TAXONOMY AND EVOLUTION OF
ISOGRAPTUS MOBERG IN AUSTRALASIA

by R. A. COOPER

ABSTRACT. *Isograptus* Moberg is one of the most diverse, abundant, and stratigraphically useful graptolite genera in Australasia. It first appears in the Chewtonian stage (mid Arenigian), dominates the faunas of the following Castlemainian and Yapeenian stages, and becomes extinct by the end of the Darriwilian (Late Llanvirn or Llandeilo).

The genus *Isograptus* is diagnosed and is distinguished by its proximal symmetry, apparently unique among reclined didymograptids; the sicula and theca 1¹ form a symmetrical pair such that the axis of rhabdosome symmetry passes between them. The relationships of *Isograptus* to *Oncograptus*, *Cardiograptus*, and *Meandrograptus* are discussed. The inferred phylogeny of the isograptid stock is presented.

The Australasian isograptids are described from the viewpoint of population systematics, particular attention being paid to the wide range of morphologic variation exhibited both within and between species. 8 species, comprised of 14 subspecies and 3 informal forms, are recognized, and grouped in 4 main groups.

The first, the *victoriae* group, comprises the subspecies of *Isograptus victoriae* described by Harris (1933), namely *lunatus*, *victoriae*, *maximus*, *maximodivergens*, and *divergens*, which represent successive stages in a continuously evolving lineage. The second group, the *caduceus* group, comprises those forms related to *I. caduceus imitatus* Harris, and the third group, the *manubriatus* group, is distinguished by the presence of a manubrium. Phyletic increase in rhabdosome size is a general trend exhibited by each of the three groups and is discussed in some detail.

The fourth group comprises the earliest species, *I.* [*caduceus*] *primulus* and is tentatively regarded as distinct from the other three groups; its closest relative is thought to be the European form *I. gibberulus* (*sensu* Moberg 1892). Brief comments are given on other described Australasian isograptids.

Growth and allometry of the isograptid rhabdosome are described, and variation within and between species is quantitatively described and discussed. The principal phyletic trends in the group are outlined.

The utility of *Isograptus* lineages for local and inter-regional correlation is discussed.

CONTENTS

INTRODUCTION

Isograptus is the dominant graptolite genus in the Castlemainian and Yapeenian stages (Upper Arenigian) of Australia and New Zealand, both in number of species and in number of individuals. A conspicuous feature of the genus is the wide range of morphologic variation shown within, and throughout its member species and subspecies; the taxonomist is confronted by a bewildering array of forms.

The genus is stratigraphically important, the succession of species and subspecies forming the basis of the three Castlemainian zones (Ca1–3) in Australasia (Harris and Thomas 1938, Thomas 1960). Further, considerable importance has been placed on the range of the genus for world correlation (Skevington 1963*b*).

The first attempt at a systematic subdivision of the genus in Australasia was that of Harris (1933) who recognized 6 species (2 of which were described as new) and 11 subspecies (all of which were described as new). It is to Harris's great credit that his classification has been accepted and used by graptolite systematists for nearly 40 years without significant change. No subsequent worker has attempted a revision of the group. However, Harris's type illustrations were at natural scale and many subspecies were not described beyond a brief indication; they have thus been difficult to recognize outside Australasia and a revision of the group is overdue.

In this study the New Zealand isograptids are described and compared with Harris's types. Particular attention is paid to their stratigraphic succession. Four main groups are distinguished within the genus in Australasia. The first, the *victoriae* group, comprises the subspecies of *I. victoriae* named by Harris: *lunatus, victoriae, maximus, maximodivergens,* and *divergens.* The second group, the *caduceus* group, comprises the forms *I. caduceus imitatus, I. c.* aff. *imitatus, I. c. australis* (sp. nov.), *I. forcipiformis, I.* cf. *forcipiformis,* and, tentatively, *I. c. tenuis, I. c. spinifer,* and *I. ovatus.* The third group, the manubriate group, comprises *I. dumosus, I. hastatus,* and *I. manubriatus,* while the fourth group contains the sole species, *Isograptus* [*caduceus*] *primulus.*

The stratigraphic succession of subspecies of *Isograptus victoriae,* represented in New Zealand by relatively large populations, is described in detail and supplemented by quantitative data, and is inferred to represent an evolutionary lineage. The phylogenetic relationships of other taxa are inferred, less certainly, from generally smaller samples (fewer than 20 specimens) or less complete successions. The work largely substantiates Harris's classification and provides it with a firmer taxonomic basis; the recognition and use of populations rather than of morphological types being the main point of difference from Harris in approach to classification.

Over 1000 specimens have been examined, but only about 500 of them were of sufficiently mature development, or well enough preserved, to be measured. Morphologic variation, both within and between, taxa, is quantitatively described, and basic statistics are given in the appendix.

With the wide range of forms referred to *Isograptus* it has proved difficult to frame a satisfactory and workable diagnosis for the genus and the only published diagnosis since that of Moberg (1892, which has proved unusable), is by Bulman (1955 and 1970). Difficulty in applying Bulman's diagnosis to Australasian specimens led the writer to re-examine the genus and its distinctive features. As a result, a new diagnosis

is proposed, in which attention is drawn to the symmetry of the proximal region enabling the ready distinction of *Isograptus* from other reclined didymograptids, such as *Didymograptus hemicyclus* Harris and *Meandrograptus* Moberg.

Astogenetic growth and phyletic growth of the isograptid rhabdosome are examined and allometric changes are outlined. The inferred phylogeny of the isograptid stock is presented.

Fossil locality numbers cited (S2/552, etc.) are those of the New Zealand Fossil Record File; all are in NZMS1 sheet S2, Kahurangi. Collections are given collection numbers prefixed according to the institution in which they are housed. A list of localities with their respective collections is given in Table 1.

TABLE 1. Fossil localities and their collection numbers, Aorangi Mine district (NZMS1), sheet S2.

| Fossil Locality Sheet S2	Collection no. Victoria University Wellington	Collection no., N.Z. Geological Survey, Lower Hutt
540	V 1043	GS 9949
552	V 1493	GS 9952
565	V 1566b	GS 10659
586	V 1602	GS 547, 740
599	V 1920	GS 9979
600	V 1921	GS 9980
602	V 1923	GS 10789
603	V 1924	GS 9981, 10788
714	–	GS 10670
744	–	GS 10722

Prefixes for type specimens similarly signify the institution in which they are housed as follows:

GSV   Geological Survey of Victoria, Melbourne, Victoria;
NMV   National Museum, Melbourne, Victoria;
PR   New Zealand Geological Survey, Lower Hutt, New Zealand;
VG   Victoria University Geology Department, Wellington, New Zealand.

Part of the work for this paper was included in a thesis presented for the degree of Ph.D. at Victoria University in 1969. Subsequent work has been done at New Zealand Geological Survey, Lower Hutt, and at the National Museum, Melbourne.

STRATIGRAPHY

The samples on which this study is based are from fossil localities exposed in stream sections in Little Slaty Creek and its tributaries, in the Aorangi Mine district, north-west Nelson (text-fig. 1). The rocks are mapped as Aorangi Mine Formation (Grindley 1961). Detailed description of the geology of the Aorangi Mine district
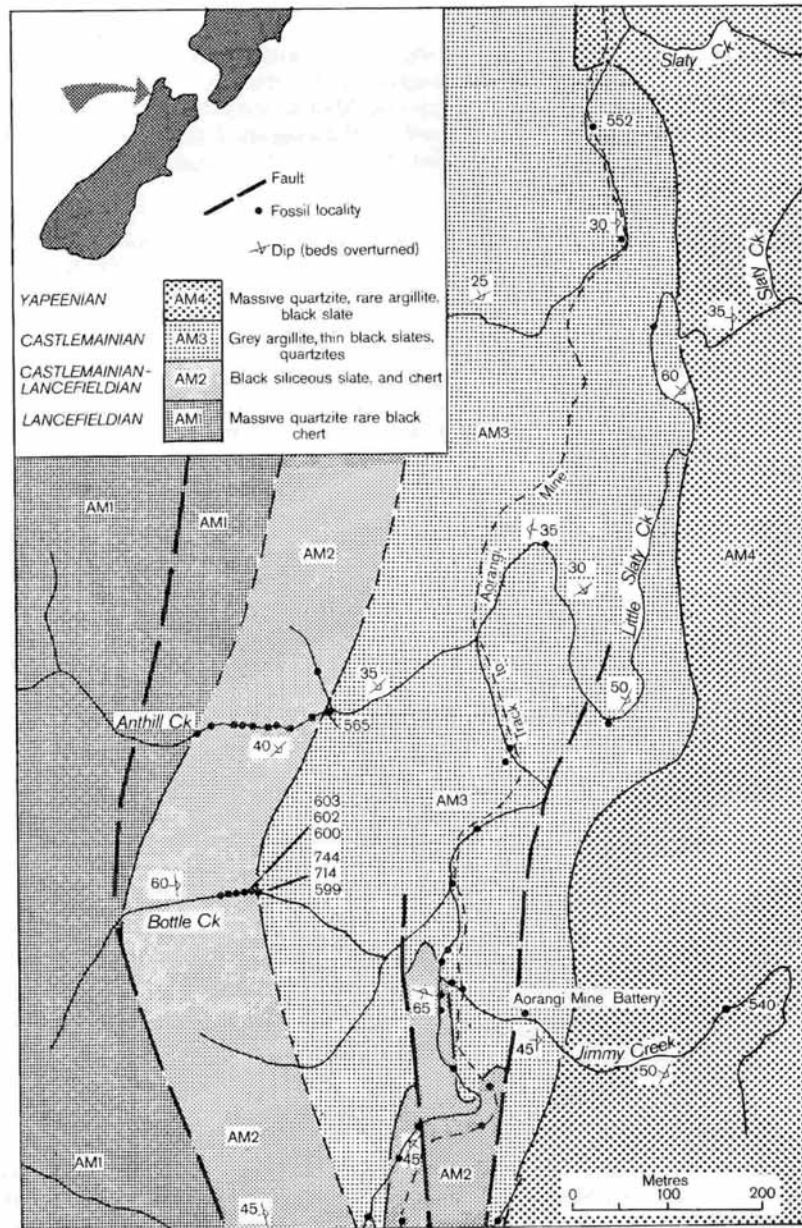
TEXT-FIG. 1. Sketch map of Little Slaty Creek and its tributaries, Aorangi Mine, showing distribution of Aorangi Mine Formation, members AM1, AM2, AM3, and AM4, and of localities of samples used in this study (numbered localities); other fossil localities are also shown. Note that the entire sequence is inverted.

is in preparation by the writer. It should be noted that the entire sequence mapped in text-fig. 1 is inverted.

The composite stratigraphic column shown in text-fig. 2 is compiled from well-exposed sections in Bottle Creek, Anthill Creek, Jimmy Creek, and on the Aorangi Mine track. These sections were chosen because they are relatively closely spaced and can be correlated with certainty, both by lithology and by non-isograptid grapto-lites.

Fossiliferous horizons are shown, those accompanied by their locality numbers being horizons of samples used in this study.

The Aorangi Mine Formation consists of 4 members, the 3 youngest of which are represented in the column (text-fig. 2). Member AM1, the oldest member, comprises mainly massive pale orthoquartzite and is mid Lancefieldian. Member AM2 is composed of hard, black, siliceous, carbonaceous slate, with thin bands of black medium grained sandstone, and rare non-carbonaceous orthoquartzite. It ranges in age from Lancefieldian, La2, to Castlemainian, Ca2. The overlying member, AM3, is hetero-geneous, being composed of mainly massive blue-grey argillite with bands of black slate, pale and dark quartzite, and dark sandstone. It is Castlemainian in age, ranging from Ca2 to Ca3. The youngest member, AM4, contains massive hard pale quartzite in its upper and lower parts and pale blue-grey argillite, graded sandstones and quartzite with rare black slate bands, in its middle part. It is Yapeenian in age, ranging from Ya1 to Ya2. Calcareous and coarse-grained beds are conspicuously absent from the entire succession.

Isograptids have been collected and examined from many other sections in the Aorangi Mine district, some being more and others less complete than those listed above. The sequence of forms in the other sections agrees with that shown in the composite section (text-fig. 2).
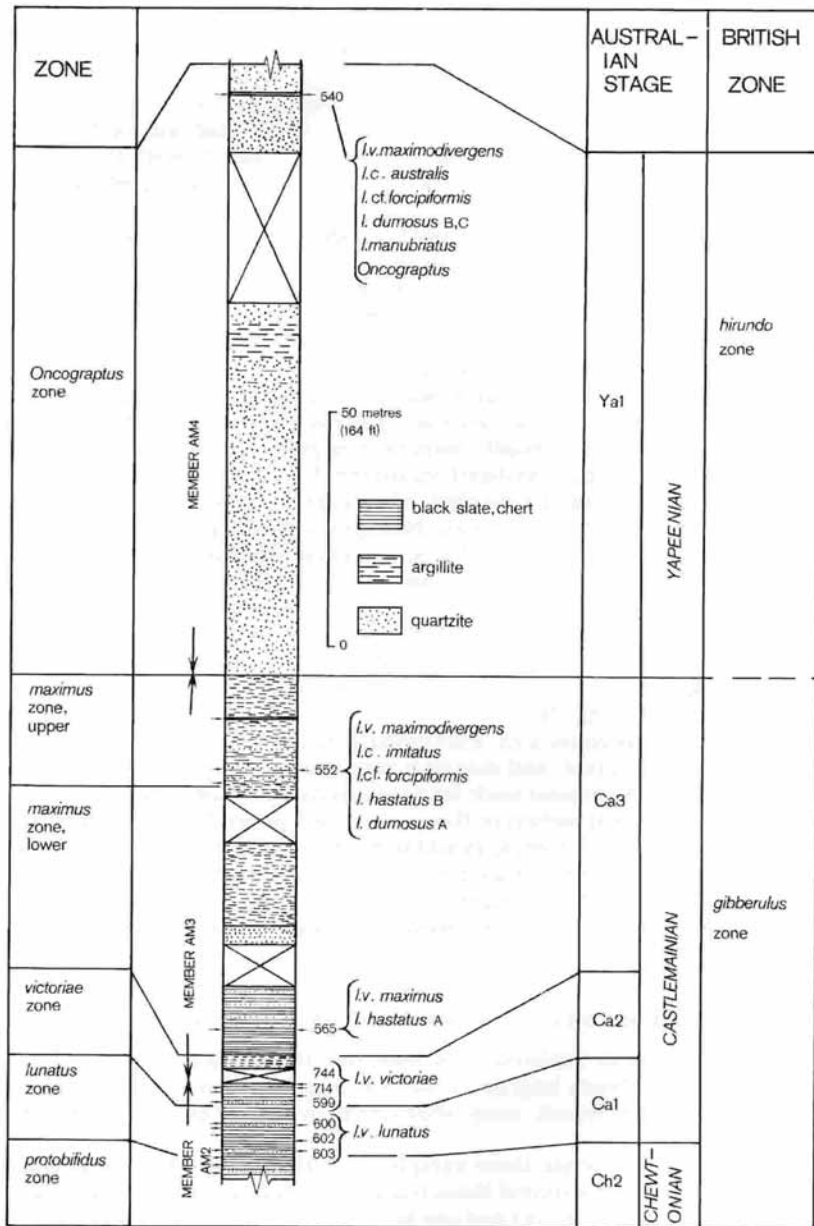
The 3 Castlemainian zones, Ca1–3 are based on the 3 index subspecies of *Isograptus victoriae*: *lunatus*, *victoriae*, and *maximus* respectively (Harris and Thomas 1938). The implications of the present work for zoning and correlation of the Castlemainian are discussed in the final section of this paper; the 3 zones, however, are used here as erected by Harris and Thomas. In addition, in both Victoria and New Zealand it is useful to distinguish, within Ca3, a lower part (that containing *maximus*) and an upper part (that containing *maximodivergens*).

The zonal distribution of species, revised in the light of the present work, is given in text-fig. 3.

SUMMARY OF NOMENCLATURAL CHANGES

The name *Isograptus* 'caduceus' has been traditionally used in Australasia for almost all non-manubriate isograptids and has been regarded as a large and widely variable species. The present study shows that two main groups can be readily distinguished.

The first group comprises those subspecies of the lineage, *Isograptus caduceus lunatus–divergens*, and the second those related to *I. caduceus imitatus*. The *lunatus–divergens* lineage is quite distinct and can be clearly traced in time; it is an exception-ally well-documented bioseries and is here given separate specific status. *Isograptus*

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ZONE			AUSTRAL-IAN STAGE	BRITISH ZONE

Column labels (left to right):

ZONE column:
- *Oncograptus* zone
- *maximus* zone, upper
- *maximus* zone, lower
- *victoriae* zone
- *lunatus* zone
- *protobifidus* zone

Members:
- MEMBER AM4
- MEMBER AM3
- MEMBER AM2

Fossiliferous horizons (left of column):
- 540
- *I.v. maximodivergens*
- *I.c. australis*
- *I.* cf. *forcipiformis*
- *I. dumosus* B,C
- *I. manubriatus*
- *Oncograptus*

Scale:
- 50 metres (164 ft)
- 0

Legend:
- black slate, chert
- argillite
- quartzite

- *I.v. maximodivergens*
- *I.c. imitatus*
- *I.*cf. *forcipiformis*
- *I. hastatus* B
- *I. dumosus* A
- 552

- *I.v. maximus*
- *I. hastatus* A
- 565

- 744
- 714 } *I.v. victoriae*
- 599

- 600
- 602 } *I.v. lunatus*
- 603

AUSTRALIAN STAGE column:
- Ya1
- YAPEENIAN
- Ca3
- Ca2
- Ca1
- Ch2
- CASTLEMAINIAN
- CHEWT-ONIAN

BRITISH ZONE column:
- *hirundo* zone
- *gibberulus* zone

TEXT-FIG. 2. Stratigraphic column compiled from stream sections exposed in Anthill Creek, Bottle Creek, Jimmy Creek, and on the Aorangi Mine track. Fossiliferous horizons are indicated on the left of the column, those yielding samples used in this study are shown on the right. Unexposed intervals are also shown.

Australian stage	Chewtonian	Castlemainian			Yapeenian		Darriwilian			
substage	Ch2	Ca1	Ca2	Ca3	Ya1	Ya2	Da1	Da2	Da3	Da4
Isograptus primulus	▬									
I. victoriae lunatus	•	▬								
I. v. victoriae	•	•	▬							
I. v. maximus	•	•	•	▬						
I. v. maximodivergens	•	•	•	▬▬▬						
I. v. divergens	•	•	•	•	•	▬▬▬	▬ ▬ ▬		▬	
I. caduceus imitatus	•	•	•	▬▬						
I. c. aff. imitatus	•	•	•	▬▬						
I. c. australis	•	•	•	•	▬▬▬					
I. c. tenuis	•	•	•	▬ ▬ ▬	▬	▬	▬ ▬	▬	▬ ▬	▬
I. c. spinifer	•	•	•	•	•	•	•	•	•	▬
I. ovatus	•	•	•	•	•	•	•	•	▬▬	▬
I. forcipiformis	•	•	•	•	•	•	▬ ▬	▬		
I. cf. forcipiformis	•	•	•	▬▬▬						
I. hastatus form A	•	•	•	▬						
I. hastatus form B	•	•	•	▬						
I. dumosus form A	•	•	•	▬						
I. dumosus form B	•	•	•	•	▬▬					
I. dumosus form C	•	•	•	•	▬▬					
I. manubriatus	•	•	•	▬▬						
Meandrograptus tau	•	•	•	▬▬						
M. aggestus	•	•	•	▬						
Didymograptus cf. eocaduceus	•	▬▬ ▬ ▬ ▬▬								

New Zealand Zone	protobifidus	lunatus	victoriae	maximus	Oncograptus	Cardiograptus	Paraglossograptus		decoratus & teretiusculus	

TEXT-FIG. 3. Zonal distribution of species revised in light of present work.

caduceus, sensu stricto, is now known to be not part of the lineage (Cooper 1971) but to belong to the *imitatus* group. The name *I. victoriae* was thus proposed, for the lineage, as Harris (1933, p. 90) regarded the variety as the *'forma typica'*. The name, *caduceus*, is here used for the *imitatus* group. *Isograptus caduceus norvegicus* Monsen 1937 is synonymized with *I. v. lunatus*, *I. walcottorum* Ruedemann 1947, with *I. v. maximodivergens*, and *I. furcula* Ruedemann 1947, with *I. v. divergens*. *I. caduceus primula* Harris 1933 is separated as a distinct species.

A third, and easily distinguished, group of isograptids comprises the manubriate species. *I. hastatus* and *I. dumosus* are each represented in New Zealand by populations which show somatic shift in time and which are distinguished informally as 'forms'. *I. caduceus* var. *gracilis* Ruedemann 1947 is synonymized with *I. hastatus* form B, and *I. caduceus velata* Harris 1933 is thought to be probably synonymous with *I. dumosus* form B.

The third manubriate species, *I. manubriatus*, is provisionally regarded as a single, widely variable species. The affinities of other forms are tentative.

TERMINOLOGY

Most of the terms used in discussion are in general usage, some require explanation and are discussed below. All refer to flattened specimens.

Measured characters

In order to interpret measurements of flattened graptolite rhabdosomes it is assumed that the flattening process produces essentially standard changes in rhabdosome dimensions from specimen to specimen, an assumption which is consistent with observations of both flattened and unflattened, pyritized, graptolites. Some characters such as sicular length, stipe length, and possibly stipe width are unlikely to have changed at all.

Because of their initial bilaterally flat shape (text-fig. 4) it can be safely assumed that isograptid rhabdosomes were similarly orientated prior to burial, with one lateral surface in contact with the sea floor, that is, parallel to the present plane of bedding.

The following characters were chosen for measuring as they are easily recognizable, readily measured, and present in most species. Measured rhabdosome characters are illustrated in text-fig. 5.

Stipe width refers to dorso-ventral stipe width as seen in profile view. *Proximal stipe width* (text-fig. 5e) is measured immediately past the sharp initial stipe flexure in the proximal region, *distal stipe width* in the distal part of mature rhabdosomes. Where maximum stipe width occurs in neither the proximal nor distal regions, as in *Isograptus victoriae maximodivergens*, it is recorded separately. *Stipe divergence* angle is measured between the distal portions of stipes. *Stipe length* extends from the initial stipe flexure to the distal stipe end. *Thecal inclination* is taken as the distal angle between the tangents on the dorsal stipe margin and the adjacent ventral thecal wall; it is only an approximate measure in isograptids in which thecae are curved, inclination changing continuously throughout their growth.

In Nelson isograptids, the sicula cannot be distinguished from the first theca (th1^1), but because of their closely similar shape and size (see generic diagnosis of *Isograptus*), measurements of either one can be regarded, for the purposes of this discussion, as those of the sicula. *Length* and *width* of the sicula are thus measured as shown in text-fig. 5 (*a* and *b* respectively). The *free length* refers to the free ventral wall, excluding that portion obscured by a peridermal film. The *supradorsal length* (5d) is the length of that portion of the sicula and first theca protruding above the dorsal stipe margins; the *supradorsal width* (5c) is measured across the sicula and first theca at the points of intersection with the dorsal stipe margin.

The number of *pendent thecae* in the proximal region is a useful and easily determined allometric character. The rhabdosome is orientated so that the midline—that line passing through the apex of the sicula and centrally between the free ventral margins of the sicula and first theca—is vertical. Pendent thecae are those whose apertural margins lie wholly below the level of the dorsal thecal wall (interthecal septum), and are denoted '*p*' in text-fig. 5. The number of pendent thecae is a function of the spacing, inclination,
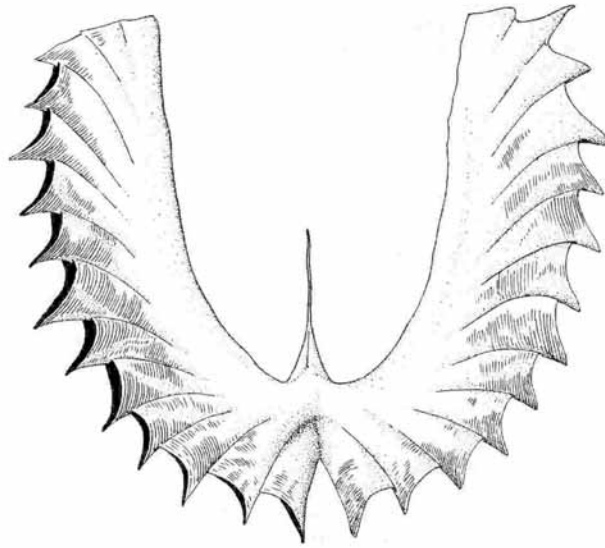
TEXT-FIG. 4. Reconstruction of *Isograptus victoriae victoriae* Harris 1933, based on specimen VG 42, ×10. Structural details inferred from flattened Nelson rhabdosomes and, by analogy, from the few isograptids described from unflattened material, particularly *Isograptus gibberulus* Nicholson.
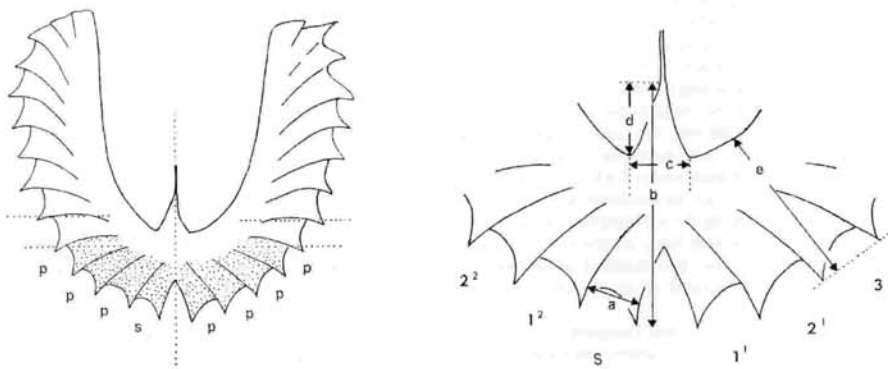
TEXT-FIG. 5. Measured characters of *Isograptus*. *a*, width of sicula at the aperture; *b*, sicular length; *c*, supradorsal width and, *d*, supradorsal length of sicula and theca 1^1; *e*, stipe width; *p*, pendent thecae; *s*, sicula. See text for discussion.

curvature, and length of thecae in the proximal region and the sharpness of the initial stipe flexure; it reflects the degree of 'proximal crowding' of thecae.

The *manubrium* refers to that structure, characteristic of manubriate isograptids, formed by the proximal parts of the sicula, theca 1^1, and those subsequently formed proximal thecae which commence their growth in a downward direction. In all Australasian manubriate isograptids stipes initially grow downwards; after budding their second or later thecal pair, direction of growth changes sharply and stipes attain a reclined attitude, the point of flexure marking the base of the manubrium. *Width* of the manubrium is measured across its base, *length* from its base to the apex of the sicula.

Significance of measured characters

From inspection the most obvious variation both within and between the species of any group is that in the overall size of the rhabdosome or of part of it. Rhabdosome size is a consequence of the size and number of individual thecae. Measured characters relating to thecal (and thus to rhabdosome) size and, by extrapolation, to the volume of the space available to the colonial graptolite organism, are length and width of the sicula, proximal and distal width of the stipes. Stipe length and divergence directly measure astogenetic rhabdosome characters. Supradorsal length and width, manubrium length and width, and number of pendent thecae, are allometric rhabdosome characters most of which are shown below to correlate positively with those relating to rhabdosome size. Variation in free sicular length may be little more than growth irregularity of the sicula and first theca.

