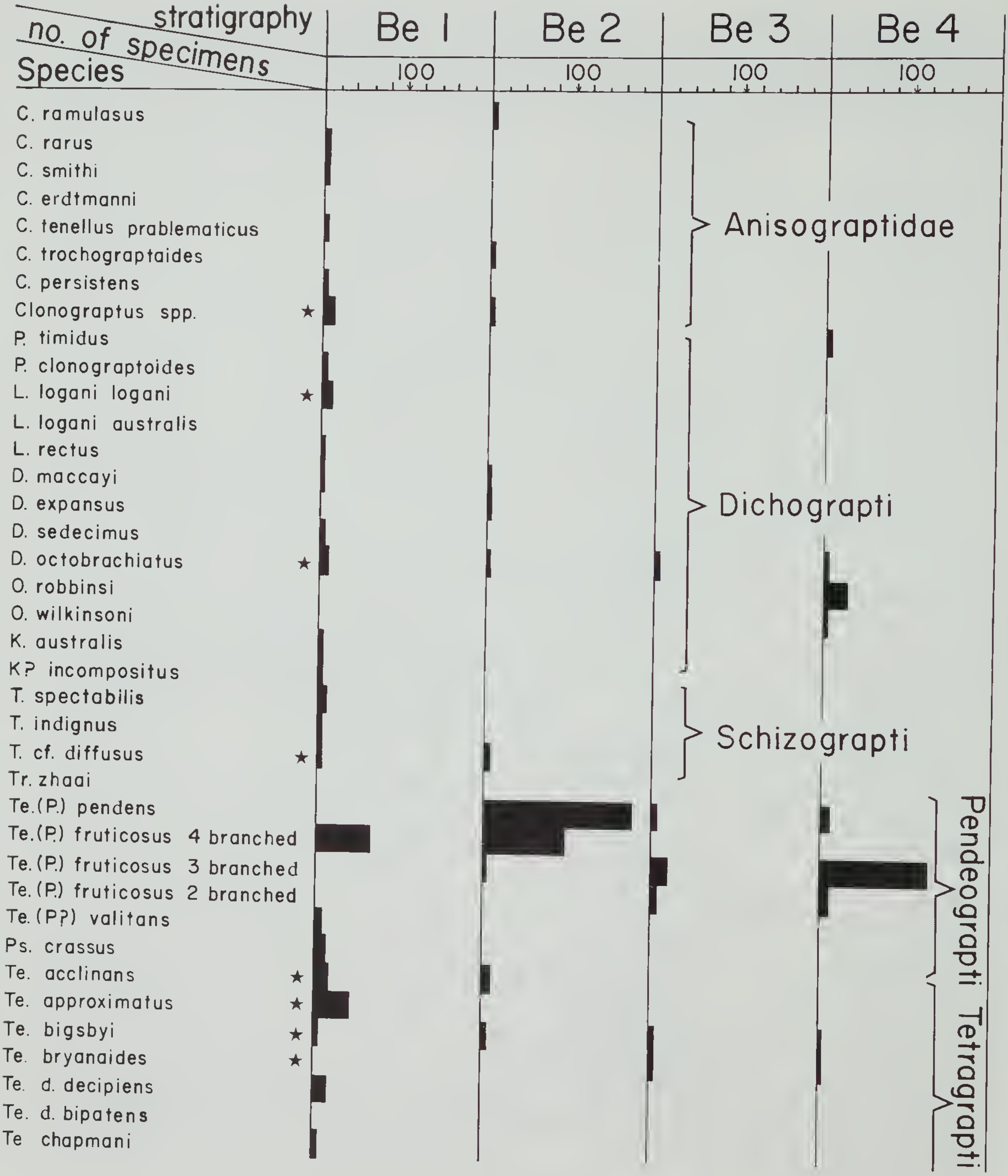


Table 2. Numbers of specimens of Bendigonian species per zone deduced from the collections, type and supplementary, in the Museum of Victoria. Over 1000 slabs were examined, about half from identified and largely curated collections, the remainder from unsorted, unidentified collections. Further discussion in text. Asterisks indicate species not described in this paper.

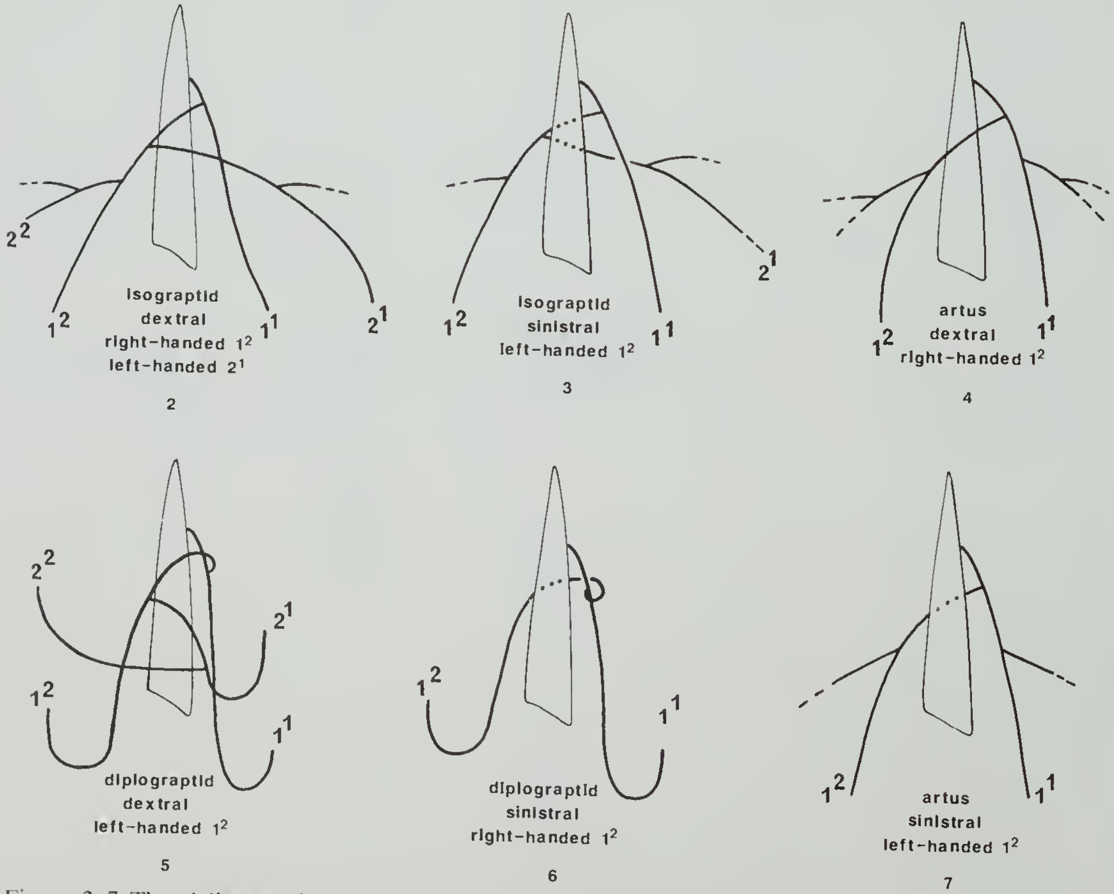

Be 1
Be 2
Be 3
Be 4
Te. quodribrochiatus
Te. serro
Ph. spp ★
Di. perditus
Di. odomontinus
Di. obnormis ★
Di osperus
Di. bolticus ★
Di. dilatans
Di. ensjoensis ★
Di. eacaduceus
Di. extensus ★
Di. grocilis ★
Di. hemicyclus
Di. latus latus
Di. latus aequalis
Di. procumbens
Di. protobifidus ★
Di. deflexus ★
Di. similis ★
Di. cf. suecicus ★
Di. suecicus robustus ★
Di. cf. urbonus ★
Di. elongatus
Di. mundus
Di. vicinus
Di. aureus
Di. lotens
Z. abnormis
Z. stewarti
S. crinitus
S. yandoitensis ★
S. laxus
Sigmagroptus spp. ★
G. thureaui
G alternons
G. macer
G. tumidus
G. velatus
Tric. fergusani
Tric. triogroptoides
E. harti.
B. etaformis ★
Didymograpti
Temnograpti
Sigmagraptinae

D. protobifidus, D. ensjoensis, D. extensus, Di. octobrachiatus etc.

Rhabdosome terminology

The descriptive terminology used in this paper is essentially that of Bulman (1970) with additions by Cooper and Fortey (1982) and those necessitated by the present work which are defined in this section and the next, dealing with branching patterns. We entirely support the conclusions of Cooper and Fortey with respect to designation and significance of *artus* and isograptid development and their contention that there is more hope of deducing dichograptid phylogeny from proximal structure than from developmental type as such.

The same authors rightly draw attention to the distinction between what is (biologically) right or left handed and what in developmental terms is dextral or sinistral. A right handed origin for a theca is when it originates, with respect to the parent sicula or theca, in right handed fashion, that is, on the right (figs 2–7) *when viewed (laterally) in "reverse" view as opposed to "obverse" view* (obverse view is that which in most graptolites gives the clearest view of the metasicula; the early thecae grow over the reverse wall of the sicula). A dextral mode of development is where a crossing canal grows in a clockwise (or dextral) sense with respect to the sicula, *when viewed from the more proximal position of the sicular apex* (if viewed from the more distal position of the sicular aperture it would grow in an anticlockwise fashion). Th1^1 is to the right of the sicula in reverse aspect (i.e. the aspect in which the early developing thecae obscure the sicula to a greater or lesser degree). Figs 2 to 7 depict what we take as the distinctions between right and left handedness, and between dextral and sinistral growth. Although we have redrawn some of these figures after Cooper and Fortey we have added others for clarity, and have not distin-



Figures 2–7. Thecal diagrams illustrating various types of proximal development and left and right handedness; 6 and 7 are hypothetical only; full explanation in text.

guished those which have actually been found to occur in nature. and those which are merely hypothetical possibilities for descriptive purposes. We can imagine that in some species (say of diplograptid genera) where the thecal tubes grow in tight profusion at the proximal end, to decide whether a particular thecal origin is right or left handed could be exceedingly difficult, but whether a tube is dextral or sinistral as defined above, should remain a relatively straightforward matter.

In terms of thecal notation it does seem to us that there may be a case for dual terminology, using the Bulman scheme (1970: fig. 53) where the proximal budding is not known. and the (preferred) Cooper and Fortey scheme (1982: fig. 5) where it is. However, the Bulman scheme could be abandoned completely if the Cooper and Fortey (1981, 1982) rule of thumb guide to distal dichotomy becomes "law": that distal dichotomies are achieved by a process which repeats the process of division taking place in the proximal region of the same species. We are inclined to the view that Cooper and Fortey are correct, and we agree with their suggestion to use their new notation scheme for the second dicalycal theca(e) onwards in the case of isograptid development types (*artus* terminology being unaffected by a change).

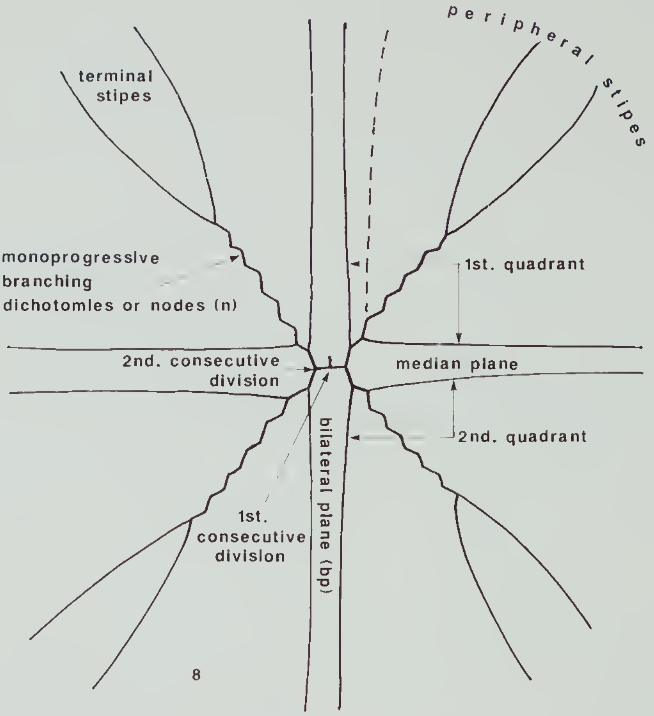
Dichograptid branching patterns

Considerable doubt has been expressed as to the distinction between dichotomous and lateral branching (e.g. Bulman, 1970: V82 et seq.; Rickards, 1976; Cooper and Fortey, 1982). It seems to us that there may be no fundamental distinction possible in terms of development of the thecal tubes and that the practical definition must remain a simple one: a dichotomous division is one in which the two diverging stipes do so at a similar angle with respect to the parent stipe; a lateral division is one in which the parent stipe continues in a more or less straight line, and in which the new stipe grows away as a side branch (figs 21, 25).

Both branching divisions are extensively used by multiramous dichograptids and on occasion it is difficult to distinguish the two, perhaps suggesting that the overall branching pattern and distribution of stipes and thecae is rather more important than the mechanism of branching. Our definitions and usage of consecutive dichotomy, delayed dichotomy, progressive branching, and monoprogressive branching exactly follow Cooper and Fortey (1982) and are illustrated in figs 8–21. However, we do of necessity introduce some new concepts below as a result of our examination of *Goniograptus* in particular. Although we agree with the Cooper and Fortey stipe notation system we have found in practice very little need to use it and have as a rule used simple reference to 1st, 2nd or nth order stipes. Fig. 8 depicts the rhabdosome orientation terminology adopted in this paper.

Fig. 8 also illustrates what we consider the definitive stipes and their arrangement in *Goniograptus*. The bilateral and median planes are each flanked by two pairs of stipes usually derived respectively from the first and second monoprogressive branching divisions. The funicle is defined by the first progressive dichotomy (in this genus = consecutive dichotomy) resulting in two short stipes growing in opposite directions, at right angles to the base region of the sicula (in all these diagrams we show the sicula, for convenience, as though it were in the same plane as the stipes, but in reality the rhabdosome midline is normal to that plane). The second consecutive dichotomy helps define the tetragraptid proximal template from which the whole colony then develops.

From the four established nodes grow four (zig-zag) monoprogressive stipes with monoprogressive branching, one lateral stipe growing from each node. The number of peripheral stipes can be deduced by counting the number of nodes (= monoprogressive branching points) and adding one for each main stipe. For fig. 8, an example of *G. thureaui* based upon the holotype, there are 11 nodes in each quadrant, giving 48 peripheral stipes. Only when the monoprogressive stipe has ended its growth does a pair of terminal stipes develop. Stated in converse, the recognition of the pair of terminal stipes can be taken as proof that the colony is complete in its pattern of stipes. Strictly speaking the terminal dichotomy resulting in the terminal stipe pair is not a monoprogressive division but it forms a distinct node and we have included it in node counts. Different *Goniograptus* species vary not only in the number of nodes in the four main stipes but also in the lengths of the internodes and in the more usually appreciated differences of thecal spacing, length, angle of thecal inclination, dorsoventral stipe width, and stipe length. It should be emphasised that even within one specimen, as well as within one species, there is considerable variation in the number of nodes in the four main stipes. Thus *G. alternans* (fig. 9) has, reading clockwise from the first quadrant, 8, 10, 14, and 11, giving 43 nodes and 47 peripheral stipes; whereas *G. macer* (fig. 17) has 2, 2,


terminal stipes
peripheral stipes
monoprogressive branching dichotomies or nodes (n)
1st. quadrant
median plane
2nd. consecutive division
2nd. quadrant
bilateral plane (bp)
1st. consecutive division

8

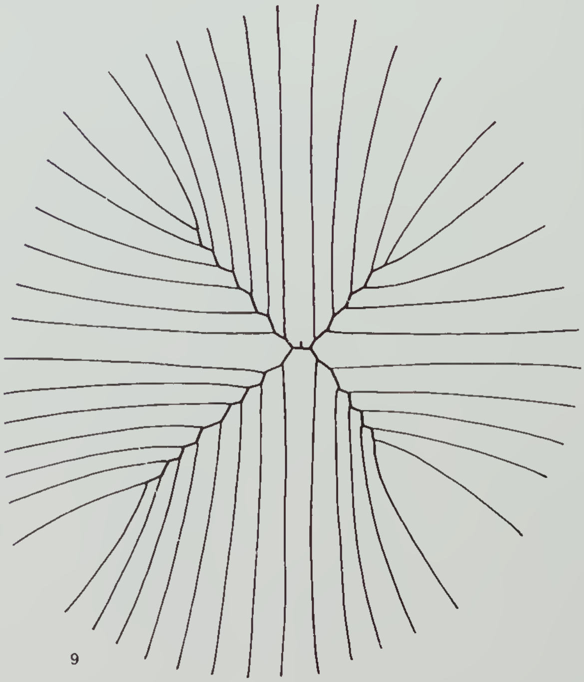


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Figure 8. Basic rhabdosomal elements of *Goniograptus*, based upon the lectotype of *Goniograptus thureaui thureaui* (P12215) which has 11 nodes (n) in each quadrant, 12 peripheral stipes in each quadrant and hence 48 peripheral stipes in total; remaining terminology is applicable to most dichograptids; in following figures the nodal formula (which includes the terminal dichotomy) is given 1st quadrant to 4th as follows (in this case) 11/11/11/11. Figs 8–20 are only roughly to scale and are largely diagrammatic to illustrate rhabdosomal geometry.

Figure 9. Rhabdosomal geometry of *Goniograptus alternans* based upon holotype P14619; 47 peripheral stipes; nodal formula 8/10/14/11.

←

1, and 1, giving 6 nodes and 10 peripheral stipes, almost the minimum possible before the form would be considered referable to *Dichograptus*.

In general, reduction of the number of nodes results not only in fewer peripheral stipes but in smaller rhabdosomes. In some forms the peripheral stipes are unusually long thus maintaining an overall large rhabdosomal diameter. Figs 8–17 depict the variation of branching patterns in some *Goniograptus* species. It is clear that the number of nodes is critical in appraising the branching patterns. In the extreme case of the number of nodes being reduced to one (the terminal dichotomy) the genus *Dichograptus* results. Evolutionary considerations are discussed later. Here it is only our intention to portray the various geometries afforded by varied branching strategies.

Praegoniograptus gen. nov. differs from *Goniograptus* in that more than four zig-zag stipes are developed. That is, the number of consecutive dichotomies on any one developing line is three, the first at the sicula, the second resulting in the *Goniograptus* stage of development, the third in a possible eight main stipes. Following the three consecutive dichotomies are monoprogressive dichotomies resulting in *Goniograptus*-like zig-zag main stipes and conspicuous nodes. However, in *P. clonograptiodes*, the type species of the genus, there is a suppression of one third order dichotomy (i.e. of a third consecutive division along one line of development) resulting in seven main zig-zag stipes (fig. 19). The number of nodes is, reading clockwise from the first quadrant, 2, 4, 4, 0, 3, 4, 3, 2 giving 22 nodes and 29 peripheral stipes.

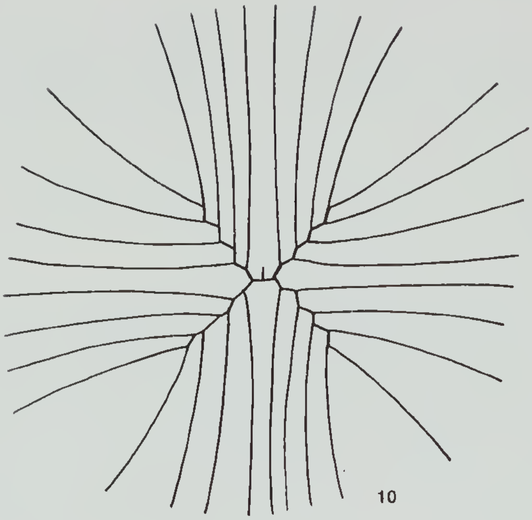
Thus the *Praegoniograptus* pattern differs from the *Loganograptus* pattern in having monoprogressive dichotomies. However, there is one species, *P. timidus*, which we have provisionally retained in *Praegoniograptus*, where the number of monoprogressive divisions *may* have been reduced to one (the terminal dichotomy) whilst retaining the three consecutive dichotomies (fig. 20). Indeed, Harris and Thomas (1939) originally described this species as *Clonograptus*. The original specimen is not well preserved and it may well be that there are some monoprogressive dichotomies present. If not, then the resemblance to *Clonograptus* is considerable and, were the terminal stipes shown to be quite long, the resemblance to *Loganograptus* would be very strong. On present evidence *Praegoniograptus* is clearly the best placement for this species. Again, the evolutionary possibilities are discussed elsewhere, but the related morphological patterns of the above genera is apparent.

Loganograptus has a proximal template like that of *P. timidus* but with elongate terminal stipes. *Clonograptus* lacks the atrophied, proximal, consecutive branching of *Loganograptus* and progressive, largely dichotomous divisions take place even towards the distal extremities of the colony (figs 21, 22).

It seems to us that *Goniograptus* is central, descriptively speaking, to any discussion of branching patterns in early multiramous dichograptids and anisograptids; and its puzzling evolutionary position is discussed later. In relation to those genera with few stipes it should be pointed out that *Sigmagraptus* is really a *Goniograptus* with two main stipes (fig. 151), that is, with only one consecutive dichotomy, the first, (but see Cooper and Fortey's (1982) remarks on *S. yandoitensis*, and comment herein) and numerous monoprogressive dichotomies. We know of no morphological patterns that could have resulted from a reduction of the number of nodes in *Sigmagraptus* to one, unless it be a diminutive "tetragraptid". *Trichograptus triograptioides* would not qualify (?) simply because the one or two upwardly directed terminal stipes are pronouncedly lateral in origin.

Preservation and reconstructions of the giant clonograptids and dichograptids

Most Bendigonian graptolites of Victoria are preserved diagenetically flattened but have not been unduly distorted tectonically except at certain localities. Contrary to popular opinion,



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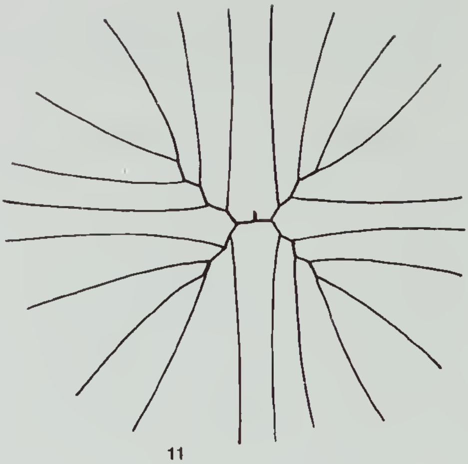

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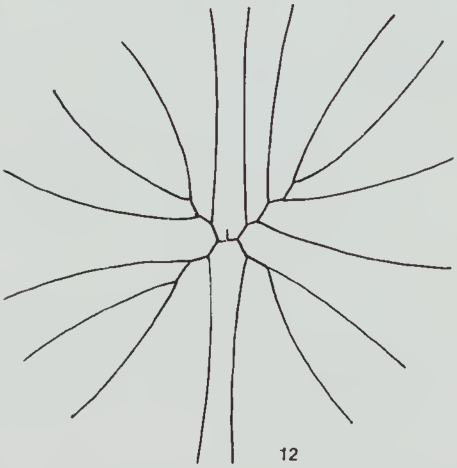

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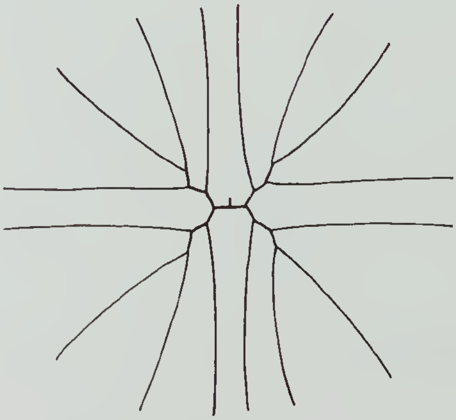

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Figure 10. *Goniograptus thureaui thureaui* based upon P34847 (35817); 32 peripheral stipes; nodal formula 7/7/7/7.

Figure 11. *Goniograptus thureaui thureaui* based upon P34861; 22 peripheral stipes; nodal formula 4/5/4/5.

Figure 12. *Goniograptus thureaui thureaui* based upon P34844 (holotype of *Goniograptus thureaui inequalis* Harris and Thomas); 17 peripheral stipes; nodal formula 5/2/3/3.

Figure 13. *Goniograptus tumidus* based upon the holotype P32168; 16 peripheral stipes; nodal formula 3/3/3/3; Bendigonian (Be1).

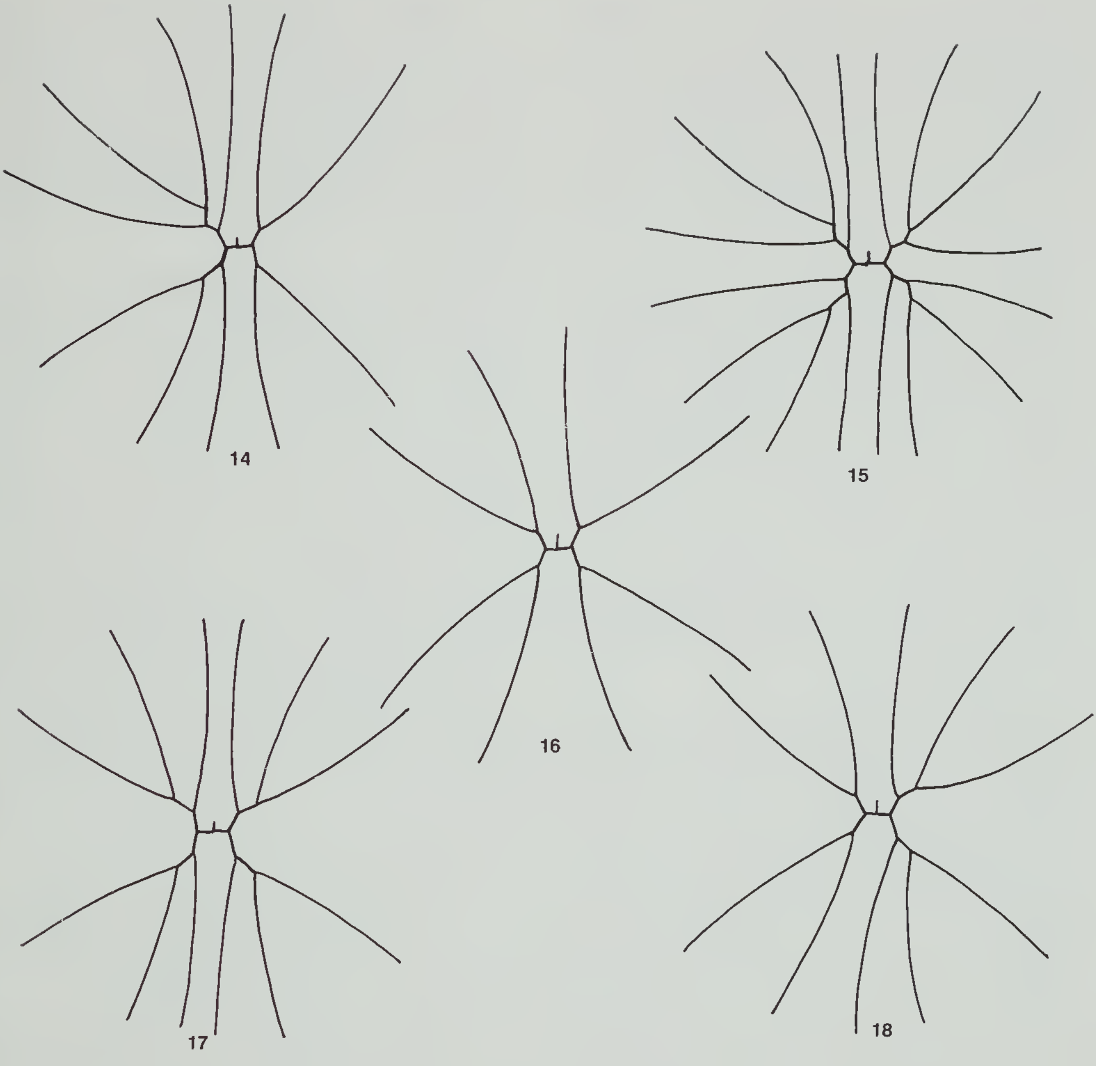
Figure 14. *Goniograptus tumidus* based upon paratype P34848; 11 peripheral stipes; nodal formula 1/1/2/3; Bendigonian (Be2).

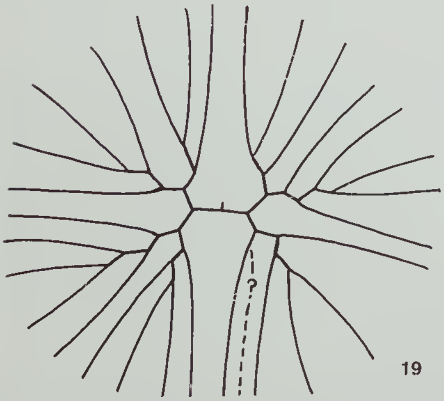
Figure 15. *Goniograptus macer* based upon P34851; 16 peripheral stipes; nodal formula 3/3/3/3.

Figure 16. *Goniograptus macer* based upon the holotype P32142; 12 peripheral stipes; nodal formula 2/2/2/2.

Figure 17. *Goniograptus macer* based upon P42707; 10 peripheral stipes; nodal formula 2/2/1/1; note that as with *Goniograptus tumidus* (Figure 14) fully one half of the rhabdosome could be described as *Dichograptus*-like.

Figure 18. Hypothetical *Dichograptus* or *Etagraptus* derived from *Goniograptus macer* of the type figured in figure 14 by loss of the last two monoprogressive nodes, leaving only the terminal nodes.





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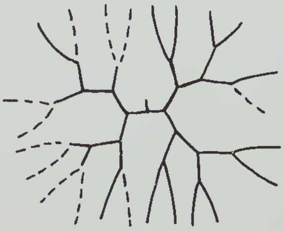

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Figure 19. *Praegoniograptus clonograptoides* based upon the holotype P32169; 29 peripheral stipes; nodal formula 2/4; 4/0; 3/4; 3/2; seven monoprogressive dividing stipes. Bendigonian (Be1).

Figure 20. *Praegoniograptus timidus* based upon holotype P32165; possibly 24 peripheral stipes; nodal formula possibly one throughout, that is including *only* the terminal pair node.

however, the early development of sicula to th2_1 can be seen often enough to make major advances in interpretation possible as, for example, in *Tetragraptus pendens* and *T. fruticosus* in this paper. This happens partly because the proximal regions, often more fully sclerotised, are not quite flat, and partly because many specimens show a little infilling with iron pyrites, albeit altered in most cases to haematite or limonite.

In addition to these considerations there is evident sedimentary (depositional) tangling and matting, particularly of clonograptids and multiramose dichograptids. Most of the tetragraptids and didymograptids show little deformation of this kind, save some stipe bending and breakage, and a clear idea of rhabdosomal shape and stipe disposition can be quickly obtained from the large numbers of specimens available for a majority of the species. Good examples would be the tetragraptids *T. approximatus* and *T. acclinans* and the didymograptids *D. eocaduceus* and *D. hemicyclus*, each pair of species being not dissimilar in general rhabdosomal aspect (plate 18a, b; plate 23a–d).

However, the preservation of clonograptids and multiramose dichograptids does cause problems of interpretation. Although Harris and Thomas often suggested a figure for overall rhabdosomal dimensions, presumably on the assumption that occasional specimens might be preserved without matting (as *Goniograptus* often is), they attempted no reconstructions. As far as we are aware our reconstructions in this paper are the first attempted, certainly for large dichograptids. We have made the reconstructions in two slightly different senses. In the first place we have tried to deduce the preserved shape of a specimen which might be deemed to have sunk quietly to the bottom and not become tangled with other specimens or had its own stipes matted by rolling (which seems common in clonograptids). And secondly we have in some instances attempted to deduce the aspect of the rhabdosome during life and to tentatively suggest a mode of life. The first approach is certainly justified by the occasional finds of such specimens, usually not later than middle growth stages, in which depositional deformation has not taken place and in which the disposition of the stipes to the funicle is remarkable symmetrical and constant. Further, there is no strong evidence in graptolite research that same order stipes are of markedly different lengths on the one specimen, particularly terminal stipes which contribute largely to the overall size of the colony and determine the shape of its periphery. Therefore in reconstructing the rhabdosomes we have taken the preserved maximum length of the stipes as applying also to those that are clearly broken. In many cases the stipes might be longer; but in taking this approach (usually selecting one good specimen, often the holotype) the overall rhabdosomal symmetry is maintained and the rhabdosomal diameter probably approaches that in life.

Detailed comments on the reconstructions for each of several species are given in the Systematics Section at appropriate points, but there are several general points which arise from this study. In multiramous forms where the sicula has been observed it is always in a different plane to the rest of the rhabdosome, which explains the rarity in the literature of figured funicular areas with a sicula depicted. We have found that preparation of the specimen in the line of the rhabdosomal axis, on either side of the funicle, often reveals the sicula. The apex of the sicula commonly occurs well below the level of the bedding plane upon which the remainder of the rhabdosome rests. In other specimens the sicula seems to be at right angles to the bedding plane (and the rhabdosome) and may be represented by a slight expansion, centrally, of the funicle.

Taking this fact as a starting point, we have recognised three basic rhabdosome orientations relative to the sicula:

1. Those species in which the rhabdosome is horizontally disposed *Clonograptus ramulosus*; *Trochograptus indignis*; *Orthodichograptus robbinsi*; *O. wilkinsoni*; *Kellamograptus australis* and possibly *Loganograptus logani*.

2. Those species in which the rhabdosomes were probably declined or reclined (*Tridensigraptus zhaoi*; *Triaenograptus neglectus*; *Clonograptus erdtmanni*.

3. The *Goniograptus* type of orientation (probably most species of *Goniograptus*, *Sigmagraptus* and possibly *Zygograptus* and *Yushanograptus*) in which the orientation of the main branching areas (4 in *Goniograptus*; 2 in *Sigmagraptus*, *Zygograptus* and *Yushanograptus*) may have been disposed to each other either in the same horizontal plane or in the form of a propeller shape, each set being at a slight angle to the other (fig. 30).

Type 1. Most of these forms give the impression of a very symmetrical rhabdosome, even such very large species as *Kellamograptus australis*. Despite the size, and length of stipes, there is very little overlap of adjacent stipes that can-

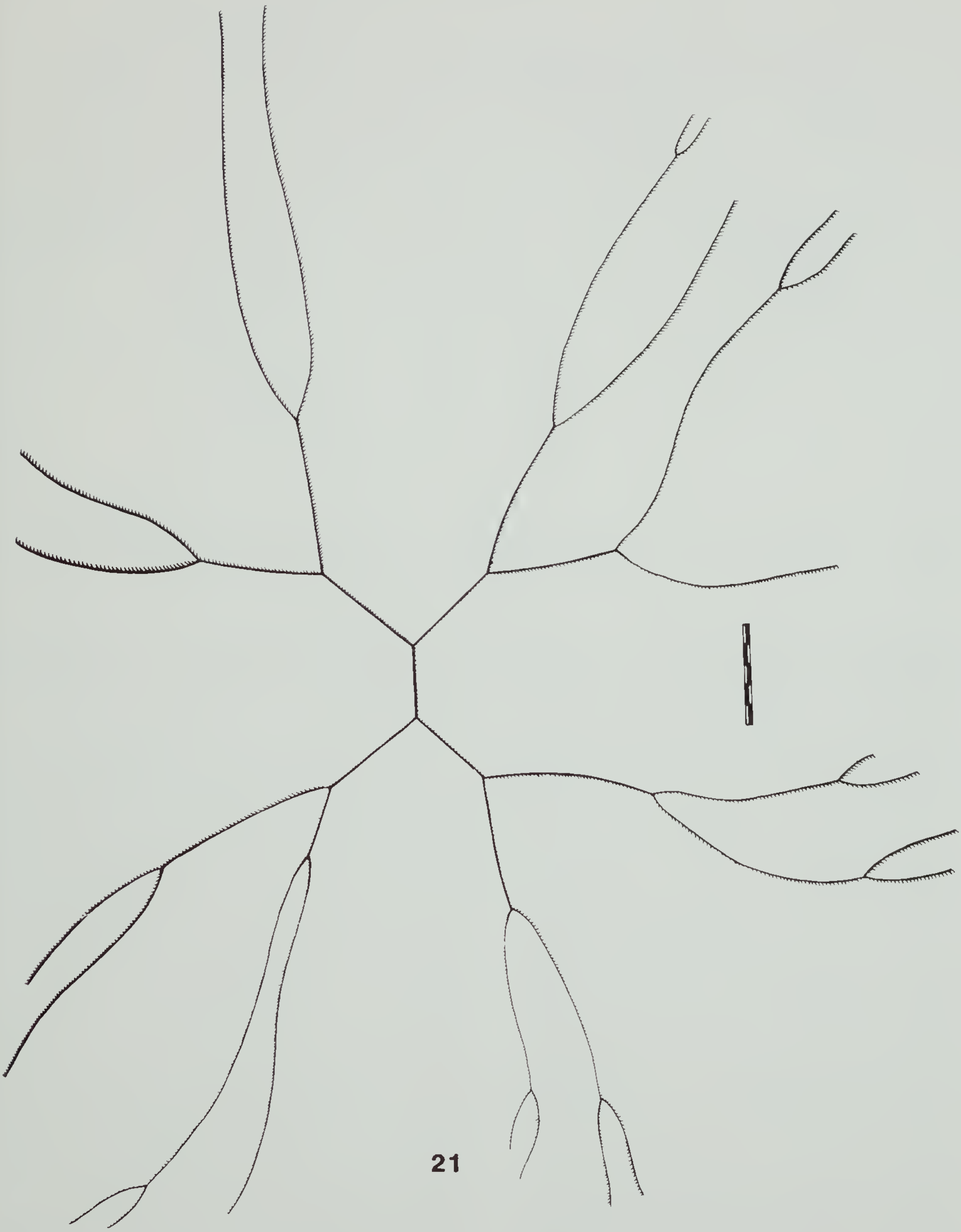

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Figure 21. *Clonograptus ramulosus*, reconstruction based upon lectotype P32082; full explanation in text. Scalebar 50 mm.

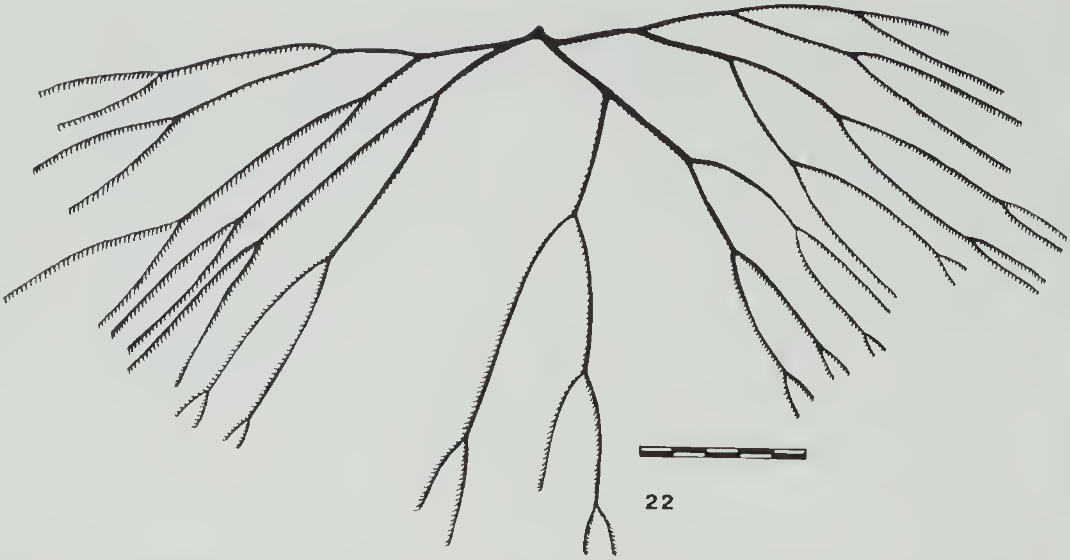

Figure 22. *Clonograptus erdtmanni* sp. nov., reconstruction of rhabdosome with tangles and breakages removed, emphasising gently declined profile; based upon holotype P34260. Scalebar 50 mm.

not be attributed to preservational tangling. Coupling this with the fact that the sicula is demonstrably at right angles to the bedding plane which preserves the rest of the rhabdosome, the most reasonable interpretation is that the rhabdosome was disposed horizontally, that it reached the bottom upon death in a horizontal position, and that during life it was probably mostly in horizontal orientation. Although these giant dichograptids would not have the solid body of a modern disc-shaped jellyfish they might be expected to have maintained the roughly horizontal position of the latter, whilst recognising that such jelly fish (if observed for several hours) may tilt at various angles to the horizontal, and even turn over occasionally, the whole process being very slow. Web, or central disc structures (Bulman, 1970), probably multilayered, are quite common in this group, except in *Clonograptus ramosus* and *Dichograptus expansus*, though they do occur in the latter rarely. Presumably the unusually long, slender stipes gave sufficient retardation of sinking effect and that positive buoyancy additions were not necessary. Webs are usually features of robustly stiped, presumably heavy species, not of those with long, slender stipes and any horizontal, planar structure, such as webs, would contribute to lift. *Dichograptus expansus* is the odd man out in our group of Victorian dichograptids (Type 1) in another respect. It has so few stipes that it is almost referable to *Tetragraptus* (*Tetragraptus*)! That some of the latter had a horizontal orientation with respect to the sicula is beyond doubt.

Type 2. There are clear indications in these forms of a declined or reclined rhabdosome. In *Triaenograptus neglectus* (fig. 28) this may be very slight and is only indicated by the slightly bulbous nature of the few cm at the centre of the rhabdosome on the holotype. It is possible that the bulk of the rhabdosome was horizontal and the proximal region only slightly reflexed. In this respect it is of interest that it is the only species in type 2 which has a proximal web structure. It would seem that strongly declined or reclined species have no need of a web. That the bowl shape of the rhabdosome (figs 22, 27) itself confers sufficient buoyancy/retardation of sinking effect. It would seem unlikely to us that *Tridensigraptus zhaoi* with its heavy stipes and reclined attitude could maintain a sicula-apex-upwards orientation. It would surely turn turtle in the manner depicted (fig. 27) unless actually in the process of sinking. It is of interest that whatever orientation this species adopted the thecal apertures were on the outside of the bowl-shape, not the inside as in most dendroids, or as in *Clonograptus erdtmanni* (fig. 22).

Type 3. It is likely that most goniograptids were horizontally disposed with respect to the sicula if the latter is orientated vertically.

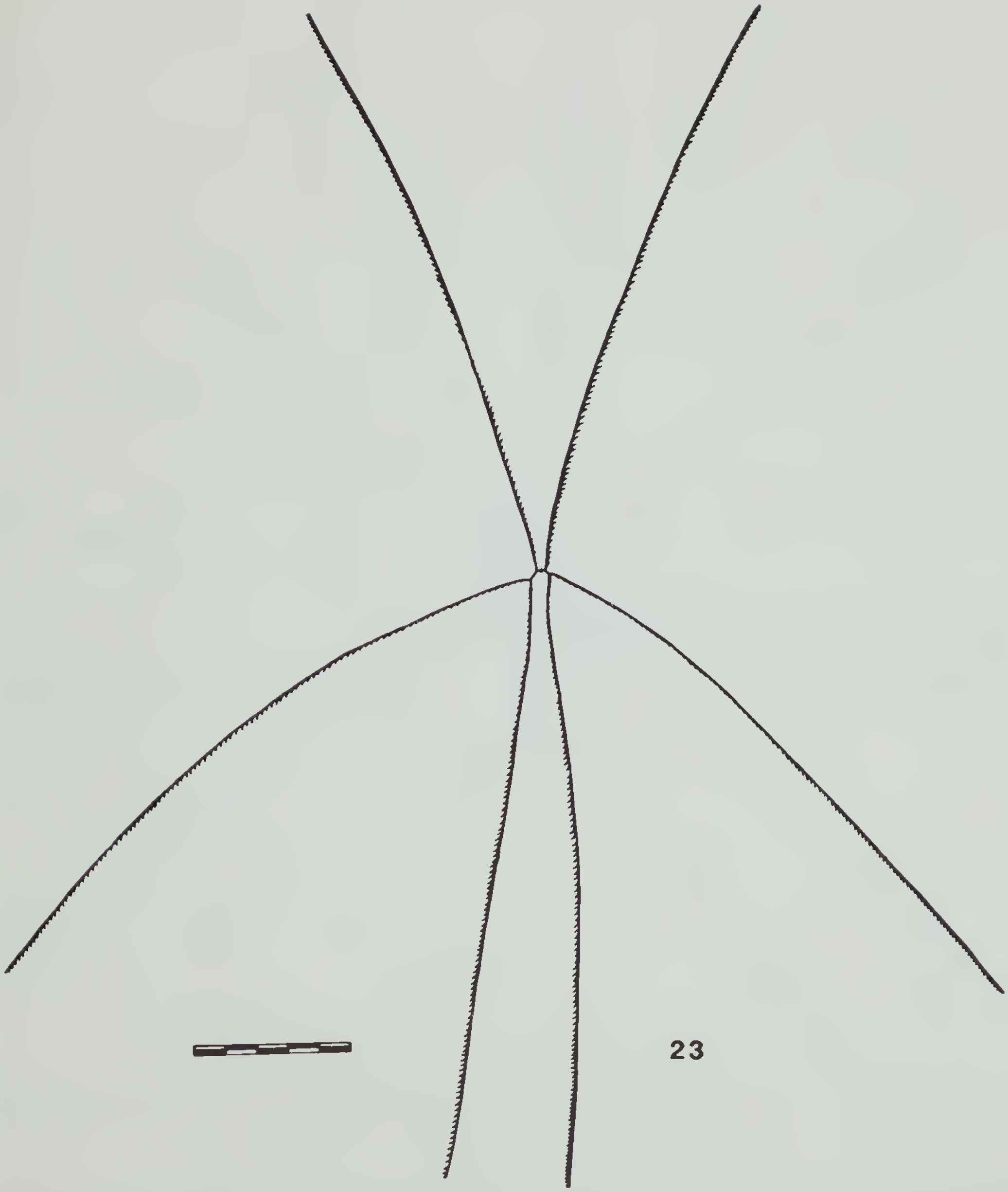

Figure 23. *Dichograptus expansus*, reconstruction of rhabdosome based upon the holotype P32076 with tangles and twists removed. Scalebar 50 mm.

However, several facts lead us to question this in some cases. For example many specimens of *Goniograptus* spp. have the peripheral stipes of adjacent branching areas (which are integral with respect to the monoprogressive branching line) somewhat tangled, even (see Ruedemann, 1904, 1947) very strongly overlapping. This can hardly be a result of overlapping growth, during life, in the same horizontal plane, and the obvious deduction is that during life each of the four branching sets was inclined in a different plane. That the rhabdosome as a whole approached a propeller in outline. The implications of such a structure in any passive model (Rickards, 1976) would be considerable.

Secondly, whilst the sicula in *Goniograptus* is

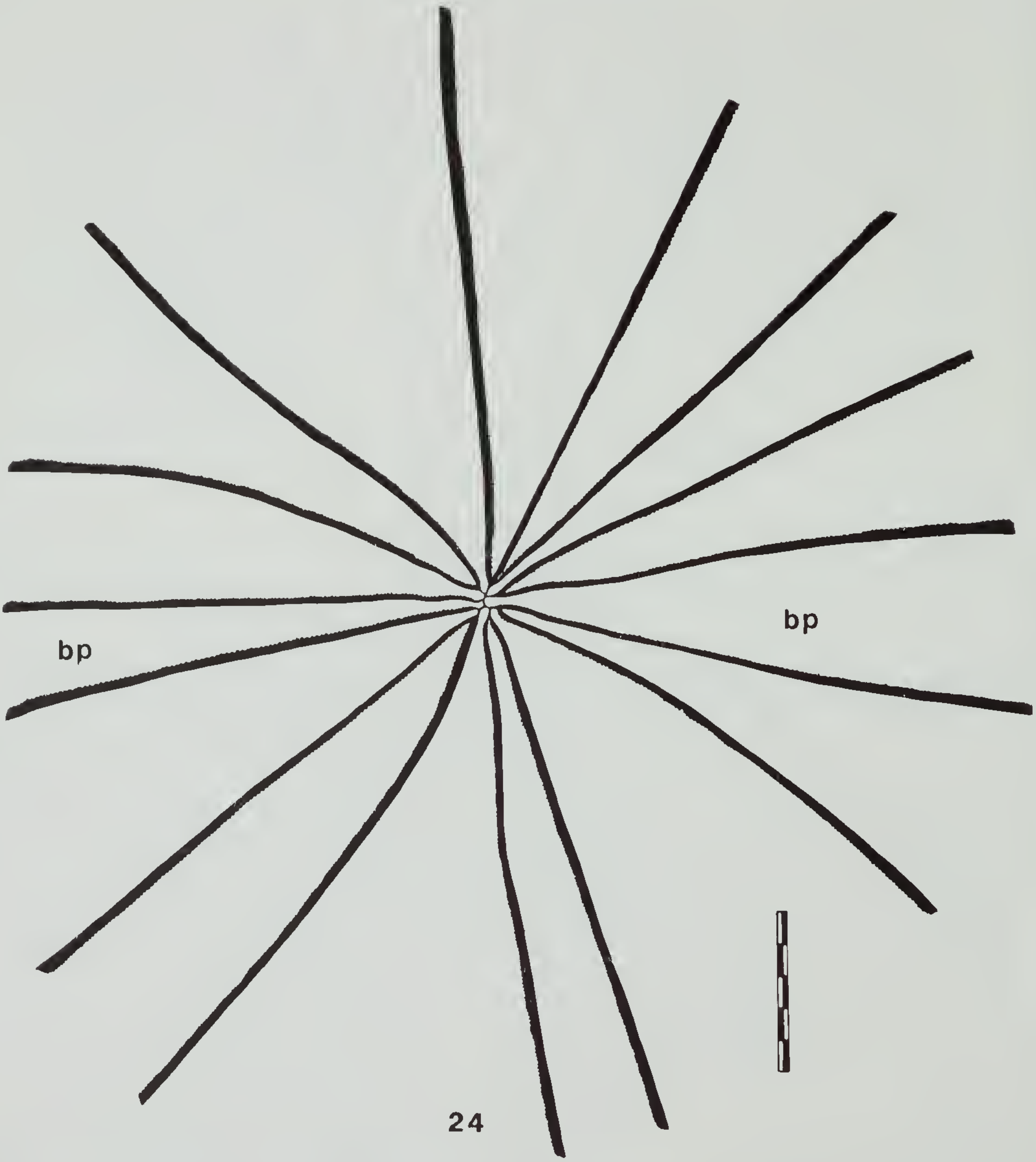

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Figure 24. *Loganograptus logani australis*, reconstruction of rhabdosome as preserved with secondary distortions removed, probably in life position (plan view). Scalebar 50 mm. bp = bilateral plane.

demonstrably at right angles to the general disposition of the colony, this is far from certain in *Sigmagraptus*. Indeed, although the sicula seems occasionally to be at a slight angle to the bedding containing the stipes, more commonly it is preserved in that very bedding plane, explaining why the proximal end development of *Sigmagraptus* is better known than *Goniograptus* (and why Cooper and Fortey (1982) could only place *Goniograptus* in their Sigmagraptinae with some question). It seems likely to us that the two sets of *Sigmagraptus* stipes (each integral with its own monoprogressive series) were set in life at an angle to each other and to the sicula. The angles could vary with the species. Such an idea seems preferable to having the sicula oriented

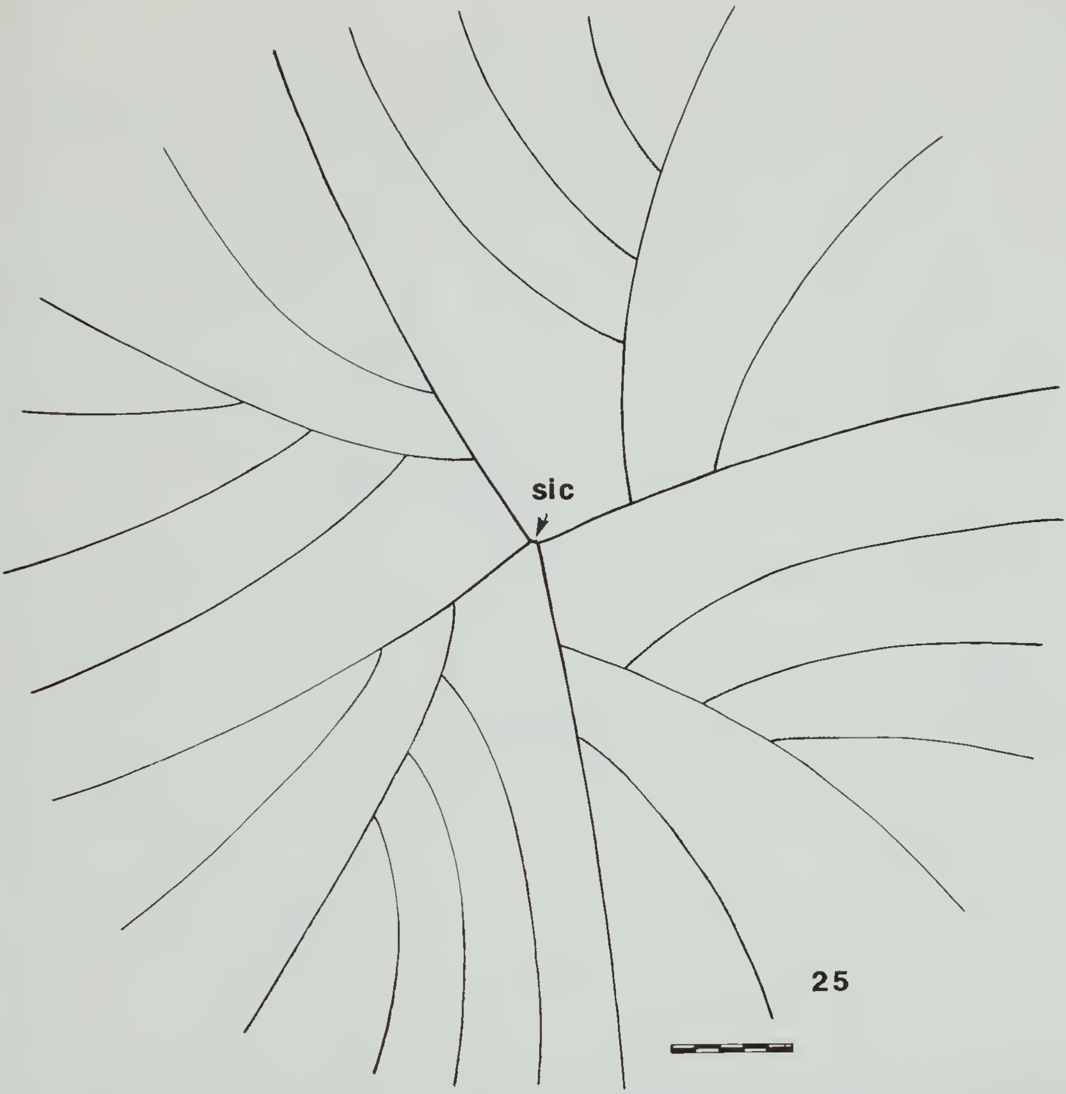

Figure 25. *Trochograptus indignis*, reconstruction of rhabdosomes based upon lectotype, P83291, probably in plan view of life position. sic = position of sicula and funicle. Scalebar 50 mm.

vertically, with two sets of often very long stipes also arranged vertically, the whole looking like, and having the orientation of a garden fence. Thus we regard *Sigmagraptus* species as having a two-vaned propeller-like structure and its mode of life orientation, like that of *Goniograptus*, would recall that of satellite antennae grids. Similarly some other genera such as *Yushanograptus* (also sigmagraptine) which share with *Goniograptus* and *Sigmagraptus* the unusual feature of monoprogressive branching series, may have had similar orientations.

Evolutionary notes

Despite the extensive work of T.S. Hall, Harris, Thomas and others over many years the time is not yet ripe for a detailed appraisal of evolutionary lineages. The overall evolutionary framework is fairly clear, and is in accord with the generalisations summarized, for example, by Bulman (1970). Thus the Anisograptidae of the Lancefieldian and Bendigonian, (already involved in stipe reduction in the Lancefieldian) gave rise to the Dichograptidae in the latter

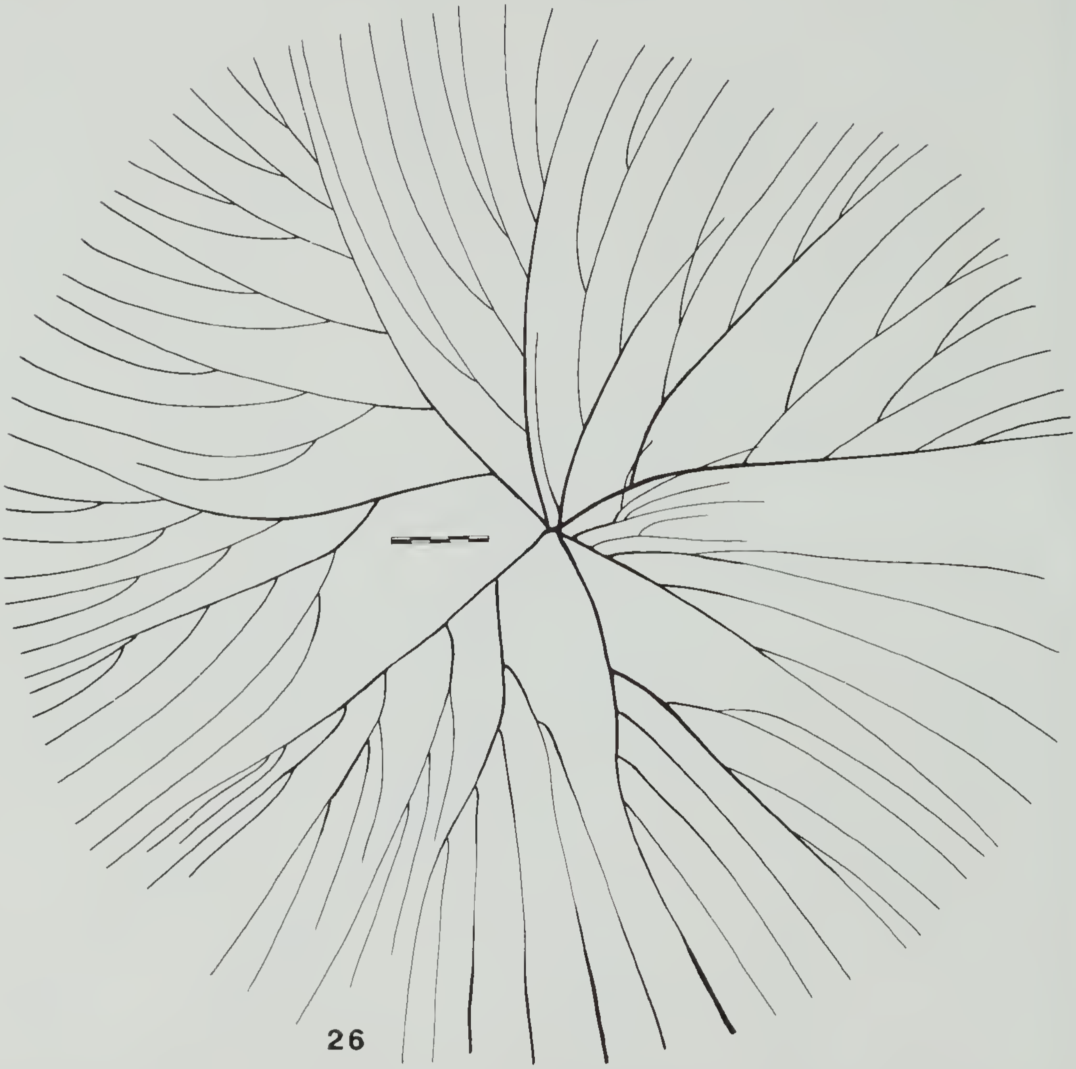

Figure 26. *Kellamograptus australis*, reconstruction of rhabdosome probably in plan view of life position; based largely upon holotype P32081. Scalebar 50 mm.

half of the Lancefieldian. The Dichograptidae reached a peak in the lower half of the Bendigonian (see Beavis, 1976) where the subfamily Sigmagraptinae became established. (The Isograptidae did not appear until the Chewtonian and the biserials until later but Cooper and Fortey's (1982) genus *Pseudophyllograptus* is typically first seen in the low Bendigonian.)

