

# APIOGRAPTUS GEN. NOV. AND THE ORIGIN OF THE BISERIAL GRAPTOLOID RHABDOSOME

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ABSTRACT. *Apiograptus* Cooper and McLaurin, gen. nov., with *Glossograptus? crudus* Harris and Thomas, 1935 as its type species, is a scandent biserial graptolite in the Yapeenian (upper Arenigian) of Australasia, and has early developmental stages which parallel those of *Pseudisograptus manubriatus* (T. S. Hall, 1914). The general aspect of its proximal region consequently resembles that of dichograptids whereas its distal region, in profile, resembles that of glossograptids. Details of development, inferred from growth stages, sparse structural evidence, and by analogy with *P. manubriatus*, suggest that the rhabdosome could be readily derived from that of *P. manubriatus* by a continuation of the tendency for the dorsal stipe margins to develop a loop at their points of flexure and to approach scandency. Such derivation is consistent with the stratigraphic relation and similarity of thecal form of the two species and is thought to reflect their phylogeny. The relationship of *Apiograptus crudus* to the glossograptids is uncertain and its postulated significance as indicating the origin of that group remains open. Closest affinities of the new genus lie with the dichograptids and it is thus included within the Family Dichograptidae.

*Pseudisograptus manubriatus* is discussed and some new material illustrated; four informal members are recognized, designated as forms A, B, C, and D. Growth stages of form C resemble those of *Apiograptus crudus* more closely than equivalent stages of the other forms.

*GLOSSOGRAPTUS? CRUDUS* Harris and Thomas, 1935 is a little-known, but truly biserial, graptolite somewhat resembling later biserial forms particularly the glossograptids. Yet its development resembles that of a dichograptid, *Pseudisograptus manubriatus* (T. S. Hall, 1914), more closely than that of any known biserial form. That it might represent a morphological intermediate between *Isograptus* Moberg and the glossograptids was suggested long ago by Harris and Thomas (1935, p. 303) and again later by Thomas (1960, p. 10), but without a detailed description of the species the suggestion has received little support (Bulman 1963, p. 408).

Some details of the structure and development of the rhabdosome can be inferred from new collections of the species which contain a range of growth stages, and probable development of the rhabdosome is discussed. Its unique proximal structure distinguishes it from all other biserial forms and warrants the erection of a new genus, *Apiograptus*. The genus is here considered to be most closely related to *Pseudisograptus* Beavis and is probably best regarded as a scandent dichograptid, rather than as a true glossograptid or diplograptid. Thus the species is thought to represent yet another line of evolution leading from a uniserial to a biserial rhabdosome but, unlike the other suggested lines—those giving rise to *Skiagraptus* Harris and *Oncograptus/Cardiograptus* Harris and Keble—may not be an evolutionary 'blind alley'. The glossograptid features, which led Harris and Thomas tentatively to refer the species to *Glossograptus* Emmons, may well indicate the origin of that otherwise cryptogenic group. However, on the presently available material, such speculation, with its implied retrogression from an isograptid to dichograptid type of development and platycalycal to pericalycal mode, is premature. Inasmuch as the close relationship

between *Apiograptus* and *Pseudisograptus* is asserted, the present paper accords with the view of Harris and Thomas.

*Pseudisograptus manubriatus* is discussed and some new specimens are figured to illustrate points of rhabdosome morphology and growth.

The material on which this discussion is based includes specimens from Chinaman's Creek, Muckleford, Victoria, type locality for three of the four type specimens of *Glossograptus? crudus*. The graptolites are preserved in soft weathered siltstone, and most are completely flattened showing only the rhabdosome outline. In a few specimens, the interthecal boundaries can be traced. The age of the Chinaman's Creek fauna is upper Yapeenian, Ya 2. *Apiograptus crudus* has been recorded from several other Victorian localities (Harris and Thomas 1935, p. 304; McLaurin, unpubl.) and is known from New Zealand. It appears to be restricted to a short interval of time in the late Yapeenian, and thus appears immediately before the appearance of the earliest glossograptids and during the waning of the isograptids.

The conclusion that *Glossograptus? crudus* warranted the erection of a new genus was arrived at independently by each of the writers. Preparation of the present paper has been by Cooper.

