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# CONTENTS

	Part	Page
ADAMS, C. G., KNIGHT, R. H., and HODGKINSON, R. L. An unusual agglutinating foraminifer from the Upper Cretaceous of England	3	637
ALLEN, P., KEITH, M. L., TAN, F. C., and DEINES, P. Isotopic methods and Wealden environments	3	607
ANDERSON, E. J., and MAKURATH, J. H. Palaeoecology of Appalachian gypidulid brachiopods	2	381
BATTEN, D. J. Use of palynologic assemblage-types in Wealden correlation	1	1
— Palynology of early Cretaceous soil beds and associated strata	2	399
BRAUCKMANN, C. See HAHN, G.		
BREED, W. J. See FORD, T. D.		
BRETT, D. W. See FOWLER, K.		
BROOKFIELD, M. The Palaeoenvironment of the Abbotsbury Ironstone (Upper Jurassic) of Dorset	2	261
BUTLER, M. Lower Carboniferous conodont faunas from the Eastern Mendips, England	3	477
CHALONER, W. G., and GAY, M. M. Scanning electron microscopy of latex casts of fossil plant impressions	3	645
CLARKSON, E. N. K. The eyes of <i>Asaphus raniceps</i> Dalman (Trilobita)	3	425
— Morphology and evolution of the eye in Upper Cambrian Olenidae (Trilobita)	4	735
COLLINS, J. S. H., and MORRIS, S. F. A new crab from the Middle Eocene of Libya	2	283
COOPER, R. A. Taxonomy and evolution of <i>Isograptus</i> Moberg in Australasia	1	45
COPPER, P. <i>Bifida</i> and <i>Kayseria</i> (Brachiopoda) and their affinity	1	117
CROXTON, C. A. See HUGHES, N. F.		
DALINGWATER, J. E. Trilobite cuticle microstructure and composition	4	827
DEINES, P. See ALLEN, P.		
DOWNIE, C. Observations on the nature of acritarchs	2	239
EDWARDS, N. See FOWLER, K.		
ELLIOTT, G. F. A Miocene solenoporoid alga showing reproductive structures	2	223
FORD, T. D., and BREED, W. J. The problematical Precambrian fossil <i>Chuarina</i>	3	535
FOWLER, K., EDWARDS, N., and BRETT, D. W. <i>In situ</i> coniferous (Taxodiaceae) tree remains in the Upper Eocene of southern England	1	205
GAY, M. M. See CHALONER, W. G.		
HAHN, G., and BRAUCKMANN, C. Lower Viséan trilobites from Feltrim, Ireland	2	391
— and HAHN, R. Viséan trilobites from Holwell, Somerset	3	551
HAHN, R. See HAHN, G.		
HAMILTON, W. R. A Lower Miocene mammalian fauna from Siwa, Egypt	2	275
HANCOCK, C. D. See PALMER, T. J.		
HARLAND, R. Dinoflagellates and acritarchs from the Bearpaw Formation (Upper Campanian) of southern Alberta, Canada	4	665
HARRISON, C. J. O., and WALKER, C. A. <i>Wyleyia</i> : a new bird humerus from the Lower Cretaceous of England	4	721
HODGKINSON, R. L. See ADAMS, C. G.		
HUGHES, N. F., and CROXTON, C. A. Palynologic correlation of the Dorset 'Wealden'	3	567
JAIN, S. L. New specimens of Lower Jurassic holostean fishes from India	1	149
JACKSON, D. E. On the mode of branching in a new species of <i>Clonograptus</i>	4	707
KEITH, M. L. See ALLEN, P.		
KEMPF, E. K. Transmission electron microscopy of fossil spores	4	787
KIER, P. M. A new Silurian echinoid genus from Scotland	4	651
KNIGHT, R. H. See ADAMS, C. G.		
KRASSILOV, V. A. Upper Cretaceous staminate heads with pollen grains	1	41

	<i>Part</i>	<i>Page</i>
MCLEAN, D. M. A problematical dinoflagellate from the Tertiary of Virginia and Maryland	4	729
MAKURATH, J. H. See ANDERSON, E. J.		
MATTHEWS, S. C. Lapworthellids from the Lower Cambrian <i>Strenuella</i> Limestone at Comley, Shropshire	1	139
— Notes on open nomenclature and on synonymy lists	4	713
— and NAYLOR, D. Lower Carboniferous conodont faunas from southwest Ireland	2	335
MORRIS, S. F. See COLLINS, J. S. H.		
MORTON, N. The aptychi of <i>Sommitia</i> (Ammonitina) from the Bajocian of Scotland	1	195
MURRAY, J. W. Wall structure of some agglutinated Foraminiferida	4	777
MUTVEI, H., and RAYMENT, R. A. Buoyancy control and siphuncle function in ammonoids	3	623
NAYLOR, D. See MATTHEWS, S. C.		
PALMER, T. J., and HANCOCK, C. D. Symbiotic relationships between bryozoa and gastropods and bryozoa and hermit crabs from the French Jurassic	3	563
PANCHEN, A. L. On <i>Crassigirinus scoticus</i> Watson, a primitive amphibian from the Lower Carboniferous of Scotland	1	179
PHILLIPS, W. E. A. See RUSHTON, A. W. A.		
POWELL, H. P. See WALTER, B.		
REYMENT, R. A. See MUTVEI, H.		
RUSHTON, A. W. A., and PHILLIPS, W. E. A. A <i>Protospongia</i> from the Dalradian of Clare Island, Co. Mayo, Ireland	2	231
SAVAGE, N. M. Lower Devonian conodonts from New South Wales	2	307
STINTON, F. C. Fish otoliths from the English Cretaceous	2	293
TAN, F. C. See ALLEN, P.		
TAYLOR, J. D. The structural evolution of the bivalve shell	3	519
TAYLOR, T. N. Combined transmission and scanning electron microscopy of <i>in situ</i> Palaeozoic spores	4	765
THUSU, B. Acritarchs of the Middle Silurian Rochester Formation of Southern Ontario	4	799
WALKER, C. A. See HARRISON, C. J. O.		
WALTER, B., and POWELL, H. P. Exceptional preservation in cyclostome Bryozoa from the Middle Lias of Northamptonshire	1	219
WEBBY, B. D. <i>Remopleurides</i> and other Upper Ordovician trilobites from New South Wales	3	445

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Cover illustration: *Ancyrodella* element (Conodont), Cashaqua Shale, Upper Devonian, New York State, ×70.

# USE OF PALYNOLOGIC ASSEMBLAGE-TYPES IN WEALDEN CORRELATION

by D. J. BATTEN

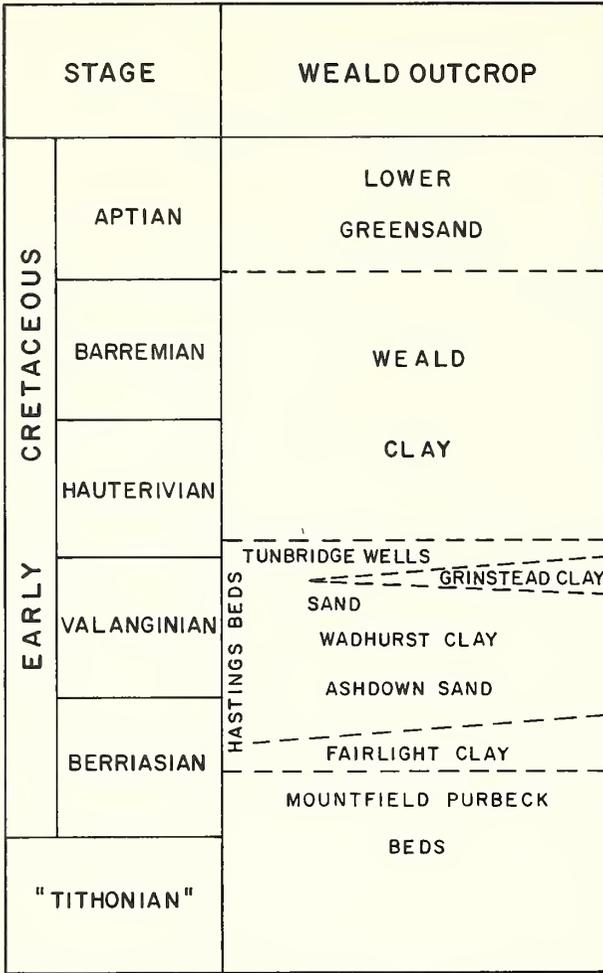
**ABSTRACT.** Analysis of extensive palynologic data from the English Wealden (Early Cretaceous) has enabled a comprehensive set of 17 palynologic assemblage-types to be defined in detail. This has been done in such a way that a rapid preliminary survey of a preparation will enable it to be placed in one of the assemblage-types so that its value for stratigraphic correlation or palaeoecology can be predicted without long and possibly uneconomic use of observation time. With the exception of *Celyphus rallus* gen. and sp. nov. of uncertain affinity, which is described because its presence is important in some assemblages, spore and pollen taxonomy is confined to brief comments on the sense in which some of the genera and species are used here.

THE method of stratigraphic comparison of palynologic assemblages practised by many palynologists is inadequate and often misleading. The descriptions of many spore and pollen taxa are unsatisfactory, the original concept of a genus or species is frequently distorted by later emendations and attributions to it, and personal opinions have to be interpreted. The ranges of taxa grow both geographically and chronologically. Facies relationships are usually ignored. Dating is, at best, usually possible only to an Age/Stage.

Refinements in the application of palynology to stratigraphic correlation will be possible only when taxa are described and compared more accurately (Hughes and Moody-Stuart 1967*b*, 1969, Hughes 1970) and the effects of the factors which have controlled the distribution of plant microfossils are more fully understood. The recognition of relationships between independent palynomorph taxa and the assemblages in which they occur is obviously necessary and is the subject of this paper.

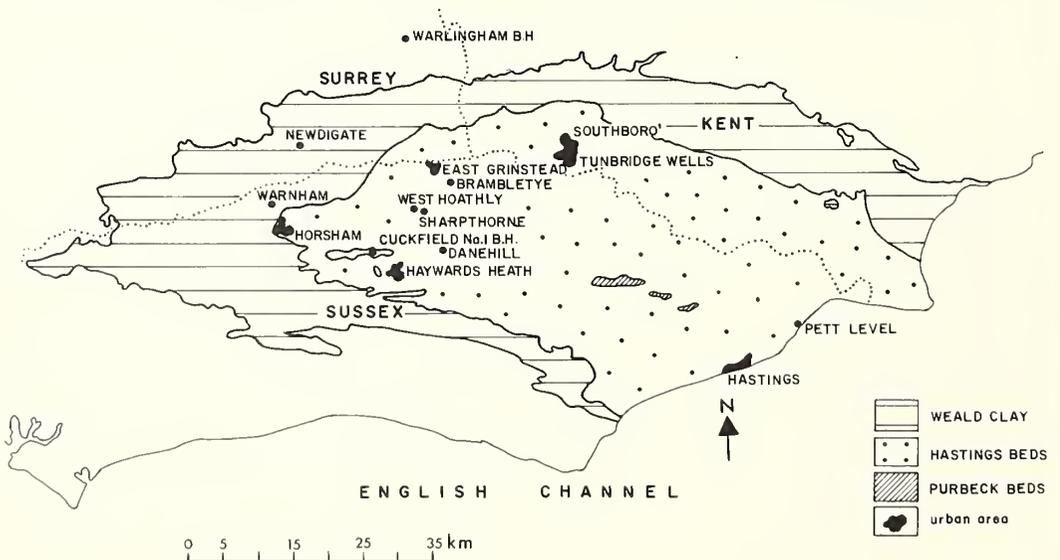
The first step is to identify and define by their contents kinds of assemblages that are in some degree related to the other characters of the sedimentary rock involved. This has been done for material from the main succession of the Hastings Beds and Weald Clay (Wealden) in the Early Cretaceous of southern England (text-figs. 1-3). The full organic palynomorph content observable with an optical microscope was recorded for 340 productive miospore preparations. Observations on recurrent associations of assemblage characters including abundance, average size, and preservation state of various palynomorphs, led to a grouping of all the assemblages into 17 assemblage-types. The grouping was aided and subsequently confirmed by a cluster analysis procedure.

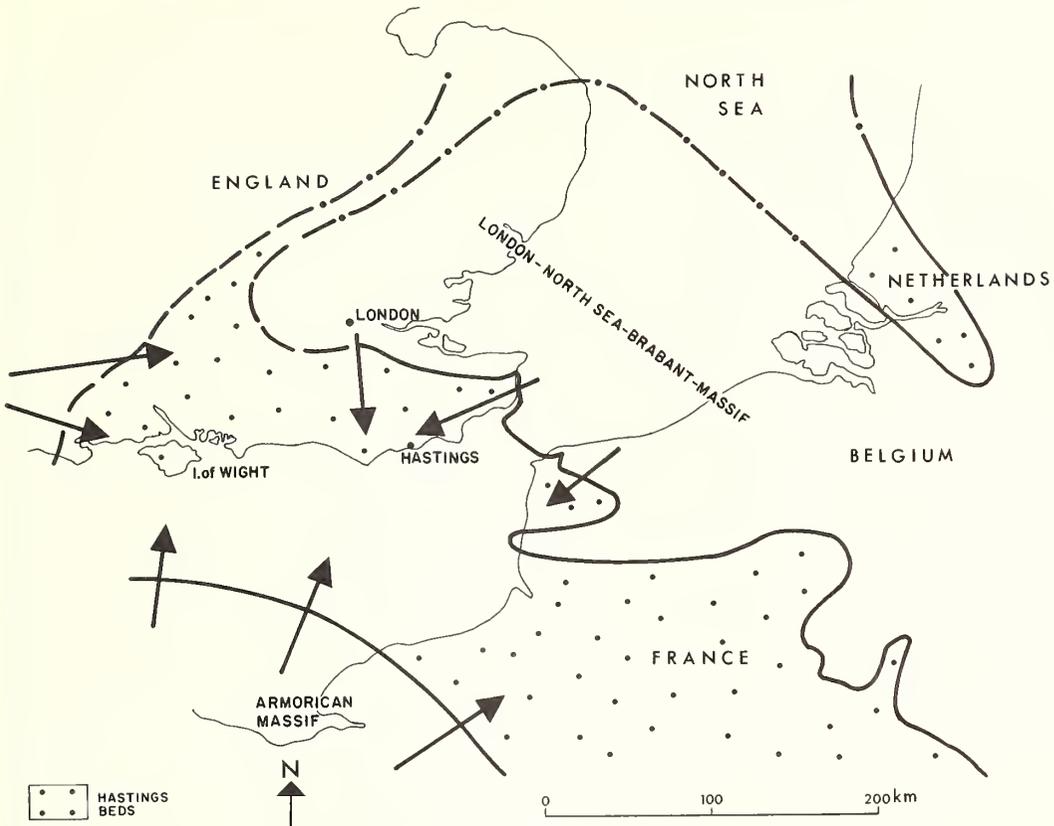
The determination of assemblage-types can now be made by a rapid survey of any preparation from these rocks by comparing its characters with those of the 17 types. As a result, it is now possible to predict, before committing the palynologist to long detailed observation, whether a preparation can contain a certain character. It is thus possible to select preparations (*a*) to avoid waste of time in searching for characters unlikely to be present, and (*b*) positively to search for selected characters thought to be present on evolutionary sequence grounds.



TEXT-FIG. 1. Suggested time-correlation of the Wealden outcrop of south-east England (from Harland *et al.* 1967, and latest published information). Lithologic boundaries appear as broken lines. The Ashdown Sand and Fairlight Clay are often grouped as the 'Ashdown Beds' (Howitt 1964, Gallois 1965, Dines *et al.* 1969); it is probable that the two units are diachronous. The Tunbridge Wells Sand is subdivided into three units (upper and lower sandy members separated by the Grinstead Clay) only in the western part of the High Weald. The formation thicknesses are not to scale. Thicknesses (from Gallois 1965): Ashdown Beds, 152-213 m; Wadhurst Clay, 30-70 m; Lower Tunbridge Wells Sand, 15-46 m; Grinstead Clay, 0-21 m; Upper Tunbridge Wells Sand, 30-76 m; Weald Clay, 122-475 m.

TEXT-FIG. 2. Map showing Purbeck Beds, Hastings Beds, and Weald Clay outcrop in south-east England. Place-names mentioned in text are included.





TEXT-FIG. 3. Inferred extent of the Hastings Beds (modified after Allen 1965, 1967a): southern England and part of north-west Europe. The succession is generally thought to have accumulated at the northern end of an elongate subsiding shallow-water essentially non-marine basin (the Anglo-Paris Basin) which ran southwards and connected with the Tethyan Sea in central France. The succession in southern England can be taken, for present purposes, to represent the development of a complex of sandy deltas (probably southward facing), bars and lagoons, and offshore silts and clays (see Allen 1959, 1967b).

Although the classification of preparations and the recognition of assemblage-types are primarily intended to provide a basis for improvements in the application of palynology to fine stratigraphy, they also form the main preliminary step towards a plant palaeoecologic study which will require the integration of this information with plant megafossil and other stratigraphic and sedimentologic information. Some assemblage-types here defined cannot be used directly in other geologic periods, but it is hoped that parallels can be produced relatively quickly on similar grounds and that the Wealden types will form a useful basis for comparison.

The development of the assemblage classification and detail of all the assemblage-types is fully worked out here. Comments are provided on the lithologic and stratigraphic distribution of the types within the succession studied. An evaluation of the types by cluster analysis and multidimensional scaling procedures is included.



TABLE 2. Abbreviations employed in text and on tables

AT	assemblage-type; ATs assemblage-types.	
P	< 3%, present	} Miospore abundances excluding <i>Inapertisporites</i>
C	3- < 15%, common	
V	15- < 30%, very common	
F	30% or more frequent	
P	present	} Relative abundances of <i>Inapertisporites</i> and of all other entities except for those listed below.
C	common	
F	frequent	

Pyrite corrosion: recorded as P if miospores affected are common or frequent. Fungal remains, rootlets, and other trace fossils, rhizomes and stems *in situ*, ironstones: P if recorded.

Trilete spore size: S = small forms dominate trilete spore content  
A = average-sized forms dominant  
L = large forms dominant

Miospore diversity: S = little diversity  
A = average  
L = large

Preservation state: B = poor (bad)  
M = fair (mediocre)  
G = good

Sorting: B = poor  
G = good

Rocks: FC, Fairlight Clay; AS, Ashdown Sand; WC, Wadhurst Clay; TWS, Tunbridge Wells Sand excluding Grinstead Clay; GC, Grinstead Clay; WEC, Weald Clay.

Publication of the detail of their application will, however, for reasons of space, have to be presented later. Details on the materials and methods and brief comments on some of the taxa employed are provided for reference.

*Definition of terms.* I use the term 'assemblage' to refer to the total organic content of a preparation from a single rock sample. A combination of recurrent associations of assemblage characters forms the basis of an 'assemblage-type'. Some, in particular Soviet, authors employ 'spectrum' for the spores and pollen extracted from a selected sample and use 'assemblage' to refer to the typical spore/pollen spectrum of a given horizon, suite, stage, etc. (Vakhrameev 1970).

#### THE ASSEMBLAGE-TYPE CLASSIFICATION

The 17 assemblage-types identified from the Wealden are presented on Table 1. Each type consists of a set of recurrent associations for a 'key character' or 'identifier'. For convenience, the types are numbered 1-17. Details are given below in a systematic section which amplifies Table 1.

#### *Method of determination of assemblage-type*

Palynologic preparations can be assigned to these assemblage-types after about 10 minutes' examination. The procedure is as follows:

1. Note preservation state, diversity of miospores, average size of trilete spores, and abundance of brown wood; assign preparation to AT1-6, or if in doubt, to AT17.

2. If considered useful, attempt to assign preparation to AT7-16, the more detailed level; in some cases it may not be possible to do so (see Table 6). If necessary,

a rapid count of 100 miospores may be made, only recording the taxa which could be key characters and treating all other taxa as one group. Successful assignment at this level cancels the initial assignment to AT1-6 and 17.

3. The following secondary characters, discussed separately below, can be noted at either stage: *Inapertisporites* F, *Celyphus rallus* C or F, microplankton, microforaminifera, and megaspores C or F. Their identification is not essential for the determination of assemblage-types.

The associations listed for each AT occur in at least 80% of the assemblages I have assigned to that type. An identified assemblage will not, therefore, necessarily display every character listed for the type. Attribution to more than one assemblage-type may be necessary because assemblage character variation is continuous. An order of priority for assemblage-type usage described elsewhere (Batten 1972) is not considered here because it has been found to be too cumbersome for general use.

Table 6 gives data on 100 selected productive samples and the identifications possible. The application of the procedure is considered later (p. 19).

### *Secondary characters*

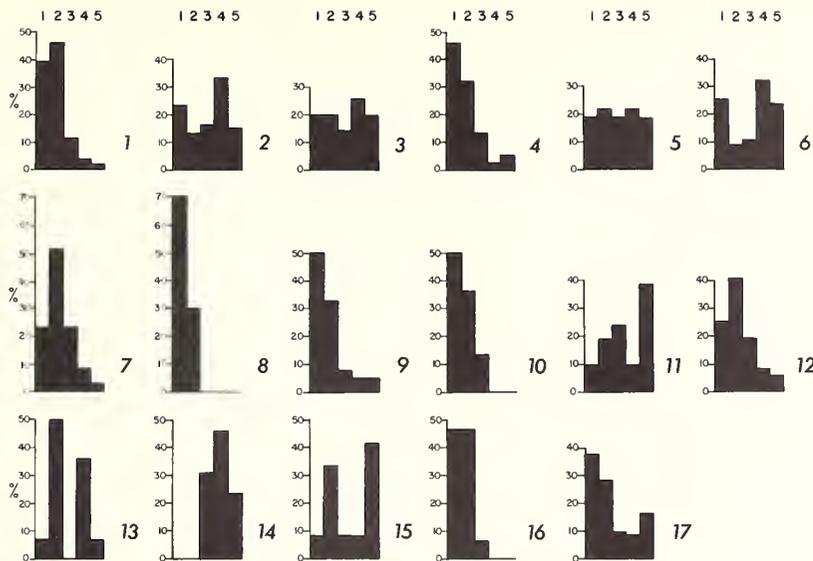
Certain palynomorph groups are considered separately from the classification because: (1) their distribution patterns differ significantly from those of the bulk of the miospores; (2) they occur in a variety of, and therefore superimpose, assemblage-types; and (3) their value in the context of Wealden miospore preparations is primarily palaeoecologic rather than stratigraphic. These groups include megaspores, charalean gyrogonites, seeds, *Botryococcus*, dinoflagellates and acritarchs, microforaminifera, reworked spores, and certain other palynomorphs. Dinoflagellates and acritarchs would probably assume greater importance in assemblage classifications developed for other regions but they are not common enough to have much other than palaeoecologic value in the Wealden.

Five categories of secondary characters which I have found useful to record are those listed on Table 5 together with their recurrent assemblage associations; details are presented for reference below. Their recognition is not, however, essential for and merely refines an identification. The occurrence of secondary characters is recorded for the assemblages listed on Table 6.

## RECORD OF ASSEMBLAGE-TYPES

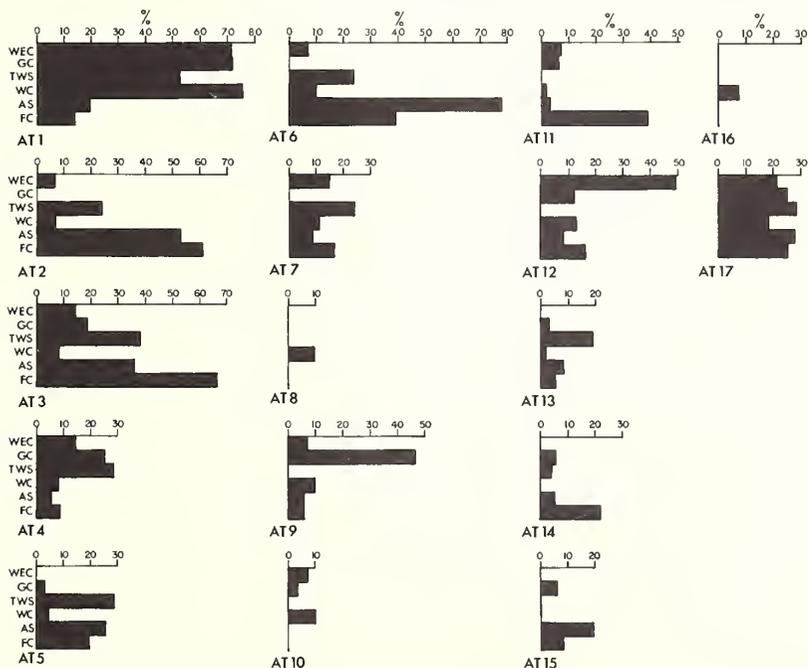
This section is intended to supplement the information given on Table 1 and text-figs. 4 and 5. Details of the assemblage-types are discussed and the key characters and associations which I consider to be important (modified since Batten 1972) are noted; reference to other associations listed on the table and to lithologic and stratigraphic distribution is restricted to information unobtainable or not obvious from the table and text-figures.

All percentages given are accurate to the nearest whole number and are derived from data on 340 productive Wealden miospore preparations (see section below: 'Development'). The number of assemblages on which each assemblage-type is based



TEXT-FIG. 4. Histograms showing relationship between assemblages containing key characters (1-17) and grain size of samples from which they were extracted. % = percentage of total number of preparations of rock samples containing key character. 1 = clay, 2 = fine-medium silt (mostly finely laminated clay/fine silt and medium silt), 3 = medium silt, 4 = medium-coarse silt, 5 = coarse silt and sand.

TEXT-FIG. 5. Histograms showing the frequency of occurrence in the Wealden of assemblages containing the key characters of the 17 assemblage-types. % = percentage of total number of productive samples processed from each formation. Percentages for Weald Clay unreliable because of insufficient data. FC = Fairlight Clay, AS = Ashdown Sand, WC = Wadhurst Clay, TWS = Tunbridge Wells Sand excluding Grinstead Clay, GC = Grinstead Clay, WEC = Weald Clay.



is given on Table 3. For abbreviations employed in the text and on tables and text-figures, see Table 2. Important associations below the 80% level of affinity of selected taxa mentioned in the text are summarized on Table 4.

TABLE 3. Number of assemblages on which each assemblage-type is based

AT	Number of assemblages	AT	Number of assemblages
1	207	10	22
2	61	11	21
3	70	12	47
4	37	13	14
5	32	14	13
6	68	15	12
7	39	16	15
8	20	17	72
9	40		

TABLE 4. Degrees of association of important taxa with certain assemblage-types, below the 80% level of affinity

<i>Concavissimisporites</i>	> 60% in ATs 13 and 14
<i>Pilosiporites</i>	> 70% in AT14, > 60% in ATs 3 and 5
<i>Verrucosiporites</i>	> 70% in AT11, > 60% in ATs 2 and 3
<i>Staplinisporites</i>	> 60% in ATs 2, 5, and 11
<i>Trilobosporites</i>	> 70% in ATs 3, 11, 13, and 15
<i>Eucommiidites</i>	> 60% in ATs 2, 9, and 14
<i>Cycadopites</i>	> 50% in AT11
<i>Exesipollenites</i>	> 70% in ATs 1, 3, 7, and 10, > 60% in AT6
<i>Schizosporis</i>	> 50% in AT14

### AT1

*Key character.* General state of preservation of miospores poor.

*Important associations.* Miospore content shows average or little diversity; *Inaperturopollenites* C or V.

*Remarks.* *Exesipollenites* occurs in 71% of the assemblages referable to AT1. Brown wood occurs in only 37% (C in 14% and F in 4%) and cuticle in 50% (C in 8% and F in < 1%). The preservation state of miospores in assemblages containing an abundance of black wood, but little or no brown wood or cuticle, is generally poor or fair.

The spores of taxa which have been most susceptible to folding, tearing, and corrosion are the thin-walled smooth or lightly sculptured triletes, the thin-walled inaperturates (*Inaperturopollenites* species), and the bisaccates. Many poorly preserved assemblages are composed almost entirely of spores with pale coloured 'thinned' and roughened (pitted/etched) exines. The recognition of various types of corrosion has been employed (unpubl.) to refine assemblage identifications.

*Distinction.* Well and fairly well preserved assemblages usually occur in association with an abundance of brown wood and/or cuticle and tend to contain a greater

variety of miospore taxa than poorly preserved assemblages. The majority of assemblages recorded as showing little diversity are poorly preserved.

*Lithologic associations.* Assemblages referable to AT1 are most often recovered from (calcareous) fine-medium siltstones, claystones (text-fig. 4), and argillaceous limestones. Those from the fine siltstones and claystones generally contain very flattened miospores but those from limestones and clay (sideritic) ironstones tend to be slightly inflated.

*Stratigraphic distribution.* Although poorly preserved assemblages are most often recovered from the Wadhurst, Grinstead, and Weald Clays, a high proportion of Tunbridge Wells Sand samples have also yielded them (text-fig. 5); this can be attributed to the fact that many of the samples processed from this unit were well sorted.

## AT2

*Key character.* General state of preservation of miospores good.

*Important associations.* Trilete miospore content dominated by average sized or large forms; brown wood C or F; cuticle P, C, or F.

*Remarks.* The miospore content of 49% of the AT2 assemblages is diverse, but shows little diversity in 25%. Brown wood is F in 70%. *Verrucosisporites*, *Staplinsporites*, *Eucommiidites*, and miospore masses and/or tetrads occur in more than 60%. Assemblages in which no spores show signs of corrosion have not been recovered and those with very few corroded forms are exceptional.

*Distinction.* The usual lack of diversity of miospores and scarcity or absence of brown wood and cuticle in assemblages in which miospores are poorly preserved contrasts with the frequent association of abundances of brown wood and cuticle and the generally greater diversity of the miospore content with well-preserved assemblages. The greater diversity in well-preserved assemblages is partly the result of the fact that it is easier to identify well-preserved miospores than poorly preserved, but it is also frequently a reflection of closer proximity of the depositional environment to source and other factors.

*Comparison.* Assemblages which contain the identifiers of ATs 5, 6, 8, 13, 14, and 15 are more likely to contain well-preserved miospores than other assemblages.

*Lithologic associations.* The best-preserved assemblages are most often extracted from sandy siltstones, sandy claystones, and poorly sorted (but not bioturbated) siltstones containing megascopic remains of plants. Many of the others in good condition were extracted from medium and coarse siltstones and very fine sandstones (text-fig. 4). Miospores are frequently preserved in an uncompressed state in these lithologies, probably because they were shielded from compression in the interstices between the grains.

The quantity of plant fragments in a rock can usually be used as an indicator of the state of preservation of miospores which can be expected. Although well-preserved assemblages can be recovered from rock samples lacking megascopic plant remains, any fine-grained sandstone and finer sediment containing F well-preserved megascopic plant fragments (brown wood and/or cuticle) usually contains

a spore assemblage that is at least in a fair state of preservation. 84% of the samples which yielded well-preserved assemblages contain megascopic plant fragments and they are C or F in 51%.

### AT3

*Key character.* Miospore content diverse.

*Important associations.* Trilete spore content dominated by average-sized or large forms; *Eucommiidites* P or C.

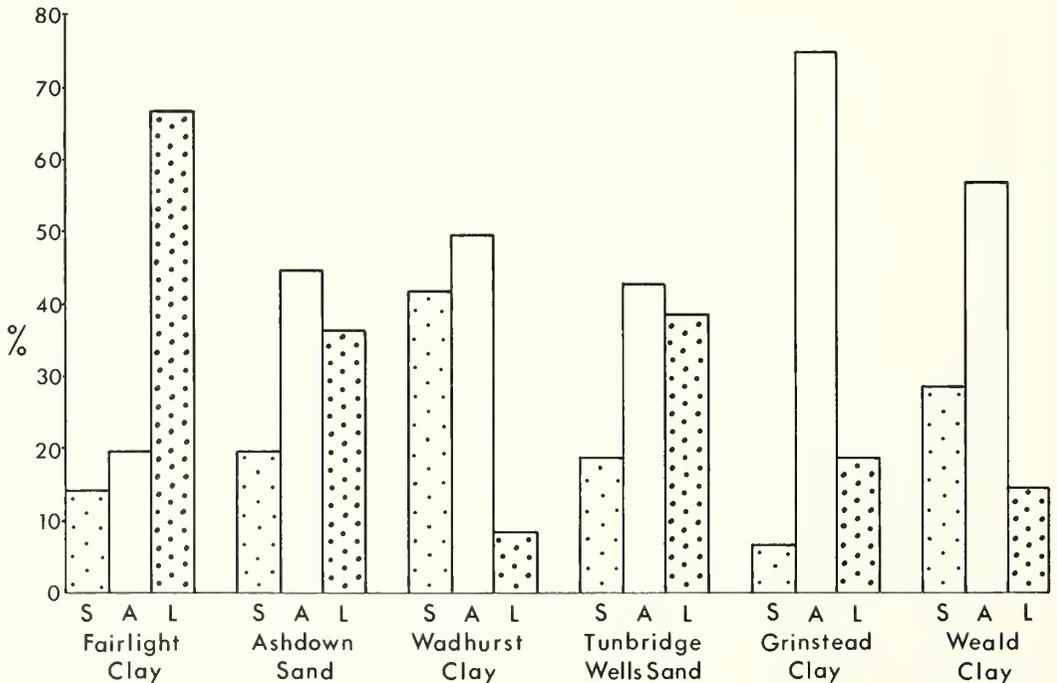
*Remarks.* Preservation was listed as good or fair for 77% of the assemblages referable to AT3. Both *Exesipollenites* and *Trilobosporites* occur in more than 70%, *Verrucosiporites* occurs in 69%, and *Pilosiporites* in 67%. Further examination of a diverse assemblage after a count of 200 miospores will usually reveal several other taxa which have not already been identified.

*Stratigraphic distribution.* The mean number of miospore taxa recorded during counts of 200 miospores from FC assemblages is 19, AS is 17, WC 14, TWS 17, GC 16, and WEC 15 (see also text-fig. 6).

### AT4

*Key character.* Small triletes dominate the trilete spore content.

*Important associations.* Miospore diversity small or average; general state of preservation of miospores poor or fair.



TEXT-FIG. 6. Histograms showing percentage of assemblages from each formation in which the diversity of the miospore content has been recorded as small, average, and large.

*Remarks.* Cuticle was recorded (P and C) from 40% and brown wood (P and C) from only 19% of the assemblages referable to this AT.

*Comparison.* Assemblages referable to ATs 7, 9, and 10 are most likely to contain trilete spores dominated by small forms. Many lack or contain very few large and/or heavily sculptured 'fern' spores and megaspores, their bulk being a 'light fraction', viz. small and light weight miospores and those which were capable of floating for long periods (e.g. bisaccates).

#### AT5

*Key character.* Large triletes dominate the trilete spore content.

*Important associations.* Miospore diversity average or large; general state of preservation of miospores good or fair; brown wood P, C, or F and cuticle P or C; *Cicatricosisporites* C or V.

*Remarks.* Brown wood occurs in more than 70%, *Pilosisporites*, *Staplinisporites*, and miospore masses and/or tetrads in more than 60%, and megaspores in 50% of the assemblages referable to this AT.

#### AT6

*Key character.* Brown wood F.

*Important associations.* General state of preservation of miospores good or fair; cuticle P, C, or F.

*Remarks.* The miospore content of 40% of the assemblages referable to this AT is diverse but 26% of the assemblages show little diversity. Miospore masses and/or tetrads were recorded from 72% and *Exesipollenites* from 66%.

*Lithologic associations.* 79% of the rock samples from which AT6 assemblages were recovered contain megascopic plant fragments.

#### AT7

*Key character.* *Inaperturopollenites* V or F.

*Important associations.* Trilete spore content dominated by average-sized or small forms; miospores show average or little diversity; general state of preservation of miospores poor or fair.

*Remarks.* *Exesipollenites* occurs in more than 70% and *Inapertisporites* in 59% (F in 26%) of the assemblages referable to this AT. Brown wood and cuticle occur in only 46% and 33% respectively.

#### AT8

*Key character.* *Pilasporites* F.

*Important associations.* Trilete spore content shows average or little diversity; miospore preservation good or fair; brown wood and cuticle C or F; miospore masses and/or tetrads P or C.

*Remarks.* Black wood occurs in 85% but is F in only 45% of the AT8 assemblages.

Brown wood occurs in all and is F in 70%. A large proportion of the miospore masses are of *Pilasporites*.

*Comparison.* Although the general aspect of AT8 is similar to that of ATs 13, 14, and 15, *Pilasporites* is never common in these ATs; it is, however, F in 40% of the assemblages referable to AT16.

*Lithologic associations.* All assemblages identified as AT8 are associated with *Equisetites* soil beds and fragment partings (Allen 1947, Batten 1968). 70% contain megascopic fragments of (*Equisetites*) plants.

*Stratigraphic distribution.* AT8 has so far only been recorded from the Wadhurst Clay (text-fig. 5) but it may also occur in both the Grinstead and Weald Clays.

#### AT9

*Key character.* *Exesipollenites* C or V.

*Important associations.* Trilete spore content dominated by average-sized or small forms; miospores show average or little diversity and poor preservation; *Classopollis* C or V.

*Remarks.* Cuticle was recorded as P or C in 58% of the assemblages referable to this AT but brown wood occurs in only 27%. *Inapertisporites* was recorded from 71% and is F in 21%. *Eucommiidites* occurs in 66%. Pyrite crystals or their relict structures are common or frequent in the exines of miospores in 68%.

#### AT10

*Key character.* *Classopollis* F.

*Important associations.* Trilete spore content dominated by small or average-sized forms; miospores show average or little diversity and poor or fair preservation.

*Remarks.* The miospore content of 64% of the assemblages referable to this AT show little diversity. Brown wood occurs in only 36% and cuticle in only 23%. *Exesipollenites*, masses or tetrads of *Classopollis*, and pyrite crystals or their relict structures in the exines of miospores occur in more than 70%; *Classopollis* tetrads are C in 18% and F in 14%. *Inapertisporites* occurs in 68% and is F in 36%.

#### AT11

*Key character.* *Eucommiidites* C.

*Important associations.* *Cicatricosisporites* C or V, *Exesipollenites* P or C.