The concept of stipe reduction, generally correct though it must be, has attendant difficulties. For example, several of the Sections which we define in the Dichograptinae actually have what may be secondarily multiramose forms at a later date. Thus the Dichograpti develop *Orthodichograptus* in Be4; the Temnograpti, *Zygograptus* in Be4; the Schizograpti, *Tridensigraptus* (horizon unknown) and *Triaenograptus* (Ca1); the Pendeograpti possibly *Pterograptus* in the Darriwilian. It is also possible that *Tridensigraptus* is a late astogenetic development of a Tetragrapti; whilst the Mimograpti (monospecific) may be a late offshoot (Ch2) of the Didymograpti. The only obvious exceptions to this scheme are *Kellamograptus* and *Trochograptus* which are Be1 in age: their resemblance to a *Loganograptus* stage of growth, with secondary (lateral) stipes

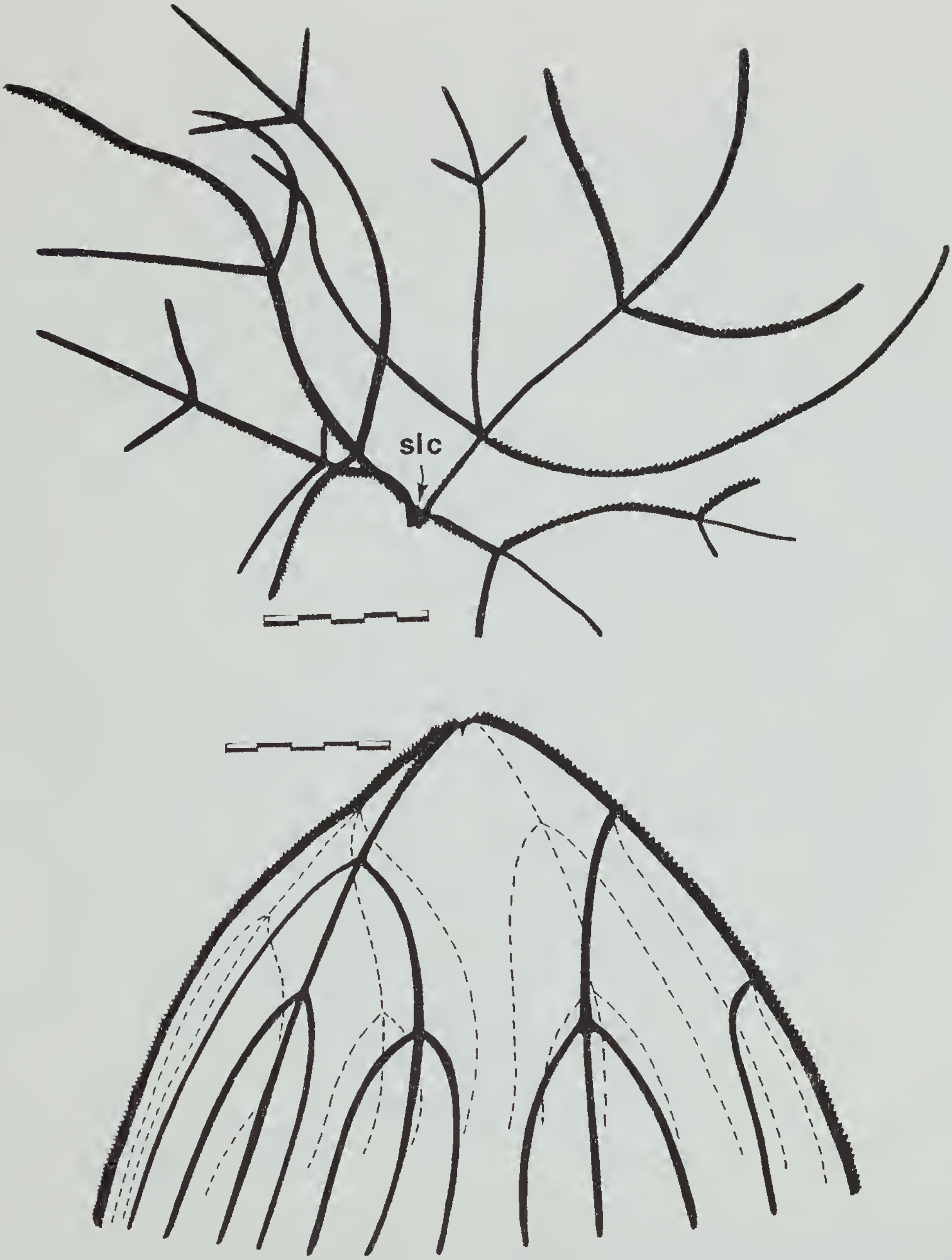

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Figure 27. *Tridensigraptus zhaoi* sp. nov. (a) drawing of holotype P31193A,B; (b) suggested reconstruction in life position, full explanation in text. sie = sicula. Scalebar 50 mm.

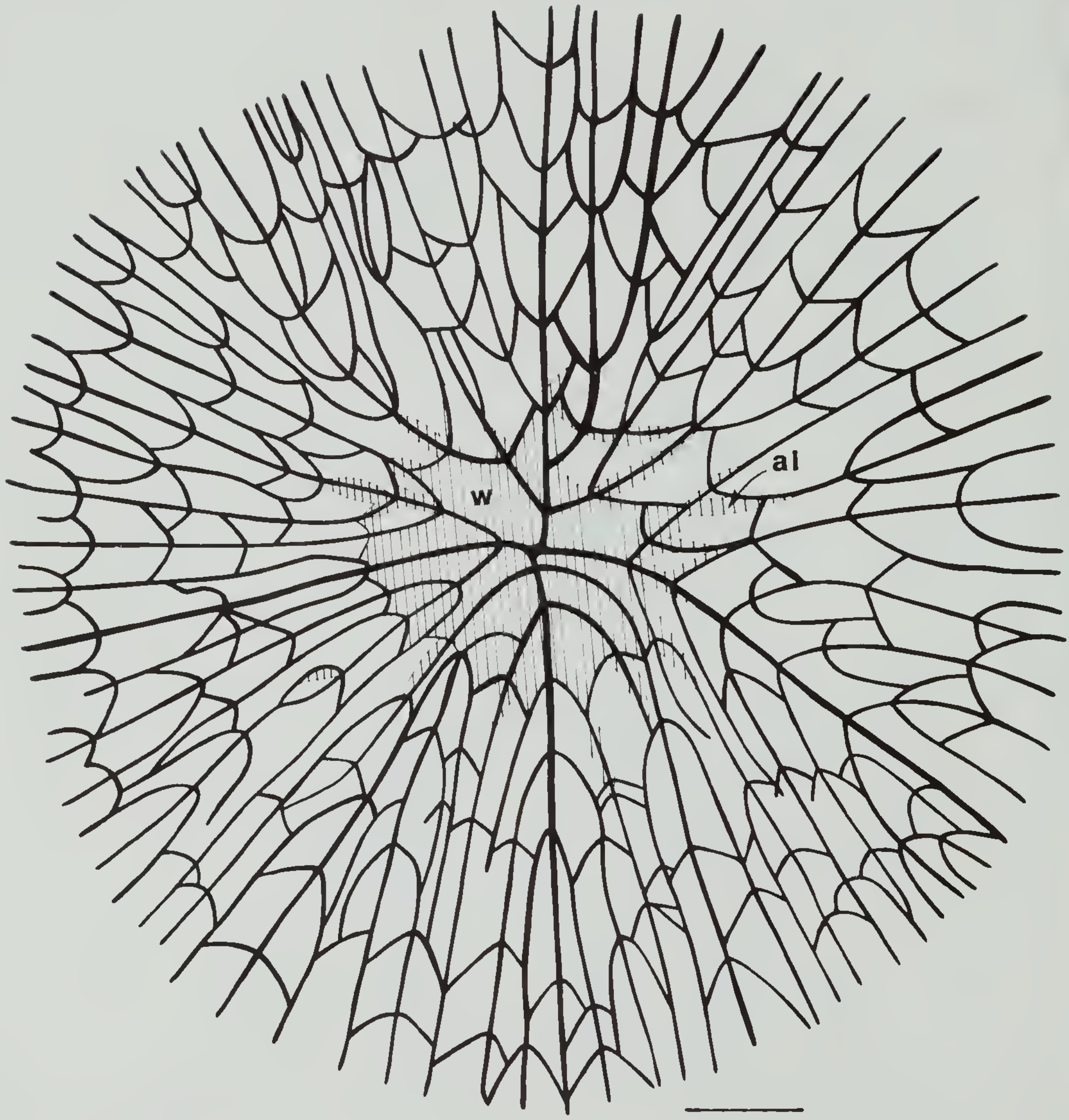

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Figure 28. *Triaenograptus neglectus*, based upon holotype P13125, only slightly reconstructed, shown as preserved; full explanation in text. w = central large web. al = alae. Scalebar 50 mm.

added is remarkable. Be2 and Be3 seem to a considerable extent lacking in such secondarily derived multiramous species, and it may be that *Kellamograptus* and *Trochograptus* represent the early acquisition of morphological features which found more widespread recognition in a later period (see Rickards, 1977).

Another problem concerns the astogenetic development of certain forms, or rather the lack of information. For example, what are the early growth stages of *Kellamograptus australis*? Could it be that *Trochograptus indignis* or *K*? *incompositus* are early growth stages of *K. australis*? Is *T. spectabilis* a yet earlier growth stage than any of the above? All occur at the same horizon and localities, and the multiramous forms are notoriously rarer. And how could we distinguish an early growth stage of *T. spectabilis*

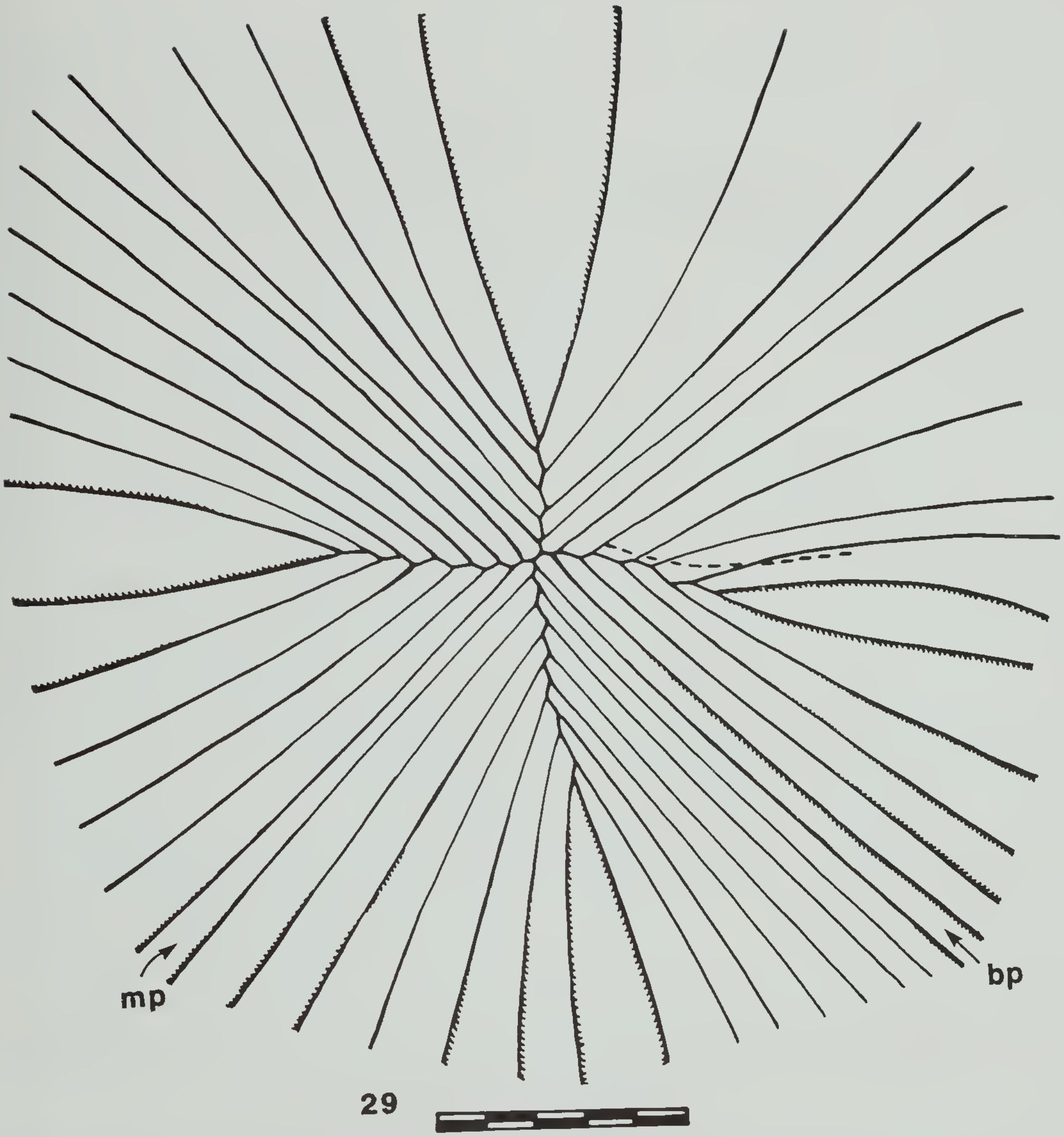

Figure 29. *Goniograptus alternans*, diagrammatic, based upon holotype P14619 shown as preserved; an abnormal stipe shown dashed. mp = median plane. bp = bilateral plane. Scalebar 50 mm.

from a *Tetragraptus* species such as *T. decipiens*? Are all these forms one species? It would certainly reduce the early Bendigonian diversity index if they were! Much more material than is at present available will be necessary to confirm or deny this. Spjeldnaes (1986) has already drawn attention to similar problems in his work on Scandinavian multiramose species.

Arguments which might apply to *Kellamograptus* will also need examining with respect to several species of *Goniograptus*, *Sigmagraptus*, *Loganograptus*, and *Dichograptus*. Presumably some multiramous genera can be excluded from such doubts (*Orthodichograptus*, *Triaenograptus*) partly because of their development characteristics (*O. robbinsi* is *not* a *Dichograptus octobrachiatus* with added stipes) and partly because of their restricted stratigraphic occurrence relative to their nearest possible ancestors.

Finally, in these general remarks we would comment upon the nature of the speciation in the Lancefieldian to Chewtonian, much of the

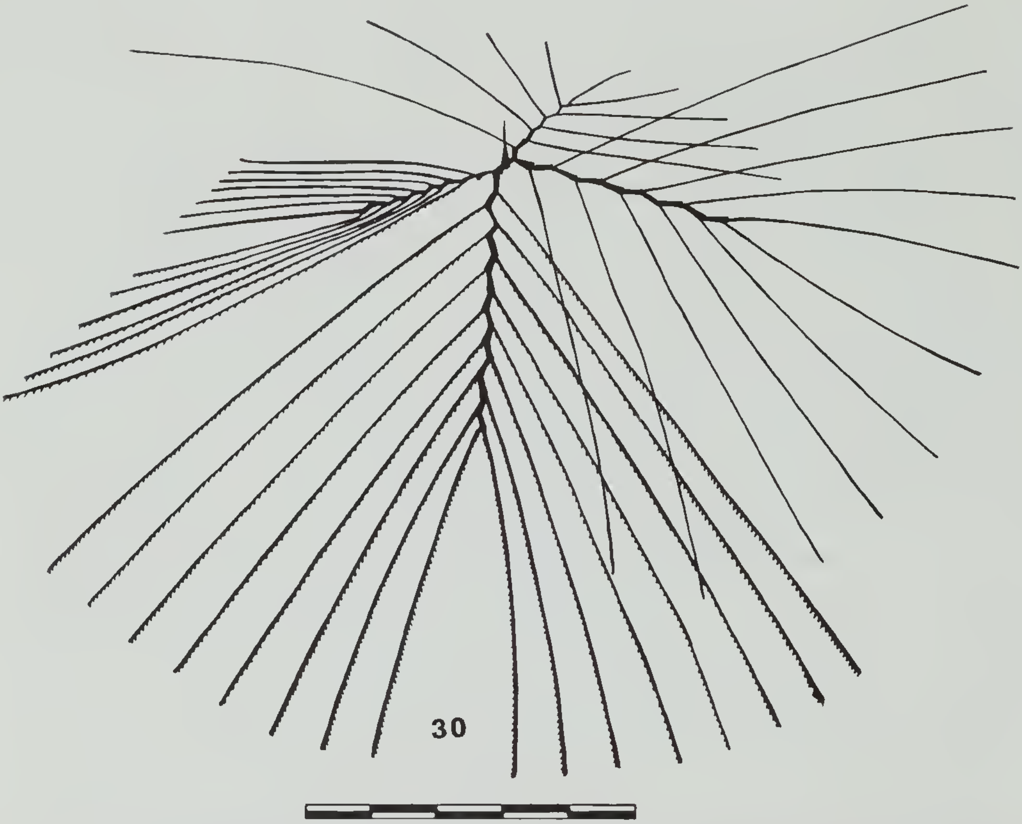

Figure 30. *Goniograptus alternans*, suggested mode of life position, hypothetical; although the orientation of the four quadrants is shown slightly pendent with respect to the sicula, it could have been horizontal; full explanation in text. Scalebar 50 mm.

marshalled information for which was provided by O.P. Singleton. This is summarized in Fig. 31. The percentage change in assemblages between neighbouring zones mirrors this distribution. It is of interest that the greatest changes are at the beginning and in the middle of what is elsewhere regarded at the *approximatus* Zone, that is at the beginning of La3 and Be1. The Chewtonian peak (Fig. 31) obviously began in Be4 with Be3 forming a trough and confirming our impressions from Table 2 that Be3 had the least diverse faunas in the Bendigonian.

More specifically there are several possible evolutionary lineages unearthed by the present work and by earlier work of Harris and Thomas. Of these latter (1942) one of the more convincing is their suggested lineage that early (multiramous) forms of *Goniograptus macer* (figs 15–17) gave rise to later (pauciramous) forms of the same species and hence by further loss of peripheral stipes (in our terminology by reduction in the nodal number) to *Dichograptus tenuissimus*, *Etagraptus harti*, *Trichograptus triograptoides* and *Didymograptus gracilis*. The general stipe dimensions support the suggestion: all have a thecal spacing in the range 7–10 in 10 mm and a dorsoventral width in the range 0.3–0.5 mm. Moreover, as we show in this paper, the thecae are very similar, simple, low angled, of dichograptid type. The only problems concern their occurrence in time. Whereas *G. macer* ranges through the Bendigonian into Ch2, *E. harti* and *T. triograptoides* are considerably earlier than *D. tenuissimus* (Table 1), so that it would be necessary to have at least two lines of evolution leading from *G. macer*. The change to *Trichograptus triograptoides* is actually much greater than might appear at first glance, reflected in our attribution of the species to *Trichograptus* rather than to *Tetragraptus*. It necessitates the development of a didymograptid rather than a tetragraptid template: whilst this then renders the derivation of *D. gracilis* from *T. triograptoides* more likely, it also suggests that *T. triograptoides* is just as likely to derive directly from *G. macer* as from *E. harti*. Should this evolutionary scheme prove correct there would be a case for expanding the definition of *Etagraptus* (see also fig. 144) to embrace the whole group except for *G. macer* perhaps. Other goniograptids have either high, isolate thecae of clonograptid Group A type, or robust dichograptid thecae, and were probably not involved in this particular story. However, *Trichograptus fergusoni*, from Be1 and Be2 (as *T. triograptoides*) is almost certainly part of the lineage leading to *D. gracilis*. *Tetragraptus whitelawi* may be a late derivative of either *G. macer* or *D. tenuissimus*.

Consideration of thecal type led us to informally divide *Clonograptus* into two groups: A, with high, more or less isolate metathecae; B, with simple dichograptid thecae. The same division can be made amongst *Goniograptus* species: *G. macer*, *G. velatus*, *G. tumidus* having simple dichograptid thecae; *G. thureaui*, *G. alternans*, *G. palmatus* having distinctly high, isolate metathecae. The genus *Dichograptus* as presently recognised may also have species falling readily into two groups (compare, for example, *D. maccoyi* and *D. sedecimus*). It is, therefore, tempting to envisage two stocks deriving from Lancefieldian clonograptids where the separation presumably took place. By this argument a clonograptid such as *C. rarus* (Be1) could have evolved into *Dichograptus sedecimus* (Be1) and *Tetragraptus chapmani* (Be1), all having remarkably similar stipe dimensions and basic thecal structure (it would be difficult to separate distal fragments, for example).

Attention has been drawn in the *Systematics* section to the similarity of thecal type and early development of the didymograptids *D. adamantinus* and *D. perditus* to *Adelograptus pritchardi*. The problem of suggesting any direct connection is that there is a considerable time gap, *A. pritchardi* being late Lancefieldian and the two didymograptids being late Bendigonian. We have seen nothing in the Victorian faunas to suggest that the gap could be bridged in this region,

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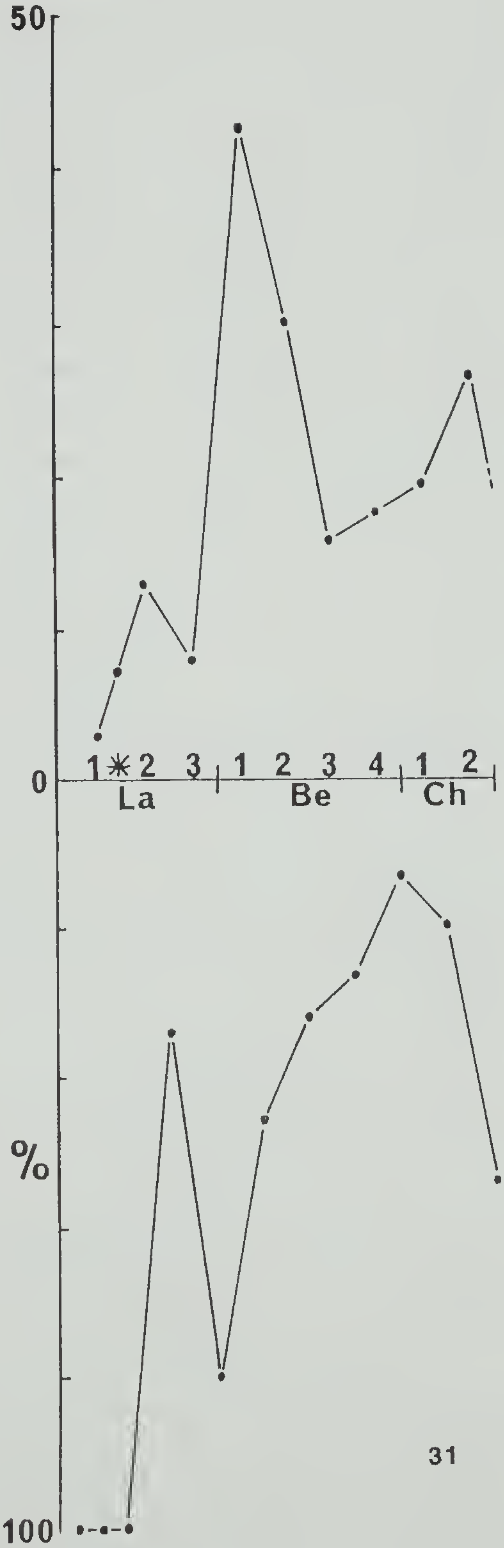

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Figure 31. Diversity of Lancefieldian to Chewtonian graptolites; upper graph shows number of species at each horizon, lower graph the percentage change over between divisions; data from O.P. Singleton (pers. comm.) modified only to include new forms and synonomies in the Bendigonian; Lancefieldian La 1.5 is shown with an asterisk.

although it is perfectly feasible that the lineage continued elsewhere. In spite of this particular problem we are inclined to link these didymograptids with *Adelograptus pritchardi* or like adelograptid.

Zygograptus is a difficult genus to place, not only in terms of the informal dichograptid classification we have adopted but in an evolutionary setting. It is essentially a late Bendigonian to Darriwilian genus with *Clonograptus* affinities. However, the derivation of *Zygograptus* from a *Clonograptus* lineage requires that the stipe lengths from 2nd order upwards become much shorter (in *Z. stewarti* they are consecutive dichotomies). The range of thecal type in *Zygograptus* has not yet been fully appraised; some appear to be simple dichograptid, others rather high possibly isolated types.

However, the most puzzling group in broad evolutionary terms are the goniograptids. On the one hand we have suggested that a *Dichograptus* species may derive from *G. macer* by reduction of the nodes to 1; on the other that *Clonograptus* is the presumed ancestor of *Goniograptus* which would have involved the introduction for the first time of zig-zag stipes and monoprogressive (nodal) branching. We are of the opinion that the introduction of this unusual stipe feature is a response to a particular mode of life and that as the requirement for this mode changed, the overriding tendency to stipe reduction prevailed and the number of nodes was reduced. Clearly much more work is needed on the individual lineages than is possible at present, and in particular the (assumed) link with species of *Clonograptus*.

Systematics

Class **Graptolithina** Bronn, 1846

Order **Dendroidea** Nicholson, 1872

Anisograptidae Bulman, 1950

(Note: the present authors are not entirely convinced by the arguments of Fortey and Cooper (1986) which place the Anisograptidae in the Graptolidea and prefer for the present to retain the family in the Order Dendroidea).

Clonograptus Nicholson, 1873
(ex J. Hall ms.)

Type species. Graptolithus rigidus Hall 1858: 146.

Diagnosis. Rhabdosome bilateral, dichotomous divisions to 8th or 9th order; branching initially diverging, becoming more parallel distally, autothecae denticulate, with variable inclination, either dichograptid-like, or with strongly isolated distal parts; stolothecae and bithecae in older species.

Remarks. Of the Bendigonian clonograptids recorded by Thomas (1960a; ranges emended herein), originally described by T.S. Hall (1899) and by Harris and Thomas (1938a, 1939), one species (*C. timidus* Harris and Thomas, 1939) is referred to *Praegoniograptus* (see discussion below) whilst the remainder fall readily into two groups:

Group A: forms having strongly denticulate and usually isolated thecal apertures (*C. ramulosus* Harris and Thomas, 1938; *C. rarus* Harris and Thomas, 1938; *C. smithi* Harris and Thomas, 1938; *C. tenellus problematica* Harris and Thomas, 1938);

Group B: forms having dichograptid thecae (*C. trochograptoides* Harris and Thomas, 1939; *C. persistens* Harris and Thomas, 1939).

In the "Treatise" diagnosis of the genus Bulman (1970) included the phrase "autothecae denticulate with moderate inclination, some species with low inclination and negligible overlap, some with exaggerated apertural spines" implying that the last were not common. In the Bendigonian clonograptids (and in the Lancefieldian species) strongly denticulate or isolated thecal apertures (Group A above) are quite common if not the norm. It is also clear from examining various forms of preservation that specimens which at first sight appear to have thecae with a low angle of inclination may in fact have thecae which are almost isolate and at a high angle, aperturally, when true profile preservations are seen. In addition the late metathecal parts do often appear to have thin periderm making their detection in the rock a matter of some difficulty. It is of interest that Harris and Thomas described the Group A forms in 1938a and the Group B forms in 1939, yet they do not comment on this and even regarded the dichograptid thecae as "normal" clonograptid (Harris and Thomas, 1938a: 73, description of *C. tenellus problematica*). It follows from the above and the following descriptions that in group A forms, despite apparent proximal thickening of stipes, the true *dorsoventral width* and thecal spacing of the stipes alters little throughout the colony, a feature typical of dendroid stipes. The two Group B species, *C. trochograptoides* and *C. persistens*, whilst having typically dichograptid thecae, in fact show little or no increase in dorsoventral width distally (i.e. no obvious increase in thecal size) and in this sense they also retain some dendroid character.

Clonograptus ramulosus Harris and Thomas

Plate 1 figs a, b; text-figs 21, 35

Clonograptus ramulosus Harris and Thomas, 1938a: 73, pl. 3 fig. 10, pl. 4 fig. 9.

Type specimen and material. Holotype, the specimen figured by Harris and Thomas as plate 3, fig. 10, P32082A and B (41318), from Be2 in NW corner of allotment 30A, sect. II, Parish of Cambelltown. The specimen is somewhat tangled and distorted but the funicle, the distal stipes, and the thecae are preserved: the stipes may become even more slender as they are not completely seen though the type slab is some 350 mm across. Harris and Thomas (1938a) mentioned a second specimen from the same locality, showing the sicula, but this specimen seems not now to be available. A paratype specimen P32030 (35908) of which a few thecae were purportedly figured by Harris and Thomas (1938a, pl. 4 fig. 9) shows neither a sicula nor funicle, but does show the thecae quite well and is certainly referable to the same species. Although this slab is marked with the supposed position of pl. 4 fig. 9, we can find no part of the slab that conforms to the figure: the marked position of the slab has thecae pointing in the wrong direction. Other specimens from Be2 are in the T. Smith collection of the Museum.

Associates. The type slabs have a rich fauna of *T. pendens*, four-stiped, mature *T. fruticosus*, *Sigmagraptus* sp., and at least four species of *Didymograptus* (*Expansograptus*).

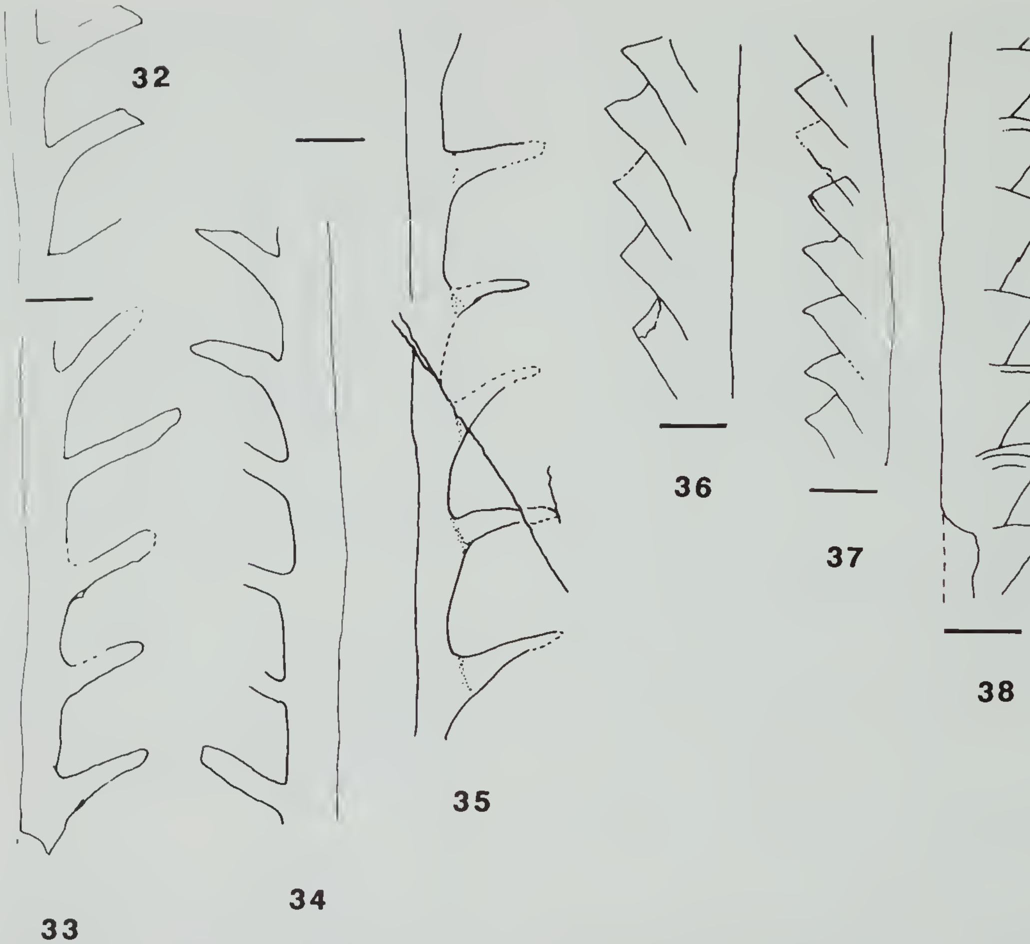
Description. The rhabdosome is certainly more than 50 cm in diameter, probably nearer 60–70 cm when due allowance is made for the tangled, very slender stipes. Dichotomous division takes place up to the 5th order quite conspicuously and with considerable distances between divisions: thereafter it is difficult to unravel divisions in the tangle of stipes but divisions of more orders may take place. The funicle is 48 mm long, and 23.5 mm from the right hand dichotomy of P32082A (the holotype) is an area which looks as though it may contain not only the remains of a sicula (fig. 21) but also the isolate distal parts of the early autothecae. If this is so then the sicula probably has a length of at least 2 mm, as claimed by Harris and Thomas, and the dorsoventral width may also be of the order of 2 mm. The width most easily seen is not the true profile width and must be largely a flattened dorsal view giving a (flattened) lateral width. Even so the early parts of the funicle and the second order stipes are quite robust, being 1 mm "wide". There is a very gradual decline of "width" towards the distal extremities but, as can be seen from fig. 21, the true dorsoventral width in these regions is still almost 2 mm. There are at least two possible explanations for this discrepancy: either we have underestimated the dorsoventral width in the funicle region, which would be easy to do since the thecal extremities do not lie in the same plane as the rest of the preserved stipe, or the prothecal width decreases distally (or a combination of the two). In any event it is clear that the thecae remain either strongly denticulate or isolate throughout the rhabdosome. Their spacing is about 6–7 in 10 mm, and is a little variable in that in some places the proximal thecae are more closely spaced, whilst in other places the opposite obtains. This may reflect varied flattening of the rhabdosome.

The lengths of the stipe orders on the holotype are approximately as follows: 1st order, 2.3–2.4 cm; 2nd order, 3.5–7.0 cm; 3rd order, 5–10 cm; 4th order, at least 7 cm; 5th order, at least 7 cm.

The "prothecal" parts of the stipe are more heavily sclerotised than the thecal apertural regions, and it cannot be assumed that bithecae and stolothecae are absent: their presence would, for example, increase the appearance of sclerotization in that part of the stipe simply because it would be multilayered on flattening.

Remarks. This species is highly distinctive and must be one of the largest clonograptids known, with some of the most widely spaced dichotomies. As Harris and Thomas rightly said it can be distinguished from *Dichograptus sedecimus* Harris and Thomas (1938a) on the size of the funicle which reaches only 10 mm in the latter species (see below, fig. 54). The species is however, extremely rare. The type series consisted of only three specimens, the two figured ones now remaining.

Reconstruction. Fig. 21 is based largely upon the holotype where we have been able to detect the true nature of the high, isolate thecae and the dorsoventral width. We have shown, in effect, no change in the dorsoventral width though it is just possible that the proximal regions would be slightly more robust if seen in full profile. We have also "preserved" the distal ends of the stipes in full profile. Although this occurs on the holotype, increasingly, in fact, towards the extremities of the rhabdosome, it would be unusual for all distal extremities to be flattened and preserved in quite this way. We have shown some of the distal twisting of stipes which com-



Figures 32–33. *Clonograptus rarus* Harris and Thomas, distal thecae of holotype, P32053, the 2nd theca of Figure 39 is possibly nearest true profile. Scalebar 1 mm.

Figure 34. *Clonograptus erdtmanni* sp. nov., distal thecae of holotype, P34260. Scalebar 1 mm.

Figure 35. *Clonograptus ramulosus* Harris and Thomas, distal thecae, paralectotype P32030. Scalebar 1 mm.

Figure 36. *Clonograptus trochograptoides* Harris and Thomas; distal thecae on 8th order stipe of holotype, P32166. Scalebar 1 mm.

Figure 37. *Clonograptus persistens* Harris and Thomas, distal thecae a 6th order stipe of holotype, P32167. Scalebar 1 mm.

Figure 38. *Clonograptus trochograptoides* Harris and Thomas; distal thecae on 7th order stipe of holotype, P32166. Scalebar 1 mm.

monly occurs, and we have unravelled the tangling of stipes which must have taken place as the holotype was rolled along the bottom. The stipe lengths and positions of branching points are as indicated on the holotype.

Clonograptus rarus Harris and Thomas

Plate 2 fig. a: text-figs 32, 33

Clonograptus rarus Harris and Thomas, 1938a: 73, pl. 1 fig. 8c; pl. 3 fig. 8a; pl. 4 fig. 7 (non plate 1 fig. 8b).

Type Material. The holotype (designated "type" by Harris and Thomas) is P32053 (41311b) from the "good bed" rather more than 200 m WSW from NE corner of allotment 16A, sect. II, Parish of Campbelltown, figured by Harris and Thomas, 1938a, plate

3 fig. 8a (a drawing, not a photograph). Also figured were plate 1 fig. 8b P34260 (41311a) and plate 1 fig. 8c, which is on P32053 and may be part of the holotype.

Horizon. Bendigonian Be1.

Description. The original dimensions suggested for the complete rhabdosome by Harris and Thomas was 60 cm. However, this was based upon the decision to include P32053 and P34260 in the same species (see *Remarks* below). We recognise only the former (the holotype) and on this basis the rhabdosome would have an overall diameter of at least 40 cm, more probably 50 cm. The proximal end is not known with certainty unless it is the specimen described by Harris and Thomas as *C. smithi* and, in the absence of the type and figured (? only) specimen, we can add nothing to their original figure and description. The holotype stipes have a maximum dorsoventral width (seen) of about 2 mm (flattened lateral width of about 1 mm) but proximally it could be more. However, even the most distal parts of stipe seen have a dorsoventral width of only just less than 2 mm. Thecal spacing seems to be 7–8 "proximally" and about 7 distally.

The holotype may show a tangled mat of stipes and dichotomies resulting from one half of a specimen: that is, those clustered at the top of the slab (plate 2 fig. a) would be from the top left of the funicle and those at the bottom from the bottom left of the funicle. If that is the case the eight terminal stipes at the top are possibly of the 5th order and are upwards of 15 cm long; the only 4th order stipe seen is 8 cm long; and full 3rd order stipes are not seen. The lower bunch of terminal stipes on the slab also number eight which suggests the above interpretation to be correct.

Remarks. The holotype and only specimen of *C. smithi* is missing, which renders difficult a decision on the synonomy or otherwise of this form with *C. rarus*. It seems to us that the proximal end of *Clonograptus smithi* figured by Harris and Thomas as plate 1 fig. 9 could be the proximal end of *C. rarus* which comes from the same locality. The latter is known only from distal fragments and there is no evidence that the earliest dichotomies seen on P32053 are second order as claimed by Harris and Thomas. They seem more likely to be 3rd and 4th order and could be quite distal fragments. The general dimensions of stipes and thecae, and the nature of the thecae and dichotomies seem very similar to those figured as *C. smithi*. It should be noted, however, that the paratype figured by Harris and Thomas as plate 1 fig. 8b (P34260 is, in our view, a new species of *Clonograptus* (see next description) quite different from either *C. rarus* or *C. smithi*.

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Figure 39. *Clonograptus trochograptoides* Harris and Thomas; dichotomy leading to 9th order stipes on holotype, P32166. Scalebar 1 mm.

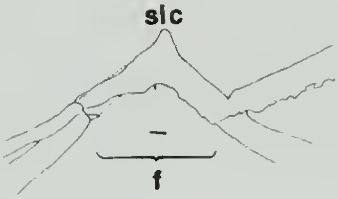

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Figure 40. *Clonograptus erdtmanni* sp. nov., funicle, sicula (sic) and 2nd order stipes of holotype, P34260. Scalebar 1 mm.

Clonograptus erdtmanni sp. nov.

Plate 3 fig. a; text figs 22, 34, 40

Clonograptus rarus (pars).—Harris and Thomas, 1938a: 73, plate 1 fig. 8b (non plate 1 fig. 8c; plate 3 fig. 8a).

Holotype. P34260 (41311a), labelled hypotype, and figured by Harris and Thomas as *C. rarus* (in fact a paratype from the Bendigonian (Be1), same locality and horizon as *C. rarus* (preceding description)). The holotype is the only known specimen. Associates are the same as for *C. rarus* and *C. ramulosus*.

Derivation of name. In recognition of the work done by Dr Bernd-Dietrich Erdtmann on early Ordovician and Tremadoc graptolites.

Description. The rhabdosome would have had an overall diameter of at least 30 cm, possibly 40 cm, were it disposed horizontally. However, it is possible that the rhabdosome was slightly declined, and the holotype may be preserved in partial profile (plate 3 fig. a; reconstruction, fig. 22). The part labelled Sic and F in fig. 40 is almost certainly the sicular region and funicle with dichotomies taking place within 10 mm of each other and within 5 mm either side of the sicular region. This latter part was not fully prepared when we first examined it, but on uncovering it carefully we found the "bend" to be in reality a rather sharply rounded, typically conical funicular region.

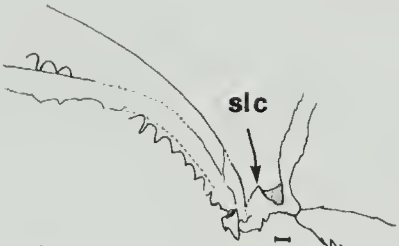


Figure 41. *Goniograptus palmatus* Harris and Keble, web arrangement near proximal end of holotype, P26448. Scalebar 1 mm.

Figure 42. *Tridensigraptus zhaoi* sp. nov., funicle (f), sicula (sic) and proximal end of holotype, P31193A, B.

The length of the sicular region is 3.2 mm and there is a slight, rounded hollow at its base suggesting a sicular apertural region. The "width" of the stipes of the first order (thecae not visible) is just under 2 mm, which is maintained to the beginnings of the second order stipes. However, almost the whole rhabdosome has the highly denticulate or isolated thecal apertures visible, presumably because the view is largely a profile view, and the dorsoventral width probably changes from 3.0 mm proximally to 2.5 mm mesially and perhaps 2 mm most distally. Dichotomous divisions take place until at least the 5th order, although a few divisions (that nearest the sicula, for example) appear to be lateral divisions: this appearance may result from the profile view of the rhabdosome. The tapering of the stipe "width", that is excluding the thin-walled thecal apertural regions, is quite rapid (from just under 2 mm proximally) and at 10 cm from the funicle the width is less than 1 mm.

Reconstruction. Fig. 22 is based upon the holotype, and upon the inference made above that the funicle region is slightly pendent, robust, and probably secondarily thickened. Almost all the divisions shown on the reconstructions are present on the holotype, and what is more important is that the more proximal stipes do branch in the positions shown, which strongly reinforces our argument in the above description. As in some other clonograptids the distal dorsoventral width is the same as that proximally, as far as can be ascertained, but we have shown less peridermal thickening distally than proximally. In view of the profile view of the rhabdosome it is unlikely that *C. erdtmanni* was a horizontally disposed form and was more likely to have been gently declined as shown. The drawing, however, does not purport to show a life position, but rather profile preserved aspect as seen on the bedding plane, but with bends and breakages removed.

Remarks. From the above it is clear that there are several lines of evidence supporting our claim that this is a profile view of a robust clonograptid with the funicular area preserved. It is unlike other Victorian clonograptids except *C. tenellus problematicus* in that the first pair of dichotomies takes place close to the sicula to be followed by 20–30 mm before the next divisions on three (possibly four) of the second order stipes. Thereafter the divisions, and rhabdosome as a whole, resemble *C. rarus* and to a greater extent the stratigraphically earlier *C. ramulosus.* The tapering of the stipe "width" is greater than in *C. rarus* and *C. ramulosus,* indeed greater than in any other Victorian clonograptid except possibly *C. trochograptoides* (see below).

Clonograptus tenellus problematicus
Harris and Thomas

Plate 2 fig. b

Clonograptus tenellus (Linnarsson) var. *problematica* (sic) Harris and Thomas, 1938a: 73, plate 1 fig. 11; plate 4 figs 10a, b.

Type material. The holotype (P32187 (41319)) and only specimen is from the same locality and horizon as *C. rarus, C. smithi* and *C. erdtmanni* sp. nov. On the type slab is a good specimen of *Tetragraptus approximatus.*

Description. The diameter of the rhabdosome is probably in excess of 14 cm. The nearly profile view of the funicle and sicula is almost certainly a result of the tangled form of the rhabdosome. Dichotomous divisions take place up to the sixth order at fairly regular intervals as follows: 1st dichotomy after 3 mm; 2nd after a further 3–5 mm; 3rd after a further 6–8 mm (one at 12 mm); 4th after a further 15–20 mm; 5th after a further 20 mm or more. Further divisions may occur.

The stipe width gradually changes from 0.5 mm proximally to 0.2 mm most distally, although this is a lateral width rather than a true profile, dorsoventral width. Such unambiguous measurements as we have made make us doubt the Harris and Thomas thecal spacing figures which were probably arrived at by counting rather conspicuous notches on the main body of each stipe. Distally these number two to each theca and, furthermore, they are not always regularly spaced but seem often to occur in pairs. They may represent bithecae and autothecae so that counting both gives twice the certain autothecal spacing when the stipe is seen in true profile. In those parts of the stipes showing the latter condition the notches are not seen, strongly suggesting that they represent autothecal and bithecal apertures pressed through; or possibly the autothecal apertures and bases of interthecal septa. In the proximal region the thecal spacing may be 11–12 in 10 mm as noted by Harris and Thomas, but distally it is as low as 6 in 10 mm and the thecal apertures, though badly preserved, are strongly denticulated and isolated giving a true dorsoventral width of about 0.75 mm.

Remarks. C. tenellus problematicus is, therefore, of essentially Group A type and does not, as Harris and Thomas (p. 73) claimed, have "normal" thecae, by which they meant dichograptid thecae. The species differs from the above described forms in having a smaller, more slender rhabdosome, and probably with more regular dichotomies.

Clonograptus trochograptoides Harris and Thomas

Plate 4 figs a, b; text figs 36, 38, 39

Clonograptus trochograptoides Harris and Thomas, 1939: 57–58, fig. 13.

Type material. Holotype, P32166 (38445), from the Bendigonian at allotment 7b, sect. II, Parish of Campbelltown.

Description. The rhabdosome is roughly circular with a diameter of more than 25 cm, and may well be almost complete. Branching up to the 8th or 10th order may take place, but some stipes reach only the 4th order, in which cases the terminal stipes may continue to grow almost to the rhabdosomal periphery. Some such dichotomies possibly take place at an early stage for adjacent stipes are extremely robust and may have added thickening during astogeny. In these instances a stipe which undergoes no further division remains relatively slender and the dichotomy itself has the appearance almost of a lateral division. There are approximate radii at which the bulk of divisions take place, but there are numerous exceptions: these radii are at 2 cm, 3.5–4 cm, 5–6 cm. Divisions up to third order stipes take place at very close intervals of 2–4 mm; thereafter divisions are at increasing but rather irregular intervals. The whole manner of development suggests an arrangement of stipes to fit a horizontally disposed rhabdosome.

Proximal thecae are indiscernible but mesial and distal thecae are clearly dichograptid (figs 38, 39), inclined to the stipe axis at some 30°–40°, and are spaced at approximately 9 in 10 mm. The free ventral wall is almost straight, but the apertural margin commonly gently convex. A few widely spaced growth lines are visible near the apertures, perhaps suggesting that the apertural parts of the thecae are less sclerotised. The thecae shown in fig. 38 may not be quite typical or true profile because in several places, quite distally, those types shown in figs 36 and 39 are seen. Although typically dichograptid they show considerable overlap. We are inclined to regard these as the true profile thecal shapes. The branching division to the 9th order stipes seems to originate from the marked lump close to the dorsal stipe margin, but this is not certain.

Remarks. Although Harris and Thomas disclaimed the marked increase in branch spacing between the fourth and fifth orders typical of *C. norvegicus* Monsen, there is nevertheless a change at this point in the rhabdosome, and the two can reasonably be grouped together as being closely related. We are at a loss to understand the reasoning behind the Harris and Thomas suggestion that *C. trochograptoides* might be intermediate between *Trochograptus* and *Clonograptus.* It seems to us to bear little or no resemblance to *Trochograptus.*

Clonograptus persistens Harris and Thomas

Plate 1 fig. c; text fig. 37

Clonograptus persistens Harris and Thomas, 1939: 59, fig. 11.

Type material. Holotype, P32167A, B, (42534), from the Bendigonian (Be1), NW corner of allotment 19, sect. II, Parish of Campbelltown. (Harris and Thomas gave the locality (p. 59) as:"good bed, allotment 16A, sect. 2, Parish of Campbelltown", but the museum register gives allotment 19 and points out that the Harris and Thomas (p. 59) attribution is incorrect. It is clear that Harris and Thomas wished to indicate that *Goniograptus thureaui* and subspecies occurred at the same locality).

Description. The overall rhabdosome diameter is some 14 cm, and the disposition probably horizontal. Dichotomous divisions up to the 7th order take place. In several places the distal dorsoventral width and the thecal profile is seen (fig. 37) where it is up to 1.5 mm and with a thecal spacing (6th order stipe) of 12 in 10 mm. In the first few stipe orders the dorsoventral width cannot be seen, and the thecae but rarely, and not in profile. In all probability the rigidity of the proximal regions ensures that upon flattening the thecae remain facing downwards (or upwards), whereas on the periphery of the colony a few stipes turn over and are seen more nearly in profile. Thus with this species, we cannot give true dorsoventral width figures for the early divisions, but would estimated them to be about the same distally as proximally, as in other clonograptids from the Bendigonian.

Remarks. The original figure of Harris and Thomas (fig. 11) is misleading in suggesting a much greater stipe width proximally than can actually be seen. The close similarity of thecal type to those we have described for *C. trochograptoides* is obvious, although in *C. persistens* they are much more closely spaced. As in *C. trochograptoides*, a thecal view which is not true profile results in an appearance where the overlap is not obvious and in which the apertural regions appear more isolate and/or denticulate.

Order **Graptoloidea** Lapworth, 1875

Suborder **Dichograptina** Lapworth, 1873

Superfamily **Dichograptacea** Lapworth, 1873
(emend. Fortey and Cooper, 1986)

Dichograptidae Lapworth, 1873
(emend. Cooper and Fortey, 1982 and herein)

Remarks. Cooper and Fortey (1982) logically changed the "Treatise" (1970) concept of the family as a result of their detailed studies of Spitsbergen graptolites. In effect they removed from Bulman's (multiramous) Section Goniograpti a number of genera based upon *Sigmagraptus* and erected a new subfamily the Sigmagraptinae to include the genera *Sigmagraptus*, *Trichograptus*, *Etagraptus*, *Acrograptus*, *Laxograptus* and possibly *Goniograptus*, *Brachiograptus* and *Yushanograptus*. The subfamily's main features include isograptid dextral development with th1^1 originating high on the ventral side of a long sicula; th^1 and 1^2 diverging from the sicula at a high angle, th1^1 being *above* the level of 1^2 at this point; dichotomies up to 10 or more orders, consecutive or delayed; branching progressive or monoprogressive. Overall rhabdosomal shape and stipe number was regarded as less important than the above developmental details. We entirely support their decision to erect the Sigmagraptinae and, furthermore, are able to add, in the following descriptions, quite considerably to the developmental information on several of the constituent genera and species (as, for example, in *Praegoniograptus*, *Kellamograptus*, *Trochograptus* and *Pendeograptus pendens*). In addition Cooper and Fortey recognised the subfamilies Isograptinae Harris (1933) and Dichograptinae Lapworth (1873), the former being tightly defined and the latter being a portmanteau taxon, admittedly polyphyletic, from which further closely defined groups might be removed in the future. Finally the same authors recognised the family Phyllograptidae Lapworth 1873 including in it *Phyllograptus sensu stricto* and *Xiphograptus* Cooper and Fortey (1982) the latter comprising some forms hitherto regarded as extensiform didymograptids.

Thus from the point of view of the Bendigonian faunas being studied here the Didymograptina is subdivided as follows:

Family Dichograptidae (subfamilies Dichograptinae and Isograptinae)
Family Phyllograptidae

We intend, in the portmanteau subfamily Dichograptinae discussed below, to completely reorganise the constituent genera in an informal way, as did Bulman (1970), without pretending that the grouping is in any monophyletic. However, it is more convenient and logical than the scheme perforce adopted by Bulman.

Dichograptinae Lapworth, 1873
(emend. herein)

Diagnosis. Sicula usually gently curved aperturally towards second stipe: development isograptid, rarely *artus*-type, but may lack isograptid symmetry of early thecae; dichotomies zero to many; peripheral stipes one to many; stipe dispositions variable.

Remarks. In erecting the Sigmagraptinae, Cooper and Fortey (1982) effectively dismantled Bulman's Section Goniograpti which he included with his multiramous forms of the Dichograptidae. In doing so they left all other dichograptids (except the Isograptinae) in a portmanteau subfamily the Dichograptinae, emending its diagnosis accordingly, but not redefining the various Sections which Bulman used relatively informally in 1970 (Goniograpti,

Table 3. Classification of the subfamily Dichograptinae adopted in this paper, with informal divisions and their current status to the left; and the structure of the rhabdosome to the right. The dichograptid template is one in which there are either 2 or 3 progressive (consecutive) dichotomies resulting then in a large number (at least 8) terminal stipes as in *Dichograptus* or *Loganograptus*.

Section	Subsection	status	template	rhabdosome branching	disposition	genera
ANOMALOGRAPTI		nov.	clonograptid	clonograptus dichotomy	horizontal to ?declined	*Anomalograptus*, ?*Anthograptus*
DICHOGRAPTI	A. dichotomous branching	emend.	dichograptid	dichotomous	horizontal	*Dichograptus*×, *Loganograptus*×, *Stellatograptus*, *Praegoniograptus*×
	B. lateral branching	emend.	dichograptid	dichotomous	horizontal	*Orthodichograptus*×, "*Schizograptus*" *incompositus*, "*Trochograptus*" *australis*×
TEMNOGRAPTI		emend.	tetragraptid	clonograptus dichotomy	horizontal	*Temnograptus*, ?*Zygograptus*×, *Calamograptus?*
SCHIZOGRAPTI	A. lateral, unpaired	emend.	tetragraptid	lateral	horizontal	*Schizograptus*×, *Trochograptus*×, *Holograptus*
	B. lateral, paired	nov.	tetragraptid	lateral	horizontal to reclined	*Tridensigraptus*×+, ?*Triaenograptus*×
PENDEOGRAPTI		nov.	tetragraptid	dichotomous	pendent	*Pseudobryograptus*×, ?*Pterograptus*, *Pendeograptus*×+
TETRAGRAPTI		emend.	tetragraptid	"dichotomous"	horizontal to declined	*Tetragraptus* (*Tetragraptus*)×+
MIMOGRAPTI		nov.	didymograptid	lateral	?declined	*Mimograptus*×, ?*Pterograptus*
DIDYMOGRAPTI		emend.	didymograptid		horizontal to deflexed to pendent	*D.* (*Didymograptus*) s.l.×+, *D.* (*Expansograptus*) ×+, *D.* (*Corymbograptus*)×, *D.* (*Didymograptellus*)

× taxa described in this work
+ taxa in which some proximal and developmental structure is known

Temnograpti, Schizograpti, Dichograpti, Tetragrapti, Didymograpti).

Our work on the Bendigonian graptolites, involving as it does many multiramous specimens and species, has given us further insight in the problems faced by Bulman in grouping the dichograptid genera. As he stated in the "Treatise", and as confirmed both by Cooper and Fortey (1982) and ourselves in this paper, the time is not yet ripe for wholesale reclassification, on a phylogenetic basis, of the dichograptids. Nevertheless we are now in a position to sensibly amend Bulman's Sections and to make further comment on the early development of some forms. The main variables to consider are as follows: *a*, detail of proximal development; *b*, dichotomous and lateral branching (see also section on branching patterns); *c*, basic proximal end plan (whether dichograptid, didymograptid etc). The first is not really applicable across the board, hence our reluctance to formally erect more subfamilial divisions. Category *c* is not the same as *a* because it depends only upon the proximity, number and arrangement of dichotomous divisions relative to the sicula, and not necessarily to the early growth of th1^1–2^1 (information about which is almost our ultimate objective). Therefore a combination of broad proximal region plan with branching pattern should give us at least an informal, descriptive and perhaps non-phylogenetic grouping. In the 1970 "Treatise", Bulman used similar criteria, but leaned heavily on the recognition of multiramous and pauciramous forms, a convenience at the time but one demoted by Cooper and Fortey, and by ourselves, as being at best only a very broad guide to evolution. Our proposed grouping within the Dichograptinae is shown in Table 3.

It will be immediately obvious that neither the number of stipes nor their attitudes has been taken as a matter of prime importance. For example, the basically 4-stiped *Pendeograptus* (redefined in this paper) is grouped with *Pseudobryograptus* and *Pterograptus*. Similarly in redefining the Sigmagraptinae Cooper and Fortey (1982) included genera such as 2-stiped *Acrograptus* with 4-stiped *Etagraptus* and several multiramous genera.

However, the template column of Table 3, emphasizing the basic proximal region plan upon which the rhabdosome is based, shows a gradation from complex (clonograptid) in the Anomalograpti to the relatively simple (didymograptid) of the Mimograpti and Didymograpti. This is not to say that the proximal end detailed development is necessarily known in all these cases.

When viewed stratigraphically there is clear supporting evidence for the above informal scheme, and the stratigraphy and classification were related to the broad evolutionary pattern earlier.

Anomalograpti (nov.). Probable *Clonograptus* proximal end and clonograptid dichotomies; if proximal template proves to be tetragraptid, could be related to *Temnograptus*. *Anthograptus* is provisionally grouped here although the proximal region is unknown: it may be more closely related to *Mimograptus* should the presumed elongate ?second order stipe prove to be part of a didymograptid plan.

Dichograpti (emend.). Dichograptid template with either dichotomous branching or lateral branching. *Orthodichograptus* is a dichograptid with lateral branches of several orders developed on the main stipes, whilst "*Trochograptus*" *australis* Harris and Thomas (1938a), which we refer to our new genus *Kellamograptus*, is based upon the dichograptid (six or seven branched) proximal end and has numerous lateral branches of several orders. "*Schizograptus*" *incompositus* Harris and Thomas (1938a) (figs 89, 90) should probably also be referred to *Kellamograptus*. It has a dichograptid (five or six branched) proximal end with secondary lateral branches of one order (it is not impossible that it represents an early growth stage of *Kellamograptus australis*. *Loganograptus* is really a *Dichograptus* in which one further division takes place (often incompletely: see systematic descriptions, and section on branching patterns prior to systematics), whilst *Stellatograptus* is essentially the same but with additions of thick central web and lateral alae on the stipes.

Temnograpti (emend.). Tetragraptid plan coupled with clonograptid dichotomies and large rhabdosomes. The section is amended only to include, possibly, *Zygograptus*. In the systematics it will be noted that the funicular region of *Zygograptus* can be very elongate, essentially didymograptid, or may involve only two thecae each side of the sicula. Basically it seems like an elongate tetragraptid plan, and coupling this with the subsequent, numerous, clonograptid dichotomies and large rhabdosomal size often achieved, it seems to us the genus fits somewhat awkwardly into the Temnograpti. However, *Zygograptus* does raise the whole question not only of the distinction between didymograptid and tetragraptid ground plan, but between these and dichograptids and clonograptids.

Schizograpti (emend.). Dichograptids with tetragraptid template, lateral branches, large rhabdosomes, the branches being either unpaired or paired. The section is amended to exclude forms with didymograptid template, and to include *Tridensigraptus* Zhao (1964) and other forms with paired lateral branches resulting in a trident-like branching system. Whether or not the lateral branches are on one side of the main stipe is probably a generic (?specific) character but may at times be a preservational feature. *Tridensigraptus zhaoi* sp. nov. has a moderately well preserved proximal end of tetragraptid template (fig. 42) and at a stage of growth without later branches could easily be mistaken for *Tetragraptus* ex gr. *serra*. *T. zhaoi* sp. nov. is strongly declined, unlike most of the large dichograptids which appear to be of horizontal disposition. *T. zhejiangensis* Zhao (1964), the type species of the genus, also seems to be horizontal.

Pendeograpti (nov.). Pendent dichograptids with a tetragraptid template and two to numerous stipes, usually 4–6, development isograptid dextral. *Pseudobryograptus* has a long range in time if *Bryograptus crassus* Harris and Thomas (1938a) is correctly referred to that genus in this paper. We note that Cooper and Fortey (1982) placed *B. crassus* in *Tetragraptus* (*Pendeograptus*) on the not unreasonable assumption that since *T.* (*P.*) *fruticosus* can have 2–4 stipes it is not stretching the definition unduly to have forms with up to 6 stipes. However, *B. crassus* and other *Pseudobryograptus* species do show third order stipes and for this reason we prefer to continue recognition of the genus for the present. In this paper we show that *P. pendens*, the type species, has an isograptid dextral initial development, followed probably by isograptid dextral dichotomies. *P. fruticosus* is also shown to have the same structure, thus supporting the Cooper and Fortey (1982) more tentative conclusions about the similarity of development of the two. Furthermore, it is likely that *Pseudobryograptus crassus* has identical development initially, so that the inclusion of the two in the same section, if not the same genus, is very reasonable. *Pterograptus* is speculatively placed here but if the proximal development proves to be based upon a didymograptid plan it would fit more naturally into the Mimograpti.