#### SCANDENT DICHOGRAPTIDS

The evolution of the biserial rhabdosome represents a major structural advance in development of the graptoloids (Bulman 1963, p. 406). The two major biserial groups—the Suborders Glossograptina Jaanusson, 1960, and Diplograptina Lapworth, 1880—each appear abruptly in the late Arenigian and each are without apparent immediate ancestors in the dichograptid fauna. A third, small, group of biserial forms appears at a similar horizon but its members are not generally thought to be related to either of the major groups. Despite their apparent lack of descendants and limited duration, members of the group are of special interest inasmuch as they bear closest affinity with the dichograptids and appear to have arisen from them. At least three phyletically distinct lines are represented, two at least of which (those leading to *Skiagraptus* and *Apiograptus*) appear likely to have involved a trend towards scandency in a biramous, uniserial rhabdosome, like a butterfly closing its wings in the analogy of Bulman. The nature of the third phyletic line, leading to *Oncograptus* and *Cardiograptus*, is uncertain.

Of the biramous genera, it was perhaps inevitable that *Isograptus*, with its already reclined stipes, has been the genus most frequently suggested to have given rise to biserial forms in this way. Harris (1933) noted the tendency for the dorsal stipe margins in the proximal region of the rhabdosome of *Isograptus victoriae maximodivergens* to approach each other in some variants of Yapeenian populations and suggested in his figure (p. 88) that this trend eventually gave rise to the initially biserial rhabdosome of *Oncograptus* and, by arrested development of the uniserial stipes, to the wholly biserial *Cardiograptus*. Bulman's (1936) later work on the structure and development of *Oncograptus* shows that such a derivation would involve major changes in the structure of the proximal region and a reversion to a stage of development generally regarded as more primitive than that known in *Isograptus*. The presence of a supplementary theca, 2<sup>1</sup>b, which could be regarded as the remnant of a reduced stipe, 1b,

led Bulman to suggest that the ancestor of *Oncograptus* was more likely to have been a tetragraptid than an isograptid. However, an isograptid derivation has again recently been advocated by Skevington (1968, p. 316) who claims a close, possibly specific, relationship between *Oncograptus* and *Pseudisograptus manubriatus*. The difficulties raised by Bulman's work still apply, and, as no further light has been shed on the problem, the origin of *Oncograptus* and *Cardiograptus* remains in considerable uncertainty.

In an apparently more definite development, the biserial rhabdosome of *Skiagraptus* was suggested by Harris (1933, p. 95) to have been derived, by concrecence of the dorsal stipe margins, from a small *Isograptus forcipiformis*-like form of the type associated with *Skiagraptus* in Yapeenian beds in Australia. Specimens thought to represent transitional stages were figured by Harris (1933, text-fig. 28) and Cooper (1973, text-fig. 17e, f, g) and Skevington (1968) has even suggested that the two forms, *Isograptus* cf. *forcipiformis* and *Skiagraptus* are variants of a single species. The only evidence of proximal structure described for *Skiagraptus* is that of Whittington and Rickards (1969) who deduce an earlier (theca 1<sup>1</sup> dicalycal) stage of development in their Newfoundland material than that likely in the isograptid ancestor. The Newfoundland form differs in several respects from the Australian *Skiagraptus gnomonicus*, however, and their relationship is uncertain.

A similar, though more complex, trend is here thought to have led from the manubriate isograptid, *Pseudisograptus manubriatus*, to the initially manubriate biserial form, *Apiograptus*, gen. nov. and is outlined below.

#### SYSTEMATIC DESCRIPTIONS

##### Genus PSEUDISOGRAPTUS Beavis, 1972

##### *Pseudisograptus manubriatus* (T. S. Hall, 1914)

Text-fig. 1a-g

For synonymy, see Cooper (1973).

*Discussion.* Several recent papers have described or discussed the species. From his study of an unflattened specimen from the Fort Peña Formation, Texas, Bulman (1968) clarified the proximal structure of the species, describing its development as *platycalycal*, and distinct from the *pericalycal* glossograptid type, but pointing out that with the pronounced curvature of its proximal thecae, it imitates the pericalycal (glossograptid) mode. Cooper (1973) described variation in rhabdosome form in New Zealand populations and listed the essential features of the species. Further features of rhabdosome morphology and the supposed affinity of the species has been discussed by Skevington (1968) and Beavis (1972). Comments here are confined to a comparison of the proximal structure with that of *Apiograptus*.