Other terms

The term *character* is used in a general sense for any feature of rhabdosome morphology that can be readily recognized and measured. These include simple characters, such as sicular length, and character complexes, such as number of pendent thecae. *Astogeny* is used for growth of the individual rhabdosome by asexual budding; *phyletic growth* is used for increase in rhabdosome size in a phyletic series. *Allometry* refers to change in proportion as a result of change in absolute magnitude of the rhabdosome, in either astogeny (heterauxesis, Simpson 1953, p. 6), or phylogeny (lineage allomorphosis, Westoll 1950).

Maturity of the rhabdosome denotes astogenetic development of the rhabdosome beyond the stage necessary for recognizing its taxonomic identity; it does not refer to sexual maturity.

Populations, subspecies, type specimens

In this discussion, the term 'population' refers to all specimens of one species or subspecies present within a single bed or narrow interval of strata (Sylvester-Bradley 1951, p. 89). Specimens collected from the bed (at any one locality) comprise the sample from which inferences are made about the population. The time span represented by such a population is insignificant in terms of detectable somatic change (Simpson 1961, p. 163).

In the *I. victoriae* lineage, the concept of successive populations with wide, overlapping ranges of variation (biospecies of Cain 1954) differs from Harris's view of morphological 'varieties' (morphospecies of Cain 1954). Thus, a single Nelson population can include more than one of Harris's named 'forms': for example, the smallest mature specimens here referred to *victoriae* match his var. *lunatus*, while the largest specimens match his var. *maximus* (Table 4). The stratigraphic ranges given by Thomas (1960) for the Victorian 'varieties' are consequently greater than those given by the writer for the same forms in Nelson (text-fig. 35), the significance of which is discussed in the final section of this paper. The size variation discussed here should not be confused with astogenetic growth variation, which is readily distinguished and is discussed following the systematic descriptions.

'Subspecies', as used here, comprises two categories. The first category, represented by the subspecies of *Isograptus victoriae*, is comprised of successive populations in a gradually evolving lineage and is equivalent to the successional subspecies of Simpson (1961) or chronological subspecies of Sylvester-Bradley (1951).

The nature of the second category of subspecies is less certain; the category includes some of those 'taxa' for which the name *variety* was formerly used, e.g. '*Isograptus caduceus* var. *imitata*'. Some of these doubtless correspond to chronological subspecies, whereas others probably correspond to *geographic* subspecies in which two or more contemporaneous populations of one species have diverged through being reproductively isolated, either by a geographic barrier, or by some other mechanism (Mayr 1963). The problem of determining the nature of a subspecies is a general one among graptolites, in which life

history, mode of life, and ecology are poorly understood. Incomplete sampling, poor stratigraphic control, or imprecise correlation frequently further complicate their interpretation (see Packham 1962, p. 523; also Bulman 1963a, p. 679).

The role of the type specimen or *type* in population systematics is now generally held to be confined to that of name bearer (Simpson 1945, 1961; Mayr *et al.* 1953). Mayr, Linsley, and Usinger stress the importance of the type locality (and thus stratigraphic horizon) in defining subspecies. In his description of the Victorian isograptids, Harris (1933) nominated types for only 3 of the 17 new taxa erected—*Isograptus hastatus* (holotype figured by Harris 1933, fig. 36), *Meandrograptus aggestus* (fig. 51), and *M. tau* (figs. 5a, d). The selection of lectotypes should, ideally, be delayed until the type localities have been precisely determined and adequately sampled so that the most suitable, modal, specimen can be chosen. However, Harris's descriptions of type localities are such that few could be precisely relocated, and the whereabouts of several of his (1933) figured specimens is unknown, reducing the choice. The advantages of permanently stabilized nomenclature are thought to justify nomination of lectotypes at this stage, and this course has been followed. Where possible, lectotypes are refigured here.

SYSTEMATIC DESCRIPTIONS

Genus ISOGRAPTUS Moberg 1892

Type species. Didymograptus gibberulus Nicholson 1875, by original designation.

Diagnosis (emend.). Rhabdosome biramous, reclined; first theca arises near apex of sicula, the two forming a symmetrical pair such that the axis of rhabdosome symmetry passes between their free ventral walls; subsequent development isograptid, proximal thecae relatively highly inclined and pendent; prothecal folds generally absent.

Remarks. Moberg's (1892, p. 346) original definition of *Isograptus* was vague; he misinterpreted the proximal end (Holm 1895, p. 19; Bulman 1932, p. 22) and his generic description is no longer usable. Bulman stressed the importance of the isograptid type of proximal end development as a generic character and in 1955 diagnosed the genus as follows: '[rhabdosome] reclined; thecae elongate with high inclination and large overlap, especially proximally; development isograptid, first few thecae growing entirely downward.'

Skevington (1965, pp. 44–45) pointed out the difficulty of distinguishing the genus from *Meandrograptus* Moberg 1892, and, in particular, the uncertain generic position of such species as *I. manubriatus* (T. S. Hall), *I. hastatus* Harris, and *I. dumosus* Harris in which distal thecae have low inclination and small overlap, and proximal thecae do not grow strictly downward. The generic position of Nelson specimens of *I. victoriae lunatus* Harris, in which proximal thecae are only moderately inclined, is also uncertain.

Extremely diverse forms have been referred to *Isograptus* and it is difficult to find common characters uniting the group. Yet most workers would probably agree that the bulk of forms referred to the genus constitute a distinct morphological group. From a study of the New Zealand isograptids and from the published descriptions of other species, several features of morphology appear to be present throughout: 1, The stipes are always reclined, usually strongly so. 2, Development, where known or inferred, is of isograptid type. 3, Proximal thecae are moderately, or highly inclined, and pendent. 4, The sicula and the first theca attain almost identical proportions and form a symmetrical pair about the rhabdosome midline.

The first 3 features are well known; the fourth needs discussion. The first theca (th1¹) arises near the apex of the sicula and grows down beside its ventral margin, attaining an almost identical outline in mirror image, to that of the sicula itself (Elles and Wood 1901, p. 52), a feature that misled Moberg into believing that the sicula was divided in two. The axis of symmetry of the rhabdosome passes *between* the free ventral walls of the sicula and first theca, rather than *through* the sicula (text-fig. 6).

Although not definitely determinable from Elles and Wood's figure of the type specimen of *I. gibberulus* (Elles and Wood 1902, p. 53, text-figs. 33a–b) the feature is described by them (on p. 53) and it is well shown by Bulman's figures (1932, p. 24, text-figs. 1a–b, pl. 8, figs. 1–4) of Swedish specimens of the type species. Similarly, all New Zealand members of the *caduceus* group, despite their variable shape, stipe width, and thecal curvature, possess this proximal symmetry. The problematical manubriate species of *Isograptus* are generally poorly known, but Bulman's illustrations (1968, figs. 1, 2) of a Texan specimen of *I. manubriatus* show, as do all manubriate species described here, that there is a similarly symmetrical arrangement of the sicula and first theca, though the mid portions of each overlap each other and the distal extremities are directed outwards, away from the midline of the rhabdosome.
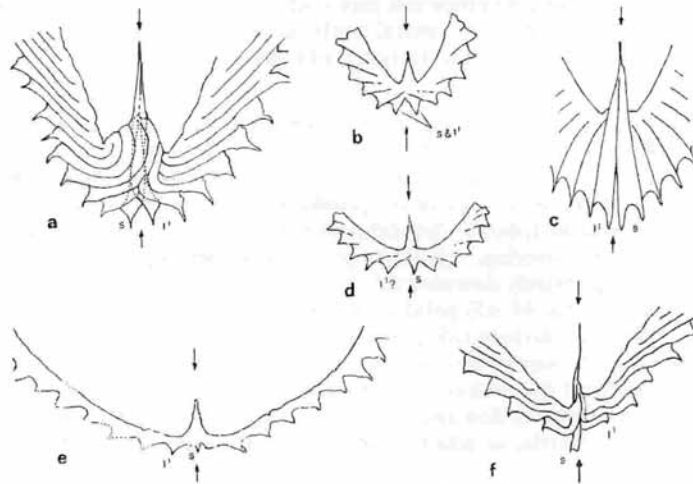
TEXT-FIG. 6. Proximal symmetry in *Isograptus* (*a, b, c*) compared with that in re-clined *Didymograptus* (*d, e*) and *Meandrograptus* (*f*). Sicula (*s*) and theca 1¹ (1¹) are indicated together with the axis of rhabdosome symmetry (arrows). *a, Isograptus manubriatus* (T. S. Hall), from Marathon, Texas. After figure by Bulman (1968, p. 112, figs. 1, 2). *b, Isograptus victoriae lunatus* Harris, from Nelson, VG31. *c, Isograptus gibberulus* (Nicholson), from Sweden. After figure by Bulman (1932, p. 25, text-fig. 1). *d, Didymograptus* cf. *eocaduceus* Harris, from Nelson; GR 109. *e, Didymograptus hemicyclus* Harris, Victoria. After Berry (1966, pl. 49, fig. 6). *f, Meandrograptus schmalenseei* Moberg, Sweden. From Bulman (1932, p. 27, text-fig. 2a). All figs. ×5 approximately.

The above diagnosis is therefore proposed and serves to distinguish the genus from reclined species of *Didymograptus*, such as *D. hemicyclus* Harris 1933 (refigured by Berry 1966, pp. 427–428, pl. 79, figs. 5,6), but to include *I. victoriae lunatus* Harris, in which proximal thecae have only moderate inclination and small overlap.

Meandrograptus Moberg is distinguished by the marked difference in form between the sicula and first theca, the rhabdosome midline passing through the sicula (as shown by the type species, *M. schmalenseei* Moberg, figured by Bulman 1932, text-figs. 2a–b, pl. 2, figs. 6–8), and by the prominence of prothecal folds (Skevington 1965, p. 44). Other distinctive features are given by Skevington (1968, p. 313) and the genus is further discussed by Bulman (1969, p. 14).

Isograptus primulus Harris 1933

Text-figs. 7a–e

1933   *Isograptus caduceus* var. *primula* Harris, p. 90, text-figs. 1, 2.
1933   *Isograptus caduceus* var. *lunata* Harris (*pars*), p. 90, text-fig. 3 only.
1935   *Isograptus caduceus* var. *primula* Harris; Benson and Keble, p. 287.
1935   *Isograptus caduceus* var. *lunata* Harris; Benson and Keble, p. 288, pl. 30, fig. 30.

Lectotype. GSV 64425, Geological Survey Museum, Victoria.

Material, age. 4 complete rhabdosomes: PR 3–5, VG 33, from S2/586, Coffee Creek, Aorangi Mine district; Chewtonian, Ch1.
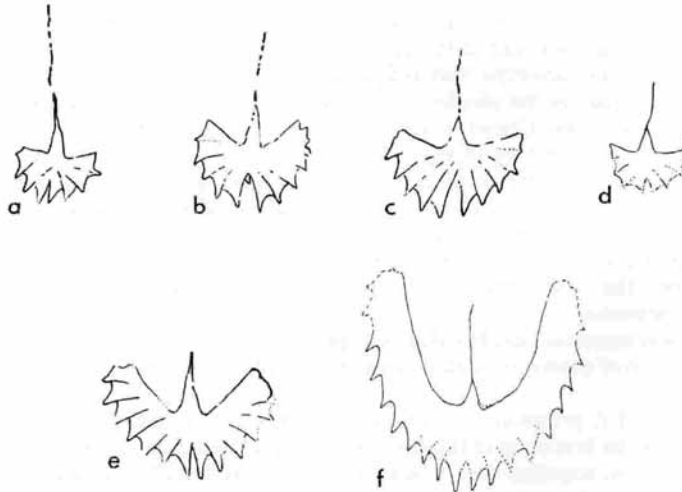
TEXT-FIG. 7. *a–f—Isograptus primulus* Harris. *a*, PR 5, S2/586; *b*, VG 33, S2/586; *c*, PR 4, S2/586; *e*, PR 3, S2/586; Aorangi Mine. *d*, GSV 64425, lectotype, figured by Harris (1933, fig. 1) from 'south of Blacksmith's Gully', Chewton–Fryerstown Road, Victoria. *f*, GSV 64426, figured by Harris as *Isograptus* '*caduceus*' *lunatus* (1933, fig. 3), from same locality as (*d*). Chewtonian, Ch2. All specimens ×5, except for *d*, which is ×4·4.

Description. The Nelson rhabdosomes are small, and stipes are barely developed, bearing only 6–7 thecae each in the largest specimen. The sicula is 2·5–4·5 mm long and about 0·7 mm wide at the aperture. It bears a fine nema up to 8 mm long. Measurements of the 4 complete specimens are given in Table 2. Thecae are almost straight, in contact for more than three-quarters of their length, and highly inclined to the stipe axis. Thecal apertural margins are concave and 'denticulate'; the indentation formed by the free ventral margins of the sicula and first theca is relatively narrow and deep.

TABLE 2. Dimensions of *Isograptus primulus* Harris (mm).

Spec. no.	Sicula				Proximal stipe width	Number of pendent thecae	Number of thecae per stipe
	length	width at aperture	Supra-dorsal width	Supra-dorsal height			
PR3	3.4	0.50	.9	1.3	1.6	8	6–7
PR4	3.0	0.45	.6	0.9	–	6+	3–4
PR5	2.6	0.40	.6	1.1	–	5?	2–3
VG33	3.2	0.55	.7	1.2	–	6+	3–4

Remarks. Isograptus primulus is the earliest representative of the genus in Australia and New Zealand, occurring with *Didymograptus protobifidus* Elles in the Chewtonian. Unfortunately, the form is extremely rare in both regions and only a few specimens are available for study. Of the 2 syntypes (Harris 1933, text-figs. 1, 2) only one is now known and is in the Geological Survey of Victoria museum; it is here nominated as lectotype and refigured (text-fig. 7*d*). The specimen is poorly preserved but matches the smaller Nelson specimens well. It comes from 'south of Blacksmith's Gully on Chewton–Fryerstown road'. A second specimen from this locality was also figured by Harris (text-fig. 3)—as '*Isograptus caduceus lunatus*'— and is also refigured here (text-fig. 7*f*). The 2 specimens, together with Harris's figure (text-fig. 2) of the second syntype of *primulus*, differ from *lunatus* populations of later horizons in having longer straighter proximal thecae, more of which are pendent, giving a 'deeper' and more crowded aspect to the proximal region of the rhabdosome. The 3 specimens are here considered to be conspecific and are all referred to *primulus*.

The Nelson material matches Harris's specimens well and shows more clearly the high inclination of thecae, though no specimen reaches the size of the largest Victorian form.

The origin of *I. primulus* is unknown. Concerning its descendants, Harris considered it to be the first stage in the *lunatus–divergens* lineage; however, the differences mentioned above, together with a lack of populations transitional between *primulus* and *lunatus*, lead the writer to regard the relationship as doubtful. Certainly the changes involved in passing from *primulus* to *lunatus* have no continuity with the changes in the transition from *lunatus* to *victoriae*, and the form is here regarded as a separate species.

I. primulus more closely resembles the later *I. caduceus imitatus* but, again, the transition is not well documented.

The large forms (text-figs. 7*e*, *f*) bear a striking resemblance to the well-known European species, *I. gibberulus* Nicholson as figured by Bulman (1932, pl. 8), particularly in their relatively straight and highly inclined thecae. When better known, *I. primulus* may well prove to be conspecific with *D. gibberulus*, *sensu* Moberg 1892, Törnquist 1901, and Bulman 1932.

Distribution. The species is known from Australasia only. Benson and Keble (1935, p. 287) reported it from the C5 zone (= CH2) of Preservation Inlet. The specimen figured by them as *I. caduceus lunatus* (pl. 30, fig. 30) more closely resembles *primulus*; its stratigraphic position is unknown.

Isograptus victoriae Harris 1933

1874   *Tetragraptus bryonoides* Etheridge (*pars*), p. 2, pl. 3, figs. 3, 4.
1874   *Graptolites* (*Didymograpsus*) *caduceus* Salter; M'Coy, p. 30, pl. 20, figs. 3–5, 5a.
1896   *Didymograptus caduceus* Salter; T. S. Hall, p. 69.
?1904   *Didymograptus* (*Isograptus*) *caduceus* Salter; Ruedemann, p. 693, pl. 15, figs. 6, 7.
1933   *Isograptus caduceus* (Salter); Harris (*pars*), pp. 90–91, text-figs. 1–18 only.
1935   *Isograptus caduceus* (Salter); Benson and Keble (*pars*), p. 287, pl. 30, fig. 28 (not fig. 30); pl. 31, fig. 24.
?1947   *Isograptus caduceus* (Salter); Ruedemann (*pars*), pp. 350–351, pl. 57, figs. 10, 11, 14, 17, 18, 19, 20, 25 (not figs. 12, 13, 15, 16).
1947   *Isograptus walcottorum* Ruedemann, p. 354, pl. 57, figs. 26–29?, 30–36.

Diagnosis. Proximal thecae directed downwards and not manubriate; 2 to 13 or more pendent thecae; thecal ventral walls curved, concave ventrally, throughout rhabdosome; apertural margins concave and denticulate; stipes of uniform width throughout or narrowest in the region of their initial flexure.

Remarks. When erecting his 'varieties' of *Isograptus caduceus*, Harris gave only brief descriptions and no diagnoses. The above diagnosis is based on a study of New Zealand and Victorian isograptids. The species here comprises 5 subspecies—*lunatus, victoriae, maximus, maximodivergens, divergens*—considered to be members of one lineage, and thus excludes the 'varieties', *primulus, imitatus, horrida, pertensa, velata, tenuis,* which are not part of the lineage.

In a recent redescription of *Isograptus caduceus* (Salter) *sensu stricto* from Lévis (Cooper 1971), the nomenclature of Australasian and North American forms referred to this species was discussed. It was shown that the Lévis form is distinct from Harris's Australasian series for which a new name is thus required. The name *victoriae* was proposed as Harris (1933, p. 90) considered his variety under this name to be the '*forma typica*'. The species ranges from Castlemainian (Ca1) to Darriwilian (Da3).

The 5 subspecies are discussed in order of their appearance in the series.

Isograptus victoriae lunatus Harris 1933

Text-figs. 8*a–k, n*

1933   *Isograptus caduceus* var. *lunata* Harris, p. 90, text-figs. 4–6 (not fig. 3).
1936   *Isograptus caduceus norvegicus* Monsen (*pars*), p. 154, pl. 5, fig. 14.
1947   *Isograptus caduceus* (Salter); Ruedemann (*pars*), pp. 350–351, pl. 57, figs. 10, ?11.
?1953   *Isograptus lunata* Harris; Spjeldnaes, p. 176, pl. 1, fig. 3; text-fig. 1D.
1953   *Isograptus norvegicus* Monsen; Spjeldnaes (*pars*), pp. 174–176, pl. 1, fig. 4; text-fig. 1c (not pl. 1, fig. 6; text-fig. 1f).

Lectotype. Of Harris's 3 figured specimens here referred to *lunatus*, that figured as text-fig. 4 (GSV 29624) is held by the Geological Survey of Victoria and is here nominated as lectotype, and refigured (text-fig. 8*n*). The specimen figured by Harris as text-fig. 5, is listed by him (p. 110) as 'no. 6293, Coll. Geol. Surv. Vict.' Its whereabouts, together with that of the third specimen (text-fig. 6), is unknown. Type locality is 'Quartz Hill, Castlemaine'.

Measured material, localities, age. 75 specimens: PR 179–225 from S2/600; PR 226–235 from S2/602; PR 236–254 from S2/603; Bottle Creek, Aorangi Mine; Castlemainian, Ca1.

Description. The rhabdosome is of variable size, generally U-shaped. A nema is present in most specimens, the longest being 8 mm. The sicula bears a 'denticle' or blunt spine; mean sicular length is 2·5 mm (1·7–3·3 mm, text-fig. 26). It is free for about 0·6 mm. Width of the sicula at its aperture ranges from 0·3 to 0·8 mm, with a mean value of 0·6 mm. As a general rule, the smaller rhabdosomes are those with the shorter and narrower siculae. The mid portions of the sicula and first theca overlap each other, their distal portions curving away from the midline so that their free ventral walls form a wide, but not deep indentation. The origins of theca 1^2 and 2^1 cannot be seen, but the general aspect of the proximal end (text-figs. 8*c, g*) suggests that development is of isograptid type (Bulman 1970).

The number of pendent thecae ranges from 2 to 5, averaging 4 (text-fig. 29). Stipes are of approximately even width, ranging throughout the population from 0·9 mm wide to 2 mm wide, and averaging 1·3–1·4 mm wide (text-figs. 27, 28). Maximum stipe length is 8 mm. Stipes are curved upwards (dorsally), the degree of curvature and angle of divergence varying widely from specimen to specimen.

Thecal spacing, measured in a few large forms only, is 6 in 5 mm. Thecal ventral walls are slightly or moderately concave, those of distal thecae are inclined at from 25° at their origins to 75° near their apertures. Thecal apertural margins are concave, 'denticulate', and moderately inclined to the stipe axis.

Discussion. The Nelson specimens are considered to represent a population with a wide and continuous range of morphologic variation, hardly any two specimens being closely similar.

The 3 specimens figured by Harris (1933, p. 112, text-figs. 4–6, *non* fig. 3 = *primulus*) indicate considerable variation also, his figures 5 and 6 closely resembling the common New Zealand forms.

In a few Nelson specimens (text-fig. 8*b*) the stipes taper slightly distally and the sicula and first theca are relatively long, giving the rhabdosome a V-shape rather than U-shape. The specimens approach the later form *I. caduceus imitatus.* The common form of *lunatus* however (text-figs. 8*d–g*) is that which gave rise to the *lunatus-divergens* lineage.

Of particular interest are a few Nelson specimens with weak isograptid symmetry, and which appear to be transitional towards the contemporaneous form *Didymograptus* cf. *hemicyclus* (text-fig. 8*m*). They suggest a possible origin for *lunatus* and the *victoriae* lineage, by the acquisition of isograptid symmetry (and, presumably, isograptid development) in an already reclined didymograptid rhabdosome. Further work, particularly on the structure and development of transitional forms, is needed to substantiate the transition and possible origin of the isograptid rhabdosome.
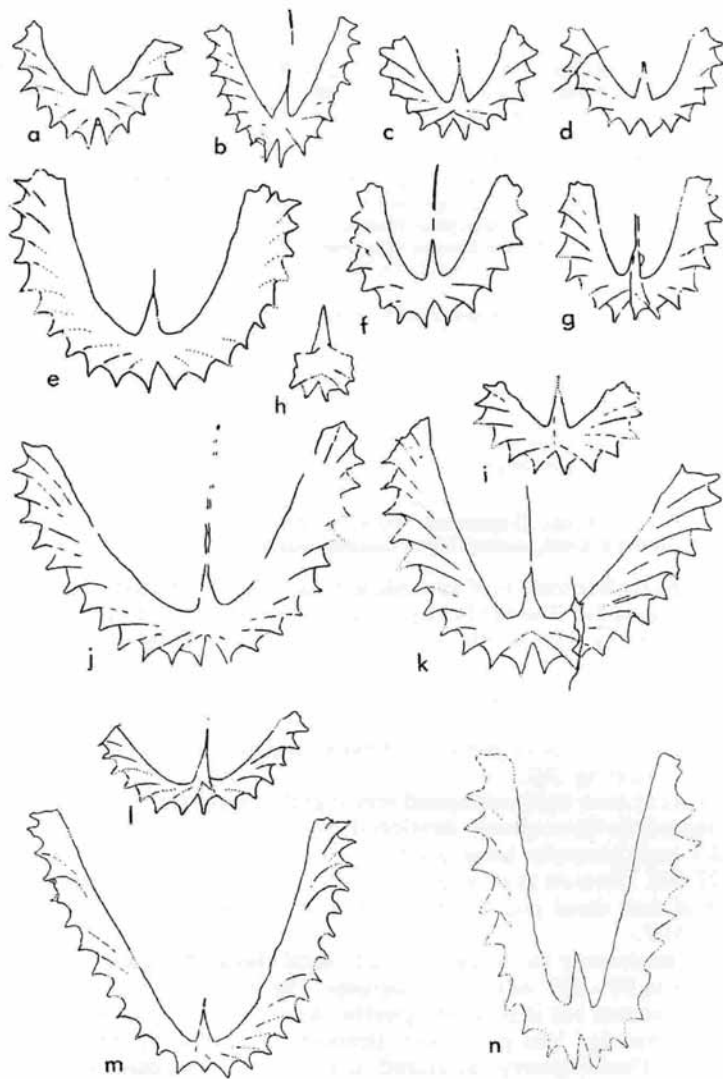
TEXT-FIG. 8. *a–k—Isograptus victoriae lunatus* Harris, Aorangi Mine area, Nelson.
a, PR 217, S2/600; *b*, VG 107, S2/593; *c*, VG 31, S2/579; *d*, VG 163, S2/562; *e*, PR 207,
S2/600; *f*, VG 38, S2/579; *g*, VG 37, S2/562; *h*, growth stage, VG 35, S2/593; *i*, VG 136,
S2/602; *j*, VG 39, S2/562; *k*, PR 224, S2/600. Castelmainian, Ca1.

n—Isograptus victoriae lunatus Harris, lectotype GSV 29624 figured by Harris
(1933, text-fig. 4). Specimen probably tectonically distorted, maximum relative shorten-
ing direction approximately normal to midline. From 'Quartz Hill, Castlemaine',
Castlemainian, Ca1.

l, m—Didymograptus cf. *hemicyclus* Harris. *l*, PR 109, S2/552; Aorangi Mine,
Castlemainian, Ca3 (upper). *m*, VG 40, S2/579; Aorangi Mine, Castlemainian, Ca1.
All figures ×5.

Distribution. The specimen from Preservation Inlet figured by Benson and Keble (1935, pl. 30, fig. 30) as *I. v. lunatus* belongs to *primulus*. Specimens from the Deepkill shale listed by Ruedemann (1947, pl. 57, figs. 10, ?11) as *I. caduceus* closely resemble New Zealand members of *I. v. lunatus*, though the subspecies was not recorded by Berry (1962) in his revision of the biostratigraphy of the Deepkill shale.

The form described by Spjeldnaes (1953) as '*Isograptus lunata*' from Layer III of the upper part of the Lower *Didymograptus* Shale (zone 3b) at Slemmestad, Oslo, differs slightly from the larger Nelson forms in having more pendent thecae, and in the angle of thecal inclination being generally higher. His figures (particularly fig. 1c, pl. 1, fig. 4) of *I. norvegicus* Monsen, however, from 'just below' Layer III closely match the intermediate and small Nelson member of *lunatus*.

Isograptus victoriae victoriae Harris 1933

Text-figs. 9*a–f*

1933 *Isograptus caduceus* var. *victoriae* Harris, p. 90, figs. 7–10.

Lectotype. Of the 4 syntypes, only that figured by Harris as text-fig. 8 is now known and is held by the Geological Survey of Victoria (specimen GSV 63310); it is here nominated as lectotype and refigured (text-fig. 9*f*). Type locality is 'spoil heap from a small mining shaft on the east side of the [Victoria] gully', Chewton.

Measured material, localities, age. 23 specimens: VG 42–44, PR 255–265, S2/599; PR 176–178, S2/744; PR 266–271, S2/714; Bottle Creek, Aorangi Mine; Castlemainian, Ca2.