Tetragrapti (emend.). This section is amended only to exclude *Pendeograptus* and certain tetragraptids now placed in *Etagraptus* Ruedemann (1904) (see discussion of Sigmagraptinae). Further discussion of Bendigonian *T.* (*Tetragraptus*) will be found under discussion of *Tetragraptus* below.

Mimograpti (nov.). Probably a declined dichograptid with didymograptid template and irregularly positioned lateral stipes of two orders.

Didymograpti. Reclined, horizontal, deflexed or pendent didymograptids, with no secondary branches.

Section **Dichograpti** (emend. herein)

DICHOTOMOUSLY BRANCHING FORMS

Loganograptus Hall, 1868

Type species. Graptolithus logani Hall, 1858: 142.

Diagnosis. Usually 16–18 peripheral stipes, rarely more than 4th order, from proximally concentrated progressive dichotomy; central web or webs commonly present; thecae typical dichograptid, moderately inclined to stipe axis.

Remarks. Comment is made below on the speciation of Victorian loganograptids into *L. logani logani*, *L. l. australis*, and *L. rectus*. It is conceivable that they are all one form, but that they differ from *L. logani* s.s. in its Northern Hemisphere development, irrespective of established faunal province. *Loganograptus* is readily distinguished from most dichograptid genera by the pattern of its proximal dichotomies, but not so readily from some goniograptids (see figs 12–17).

Loganograptus logani australis (McCoy)

Plate 6 fig. c; text figs 24, 69

Graptolites (*Didymograpsus*) *logani* (Hall) var. *australis* McCoy, 1874: 18–20, pl. 2 fig. 6.

Loganograptus logani.—Harris and Thomas, 1940 (? pars, text), 130–131, (non pl. 2 figs 7a, b; text-fig. 2, 3).

Type specimen. Holotype, P12280, from GSV locality Ba 78, Barker Street, Castlemaine.

Diagnosis. L. logani in which the rhabdosome may be very large, the dorsoventral stipe width almost 3 mm (possibly more in some), and the thecal spacing only 6 in 10 mm.

Description. We have managed to uncover a trace of the sicula on McCoy's holotype (fig. 69) where it can be seen to be somewhat curved with a length of 1.5 mm, although nothing further is visible. The funicle has a length of 3 mm, with one theca either side of the sicula and a maximum width of 0.75 mm. It is by no means certain that: *a*, this is a thecal profile width, although there is some suggestion of profile in the early thecae, or *b*, that the sicula itself is parallel with the bedding plane. The 2nd order stipes are between 1 and 2 mm long and probably comprise only one theca in each stipe (ignoring overlap, which cannot be discerned). The third order stipes are some 1–3 mm long, with a width of up to 1.5 mm; so that the whole dichotomous division of the species is accomplished within 5 mm of the sicula. The distal dorsoventral width, of the fourth order stipes, reaches almost 3 mm and the thecal spacing is as low as 6 in 10 mm. The thecae themselves are dichograptid, with free ventral walls inclined to the stipe axis at 40–50°. The holotype has eighteen peripheral stipes. Sixteen of these are joined in normal loganograptid fashion as terminal pairs from the fourth progressive dichotomy, but two branches (arrowed in plate 6, fig. c) *seem* to be lateral. In all other respects these resemble terminal stipes.

Remarks. Harris and Thomas (1940: 131) by implication included McCoy's form in their description of *L. logani*, but do not record it in this fashion in their synonomy list (1940: 130). They seemed to be of the opinion that Victorian specimens of *L. logani* were more robust with dorsoventral widths in excess of typical North American and British material (reaching almost 2 mm compared with 0.8 mm and 1.6 mm respectively). Our study of the Victorian specimens confirms that many *are* more robust, but that narrower stiped specimens are not uncommon. All these we would include, as did Harris and Thomas, in *L. logani logani*. However, McCoy's form is noticeably more robust with a dorsoventral width of 3 mm and, apparently, some lateral stipes (or, at least, abnormal, irregular dichotomies) as well as a low thecal spacing of only 6 in 10 mm. It is not as common as the nominal subspecies, and we prefer to retain its taxonomic status at present. Although Elles and Wood (1901–1918) recorded a dorsoventral width of 1.6 mm for British forms it is clear from some of their illustrations, as well as from our own observations, that the distal dorsoventral width occasionally reaches 2 mm, as it does in North American material we have examined. The *total* range of variation is probably similar to Victorian specimens but the latter are more commonly robust with fewer slender specimens. It is possible that some stratigraphic variation will eventually be shown, as hinted at by Ruedemann (1904: 633). The specimen figured by Harris and Thomas as *L. logani* (1940, text-fig. 3) has 4th order stipes possibly 15 cm long, giving a total rhabdosomal diameter of more than 30 cm. The distal dorsoventral width is 3.4 mm, which is considerably greater than previously recorded (thecal spacing at this stage is 10 in 10 mm): a dorsoventral width of 3.0 mm is achieved within 5 cm of the sicula.

Loganograptus rectus Harris and Thomas

Plate 7 figs a–d; text-figs 67, 68

Loganograptus rectus Harris and Thomas, 1940a: 131, pl. 1 fig. 6a, b, pl. 2 figs 8a–c.

Type specimens. Holotype, P32034 (42563), from the Bendigonian (Be1) of allotment 25B, Parish of Sandon, figured by Harris and Thomas as pl. 1 fig. 6a and pl. 2 fig. 8c. Paratype, P32054 (42564), figured by Harris and Thomas as pl. 1 fig. 6b and pl. 2 fig. 8a, b, from the Bendigonian (Be1) of allotment 16A, Parish of Campbelltown.

Diagnosis. Loganograptid with small stiff rhabdosome, less than 10 cm diameter; maximum dorsoventral stipe width about 2 mm; thecal spacing 8 in 10 mm; 4th order stipes straight; up to 45 mm; funicle 2.5–3.0 mm.

Description. The paratype (P32054) was originally figured (pl. 2 fig. 8b) with the position of the sicula shown. We have now uncovered much more of the sicula (fig. 67) where it can be seen to have a length of well over 1 mm in a funicle of some 2.5–3.0 mm. There is a suggestion that the sicula is not in the same plane as the rest of the early part of the rhabdosome. The holotype itself confirms this last observation: the sicula seems to be at right angles to the bedding plane, and the funicular region and early dichotomies are gently domed. Whilst this may be an artefact of preservation it may, equally, reflect an original arching incompletely flattened into the bedding. Small portions of web are irregularly distributed in the proximal parts of the rhabdosome (fig. 67). Th1^2 may leave the sicula at a slightly lower level than th1^1 (if the latter is correctly identified by its closer position to the sicula: fig. 67). The 1st, 2nd and 3rd order stipes are short, 1.5–2.0 mm, probably involve only a single theca, and are completed within 6 mm of the sicula. 4th order stipes are stiff and straight, and up to 45 mm long with a maximum distal dorsoventral width (seen on the holotype) of 1.9–2.0 mm when viewed in near profile. The thecae are not well seen on any of our specimens but are distally spaced at 8 in 10 mm and appear to be "normal" overlapping dichograptid thecae (fig. 68).

Remarks. Harris and Thomas distinguished this species on three counts from *L. logani*: *a*, the more rigid habit (stiffer stipes); *b*, the more constant (stipe) width; *c*, the lower angle of thecal inclination and straighter ventral margins. *b* and *c* may be invalid distinctions in that the true stipe profile is not seen on either of the two types. Thus fig. 68 depicts the distal thecae on the paratype (thecae are difficult to see at all on the holotype) and it is apparent that they are not in true profile but a subdorsal view: this results in a lower dorsoventral width figure, a lower angle of thecal inclination, and a straighter ventral margin. The relatively small, stiff rhabdosome remains the only reasonable criterion for distinguishing the two, and it may well be that future work on the variation of *L. logani* will show even this to be invalid. We have the strong impression, looking at numerous Victorian specimens of *L. logani*, that when the stipes reach great length they become (preservationally) more flexuous (e.g. P32056, figd. Harris and Thomas, 1940, fig. 3; and herein plate 6 fig. a). Smaller specimens often appear distinctly rigid; and it is equally obvious that only a small number of Museum of Victoria specimens have been identified as *L. rectus*.

Dichograptus Salter, 1863

Type species. Dichograptus sedgwickii, Gurley, 1896.

Diagnosis. 8 or fewer stipes, progressive dichotomies to 3rd order, which are terminal and often long; thecae long, moderately inclined dichograptid, denticulate, with considerable overlap; rarely with long apertural spines.

Dichograptus maccoyi maccoyi
Harris and Thomas

Plate 8 figs a–d; text figs 44, 46–48

Dichograptus maccoyi Harris and Thomas, 1940a: 129, pl. 1 figs 1a–d; pl. 2 fig. 2.—Cooper, 1979: 58–59, pl. 5f; fig. 25.

Dichograptus maccoyi maccoyi.—Cooper and Fortey, 1982: 185–186, fig. 11.—Henderson, 1983: 157, fig. 8b.

Type specimens and other material. Holotype, P32061 (42550), from the Bendigonian (Be2) of allotment 20, Parish of Campbelltown. Paratypes P32035 (34853); P32063 (42552); P32062 (42551); from the Bendigonian (Be1) of allotment 16A, Parish of Campbelltown; in the case of the first from the SW corner "on A of 16A". Ten specimens in the collections of the Museum of Victoria.

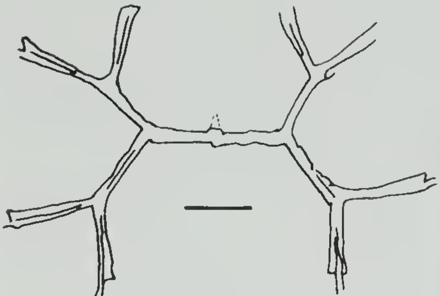
Diagnosis. Sicula 1.5 mm+; funicle 3 mm; 2nd order stipes 1–2 mm; thecae elongate dichograptid, 8–10 in 10 mm; distal dorsoventral width 1.8–2.0 mm; maximum stipe length 47 mm.

Description. The sicula has now been fully exposed on the holotype and when initially prepared showed a short, fine nema (fig. 44): this subsequently deteriorated in the somewhat crumbly rock. The length of the holotype sicula is over 1.5 mm. It is clear from the slight shoulder joining the sicula and $th1^1$ that the latter arises at the very least one third up the sicula (probably much higher) and gives rise to $th1^2$ which then leaves the apertural region of the sicula at a lower level than does $th1^1$. Again, this is on the assumption that that theca, the aperture of which is closest to the sicula, is $th1^1$. (This does seem to be a general rule in forms where it can be ascertained). The sicula is in a slightly different plane to the rest of the rhabdosome. The funicle is about 3 mm long, and the 2nd order stipes 1–2 mm. Thereafter the thecae become clearly visible and are elongate dichograptid becoming rapidly higher: a distal dorsoventral width 1.4–1.6 mm is reached in most stipes, but where a true profile is seen (figs 44, 48) 1.8–2.0 mm is more common, from a proximal width (?true profile) of 0.6 mm. Thecal spacing is 8-10 in 10 mm, and the maximum stipe length seen is 47 mm. When seen in true profile (fig. 44) there is a certain flaring of the aperture and an increasing angle of inclination of the free ventral wall as the distance increases from the dichotomy point (30° to 50°).

The paratype to which Harris and Thomas (1940a: 129) referred as "showing atrophy of branches" (plate 1 fig. 1d, not 2d as stated in their text) actually has eight peripheral stipes (not 6 or 7 as claimed): one is folded back over part of the funicle area, and a dichotomous division is just visible in the bottom left hand corner of the slab.

Remarks. We have questioned the attribution of Cooper's (1979) forms only because Cooper and Fortey consider them closer to *D. maccoyi densus* Cooper and Fortey. We have not identified the latter in Victoria.

The stipes are more truly robust than intimated by Harris and Thomas and certainly reach 2 mm distally. Also the angle of inclination of the theca is clearly much greater than they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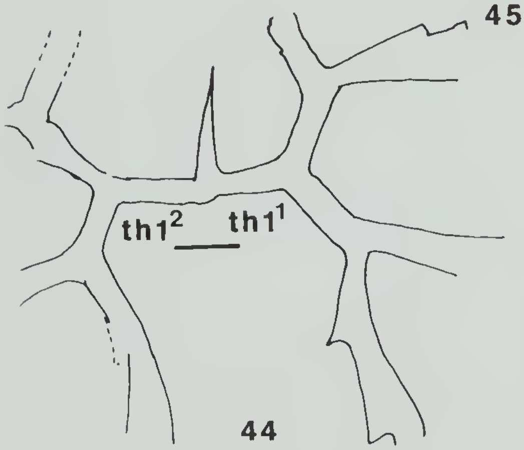

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Figures 43, 45. *Dichograptus tenuissimus* Harris and Thomas, proximal region and distal thecae respectively of the holotype, P32110. Scalebar 1 mm.

Figures 44, 46–48. *Dichograptus maccoyi maccoyi* Harris and Thomas, respectively proximal end of the holotype P32061 (42550) with short nema (later destroyed during further preparation attempts), distal thecae of holotype, and distal thecae of paratypes P32035 and P32063. Scalebar 1 mm.

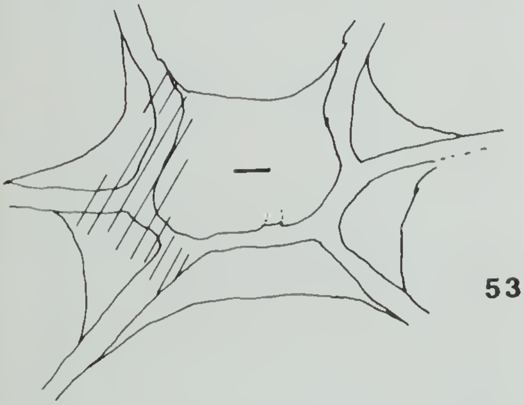
Figure 49. *Dichograptus sedecimus* Harris and Thomas, portion of 3rd order stipe of holotype P32010. Scalebar 1 mm.

Figure 50. *Dichograptus expansus* Harris and Thomas, distal thecae of holotype, P32076. Scalebar 1 mm.

supposed, bringing the definition of this species even closer to *D. sedgwickii* Salter and *D. tenuis* Monsen; as does the flaring of the thecal apertures. The most distinctive feature of *D. maccoyi*, relative to these other dichograptids, is the lower thecal spacing; and *maccoyi* differs from *D. octobrachiatus* in being smaller and with much narrower stipes. Nevertheless the differences between all these species seem to us to be very slight and, in part at least, may be due to the age of the colony. The older (Be1) specimens from the Bendigonian seem slightly more robust than the holotype and the other specimens from Be2: however the latter rarely seem to show the thecae very well. *D. solidus* Harris and Thomas is a more robust species than *D. maccoyi*, with short curved stipes and a strong suggestion in the holotype (P32059 (42555)) of at least slightly declined stipes. The holotype of *D. solidus* was figured by Harris and Thomas as pl. 1 fig. 3. On this specimen the lowermost two 3rd order stipes are on one bedding plane; the next two

Figures 51, 52. *Dichograptus expansus* Harris and Thomas, part and counterpart of funicular region of P73512 from Whittings Quarry. Scalebar 1 mm.

above (one to the left; one to the right) are on a second plane fractionally higher; and the uppermost four stipes are on a third plane slightly higher still. Should the rhabdosome be declined, as suspected, this is exactly the kind of flattening we would expect from a multistiped form which would only rarely be seen in either true profile of true plan view. Thus *D. solidus* is a somewhat unusual dichograptid and may, of course, be related to some of the robust declined tetragraptids. *D. tenuissimus* and *D. sedecimus* are dealt with elsewhere in this paper and are quite different from the *D. octobrachiatus* group. *D. expansus* is described below and the differences with *D. maccoyi* are discussed there.



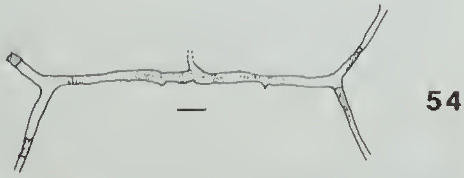


Figure 53. *Dichograptus expansus* Harris and Thomas, proximal region of paratype P32077 showing proximal web; shaded area is where a second layer of web is visible. Scalebar 1 mm.

Figure 54. *Dichograptus sedecimus* Harris and Thomas, badly preserved funicle of holotype, P32010A. Scalebar 1 mm.

Dichograptus expansus Harris and Thomas

Plate 9 fig. a; text figs 23, 50–53

Dichograptus expansus Harris and Thomas, 1940a: 130, pl. 1 fig. 5; pl. 2 figs 6a, b.

Type specimen and other material. Holotype, P32076A and B (42559) from the Bendigonian (Be2) of allotment 30A, Parish of Campbelltown. Paratype, P32077 (42560), from the same locality and horizon. Numerous fragments of the long stipes which may be referable to this species; and one well preserved specimen (P73512) from Whitting's Quarry, Bendigo (GSV Bendigo locality 2645 which we refer to this species).

Diagnosis. Giant dichograptid, with 6 long, relatively slender, terminal stipes; funicle 3–4 mm; thecal spacing 6–7 in 10 mm; dorsoventral width 1.7 mm.

Description. The overall rhabdosomal diameter was probably in excess of 40 cm, and is characterised by six peripheral stipes of great length, all progressive dichotomies being completed within 5 mm of the centre of the funicle. The sicula has not been clearly seen, but the funicle on the paratype is perhaps 4 mm long, with a trace of a sicula nearer one side (fig. 52). The funicle in the holotype is 3 mm long, and this specimen lacks the 6–10 mm diameter web of the paratype. In the shaded area of fig. 53 we indicate where a second layer of web is visible.

Stipes are relatively slender, possibly with a maximum dorsoventral width of 1.7 mm and a thecal spacing of 6–7 in 10 mm. It is not certain whether true stipe profile is displayed by these specimens.

Remarks. D. expansus differs from *D. maccoyi* in all measurements and dimensions and in overall rhabdosomal aspect. As stated by Harris and Thomas it is closest to *D. separatus* Elles, but has a shorter funicle, more robust stipes, and a lower thecal spacing than that form.

Dichograptus tenuissimus Harris and Thomas

Plate 9 fig. e; text figs 43, 45

Dichograptus tenuissimus Harris and Thomas, 1942: 366, pl. 1 figs 3, 3a.

Etagraptus tenuissimus.—Cooper and Fortey, 1982: 267–268, fig. 63a.

Type specimen and other material. Holotype P32109 (45368) referred to in text as the type but not figured by Harris and Thomas; paratype P32110 (45366); both from the Chewtonian (Ch2) of allotment 41B, Parish of Campbelltown.

Diagnosis. Small slender dichograptid with 8–6 third order, stiff, peripheral stipes developed from dichotomies completed within 2.0 mm of the sicula.

Description. Overall rhabdosomal diameter 5 cm; third order stipes (6–8) reach 25 mm in length and a maximum dorsoventral width of 0.4–0.5 mm, and a thecal spacing of 8 in 10 mm. The funicle is 2 mm long, comprising one theca each side of the sicula; and the 2nd order stipes are about 1–1.3 mm long and are composed of only one theca. Thecal overlap is considerable (fig. 45). The dorsal stipe margin shows gentle undulations in places.

Remarks. This species is the smallest and most slender dichograptid known and can be distinguished readily from all other species including *D. separatus* Elles which is robust by comparison. The relationships of *D. tenuissimus* within an evolutionary setting are discussed elsewhere in the paper. As a consequence of these evolutionary possibilities, we prefer to retain the species in the genus *Dichograptus* rather than attempt, at this stage, an expanded redefinition of *Etagraptus* to embrace several related species with the exception of *G. macer*.

Dichograptus sedecimus Harris and Thomas

Plate 9 fig. b; text figs 49, 54

Dichograptus sedecimus Harris and Thomas, 1938a: 73, pl. 1 fig. 12; plate 4 fig. 11.

Laxograptus sedecimus.—Cooper and Fortey, 1982: 269.

Type specimens and other material. Holotype, P32010A and B (41320a, b) from the Bendigonian (Be1) from the "Good Bed" rather more than 200 m WSW from NE corner of allotment 16a, sect. 2, Parish of Campbelltown; and several fragmentary specimens in the Museum of Victoria from the same horizon.

Diagnosis. Clonograptid-like dichograptid with high, isolate thecae contributing much to the dorsoventral width of 1.5 mm, and spaced at 8 in 10 mm.

Description. The funicle of the holotype is some 10 mm long, possibly with 3–4 thecae either side of a small sicula (approximately 1 mm long). The sicula seems not to be in quite the same plane as the primary stipes or rhabdosome, and we had to uncover it on the holotype by removing matrix. Proximal thecae are not clearly visible but distal thecae (on 2nd and 3rd order stipes) number 8 in 10 mm and the distal dorsoventral width is fully 1.5 mm, most of which is made up of high, denticulate thecae which may have isolated apertures. There is no evidence that early rhabdosomal thecae are more elongate as suggested by Harris and Thomas. The presence of bithecae and stolons cannot be entirely excluded. In places there are faint suggestions of both but this could be a quirk of preservational folding of the periderm. The second order stipes are about 2 cm long, and the third order stipes up to 3.5 cm.

Remarks. The species is clearly close to the genus *Clonograptus* from which it differs largely in having reached only the *Dichograptus* stage of development with delayed second and third order dichotomies. It does not seem to fit readily into the genus *Laxograptus* as defined by Cooper and Fortey (1982) in the sense that the thecae are high and the apertural regions almost isolate, not low and axially elongate as implied in their discussions of *Laxograptus*. Furthermore we have not in this paper recognised *Laxograptus* partly on the grounds that we consider *L. irregularis*, the type species, to be a more or less typical *Zygograptus* species.

Section **Dichograpti**

FORMS WITH LATERAL BRANCHES

Orthodichograptus Thomas, 1973

Type species. Orthodichograptus robbinsi Thomas, 1973 (original designation).

Diagnosis. (emend. herein). Forms with dichograptid template, rapid, proximal, progressive dichotomies, followed by long third order stipes which show irregular lateral branches to the fourth order, rarely fifth order, and rarely with paired lateral branches.

Remarks. The recognition of a second species *O. wilkinsoni* sp. nov. necessitates a redefinition of the genus in that the proximal end development resembles *Dichograptus* as a genus, rather than *D. octobrachiatus* in particular. In addition we have detected 5th order stipes, and define paired lateral branches both in *Orthodichograptus* and in *Triaenograptus* where they are developed *par excellence. O. robbinsi* has recently been found in Spitsbergen (Cooper and Fortey, 1982) which is still the only locality known outside Victoria, where it is known from only two quarries in Bendigo, namely Whitting's Quarry at Quarry Hill, and Dixon's Quarry. Specimens of the two species are extremely rare and total only seventeen as far as we know.

Orthodichograptus robbinsi Thomas

Plate 10 figs a–c; text figs 59, 60

"New giant graptolite".—Robbins, 1971: 50–51, cover vol. 4, no. 3; 2 text-figs.

Orthodichograptus robbinsi Thomas, 1973: 529–530, pl. 1 figs a, b; pl. 2 fig. a; text-fig. 1.—Cooper and Fortey, 1982: 184–185, fig. 10.

Orthodichograptus cf. *robbinsi*.—Williams and Stevens, 1988: 26–27, textfig. 15.

Type material. The holotype is P73827 and the paratype P83089. Both are on the same slab numbered GSV 64420 from the Bendigonian (Be4) of Dixon's Quarry. Although Thomas did not state in his paper which of two quarries yielded the holotype we have ascertained this fact from Mr Jack Kellam and Mr Frank Robbins, and the latter states the same in his preliminary account in *Bendigo Naturalist* 4(3). One counterpart of the holotype slab is held in the private collection of Mr Jack Kellam, and the counterpart, used by Thomas in his paper, is now in the Museum of Victoria. We have been able to examine the specimen belonging to Mr Kellam, at our leisure, and have been able to photograph it, and have the use of Mr Robbin's photographs and drawings which were used to illustrate his 1971 paper.

Other material. A number of specimens in the private collections of J. Kellam and F. Robbins of Bendigo, and other specimens in the Geological Survey collection at Bendigo and the Museum of Victoria. Only one specimen (P73498) is possibly from another locality than Whitting's Quarry or Dixon's Quarry, namely the C. C. Extension (locality D1) of Bendigonian (Be1) age.

Diagnosis. Orthodichograptid in which 3rd order stipes produce lateral branches usually around 3–4 cm from the proximal end; these divide again up to order 5 at least; paired lateral branches may occur.

Description. The overall diameter of the rhabdosome was certainly in excess of 30 cm, and one specimen (P73486) may have been more than 50 cm across. All the specimens with a proximal end preserved have a web structure surrounding the early progressive dichotomous (dichograptid) divisions. This has a diameter of 7–22 mm but is not always as symmetrical with respect to the stipes as on the holotype. For example P73488 is about 7 mm across at its narrowest, but 22 mm wide at right angles to this where it grows out further along some stipes than others. Furthermore, some specimens suggest that the web structure is in more than one layer (P73487, P73488) a feature we have noted in other dichograptids.

Details of the most proximal development are obscured by the proximal web and the general preservation. However, the dichotomies are demonstrably dichograptid, the funicle being at the most 2 mm long, and the second order stipes little more than 1 mm long, suggesting that both first and second order stipes can involve no more than one theca. In all the specimens the 1st, 2nd and 3rd order dichotomies are completed within 5 mm of the centre of the funicle, so that the proximal web extends well beyond it. In addition to the proximal web there are traces of webs in the acute angle of some later branching divisions (P73486; fig. 60).

Branching on the 3rd order stipes is one of the most striking features of the species (and the genus). It is our opinion that the divisions are essentially lateral, not dichotomous, although the main stipe certainly undergoes an angular change, which is probably original, in many instances. More commonly the 3rd order stipe is gently curved and the lateral branch grows off it at angles of 30°–60° in a manner which almost simulates dichotomous divisions in places. In addition there are paired lateral branches on some stipes: stipe 6 on the holotype (using Thomas' 1973: 529 terminology); possibly two such divisions on P73488. The nature of the branches suggests that they cannot be added, as a rule at a late stage of astogeny, but rather grew simultaneously with the growing periphery of the rhabdosome. However, growth stages will be needed to verify this.

In the accompanying table (Fig. 59) we give the length of the third order stipes for all the material at our disposal. This not only gives direct comparison with Thomas's (1973) table, but directly indicates the distance from the 3rd order dichotomy of the first lateral stipe branch. A total of five stipes are unbranched at upward of 5 cm length (we have ignored very short, broken stipes). The holotype seems to be the most regular in its branch positions on the third order stipes, whilst the paratype on the same slab has its divisions somewhat more distally,

Fig. 58 shows what we believe is a proximal end of *Orthodichograptus robbinsi* from Whitting's Quarry. It has a web structure, clearly at several levels, a funicle of 2 mm length, and all dichograptid dichotomies are completed within 5 mm of the centre of the funicle resulting in at least seven 3rd order stipes. The sicula is not in the same plane as the diverging stipes: its position is indicated by a slightly rounded area. The dorsoventral width at 5 mm from the sicula is 2 mm and the thecae are denticulate dichograptid.

Further branching takes place distally on a seemingly irregular basis. It may occur on both sides of what we continue to assume is the main (3rd order) stipe, and some such stipes have as many as 4 essentially lateral branches (only 2 on the holotype slab). These latter lateral branches may themselves branch again producing two further branches (as in P73488) on two stipes, and possibly divisions to higher order still on P73486. Certainly branches to the 5th order are not uncommon.

The distal dorsoventral stipe width seems not to exceed 2.5 mm and the thecal spacing varies from approximately 8 in 10 mm proximally, perhaps more closer to the proximal end, to 6 in 10 mm distally.

Remarks. Although the early growth stages should be difficult to distinguish from dichograptids like *D. octobrachiatus*, a form with no lateral branches on the 3rd order stipes and a rhabdosomal diameter of more than 7–8 cm is unlikely to be an orthodichograptid. The dimensions of the proximal end (P73487 fig. 59) which we think is referable to *O. robbinsi* are not in themselves sufficient to prove the case: in *Dichograptus octobrachiatus* the early stipes rapidly achieve considerable width, but in Victorian specimens seem to be relatively slender (up to 1.8 mm) and the funicle is longer than in *O. robbinsi* (2.4 mm cf. 2.0 mm).

The trident-like paired lateral branches we have also seen in *O. wilkinsoni* and (in abundance) in *Triaenograptus neglectus* T.S. Hall, described below. The form described by Williams and Stevens (1988) seems to have much longer third order stipes than either *O. robbinsi* or *O. wilkinsoni* sp. nov. (see below).

Orthodichograptus wilkinsoni sp. nov.

Plate 11; text fig. 59

Holotype and only specimen. P73489 from the Bendigonian (Be4) of Whitting's Quarry, Quarry Hill, Bendigo; collected by W. Whitting; presented Frank Robbins, 1982.

Derivation of name. In recognition of Eric Wilkinson, District Geologist of the Department of Minerals and Energy at Bendigo, and the work he has done for graptolite research and Ordovician biostratigraphical studies.

Description. The rhabdosome as preserved has a diameter of 24 cm, but if the development is even partly comparable to *O. robbinsi* the total diameter could have approached twice this size. At the centre is a large web, comprising two layers perhaps 0.5 mm apart: the webs seem to have a length of 4.5 cm and a width of just under 3 cm. The maximum dimension of the web is almost at right angles to the direction of the funicle, assuming we have deduced the position of the latter correctly. The funicle length is possibly 3 mm or a little more. The 1st to 3rd order progressive dichotomies all take place within the proximal web, but their course is roughly determinable, and all such divisions have ceased within 10 mm of the centre of the funicle. A relatively short distance outside the web, seven of the 3rd order stipes divide again (mostly as quite clear lateral divisions) between 20 and 50 mm from the centre of the funicle (Fig. 59). One third order stipe is undivided after 7.5 cm; whilst two fourth order stipes produce lateral branches of the fifth order, both at 8 cm from the centre of the funicle; and one has a paired lateral division at 9 cm from the centre.

The stipe widths (not in true profile) where they leave the web are 3–4 mm, although this may be thickened to some extent by secondary tissue (small amounts of web occur in the acute angles of stipe divisions). The most distal stipe width is of the order of 2 mm,and where thecae are seen in profile they are typically denticulate dichograptid with a thecal spacing of 8–9 in 10 mm.

Remarks. Thomas (1973) may have seen this specimen and obtained his dorsoventral stipe width figure of 3 mm from it, for such widths are not seen on *O. robbinsi* in the material we have examined. There is, however, no other indication in his paper that he did see the specimen. The rhabdosome is altogether larger and more robust than *O. robbinsi* with the 4th order divisions closer to the centre, whilst the rhabdosome as a whole seems to have clearer bilateral symmetry (i.e. at right angles to the funicle direction).

Kellamograptus gen. nov.

Type species. Trochograptus australis Harris and Thomas, 1938a.

Derivation of name. After Mr Jack Kellam of Bendigo in recognition of many years indefatigable and skilled collecting of Victorian graptolites.

Diagnosis. Dichograptid proximal end template; up to seven 3rd order stipes which have numerous and highly irregular lateral branches at least to 6th order; main stipes thickened proximally but with little trace of web structure; lateral branches on both sides of main stipes, although more commonly on one side.

Remarks. Kellamograptus differs from *Trochograptus* which has a tetragraptid ground plan and relatively fewer lateral branches which, although mostly on one side of the four main stipes, are proportionately further apart and more regular in distribution.

Kellamograptus australis (Harris and Thomas)

Plate 12 fig. a; text-figs 26, 82

Trochograptus australis Harris and Thomas, 1938a: 71, pl. 3 fig. 1a.

Type specimen and other material. Holotype, P32081 (41305) from the Bendigonian (Be1) on the northern boundary of allotment 25B, sect. III, Sandon, Victoria. The holotype was the only known specimen: however, another, P73469, which to judge from the nature of the branching is referable to this species, is from the Bendigonian (Be2), probably of allotment 16A, Parish of Campbelltown.

Diagnosis. Huge dichograptid with *Dichograptus* proximal end plan, seven major stipes of 3rd order, and numerous and highly irregularly distributed lateral branches, usually on one side of main stipes, but not always, and developed to at least 6th order; thecae dichograptid numbering 8 in 10 mm, rarely 9 in 10 mm.

Description. The overall rhabdosome diameter is probably in excess of 60 cm, and with seven 3rd order stipes robustly developed (four prominently so) the overall shape could be roughly circular. The funicle is about 3 mm long and 2.5 mm wide. Two 2nd order and two (possibly 3) 3rd order dichotomies take place within 5 mm of the centre of the funicle resulting in seven major stipes of which at least four are long and robust. All carry numerous and irregularly spaced lateral branches. The most robust proximal stipes have a width of up to 2.2 mm, but they may be thickened slightly (there are traces of web structures) and they are not in profile. Distally the stipes become more slender and the dichograptid thecae are seen more commonly in profile where they number 8 in 10 mm.

Reconstruction. Fig. 26 is based on the holotype which occurs on a large slab amongst a tangled mat of graptolites. The number of peripheral stipes is probably not exaggerated in this reconstruction for the divisions are seen more or less fully developed (though a little bent) along one of the main stipes, and comparable, thick, stipes are seen at corresponding points on several of the other main stipes. *K. australis* must have been one of the largest graptolites in existence.

Remarks. Kellamograptus australis has longer, more robust, and more gradually tapering stipes than *Trochograptus* species such as *T. indignis* and *T. diffusus* which we place in the Schizograpti. It is conceivable that *K. australis* represents an unusually late stage of astogenetic development of *Trochograptus* but this suggestion hardly explains the clear dichograptid template and the growth of 6–7 3rd order stipes. Early growth stages are as yet unknown or unrecognised: they are presumably similar to other dichograptids from early growth until the main stipes become a few cm long, but the secondary branching must have begun before the main stipes reached 7–8 cm (for further discussion of possible astogenetic problems relating to large sized dichograptids, see earlier section).

Kellamograptus? incompositus

(Harris and Thomas)

Plate 12 figs b, c; text-figs 89, 90

Schizograptus incompositus Harris and Thomas, 1938a: 72, pl. 1 figs 3a, b; pl. 4 fig. 2.

Type specimens and other material. Holotype, P34969 (41302), from the Bendigonian (Be1), of the "good bed" rather more than 200 m WSW from NE corner of allotment 16A, sect. 11, Parish of Campbelltown and paratype, P32046A and B (41303,4), from the same horizon and locality. A further fragmented specimen is in the T. Smith collection also from the "good bed" Parish of Campbelltown, showing lateral branching similar to the holotype.

Diagnosis. Dichograptid ground plan, six main stipes, four of which are 3rd order and two 2nd order, with lateral branches developed on one side of main stipes more or less regularly.

Description. The holotype has a maximum rhabdosomal diameter of 35 mm, and has lateral branches all less than 7 mm long, whilst the paratype has a maximum diameter of 30 mm and no lateral branches developed. Harris and Thomas (1938a), correctly we feel, considered the paratype as an earlier growth stage before the lateral stipes were developed. Our examination, involving removal of a little matrix, establishes that there are six conspicuous stipes on the holotype, and probably six on the paratype but preservational deformation of the proximal end has contorted one stipe badly. In addition we have noted that one of the main stipes on the holotype, superficially lacking a branch, actually has one partly obscured in subdorsal view (Harris and Thomas may have depicted this in their fig. 3a).

The funicle is about 2 mm long, and all early progressive dichotomies are completed within 2 mm of the sicula, indicating that only one theca is involved in each case. The sicula has been uncovered in the paratype where it can be seen (fig. 89) to be approximately 1.5 mm long with a short nema, and possible nemaphorous attachment. The sicula is not quite in the same plane as the early stipes indicating that it had a different orientation in life.

The maximum dorsoventral width is 1.3–1.4 mm; and the thecal spacing 10 in 10 mm, of simple dichograptid thecae rather longer than high in the early parts of each stipe.

Remarks. This specimen has a more ordered appearance than does *K. australis*, but it is possible that it represents early growth stages of the latter. It certainly has the dichograptid proximal template of our section Dichograpti, and is different in this respect from *Schizograptus* species. With only two specimens showing lateral branches, and those at an early stage of growth it cannot be claimed that the branching is regular. However, it is likely that the stipes in *K*? *incompositus* are more slender than in *K. australis* and the thecae more closely spaced. Despite the differences in (apparent) rhabdosome size *K*? *incompositus* is closer to *Kellamograptus* than to any other genus.

Section **TEMNOGRAPTI** emend. herein

Zygograptus Harris and Thomas
(= *Laxograptus* Cooper and Fortey, 1982)

Type species. Graptolithus abnormis J. Hall, 1857.

Diagnosis. (emend. herein). Exaggerated funicle up to 45 mm long, comprising 4–22 thecae, followed by repeated progressive dichotomies at close intervals of 1–3 thecae, up to 5th order; development probably sigmagraptine, isograptid, dextral.

Remarks. On present evidence it seems to us that the zygograptids form a relatively tightly knit group, including *Z. irregularis* Harris and Thomas, 1941 which Cooper and Fortey (1982) made the type species of their new genus *Laxograptus*. *Z. irregularis* is one of the most slender species of the group but is not as irregular as claimed by Harris and Thomas and such irregularities as exist seem to be the result of tangled preservation. Nor is the funicle unusually long for the group: although the funicle length is a species specific character, it does in fact vary with the species from about 5 mm to 30 mm, and there is considerable variation within each species (see following species descriptions). For these reasons we continue to recognise the genus and suggest that *Laxograptus* is a junior synonym (see further discussion under *Remarks* on *Z. irregularis*). *Z. irregularis* does not, in fact, have a lax habit, which is a prime criterion in the definition of *Laxograptus*: clonograptid-like thecae, delayed dichotomies and sigmagraptine development are common to *Laxograptus* and *Zygograptus*. The placement of *Zygograptus* in the dichograptids is difficult. The development of *Z. abnormis* has never been elucidated in the type Quebec material, and is not unequivocable in the Victorian material. However, it may well be isograptid and generally sigmagraptine, a development we can also suggest for *Z. irregularis*.

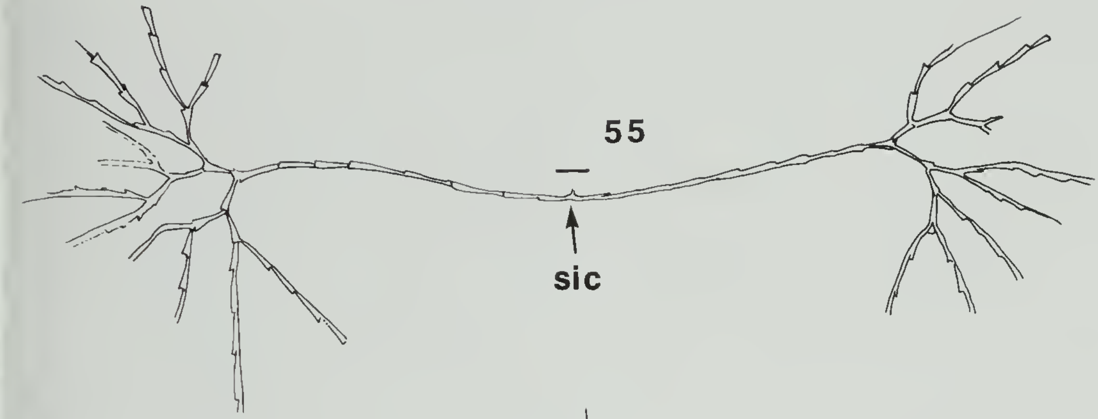
Zygograptus abnormis (J. Hall)

Plate 26 figs a–c; text-figs 63–65

Graptolithus abnormis J. Hall, 1857–58: 117.—J. Hall, 1859a: 503.—J. Hall, 1859b: 51.—J. Hall, 1865: 1106, pl. 11 fig. 6.

Graptolithus (*Monoprion*) *abnormis*.—J. Hall, 1868: 226.—J. Hall, 1870: 223, 261.

Dichograptus rigidus Herman, 1885: 210.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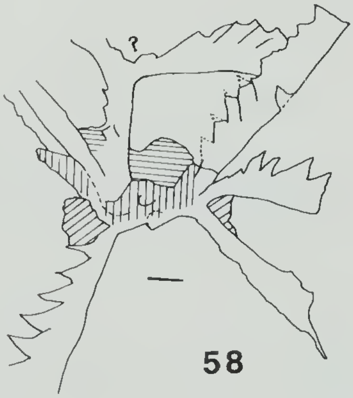
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Figure 55. *Zygograptus stewarti* sp. nov., holotype, P73482. approx. Scalebar 1 mm.

Figure 56. *Triaenograptus neglectus* T.S. Hall, branching point of "trident" on holotype, P13125, showing dichograptid thecae, and web arrangement (alae) along parts of stipes.

Figure 57. *Goniograptus thureaui thureaui* (McCoy), proximal end of holotype, P12215. approx. Scalebar 1 mm.

Figure 58. cf. *Orthodichograptus robbinsi* Thomas, proximal end of P73487, showing webs at three levels, funicular region and at least six primary stipes. approx. Scalebar 1 mm.

Dichograpsus abnormis Gurley, 1896: 65, 95.
Clonograptus abnormis.—Elles and Wood, 1903: 51.—Hart, 1908: 284.—T.S. Hall, 1912: 210, pl. 26 fig. 4.—Bassler, 1915: 245.—Benson and Keble, 1935: 270, pl. 32 fig. 8.
Zygograptus abnormis.—Harris and Thomas, 1941: 308–309, pl. 1 figs 1–3.—Ruedemann, 1947: 282–283, pl. 44 figs 2–3 (non fig. 1).
?*Zygograptus ferrarius* Harris and Thomas, 1941: pl. 2 fig. 1.

Material. P32126 from allotment 41B, Campbelltown (Ch2); P32127 (44669) from between Chewton and Fryerstown (Be4); P34279A, B from Chewton Railway Station (Ch2); P73481, locality unknown.

Description. The funicle varies from 6 mm to a little over 10 mm and comprises as few as two thecae either side of the sicula to the more usual 4 in one series, probably the 1^2 series, and 5 in the other. One specimen (P32127) has 9 first order thecae before the dichotomy, so the funicle would be in excess of 10 mm unless irregular. The disposition of the two stipes relative to the sicula is approximately horizontal, with the second series leaving the sicula fractionally lower than does the first series. The sicula may be less than 1 mm long. Nothing further has been deduced about the development, but the early

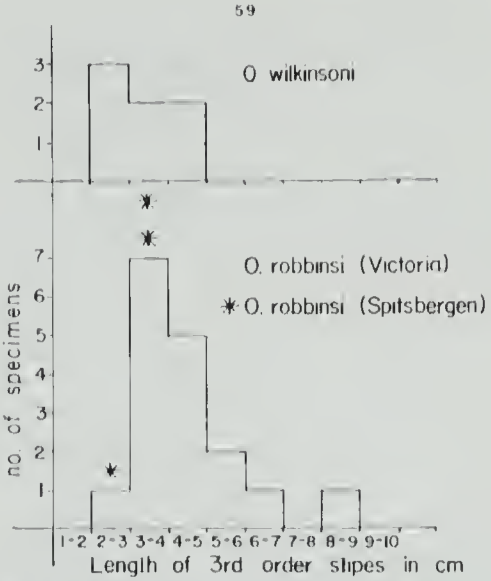

Figure 59. Comparison of *Orthodichograptus robbinsi* Thomas and *O. wilkinsoni* sp. nov. based upon length of 3rd order stipes; asterisks indicate measurements from Spitsbergen specimen referred to in text.

thecae can be discerned where they can be seen to be sigmograptid (fig. 63) of unknown overlap. They are spaced at 7 in 10 mm, and similarly on the terminal stipes, possibly even 8 or 9 in 10 mm in some. Fourth order stipes are quite common, fifth order stipes rarer, but all terminal stipes may be quite long. The number of thecae in successive orders is variable, but low: 2nd order, 1 or 2 thecae; 3rd order, 2; 4th order, 1–5 (where not terminal); 5th order, 1–5 (where not terminal). Successive orders increase in length, therefore, but only rather gradually, and the bulk of dichotomies occur well within 15 mm of the sicula. Thereafter the terminal stipes are not well seen in the Victorian specimens: fragmentary material often associated with the proximal ends of rhabdosomes suggests that they may reach a considerable overall diameter, and that the distal dorsoventral width may be much greater than the 0.5 mm maximum that we have seen in the proximal regions.

Remarks. Victoria material does not usually seem to reach the overall large rhabdosomal size of the Quebec specimens, nor the distal dorsoventral width, but otherwise the dimensions are closely similar. However, we do have doubts about the distinction of the Ch2 species *Z. ferrarius* Harris and Thomas, 1941 from *Z. abnormis*. Specimens of the former may represent mature specimens of *Z. abnormis*, as the proximal dichotomy pattern and dimensions are essentially the same, even to thecal spacing and dorsoventral width. Seen in this light a combination of the two would match very closely Hall's original material of *Z. abnormis*. One particularly good specimen (P73481) is to all intents and purposes a *Z. abnormis* proximally, and a *Z. ferrarius* when considered as a whole rhabdosome (plate 26 fig. a). All the dichotomies to 5th order (except one) are completed within 10 mm of the sicula and the number of thecae involved in the stipes are as follows: 2nd order, 1; 3rd order, 2; 4th order, 3–5 (one of 10); 5th order where not terminal, 7. The distal thecal spacing is 8, and the dorsoventral width 1.0–1.4 mm. The maturity of the rhabdosome, as far as branching is concerned, is indicated by the presence or absence of terminal stipes, and clearly there is some variation in this within the species as in species of other dichograptid genera, such as *Goniograptus*.

Zygograptus irregularis Harris and Thomas

Text-figs 61, 62, 73, 80

Zygograptus irregularis Harris and Thomas, 1941: 310, pl. 1 figs 7–9; pl. 2 fig. 5.—Cooper, 1979: 57–58, pl. 3f.

Laxograptus irregularis.—Cooper and Fortey, 1982: 269–270, figs 65a–d; plate 4 fig. 1.

Type specimens and other material. Holotype, P32124 (44661) from the Chewtonian (Ch2) of Scotts Gully, Castlemaine, figured by Harris and Thomas (1941: plate 1 fig. 7, pl. 2 fig. 5). Paratypes, P32125 (44663) (Harris and Thomas, 1941: pl. 1 fig. 8), P83290 (44663) (Harris and Thomas, 1941: pl. 1 fig. 9). Numerous other specimens from Ch2 and some from Be4/Ch1 of Spring Gully Reservoir, Bendigo. In addition, several museum specimens from various localities of either late Bendigonian or Chewtonian (Ch1 and 2) age. Paratypes are P32125 (44663) (Harris and Thomas, 1940: pl. 1 fig. 8) and P83290 (44663) (Harris and Thomas, 1940: pl. 1 fig. 9).

Diagnosis. Zygograptid with rather long 2nd–5th order stipes involving 5–10 thecae; and a long funicle of 25–45 mm.

Description. The sicula on the holotype is not fully seen (fig. 61) but the apertural region is fairly clear and has a sigmagraptine appearance, probably coupled with an early isograptid, dextral growth of th1^1–2^1. Th1^1, the aperture of which is closest to the sicula, leaves the base of the sicula at the level of the proximal part of the sicular aperture. Th1^2 derives from th1^1 and leaves the sicula at a slightly lower level than

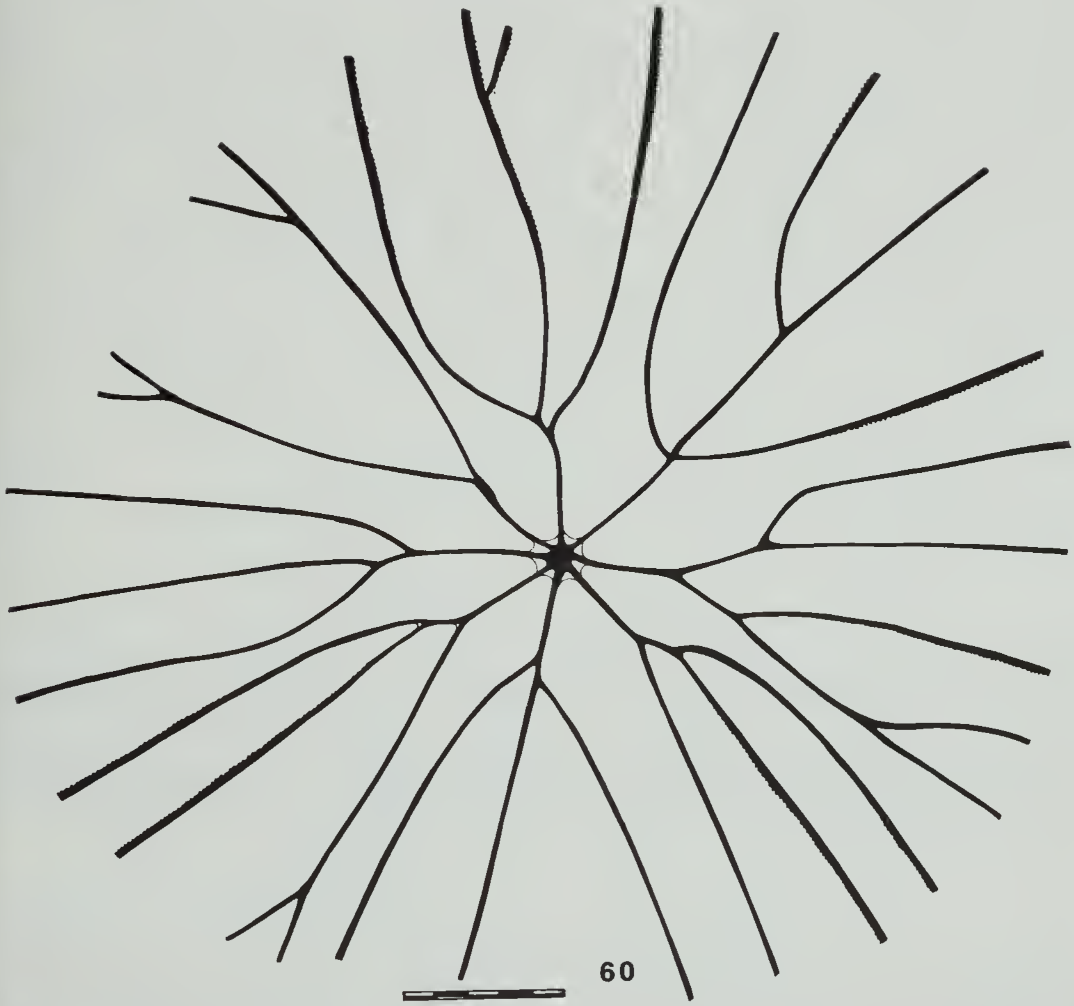

Figure 60. *Orthodichograptus robbinsi* Thomas, diagrammatic reconstruction based upon holotype P73827; approx. Scalebar 50 mm.

th1[1], the two thecae being more or less horizontally disposed to the sicula. The early thecae are relatively high and a dorsoventral width of 0.5 mm is achieved immediately. On the most distal stipes a width of almost 1 mm is reached and the thecae are proportionately higher and more triangular (fig. 62). Numerous other specimens confirm this interpretation of the holotype. Thecal spacing varies from 8 in 10 mm proximally to 8–9 in 10 mm distally.

The holotype has 11 thecae in the first series before the first dichotomy. The full funicle is not preserved but is likely to have been of the order of 28 mm. Dichotomous division takes place quite regularly so that the thecae involved are as follows: 1st order 11; 2nd order, 5; 3rd order, 6–7; 4th order, 10 (seen on only one stipe; the fig. 7 of Harris and Thomas showing several distal divisions at the top left is quite wrong as these divisions belong to a tangled fragment of another specimen).

Other specimens confirm that whilst some examples are pendent (e.g. Harris and Thomas, fig. 8) and very occasionally reclined, the vast majority are horizontal with more or less regular dichotomies at gradually increasing and widely spaced intervals.

In the Victorian material the funicle varies from around 25 mm to 45 mm, involving 10–18 thecae either side of the sicula.

Remarks. We have uncovered the holotype much more fully than was done by Harris and

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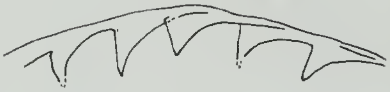

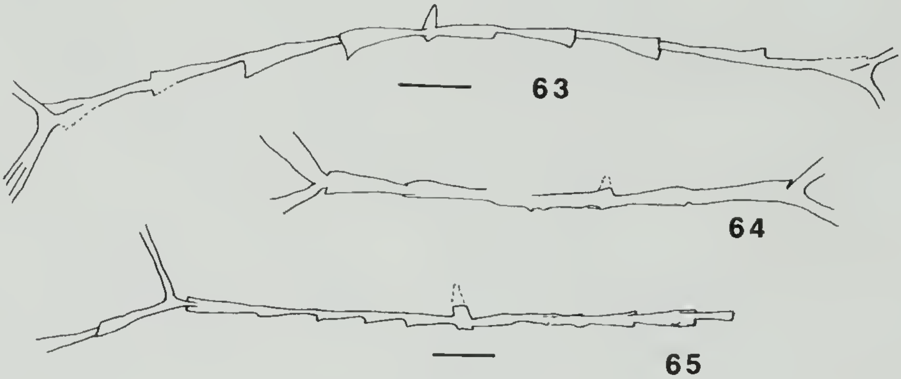

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Figures 61, 62. *Zygograptus irregularis* Harris and Thomas, respectively proximal end of holotype, P32124, and distal thecae on 4th order stipe of same; 68 shows characteristic sigmagraptine proximal end. approx. Scalebar 1 mm.

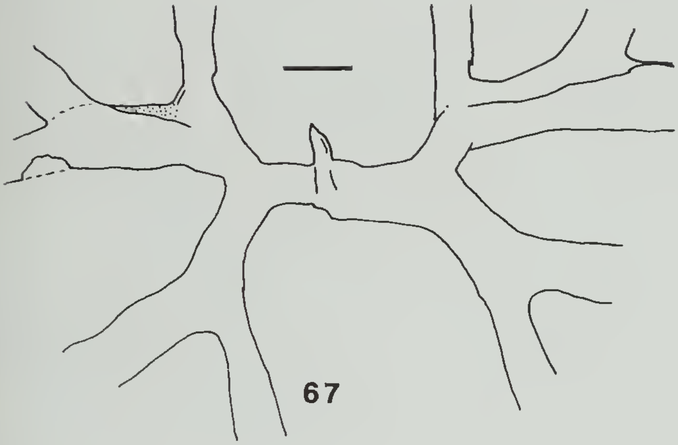
Figures 63–65. *Zygograptus abnormis* (J. Hall), 63, 64 respectively from allotment 41B, Campbelltown, (Chewtonian 2) and Chewton Railway Station (Chewtonian 2), P32126 and P34279B; 65 from between Chewton and Fryerstown, Bendigonian (Be4), P32127 (44669). approx. Scalebar 1 mm.

Figure 66. *Zygograptus stewarti* sp. nov. proximal end of holotype, P73482. approx. Scalebar 1 mm.

Thomas (fig. 73) and the regular dichotomous branching is quite clear. Furthermore such branching is apparent in the other figured specimens, on close examination of the specimens, and on much other material. It is clear from our description that Harris and Thomas misunderstood not only the branching, but the nature of the thecae, the dorsoventral stipe width and the thecal spacing. Cooper's (1979) specimens may have a yet longer funicle and more delayed dichotomies, but they are from a rather higher horizon (Zone of *I. v. lunatus* (Ca1)). The Cooper and Fortey (1982) Spitsbergen specimens seem to be rather closer to the Victorian material, and they record the species both from the Bendigonian and Chewtonian equivalents: in this latter material the funicle is some 10–24 mm long, and has upwards of 5 thecae either side of the sicula. Our impression is that in the Victorian material we have seen the funicle is shorter at lower horizons.

A further point of interest is that we can show that the thecae of *Z. irregularis* are high with strongly denticulate apertures (possibly even slightly isolated). Similarly our re-examination of *Dichograptus sedecimus* Harris and Thomas (1938a) and *Tetragraptus whitelawi* T.S. Hall (1914) (included in *Laxograptus* by Cooper and Fortey, 1982) shows that these too have thecae much higher than previously noted, in the case of *D. sedecimus* being strongly isolate to denticulate (fig. 49). These and *Z. irregularis* type thecae do recall the type commonly seen in clonograptids rather than in true dichograptids. Other *Zygograptus* species may well have similar thecae. It cannot be emphasised too strongly that in such slender graptolites, where, because of the roughly horizontal rhabdosomal attitude the thecae are often buried from view, detection of the true thecal profile is extremely difficult: what appear to be elongate, slim tubes of dichograptid type have often been proved in this work, to be high, denticulate or even aperturally isolated thecae.

If *Zygograptus* species are considered to represent a cohesive generic group, possibly phylo-



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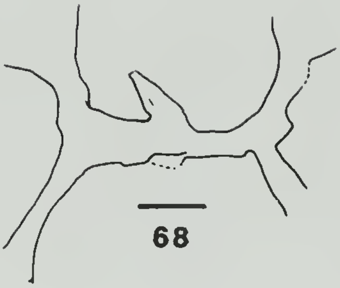

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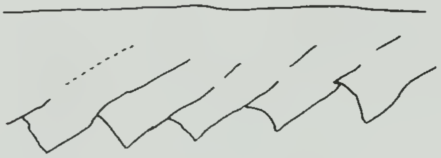

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Figures 67, 68. *Loganograptus rectus* Harris and Thomas, proximal region and distal thecae (possibly not in full profile) of paratype, P32054 (42654); stippled area in 67 indicates partial web; stippled area in 68 indicates overlying sediment. Scalebar 1 mm.

Figures 69, 70. *Loganograptus logani* (J. Hall), respectively proximal end of P12280 holotype of *L. l. australis* (McCoy); and thecae 2 cm from sicula on P15753, form identified by Harris and Thomas (1940) as *L. logani* which we refer to *L. logani logani*. Scalebar 1 mm.

genetically related, then the genus *Zygograptus* should take priority over *Laxograptus*. It depends whether one regards *Z. irregularis* as part of such a group or as the type species of a different genus, *Laxograptus*. We are inclined at present to regard it as a *Zygograptus*. If the opposite standpoint was adopted the genus *Laxograptus* would need redefining, emphasising not the supposed lax habit but the clonograptid-like thecae, delayed dichotomies and sigmagraptine development, although the last two of these features, at least, are shared by *Zygograptus* species.

Zygograptus stewarti sp. nov.

Plate 20 figs d, e; text-figs 55, 66, 71, 72

Holotype. P73482 from ridge and low saddle immediately S of Spring Gully Road, E of turn off to Spring Gully Reservoir, Bendigo, from the Bendigonian (Be4) collected by I. Stewart, 1982. The holotype and paratypes (P73483, P73484) are associated with 3-stiped *T. fruticosus* and a *Tetragraptus* of *serra* type.

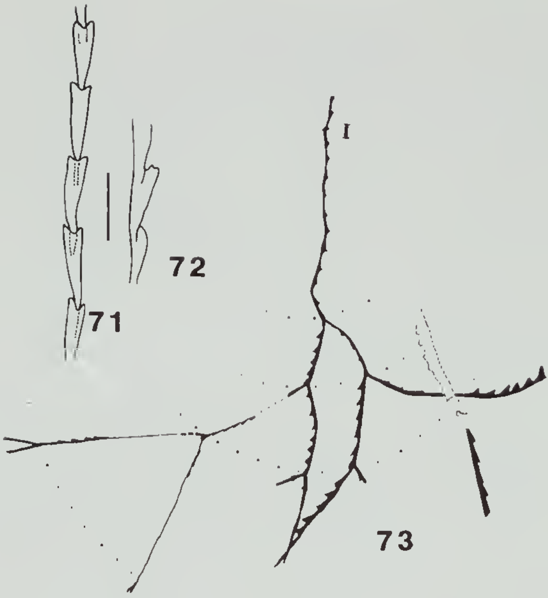
Other material. Numerous specimens from the same locality.

Derivation of name. After I.A. Stewart, collector of many Victorian graptolites.

Diagnosis. Zygograptid with long funicle of 15–20 mm, very slender, 5th order stipes developed, all except 1st and terminal stipes consisting of 1 theca only.

Description. The sicula and proximal end are so slender and small that the development could not be worked out. The sicula (fig. 55) is 0.90 mm long and the first order stipes on the holotype have a dorsoventral width (low relief) of 0.10–0.15 mm and a thecal spacing of about 8 in 10 mm. The maximum, distal, dorsoventral width seen (low relief) is 0.25–0.35 mm; and the distal thecal spacing is 10 in 10 mm. Thecae are low dichograptid, yet despite this have slightly isolate apertures (fig. 72, P73483) and considerable thecal overlap. A ventral view of the thecae (fig. 71) suggests a ventral apertural saddle of some size, a feature not previously noted in zygograptids.