The genus *Pseudisograptus* was proposed by Beavis (1972) and is here used for the manubriate isograptid species, *Didymograptus manubriatus* T. S. Hall, *Isograptus dumosus* Harris, and *Isograptus hastatus* Harris. As pointed out previously (Cooper 1973) the manubriate species differ from all other isograptids in the structure of the proximal region and comprise a phylogenetically distinct group, although they possess isograptid proximal symmetry.

For convenience in the following discussion, four informal forms of *Pseudisograptus manubriatus* are recognized. Although they are linked by intermediates and are unlikely to prove to be distinct taxa, they do appear to represent end points along different lines of variation.

1. *P. manubriatus*, form A (text-fig. 1a-d), includes the type, as figured by Hall (1914, pl. 17, fig. 12) and specimens figured by Bulman (1968, fig. 1) from Marathon, Texas, and by Skevington (1968, fig. 2A) from the probable type locality—Willey's Quarry, Macedon, Victoria. It is distinguished by the pronounced shoulders and rapid expansion of the manubrium, which, from Bulman's (1968) work, results from the extreme concentration of thecal origins following the budding of thecae 1<sup>2</sup> and 2<sup>1</sup>. Stipes are variable in attitude but are generally strongly reclined. Growth stages are represented by specimens from Chinaman's Creek (fig. 1a, b) and from Willey's Quarry (Skevington 1968, fig. 1A-D).

2. *P. manubriatus*, form B, differs from form A in having a more gradually expanding manubrium without conspicuous shoulders and with a rather smooth-sided wedge shape and in generally having curved stipes. Distal thecae are extremely long and slender and stipe attitude increases from initially weakly reclined to distally strongly reclined. Mature rhabdosomes are known from Aorangi Mine, Nelson (Cooper 1973, fig. 22a-g, l), and from Willey's Quarry (Cooper 1973, fig. 22c). Growth stages are figured by Cooper (fig. 22b, g) and by Skevington (fig. 1E).