*Remarks.* *Verrucosisporites*, *Trilobosporites*, and miospore masses and/or tetrads occur in more than 70% and *Staplinisporites* in 67% of the assemblages which can be referred to AT11. Although *Cycadopites* was recorded from only 21% of the 340 productive preparations, it occurs in 57% of AT11 assemblages.

*Comparison.* The characters of ATs 9 and 14 are closest to those of AT11 and 39% of the AT14 assemblages (all from the Fairlight Clay) contain the identifier of AT11. This overlap is the result of the fact that both *Eucommiidites* and *Trilobosporites* occur together more frequently in abundance in the Fairlight Clay than elsewhere in the succession. Only 5% of the AT9 assemblages contain the identifier of AT11.

*Lithologic associations.* 62% of the rock samples which yielded AT11 assemblages contain megascopic plant fragments. The one Ashdown Sand and 13 of the 14 Fairlight Clay AT11 assemblages recorded are well or fairly well preserved whereas the 6 Wadhurst, Grinstead, and Weald Clay assemblages are poorly preserved.

## AT12

*Key character.* *Cicatricosisporites* V or F.

*Important associations.* General state of preservation of miospores poor or fair.

*Remarks.* *Cicatricosisporites* is the most frequently recovered sculptured trilete spore in the Wealden. It occurs in nearly all (99%) productive samples, is C in 68% of these, V in 13%, and F in 1%. Miospore masses and/or tetrads were recorded from 62% of the assemblages referable to this AT; brown wood occurs in 55% and cuticle in 60%.

## AT13

*Key character.* *Pilosisorites* C.

*Important associations.* Trilete spore content dominated by average-sized or large forms; miospore diversity average or large; general state of miospore preservation good or fair; brown wood and cuticle P, C, or F; *Cicatricosisporites* C or V.

*Remarks.* More than 70% of the assemblages referable to this AT are diverse and contain *Trilobosporites*. *Concavissimisorites*, megaspores and miospore masses and/or tetrads occur in more than 60%.

## AT14

*Key character.* *Trilobosporites* C.

*Important associations.* Trilete spore content dominated by average-sized or large forms; miospore diversity average or large; general state of preservation of miospores good or fair; brown wood and cuticle P, C, or F; *Perinopollenites* P.

*Remarks.* Brown wood was recorded as C or F in 77% of the assemblages identified as this AT. *Pilosisorites* occurs in more than 70%, *Eucommiidites* in 69%, *Concavissimisorites* in 62%, *Schizosporis* (recorded from only 18% of the 340 productive preparations) in 54%, and miospore masses and/or tetrads in 77%.

The association between *Trilobosporites* C and *Perinopollenites* P is partially accounted for by the fact that 62% of the AT14 assemblages came from the Fairlight Clay. Representatives of both genera are recovered more often and are more frequently abundant in the Fairlight Clay than higher in the succession. *Perinopollenites* was recorded from 59% of the productive Fairlight preparations but from only 18% of the total prepared.

*Lithologic associations.* Megascopic plant fragments are present in 69% of the samples which yielded AT14 assemblages.

## AT15

*Key character.* *Concavissimisorites* C.

*Important associations.* Trilete spore content dominated by average-sized or large

forms; miospore diversity average or large; general state of preservation of miospores good or fair; brown wood and cuticle P, C, or F; *Pilosporites* P or C, *Cicatricosisporites* C or V.

*Remarks.* *Trilobosporites* occurs in more than 70% of the assemblages referable to this AT.

#### AT16

*Key character.* *Ischyosporites* C or V.

*Important associations.* Miospore content shows average or little diversity; cuticle P, C, or F; *Pilasporites* C, V, or F.

*Remarks.* The miospores are poorly preserved in 47% but well preserved in 33% of the assemblages on which this AT is based.

*Comparison.* *Pilasporites* F (identifier of AT8) was recorded from 40% of the AT16 assemblages.

*Lithologic associations.* AT16 assemblages are commonly associated with *Equisetites* soil beds and fragment partings (see AT8).

#### AT17

*Key character.* Miospores in a fair state of preservation.

*Remarks.* Many of the 72 assemblages in which the miospores are in a fair state of preservation contain identifiers of other ATs. AT17 is intended to be a 'port-manteau' type for the inclusion of only those assemblages which cannot be referred to ATs 1-16. Only 3% of the assemblages examined had to be referred to this type.

### RECORD OF CATEGORIES OF SECONDARY CHARACTERS

The most important recurrent assemblage associations of the secondary characters at the 80% level of affinity are noted; all are given on Table 5. Lithologic associations and stratigraphic distributions are summarized on text-fig. 7; reference to these aspects here is chiefly restricted to information unobtainable from this text-figure.

#### S1: *Inapertisporites* F

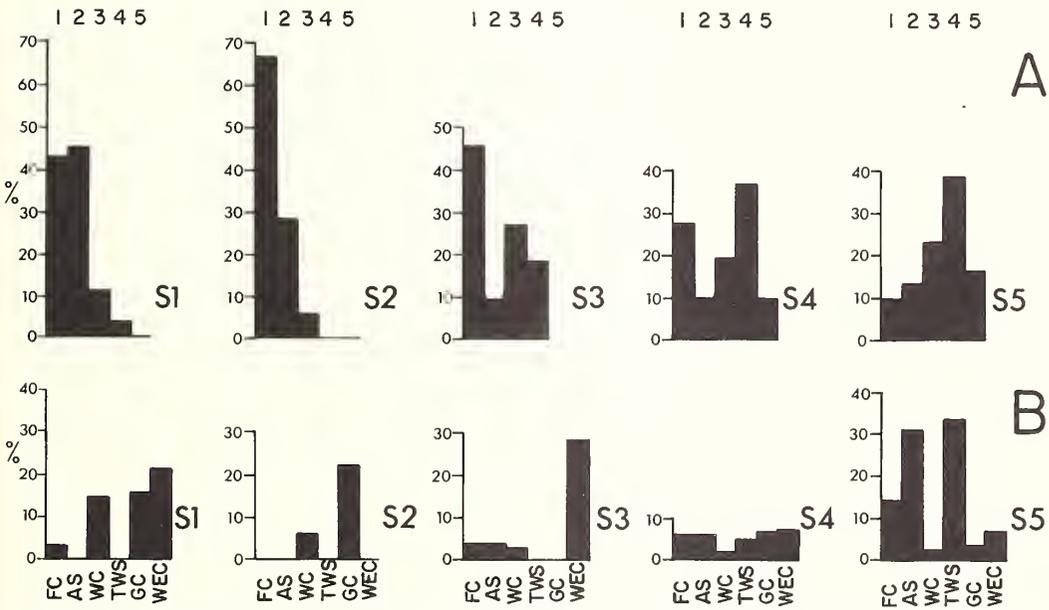
*Important associations.* Poorly preserved miospore assemblages in which average-sized or small spores dominate the trilete spore content.

*Remarks.* The distribution of *Inapertisporites* is not clearly related to kinds of assemblages. It was recorded as F from 38 productive preparations for miospores (26%, 5%, 21%, 36%, 9%, 8%, and 8% of ATs 7, 8, 9, 10, 11, 12, and 15 respectively). Brown wood is F in only 3%, C in 16%, and P in 10% of the assemblages and cuticle is F in only 5%, C in 5%, and P in 23%.

*Lithologic associations.* The distribution of *Inapertisporites* is irregular. Abundances vary considerably in samples lithologically similar, stratigraphically separated at a single locality by only one or two centimetres. When F (or C), it is usually associated with fine-grained lithologies (clay or medium silt, text-fig. 7). 60% were extracted from fossil rootlet bearing samples.

TABLE 5. Recurrent associations at the 80% level of affinity for secondary characters S1-5. For abbreviations employed, see Table 2; for use of terms 'wood' and 'cuticle', see 'Development'; for taxonomic usage, see 'Miospore Record'. CVF, SAL, etc. = C, V, or F; S, A, or L. § = key character; ¶ = important character; 1 = other.

SECONDARY CHARACTERS		RECURRENT ASSOCIATIONS																									
		SMOOTH TRILETES	PILOSISPORITES	CICATRICOISPORITES	GLEICHENIIDITES	TOTAL TRILETES	ARAUCARIACITES	INAPERTISPORITES	INAPERTURPOLLENITES	TSUGAPOLLENITES	BISACCATES	EUCOMMIDITES	CLASSOPOLLIS	EXESIPOLLENITES	CELYPHUS RALLUS	TRILETE SPORE SIZE	MIOSPORE DIVERSITY	INDETERMINABLE MIOSPORES	BROKEN MIOSPORES	PRESERVATION	PYRITE CORROSION	BLACK WOOD	BROWN WOOD	CUTICLE	MICROPLANKTON	MICROFORAMS	MEGASPORES
		CVF	PC	PC	VFC	VFC	FC	FC	VFC	CVF	PC	PC	CVF	PC	CF	ALS	AL	PC	CF	BM	CF	CF	CF	CF	CF	CF	CF
INAPERTISPORITES F	S1	.11	.11	.11	111111	.11111111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111
CELYPHUS RALLUS C or F	S2	.11	.11	.11	111111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111
MICROPLANKTON	S3	.11	.11	.11	1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111
MICROFORAMINIFERA	S4	.11	.11	.11	111111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111
MEGASPORES C or F	S5	.11	11	11	1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111	.1111



TEXT-FIG. 7. A, Histograms showing relationship between assemblages containing secondary characters (S1-5) and grain size of samples from which they were extracted. % = percentage of total number of preparations of rock samples containing secondary character. 1 = clay, 2 = fine-medium silt (mostly finely laminated clay/fine silt and medium silt), 3 = medium silt, 4 = medium-coarse silt, 5 = coarse silt and sand. B, Histograms showing the frequency of occurrence in the Wealden of assemblages containing secondary (S) characters. % = percentage of the total number of productive samples processed from each formation.

S2: *Celyphus rallus* C or F

*Important associations.* Poorly preserved miospore assemblages which show average or little diversity, pyrite crystals or their relict structures in the exines of miospores, bisaccates V or F and *Exesipollenites* P or C.

*Remarks.* *C. rallus* was recorded as C or F in 18 productive preparations (8%, 18%, 2%, and 17% of AT7, 9, 12, and 16 assemblages respectively).

*Lithologic associations.* The distribution of *C. rallus* is restricted but irregular. Abundances vary considerably in samples lithologically similar, stratigraphically separated by only one or two centimetres. The productive samples are all medium siltstones and finer grained rocks.

## S3: Microplankton

*Recurrent associations.* The associations listed on Table 4 are unreliable because dinoflagellates and acritarchs have been recorded from only 11 and are abundant in only 2 of the 340 productive preparations.

*Remarks.* Most forms of Wealden microplankton are attributable to *Palaeoperidinium*, and the acritarch genera *Micrhystridium*, *Baltisphaeridium*, and *Veryhachium*. Of the AT7-16 assemblages, microplankton occur in 5%, 4%, 5%, 10%, 7%, and 15% of those referable to ATs 9, 10, 11, 12, 13, and 14 respectively.

*Stratigraphic distribution.* Weald Clay preparations are more likely to contain microplankton than preparations of Hastings Beds material (text-fig. 7).

## S4: Microforaminifera

*Recurrent associations.* The associations listed on Table 4 are unreliable because microforaminifera have been recorded from only 11 preparations and are not abundant in any of these.

*Remarks.* Brown wood occurs in 8 and is F in 5. Cuticle is P in 5. Of the assemblages referable to ATs 7-16, microforaminifera occur in 5%, 5%, 9%, 5%, 4%, 7%, and 8% respectively of ATs 7, 9, 10, 11, 12, 13, and 14.

*Stratigraphic distribution.* Sporadic occurrences in both the Hastings Beds and Weald Clay (text-fig. 7).

## S5: Megaspores C or F

*Important associations.* Average or diverse miospore assemblage in a good or fair state of preservation. Trilete spore content dominated by average-sized or large forms. *Pilosisporites* P or C, brown wood and cuticle P, C, or F.

*Remarks.* Megaspores are seldom abundant in preparations for miospores. Abundance (C or F) in a rock sample is usually suggested by the occurrence of only a few specimens in a miospore preparation; when only P in a rock sample an occurrence in a preparation is fortuitous.

Brown wood is F in 40% and C in 33% of the 30 preparations in which megaspores occur. Cuticle is C in 37% but F in only 7%. Abundances of megaspores in rock samples were not suggested for any of the samples from which ATs 1, 8, 10, 11, or

17 were recorded (confirmed after subsequent preparations for large plant microfossils). Of the remaining ATs, megaspores are most often associated with assemblages identified as ATs 2, 3, 5, 6, 13, and 14.

*Lithologic associations.* Megaspores are most often abundant in medium-coarse and poorly sorted siltstones (text-fig. 7; see also Batten 1969).

*Stratigraphic distribution.* Fairlight Clay, Ashdown Sand, and Tunbridge Wells Sand samples have been the most productive (text-fig. 7).

## EVALUATION

### *Omissions*

Some kinds of assemblages seldom occur in the Wealden succession. One important omission is a set of associations for *Cycadopites*/*Monosulcites* grains. Hughes and Moody-Stuart (1967a) reported that *Monosulcites* species are usually associated with inaperturate abundances in higher parts of the Wealden. The low frequency of occurrence of pollen referable to this genus or to *Cycadopites* through the whole of the succession (recorded as P during counts of 200 grains from 18% of the productive preparations, C in only 3 preparations), has, however, prevented the determination of a reliable set of associations for these genera. Greater abundances have been reported elsewhere from the Jurassic (e.g. Couper 1958, Chaloner and Muir 1968) and Early Cretaceous (e.g. Singh 1964).

### *Taxa of little value*

Many of the taxa that have been recorded cannot be considered in the identification procedure because they are seldom common in the Wealden. On the other hand, others which are often abundant (e.g. the bisaccates, *Araucariacites*, *Tsugaepollenites*, and *Gleicheniidites*) have little value because few of their associations are distinct. I had expected 'bisaccates F' to be an identifier of an AT but its usefulness was limited because of the frequency of occurrence of assemblages containing this character (102 of the 340 productive preparations) and because neither its palynologic nor its lithologic associations are distinct (although 28 of the 30 assemblages in which the bisaccates constitute 40% or more came from medium siltstones and finer grained samples).

The only significant associations noted for the other taxa mentioned above are as follows: *Araucariacites* C or V mostly in assemblages containing miospores in a poor or fair state of preservation recovered from the finer grained siltstones; *Tsugaepollenites* C or V mostly in poorly preserved assemblages of average or little diversity; trilete spore content of assemblages containing 5% or more *Gleicheniidites* usually (44 of 45) dominated by average-sized or small forms.

### *Lithologic and stratigraphic control*

The distribution of the assemblage-types is closely related to both lithology and stratigraphy reflecting changes through time of both depositional and source environments. The dominant factor controlling the distribution of plant remains and their preservation in the Wealden was probably a delta complex (text-fig. 3) which would

have acted both as the chief source of the material and as a major transport agency. Other factors would have included the geologic and climatic events which affected the water level in the delta and caused changes in the pattern and amount of discharge of the rivers draining into the basin, the relationships between currents in the basin, the rate of deposition of palynomorphs and detrital material, and the degree of reworking.

The relationship between assemblages containing the key characters of the assemblage-types and the average grain-size of the rocks from which they were extracted has been considered in the 'Record of Assemblage-types' and is summarized on text-fig. 4. Some assemblages are more likely to be, or are only associated with fine-grained rocks (maximum average grain-size, medium silt), others are restricted to medium silts and coarser grained rocks, and some distributions show no clear trends (e.g. those of ATs 13 and 15). The last suggests that the assemblage-types are fairly evenly distributed throughout the grain-size range, but it is possible that a trend might have become apparent if the histograms concerned had been based on a greater number of preparations.

Several assemblage-types show a selective distribution in the succession (text-fig. 5). AT10, for example, has so far been recorded only from the more argillaceous formations whereas AT15 has been recovered only from the more arenaceous. AT9 has been recorded most often from the Grinstead Clay, AT12 from the Weald Clay, and ATs 11 and 14 from the Fairlight Clay. ATs 8 and 16 have only been recorded from the Wadhurst Clay. It is likely that AT8 will eventually be recovered from both the Grinstead and Weald Clays; equally, AT16 may well occur elsewhere in the succession. AT8 is usually, and AT16 commonly associated with *Equisetites* soil beds and adjacent strata.

#### *Numerical analysis of relationships*

In order to determine the relationships between the assemblage-types, all 340 assemblages on which the classification was based were identified after counts of 200 miospores. The total data on each of the assemblages, and sections of it, were then compared with the data on all the others using coefficients which express relationships of both similarity and difference (see Cheetham and Hazel 1969) followed by cluster analysis and nonmetric multidimensional scaling techniques (Bonham-Carter 1967, Kruskal 1964*a, b*). The clusters produced by programs operating on the matrices of coefficients derived were subsequently examined to determine whether they were meaningful in the light of the assemblage identifications (for further details, see Batten 1972).

It was found that most of the assemblages referable to ATs 1, 4, 7, 9, and 10 and most of those identified as ATs 2, 5, 6, 13, 14, and 15 are more closely linked to each other than to those which were identified as the other ATs. These groupings chiefly result from differences in state of preservation of assemblages, diversity of miospore content, abundance of organic matter in rock sample, and grain size of sample. Of the assemblages referable to ATs 3, 11, 12, and 17 (transitional ATs), some are closely linked to the components of the two large groups and some are isolated or constitute (small) clusters which are less well linked to the rest of the set. Assemblages referred to AT8 and most of those identified as AT16 are more closely linked to each other than to any other type.

Examination of the sub-clusters which comprise the major clusters revealed that, for the most part, assemblages referable to particular assemblage-types or to types within the groups mentioned above, tend to be well linked internally in spite of the fact that all the data and not just the recurrent associations of the assemblage-types were taken into account. Some sub-clusters do, however, contain one or two anomalies and some are composed of a variety of (not only transitional) types. Both situations result from the continuous variation of assemblage characters.

The relationships determined here are demonstrated below with the aid of Table 6. This table gives data on 100 selected productive samples. To the right of the data block is a list of the assemblage-types to which the assemblages can be referred. Whilst many can be referred to more than one assemblage-type, the bulk of the multiple assignments are to the general types which take second place to reference to one of the ATs 7-16.

Most are referable to types within the two major groups delimited above, or to an assemblage-type from one of these groups and a transitional form. An assemblage identified as AT13, for example, cannot also normally be referred to types other than ATs 11, 12, 14, or 15. Even when the general assemblage-types are taken into account, reference to ATs 2, 5, or 6 is much more common than to 1 or 4. Similarly an assemblage identified as AT7 is more likely to be also referable to ATs 9 or 10 of the specific and 1 or 4 of the general types than to any of ATs 2, 5, 6, 13, 14, or 15. Atypical groupings do, however, occur (e.g. Table 6, examples 19 and 24).

#### APPLICATION

##### *In the Wealden*

An assemblage-type identification enables an immediate assessment to be made of the potential of an assemblage for either stratigraphic or palaeoecologic purposes. A set of identifications provides a useful record of the general aspect of palynologic preparations in a stratigraphic succession. The use of any stratigraphic marker microspore can now be closely examined in the light of the kinds of assemblages from which it has been recorded. The determination of facies patterns in (local) distributions of kinds of assemblages is facilitated because the assemblage-types reflect both depositional and source environments. Together with plant megafossil and other stratigraphic and sedimentologic information, the assemblage classification procedure provides a basis for more reliable palaeoecologic interpretations than have hitherto been possible. It is now possible to select preparations in which certain characters can be expected or not expected to occur. The type of assemblage which occurs in a given rock type or in a given part of the succession can also be predicted. This allows selective preparations to be made, saving time when large numbers of samples are involved.

On a more specific level, it might, for example, be considered necessary to rely on a certain taxonomic group for correlation, e.g. species of *Trilobosporites*. Preparations which contain, or are likely to contain, these spores in relative abundance can now be selected from a set of identified preparations. Those identified as AT14 can be examined first because *Trilobosporites* species are common in this assemblage-type and are generally well or fairly well preserved. If it is necessary to examine further

TABLE 6. Data on 100 productive samples from the Wealden. Sample numbers on left-hand side of table. Possible identifications on right-hand side; reference to secondary characters is included. Number of samples selected from each formation (Fm) proportional to total prepared from that formation. Samples initially chosen at random but numbers then adjusted so that at least two representatives of each AT could be incorporated in table; for localities, see Appendix. Formation boundaries in the Cuckfield No. 1 Borehole given in Gallois (1970); (unregistered) Cuckfield sample numbers prefixed by CUC. The taxa are arranged in the same order as they appear in 'Miospore Record'. A period (.) indicates 'no information' (for columns 1-68 = no information after a count of 200 miospores).

Average grain size: 1 = clay-fine silt; 2 = fine-medium silt (mostly finely laminated clay/fine silt and medium silt); 3 = medium silt; 4 = medium-coarse silt; 5 = coarse silt; 6 = coarse silt-very fine sand; 7 = very fine sand; 9 = fine sand.

	1	2	3	4	5	6	7	9	ATS	1-6	SL-5 Fm
1	FC	FC	FC								
2	FC	FC	FC								
3	FC	FC	FC								
4	FC	FC	FC								
5	FC	FC	FC								
6	FC	FC	FC								
7	FC	FC	FC								
8	FC	FC	FC								
9	FC	FC	FC								
10	FC	FC	FC								
11	FC	FC	FC								
12	FC	FC	FC								
13	FC	FC	FC								
14	FC	FC	FC								
15	FC	FC	FC								
16	FC	FC	FC								
17	FC	FC	FC								
18	FC	FC	FC								
19	FC	FC	FC								
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27	FC	FC	FC								
28	FC	FC	FC								
29	FC	FC	FC								
30	FC	FC	FC								
31	FC	FC	FC								
32	FC	FC	FC								
33	FC	FC	FC								

1. A. ...  
 2. P. ...  
 3. P. ...  
 4. P. ...  
 5. P. ...  
 6. P. ...  
 7. P. ...  
 8. P. ...  
 9. P. ...  
 10. P. ...  
 11. P. ...  
 12. P. ...  
 13. P. ...  
 14. P. ...  
 15. P. ...  
 16. P. ...  
 17. P. ...  
 18. P. ...  
 19. P. ...  
 20. P. ...  
 21. P. ...  
 22. P. ...  
 23. P. ...  
 24. P. ...  
 25. P. ...  
 26. P. ...  
 27. P. ...  
 28. P. ...  
 29. P. ...  
 30. P. ...  
 31. P. ...  
 32. P. ...  
 33. P. ...

97. Large Plant Fragments  
 96. Bladder/Stem  
 95. Bladder  
 94. Pinnule  
 93. Pinnule  
 92. Pinnule  
 91. Pinnule  
 90. Pinnule  
 89. Pinnule  
 88. Pinnule  
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 86. Pinnule  
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	ATS 7-16	ATS 1-6	SL-5	Fm
67	DJB291	or 17	12,13	WC
68	DJB294	5	8	WC
69	DJB347A	1,3	7	WC
70	DJB125	3	16	WC
71	DJB352A	1	7	WC
72	DJB126	1	16	WC
73	DJB163	1,4	3	WC
74	CIC698	3,5,6	9,12	TWS
75	CIC635/6	3,6	4	TWS
76	CIC513	2,3,5	13	TWS
77	CIC499	2,3	13	TWS
78	CIC443	5	6	TWS
79	CIC379	5	3,5	TWS
80	CIC345	1	1	TWS
81	CIC296	4,5	7	TWS
82	CIC295	1	1	TWS
83	DJB161	1,4	7	TWS
84	CIC563	17	17	GC
85	DJB12	1	1	GC
86	DJB137	1,3	1,3	GC
87	DJB11	9	9	GC
88	DJB143	1,3	1,3	GC
89	DJB9	1,3	10	GC
90	DJB1	2,4	1,3	GC
91	DJB3	1	1	GC
92	DJB5	1	1	GC
93	DJB6	1,4	9	GC
94	DJB16	1	9	GC
95	DJB17	1,4	9	GC
96	DJB18	1,4	9	GC
97	DJB158	12,13,14	3,5	GC
98	DJB159	11	11	WEC
99	WM1212/7	12	12	WEC
100	WM1198/5	12	12	WEC

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preparations to establish a more complete picture, assemblages identified as ATs 3, 13, and 15 could then be selected because more than 70% of these contain *Trilobosporites* (see 'Record of Assemblage-types' and Table 4). If more preparations are needed, only medium siltstones and coarser grained samples need be considered initially (text-fig. 4).

An examination of assemblages from a larger number of both coarse-grained and Weald Clay samples remains to be accomplished and could lead to the erection of one or two additional assemblage-types; many of the coarse-grained samples proved, as expected, to be devoid of palynomorphs. The sequential appearance and development of recurrent groupings of taxa also need to be fully investigated. It is hoped that eventually it may be possible to identify preparations in which any selected spore, pollen, or other palynomorph species can be expected to occur.

### *Outside the Wealden*

Although it is probable that the assemblage classification cannot be applied in its entirety in (Early Cretaceous) successions outside of the English Wealden, the method of tackling the facies problem can be applied to any rocks containing palynomorphs and many of the associations recognized may provide a useful basis for comparison for both stratigraphic and palaeoecologic purposes.

## DEVELOPMENT

The materials and methods employed in the development of the assemblage classification are here described.

### *Samples*

The 340 productive field and borehole samples from southern England were used for the project. They range from Berriasian to Late Barremian/Early Aptian in age (Table 7, text-fig. 1).

TABLE 7. Samples prepared for the microscopic examination of their organic contents

	<i>Total miospore preparations</i>	<i>Total productive miospore preparations</i>	<i>Preparations for larger plant microfossils</i>
Fairlight Clay	51	36	19
Ashdown Sand	46	36	19
Wadhurst Clay	203	201	22
Tunbridge Wells Sand (excluding GC)	44	21	15
Grinstead Clay	39	32	2
Weald Clay	14	14	3
Total	397	340	80

### *Preparations*

Rock samples weighing about 15 g and from not more than 2 cm stratigraphic thickness were processed for miospores. To enable the assemblages extracted to be compared as accurately as possible, the preparations were carried out in a standard manner using 50% hydrochloric acid, HF, nitric acid or Schulze solution, ammonium hydroxide and zinc bromide (sp. gr. c. 2.2). Oxidation time was kept to a minimum, usually 30 minutes or less in concentrated nitric acid or 5–10 minutes in Schulze solution. The residues were cleared with 5% ammonium hydroxide for 5 minutes. Fine material was removed by short centrifuging. Strew slides were made with Clearcol; Euparal or DePeX sealed the cover-slips to the slides. The method of retrieval and examination of megaspores and other large plant microfossils was as described in Batten (1969).

### *Documentation of lithologic information*

All samples prepared for the microscopic examination of their organic contents were examined under a stereoscopic microscope prior to processing. Abundances of plant megafossils, bivalves, ostracods, and fish remains were estimated and recorded as P, C, or F (Table 2). If present, rootlets and other trace fossils, plant stems and rhizomes *in situ*, and ironstones were recorded as P; abundances were not considered. Information on colour, sorting, cross-bedding, bedding disturbance (bioturbation), slickensiding, presence of pyrite, spherulitic siderite, mica, gastropods, etc., was also documented. The colour of the samples was determined after they had been allowed to dry, by comparing them with the Rock Color Chart (1963) published by the Geological Society of America.

### *Documentation of palynologic information*

*Counts.* The number of objects that should be counted to ensure that a recorded assemblage is reasonably representative of their distribution in a sample has been considered by several authors both within and outside of the field of palynology. The diversity of the assemblage, the relative abundance of individuals, and particularly the purpose for which the count is required have to be taken into consideration. It is generally known that in a count of  $n$  grains, the probable error of the recorded number of abundant objects is much lower than that for the rare forms.

Many of the miospores which are stratigraphically useful are uncommon in preparations. It is, therefore, necessary to undertake counts which ensure their adequate representation; a count of 500 miospores is probably best in most cases (cf. Smith and Butterworth 1967, p. 96). For palaeoecologic purposes, however, comparison of only the broad features of palynomorph distribution in beds is the usual aim. There was little advantage in counting more than 200 grains for this study because the characters of an assemblage are established with this number and the occurrence of rare spores, and low percentages can have little value for rapid identification of assemblages, at least for the present, in the Wealden. Broken miospores were included in the counts if they constituted  $> 50\%$  of a spore. Tetrads and masses were recorded as single grains only to reduce bias (but their presence in an assemblage was also documented; see p. 28). Unequivocally reworked grains (from Jurassic and older rocks) were recorded separately.

Bias differences can occur between observers when examining the more abundant species, and in the counting of the same worker at different times. The differences arise largely from variations in the procedure adopted for rejecting broken and badly preserved grains (Tomlinson 1957). The possibility of error due to bias can usually be removed by check counting (Smith and Butterworth 1967) but it is sometimes difficult to avoid bias when preparing counts from poorly preserved assemblages because some miospore taxa are more easily recognizable in a poorly preserved state than others. To reduce the possibility of error due to bias and to facilitate comparison of assemblages, I documented the percentages of miospore taxa as P, C, V, and F for < 3%, 3-14.5%, 15-29.5%, and 30% or more respectively (Table 2).

*'Fern' spore size index.* The maximum diameters of 100 trilete spores were measured from each assemblage and placed in one of three size groupings (small, < 30  $\mu\text{m}$ ; average, 30-50  $\mu\text{m}$ ; and large, > 50  $\mu\text{m}$ ) following Hughes and Moody-Stuart (1967b, 1969). The majority of triletes were referred to the 30-50  $\mu\text{m}$  category.

I considered small triletes to dominate the trilete spore content of an assemblage if either (1) the number of these was greater by more than 15 than the totals of both the average-sized and large spores, or (2) the difference between the totals of small and average-sized spores was 15 or less and if both were greater by more than 15 than the total of large spores. Domination by large triletes was determined in a comparable way.

*Miospore diversity.* A large number of miospore taxa were recorded during this study but many are rare forms and 44 of the 85 taxa employed in the assemblage comparisons (see 'Evaluation') do not constitute 3% or more of the counts from any palynologic preparation. I therefore considered assemblages from which 13 or fewer taxa were identified during a count of 200 miospores to be those showing little diversity (restricted); from which 20 or more were recorded, to be diverse; and between these limits, to show average diversity. The subdivision is not ideal chiefly because the true diversity of an assemblage may be obscured during a count of 200 by considerable abundances of one or a few taxa. To determine the true diversity in such a case, the exceptionally abundant taxa should be excluded from the count. The numerical limits of the divisions selected were found to be the most reasonable for present data but they will have to be adjusted when future systematic work increases the number of taxa which can be readily identified.

*Preservation.* The general state of preservation of assemblages was recorded as 'good' (G), 'fair' (M), and 'poor' (B; Table 2). The use of these gradings (they refer more to corrosion than to damage from breakage; see below) has depended to some extent on experience. 'Good' indicates that the majority of spores are well preserved; 'poor', that the majority are poorly preserved; and 'fair' is an intermediate category (indicates that badly damaged (corroded) and well-preserved grains are more or less equally abundant).

The preservation state of, in particular, the common Wealden plant microfossil taxa has been examined. Information was sought regarding the degree of inflation/compression; surface compression (flattening of sculptural elements and crumpling of exine); pitting (whether pits are circular, irregular, or dendritic and whether they

are the products of bacterial or fungal attack or the result of diagenesis); modification of exines by pyrite (see Neves and Sullivan 1964; recorded as P if common or frequent); softening and thinning with and without corrosion; breakage and opacity. Some of these effects on the sculptural and structural features of Wealden *Cicatricosisporites* have been demonstrated by Hughes and Moody-Stuart (1969, p. 104, text-fig. 3).

'Degraded' and 'corroded' are terms which have been used by Cushing (1967), Birks (1970), and others to refer to different classes of preservation of deteriorated grains but I have not attempted to distinguish the two.

*Wood and cuticle.* P, C, and F were used for expressing the relative abundance of black and brown 'wood' and 'cuticle' (Table 2). Black wood (Pl. 1, figs. 1-3) includes both structured (e.g. fibrous, with tracheids) and unstructured plant fragment material. The fragments are usually angular (with sharply defined edges) and platey, but are sometimes splintered. When thin, they are translucent (brownish black-dark brown-medium brown). In reflected light, two kinds are recognizable, one which reflects light and another which is dull black. It has not been possible, however, to make distinctions of this nature in transmitted light. Some is vitrain derived from woody plant tissues and leaves which have been affected by anaerobic decay, diagenesis, and compression, but much is probably fusain (resembles Recent charcoal; see Harris 1958).

Brown wood (Pl. 1, figs. 4-6) includes dark and light brown, reddish brown, and orange fragments of plant material. In transmitted light, distinction from black wood is usually only difficult when the fragments are thick and therefore opaque. Two kinds have been recognized: (1) fragments which lack any recognizable structure and are probably decomposition products of plants; (2) fragments of lignite from tree trunks, branches, and leafy twigs preserved in anaerobic conditions. Brown wood is particularly common in the Fairlight Clay, Ashdown Sand, and Tunbridge Wells Sand.

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#### EXPLANATION OF PLATE 1

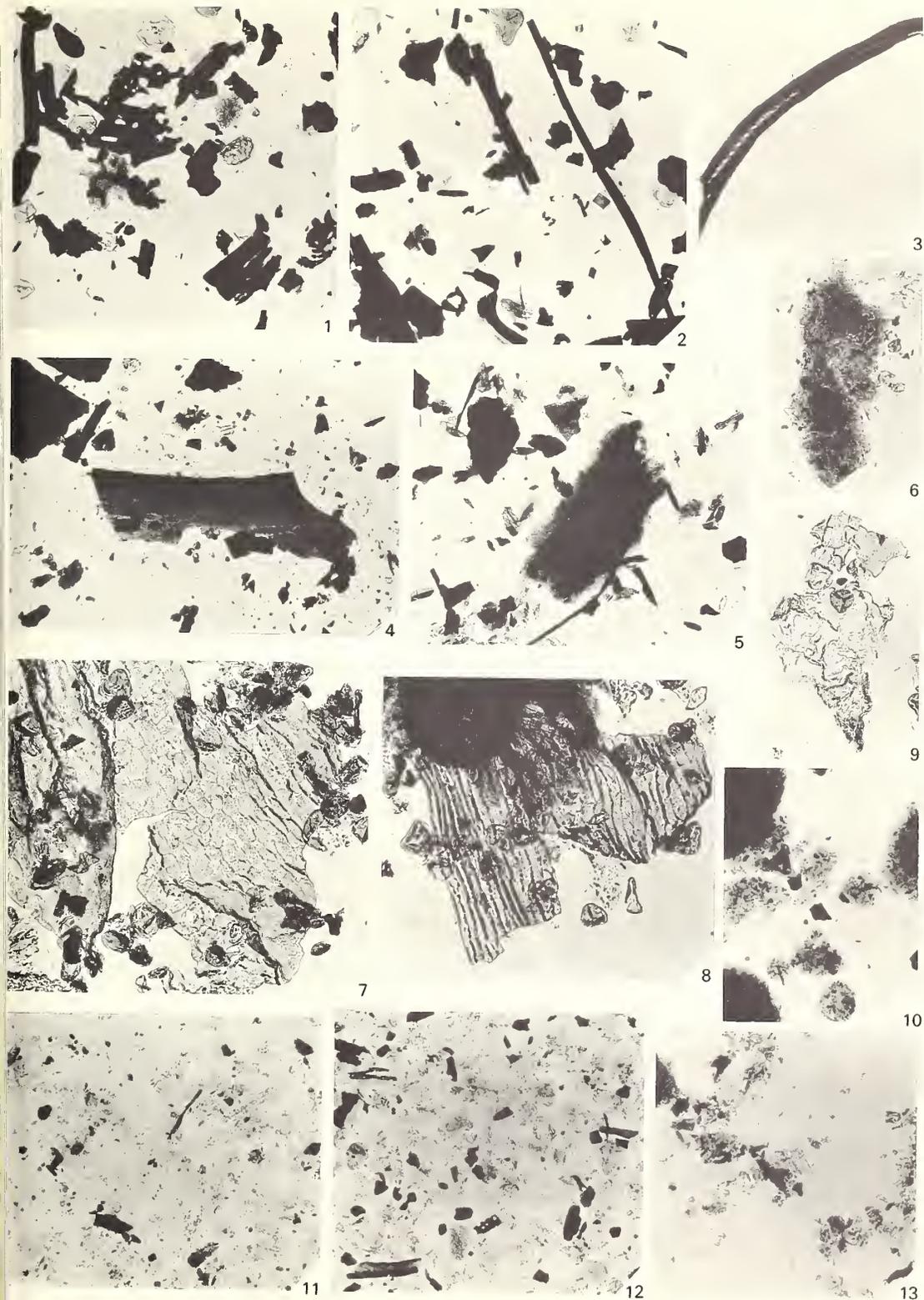
All figures  $\times 100$ . Stage coordinates refer to Leitz Laborlux (L1) microscope, number 557187, Department of Geology, Sedgwick Museum, Cambridge.

Figs. 1-3. Black 'wood'. 1, Fragments of black wood, some structured (including bordered pits), DJB18, prep. T061/1, L1 51.9 123.5. 2, Black wood fragments, some structured, DJB18, T061/1, L1 48.8 120.8. 3, Bordered pits, CUC799/6, T354/2, L1 50.8 116.4.

Figs. 4-6. Brown 'wood'. 4, All fragments are brown wood, opaque-reddish brown, DJB38, T056/1, L1 40.6 118.9. 5, Large piece in centre of figure and most of the smaller fragments are brown wood, some structured; small fragments with sharp outlines are black wood, DJB51, T025/2, L1 40.9 116.1. 6, Amorphous, light brown, DJB346, T325/1, L1 49.0 113.0.

Figs. 7-9. 'Cuticle.' 7, Large piece, CUC971, T294/2, L1 44.9 122.2. 8, Cuticle and part of *Thomsonia* megaspore, CUC971, T294/2, L1 40.1 121.7. 9, Poorly preserved, mostly unstructured; relict structures of pyrite crystals present but only just visible in figure, CUC971, T294/2, L1 57.8 120.9.