The funicle may have 6–8 thecae on either side of the sicula; the holotype has 7 on one side



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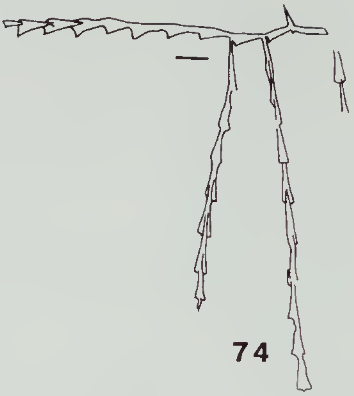

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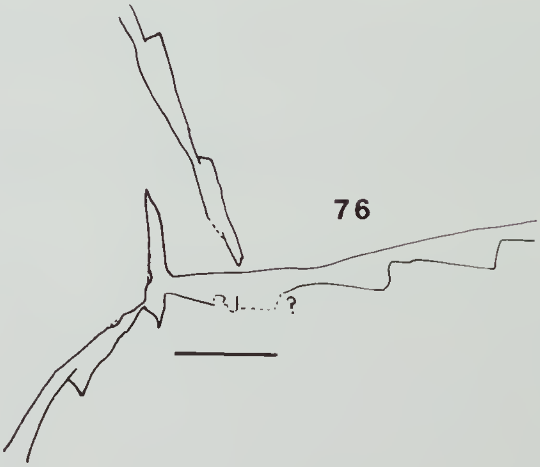

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Figures 71, 72. *Zygograptus stewarti* sp. nov. respectively ventral view of distal thecae and profile view of paratype, P73483; Scalebar 1 mm.

Figure 73. *Zygograptus irregularis* Harris and Thomas, holotype P32124, as uncovered by authors; dotted lines indicate successive dichotomies. Scalebar 1 mm.

Figures 74, 75. *Trichograptus fergusoni* T.S. Hall, respectively P32017 (Scalebar 1 mm) and lectotype P34966 (Scalebar 1 mm).

Figure 76. *Trichograptus triograptoides* (Harris and Thomas), proximal end of holotype P31999. Scalebar 1 mm.

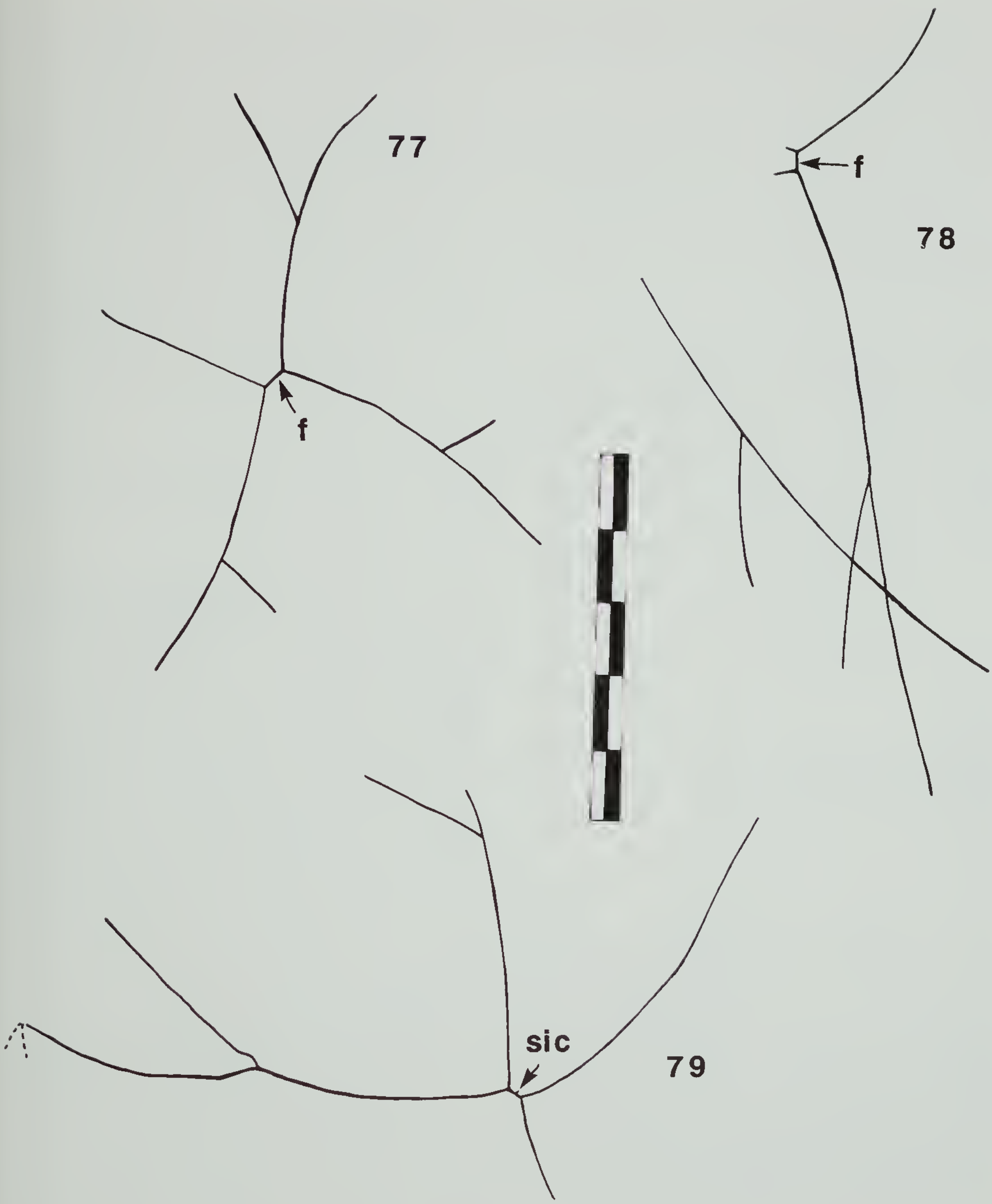

Figure 77. *Trochograptus spectabilis* (Harris and Thomas), holotype P34968. Scalebar 50 mm.

Figure 78. *Trochograptus spectabilis* (Harris and Thomas), P34803. Scalebar 50 mm.

Figure 79. *Trochograptus indignus* Harris and Thomas P73513. Scalebar 50 mm.

(probably the th1[1] series) and 8 on the other. Th1[1] may leave the sicula at a slightly higher level than does th1[2], but with such slender stipes this is not certain (fig. 55).

Dichotomies up to the 5th order commonly occur, occasionally more, and without exception these involve only one theca in each order unless it be a terminal stipe. Terminal stipes may have up to 11 thecae developed. All dichotomies are completed within 7 mm of the first order/second order dichotomy, and well within 15 mm of the sicula as a general rule.

Remarks. Z. stewarti differs from all previously described zygograptids in having only one theca in each order of stipes save the first and terminal stipes. In addition the rhabdosome is perhaps the most slender of the genus and the funicle very long. There are other Chewtonian zygograptids just as slender (Stewart, pers. comm.) which may be undescribed species.

Section **SCHIZOGRAPTI** (emend. herein)

FORMS WITH UNPAIRED LATERAL BRANCHES

Trochograptus Holm, 1881

Type species. Trochograptus diffusus Holm, 1881.

Diagnosis. Schizograptus-like rhabdosome, two progressive dichotomies to four main (2nd order) stipes; followed by widely spaced lateral branches of two orders, 3rd and 4th, the latter quite common.

Remarks. Whether *Trochograptus* can really be distinguished from *Schizograptus* is surely debatable. Rhabdosome size is at best a difficult criterion to apply. We retain the genus here, and *Holograptus*, in our Section Schizograpti (forms with unpaired lateral branches) partly because there seems to be a morphological sequence at least from *Trochograptus - Schizograptus - Holograptus* and *Kellamograptus*. Clearly some species will be difficult to place where one genus grades into the other; and early growth stages of one genus will be difficult to distinguish from later growth stages of another.

Trochograptus indignus Harris and Thomas

Text-figs 25, 79, 80, 81, 88

Trochograptus indignus Harris and Thomas, 1938a: 71, pl. 3 figs 1b, c.

Trochograptus cf. *diffusus*.—Harris and Thomas, 1938a: 71, pl. 1 figs 2a, b; pl. 4 fig. 1.

Type specimens and other material. The two syntypes (Harris and Thomas's cotypes) are on the same slab as the holotype of *Kellamograptus australis*, (41305), from the Bendigonian (Be1) of Sandon. We choose as lectotype the specimen, P83291, illustrated by Harris and Thomas (fig. 1b) since it most clearly conforms to the generic definition, and as paralectotype, P83292 (fig. 1c). It should be noted that many stipes and preservational gaps along stipes have been pencilled on the type slab, possibly by Harris and Thomas to assist the tracings they made, and great care is now needed to interpret which stipe branches from which. There are several specimens of *T. approximatus* and *T. acclinans* on the type slab. Also on the type slab is another specimen of *T. indignus* showing the funicle and four main stipes, and numerous fragments probably referable to *T. indignus*. P73513A and B from SRWSC pipe extension, Race St, Flora Hill, Bendigo, just W of corner of Race St and Wirth St, Bendigonian (Be1), with other fragmentary specimens on the same slab.

Diagnosis. Very large rhabdosome with tetragraptid proximal template, and with 3rd and 4th order lateral branches widely and fairly regularly spaced at 30–40 mm.

Description. The species has a short tetragraptid funicle, at most 3 mm long (lectotype), but a little over 2 mm on the other specimens on the type slab. The sicula is not seen in profile on any of the specimens, but its position is clear on the lectotype and on the unfigured proximal end on the slab. The 1st order stipes have only one theca: the second order progressive dichotomies are complete within 2 mm of the sicula and thereafter the thecae are often very visible in oblique view, are dichograptid, and number 10 in 10 mm. In distal parts of the colony the thecal spacing varies from 7–9 in 10 mm; and the width from 1.1 mm close to the proximal end (possibly a lateral width figure) to 1.0 mm or a little less distally (in true thecal profile).

The general rhabdosomal profile is, therefore, probably horizontal. The first lateral stipes (i.e. 3rd order) occurs at 40 mm from the funicle on the lectotype, and at 35 mm from the funicle on the paralectotype; the second lateral stipes also occur at 35–40 mm from the first, and on the lectotype the 3rd order stipes have 4th order, lateral branches at 30–35 mm intervals. The rhabdosome diameter is probably of the order of 50 cm. Small amounts of web are visible in places at branching points. All the lateral branches are on the same side of the main stipe (fig. 81).

Remarks. The possibility is remarked upon elsewhere that *T. indignus* is an earlier growth stage of *Kellamograptus australis* and a later growth stage of *Schizograptus* sp. For the present

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Figure 80. *Trochograptus indignus* Harris and Thomas, P83292, Scalebar 50 mm.

we note that the spacing of the 3rd order stipes is similar in all three, but that lateral branching in *T. indignus* and the rhabdosomal pattern as a whole falls well within the established concept of *Trochograptus*. If the specimens referred by Harris and Thomas to *T.* cf. *diffusus* (pl. 13a, b). are *T. indignus*, and we feel this more than likely, then the distal dorsoventral width figure given above would be increased to 2 mm.

Trochograptus spectabilis
(Harris and Thomas)

Plate 13 fig. e; text-figs 77, 78, 87

Schizograptus spectabilis Harris and Thomas, 1938a: 72, pl. 1 fig. 4; pl. 4 fig. 3.

Type specimen and other material. Holotype, P34968 (41301), from either late Lancefieldian (La3) or early Bendigonian (Be1) of Providence Gully, about 25 chains north of NE corner of allotment 32, sect. II, Parish of Sandon. Other fragmentary specimens on the type slab, probably referable to the species; and specimens probably from Providence Gully (P34803); other museum specimens without location.

Description. The funicle is 2 mm long, but no trace of the sicula could be found. Four main stipes are developed from the two 2nd order dichotomies and are developed to a length of up to 45 mm on the holotype, and 90 mm on a second very good specimen (P34803). Each main stipe develops a short lateral stipe. Three

Figure 81. *Trochograptus indignus* Harris and Thomas, lectotype P83291.
Figure 82. *Kellamograptus australis* (Harris and Thomas), holotype, P32081.
Scalebar 50 mm.

of these project from the ventral side of the main stipe, and one from the dorsal side. A branching point on the type slab is also well seen in dorsal view (fig. 87). The lateral branches are 8, 11, 11.5 and 18 mm long, developed respectively at 25 mm, 26 mm (th 20), 21 mm and 21 mm (th 16) from the centre of the funicle. P34803 has a lateral branch at a distance of 45 mm (th 34) from the centre of the funicle.

The maximum distal dorsoventral width is 1.0–1.1 mm and the thecal spacing 7–8 in 10. Thecae themselves are dichograptid, moderately inclined at about 40° to the stipe axis. Thecal spacing and stipe widths are the same on the lateral branches.

Remarks. There is clearly some variation in rhabdosomal pattern though general style and dimensions of stipes and thecae are roughly constant.

FORMS WITH PAIRED LATERAL BRANCHES

Tridensigraptus Zhao, 1964

Type species. Tridensigraptus zhejiangensis Zhao, 1964.

Diagnosis. Rhabdosome huge, horizontal to strongly reclined, based upon tetragraptid proximal template; two progressive dichotomies to four main 2nd order stipes on which, at more or less regular intervals, are paired lateral stipes ("tridents"); these 3rd order stipes may also develop paired lateral branches less frequently and less regularly; occasionally three lateral branches from one point on main 2nd order stipe: thecae dichograptid, highly inclined, and strongly overlapping.

Remarks. The holotype of *Triaenograptus neglectus* T.S. Hall (P13125) has small areas with not dissimilar stipe division to that in the two *Tridensigraptus* species, but the latter lack the spectacular anastomosis of *Triaenograptus*, as well as having far fewer stipes. Assuming *Triaenograptus* is a dichograptid it is still preferable to keep the two genera as separate taxa on account of the anastomosis which seems unlikely to be a late astogenetic developmental stage.

Tridensigraptus zhaoi sp. nov.

Text-figs 27, 42

Holotype. P31193A and B (two parts of a slab, a major crack of which goes nearly through the funicle). Almost certainly from Barkers Creek Slate Quarry, N of Castlemaine, of Castlemainian age (Ca1), the same locality as the holotype and the other "trident" specimens of *Triaenograptus neglectus.*

Derivation of name. After Y.T. Zhao.

Diagnosis. Strongly reclined, robust, large dichograptid, with widely spaced (at least 2) paired lateral branches on each 2nd order stipe, and paired lateral branches on several 3rd order stipes.

Description. The measurable preserved diameter of the holotype, assuming average dichograptid symmetry is 40 cm: the profile height of the (reclined) rhabdosome is 15 cm. In all probability the complete specimen was much later. The region of the funicle is strongly reminiscent of some robust, reclined tetragraptids. The funicle is robust, perhaps 4 mm long, and the sicula about 2 mm long (though strongly thickened or overgrown on its sides). First order stipes are less than 2 mm; 2nd order long, up to 20 cm, and with a maximum dorsoventral width of 4.2 mm and a thecal spacing of 8 in 10 mm. The proximal end of each 2nd order stipe rapidly reaches a dorsoventral width of 3.5–4 mm and has a thecal spacing of about 8 in 10 mm.

The first paired lateral stipes ("tridents") on each 2nd order stipe are at 35, 30, 35 and 30 mm from the funicle (including one with three lateral branches); and the second paired lateral stipes respectively at 80, 90 and 90 mm. On four of the first paired lateral stipes another "trident" is formed. One of the lateral branching points produces not two, but three lateral stipes: two grow further "tridents" but one is long and unbranched.

Reconstruction. In fig. 27b we have retained the stipe lengths and branching faithfully, but have inverted the colony and spaced the stipes more or less evenly embracing a conical envelope. It is unlikely that the cone had a broader base a) because of the stipe length and b) because it would have been unlikely to be preserved in profile as it is.

Remarks. T. zhaoi sp. nov. differs from the type species of the genus in being strongly reclined. The actual pattern of lateral branching is quite different and since the overall diameter of the rhabdosome is considerably greater (18 cm cf. 40 cm) the appearance is of a species with sparser, more robust, stipes than *T. zhejiangensis.* In order that such a large rhabdosome could be preserved almost in full profile the angle of reclination of the stipes must have been in excess of 45° from the horizontal. We have shown a reconstructed rhabdosome in fig. 27 in presumed life position. At a radius of 15 cm from the origin the number of peripheral stipes on *T. zhaoi* is about 16. On *Triaenograptus neglectus*. the number of peripheral stipes is well over 80.

Triaenograptus T.S. Hall, 1914

Type species. Triaenograptus neglectus T.S. Hall, 1914.

Diagnosis. ?Dichograptid of large size with numerous paired lateral branches ("tridents") which anastomose laterally with adjacent branches and possibly with "main" stipes in places; overall rhabdosome shape probably circular, either gently declined or deflexed; proximal end not known; number of "main" stipes probably four; growing ends of stipes rounded or blunt, lateral branches almost keeping pace with mother branch.

Remarks. We place this graptolite in the Section Schizograpti, not the Goniograpti as Bulman (1970) did, solely on the grounds that the trident-like divisions closely resemble those in *Tridensigraptus* although in that genus no anastomosis takes place. An alternative taxonomic position would be in the Section Dichograpti alongside *Orthodichograptus* which itself has rare trident-like divisions of the branches: this would imply a dichograptid template, which on present evidence seems unlikely, and hence the possibility of more peripheral stipes (*T. neglectus* has at least 80 in the holotype). Fig. 56 suggests the possibility that the "trident"-like divisions could be lateral branches from two successive thecae. We have established that the holotype of the type species has dichograptid theca, and whilst anastomosis is more or less unknown amongst graptoloids the preserved dichograptid thecae does increase the possibility that *Triaenograptus* is correctly referred to the dichograptids. Furthermore, although the proximal region of P13125 is difficult to discern we gain the strong impression that there are four main stipes reaching to the centre from the periphery, and when preparing the reconstruction of fig. 28, working from the periphery inwards, all stipes seemed eventually to concentrate in the four regions as shown.

Triaenograptus neglectus T.S. Hall

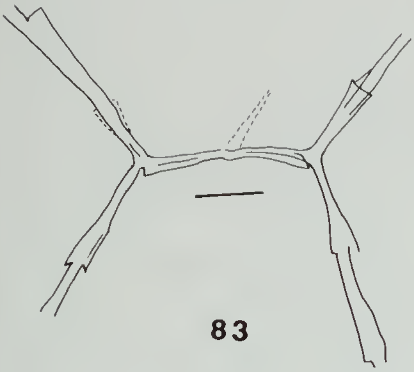
Plate 14; plate 15 figs a, b; plate 16 fig. d; text-figs 28, 56, 110

Triaenograptus neglectus T.S. Hall, 1914: 115, fig. 7.

Holotype and other material. Holotype P13125, from Barkers Creek Slate Quarry, north of Castlemaine, of Castlemainian age (Ca1). P31195–P31197, numerous distal fragments and growing ends of "tridents" associated with *Didymograptus extensus* s.l., *Phyllograptus* sp., *Clonograptus* sp., locality uncertain but possibly same as holotype.

Description. The overall diameter of the rhabdosome is 40 cm measurable, possibly more, with at least 80 peripheral stipes including paired lateral branches close to the distal extremities. The proximal end is indiscernible but its rough position can be seen on the holotype where the central area of a roughly circular (?flabellate, declined or deflexed) is slightly domed yet very badly preserved. The main stipes, and a large number of lateral branches reach a dorsoventral width of 3–4 mm when a true profile is seen: these latter are rare on the type specimen but indicate that the thecal spacing is of the order of 8–10 in 10 mm. The thecae themselves are denticulate dichograptid in type. On P31195 (fig. 110) the nature of the thecae can be fairly clearly seen. The stipes have web structure in places, often along the stipe lengths as alae, but certainly well developed in some of the acute angles of the branching points. The growing ends (as on P31159) show either a rather blunt termination (the most usual and typically dichograptid) or a roughly rounded appearance. Whether this latter is a preservational feature is not clear. Even on the growing periphery of the rhabdosome, represented by P31159, anastomosis has taken place within 50 mm of the edge of the colony. Quite how anastomosis of the lateral branches with other stipes is achieved cannot be seen. It is possible that it is accomplished by deposition of the web material which is certainly present. Careful examination reveals numerous faint bleb-like accompaniments along the stipes. Under ultraviolet light the proximal region, though badly preserved, shows more and denser webs than expected and we gained the distinct impression that the whole colony is developed from four robust stipes, along which much of the proximal web structure grows.

Reconstruction. This is hardly a reconstruction at all in the sense that the diameter, number of peripheral stipes and majority of the trident-like divisions are all preserved on the holotype. A certain amount of reconstruction was necessary near the centre because a number of divisions was not all that clear and the web itself is a little obscure in places. In addition the tetragraptid template at the centre is deduced by following



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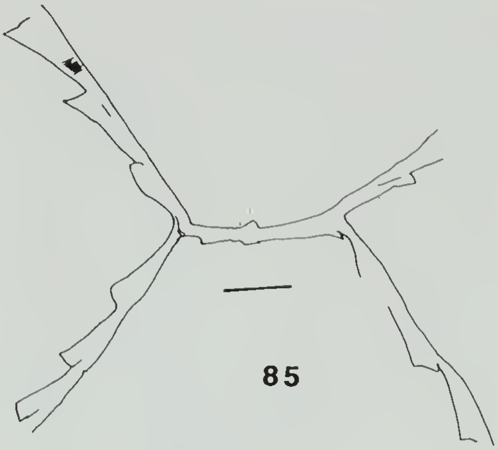

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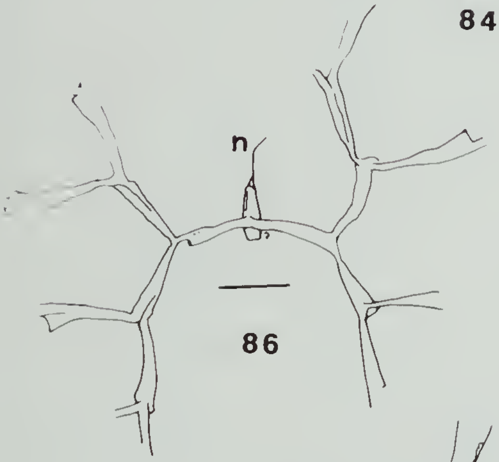

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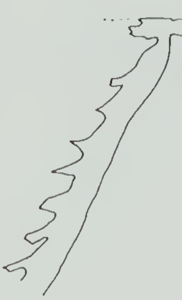

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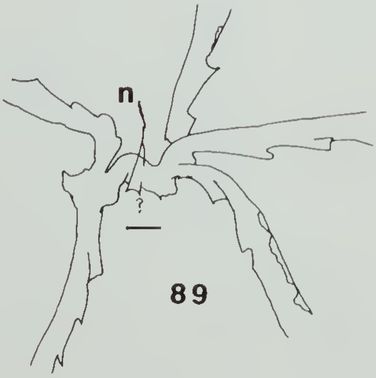

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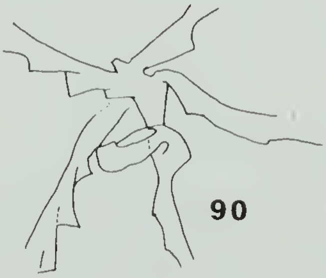

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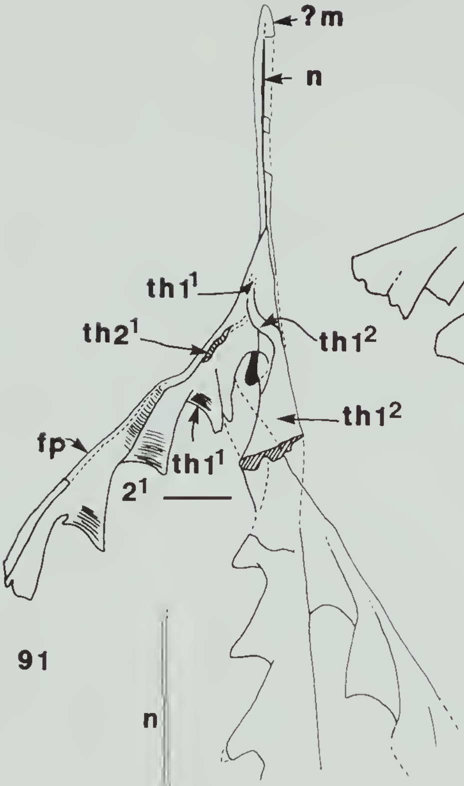
Figures 83–85. *Etagraptus harti* (T.S. Hall). 83/84 proximal end of holotype, P31955, and distal thecae of same (2nd order stipe, beginning with th5 on figure). 85, paratype P14288. Scalebar 1 mm.

Figure 86. *Brachiograptus etaformis* Harris and Keble; paratype P24020, for comparison with sigmagraptines of figure 144 from MO3, Strathfieldsaye, Bendigo East (Da3). Scalebar 1 mm.
Figure 87. *Trochograptus spectabilis* (Harris and Thomas), P83339. Scalebar 1 mm.

Figure 88. *Trochograptus indignus* Harris and Thomas, proximal end of P73513A (see also figure 79) showing sicula and tetragraptid template. Scalebar 1 mm.

Figures 89, 90. *Kellamograptus*? *incompositus* (Harris and Thomas), paratype P32046B and holotype P34969. Scalebar 1 mm.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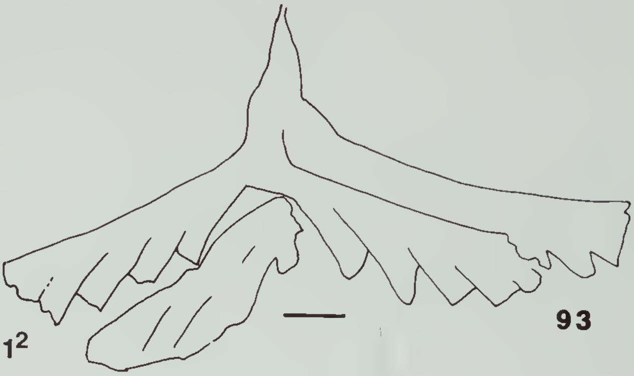

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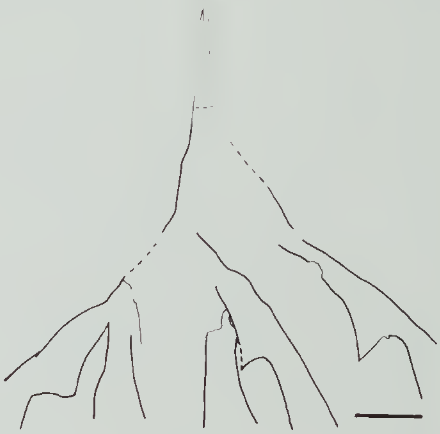

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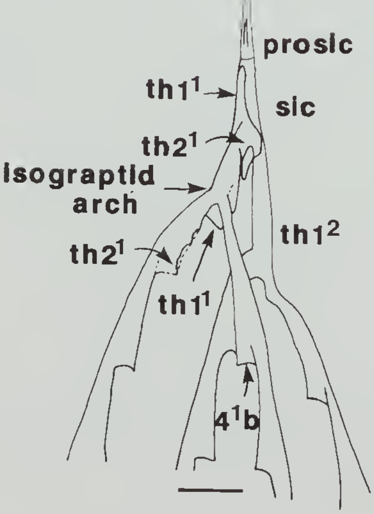
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stipe divisions from the periphery inwards. Even under ultraviolet light the central region was difficult to make out.

In examining O.M.B. Bulman's notes on Australian graptolites we came across his pencilled reconstruction of the proximal end of *Triaenograptus neglectus*, stated to be based solely upon Hall's original sketch (fig. 7), and it is of interest that he had deduced a rough tetragraptid proximal template!

Section **PENDEOGRAPTI** nov.

Remarks. In the 1970 "Treatise" Bulman divided his informal group of pauciramous forms into two sections, the Tetragrapti and the Didymograpti, the former having four stipes or less produced as second orders stipes, the latter not more than two stipes. For the purposes of the present discussion the Didymograpti are a reasonably unified group, but the definition of the Tetragrapti may need some re-examination. The genus *Pseudobryograptus*, for example, is excluded for the present from the Tetragrapti because it has stipes up to the third order.

Pendeograptus Bouček and Přibyl, 1951
(emend. herein)

Type species. Tetragraptus pendens Elles, 1898.

Diagnosis. Pendent or declined and deflexed tetragraptids, development of th1^1–2^1 isograptid, dextral; subsequent dichotomies after only one theca each side of the sicula, at most two in number, probably also dextral; sicula conspicuous, partly because of pendent habit of rhabdosome, partly because the early growth of th1^1 and 1^2 emphasises its position; nema usually long, slender, but may expand a little and may be involved in some form of membrane; stipes usually four in number, but may be three and, rarely, two-stiped forms.

Remarks. In their paper on the Ordovician graptolites of Spitsbergen, Cooper and Fortey (1982) tentatively accepted the subgenus *Pendeograptus* on the basis of their suggested development of *T. fruticosus*, whilst recognising that the type species of the subgenus is *T. pendens*. Their argument that the two are closely related is confirmed in this paper, and our material allows us not only to give a reasonable model for the development of *T. pendens* but to confirm and add to the Cooper and Fortey preferred model for the development of *T. fruticosus*. Our discoveries, therefore, reinforce the general arguments put forward by them for the early evolution of graptoloids, particularly in emphasising the important role of the isograptid development stage in Bendigonian faunas and the subsequent derivation of the *artus* stage. It can also be used as an argument against the *artus* stage development claimed for *Sigmagraptus praecursor* by Rickards (1976). This particular question is remarked upon further in the section on the Sigmagratinae. More recently, Fortey and Cooper (1986) have questioned whether *T.* (*Pendeograptus*) should remain in the Dichograptinae. We retain it for convenience until such time as its true affinities are surer.

Pendeograptus pendens Elles

Plate 15 figs c–e; text-figs 92, 96

Tetragraptus pendens Elles, 1898: 491, fig. 13.—Elles and Wood, 1903: 63–64, text-fig. 38, pl. 6 figs 3a–d.—Ruedemann, 1904: 653–655, text-fig. 55, pl. 11 figs 17–20.—Raymond, 1914: 529.—Bassler, 1915: 1269.—Ruedemann, 1926: 27.—Benson and Keble, 1935: 276, pl. 33 fig. 26.—Keble and Benson, 1939: 87.—Cooper, 1979: 65, pl. 6f; text-fig. 34b.—Henderson, 1983: 161, figs 8e, f.—Lenz and Jackson, 1986: figs 5L, O.

Tetragraptus sp. cf. *T. pendens*: Cooper, 1979: 66, pl. 6c; fig. 34a.

Pendeograptus pendens.—Williams and Stevens, 1988: 38, pl. 6 fig. 4.

Material. Very abundant specimens in the collections of the Museum of Victoria, from many localities, of Bendigonian age (Be2–Be4). Numerous well preserved specimens from allotment 31A, Parish of Campbelltown; and many other specimens and localities. Figured specimens are P32002, P32005, P13067.

←

Figure 91. *Pendeograptus fruticosus* (J. Hall), P73485 showing development of proximal end, full explanation in text. Scalebar 1 mm.

Figure 92. *Pendeograptus pendens* Elles, P32002, from the Bendigonian (Be2), full explanation in text; arrow indicates "isograptid arch" of th1^2 and 2^1. Scalebar 1 mm.

Figure 93. *Pendeograptus volitans* Harris and Thomas, holotype, P31995. Scalebar 1 mm.

Figures 94, 95. *Pseudobryograptus crassus* (Harris and Thomas), respectively P83340 and holotype P32009, both on same slab; P83340 shows nema, possible prosicula, and possible longitudinal rods on the prosicula. Scalebar 1 mm.

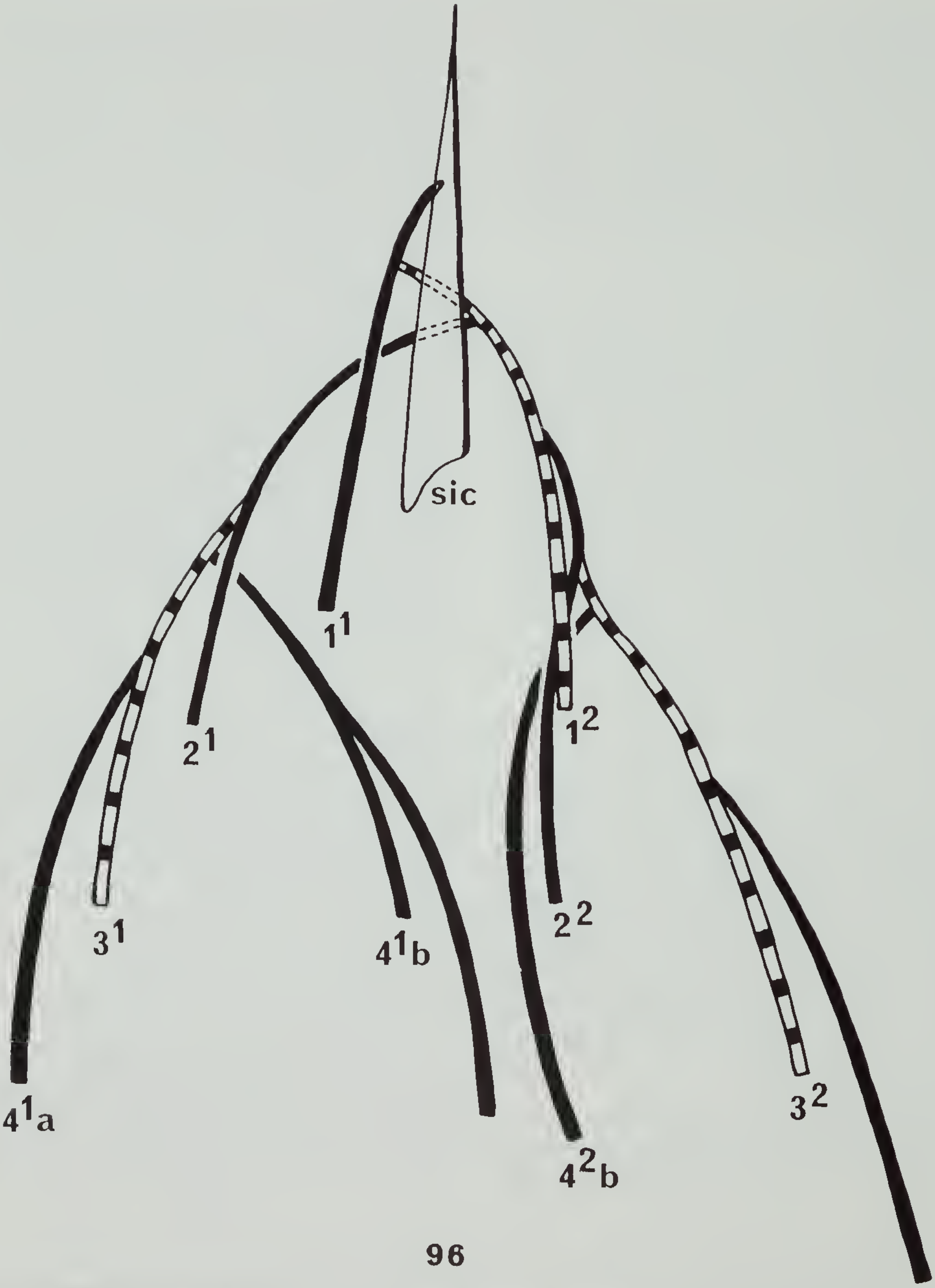

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Figure 96. *Pendeograptus pendens* Elles, development diagram deduced from P32002, figure 92.

Horizon. T. pendens occurs throughout the Bendigonian and we have examined material from most horizons and localities.

Diagnosis. Pendent tetragraptid with slim stipes, long sicula (2–3 mm) long nema (up to 6 mm) (often slightly thickened or with membrane), isograptid, dextral initial development, probably followed by isograptid dichotomies; th1^1 and 1^2 highly pendent and typically elongate; stipe widths not exceeding 1.0 mm and thecal spacings after initial dichotomies 8–12 in 10 mm, usually 8–10.

Description. In the present material, particularly from allotment 30A, there is some trace of tectonic deformation visible as a lineation on the bedding surfaces, so that occasional dorsoventral stipe widths are met with in excess of 1 mm, and thecal spacings may be as low as 6 or as high as 14. Similarly the angle of divergence of the pendent stipes varies with the deformation, some specimens having all four stipes pushed almost together. The diagnosis above allows for these extreme cases and gives the probable dimensions of undeformed, flattened, specimens; figures to which those specimens lying at 45° to the lineation largely conform.

The proximal end development is well shown in several specimens, but particularly in P32002 from Campbelltown (fig. 92). The specimen is inconvenient in that the sicular apertural process is to the left, but the thecae are well seen pressed through and it can be demonstrated that the early parts of th1^1, 1^2 and 2^1 are overlain by the later metasicular parts. Th1^1 originates high on the sicula, just below the prosicular boundary, though this cannot be certain (traces of longitudinal threads may be visible on the prosicula) and forms a slight lump in the left side of the sicula as seen in fig. 92. About 1 mm above the distal extremity of the sicular process the downward growing tube of th1^1 gives rise to th1^2 which grows across the sicula rapidly becoming pendent, before the level of the sicular aperture is reached. Before this, however, there is a clear trace of a crossing canal leading from the early part of 1^2 to the left side of the sicula (as drawn): this can only be th2^1, and the development at this level can be described as isograptid, dextral with a characteristic, though slim, isograptid arch of th1^2 and 2^1 (see opposite arrow on fig. 92). Th1^1 grows down at an angle of perhaps 15° to the rhabdosomal/sicular axis producing a second shoulder or bump on that side of the sicula as viewed. Some 0.75–1.0 mm below the distal sicular extremity is the aperture of th1^1, but on its presumed dorsal side, 0.50 mm earlier, a branching division is clearly visible. The further development of this series is discussed two paragraphs below.

Th1^2 also grows downwards, almost vertically, its aperture being below that of th1^1, and just over 1 mm below the distal extremity of the sicular aperture. In the region of the aperture of th1^2 (only approximately estimable on fig. 92) a branching division is clearly demonstrable. The strongly pendent and elongate nature of th1^1 and th1^2 is highly characteristic of the species.

The branching division visible near the aperture of th1^1 cannot be interpreted with certainty. On the face of it th2^1 could be dicalycal, giving rise to th3^1a and 4^1b, perhaps suggested by the high angle of divergence of 4^1b from th2^1. A more likely interpretation, however, is that th3^1a is much more elongate than one can demonstrate, that it has a long, narrow prothecal part (shown by dotted line) and that *it* gives rise to th3^1b and is therefore dicalycal. Such would be in accord with the isograptid early development of th1^1-2^2 in that it also would be isograptid dichotomy, possibly dextral. Perhaps supporting this viewpoint is that th4^1b is demonstrably very long and would be of about the same length as th3^1a and all later thecae. The same argument could be applied to the second branching division of the rhabdosome and the total development would be as shown in fig. 96. Fig. 96 is labelled for convenience upon this interpretation, but it should be emphasised that if th2^1 were dicalycal then the branching dichotomy would be of *artus* type, following an earlier isograptid initial division of th1^1-2^1. This is not unknown (see Cooper and Fortey, 1982, for a description of the development of *Didymograptus* (*Didymograptellus*) *multiplex*) but it seems rather unlikely in this case.

Remarks. See under *Pendeograptus* for further comment. *P. pendens* although having a similar proximal development to *P. fruticosus* (see Cooper and Fortey, 1982 differs in its slim stipes and elongate portions of th1^1 and th1^2, in particular the latter (see also fig. 92 herein).

Pendeograptus fruticosus (J. Hall)

Plate 16 figs a–c; text-fig. 91

Graptolithus fruticosus J. Hall, 1858: 128.—J. Hall, 1865: 90–91, pl. 5 figs 6–8; pl. 6 figs 1–3.

Graptolites (*Didymograpsus*) *fruticosus.*—McCoy, 1874: 13, pl. 1 figs 9–14.

Didymograptus pantoni Etheridge, 1874: 7, pl. 3 figs 21–22.

Tetragraptus fruticosus.—Elles and Wood, 1902: 61, pl. 6 figs 2a–b.—Benson and Keble, 1935: 275–276, pl. 30 fig. 41, pl. 33 figs 25, 27.—Ruedemann, 1947: 304–305, pl. 51, figs 25? 26-32.—Berry, 1960: 54–55, pl. 6 figs 7, 11, 12; pl. 7 fig. 14, pl. 8 figs 1, 3; pl. 9 fig. 3.—Thomas, 1960: pl. 3 figs 26–28.—Cooper, 1979: 64–65, pl. 6b, e, g, figs 32a–c.—Kilpatrick and Fleming, 1980: 70–73, figs 3, 4—1983: 159–161, figs 7c, f, k.—Lenz and Jackson, 1986: Fig. 6B.

Bryograptus crassus Harris and Thomas, 1938a: pl. 1 fig. 7d (non 7a–c).

Pendeograptus fruticosus.—Williams and Stevens, 1988: 39–41, pl. 9 figs 3, 8–12; pl. 10 figs 5, 9–14; pl. 11 figs 1, 2, 6, 7, 12; pl. 30 fig. 12; text-figs 27 A–U.

Tetragraptus (*Pendeograptus*) *fruticosus.*—Cooper and Fortey, 1982: 210-213, text-figs 30a–f; pl. 3 fig. 4, pl. 4 fig. 2.

Material. Numerous 4-stiped and 3-stiped forms, total range Bendigonian (Be1–4) to Chewtonian (Ch1); 3-stiped forms from Be2–Ch1, fairly common at most localities where these horizons occur except in Be2 where they are rare. We have recorded no 4-stiped forms above Be2 (see table 2), but Webby et al. (1981) recorded them as rare in Be3, Be4 and possibly in Ch1. Specimens figured P73485, P83326–P83329.

Diagnosis. Robust pendent tetragraptid, proximally pendent to declined, distally deflexed; sicula large and both it and nema prominent; development isograptid dextral initially, and branching divisions same; four stipes in early strata, commonly 3-stiped in later strata; rarely 2-stiped.

Description. One particular proximal end of a 3-stiped specimen, P73482 (Spring Gully Reservoir, Bendigo) (fig. 91) shows the early development unusually well. The sicula is fully 2.5 mm long, though much of the mesial and apertural area is lifted off, fortuitously exposing the developing tubes. At its apex is a long slender nema seemingly enclosed in a membranous structure. However, this cannot be altogether certain (even though reported commonly in *P. fruticosus*) because parts of the colony are also shrouded in a thin layer of fibrous penninite.

Th1^1 arises 0.7 mm below the sicular apex, possibly on the prosicula and grows downwards, its outer surface forming an angle of some 20° with the rhabdosomal/sicular axis, and resulting in the whole sicular region having a broadly conical appearance rather than the narrow cone of most graptolite origins (contrast, for example, *P. pendens*, fig. 92, of the preceding description).

Th1^2 originates fairly high on th1^1 about 1 mm from the sicular apex, and then grows across to the opposite side of the sicula as a narrow tube before turning downwards parallel to the sicular wall, simultaneously increasing considerably in diameter. The aperture of th1^2 is fully 1 mm below the sicular aperture and more than 0.5 mm below the aperture of th1^1. Th1^1 and 1^2 taken as a whole diverge from each other at an angle of 40° (contrast 20° in *P. pendens*) although their apparent ventral walls remain roughly parallel as in several other pendent tetragraptids.

Subsequent to this, development becomes more difficult to unravel though a little judicious dissecting has improved matters. Arising almost certainly from th1^2 is a very narrow tube, with some growth lines preserved, and this continues across to the opposite side to th1^2 – to the th1^1 side – and thereafter grows downwards along the dorsal side of th1^1 to become th2^1. Thus so far the development is isograptid, dextral.

Dorsally to the prothecal part of th2^1 is another narrow tube, extremely long, which grows downwards to eventually become the apertural part of th3^1. Its origin cannot be seen but it can reasonably be suggested that the only possible origin is from th2^1, and moreover that th3^1 gives rise to th4^1b (shown by dashed line in its mesial parts where it is still beneath sediment) as the divergence of the two stipes visibly takes place just over 0.5 mm proximally to the aperture of th1^1.

Such an interpretation means that the dichotomy is isograptid, dextral, as is the earlier development, and that the thecae 2^1 et seq. and 1^2 et seq. are of comparable total lengths, with no foreshortened or "abnormal" thecae, save th1^1 itself which is a little shorter at 2.25 mm. Th2^2 presumably develops from th1^2, but this cannot be seen: there seems no real alternative. This particular series does not branch and the rhabdosome on this specimen (from Be4) remains 3-stiped.

Taking the many other specimens at our disposal a maximum stipe length of 25 cm is achieved, the striking deflexion taking place at th10–th15, bringing the remainder of the stipe at right angles to the earlier part. A distal dorso-ventral width (flattened) is of the order of 4 mm; and the thecal spacing 8–6 in 10 mm proximally to 6–5 in 10 mm distally. The maximum stipe length, of the order of 25 cm, gives a potential span of 50 cm.

Remarks. The species in our most abundant material is clearly distinguished from *P. pendens* as noted above, yet is important in lending corroboration to the interpretation suggested for *P. pendens* which is the type species of *Pendeograp-*

tus (see above under discussion of the Pendeograpti).

?Pendeograptus volitans Harris and Thomas

Plate 17 figs c–d; text-fig. 93

Tetragraptus volitans Harris and Thomas, 1938a: 74, pl. 2 figs 16a–d; pl. 4 fig. 15.

Type specimens. Holotype, P31995 (41329), Harris and Thomas (1938a, pl. 2 fig. 16a, pl. 4 fig. 15) from loc. 1, "good bed" rather more than 200 m WSW from NE corner allotment 16A, sect. II, Parish of Campbelltown; and paratypes P32006A and B (41330), P32007 (41331) P32008 (41354); respectively figured by Harris and Thomas (1938a: pl. 2 figs 16b–d); all from loc. 1, Bendigonian (Be1).

Description. The sicula in the type series is not easily seen because its later parts are obscured by the four developing stipes, but it must have a length of between 1 and 2 mm probably nearer the latter figure in the holotype (fig. 93), and an average width of about 0.5 mm. The origins of the first thecae are not clear but the holotype does show distinct shoulders to the left and right at about 1 mm, and the one to the left (fig. 93) probably represents the division of the first stipe which quite clearly branches just below it. Similarly the shoulder, or asymmetry, to the right probably represents the development of the second primary stipe from the first coupled with its rapid division. Thus within 2 mm of their origin on the sicula the four tetragraptid stipes are developed. They are conspicuously subhorizontal, any pendency being represented by the growth down the sicula and the initial branching. The curve of the stipes suggests that distally they will be fully horizontal in aspect, not pendent. The simple dichograptid thecae are spaced at 10–12 in 10 mm and are inclined to the stipe axis at up to 35°. The maximum dorsoventral width seen (flattened) is 1.4 mm.

Remarks. We have been unable to find any evidence from the literature or from collections to substantiate the claim by Thomas (1960a) that *P. volitans* occurs in both Bendigonian 1 and 2 and we note that Singleton (pers. comm.) came to the same conclusion. It is extremely rare. We only have the type series and a few doubtful specimens from the same locality, and extensive collecting of the type locality by Messrs Wilkinson and Cooper some years ago failed to turn up any further specimens. Harris and Thomas (1938a: 74) allude to a vague similarity to *T. approximatus* "... in which the funicle instead of being horizontal was dependent ..." The similarity may, in fact, be much closer. We have a feeling that the very rare *P. volitans* actually represents very rare *profile* views of the early stages of growth of *T. approximatus* which occurs commonly at the same locality. *P. volitans* is not known from late growth stages. However, there is no direct evidence of this idea at present so we retain *P. volitans* doubtfully in *Pendeograptus*.

Pseudobryograptus Mu, 1957

Type species. Pseudobryograptus parallelus Mu, 1957.

Diagnosis. Rhabdosome small, pendent, branching progressively dichotomous up to 3rd order, thecae dichograptid.

Remarks. Mu distinguished species of *Pseudobryograptus* from *Bryograptus*, where they had been placed previously, because development only took place to the 3rd order: that they were to all intents and purposes dichograptids. More recently Cooper and Fortey (1982) have placed *B. crassus* Harris and Thomas (1938a) in the genus *Pendeograptus* and it could reasonably be argued that what applies to this species, a typical pseudobryograptid, applies to most if not all other *Pseudobryograptus* species. We prefer for the present to retain the genus *Pseudobryograptus* for the Harris and Thomas (1938a) species *Bryograptus crassus*.

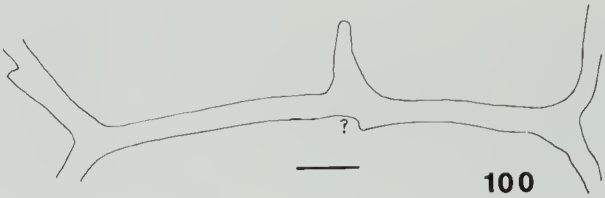
Pseudobryograptus crassus
(Harris and Thomas)

Plate 17 figs a, b; text-figs 94, 95

Bryograptus crassus Harris and Thomas, 1938a: 72–73, pl. 1 figs 7a–c (non 7d) pl. 4 fig. 6.

Type specimens and other material. Holotype, P32009 (41365), from the "good bed" rather more than 200 m WSW from NE corner of allotment 16A, sect. II, Parish of Campbelltown. The paratype series all from the same locality and horizon (Bendigonian, Be1), P32047 (41316), P32048 (41314), P34974 (41315): P32048 (41314) we refer to *T. fruticosus*. Several poor specimens in the general collections of the Museum of Victoria, from the same locality or at least the same region; horizon probably the same, namely low Bendigonian (Be1).

Remarks. It seems to us that the type series and other material of *P. crassus* is distinctly more slender than *T. fruticosus* specimens at the same locality. Thus at 1 cm along the stipes *T. fruticosus* specimens are 2 mm wide and *P. crassus* barely 1 mm wide. The thecal spacing and shape are about the same but the rhabdosome shape is more declined than pendent, and explains the frequency with which *P. crassus* occurs in plan



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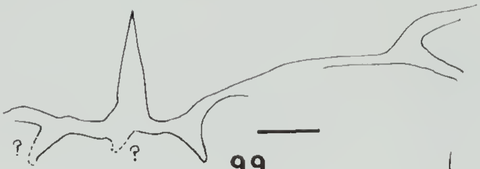

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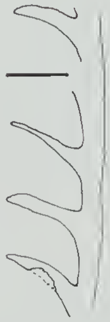

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Figures 97, 98. *Tetragraptus* (?*Tetragraptus*) *chapmani* Keble and Harris: 97, thecae on 2nd order stipe of holotype P14378A thecae, partly infilled with opaline silica, and apertural regions thinly sclerotised; 98, specimen of distal thecae on P83341A on same slab as P14378A, and probably referable to the same species. Scalebar 1 mm.

Figure 99. ?*T.* (?*T.*) *chapmani* or ?*Clonograptus* sp.; P83342A on same slab as P14378A (figures 97, 98, 100).

Figure 100. *Tetragraptus* (?*Tetragraptus*) *chapmani* Keble and Harris, funicle of holotype, P14378A. Scalebar 1 mm.

Figure 101. *Tetragraptus* (*Tetragraptus*) *decipiens decipiens* T.S. Hall, holotype, P14368. sic = sicular aperture. n = nema. Scalebar 1 mm.

view as well as profile. Therefore we cannot support Harris and Thomas (1938a: 73–74) where they strongly imply that *T. fruticosus* and *P. crassus* are conspecific but that "... according to the artificial classification in use they must be placed in different genera". The 4-branched form "described" by Harris and Thomas is, in fact, *T. fruticosus* and even on their rough drawings it seems distinctly more robust than the others, and certainly more so than a plan view *P. crassus* on the same slab. Nor can we support their suggestion that distally the stipes take on the deflexed attitude typical of *T. fruticosus*. We have seen no forms we would refer to as 4-stiped *P. crassus* but have seen a single specimen with five stipes which we would refer to *T. fruticosus*.

Section **Tetragrapti**

Tetragraptus (Tetragraptus) Salter, 1863 (sensu Cooper and Fortey, 1982)

Type species. Fucoides serra Brongniart, 1828.

Remarks. It is of interest that we have few Victorian Bendigonian tetragraptid species which can be strictly referred to this subgenus. *T. decipiens* which we briefly describe below, appears first in the Lancefieldian and ranges up into Be1, whilst *T. decipiens bipatens* has been recorded from the Bendigonian of Blackwood by Keble and Harris, 1934; *T. pendens*, *T. fruticosus* and possibly *T. volitans*, are referable to *Pendeograptus* and *T. harti* to *Etagraptus* as redefined by Cooper and Fortey (1982). *Tetragraptus chapmani* Keble and Harris (Be1) closely resembles *Clonograptus* fragments on the holotype slab, has clonograptid-like thecae of the isolate type (i.e. quite different from what one normally regards as typical of *T.* (*Tetragraptus*) and may have evolved by stipe reduction from a *Clonograptus* species in the low Bendigonian: we place it provisionally in *T.* (*Tetragraptus*). *T. whitelawi* (T.S. Hall) (Ch1 and 2) has up to 10 thecae in the funiclar region before the second order dichotomy occurs, making it a borderline tetragraptid by any definition. The species has dichograptid thecae and we regard it as likely to have developed from a dichograptid ancestor in the Bendigonian, or a clonograptid species of the group with dichograptid thecae. We describe it here under *T.* (*Tetragraptus*) with reservation.

Tetragraptus (Tetragraptus) decipiens decipiens T.S. Hall

Plate 19 figs a–d; text-fig. 101

Tetragraptus decipiens T.S. Hall, 1898: 168, plate 17 figs 13–15, plate 18 figs 16–19.

Type specimen. Holotype P14368 from a small quarry about 0.4 km N of site of old Mt William railway station and about 8 km NE of Lancefield. Type loc. is PL1144, allotment 56, Parish of Goldie; from the Lancefieldian (La2).

Other material. Figured specimens P14368, P31952, P31953, P14240. Numerous specimens from La2, La3, and Be1 of numerous localities. Despite Thomas' (1960) table which shows the species from Be2, we have been unable to substantiate this. In Be1 the species is as abundant at *T. acclinans* (Table 2) and almost as common as *T. approximatus*.

Diagnosis. Distinctive rhabdosome with four slender, stiff stipes, mutually at right angles and developed within 1 mm of the sicula, which is conspicuous, and nematophorous; little change in stipe width distally; thecal spacing constant at about 7 in 10 mm.

Description. A short nema is commonly seen, as on the holotype, where it is over 2 mm long. The early development is not known but four stipes are established within 1 mm either side of the sicula, and there is a suggestion that th1^1 arises very high on the sicula. The stipes have a uniform width from close to the sicula of just over 1 mm (flattened), and a fairly constant low thecal spacing of 7 in 10 mm. The thecae themselves seem to be simple dichograptid inclined to the stipe axis at about 25–30°.

Remarks. We have figured for comparison specimens of *T.* (*T.*) *decipiens bipatens* Keble and Harris which occurs at essentially the same horizon, and perhaps a little higher, at Antimony Mine, Blackwood.

Tetragraptus (?Tetragraptus) chapmani Keble and Harris

Plate 20 fig. e; text-figs 97–100

Tetragraptus chapmani Keble and Harris, 1934: 169, pl. 20 figs 3a, b.

Tetragraptus cf. *chapmani*.—Lenz and Jackson, 1986: fig. 6A.

Type specimen and other material. Holotype, P14378A and B (24984, 5) from Fossil Gully, near junction of Kangaroo Creek and Lerderberg River, left bank, 3.6 km below Blackwood. Paratype P26452 (25080) from Antimony Mine, Lerderberg River, 1.6 km below Blackwood. Several other specimens and fragments on the holotype and paratype slabs. Bendigonian (Be1 and Be2 according to Thomas (1960) but possibly restricted to Be1 from our observations).

Diagnosis. 8 mm long funicle, possibly with several thecae; distal thecae high, triangular, aperturally isolate, spaced at 8 in 10 mm.

Description. We have prepared the holotype so that the sicula is now exposed. It has a length of about 1.7 mm, but is not in the same plane as the stipes. The sicular aperture is not clear. The funicle is rather long, being almost 8 mm, so that there is room for several thecae to be developed before the 2nd order dichotomy gives rise to the four stipes. No thecae are, however, apparent on the holotype. Early growth stages associated with the holotype, and having a similar funicle length (fig. 99) and sicular size, have thecae which in profile are conspicuously isolated and rather clonograptid-like. The distal thecae of *T. chapmani* (figs 97–98) are very similar: a dorsoventral width of 1.3 mm is achieved of which fully 1 mm comprises the isolated metathecal portion. The prothecal parts of several specimens are in low relief, infilled with opaline silica, but the metathecal parts are not infilled, are flattened, and may have thin periderm. The thecal spacing is 8 in 10 mm.

Remarks. *T. chapmani* has thecae which closely recall those of some clonograptids such as *C. ramulosus*, *C. rarus*, and *C. smithi*. Indeed the slender *C. tenellus problematica* may have given rise to *T. chapmani* by stipe reduction.

Tetragraptus (?Tetragraptus) whitelawi T.S. Hall

Text-figs 151, 154

Tetragraptus whitelawi T.S. Hall, 1914: 114, pl. 17 fig. 16.—Benson and Keble, 1935: 279, pl. 30 fig. 234.—Skwarko, 1961: 103–105, fig. 2.

Type specimen. Holotype P14287A and B (9756, 9761) from Geological Survey of Victoria locality 79/BO, Sheepshead Line, Bendigo, from the upper part of the Chewtonian. What rare material there is of this species suggests that the age is the upper part of the Chewtonian, possibly only Ch2, although Thomas (1960) recorded it from Be4. None of the collections of Be4 in the Museum of Victoria have specimens which we could refer to *T. whitelawi*. A *Sigmagraptus* cf. *crinitus* occurs on the holotype slab; and T. S. Hall records *T. serra*, *S. laxus* and *I. caduceus*, referring the Sheepshead Line locality to the "Upper Bendigonian".

Diagnosis. Slender, 4-stiped dichograptid with long funicle of 10 thecae; one dichotomous division on each stipe resulting in four 2nd order stipes of usually less than 2 cm; thecae dichograptid, of low angle to the stipe axis.

Description. The sicula on the holotype has a length of a little over 1 mm, allowing for a small portion missing near the apex. It is slightly curved, particularly adaperturally (fig. 154) where the aperture curves towards th1^2. The origin of th1^1 is unclear, but th1^2 can be seen as a narrow tube which eventually turns almost at right angles to the axis of the sicula and grows away in horizontal disposition. The mesial parts of th1^1, those along the metasicula, may be obscured by the early growth of th1^2, but the metathecal part of 1^1 is clearly visible. Moreover, a small tube in a dorsal position to that where th1^1 leaves the sicula, could be the early growth of a slender th1^1. The funicle is about 10 mm long.

The early thecae on the holotype are seen in apertural view, suggesting that the sicula (seen here in good profile) is not in the same plane as the two early stipes, and that the overall rhabdosomal disposition is horizontal with the sicula upright. The thecal spacing on the first order stipes is 9 in 10 mm, and those stipes have five thecae developed before the second order dichotomy. The second order stipes have thecal spacings of 8–10 in 10 mm; with a free ventral wall inclined to the stipe axis at 20°–30° (flattened specimens); and a dorsoventral width of a little more than 0.5 mm. The thecal apertures are conspicuous (fig. 151), almost denticulate, and often with a slightly convex profile. The dorsoventral stipe width is 0.6–0.7 mm.

Remarks. *T. whitelawi* has an unusually long funicle for a tetragraptid and resembles rather a slender dichograptid or late clonograptid in which stipe reduction has reached four. The question is discussed again under *Evolutionary notes*. The species is not dissimilar to *Etagraptus harti* but differs in that the latter has a short funicle. *T. whitelawi* was placed in their genus *Laxograptus* by Cooper and Fortey (1982) but the rhabdosome is stiff rather than lax: and in this paper we regard the type of *Laxograptus* (*Z. irregularis*) as a slender but more or less typical representative of *Zygograptus*.

Section **Mimograpti** nov.