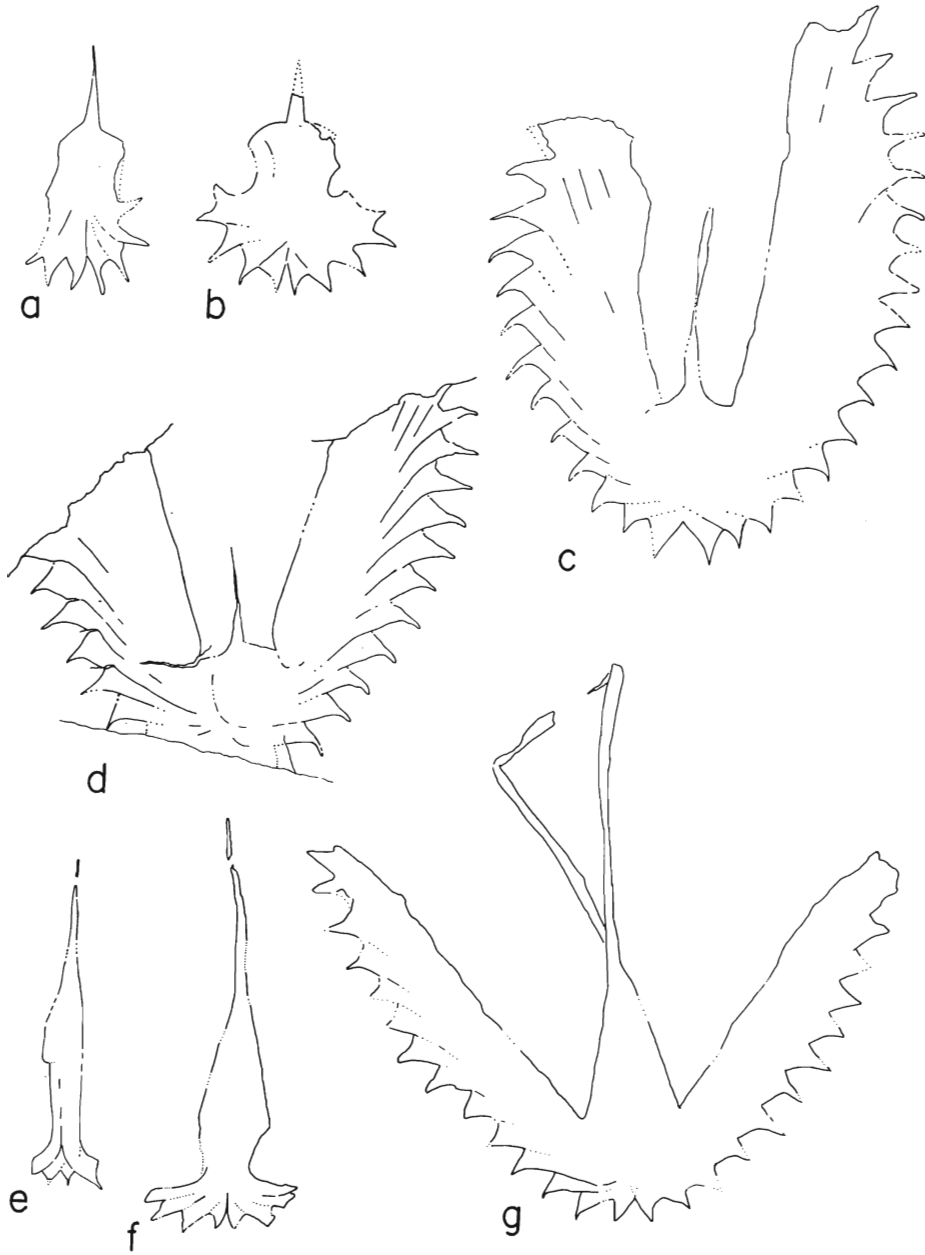
3. *P. manubriatus*, form C (text-fig. 1e-g) is distinguished by its extremely long sicula and massive wedge-shaped manubrium. Stipes are straight and moderately reclined. From Aorangi Mine, Cooper (1973) has figured mature specimens (fig. 22h, i) and growth stages (fig. 22j, k).

4. *P. manubriatus*, form D, bears nearly scandent stipes which 'encroach' upon or envelope a comparatively inconspicuous manubrium. Stipes are straight and broad and distal thecae are extremely long and slender. Mature forms have been figured from Aorangi Mine by Cooper (1973, fig. 22p) and Willey's Quarry, Skevington (1968, fig. 2B).

*Structure of the proximal region.* Proximal structure and arrangement of thecae are known in only form A (Bulman 1968). However, some features of rhabdosome morphology of the other forms can be explained by homology with form A. The following points are noted:

1. The sharp shoulders and rapidly expanding manubrium of form A equate with less conspicuous shoulders and more gradually expanding manubrium in forms B and D, and almost imperceptible shoulders and a wedge-shaped manubrium in form C. Thus the concentration of thecal origins is inferred to be less extreme in forms B, C, and D than in form A, and the growth paths of proximal thecae are likely to be somewhat less curved. However, the manubrium appears to be comprised of a similar number of thecal origins, approximately five or six pairs, in each of the four forms.

2. Although development takes place entirely on the reverse side, proximal thecae beyond the second thecal pair do not commence their growth strictly downwards in the plane of the rhabdosome, as they do in the non-manubriate isograptids, and in most other biramous dichograptids, but laterally towards the obverse side of the rhabdosome and then downwards in the first thecal series, or towards the reverse side



TEXT-FIG. 1. *Pseudisograptus manubriatus* (T. S. Hall) *sensu lato*. a-d. *P. manubriatus*, form A, from Chinaman's Creek, Muckleford, Victoria. Yapeenian, Ya 2. a, growth stage, NMV P28725. b, growth stage, GSV 64436a. c, mature rhabdosome, NMV P30513. d, mature rhabdosome, NMV P28730. e-g. *P. manubriatus*, form C, from Jimmy's Creek, north-west Nelson, New Zealand. e, growth stage, PR 434. f, growth stage, PR 398. g, mature rhabdosome, PR 403. All figures  $\times 5$  approx.

and downwards in the second thecal series (Bulman 1968, fig. 2*b, c*). The downward growth is along a curving path which is first directed towards the side of the opposite thecal series, then around and across to end with the thecal aperture facing away from the rhabdosome midline. Proximal thecae of one stipe are thus superposed in part upon those of the other, and the sicula is partially enveloped in simulated pericalycal style. The initial lateral growth is most marked in form A, where it is preceded by brief upward growth, but is probably developed to some extent in other forms.