Figs. 10-13. 'Mush.' 10, Mush resulting from faulty preparation technique, CUC799/6, T354/2, L1 48.2 120.1. 11, 'Ghosts' of cuticle together with finely divided organic and mineral debris, DJB160, T145/1, L1 31.8 120.8. 12, Chiefly 'ghosts' of miospores together with mineral debris, DJB334, T350/2, L1 49.5 126.5. 13, Finely comminuted plant fragments and spores, DJB228, T085/1, L1 30.0 120.2.



BATTEN, Cretaceous palynologic preparations

Cuticle (Pl. 1, figs. 7–9) is used here both for probable epidermal tissue and for the waxy layer formed on the outer layer of epidermal cells. The bulk of the cuticle in Wealden palynologic preparations is probably of gymnospermous origin.

It was difficult to obtain a consistent representation of wood and cuticle in each slide of a preparation, especially when many of the fragments were relatively large. The average size of the fragments is not considered here; it was not recorded unless small or large pieces ( $< 75 \mu\text{m}$  or  $> 200 \mu\text{m}$  respectively) were unusually abundant.

*Mush.* In some assemblages, various homogenized, frequently coagulated, combinations of the following occur, constituting 'mush' (Pl. 1, figs. 10–13: cf. in part 'sapropelic material' in Correia 1971, p. 611): minute fragments of poorly preserved miospores; entire but pale, crumpled 'ghosts' of miospores; small fragments of wood; very pale flimsy structureless tissue, probably partly cuticular–epidermal; finely divided organic (soft tissues of plants and animals) and inorganic (pyritous?) material; and mineral debris.

*Other characters.* The ratios of determinable to indeterminate grains and broken grains and fragments to entire grains were noted for each assemblage, expressed as percentages and recorded as P ( $< 3\%$ ), C (3–29.5%), or F (30% or more). P, C, and F were also used (Table 2) for expressing the relative abundance of other fossils in the assemblages, namely, *Celyphus rallus* gen. and sp. nov., *Inapertisporites*, spore masses and tetrads, sporangia, megaspores, megaspore fragments, reworked palynomorphs, seeds, charalean gyrogonites, *Dictyothylakos*, dinoflagellates, acritarchs, microforaminifera, and *Botryococcus* (some of these not considered here). Grains referable to *Inapertisporites* were not included in the miospore counts of 200 because they tend to be overlooked on account of their very small size, and when frequent, considerably distort a count. Fungal remains (hyphae and spores) were recorded as P if present; abundances were not considered. Palynomorphs not considered at all include possible animal tissues and algae.

*Data storage and handling.* The Cambridge Titan computer was used to store and handle both the lithologic and palynologic data.

#### *Determination of assemblage-types*

The major difficulty in deriving a practical system for the rapid identification of palynologic assemblages was the large number of variables involved. The data on the preparations for miospores were grouped in various ways. Assemblage characters which I had found were easy to identify and/or appeared to be indicative of certain facies were used as a basis for grouping. The recurrent associations of the other characters displayed by the grouped assemblages were then determined for several levels of affinity. Those at the 70% (0.7) and 80% (0.8) levels of 37 groupings were selected from 69 as potentially useful for assemblage identification (for characters used as a basis for the 37 groupings, see Table 8).

A cluster analysis procedure was then used to facilitate the selection of assemblage-types from this number and at the same time to show the levels of similarity between them. The analysis started with a measure of similarity by comparing the binary data (presence/absence of variables) comprising each pair of objects (potential assemblage-

types) and counting the frequency of 'matches' and 'mismatches' between them. A positive match indicated a match of 1 with 1, a negative match, 0 with 0, and a mismatch, 1 with 0.

Because every type of coefficient has some bias which can effect different patterns of clustering, several measures of similarity were used for comparison, including the Simple Matching Coefficient,  $\frac{C+A}{N_1+A}$  (see Cheetham and Hazel 1969) and the Jaccard Coefficient  $\frac{C}{N_1+N_2-C}$ .

A Fortran IV program took the profiles of the 37 potential assemblage-types and computed the similarity coefficient values as a matrix. The values ranged between 1.0 (complete similarity) and 0.0 (complete dissimilarity). A modified version of Bonham-Carter's (1967) Fortran IV cluster analysis program was used to operate

TABLE 8. Characters used as a basis for grouping assemblages. Other characters which occurred in association with these in at least 70% and 80% of the assemblages formed the bases of 37 potential assemblage-types

General state of preservation of miospores good. General state of preservation of miospores poor. Black wood F, brown wood P or not recorded. Brown wood C. Brown wood F. Cuticle C. Cuticle F. Miospore diversity large. Miospore diversity small, poor preservation. Miospore diversity small, good preservation. Small triletes dominate the trilete spore content. Large triletes dominate the trilete spore content. *Concavissimisporites* C. *Pilososporites* C. *Verrucosiosporites* C. *Cicatricosiosporites* V or F. *Ischyosporites* C or V. *Trilobosporites* C. *Araucariacites* C. *Araucariacites* V. *Inaperturopollenites* V or F. *Pilasporites* F. *Tsugapollenites* C or V. *Bisaccates* F. *Eucommiidites* C. *Classopollis* V. *Classopollis* F. *Exesipollenites* C or V. *Inapertisporites* C. *Inapertisporites* F. *Celyphus rullus* C or F. *Microplankton*. *Microforaminifera*. *Megaspores* P. *Megaspores* C or F. Light weight megaspores dominate megaspore content. Megaspores mixed.

on the similarity data matrix using the unweighted pair-group linkage method (Sokal and Michener 1958, Sokal and Sneath 1963; both programs courtesy A. K. Yeats and P. D. Alexander-Marrack, Cambridge). The objects (potential assemblage-types) were related to each other on the basis of their attributes (characters); they were either paired or not paired. The paired categories formed single categories for the next and subsequent computation cycles. New coefficients were computed between the new categories at each cycle. The program printed out the level of similarity of successive linkages and a list of the object names in an order suitable for drawing a dendrogram.

The clusters produced using the different similarity coefficients were then compared and the number of potential assemblage-types was reduced from 37 to 22. Use of the data derived from comparison of the recurrent associations at the 0.7 level of association was abandoned at this stage in favour of those derived from comparison at the 0.8 level. I then tried to categorize the 340 productive miospore preparations by comparing their characters with those of the 22 potential assemblage-types. 97% were usefully referred to 16 of these (ATs 1-16). The remaining 3% could not be identified and were subsequently referred to a 17th 'portmanteau' type (AT17) erected purely for recording convenience.

## MIOSPORE RECORD

Comments are made with regard to the usage, distinction, and comparison of the miospore taxa referred to in the text and listed on Table 6. The authors of both the taxa used and compared are given once only. The Ages/Stages from which the published species (but not genera) referred to were described are given in parentheses after the author(s)' name(s) if they were originally described from rocks outside the Cretaceous period. The taxa are arranged in the same order as they are set out on Table 6. The groupings approximately correspond to some of the ranks in the suprageneric classification systems of Potonié (1960, 1966) and Dettmann (1963); these are given in parentheses. Within each grouping the taxa are arranged in alphabetical order.

Systematic and nomenclatural problems raised during the course of this study were numerous despite the fact that for the most part I have dealt only with genera. I have had to use some generic names originally erected to incorporate Palaeozoic species for Wealden spores (e.g. *Granulatisporites*, *Converrucosisporites*, *Verrucosisporites*, *Acanthotriletes*, *Apiculatisporis*, and *Reticulatasporites*). Because they are so greatly separated in time, their use, at least for Late Mesozoic spores, should eventually be discontinued when suitable Mesozoic genera become available (see Hughes 1969). The large volume of literature which has to be perused renders comparison of Palaeozoic with Late Mesozoic taxa impracticable.

(Turma TRILETES Reinsch emend. Dettmann 1963)

(Infraturma LAEVIGATI Bennie and Kidston emend. Potonié 1956)

1. AURITULINASPORITES Nilsson 1958: miospores recorded as *Auritulinasporites* are closely similar to *A. complexis* Burger 1966 and *A. deltaformis* Burger 1966.
2. CONCAVISPORITES Pflug 1952 and in Thomson and Pflug 1953 emend. Delcourt and Sprumont 1955/*Concavisporites juriensis* Balme 1957: *Concavisporites* was not used unless specimens could be referred to *C. juriensis* (Jurassic) because of frequent difficulties with reliable determination; they were counted as 'smooth triletes' instead.
3. STEREISPORITES Pflug in Thomson and Pflug 1953.
4. UNDULATISPORITES Pflug in Thomson and Pflug 1953: spores with undulating laesurae almost as long as their radii and with exines which are smooth externally but often irregular (fossulate) internally have been recorded as *Undulatisporites*. The fossulate specimens are similar to *U. pseudobrasiliensis* Krutzsch 1959 (Tertiary), *U. takutuensis* van der Hammen and Burger 1966, and *U. major* Danzé and Laveine 1963 (Jurassic).
5. Smooth triletes: separation of most of the smooth walled trilete spores (*Biretisporites* Delcourt and Sprumont 1955 emend. Delcourt, Dettmann, and Hughes 1963, *Deltoidospora* Miner 1935, *Cyathidites* Couper 1953, *Leiotriletes* Naumova 1937 emend. Potonié and Kremp 1954, *Laroccatriletes* Burger 1966, *Todisporites* Couper 1958, *Triplanosporites* Pflug in Thomson and Pflug 1953, *Dictyophyllidites*, and *Concavisporites* (excluding *C. juriensis*) etc. is generally not practicable at present because of frequent identification difficulties; although the plants concerned

were many, reliable characters for their separation are few. Observations of some trilete spores which show the outer sculptured layer of the exine partially removed suggests that a few (< 1%) of the miospores recorded as 'smooth trilete' may originally have been sculptured.

(*Infraturma* APICULATI Bennie and Kidston emend. Potonié 1956)

6. ACANTHOTRILETES Naumova 1937 emend. Potonié and Kremp 1954: I referred to this genus spores which are ornamented with closely spaced, tapered, occasionally blunt-ended spines more than twice as long as their basal diameter. Some are clearly comparable to *Acanthotriletes varispinosus* Pocock 1962.

7. APICULATISPORIS Potonié and Kremp 1956.

8. BACULATISPORITES Thomson and Pflug 1953.

9. CERATOSPORITES Cookson and Dettmann 1958.

10. CONCAVISSIMISPORITES Delcourt and Sprumont 1955 emend. Delcourt, Dettmann, and Hughes 1963: *Concavissimisporites* has, by definition, concave to almost straight sides.

11. CONVERRUICOSISPORITES Potonié and Kremp 1954: I used *Convverrucosisporites* for slightly concave to convex sided verrucate spores.

12. CYCLOGRANISPORITES Potonié and Kremp 1954/GRANULATISPORITES Ibrahim 1933 emend. Potonié and Kremp 1954.

13. FORAMINISPORIS Krutzsch 1959: Potonié (1966) is of the opinion that the character which distinguishes this genus from other genera is the presence of foveolae in the exine, provided that they are not of secondary origin. Dettmann (1963), on the other hand, has attributed miospores with a narrow sculptured cingulum to the genus although a cingulum was not diagnosed by Krutzsch. The exines of Wealden specimens referred to the genus lack perforations but are probably slightly thickened equatorially; they resemble the holotype of *F. foraminis* Krutzsch 1959 (Tertiary).

14. KUYLISPORITES Potonié 1956.

15. LEPTOLEPIDITES Couper 1953 emend. Norris 1968.

16. NEORAISTRICKIA Potonié 1956.

17. OSMUNDACIDITES Couper 1953: I included in this genus specimens showing considerable variation in wall thickness and sculpture. Forms with exines less than 1  $\mu$ m thick, sculptured with small widely spaced grana and occasional bacula, and those with thicker exines possessing closely spaced grana (sometimes with coalescent bases) are grouped together. Most could have been included in the species *O. wellmanii* Couper 1953 (Jurassic). Similar grains but with predominantly baculate sculpture have been included in *Baculatisporites*.

18. PILOSISPORITES Delcourt and Sprumont 1955.

19. VERRUCOSISPORITES Ibrahim 1933 emend. Smith and Butterworth 1967: forms I included in this genus have circular to subcircular amb. The diagnoses of *Verrucosisporites* and *Convverrucosisporites* overlap.

(Infraturma MURORNATI Potonié and Kremp 1954)

20. CICATRICOSISPORITES Potonié and Gelletich 1933: I used *Cicatricosisporites* to incorporate positively and negatively sculptured forms (Hughes and Moody-Stuart 1967b) and specimens which possess exinal thickenings (appendices) in equatorial radial regions (= *Appendicisporites* Weyland and Krieger 1953).

21. CORRUGATISPORITES Thomson and Pflug 1953 ex Weyland and Greifeld 1953/RUGULATISPORITES Thomson and Pflug 1953: spores which could have been referred to *Lycopodiacidites* Couper 1953 emend. Potonié 1956 and to *Trilites* Erdtman 1947 ex Couper 1953 emend. Dettmann 1963 were included here.

22. FOVEOSPORITES Balme 1957/FOVEOTRILETES van der Hammen 1954 ex Potonié 1956/SESTROSPORITES Dettmann 1963.

23. KLUKISPORITES Couper 1958: the diagnoses of *Klukisporites*, *Reticulisporites*, *Lycopodiumsporites*, and *Retitriletes* overlap. I included non-valvate spores with distally foveo-reticulate sculpture and smooth or lightly sculptured proximal surfaces in *Klukisporites*. *Ischyosporites* is valvate.

24. LYCOPODIUMSPORITES Thiergart 1938 ex Delcourt and Sprumont 1955/RETICULISPORITES Potonié and Kremp in Weyland and Krieger 1953: I recorded distally reticulate azonate miospores with membraneous laesurate lips as *Lycopodiumsporites*. *Reticulisporites* differs from *Lycopodiumsporites* in having lower muri.

25. *Reticulisporites semireticulatus* (Burger 1966) Norris 1969 (Jurassic): *Lycopodiumsporites semimuris* Danzé-Corsin and Laveine (in Briche *et al.* 1963; Lower Lias) is similar but the muri are higher (2–4  $\mu\text{m}$ ) and generally narrower.

26. RETITRILETES van der Hammen 1956 ex Pierce 1961: I used *Retitriletes* for spores with characters which prohibit their inclusion in other, more commonly used, genera for Mesozoic reticulate spores. Some show characters similar to those of spores which have been referred to, in the literature, as *Dictyotriletes* Naumova 1937 *sensu* Smith and Butterworth (1967).

27. STAPLINISPORITES Pocock 1962/CORONATISPORITES Dettmann 1963.

28. TAUROCUSPORITES Stover 1962 emend. Playford and Dettman 1965/POLY-CINGULATISPORITES Simoncsics and Kedves 1961 emend. Playford and Dettmann 1965.

29. TRIPARTINA Maljavkina 1949 ex Potonié 1960.

(Infraturma PERINOTRILITI Erdtman 1947)

30. PEROTRILITES Erdtman 1947 ex Couper 1953.

(Infraturma AURICULATI Schopf emend. Dettmann 1963)

31. ISCHYOSPORITES Balme 1957.

32. MATONISPORITES Couper 1958 emend. Dettmann 1963.

33. TRILOBOSPORITES Pant 1954 ex Potonié 1956: spores recorded as *Trilobosporites* had differentially thickened exines and/or larger sculptural elements about the radial regions at the equator.

(Infraturma TRICRASSATI Dettmann 1963)

34. GLEICHENIIDITES Ross 1949 ex Delcourt and Sprumont 1955 emend. Dettmann 1963: I included in this genus forms which could have been included in some of Krutzsch's (1959) subgenera or in *Clavifera* Bolkhovitina 1966. Sculptured forms comparable with *Ornamentifera* Bolkhovitina 1966 (= subgenus *Peregrinisporis* Krutzsch 1959) have not been recovered.

35. *Gleicheniidites apilobatus* Brenner 1963: miospores recorded as this species have differentially thickened distal exines and distal ridges crossing the apical lobes (Kemp 1970). The ridges have been interpreted (Kemp 1970) as upturned margins of the thickening. Reference to *Gleicheniidites* is therefore inaccurate but there is at present no other suitable genus available. *Concavisporites jurienensis* differs in having kyrtomes which extend from the proximal face on to the distal.

(Infraturma CINGULATI Potonié and Klaus emend. Dettmann 1963)

36. CINGUTRILETES Pierce 1961 emend. Dettmann 1963.

37. CONTIGNISPORITES Dettmann 1963.

38. DENSOISPORITES Weyland and Krieger 1953 emend. Dettmann 1963.

39. *Densoisporites velatus* Weyland and Krieger 1953 emend. Krasnova 1961.

(Infraturma PATINATI Butterworth and Williams 1958)

40. PATELLASPORITES Groot and Groot 1962 emend. Kemp 1970: *Patellasporites* was used for spores which are equatorially and distally thickened and strongly sculptured. The distal exine of the type species of this genus (*P. tavadensis* Groot and Groot 1962) is dissected by narrow canals into areas of exine of varying shape and size. I included here forms which superficially resemble *Bullasporis aequatorialis* Krutzsch 1959 (Tertiary).

(Turma HILATES Dettmann 1963)

41. AEQUITRIRADITES Delcourt and Sprumont 1955 emend. Cookson and Dettmann 1961.

42. COOKSONITES Pocock 1962 emend. Dettmann 1963.

43. COPTOSPORA Dettmann 1963.

44. COUPERISPORITES Pocock 1962 (*C. complexus* (Couper 1958) Pocock 1962).

45. ROUSEISPORITES Pocock 1962.

46. Sculptured triletes indet.

47. Total triletes.

(Turma MONOLETES Ibrahim 1933)

48. MONOLITES Cookson 1947 ex Potonié 1956.

49. MARATTISPORITES Couper 1958.

50. PEROMONOLITES Erdtman 1947 ex Couper 1953.

(Turma ALETES Ibrahim 1933)

51. ARAUCARIACITES Cookson 1947 ex Couper 1953.

52. INAPERTISPORITES van der Hammen 1955 ex Rouse 1959: I used *Inapertisporites*

to incorporate small (7–16  $\mu\text{m}$  diameter), smooth or scabrate, alete, circular to sub-circular grains which have an exine 0.5–1.0  $\mu\text{m}$  thick. Most are probably comparable with forms described by Norris as *Inaperturopollenites* sp. (Norris 1969, pp. 597–598; Upper Jurassic).

53. INAPERTUROPOLLENITES Pflug 1952 ex Thomson and Pflug 1953 emend. Potonié 1966: Inaperturates occur in nearly all productive preparations. They are a difficult group to deal with owing to a paucity of characters and a tendency to fold. *Inaperturopollenites* was used here to incorporate all more or less smooth relatively thin walled (exine c. 1  $\mu\text{m}$  thick) forms distinct from those referable to *Araucariacites*, *Pilasporites*, *Inapertisporites*, and representatives of the acritarch group.

54. PILASPORITES Balme and Hennelly 1956 (*P. allenii* Batten 1968).

55. RETICULATASPORITES Ibrahim 1933 emend. Potonié and Kremp 1954.

(Turma SACCITES Erdtman 1947)

56. CEREBROPOLLENITES Nilsson 1958 (*C. mesozoicus* (Couper 1958) Nilsson 1958; Jurassic).

57. TSUGAEPOLLENITES Potonié and Venitz 1934 emend. Potonié 1958: considerable confusion exists in the literature with regard to the usage of *Zonalapollenites* Pflug in Thomson and Pflug 1953, *Calliasporites* Dev 1961, *Applanopsis* Döring 1961, *Triangulopsis* Döring 1961, *Cerebropollenites*, and *Tsugaepollenites* for morphologically similar saccate pollen grains (see Potonié 1966, Pocock 1968). The genus *Tsugaepollenites* is used here but not strictly in the sense of Potonié (1958) because *Cerebropollenites mesozoicus* has been recorded separately.

58. Bisaccates (excluding VITREISPORITES): most of the published Late Mesozoic bisaccate species and genera are insufficiently well described (see Kemp 1970) to have much value for stratigraphic purposes in the Wealden. Variations in preservation and orientation continually cause difficulties with identification. The most common forms are *Alisporites* types, e.g. forms similar to *Alisporites thomasii* (Couper 1958) Pocock 1962 (Jurassic) and *A. microsaccus* (Couper 1958) Pocock 1962 (Jurassic) but specimens referable to *Parvisaccites* Couper 1958 (e.g. *P. radiatus* Couper 1958), *Podocarpidites* Cookson 1947 ex Couper 1953, and *Vitreisporites* also occur.

59. VITREISPORITES Leschik 1955 emend. Jansonius 1962.

(Turma Plicates Naumova emend. Potonié 1960)

60. EUCOMMIDITES Erdtman 1948 emend. Hughes 1961.

61. CYCADOPITES Wodehouse 1933 ex Wilson and Webster 1946: I recorded all monosulcate grains, including those which could, perhaps, have been included in *Monosulcites* Cookson 1947 ex Couper 1953, as *Cycadopites*. All were elongate to subcircular and had smooth to microgranulate exines.

(Turma POROSSES Naumova emend. Potonié 1960)

62. CLASSOPOLLIS Pflug 1953 emend. Reyre 1970.

63. EXESIPOLLENITES Balme 1957: the characters of *Exesipollenites* and *Spheripollenites* Couper 1958 overlap. *Exesipollenites* possesses a circular depression sur-

rounded by an area of exinal thickening; the depression may represent a pore although actual perforation of the exine has not been recorded. According to the original definition, the exine can be smooth or with occasional granules (Balme 1957). *Spheripollenites*, as originally defined, lacks an exinal thickening and, as a result, is more often found in a folded state.

Most of the Wealden forms probably fall within the character range of *E. tumulus* Balme 1957 (Jurassic). Few definitely lack an area of exinal thickening.

Muller (1968) expressed some doubt as to whether *Exesipollenites* can be considered a pollen grain because of the absence of any structural differentiation in the wall and because the circular depression in the wall cannot be considered an aperture. He suggested that its occurrence in floods in Cretaceous marine facies of Sarawak, Malaysia, may be because its origin is planktonic. There is no evidence so far, however, to suggest that Wealden forms referable to the genus have such an origin.

64. PERINOPOLLENITES Couper 1958: grains with a firmly attached but loosely enveloping perine were included in *Perinopollenites*. Reference to *Ballosporites* Mädlar 1964 may, however, have been more appropriate for split specimens lacking a pore. Oval, split forms resemble *P. pseudosulcatus* Danzé-Corsin and Laveine 1963 (in Briche *et al.* 1963; Lower Lias).

(MIOSPORES INCERTAE SEDIS)

65. SCHIZOSPORIS Cookson and Dettmann 1959.

66. *Schizosporis parvus* Cookson and Dettmann 1959.

67. *Schizosporis reticulatus* Cookson and Dettmann 1959.

#### RECORD: INCERTAE SEDIS

*Celyphus rallus* gen. and sp. nov.

Plate 2, figs. 1-15

*Type sample.* CUC 869, Cuckfield No. 1 Borehole, Sidnye Farm, Sussex (TQ 2961 2731), depth 869 feet (264.9 m); Wadhurst Clay, Valanginian? Medium to medium dark grey (N5-N4) fine siltstone, slightly calcareous. Preparation T400; 20 mins HNO<sub>3</sub>, cleared in dilute NH<sub>4</sub>OH, mineral separation, strew slides with Clearcol. AT9:S2,4.

*Generic diagnosis.* As for specific diagnosis.

*Specific diagnosis.* Palynomorph body elongate, tapered, with rounded or flattened ends. Mean maximum length of body 55.5  $\mu$ m, standard deviation 9  $\mu$ m (100 specimens). Mean maximum width of body 19.5  $\mu$ m. Body wall 0.5-1.0  $\mu$ m thick except near the B end (Pl. 2, fig. 1) where it becomes very thin (*c.* 0.25  $\mu$ m) and is often folded (folds small, narrow, irregular). The B end is open, has a variable outline and frequently appears to have been torn. At the A end (Pl. 2, fig. 1) there is a circular or sub-circular opening (pore) 3-10  $\mu$ m in diameter, with a smooth (? unthickened) or serrated margin. Unevenly spaced (usually 4-11  $\mu$ m apart) concentric bands of thin wall may be faintly, sometimes clearly, distinguishable. They are generally 2-4 in number and 0.5-3  $\mu$ m wide (Pl. 2, fig. 2).

*Holotype.* Slide preparation T400/6, L1 35.8 127.2; Pl. 2, fig. 5.

*Description.* The observed limits of the maximum length of the body are 39–74  $\mu\text{m}$  (coefficient of variation 16.2%), and of the maximum width are 16–23  $\mu\text{m}$ . The serrated margins of the pores of some specimens appear to have been the result of expansion and splitting of the pore margin; sometimes the splits continue for up to 25  $\mu\text{m}$  along the length of the body.

*Preservation and compression.* This palynomorph has been susceptible to corrosion; specimens are commonly pale (thinned) and poorly preserved, and damage by pyrite is common (Pl. 2, fig. 6). Poorly preserved specimens were included in the 100 examined.

*Remarks.* Specimens are commonly preserved aligned sub-parallel to each other in circular or oval shaped masses (Pl. 2, figs. 9, 11, 12). The A ends face the centre of a mass unless specimens have been dislodged. Individuals separate easily from the masses; perhaps before fossilization they were held together by mucilage. The affinity of the palynomorph is uncertain (? egg cases, ? algae).

Preparations of the same type as used for the recovery of large plant microfossils enabled the recovery of masses larger than those generally seen in preparations for miospores. The holotype specimen is present with topotype specimens in a strew slide of a single preparation. The figured specimens are housed in the palynology collection of the Sedgwick Museum, Cambridge. Representative specimens are also deposited in the Institute of Geological Sciences, Leeds.

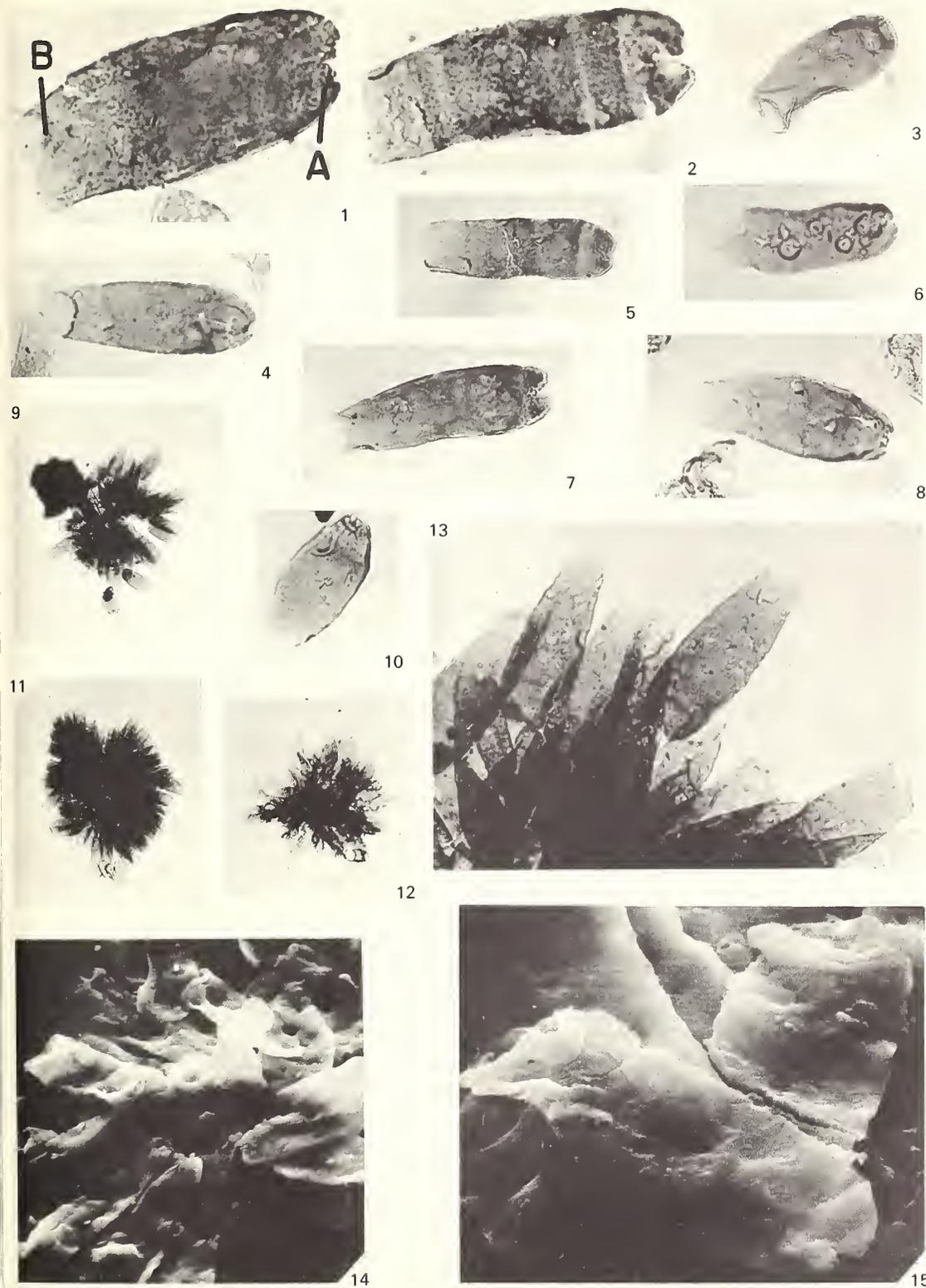
*Acknowledgments.* The work for this paper was carried out whilst I was in receipt of a N.E.R.C. grant. It is partially based on material from the Cuckfield No. 1, Warlingham, and Whites Bridge boreholes made available to Mr. N. F. Hughes by the Institute of Geological Sciences. I am grateful to the Institute for access to the log of the Cuckfield No. 1 Borehole. I thank Mr. N. F. Hughes and Miss J. E. Hutt for discussion.

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#### EXPLANATION OF PLATE 2

Stage coordinates refer to Leitz Laborlux (L1) microscope, number 557187, Department of Geology, Sedgwick Museum, Cambridge.

Figs. 1–15. *Celyphus rallus* gen. and sp. nov. 1, Indicating A and B ends, T400/6, L1 52.0 119.6,  $\times 1000$ . 2, Concentric bands of thin wall distinguishable, T400/6, L1 53.1 116.0,  $\times 1000$ . 3, Pore at A end, B end open, T400/6, L1 53.8 108.9,  $\times 500$ . 4, Tapered specimen, pore clearly visible, T400/6, L1 22.1 126.9,  $\times 500$ . 5, Holotype, T400/6 L1 35.8 127.2,  $\times 500$ . 6, Specimen with pyrite relict structures in wall, T400/6, L1 40.1 128.1,  $\times 500$ . 7, T400/6, L1 40.2 120.9,  $\times 500$ . 8, Small pyrite relict structures in wall, T400/6, L1 37.1 127.4,  $\times 500$ . 9, Mass, several specimens dislodged, T400/4, L1 34.4 115.9,  $\times 100$ . 10, Small specimen, T400/6, L1 26.9 125.9,  $\times 500$ . 11, Cohesive mass, T400/4, L1 31.6 120.1,  $\times 100$ . 12, Poorly preserved mass, T400/4, L1 32.8 114.8,  $\times 100$ . 13, Part of mass, T400/4, L1 34.3 115.9,  $\times 500$ . 14, S.E.M. of part of mass, prep. T400, stub (SH)DB 55,  $\times 400$ . 15, S.E.M. of specimen in mass, prep. T400, stub (SH)DB 55,  $\times 1500$ . (Scanning electron micrographs courtesy Dept. of Environmental Sciences, U.E.A. Norwich: specimens were mounted on double sided 'Sellotape' and coated with carbon.)



BATTEN, early Cretaceous palynomorph

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D. J. BATTEN

Department of Geology  
Sedgwick Museum, Cambridge

Present address:

c/o Robertson Research International Ltd.  
Ty'n-y-coed  
Llanrhos, Llandudno  
North Wales

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## APPENDIX

### *Localities of samples listed on Table 5*

*Fairlight Clay (FC)*. 1, FC 'd' (see White 1928), Goldbury Point, near Hastings, Sussex (TQ 8789 1163). 2, FC 'd', in proximity of Fairlight Glen, near Hastings (TQ 8552 1067). 3, as above (TQ 8523 1063). 4–6, as above (TQ 8548 1072). 7, as above (TQ 8548 1073). 8–10, as above (TQ 8533 1070). 11, FC 'b', west of Haddocks Rough, near Hastings (TQ 8818 1222). 12–14, Warlingham Borehole, Surrey (TQ 3476 5719); sample numbers indicate depth.

*Ashdown Sand (AS)*. 15, 16, Ecclesbourne Glen, near Hastings (TQ 8372 0996). 17–24, Cuckfield No. 1 Borehole, Sussex, second redrilling (TQ 2961 2731), sample numbers indicate depth, most (rounded) to the nearest foot. 25, east of Haddocks Rough, near Hastings (TQ 8812 1206). 26, west of Ecclesbourne Glen, near Hastings (TQ 8352 0981). 27, near Pett Level, Sussex (TQ 8872 1288).

*Wadhurst Clay (WC)*. 28–34, Cuckfield No. 1 Borehole (TQ 2961 2731). 35–45, Cuckfield No. 1 Borehole, first redrilling (TQ 2962 2729). 46–48, Cuckfield No. 1 Borehole, original site (TQ 2962 2729). 49–57,

Railway Brickyard, Sharpthorne, Sussex (TQ 3740 3294). 58-60, Freshfield Lane Brickworks, Danehill, Sussex (TQ 3813 2659). 61-72, High Brooms Brick and Tile Company's pit, Southborough, Kent (TQ 5948 4189). 73, Brambletye Bend (A.22), Sussex (TQ 419 363).

*Tunbridge Wells Sand (TWS)*. 74-82, Cuckfield No. 1 Borehole (TQ 2962 2729). 83, Philpots Quarry, West Hoathly, Sussex (TQ 3548 3221).

*Grinstead Clay (GC)*. 84, Cuckfield No. 1 Borehole (TQ 2962 2729). 85-96, Philpots Quarry, West Hoathly (TQ 3548 3221).

*Weald Clay (WEC)*. 97, Warnham brick pit, Sussex (TQ 173 345). 98, Newdigate Brickworks clay pit, Surrey (TQ 204 425). 99, 100, Warlingham Borehole (TQ 3476 5719).

# UPPER CRETACEOUS STAMINATE HEADS WITH POLLEN GRAINS

by V. A. KRASSILOV

ABSTRACT. *Tricolpopollianthus burejensis* gen. et sp. nov., the staminate heads with tricolpate grains *in situ*, are described from the Upper Cretaceous of the Amur Basin, Far East of the U.S.S.R.

DIFFERENT types of angiosperm pollen grains of obscure affinities have been described from Upper Cretaceous and Palaeogene deposits. The discovery of pollen grains within the pollen-bearing structures is of interest in linking the angiosperm mega- and microfossils. Unfortunately, angiosperm fossil flowers are extremely rare. Few fossil flowers with pollen grains have been reported from the Tertiary of Europe and the staminate heads described in this paper are the only ones known so far from the Cretaceous. They have been collected (Krassilov 1971) from the Tsagajan Formation near the mouth of the Bureja River, a tributary of the Amur. The Tsagajan Formation is composed of conglomerates, gravels, and sands containing fossiliferous clay and siltstone lenses. These rocks are of alluvial origin. Dinosaur remains have been collected from the beds somewhat older than the plant-bearing strata. Plant megafossils from Tsagajan Beds have been described by Heer, Kryshtofovich, Baikovskaya, and others. Kryshtofovich (in Kryshtofovich and Baikovskaya 1966) assigned the Tsagajan fossil flora to the Danian stage whereas Bratzeva (1969) advocated a Maastrichtian age on the plant microfossil evidence. The Tsagajan flora comprised about 60 species of conifers and angiosperms. This fossil assemblage was dominated by *Sequoia* and *Trochodendroides* and represented a lowland-valley forest of temperate aspect.

*Methods.* Balsam transfer preparations of heads have been prepared and the stamen fragments have been macerated with  $\text{HNO}_3$  and  $\text{KOH}$ .

## SYSTEMATIC DESCRIPTION

Genus TRICOLPOPOLLIANTHUS gen. nov.

*Diagnosis.* As for species diagnosis below.

*Tricolpopollianthus burejensis* sp. nov.

Plate 3, figs. 1-13

*Diagnosis.* Staminate heads, globular, 7-8 mm in diameter borne singly or in spikes. Stamens with inconspicuous filaments and long anthers. Connective distally expanded. Pollen small, tricolpate.

*Holotype.* Specimen 571-331 and slide 571-331a, Far East Geological Institute Collections; Pl. 3, figs. 4, 7.

*Occurrence.* Right bank of the Bureja River near the bottom of Belaja Mountain, Tsagajan Formation.

*Age.* Maastrichtian–Danian.

*Description.* There are five heads of uniform size (7–8 mm in diameter). Only short pieces of peduncle (or spike axis) preserved. Peduncle about 1 mm thick. Receptacle relatively massive. Individual flowers not distinguishable. Stamens in surface view are seen in split heads (Pl. 3, figs. 2–3). They are about 3 mm long, 0.8 mm wide, distally expanded in a shield with leaf-like process. The latter triangular, often curved or reflexed. Two ridges below the distal expansion of connective represent pollen sacs. On imprints of head surface, distal expansions of stamens are seen as polygonal shields 1 mm wide (Pl. 3, figs. 1, 4–6). Cuticle of connective delicate. Cells elongated, with straight walls. Stomata were not observed.

Masses of pollen grains adhere to stamen and connective cuticles. It was difficult to separate the individual pollen grains and they have been photographed lying on the cuticle. Pollen tricolpate, spherical, trilobate in polar view, elliptical in equatorial view. Diameter 18  $\mu\text{m}$ , equals the polar axis. Exine *c.* 1  $\mu\text{m}$  thick, ectexine clavate-microreticulate. Colpi long, almost reaching the poles.

*Remarks.* *Tricolpopollianthus* stamens may be compared with those of *Nymphaea*, some members of the Magnoliaceae, and to some extent, with *Platanus* and *Nelumbo*, which have distally expanded connectives. However, if this interpretation of *Tricolpopollianthus* morphology is correct, it differs from the staminate structures of these modern genera.