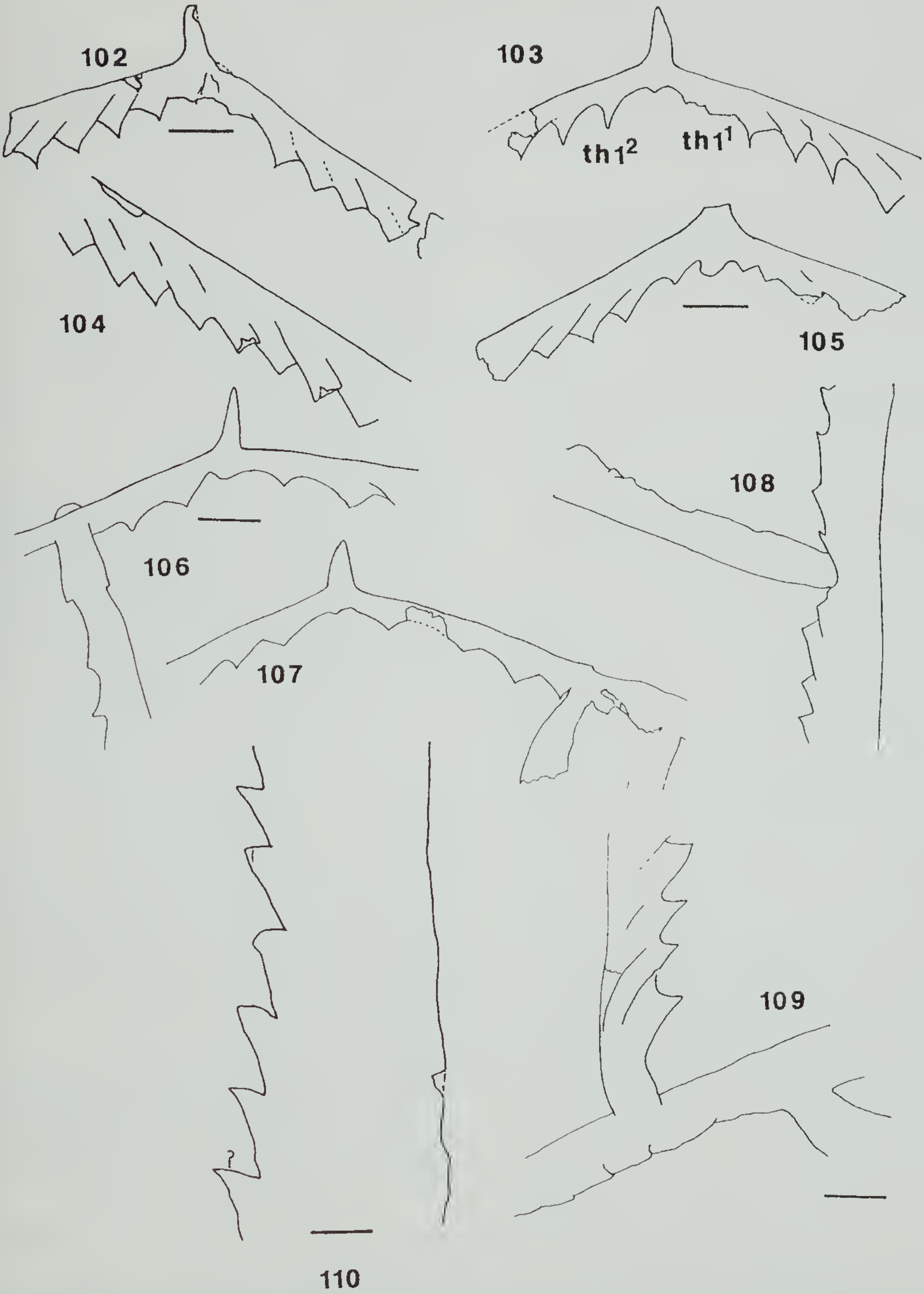
Mimograptus Harris and Thomas, 1940b

Type species. Mimograptus mutabilis Harris and Thomas, 1940b.

Diagnosis. (emend. herein). Proximal template undoubted didymograptid, that is with one progressive dichotomy resulting in two main stipes; main stipes gently declined; irregular development of lateral stipes of 2nd and 3rd orders; 2nd order stipes on both sides of main stipes; thecae simple dichograptid tubes, slightly denticulate.

Remarks. In his (1970) "Treatise" definition of the genus Bulman stated "forms with few or no lateral branches also occur". In fact, in the type series just one specimen lacks lateral branches, and the others have one, two, five and eight, the last two including single 3rd order stipes: they look like growth stages of the colony. *Mimograptus* has a distinctly didymograptid aspect and without the lateral branches would be close to *Didymograptus dilatans* or *D. mundus*.

The genus differs from *Adelograptus* in the pronounced lateral nature of the branches, the



Figures 102–109. *Mimograptus mutabilis* Harris and Thomas. 102, holotype P34927B; 103, P34929; 104, P34927, (8 cm from sicula on main stipe); 105, P34927A (counterpart of figure 109); 106, P34928; 107, P34930; 108, P34927 (only 3rd order stipe known, from first 2nd order stipe); 109, P34927B (only stipe on dorsal side of main stipes of holotype, showing 2nd order thecal form). Scalebar 1 mm.

Figure 110. *Triaenograptus neglectus* T.S. Hall, distal thecae of holotype, P31195. Scalebar 1 mm.

robust and distinctly dichograptid thecae, and the overall appearance of the colonies.

Mimograptus mutabilis Harris and Thomas

Plate 21 figs a–d; text-figs 102–109

Mimograptus mutabilis Harris and Thomas, 1940b: 197–198, figs 1–8.

Type series and only specimens. Holotype, P34927A, B (44344 and 5) from the Chewtonian (Ch2) of allotment 41B, Parish of Campbelltown; and paratype P34928–P34931 (44346–9) from the same locality and horizon.

Description. The sicula is about 1.5 mm, seemingly slightly curved, with its aperture turned gently towards the th1^2 series although this is not quite certain. Early development cannot be deduced and there is some ambiguity about the apertures of th1^1, th1^2 and the sicular aperture. The holotype (fig. 102) has a relatively robust proximal end with the early thecae inclined at a high angle (50°) to the stipe axis and the sicular aperture not all that clear. Other specimens (figs 103 and 105) show the early thecae inclined at 40° to the stipe axis, but the proximal end as a whole still resembles that of a relatively robust, declined didymograptid. The proximal thecal spacing is high at 12–15 in 10 mm and the dorsoventral width at theca 5 on either main stipe is fully 1 mm. The most distal parts of the main stipes have a dorsoventral width of 1.0–1.2 mm with a thecal spacing of nearer 12 in 10 mm, a figure maintained on the lateral stipes. The lateral stipes, however, may be more robust reaching a dorsoventral width of 1.3–1.5 mm.

The origin of the branches cannot be seen in terms of thecal details, but specimen P34929 shows a dorsal bulge to the main stipe before the lateral stipe depends ventrally whilst others have the appearance of a strong lateral position which is not always clearly related to a thecal aperture on the parent stipe. The lateral branches of the 2nd order are positioned as follows:

holotype: one, th27; two, 30 mm; three, 39 mm; four, 41 mm.

P34930: one, th4; two, th6 (each on first stipe pendent)

P34929: one, th23; (second stipe, pendent)

P34928 (4 specimens): one, th9; two, th13 approx. (first stipe, reclined); and one, 17 mm (first stipe, pendent); and one, 12.5 mm; two, 17 mm; three, 22 mm (second stipe, reclined); and one, th3; (second stipe, pendent).

Remarks. In several respects *Mimograptus mutabilis* differs from other didymograptids, but particularly in the relatively robust stipes coupled with a high thecal spacing a high angled dichograptid thecae. Most multiramous dichograptids with robust stipes have a thecal spacing less than 10 in 10 mm, usually 8–9. In other respects *M. mutabilis* is close to certain didymograptids, such as *D. mundus* and *D. dilatans*. Ge (1979, in Mu et al.) divided *M. mutabilis* into two species, after examination of the original figures (*D. mutabilis* = figs 2 and 4; *D. australis* = figs 1, 3, 5, 6, 7 and 8). We can find no basis for this and do not support it. *M. mutabilis* differs in most measurable dimensions from *M. reclinatus* Ge and *M. dubius* Ge, and is distinctly stiffer and more robust than the latter, and has dependent stipes in marked contrast to the former.

Section **Didymograpti** emend. herein

Didymograptus McCoy, 1851

Type species. Graptolithus murchisoni Beck, 1839.

Remarks. Using the genus sensu lato as defined earlier, the didymograptids from our Bendigonian material do fall into several groups. We do not consider, however, that the genera *Expansograptus*, *Corymbograptus* and *Acrograptus* are sufficiently well defined to justify our formal use of the terms.

D. adamantinus and *D. perditus* have a distinctly archaic appearance about them with a full stipe width (and hence thecal size) achieved almost immediately, and a metasicular region barely distinguishable on shape and size from

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Figures. 111–113. *Didymograptus elongatus* Harris and Thomas, respectively holotype P32074; th19–22 of same; and paratype P32075. Scalebar 1 mm.

Figures 114, 115. *Didymograptus procumbens* T.S. Hall, respectively holotype P31974 and specimen on the same slab. Scalebar 1 mm.

Figure 116. *Didymograptus latens* T.S. Hall, holotype, P31976. Scalebar 1 mm.

Figures 117, 118. *Didymograptus asperus* Harris and Thomas. 117, paratype P32041; 118, holotype, P32011. Scalebar 1 mm.

Figure 119. *Didymograptus aureus* T.S. Hall, holotype, P31977. Scalebar 1 mm.

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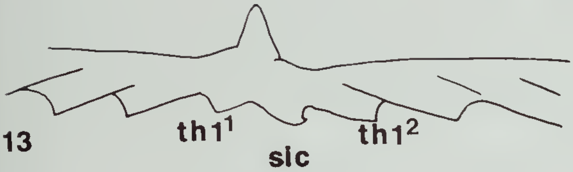

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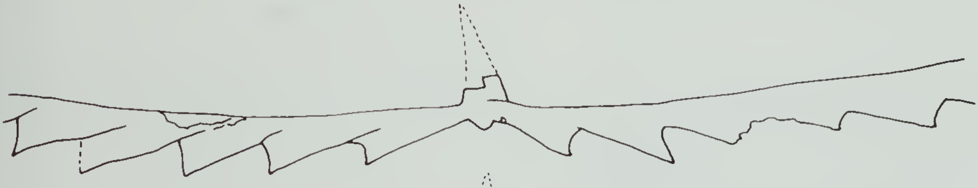

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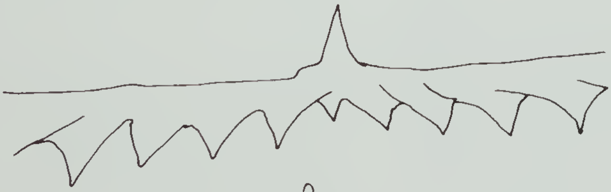

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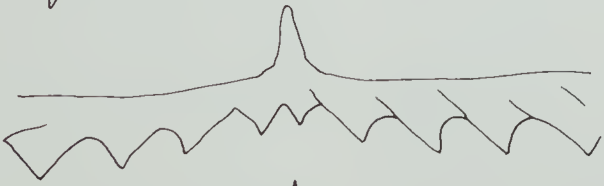

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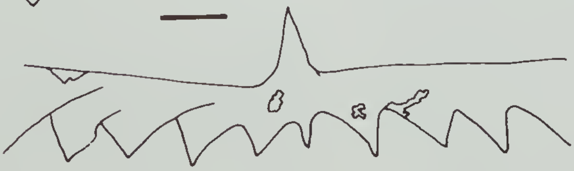

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adjacent thecae. Although it seems unlikely on preservational grounds the presence of bithecae would not altogether be a surprise. Their similarity to a slim *Kiaerograptus* is striking, but they occur in the upper Bendigonian and higher (Table 1).

D. hemicyclus and *D. eocaduceus* share the general stipe characters of the above two species yet are strongly reclined, as well as being fairly robust, a most unusual and distinctive combination of didymograptid characters. Both species are relatively early being confined to Bendigonian Be1.

D. dilatans (Be2, Be3) is possibly referable to the subgenus *D.* (*Acrograptus*), that is a didymograptid which is slender, gently declined, but otherwise little different in diagnosis from similar *D.* (*Expansograptus*) species (but see Cooper and Fortey (1982)).

D. mundus and *D. vicinus* are relatively robust, declined/deflexed (but not pendent) didymograptids which would be referred by most modern workers to *D.* (*Corymbograptus*). However, *D. mundus*, if not *D. vicinus*, seems to us to be little more than a *D. nitidus* type and we prefer, therefore, to retain them under *Didymograptus* or *D.* (*Expansograptus*). In fact we have grave doubts about the definition and value of the subgenus *Corymbograptus*: *D. nitidus*, as well as *D. mundus* and *D. vicinus* would fit into Boucek's (1973) definition, yet it seems to be based upon little more than the deflexed flexuous nature of the stipes, surely a variable and gradational feature.

The remainder of the didymograptids we describe are referable to *D.* (*Expansograptus*), that is more or less horizontally disposed forms with isograptid dextral development and a sicula lacking a virgella. Some of those last Victorian forms may be synonymous with Scandinavian species described by Monsen (1937), but the latter are in such need of revision that we have confined our remarks on possible synonomies to the Remarks sections in the systematic descriptions pending modern work on Scandinavian material. *D. elongatus* Harris and Thomas (1940a), regarded by Cooper and Fortey (1982) as belonging to *Xiphograptus* in fact lacks a virgellar spine, and is almost certainly referable to *D. (Expansograptus)* as defined by them, and as adopted herein.

Didymograptus perditus T.S. Hall

Plate 22 fig. b; text-figs 126–128

Didymograptus perditus T.S. Hall, 1914: 104–105; pl. 17 fig. 2.

Didymograptus cf. *perditus*.—Monsen, 1937: 110, pl. 1 figs 15, 51, pl. 7 fig. 9.

Type specimen and other material. Holotype, P14294, from locality H7 of the T.S. Hall Collection, Daphne Reef, Lost Gully, Chewton. T.S. Hall recorded it from the "highest zone in the Bendigonian" (i.e. Chewtonian today), and Thomas (1960a) therefore extended the range of the species to include the Chewtonian, whilst modern revision of Thomas' ranges (Singleton, pers. comm.) restricted it to the Chewtonian. The Daphne Reef locality may well be Chewtonian and the only other material we have seen (in the Kellam Collection at Bendigo) is Chewtonian in age, with some of doubtful Be4.

Diagnosis. Horizontal didymograptid proximally, becoming very gently reclined distally; uniform sized thecae; dorsoventral width 0.90–0.95 mm at th5 to 1.2–1.3 mm distally, inclined at relatively high angle of 35°-40° throughout; thecal spacing of 6.4–7.5 mm in 10 mm; sicula 2 mm.

Description. Th1^1 and 1^2 originate high on the sicula and grow away from it after about one third of the sicular length so that much of the distal part of the sicula is free and isolated. It has a length of 2 mm and its aperture faces strongly to the side of the second stipe of which it appears almost as a proximal continuation (fig. 126). The sicular aperture has a width of fully 0.7 mm.

Both th1^1 and 1^2 grow downwards quite strongly, reaching the distal extremity of the sicula in position and forming with the sicula a very characteristic proximal end with three apertures quite close together. Succeeding thecal apertures are more widely spaced, but a similar high angle of thecal inclination persists distally. The early parts of the th1^1 and 1^2 also form a characteristic dip in the dorsal stipe profile adjacent to the sicula. Subsequent to this the stipes become horizontal and, more distally, gently reclined. The early part of the stipes has a gently undulating dorsal profile.

Remarks. The overall rhabdosomal aspect recalls some kiaerograpatids although there is in our material no sign of bithecae and the horizon, Chewtonian, is rather high. Nevertheless it is tempting to consider *D. perditus*, and *D. adamantinus* for the same reasons, to have evolved directly from a *Kiaerograptus*-like ancestor rather than belonging to the plexus of extensiform didymograptids described below.

Didymograptus adamantinus T.S. Hall

Plate 22 fig. c; text-fig. 125

Didymograptus adamantinus T.S. Hall, 1914: 106–10 7, pl. 17 fig. 8.—Benson and Keble, 1935: 280, pl. 31 fig. 23.

Type specimen and other material. Holotype, P31975, from T.S. Hall locality H45 at Diamond Hill, Bendigo. Hall gave the horizon as Bendigonian, Thomas (1960) the range as Be3–Ch1, and modern studies (e.g. Singleton, pers comm. and our own observation) as Be4–Ch1 (as in the Kellam Collection at Bendigo).

Diagnosis. Gently declined didymograptid with archaic proximal end, slender stipes, and overall *Kiaerograptus*-like aspect.

Description. The stipes are almost uniformly narrow with a maximum dorsoventral at about th6/7 of 1.10–1.15 mm, thereafter decreasing a little to around 1 mm. The sicula has a short nema, and a total length of 1.5 mm. It is slightly curved towards th1^2, the aperture of which is fully 1 mm away from that of the sicula. Th1^1 grows downwards opening quite close to the sicular aperture but facing in the opposite direction (fig. 125). The distal extremities of the sicula and th1^1 thus form a highly characteristic dependent pair symmetrically disposed beneath the sicular apex: the rhabdosomal/sicular axis passes between the two apertures equidistantly. The thecae throughout are conspicuous, apertures normal to thecal length or slightly denticulate, spaced at 7–8 in 10 mm, and are inclined, adaperturally, at about 35°–45° to the stipe axis. The early parts of each theca may be inclined as low as 15° so that the free ventral wall is concave.

Remarks. D. adamantinus differs from *D. perditus* in the nature of the proximal end, which has two clustered apertures rather than three, and in its general stipe dimensions. It is not dissimilar in appearance to *Adelograptus antiquus* the Lancefieldian form (see also remarks under the preceding description of *D. perditus*, and plate 3 fig. b for comparison).

Didymograptus hemicyclus Harris

Plate 23 figs c, d; text-figs 132, 152

Didymograptus hemicyclus Harris, 1933: 109–110, pl. 6 fig. 4, text-fig. 68.—Harris and Thomas, 1938a: 76, pl. 2 figs 21a–c.—Berry, 1966: 427–428, pl. 49 figs 5, 6.—Beavis and Beavis, 1974: 191–193, figs 4c, d.

Didymograptus sp. cf. *D. hemicyclus*.—Cooper, 1979: 71, pl. 13d, text-figs 43a–c.

Didymograptus cf. *hemicyclus*.—Lenz and Jackson, 1986: Fig. 6L.

Type specimens. Lectotype, P13797 (designated by Berry, 1966) from the Bendigonian (Be1) of the Parish of Campbelltown: "17"' on the specimen slab apparently refers to Bed 17 of Thomas Smith which is equivalent to "Good Bed 16A" (S.17 in T. Smith Collection Index). Harris and Thomas (1938a) referred to this as the "type locality" and its exact placing is 240 m WSW from NE corner of allotment 16A, sect. II Parish of Campbelltown. In addition there is a well preserved specimen, P83293, on the same slab as P32048, a paratype of *Pseudobryograptus crassus*; and numerous other Bendigonian (Be1) specimens. Berry (1966) gave the locality erroneously as allotment 19, presumably due to misinterpretation of the pencilled 17 as 19.

Diagnosis. Strongly reclined didymograptid with short curved stipes, giving unique overall semicircular rhabdosomal aspect; isograptid proximal development and strongly denticulate, high angled thecae.

Description. The sicula has a total length of about 2 mm although a quarter of this is certainly taken up by a pronounced mucronate apertural process adjacent to an aperture which faces the second thecal series. P32048 has a trace of a possible nema. Th1^1 originates high on the sicula (fig. 132) and gives rise to th1^2 seemingly about half way down the sicula (or, at least, th1^2 is seen at this point growing away from th1^1: its origin could be higher though there are no bumps to indicate this). Th2^1 undoubtedly originates from th1^2 at about the same level as th1^2 (apparently) does from th1^1 and, presumably, th2^2 grows from th1^2 shortly after this (fig. 132). Thus the development is isograptid.

The cluster of the apertural regions of the sicula and th1^1 and th1^2 makes a characteristic grouping, particularly as each is downwardly directed very strongly and th1^1 and the sicular process are back-to-back with a highly typical V-shaped excavation between them.

Subsequent thecae of both series are very similar to the first two thecae, notably in their high angle of inclination to the stipe axis (up to 60°–80°), their prominent, (?) rounded, ventral processes, and their wide apertures (approximately 0.7 mm). The total dorsoventral stipe width is about 1 mm, and the thecal spacing of the order of 12 in 10 mm (allowing for the curvature of the stipes). Thecal overlap is difficult to estimate but is certainly at least 50%.

Remarks. If it could be imagined that the stipes were pulled down to the horizontal position there would be a close similarity between *D. hemicyclus* (and, for that matter *D. eocaduceus* described next) and the two previously described didymograptids *perditus* and *adaman-*

tinus: all have the relatively "primitive" downward growing early cluster of thecae, in contrast to the extensiform didymograptids described below. *D. hemicyclus* cannot be confused with any described species: reclined didymograptids are quite rare and only *D. cocaduceus* is both robust *and* reclined and it has a quite different rhabdosomal shape. Indeed the semicircular outline of *D. hemicyclus* is not only highly characteristic, but of considerable aesthetic appeal.

Didymograptus cocaduceus Harris

Plate 23 figs a, b

Didymograptus cocaduceus Harris, 1933: 109, pl. 6 figs 8A, B, text-figs 64–67.—Beavis and Beavis, 1974: 191, fig. 4a, b.

Didymograptus cf. *cocaduceus*.—Cooper, 1963: 56, fig. 6d.

Type specimens and other material. Lectotype selected by Beavis and Beavis (1974), P13800, same locality as *D. hemicyclus* types, previous description. Paralectotypes include P42445, P34789, the former having stipes which touch dorsally. Specimens figured by Harris as his figs 65, 67, pl. 6 fig. 8B are missing.

Diagnosis. Tiny *Didymograptus*, U-shaped rhabdosome, with strongly reclined stipes so that they are sub-parallel or occasionally touching; dorsoventral width 1.7 mm; thecal spacing 11–12 in 10 mm.

Description. The sicula is fully 2 mm in length, with a short nema commonly preserved, and an apertural process some 0.5 mm in length, the tip of which reaches the level of the ventral apertural processes of the thecae. Nothing further can be said about the development at the proximal end except that th1^1 and 1^2 grow downwards quite strongly, and th1^1 must originate high on the sicula. The dorsoventral stipe width (flattened) is narrowest at the level of the first four thecae of the rhabdosome (where flexure is greatest) but thereafter is uniform and from 1.5–1.7 mm including processes.

Remarks. It is likely that *D. cocaduceus* has similar development to *D. hemicyclus* but none of the material is as well preserved as the latter. The distinction between the two species is given in the preceding description. It should be remarked that *D. cocaduceus*, more so than *D. hemicyclus*, has the appearance of a two-stiped tetragraptid and its ancestry may lie in one of the small reclined *Tetragraptus* species.

Didymograptus vicinus Harris and Thomas

Plate 25 fig. b; text-figs 133, 134

Didymograptus vicinus Harris and Thomas, 1938a: 76, pl. 2 figs 24a–c; pl. 4 fig. 22.

Didymograptus sp. cf. *D. vicinus*.—Cooper, 1979: 72, text-fig. 45.

Type specimens. Holotype, P32015 (41344), from "good bed" rather more than 200 m WSW from NE corner of allotment 16A, sect. II, Parish of Campbelltown; paratype P32016 figured by Harris and Thomas (pl. 2 fig. 24b) from Allotment 22A, Section II, Parish of Campbelltown, Bendigonian (Be1). Paratype figured by Harris and Thomas (pl. 2 fig. 24C and pl. 4 fig. 22) is missing.

Diagnosis. Deflexed proximally and more or less horizontal distally, with about 5 thecae on each stipe involved in the flexure: thecal spacing 8–10 in 10 mm; dorsoventral width about 2 mm maximum.

Description. The sicula on the holotype and paratype is well over 2 mm long, with, on the former, a trace of a short nema (and, indeed, an adjacent sicula (fig. 133) suggestive of a synrhabdosome arrangement). The sicular apertural region curves towards the second thecal series and its aperture (or process thereon) is relatively close to that of th1^1. Th1^1 originates high on the sicula but further development has not yet been discerned.

A dorsoventral width (almost flattened) of 2 mm is achieved by th3^2 or th4^1 on the holotype, and similarly on other specimens, that is shortly before the stipes become horizontal. Distally there is little further increase and in the most distal parts, at 20 mm or so, there is a slight diminution in width. The angle of inclination of the free ventral wall to the stipe axis is about 40°.

Remarks. The development, so far as it is known, and the deflection of the proximal end region is very little different from in the type series of *D. nitidus* J. Hall, of which Dr J. Riva kindly made us aware some years ago. Therefore, we are inclined to group *D. vicinus* with *D. nitidus* as an essentially extensiform didymograptid with a small amount of deflection at the proximal end: several species of extensiform didymograptids show some variation of this feature. It should be noted that the sicula is considerably longer than stated by Harris and Thomas (see fig. 133) and it is possible that they misinterpreted the apertural region of the sicula.

Didymograptus mundus T.S. Hall

Plate 25 fig. a; text-fig. 135

Didymograptus mundus T.S. Hall, 1914: 107, pl. 17 fig. 9.—Benson and Keble, 1935: 284, pl. 31 fig. 22.—Berry, 1966: 428–429, pl. 46 fig. 2.

Type specimen and other material. Holotype, P14270, from T.S. Hall locality H46 in Lost Gully, Chewton.

There is some agreement between Thomas (1960a) who gave the range of the species as Chewtonian and Castlemainian (Ca1, Ca2) and T.S. Hall (1914) who noted that it is characteristic of "the Upper Bendigonian, and Lower and Middle zones of the Castlemainian". The above locality is probably Chewtonian in age. What is puzzling is that T.S. Hall (1914: 117) gave Bendigo as the type locality and, as pointed out by Berry (1966: 428) Keble cited Diamond Hill, Bendigo as the type locality. It is known that T.S. Hall's locality H45 *is* at Diamond Hill, Bendigo.

Diagnosis. Essentially horizontal didymograptid with a deflexed proximal portion encompassing up to 5 thecae either side of the sicula, the total amplitude of the deflection being about 3 mm; dorsoventral width 1.0–1.5 mm; thecal spacing 10–9 in 10 mm.

Description. The sicula is probably almost 2 mm long and is without question curved gently, in the apertural region, towards the second thecal series (fig. 135). There is a distinct shoulder formed as th1^2 grows away from th1^1, which latter is initiated high on the sicula (on the holotype both the part and counterpart must be examined to detect this shoulder). It is not possible to see further development details.

The dorsoventral stipe width is 1.0 mm at the level of th1^1, 1.10–1.15 at th5 (on either stipe) and up to 1.50 mm at th18. The change in width is gradual. The proximal thecal spacing is approximately 10 in 10 mm and more distally 10–9 in 10 mm, and the free ventral thecal wall is inclined at 30-50° to the stipe axis.

Remarks. T.S. Hall was surely correct to compare this form closely with *D. nitidus* (J. Hall). *D. mundus* has a larger sicula (we note that it is longer than T. S. Hall considered) and the thecae themselves are inclined at a lower angle to the stipe axis and number only 9–10 in 10 mm (cf. 12–13 in 10 mm in *D. nitidus*). Nevertheless *D. mundus* should be grouped with *D. nitidus* and it seems to us that neither these nor *D. vicinus* should on present evidence be equated with *D.* (*Corymbograptus*). In the Victorian sequences *D. mundus* occurs at about the same stratigraphic level as *D. nitidus*. But *D. vicinus* precedes them. Thomas (1960a) compared *D. mundus* to *D. balticus* Tullberg, but in our view this latter is much nearer the common concept of *Corymbograptus* and has particularly elongate thecae and sicula.

Didymograptus elongatus Harris and Thomas

Plate 24 figs e–f; text-figs 111–113

Didymograptus elongatus Harris and Thomas, 1940: 132–133, pl. 1 figs 12a, b, pl. 2 figs 14a, b.

non ?*Xiphograptus elongatus*.—Cooper and Fortey, 1982: 289–291, pl. 1 fig. 11; text-figs 83a–c.

Type specimens. Holotype, P32074 (43204) from the dam, allotment 17A, Parish of Campbelltown (Harris and Thomas, 1940, pl. 1 fig. 12a) and paratype P32075 (43205) from Bendigo (Harris and Thomas, 1940: pl. 1 fig. 12b, pl. 2 figs 14a, b). The holotype is Bendigonian Be2 and the paratype from Be3.

Diagnosis. Extensiform didymograptid with characteristically low angled th1^1 and 1^2 strongly diverging from each other at less than 180°; sicular aperture curves towards 1^2 but it is basically closer to 1^1; thecae about 8 in 10 mm; dorsoventral width maximum of 2 mm.

Description. The proximal ends of the later forms tend to be slightly more robust (cf. figs 111, 113 and 120) but otherwise the overall appearance of the stipes is the same with a stipe length of more than 5 cm in some, roughly horizontally disposed, and with a distal dorsoventral width of 1.5–2.0 mm. At the level of the aperture of th1^1 the dorsoventral stipe width is a little over 0.5 mm in the early forms and just over 1 mm in the later ones. The sicula has a length of up to 1.3 in early forms and over 1.7 in later forms. In both, however, the apertural region curves towards and becomes effectively part of the second thecal series. There is a blunt rounded apertural process to the sicula. Early development is not clear but there are often distinct shoulders near the points where th1^1 and 1^2 leave the sicula: these are presumably the early growth parts of th2^1 and 2^2. Thecal overlap is approximately one-third proximally and a little over half distally. The thecae are simple dichograptid throughout, with even apertures and an inclination of the free ventral wall of about 25°–30°.

Remarks. Pl. 2 fig. 14B of Harris and Thomas apparently shows a virgellar spine which in part led Cooper and Fortey to include the species in *Xiphograptus*. This was almost certainly a draughting or printing error for the original (P32075) shows no such structure (see fig. 111). In all senses *D. elongatus* is an extensiform didymograptid.

Didymograptus procumbens T.S. Hall

Plate 23 fig. e; text-figs 114, 115

Didymograptus procumbens T.S. Hall, 1914: 106, pl. 17 figs 6, 7.—Benson and Keble, 1935: 286.

Type specimens and other material. Holotype P31974 (Hall 1914, pl. 17 fig. 6), paratype P14279 (pl. 17, fig. 7) from Diamond Hill, Bengido, T.S. Hall locality H45. The type specimens are probably Bendigonian (Be4), but the species according to T.S. Hall and

Thomas (1960a) ranges from Be4 into Castlemainian Ca2. There are other specimens in the Museum of Victoria, from these horizons and various localities, probably referable to the species, although not always labelled as such.

Diagnosis. Very gently reclined rhabdosome with a strikingly prominent sicula, extensiform development, and a rather low thecal spacing of 6 in 10 mm proximally, possibly 8 in 10 mm distally in some later specimens.

Description. The sicula is rather narrow, often less than 0.5 mm, and fully 2 mm long, its axis more or less at right angles to the initial growth of the stipes which are at 180°, but gradually become gently reflexed. Th1^1 may arise about one-third of the sicular length below the apex but development is not clear. The sicular aperture is slightly curved towards the th1^2 series, and it has a robust, rounded process. The aperture of th1^1 is slightly closer to the sicula than that of 1^2. The thecae are simple dichograptid tubes, with overlap less than , and an inclination to the stipe axis of around 25° in the stratigraphically earlier forms, and perhaps 30° in the later forms and in the more distal thecae of all forms. Thecal spacing is 6–8 in 10 mm, and the distal dorsoventral width 1.8 mm.

Remarks. It would be premature to separate the early from the late forms before the *D. extensus* group itself is fully revised. The most striking features of *D. procumbens*, readily distinguishing it from other Victorian extensiform didymograptids are the long narrow sicula and the very widely spaced early thecae, giving the whole proximal end a "stretched" appearance. *D. extensus* for example, has a thecal spacing more typical of the group of 8–9 in 10 mm, and is narrower with a less conspicuous sicula. Most other extensiform species have thecae inclined at a higher thecal angle.

Didymograptus latens T.S. Hall

Plate 25, fig. c; text-fig. 116

Didymograptus latens T.S. Hall, 1914: 106, pl. 17 fig. 5.

Type specimen. Holotype, P31976, from T.S. Hall locality H45, Diamond Hill, Bendigo; Bendigonian, probably Be4.

Diagnosis. Extensiform didymograptid with short, 1 mm sicula curved aperturally to the th1^2 series; stipes gently reflexed initially, becoming horizontal; thecae inclined at 30° proximally, to 40° distally, spaced at 10 in 10 mm throughout, simple dichograptid; dorsoventral width rarely exceeds 1 mm.

Remarks. Hall was in error in describing the sicula as being in excess of 1.5 mm *broad* as well as long. It can be seen from fig. 116 that he included the later growth of th1^1 in that measurement thus giving the abnormally wide sicula. Nor are we certain that the sicular length is as he claims: it seems around 1 mm rather than 1.5 mm. This is clearly important for it removes one of the main distinctions between *D. latens* and *D. decens* Törnquist and *D. suecicus* Tullberg referred to by Hall. However, *D. suecicus* is now known to have more highly inclined thecae than does *D. latens*. What is probably more important is that *D. latens* must be very close to *D. extensus* and we only retain the integrity of the former here until the *extensus* group is revised. *D. similis* (J. Hall) is very close to *D. latens*, having the same dimensions though possibly with a longer sicula.

Didymograptus asperus Harris and Thomas

Plate 22 fig. a; plate 23 fig. f; text-figs 117, 118

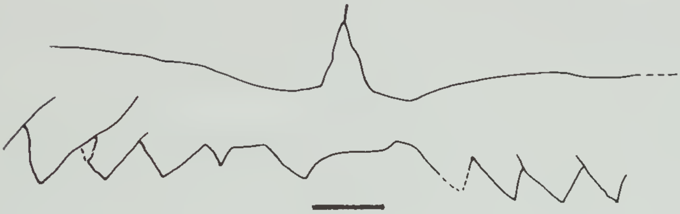
Didymograptus asperus Harris and Thomas, 1938a: 76–78, pl. 2 figs 25a–c, pl. 4 fig. 23.

?*Didymograptus* cf. *asperus*.—Skwarko, 1961: 105, fig. 3.

Type specimens and other material. Holotype, P32011 (41347) from the "good bed" rather more than 200 m WSW from the NE corner of allotment 16A, sect. II, Parish of Campbelltown; Bendigonian (Be1); and paratypes P32041 (35861) (Harris and Thomas 1938a: pl. 2 fig. 25b), P34973 (41346) (pl. 2 fig. 25c; pl. 4 fig. 23). A small number of other specimens in the Museum of Victoria collections from 16A are probably referable to this species.

Diagnosis. Extensiform didymograptid, almost horizontal to gently reflexed stipes up to 5 cm long; distally reaching width of 1.6 mm; thecal spacing 9 in 10 mm proximally, 8 in 10 mm distally; sicula up to about 1.75 mm with distinct shoulder where 1^1 and 1^2 leave sicula, curved gently to 1^2 series; thecae simple dichograptid tubes, overlap rather less to rather more than one half; inclined to stipe axis at 40°–60°.

Remarks. D. asperus is distinctive in its relatively long elegant sicula with one or more shoulders or bumps as the stipes leave it. It is clearly of *extensus* type but the proximal end is more robust and the sicula larger. No other Victorian forms have this particular combination of characters. *D. aureus* T.S. Hall is similar but the early thecae in particular are more tightly



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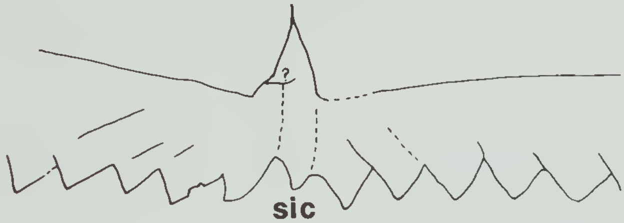

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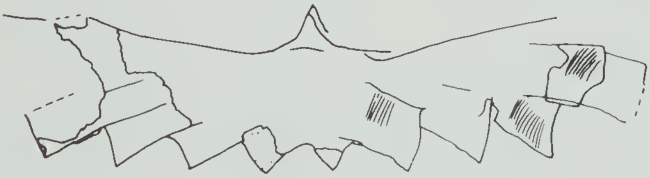

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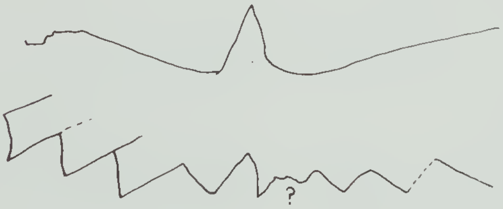

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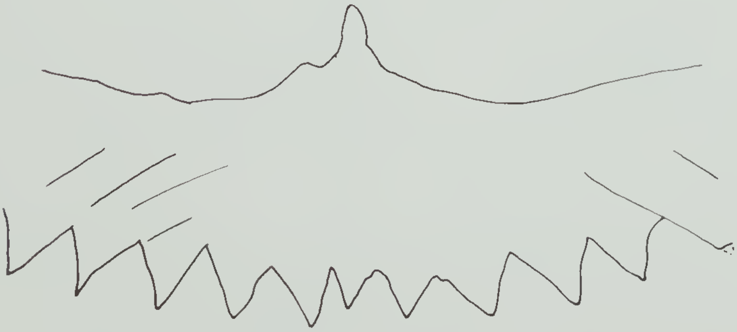

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Figures 120–123. *Didymograptus latus latus* T.S. Hall. 120, P14283; 121, P14283A (counterparts); 122, P32025; 123, P32023. Scalebar 1 mm.

Figure 124. *Didymograptus latus aequalis* Harris and Thomas, P34970. Scalebar 1 mm.

packed and dependent (cf. figs 118 and 119). There is a slight overall resemblance to *D. perditus* described above.

Didymograptus aureus T.S. Hall

Plate 25 figs c, d; text-fig. 119

Didymograptus aureus T.S. Hall, 1914: 105, pl. 17 fig. 4.

Didymograptus cf. *aureus*.—Benson and Keble, 1935: 281.

?*Didymograptus* cf. *aureus*.—Monsen, 1937: 109, pl. 8 fig. 7.

Type specimen and other material. Holotype P31977, from Bendigo, "Lower Bendigonian" according to T.S. Hall. Benson and Keble (1935) note that the species ranges from L1–B5 (i.e. from Lancefield, uppermost Lancefield, into Bendigonian Be1, see Harris and Thomas, 1938b). Other specimens on same slab are paratypes.

Diagnosis. Extensiform didymograptid with sicular aperture barely curved towards second thecal series, and with a prominent, rounded, apertural process; stipes begin faintly reflexed, are essentially horizontal, but with a typical double curvature; sicula elongate conical, over 2 mm long, slight shoulders where stipes leave it; thecae slightly "denticulate", 8 in 10 mm; dorsoventral width over 1 mm at th1^1 rapidly reaching 1.5 mm which is maintained distally; free ventral walls inclined at 40°–45°.

Remarks. The species differs from *D. extensus* ,to which group it clearly belongs, by its more robust proximal region and more dependent thecae: the actual thecal spacing is not dissimilar. *D. aureus* is clearly close to *D. asperus* but differs in the same manner as from *D. extensus*.

Didymograptus latus latus T.S. Hall

Plate 24 fig. a; text-figs 120–123

Didymograptus latus T.S. Hall, 1907: 141–142, pl. 15 fig. 7.—Benson and Keble, 1935: 284, pl. 30 fig. 31.—Harris and Thomas, 1938a: 74–75, pl. 2 figs 18a–d; pl. 4 fig. 17.—Legg, 1976: 29, pl. 9 figs 32, 33.—Lenz and Jackson, 1986: Fig. 7 J, R.—Williams and Stevens, 1988: 48–49, pl. 12 fig. 14, text-figs 34A–H.

Type specimen and other material. Holotype, P14283A, B (1425, 1427 counterparts) from Smith Street East, 60 m from Arnold Street, Bendigo; Bendigonian (Be1). The red shale of the locality has tetragraptids, *Clonograptus* cf. *flexilis* and *Ceratiocaris* on the type slabs. There are numerous additional specimens in the Museum of Victoria collections from other localities including P34970 (41333) (Harris and Thomas, 1938a: pl. 2 fig. 18a) from dam in allotment 17, section II, Parish of Campbelltown (Be2); and P32023 (41332) (pl. 2 fig. 18b), P32024 (41349) (pl. 2 fig. 18c) and P32025 (41350) (pl. 2 fig. 18d) all from "good bed", Bendigo (Be1).

Diagnosis. Robust extensiform didymograptid with stipes slightly reflexed: proximal dorsoventral width 1.5–1.8 mm; thecal spacing 11–14 in 10 mm; maximum dorsoventral width approximately 2 mm; thecal inclination, of free ventral wall, up to 50° proximally, a little less, 35–45°.

Description. The sicula has a length of 2.2–2.4 mm and is aperturally curved towards the second thecal series, though its rounded, blunt, process is quite close to the ventral edge of th1^1. Much of the sicula is enclosed by the developing early thecae (fig. 122) and the apertural region is only free for the length of the sicular process in consequence of the strongly downward direction of growth of all the early thecae. This is ultimately reflected in the very robust nature of the proximal end, and the maximum dorsoventral width is usually achieved between the first and fifth thecae on any stipe.

The thecal spacing is a little variable, the types having as few as 11 in 10 mm (fig. 122). In these latter specimens the angle of inclination is possibly a little less (cf. figs 121 and 122) but in general is commonly 50° proximally, falling

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Figure 125. *Didymograptus adamantinus* T.S. Hall, holotype, P31975, proximal regions. sic = sicular aperture. Scalebar 1 mm.

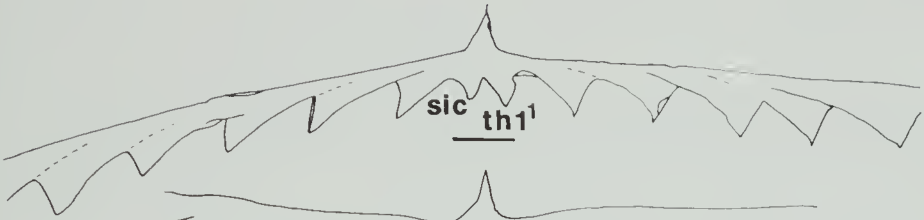
Figures 126–128 *Didymograptus perditus* T. S. Hall, holotype, P14294, respectively proximal end; th4–6; distal th28–32 on th1^1 series. Scalebar 1 mm.

Figures 129–131 *Didymograptus dilatans* T.S. Hall. 129 P83343 from Bendigonian (Be2); 130, holotype P31978 from Daylesford Bendigonian (Be3); 131, P32073 on same slab as P83343. Scalebar 1 mm.

Figure 132. *Didymograptus hemicyclus* Harris, P83293. Scalebar 1 mm.

Figures 133, 134. *Didymograptus vicinus* Harris and Thomas, holotype P32015 with associated pro and ?metasicula; and paratype P32016. Scalebar 1 mm.

Figure 135. *Didymograptus mundus* T.S. Hall, holotype P14270. Scalebar 1 mm.



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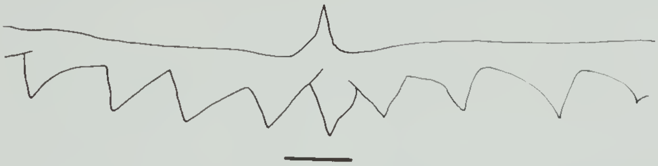

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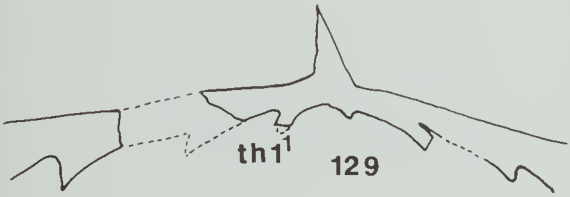

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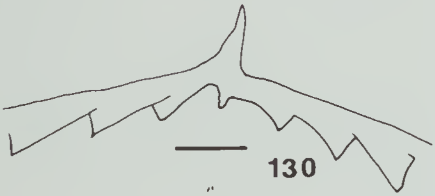

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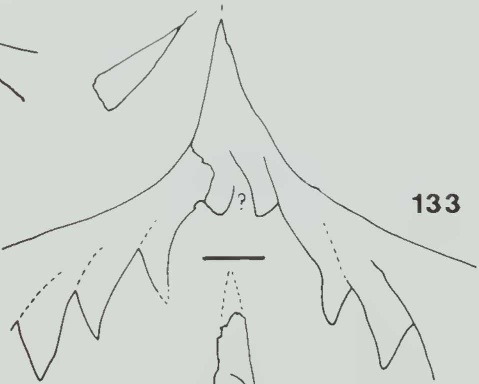

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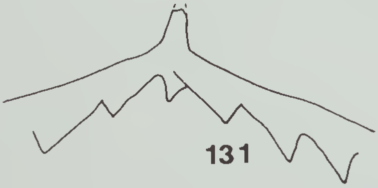

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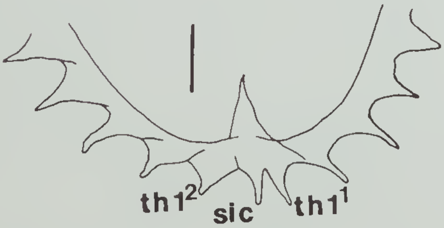

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gradually towards the distal extremities of the stipes, which are at about 1 cm or less. A short nema has been detected on several specimens, including the holotype.

Remarks. Harris and Thomas (1938a) gave a thorough account of the use of the species name *latus*, and of their reinterpretation of Hall's original description. Two puzzling features arise from the Harris and Thomas account. One is their doubt of the Hall thecal spacing figure of 14 in 10 mm, clearly confirmed as 14 in 10 mm by our work. The second is their statement that *D. latus* differs from *D. hirundo* in that the former has the greater width. It is our view that *D. l. latus* is nowhere near as robust at the proximal end, nor are the early thecae so dependent or long (cf., for example, our figures of the holotype of *D. latus* with Elles' figures of *D. hirundo*, 1933 fig. 12). There is, however, clearly some resemblance between *D. latus latus* and *D. suecicus* Tullberg and *D. praenuntius* Törnquist: the type specimens of *D. l. latus* certainly have a higher thecal count than either of the two Scandinavian species, but our specimens from Campbelltown (and, indeed, Harris and Thomas' (1938a) "concept" of *D. latus*) are obviously extremely close to *D. suecicus*. For the present we prefer to keep *D. l. latus* intact until further revision of extensiform didymograptids has taken place. *D. suecicus robusta* Monsen (1937) seems similar in many respects to *D. l. latus* but differs on thecal spacing.

Didymograptus latus aequalis
Harris and Thomas

Plate 24 figs b–d: text-figs 124, 136

Didymograptus latus var. *aequalis* Harris and Thomas, 1938a: 75, pl. 2 figs 19a, b; pl. 4 fig. 18.

Type specimens and other material. Harris and Thomas (1938a) did not designate a type but there are two syntypes (=cotypes of Harris and Thomas), P34971 (41334) and P31994 (41335). Both are from the Bendigonian (Be2) of the NW corner of allotment 30A, sect. II of the Parish of Campbelltown: the first was figured by Harris and Thomas as pl. 2 fig. 19a, and the second as pl. 2 fig. 19b, pl. 4 fig. 18. We designate P34971 (fig. 136 and plate herein) as lectotype. We have examined about fifteen other specimens from Be2 in the collections of the Museum of Victoria; Thomas (1960a) gives the total range as Be1–Be2 (the same as *D. l. latus*; O.P. Singleton, pers. comm.) but in the collections we could only identify specimens from Be2.

Diagnosis. Extremely robust extensiform didymograptid, slightly reflexed to horizontal; maximum dorsoventral width 3.8–4.0 mm at th1^1 and th1^2; thecae inclined at 60°+ proximally and 40°–60° distally; stipes up to 4cm; thecal spacing 7–8 in 10 mm.

Description. The sicula may be as much as 4.5 mm long in some specimens. The early development of thecae is not known but there are robust shoulders along the sides of the sicula as the stipes leave it (fig. 124). The sicula curves, presumably towards the second thecal series. Early thecae may have a length of 3.5–4.0 mm and th1^1 and 1^2 grow downwards at a very high angle, certainly 70° in some specimens. However, by th5 the angle of thecal inclination has fallen to well below 60° in most specimens. The stipes are usually 2–3 cm long and there is a gradual loss of dorsoventral width away from the most proximal regions where it may be as high as 4 mm. Thecal overlap is around three-quarters but the thecae are more or less straight, simple dichograptid, with only the most proximal parts of each theca inclined at a lower angle to the stipe axis.

Remarks. D. l. aequalis is closer in general dimensions to *D. hirundo* than *D. l. latus*, but the sicula and first pair of thecae are certainly much longer in *D. l. aequalis*. Nor do the thecae have quite the same dependent aspect and concave ventral surface. In both these respects *D. l.*

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Figure 136. *Didymograptus latus aequalis* Harris and Thomas, lectotype, P34971. Scalebar 1 mm. ►

Figures 137, 138. *Sigmagraptus laxus* T.S. Hall, respectively from Museum of Victoria cabinet 328, drawer 10; and holotype P32141A. Scalebar 1 mm.

Figure 139. *Sigmagraptus laxus* (T.S. Hall), P34796, probably from Bendigo. Scalebar 1 mm.

Figure 140. *Sigmagraptus crinitus* (T.S. Hall), same slab as C2200 (tray 2) near a single *Phyllograptus* sp. and ventral side of a stipe of *P. fruticosus*. Scalebar 1 mm.

Figures 141, 142. *Praegoniograptus timidus* (Harris and Thomas): 141, P83314, paratype; 142, P83315 on the same slab. Scalebar 1 mm.

Figure 143. *Praegoniograptus clonograptoides* (Harris and Thomas), holotype, P32169 distal thecae of terminal stipe, shaded area is heavier sclerotisation, black threads visible are possible stolons. Scalebar 1 mm.

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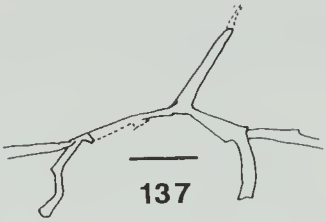

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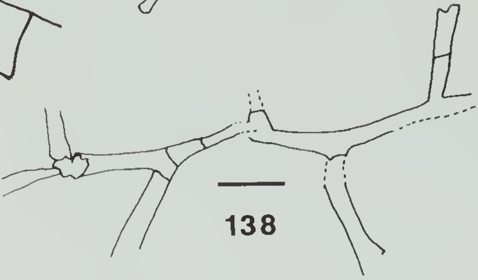

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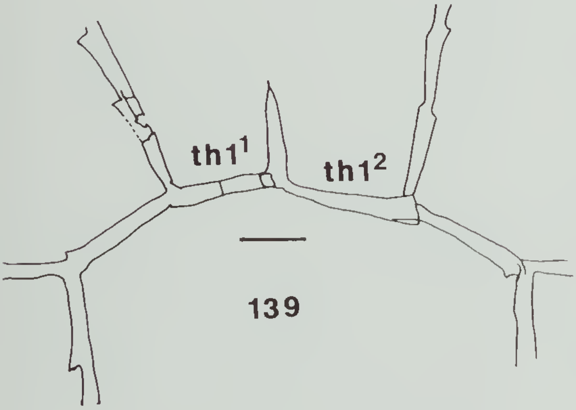

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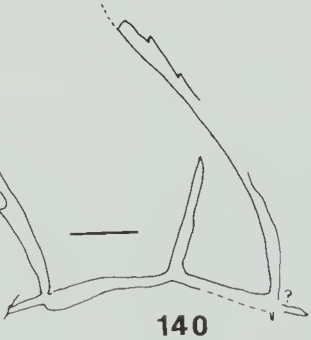

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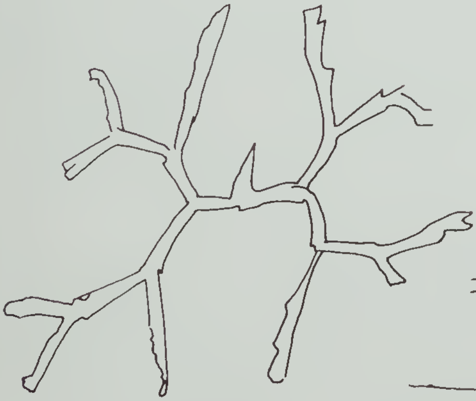

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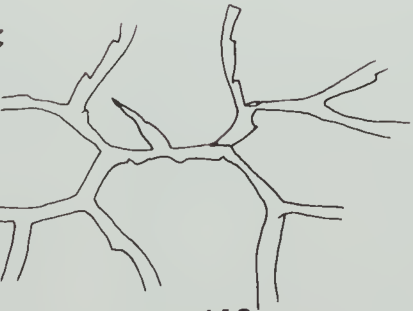

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aequalis is closer to *D. praenuntius* Törnquist, but this latter species, like *D. hirundo* has a much closer thecal spacing than *D. l. aequalis* 12 in 10 mm cf. 7–8 in 10 mm. Victorian forms usually recorded as *D. praenuntius* or *praenuntius-hirundo* transients (e.g. Harris and Thomas, 1940) are actually rather different to *D. l. aequalis* in being narrower and with a much higher thecal spacing. That form recorded by Elles (1933: fig. 11) is quite similar (except in thecal spacing) to *D. l. aequalis* but is not certainly referable to *D. praenuntius* in our view. It is possible that at some Be2 localities *D. l. latus* may grade into *D. l. aequalis* suggesting that the origin of the latter, later subspecies may lie in the former.

Didymograptus dilatans T.S. Hall

Plate 22 figs d, e; text-figs 129–131

Didymograptus dilantans T.S. Hall, 1914: 107–108, pl. 17 fig. 10.—Harris and Thomas, 1940a: 131–132, pl. 1 figs 7a–c; pl. 2 figs 9a–b.

Type specimen and other material. Holotype, P31978, from the Bendigonian (Be3) of Daylesford; other specimens including P32072 (42565) figured (Harris and Thomas, 1940a: pl. 1 fig. 7a, pl. 2 fig. 9) and P32073 (42566) figured by Harris and Thomas, 1940a: pl. 1 fig. 7b) from allotment 20, section II, Parish of Campbelltown, Bendigonian (Be2). The stratigraphic range of the species was given by Thomas (1960a) and modern workers (O.P. Singleton, pers comm.), as Be2–Be3 and this is confirmed by our own examination of collections.

Diagnosis. Stiffly declined didymograptid stipes diverging at 140°–160°, commonly the former; thecal spacing 7–9; distal width 1.8–2.0 mm maximum; thecae inclined at 20°–30° proximally and nearer the latter figure distally.

Description. The sicula is conspicuous, elongate conical with a length of 1.7 mm. It has a pronounced, rounded, apertural process and the sicular aperture faces towards the second thecal series. Details of development have not been seen, but the slim conical shape of the sicula may mean that th1^1 originates lower down the sicula than on those didymograptids of the preceding descriptions. The thecal spacing may be as low as 7 in 10 mm proximally or as high as 9. In most specimens the thecal spacing decreases distally. The stipes may occasionally be upwards of 5 cm long and the increase in dorsoventral width is gradual from a proximal 0.6–0.7 mm to a distal 2.0 mm maximum. The thecae throughout are simple, dichograptid low angled tubes, the apparent denticulation of which is probably caused by flattening.

Remarks. In our material *D. dilatens* resembles, superficially, only *D. adamantinus* which has a quite different arrangement of proximal thecae. We are uncertain whether the subgenus *D.* (*Acrograptus*) has any real value: in its horizontal or gently reflexed stipes *D. dilatans* is similar to *D. asperus* or *D. procumbens*. Thus the only feature of distinction is the gentle declination of the stipes. It would not surprise us to learn that elsewhere, if not in this one species, there is every gradation between horizontal and declined forms.

Sigmagraptinae Cooper and Fortey, 1982

Original diagnosis. Sicula long and slender, th1^1 originating high on ventral side: th1^1 leaves sicula at right angles but above the level at which th1^2 does the same on the opposite side; protheca of th2^1 very slender, inconspicuous; dichotomies up to 10 or more orders; terminal stipes 3–20 or more; dichotomies consecutive or delayed; branching progressive or mono-progressive; development isograptid, dextral.

Remarks. It is clear from the above diagnosis that the subfamily Sigmagraptinae was erected on more refined information than many other dichograptids, but this has to some extent been remedied by our reappraisal of some aspects of the subfamily Dichograptinae (see above). In defining the sigmagraptines Cooper and Fortey (1982, leant heavily on the early development, thecal type and rhabdosomal stipe aspect; and less so upon whether the proximal plan was didymograptid, tetragraptid or dichograptid (and, in effect, less on the branching pattern). Figure 144 is a summary of their sigmagraptine genera with the several variables included.

Sigmagraptus Ruedemann, 1904

Type species. Sigmagraptus praecursor Ruedemann, 1904.

Diagnosis. Sigmagraptines with one order of progressive branching, plus many orders of monoprogressive branching, the undivided stipes lying alternately on opposite sides of main axis formed by dicalycal thecae; main axis commonly of alternating long and short units between "lateral" stipes; dichotomies consecutive throughout rhabdosome; sicula long and slender; 1^1 originates high on ventral side of sicula; thecae generally slender.

Remarks. We are inclined to support the opinion of Cooper and Fortey (1982) concerning Rickards' (1974) interpretation of the development of *S. praecursor* from Quebec. The early parts of

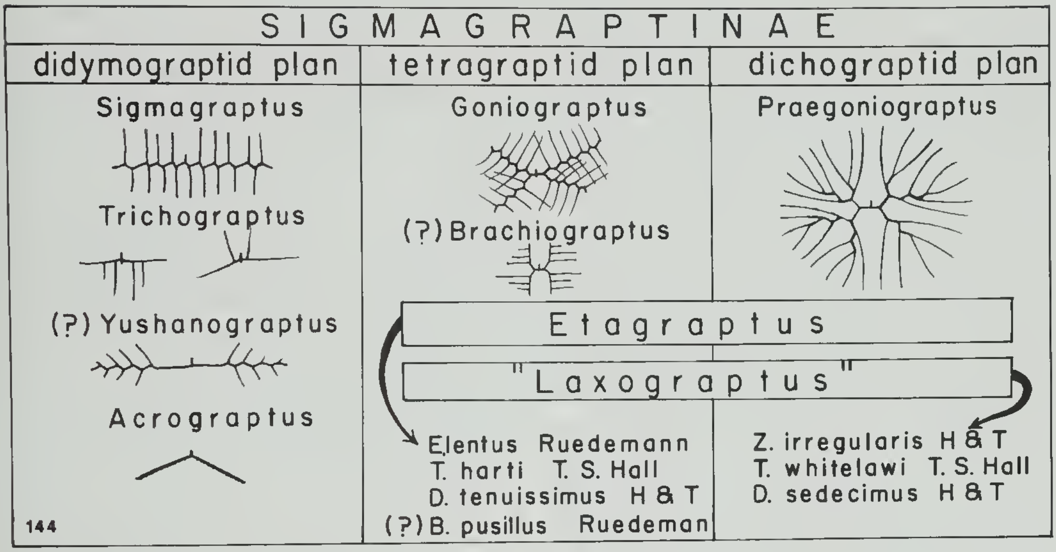

Figure 144. Suggested classification of the subfamily Sigmagraptinae, modified slightly after Cooper and Fortey (1982).

th2^1 are so very slender and inconspicuous even in the isolated material available to Cooper and Fortey, that it might be indiscernible in most pyritised and almost all flattened material. It seems likely, therefore, that the *artus* development attributed to the Quebec specimens is incorrect. There does remain an element of doubt about this conclusion. In the first place, the strange proximal spines detected by Rickards (1974) were not seen in the Spitsbergen specimens, yet they occur in Australian material (fig. 155 albeit rarely in *S. laxus*; so that the specific identify of the Spitsbergen (or Quebec) specimens cannot be held as altogether sure. Secondly, the branching pattern of the stipes for the Quebec material does seem to us to be different from that described by Cooper and Fortey for their material which is the same as described for *Goniograptus* by Jaanusson (1965). Again, it is quite possible that in such material Rickards (1974) was unable to discern the crucial early growth of the thecal tubes; yet against that is the very high angular change of growth direction seen where the side branch leaves the main stipe (see Rickards, 1974: fig. 2, particularly 2G and H). It is not impossible that the Quebec specimens are of a different species, with different development, but if this is so it could call into question what we consider a very reasonable and likely general interpretation of Cooper and Fortey (1982) that the *artus* stage of development probably evolved from the *Isograptus* stage.

Sigmagraptus laxus (T.S. Hall)

Plate 27 figs b, c; text-figs 137, 138, 139, ?155

Goniograptus laxus T.S. Hall, 1914: 113, text-fig. 4.

Sigmagraptus laxus.—Benson and Keble, 1935: 272–273, plate 32 figs 10, 11, 12.—Cooper, 1979: 57, plate 4g; text-fig. 22.