3. At about the level of the 5th or 6th thecal pair the stipes change sharply in direction of growth from pendent to strongly reclined, the point of change marking the base of the manubrium. Because of the initial lateral deflection of thecae the dorsal stipe margin develops a lateral fold at the point of flexure and tends to grow back on itself before commencing its upward growth, forming a sharp notch in the dorsal stipe margin. The feature is clearly shown in Bulman's (1968) fig. 2*C* of stipe 1 and is thought to be present in both stipes of other specimens of form A (see Skevington 1968, fig. 2*A*, p. 316) and in specimens of forms C and D (Cooper 1973, fig. 22; Skevington 1968, fig. 2*B*). Indeed, the best interpretation of such specimens as those figured here (text-fig. 1*c, d*) and Skevington (fig. 2*A*) in which the manubrium margin apparently extends beyond its point of contact with the reclined stipe, is that the dorsal stipe margin actually grows around in a loop, recrossing the line of its earlier path. It is this tendency which is here regarded as of particular importance and which is thought to be developed to an extreme degree in the rhabdosome of *Apiograptus*.

#### Genus APIOGRAPTUS gen. nov.

*Type Species.* *Glossograptus? crudus* Harris and Thomas, 1935.

*Diagnosis.* Rhabdosome biserial; first four to six pairs of thecae with pronounced initial downward growth before curving away from midline and upwards; distal thecae straight and with apertural ventral margins extended into a prominent denticulate process.

*Species.* *Glossograptus? crudus* Harris and Thomas, 1935. *Glossograptus? crudus* var. *gisbornensis* Harris and Thomas, 1935. *Paracardiograptus abnormis* Yao, 1965.

*Discussion.* The essential feature of *Apiograptus* is the large number of proximal thecae—four to six pairs—with pronounced downward initial growth. The rhabdosome passes through developmental stages, including the formation of a manubrium, which are similar, at least in outline, to those of *Pseudisograptus manubriatus*, and development thus resembles that of a dichograptid rather than that of any known diplograptid or glossograptid. Details of proximal structure and development are discussed in more detail in the description of *Apiograptus crudus*, the type species. *Glossograptus? crudus* var. *gisbornensis* Harris and Thomas is a closely related form and may prove, when the full range of variation in the type species is known, to be a synonym of *crudus*, *sensu stricto*.

*Paracardiograptus abnormis* Yao (1965, p. 115) from the Tzishui Valley, Hunan, closely resembles *Apiograptus crudus*. It is found with *Allograptus* sp., *Holmograptus? orientalis* Mu, *Paracardiograptus intermedius latus* Yao, representing the

*Didymograptus hirundo* Zone of Yenchi, Hunan, a similar horizon to its Australasian occurrence.

Of the two forms (*Glossograptus? crudus* and *G.? crudus* var. *gisbornensis*) available for nomination as type species, *G.? crudus* is chosen because its morphology and growth stages are better known.

*Comparison with other genera.* *Skiagraptus* Harris, as represented by the genotype *S. gnomonicus* Harris and Keble (see Skevington 1968, fig. 5d) shows, in its proximal region, none of the structural complexity of *crudus* and there is no resemblance in thecal form. The Newfoundland specimens referred to *Skiagraptus* by Whittington and Rickards (1969, p. 814, figs. 9, 10) resemble the Australasian form more closely, but differ markedly in the form, curvature, and direction of growth of proximal thecae and in the fusion of the apertural processes of the sicula and theca 1<sup>1</sup>.