Description. The rhabdosome is of variable size, generally U-shaped, and commonly bears a long stout nema. The sicula ranges in length from 2·8 to 4 mm, mean length being 3·3 mm (text-fig. 26); width at the aperture is about 0·7 mm. A prominently extended ventral process takes up one-quarter to one-eighth of the total sicular length. The indentation between the free ventral walls of the sicula and the first theca is wide and deep. In many specimens the apex of this indentation is bridged, presumably by a thin sheet of periderm. Pendent thecae range in number from 5 to 9 and average 7 (text-fig. 29).

The stipes are of even width or expand very slightly, except for the distal 3 or 4 mm where the thecae are incompletely developed. Width averages 2·1–2·3 mm, ranging from 1·6–2·7 mm, generally being greatest in rhabdosomes of largest overall size (text-figs. 27, 28). Greatest stipe length is 14 mm. Stipes curve markedly, the divergence angle of their distal portions being extremely variable (V = 80), and ranging from 360° to 310°.

Thecae are moderately to strongly curved, distal thecae being inclined from 20° at their origins to 90°–100° near their apertures. The inclination of proximal thecae is not easily measured but is generally greater. Apertural margins are strongly concave, and are extended into prominent 'denticles' at their junctions with ventral thecal margins. Thecal spacing, measured in a few large specimens only, is about 11 in 10 mm.

Discussion. Isograptus victoriae victoriae differs from the preceding subspecies *I. v. lunatus* in containing generally larger forms with a greater number of pendent thecae. In *victoriae*, thecae attain a higher angle of inclination and have more overlap than in *lunatus*; the most common or 'typical' forms of each subspecies are easily distinguished, but the smallest members of *victoriae* are of similar size to the largest members of *lunatus*.
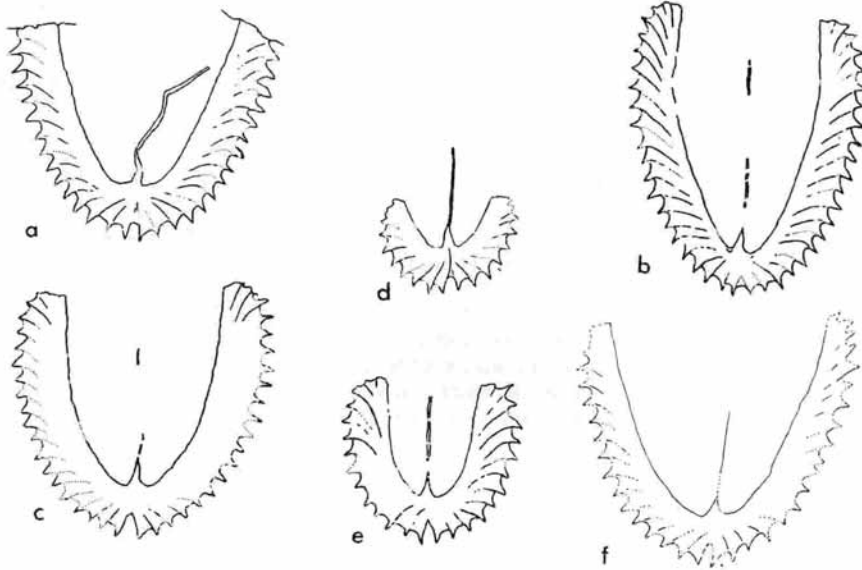
TEXT-FIG. 9. *a–f—Isograptus victoriae victoriae* Harris. *a*, PR 267, S2/714; *b*, VG 43, S2/599; *c*, PR 265, S2/599; *d*, PR 268, S2/714; *e*, VG 42, S2/599. Aorangi Mine area, Nelson; Castlemainian, Ca2. *f*, *Isograptus victoriae victoriae* Harris, lectotype GSV 63310 figured by Harris (1933, text-fig. 8) from 'Victoria Gully, Castlemaine'; Castlemainian, Ca2. All figures ×3.

Harris's 4 figured specimens (1933, text-figs. 7–10) indicate a similar range of morphology to that shown by the Nelson material. The lectotype (Harris's text-fig. 8) is refigured here for comparison (text-fig. 9*f*).

Distribution. I. v. victoriae has been widely recorded in North America. Berry (1960) recorded it from the lower part of the Fort Peña Formation (zone of *Isograptus caduceus*) in the Marathon sequence of Texas, but the specimen figured by him (pl. 11, fig. 7) more closely resembles the later subspecies *maximodivergens* (see text-fig. 12*d*); it is associated with *Cardiograptus morsus, I. v. divergens, I. v. maximodivergens,* and *Oncograptus upsilon,* all of which first appear at a later horizon than that of *victoriae* in Australasia. Ross and Berry (1963) recorded *I. victoriae* cf. *victoriae* from the Palmetto Formation, Basin Ranges, Western U.S.A. Kindle and Whittington (1958) recorded the form from Newfoundland; *I. v. victoriae* was listed from the top of their section at Martin Pt., and *I. v.* cf. *victoriae* from locality (5) at St. Paul's Inlet.

I. v. cf. var. *victoriae* has been listed from Rioux Quarry, near Cowansville, Southern Quebec, by Riva (1966, p. 221), together with '*I.* cf. *caduceus*'. Jackson (1964, p. 525, fig. 1) recorded the subspecies from near the base of the zone of *I. caduceus,* at the type locality of the Road River Formation in the Richardson Mountains, Northern Yukon, and Jackson, *et al.* (1965) listed it from Cloudmaker Mountain (zone of *I. caduceus*) in north-eastern British Columbia.

Isograptus victoriae maximus Harris 1933

Text-figs. 10*a–e*

1933   *Isograptus caduceus* var. *maxima* Harris, p. 91, fig. 13.
1960   *Isograptus caduceus* var. *maxima* Harris; Berry, pp. 66–67, pl. 11, fig. 8.

Type specimens. Neither of the 2 syntypes figured by Harris are now known and apparently no other specimens from either of the type localities given by him (p. 110) have been figured. Harris's figures and brief description (p. 91) are therefore the only, rather unsatisfactory, basis for comparison.

Measured material, locality, age. 50 specimens: VG 41, PR 115–117, PR 123, PR 128–141, PR 143–169, PR 171–175, S2/565, Anthill Creek, Castlemainian, Ca3, lower part.

Description. Rhabdosome of variable shape and size, the smaller forms generally U-shaped and the larger forms generally V-shaped. The sicula ranges in length from 2·5 mm to 5·6 mm, averaging 4·2 mm (text-fig. 26). The ventral indentation between sicular, and first thecal, ventral walls is relatively narrow and deep and is generally bridged by a peridermal sheet which extends about half-way down from the apex. Pendent thecae range in number from 6 to 12 and average 8·7 (text-fig. 29).

Proximal stipe width ranges from 1·6–3·2 mm, averaging 2·6 mm, whereas distal stipe width ranges from 1·7–4·6 mm and averages 3·4 mm (text-figs. 27, 28). The population ranges from forms in which stipe width is uniform throughout as in *victoriae* and *lunatus*, to forms in which proximal stipe width is only about 0·6 distal stipe width. The average ratio of proximal to distal stipe width is 0·82. Simi-
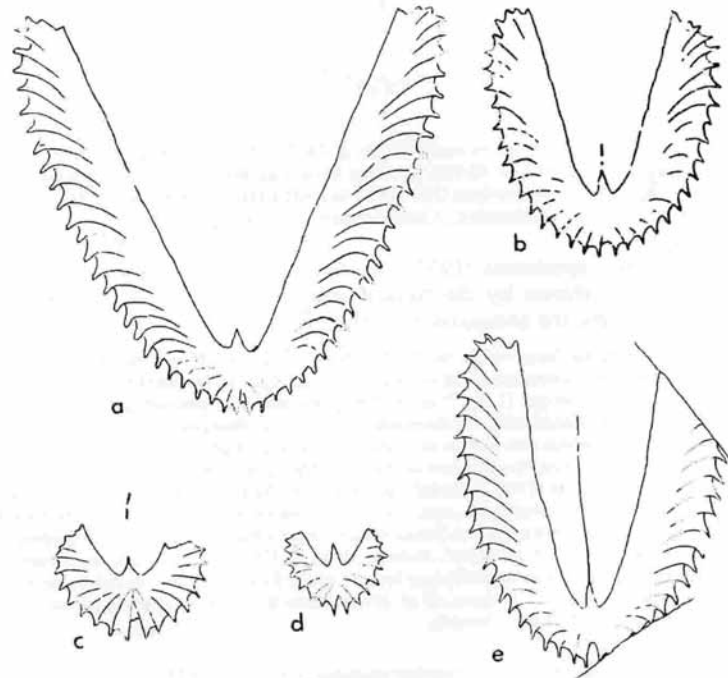
TEXT-FIG. 10. *a–e—Isograptus victoriae maximus* Harris. *a*, PR 162; *b*, VG 41; *c*, PR 146; *d*, PR 111; *e*, PR 141. All from S2/565, Aorangi Mine area, Nelson; Castlemainian, Ca3 (lower). All figures ×3.

larly, stipe curvature ranges from continuous dorsal concavity, giving the rhabdosome a U-shape, to straight (after the initial flexure) or slight dorsal convexity giving a V-shape. The angle of stipe divergence is very variable, ranging from 345°–290° (averaging 324°). Greatest stipe length is 24 mm.

Thecae are strongly curved, inclined from 20°–30° near their origins to 100° near their apertures. Apertural margins are concave, and extended into a ventral 'denticle'. Thecal spacing ranges from 9·5 to 13·5 in 10 mm, averaging 10·7.

Discussion. The appearance of forms with stipes that are conspicuously narrower in their proximal regions than in their distal regions marks a departure from the progression of successively larger rhabdosomes without significant change in over-all proportion. Specimens with stipes of uniform width resemble an enlarged *victoriae*, whereas specimens in which stipes are conspicuously narrower in the proximal region than distally resemble the succeeding subspecies *maximodivergens*. The mean values for proximal and, particularly, distal stipe width (text-figs. 27, 28), also for the number of pendent thecae and sicular length (text-figs. 26, 29) are all greater than in *victoriae*, but the range for each character overlaps between the 2 subspecies. A few exceptionally small specimens of *maximus*, however, lie well down within the *victoriae* range.

Harris's 2 figured specimens of *maximus* (Harris 1933, figs. 11, 12) correspond to those members of the New Zealand population in which stipes are of uniform width, rather than to those in which stipes narrow proximally.

Distribution. Berry (1960, pl. 11, fig. 8) figured a specimen from the lower Fort Peña Formation which matches the common Nelson forms and most probably lies within the subspecies.

Isograptus victoriae maximodivergens Harris 1933

Text-figs. 11*a*–*f*, 12*a*–*g*, 13*a*

?1931   *Didymograptus (Isograptus) caduceus* Salter emend. var.; Bulman, pp. 42–43, text-fig. 17.
1933   *Isograptus caduceus* var. *maximodivergens* Harris, p. 91, fig. 13.
1947   *Isograptus walcottorum* Ruedemann (*pars*), p. 354, pl. 57, figs. 26?, 29?, 30–36 (not figs. 27, 28).
1960   *Isograptus caduceus* var. *maximodivergens* Harris; Berry, p. 67, pl. 11, fig. 11.
1963   *Isograptus caduceus* cf. *I. c.* var. *maximodivergens* Harris; Ross and Berry, p. 93, pl. 5, fig. 14.
1964   *Isograptus caduceus* var. *maximodivergens* Harris; Jackson, fig. 3, no. 9.

Lectotype. Although Harris figured only a single specimen it is clear from his comment in the figure caption to text-fig. 13 (p. 110) that he had further specimens. The figured specimen, NMV P28770 held by the National Museum, Victoria, is therefore here nominated as lectotype and refigured (text-fig. 13*a*). Type locality is 'between Castlemaine Military Rifle Range and town', Castlemaine.

Measured material, localities, age. 57 specimens; 39 from S2/552: VG 47–49, 51–52, 54, 62, 65, 89, 137–139, 142, 144–145, 147, 149, 150, 153; PR 38, 272–278, 283, 285, 287–288, 293–294, 296, 301, 302, 304, 305, 309; Castlemainian, Ca3 (upper); 17 specimens from S2/540: VG 46, 64, 70; PR 320, 323, 327, 329, 337, 344, 358, 359, 378, 379, 390, 396, 397, 409; Yapeenian, Ya1.

Description. The rhabdosome is large, U- to V-shaped, and commonly bears a short nema. The sicula ranges from 4·0–5·6 mm long, averaging 4·5 mm. Width at the aperture is 0·6–0·9 mm. In most mature specimens from the Yapeenian, Ya1 (locality S2/540), the sicula and proximal portion of the nema are enmeshed in a peridermal

E

film, the 'axilar film' of Harris, which generally extends to the dorsal stipe margins
(text-figs. 12a, e). Probably a thin sheet of periderm, the film is not present in early
growth stages and is apparently formed only after maturity of the rhabdosome has
been reached. It generally obscures the sicula and dorsal stipe margins in the axilar
region and, in some specimens, appears to be irregularly thickened. The indentation
formed by the free ventral margins of the sicula and the first theca is partly bridged
by a similar sheet of periderm leaving in most forms an excavation only slightly
deeper than that of a normal thecal aperture. Formation of the ventral sheet follows
shortly after the proximal thecae are fully developed (text-figs. 11a–f). The number
of pendent thecae ranges from 8 to 13, averaging 10.

Stipe width is remarkably variable, both within individual specimens, and from
specimen to specimen. Stipes are narrowest in the region of their maximum flexure,
in the proximal region, and widest in the middle third of their length. Proximal
width averages 3·1 mm (2·4–4·7 mm) and is generally about three-quarters maximum
width, which averages 4·4 mm (3·1–5·6 mm). The stipes of a few exceptional speci-
mens in the Upper Castlemainian (S2/552) widen and narrow repeatedly along
their length.

The direction of growth of the stipes is also variable both within and between
specimens. Following the sharp initial concave curvature, the dorsal stipe margins
generally show a gentle convex recurvature, after which they become straight or,
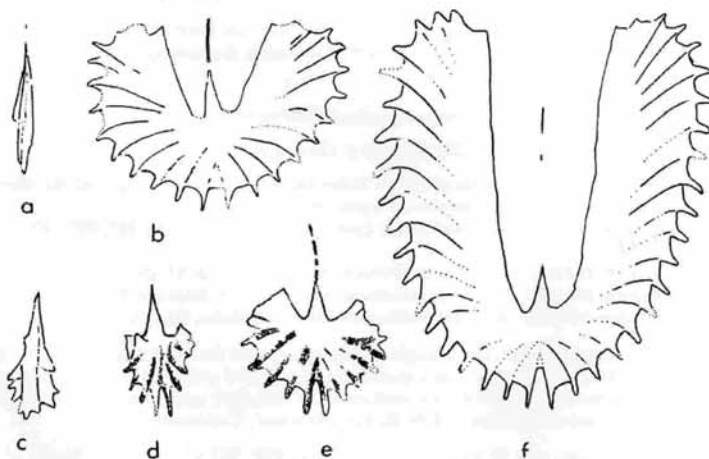
TEXT-FIG. 11. a–f—Growth stages of *Isograptus victoriae maximodivergens* Harris.
a, sicula and initial bud, VG 69. c, d, later stages with immature proximal thecae;
VG 34, VG 68 respectively. e, stage in which proximal thecae are almost fully formed,
but in which the ventral indentation between the sicula and first theca is still open;
VG 67. b, stage in which proximal thecae are apparently fully formed and the ventral
indentation has been bridged by a web of periderm; VG 66. f, mature rhabdosome;
PR 304. All specimens from S2/552, Aorangi Mine; Castlemainian, Ca3 (upper);
all × 5.

less commonly, gently flexuous. In a few Upper Castlemainian specimens the dorsal stipe margins retain concave curvature throughout their growth, becoming almost parallel. The stipes of most Yapeenian specimens are straight and sharply flexed in the proximal region. Divergence angle is highly variable though less so than in *victoriae*, and ranges from 315° to 360°, averaging 332°.

Thecal spacing ranges from 10 to 12 in 10 mm, most forms having 10·5; thecae are strongly curved, being inclined from 20° at their origins up to 90°–100° near their apertures. They overlap almost their entire length. Thecal apertures are strongly concave and prominently 'denticulate'; they are generally inclined to the stipe axis at a lower angle than in the earlier members of *I. victoriae*.

Discussion. Most specimens resemble Harris's figured specimen of var. *maximo-divergens* (lectotype, Harris 1933, fig. 13; this paper, text-fig. 13*a*); however, a few Upper Castlemainian forms, in which stipe width is nearly constant (e.g. text-fig. 12*c*), more closely match his figure 12, *maximus*, while others from the Castle-mainian and Yapeenian (text-fig. 12*g*) resemble his figures 14 and 17, *divergens*. They are linked with the most common form by intermediates, and are regarded here as 'variants', or members, of a variable population centred around forms which correspond to *maximodivergens*, rather than as distinct subspecies.

Average dimensions of sicular length, free sicular length, and sicular width do not differ significantly from those of *I. victoriae maximus*; however, the supra-dorsal length and width of the sicula and first theca are considerably less, whereas average proximal, and distal stipe width, and number of pendent thecae are significantly greater (text-figs. 27–29). The net effect is a larger over-all rhabdo-some size.

The divergence angle of stipes in the axilar region in a few specimens (text-figs. 12*b*, *g*) is 360°, becoming less distally with the convex dorsal curvature. The specimens are particularly interesting as they approach the *Oncograptus* rhabdosome with an initial biserial portion, and accord with Harris's suggestion (1933, pp. 95–96) that *Oncograptus* was derived from *I. v. maximodivergens*. Bulman's evidence (1936) for a 'primitive' pre-*minutus* stage of development in *Oncograptus*, however, appar-ently contradicts Harris's suggestion, and the derivation of *Oncograptus* is still uncertain.

Distribution. Ruedemann's figures of *I. walcottorum* from the Glenogle shale, British Columbia, and from Nevada (Ruedemann 1947, pl. 57, figs. 26–36) agree well with *I. victoriae maximodivergens* as described here, with the exception of figs. 27 and 28 which probably represent manubriate species of *Isograptus*.

Jackson (1964, fig. 3, no. 9) figured a specimen from the '*I. caduceus* Zone, Glenogle Formation', British Columbia, which closely resembles Nelson Yapeenian specimens. *I. victoriae* cf. *maximodivergens* has been listed by Kindle and Whittington (1958) from Newfoundland (from Bed 13 on Cow Head Peninsula, and from locality (5) at St. Paul's Inlet). Berry (1960, p. 67, pl. 11, fig. 7) recorded the form from zone 8 in the Marathon Sequence, Texas, and Ross and Berry (1963, p. 93, pl. 5, fig. 14) recorded it from the Basin Ranges (Phi Kappa Formation).

Bulman (1931, pp. 42–43, text-fig. 17) described and figured an incomplete specimen which probably corresponds to *maximodivergens*, from the 'lower Llanvirnian' beds of Korpa, Bolivia. The specimen was associated with *Didymograptus murchisoni* var. *geminus*. Turner's *I. gibberulus* var. *a* (1960, p. 82, pl. 9, fig. 6) from Argentina, which is stated to bear 'certain similarities to *I. walcottorum*' probably also belongs to *maximodivergens*.
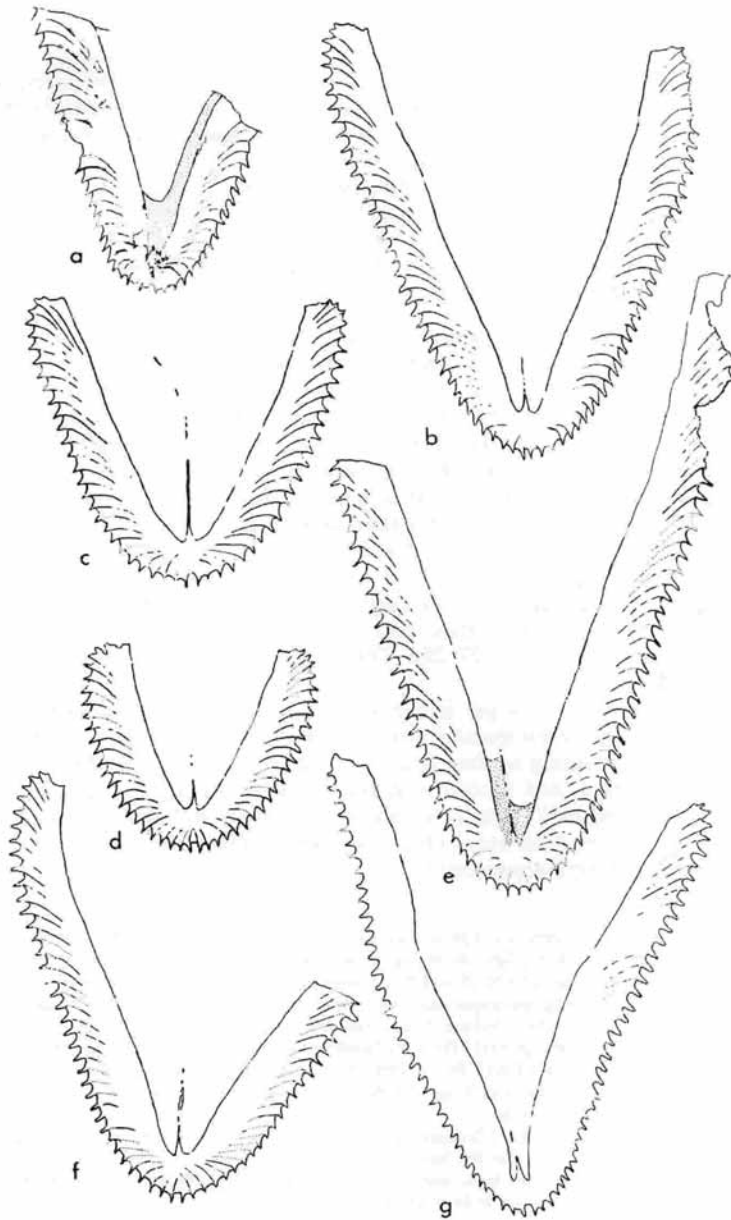
TEXT-FIG. 12. *a–g—Isograptus victoriae maximodivergens* Harris. *a, e*—from S2/540, Yapeenian, Ya1. *a*, VG 64; *e*, VG 46. *b, c, d, f, g*—from S2/552, Castlemainian, Ca3 (upper). *b*, VG 54; *c*, VG 51; *d*, VG 48; *f*, VG 49; *g*, VG 52. All figures ×2.
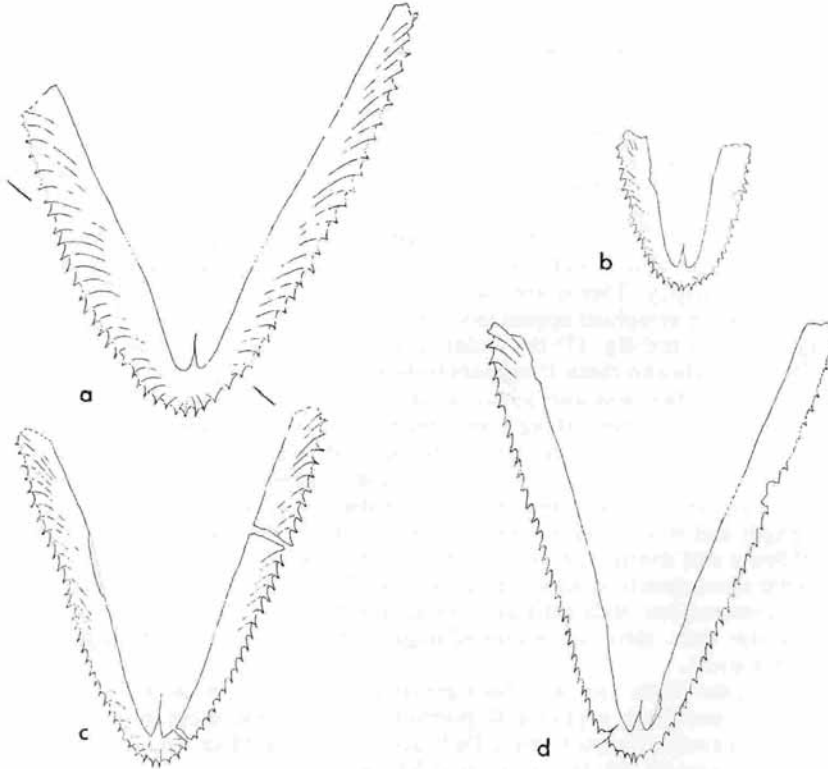
Isograptus victoriae divergens Harris 1933

Text-figs. 13*b–d*

1933   *Isograptus caduceus* var. *divergens* Harris, p. 91, text-figs. 14–18.
1947   *Isograptus furcula* Ruedemann, p. 353, pl. 57, fig. 48.

Lectotype. Of the 5 syntypes, 4 are held by Geological Survey of Victoria. The most complete and best preserved and most nearly modal specimen (GSV 63301, Harris, text-fig. 15) is here nominated as lectotype and refigured (text-fig. 13*d*). Paralectotypes are GSV 63648 (Harris, text-fig. 16), GSV 63649 (text-fig. 18), and No. 31361 LL/18(4) (text-fig. 17). The fifth syntype, that figured by Harris as text-fig. 14, is apparently lost. Type locality is 'Chinaman's Creek, Muckleford'.

TEXT-FIG. 13. *a–d—Isograptus victoriae maximodivergens* Harris, *I. v. divergens* Harris. *a, I. v. maximodivergens*, lectotype NMV P28770, from 'between Castlemaine Military Rifle Range and town', Victoria; figured by Harris (1933, text-fig. 13). Slight tectonic distortion, approximate direction of maximum shortening indicated. Castlemainian, Ca3. *b–d—I. v. divergens. b*, PR 442, S2/558, Aorangi Mine. *c*, PR 443, Chinaman's Creek, Muckleford, Victoria, collected by the writer. Yapeenian, Ya2. *d*, lectotype GSV 63301 figured by Harris (1933, text-fig. 15), from same locality as *c*. All figures ×2.

Material, localities, age. VG 50, VG 162, S2/545; PR 442, S2/558; several incomplete specimens; Yapeenian, Ya2.

Description. Rhabdosome large to moderate size, generally V-shaped. Sicula 3·5–4·0 mm long and about 0·6 mm wide at the aperture. The supradorsal portion of the sicula and theca 1^1 are conspicuous and 1·5 mm long. Stipes are only about 2 mm wide proximally, and widen gradually and evenly to about 4–5 mm wide near their distal ends, though in a few specimens, the stipes widen more abruptly, as in *I. v. maximodivergens.* Stipes are generally straight and diverge at about 340°.

Thecae are spaced about 9 in 10 mm and bear prominent denticles. Distal thecae are relatively straight and inclined at a low angle but their apertural portions are sharply flexed and directed downwards.

Discussion. With only a few New Zealand specimens available for study, the range of variation cannot be estimated. The specimens match Harris's types well and are confined to the Upper Yapeenian (Ya2) where they are associated with *Cardiograptus.* In Victoria the form ranges into the Darriwilian (Thomas 1960).

A syntype, figured by Harris (1933, text-fig. 15) from Chinaman's Creek (Muckleford, Victoria), is refigured here (text-fig. 13*d*) together with a topotype (text-fig. 13*c*).