Type and other material. Holotype P32141A, B from Bendigo (Geological Survey of Victoria loc. 38BO), 100 m NW from Garden Gully United Shaft, collected 1910 by H. S. Whitelaw, figured by T.S. Hall, 1914, text-figure 4; upper Bendigonian. Numerous specimens from the upper two divisions of the Bendigonian and from the Chewtonian.

Diagnosis. Sicula probably at least 1.5 mm; funicle about 2.5 mm; most rhabdosomes begin with a downward growing pair, one each side of the sicula (less commonly an upward growing pair); in some specimens two thecae may be developed each side of the sicula before the first lateral stipes; rhabdosome up to 6 cm wide and may be 6 cm wide in the bilateral plane; thecae 10 in 10 mm on lateral branches.

Description. The very proximal end of the holotype is not all that well preserved but we have uncovered part of the sicula: this, and other specimens strongly suggest that the sicula is not in exactly the same plane as the rhabdosome as a whole. Less than 1 mm of the sicula is seen on the holotype, but it is the apertural part. Other specimens suggest that the sicula is 1.5 mm long. Th1^1

and th1^2 leave the sicula low down but at quite different levels (fig. 138) and our impression is that th1^1 leaves at a higher level than th1^2 and its aperture is fractionally nearer the sicular aperture than that of th1^2. The funicle on the holotype is about 2.5 mm, the free portion of th1^1 being about 1 mm. The first pair of side branches are downward growing, with respect to the sicula, in most specimens, but a few have been seen in which they grow upwards.

There may be some variation in the proximal end characters. Thus one specimen is a proximal end on the same slab as an undoubted, large *S. laxus*. It seems to differ from the holotype in that two thecae are developed, possibly on the first series, before the normal downward growing branch. It is not clear whether the other series has 1 or 2 thecae before the downward growing branch. It seems to be the same species and the funicle and other measurements are the same as on certain *S. laxus* specimens.

A second specimen (fig. 155), on a slab labelled by R. A. Cooper as *S. laxus*, is also one of the very few exhibiting the kind of pseudovirgula spine described by Rickards (1974), although few suitable early growth stages, sufficiently well preserved, are available for study. The mature *S. laxus* on this slab has an upward growing first pair of branches and the funicle is of the same length as the holotype, unlike that of fig. 155 which is 6 mm. The latter may not be referable to *Sigmagraptus laxus*.

The overall rhabdosome size is some 60 mm wide by 30 mm+ wide, and individual lateral branches commonly exceed 15 mm. A few specimens, however, have a height in excess of 60 mm for the normal 60 mm width; that is, individual lateral branches may exceed 30 mm. We are inclined to regard these as the fully mature rhabdosomes.

Although Hall claimed that thecae were not visible they are, in fact, moderately clear on the holotype, numbering about 10 in 10 mm on the lateral branches. The two main stipes do not have a pronounced zig-zag, each successive monoprogressive dichotomy diverging but 30° from the last (or 15° from the stipe axis). All zig-zags tend to lessen distally. Up to 20 dichotomies have been observed on the main stipes.

The dorsoventral stipe width of the two main stipes is up to 0.25 mm near the thecal apertures, but often only 0.20 mm. The lateral branches tend to be narrower still and in the most distal extremities of the stipes 0.10 mm or even less is more usual.

Spacing of the nodes changes along the main stipes. The first node of the first series is some 1.0–1.1 mm from the sicula, subsequent nodes quickly reaching 1.5 mm (by nodes 7–9), and more distally the spacing changes to 2.0 mm. Not only does the zig-zag angle lessen in these latter areas, but the lateral branches need not be at 90° to the main stipe, and may tend to lean distally.

The holotype has what is almost certainly an abnormality towards the distal end of the first series main stipe (plate 27, fig. b). The 14th node, instead of continuing the general line of the main stipe, turns at right angles and grows by monoprogressive dichotomies for a further 5 or 6 nodes producing lateral branches as usual and superficially resembling a *Goniograptus*. It can be established that this is not a preservational feature for if the upwards growing portion were bent backward to the general direction of main stipe growth it would result in two downward (or two upward) growing lateral branches adjacent to each other. Node divisions on this abnormal stipe also revert to a closer spacing (1.1–1.4 mm) at first before increasing to 1.5 mm, but never to the full 2 mm of the normal main stipe: this strongly suggests that it represents an aberrant and delayed attempt to produce a new main stipe. This phenomenon has not been seen on any other specimens.

Considered in dorsal view, the lateral branches may be given off first to one side of the zig-zagging main stipe, and then to the other. In the holotype the first cladium of the first series seems to grow downward to the left.

Remarks. Unlike Cooper and Fortey (1982) we do not regard *S. laxus* as synonomous with *S. praecursor* Ruedemann. It differs consistently in that the dichotomies are closer spaced throughout the rhabdosome, although showing the same proportion of distal increase in spacing. The dorsoventral stipe width is also less, and the thecae slightly more closely spaced (10 in 10 mm, cf. 7–9 in 10 mm). In terms of these dimensions *S. praecursor sensu* Rickards (1974) compares closely with Ruedemann's species and with the material described from Spitsbergen by Cooper and Fortey (1982) and these, and Ruedemann's originals, can be contrasted with the T.S. Hall holotype and numerous topotypes.

Whether the upward or downward growing first pair of lateral stipes has any significance we are not certain. In the Quebec material most of the first pair grow upwards, with a minority (often on particular bedding planes) growing downwards. In the Bendigonian specimens the majority of first pairs grow downwards, but several have been recorded with an upward disposition. The Cooper and Fortey specimens have the first pair of lateral branches upward growing as far as is known, as do the Ruedemann originals.

As stated earlier we do not regard *S. praecursor sensu* Rickards (1974) as having with certainty the isograptid development of the Spitsbergen specimens, although on balance we think it likely. However, *S. laxus* does have the silhouette appearance of a typical sigmagraptine as defined by Cooper and Fortey (1982) and this in itself lends further support to their development model.

The manner in which the lateral branches may originate first on one side of the main stipe, then on the other, recalls *S. praecursor sensu* Rickards (1974) and the genus *Pterograptus* where the feature occurs more strikingly.

Sigmagraptus crinitus (T.S. Hall)

Plate 27 figs a, d, e; text-fig. 140

Goniograptus crinitus Hall, 1914: 111–112, text-figs 2, 3.—Benson and Keble, 1935: 272.

Sigmagraptus crinitus.—Harris and Thomas, 1939: 59, fig. 14.

Sigmagraptus? crinitus.—Cooper and Fortey, 1982: 265–266, plate 2 fig. 4.

Type and other material. The holotype figured by T.S. Hall appears to be missing, and it had received neither a Mines Department nor a Museum of Victoria registration or number. This is presumably why Harris and Thomas (1939) figured a different specimen (also figured herein). Fortunately there can be no doubt that this specimen is conspecific with the Hall type. T.S. Hall did not give the type locality of the original material but in 1914 (p. 111) he stated that he earlier recorded *Goniograptus? crinatus* as *Thamnograptus* which he said does not occur in the Bendigonian or Castlemainian. The earliest record of *Thamnograptus* is by Hall (1893: 1) from Lost Gully between Chewton and Fryers, near Castlemaine. We have found no other records of *Thamnograptus* by Hall between 1893 and 1914 and since his 1914 paper includes several specimens from the region of Castlemaine it is possible that the type locality of *Sigmagraptus crinatus* is Lost Gully. Age Upper Bendigonian to Chewtonian, a number of well preserved, more or less complete, large rhabdosomes, and numerous fragments.

Diagnosis. Very large *Sigmagraptus* with extensive secondary thickening; branching nodes 1.2–3.0 mm, increasing distally; distal dorsoventral lateral stipe width 0.2 mm; thecal spacing on lateral stipes 10 in 10 mm; spacing of branching nodes alternately long and short.

Description. The rhabdosome width along the main stipes is of the order of 12 cm, and the width at right angles to this some 15 cm. The two main stipes have every appearance of being secondarily thickened, and no proximal ends are known which grow initially at this degree of robustness. In places the thickening forms distinct blobs or membranes. Near the proximal end the width is up to 1 mm, but it does not obscure the main stipe apertures, as implied by Hall, and these can be detected at the branching nodes quite frequently: thecal spacing is, of course, that of the branching nodes, and there is no evidence of more than one theca between nodes. However, such a statement of thecal spacing takes no account of the possible isograptid, dextral mode of development, with intercalatory non-dicalycal thecae (which would, in effect, about double the thecal spacings though thecal spacing figures in such cases are meaningless if branches occur so frequently).

Branching nodes are spaced at 1.2 mm intervals near the proximal end and at 1.5–2.0 mm intervals slightly more distally, reaching 2.0 mm–2.5 mm at about nodes 8–11. By about the fifteenth node spacing may be 3 mm. However, these figures obscure an interesting feature, namely that, roughly speaking, the distances between nodes are alternatively long and short, as noted by Harris and Thomas for some other species. On the gently declined and reflexed specimen (usually the main stipes are horizontal) the upward branches of the first thecal series are preceded by a long division, whilst in the second main stipe series the opposite obtains.

The most distal branches have a dorsoventral width of less than 0.20 mm and a thecal spacing around 10 in 10 mm, although on none of the specimens is the thecal spacing easy to see. As with the mature specimens proximal ends associated with them have the first pair of lateral branches directed either upwards or downwards.

Proximal ends associated with mature rhabdosomes (fig. 140) are almost certainly referable to *S. crinitus*. They show standard sigmagraptid development in silhouette and despite the extremely slender nature of the sicula and thecae it is clear that $th1^1$ and 1^2 leave the sicula at slightly different levels. The sicula is fully 2 mm long.

Remarks. There is clearly a great similarity of this species to *S. laxus*, and they seemingly differ only in that *S. crinitus* shows extensive thickening of the two main stipes. Otherwise the dimensions and development are very close. *S. crinitus* although overlapping in time is essentially a later form and pending further work we suggest leaving it as a separate taxon.

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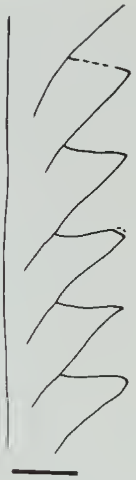

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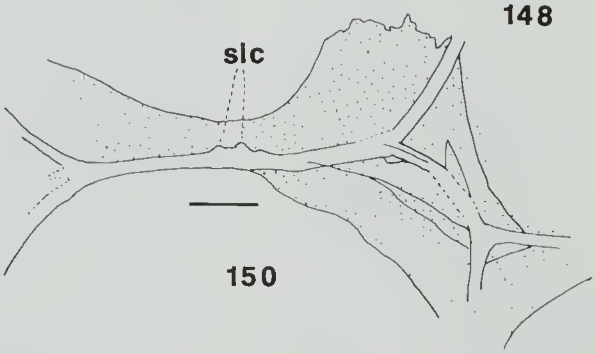

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Figure 145. *Goniograptus alternans* Harris and Thomas, distal thecae on stipe following an 8th monoprogressive node, holotype, P14619. Scalebar 1 mm.

Figures 146 and 150. *Goniograptus palmatus* Harris and Keble: 146, distal thecae of holotype, P26448A; 150, funicular region of holotype, P26448B, counterpart of specimen originally figured as holotype; shaded area shows position of web/s. Scalebar 1 mm.

Figure 147. *Goniograptus velatus* Harris and Thomas, branching division on holotype, P34849. Scalebar 1 mm.

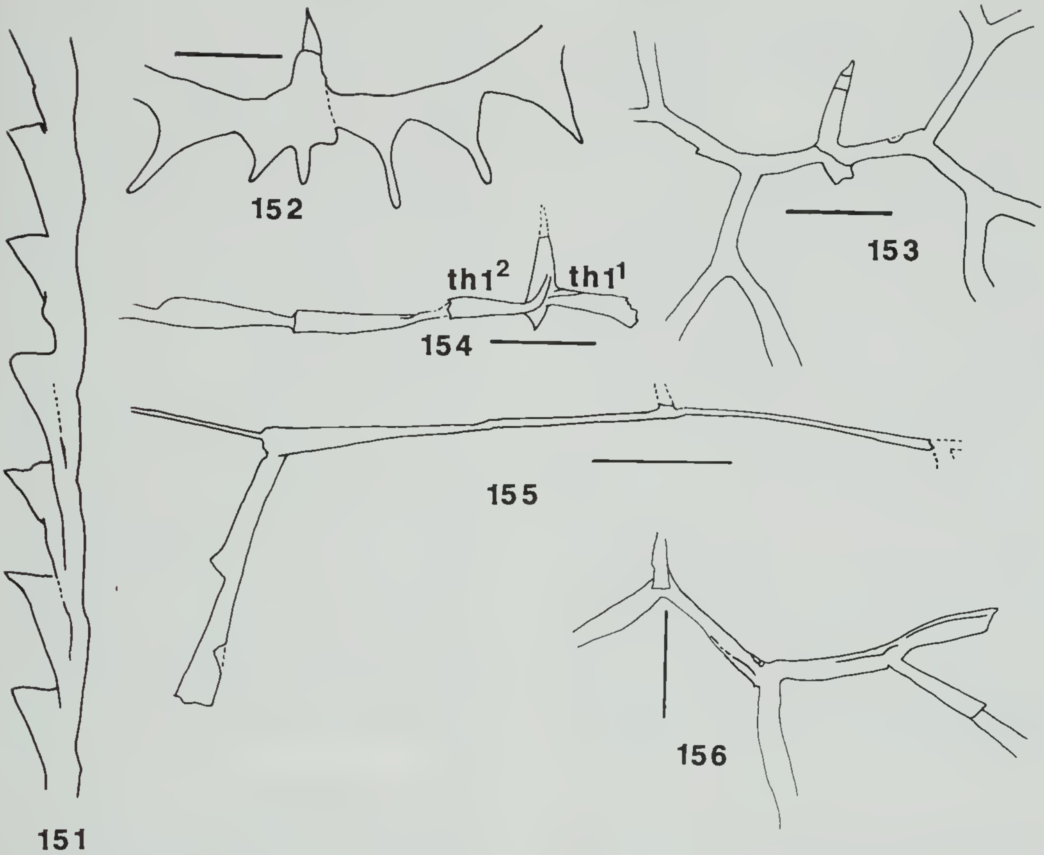
Figure 148. *Goniograptus tumidus* Harris and Thomas, distal thecae of holotype, P32168 (42526). Scalebar 1 mm.

Figure 149. *Goniograptus thureaui thureaui* (McCoy), distal thecae of holotype, P12215. Scalebar 1 mm.

A note on **Sigmagraptus yandoitensis**

This rare species was described by Harris and Thomas in 1938a to encompass forms having, seemingly, several thecae between dichotomies unlike other species of *Sigmagraptus* where only one theca spans the monoprogressive divisions. Unfortunately the type (41312) from locality 1 at Campbelltown "good bed" appears to be missing and there are no specimens at all in the Museum of Victoria. However, Dr O.P. Singleton has kindly loaned us a specimen from the University of Melbourne (F6058), probably identified by Thomas originally, and labelled "Allot. 30A, Campbelltown, Victoria" "Bendigonian-Be2". It is presumably not the counterpart of the type specimen because the funicle length is slightly different.

What is unusual about this species (if F6058 is correctly referred to it, as seems likely) is that the inter- node spacing *decreases* distally, the exact opposite of any other *Sigmagraptus* species or specimens that we have examined. Furthermore the inter-node spacings are quite long (4.5 mm



Figures 151, 154. *Tetragraptus* (?*Tetragraptus*) *whitelawi* T.S. Hall: 151, distal thecae, probably of holotype; and proximal end of holotype P14287A and B (9761).

Figure 152. *Didymograptus hemicyclus* Harris, proximal end of lectotype, P13797 (it is far from certain that apertural processes are as rounded as shown).

Figure 153. *Goniograptus macer* T.S. Hall, proximal end of holotype, P32142A.

Figure 155. ?*Sigmagraptus laxus* (T.S. Hall), P83344 from School Reserve, Fryerstown.

Figure 156. *Goniograptus macer* (T.S. Hall), 1st, 2nd, 3rd and terminal (order) stipes on P42707 from the Chewtonian (Ch2) showing possible overlap of thecae.

initially in F6058, reducing after 10 dichotomies to 2 mm) and may well have several thecae involved: strangely this is more likely distally than proximally where the thecal tubes are very elongate. The funicle itself is 6 mm long and there may well be two thecae in the first part of the second thecal series. The sicula is not quite central in the funicle, being 2.4 mm from the left hand dichotomy (as viewed) which we think is the one leading from th1^1. Of the sicula 1 mm is visible and it may not be much longer than that, though this is uncertain. The stipes seem to become slightly more robust distally both on the lateral branches and on the zig-zag stipes. Clearly we still need more information about this species for if it has the characters described above then it does raise some doubts about the present definition of the subfamily Sigmagraptinae (see also Cooper and Fortey, 1982).

Goniograptus McCoy, 1876

Type species. Goniograptus thureaui McCoy, 1876: 129.

Remarks. The question of the similarity of *Goniograptus* to *Sigmagraptus* and some other sigmagraptine genera is discussed elsewhere in this paper but we feel that these genera should retain their integrity at least for the time being.

Goniograptus thureaui thureaui (McCoy)

Plate 28 figs a–e; text-figs 10–12, 57, 149

Didymograpsus thureaui McCoy, 1876: 129, unnumbered text fig.

Graptolites (*Didymograpsus*) *thureaui*.—McCoy, 1877: 39–40, pl. 50 figs 1–4.

Goniograptus thureaui McCoy and *Goniograptus thureaui* McCoy var. *postremus* Ruedemann, 1904: 621–624, pl. 6 figs 1–14, (non 15) text-figs 37–38.

Goniograptus thureaui.—Harris and Thomas, 1939: 55, figs 1a, b.—Cooper, 1959: 56, pl. 5d.—Williams and Stevens, 1988: 81, 83, pl. 25 figs 1, 2, 4, 5, 7; pl. 26 figs ?16, ?17; pl. 31 fig. 7; text-figs 76A–D, F–H.

Goniograptus thureaui var. *inaequalis* Harris and Thomas, 1939: 56, fig. 3.

(Further references for consideration in such a synonomy can be seen in Ruedemann, 1904 and 1947, and Williams and Stevens, 1988).

Type material. Lectotype selected herein, P12215, from the lower Ordovician of Bendigo, Victoria, figured McCoy (1876); syntype P12200; both from "black and red slates of the Llandeilo flag age of the Bendigo goldfield, Sandhurst, Victoria. The holotype of *G. t. inaequalis* Harris and Thomas (1939), P34844 (42544), regarded by us as a junior synonym of Hall's species, is from the Bendigonian (Be1) of the "good beds" allotment 16A, sect. H, Parish of Campbelltown. Numerous specimens in the collections of the Museum of Victoria.

The other specimens figured by McCoy (1877) are:

P12216 (McCoy, 1877: pl. 50 fig. 3) from locality Bd2 = branch of Parwan Creek, approx. 3.6 km SE of Ingliston (Harris and Thomas, 1939, state that this specimen is from a higher horizon and is probably more closely allied to *Goniograptus speciosus* T.S. Hall. They also stated that the specimen is lost).

P12214 (McCoy, 1877: pl. 50 fig. 4) described by McCoy as an "allied form" – i.e. presumably not *G. thureaui*. From the lower Ordovician at Bendigo.

Specimens of *G. thureaui* figured by Harris and Thomas (1939) are:

P34846 (42521) (fig. 1a) and P34847 (35817) (fig. 1b), both from the "good bed", allot. 16A, etc., Parish of Campbelltown.

There is one other specimen of *G. thureaui*, P34861 (1530), figured by David (*Geology of Australia*), pl. 15 fig. g, from Windmill Hill, New Chum Line, Bendigo.

Diagnosis. Rhabdosome may exceed 70 mm in diameter, roughly quadrate; number of peripheral stipes in mature specimens 18–48; branching nodes 3–11; dorsoventral distal stipe width up to 1.5 mm and thecal spacing 8–9 in 10 mm throughout the rhabdosome; sicula 1.2–1.3 mm long; funicle 3 mm long; second order stipes 1.5–2.0 mm long; distal thecae high, isolate, clonograptid-like.

Description. The rhabdosome as a whole may have a diameter commonly of 5 cm, occasionally 7 cm, but a few specimens do suggest a much greater diameter. There is a generally quadrate appearance caused by the fact that the early lateral thecae grow to a considerable length presumably keeping pace with growth of the main stipe and later lateral branches: what growth stages are available support this interpretation. The number of stipes developed at the periphery varies from 18–48 in the material we have examined. Each of the four monoprogressive stipes after the initial tetragraptid template, may have as many as 11 nodes or as few as 3, the latter resulting in smaller colonies: that each is a mature colony is proved by the presence of a terminal division producing a pair of undivided (?lateral) stipes. Despite this variation in rhabdosome size and number of peripheral stipes the dorsoventral width and thecal spacing are comparable in similar parts of the rhabdosome: respectively up to 1.5 mm distally and 8–9 thecae in 10 mm throughout the rhabdosome. The dorsoventral width is never easily seen near the centre of the rhabdosome because dorsal and ventral views are almost always preserved and unless a stipe is twisted a true profile is not seen. Many specimens show the stipe bent over in true profile towards the periphery of the rhabdosome.

On the holotype the sicula is less than 1.5 mm, possibly of the order of 1.2–1.3 mm: we could not fully uncover it, and it is clearly not in the same plane as the rest of the colony. The funicle is some 3 mm long; and the second order stipes only 1.5–2.0 mm. Th1^1 and 1^2 leave the base of the sicula at different levels, probably with th1^2 at the lower level. There is no virgella. The distal thecae are rather high, isolate thecae of dichograptid/clonograptid type (fig. 149).

Remarks. We regard the holotype *G. thureaui inaequalis* as an abnormal specimen of *G. t. thureaui*. It is the only specimen known, and whilst it is true that *G. t. thureaui* is remarkably constant in the number of stipes in each quadrant and, therefore, the number of nodal divisions along the four main monoprogressive stipes, there is some variation. The lectotype of *G. t. thureaui* has 11 nodes in each quadrant (probably), that is 12 or 13 stipes, giving a total of 51 around the periphery of the colony; but P34861 (1530) has 22 stipes; P34846 (42521) 36 stipes; P34847 (35817) 32 stipes; each being complete in the sense that nodal division had ceased and the terminal, unbranched pair of stipes is demonstrably present. The type of *G. t. inaequalis* has only 17 stipes but is otherwise of typical appearance and has identical thecal spacings, nodal spacings, and funicular size: for some reason development was foreshortened. Nor can the irregular distribution of stipes per quadrant (6, 3, 4, 4) be taken as diagnostic: it simply indicates that one monoprogressive series achieved further divisions (in the "first series") testifying to the abnormality of the specimen. Furthermore, other specimens of *G. t. thureaui* do show some variation per quadrant: P34861 (1530) has 5, 6, 5, 6, (going clockwise around the colony).

Goniograptus tumidus Harris and Thomas

Plate 31 fig. d; plate 32 figs a, b; text-figs 13, 14, 148

Goniograptus tumidus Harris and Thomas, 1939: 57, figs 7a, b.

Type specimens and other material. Holotype, P32168 (42526), from the Bendigonian (Be1) of the "good bed" allotment 16A, sect. II, Parish of Campbelltown, collected by T. Smith. Paratype P34848 (42527) from allotment 20, Section 11, Parish of Campbelltown, Bendigonian (Be2) and other specimens from Be1 and Be2.

Diagnosis. Goniograptid with unusually long (up to 7 cm) peripheral stipes and few monoprogressive divisions, coupled with a large rhabdosome size of some 14 cm.

Description. The rhabdosome may reach a diameter of some 14 cm, with as few as 11 or as many as 18 peripheral stipes, with 1 progressive dichotomy after the funicle and up to 3 monoprogressive dichotomies (including terminal dichotomy). The distal dorsoventral stipe width is about 2 mm, and the thecal spacing 7–8 in 10 mm. The thecae are high, almost isolate, dichograptid thecae with a free ventral wall inclined to the stipe axis at 40°. The funicle is 3 mm long, and the second order stipes 1.4–2.0 mm. Thecae are visible after the first progressive dichotomy where the dorsoventral width is already at least 1 mm, but it is not clear that they are in true profile. The latest formed peripheral stipes are all established within 10 mm of the sicular region and may reach a length of 6–7 cm in the case of those formed nearer the proximal end. The number of stipes in one quadrant may be as few as two (P34838 for example), but no specimens have been seen having fewer than eleven stipes in total.

Remarks. The paratype P34848 (fig. 14) resembles species of *Dichograptus*. With the loss of three stipes the result would be remarkably like *Dichograptus octobrachiatus*, not only in rhabdosomal size and stipe dimensions, but in the shape of the thecae.

G. tumidus is unlike any other goniograptid in that although the rhabdosome is one of the largest of the genus the number of monoprogressive dichotomies is few and the peripheral stipes are unusually long.

Goniograptus velatus Harris and Thomas

Plate 32 fig. b; text-fig. 147

Goniograptus velatus Harris and Thomas, 1939: 57, figs 8, 9.

Type material. Holotype, P34849 (42523) figured by Harris and Thomas (1939: fig. 8) from the Bendigonian (Be2) of allotment 30A, sect. II, Parish of Campbelltown, collected T. Smith. The other figured specimen of Harris and Thomas (1939: fig. 9) provisionally referred to *G. velatus* is certainly that species.

Diagnosis. Heavily thickened funicle and stipes and, relatively, a small rhabdosome giving the impression of robustness and rapidly tapering stipes. One progressive dichotomy followed by up to 9 monoprogressive dichotomies; distal thecae dichograptid, numbering 8–9 in 10 mm.

Description. The overall rhabdosomal diameter would be about 9 cm, but no complete specimens are known. The stipes and proximal end are heavily thickened and no detail can be discerned except the funicle itself which may be about 3–4 mm long. Two of the (presumed) four main stipes are visible and one of these has 9 monoprogressive dichotomies indicating possibly as many as 34–40 stipes peripherally in the rhabdosome as a whole. The thecae in fig. 147 are fairly close to the proximal end, at the third monoprogressive dichotomy of one of the main stipes, and they are clearly of relatively simple dichograptid type, numbering 8–9 in 10 mm.

Remarks. The type specimen may be a thickened late growth stage of another species but we have been unable to match the dimensions with any described forms, and despite the paucity of information at present we are inclined to let the taxon stand.

Goniograptus alternans, Harris and Thomas

Plate 30; text-figs 9, 29, 145

Goniograptus alternans Harris and Thomas, 1939: 56, fig. 12.

Type specimens. Holotype, P14619 (42524), from the Bendigonian (Be2) of allotment 20, sect. II, Parish of Campbelltown. Several additional specimens in the collections of the Museum of Victoria.

Diagnosis. The largest known goniograptid with a diameter of over 300 mm, the first progressive dichotomies followed by up to 14 monoprogressive dichotomies, and as many as 47 peripheral branches; four monoprogressive stipes almost at right angles to each other; stipes up to 12 cm long; terminal stipe pairs up to 9 cm.

Description. The stipes are quite straight giving a remarkably symmetrical appearance to the whole colony. There is, in effect, a small offset caused by the 3 mm funicle, but otherwise the four main stipes are set at about 90° to each other. The monoprogressive dichotomies are proximally about 3 mm apart, and distally as much as 5 mm, but there is also a clear tendency for short monoprogressive stipes to alternate with longer ones: this is particularly conspicuous in the holotype. Distal thecae are spaced at 8–9 in 10 mm, and the distal dorsoventral width, mostly caused by the high, isolate thecae is up to 1.8 mm (fig. 145). The angle of zig-zag along the main stipes decreases distally.

Remarks. G. alternans is a highly distinctive form in its size at least, perhaps closest to *G. thureaui*. On close comparison with *G. thureaui* it must be admitted that all dimensions, and rhabdosome plan, correspond, and it would be exceedingly difficult to separate the two after a similar number of monoprogressive dichotomies. The nodes are further apart in *G. alternans* than in *G. thureaui*.

Goniograptus macer T.S. Hall

Plate 29; text-figs 15–17, 153, 156

Goniograptus macer T.S. Hall, 1899: 449, figs 9, 10.—T.S. Hall, 1914: 110, pl. 17 fig. 15.—Harris and Thomas, 1939: 56, fig. 4a, b.—Harris and Thomas, 1942: 365–366, pl. 1 figs 2, 2a; figs 1a–c.—Cooper, 1979: 55, plate 5c.—Lenz and Jackson, 1986: fig. 5B.

Goniograptus(?) *macer*.—Benson and Keble, 1935: 272, pl. 30 fig. 36; pl. 32 figs 6, 7.

Type material. Holotype P32142A and B (25500, 25501, counterparts) from locality H46 (T.S. Hall locality) of Bendigo, Victoria, collected J.O. Liddell (figured by Hall, 1899: fig. 9 and Hall, 1914: pl. 17 fig. 15). Numerous other specimens in the Museum of Victoria collections.

Other figured specimens in the type index are as follows:

P34850 (42533) from north of Ballark Pre-emptive Right, east branch of Moorabool River (Harris and Thomas, 1939: fig. 4a) (Bendigonian, Be4).

P34851 (42532) from Lost Gully, Chewton (Bendigonian, Be4) (Harris and Thomas, 1939: fig. 4b).

P42707 (45369) from allot. 41B, Parish of Campbelltown (Chewtonian, Ch2) (Harris and Thomas, 1942: pl. 1 fig. 2, 2A).

Diagnosis. Small, slender goniograptid with 1 or 2 monoprogressive dichotomies, as few as 10 stipes or as many as 16; thecae dichograptid numbering 8 in 10 mm, dorsoventral width 0.6–0.8 mm; rhabdosome approaching *Dichograptus* in appearance up to 80 mm in diameter.

Description. The sicula is conspicuous in the holotype although clearly set in a different plane to the stipes. It has a length of about 1.5 mm but is strongly curved towards what is probably the th1^2 side. Th1^1 and 1^2 leave the sicula fairly low down at a high angle (fig. 153), one being lower than the other: judging from the distances to the first dichotomies th1^2 is the lower of the two.

The rhabdosome has a characteristically sparse appearance with relatively few, thin stipes which are straight when well preserved but commonly bent and twisted in angular fashion.

A few specimens (e.g. P42707; (45369)) have one or more quadrants reduced to two stipes but the rhabdosome does not fully conform to *Dichograptus* in that in some quadrants limited monoprogressive dichotomy takes place. The holotype has two stipes in one quadrant, but three in each of the others, giving a total of 11 peripheral stipes.

Remarks. Some specimens are almost referable to *Dichograptus*. It is unlike any other *Goniograptus* species. There is a superficial resemblance of sparsely stiped specimens to *Brachiograptus* but in reality the orientation of these rhabdosomes is at 90° to *Brachiograptus* to achieve the same outline. *G. macer* differs from *Dichograptus tenuissimus* in having progressive dichotomies, but if the latter evolved from the former in the Chewtonian, then some morphological transition might perhaps be expected.

Goniograptus palmatus Harris and Keble

Plate 31 fig. c; text-figs 41, 146, 150

Goniograptus palmatus Harris and Keble, 1932: 45, text-fig. 5, pl. 6 fig. 5.

Goniograptus aff. *palmatus*.—Monsen, 1937: 193, pl. 6 fig. 4.

Type specimens and other material. Holotype, P26448A and B, part and counterpart (Harris and Keble's "cotypes") from the Chewtonian (Ch2) of Campbell's Creek, Castlemaine; figured Harris and Keble (1932) plate 6 fig. 5; text-fig. 5. A few specimens from Geological Survey of Victoria locality Ba 83 at a bend of the Loddon River at the mouth of Hit or Miss Gully, W of Vaughan, Victoria.

Remarks. We have illustrated *G. palmatus* because it is one of the few sigmagraptine to show web structures, which are irregular and probably at more than one level (fig. 41). Although it is a relatively late species, the thecae are quite high and aperturally isolate, recalling the clonograptid thecae of *Clonograptus* Group A described below.

Praegoniograptus gen. nov.

Type species. Goniograptus thureaui clonograptoides Harris and Thomas, 1939.

Diagnosis. Rhabdosome intermediate between *Clonograptus* and *Goniograptus*, with 6–7 main stipes, developed from up to 3 progressive dichotomies, dichograptid proximal template, and some monoprogressive divisions developed; general *Clonograptus*-like rhabdosomal aspect, and unbranched cladia not convincingly lateral.

Remarks. P. clonograptoides (Harris and Thomas) and *P. timidus* (Harris and Thomas) respectively from Be1 and Be4 are the only two species which we currently recognise in our new genus. Morphologically they are certainly intermediate between *Clonograptus* and *Goniograptus*: stratigraphically they occur at the same time as the earliest *Goniograptus* spp. It is possible that *P. clonograptoides* could have given rise to *G. thureaui*, but it is equally possible that it represents an offshoot, as seems likely in the case of *P. timidus*; which latter has indications of neotonous growth. *Praegoniograptus* differs from *Goniograptus* in having up to 3 progressive dichotomies, followed by limited monoprogressive dichotomies. *Goniograptus* has no more than 2 progressive dichotomies and no more than 4 main stipes.

Praegoniograptus clonograptoides (Harris and Thomas)

Plate 5 fig. f; text-fig. 19, 143

Goniograptus thureaui postremus Ruedemann 1904: (pars) pl. 6 fig. 15 (non pl. 6 figs 1–14).

Goniograptus thureaui var. *clonograptoides* Harris and Thomas, 1939: 55, fig. 2.

?*Goniograptus thureaui clonograptoides*.—Lenz and Jackson, 1986: Fig. 5A.

Type specimens. Holotype, P32169 (42529) from the Bendigonian (Be1) of the "good bed", allotment 16A, sect. II, Parish of Campbelltown.

Diagnosis. Goniograptus-like species with dichograptid proximal template; 29 peripheral stipes; 7 main stipes; 2–3 monoprogressive stipe divisions following 3 progressive dichotomies.

Description. The rhabdosome has a diameter of about 7 cm or a little more, has 29 peripheral stipes, and 7 main stipes, one not achieving the third progressive dichotomy typical of the other three or the four second order stipes. The funicle is approximately 3 mm long; the distal stipe dorsoventral width is 1.6 mm, and the thecal spacing distally 7–8 thecae in 10 mm. The thecae themselves are dichograptid but rather denticulate and isolate, the free ventral wall being at a relatively high angle to the stipe axis (fig. 143). Furthermore the metathecae seems thinly sclerotised in the holotype, whilst the dorsal margin and prothecal parts are more strongly sclerotised, dark brown in colour. The proximal dorsoventral width and thecal spacing cannot be deduced, but when the thecae are first seen in profile (plate 5 fig. f) they are clearly quite high and the dorsoventral width considerable. We suspect there is almost no change proximally. In some places a fine black thread is visible in the heavily sclerotised dorsal stipe wall. This may be part of a stolonal chain. There is no preserved trace of bithecae in the distal regions. The sicula is not visible on our material and the early development of thecae cannot be seen.

Remarks. There is a strong case for making Harris and Thomas' *G. t. clonograptoides* the basis of a new genus, for it is intermediate between *Clonograptus* on the one hand and *Goniograptus* on the other. Its probable important evolutionary position was recognised by Harris and Thomas (1939: 55) but they did not elucidate. The question was discussed more fully earlier; but stated another way, further progressive dichotomies on the main stipes of *G. t. clonograptoides* would make it, by definition, a clonograptid. Until now it has been considered a goniograptid of dichograptid proximal plan, whereas all other goniograptids have a tetragraptid template.

The distal thecae and stipe details (fig. 143) strongly recall those of some *Clonograptus* species, and it cannot be ruled out that the heavy sclerotisation of the dorsal parts, and the fine black thread sometimes visible, represents the stolothecal and stolon system. The thecae shown in fig. 143 differ from the distal thecae of *Clonograptus persistens* (fig. 37) in that they are larger, more isolate, and perhaps are more suggestive of earlier clonograptid thecae than those like *C. persistens* and *C. trochograptoides* which have more truly dichograptid thecae.

Praegoniograptus timidus (Harris and Thomas)

Plate 5 figs a–c; text-figs 20, 141, 142

Clonograptus timidus Harris and Thomas, 1939: 58–59, figs 10a–c.

Type specimens. Holotype P32165 (42535) figured by Harris and Thomas (1939: fig. 10a) and three paratypes, P83313 (Harris and Thomas 1939: fig. 10b), P83314 (1939, fig. 10c) and P83315, all on same slab, N of Nell Gwynne Mine, Bendigo. Age Bendigonian (Be4). Other fragmentary specimens are on the type slab and as far as we are aware these are the only specimens known, even though Harris and Thomas (1939) claimed it to be abundant. However, we have seen a few specimens in the J. Kellam collection at Bendigo which certainly resembled *P. timidus*. Horizon is Bendigonian Be4.

Diagnosis. Diminutive goniograptid-like form, certainly with some clonograptid-like dichotomies; development insufficient to deduce whether monoprogressive series are established, though specimens seem mature; 4–6 main stipes.

Description. The sicula is perhaps 1.5 mm long, not quite in the same plane as the rest of the rhabdosome; although the sicula was missed by Harris and Thomas one of their figures (10c) has a suggestion of it. Thecal spacing is 10 in 10 mm, and each dichotomy prior to a "lateral" branch is preceded by only one theca (ignoring, for the present, possible thecal overlaps). The funicle is 1.8–2.0 mm, and successive stipe orders are very short, being less than 2 mm. The total number of peripheral stipes is up to 16 or 17; and the total rhabdosomal diameter (possible quite mature) is about 12 mm.

Remarks. Harris and Thomas, quite correctly we feel, implied that this is a tiny *Clonograptus*-like form with *Goniograptus* affinities. It differs from species of *Goniograptus*, as does *P. clonograptoides*, in having more than 4 primary stipes, in this case up to 6. *P. timidus* is, however, even closer to *Goniograptus* at least in the sense that one cannot entirely rule out the presence of several monoprogressive series. We are inclined to regard both our species of *Praegoniograptus* as belated evolutionary "attempts" to produce a *Goniograptus* from a *Clonograptus* stock (Rickards, 1977).

Etagraptus Ruedemann, 1904
(emend. Cooper and Fortey, 1982)

Type species. Etagraptus lentus Ruedemann, 1904.

Diagnosis. Sigmagraptines with stipes of 2, 3 or more orders in which dichotomies of the first two orders are consecutive. Branching of progressive type.

Remarks. Tetragraptus harti T.S. Hall (1914) was included in this genus by Cooper and Fortey (1982) and our examination of the types and other specimens confirms the general sigmagraptine appearance of the proximal end and hence this assignment. However, it must be said that th1^1 and th1^2 do not noticeably leave the sicula at different levels. The most useful features of *Etagraptus* seem to be that it has slender stipes, disposed in horizontal to pendent fashion, with low angled, widely spaced thecae. Harris and Thomas (1942) placed *E. harti* in an evolutionary series involving *Dichograptus tenuissimus*, *Goniograptus macer* and *Didymograptus gracilis*, a theory that we discuss elsewhere in this paper.

Etagraptus harti (T.S. Hall)

Plate 35 figs b–d; text-figs 83–85

Tetragraptus harti T.S. Hall, 1914: 113–114, text-figs 5, 6.—Harris and Thomas, 1938a: 73, pl. 2 figs 14a, b; pl. 4 fig. 13.—Cooper, 1979: 65, pl. 7f, fig. 33.—Lenz and Jackson, 1986: Fig. 6F.

?*Tetragraptus zhejiangensis* Ge, 1964: 393–394, pl. 1 figs 1–8.

Etagraptus harti.—Cooper and Fortey, 1982: 268–269, fig. 64.—Henderson, 1983: 158, fig. 7A.—Williams and Stevens, 1988: 84, text-figs 78A–I.

Type specimens and other material. Holotype, P31955 (9750) from a point 60 m (298 links) from the bend on the E side of Lester St, SE from the corner of Treveas St, and Lester St, Bendigo; and paratype P14288 (12820) from the junction of Jim Crow and Spring Creek, Daylesford, Bendigonian (Be4). Several specimens from various localities, in the collections of the Museum of Victoria.

Diagnosis. Diminutive, slender, tetragraptid, probably with sigmagraptine development, second order stipes slender and occasionally long; funicle 2.5 mm; thecal spacing 8–9 in 10 mm; maximum dorsoventral width 0.8 mm.

Description. Hall (1914) noted that the sicula was unknown. However, the holotype shows its position (fig. 83) and the paratype a little more of it (fig. 85). The first order stipes comprise one theca only (apart from any overlapping later thecae which cannot yet be proven) giving a funicle of about 2.5 mm. Following this is a single dichotomy with the two new stipes diverging stiffly from each other at about 90°. They *may* reach considerable length but in specimens with a funicle preserved have only been observed to 3 cm. The maximum dorsoventral width is approximately 0.8 mm and the thecal spacing 8–9 in 10 mm. Th1^1 and th1^2 form 180° and each grows at 90° to the sicula, but there is little or no discernible difference in the levels of their free ventral walls relative to the sicula.

Trichograptus Nicholson, 1876

Type species. Dichograptus fragilis Nicholson, 1869.

Diagnosis. (emend. herein). Two slender primary stipes disposed horizontally to the sicula, more or less straight, each with lateral, pendent or reclined, undivided stipes, numbering 1–6, possibly more; development almost certainly sigmagraptine, but not proven.

Remarks. Trichograptus bears the same relationship to *Sigmagraptus* as does *Brachiograptus* to *Goniograptus.* However, *Tetragraptus triograptoides* should, we feel, be referred to *Trichograptus. Trichograptus* thus has further parallels with *Sigmagraptus*, namely the ability of the lateral stipes to grow upwards or downwards from the primary stipes.

Trichograptus fergusoni T.S. Hall

Plate 34 figs a–c, e; text-figs 74, 75

Trichograptus fergusoni T.S. Hall, 1912: 210, pl. 26 figs 1, 2.—Harris and Thomas, 1938a: 72, pl. 1 figs 6a–c; pl. 4 fig. 5.—Lenz and Jackson, 1986: Fig. 5C.

Type specimen and other material. Lectotype herein selected, P34966A, B, (4615, 4650, counterparts). Mines department locality R13 from SE corner of allotment 1c, sect. VIII (86° for 280 m to old shaft on Welsh and Slater N reef, Parish of Dean). Good specimens from the Bendigonian (Be1), Parish of Tarnagulla associated with *Tetragraptus acclinans*, *T. decipiens*, *Dichograptus octobrachiatus*, *D. f. similis* and *Goniograptus macer* as well as numerous 4-stiped *P. fruticosus.*

Specimens of *T. fergusoni* figured by Harris and Thomas (1938a) are as follows: P32017 (41351) Harris and Thomas, pl. 1 fig. 6c), P32049 (41309) (Harris and Thomas, pl. 1 fig. 6a, pl. 4 fig. 5), and P32050 (41310) (Harris and Thomas, pl. 1 fig. 6b), all from "Locality 4, 19 North West, 4 chains E of N.W. corner of allotment 19, sect. II, Parish of Campbelltown". Bendigonian, Be2.

Diagnosis. Two horizontally disposed main stipes, with 1–3 pendent lateral branches each side of the sicula; sicula small; stipes slender 0.3–0.5 mm; thecal spacing 7–10 in 10 mm.

Description. The early development is probably typically sigmagraptine. The sicula is 1.0–1.3 mm long, curved gently towards the th1^1 side, particularly in the apertural region, and th1^1 and 1^2 leave the sicula at slightly different levels, the latter lower down near the sicular aperture. The development of other early thecae cannot be seen. The two main stipes are disposed essentially horizontally except for th1^1 and th1^2 which depend slightly from the sicula. In profile th1^1 has its aperture closer to the sicula than that of th1^2.

There may be an equal number of lateral stipes each side of the sicula (P32050 3:3) but more usually there are more on the th1^1 side (2:1; 3:2). Those nearest the sicula are longer but rarely reach 10 mm. Thecal spacing on the lateral stipe is 7–9 in 10 mm; and 7-10 on the main stipes. After the lateral branches the two main stipes continue without further division for up to 11 thecae. The undulating nature of the dorsal stipe wall is caused by the fact that the thecae are seen in ventral or dorsal view, not in true profile (fig. 74), so that a part of them overlaps the dorsal wall, obscuring it. The prothecae are pyritised in some specimens and the thecal overlap can be seen to be considerable, lending support to the idea that the early development of th1^1–1^2 could be typically sigmagraptine.

The Tarnagulla specimens are the largest seen with pendent lateral branches of 4 cm, and main stipes of 2.5 cm. Other characters are exactly the same.

Trichograptus triograptoides (Harris and Thomas)

Plate 34 figs d, f: text-fig. 76

Tetragraptus triograptoides Harris and Thomas, 1938a: 74, pl. 2 figs 15a, b; pl, 4 fig.14.

Type specimens. Holotype, P31999 (413551), figured by Harris and Thomas (1938a: pl. 2 fig. 15a, pl.4 fig. 14); paratype P32000 (41356) figured by Harris and Thomas (pl. 2 fig. 15b) both from the Bendigonian (Be2), 80 m E of the NW corner of allotment 19, sect. II, Parish of Campbelltown; associated with *Trichograptus fergusoni* and others at the same locality. Several topotypes.

Diagnosis. Only rarely with four stipes, usually three: with two more or less horizontally disposed primary stipes; stipes three and four grow upwards, strongly reclined, respectively from th1^1 and th1^2, almost at right angles to the primary stipes.

Description. A sparse and diminutive dichograptid with either three or four stipes, not usually the latter, and none longer than a centimetre or two. The holotype has three stipes but a specimen from the same locality and horizon (P42528) has four stipes although the junction of one with the others is unclear. The maximum dorsoventral stipe width is 0.25–0.30 mm and the thecal spacing is 8 in 10 mm: consequently the angle of inclination of the free ventral wall is low, about 15°. Overlap of the thecae occurs but the extent cannot be discerned on any specimens we have examined.

The sicula is about 1.5 mm long, narrow, and gently curved with its aperture turned towards th1^2. Th1^1 may originate quite high on the sicula but th1^2 leaves the sicula much lower down, at the level of the most proximal part of the sicular aperture. Th1^2 and th1^1 diverge from the sicula at an angle of 140°, and have an approximate *Didymograptus*-like appearance relative to each other and the sicula. The third stipe, always directed upwards originates from near the aperture of th1^1 although its relationship to that aperture has not been seen. When a second reclined stipe is developed its relationship to the aperture of th1^2 is equally obscure.

Remarks. We have grave doubts about the specific validity of this form and recognise it at present only because of its distinctive overall shape. In all its other characters and measurements as well as locality and horizon, it is identical to *Trichograptus fergusoni* Hall, also described by Harris and Thomas in the same paper. Indeed if a single specimen was found with a fifth stipe, directed either upwards or downwards, then we would regard the two "species" as forming a continuous morphological series. At present this has not been shown. In the case of *Sigmagraptus* species (see Rickards, 1974; and this paper) the initial lateral stipes may be directed either upward or downwards (this may reflect the mode of life of early growth stages; Rickards, 1974) so that a discontinuous morphological series is possible; some may have the first few stipes directed upwards, others downwards, but it is unlikely that a mixture of the two would occur (see Mimograpti).

It will be clear from the foregoing that we do not regard the species as a *Tetragraptus* because it has two primary stipes and either 1 or 2 lateral stipes, in a similar way that *Trichograptus fergusoni* has 1–3 lateral stipes on one side of the sicula, and 1–3 on the other. Both show the same relationship to *Sigmagraptus* and *Brachiograptus* (plate 35 figs a, e) does to *Goniograptus*.

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Plate 1

a, b. *Clonograptus ramulosus* Harris and Thomas: a, P32030, showing distal stipe dichotomies, in association with *Didymograptus ensjoensis* Monsen, from Campbelltown; b, lectotype, P32082, (funicle arrowed) in association with *D. ensjoensis* and *P. pendens* Elles, from Campbelltown (see reconstruction based upon this specimen, fig. 21).

c. *Clonograptus persistens* Harris and Thomas: holotype, P32167a, from Campbelltown.

Scale bars respectively 10 mm, 20 mm, 10 mm.

Plate 2

a. *Clonograptus rarus* Harris and Thomas: holotype, P32053, in association with *P. fruticosus* (J. Hall). *Didymograptus* and *Goniograptus* species and extensiform didymograptids, from the "Good Bed", Campbelltown.

b. *Clonograptus tenellus problematicus* Harris and Thomas: holotype, P32187, in association with *T. approximatus* Nicholson, from the "Good Bed", Campbelltown.

Scale bars respectively 10 mm, 5 mm.

Plate 3

a. *Clonograptus erdtmanni* sp. nov.: holotype, P34260, funicle arrowed in association with *Pseudobryograptus crassus* (Harris and Thomas), *Goniograptus* and *Tetragraptus* species, from the "Good Bed", Campbelltown.

b. *Adelograptus*? *antiquus* (T.S. Hall): holotype, P14241, proximal end showing sicula and thecal form of proximal thecae, and lateral branch near margin of slab, from Lancefield quarry near old Mount William railway station, for comparison with *Didymograptus adamantinus*, plate 22c.

Scale bars respectively 10 mm, 5 mm.

Plate 4

Clonograptus trochograptoides Harris and Thomas: a, b, complete rhabdosome and funicular region of holotype, P32166, from Campbelltown.

Scale bars respectively 10 mm, 5 mm

Plate 5

a–e. *Praegoniograptus timidus* (Harris and Thomas): a, whole slab showing association of type series (P32165, P83313–P83315) with *P. fruticosus* (J. Hall), *T. sp.*, and *Phyllograptus* sp.; b, holotype, P32165, labelled "a" on figure a; c-e, enlargements of the paratypes P83315, P83313 and P83314 respectively, from Bendigo.

f. *Praegoniograptus clonograptoides* (Harris and Thomas): holotype, P32169, from the "Good Bed", Campbelltown.

Scale bars respectively 5 mm, 1 mm, 1 mm, 1 mm, 1 mm, 10 mm.

Plate 6

a, b. *Loganograptus logani logani* (J. Hall): P32056 from Castlemaine and P15753 from Parish of Mandurang.

c. *Loganograptus logani australis* (McCoy): holotype, P12280, from Castlemaine.

d, e. *Loganograptus* cf. *logani* (J. Hall): d, P33168 juvenile from "28b", Muckleford, showing part of sicula; e, specimen from P90, Parish of Darriwil.

Scale bars respectively 20 mm, 10 mm, 10 mm, 1 mm, 10 mm.

Plate 7

a–d. *Loganograptus rectus* Harris and Thomas: a, b, paratype P32054, and proximal end showing newly prepared funicle and sicula from Campbelltown; c, d, holotype, P32034, from Parish of Sandon.

Scale bars respectively 10 mm, 1 mm, 20 mm, 5 mm.

Plate 8

a–d. *Dichograptus maccoyi maccoyi* Harris and Thomas: respectively holotype P32061; paratypes P32035; P32063; P32062; all from Campbelltown.

Scale bars respectively 5 mm, 5 mm, 5 mm, 10 mm.

Plate 9

a. *Dichograptus expansus* Harris and Thomas: holotype, P32076a, from Campbelltown.

b. *Dichograptus sedecimus* Harris and Thomas: holotype, P32010, from the "Good Bed", Campbelltown.

c. *Dichograptus tenuissimus* Harris and Thomas: holotype, P32110, from Campbelltown.

Scale bars respectively 20 mm, 5 mm, 5 mm.

Plate 10

a–c. *Orthodichograptus robbinsi* Thomas: a, slab with holotype (bottom) and paratype, in Jack Kellam collection (counterpart in NMV, holotype P73827, paratype P83089); from Dixons Quarry, Bendigo, in association with *P. pendens* Elles, *Phyllograptus s. l.* sp.; b, P73488 showing irregular proximal web; c, specimen in Jack Kellam collection showing large proximal web.

Scale bars 20 mm.

Plate 11

Orthodichograptus wilkinsoni sp. nov.: holotype, P73489, donated in 1982 by Frank Robbins, from Whittings Quarry, Bendigo; shows probably biform proximal web, thecal spacing and one trident-like stipe division, which suggests that tridents could be consecutive dichotomies. Scalebar 10 mm.

Plate 12

a. *Kellamograptus australis* (Harris and Thomas): holotype, P32081, from Sandon (the funicular region has a small, inked, letter "a" to the right of it, bottom right of slab. (counterpart of figure 82).

b, c. *Kellamograptus*? *incompositus* (Harris and Thomas): respectively holotype, P34969 from the "Good Bed", Campbelltown and P32046B from the same locality.

Scale bars respectively 20 mm, 5 mm, 5 mm.

Plate 13

a, b. *Trochograptus* cf. *diffusus* Holm: respectively P32051 figured by Harris and Thomas (1939) and P32052 figured by Harris and Thomas (1938a: pl. 1 fig. 2a, pl. 4 fig. 1) from Providence Gully, Sandon.

c. *Trochograptus spectabilis* (Harris and Thomas): holotype, P34968, from Providence Gully, Sandon.

Scale bars 10 mm.

Plate 14

Triaenograptus neglectus T. S. Hall: holotype, P13125, from Castlemaine; showing numerous trident-like divisions and numerous examples of stipe anastomosis; several stipe divisions produce more than 3 stipes.

Scale bar 20 mm.

Plate 15

a. *Triaenograptus neglectus* T. S. Hall: P31195B with some growing trident-like divisions and associations of *Tetragraptus* of *serra* type; b, part of P31196B, locality of both specimens not known.

c–e. *Pendeograptus pendens* (Elles): respectively P32002, P32005 and P13067, from Campbelltown; c, and d may be deformed tectonically in opposing senses.

Scale bars respectively 10 mm, 5 mm, 5 mm, 1 mm, 1 mm.

Plate 16

a–c. *Pendeograptus fruticosus* (J. Hall): a, P83326 (small specimen at top, left of centre), P83328 (large specimen just below and to left of P83326) and P83327 (3- branched specimen at bottom); b, P83329; both from Allotment 17, Parish of Campbelltown; c, P73485 from Spring Gully Mine, Bendigo.

d. *Triaenograptus neglectus* T.S. Hall: P31196A, counterpart of specimen in pl. 15 fig. a.

Scale bars respectively 10 mm, 1 mm, 1 mm, 10 mm.

Plate 17

a, b. *Pseudobryograptus crassus* (Harris and Thomas): holotype, P32009, from the "Good Bed",Campbelltown, and enlargement of holotype.

c, d. ?*Pendeograptus volitans* Harris and Thomas: respectively holotype P31995, and P32008, both from the "Good Bed", Campbelltown.

e. *Pendeograptus fruticosus* (J. Hall): P83330 (right) and P32048 from the "Good Bed", Campbelltown; P32048 originally figured by Harris and Thomas (1938a) as a four branched *P. crassus.*

Scale bars respectively 10 mm, 1 mm, 1 mm, 1 mm, mm.

Plate 18

a. *Tetragraptus approximatus* Nicholson: P13068, from Campbelltown.

b. *Tetragraptus acclinans* Keble: P13069, from Yandoit Hill.

c–g. *Tetragraptus bryonoides* J. Hall: c, P83331 from Bendigo; d, Jack Kellam collection; e, P13089 from Yandoit; f, P13090 from Yandoit; g, P32928 from Campbelltown.

Scale bars respectively 5 mm, 5 mm, 5 mm, 2 mm, 1 mm, 1 mm.

Plate 19

a–d. *Tetragraptus decipiens decipiens* T.S. Hall: respectively P31953; P31952; holotype, P14368; P14240, all from Lancefield.

Scale bars respectively 2 mm, 5 mm, 2 mm, 2 mm.

Plate 20

a–d. *Tetragraptus decipiens bipatens* Keble and Harris: respectively paratypes P14399; P14395; P14393, holotype P14393, all from Antimony Mine, Blackwood.

e. *Tetragraptus* ?(*Tetragraptus*) *chapmani* Keble and Harris: holotype, P14378, from Fossil Gully, Blackwood.

Scale bars respectively 2 mm, 2 mm, 2 mm, 2 mm, 5 mm.

Plate 21

a–d. *Mimograptus mutabilis* Harris and Thomas: a, paratype P34929; b, paratype P34928; c, d, holotype, P34927B.

Scale bars respectively 5 mm, 5 mm, 10 mm, 1 mm.

Plate 22

a. *Didymograptus asperus* Harris and Thomas: holotype, P32011, from the "Good Bed", Campbelltown.

b. *Didymograptus perditus* T. S. Hall: holotype, P14294, from Chewton.

c. *Didymograptus adamantinus* T. S. Hall: holotype, P31975, from Bendigo.

d, e. *Didymograptus dilatans* T. S. Hall: respectively P32073 from Campbelltown and holotype, P31978 from Daylesford.

Scale bars respectively 2 mm, 5 mm, 2 mm, 10 mm, 5 mm.

Plate 23

a, b. *Didymograptus eocaduceus* Harris: respectively lectotype, P13800 and paralectotype P42445 both from Campbelltown.

c, d. *Didymograptus hemicyclus* Harris: respectively lectotype, P13797, and P83293, both from Campbelltown, latter from the "Good Bed".

e, *Didymograptus procumbens* T. S. Hall: holotype, P31974 from Bendigo.

f. *Didymograptus asperus* Harris and Thomas: paratype, P32041.

Scale bars respectively 1 mm, 2 mm, 1 mm, 1 mm, 2 mm, 2 mm.

Plate 24

a. *Didymograptus latus latus* T.S. Hall: holotype, P14283 (counterpart is P14289) from Bendigo.

b–d. *Didymograptus latus aequalis* Harris and Thomas: b, P34970 from Campbelltown; c, d, respectively lectotype, P34971 and paralectotype P31994 both from Campbelltown.

e, f. *Didymograptus elongatus* Harris and Thomas: respectively holotype, P32074 from Campbelltown and P32075 from Bendigo.

It should be noted that c and e are not retouched but that the specimens have a natural, pale, preservational halo.

Scale bars respectively 2 mm, 2 mm, 5 mm, 5 mm, 5 mm, 5 mm.

Plate 25

a. *Didymograptus mundus* T. S. Hall: holotype P14270B, from Chewton.

b. *Didymograptus vicinus* Harris and Thomas: holotype, P32015 from the "Good Bed", Campbelltown.

c, d. *Didymograptus aureus* T. S. Hall: c, slab with holotype P31977 (specimen with sicula on upper right) and paratypes, including P83333 (with sicula in centre) and P83334 (with sicula on left, upside down); d, enlargement of holotype, from Bendigo.

c. *Didymograptus latens* T.S. Hall: holotype, P31976, from Bendigo.

Scale bars respectively 5 mm, 5 mm, 5 mm, 1 mm, 1 mm.

Plate 26

a–c. *Zygograptus abnormis* (J. Hall): respectively P73481 (locality unknown), and P34279A, B (part and counterpart) from Chewton.

d, e. *Zygograptus stewarti* sp. nov.: paratypes P73484 and P73483, from Spring Gully Mine, Bendigo.

Scale bars respectively 10 mm, 1 mm, 5 mm, 2 mm, 5 mm.

Plate 27

a, d, e. *Sigmagraptus crinitus* (T.S. Hall): a, P34852 from Langwerner; d, e, P34798A, from Bendigo.

b, c. *Sigmagraptus laxus* (T.S. Hall): respectively holotype, P32141B, showing abnormal division, referred to in text, at bottom left; and P6972 showing considerable length of lateral stipes; both from Bendigo.

Scale bars respectively 10 mm, 5 mm, 5 mm, 20 mm, 5 mm.

Plate 28

a–e. *Goniograptus thureaui thureaui* (McCoy): respectively P34847 and P34846 from the "Good Bed", Campbelltown; P34844 (holotype of *G. t. inaequalis* Harris and Thomas; lectotype (or paralectotype) P12215 and P34861, both from Bendigo.

Scale bars respectively 5 mm, 5 mm, 5 mm, 10 mm, 10 mm.

Plate 29

a–c. *Goniograptus macer* T.S. Hall: respectively P112 from Newham, labelled *G. macer* but note the similarity to an early growth stage of *Brachiograptus* and biserials on slab suggest a higher horizon than usual *G. macer* levels; holotype, P32142A from Bendigo; P34851, Lost Gully, Chewton; both b, and c show distinction from *Brachiograptus*.

Scale bars respectively 2 mm, 5 mm, 5 mm.

Plate 30

Goniograptus alternans Harris and Thomas: holotype, P14619A, from Campbelltown,

Scale bar 10 mm.

Plate 31

a. *Goniograptus alternans* Harris and Thomas: P47017 from Allotment 30A, Parish of Campbelltown.

b. *Goniograptus macer* T. S. Hall: P83335 from the "Good Bed", Campbelltown.

c. *Goniograptus palmatus* Harris and Keble: holotype, P26448A from Campbells Creek, Castlemaine ("cotypes" of Harris and Keble are part and counterpart of the same specimen).

d. *Goniograptus tumidus* Harris and Thomas: P34848 from Allotment 20, Section II, Parish of Campbelltown.