Like *Skiagraptus*, *Cardiograptus* Harris and Keble apparently differs fundamentally in the lack of proximal complexity and in thecal form, though until the type species, *C. morsus* Harris and Keble is known in more detail, affinities of the genus remain in dispute (see Skevington 1968, p. 316; Mu and Lee 1958). In *Paracardiograptus* Mu and Lee (1958) there is a suggestion of proximal complexity in the outward deflection of initial thecae but the deviation from *Cardiograptus* is apparently not great, and was not thought to warrant separation as a distinct genus by Bulman (1970, p. V116).

From the diplograptids and glossograptids, the new genus is distinguished by the downward growth of many of its proximal thecae and their gradual transition from a pendent to scandent attitude.

*Stratigraphic range.* The type species is confined to a narrow interval in the upper Yapeenian (Ya 2, Thomas 1960). *Apiograptus gisbornensis* is found at a similar, or slightly higher, level in the upper Yapeenian. Range of the genus thus appears to be within the upper Yapeenian.

### *Apiograptus crudus* (Harris and Thomas, 1935)

Text-fig. 2a-h

- 1935 *Glossograptus? crudus* Harris and Thomas, pp. 303-4, fig. 1, no. 13; fig. 2, nos. 15-17.  
 1960 *G.? crudus*, Thomas, fig. 62.  
 1965 *Paracardiograptus abnormis* Yao, pp. 114-115, pl. 1, fig. 8 1-d; text-fig. 3.

*Lectotype.* Of the four syntypes figured by Harris and Thomas, those of fig. 1, no. 13, and fig. 2, no. 17 are immature; that of fig. 2, no. 16 is apparently missing (C. Abele, pers. comm.). The specimen of fig. 2, no. 15 (no. 37406 in the Geological Survey of Victoria), though somewhat broader than average, is therefore nominated as lectotype.

*Horizon.* Upper Yapeenian, Ya 2.

*Description.* The mature rhabdosome is biserial, short, and squat, the largest specimens being only 14 mm long. Most specimens have a prominent virgula which extends beyond the somewhat emarginate distal end. Proximal width apparently is variable, ranging from 2.5 to 5 mm, and most rhabdosomes have a slight distal taper. The proximal margin is broadly rounded and proximal thecae change only gradually from pendent to obliquely upward in direction of growth. The sicula is about 8 mm long and probably about 0.6 mm wide at the aperture, though the apertural region is partly obscured by theca 1<sup>2</sup>. In profile view the sicular apertural margin is concave in

outline. Theca 1<sup>1</sup> appears to arise from near the apex of the sicula and grows to approximately the same length, the apertural regions of the two facing away from each other. Subsequent development is very similar to that in *Pseudisograptus manubriatus*, particularly form C, with the concentration of thecal origins and long, downward-growing early thecae forming a large wedge-shaped manubrium. The point of origin of theca 1<sup>2</sup> is inferred to correspond to the rounded shoulder on the manubrium, about 2.6–3.0 mm below the apex of the sicula. The growth paths of proximal thecae can be partially traced in a few specimens (text-fig. 2*b, d, g*) and correspond well with the assumption that proximal structure is essentially similar to that of *P. manubriatus*.

Distal thecae are long and narrow, of low inclination, and are spaced about 5 in 5 mm. Apertural margins, in biprofile view, are inclined to the stipe axis nearly at right angles and their ventral margins are extended, together with the free ventral walls, into a prominent projecting process. Slightly raised lateral lappets are inferred from the commonly arched outlines of apertural margins. Spines of glossograptid type were not observed.