Pollen grains resemble *Tricolpopollenites micromunus* Groot et Penny which have been reported from several Upper Cretaceous and Lower Tertiary localities in Asia and North America (see Drugg 1967). Brenner (1963, p. 93) compared *T. micromunus* with pollen grains of living *Trochodendron*. Similar pollen grains were obtained from the staminate heads assigned to the Tertiary *Platanus neptuni*; Bužek *et al.* (1967) compared these pollen grains with *Tricolpopollenites microhenrici*.

According to Chang (1964) the pollen grains of *Platanus* are tricolpate, spherical, 18.5–22.5  $\mu\text{m}$  in diameter, with ectexine microreticulate. However, they differ from the pollen grains of *Tricolpopollianthus burejensis* in comparatively short and broad colpi. The pollen grains of *Trochodendron aralioides* Sieb. et Zucc. differ from those of the present species in more elongate form (polar axis up to 26  $\mu\text{m}$ , diameter 20  $\mu\text{m}$ ) and in having larger meshes of the exine reticulum. *Corylopsis pauciflora* Sieb. et Zucc. has comparable but somewhat larger pollen grains.

*Tricolpopollianthus* supplements the record of Cretaceous angiosperm reproductive structures which are mostly unisexual, devoid of conspicuous perianth, and clustered in spikes, racemes, or heads. It illustrates the primitive type of stamen retained with some modifications in several living genera.

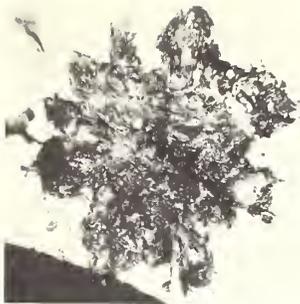
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#### EXPLANATION OF PLATE 3

Figs. 1–13. *Tricolpopollianthus burejensis* sp. nov.; staminate heads with pollen grains from the Upper Cretaceous of the Bureja River. 1, 5–6, Heads showing distal expansions of stamens,  $\times 7$ . 4, Part of fig. 1,  $\times 12$ . 2–3, Split heads showing stamens,  $\times 7$ . 7, Pollen grains on the connective cuticle,  $\times 395$ . 8–13, Pollen grains,  $\times 1000$ .



1



2



3



4



6



5



8



9



7



10



11



12



13

KRASSILOV, Cretaceous flower with pollen

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Typescript received 15 February 1972

V. A. KRASSILOV  
Institute of Biology and Pedology  
Vladivostok 22, U.S.S.R.

# 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 <sup>1</sup> 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	Page 46
STRATIGRAPHY	47
SUMMARY OF NOMENCLATRURAL CHANGES	49
TERMINOLOGY	52
Measured characters; significance of measured characters; other terms; populations, subspecies, type specimens	
SYSTEMATIC DESCRIPTIONS	55
<i>Isograptus</i> Moberg	55
<i>primulus</i> group	57
<i>victoriae</i> group ( <i>lunatus</i> , <i>victoriae</i> , <i>maximus</i> , <i>maximodivergens</i> , <i>divergens</i> )	59
<i>caduceus</i> group ( <i>caduceus</i> , <i>imitatus</i> , <i>australis</i> , <i>forcipiformis</i> )	71
<i>manubriatus</i> group ( <i>dumosus</i> , <i>hastatus</i> , <i>manubriatus</i> )	78
NOTES ON OTHER FORMS	88
GROWTH, VARIATION, PHYLETIC TRENDS	92
Growth, allometry	92
Intraspecific variation	94
Interspecific discrimination	96
Phyletic trends	103
PHYLOGENY OF <i>ISOGRAPTUS</i>	104
STRATIGRAPHIC SIGNIFICANCE	105
Local stratigraphic significance	105
Significance for world correlation	105
ACKNOWLEDGMENTS	109
REFERENCES	109
APPENDIX (with tables)	111

## 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

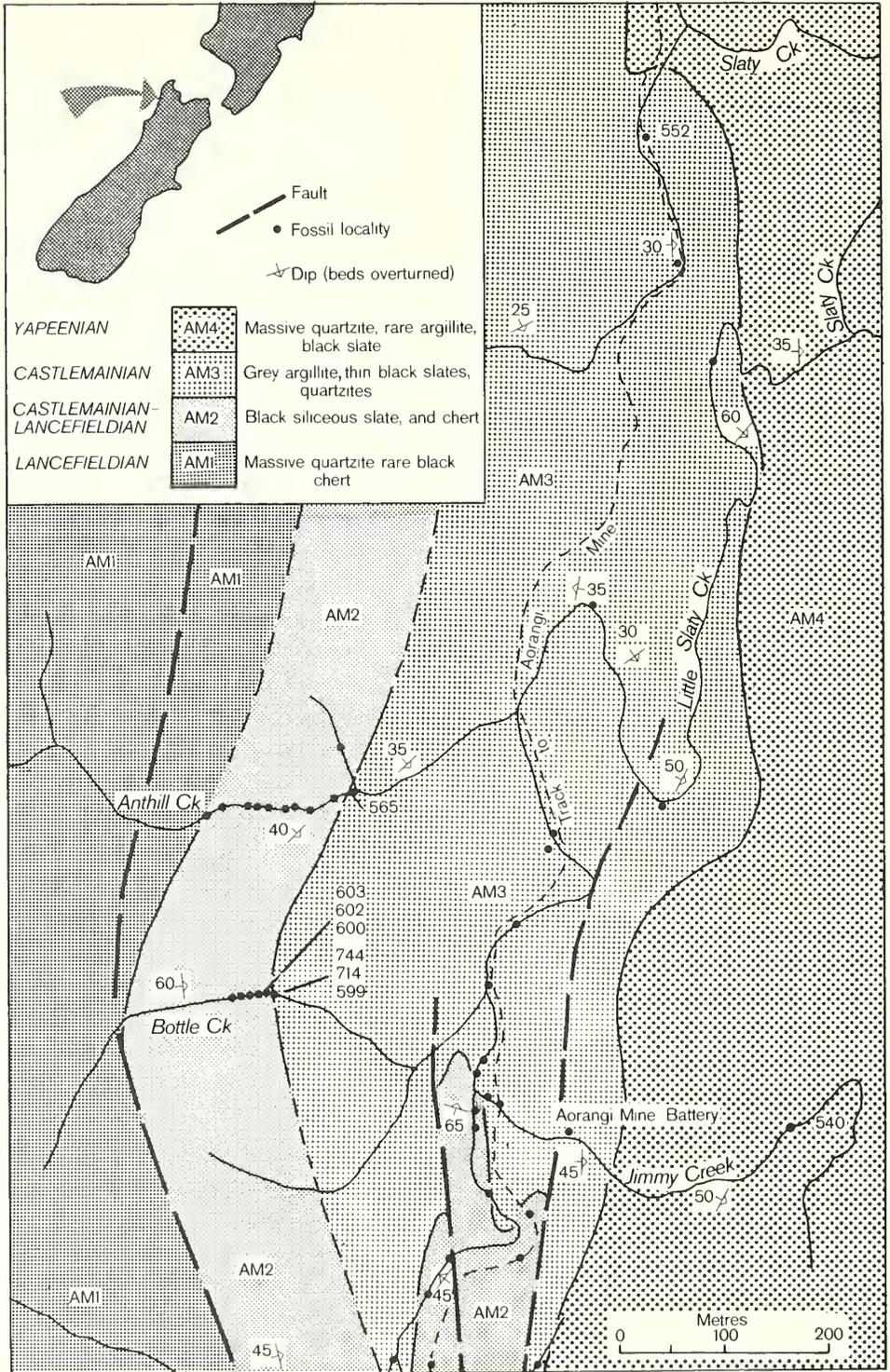
Prefixes for type specimens similarly signify the institution in which they are housed as follows:

- 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 graptolites.

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 heterogeneous, 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).

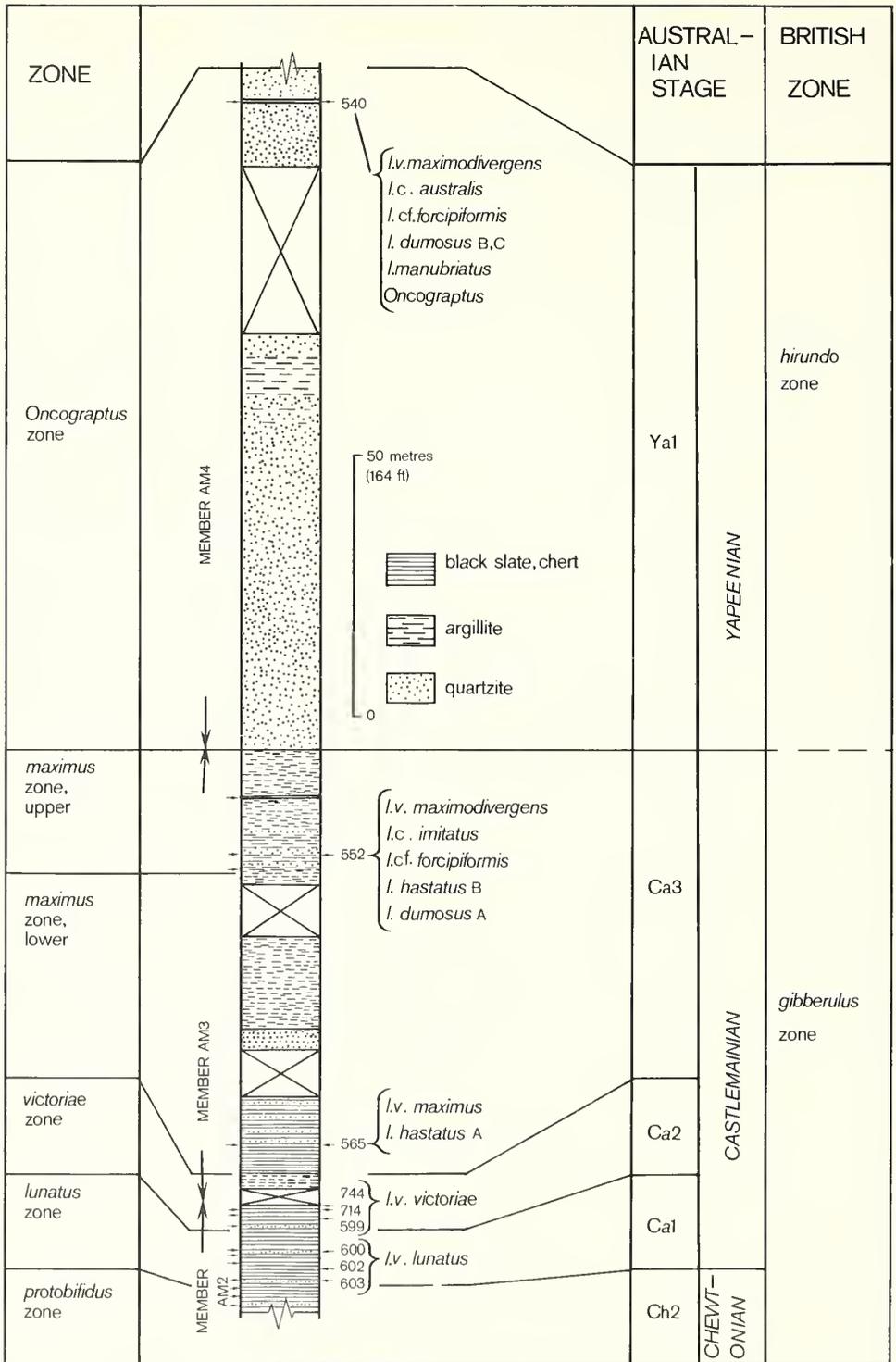
The 3 Castlemainian zones, Ca1-3 are based on the 3 index subspecies of *Isograptus victoriae*: *lunatus*, *victoriae*, and *maximus* respectively (Harris and Thomas 1938). The implications of the present work for zoning and correlation of the Castlemainian are discussed in the final section of this 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 exceptionally well-documented bioseries and is here given separate specific status. *Isograptus*



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		Darrivilian			
	substage	Ch2	Ca1	Ca2	Ca3	Ya1	Ya2	Da1	Da2	Da3	Da4
<u>Isograptus primulus</u>	—										
<u>I. victoriae lunatus</u>	•	—									
<u>I. v. victoriae</u>	•	•	—								
<u>I. v. maximus</u>	•	•	•	—							
<u>I. v. maximodivergens</u>	•	•	•	—		—					
<u>I. v. divergens</u>	•	•	•	•	•	—		—			
<u>I. caduceus imitatus</u>	•	•	•	—		—					
<u>I. c. aff. imitatus</u>	•	•	•	—		—					
<u>I. c. australis</u>	•	•	•	•	—		—				
<u>I. c. tenuis</u>	•	•	•	—		—		—			
<u>I. c. spinifer</u>	•	•	•	•	•	•	•	•	•	•	
<u>I. ovatus</u>	•	•	•	•	•	•	•	•	•	•	
<u>I. forcipiformis</u>	•	•	•	•	•	•	•	•	•	•	
<u>I. cf. forcipiformis</u>	•	•	•	—		—					
<u>I. hastatus form A</u>	•	•	•	—		—					
<u>I. hastatus form B</u>	•	•	•	—		—					
<u>I. dumosus form A</u>	•	•	•	—		—					
<u>I. dumosus form B</u>	•	•	•	—		—					
<u>I. dumosus form C</u>	•	•	•	—		—					
<u>I. manubriatus</u>	•	•	•	—		—					
<u>Meandrograptus tau</u>	•	•	•	—		—					
<u>M. aggestus</u>	•	•	•	—		—					
<u>Didymograptus cf. eocaduceus</u>	•	—									
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* Mosen 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.

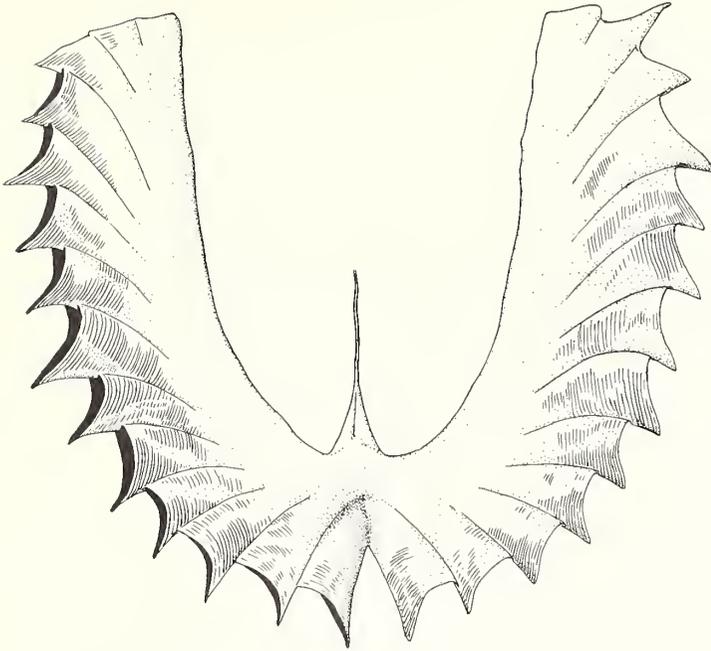
Because of their initial bilaterally flat shape (text-fig. 4) it can be safely assumed that isograptid rhabdosomes were similarly orientated prior to burial, with one lateral surface in contact with the sea floor, that is, parallel to the present plane of bedding.

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.

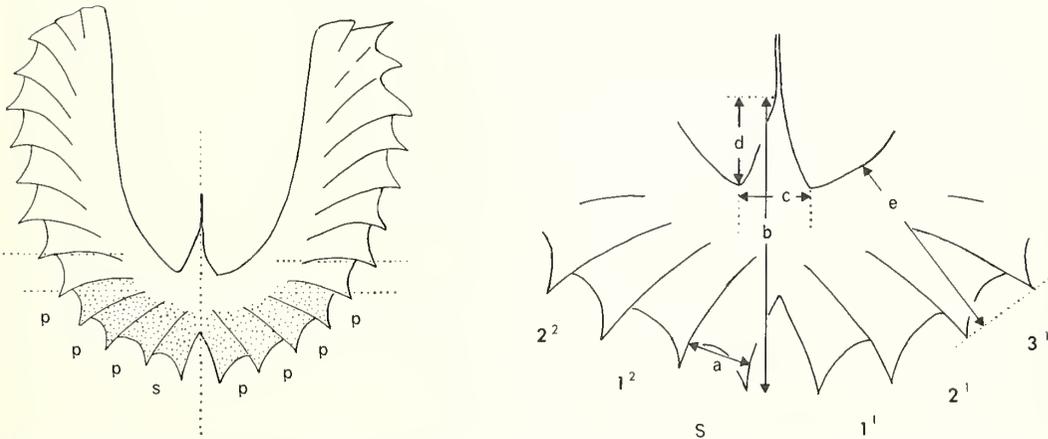
*Stipe width* refers to dorso-ventral stipe width as seen in profile view. *Proximal stipe width* (text-fig. 5e) is measured immediately past the sharp initial stipe flexure in the proximal region, *distal stipe width* in the distal part of mature rhabdosomes. Where maximum stipe width occurs in neither 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 (th<sup>1</sup>), 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,  $\times 10$ . 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*, supra-dorsal width and, *d*, supra-dorsal length of sicula and theca 1<sup>1</sup>; *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<sup>1</sup>, 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 allomorphy, 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.

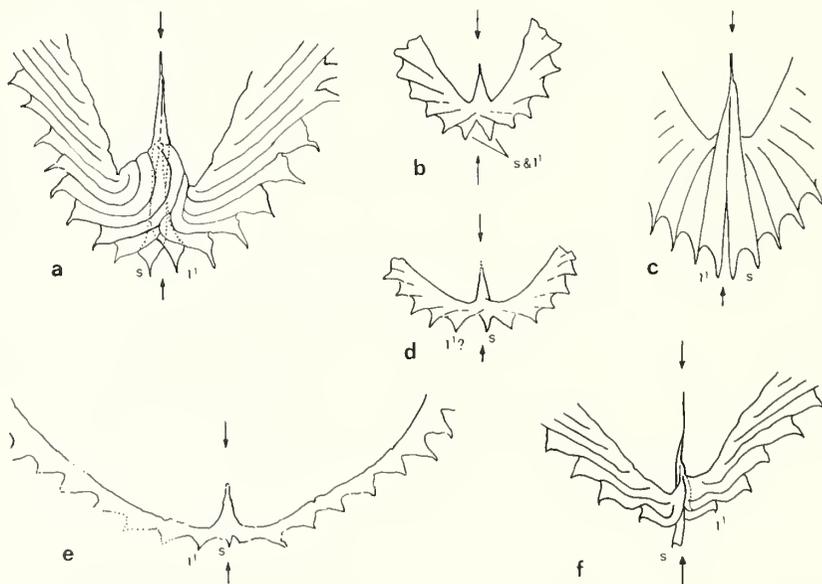
*Remarks.* Moberg's (1892, p. 346) original definition of *Isograptus* was vague; he misinterpreted the proximal end (Holm 1895, p. 19; Bulman 1932, p. 22) and his generic description is no longer usable. Bulman stressed the importance of the isograptid type of proximal end development as a generic character 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 ( $th1^1$ ) 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 reclined *Didymograptus* (d, e) and *Meandrograptus* (f). Sicula (s) and theca  $1^1$  ( $1^1$ ) 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 schmalensei* Moberg, Sweden. From Bulman (1932, p. 27, text-fig. 2a).

All figs.  $\times 5$  approximately.

The above diagnosis is therefore proposed and serves to distinguish the genus from reclined species of *Didymograptus*, such as *D. hemicyclus* Harris 1933 (re-figured 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).

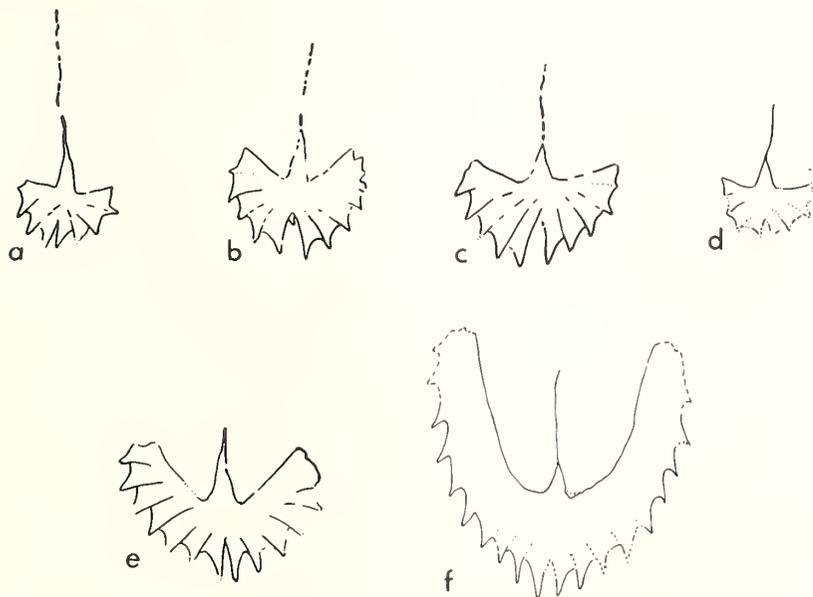
### *Isograptus primulus* Harris 1933

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  $\times 5$ , except for d, which is  $\times 4.4$ .

*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						
	length	width at aperture	Supra-dorsal width	Supra-dorsal height	Proximal stipe width	Number of pendent thecae	Number of thecae per stipe
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. 7d). 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. 7f). 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. 1*D*.  
 1953 *Isograptus norvegicus* Monsen; Spjeldnaes (*pars*), pp. 174-176, pl. 1, fig. 4; text-fig. 1*c* (not pl. 1, fig. 6; text-fig. 1*f*).

*Lectotype.* Of Harris's 3 figured specimens here referred to *lmatus*, 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. 8n). 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, Cal.

*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<sup>2</sup> and 2<sup>1</sup> cannot be seen, but the general aspect of the proximal end (text-figs. 8c, 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.

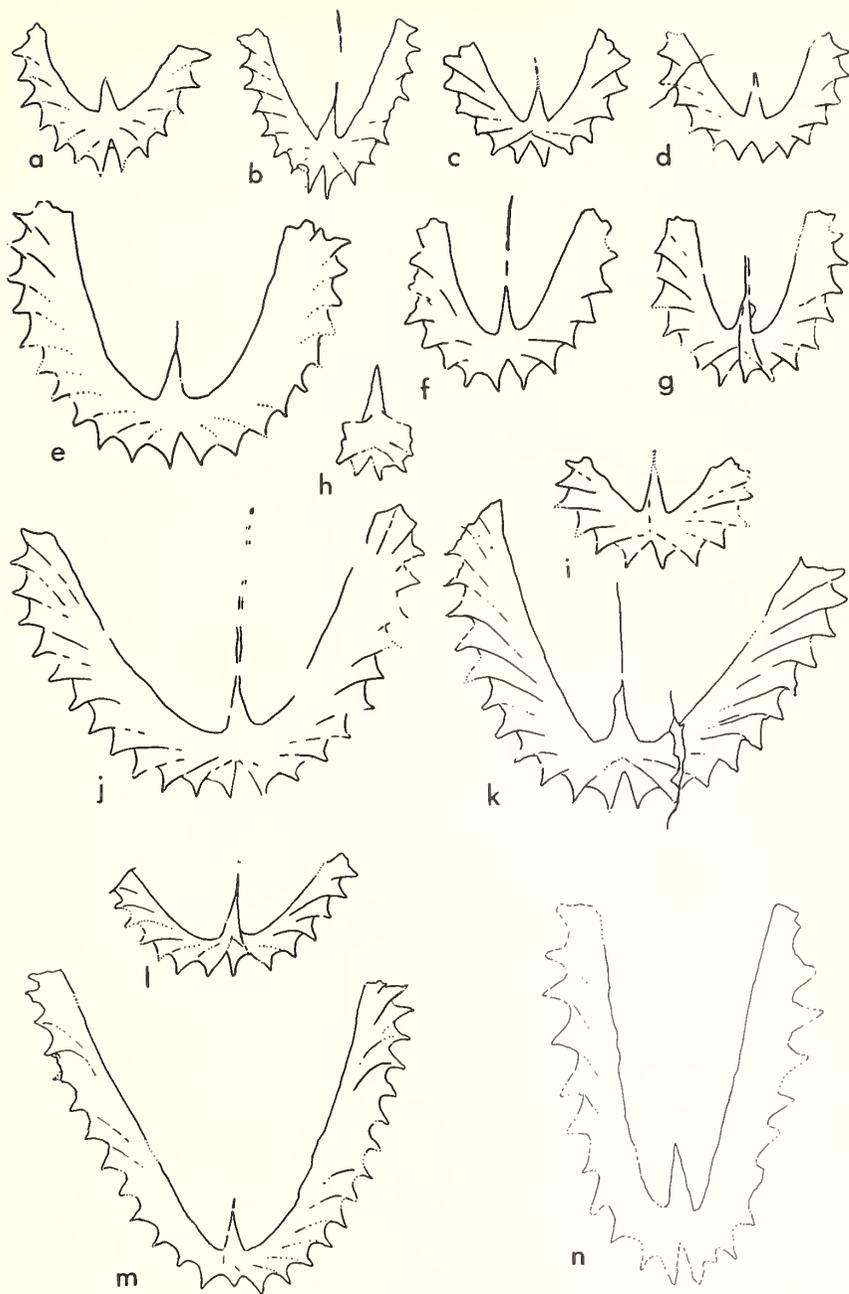
Thecal spacing, measured in a few large forms only, is 6 in 5 mm. Thecal ventral walls are slightly or moderately concave, those of distal thecae are inclined at from 25° at their origins to 75° near their apertures. Thecal apertural margins are concave, 'denticulate', and moderately inclined to the 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. 8b) 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 *lmatus* however (text-figs. 8d-g) is that which gave rise to the *lmatus-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. 8m). They suggest a possible origin for *lmatus* 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. Castlemainian, Ca1.

*n*—*Isograptus victoriae lunatus* Harris, lectotype GSV 29624 figured by Harris (1933, text-fig. 4). Specimen probably tectonically distorted, maximum relative shortening 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  $\times 5$ .

*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. 9a-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. 9f). Type locality is 'spoil heap from a small mining shaft on the east side of the [Victoria] gully', Chewton.

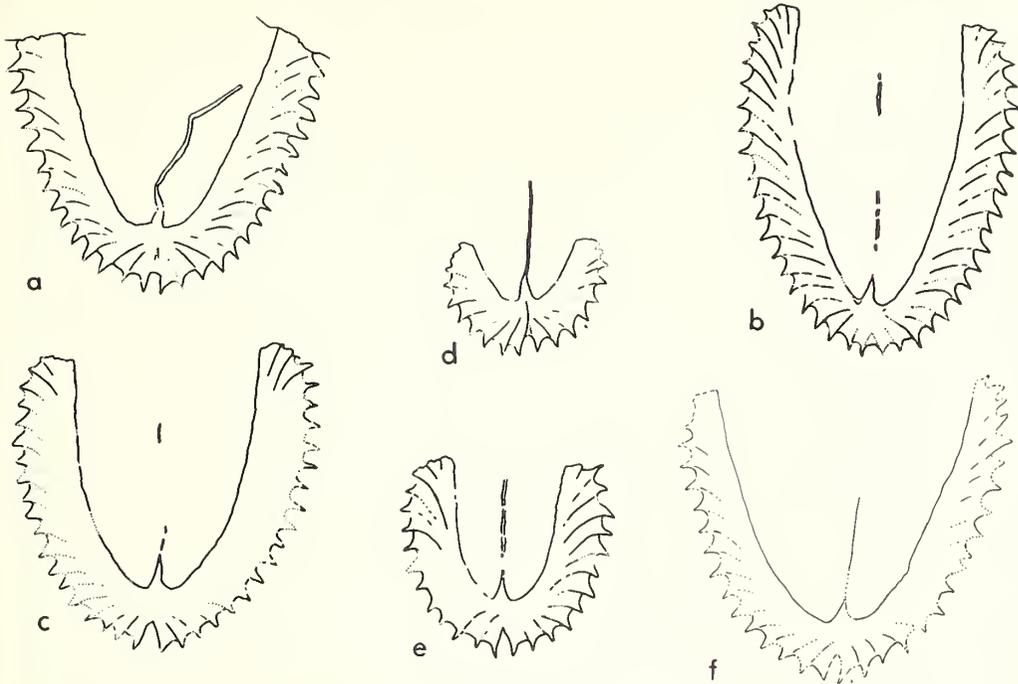
*Measured material, localities, age.* 23 specimens: VG 42-44, PR 255-265, S2/599; PR 176-178, S2/744; PR 266-271, S2/714; Bottle Creek, Aorangi Mine; Castlemainian, Ca2.

*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  $360^\circ$  to  $310^\circ$ .

Thecae are moderately to strongly curved, distal thecae being inclined from  $20^\circ$  at their origins to  $90^\circ$ - $100^\circ$  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  $\times 3$ .

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. 9f).

*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. 12d); 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. 10a-e

1933 *Isograptus caduceus* var. *maxima* Harris, p. 91, fig. 13.

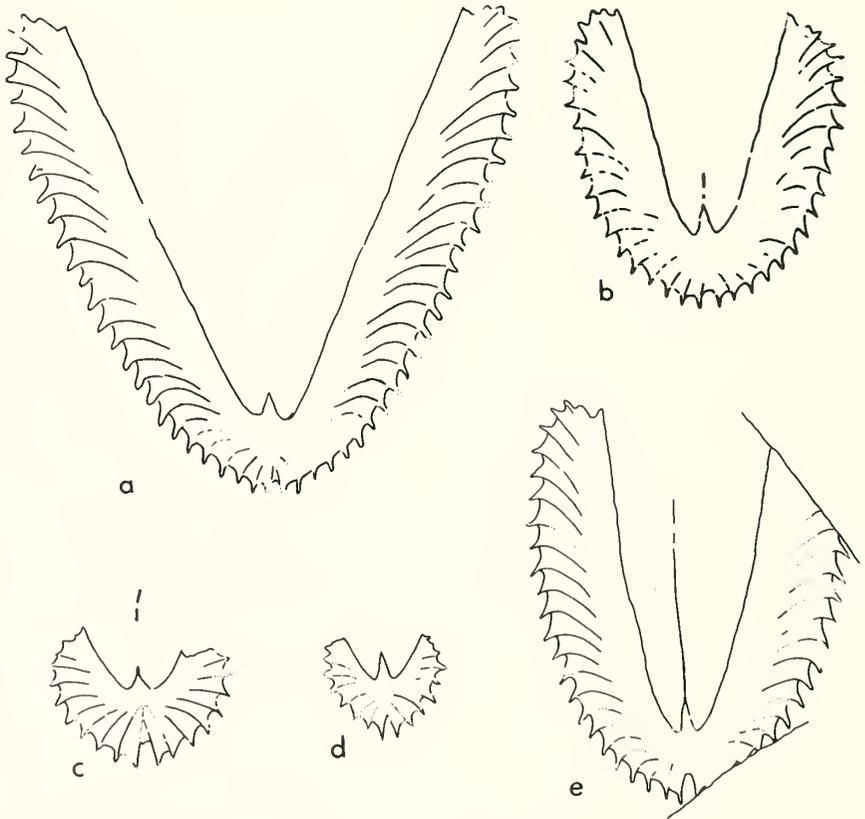
1960 *Isograptus caduceus* var. *maxima* Harris; Berry, pp. 66-67, pl. 11, fig. 8.

*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  $\times 3$ .

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. 11a–f, 12a–g, 13a

- ?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. 13a). Type locality is 'between Castlemaine Military Rifle Range and town', Castlemaine.

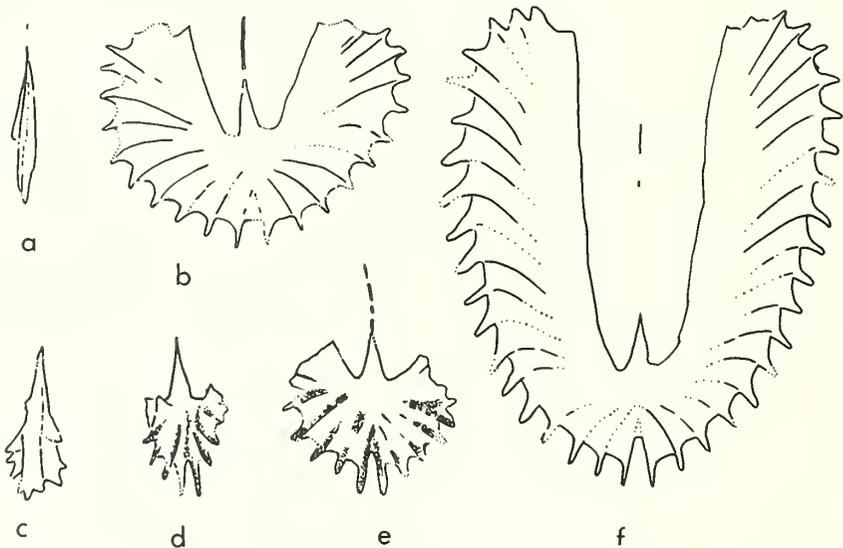
*Measured material, localities, age.* 57 specimens; 39 from S2/552: VG 47–49, 51–52, 54, 62, 65, 89, 137–139, 142, 144–145, 147, 149, 150, 153; PR 38, 272–278, 283, 285, 287–288, 293–294, 296, 301, 302, 304, 305, 309; Castlemainian, Ca3 (upper); 17 specimens from S2/540: VG 46, 64, 70; PR 320, 323, 327,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

*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, Yal (locality S2/540), the sicula and proximal portion of the nema are enmeshed in a peridermal

film, the 'axilar film' of Harris, which generally extends to the dorsal stipe margins (text-figs. 12*a*, *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. 11*a-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 specimens 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  $\times 5$ .

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  $315^\circ$  to  $360^\circ$ , averaging  $332^\circ$ .

Thecal spacing ranges from 10 to 12 in 10 mm, most forms having 10.5; thecae are strongly curved, being inclined from  $20^\circ$  at their origins up to  $90^\circ$ – $100^\circ$  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. *maximodivergens* (lectotype, Harris 1933, fig. 13; this paper, text-fig. 13a); however, a few Upper Castlemainian forms, in which stipe width is nearly constant (e.g. text-fig. 12c), more closely match his figure 12, *maximus*, while others from the Castlemainian and Yapeenian (text-fig. 12g) 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.

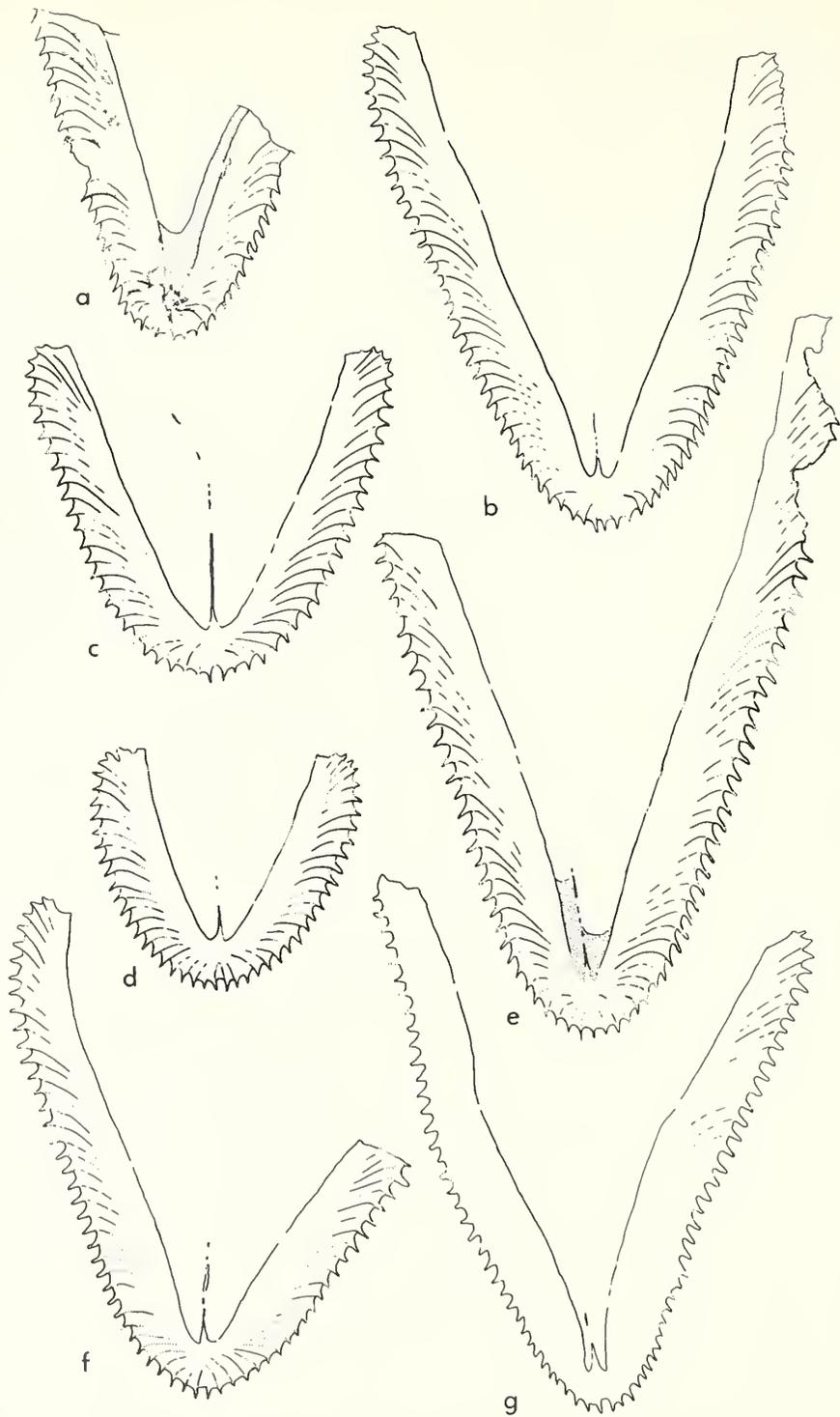
Average dimensions of sicular length, free sicular length, and sicular width do not differ significantly from those of *I. victoriae maximus*; however, the supra-dorsal length and width of the sicula and first theca are considerably less, whereas average proximal, and distal stipe width, and number of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

The divergence angle of stipes in the axilar region in a few specimens (text-figs. 12b, g) is  $360^\circ$ , 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, apparently 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).