Scale bars respectively 10 mm, 2 mm, 10 mm, 10 mm.

Plate 32

a. *Goniograptus tumidus* Harris and Thomas: holotype. P32168 from the "Good Bed", Campbelltown.

b. *Goniograptus velatus* Harris and Thomas: holotype, P34839, from Campbelltown.

Scale bars 5 mm.

Plate 33

a, b. *Goniograptus speciosus* T. S. Hall: respectively P34845 and P47065 from Willeys Quarry, Macedon, SW of Woodend. (Ya2).

Scale bars 5 mm.

Plate 34

a–c, e. *Trichograptus fergusoni* T. S. Hall: respectively P32049 from Campbelltown; lectotype, P34966A from Dean; P83336 and P32050 both from NW corner of Allotment 19, Section II, Parish of Campbelltown.

d, f. *Trichograptus triograptoides* (Harris and Thomas): respectively P42528 and holotype, P31999, both from Campbelltown.

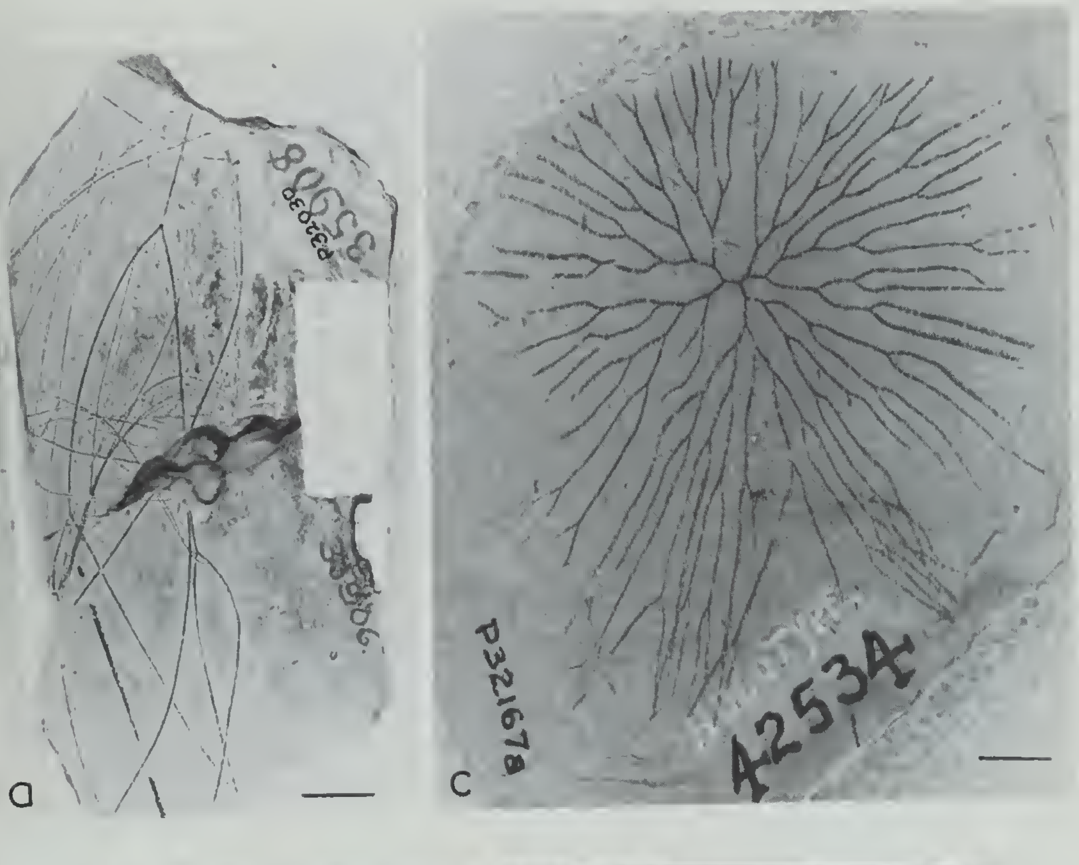
Scale bars 1 mm.

Plate 35

a, e. *Brachiograptus etaformis* Harris and Keble: respectively holotype, P24019B and paratype P24020, from Strathfieldsaye.

b–d. *Etagraptus harti* (T.S. Hall): respectively holotype P31955 from Bendigo; paratype P14288 from Daylesford; unnumbered specimen J. Kellam collection.

Scale bars respectively 1 mm, 1 mm, 5 mm. 2 mm, 1 mm.



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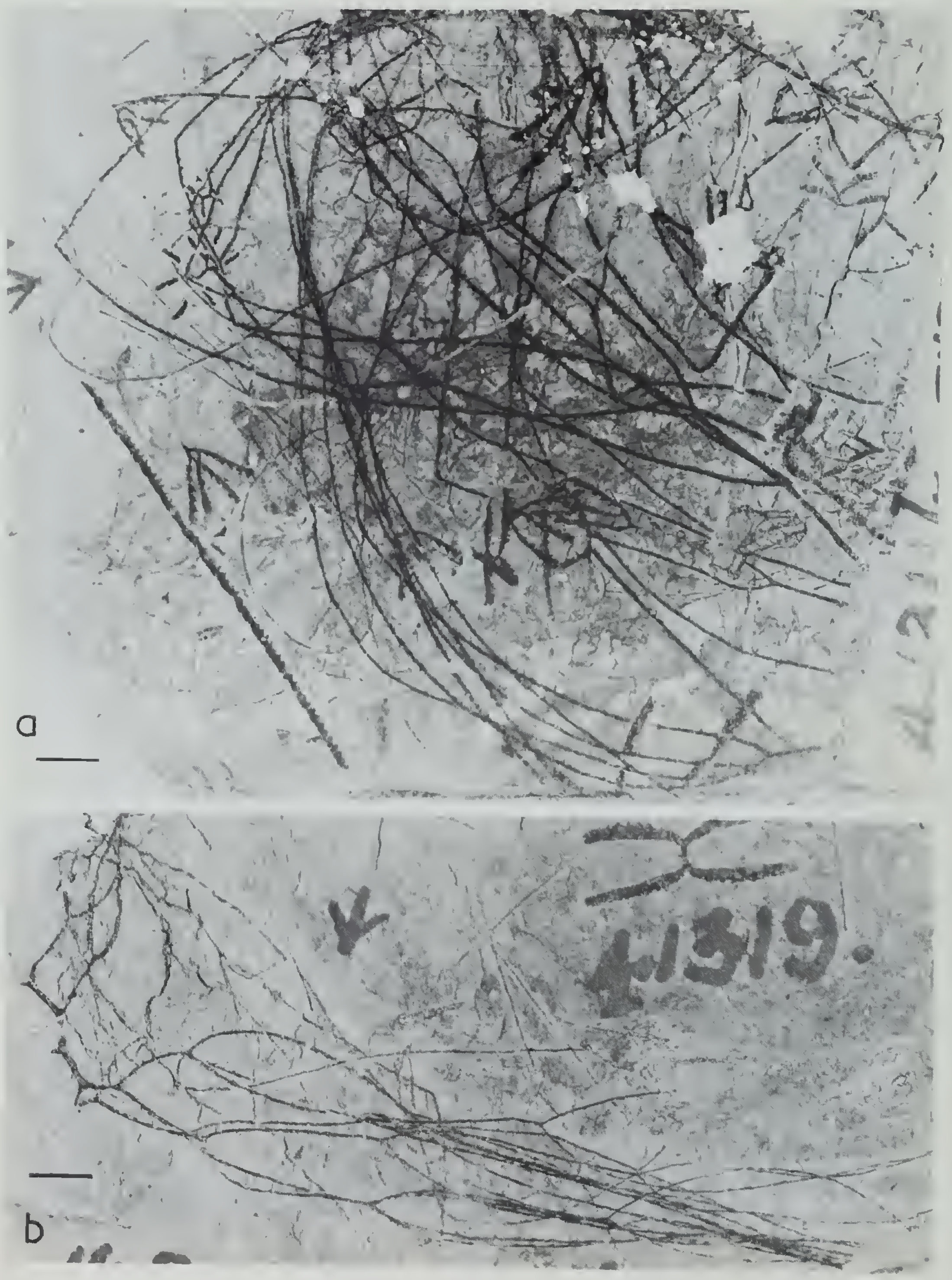
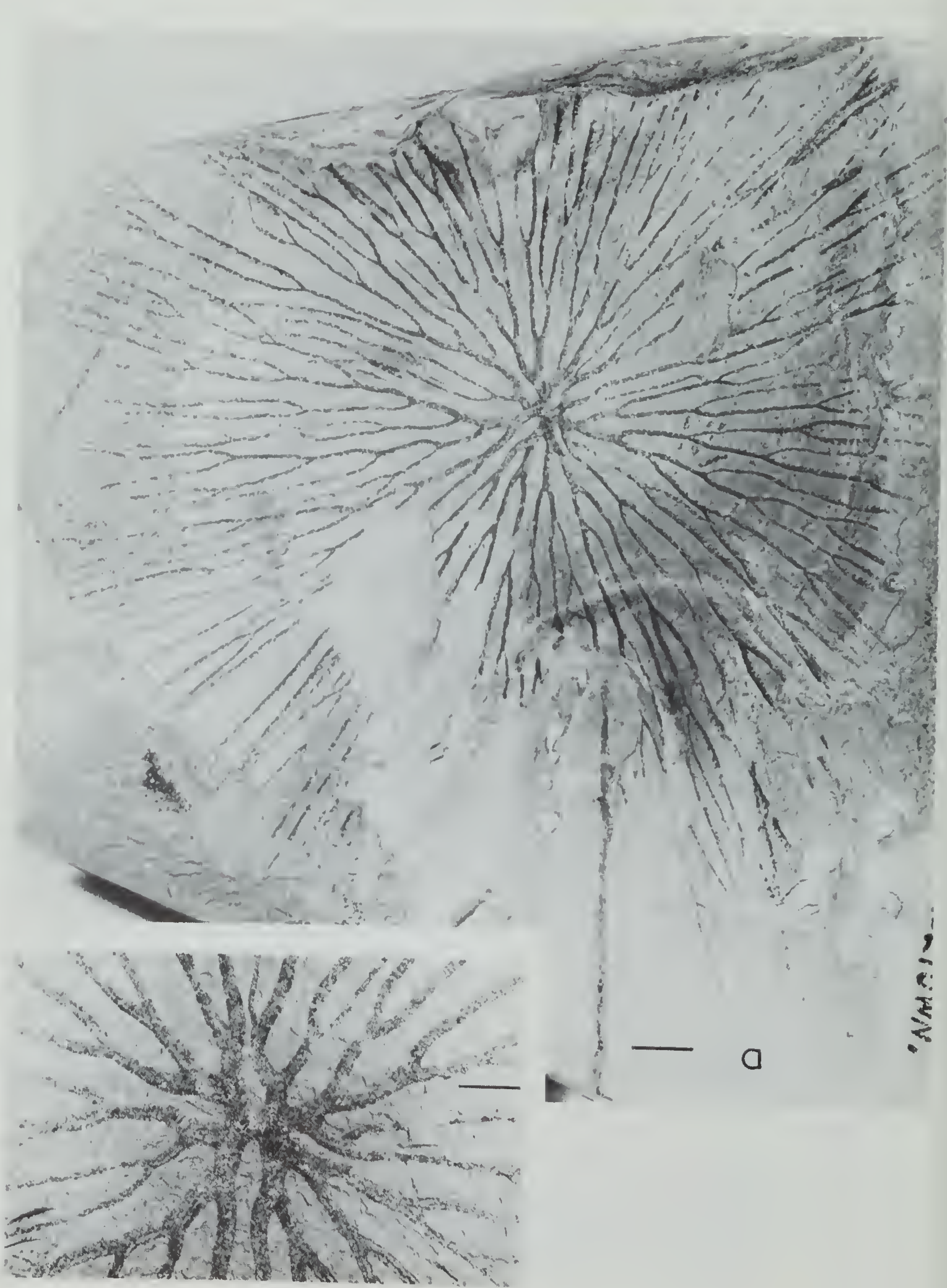


PLATE 2

PLATE 3



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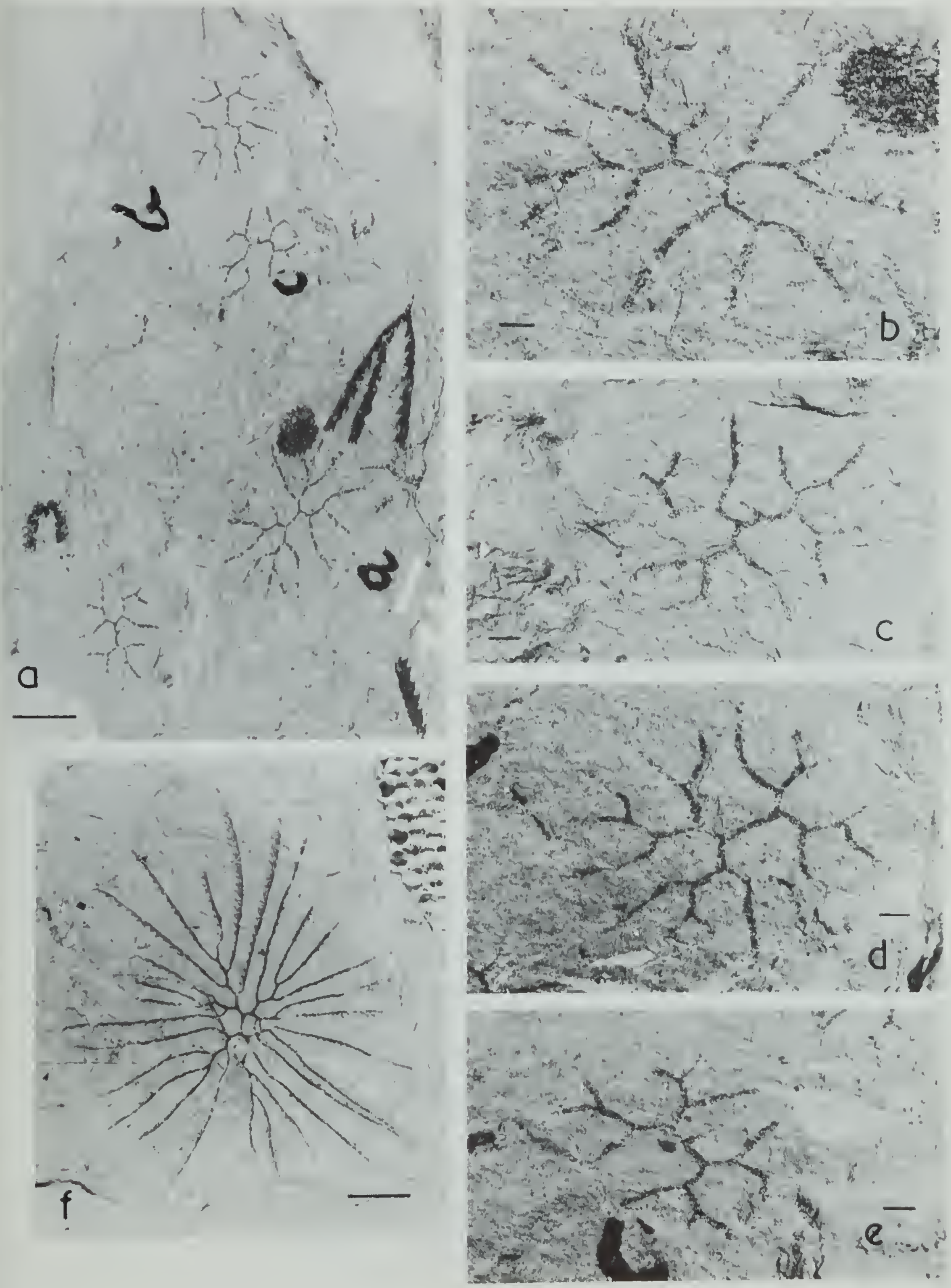

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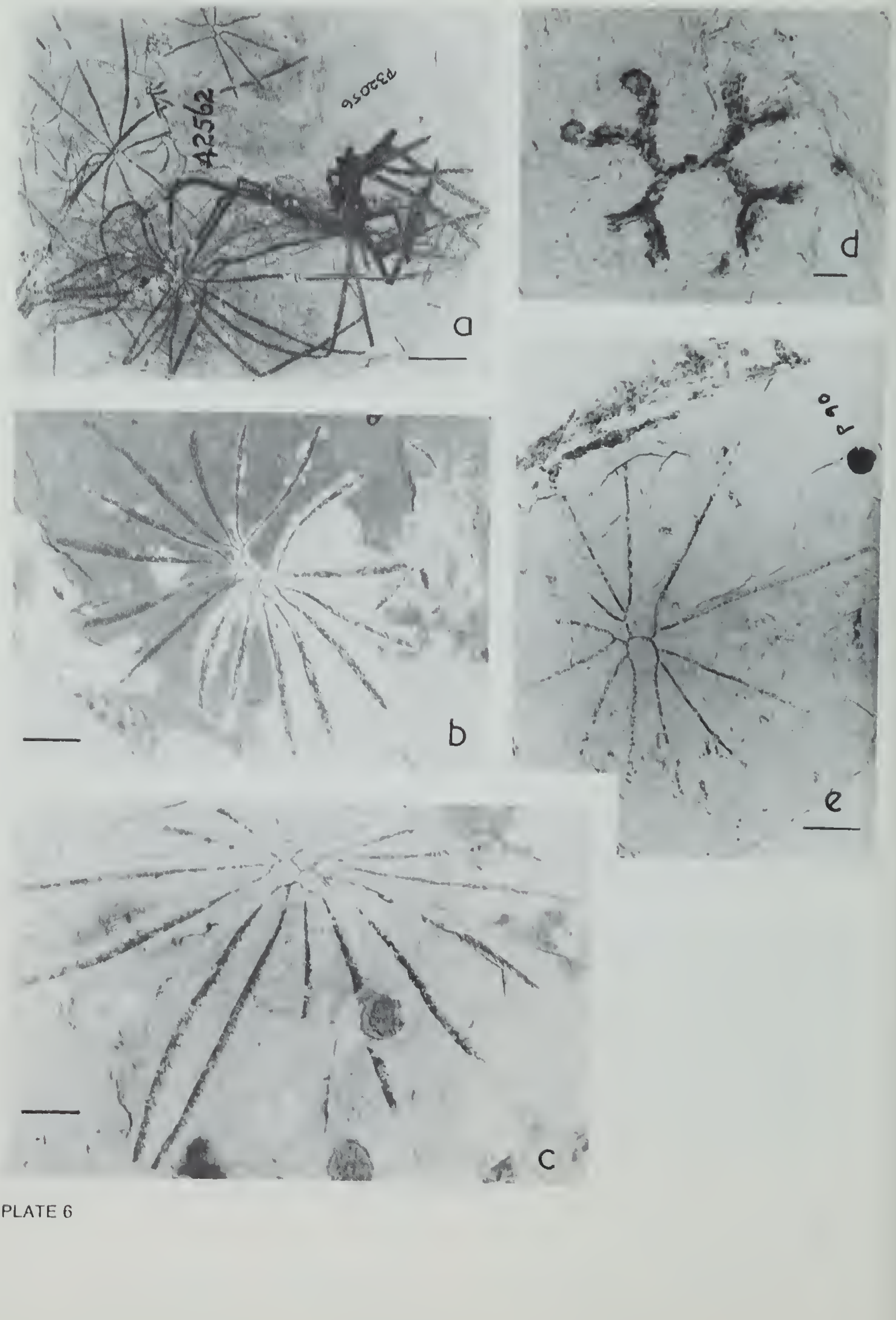

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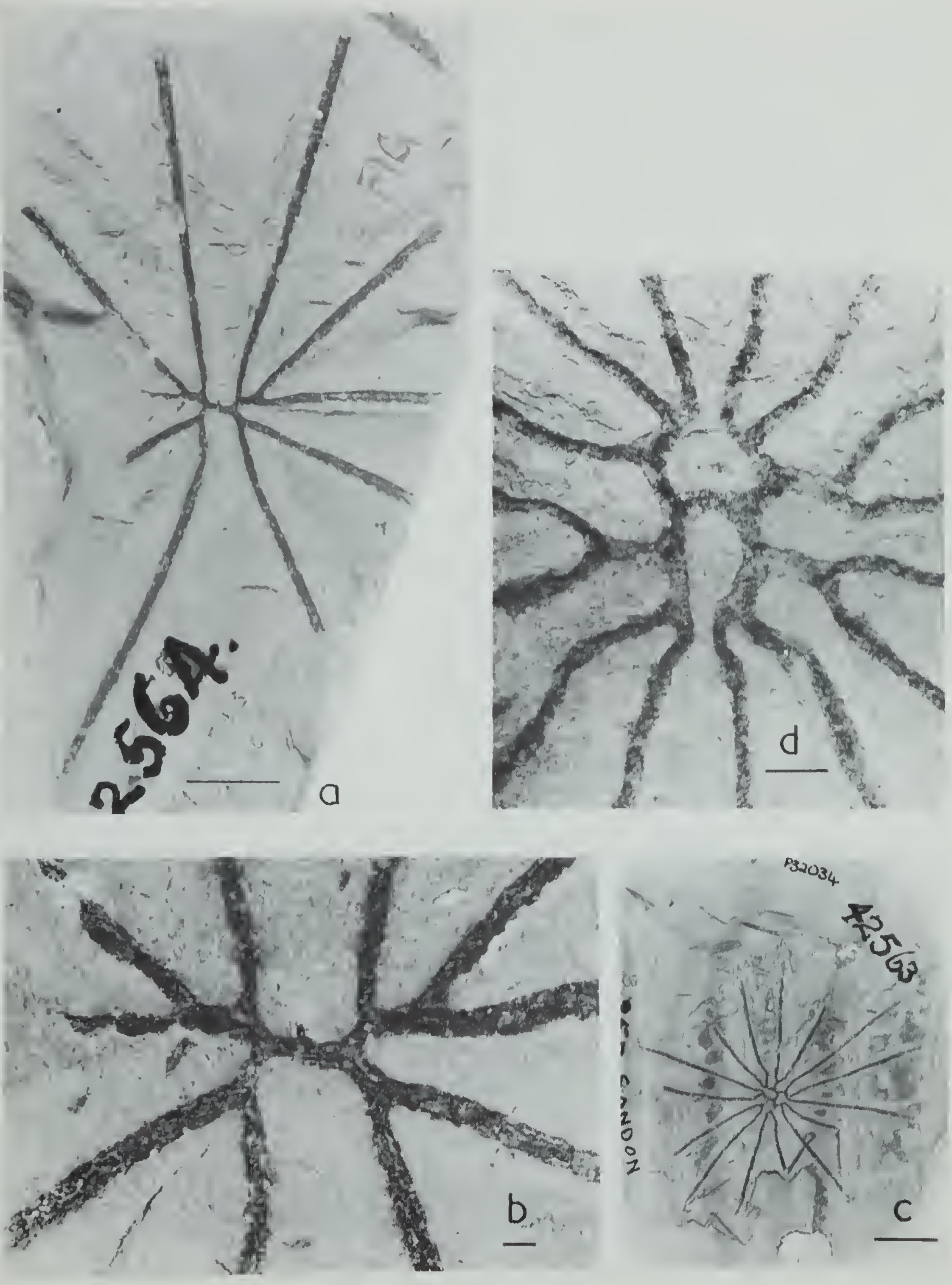

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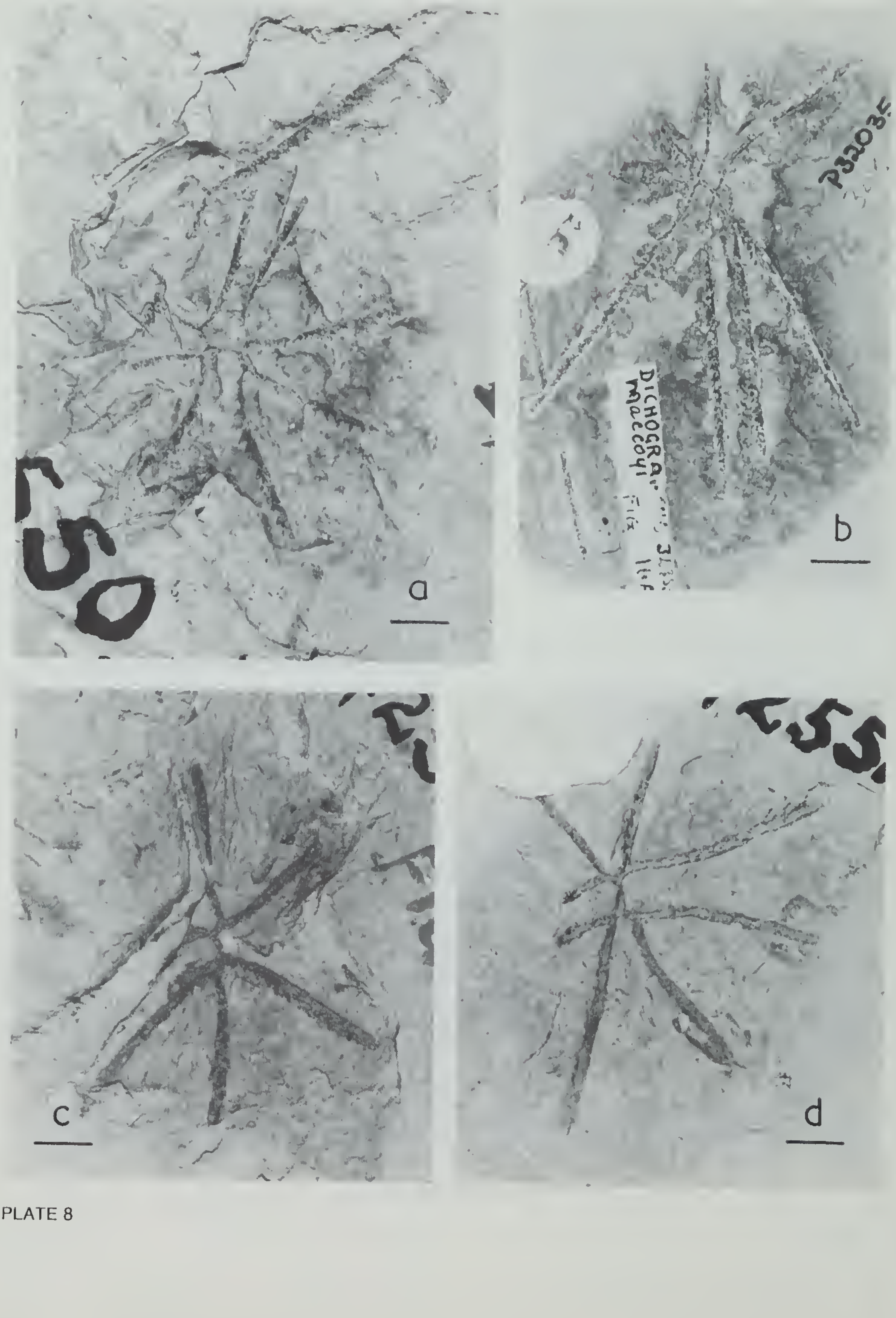

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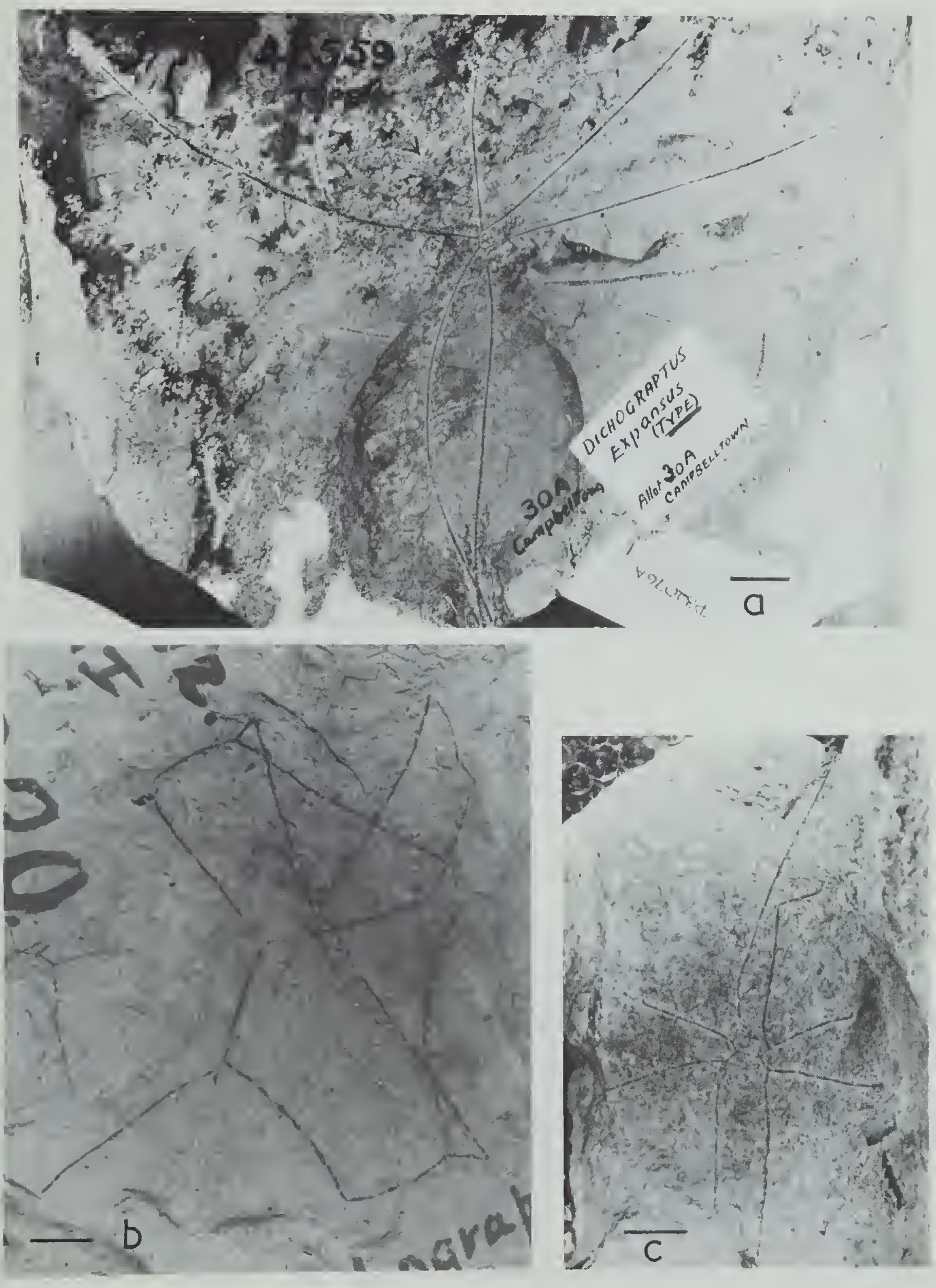

41559
DICHOGRAPTUS
Expansus
(TYPE)
Allot 30A
CAMPBELLTOWN
30A
Campbelltown
a
b
c

PLATE 9

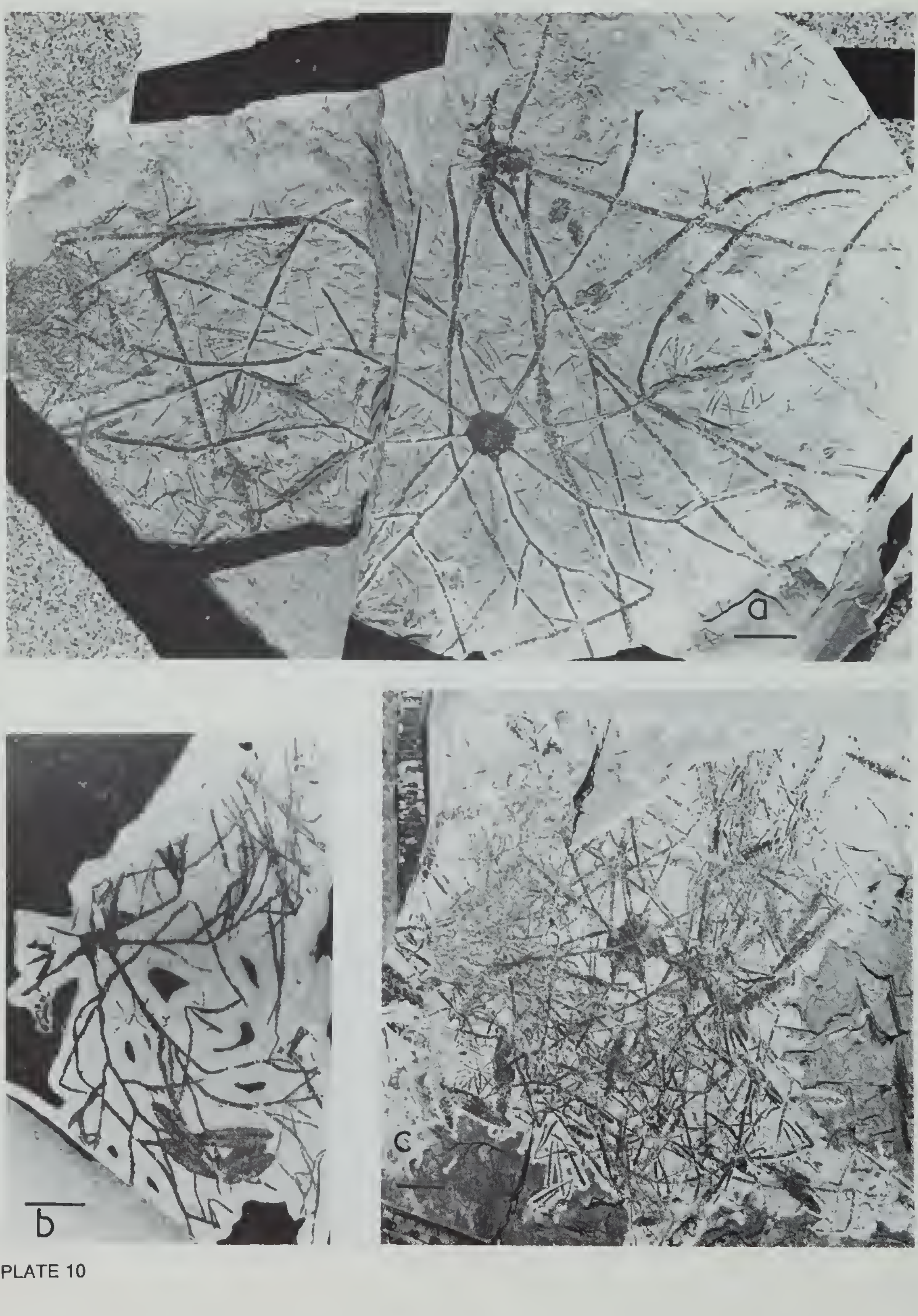


PLATE 10

PLATE 11

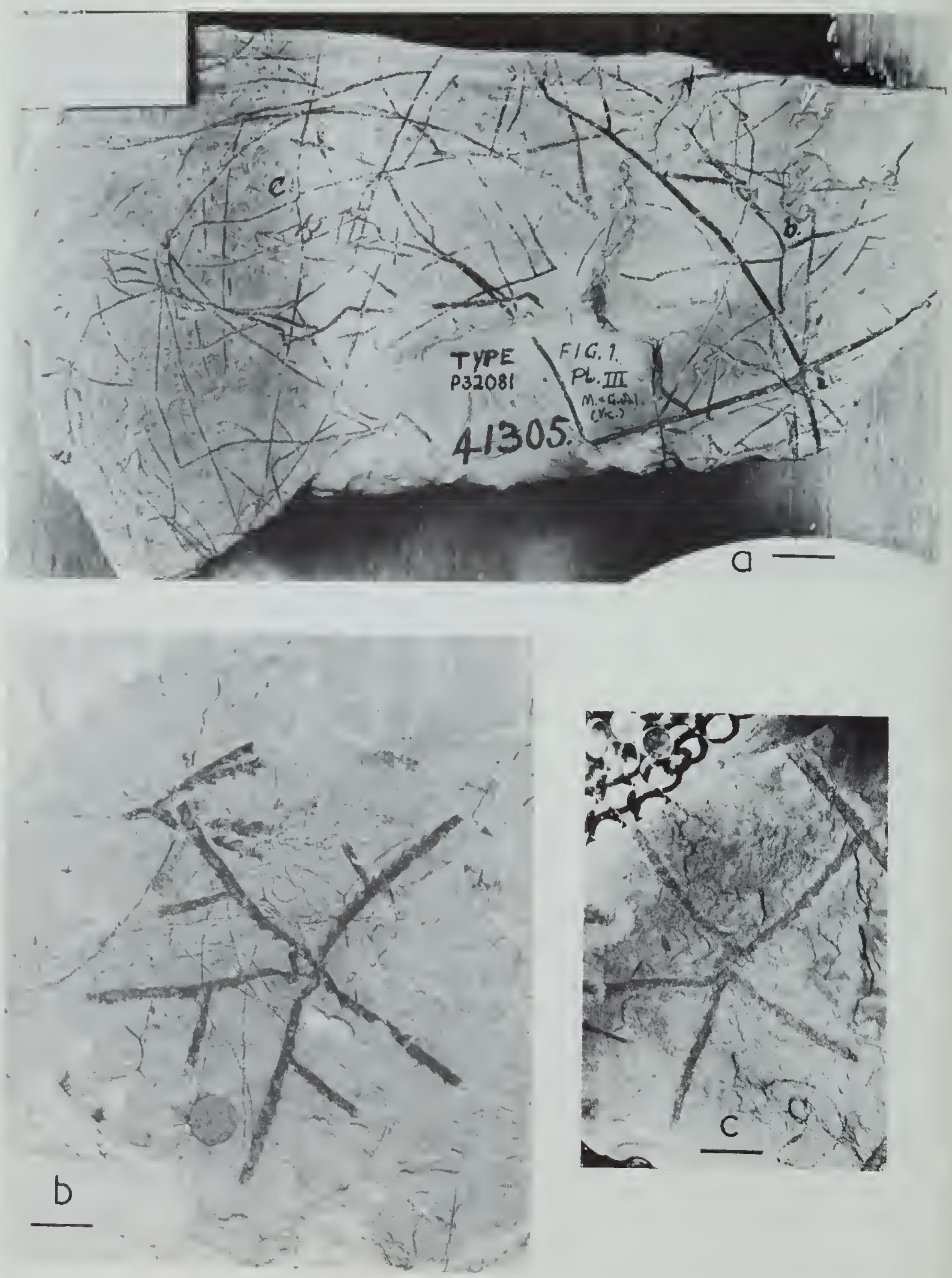


PLATE 12

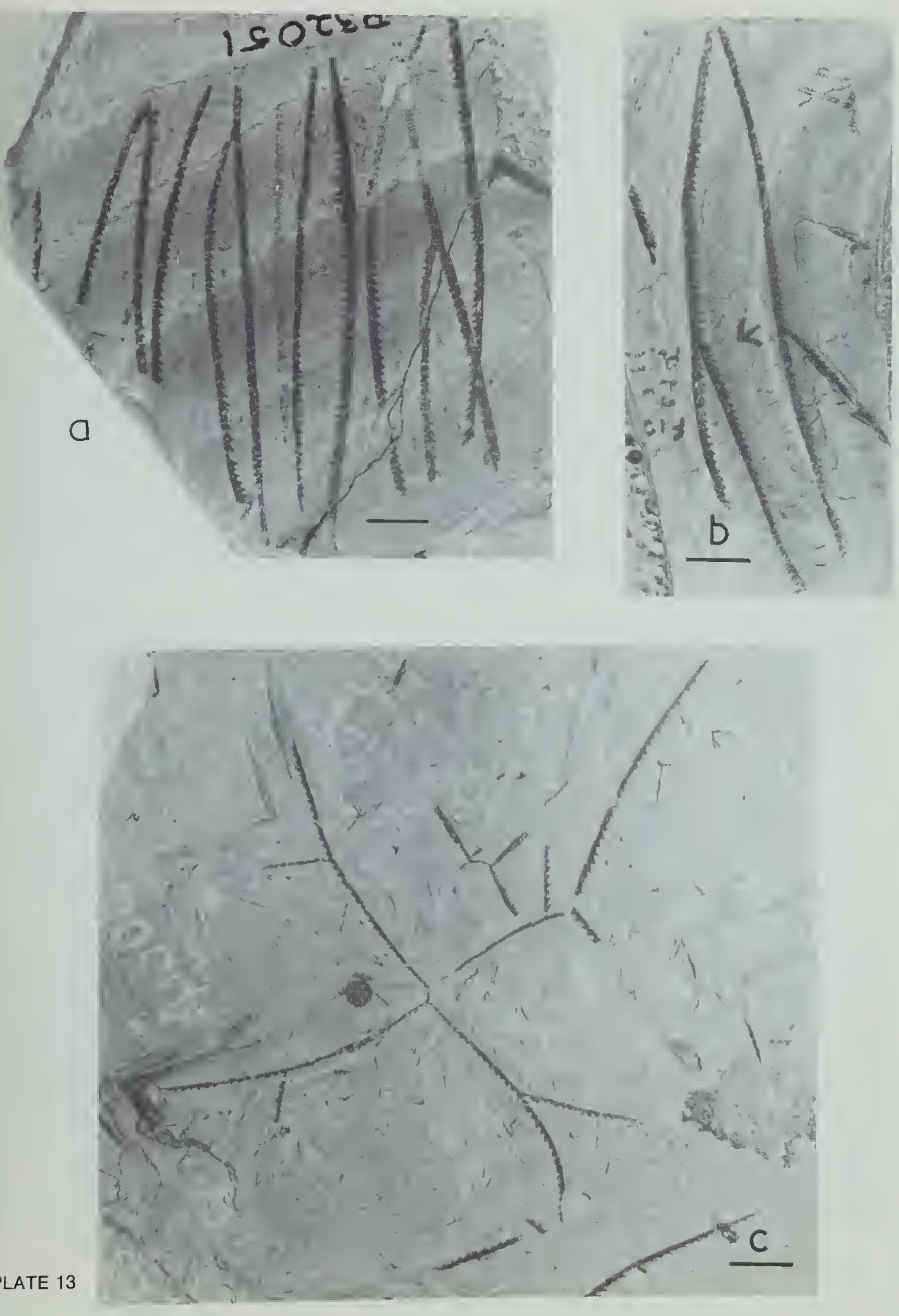
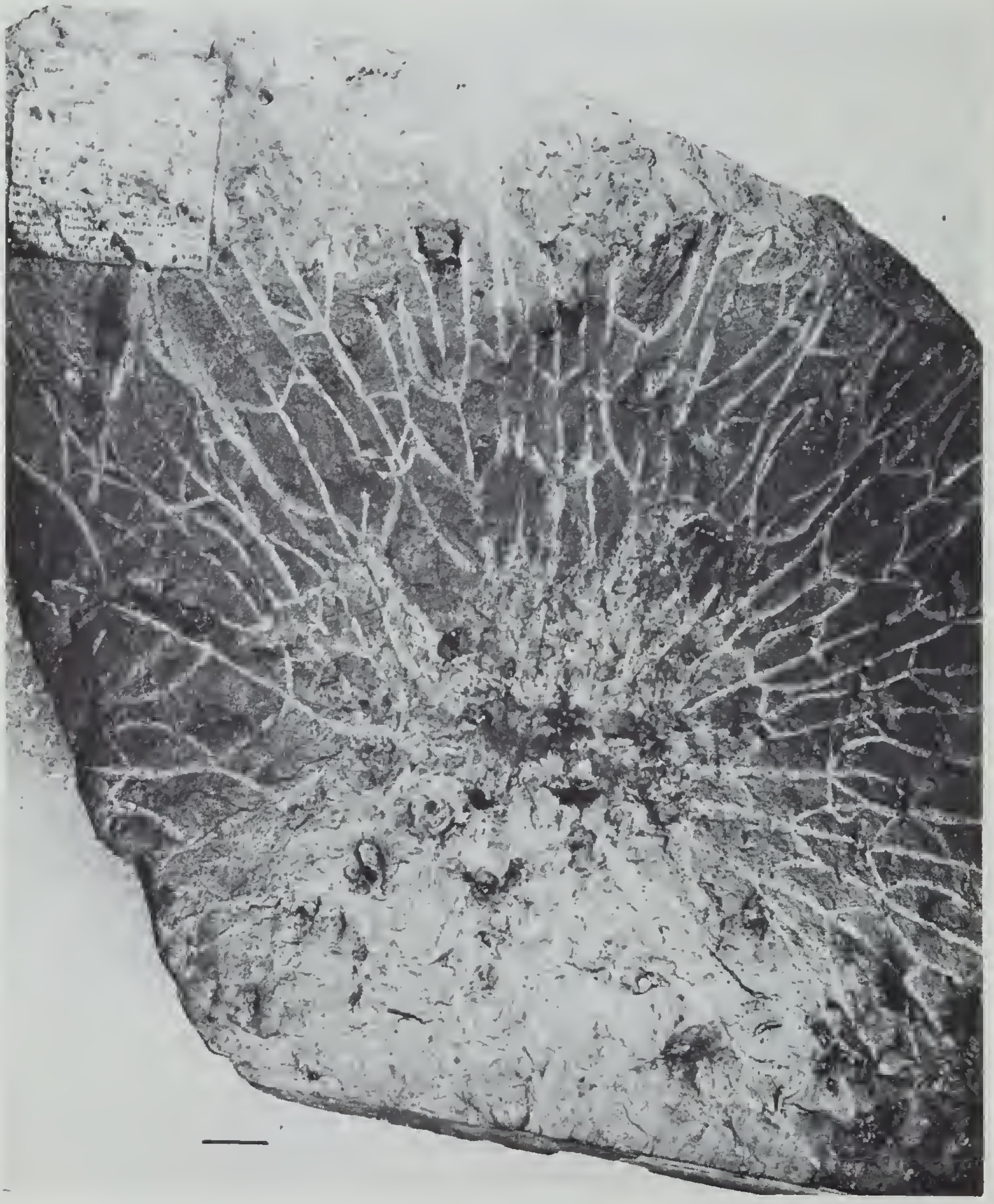


PLATE 13



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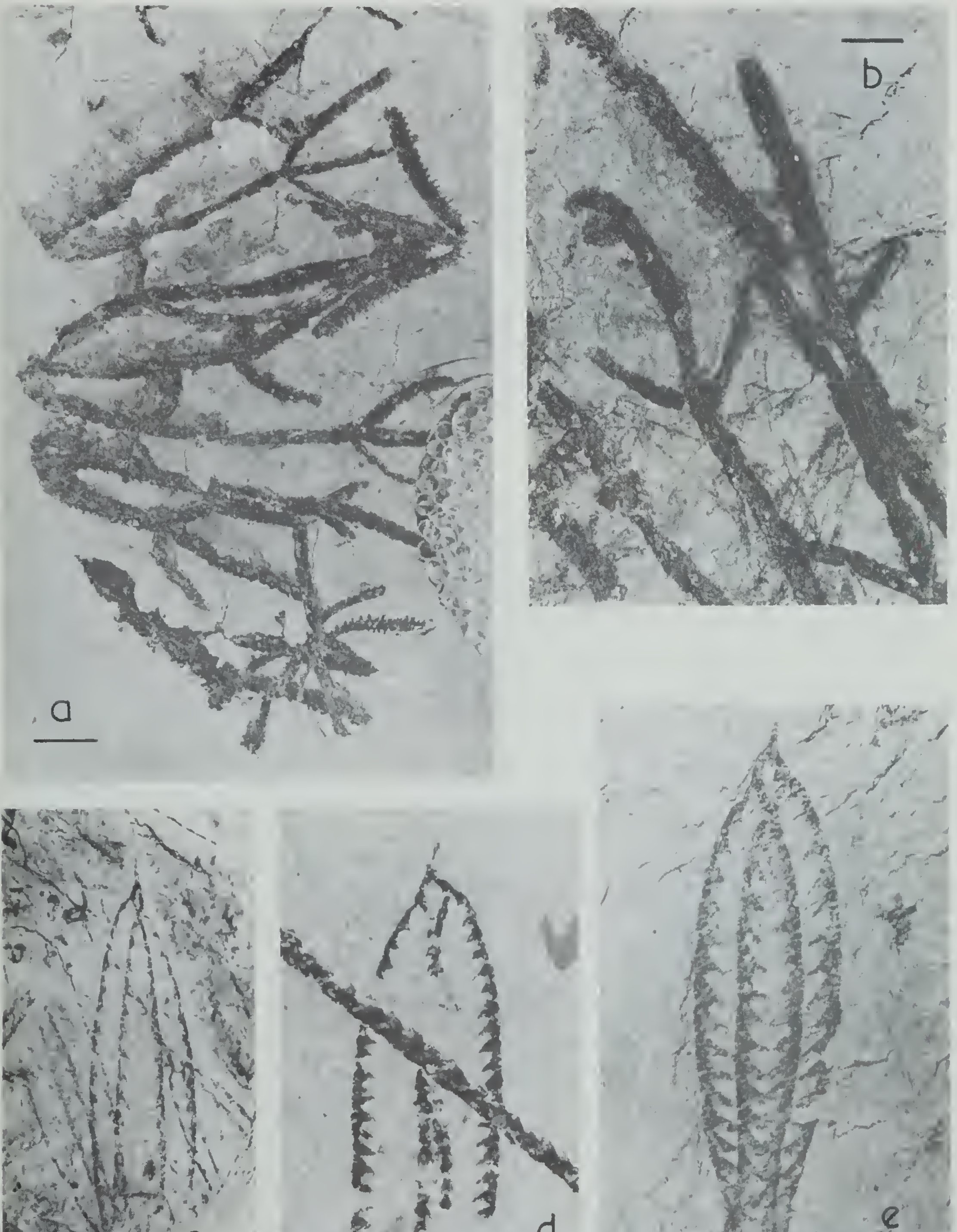


PLATE 15

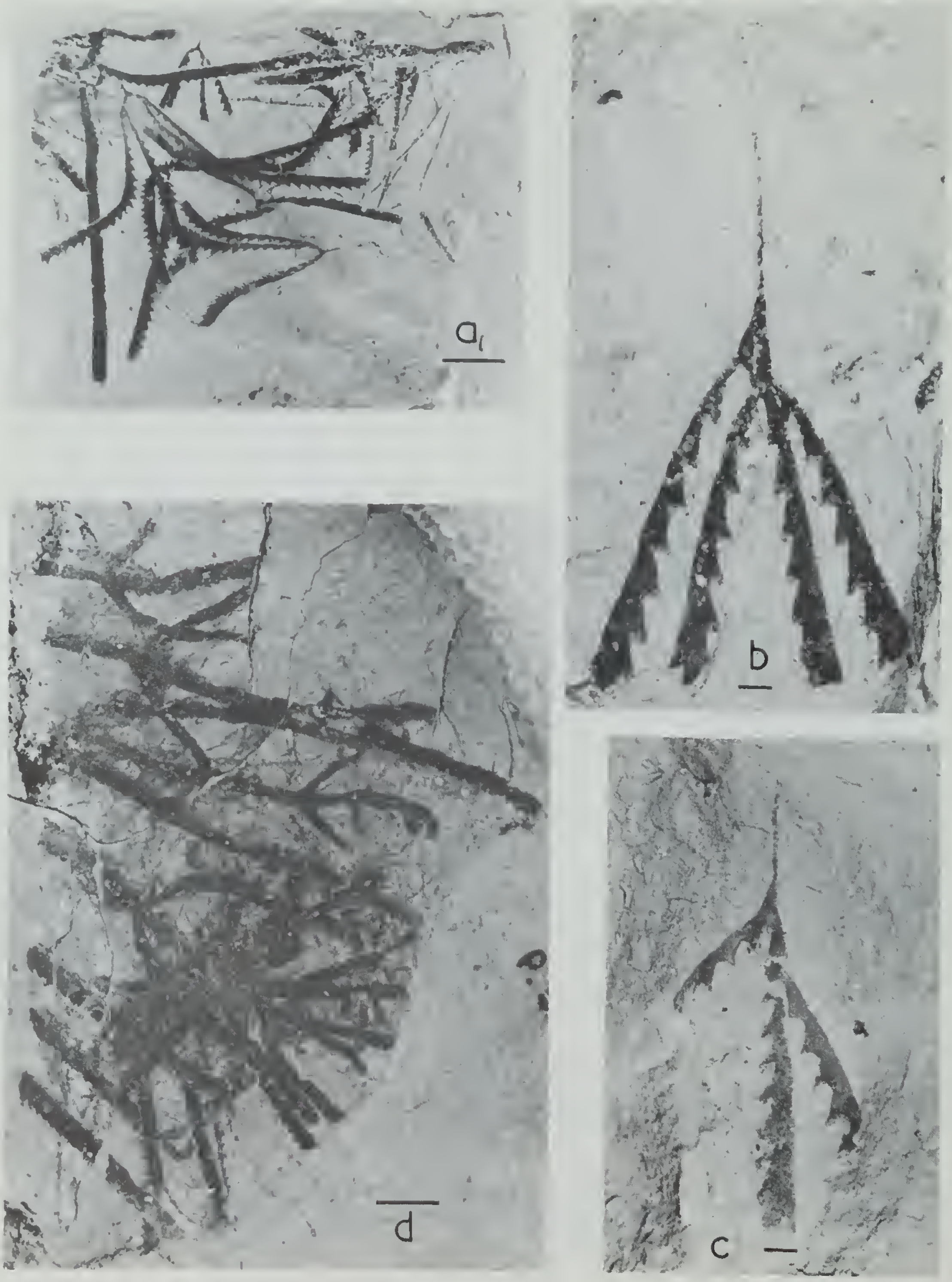
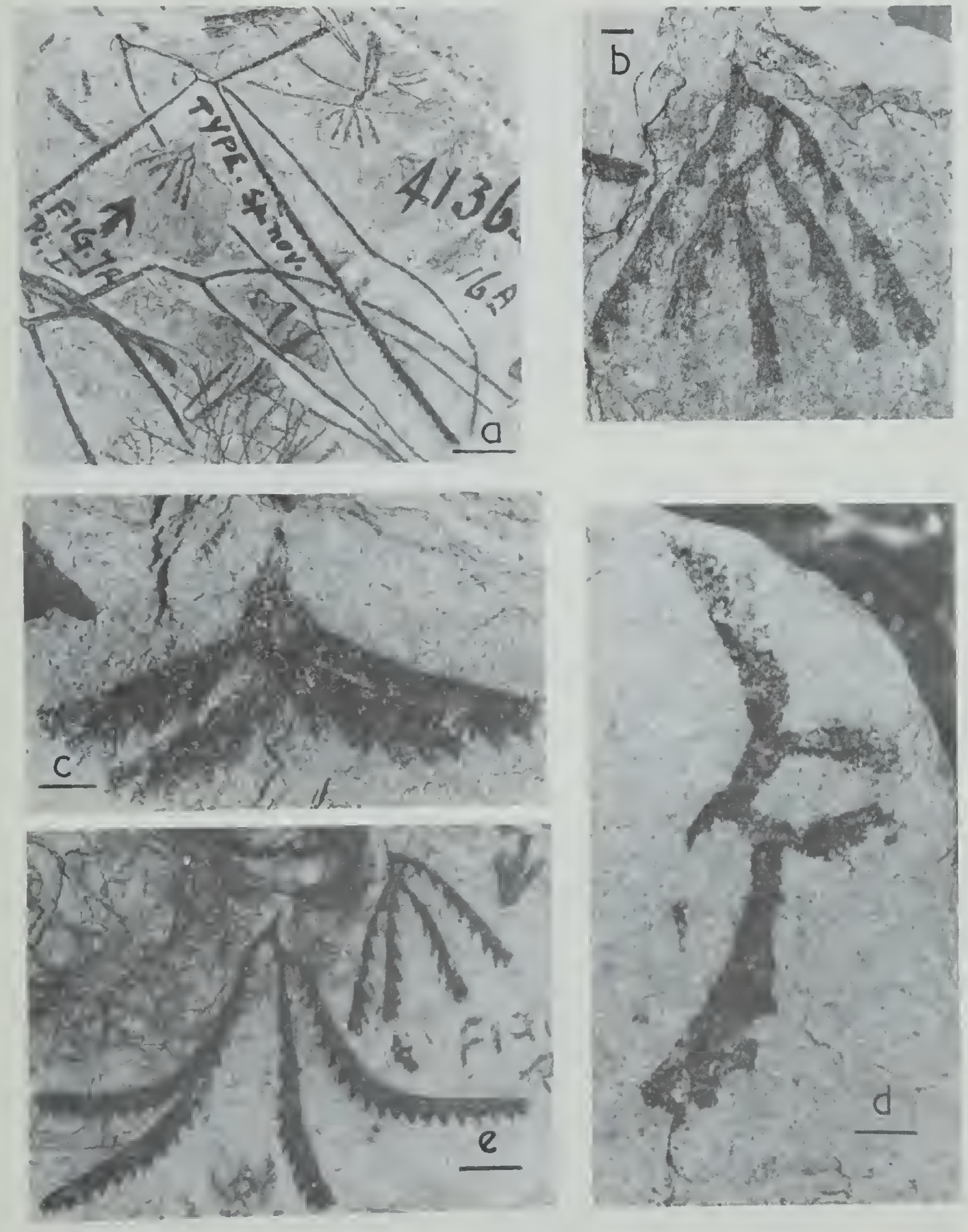


PLATE 16



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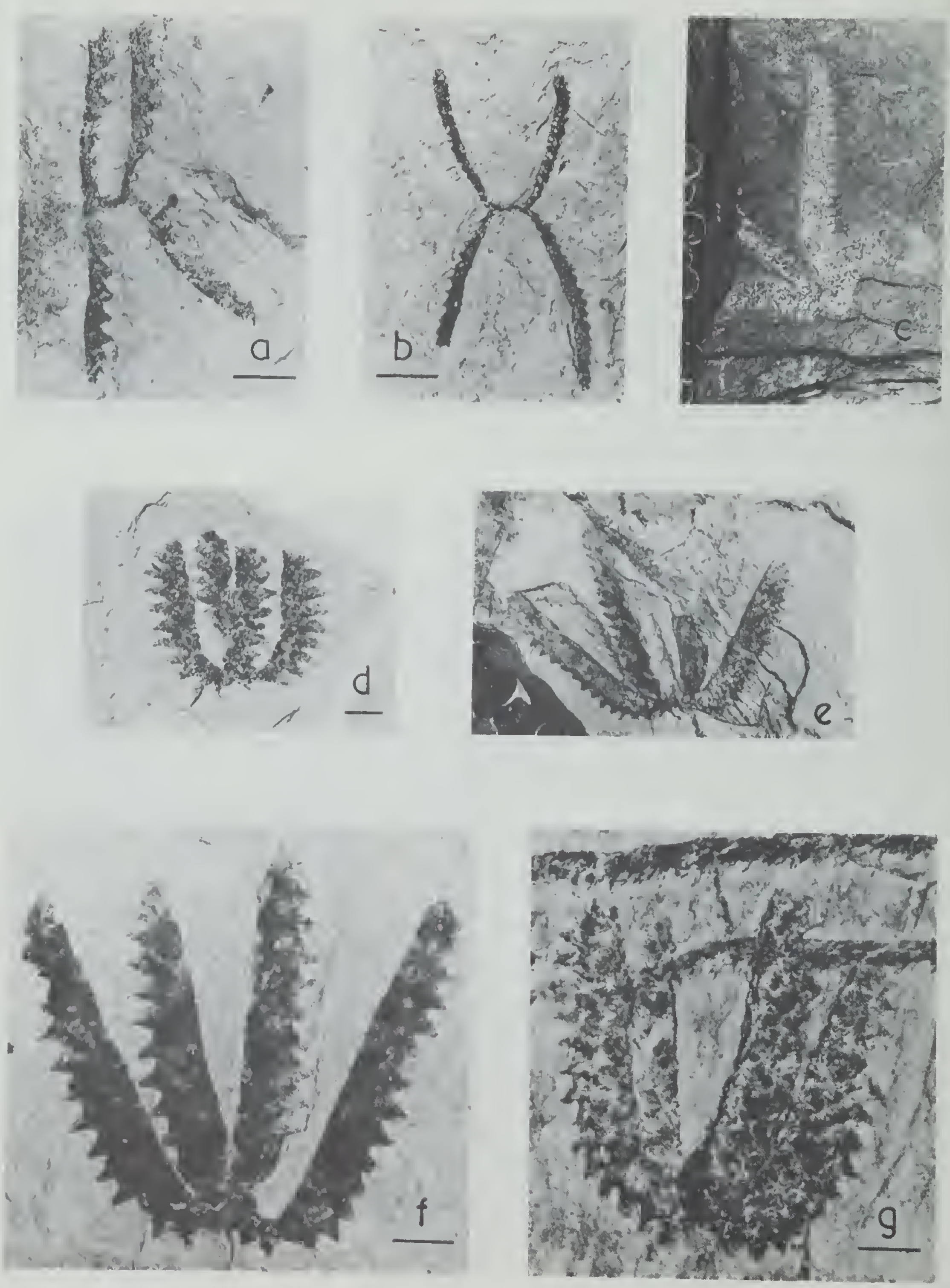