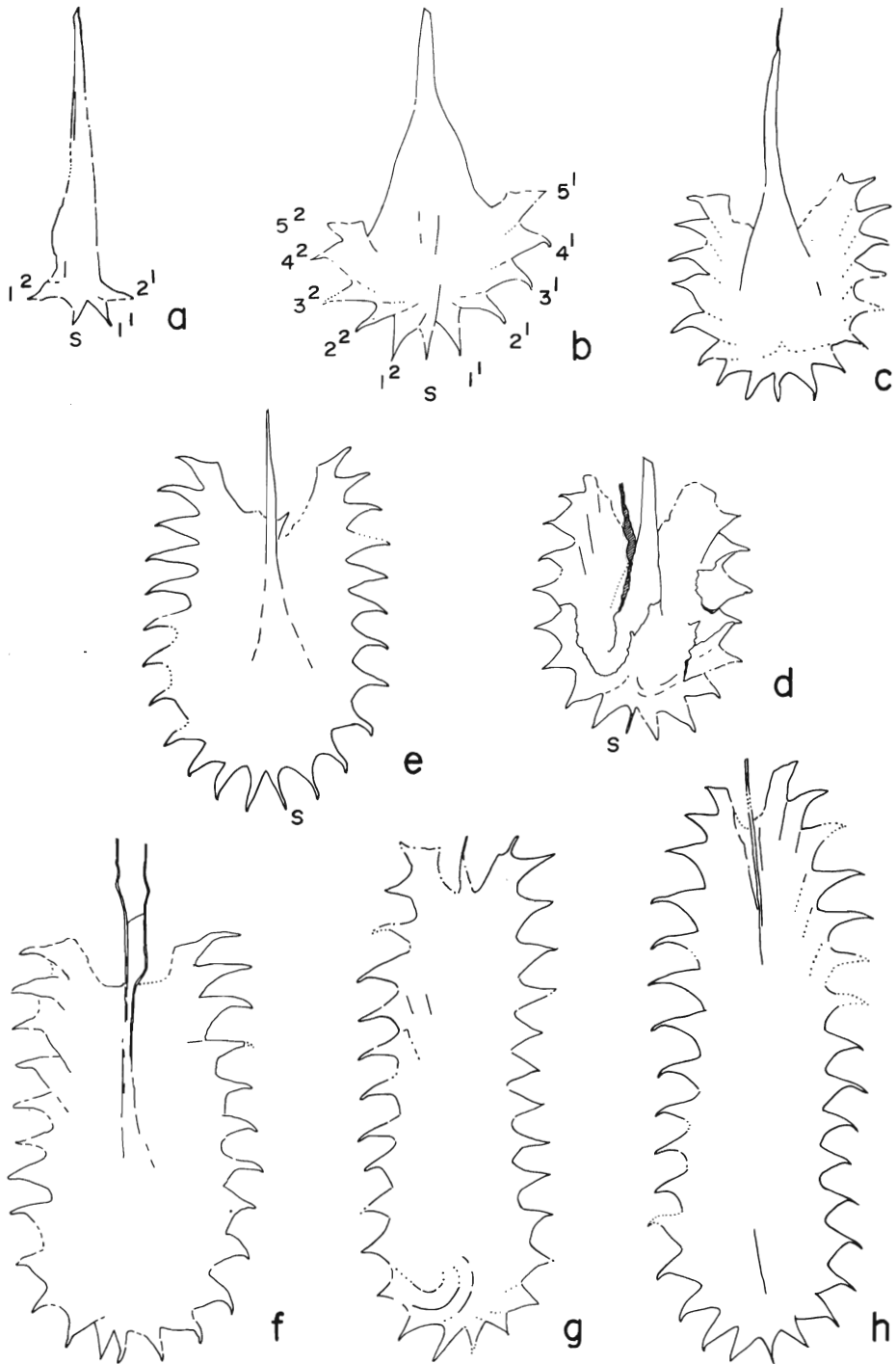
*Growth series and inferred structure.* The earliest growth stages (text-fig. 2*a, b*) show the distal outward deflection of the initial thecae and the formation of a large wedge-shaped manubrium comprised of the proximal portions of at least the first five thecal pairs. Development to this point presumably takes place on the reverse side. The sharp change to scandent growth immediately follows, the dorsal stipe margin apparently curving around and back, across the lateral face of the manubrium to about the region of the midline before attaining full upward growth (text-fig. 2*c, d*). During subsequent growth, the stipes remain in contact firstly with the manubrium and then with each other. From a specimen preserved with slight relief (text-fig. 2*d*), the two stipes appear to lie on opposite sides of the manubrium and later stages suggest that they may even partly overlap each other laterally, in an incipiently monopleural arrangement. If correctly interpreted, the sicula and upper part of the manubrium would thus be enveloped by the scandent stipes in a simulated pericalycal fashion, following an otherwise presumably platycalycal initial development.

In the final stages of growth the rhabdosome has assumed, except for the lack of spines, a more 'normal' glossograptid outline (text-fig. 2*g, h*).