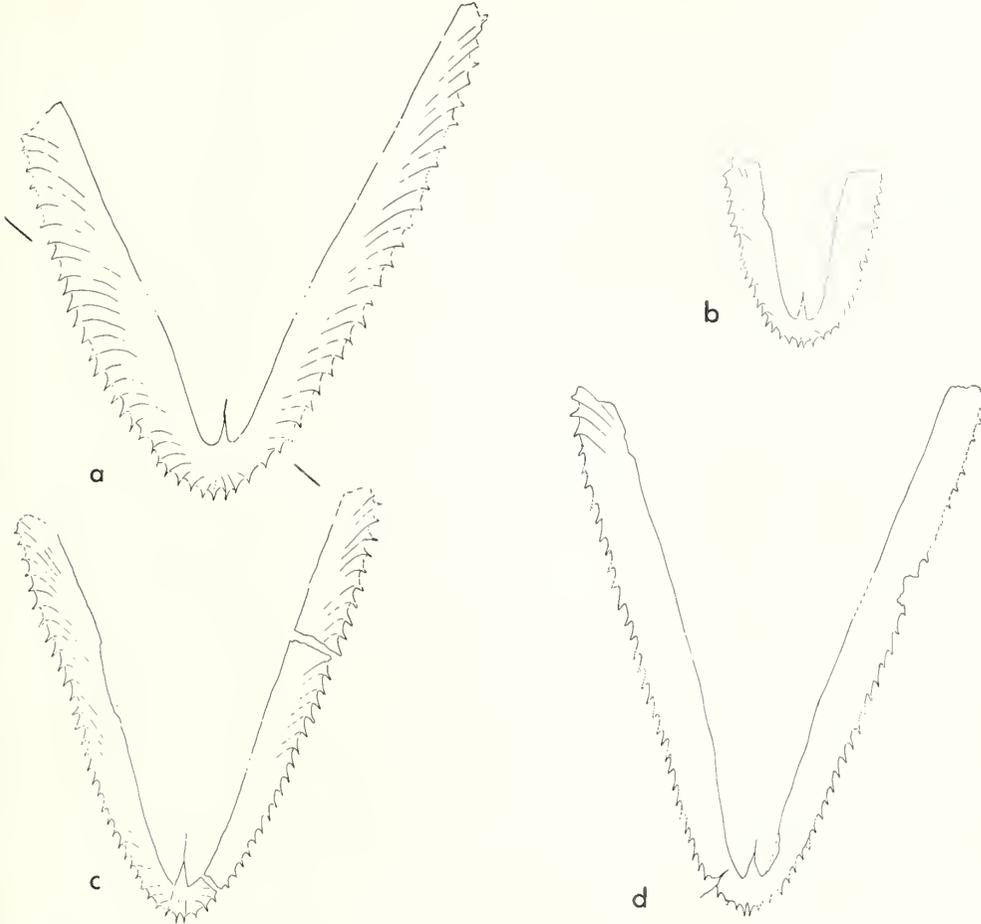
Bulman (1931, pp. 42–43, text-fig. 17) described and figured an incomplete specimen which probably corresponds to *maximodivergens*, from the 'lower Llanvirnian' beds of Korpa, Bolivia. The specimen was associated with *Didymograptus murchisoni* var. *geminus*. Turner's *I. gibberulus* var. *a* (1960, 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, Yal. *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  $\times 2$ .

*Isograptus victoriae divergens* Harris 1933Text-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 maximo-divergens* Harris, *I. v. divergens* Harris. *a*, *I. v. maximo-divergens*, 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  $\times 2$ .

*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<sup>1</sup> 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<sup>1</sup> 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-theal 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. 14a–i

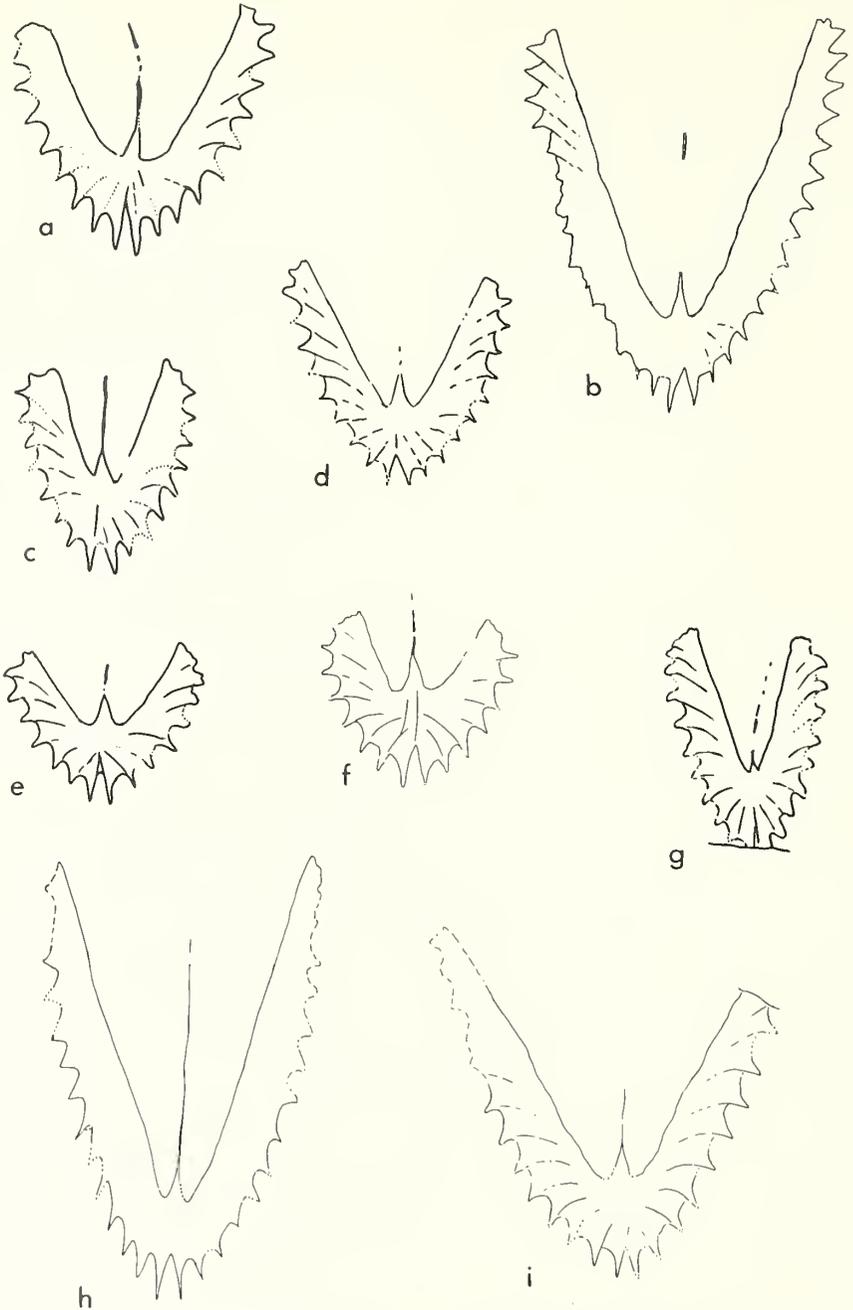
- 1933 *Isograptus caduceus* var. *imitata* Harris, p. 92, figs. 55–59.  
 ?1933 *Isograptus caduceus* var. *horrida* Harris, p. 92, fig. 32.  
 1961 *Isograptus forcipiformis* var. *harrisi* Skwarko, p. 106, fig. 4.

*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. 14i). Paralectotypes are GSV 63644 (Harris, text-fig. 55), and GSV 63303 (Harris, text-fig. 56; this paper text-fig. 14h). 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  $\times 5$ .

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 sicula 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 *lumatus*). In general accordance with Harris's view, the writer considers it to have probably descended from such V-shaped forms as *I. v. lumatus* (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. 16a-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).

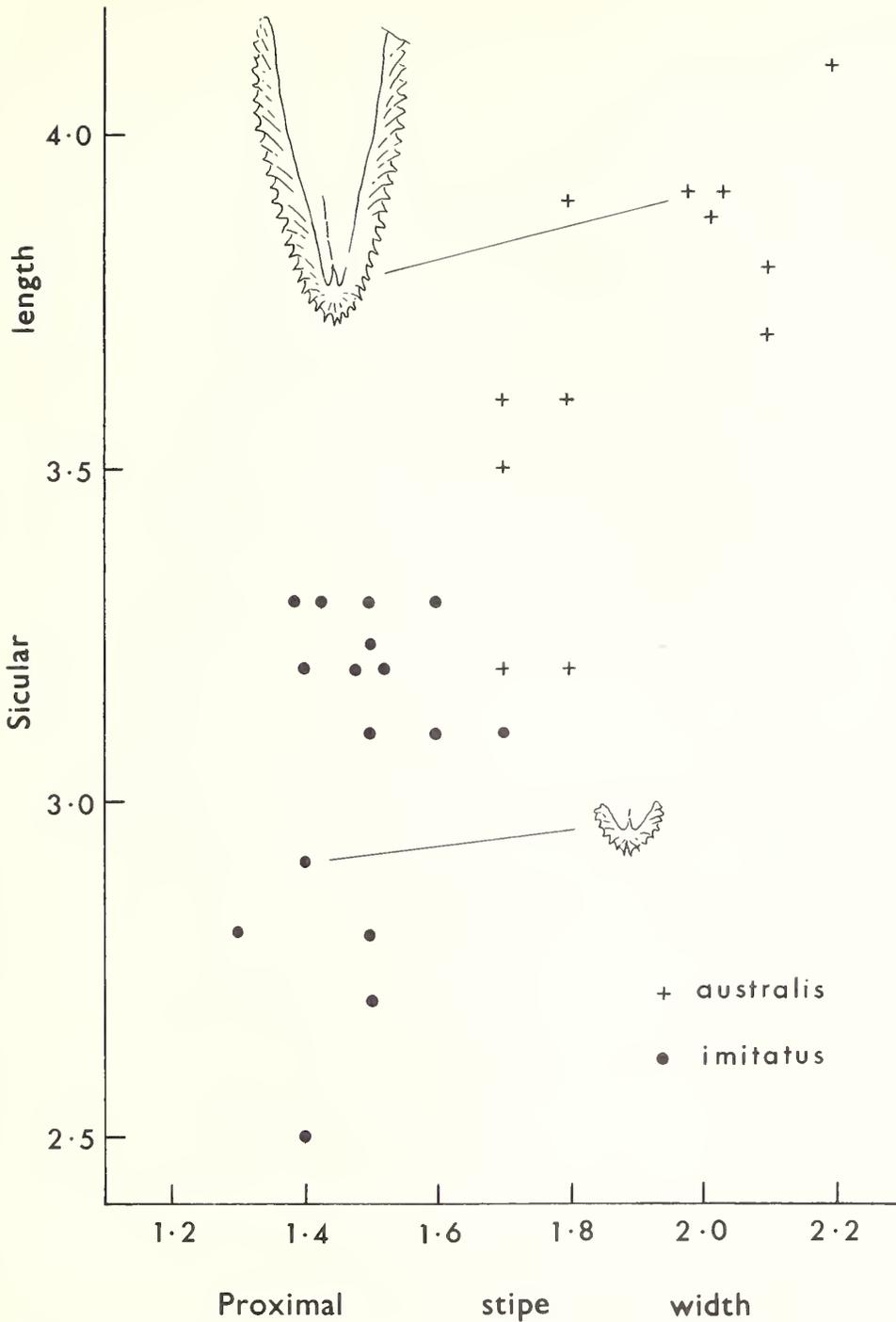
*Measured material (paratypes), localities, age*. 17 specimens from S2/540 (*Oncograptus* zone); VG 133; PR 8, 312, 314, 334-336, 346, 351, 361, 370, 372, 387, 392-393, 421; Yapeenian, Ya1, in New Zealand, Ya1-2 in Victoria.

*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.

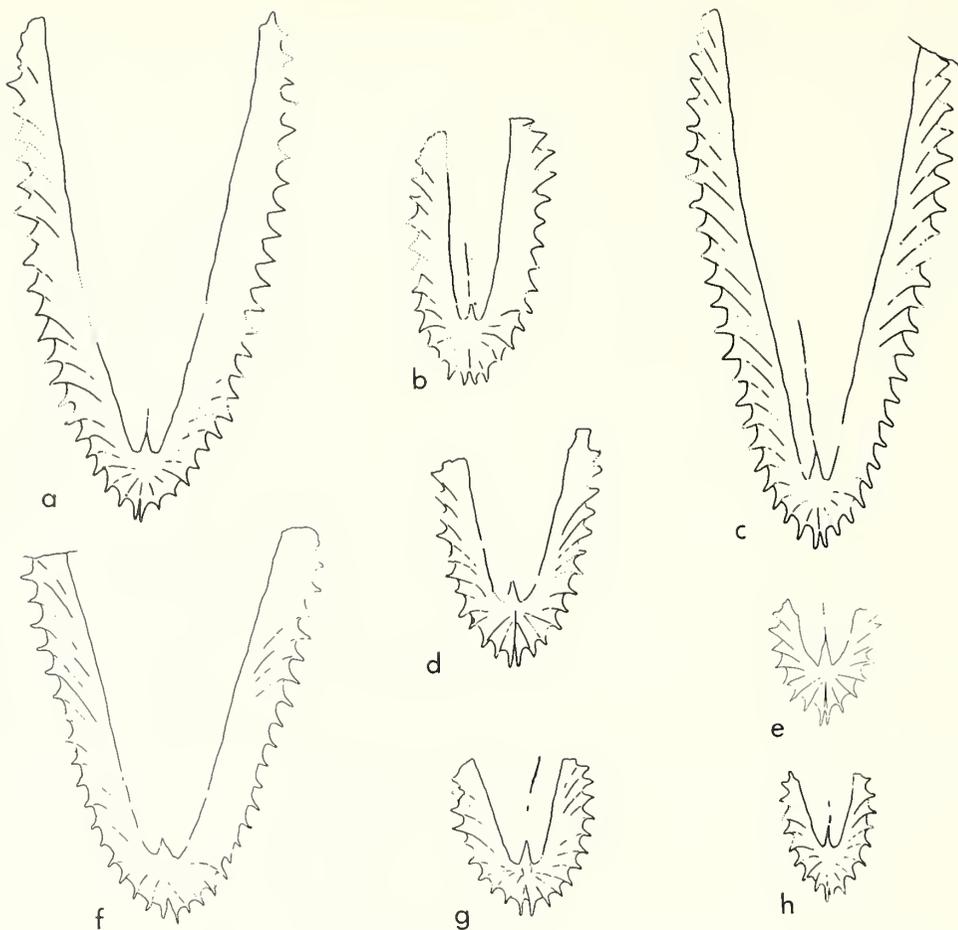
The stipes, following their initial flexure, are straight or slightly curved, dorsally concave, grow to a considerable length (up to 25 mm), and diverge at from 330° to 360° (average 342°). They are widest in the region of the sicula, but thereafter are either parallel sided or taper gradually throughout 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. 16a, 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  $\times 3$ .

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. 16*h*), however, more closely match *imitatus*, reflecting its phylogeny.

*Distribution.* Several records of *I. 'caduceus' divergens* are more probably attributable to *I. caduceus australis*. 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).

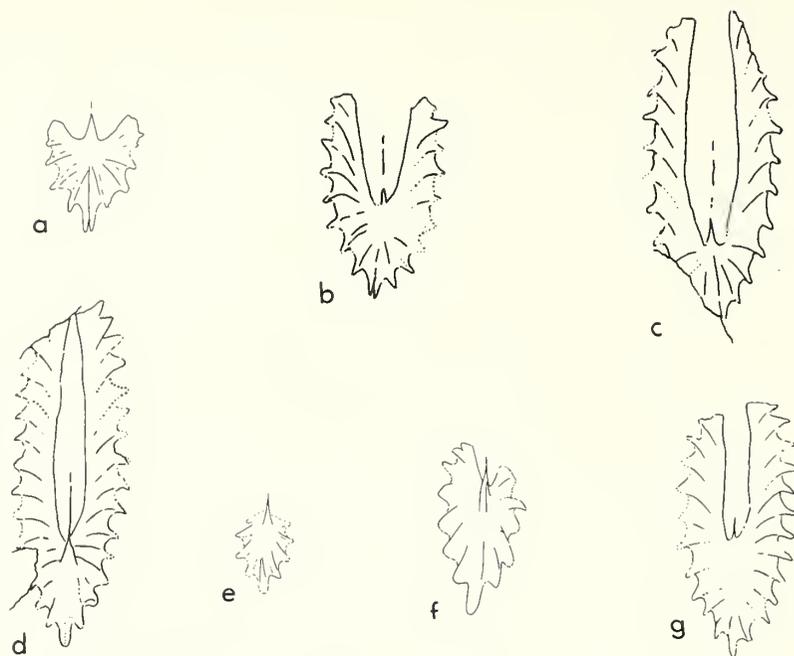
*Material, locality, age.* 5 specimens: VG 55, 62, 63; PR 422; and several incomplete or poorly preserved specimens from S2/552; Castlemainian, Ca3 (upper). PR 357 from S2/540; Yapeenian, Ya1.

*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. Intertheal 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  $\times 5$ .

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*.

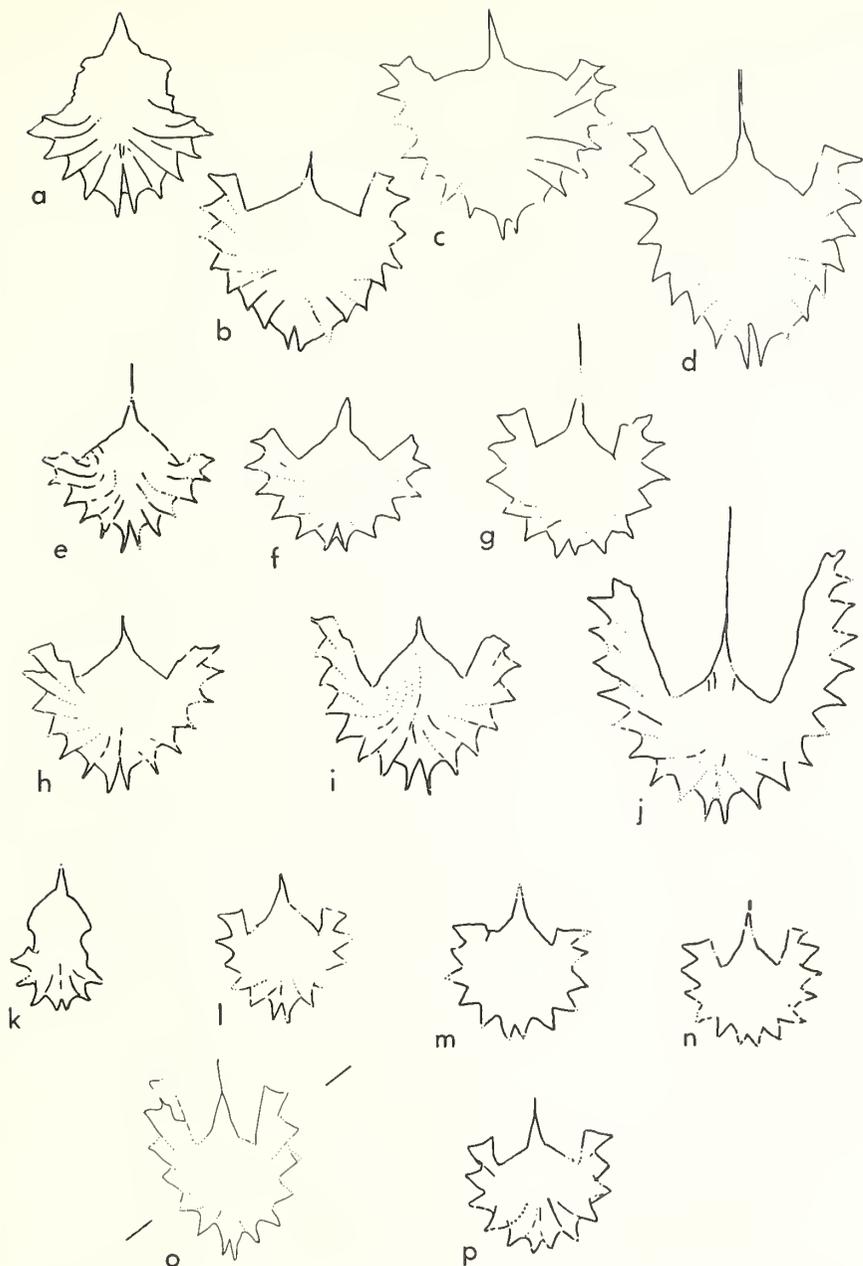
### *Isograptus dumosus* Harris 1933

Text-figs. 18a-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. 18o). 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  $\times 5$ .

*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.

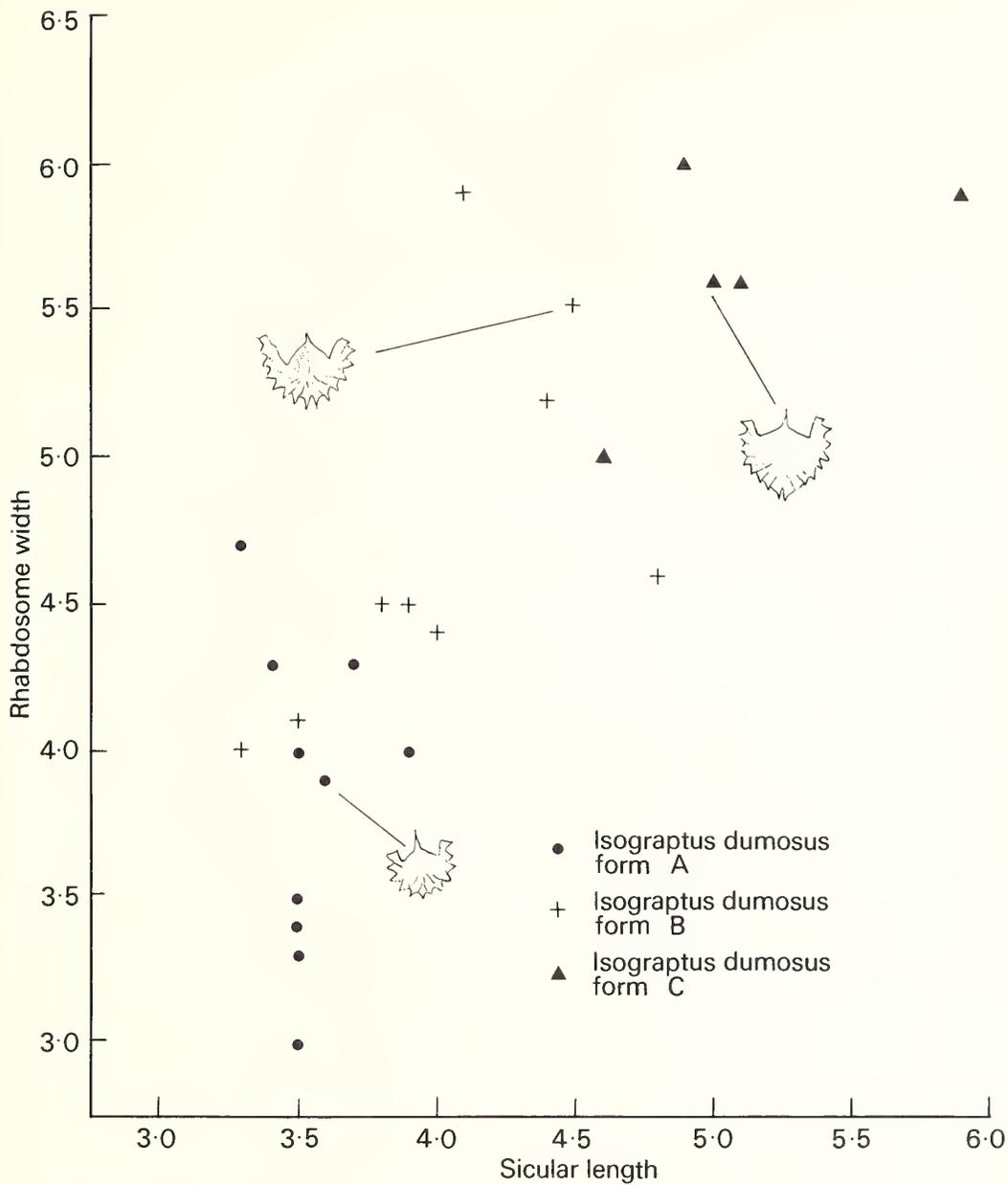
In form A, the smallest form, the sicula averages 3.6 mm (3.3–4.0) long, and 0.29 mm wide at the aperture. The apex of the sicula and first theca protrude about 1 mm above the shoulder of the manubrium, which expands rapidly to an average basal width of 1.8 mm. The apertural portions of proximal thecae 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. 18*o*). 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).

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. 20a–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. 20k). 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 1<sup>1</sup> 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. 20l) 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.

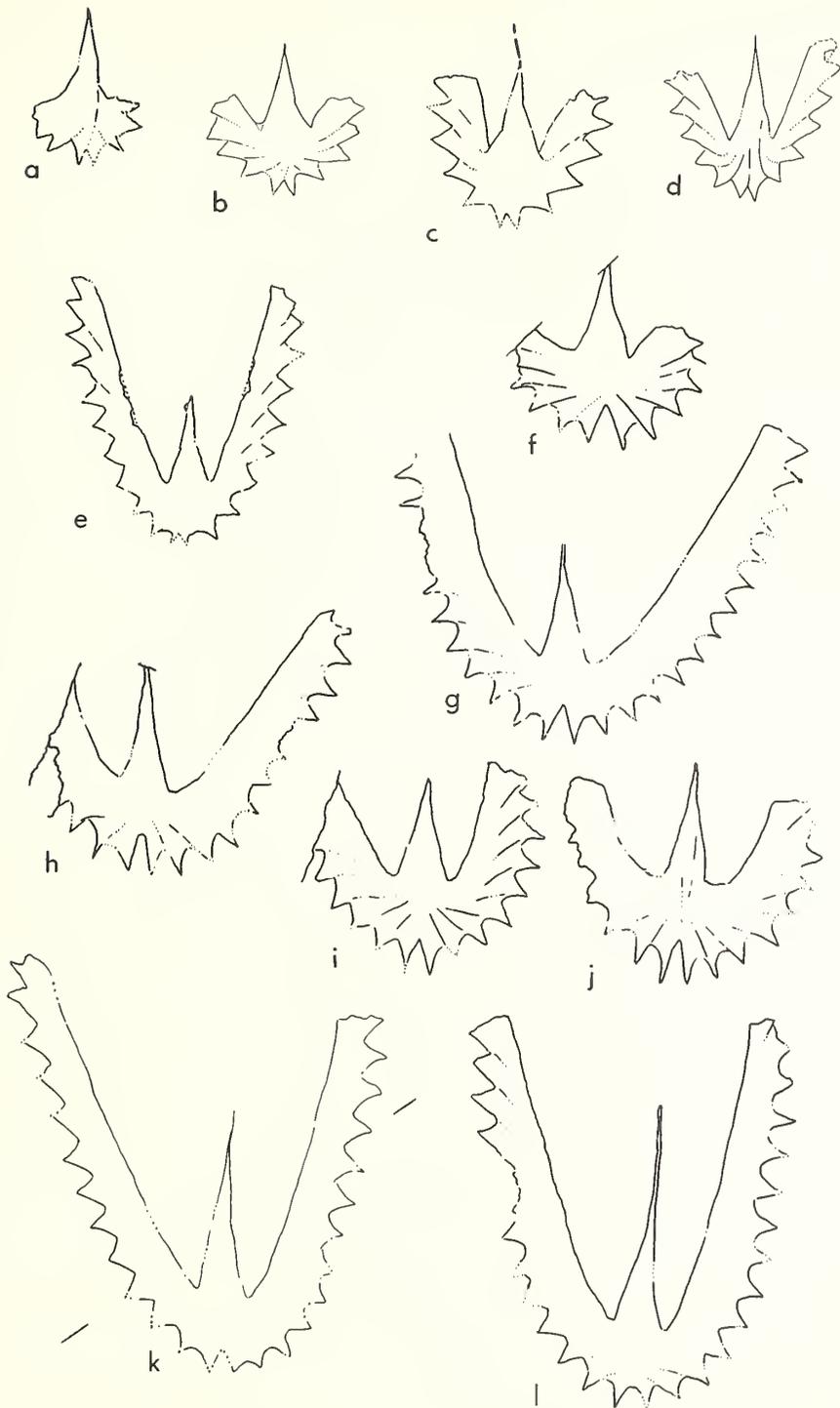
Thecae are spaced 5–6 in 5 mm, and are inclined at about 30°–40° to the stipe axis. Proximal thecae are markedly denticulate, the apertural margins of distal thecae are concave and highly inclined to the stipe axis.

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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. 20*b*, *d*) are well enough preserved to show that the manubrium comprises, in addition to the sicula and theca 1<sup>1</sup>, 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<sup>2</sup>. 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. 20*l*, matches the holotype of *Isograptus hastatus* Harris (1933, fig. 36), refigured here for comparison (text-fig. 20*k*), 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. 10*d* and 20*i*) 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).

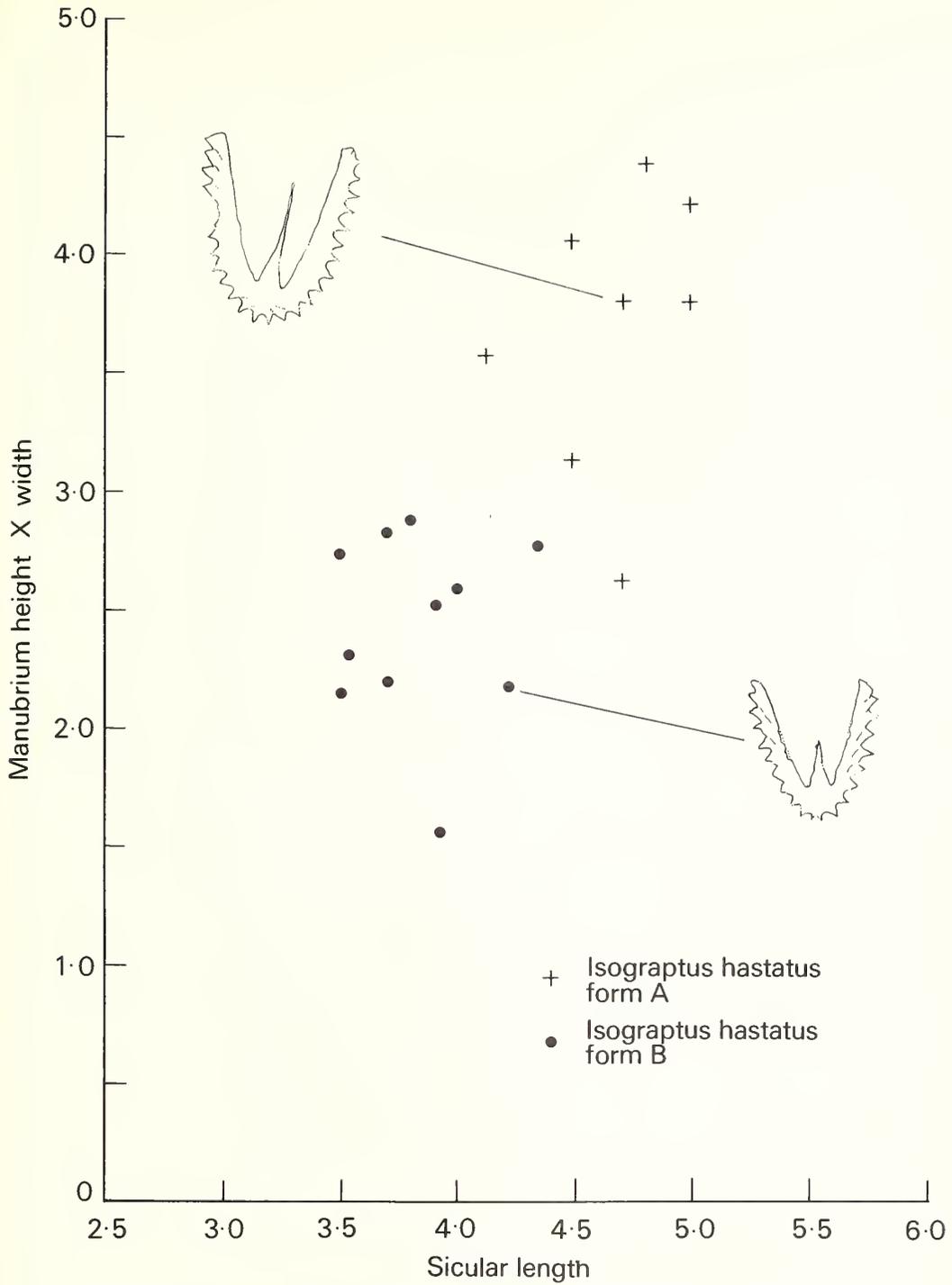
### *Isograptus manubriatus* (T. S. Hall 1914) *sensu lato*

Text-figs. 22*a–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. 2*a–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<sup>1</sup>. 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.

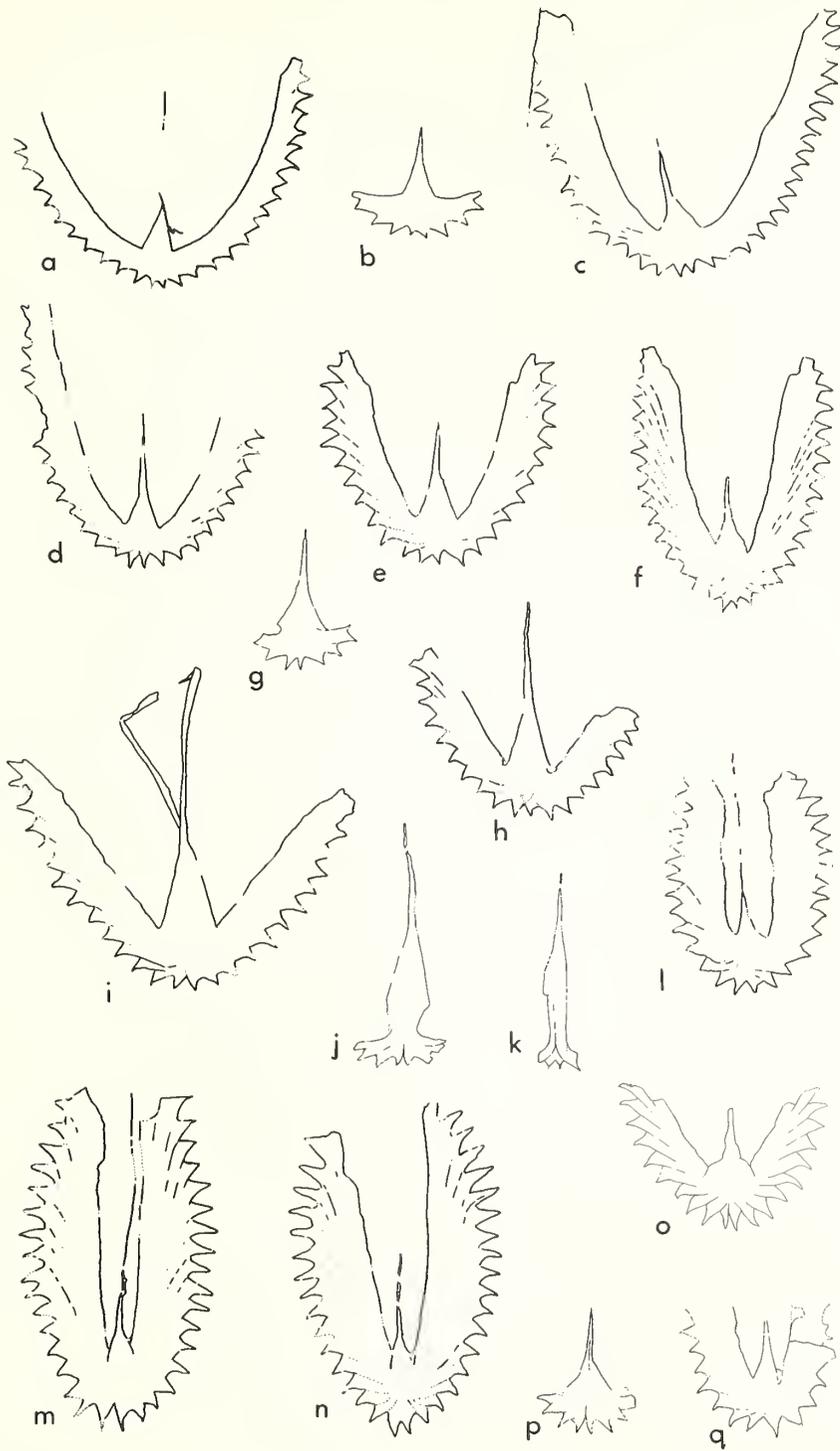
Thecae are extremely long and their apertural margins bear a prominent ventral process; inclination of distal thecae decreases from about 20°–30° at mid stipe to 10° or less at the distal extremity. Apertural margins are nearly straight and inclined at about 90° to the stipe axis.

*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. 22o) 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

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  $\times 3$ .