I. victoriae divergens differs from its predecessor *maximodivergens* chiefly in its less robust rhabdosome, with narrower stipes which widen gradually and evenly rather than abruptly. Thecae are inclined at lower angles, and the whole rhabdosome has a more atrophied appearance. With the exception of the specimen figured by Harris (1933, text-fig. 17) the axilar film is absent and the ventral indentation between the sicula and theca 1^1 appears to be open and not bridged by periderm.

The loss of robustness and apparent atrophy of the *divergens* rhabdosome are accompanied by its diminishing abundance in the Upper Yapeenian and Darriwilian faunas of both Victoria and New Zealand. The stages through which the species passed during its phyletic growth are not, however, reoccupied during its waning; from the few specimens available for study it appears that the reduction in stipe length and width results from 'shrinking', rather than solely from the formation of fewer and shorter thecae. Thus thecae are much narrower, less inclined, and somewhat more closely spaced than in *maximodivergens.* Inter-thecal septa are not clearly preserved but, with their apparently lower inclination, distal thecae may be little shorter than those of *maximodivergens,* despite considerable reduction in distal stipe width.

Similarly, the sicula and first theca are only slightly shorter than those of *maximodivergens* and their supradorsal portions thus become more prominent. The latest representatives known, from Da3, are much reduced in size and robustness (Harris 1933, text-fig. 16; this paper, text-fig. 34).

Isograptus furcula Ruedemann 1947 from the Glenogle Shale of British Columbia bears the characteristic proximal features and low inclination of distal thecae of *I. victoriae divergens,* although stipes are more slender and grow to a greater length than known in Australasia. There seems little doubt, however, that Ruedemann's figured specimen belongs in Harris's species and is here synonymized accordingly.

Isograptus caduceus (Salter) 1853

1853   *Didymograpsus caduceus* Salter, p. 87, fig. 1.
1933   *Isograptus caduceus* (Salter); Harris (*pars*), pp. 89–93, text-figs. 55–59, 31?, 32?
1971   *Isograptus caduceus* (Salter); Cooper, p. 905, figs. 2a–f.

Diagnosis. Proximal thecae directed downwards and not manubriate; 4 to 7 pendent thecae; thecal ventral walls curved, concave ventrally, throughout rhabdosome; sicula and thecae somewhat denticulate; sicula and proximal thecae ventrally extended, giving stipes their greatest width at their origins, thereafter stipes tapering or, rarely, of constant width; stipes generally straight and diverging at high angles.

Remarks. Description of *Isograptus caduceus* at its type locality, Lévis, Quebec, and comments on its affinities are given by Cooper (1971). Two chrono-subspecies are formally recognized in Australasia—*I. c. imitatus* Harris and *I. c. australis* ssp. nov.; the nominate subspecies, however, is apparently not represented. The species is distinguished from *Isograptus victoriae* by its longer sicula and proximal thecae and consequently 'deeper' proximal region, its more constant number of pendent thecae (generally 5), its straighter stipes, and more commonly V-shaped rhabdosome. The species ranges from Castlemainian, Ca3 (upper part), to Yapeenian, Ya2, in Australasia, and is found in the Lower Darriwilian (*G. dentatus* zone) at Lévis, Quebec.

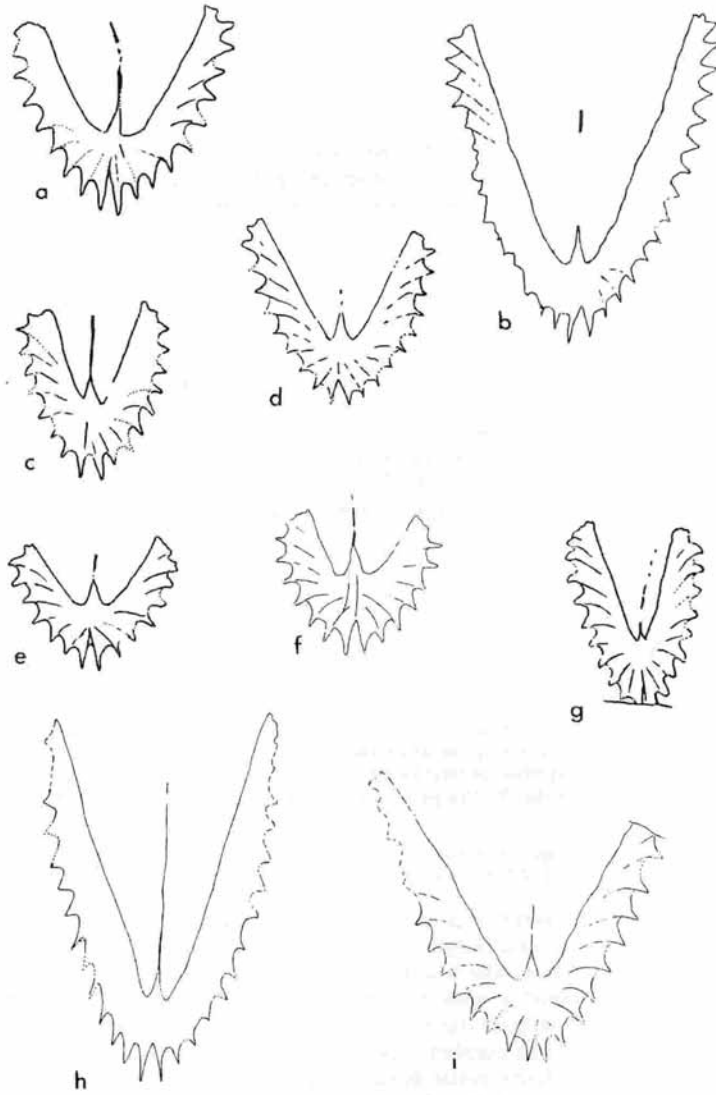## *Isograptus caduceus imitatus* Harris 1933

Text-figs. 14*a–i*

1933   *Isograptus caduceus* var. *imitata* Harris, p. 92, figs. 55–59.
?1933 *Isograptus caduceus* var. *horrida* Harris, p. 92, fig. 32.
1961   *Isograptus forcipiformis* var. *harrisi* Skwarko, p. 106, fig. 4.

Lectotype. Of the 5 syntypes, 3 are held by the Geological Survey of Victoria. The best preserved form (GSV 63650, figured by Harris, text-fig. 59) which also closely matches the common forms described here, is nominated as lectotype and refigured (text-fig. 14*i*). Paralectotypes are GSV 63644 (Harris, text-fig. 55), and GSV 63303 (Harris, text-fig. 56; this paper text-fig. 14*h*). Type locality is 'Ba 71, Gisborne Creek', Victoria.

Measured material, locality, age. 16 specimens: VG 30, 57–59, 61, 88, 141, 143, 146, 151, 157; PR 284, 286, 290, 292, 295; all from S2/552, Aorangi Mine Track; Castlemainian, Ca3 (upper part).

Description. The rhabdosome is generally V-shaped and small. The sicula commonly bears a thin short nema and ranges in length from 2·5–3·3 mm, averaging 3·1 mm; it is free for about 1·1 mm, and is about 0·5 mm wide at the aperture. The indentation between the free ventral walls of the sicula and first theca is narrow and deep; the apertural margins of both the sicula and first theca being extended into a prominent ventral process. The number of pendent thecae ranges from 4 to 7, averaging 6. The stipes, after their sharp initial flexure, remain straight or only slightly curved. Stipe divergence is less variable than in *victoriae*, being about 325° (300°–350°), giving the rhabdosome its characteristic 'V' shape. They are widest in the sicular region, and taper distally; proximal width averages 1·5 mm (1·4 mm–1·6 mm), and distal width averages 1·3 mm (1·1 mm–1·4 mm). Greatest stipe length is 15 mm.

Thecae are spaced about 7 in 5 mm. The initial one or two thecae of each stipe are

TEXT-FIG. 14. *a–i—Isograptus caduceus imitatus* Harris. *a*, VG 61; *b*, VG 88; *c*, VG 58; *d*, PR 286; *e*, VG 59; *f*, VG 30; *g*, VG 57. All from S2/552, Aorangi Mine area; Castlemainian, Ca3 (upper). *h*, paralectotype GSV 63303 figured by Harris (1933, text-fig. 56), from 'McKenzies Hill, Castlemaine'. *i*, lectotype GSV 63650 figured by Harris (1933, text-fig. 59) from 'Ba 71, Gisborne Creek', Victoria; Yapeenian, Ya1. All figures ×5.

relatively long and nearly straight, and are followed by shorter, curved thecae which are highly inclined to the stipe axis. Distal thecae are less curved and are inclined at lower angles. Thecal apertures are concave, markedly denticulate, and moderately inclined to the stipe axis, as in the smaller members of the *victoriae* series.

Discussion. Specimens referred to *I. caduceus imitatus* are considered to represent a variable population, the most common forms of which (text-figs. 14*d*, *e*) agree well with Harris's illustrations of the type specimens (Harris 1933, figs. 55-59). The most distinctive feature of the form is the shape of its stipes—they are widest in the sicular region, and taper distally. The typical, though not invariable, V-shape of the rhabdosome, together with its small size, also distinguishes it from subspecies of *I. victoriae*.

I. caduceus imitatus differs from *I. caduceus caduceus* (Salter), as redescribed from the type locality, Lévis, Quebec, by Cooper (1971), in having a shorter sicula and proximal thecae, giving a shallower outline to the ventral margin in the proximal region of the rhabdosome, and in its much shorter stipes.

The subspecies varies considerably in shape, and variants approach several described species. In a few specimens proximal thecae are longer than average and stipes are sharply flexed and more reclined (text-fig. 14*g*). The periderm appears to be thickened along the ventral thecal margins, and the ventral indentation between the sicula and first theca is almost completely closed. In general shape the specimens approach the form described here as *I.* cf. *forcipiformis* Ruedemann in the same beds and are inferred to indicate the derivation of that form.

The specimen in text-fig. 14*f*, with a more rounded ventral outline, approaches Swedish specimens of *I. gibberulus* Nicholson (Bulman 1932, pl. 8, figs. 3, 4). It is distinguished by having fewer thecae in the proximal region and by the much lower inclination of distal thecae.

A few specimens are of larger over-all size, with long stipes that do not taper and with a more rounded ventral outline (text-figs. 16*f*, *g*). They appear to form a distinct group and are here referred to as *I. caduceus* aff. *imitatus*.

While the contemporaneous form *I. v. maximodivergens* can be readily related to preceding subspecies of *I. victoriae*, the ancestry of *I. imitatus* is not so easily traced. Harris regarded it as a 'catagenetic variety' of *I. victoriae* and implied that it evolved from an earlier subspecies (*victoriae* or *lunatus*). In general accordance with Harris's view, the writer considers it to have probably descended from such V-shaped forms as *I. v. lunatus* (text-fig. 8*b*) in Ca1 and *I. v. maximus* (text-fig. 10*d*) in the lower Ca3, becoming a distinct species in the upper part of Ca3.

In New Zealand *I. caduceus imitatus* is confined to the upper part of Ca3 and is replaced by *I. caduceus australis*, which occurs with abundant *Oncograptus* and *Isograptus manubriatus* (s.l.) in Ya1. A possible intermediate population ranging from 'typical' *imitatus* to 'typical' *australis* was collected at Gisborne Creek (Ba 71) in Victoria, and occurs with *Oncograptus* but with little or no *I. manubriatus* and may, therefore, represent an intermediate horizon. Elsewhere in Victoria the form is found in the Upper Castlemainian (Harris 1933, p. 92).

I. caduceus imitatus is important as it apparently gives rise to the whole *caduceus* group, through rapid radiation at about the level of the Castlemainian-Yapeenian

boundary. All members of the group share with *imitatus* the distinctive long sicula and initial thecae, giving a 'deep' aspect to the proximal end, and the relatively stable number of pendent thecae (about 5 or 6). Although the subspecies has not been recorded outside Australasia, it has been observed in collections from the Lévis shales of Quebec and the Marathon sequence (probably Fort Peña Formation) of Texas, by the writer.

Skwarko's description and illustration of *I. forcipiformis* var. *harrisi* Skwarko (1961, p. 106, fig. 4) from the Aorangi Mine area, Nelson, agree well with larger members of *I. imitatus* and it is here included within the species. The poorly known form *I. caduceus* var. *horrida* Harris 1933 is closely related to *imitatus* (Harris 1933, p. 92) and when better known will probably prove to be conspecific.

Isograptus caduceus australis subsp. nov.

Text-figs. 16*a–h*

1962 *Isograptus caduceus* var. *divergens* Harris; Blake, pp. 231–232, pl. 1, figs. 8–9; pl. 2, figs. 7, ?8.
1963 *Isograptus caduceus* cf. *I. c.* var. *divergens* Harris; Ross and Berry, pl. 5, fig. 22.

Holotype. PR 389, held by New Zealand Geological Survey, Lower Hutt. Type locality is 20 chains up Jimmy's Creek from its junction with Little Slaty Creek, Aorangi Mine, Nelson, New Zealand (S2/540).

Measured material (paratypes), localities, age. 17 specimens from S2/540 (*Oncograptus* zone); VG 133; PR 8, 312, 314, 334–336, 346, 351, 361, 370, 372, 387, 392–393, 421; Yapeenian, Ya1, in New Zealand, Ya1–2 in Victoria.

Description. The rhabdosome is of moderate size and is generally V-shaped. The sicula ranges in length from 3·0 mm to 4·1 mm, averaging 3·6 mm, it is free for about 0·71 mm and averages 0·6 mm wide at the aperture. The ventral indentation between sicula and first theca is generally narrow and not deep. Pendent thecae range in number from 5 to 7, averaging 6.

The stipes, following their initial flexure, are straight or slightly curved, dorsally concave, grow to a considerable length (up to 25 mm), and diverge at from 330° to 360° (average 342°). They are widest in the region of the sicula, but thereafter are either parallel sided or taper gradually throughout their length. Average proximal stipe width is 1·9 mm, ranging from 1·3 mm–2·5 mm; distal stipe width ranges from 1·6 mm–2·2 mm and averages 2·0 mm.

Thecae are spaced from 9·5 to 10·5 in 10 mm, averaging 10·2. Inclination of thecae in the mid and distal portions of the rhabdosome is initially low (20°–30°), increasing rapidly to 50°–90° near the thecal aperture.

Discussion. The Nelson specimens are from the *Oncograptus* zone and represent a widely variable population, including some which closely approach *Isograptus caduceus caduceus* from Zone D (*Glyptograptus dentatus*) of the Lévis Shales of Quebec (text-figs. 16*a, c*). The neotype of the Lévis form, however, differs from all Nelson specimens in having a relatively longer sicula and first theca, giving a 'deeper' aspect to the proximal end, and more slender, gradually tapering stipes, which diverge at a greater angle. The New Zealand population most probably represents the Australasian equivalent of either *I. caduceus caduceus* or its immediate ancestor, and is named accordingly. Victorian specimens of the same form are common at
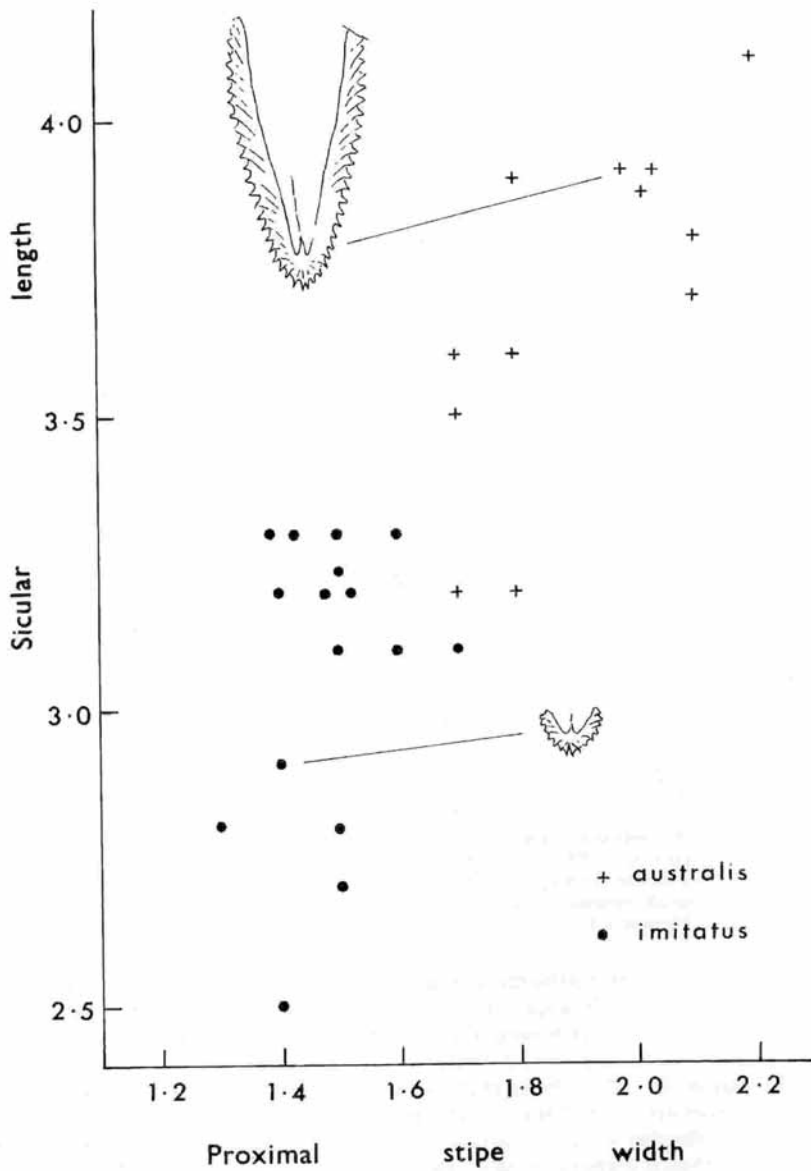
TEXT-FIG. 15. Sicular length plotted against proximal stipe width (mm) in 16 specimens of *Isograptus caduceus imitatus* Harris (Ca3, upper), and 12 specimens of *I. c. australis* subsp. nov. (Ya1).
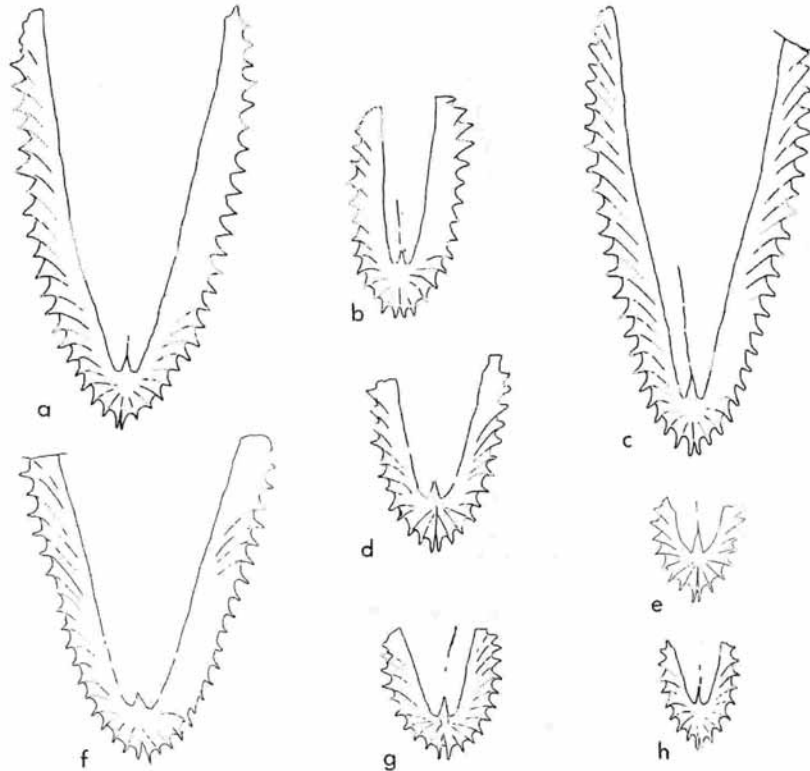
TEXT-FIG. 16. *a–h—Isograptus caduceus australis* subsp. nov., *I. caduceus* cf. *imitatus* Harris.
a–e, h—I. c. australis. a, PR 346; *b*, PR 370; *c*, PR 389, holotype; *d*, VG 133; *e*, PR 334;
h, PR 8. All from S2/540, Aorangi Mine; Yapeenian, Ya1.
   f, g—I. caduceus aff. *imitatus. f*, VG 60; *g*, VG 56; from S2/552, Aorangi Mine; Castlemainian,
Ca3 (upper). All figures ×3.

the Yapeenian localities, Gisborne Creek (Ba 71, Ya1), Chinaman's Creek (Ya2),
and Willey's Quarry (Ya2), a specimen of which is illustrated in text-fig. 34.

   The form is distinguished from contemporaneous subspecies of *I. victoriae*—and
resembles the preceding species, *I. imitatus*—in bearing stipes which are widest in
the sicula region. It differs from *imitatus* in being larger and more robust (text-
fig. 15); the stipes are wider, longer, and taper less markedly, and the sicula and first
theca are less extended ventrally, giving the ventral rhabdosome margin a rounded
outline, rather than a V-shape. Smaller members of *australis* (text-fig. 16h), however,
more closely match *imitatus*, reflecting its phylogeny.

Distribution. Several records of *I. 'caduceus' divergens* are more probably attributable to *I. caduceus aus-
tralis.* The specimen figured by Ross and Berry (1963, pl. 5, fig. 22) as *I. v. divergens*, from Pine Valley

quadrangle, Nevada, has stipes which are widest at their proximal ends, and thus cannot be referred to *divergens*. The specimen matches those Nelson forms of *I. caduceus australis* with narrow stipes.

Blake (1962, pp. 231–232, pl. 1, figs. 8, 9; pl. 2, figs. 7, 8) figured 4 specimens from the Bogo Shale of the Trondheim region, Norway, as *I. victoriae divergens*. From his figures the stipes appear to be widest at their proximal ends, and match *I. caduceus australis*, rather than *divergens*. The Bogo Shale fauna has been correlated with the *Didymograptus hirundo* zone of Britain by Skevington (1963a) and by Dewey *et al.* (1970); a somewhat younger British equivalent is advocated by Berry (1968). In South America, Turner (1960, pp. 83–84, pl. 9, figs. 10, ?11) described a similar form as *Isograptus gibberulus* var. *c* from 'Lower Llanvirnian' beds.

I. caduceus australis is thus likely to have a wide distribution; its stratigraphic range appears to be restricted and it should prove useful for correlation of the Yapeenian stage.

Isograptus sp. cf. *I. forcipiformis* Ruedemann 1904

Text-figs. 17a–g

cf. 1904   *Didymograptus forcipiformis* Ruedemann, pp. 699–700, fig. 91; pl. 15, figs. 10–13.
   1933   *Isograptus forcipiformis* (Ruedemann); Harris (*pars*), fig. 28 (not fig. 27).
   1968   *Isograptus forcipiformis* Harris; Skevington (*pars*), fig. 5c (not 5b).

Material, locality, age. 5 specimens: VG 55, 62, 63; PR 422; and several incomplete or poorly preserved specimens from S2/552; Castlemainian, Ca3 (upper). PR 357 from S2/540; Yapeenian, Ya1.

Description. The rhabdosome is small and oval in outline. The sicula and first theca are relatively long (3 mm) and are in contact for almost their entire length; their supradorsal portions are relatively short and inconspicuous. There are 5 to 6 pendent thecae. Stipes diverge proximally at about 330° curving back to become parallel, then converging distally. Proximal stipe width is 1·3–1·4 mm, the stipes gradually tapering to about 1·1 mm near their distal ends.

Thecal inclination changes markedly throughout the rhabdosome as in *I. caduceus imitatus*, from highly inclined in the proximal region to moderately inclined distally. Thecal apertures are moderately concave and sub-parallel to the stipe axis. Interthecal walls appear to be thickened.

Discussion. Immature growth stages of the species are unknown in the *maximus* zone (Ca3); what are probably immature stages (text-fig. 17a) are known from the *Oncograptus* zone (Ya1) where, however, mature stages are not represented in New Zealand. Mature stages are well known in the Yapeenian of Victoria (Harris 1933, text-fig. 28; Skevington 1968, fig. 5c).

The Nelson material generally resembles *I. forcipiformis* Ruedemann, the syntypes of which are refigured by Cooper (1971, fig. 3) in having approximately parallel stipes, relatively long sicula and proximal thecae, and an inconspicuous supradorsal portion of the sicula. However, they are of considerably smaller over-all size, with shorter, narrower, and more curved stipes and are confined to an earlier horizon. Skevington (1968, figs. 5b, c) figured two *forcipiformis*-like forms from Victoria; the smaller form is of Lower Yapeenian (Ya1) age, from Jackson's Creek (fig. 5c, listed in the caption as '5d'), and matches the Nelson specimens well. Further Victorian specimens from the Yapeenian stage are figured here (text-figs. 17d–g). The larger form figured by Skevington is of *decoratus* zone (Da3) age, from Strathfeldsaye (fig. 5b) and, together with the specimen figured by Harris (1933, fig. 27), agrees
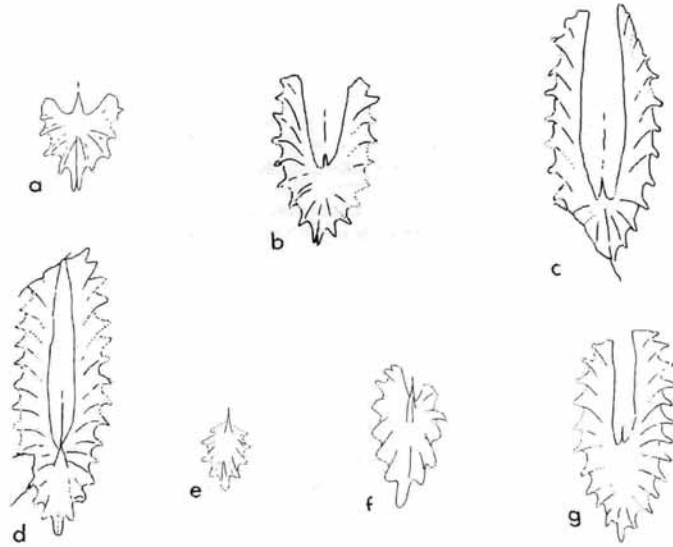
TEXT-FIG. 17. *a–g—Isograptus* cf. *forcipiformis* Ruedemann. *a*, immature rhabdosome, PR 357; S2/540, Aorangi Mine, Yapeenian, Ya1. *b*, VG 62; S2/552, Aorangi Mine, Castlemainian, Ca3 (upper). *c*, mature rhabdosome, VG 55, S2/552. *d*, GSV 63656b, Ba 71, Gisborne Creek, Victoria; Yapeenian, Ya1. *e*, immature growth stage of a form transitional between *I.* cf. *forcipiformis* and *Skiagraptus*; GSV 64427a. *f*, a subsequent growth stage (from the same slab as above); GSV 64427b. *g*, *forcipiformis*-like form (from same slab as figs. *e*, *f*); GSV 64427c. The three specimens of figs. *e*, *f*, and *g* are from the slab containing the specimens of Harris's (1933) text-figure 28, from Ba 71, Gisborne; Yapeenian (Ya1). All figures ×5.

well with Rudemann's syntypes of *Isograptus forcipiformis* from New York. The general similarity in rhabdosome form and in details of the proximal end of the Australasian cf. *forcipiformis* and the later *forcipiformis* s.s. suggest a direct phylogenetic relationship. However, until the lineage is documented in intervening strata (Darriwilian Zones 1 and 2) it remains tentative, particularly in view of the possible derivation of *forcipiformis* from *I. caduceus caduceus*.