The arrangement of proximal thecae and their sequence of budding cannot be directly determined in any Victorian specimen. However, the apparently close similarity of growth stages with equivalent stages in *P. manubriatus* lead to the assumption that the patterns of growth of proximal thecae are essentially similar in the two forms. The assumption is consistent with the inferred close genetic relationship of the two forms outlined below and with the comparatively few structural details gleaned from the Victorian specimens.

The development pattern, thus interpreted, can be readily derived from the *manubriatus* pattern by a continuation of the tendency in *manubriatus* for the dorsal stipe margin, or common canal, to grow around in a loop to the stage where it reaches the rhabdosome midline and produces a scandent rhabdosome. If the resulting rhabdosome is correctly interpreted as incipiently monopleural, it is unusual in





TEXT-FIG. 2. *Apiograptus crudus* (Harris and Thomas). Growth series from an early stage with sicle and initial three thecae to mature rhabdosome, from Slaty Creek, north-west Nelson, New Zealand (2a), and Chinaman's Creek, Muckleford, Victoria (topotypes, 2b-h). Yapeenian, Ya 2. a, PR 441. b, NMV P30514. c, NMV P30515. d, NMV P30516. e, NMV P30517. f, NMV P30518. g, GSV 64430 b. h, NMV P27485. All figures  $\times 6$  approx.

s = sicle,  $1^1$   $1^2$  = theca  $1^1$ ,  $1^2$ , etc.

combining this feature with platycalycal development, monopleural stipe arrangement otherwise being confined to the exclusively pericalycal Glossograptina.

*Discussion.* In their original description Harris and Thomas (1935) figured two mature specimens and one immature specimen from Chinaman's Creek and one immature specimen from Strathfieldsaye. Structure of the rhabdosome was not discussed. The specimens described here, from Chinaman's Creek, match Harris's and Thomas's material well.

Harris and Thomas commented on the resemblance of the form, particularly in its 'juvenile state', to *Isograptus* and suggested that it might provide a link between *Isograptus* and *Glossograptus*. This suggestion received strong support from the description of two pyritized specimens from the *Glyptograptus austrodentatus* Zone of Bendigo, Victoria, with clearly monopleural stipe arrangement, by Beavis (1962). Unfortunately, from his figures and description, the Bendigo specimens cannot be definitely identified with *crudus*. However, from the present work, the rhabdosome is inferred to have at least an incipient monopleural stipe arrangement and further glossograptid features are the long, straight, narrow thecae with ventral apertural processes. Its closest relative, however, is here thought to be *Pseudisograptus manubriatus* for the following reasons:

1. As in *manubriatus*, the sicula and first theca are long and form a symmetrical pair (or nearly so) unlike those of the glossograptids.
2. Development is inferred to be like that of *manubriatus* and unlike that known in any other biserial form, with many downward-growing thecae and the formation of a large manubrium.
3. Thecal form and apertural outline are closely similar to those of *manubriatus*.

The *Apiograptus crudus* rhabdosome, as pointed out above, can be readily derived from the rhabdosome of *Pseudisograptus manubriatus*, and such a derivation is supported by the stratigraphic relation of the two forms. Contemporaneous populations of *P. manubriatus* show a wide range of morphologic variation and a marked tendency for the stipes to fold back on themselves and approach scandency.

*Apiograptus* is therefore probably best regarded as a scandent dichograptid rather than as a true glossograptid (or diplograptid). Comments on whether or not it lies phyletically between the two sub-orders, as suggested by Harris and Thomas (1935), must await the description of better-preserved material.

#### CONCLUSIONS

1. Four informal forms of *Pseudisograptus manubriatus* can be recognized and are designated, forms A, B, C, and D. In at least three of the forms, A, C, and D, there is a tendency for the dorsal stipe margin to fold back on itself at the point of flexure.
2. *Glossograptus? crudus* Harris and Thomas represents a distinct genus here named *Apiograptus* Cooper and McLaurin, gen. nov., and is designated as its type.
3. *Apiograptus* is a scandent dichograptid with an apparently similar development plan to that of *Pseudisograptus manubriatus*, but with some features of the glossograptids. The biserial *Apiograptus crudus* rhabdosome is thought to have been derived from that of *Pseudisograptus manubriatus* by a continuation of the tendency (1) noted above.

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