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<sup>1</sup>) 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. 2*a*–*b*, pl. 2, figs. 6–8; this paper, text-fig. 6*f*) is relatively long and straight, and the initial pair of thecae (1<sup>1</sup> and 1<sup>2</sup>) 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

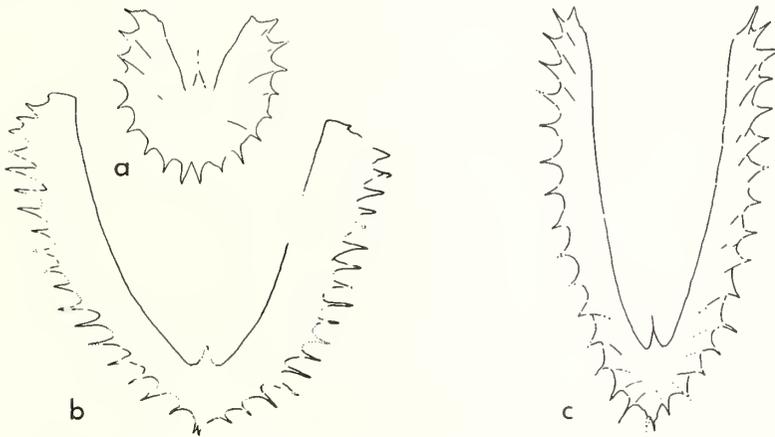
1. Several other, sparsely represented, isograptids are present in the Upper Castlemainian to Upper Darriwilian interval of Australasia. *Isograptus caduceus* var. *tenuis* Harris (1933, pp. 92–93, text-figs. 53–54) is found rarely in Ca3–Da4 beds in Victoria; it has a slender horseshoe-shaped rhabdosome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

fig. 81) 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. 23b, c). Together with the specimen from the Hendre Shales figured by Toghil (1970, fig. 2a) they are apparently the youngest representatives of the genus in the world. The holotype (counterpart) of *I. caduceus spinifer* is refigured here (text-fig. 23c) 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. 24a) for comparison with the isograptids, together with 2 other specimens from the same stage (Yapeenian) in Victoria (text-figs. 24b, d). In each specimen it can be seen that the

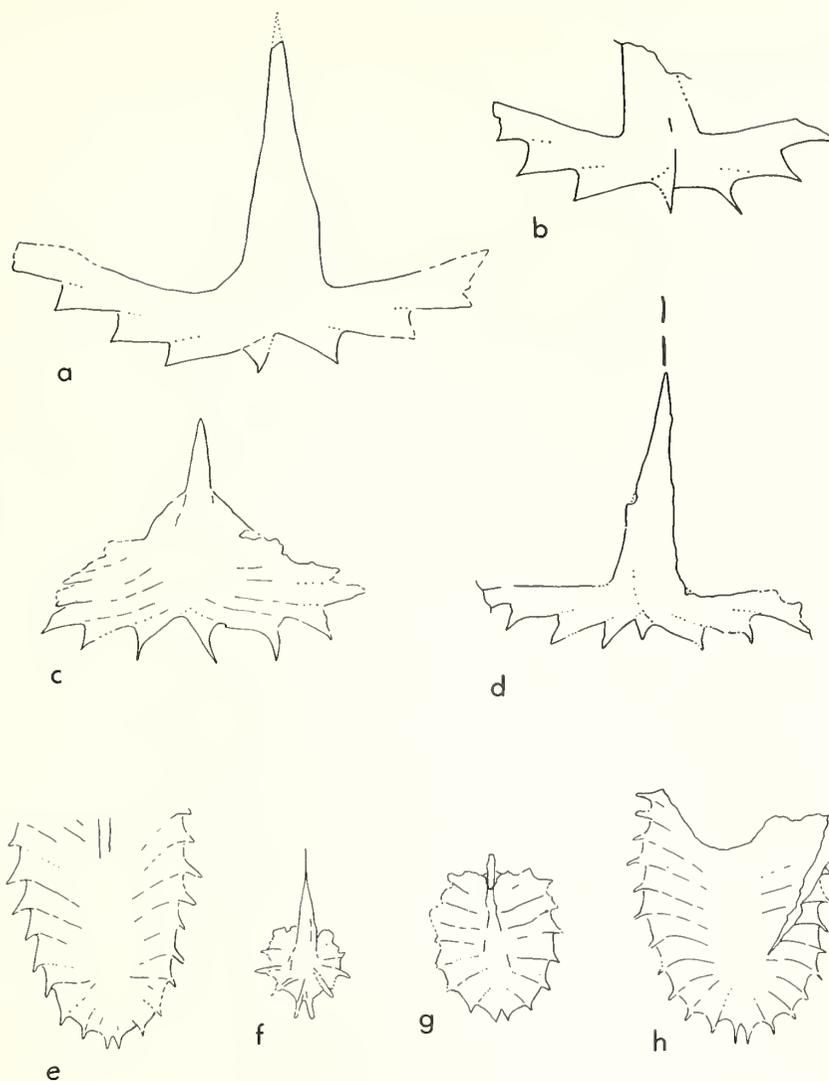


TEXT-FIG. 23. *a-c*—Darriwilian isograptids from Nelson. *a*, *Isograptus* sp., immature rhabdosome; PR 32, S2/582; Darriwilian, Da1-2.  $\times 5$ . Aorangi Mine area. *b*, *Isograptus* cf. *ovatus* T. S. Hall, tectonically distorted with approximate direction of maximum relative shortening parallel to rhabdosome midline; specimen figured by Keble and Benson (1929, pl. 104, fig. 10), from Cobb Valley; Darriwilian, Da4.  $\times 3$ . *c*, *Isograptus caduceus spinifer* Keble and Benson, holotype counterpart; Cobb Valley, Darriwilian, Da4.  $\times 5$ .

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-*minusculus* dichograptid type with the insertion of an additional theca,  $2^1b$ , 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'.  $\times 10$ .

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

*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.  $\times 5$ .

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

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. 24h) 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).

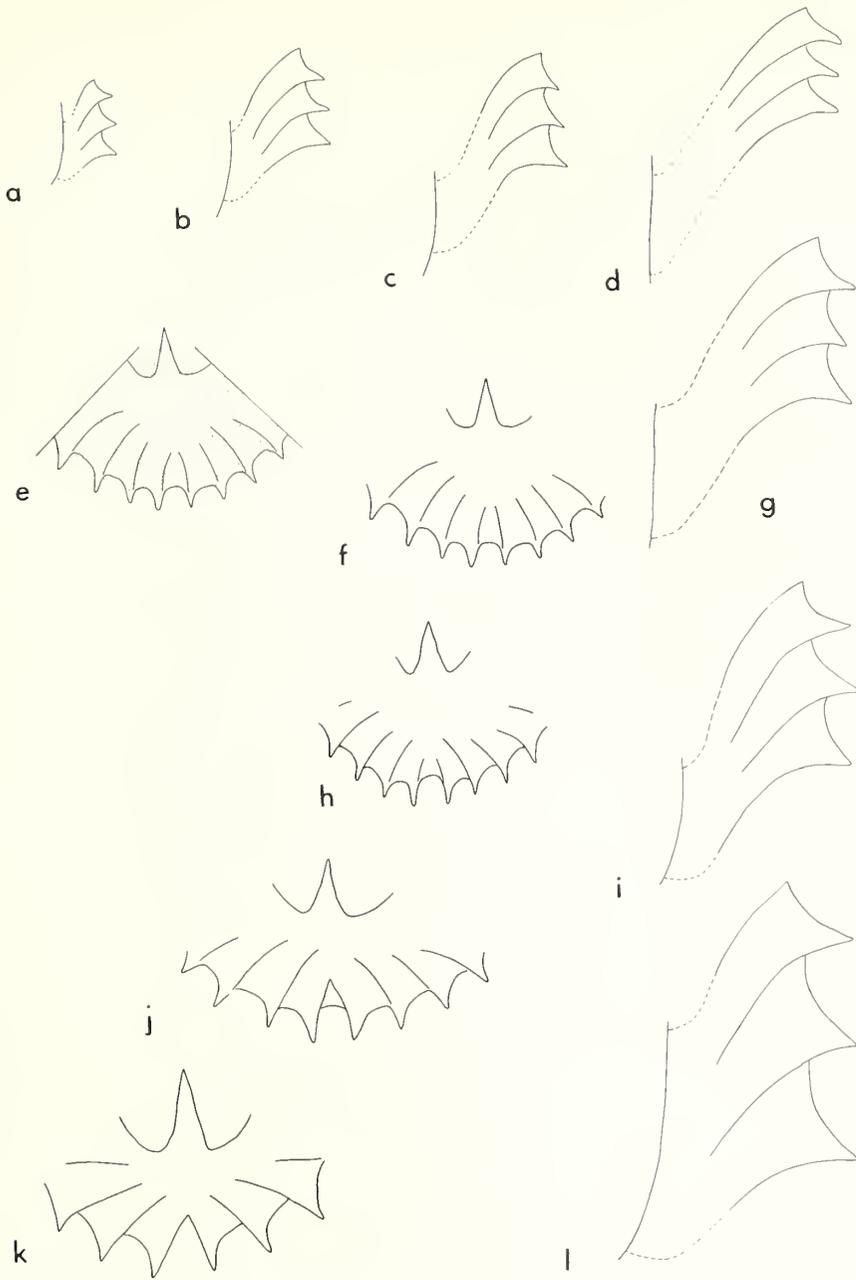
#### GROWTH, VARIATION, PHYLETIC TRENDS

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 *humatus*, *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 graptozoid. 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. 25a, 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  $\times 5$ ) 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  $\times 5$ ) 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' *lumatus* 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  $\times 1.4$ ). 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).

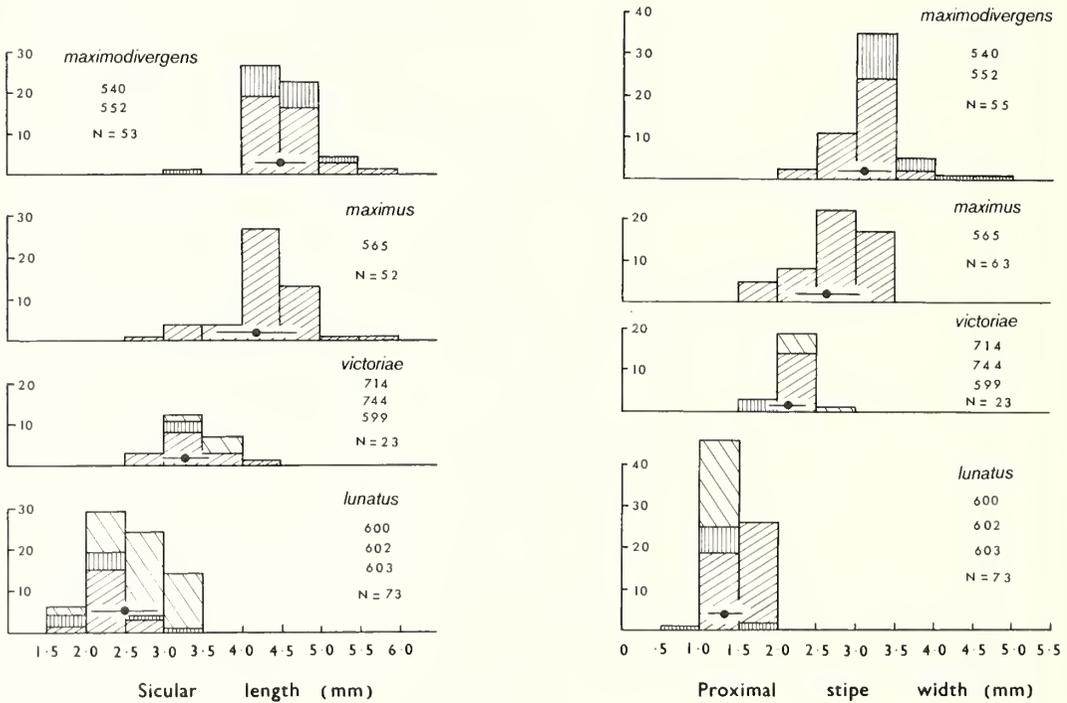
Much of the observed intraspecific (intrapopulation) variation is related to the

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

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



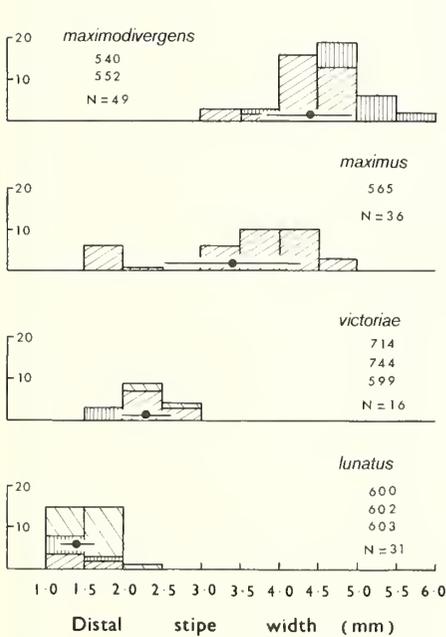
TEXT-FIG. 26. Frequency distribution of measurements of sicular length in samples of *Isograptus victoriae lunatus*, *victoriae*, *maximus*, and *maximodivergens*. The mean value and one standard deviation from the mean are indicated for each subspecies. Sample numbers are listed in their order of superposition 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.

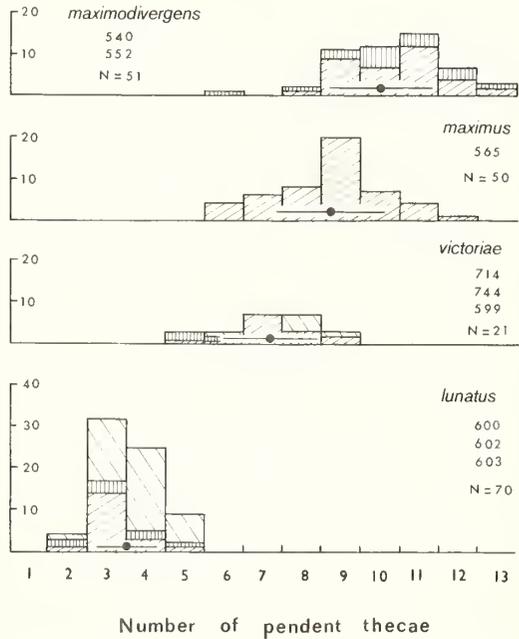
The most meaningful representation of the comparative over-all 'morphologic distance' between populations is that based on *all* measurements of *all* characters of *all* specimens (multivariate analysis).

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.

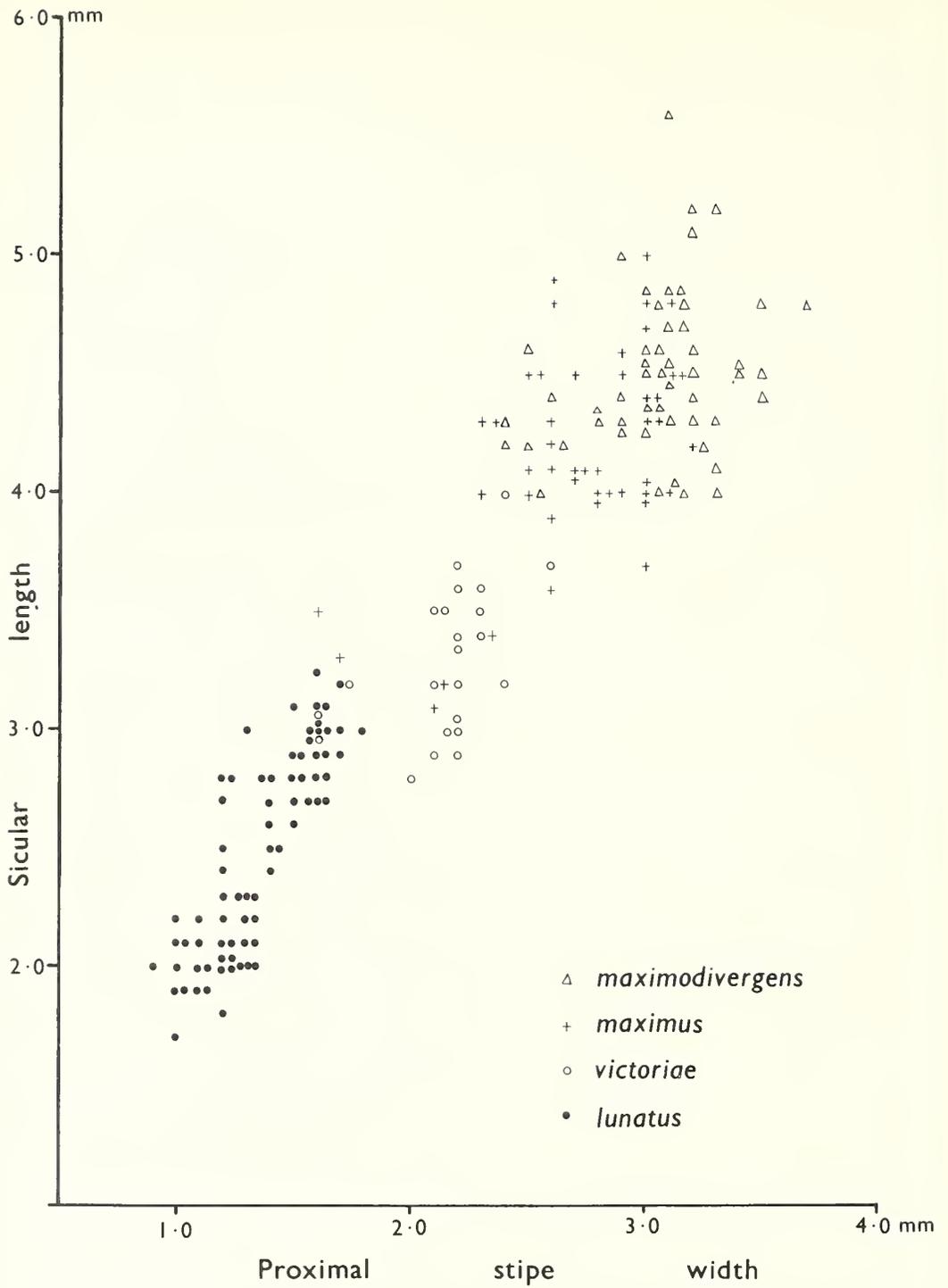
The method of computation accepts only complete data sets. Since some characters, such as distal stipe width, could not be measured in many incompletely preserved specimens they were excluded from the analysis in order to make use of the maximum number of specimens. Six of the 10 measured characters were used: sicular length, sicular width, supradorsal length, supradorsal width, proximal stipe width,



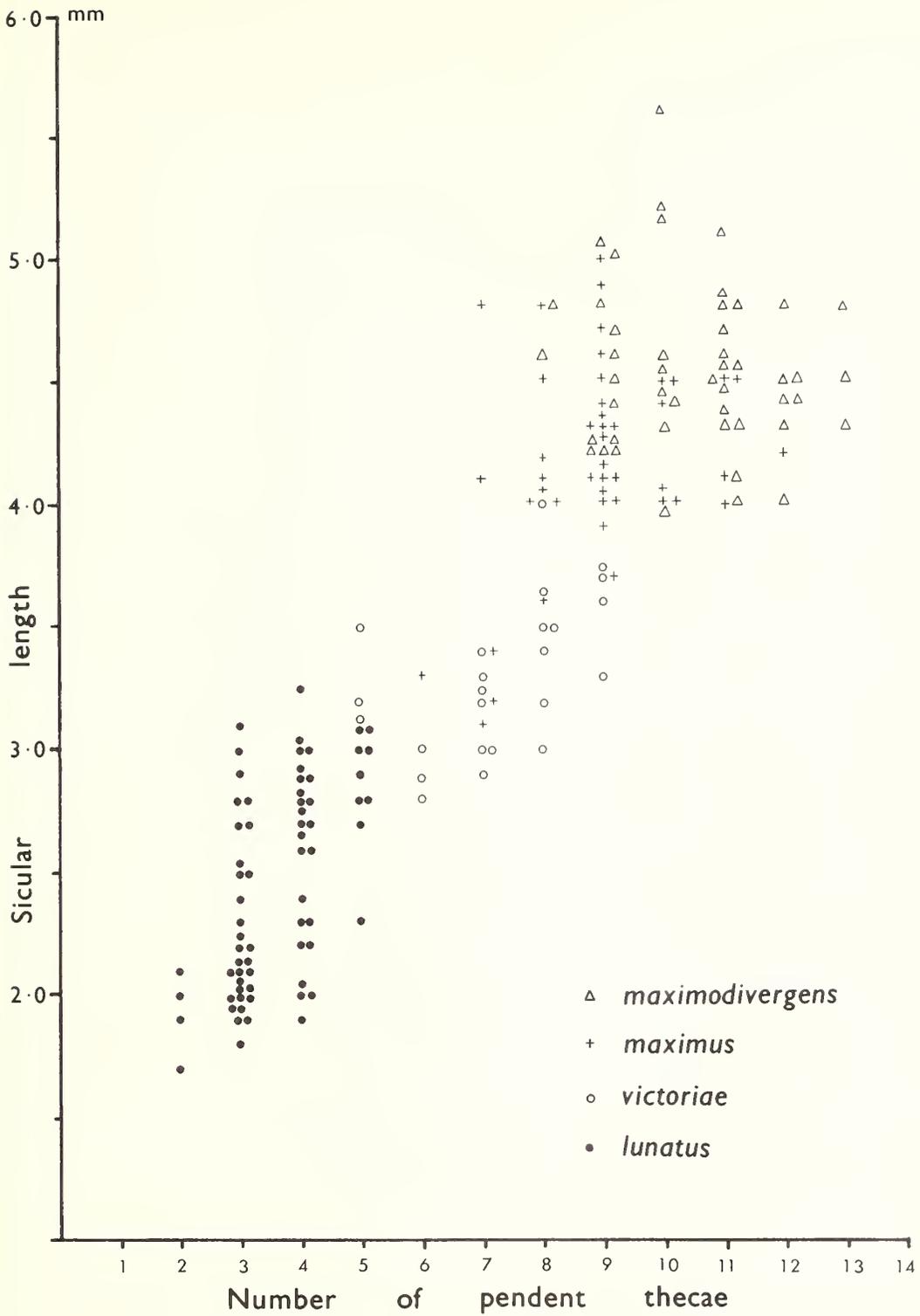
TEXT-FIG. 28. Frequency distribution of measurements of distal stipe width in *Isograptus victoriae lunatus*, *victoriae*, *maximus*, and *maximodivergens*. The mean value and one standard deviation from the mean are indicated for each subspecies. Sample numbers are listed in their order of superposition in the histograms.



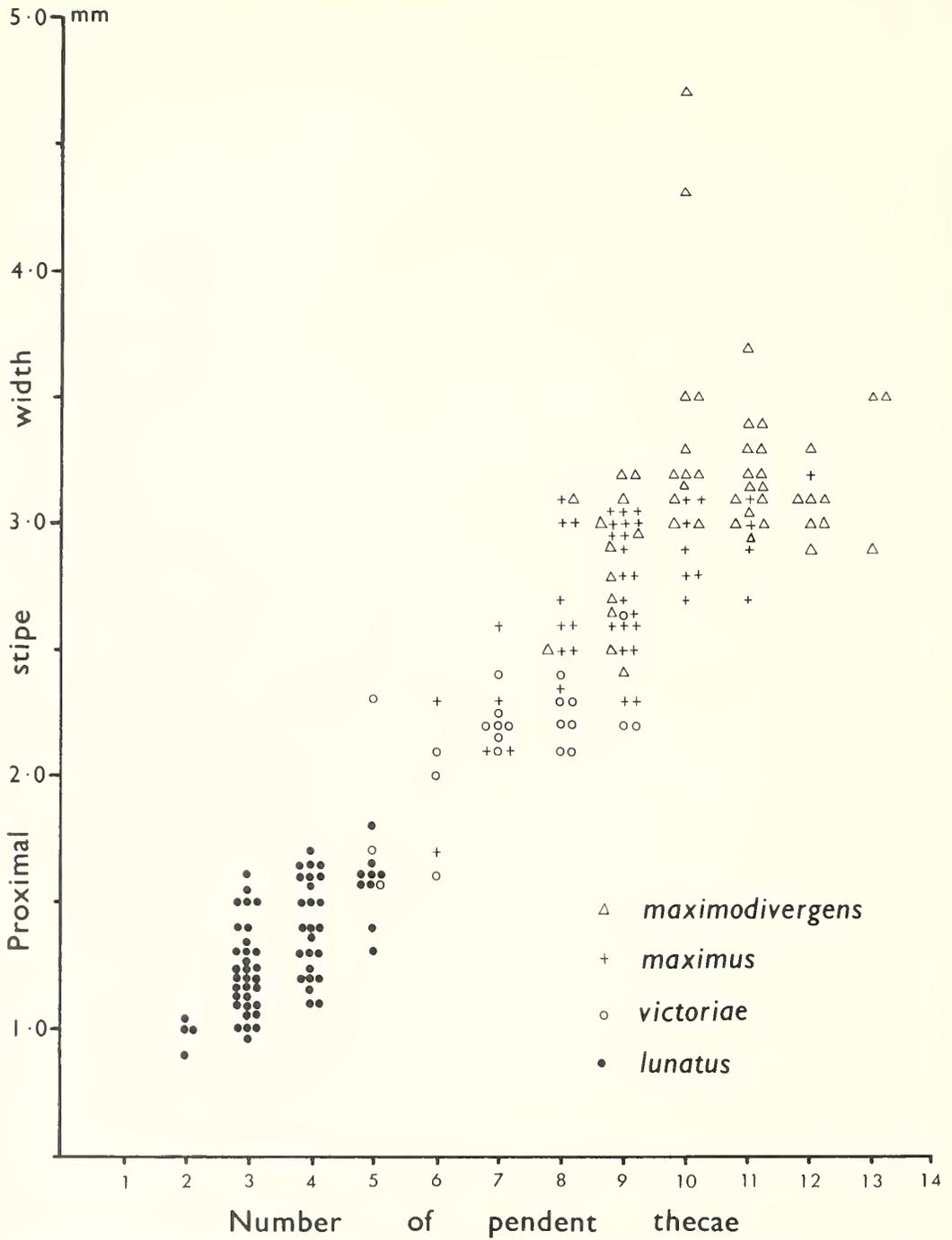
TEXT-FIG. 29. Frequency distribution of counts of number of pendent thecae in *Isograptus victoriae lunatus*, *victoriae*, *maximus*, and *maximodivergens*. The mean value and one standard deviation from the mean are indicated for each subspecies. Sample numbers are listed in their order of superposition in the histograms.



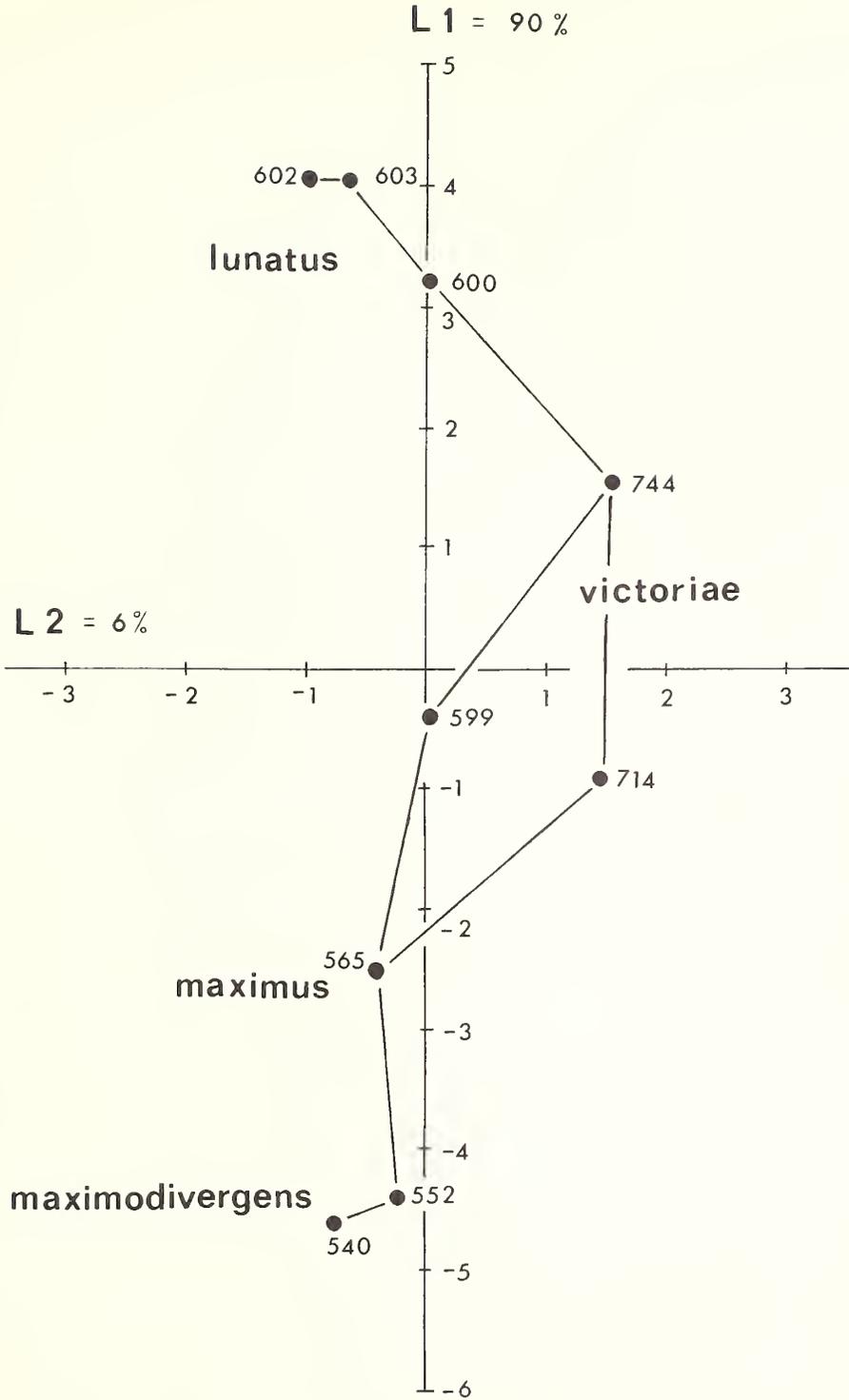
TEXT-FIG. 30. Sicular length plotted against proximal stipe width in 192 specimens of *Isograptus victoriarum* subspecies.



TEXT-FIG. 31. Sicular length plotted against number of pendent thecae in 182 specimens of *Isograptus victoriana* 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  $D^2$  (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
			<i>lunatus</i>	<i>victoriae</i>	<i>maximus</i>	<i>maximodivergens</i>	
<i>lunatus</i>	38	.028	38 (100%)	0 (0%)	0 (0%)	0 (0%)	0
<i>victoriae</i>	22	.098	1 (4.5%)	20 (91%)	1 (4.5%)	0 (0%)	2
<i>maximus</i>	46	.162	1 (2%)	4 (9%)	30 (65%)	11 (24%)	16
<i>maximodivergens</i>	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*.

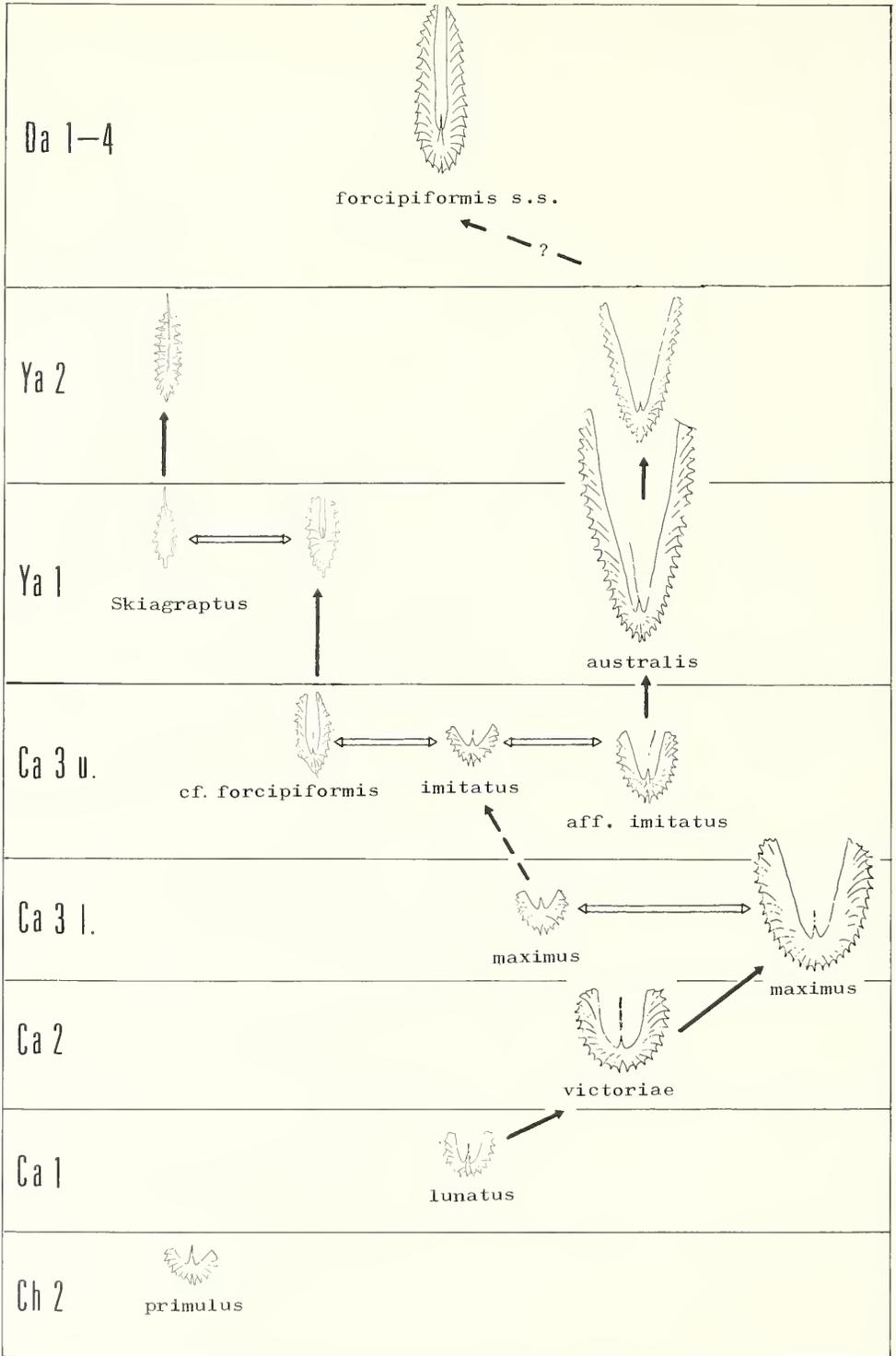
Latest representative of the group is probably *I. caduceus spinifer* in the Upper Darriwilian (Da4).

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.

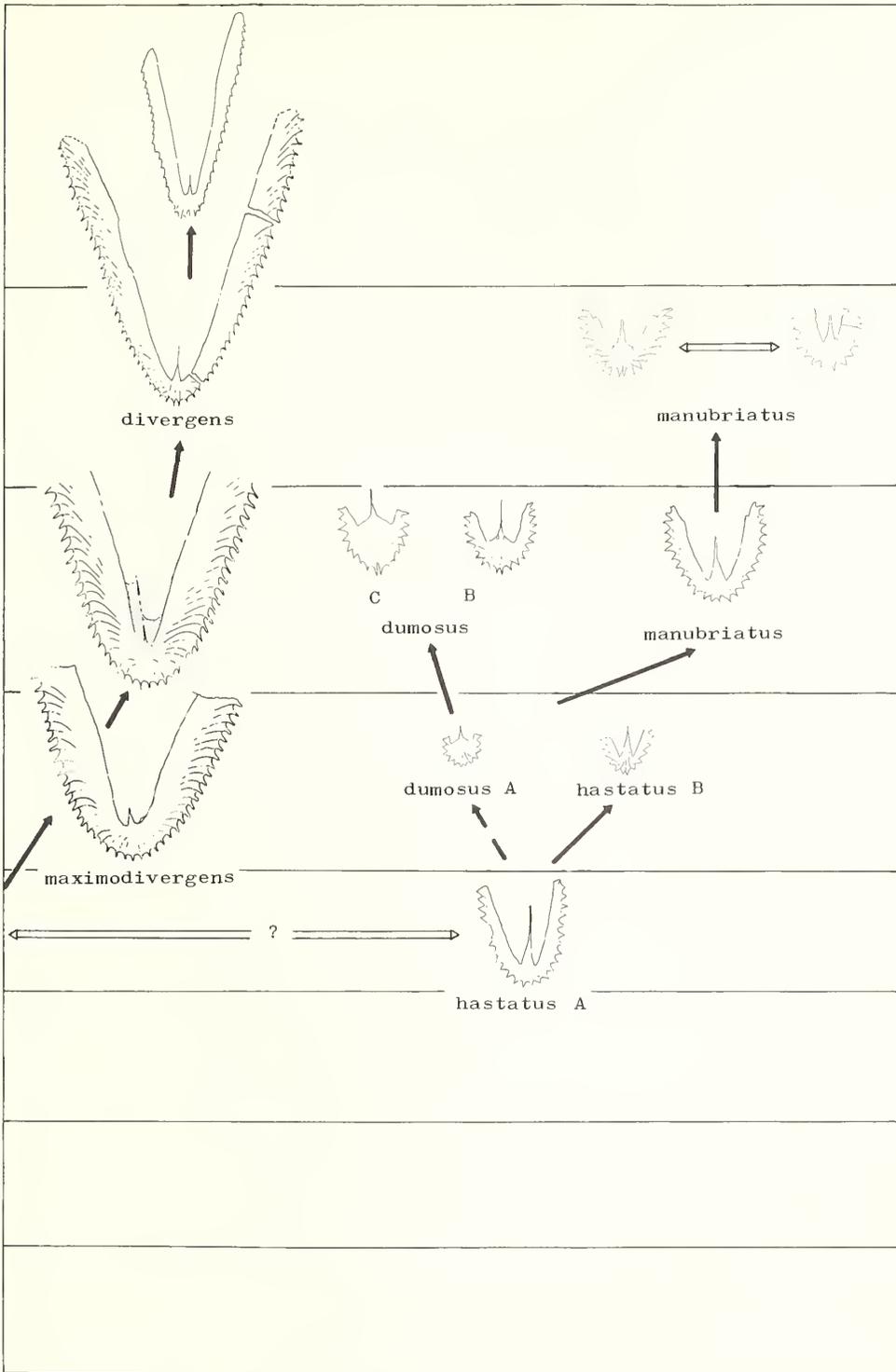
#### STRATIGRAPHIC SIGNIFICANCE

*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.