Isograptus dumosus Harris 1933

Text-figs. 18*a–p*

1933   *Isograptus dumosus* Harris, p. 94, text-figs. 37–39, pl. 6, figs. 2a–c.
?1933   *Isograptus caduceus velata* Harris, p. 93, text-fig. 40.

Lectotype. Of the 6 syntypes, Harris referred to the specimen figured as text-fig. 39 (GSV 63651, Geological Survey of Victoria) as a 'typical mature form' and it is here nominated as lectotype and refigured, text-fig. 18*o*). Paralectotypes held by the Geological Survey of Victoria are GSV 63652 (Harris, text-fig. 37) and GSV 63653 (Harris, text-fig. 38). Type locality is 'Ba 71, Gisborne Creek', Victoria.
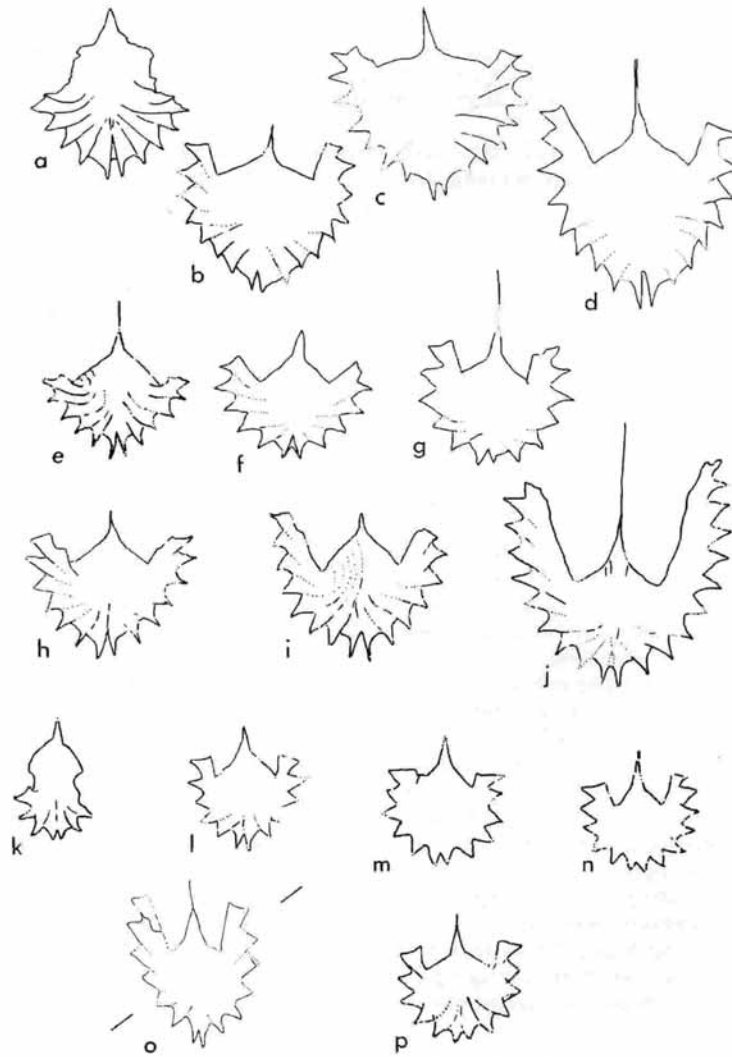
TEXT-FIG. 18. *a–p—Isograptus dumosus* Harris, 1933. *a–d—I. dumosus* form C, from S2/540, Aorangi Mine; Yapeenian, Ya1. *a*, PR 366; *b*, PR 425; *c*, PR 400; *d*, PR 384.

e–j—I. dumosus form B, from same locality as figs. *a–d. e*, PR 315; *f*, PR 377; *g*, PR 42; *h*, PR 316; *i*, PR 28; *j*, PR 414.

k–n, p—I. dumosus form A, from S2/552, Aorangi Mine; Castlemainian Ca3 (upper). *k*, growth stage, VG 89; *l*, PR 27; *m*, PR 429; *n*, PR 423; *p*, VG 140.

o—I. dumosus, lectotype GSV 63651, figured by Harris (1933, text-fig. 39), from Ba 71, Gisborne, Victoria; Yapeenian, Ya1. Slight tectonic distortion, approximate direction of maximum relative shortening indicated. All figures ×5.

Measured material, localities, age. 28 specimens: form A—VG 89, 140; PR 27, 280–281, 306, 423, 429, 432, 433, 434, from locality S2/552, Castlemainian, Ca3 (upper part); form B—PR 28, 42, 315–316, 339, 353, 374, 377, 412–415, from locality S2/540, Yapeenian, Ya1; form C—PR 338, 366, 384, 400, 410, 425, from locality S2/540, Yapeenian, Ya1.

Description. Three informal forms are recognized in the Nelson material: form A from the upper part of the *maximus* zone and forms B and C from the *Oncograptus* zone.

In form A, the smallest form, the sicula averages 3·6 mm (3·3–4·0) long, and 0·29 mm wide at the aperture. The apex of the sicula and first theca protrude about 1 mm above the shoulder of the manubrium, which expands rapidly to an average basal width of 1·8 mm. The apertural portions of proximal thecae are curved and directed outwards. Stipes are barely developed beyond the manubrium comprising only one or two thecae each, which are inclined to the stipe axis at a low angle; stipe width ranges from 0·8–1·1 mm. The rhabdosome is small and compact with an average width, at the level of the base of the manubrium, of 3·8 mm.

Form B is of similar general shape but has a slightly larger rhabdosome and its stipes attain a greater length. The sicula averages 4·0 mm (3·3–4·5) long and 0·5 mm wide at the aperture. The manubrium is of similar shape but of slightly larger size than that of form A. In a few specimens, outlines of some of the proximal thecae can be seen; they appear to be strongly curved, their apertural portions recurving somewhat so that apertures are directed away from the midline less noticeably than in form A. The general plan resembles that figured by Bulman (1968, figs. 1, 2) for *Isograptus manubriatus* but is developed to a less marked degree. Proximal thecae are somewhat denticulate.

The stipes are more robust than those of form A, bearing up to 6 thecae each beyond the manubrium, and measuring 1·1 mm (0·9–1·5) wide. Thecal inclination and shape are as in form B.

Form C has a more massive proximal region with a greater number of proximal thecae. The sicula averages 5·0 mm (4·6–5·9) long and 0·7 mm wide at the aperture. The sicula and the first two or three pairs of proximal thecae are 'denticulate' and considerably longer than in either forms A or B, giving a much 'deeper' aspect to the proximal region. Recurvature of the first two or three pairs of proximal thecae is marked, resulting in thecal apertures being directed downwards, imitating the *caduceus* condition. Subsequent thecae, however, resume the inclination and shape of forms A and B and the more normal manubriate condition. The manubrium is relatively wide and short, averaging 3·1 mm wide and 1·5 mm long. The stipes, as in form A, are barely developed beyond the manubrium and comprise only one or two thecae each.

Discussion. Form A comprises those members of *Isograptus dumosus* found in the upper part of the *maximus* zone and best matches Harris's description and figures of the types. Form B, which has undoubtedly descended from form A, has essentially a slightly larger and more developed rhabdosome, and is confined to the *Oncograptus* zone. The two forms overlap in range of morphology (text-fig. 19) and are here included within the one species. The lectotype from Ba 71, Gisborne Creek (Yapeenian, Ya1), figured by Harris (1933, text-fig. 39) is refigured here for comparison (text-fig. 18o). It is tectonically distorted and matches either form A or B.
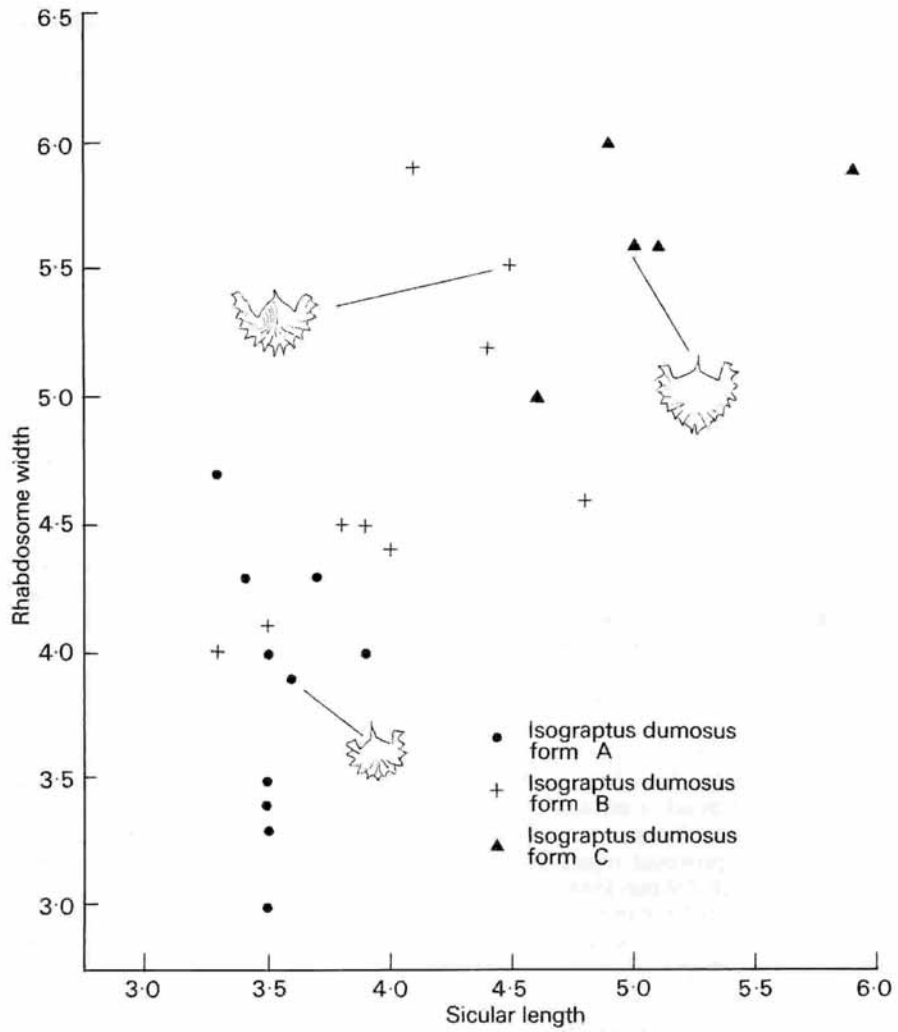
TEXT-FIG. 19. Rhabdosome width (measured at level of base of manubrium) plotted against sicular length (mm) in specimens of *Isograptus dumosus*, form A (10 specimens, Ca3, upper), form B (9 specimens, Ya1) and form C (5 specimens, Ya1).

F

Form C is found in association with form B in the *Oncograptus* zone. Its relationship with the other forms is unknown, but it does appear to constitute a distinct, though small, group.

Isograptus dumosus has been recorded from the Victorian *maximus*, *Oncograptus*, and *Cardiograptus* zones (Ca3–Ya2); its range in New Zealand is from the upper *maximus* zone to the *Oncograptus* zone (upper Ca3–Ya1).

Isograptus hastatus Harris 1933

Text-figs. 20*a–l*

1914   *Didymograptus caduceus manubriatus* T. S. Hall (*pars*), pl. 17, fig. 13.
1933   *Isograptus hastatus* Harris, p. 104, text-figs. 33–36.
1947   *Isograptus caduceus* var. *gracilis* Ruedemann, p. 351, pl. 57, figs. 15, 16.

Holotype. GSV 63654, Geological Survey of Victoria, figured by Harris (text-fig. 36) and refigured here (text-fig. 20*k*). Type locality is 'Sandy Creek Road near Bagshot, Bendigo'.

Measured material, localities, age. 24 specimens: form A—PR 114, 116, 118–122, 124–127, 166, from locality S2/565, Anthill Creek; Castlemainian, Ca3 (lower part); form B—VG 94–95, 142, 152, 156, 158; PR 282, 289, 300, 307, 310, 424, from locality S2/552, Aorangi Mine track; Castlemainian, Ca3 (upper part).

Description. The 2 populations studied are referred to 2 informal forms, form A in the lower Ca3, and form B in the upper Ca3.

In form A, the sicula averages 4·6 mm (3·6–5·0) long and 0·4 mm wide at the aperture. The manubrium is particularly large, averaging 2·7 mm (2·2–3·1) long and 1·4 mm (1·2–1·6) wide at the base. Details of its structure are not preserved but it presumably comprises the proximal portions of the sicula, theca 1¹ and the first two or three thecae of each stipe. Its smooth-sided wedge shape suggests that the successive budding of proximal thecae is spaced out and not bunched as in some later manubriate forms. A stout nema is common. Proximal thecae are generally directed downwards as in the associated form *I. victoriae maximus*, though in a few specimens (text-fig. 20*l*) they are directed outwards, foreshadowing the condition in form 'B', and in other manubriate isograptids.

The rhabdosome has the shape of an open U or V. Stipes average 1·8 mm (1·6–2·0) wide in the proximal region and taper slightly to 1·5 mm (1·4–1·6) in the distal region; they reach 0·9 mm long.

Thecae are spaced 5–6 in 5 mm, and are inclined at about 30°–40° to the stipe axis. Proximal thecae are markedly denticulate, the apertural margins of distal thecae are concave and highly inclined to the stipe axis.

TEXT-FIG. 20. *a–l—Isograptus hastatus* Harris 1933. *a–e—I. hastatus* form B, from S2/552, Aorangi Mine, Nelson. *a*, growth stage, PR 424; *b*, immature rhabdosome, PR 307; *c*, VG 95; *d*, VG 156; *e*, VG 94. Castlemainian, Ca3 (upper).

f–j, l—I. hastatus form A. *f*, PR 166; *g*, PR 125; *h*, PR 119; *i*, PR 120; *j*, PR 122; *l*, PR 118; all from S2/565, Aorangi Mine, Castlemainian Ca3 (lower).

k—I. hastatus, holotype figured by Harris (1933, text-fig. 36) from 'Sandy Creek Road, near Bagshot, Bendigo', Castlemainian, Ca3. Slight tectonic distortion, approximate maximum relative shortening direction indicated. GSV 63654. All figures ×5.
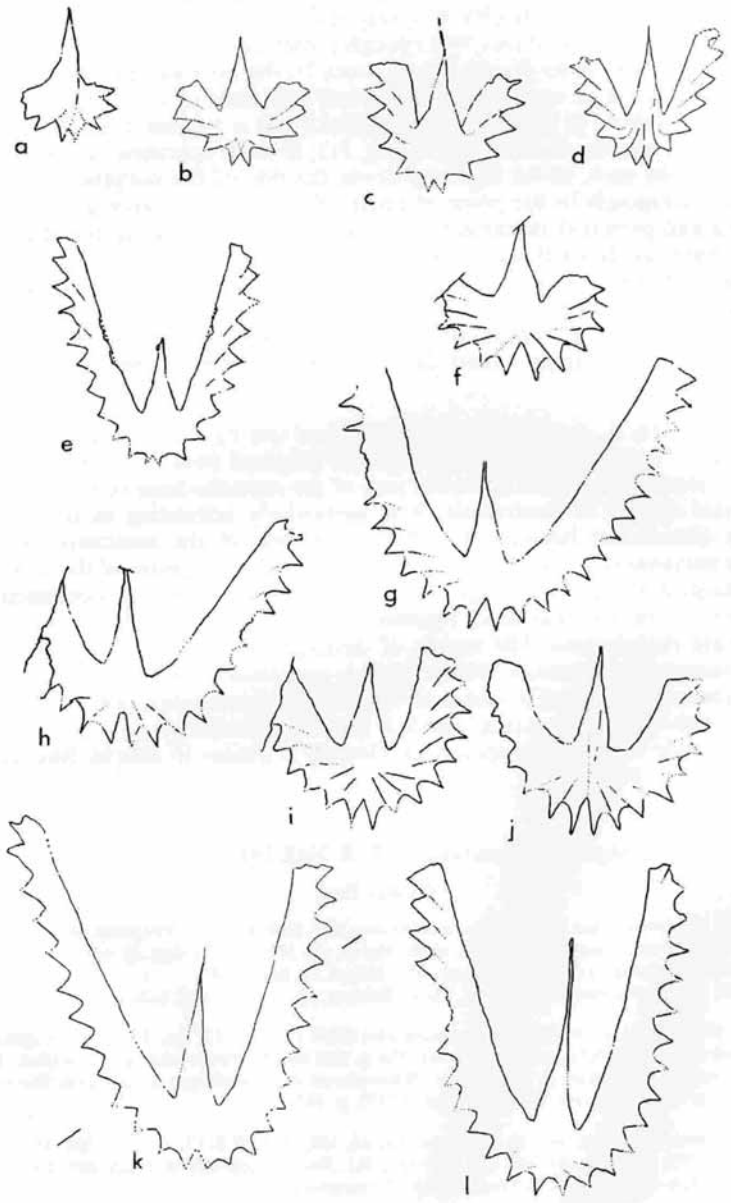
Form B has a somewhat smaller rhabdosome with straighter stipes. The sicula is shorter, averaging 3·8 mm (3·5–4·3) long and 0·6 mm wide at the aperture. A few specimens (text-figs. 20b, d) are well enough preserved to show that the manubrium comprises, in addition to the sicula and theca 1^1, the proximal portions of the first two or three thecae of each stipe, curved, and with little or no overlap of those of one stipe upon those of the other. Supradorsal width is 1·4 mm, and length 2·3 mm, considerably less than in form A (text-fig. 21); in most specimens a distinct break in slope can be seen, about half-way down the side of the manubrium, and presumably corresponds to the point of origin of theca 1^2. The apertural portions of the sicula and proximal thecae are directed outwards, away from the rhabdosome midline; there are fewer thecae in the proximal region than in form A.

Stipes are generally short, up to about 6 mm long, bearing no more than 9 or 10 thecae each after their points of flexure. They average 1·2 mm (1·1–1·3) wide proximally and are approximately parallel sided. Thecae are not denticulate; distal thecae are inclined at a low angle—about 20°–25°. Thecal apertures are relatively straight and highly inclined.

Discussion. Form A, particularly the specimen of text-fig. 20l, matches the holotype of *Isograptus hastatus* Harris (1933, fig. 36), refigured here for comparison (text-fig. 20k), and is confined to the lower part of the *maximus* zone (Ca3). The earliest manubriate species in Australasia, it is particularly interesting as it is morphologically transitional between the smaller members of the associated *Isograptus victoriae maximus* (cf. text-figs. 10d and 20i) and the later species of the manubriate group, suggesting a possible origin for the group. Form B, which is confined to the upper part of the *maximus* zone, represents a later stage in the development of the manubriate rhabdosome. The nature of development cannot be determined but, as in *I. manubriatus* (Bulman 1968, p. 212), is presumed to be of isograptid type.

Ruedemann's figures of *I. caduceus* var. *gracilis* Ruedemann, from the Glenogle Shale, British Columbia, closely match *I. hastatus*, form B.

Stratigraphic range of the species in Victoria is similar to that in New Zealand (Harris 1933, p. 104).

Isograptus manubriatus (T. S. Hall 1914) *sensu lato*

Text-figs. 22a–q

1914   *Didymograptus caduceus* var. *manubriatus* T. S. Hall, pp. 108–109 (*pars*), pl. 17, fig. 12.
1933   *Isograptus manubriatus* (T. S. Hall); Harris, pp. 102–104, text-figs. 41–44, pl. 1, figs. 2a–i.
?1947   *Isograptus lyra* Ruedemann, pp. 353–354, pl. 57, figs. 43–47.
1968   *Isograptus manubriatus* (T. S. Hall); Bulman, pp. 212–214, figs. 1–2.

Lectotype. Hall figured 2 'co-types' of *I. manubriatus* (Hall 1914, pl. 17, figs. 12, 13). The specimen of fig. 12 effectively became lectotype when Harris (1933, p. 102) transferred the other specimen (that of fig. 13) to his new species *I. hastatus*, as its holotype. Whereabouts of the lectotype is unknown. The probable type locality is Willey's Quarry, Macedon (Harris 1933, p. 102).

Measured material, localities, age. 49 specimens: VG 63, 160, 161; PR 9–13, 311, 317, 319, 321, 324, 330, 340, 348–350, 352, 355, 360, 363, 367, 375, 380–382, 385, 394–395, 398–399, 402–405, 407–408, 411, 416–417, 419–420, 426–428, 430–431, 434 from S2/540; Yapeenian (Ya1).
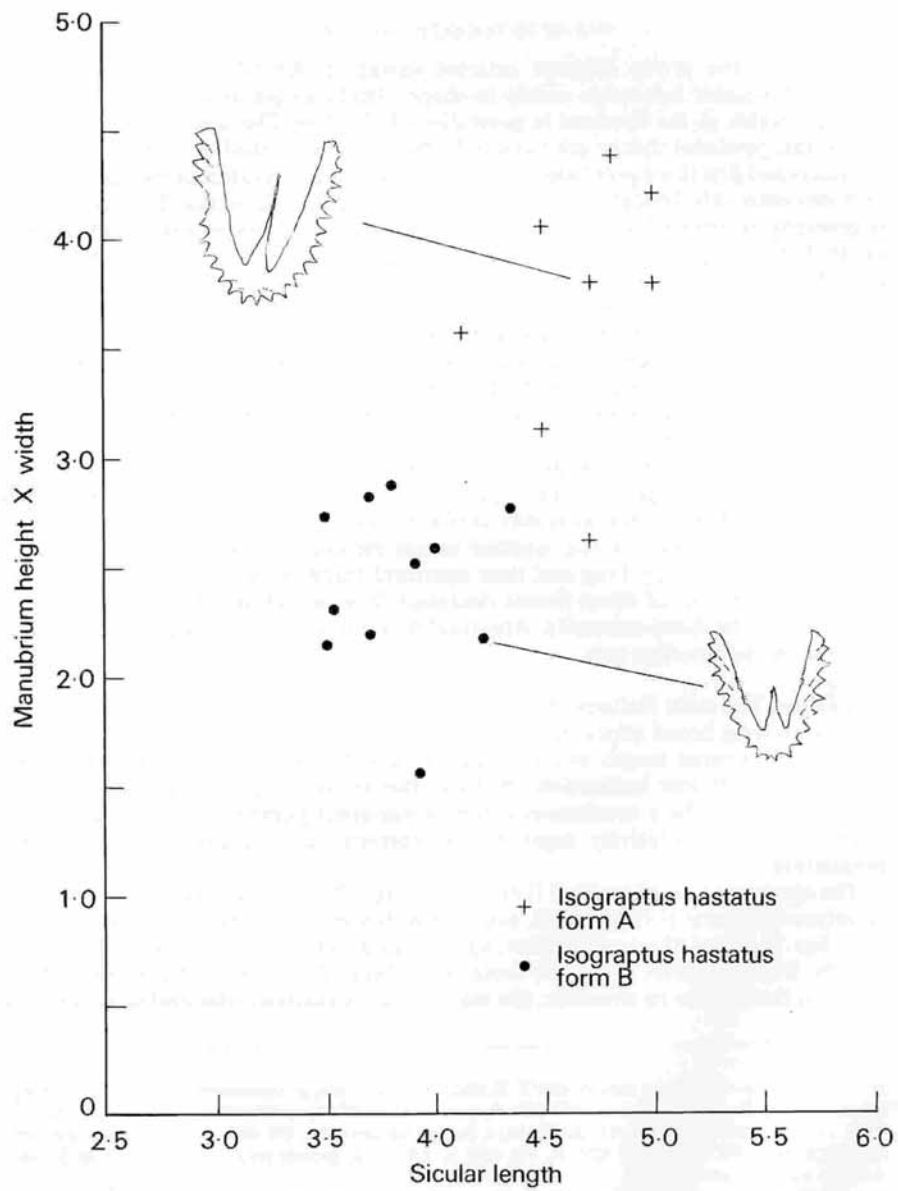
TEXT-FIG. 21. Manubrium height times manubrium width plotted against sicular length (mm) in specimens of *Isograptus hastatus* form A (8 specimens; Ca3, lower), and form B (11 specimens; Ca3, upper).

Description. The group displays extreme variation. Rhabdosomes are generally large and massive but range widely in shape. Sicula length averages 5·3 mm (3·0–8·0) and width at the aperture is generally 0·3–0·5 mm. The distal portions of the sicula and proximal thecae are outwardly curved to a marked degree. The apex of the sicula and first theca protrude about 1–2 mm above the shoulder of the manubrium, and are commonly difficult to distinguish from the base of the nema. The manubrium is generally extremely long and wedge-shaped, averaging 3 mm in length but ranging up to 5 mm long; width at the base averages 1·6 mm (0·1–2·7). Structure of the manubrium cannot be determined, but it apparently comprises the proximal portions of at least the first 3 or 4 thecae of each stipe, in addition to the sicula and theca 1^1. In a few specimens, particularly those with nearly parallel stipes, the sides of the manubrium can be seen to extend below their points of contact with the dorsal stipe margin for up to 1 mm. Stipe divergence and curvature range widely and independently. Divergence ranges from 260° to 360° with a high coefficient of variation (86); curvature varies from straight to strongly curved. Stipes reach 10–14 mm long in mature forms. Stipe width, in forms with straight stipes, is generally greatest at about mid stipe, tapering slightly proximally and distally, whereas in forms with curved stipes, stipe width is generally uniform. The result is that the ventral rhabdosome margin is always curved, whether or not the dorsal stipe margins are curved.

Thecae are extremely long and their apertural margins bear a prominent ventral process; inclination of distal thecae decreases from about 20°–30° at mid stipe to 10° or less at the distal extremity. Apertural margins are nearly straight and inclined at about 90° to the stipe axis.

Discussion. The main features of this extremely variable group are: (1) large rhabdosome with long broad stipes; (2) marked degree of outward curvature in proximal thecae; (3) extreme length of sicula and proximal thecae; (4) long wedge-shaped manubrium; (5) low inclination of distal thecae; (6) ventral, apertural process. There appears to be a continuous range of variation joining all members and the whole group is tentatively regarded as representing a single, widely variable, population.