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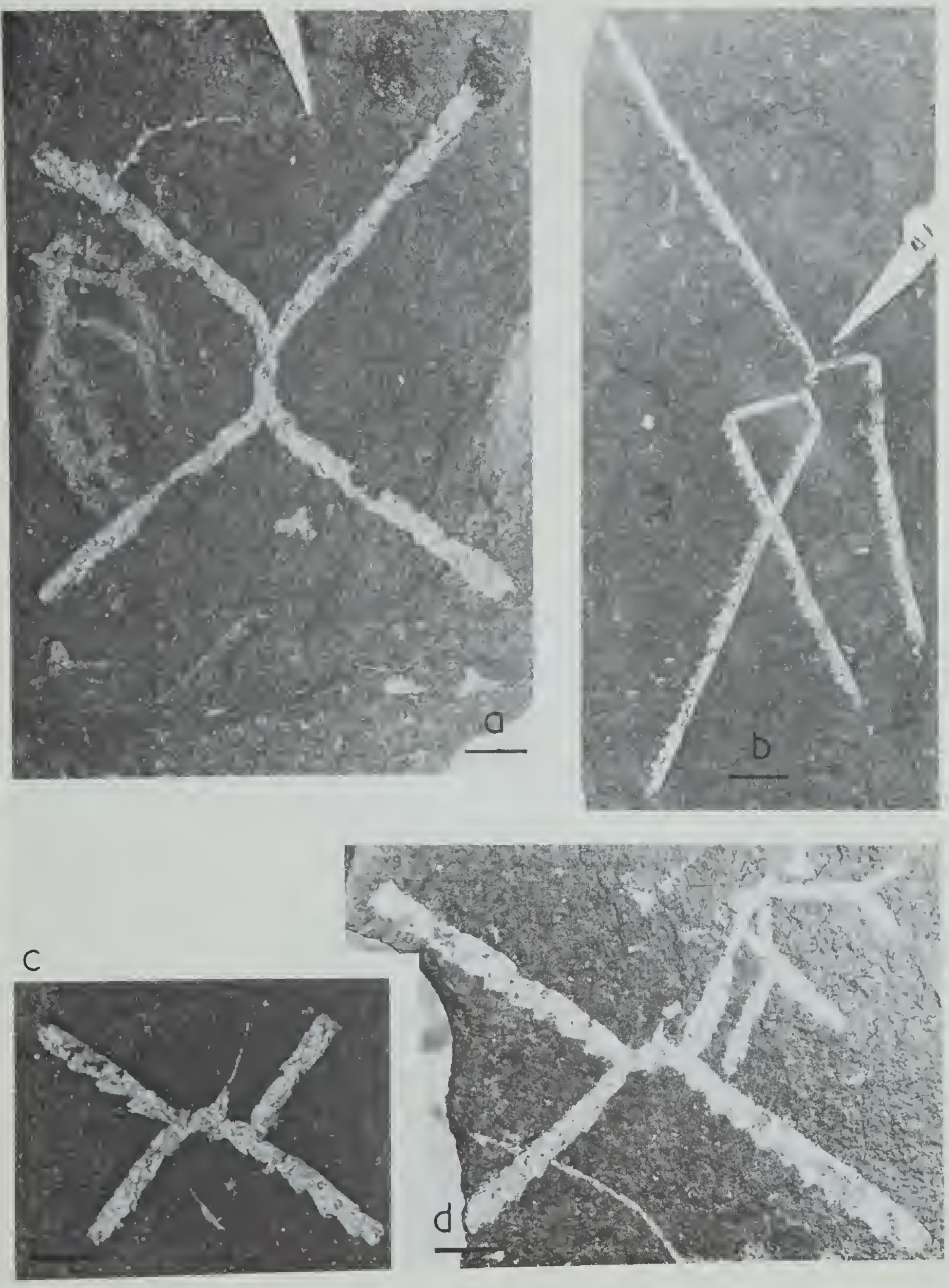

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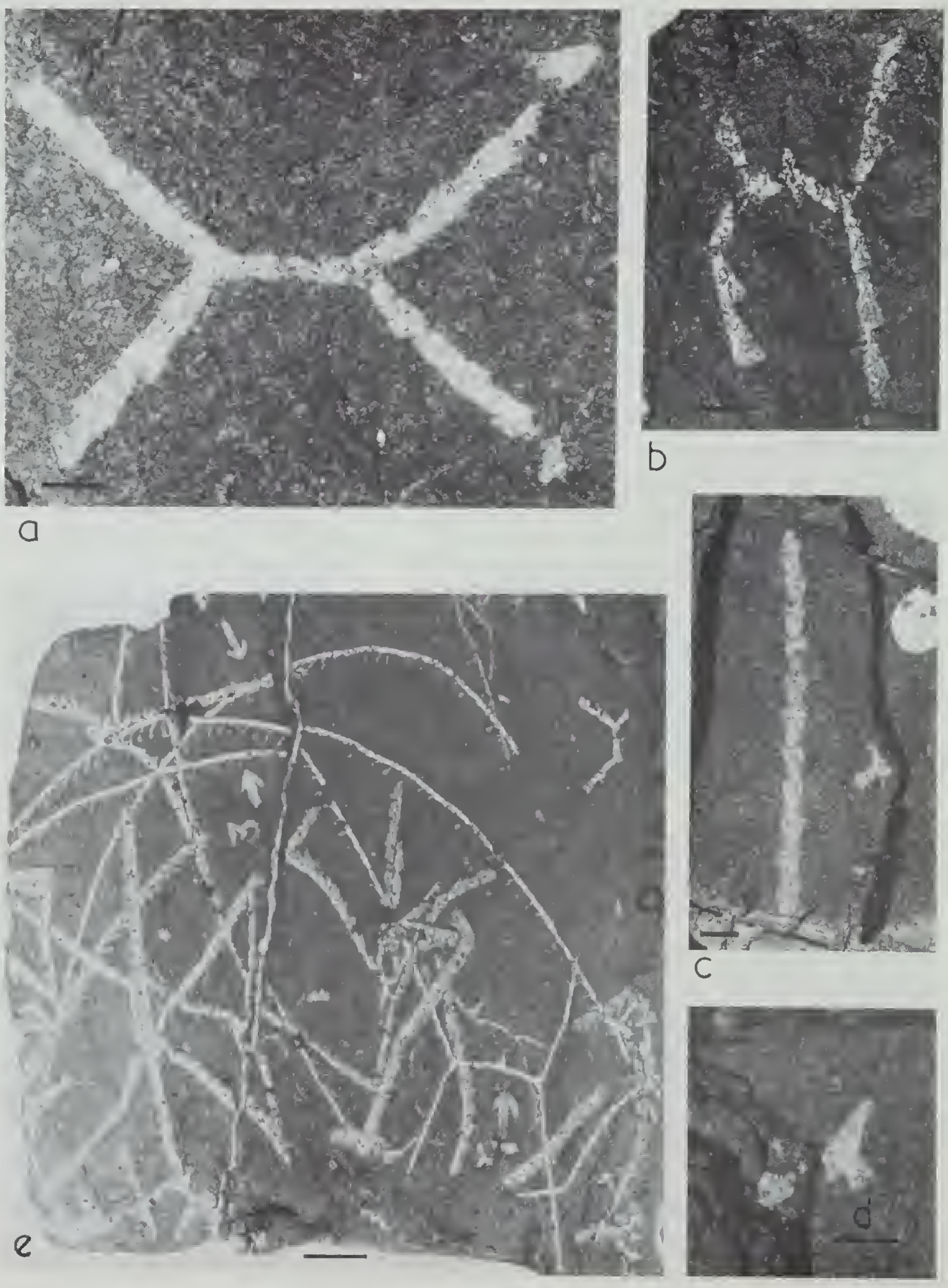

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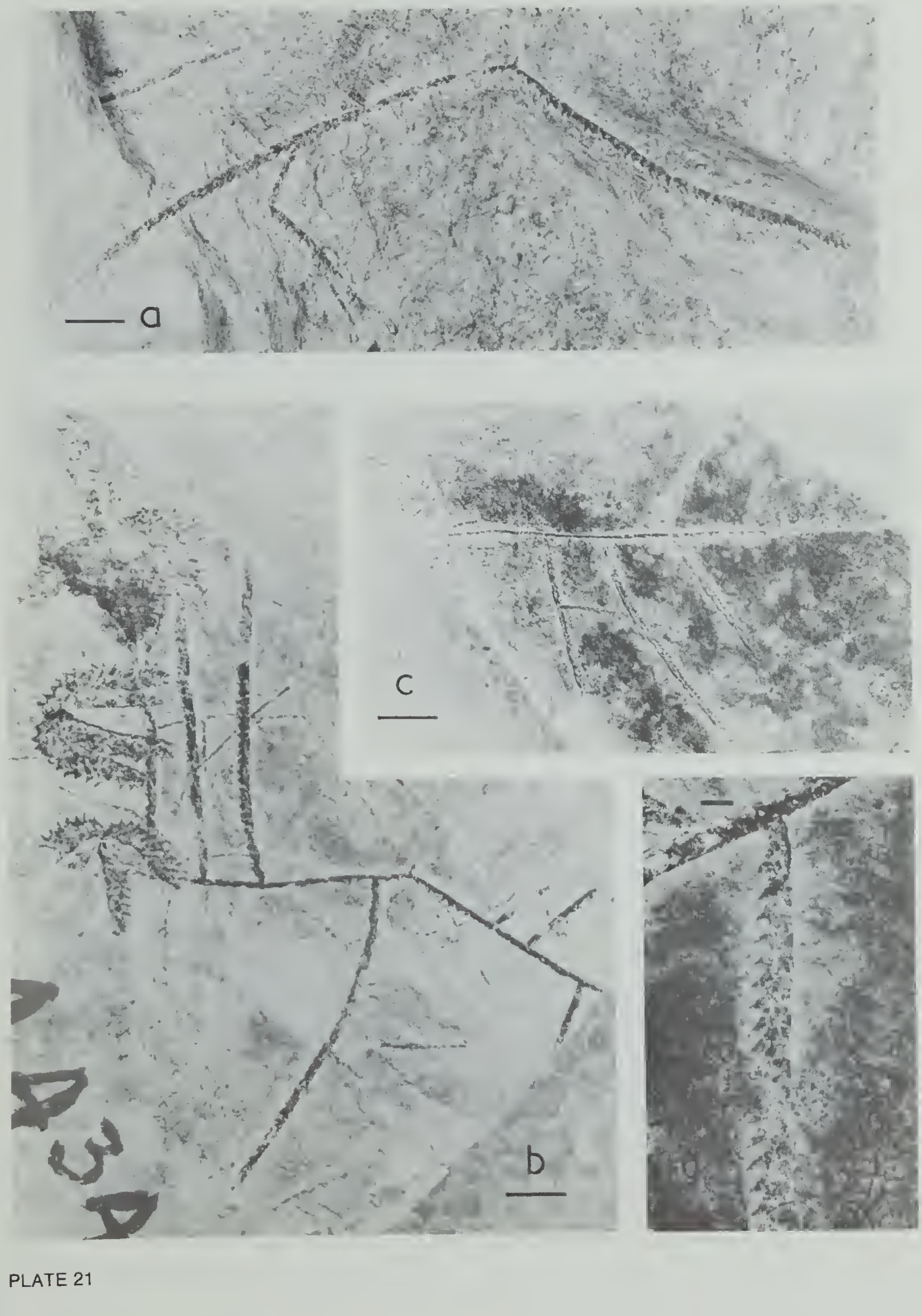

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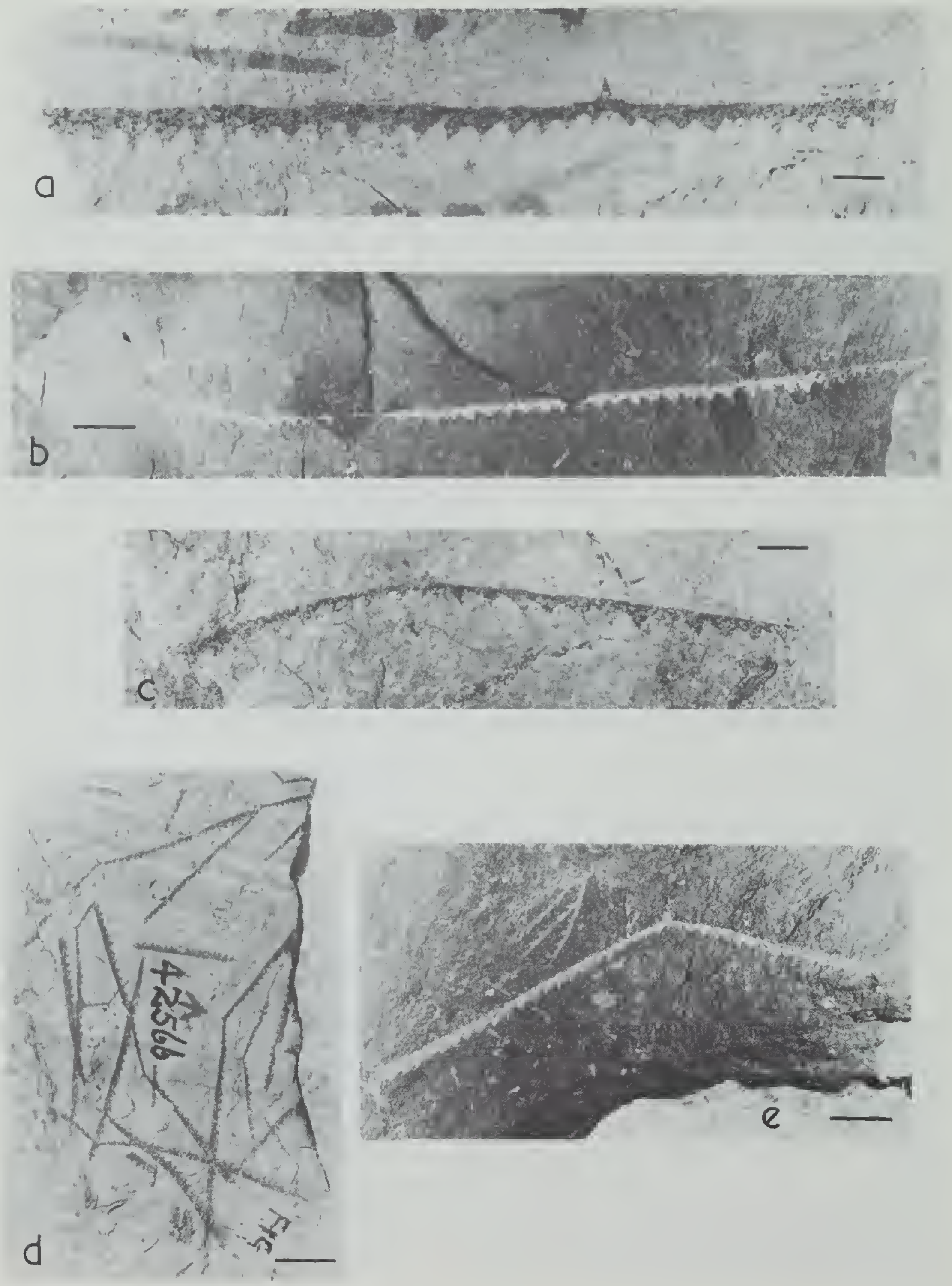

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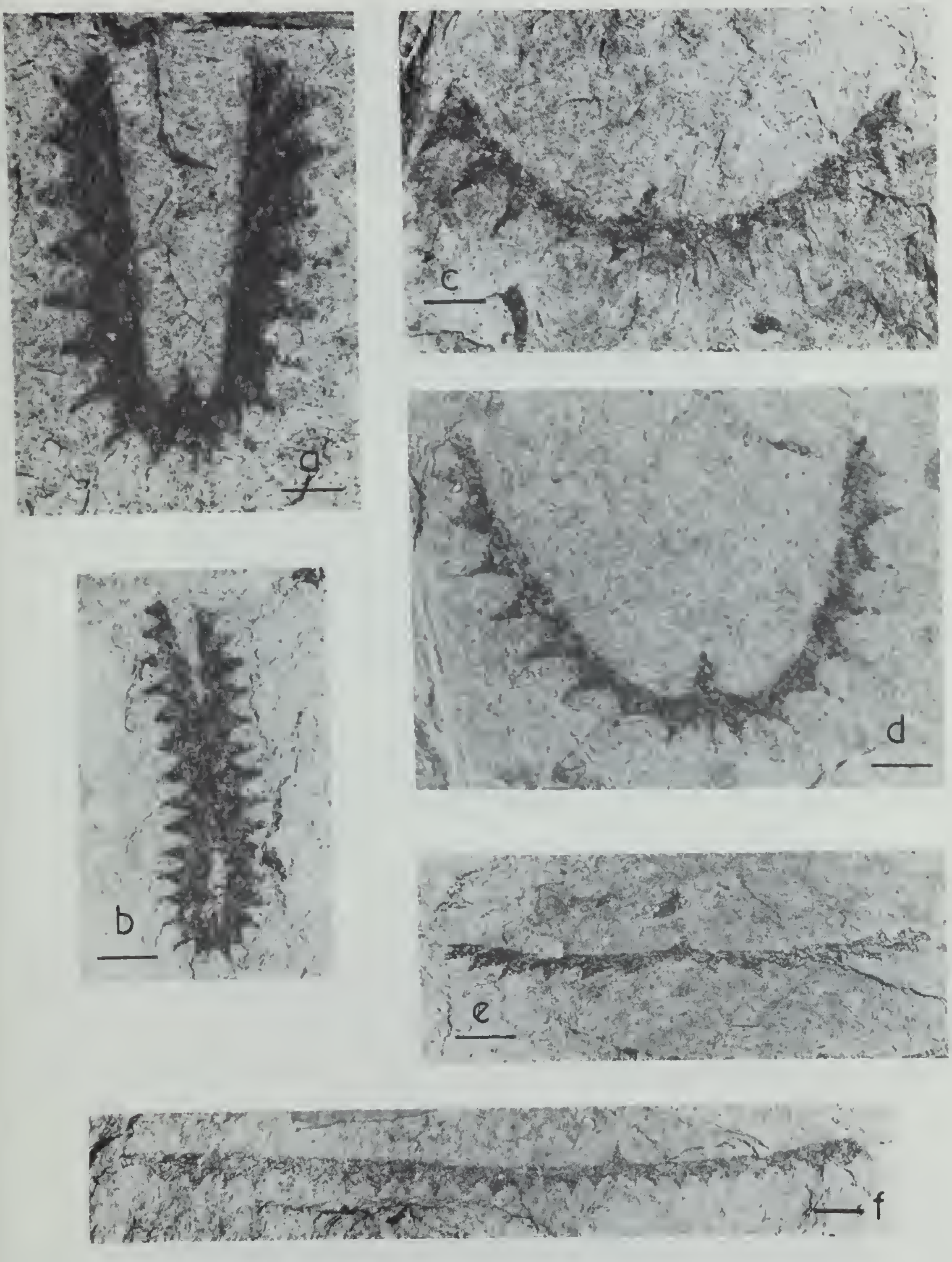

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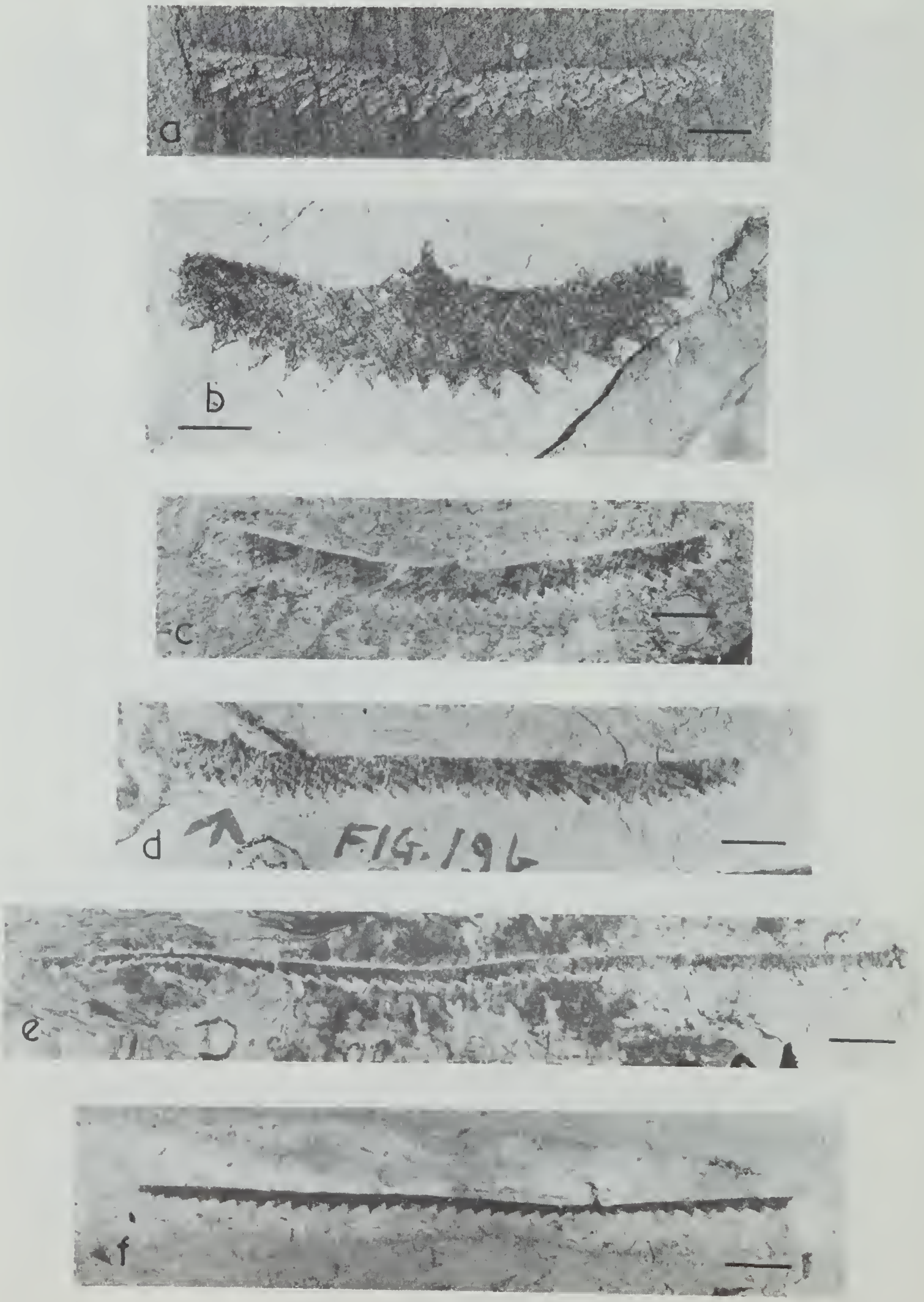

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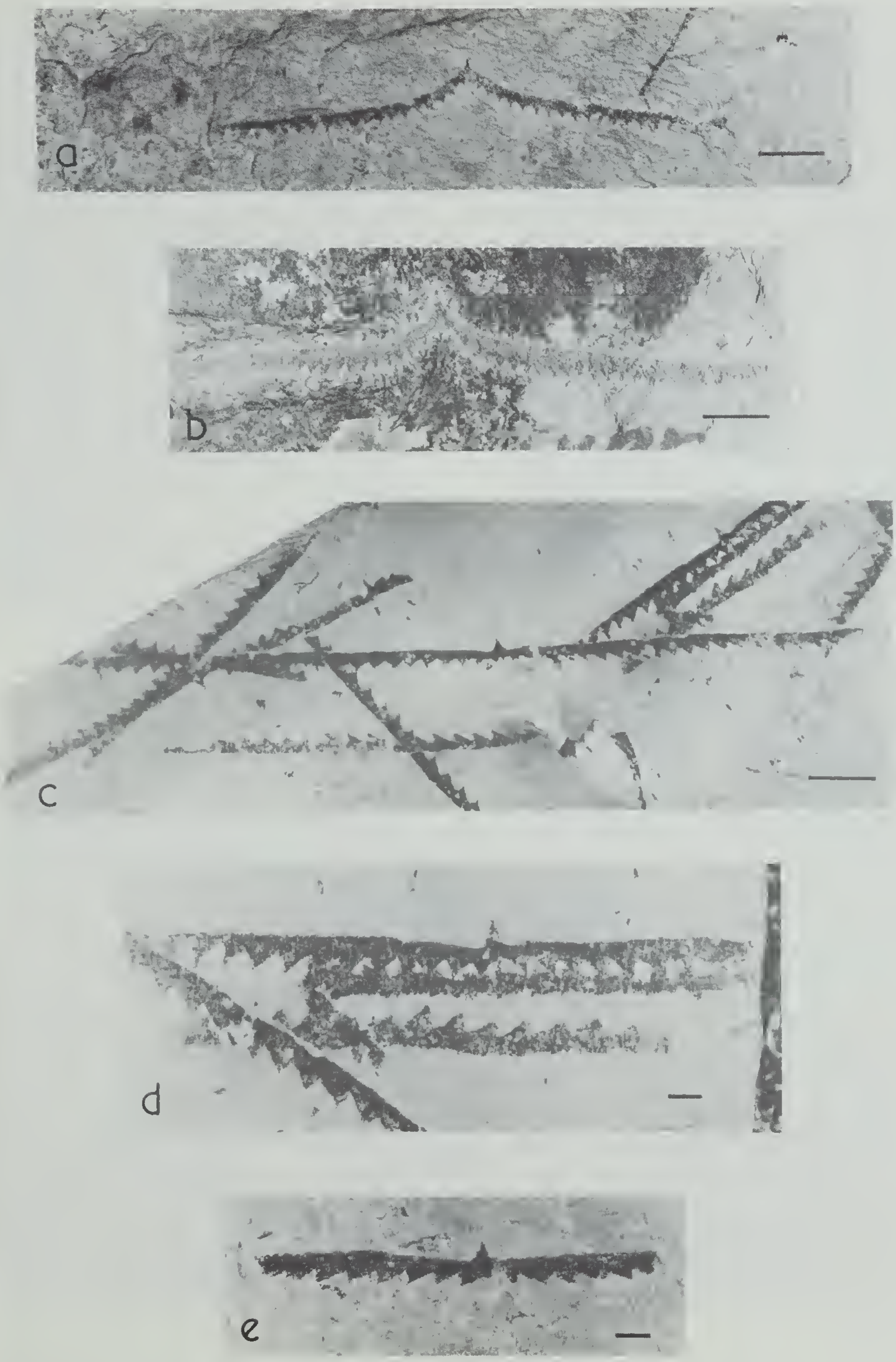

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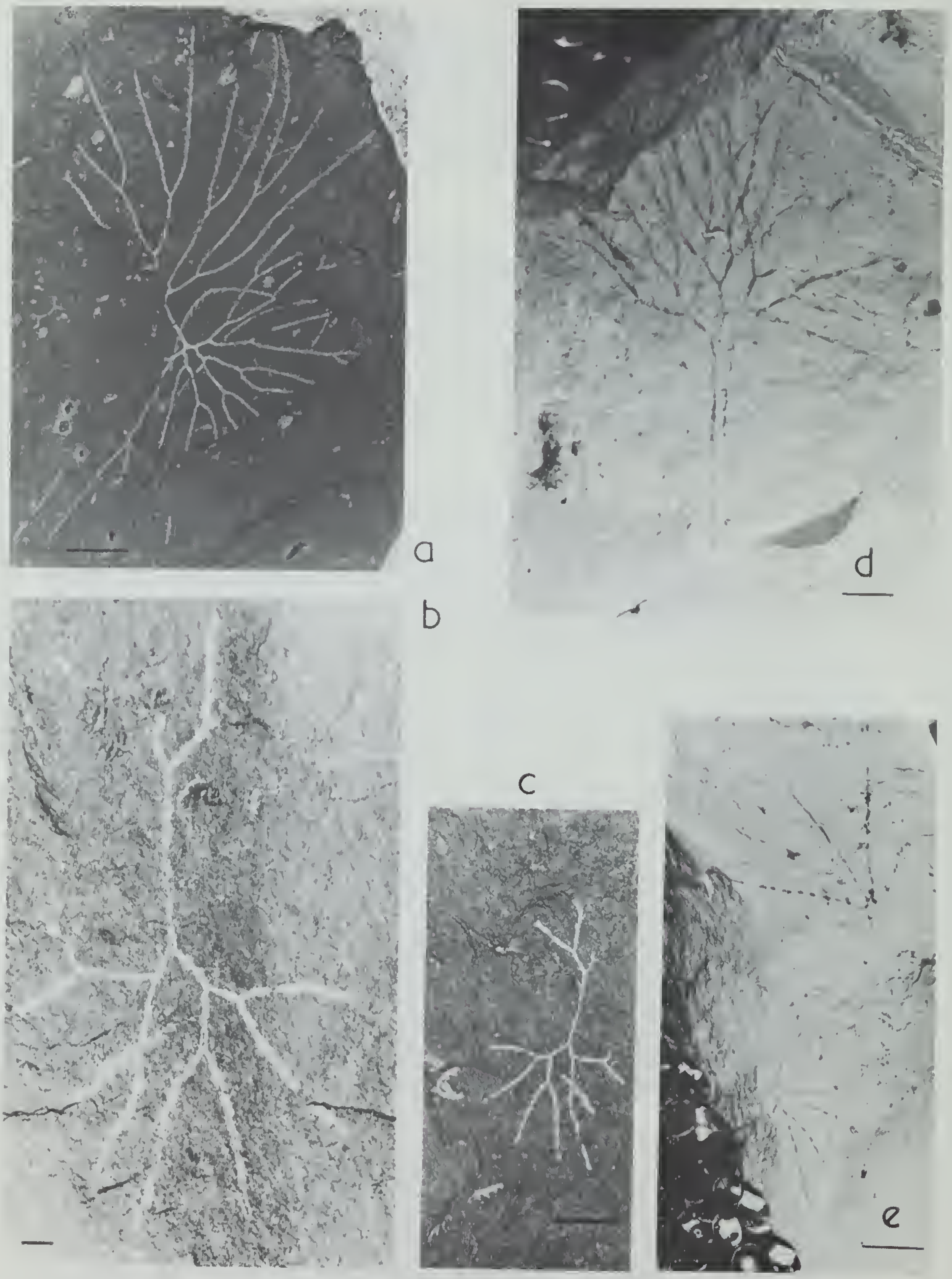

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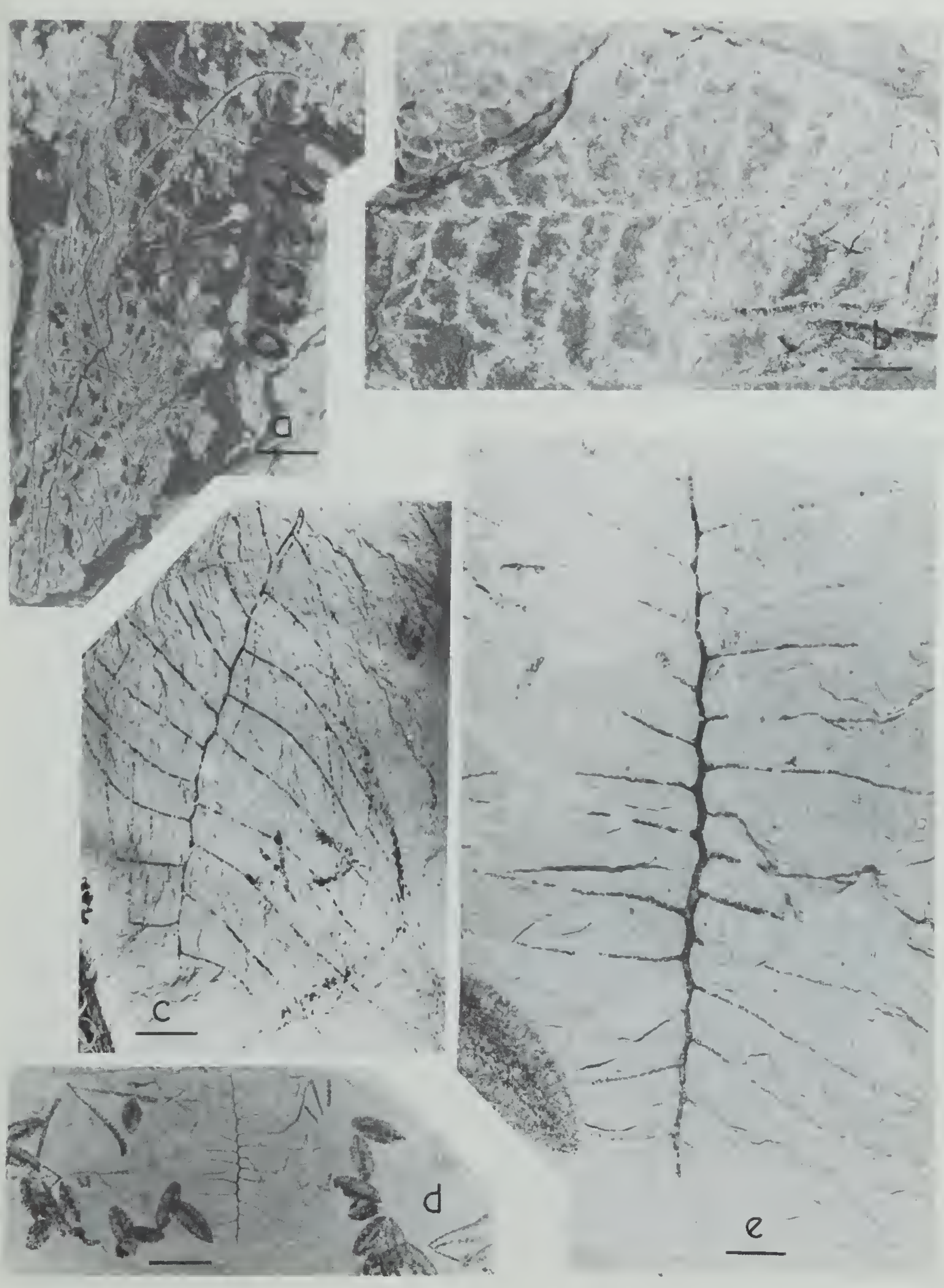

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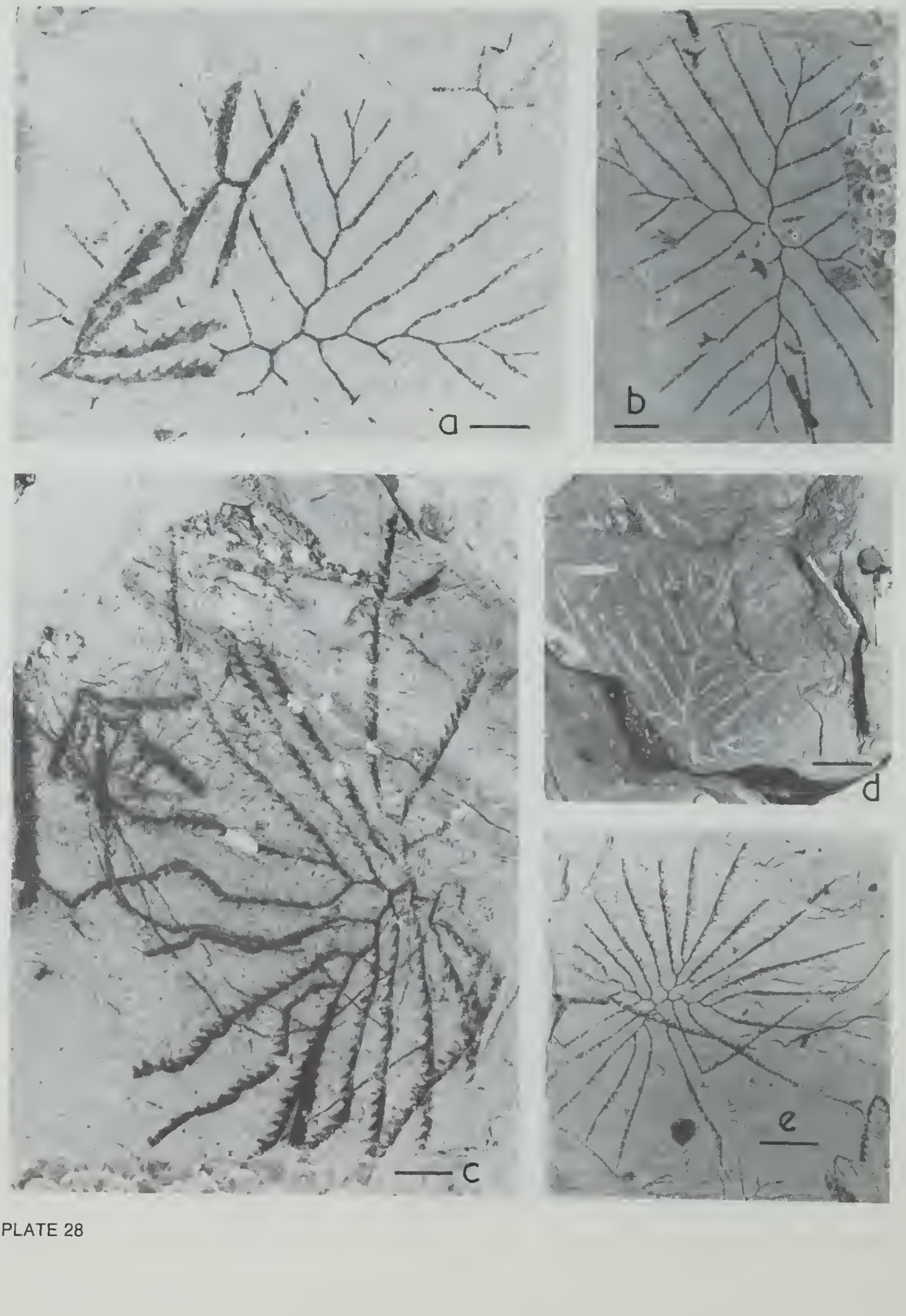

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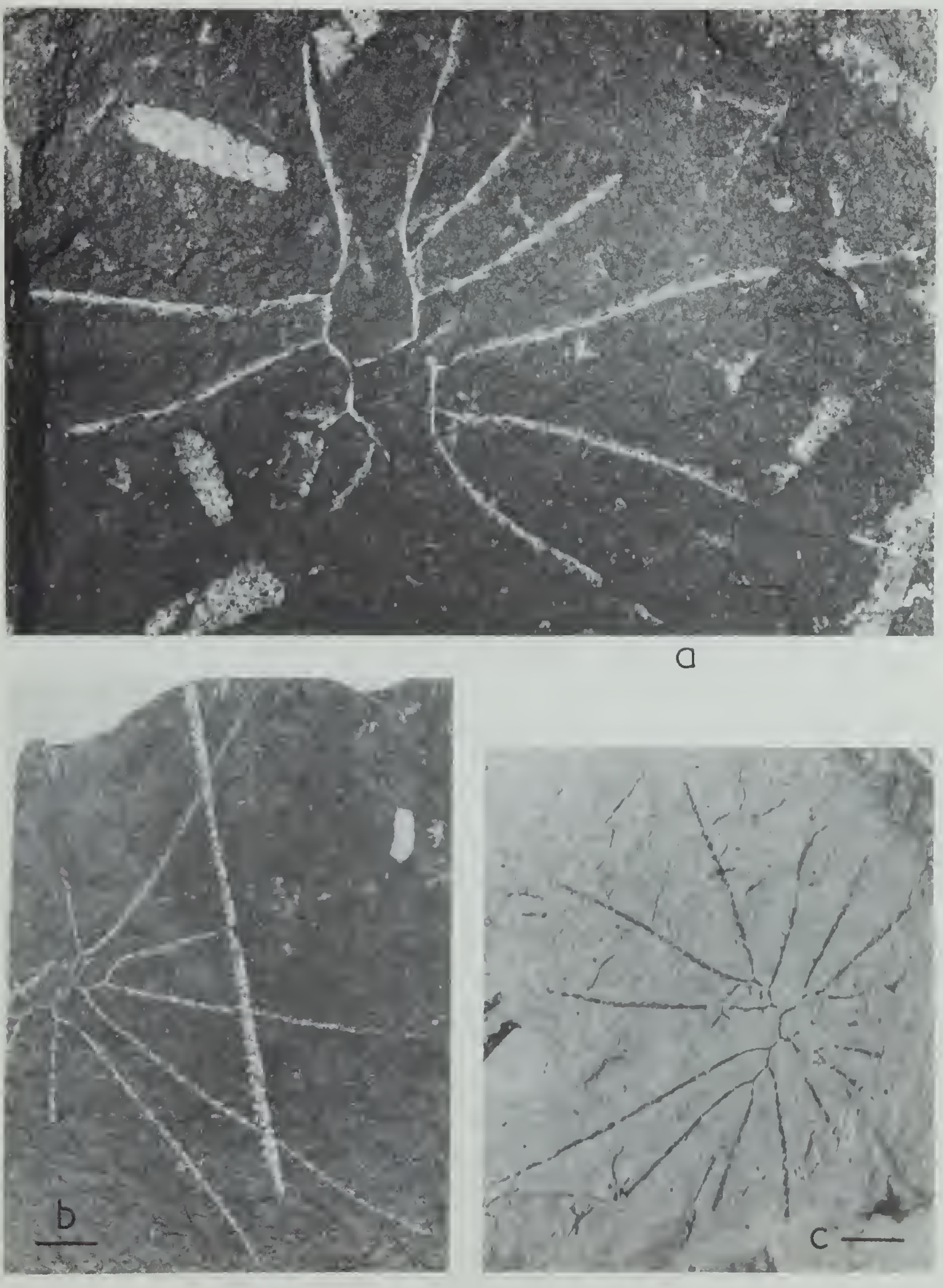
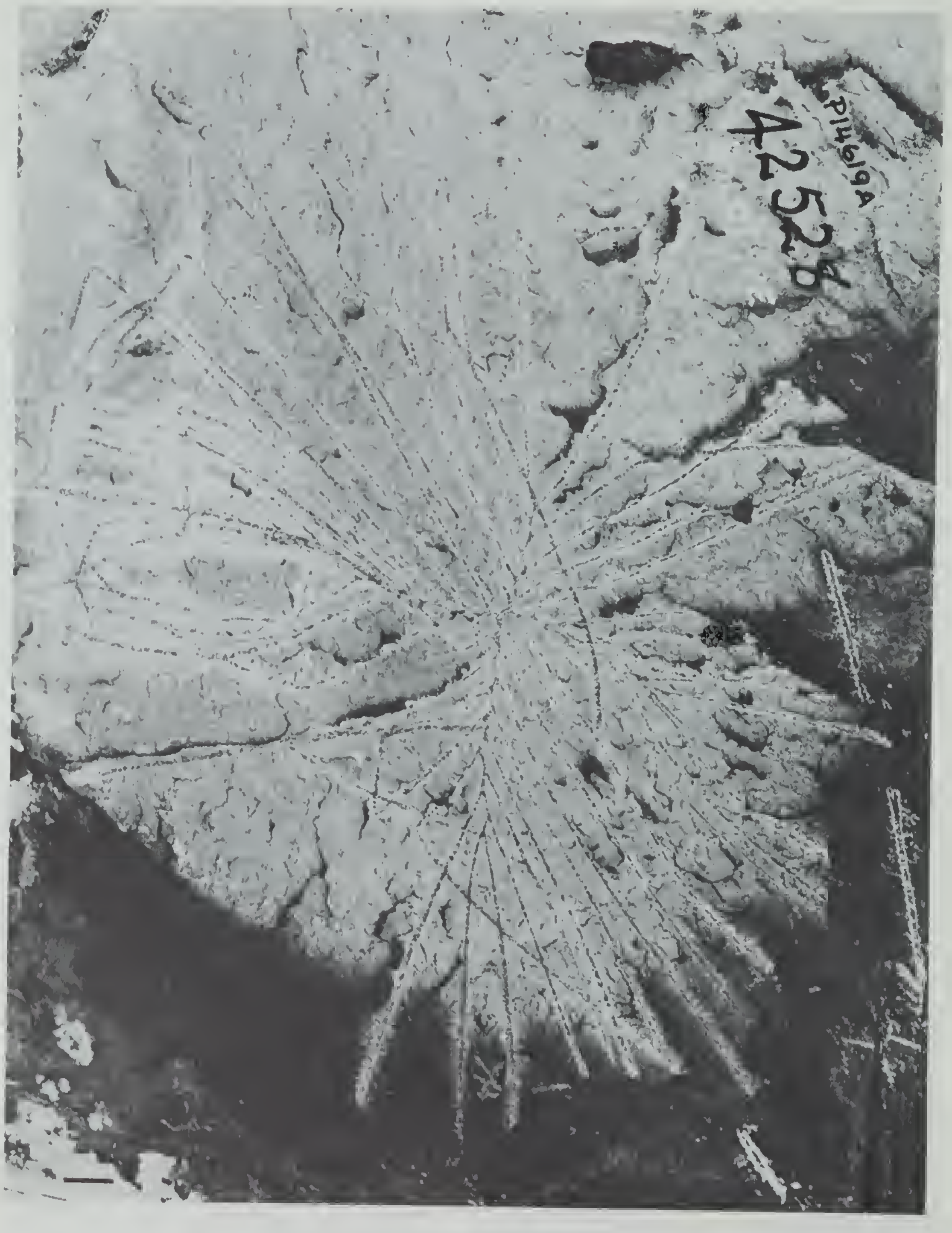


PLATE 29



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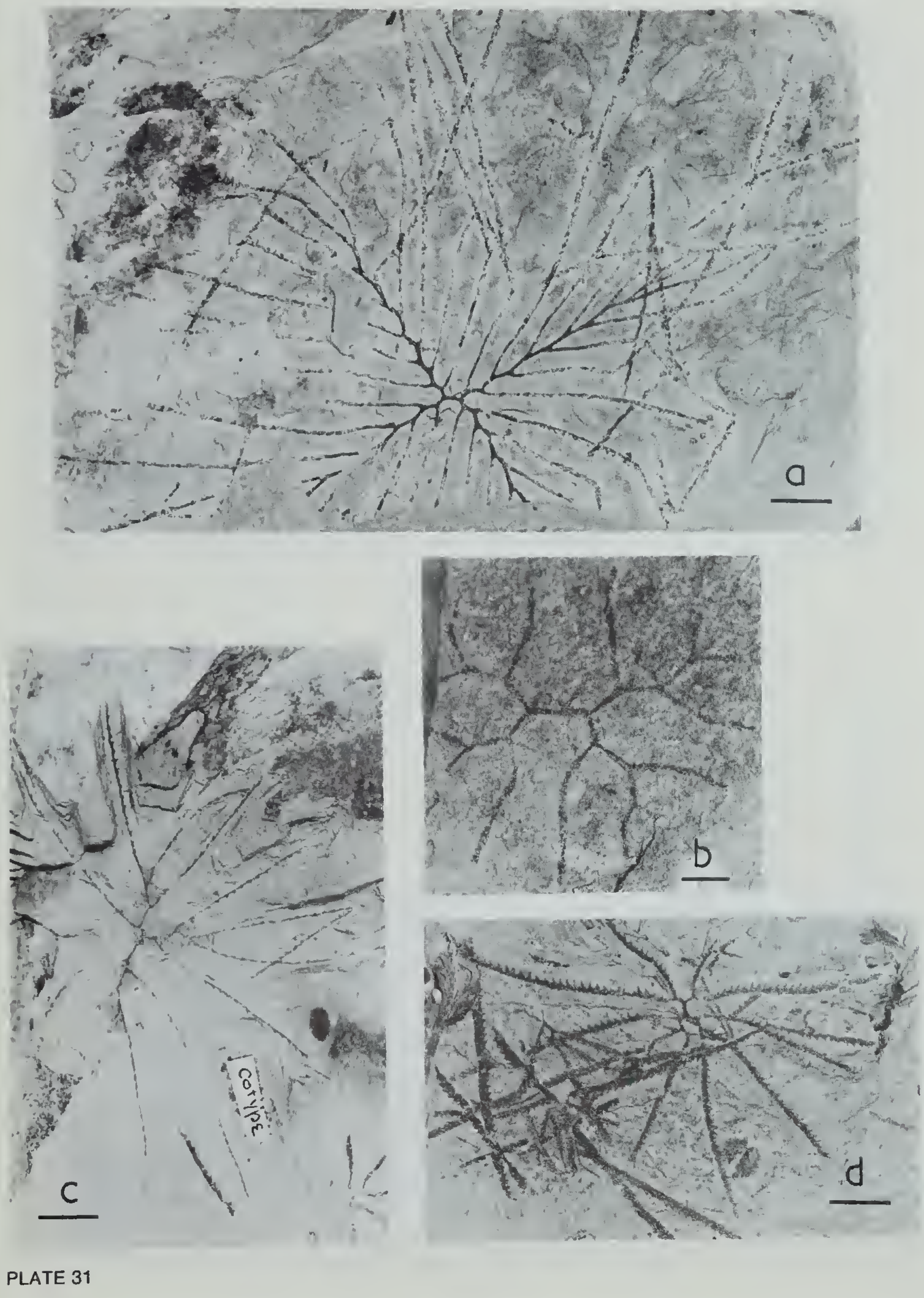

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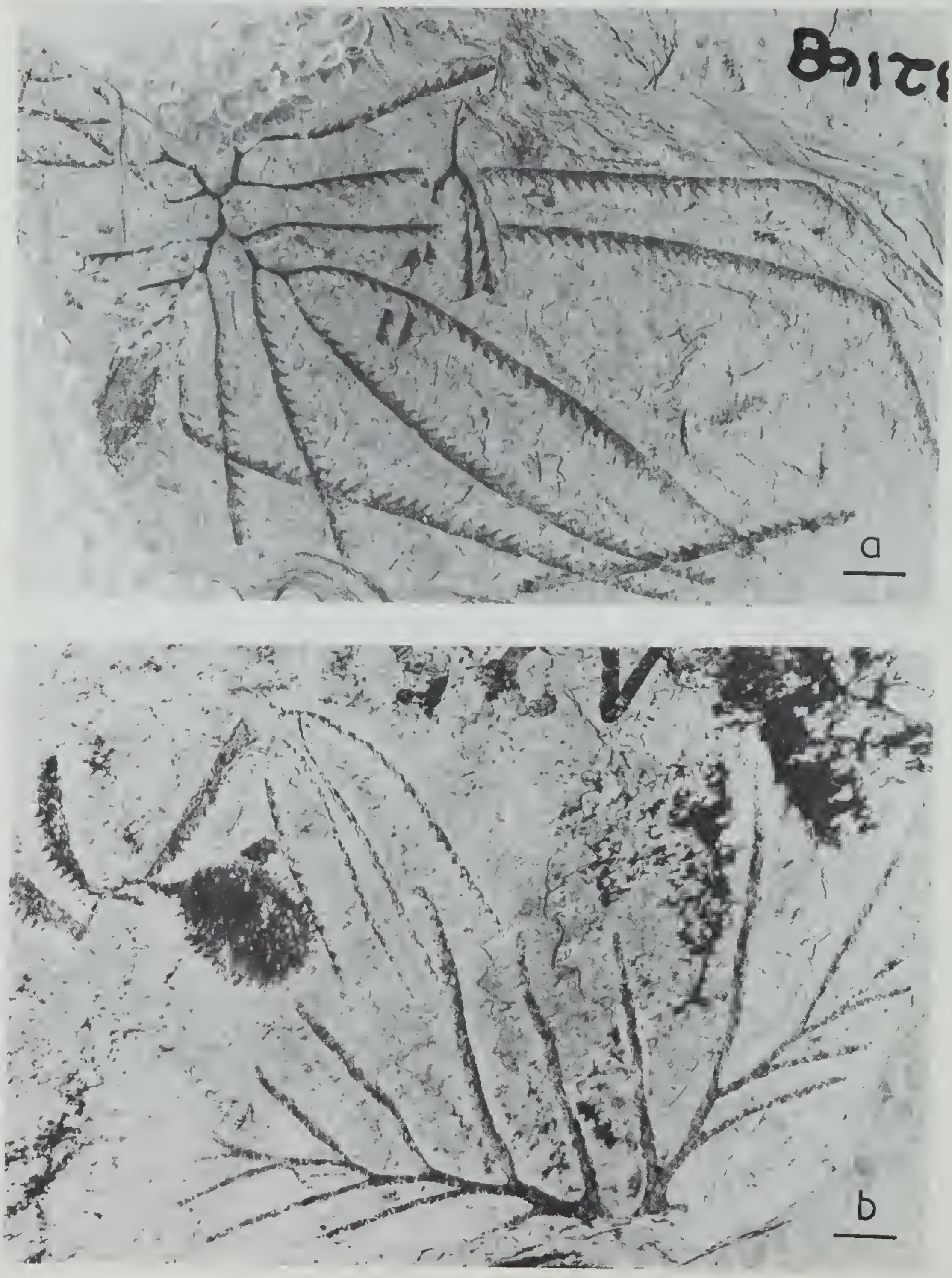

PLATE 32

PLATE 33

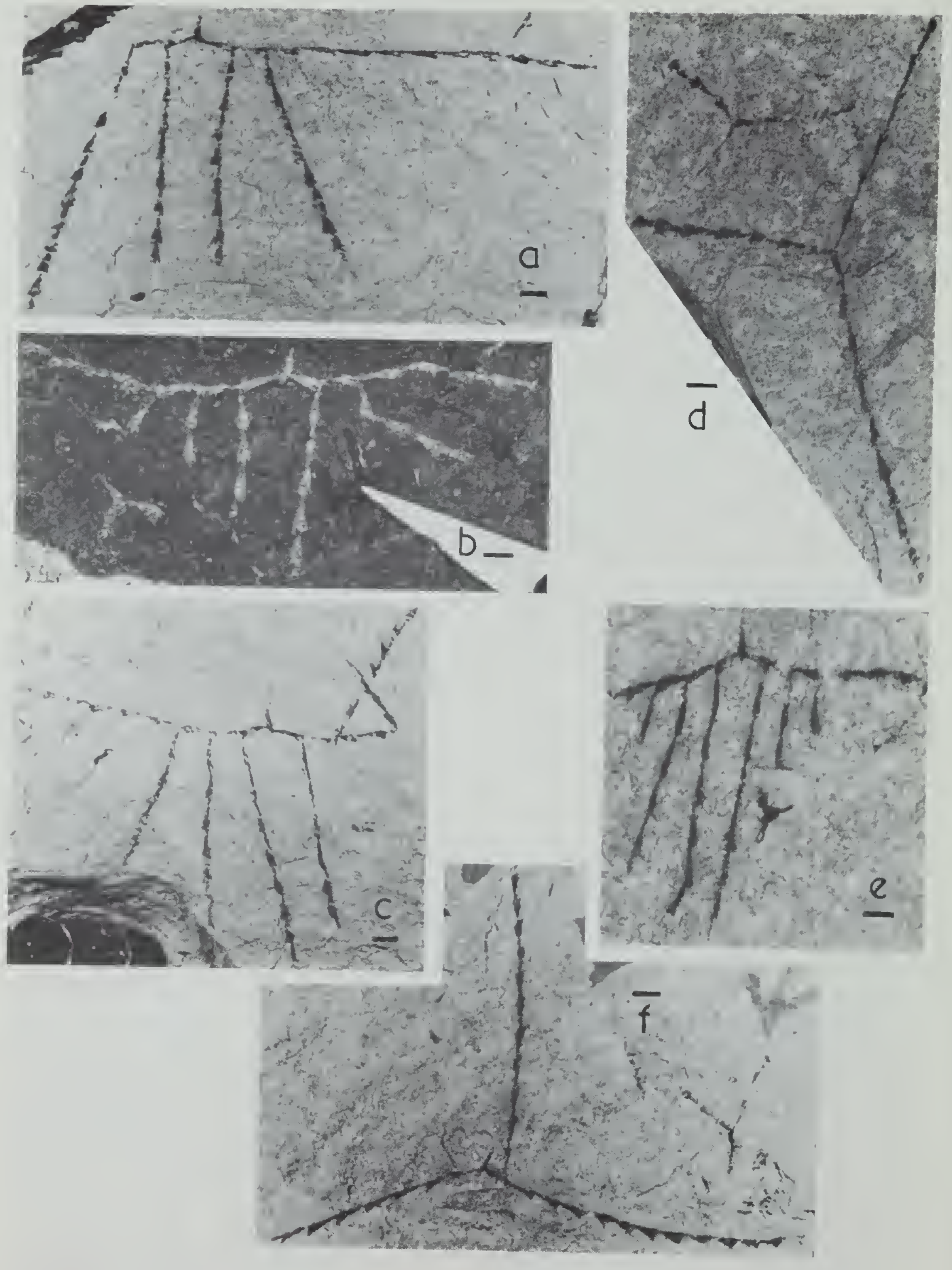

PLATE 34

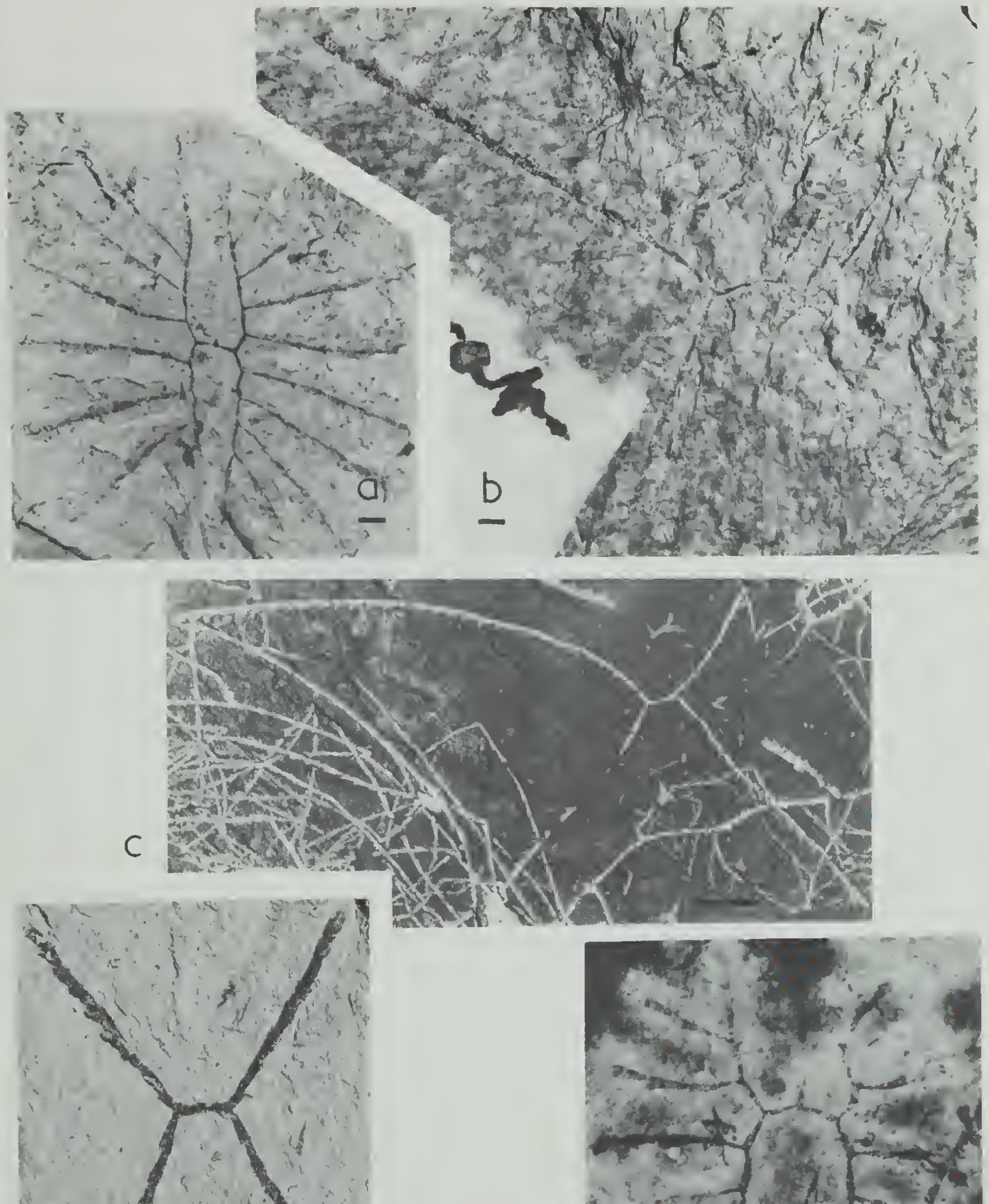

PLATE 35