Victorian substage	Ch2	Ca1	Ca2	Ca3	Ya1	Ya2
<i>I. v. primulus</i>						
<i>I. v. lunatus</i>						
<i>I. v. victoriae</i>						
<i>I. v. maximus</i>						
<i>I. v. maximodivergens</i>						
<i>I. v. divergens</i>						
New Zealand Zone	<i>protobifidus</i>	<i>lunatus</i>	<i>victoriae</i>	<i>maximus</i>	<i>Oncograptus</i>	<i>Cardiograptus</i>

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 3b $\epsilon$  Layer 2—*I. gibberulus* Nicholson  
 Layer 3—*I. lunata* Harris (? = *I. c. lunatus*)  
 Zone 3b $\delta$  *I. norvegicus* Monsen (pars = *I. c. lunatus*)  
 Zone 3b $\gamma$  *I. spinosus* Spjeldnaes

The earliest species, *I. spinosus* Spjeldnaes from zone 3b $\gamma$ , has no known equivalent in Australasia. Included in the succeeding form, *I. norvegicus* Monsen in zone 3b $\delta$ ,

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 3b $\epsilon$  through a 'continuous series of development'.

The specimen figured by Spjeldnaes (1953, text-fig. 1D) as '*I. lunata*' from Layer 3, zone 3b $\epsilon$ , 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 3b $\delta$ /3b $\epsilon$  boundary with the Ca1/Ca2 boundary (and the *D. bifidus*/*I. caduceus*' zone boundary of Texas), in agreement with the correlation advocated by Skevington (1963*b*, 1968) but in marked conflict with that proposed by Kindle and Whittington (1958, p. 328) and advocated by Berry (1960, 1968), in which 3b $\epsilon$  (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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R. A. COOPER

Victoria University of Wellington  
and New Zealand Geological Survey  
Lower Hutt

Present address:  
New Zealand Geological Survey  
Lower Hutt

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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



## 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 re-classification (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	$\frac{s}{x}$	s	V	Correlation matrix (N=29)						
								1	3	4	5	8	9	10
1. Sicular length	52	4.0	5.6	4.5	.047	.34	7	.121	-.158	<u>.340</u>	<u>.569</u>	.211	.152	-.138
2. " free length	49	.1	1.4	.90	.036	.25	28							
3. " width	50	.6	.9	.69	.009	.07	10	-.003	.002	.092	-.145	.075	.247	.144
4. " supradorsal width	49	.5	1.0	.71	.016	.11	15	.010	.000	.007	<u>.530</u>	<u>.337</u>	.205	<u>.320</u>
5. " supradorsal length	50	.7	1.5	1.1	.025	.18	16	.031	-.001	.007	.024	-.108	-.073	.072
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	<u>.683</u>	<u>.448</u>
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

*Isograptus imitatus*  
Sample S2/552. Castlemainian, Ca3, upper

Measured character	N	Min.	Max.	Mean	$\frac{s}{x}$	s	V	Correlation matrix (N=10)						
								1	3	4	5	8	9	10
1. Sicular length	12	2.5	3.3	3.1	.078	.27	9	.083	.012	<u>.656</u>	<u>.728</u>	.241	-.273	.009
2. " free length	12	.5	1.1	.77	.053	.18	24							
3. " width	12	.4	.6	.48	.018	.06	3	.000	.004	.000	.159	.429	.360	.341
4. " supradorsal width	13	.2	.6	.47	.026	.09	20	.009	.000	.002	<u>.913</u>	.000	.000	.286
5. " supradorsal length	13	.5	1.1	.87	.050	.18	21	.032	-.002	.007	.024	.175	.013	.227
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	<u>.644</u>	.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

*Isograptus caduceus australis*  
Sample S2/540. Yapeenian, Ya1

Measured character	N	Min.	Max.	Mean	$\frac{s}{x}$	s	V	Correlation matrix (N=10)						
								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							
3. " width	13	.4	.6	.55	.022	.08	14	-.006	.005	-.225	.010	.053	.081	.123
4. " supradorsal width	13	.5	.7	.55	.018	.07	12	.015	-.001	.005	.739	.442	-.120	-.609
5. " supradorsal length	13	.5	1.2	.78	.056	.20	26	.060	-.002	.012	.050	.767	.241	-.231
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

Mathematics Division, Department of Scientific and Industrial Research, Wellington) and 8B (prepared by Mr. Scott) were which again accept complete data sets only. In calculating  $D^2$  values of *I. victorae* 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 inter-population 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	.513	-.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. Rhadosome 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	$\frac{s}{\bar{x}}$	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. Rhadosome width	8	4.0	5.9	4.7	.220	.62	13

*Isograptus manubriatus*  
Sample S2/540. Yapeenian, Ya1

Measured character	N	Min.	Max.	Mean	$\frac{s}{\bar{x}}$	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	<u>.424</u>	<u>.787</u>	<u>.352</u>	<u>.368</u>	.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	<u>.723</u>	<u>.423</u>	<u>-.402</u>	<u>-.510</u>
5. " length	42	.2	5.0	3.0	.136	.88	29	.585	.338	.731	<u>.505</u>	<u>-.210</u>	<u>-.382</u>
6. Stipe length	43		16.0										
7. " divergence	36	260	360	32	4.61	28	86	7.50	.567	10.6	.060	<u>-.382</u>	<u>-.424</u>
8. " proximal width	43	1.0	3.0	1.9	.058	.38	20	.124	<u>-.086</u>	<u>-.070</u>	<u>-.365</u>	.152	<u>.907</u>
9. " distal width	41	1.4	3.5	2.3	.069	.44	19	.060	.060	<u>-.116</u>	<u>-.136</u>	.147	.174



# BIFIDA AND KAYSERIA (BRACHIOPODA) AND THEIR AFFINITY

by PAUL COPPER

ABSTRACT. The internal morphology of the European Middle Devonian brachiopods *Bifida* and *Kayseria* is truly athyridid in every character, especially with regard to the structure of the spiralia. Several previously unknown internal structures and two new species, *Kayseria alvea*, and *K. nohnensis* are described. One species of *Kayseria* is also shown to have an unusual external shell cover consisting of bushy frills located in rib troughs. It is proposed that both genera, as well as other known dayiacean brachiopods, be removed entirely from the order Atrypida and be reassigned to the suborder Athyridina (order Spiriferida).

IT is widespread practice to assign the two spire-bearing brachiopod superfamilies Atrypacea and Dayiacea to a single large group of either subordinal or ordinal rank. This is, for example, the classification followed in the two most recent brachiopod treatises, the *Osnovy* (Rzhonsnitskaya 1960) and the *Treatise on Invertebrate Paleontology* (Boucot *et al.* 1965). This usage also was followed in the Geological Society of London's symposium on the Fossil Record (Copper 1967). Re-examination of the internal structures of *Bifida* and *Kayseria*, established by Davidson in 1882, showed none of the typical characters of the true *Atrypa*. This paper attempts to show why the dayiaceans, or at least the two genera in question, are more aptly grouped with the athyridid brachiopods, where they were placed by Schuchert as early as 1894. The coiling of the spiral lophophore supports in those dayiaceans where such structures are known (e.g. *Bifida*, *Kayseria*, *Dayia*, *Aulidospira*) shows a ventral or ventro-lateral coiling direction which is the exact opposite or mirror-image to that of the true atrypids, in which the coiling direction is dorsal or dorso-medial. It is nearly impossible to visualize how two groups with such obviously opposed lophophore supports, and hence respiratory habits, can be housed under a single taxonomic roof. There is no evidence at present to indicate that the true spiriferids evolved from atrypids. It should be noted that *Bifida* and *Kayseria* are confined to the Devonian of Eurasia and northern Africa, and that they are absent in eastern North America, where they appear to have been represented ecologically by the vaguely similar probable dayiaceans *Coelospira* and *Leptocoelia*.

Stratigraphic correlations used in this paper are based on the classic work of Struve (1961) in the Eifel region of Germany. The geologic section is summarized in text-fig. 6. House and Selwood (1966) reviewed the stratigraphy of Devon in south-west England, where the type species of *Kayseria* occurs. In supplement it can be said, on the basis of the brachiopod *Kayseria*, that the Hope's Nose Beds are undoubtedly at least in part of Upper Eifelian (Freilingen) age. The Chercombe Bridge Shales, containing *Gruenewaldtia latilinguis* (Schnur), are undoubtedly in part Middle Eifelian (Junkerberg) in age.

*Methods and acknowledgements.* The internal structure of the specimens was studied with the use of aceto-butyrate peels (Triafol NB), a technique well suited to calcareous shells with a muddy matrix. The peels were inserted in 35 mm glass slide holders for photography under transmitted light in a standard petrographic microscope. To show the serial development of various structures, the slide-mounted peels were inserted in an ordinary slide projector, focused on a screen to an enlargement of 20 times, and then traced with india ink. A full three-dimensional picture of the internal structure of the shell was reconstructed by transferring peel images to a horizontal grid pattern parallel to the commissural plane. If the peels are aligned according to the plane of bilateral symmetry, then the reconstruction is accurate to within one millimetre at a scale of times 20.

Specimens photographed and sectioned were deposited in the British Museum (Natural History) (BMNH) or the Institute of Geological Sciences Museum, London, England (GSM). The work was mainly carried out during 1965-1967 under a National Research Council of Canada postdoctoral fellowship. Locality references employ the German metric grid system; most material came from the Eifel region of Germany.

The writer is extremely grateful to Drs. D. E. White and D. E. Butler of the Institute of Geological Sciences for assisting in access to type specimens of *Kayseria*, and for supplying photographs of the types, and to Dr. Hermann Jaeger in providing information about types in the Berlin museum.

### PALAEOECOLOGY

All dayiaceans are small brachiopods less than 15 mm wide. The small size factor seems to hold generally true also for most athyridids, although exceptional athyridid species may be up to 40 mm wide. Also all dayiaceans apparently lack deltidial plates or pedicle structures of some sort, and all lack a large pedicle opening, delthyrium or interarea. Even *Dayia* apparently has no deltidial plates (see Tucker 1968). So, the dayiaceans were not primarily pedicle-supported brachiopods, or if they were, their pedicle muscle must have been very slender and minute, or must have consisted of thread-like structures along the hinges. The pedicle probably atrophied in most shells during the mature stage. As a result, most adults were in all likelihood loose, sedentary forms positioned on the muddy sea bottom. There are no wide brim-type frills developed on the shell surfaces. The peculiar rib trough-located frills on *Kayseria* may have helped as anchoring devices, or as filtering screens.

Both *Bifida* and *Kayseria* seem to have preferentially lived on a calcareous muddy bottom, and associated with other small brachiopods (especially in the Late Eifelian Ahabach Beds of the Eifel region). There is no evidence that they lived in a biotope of stunted shells. They also occur in the shaly lenses in coral-stromatoporoid-crinoid rich Eifelian Freilingen Beds of the Eifel where the environment shows good evidence of aeration and current sorting. The lithology in which *Bifida* and *Kayseria* are found mainly consists of brownish to dark greyish calcareous shales or argillaceous, thin-bedded limestones. They are not present in clastic rocks such as siltstones or sandstones, or in non-argillaceous biohermal limestones. Their preference is for the normal, muddy, shallow marine Eifel type of facies in zones 5 to 6 as shown in Copper (1966, fig. 2) in relatively quiet to slightly disturbed waters.

There seem to be no specific symbiotic affinities with other invertebrates. In the Eifel region in Middle Devonian time, *Kayseria alvea* sp. nov. is commonly found in association with *Spinatrypa* (*Invertrypa*) *kelusiana* Struve, an atrypid which very probably lived anchored and partially buried in the muddy bottom. The function of fibrous projections of *Kayseria* here is not clear. The fibres are directed towards the hinge area and in such a way that they form a flat shelf-like area. *Kayseria* perhaps

lived vertically, with the shell apex near the bottom and the anterior commissure upwards. A short pedicle may have served as an anchor in the mud. No specimens were found in growth position.

*Bifida* differs from *Kayseria* in its smaller size, unequal, ventribiconvex shell, and lack of distinctive frills or fibres. The beak of *Bifida* is more strongly incurved. This genus may very well have lived attached to other brachiopods by a short pedicle.

Externally other dayiaceans such as *Coelospira* (viz. Boucot and Johnson 1967), *Leptocoelia*, and *Eocoelia* (viz. Ziegler 1966), the first two of which were confined to North America during Devonian time, are very similar to the western European *Bifida* and *Kayseria*. They were probably also very similar in their environmental requirements.

#### REDESCRIPTION OF THE TYPE SPECIES

Since the main purpose of this paper is to clarify the internal morphology and taxonomy of the two genera treated, the type species of both were re-examined. In addition, the definitions of the suborder Athyrididina, the superfamily Dayiacea, and the families Anoplothecidae and Kayseriidae are modified, since these are not clearly defined in the Brachiopod Treatise.

#### Suborder ATHYRIDIDINA

The athyridids are identified mainly by their relatively rounded shape, a lack of, or very small interarea and pedicle opening, and internally particularly by their medially directed crura, their unusually elaborate jugum with accessory lamellae, and their laterally-ventrally directed spiralia. The direction of coiling of the spiralia is most critical since it represents the mirror image or exact inside-out replica of atrypid coiling. These characters are also pertinent to *Kayseria* and *Bifida* and may be readily employed as a definition of the whole suborder. The whole superfamily Dayiacea can, in fact, be accommodated in the athyridid group without any alteration in the Treatise definition of the suborder. The only character which makes some Dayiaceans look like atrypids is the superficial one of a radial rib structure, but even a radial rib structure is not unknown in other athyridids such as the genus *Atrythyris* Struve. If the dayiaceans are accepted as true athyridids, as suggested here, then the range of the suborder Athyrididina may be extended downwards to the Middle Ordovician. Investigation of the internal structures of early, ancestral 'spirebearers' such as *Cyclospira*, *Aulidospira*, *Hindella*, and others is being carried out by the author, since there are no reliable data on the structure, orientation, and ontogenetic development of their spiralia.

#### Superfamily DAYIACEA Waagen 1883

Included in this superfamily are the Dayiidae, Anoplothecidae, Kayseriidae, and Leptocoeliidae, ranging in age from Middle Ordovician to Middle Devonian time. Primitive, Ordovician members of this group are mainly small, smooth shells. This is also true of several early atrypaceans. In fact with present knowledge there may

be some confusion in their identification. In Silurian and Devonian time most dayiaceans are ribbed, and many show a prominent median rib-pair on the pedicle valve with corresponding sinus on the brachial valve, or else a sinus on both valves. There are no distinctive long external growth lamellae in dayiaceans; very short fringes are developed in *Bifida* and in *Kayseria* but most others have overlapping growth lamellae which are not freed from the shell surface. An exception is *Leptocoelia flabellites*, a Lower Devonian athyridid common in eastern North America. *Leptocoelia* has growth fringes very much like those of *Kayseria* described in this paper. Growth interruptions may be quite numerous.

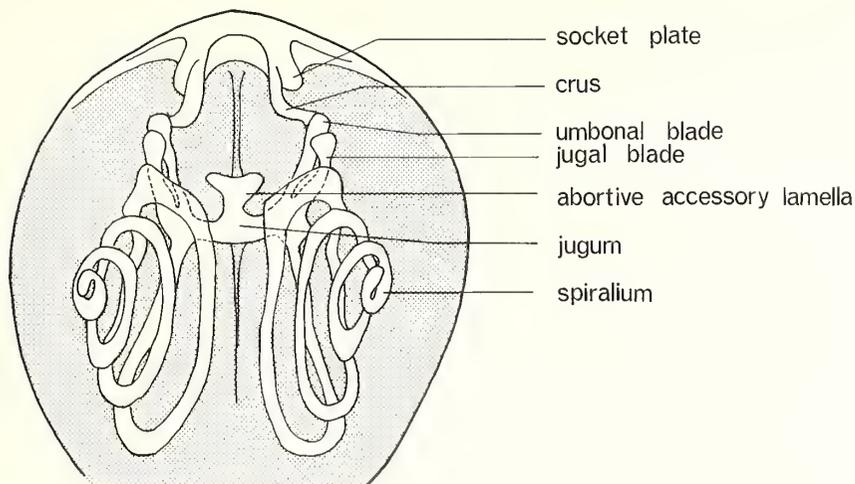
No deltidial plates, pedicle collars, or other pedicle structures are known in dayiaceans, and this is perhaps an important criterion for defining the group.

A simple type of jugum appears to be present in the early representatives of the Dayiacea, like *Dayia* as described by Alexander (1947, p. 305). According to Hall and Clarke (1893, p. 148) the earliest dayiacean *Cyclospira* lacked a jugum, but it was said to have 'two short convergent apophyses which may be construed as discrete elements of a loop'. Hall and Clarke also stated on the same page, 'As for the loop, there is as yet no satisfactory proof of its existence.' There is no recent evidence to substantiate or refute the presence of this type of structure in *Cyclospira*. There is apparently no trend for the jugum to become separated into two unconnected sections, as in Late Silurian and Devonian atrypids. Nearly all dayiaceans show a jugal saddle and accessory lamellae extending posteriorly from the jugal saddle. This feature is identical to that of the true athyridids (see Williams and Rowell 1965, p. H103), and absent in all true atrypids. In *Kayseria* the accessory lamellae lie parallel to the main spiral lamellae up to the tips of the coils. The spiralia are usually ventro-laterally directed; the dayiaceans show more of a ventrally pointed axis than other athyridids.

The crura are more or less parallel to the plane of symmetry and remain very close to the centre of the shell (in atrypids they flare to the sides directly from their point of attachment). The umbonal blades, the beginning portion leading to jugs and spiralia, show a distinctive type of attachment to the crura; instead of continuing on smoothly from the crural ends, they geniculate sharply at their point of origin, bend posteriorly and then curve around gently following the contours of the brachial valve. It is not clear why this happens. In the atrypids the crura terminate only at the jugal axis, from which point the jugal processes and spiralia are extended. In the dayiacean family Leptocoeliidae, jugs and spiralia are as yet unknown. Perhaps they were never calcified in this group. Nevertheless, external similarities allow the leptocoeliids to be referred to the Dayiacean group.

#### Family ANOPLOTHECIDAE Schuchert 1894

This group includes small, ribbed dayiaceans with short, abortive accessory lamellae developed from the ventral crest of the jugal saddle. In addition, a *jugal blade* (new term) may be initiated from the dorsal base of the jugum and directed ventro-posteriorly towards the short, abortive accessory lamellae (text-fig. 1). It may be foreseen that in some internally yet undescribed species this jugal blade in fact connects with the first accessory lamellae, to form a kind of looped structure as in



TEXT-FIG. 1. Reconstruction of the brachial valve internal morphology of *Bifida lepida* (Archiac and Verneuil) based on serial sections of specimen shown on Pl. 6, figs. 5-8. Scale  $\times 10$ .

some meristellids. Spiralia have 3 or more whorls, with the concave side of the spiral lamellae directed outwards. Spiral lamellae may be partly double-edged to form a type of embryonic double lamella (see Pl. 8, fig. 2). Included in the family are *Anoplotheca*, *Bifida*, *Dnestrina*, *Coelospirina*, *Coelospira*, and *Neocoelia*.

*Range*: Upper Silurian (Ludlovian) to Middle Devonian (Givetian).

### Genus BIFIDA Davidson 1882

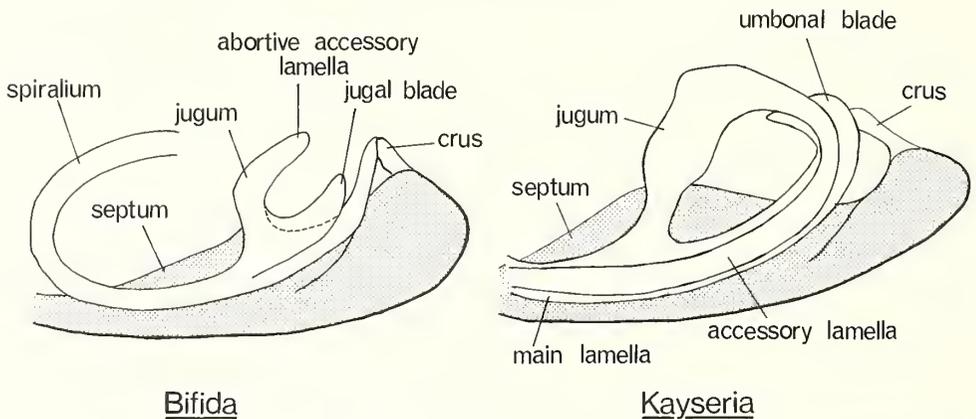
*Type species*. *Terebratula lepida* Archiac and Verneuil 1842, p. 368, pl. 35, figs. 2, 2a-c.

*Range*. Mainly known from the Eifelian-Givetian, but apparently also present in Lower Devonian (Emsian). (See LeMaitre 1952, p. 117.)

*Distribution*. Eurasia, North Africa, Nevada (N. America).

*Diagnosis*. Small, usually less than 5 mm wide, elongately rounded, ventribiconvex-planoconvex shells with numerous, even, less than 1 mm spaced concentric growth lines. Ribs few in number (commonly less than 6), non-bifurcating, tending to broaden and fade towards the commissure. Strong, elevated, mid-rib pair on ventral valve matched dorsally by a sinus flanked by two or more strong ribs and a depressed thin median rib. One or two weak ribs may appear to the sides of these. Ventral beak adpressed (squeezed against dorsal valve) and interarea and deltidial plates absent. Internally, ventrally, and laterally directed spiralia with 4-5 coils, joined by a 'wish-bone' jugum giving off two brief accessory lamellae. An additional jugal blade, projecting from base of jugum in a posterior direction, is present in at least one species. Spiral lamellae are 'embryonically' double, with a thin outer strip turning whorls into 'troughs' which are outwardly pointed.

*Comparison.* *Anoplothea* is undoubtedly closely related to *Bifida*, despite the fact that the type species *Anoplothea venusta* (Schnur 1853) from Emsian beds of the Prüm syncline (Eifel region, Germany) has not yet been revised or re-examined in detail. The two genera may even be congeneric, as Hall and Clarke (1893, p. 133) believed. Havlíček (1956) and Siehl (1862) have supported this view. Nevertheless, it seems possible to distinguish the two by their shape, size and ribbing, and possibly internal structure. *Anoplothea* is wider, more rounded and has ribs near the apex only (these are bifurcating and intersected by numerous growth lamellae), and has more coils in the spiralia and a larger cardinal process (after Boucot *et al.* 1964, pl. 125, figs. 20–25). It seems possible that there are also important differences in the structure of the jugum and accessory lamellae. *Anoplothea* may have had a type of accessory lamellae-jugum structure where the jugal blade is joined to the abortive accessory lamella (see text-fig. 2). *Anoplothea* is Lower Devonian in age and *Bifida* mainly, if not wholly, Middle Devonian.



TEXT-FIG. 2. Cut-away reconstruction in lateral view of the brachial valves of *Bifida lepida* (Archiac and Verneuil) on the left and *Kayseria dividua* (Schnur) on the right, based on serial sections. Specimens sectioned are shown on Pl. 4, figs. 1–8. Spiralia have been left out to show the connection between the crura, umbonal blades, jugs, and spiralia. Note how the dorsal septum functions as a resting site for the jugum in both shells (refer to Pl. 6, fig. 4 and Pl. 5, fig. 2).

Scale  $\times 10$ .

Havlíček (1956, p. 656) determined that his genus *Coelospirina* has spiralia with only a few coils which are ventrally directed (but did not illustrate this). It probably belongs to the Anoplothecidae, but it is very unlike either *Bifida* and *Anoplothea* externally because it has sharply edged ribs and very few growth lamellae except anteriorly. Its external features seem to indicate a much closer affinity with *Coelospira*, as the name suggests. Until internal illustrations of *Coelospirina* are given, its classification remains doubtful.

The genus *Dnestrina* Nikiforova and Modzalevskaya (1968) from the Upper Silurian of Podolia (Dzvinogorod marls, Skala horizon) is clearly an early anoplothecid perhaps ancestral to *Anoplothea*. No spiralia, however, is known, but the long median septa of the two valves are virtually identical to those of *Bifida*.

The smooth-shelled specimens referred to *Bifida* by Whidborne (1893, pp. 102–103, pl. 12, figs. 8, 8a–b) are probably not Anoplotheceidae.

*Coelospira* (see Boucot and Johnson 1967, pl. 166, figs. 20–21) is internally similar to *Bifida* but stands less closely externally and in terms of septal structures to *Bifida* than *Dnestrina*.

Species assigned to *Bifida*: *Anoplothece* (*Bifida*) *dahlia* Havlíček (1956, pp. 590–591, pl. 4, figs. 9–13), *Anoplothece nitida* Schmidt (1951, pp. 91–93, pl. 1, figs. 5a–c, text-figs. 1–3).

*Anoplothece levigata* Wolburg (1933, p. 49, pl. 10, figs. 8a–n) is a doubtful member.

### *Bifida lepida* (Archiac and Verneuil 1842)

Plate 4, figs. 5–8; Plate 5, figs. 3–4; Plate 6, figs. 1–4; Plate 7, figs. 23–24

1842 ‘*Terebratula lepida* Goldfuss, Bonn Mus’, Archiac and Verneuil, p. 368, pl. 35, figs. 2, 2a–c. Though Goldfuss is referred to as the first author, to my knowledge, no description by him of this species exists.

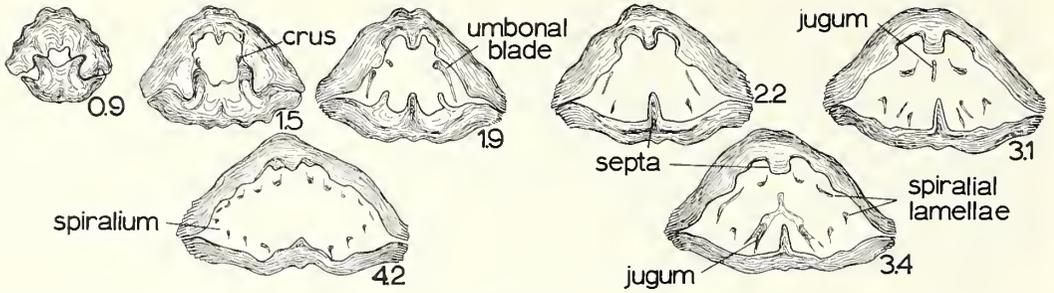
*Type specimens.* Since only one specimen was figured by Archiac and Verneuil, it automatically becomes the lectotype (see article 74b, ICZN). Syntypes are apparently lost. Hypotype BMNH:BB58557 illustrated in this paper (Pl. 7, figs. 23–26) is similar to Archiac and Verneuil’s illustration and since it comes from the source area mentioned (Eifel, Germany), it would serve as a potential neotype if further search for syntypes proves fruitless.

*Range.* With limited material available there appear to be no major differences between specimens from the Eilenberg horizon and those from higher horizons up to the top of the Ahabach beds, the upper boundary of the Eifelian sequence in the Eifel. The species is not abundant in collections, probably because of its small size.

*Distribution.* Eifel region, Germany, and Poland. The species probably has a wider geographic spread than this, but other foreign forms need to be verified.

*Diagnosis.* Small *Bifida* averaging less than 6 mm in width and length and 3 mm in depth with a ventribiconvex-planoconvex shell with a strong median rib pair flanked by 2–3 side ribs on the pedicle valve and a broad median trough lined by strong ribs and weaker lateral ribs on the brachial valve. Internally, septa are present in both valves. Double-sided spiral lamellae number about 4; laterally directed spiralia.

*Internal structure.* The species lacks deltidial plates. A distinctive median septum is present in the pedicle valve, even in a position very close to the umbo. The septum is ‘buried’ in a thick layer of calcite tissue (Pl. 5, fig. 3). The crest of the septum flattens out anteriorly to form a broad base against which the forked abortive accessory lamellae of the brachial valve, extending from the dorsal jugum, are pressed. This must have been useful as a stabilizing device to prevent the spiralia and jugum from moving when the shell was closed, and also to separate food currents produced by opposing lophophores (text-fig. 3). The teeth are short, solid (no lateral cavities), nearly vertical in growth and lack crenulated lobes or accessory lobes. On the inner margins of the teeth there are special hollows to accommodate the tips of the brachial valve’s socket plates, an unusual feature in most brachiopods (Pl. 6, fig. 1). It is possible that these are the ‘crural fossettes’ mentioned by Boucot *et al.* (1965, p. 648) but this would be a misnomer here because the crura never rest in these small hollows. The adductor muscle impressions are quite deep posteriorly and are separated by the median septum. Nevertheless the septum here is not so much a muscle separator, i.e. a myophragm, as a base of support for the jugum of the dorsal valve. In fact the term myophragm has been misused in the past and should really be dropped for spire-bearers unless there is definite proof that it served to separate the adductor muscles. The distal disappearance of the septum and broadening of the muscle scars is evident in text-fig. 3.



TEXT-FIG. 3. Serial sections of *Bifida lepida* (Archiac and Verneuil) of specimen illustrated on Pl. 4, figs. 5-8. Observe the critical development of the brachial apparatus, comparing with photographs on Pls. 5 and 6. Numbers refer to distance in mm from ventral apex. Scale  $\times 5$ .

In the brachial valve a very weak, small amorphous cardinal process is present only in the most apical portions (Pl. 5, fig. 3). The socket plates are solid, and curved slightly outwards in direction to accommodate the teeth from the opposite valve. The tips of socket plates fit into hollows on the inner margins of the teeth (Pl. 5, figs. 3-4). The crural bases appear less than 1 mm from the apex of the brachial valve, and they are tiny, slender wedge-like plates fixed to the inner and distal margins of the socket plates (Pl. 6, fig. 1). Within 0.5 mm or so of their starting-point on the socket plates, they curve around sharply more than  $90^\circ$  (like walking-cane handles), and they then turn into a rod-like shape (Pl. 5, fig. 4). Instead of continuing directly into spiralia structures, the crura make a very sharp bend to give off what are the beginnings of the spiralia and jugum. This portion of the brachidium, between the end of the crura and the point of junction of the jugum and spiralia, is called the umbonal blade.

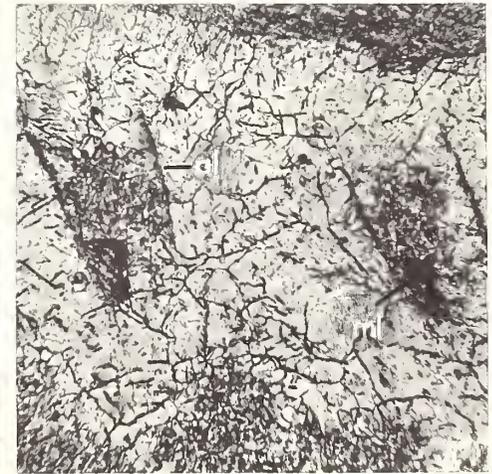
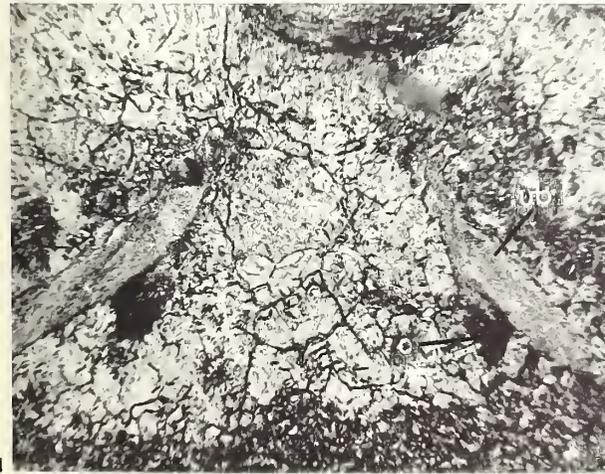
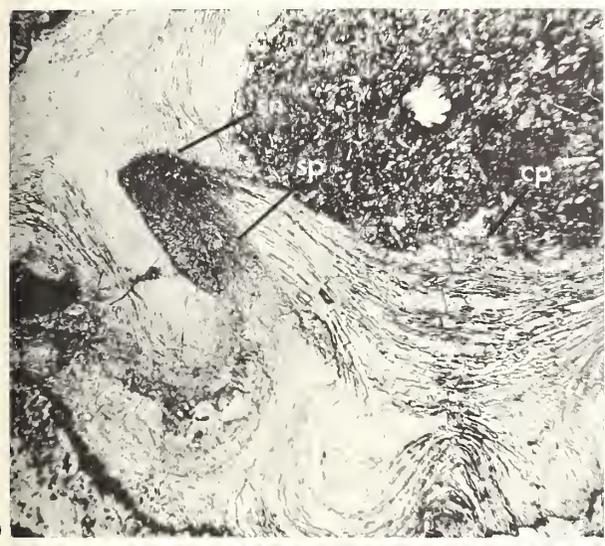
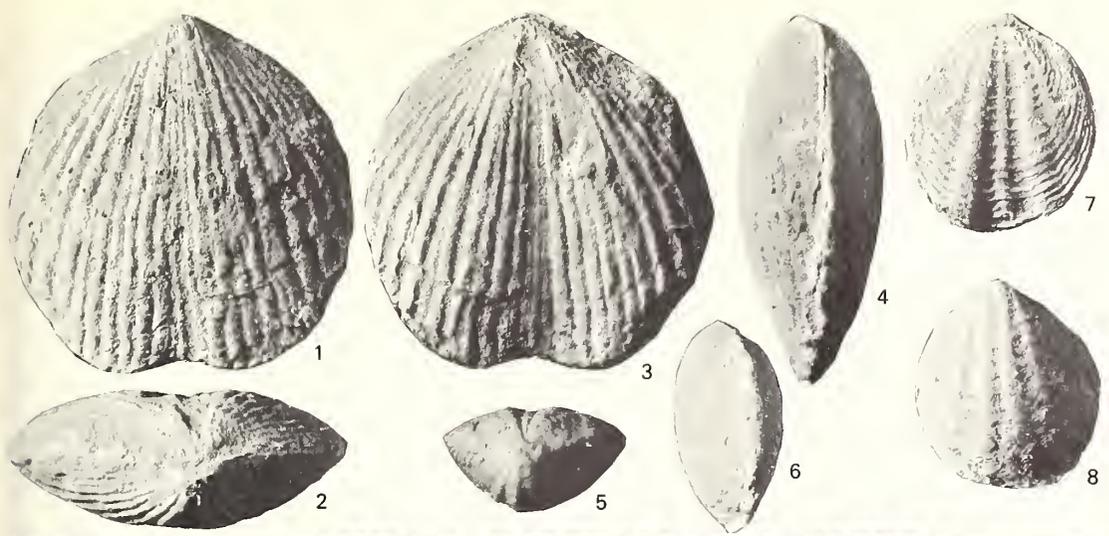
The jugum consists of an arched, angularly crested band that connects the spiralia (there is no indication of a break between the opposite sides). It is remarkable that the crest of the jugum splits off into two short prongs about 2 mm long (text-fig. 1). Each jugal prong is directed slightly towards the side, but is also pointed towards the ventral valve and the shell umbo. Then they stop abruptly in squared stubs, which appear to consist of resorbed calcite or carbonate tissue that is poorly defined or preserved. These two little prongs projecting from the jugum have given rise to the name *bifida*. They are very probably an abortive attempt at the growth of complete accessory lamellae, which are present in the genus *Kayseria*. This view is strengthened by the fact that almost identical jugal structures are present in *Kayseria* (compare Pl. 5, fig. 2 with Pl. 6, fig. 4). At the dorsal base of the jugum, where it is attached to the focal point of the umbonal blade and the beginning of the spiralium, each side of the jugum gives off another short, but more distinctly

#### EXPLANATION OF PLATE 4

*Kayseria dividua* (Schnur 1851), Upper Eifelian, Middle Devonian (Freilingen beds, Eilenberg horizon). Figs. 1-4. Ventral, posterior, dorsal, and lateral views of a typical specimen from the Eifel, MTB Dollendorf r53850:h74689, Germany. Hypotype BMNH:BB59010 ( $\times 4$ ). Figs. 9-12. Photographs of acetate peels of specimen BMNH:BB59010 shown above. 9, shows the hinge mechanism with socket plate (sp), notch for the socket plate in pedicle valve (sn), and cardinal process (cp). 10, shows the crus (c), tooth (t), and socket plate. 11, shows the terminus of crus, the umbonal blade attached to it (ub), and the ventral septum. 12, the double spiralia lamellae are separated into a thicker main lamella on the left (ml) and accessory lamellae on the right (al). All peel photographs approx.  $\times 40$ .

*Bifida lepida* (Archiac and Verneuil 1842), Upper Eifelian, Middle Devonian (Freilingen beds, Eilenberg horizon).

Figs. 5-8. Posterior, lateral dorsal and ventral views of a typical specimen (see Pls. 5 and 6 for serial peels of same specimen) from the Eifel, MTB Dollendorf r54460:h75550, Germany. Hypotype BMNH:BB58564 ( $\times 4$ ).



developed blade (here called the *jugal blade*). Each of these jugal blades is directed ventro-posteriorly towards the ends of the jugal prongs described above. But they are not connected to these prongs, stopping short at a point near the crural ends (text-fig. 1). The function of these two structures is unknown but it seems likely that they represent remnants of arrested accessory lamellae which are fused to the spirals instead of continuing freely parallel to the spirillum.

The spiralia contain 3 to 4 whorls. Each spiral lamella is double, with a lateral (or outer) and central (or inner) rim fused on the inner margins of the spiral coils (Pl. 6, fig. 2). The lateral rim of the double spirals is less well developed and occasionally becomes detached or lost completely. In three-dimensional view these spiral coils thus would resemble eavestroughs which had their open sides exposed on the outer parts of the spiral coils (i.e. concave outwards).

The double-sided spiral lamellae are very strong evidence in support of affinity with *Kayseria*. The genus *Bifida* may be visualized as a *Kayseria* in which the accessory lamellae have remained fused or become fused to the primary coils.

The only detailed information previously available on the inner structure of *Bifida* is that published by Siehl (1962, pl. 29, figs. 1-3). Siehl failed to notice the basic structure of the jugum, the jugal blades, the umbonal blades, the jugal prongs, or even the peculiar nature of the spiral lamellae. Biernat (1954, p. 518, fig. 17) illustrated sections of *Bifida* but no details are recognizable, nor were these described. Davidson (1882, p. 28), using preparations made by Glass, illustrated *Bifida* spiralia which show a coiling in exact reverse (!) to that determined in this paper. For example, Davidson's figure (ibid.) shows the right spirillum coiled counterclockwise, whereas it should be clockwise. The error was duplicated by Hall and Clarke (1893, figs. 114-121). In illustrating *Anoplothecca*, which is closely related to *Bifida*, Boucot *et al.* (1964, pl. 125, fig. 20) confirm a normal type of athyridid coiling with the right spirillum clockwise, such as shown in this paper (text-fig. 1).