The specimen figured by Hall (1914, pl. 17, fig. 12) which was later established as lectotype by Harris (1933, p. 102), together with specimens figured by Harris (1933, pl. 6, figs. 1a–i) and Skevington (1968, fig. 2a; this paper, text-fig. 22*o*) from Macedon, and by Bulman (1968, figs. 1–2) from Marathon, Texas, differ from the Nelson forms in that, below its shoulder, the manubrium is much shorter and squatter, and

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TEXT-FIG. 22. *a–q*—*Isograptus manubriatus* T. S. Hall, *sensu lato. a–n, p*—specimens from S2/540, Aorangi Mine, Nelson; Yapeenian, Ya1. *a*, VG 160; *b*, growth stage, PR 9, *c*, PR 430; *d*, PR 431; *e*, PR 427; *f*, PR 11; *g*, growth stage, PR 411; *h*, PR 10; *i*, largest Nelson form, PR 403; *j*, growth stage, PR 398; *k*, growth stage, PR 434; *l*, PR 428; *m*, PR 426; *n*, PR 13; *p*, growth stage, PR 12; all from S2/540, Aorangi Mine. Yapeenian, Ya1.

o, q—Victorian specimens from Willey's Quarry, Macedon, the probable type locality. *o*, specimen figured by Skevington (1968, fig. 2a) closely matching Hall's (1914, pl. 17, fig. 12) figure of the type; *q*, specimen with more gradually expanding manubrium, resembling the New Zealand forms (compare with fig. 22 *l*; Yapeenian, Ya2. All figures ×3.
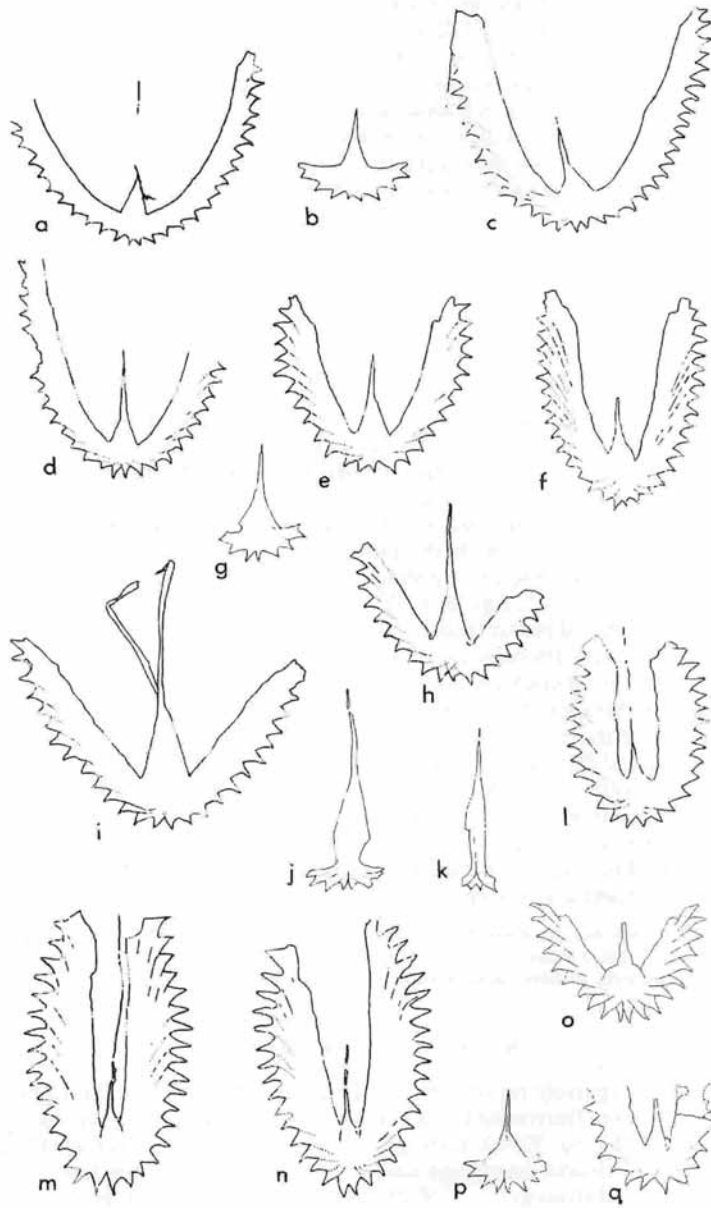
there is consequently a more pronounced bunching of proximal thecal origins. The full range of forms at Willey's Quarry, Macedon—the probable type locality of *manubriatus* (Harris 1933, pp. 102–104)—however, includes specimens (one example being figured in text-fig. 22*q*) with a long, tapering manubrium, such as in the Nelson forms and until the species is adequately redescribed and defined in Victoria, all specimens are tentatively included in '*manubriatus, sensu lato*'.

Early growth stages (text-figs. 22*b*, *g*, *i*, *k*, *p*), with their long siculae and initial thecae, are easily distinguished from growth stages of other isograptids (see Harris 1933, p. 103).

I. manubriatus first appears shortly after the appearance of *Oncograptus* in the Lower Yapeenian in Victoria; it appears to be restricted to the Yapeenian stage in both New Zealand and Victoria.

Isograptus lyra Ruedemann 1947 matches those Nelson specimens with parallel stipes but apparently comes from a younger stratigraphic horizon in the Athens Shale (Ruedemann 1947, p. 353, pl. 57, figs. 43–47).

Generic affinities. In a recent discussion of the generic affinities of *I. manubriatus*, Skevington (1968) concluded that the species is more closely related to *Meandrograptus* Moberg 1892 than to *Isograptus* Moberg 1892. However, the symmetrical arrangement of the sicula and initial theca (1^1) in *I. manubriatus* (see Bulman 1968, p. 212, fig. 1) as in the closely similar Swedish species *Meandrograptus*? *geniculatus* Skevington 1965, suggest that both species belong to *Isograptus*, as defined here. The sicula in the type species, *Meandrograptus schmalenseei* Moberg (see Bulman 1932, text-figs. 2a–b, pl. 2, figs. 6–8; this paper, text-fig. 6*f*) is relatively long and straight, and the initial pair of thecae (1^1 and 1^2) turn sharply away from it, the axis of rhabdosome symmetry passing *through* the sicula. In *M. schmalenseei*, as in other species referred to *Meandrograptus* by Skevington (1965, p. 44)—*Didymograptus leptograptoides* Monsen 1937 and *Didymograptus mobergi* Törnquist 1901—the distal portions of the initial thecae are reclined, contrasting markedly with those of *I. manubriatus* and *M.? geniculatus*. The 2 species are probably best regarded, together with the other 'manubriate' species, *dumosus* and *hastatus*, as comprising a divergent group within *Isograptus*, with the proximal symmetry and highly inclined proximal thecae of *Isograptus*, and the proximal concentration of thecal origins, the prothecal folds, and the low inclination of distal thecae of *Meandrograptus*. The group may well eventually warrant separation as a distinct subgenus within *Isograptus*.

Since the above was written, Beavis (*Geol. Mag.*, vol. 109, pp. 193–204, 1972) has proposed the name *Pseudisograptus* for the 3 manubriate species, *manubriatus* (type species), *dumosus*, and *hastatus*; the accompanying diagnosis, however, needs revision in view of the present work.

NOTES ON OTHER FORMS

1. Several other, sparsely represented, isograptids are present in the Upper Castle-mainian to Upper Darriwilian interval of Australasia. *Isograptus caduceus* var. *tenuis* Harris (1933, pp. 92–93, text-figs. 53–54) is found rarely in Ca3–Da4 beds in Victoria; it has a slender horseshoe-shaped rhabdosome and superficially resembles a small reclined didymograptid of *Didymograptus hemicyclus* Harris type (text-

fig. 8*l*) which is common in the same beds. The didymograptid is distinguished by its proximal symmetry.

2. The variety *I. caduceus* var. *pertensa* Harris (1933, p. 92, text-fig. 31) occurs sparsely, being known only from Steiglitz (Beavis and Beavis 1968, p. 117). The specimen figured by Harris has abnormally long stipes and thecal spacing is about 5 in 10 mm—approximately twice the normal isograptid spacing; it resembles those specimens of *I. caduceus* which have been tectonically distorted, with the direction of maximum relative lengthening nearly parallel to the rhabdosome midline. Until it is adequately described, true identity of the variety remains uncertain.

3. *Isograptus ovatus* T. S. Hall 1914, and *I. caduceus spinifer* Keble and Benson 1929, are of particular interest as they are the youngest isograptids in Australasia occurring, albeit sparsely, in the *teretiusculus* zone (Da4, text-figs. 23*b*, *c*). Together with the specimen from the Hendre Shales figured by Toghill (1970, fig. 2*a*) they are apparently the youngest representatives of the genus in the world. The holotype (counterpart) of *I. caduceus spinifer* is refigured here (text-fig. 23*c*) and, although poorly preserved, shows a definite resemblance in proximal region features, to members of the *caduceus* group. *I. ovatus* is an apparently similar form; both bear somewhat spinose thecae and highly inclined apertural margins on distal thecae.

4. *Meandrograptus tau* Harris 1933, *M. aggestus* Harris 1933. Harris (1933, p. 107) commented on the similarity of *Meandrograptus tau* to the manubriate isograptids and suggested that a specimen of *M. tau* with reclined stipes would be indistinguishable from *I. hastatus*. The holotype of *M. tau* is refigured here (text-fig. 24*a*) for comparison with the isograptids, together with 2 other specimens from the same stage (Yapeenian) in Victoria (text-figs. 24*b*, *d*). In each specimen it can be seen that the
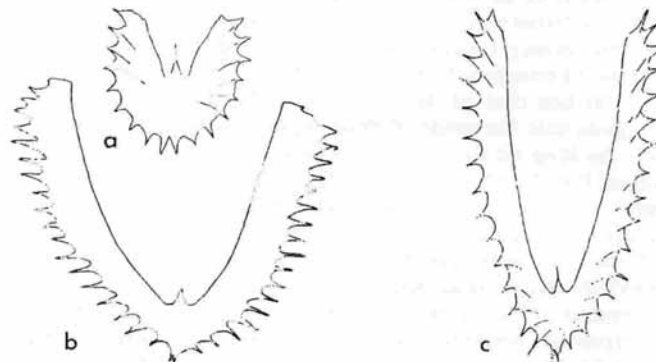
TEXT-FIG. 23. *a–c*—Darriwilian isograptids from Nelson. *a*, *Isograptus* sp., immature rhabdosome; PR 32, S2/582; Darriwilian, Da1-2. ×5. Aorangi Mine area. *b*, *Isograptus* cf. *ovatus* T. S. Hall, tectonically distorted with approximate direction of maximum relative shortening parallel to rhabdosome midline; specimen figured by Keble and Benson (1929, pl. 104, fig. 10), from Cobb Valley; Darriwilian, Da4. ×3. *c*, *Isograptus caduceus spinifer* Keble and Benson, holotype counterpart; Cobb Valley, Darriwilian, Da4. ×5.

sicula and theca th1[1] do not form a symmetrical pair as they do in *I. hastatus* and all isograptids, but that the axis of rhabdosome symmetry passes through the sicula at its aperture as in *M. schmalenseei*, and Harris's species appears to be best retained within *Meandrograptus*. However, the specimens bear the characteristic manubrium of manubriate isograptids and could well be produced by the loss of isograptid symmetry from a manubriate isograptid rhabdosome; a stage in which isograptid symmetry is barely lost might be represented by the rhabdosome of *Meandrograptus aggestus*, the holotype of which is refigured here (text-fig. 24c), and for which generic placement is less obvious. The suggested derivation of the meandrograptid rhabdosome from *Isograptus* is consistent with their similarity of development (theca 1[2] dicalycal) and with their stratigraphic relationship—*Meandrograptus* appears shortly after the appearance of the manubriate isograptids—in the Upper Castlemainian to Lower Yapeenian, or its equivalent.

5. *Oncograptus* Hall and *Cardiograptus* Harris and Keble. The similarity in form of the thecae of *Oncograptus* and *Isograptus* 'caduceus' was noted by Hall (1914, p. 109), and the series *Isograptus* 'caduceus' (*I. victoriae*)–*Oncograptus*–*Cardiograptus* was proposed by Harris as a possible line of development of the biserial rhabdosome. The hypothesis was reviewed by Bulman (1936, pp. 271–278) who described the proximal development of a Texan specimen of *Oncograptus* as being of pre-*minutus* dichograptid type with the insertion of an additional theca, 2[1]b, and who therefore concluded that *Oncograptus* cannot be closely related to *Isograptus* but is probably derived from a reclined tetragraptid ancestor. The 'primitive' stage of development may be less of an objection if the development of *Skiagraptus*, which is more certainly derived from *Isograptus* (Skevington 1968, p. 321) is also of dichograptid type (Whittington and Rickards 1969, p. 802). However, as Harris (1933, p. 96) observed, intermediate forms between *Isograptus* and *Oncograptus* are apparently lacking and the suggested relationship remains uncertain.

More recently Skevington (1968) claimed that the proximal end structure of *Oncograptus* 'matches that of *M. manubriatus* [*Isograptus manubriatus*] in every detail and suggests that the mode of development is the same in both'. He goes on to assert that 'the long sicula, the superposition of later upon earlier thecae at the proximal end of the rhabdosome, the deflection of the apertural portions of th1[1] and subsequent thecae away from the sicula to a progressively increasing degree, the form of the apertural margin and of the ventral denticle—all these features are common to both *M. manubriatus* and *O. upsilon*, and on this evidence it is concluded that . . . [they] should be regarded as conspecific'. However, in all specimens of *Oncograptus* examined by the writer in which proximal details are preserved, the curvature of proximal thecae is as shown in the Victorian specimen figured by Bulman (1936, text-fig. 1B) and in those figured here (text-figs. 24e–g). Contrary to Skevington's claims, the apertural portions of proximal thecae are *not* deflected away from the sicula, but are directed downwards as in *I. caduceus* and *I. victoriae* (compare text-figs. 22a–q with text-figs. 24e–g). The two thecal series appear to develop separately and are *not* superposed as in *I. manubriatus*; certainly there is no structure approaching the manubrium. Further, thecal apertural margins in profile view are so like those of *Isograptus victoriae maximodivergens* that distal stipe fragments of
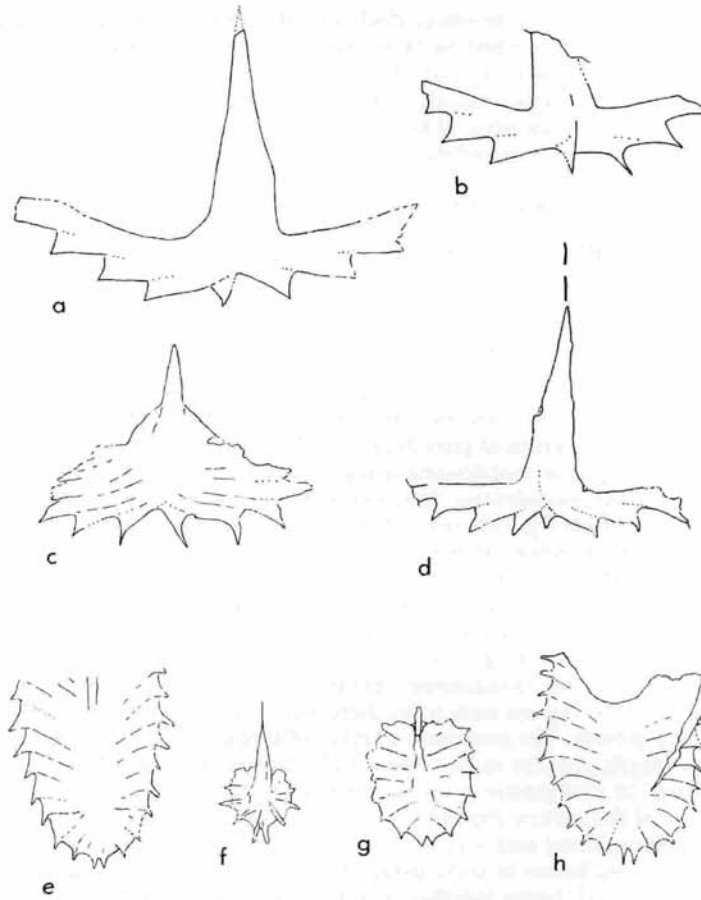
TEXT-FIG. 24. *a–h—Meandrograptus* Moberg, *Oncograptus* T. S. Hall, and *Cardiograptus* Harris and Keble illustrating proximal symmetry and thecal curvature.

a, b, d—Meandrograptus tau Harris, 1933. *a*, NMV P13798, holotype, figured by Harris (1933, pl. 6, fig. 5d); *b*, GSV 63656a; both from Ba 71, Gisborne Creek, Victoria; Yapeenian, Ya1. *d*, GSV 63655, figured by Harris (1933, text-fig. 48) from 'near Ba 71, Gisborne Creek'. ×10.

c—Meandrograptus aggestus Harris, 1933, holotype, figured by Harris (1933, pl. 6, fig. 7a), NMV P13799. Allotment 2, Section 2, Yandoit, Victoria. Castlemainian, Ca3. ×10.

e–g—Oncograptus upsilon T. S. Hall. *e*, proximal portion only, PR 439. *f*, growth stage, PR 418. *g*, later growth stage, PR 365. All three specimens from S2/540, Aorangi Mine, Yapeenian, Ya1. ×5.

h—Cardiograptus morsus Harris and Keble 1924. PR 30, S2/556, Aorangi Mine. Yapeenian, Ya2. ×5.

the two forms cannot be differentiated whereas the apertural margins of manubriate forms are readily distinguished by their high inclination to the stipe axis. Far from being conspecific, the two forms are here considered to be not closely related.

Similarly, the proximal end structure in *Cardiograptus morsus* (text-fig. 24*h*) appears to be of the same general kind as in *C. crawfordi* (Skevington 1968, fig. 5a) rather than like that of *I. manubriatus*, as suggested by Skevington (1968, p. 316).

GROWTH, VARIATION, PHYLETIC TRENDS

Because a comparatively large number of specimens is involved in this study (approximately 500) the most convenient means of describing morphologic variation and of comparing populations is by statistical analysis of the measured characters. The statistics are used as a tool to aid in description rather than as the main basis for taxonomic interpretation.

Growth, allometry. Both astogenetic growth and phyletic growth affect rhabdosome size; each is accompanied by its own kind of allometric change in rhabdosome proportions. The two kinds of growth are readily distinguished.

The earliest stages of rhabdosome astogeny are shown in a growth series such as that of *Isograptus manubriatus* Skevington (1968, fig. 1) or *Isograptus victoriae maximodivergens* (text-fig. 11 herein); the sicula and proximal thecae grow to approximately their full size while the rhabdosome is still in an early stage of development. Subsequent growth of the rhabdosome takes place principally by the distal addition of new thecae. Thus the locus of thecal growth moves progressively along the stipe, away from the sicula, the growing portion of the stipe being that composed of the newest 3 to 6 thecae forming at its distal end. With the addition of each new theca the proportions of the rhabdosome change (heterauxesis) but because thecae are formed at the same rate on each stipe, there is no loss of bilateral rhabdosome symmetry during growth. The maximum number of thecae formed, and hence the maximum stipe length, appears to be a specifically determined character.

In contrast to astogenetic growth, phyletic growth involves an increase in the over-all size of the mature rhabdosome, with accompanying change in proportions (lineage allomorphosis) and is particularly well displayed by the *I. victoriae* lineage which is discussed below in some detail. It is accomplished principally by increase in size of individual thecae together with the continued distal formation of thecae, producing a greater number in each stipe. The maximum stipe length appears to be closely related to thecal length in that part of the lineage containing *lunatus*, *victoriae*, and *maximus*, so that there is comparatively little change in the over-all rhabdosome proportions of the 3 subspecies. Stipes of *maximodivergens* and, to a lesser extent, *divergens* grow to, proportionately, a much greater length. Undoubtedly the most important increase is that of the volume of the space within the theca, that occupied by the graptozooid. Whereas most linear dimensions increase by a factor of 2 or 3 throughout the series (see figs. 26-29), thecal length increases by about 3·5 times, the dorso-ventral profile area of thecae by about 6 times, and the inferred thecal volume by at least 12 times. Width at the aperture increases only slightly; consequently, thecae change in shape from short, squat, rapidly expanding tubes to long, drawn-out, gradually expanding tubes (text-figs. 25*a*, *b*, *c*, *d*, *g*, *i*, *l*).
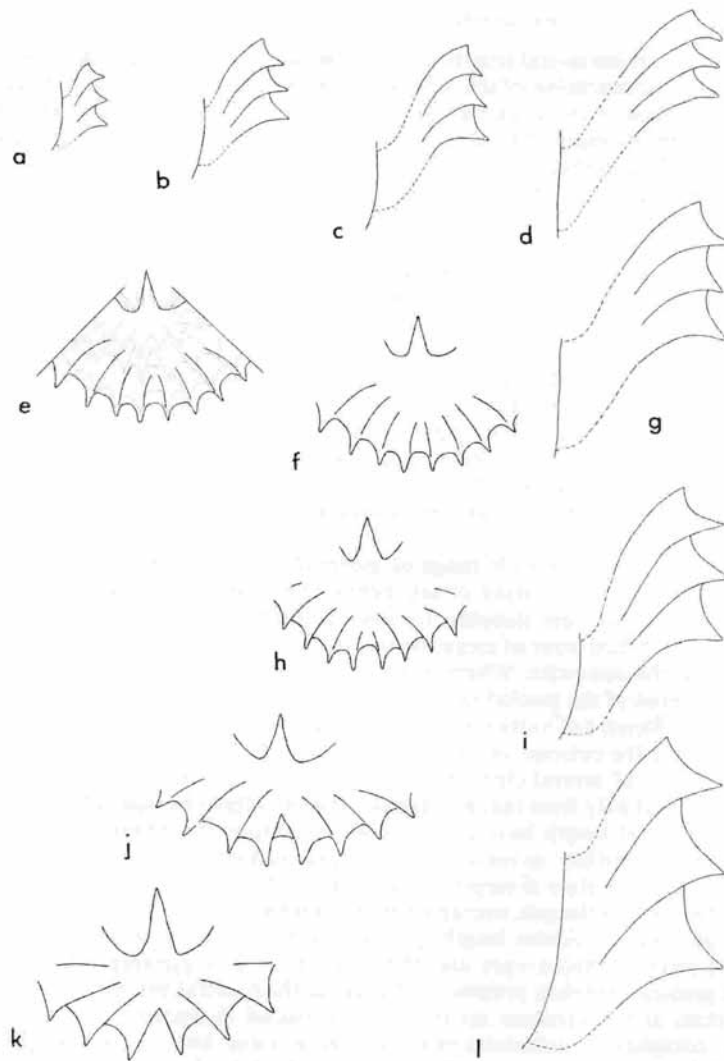
TEXT-FIG. 25. *a–l*—Allometry in the phyletic series *Isograptus victoriae lunatus-divergens* illustrated by modal forms from Nelson. *a–d, g, i, l*—Distal stipe segments drawn at same scale (*a–d*, approximately ×5) to show progressive increase in length and profile area of mature distal thecae; *lunatus* (*a*), *victoriae* (*b*), *maximus* (*c*), *maximodivergens* (*d*). Similar segments are drawn at approximately equal size in the series *l, i, g, d*, to show the progressive change in thecal proportions from relatively squat tubes to relatively slender tubes. *e, f, h, j, k*—Proximal portions of rhabdosomes superposed (*e*, approximately ×5) to show increase in length of proximal thecae and sicula, and drawn at approximately equal size to show change in thecal proportions; *lunatus* (*k*), *victoriae* (*j*), *maximus* (*h*), *maximodivergens* (*f*).

Part of the increased thecal length is accommodated by an increase in stipe width, and part by an exaggeration of the sigmoidal thecal curvature. The rate of budding per unit length of stipe does not change significantly throughout the series (approximately 10–12 in 10 mm). The long *maximodivergens* theca is thus, in essence, a 'stretched-out' *lunatus* theca with increased sigmoidal curvature.

In the proximal region, increase in rhabdosome size is achieved by an increase in thecal (and sicular) length, and a smaller increase in apertural width (less than $\times 1 \cdot 4$). The rate of expansion of individual thecae is thus much reduced, enabling a greater number to assume a pendent or downward growing attitude (text-figs. 25*f*, *h, j, k*). The size of the supradorsal portions of the sicula and first theca do not change significantly.

The one feature that appears to have at least a partially controlling influence on phyletic growth of the rhabdosome thus appears to be thecal width or, in the original rhabdosome, cross-sectional area of the theca.

As discussed in the taxonomic section above, maximum development of the *victoriae* rhabdosome (*maximodivergens* stage) is followed by a decrease in size and loss of robustness (*divergens* stage) which is the result of 'shrinking' of the rhabdosome rather than a retrogressive passage through the stages of its phyletic development.

Intraspecific variation. The wide range of morphologic variation displayed by most species of *Isograptus* is a feature of taxonomic importance and deserves particular attention. Basic univariate statistics for each character—minimum and maximum values, mean, standard error of mean, standard deviation, and coefficient of variation —are given in the appendix. Where a species is represented by several samples the statistics are those of the pooled samples.

The high coefficients of variation, generally greater than 10 and commonly greater than 20, indicate the extreme variation displayed by most species (Table 3).

The variability of several characters, such as free sicular length and supradorsal width, varies markedly from taxon to taxon, whereas other characters such as sicular length, supradorsal length have a more uniform variability. There is no apparent tendency towards either increased or decreased variability with time. The most variable character is stipe divergence angle, with an average coefficient of 48; the least variable is sicular length, averaging 10. Characters which show the most marked trends in phylogeny—sicular length, proximal stipe width, distal stipe width, and number of pendent thecae—are also the least variable, suggesting that they were under the greatest selection pressure and making them useful for specific diagnosis.

Correlation and covariance matrices for measured characters are given in the appendix; correlation coefficients range widely in value but, except for species of the manubriate group, are generally positive, indicating that an increase in value of one character is generally accompanied by an increase in value in the others (text-figs. 30–32), and suggesting that individual characters do not vary completely independently of each other but, to some extent, are related and depend on—or determine—over-all rhabdosome size. In the manubriate group, stipe width bears weak to moderate negative correlation with most other characters—which mainly relate to size of the sicula and manubrium—and suggests that increase in size of the latter is at the expense of stipe width.

Interpretation of the factors contributing to intraspecific variation is difficult; whereas the range of permissible variation is undoubtedly genetically determined, the extent to which genetic variation contributes to the total variation is unknown. Of the possible causes of nongenetic variation those of ontogeny (and astogeny) and environment are the most likely (Mayr 1963).

From the growth series referred to above and from the comparatively early development of such structures as the external peridermal film in the ventral indentation in *I. victoriae* subspecies, growth of proximal thecae would appear to be largely complete while the rhabdosome is still in an early stage of development. Thus subsequent increase in stipe length would not be accompanied by significant increase in sicular length, proximal stipe width, etc. This interpretation is consistent with the general lack of significant positive correlation of these characters with stipe length (see appendix)—which, up to the genetically determined maximum, is purely a function of astogeny. Development of the rhabdosome, beyond that stage represented in text-fig. 11*b*—the minimum stage accepted for measurement—is thus thought unlikely to be a major contributor to intra sample variation.

Because of our present poor knowledge of graptolite ecology, little can be said about the extent of variation produced by environmental modification of the genotype ('ecophenotypic' variation).

Much of the observed intraspecific (intrapopulation) variation is related to the

TABLE 3. Variability of measured characters in *Isograptus* species (coefficients of variation).

Species	Sicular length ≡	free length ≡	width ≡	supradorsal width ≡	supradorsal length ≡	Stipe divergence	proximal width ≡	distal width ≡	Number of pendent thecae
Isograptus victoriae lunatus	17	22	19	22	24	45	16	15	22
I. v. victoriae	9	31	13	15	21	80	11	15	17
I. v. maximus	12	24	11	23	34	36	16	26	16
I. v. maximodivergens	7	28	10	15	16	34	13	12	12
I. caduceus imitatus	9	24	3	20	21	37	5	9	14
I. c. australis	9	18	14	12	26	38	15	10	10
I. hastatus A	9	7	3	10	13	35	7	2	–
I. hastatus B	7	33	16	17	8	43	6	–	–
I. dumosus A	6	30	20	13	14	33	11	–	–
I. dumosus B	11	48	14	15	19	58	16	–	–
I. manubriatus	17	37	26	30	29	86	20	19	–

over-all size of the mature rhabdosome. Phyletic increase in rhabdosome size, such as in the *victoriae* lineage, undoubtedly reflects genetic change, and in terms of Darwinian selection and evolution, must draw upon a variable gene pool within the lineage. Variation in rhabdosome size within a single population is a likely expression of the gene pool and such variation in *victoriae* populations is thus thought to be at least partly the result of genetic variation, suggesting that the isograptids were not as specialized a group as has been suggested (Bulman 1963*b*, p. 408).

Interspecific discrimination. Few species can be distinguished from all others on the basis of a single character. Within most species groups, however, single character analysis is generally useful if whole populations are considered; for example, the distinction of subspecies in the *Isograptus victoriae* lineage on the basis of sicular length, proximal stipe width, distal stipe width, or number of pendent thecae (text-figs. 26–29). Bivariate plots of manubrium size are similarly useful for distinguishing manubriate forms (text-figs. 19, 21).
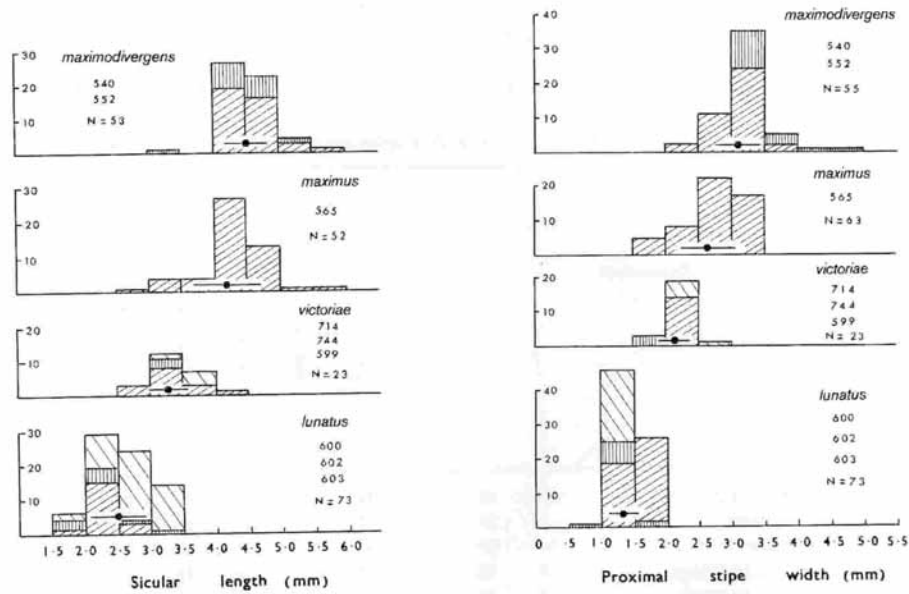
TEXT-FIG. 26. Frequency distribution of measurements of sicular length in samples of *Isograptus victoriae lunatus, victoriae, maximus,* and *maximodivergens.* The mean value and one standard deviation from the mean are indicated for each subspecies. Sample numbers are listed in their order of superposition in the histograms.
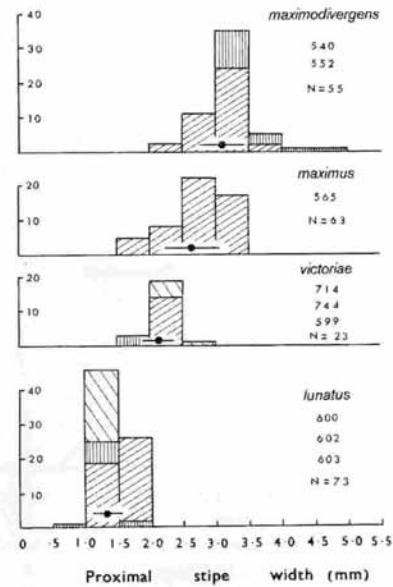
TEXT-FIG. 27. Frequency distribution of measurements of proximal stipe width in *Isograptus victoriae lunatus, victoriae, maximus,* and *maximodivergens.* The mean value and one standard deviation from the mean are indicated for each subspecies. Sample numbers are listed in their order of superposition in the histograms.

The most meaningful representation of the comparative over-all 'morphologic distance' between populations is that based on *all* measurements of *all* characters of *all* specimens (multivariate analysis).

Mahalanobis's D^2 statistic (Rao 1952) provides a useful estimate of interpopulation distance. The distribution of samples of *I. victoriae* subspecies in terms of these distances (text-fig. 33) was obtained by principal coordinate analysis of the D^2 matrix (Gower 1966). The two coordinate axes (L1, L2) together account for 96% of the variance of the D^2 matrix. Thus the two-dimensional representation is very close to that of the samples in six-dimensional hyperspace. It should be noted that the D^2 matrix is found by using the pooled sample covariance matrices. These may not be strictly homogeneous and some values of D^2 may be poor estimates of interpopulation distances.

The method of computation accepts only complete data sets. Since some characters, such as distal stipe width, could not be measured in many incompletely preserved specimens they were excluded from the analysis in order to make use of the maximum number of specimens. Six of the 10 measured characters were used: sicular length, sicular width, supradorsal length, supradorsal width, proximal stipe width,
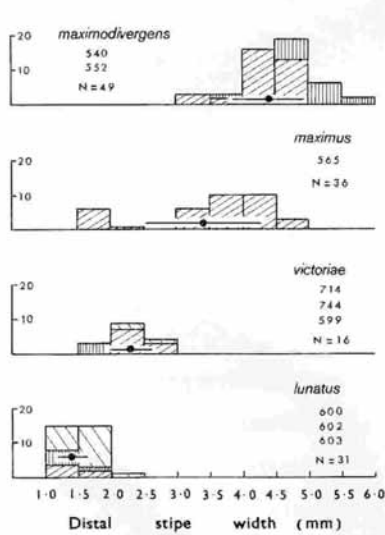
TEXT-FIG. 28. Frequency distribution of measurements of distal stipe width in *Isograptus victoriae lunatus, victoriae, maximus,* and *maximodivergens.* The mean value and one standard deviation from the mean are indicated for each subspecies. Sample numbers are listed in their order of superposition in the histograms.
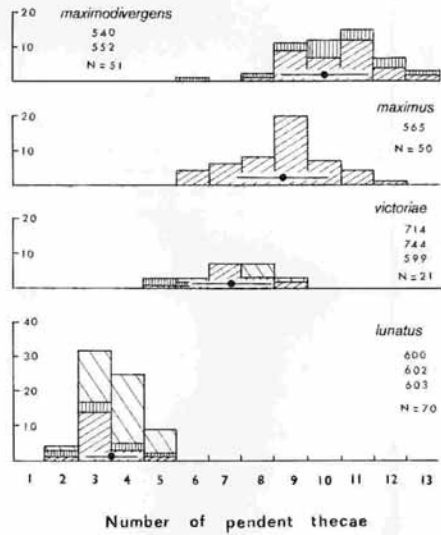
TEXT-FIG. 29. Frequency distribution of counts of number of pendent thecae in *Isograptus victoriae lunatus, victoriae, maximus,* and *maximodivergens.* The mean value and one standard deviation from the mean are indicated for each subspecies. Sample numbers are listed in their order of superposition in the histograms.

G
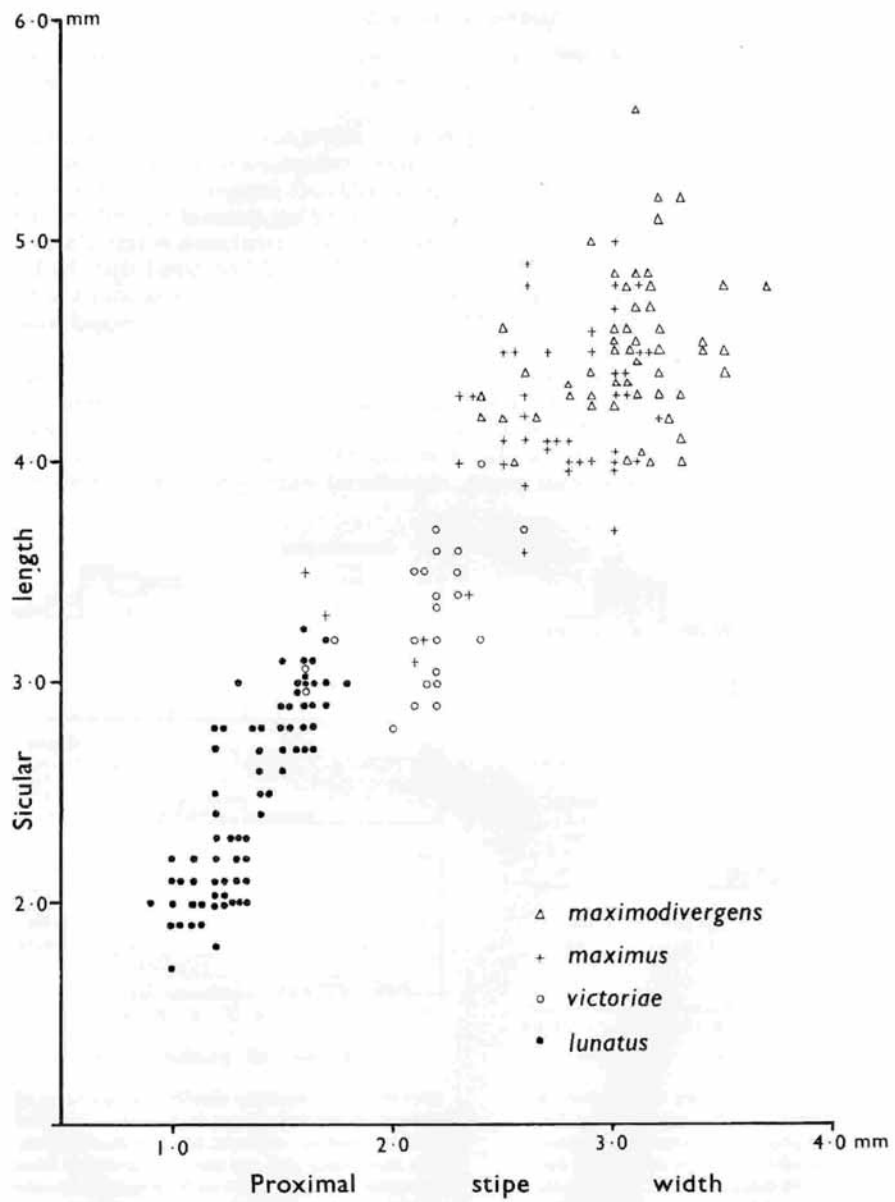
TEXT-FIG. 30. Sicular length plotted against proximal stipe width in 192 specimens of *Isograptus victoriae* subspecies.
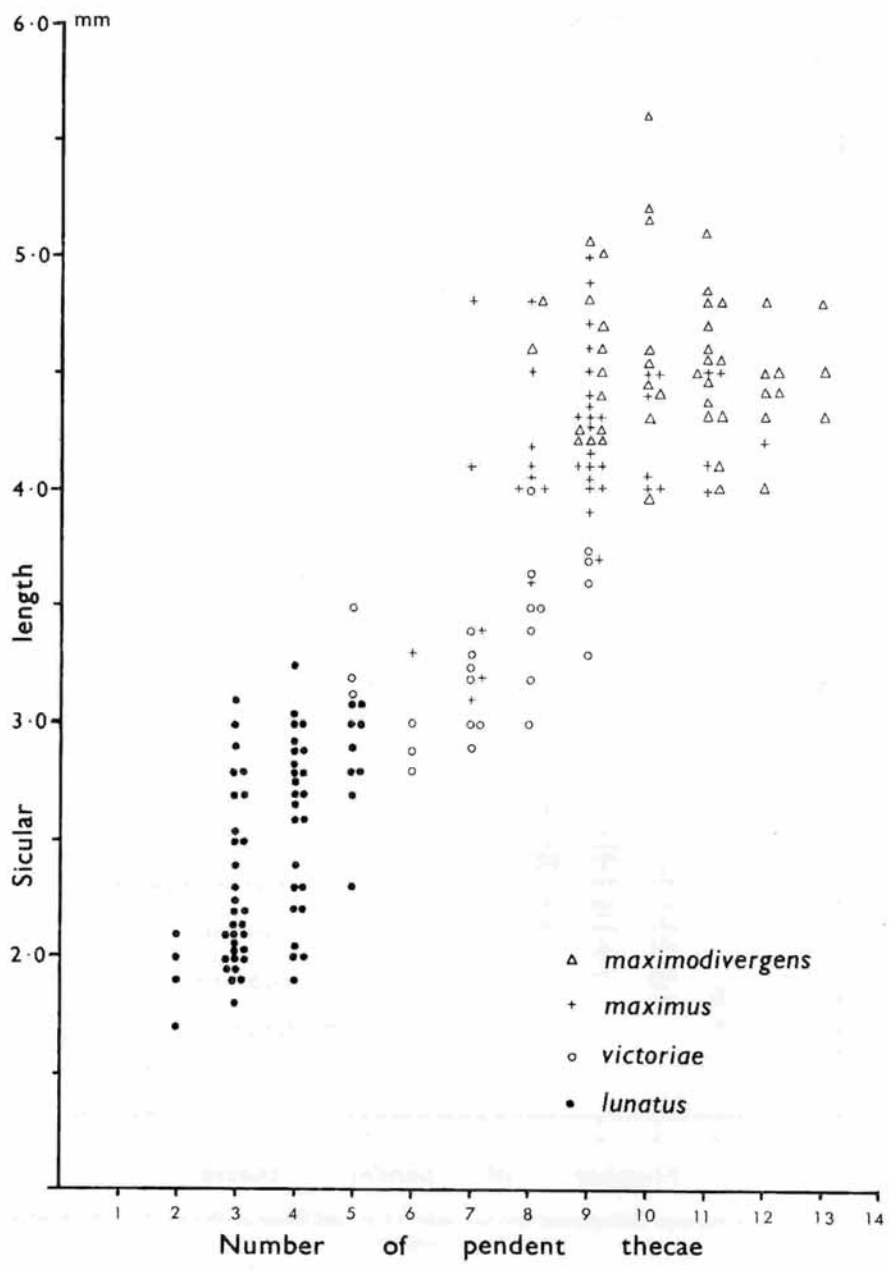
TEXT-FIG. 31. Sicular length plotted against number of pendent thecae in 182 specimens of *Isograptus victoriae* subspecies.
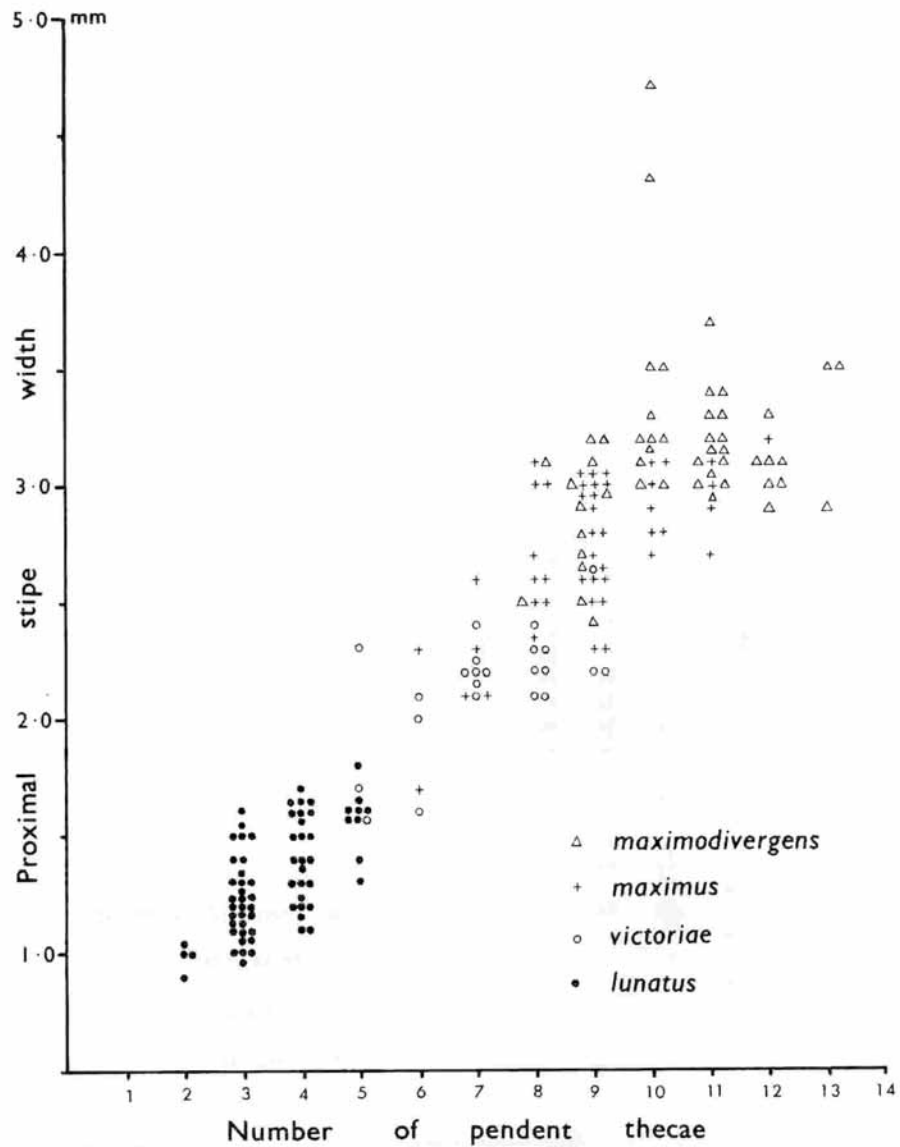
TEXT-FIG. 32. Proximal stipe width plotted against number of pendent thecae in 189 specimens of *Isograptus victoriae* subspecies.
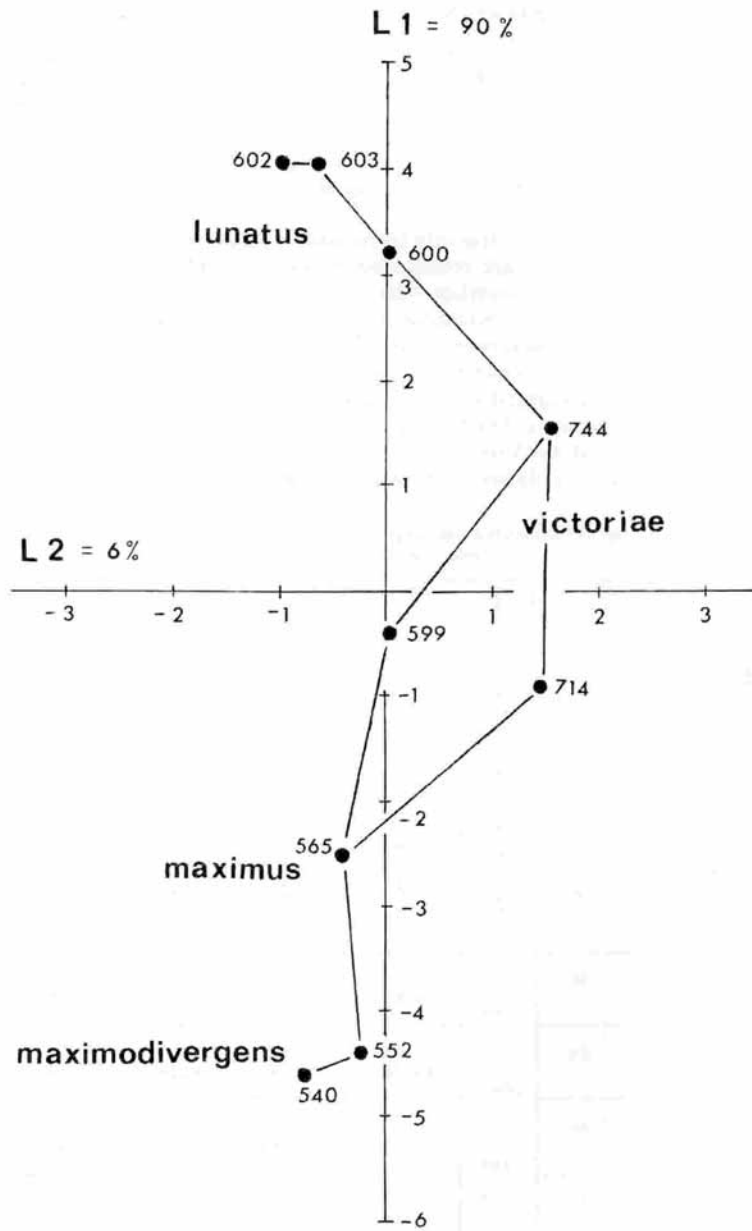
TEXT-FIG. 33. Principal coordinate analysis of *Isograptus victoriae* populations. The population means are plotted against the two principal axes (L1, L2) of the D² (squared distance) matrix, showing the multivariate distances between pairs of population means.

number of pendent thecae. From the plotted samples it can be seen that the successive subspecies are clearly distinguished. Individual samples of *lunatus* and *maximodivergens* are relatively closely spaced whereas those of *victoriae* span a distance equivalent to that separating subspecies.

An indication of interspecific overlap is given by the reclassification, by computer, of each specimen into that taxon whose morphology it most closely resembles, based on the six characters (Table 4).

I. v. lunatus is thus entirely discrete from other subspecies; 4·5% of all measured specimens of *I. v. victoriae* are reclassified in *lunatus*, and 4·5% in *maximus*. The subspecies with the greatest overlap with its neighbours is *I. v. maximus*, 2% being reclassified in *lunatus*, 9% in *victoriae*, and 24% in *maximodivergens*; 17% of the specimens of *I. v. maximodivergens* were reclassified in *maximus*.

Thus the large overlap between the New Zealand populations of *maximus* and *maximodivergens* is highlighted and some doubt cast on the validity of distinguishing them as separate subspecies. The level arbitrarily taken as a criterion for distinguishing subspecies by most workers is 25% or less overlap (Simpson 1961, p. 175) and no change to the existing classification is recommended.

TABLE 4. Computer reclassification of specimens of *I. victoriae* showing the degree of inter-subspecific overlap.

Subspecies	number of specimens	probability of misclassification	Reclassified as:				Total misclassified
			lunatus	victoriae	maximus	maximodivergens	
lunatus	38	.028	38 (100%)	0 (0%)	0 (0%)	0 (0%)	0
victoriae	22	.098	1 (4.5%)	20 (91%)	1 (4.5%)	0 (0%)	2
maximus	46	.162	1 (2%)	4 (9%)	30 (65%)	11 (24%)	16
maximodivergens	41		0 (0%)	0 (0%)	7 (17%)	34 (83%)	7

It should be noted here that in order to observe the rule of priority in taxonomic nomenclature, *Isograptus* sample populations were initially grouped in the way that best matched Harris's (1933) indications of species and subspecies (mainly by reference to Harris's figures). The statistical work supports Harris's divisions to the extent that subspecies so recognized are generally clearly distinguished, most lying well within the 25% overlap criterion, and more or less evenly spaced (text-fig. 33).

Phyletic trends. In the *I. victoriae* lineage, univariate trends in sicular length, stipe width, and in number of pendent thecae (text-figs. 26–29) reflect the progressive increase in rhabdosome size and accompanying changes in proportions, and provide a convenient means of measuring evolution of the group. Thus when mean sicular length is 2·6 mm the lineage has reached the *maximus* stage of evolution.

In the same way a possibly more reliable, though less precise, measure is obtained from bivariate scatter diagrams such as those of text-figs. 30–32, the stage reached by any sample of the lineage corresponding to the relative position of its plotted points between those of the end members.

The multivariate distance diagram (text-fig. 33) can be read in the same way as the bivariate diagrams and, being based on all measured characters, is a more truly representative picture of the trend of the lineage. Progressively younger populations plot from top to bottom.

The apparent reversal in trend of 2 samples of *I. victoriae victoriae* (samples S2/599 and 744) needs mentioning, and is a reflection of their small size (13 and 3 specimens respectively) and wide ranges of variation. The mean vectors of the 2 samples do not differ significantly at the 20% level and the apparent reversal is thought to be not significant in terms of evolution of the lineage.

The increase in rhabdosome size from *I. caduceus imitatus* to its descendant *I. c. australis* is of a similar kind to that described in *I. victoriae* and is reflected in the trends in sicular length and distal stipe width (text-fig. 15). An increase in rhabdosome size is also shown by the *I. dumosus* transition from its Upper Castlemainian form A, to its Yapeenian form B (text-fig. 19).

An exception to the general isograptid trend of phyletic size increase is found following the first appearance of the manubriate group in the lower part of Ca3. The earliest form, *I. hastatus* form A, is considerably larger than its descendant, form B. This apparent reversal may well be associated with the development of a new type of proximal structure, which does not become fully established until the upper part of Ca3, in the rhabdosomes of *I. hastatus* form B and *I. dumosus* form A.

Little can be said about the causes of phyletic size increase in isograptids. The phenomenon is a common feature of animal evolution though it is best known in noncolonial organisms. It has received little attention in other graptolite genera, although it is well known in the Arenigian–Llanvirnian series, *Didymograptus protobifidus–D. bifidus* (Elles 1933). A full discussion of phyletic size increase in invertebrates with suggested causes is given by Newell (1949).

The trend towards increased rhabdosome size in the *I. victoriae* lineage is reversed at about the level of the Ya1/Ya2 boundary, with the transition from *maximodivergens* to *divergens*. The lineage continues to wane in size and numbers becoming extinct in the Late Darriwilian (Da3). This suggests that the large size of the

maximodivergens rhabdosome became disadvantageous after the time of Ya1 and it is significant that at about this level most other dichograptids, including several large-rhabdosomed forms (*Tetragraptus* cf. *serra* (Brongniart), *T. headi* (Hall), *Goniograptus speciosus* (T. S. Hall), and *Dichograptus octobrachiatus* (Hall), large form), disappeared from the Australasian region.

PHYLOGENY OF *ISOGRAPTUS*

The inferred phylogeny of *Isograptus* is set out in text-fig. 34. The earliest form, *Isograptus primulus*, appears in the Upper Chewtonian; the genus is represented by a single though numerically abundant lineage through the Lower and Middle Castlemainian. In the Upper Castlemainian the genus suddenly begins to diversify and, in the Yapeenian, reaches its maximum diversity and abundance, dominating the fauna of that stage. At the base of the Darriwilian the isograptid fauna is largely replaced by new, mainly biserial forms and, except for the relative abundance of *I. forcipiformis* (s.s.) in Da3, it remains sparse in numbers of taxa and individuals until its final disappearance at the close of Da4.

Isograptus species evolved in 4 main groups. *Isograptus primulus*, the sole member of the first group, is somewhat enigmatic; its origin is unknown and it appears to be unrelated to the later Australasian isograptids. It already bears features seen only in much later Australasian forms, particularly the large number of pendent proximal thecae, and it seems unlikely to be the ancestor of the following, much more nearly didymograptid, *lunatus*. The species bears unmistakable resemblance to the European *I. gibberulus* Nicholson, which is probably its closest relative.

The second group is the best documented and comprises the subspecies of *I. victoriae*, the *lunatus-divergens* lineage. The origin of *lunatus*, like that of *primulus*, is unknown but its possible derivation from reclined didymograptids is especially interesting in that it carries with it the implication of recurrent evolution of the isograptid rhabdosome and a polyphyletic origin for the isograptid stock. The subspecies of *I. victoriae* represent successive stages, or populations, within a continuously evolving series. The progressive increase in rhabdosome size from the small early members to the large later members with a final loss of rhabdosome 'robustness' is the most conspicuous feature of the lineage although the most important trend is possibly the increase in thecal length and volume. The group becomes extinct by the Late Darriwilian (Da3).

Phylogeny in the third group, the *caduceus* group, is less certain but appears to have been of a branching kind rather than linear. The earliest form, *I. caduceus imitatus*, appears to have arisen from those members of *victoriae* and *maximus* with V-shaped rhabdosomes. It appears as a distinct form in the Castlemainian (Ca3, upper) and ranges widely in morphology. By a widening and lengthening of its stipes it passes into *I. caduceus* aff. *imitatus* of the same horizon, and *I. caduceus australis* in the following zone. The latter subspecies is apparently the most closely related Australasian form to *I. caduceus caduceus* of North America; it is confined to the Yapeenian.

In another trend, proximal thecae elongate and stipe divergence increases and *I. caduceus imitatus* passes into *I.* cf. *forcipiformis* in the Upper Castlemainian (Ca3).

A continuation of this trend in the Yapeenian (Ya1) could lead to the wholly biserial rhabdosome of *Skiagraptus*.

It is uncertain whether *I. forcipiformis* Ruedemann (s.s.) which is apparently confined to the *decoratus* zone (Da3) in Australia is derived through the small *forcipiformis*-like form in the Lower Yapeenian or through the *Isograptus caduceus australis–I. c. caduceus* lineage.

The proximal region of the rhabdosome is less variable in the *caduceus* group than in the *victoriae* group, both sicular length and number of pendent thecae having stabilized at about the level reached by *victoriae*.

Latest representative of the group is probably *I. caduceus spinifer* in the Upper Darriwilian (Da4).

The fourth phyletic group of isograptids, the manubriate group, is clearly distinguished by the initial downward growth and sharp flexure of its stipes, forming the manubrium, but its phylogeny is less certain than that of the *victoriae* and *caduceus* groups. Its earliest member, *I. hastatus* form A, appears in the lower part of the *maximus* zone (Ca3, lower); its origin is uncertain but it may well have been derived from the *I. victoriae* lineage by delay in the point of dorsal stipe flexure, beyond the level of the origins of the second or third thecal pair. *I. hastatus* form B appears in the upper *maximus* zone together with *I. dumosus* form A. In the Lower Yapeenian the first large manubriate forms appear and comprise a bewildering variety of rhabdosome shapes, here grouped tentatively in *I. manubriatus* (s.l.). *I. dumosus* is here represented by forms B and C, with slightly larger rhabdosomes; the point of stipe flexure is somewhat delayed, resulting in a larger manubrium. With the possible exception of *Isograptus lyra* Ruedemann (= *I. manubriatus*) in North America, the manubriate group disappeared before the Darriwilian.

STRATIGRAPHIC SIGNIFICANCE

Local stratigraphic significance. The univariate trends (text-figs. 26–29) provide a useful means of precise stratigraphic subdivision and correlation of Castlemainian and Yapeenian strata, and enable measurements on characters to be directly related to stratigraphic horizon. Zone boundaries can similarly be precisely defined and applied. Multivariate trends provide an even more reliable stratigraphic tool but their determination is more involved. Although the population (biospecies) concept means that a single specimen may not, by itself, be able to be definitely assigned to its taxon, there is no loss of stratigraphic precision. As discussed in the section on populations above, the stratigraphic ranges of *I. victoriae* biological subspecies is much shorter than those given for morphological subspecies by Thomas (1960) (see text-fig. 35). Thus the stratigraphic range assigned to a single specimen is likely to be the same under either concept. On the other hand, given a sample of several specimens, the *precise* stratigraphic horizon can be determined with much greater probability than was formerly possible.

Significance for world correlation. The Australasian isograptids have been recorded widely throughout the world but the relative stratigraphic sequence of species is poorly known outside Australasia. Stratigraphic sequences are known in Texas and Norway.
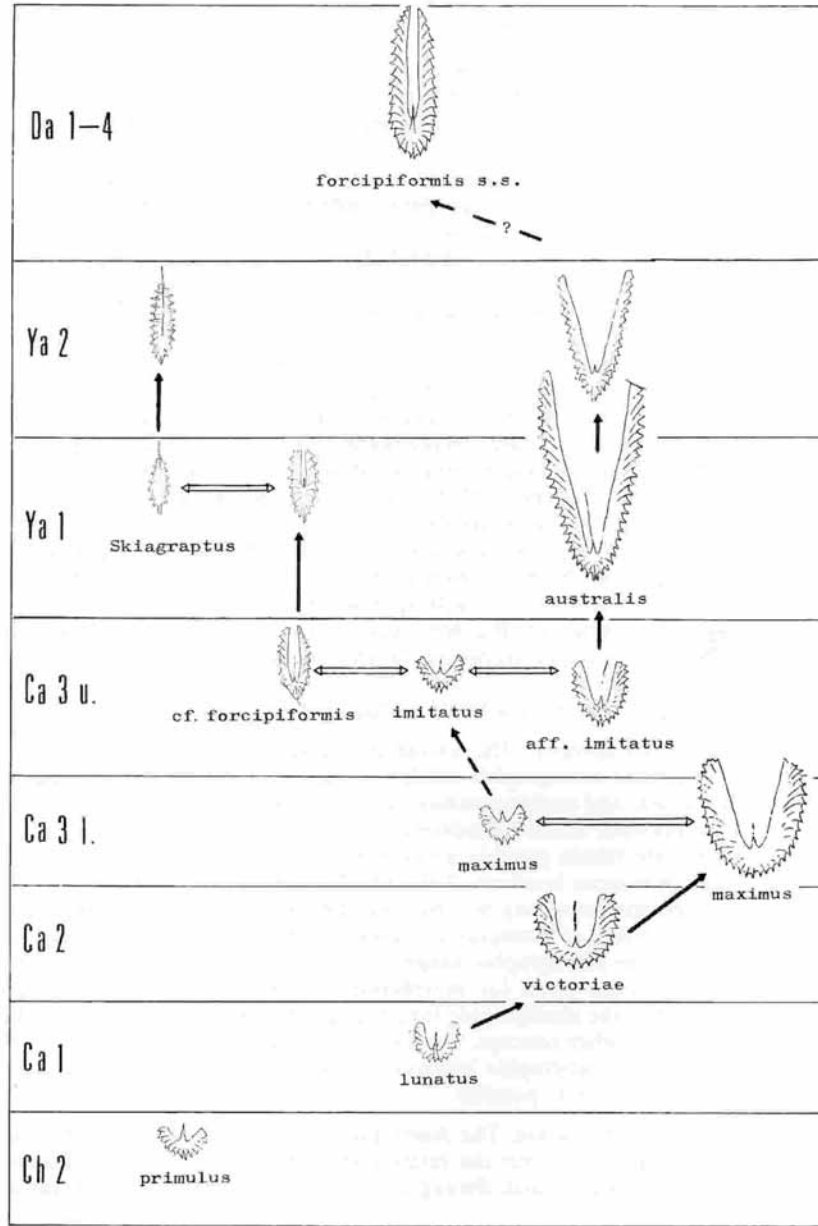
TEXT-FIG. 34. *a, b.* Inferred phylogeny of *Isograptus* and its allies. Phylogenetic transitions in time shown by solid arrows, transitions at one horizon by double-lined arrows.

divergens

manubriatus

C   B

dumosus

manubriatus

dumosus A   hastatus B

maximodivergens

?

hastatus A
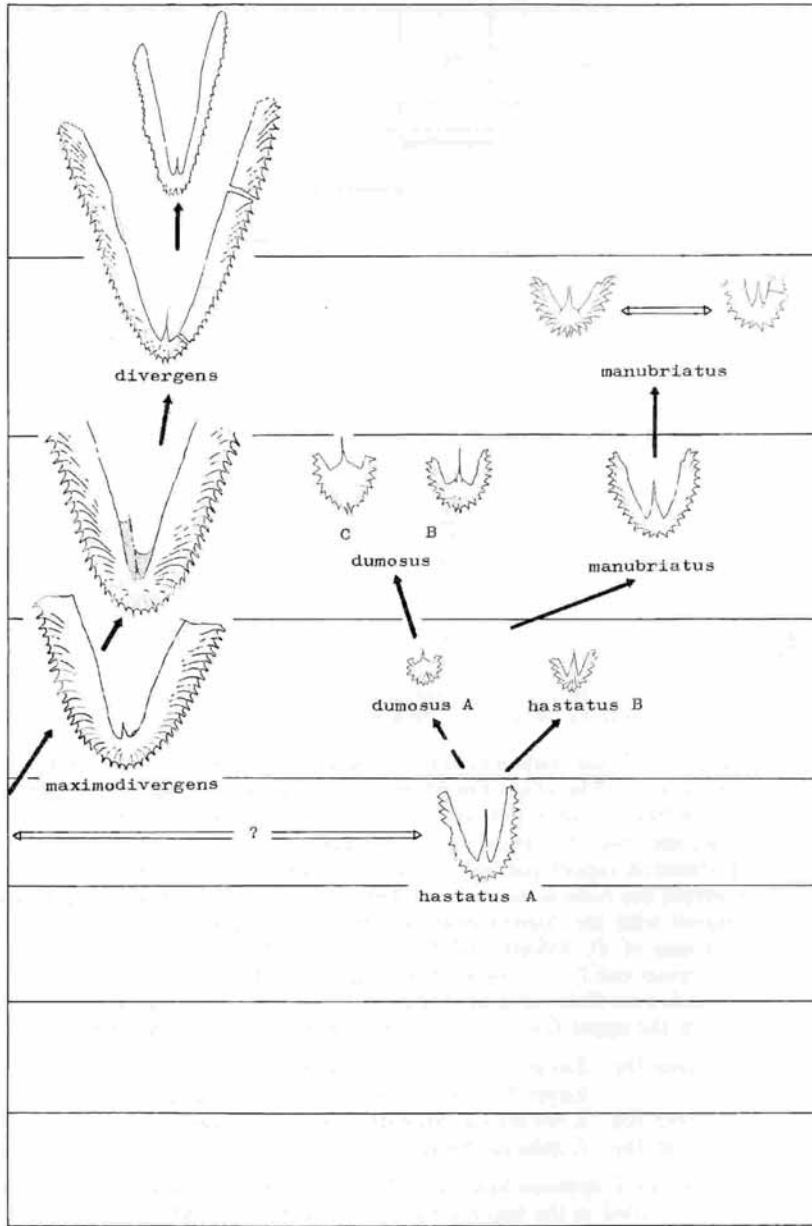
Victorian substage	Ch2	Ca1	Ca2	Ca3	Ya1	Ya2
I. v. primulus						
I. v. lunatus						
I. v. victoriae						
I. v. maximus						
I. v. maximodivergens						
I. v. divergens						
New Zealand Zone	protobifidus	lunatus	victoriae	maximus	Oncograptus	Cardiograptus

TEXT-FIG. 35. Comparison of the stratigraphic ranges given for subspecies of *Isograptus victoriae* in Victoria by Thomas (1960), and in Nelson by the writer; thin line, Thomas; thick line, the writer.

In the Marathon, Texas, sequence the earliest isograptid *I. v. lunatus*, appears in the highest beds of the Marathon limestone (*D. bifidus* zone), and extends into the overlying Alsate Shale (lower part of *I. 'caduceus'* zone, Berry 1960, p. 66). The forms *victoriae, maximus, maximodivergens*, and *divergens* are listed from the lower Fort Peña Formation (upper part of *I. 'caduceus'* zone), but their relative order of appearance within the zone is not known. The replacement of *lunatus* by the larger subspecies agrees with the Australasian sequence and suggests that the boundary between the zones of *D. bifidus* and *I. 'caduceus'* corresponds to the boundary between *I. v. lunatus* and *I. v. victoriae* (Ca1/Ca2) in Australasia.

At Slemmestad, near Oslo, several species of *Isograptus* were described by Spjeldnaes (1953) from the upper few metres of the Lower *Didymograptus* Shale.

Zone 3bε   Layer 2—*I. gibberulus* Nicholson
           Layer 3—*I. lunata* Harris (? = *I. c. lunatus*)
Zone 3bδ   *I. norvegicus* Monsen (pars = *I. c. lunatus*)
Zone 3bγ   *I. spinosus* Spjeldnaes

The earliest species, *I. spinosus* Spjeldnaes from zone 3bγ, has no known equivalent in Australasia. Included in the succeeding form, *I. norvegicus* Monsen in zone 3bδ,

are specimens which are here referred to *I. v. lunatus* and which according to Spjeldnaes grade into the youngest form, '*I. gibberulus* (Nicholson)', in zone 3bϵ through a 'continuous series of development'.

The specimen figured by Spjeldnaes (1953, text-fig. 1D) as '*I. lunata*' from Layer 3, zone 3bϵ, is only doubtfully referred to the subspecies here. Also, as Spjeldnaes (1953, pp. 182–183) notes, '*I. gibberulus*' appears at a relatively earlier stage in the British graptolite sequence than in that of Slemmestad. However, the transition from *lunatus* s.s. to larger forms agrees with the trend in Australasia and suggests correlation of the 3bδ/3bϵ boundary with the Ca1/Ca2 boundary (and the *D. bifidus*/ *I. 'caduceus*' zone boundary of Texas), in agreement with the correlation advocated by Skevington (1963b, 1968) but in marked conflict with that proposed by Kindle and Whittington (1958, p. 328) and advocated by Berry (1960, 1968), in which 3bϵ (or Upper Arenig) is correlated with Upper Bendigonian or Lower Chewtonian.

In view of the present controversy surrounding world correlation of this Upper Arenig to Llanvirn interval the isograptids would appear to provide a potentially important datum for correlation and underline the need for detailed description of the taxonomy and stratigraphy of isograptids in North America, British Isles, and Scandinavia.

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APPENDIX

A. *Basic statistics*

The number of measured specimens (N), minimum measured value (Min.), maximum measured value (Max.), mean value (Mean), standard error of the mean ($s_{\bar{x}}$), standard deviation (s), and coefficient of variation (V)—for each measured character of each species are listed below. Where a taxon is represented

by more than one sample, the statistics are those of the pooled samples. The characters are discussed in text.

The original data—the measurements on which these statistics are based—are held on open file by Palaeontological Section, New Zealand Geological Survey, Lower Hutt.

B. *Correlation, covariance*

Product-moment correlation and covariance matrices for selected characters (identified by number) for those taxa with a sufficiently large number of measured specimens are also given; in the diagonal of each matrix is given the variance of the character. Coefficients significant at the 95% level are underlined. As in the list of basic statistics, all samples of each taxon are used.

Isograptus victoriae lunatus
Samples S2/600, 602, 603 (pooled). Castlemainian, Ca1.

	Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V	Correlation matrix (N=58)					
									1	3	4	5	8	10
1.	Sicular length	73	1.7	3.3	2.5	.051	.43	17	.172	.700	.790	.713	.837	.598
2.	" free length	71	.3	.9	.59	.016	.13	22	.032	.012	.650	.560	.715	.423
3.	" width	67	.3	.8	.57	.013	.11	19	.050	.011	.023	.569	.686	.607
4.	" supradorsal width	70	.5	1.0	.65	.017	.15	22						
5.	" supradorsal length	72	.6	2.0	1.1	.032	.27	24	.083	.017	.024	.078	.535	.273
6.	Stipe length	72		8.0										
7.	" divergence	47	270	360	320	2.66	18	45						
8.	" proximal width	73	.9	1.8	1.3	.025	.22	16	.074	.017	.022	.031	.044	.648
9.	" distal width	31	1.1	2.0	1.4	.039	.22	15						
10.	Pendent thecae	70	2	5	3.5	.094	.79	22	.196	.037	.073	.060	.107	.626

(lower triangle = Covariance matrix)

Isograptus victoriae victoriae
Samples S2/744, 714, 599 (pooled). Castlemainian, Ca2.

	Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V	Correlation matrix (N=22)					
									1	3	4	5	8	10
1.	Sicular length	23	2.8	4.0	3.3	.065	.31	9	.101	.540	.271	.645	.480	.561
2.	" free length	19	.3	1.2	.69	.049	.22	31						
3.	" width	22	.5	0.8	.66	.018	.08	13	.015	.007	.446	.538	.023	.020
4.	" supradorsal width	23	.4	1.8	.65	.020	.09	15	.003	.004	.009	.637	-.223	-.111
5.	" supradorsal length	23	.4	1.3	.97	.042	.20	21	.042	.009	.012	.041	.024	.173
6.	Stipe length	23		14.0										
7.	" divergence	18	310	360	341.7	3.48	15	80						
8.	" proximal width	23	1.6	2.6	2.1	.030	.24	11	.037	.000	-.005	.001	.060	.634
9.	" distal width	16	1.6	2.7	2.3	.085	.34	15						
10.	Pendent thecae	23	3.0	9.0	7.2	.257	1.2	17	.225	.002	-.013	.044	.195	1.58

(lower triangle = Covariance matrix)

Isograptus victoriae maximus
Sample S2/565. Castlemainian, Ca3, lower

	Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V	Correlation matrix (N=29)						
									1	2	3	4	5	8	9
1.	Sicular length	51	2.5	5.6	4.2	.073	.52	12	.225	.170	.276	.415	.389	.514	.574
2.	" free length	49	.5	1.2	.85	.029	.20	24	.016	.039	-.302	.194	.068	-.077	-.113
3.	" width	49	.5	.8	.65	.010	.07	11	.008	.000	.004	.116	.197	.061	.019
4.	" supradorsal width	51	.6	1.4	.77	.025	.18	23	.035	.007	.001	.032	-.037	.025	.120
5.	" supradorsal length	52	.6	3.0	1.2	.059	.42	34	.066	.005	.004	-.002	.129	-.199	.056
6.	Stipe length	51		24.0											
7.	" divergence	36	290	345	324	2.17	13	36							
8.	" proximal width	32	1.6	3.2	2.6	.057	.41	16	.095	-.006	.001	.001	-.028	.150	.823
9.	" distal width	36	1.7	4.6	3.4	.148	.89	26	.230	-.019	.001	.018	.011	.270	.713
10.	Pendent thecae	50	6	12	8.7	.198	1.4	16							

(lower triangle = Covariance matrix)

C. *Computer programs*

For the basic statistics (part A, above) programme GSGHS 5MD prepared by Mr. G. H. Scott, New Zealand Geological Survey, was used. The programme accepts incomplete data sets enabling all measurements of a character to be utilized.

For the correlation and covariance matrices, programme GSGHS 4A (prepared by Mr. Scott) was used, which accepts complete data sets only, and thus reduces the number of usable specimens to only those in which all characters could be measured. For this reason only selected characters were studied (identified by number) in order to keep the number of usable specimens as large as possible.

For interspecific discrimination, discriminant functions, and principal coordinate analysis and reclassification (discussed in text) programmes GSGHS 8A (prepared by Mrs. M. Hamilton, Applied

Isograptus victoriae maximodivergens

Samples S2/552, 540 (pooled). Castlemainian, Ca3, upper, to Yapeenian, Ya1.

	Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V	1	3	4	5	8	9	10
1.	Sicular length	52	4.0	5.6	4.5	.047	.34	7	.121	-.158	.340	.569	.211	.152	-.138
2.	" free length	49	.1	1.4	.90	.036	.25	28	-.005	.002	.092	-.145	.075	.247	.144
3.	" width	50	.6	.9	.69	.009	.07	10	.010	.000	.007	.530	.337	.205	.320
4.	" supradorsal width	49	.5	1.0	.71	.016	.11	15	.031	-.001	.007	.024	-.108	-.073	.072
5.	" supradorsal length	50	.7	1.5	1.1	.025	.18	16							
6.	Stipe length	53													
7.	" divergence	44	315	360	332	1.45	9.6	34							
8.	" proximal width	53	2.4	4.7	3.1	.051	.39	13	.020	.001	.008	.004	.072	.683	.448
9.	" distal width	49	3.1	5.6	4.4	.079	.55	12	.024	.006	.008	.005	.082	.198	.048
10.	Pendent thecae	50	8	13	10	.179	1.3	12	.058	.009	.033	.001	.146	.259	1.47

(Correlation matrix (N=29); upper — matrix, lower — Covariance)

Isograptus imitatus

Sample S2/552. Castlemainian, Ca3, upper

	Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V	1	3	4	5	8	9	10
1.	Sicular length	12	2.5	3.3	3.1	.078	.27	9	.083	.012	.656	.728	.241	-.273	.009
2.	" free length	12	.5	1.1	.77	.053	.18	24	.000	.004	.000	.159	.429	.360	.341
3.	" width	12	.4	.6	.48	.018	.06	3	.009	.000	.002	.913	.000	.000	.286
4.	" supradorsal width	13	.2	.6	.47	.026	.09	20	.032	-.002	.007	.024	.175	.013	.227
5.	" supradorsal length	13	.5	1.1	.87	.050	.18	21							
6.	Stipe length	13			15										
7.	" divergence	12	300	350	325	3.82	13	37							
8.	" proximal width	13	1.4	1.6	1.5	.020	.07	5	.005	.002	.000	.002	.005	.644	.055
9.	" distal width	10	1.1	1.4	1.3	.034	.11	9	-.008	.002	.000	.000	.005	.012	.402
10.	Pendent thecae	13	4.0	7.0	5.5	.215	.78	14	.002	.018	.011	.029	.003	.036	.678

(Correlation matrix (N=10); upper — matrix, lower — Covariance)

Isograptus caduceus australis

Sample S2/540. Yapeenian, Ya1

	Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V	1	3	4	5	8	9	10
1.	Sicular length	13	3.0	4.1	3.6	.092	.33	9	.097	-.286	.683	.866	.737	.411	-.180
2.	" free length	14	.5	.9	.71	.034	.13	18	-.006	.005	-.225	.010	.053	.081	.123
3.	" width	13	.4	.6	.55	.022	.08	14	.015	-.001	.005	-.739	.442	-.120	-.609
4.	" supradorsal width	13	.5	.7	.55	.018	.07	12	.060	-.002	.012	.050	.767	.241	-.231
5.	" supradorsal length	13	.5	1.2	.78	.056	.20	26							
6.	Stipe length	14			25										
7.	" divergence	14	330	360	342	1.86	7.0	38							
8.	" proximal width	14	1.3	2.5	1.9	.077	.29	15	.040	.000	.006	.030	.032	.383	-.048
9.	" distal width	12	1.6	2.2	2.0	.054	.19	10	.025	.001	-.002	.011	.013	.038	.440
10.	Pendent thecae	14	5	7	5.8	.155	.58	10	-.029	.004	-.022	-.027	-.004	.044	.267

(Correlation matrix (N=10); upper — matrix, lower — Covariance)

H

Mathematics Division, Department of Scientific and Industrial Research, Wellington) and 8B (prepared by Mr. Scott) were used which again accept complete data sets only. In calculating D^2 values of *I. victoriae* populations and their representation on principal coordinate plots it is important to note that all populations were considered simultaneously, sample covariance matrices being pooled. Because the matrices may not be homogeneous the distance between any pair of sample means may be a poor estimate of interpopulation distances. The same applies to the taxonomic reclassification of specimens (Table 4, in text).

Isograptus hastatus form A

Sample S2/565. Castlemainian, Ca3, lower

Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V	Correlation matrix (N=8) 1	2	3	4	5	6	8
1. Sicular length	9	3.6	5.0	4.6	.141	4.2	9	.200	.024	.343	-.711	.379	.177	-.377
2. " free length	9	.5	1.1	.7	.065	.19	7	.001	.017	.220	-.293	-.323	.322	-.282
3. " width	9	.5	.7	.54	.024	.07	3	.011	.002	.006	-.129	.592	-.124	-.372
4. Manubrium width	8	1.2	1.6	1.4	.046	.13	10	-.041	-.005	-.001	.017	.210	-.253	.293
5. " length	9	2.2	3.1	2.7	.116	.35	13	.054	.014	.014	.009	.103	-.555	-.415
6. Stipe length	9		.9					.021	.011	-.002	-.009	-.048	.074	.243
7. " divergence	8	285	335	315	5.59	16	35							
8. " proximal width	9	1.6	2.0	1.8	.044	.13	7							
9. " distal width	4	1.4	1.6	1.5	.048	.10	2	-.023	.005	-.004	.005	-.018	.009	.018

Isograptus hastatus form B

Sample S2/552. Castlemainian, Ca3, upper

Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V	Correlation matrix (N = 9) 1	3	4	5	8
1. Sicular length	10	3.5	4.3	3.8	.078	.25	7	.057	.313	-.185	.469	-.475
2. " free length	7	.2	.5	.33	.042	.11	33					
3. " width	9	.4	.6	.44	.024	.07	16	.009	.005	-.889	.561	.184
4. Manubrium width	11	.7	1.4	1.2	.060	.20	17	-.009	-.014	.044	.425	-.395
5. " length	11	1.8	2.3	2.1	.047	.16	8	.015	.006	-.012	.019	-.134
6. Stipe length	11		6.0									
7. " divergence	9	280	340	315	6.45	19	43					
8. " proximal width	11	1.1	1.3	1.2	.023	.08	6	-.009	.001	-.007	-.002	.007
9. " distal width	2	1.1	1.1	1.1								

Isograptus dumosus form A

Sample S2/552. Castlemainian, Ca3, upper

Measured Character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V
1. Sicular length	11	3.3	4.0	3.6	.063	.21	6
2. " free length	10	.2	.5	.29	.028	.09	30
3. " width	9	.3	.5	.42	.028	.08	20
4. Manubrium width	10	1.5	2.1	1.8	.071	.23	13
5. " length	10	1.0	1.5	1.3	.060	.19	14
6. Stipe length	8		1.5				
7. " divergence	3	330	345	23	4.41	7.6	33
8. " proximal width	8	.8	1.1	.94	.038	.11	11
*9. Rhabdosome width	10	3.0	4.7	3.8	.167	.53	14

* Measured at level of base of manubrium

Isograptus dumosus form B

Sample S2/540.   Yapeenian, Ya1

Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V
1. Sicular length	11	3.3	4.8	4.1	.132	.44	11
2. " free length	11	0	.7	.39	.056	.19	48
3. " width	9	.4	.6	.5	.024	.07	14
4. Manubrium width	10	1.5	2.4	2.0	.097	.31	15
5. " length	10	1.1	2.2	1.5	.091	.29	19
6. Stipe length	9		3.0				
7. " divergence	7	285	345	44	9.72	26	58
8. " proximal width	9	.9	1.5	1.1	.057	.17	16
9. Rhabdosome width	8	4.0	5.9	4.7	.220	.62	13

Isograptus manubriatus

Sample S2/540.   Yapeenian, Ya1

Measured character	N	Min.	Max.	Mean	$s_{\bar{x}}$	s	V	Correlation matrix (N=29) 1	4	5	7	8	9
1. Sicular length	43	3.0	8.0	5.3	.137	.90	17	.755	.424	.787	.352	.368	.165
2. " free length	38	.2	1.3	.47	.028	.17	37						
3. " width	34	.3	.8	.44	.020	.12	26						
4. Manubrium width	40	.1	2.7	1.6	.076	.49	30	.202	.300	.723	.423	-.402	-.510
5. " length	42	.2	5.0	3.0	.136	.88	29	.585	.338	.731	.505	-.210	-.382
6. Stipe length	43		16.0										
7. " divergence	36	260	360	32	4.61	28	86	7.50	.567	10.6	.060	-.382	-.424
8. " proximal width	43	1.0	3.0	1.9	.058	.38	20	.124	-.086	-.070	-.365	.152	.907
9. " distal width	41	1.4	3.5	2.3	.069	.44	19	.060	.060	-.116	-.136	.147	.174