*Comparison.* *Bifida lepida* differs from the Czechoslovakian species *B. dahlia* Havlíček 1956 in its less tubular, less marked ribs which also do not extend clearly to the commissure. Havlíček reports *B. lepida* from the Prokop limestones which lie below the Zlichov beds (Emsian) in which *B. dahlia* are found.

Schmidt (1951, pp. 91-93, pl. 1, figs. 5a-c) distinguishes her *Anoplothecca* (?*Bifida*) *nitida* from *B. lepida* by their larger size, a more rounded pedicle valve, and more distinct as well as different rib structure. No inner structures are mentioned. Schmidt's species was found in Upper Givetian rocks east of the Rhine.

I have not had the opportunity to compare *B. lepida* with *Anoplothecca levigata* Wolburg 1933 mentioned by Schmidt (ibid.).

Specimens labelled as *Bifida lepida* by Davidson (1882, pl. 2, figs. 13a-b) collected at Hope's Nose, Devon, England (probably from Late Eifelian beds), show a much more rounded brachial valve than Eifel *B. lepida* and additional development of

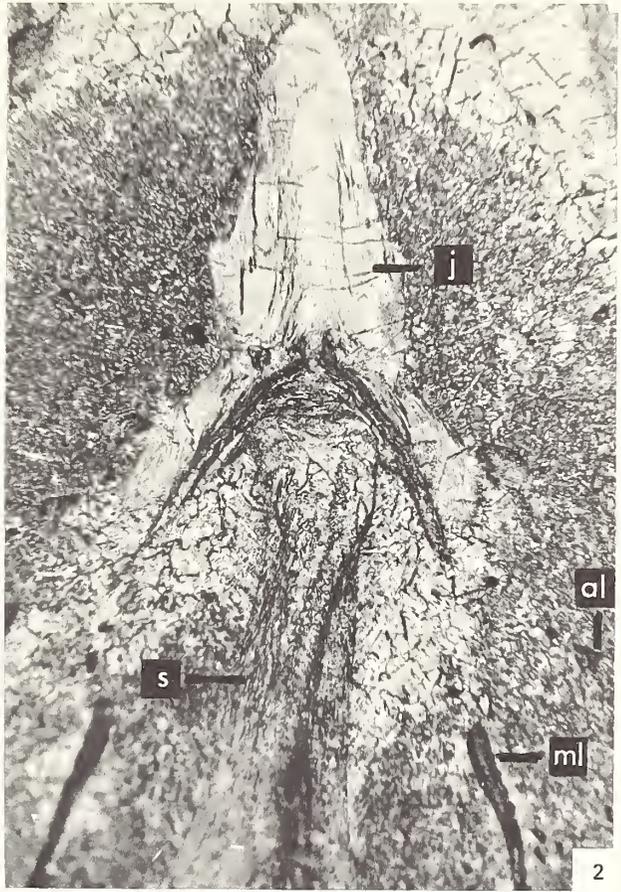
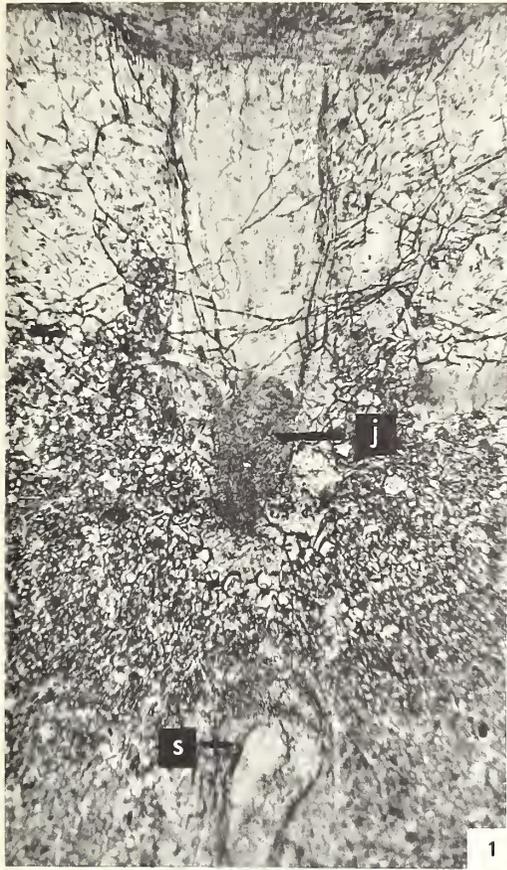
#### EXPLANATION OF PLATE 5

*Kayseria dividua* (Schnur 1851), Upper Eifelian, Middle Devonian.

Figs. 1-2. Photographs of acetate peel, of specimen shown in Pl. 4, figs. 1-4. 1, showing jugum (j) with a finely crystalline dorsal end and coarse ventral end which abuts the ventral septum, but is not fused to it. 2, more anteriorly taken, this view shows the jugum where it gives rise to the main lamella (ml) and accessory lamella (al). When the valves shut the jugum must be immobile. Scale approx.  $\times 40$ .

*Bifida lepida* (Archiac and Verneuil 1842), Upper Eifelian, Middle Devonian.

Figs. 3-4. Acetate peels of hypotype BMNH:BB58564 shown on Pl. 4, figs. 5-8. 3, view showing socket plate (sp) fitting into notch in pedicle valve, the cardinal process (cp), and ventral septum buried in calcite tissue. 4, beginning of crus (c) where attached to socket plate, and tooth, dorsal septum. Scale approx.  $\times 40$ .



more incised side ribs beside the main rib pairs. An earlier Davidson illustration of alleged *B. lepida* (1865, pl. 10, figs. 2, 2a) from near-by Barton is also different from true *lepida* in the same manner.

*Material.* For 8 specimens measured, average width 5.4 mm, length 5.8 mm, depth 3.0 mm.

Locality C317 (2 specimens), MTB Dollendorf r54460:h75550; C316 (1) r54530:h75590; C364 (1) r53650:h74580; C512 (1) r53850:h74680: all Freilingen beds. Locality C352 (1) r54940:h75890, Junkerberg beds. Locality C279j (1) r55960:h77380, Ahabach beds.

#### Family KAYSERIIDAE Boucot, Johnson, and Staton 1964

It may be better to regard the family Kayseriidae, with only a single genus *Kayseria*, as a subfamily of the Anoplothecidae to which they are most closely related. The main difference between these two families seems to be that in the Kayseriidae the accessory lamellae are separated from the main spiral lamellae, whereas in the Anoplothecidae they are fused together. Internal structures of members of both families are very similar (see Pls. 4 to 6).

The chief distinction of the Kayseriidae lies in the presence of separated double spiral coils directed latero-ventrally. In the Treatise (Boucot *et al.* 1965, p. 663), the double-spiralled Triassic athyridids which are the only other known brachiopods with double spiralia, are regarded as a subfamily of the single-spiralled Athyrididae. Schuchert (1894, p. 107) grouped Devonian *Kayseria* with the Triassic Diplospirellinae, but these genera are separated widely stratigraphically and it is difficult to demonstrate a genetic link for a time gap of about 150 million years. The development of double spirals may have been independent in unrelated stocks. Moreover, it is possible that the double spirals were developed in an entirely different fashion. The *Diplospirella* type of coil in Triassic forms may have evolved simply by prolonged extension of the accessory lamellae from the jugum right to the spiraliun apex (as suggested for *Kayseria* by Boucot *et al.* 1965, p. 649). But *Kayseria*'s double spirals may have arisen from a bifurcated jugal loop such as is known in some Silurian meristellids (Davidson 1882, pl. 5, figs. 13, 13a). Such a double jugal loop, if the dorsal end were extended parallel to the main spiral lamellae (instead of stopping), could have resulted in a new set of accessory lamellae of the *Kayseria* type. This is suggested by the spiral development of *Bifida*, in which the 'double loop' is broken but continues fused to the main spiral coils. A double loop of the meristellid sort is also known in the Devonian-Carboniferous *Camarophorella* group. It is of course feasible that a double jugal loop may also have been the starting-point of the Triassic double-spiralled forms.

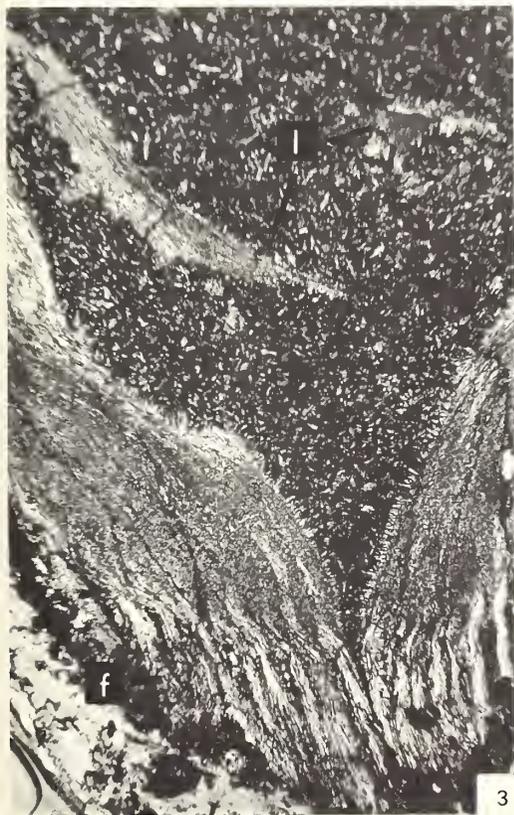
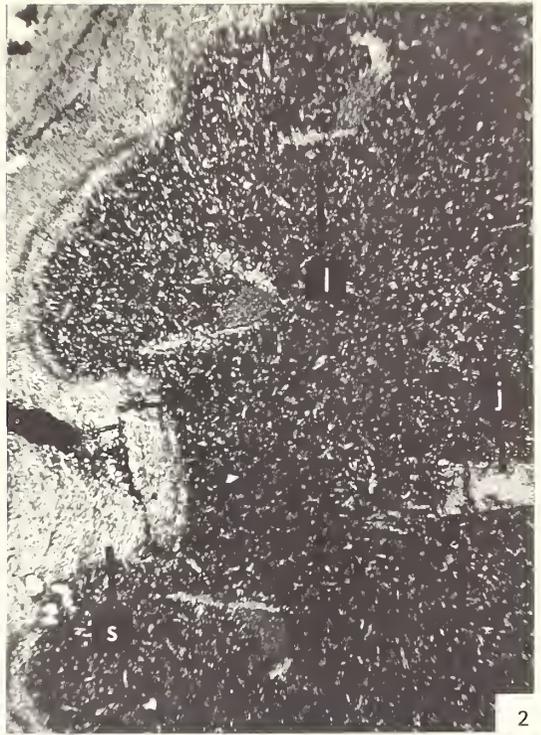
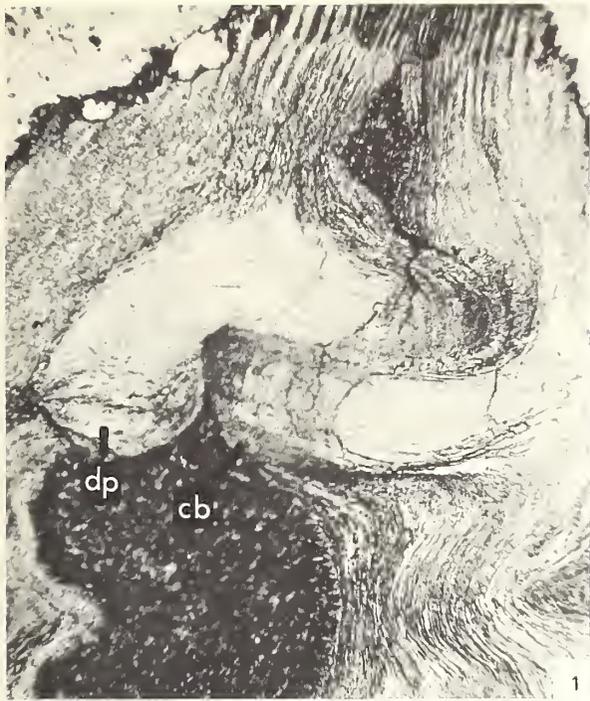
Placing the Kayseriidae in the suborder Atrypidina is a completely artificial assignment based only on the presence of surface ribbing. It should be abandoned. The

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#### EXPLANATION OF PLATE 6

*Bifida lepida* (Archiac and Verneuil 1842), Upper Eifelian. Middle Devonian.

Figs. 1-4. Acetate peels from BMNH:BB58564 shown on Pl. 4, figs. 5-8. 1, hinge mechanism with traces of crural base (cb) and dental pad (dp). 2, doubly edged spiraliun lamellae (l), trace of jugum (j) and ventral septum (s). 3, lateral portions showing frilly growth lamellae (f) and spiraliun lamellae. 4, view of jugum, jugal plate (jp), and dorsal septum (s). Scale approx.  $\times 40$ .



COPPER, *Bifida*

ventro-laterally directed spiralia, the typical athyridid jugum, the double spirals, the structure of the crura and socket plates all suggest affinities with the true spiriferids, and the suborder Athyrididina.

Genus *KAYSERIA* Davidson 1882

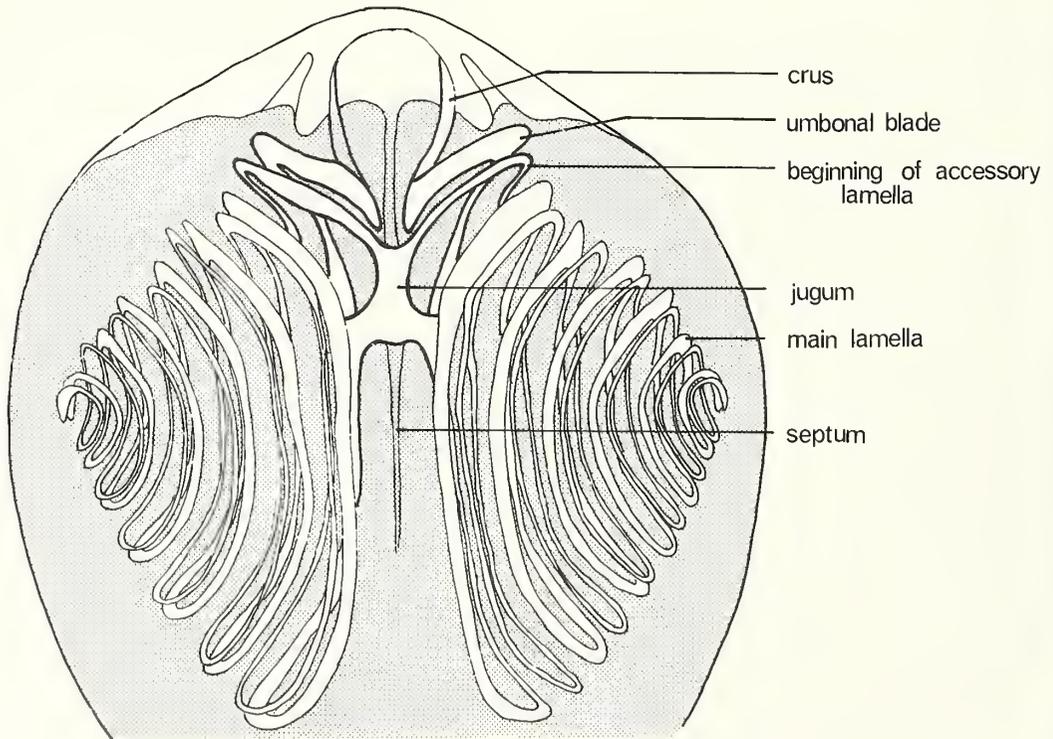
*Type species.* *Orthis lens* Phillips 1841, p. 65, pl. 26, figs. 110a-b.

*Range.* Eifelian.

*Distribution.* Eurasia.

*Diagnosis.* Relatively small, weakly biconvex, rather finely ribbed shells which occasionally preserve laterally directed frilly projections in rib troughs. Tiny beaks, minute foramens, no interareas and lack of deltidial plates are typical characters. Sulci present on both valves. Internally teeth massive, with notches for socket plate tips. Median septa occur in both valves, but more prominent in brachial valve. Spiralia begin with umbonal blades which are connected at sharp angle to crura instead of being crural continuations. Accessory lamellae stem from jugal saddle and are maintained separately to ends of spiral coils. Spiralia are latero-ventral, with about 6 double coils (text-fig. 4).

*Species included in genus.* *Orthis lens* Phillips 1841, *Terebratula dividua* Schnur 1851, *Kayseria alvea* sp. nov., *K. nohnensis* sp. nov.



TEXT-FIG. 4. Reconstruction of the brachial valve internal morphology of *Kayseria dividua* (Schnur) based on serial sections of specimen shown on Pl. 4, figs. 1-4. Scale  $\times 10$ .

*Kayseria lens* (Phillips 1841)

Plate 7, figs. 1-5

- 1841 *Orthis lens* Phillips, p. 65, pl. 26, figs. 110a, b.  
 1864 *Atrypa lens* Phillips, Davidson, pp. 51-52, pl. 10, figs. 1, 1a-d.  
 1882 *Kayseria lens* Phillips, Davidson, p. 21, pl. 2, figs. 11, 11a-c.  
 1966 *Kayseria lens* Phillips, House and Selwood, pl. 2, fig. 7.

*Type locality and stratum.* 'Hope, near Torquay' (Phillips, 1841, p. 65). This probably refers to the fossiliferous Eifelian limestones exposed on the seashore at Hope's Nose near Torquay, Devon. These limestones are probably of Freilingen age (Upper Eifelian in German reference section), as confirmed by *Kayseria*, and must overlie the *Gruenewaldtia*-bearing shales of Chercombe Bridge which are Middle Eifelian in age. If the species is rediscovered at Hope's Nose, a more precise type locality should be established (refer to House and Selwood, 1966, p. 55).

*Remarks.* Dr. D. E. Butler (pers. comm.) informed me that Phillips's syntypes were deposited in the Institute of Geological Sciences in London and supplied the following data. 'The only specimen of *Orthis lens* listed in our catalogues of that period are GSM6914, GSM50871, and GSM50872. GSM6914 has long been marked as figured by Phillips and by Davidson but the specimen is unlikely to have formed the basis of their drawings alone, as it is incomplete. Furthermore, it is probable that GSM50871-2 were included under the number 6914 before it became practice to give each specimen 2 separate numbers, especially as all three specimens were cited, until recent curation, on the same ancient museum tablet. It seems probable, therefore, that Phillips's figure 1102 and Davidson's figures are composite drawings based on all three.'

Lacking evidence to the contrary, it can be accepted that the specimens are originals from the Phillips collection, and are thus the syntypes described. Of the three specimens, all of which are damaged to some extent, GSM50872 is the best preserved and is selected as lectotype.

*Kayseria dividua* (Schnur 1851)

Plate 4, figs. 1-4, 9-12; Plate 5, figs. 1-2; Plate 7, figs. 9-11; text-figs. 2, 4, 5

- 1851 *Terebratula dividua* Schnur, p. 6.  
 1853 *Terebratula dividua* Schnur, pp. 179-180, pl. 24, figs. 2a-e.  
 1853 *Orthis eifliensis* Steininger, p. 80, pl. 5, figs. 5a-b.

*Type locality.* 'Schönecken, Prum, Gerolstein und bei Blankenheim' (Schnur 1853, pl. 180) and 'Weinsheim' (ibid., p. 234). It is impossible to establish the exact locality of Schnur's types, which are certainly not present in the Paläontologisches Institute and Museum, Berlin, DDR. (Hermann Jaeger, pers. comm.). A suitable designate type locality would be the north-east slope of Hönselberg, Dollendorf syncline, Eifel region (MTB Dollendorf r53850:h74680).

*Type stratum.* 'Im kalk . . .' (Schnur, 1853, p. 180). The most likely horizon where Schnur would have collected material would be the 'Crinoiden-Schichten' or crinoidal limestones which seem to have provided specimens for many early monographs. These beds are mainly of Freilingen (Upper Eifelian) age. The designated type locality is exposed on Hönselberg, in the Eifel, Germany (see above); the type stratum the Eilenberg horizon, Freilingen beds.

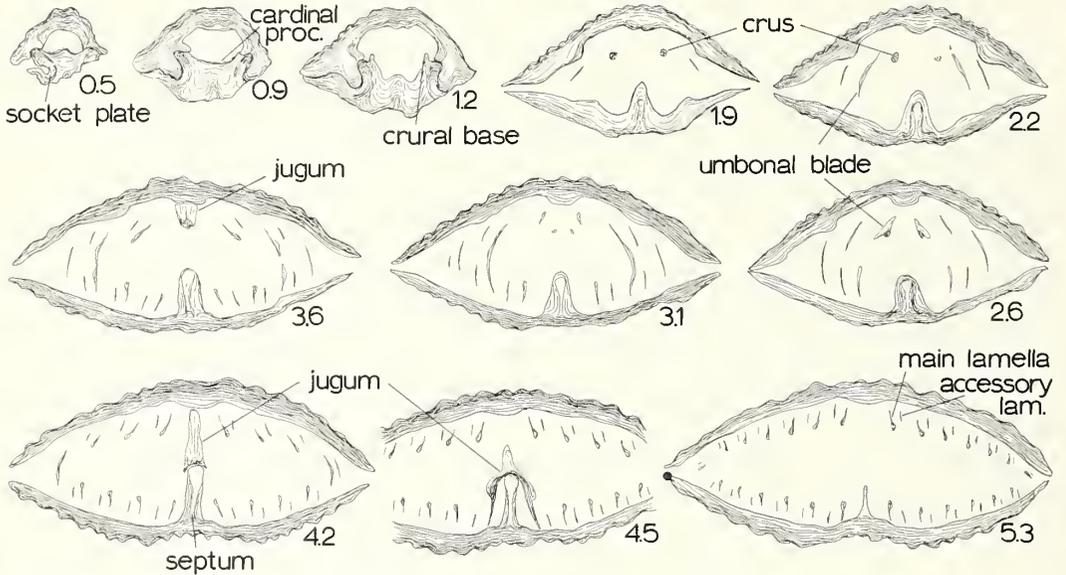
*Type material.* Holotype or syntypes apparently lost. I have selected two hypotypes for illustration which resemble Schnur's figures and are probably conspecific with them. These are BMNH:BB58558 (Pl. 7, figs. 9-11 which could be chosen as neotype if eventually the syntypes are proved to be destroyed or lost) and BMNH:BB58564.

*Diagnosis.* Small *Kayseria*, roughly as long as wide, somewhat well rounded in outline, but weakly biconvex in side view. Anterior commissure slightly lobed. Double sulcus weak with poorly defined ribs at sulcal margin. About 20 evenly sized ribs per mature specimen with 3-4 finer ribs located in the sulci. Frilly projections rare.

*External.* Shells are wider than long in early stages, but become equally long as wide or longer than wider after reaching 10 mm width. Maximum width less than 13 mm (see text-fig. 6).

*Internal.* Observations depend upon serial sections (text-fig. 5), shown in photographs on Pl. 4, figs. 1-4 and 9-12; Pl. 5, figs. 1-2.

There are no traces of deltidial plates, but a pedicle layer lines the delthyrial cavity. Teeth are short,



TEXT-FIG. 5. Serial sections of *Kayseria dividua* (Schnur) based on specimen shown on Pl. 4, figs. 1-4. Pay special attention to the labelled structures. Proc. refers to process, lam. refers to lamella. Note how the jugum is firmly held in place by the septa in both valves (section 4.2). Numbers refer to distance in mm from ventral apex. Scale  $\times 5$ .

#### EXPLANATION OF PLATE 7

All figures  $\times 2$ , except fig. 22,  $\times 10$  and figs. 23-36,  $\times 4$ .

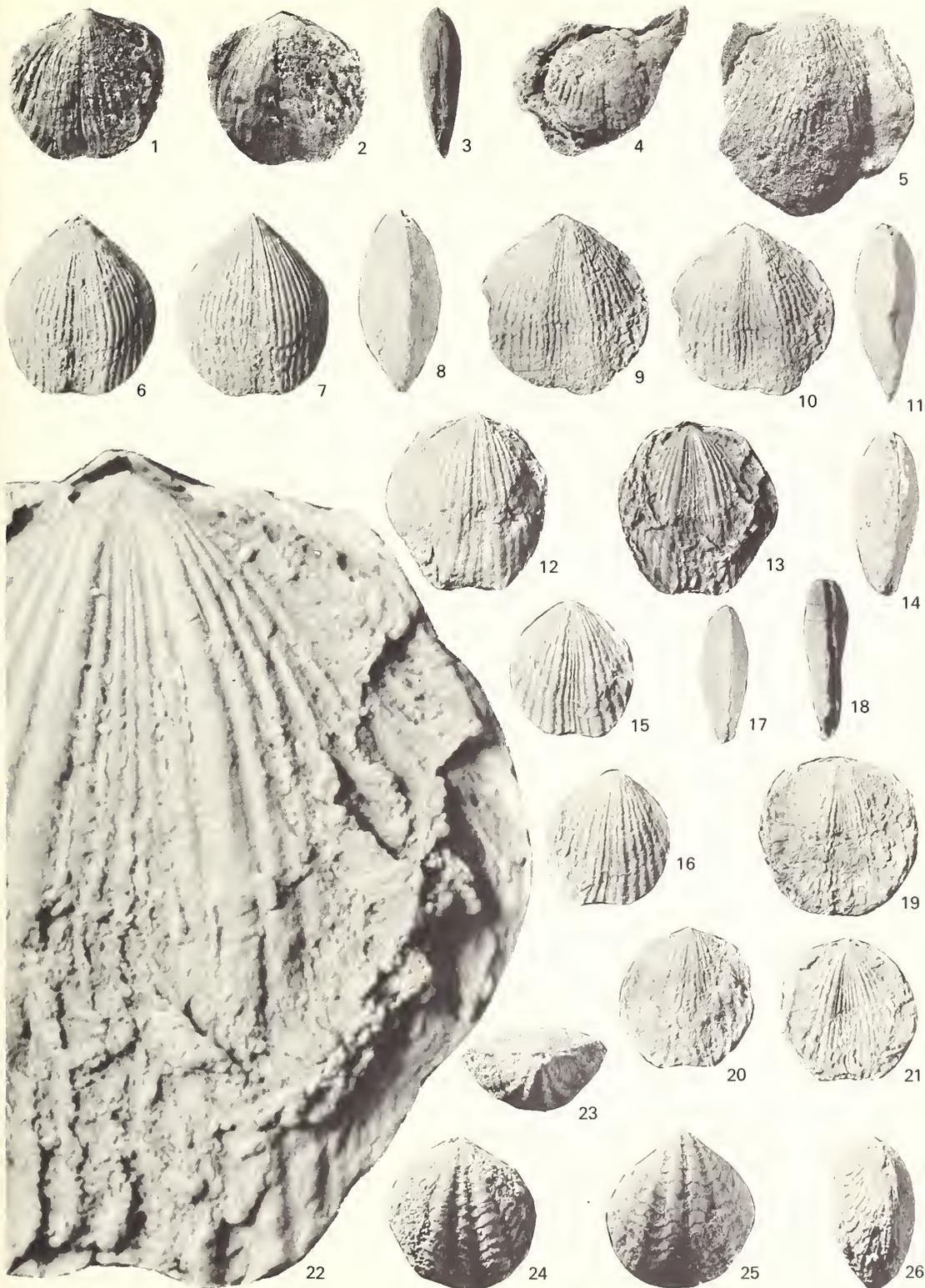
Figs. 1-5. *Kayseria lens* (Phillips 1841). Three syntypes from the Phillips collection taken from Hope's Nose, Torquay, Devon, and very likely of Upper Eifelian (specifically Freilingen) age. 1-3, Lectotype GSM50872, ventral, dorsal, and lateral views respectively. 4, small specimen GSM6914 showing the sulcus. 5, large specimen GSM50871, ventral view.

Figs. 6-8. *Kayseria nohnensis* sp. nov. Holotype BMNH:BB58563. Lower Eifelian, Nohn beds; Eifel, MTB Dollendorf r56980:h78350. Dorsal, ventral, and lateral views.

Figs. 9-11. *Kayseria dividua* (Schnur 1853). Hypotype BMNH:BB58558. Upper Eifelian, Freilingen beds; Eifel, MTB Dollendorf r53850:h74680. Dorsal, ventral, and lateral views.

Figs. 12-22. *Kayseria alvea* sp. nov. 12-14, Holotype BMNH:BB58559. Upper Eifelian, Ahabach beds; Eifel, MTB Dollendorf r55480:h77390; ventral, dorsal, and lateral views: 22, shows the frills in detail. 15-17, Paratype BMNH:BB58560; Upper Eifelian, Ahabach beds; Eifel, MTB Dollendorf r54550:h75730. Note the asymmetry common to this species; dorsal, ventral, and lateral views. 18-19, Paratype BMNH:BB58561 (same locality, horizon as 58560); this specimen clearly demonstrates the frilly projections covering the valves so that only the middle and posterior portions remain bared. Lateral and dorsal views. 20-22, Paratype BMNH:BB58562 (same locality, horizon as 58560); another specimen showing the external frills, this time clearly directed towards the shell hinge (!).

Figs. 23-26. *Bifida lepida* (Archiac and Verneuil 1842). Hypotype BMNH:BB58557. Upper Eifelian, Freilingen beds; Eifel, MTB Dollendorf r54460:h75550. Posterior, dorsal, ventral, and lateral views.



COPPER, *Kayseria* and *Bifida*

massive, and inwardly directed (no lateral cavities). Inner tooth margins are notched to accommodate tips of socket plates from the opposite valve. A median septum with a broad, flat or even concave crest presses directly against the dorsal jugal saddle when the valves are tightly closed (Pl. 5, fig. 1).

A small, delicate, ragged-edge cardinal process rests on the arch between socket plates. Tiny crura are fastened to the inner, ventral tips of the socket plates (Pl. 4, fig. 10). They project ventrally for 2–3 mm, then gradually bend around to meet the beginning of the spirallium, the umbonal blade (text-fig. 5, 2–6 mm). Crura disappear about 2·7 mm from the ventral apex (Pl. 4, fig. 11). Umbonal blades are first deflected towards the posterior shell margin, then curve back towards the anterior commissure and the dorsal valve floor in a line very close to the plane of symmetry (text-fig. 4). At about 4·5 mm from the pedicle valve apex, the jugum is thrust ventrally up from the umbonal blade, or the first main spiral coil. It projects ventrally until it touches the ventral median septum (Pl. 5, fig. 2), then it extends posteriorly towards the umbo to form the accessory lamellae. Accessory lamellae parallel the main spiral lamellae to the apices of the spiralia, at a constant distance of 0·4 to 0·5 mm (Pl. 4, fig. 12). The main lamellae have a thickened interior rim. The accessory lamellae are extremely thin and stay in a position directly across from the thin flanges of the main lamellae. Maximum coils 6 to 7.

*Comparison.* *K. dividua* and *K. lens* are superficially very similar, though adequate material for comparison of the latter is not yet available. The German *K. dividua* differs externally from *K. alvea* sp. nov. in being more rounded, generally smaller, and especially in having a rounded double sulcus which is not as clearly marked. The pedicle valve appears to have a slightly deeper sulcus. Frilly projections appear to be scarce or missing. Internal comparisons are not yet possible.

*Material.* Total 32 specimens. Freilingen beds, Eilenberg horizon C353 (3) MTB Dollendorf r54340:h75320; C360 (2) r53880:h74660; C512 (3) and C359 (11) r53850:h74680; C316 (6) r54530:h75590; C305 (4) MTB Hillesheim r52830:h73780; C361 (1) r53810:h74630.

Others provisionally assigned: C289 (1), Ahrdorf beds (top), MTB Doll r56930:h78800; C513 (1), Junkerberg beds (middle), MTB Prüm r34660:h64590.

Width-length relationships with increase in size are shown in text-fig. 6. Maximum width 12·6 mm, maximum length 13·7 mm, maximum depth 5·4 mm. Average width 10·6 mm, average length 10·4 mm, average depth 4·4 mm.

### *Kayseria alvea* sp. nov.

Plate 7, figs. 12–22; text-fig. 6

*Type locality.* Hillesheim syncline, Eifel, Germany, south-west slope of Mühlenberg, MTB Dollendorf r54550:h75730.

*Type stratum.* Mullert horizon (Upper part?), Ahabach beds, Upper Eifelian.

*Range.* Ahabach beds, Upper Eifelian (stratigraphically above Freilingen with *K. dividua*).

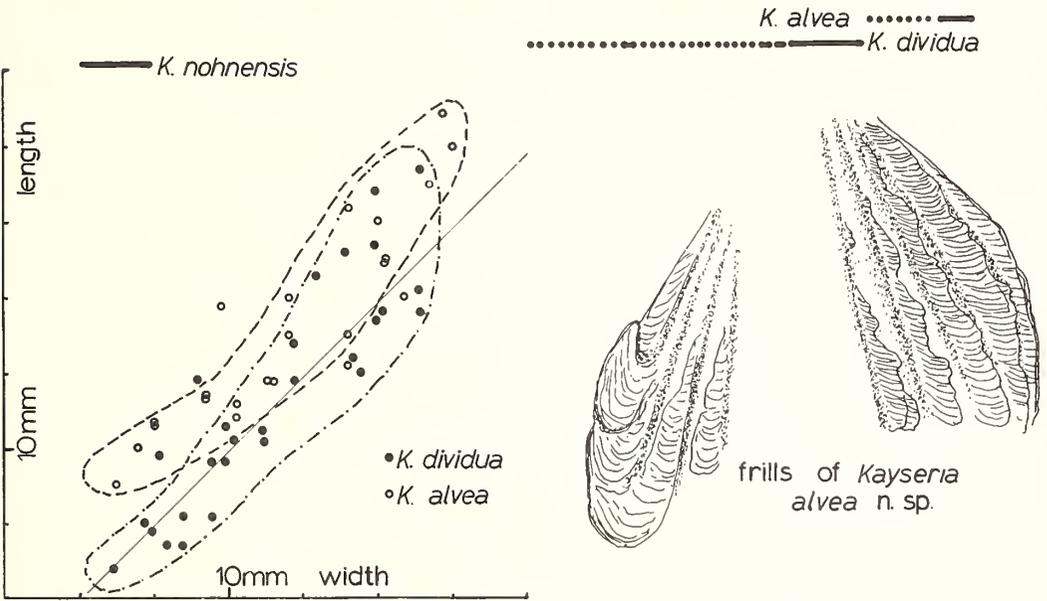
*Distribution.* Eifel, Germany.

*Type material.* Holotype BMNH:BB58559; paratypes BMNH:BB58560–58562.

*Diagnosis.* Shells flat, longer than wide, margins of sulcus on both valves sharply defined by 2 strong ribs, with 4–6 delicate ribs in dorsal sulcus. Very prominent frilly projections on most shells concentrated in rib troughs, especially around commissure.

*External.* Scatter diagrams (text-fig. 6) show that on average shells are longer than wide in comparison to shells of *K. dividua* (Schnur). Because of the frilly projections, sometimes covering the whole shell rib counts are very difficult to make. On the whole, there is a much greater size difference in ribs located in the sulci and the ribs located lateral to the sulci which are always longer. This difference in rib size is less marked in the stratigraphically older species *K. dividua* and *K. nohmensis*.

EIFELIAN											GIVETIAN
LAU.	NOHN				AHRDORF			JUNKERBERG		FREI.	
											Mullert
											Lahr
											Haller
											Nollenbach
											Eilenberg
											Giesdorf
											Nims
											Recher
											Hönselberg
											Mussel
											Klausbach
											Niederere
											Wasen
											Flesten
											Köll
											Bildstock
											Hundsdell
											Dankerath
											Hunnertsberg
											Erdel
											Markstein
											Schmitzbach
											Schleit
											Weilersbach
											Dorsel
											Wolfenbach



TEXT-FIG. 6. Composite diagram showing the stratigraphic ranges of the three *Kayseria* species in the Eifel region, (top) the width/length ratios of *K. alvea* and *K. dividua* (the diagonal line represents the line where width equals length) and to the right sketch diagrams of the frills of two specimens of *K. alvea* (scale  $\times 5$  approx.).

Frilly projections of *K. alvea* are extremely unusual and seem to be unknown in any other brachiopods except the Devonian *Leptocoelia* from North America. They are more or less flat-lying, pressed against the shell surface, are usually absent in the postero-central parts of the valves (presumably they are worn down with age) and tend to grow primarily out of the rib troughs (see text-fig. 6; Pl. 7). The crystalline fibres of the frills are directed towards the sides at a greater angle than the direction of the ribs themselves. Towards the hinge area and the postero-lateral margins the tips of these fibres are redirected towards the hinge instead of anteriorly. They could therefore have served as anchoring devices. In *Leptocoelia* (from James Hall's type collection) I have seen specimens which show very similar structures along the hinge line (Hall and Clarke 1893, pl. 53, fig. 47).

*Internal.* No serial sections were made.

*Comparison.* The thick rib pair lining the sulci on both valves, the larger ribs at the sides, the delicate ribs inside the sulci, the greater length:width ratio, and

the prominent frill development (which may also be a preservational factor), distinguish this species from *K. dividua* (Schnur) and *K. nohnensis* sp. nov.

*Material.* Müllert horizon, Ahbach beds, Upper Eifelian. 24 specimens (see text-fig. 6 for width and length dimensions). C279i (9). MTB Dollendorf r55480:h77390; C279j (7) r55460:h77380; C321 (7) r54550:h75730; C412 (1) r54900:h77960.

Maximum width 13.0 mm, maximum length 14.5 mm, maximum depth 5.1 mm. Average width 10.9 mm, average length 11.7 mm, average depth 3.7 mm.

*Kayseria nohnensis* sp. nov.

Plate 7, figs. 6–8

*Derivation of name.* After the town Nohn, less than 1 km to the west of the type locality, Eifel, Germany.

*Type locality.* Cut on Nohn–Dankerath road, MTB Dollendorf r56980:h78350, almost at type locality of Weilersbach horizon, Nohn beds, Hillesheim syncline, Eifel, Germany.

*Type stratum.* Weilersbach horizon, basal Nohn beds, Lower Eifelian, Middle Devonian.

*Range.* Nohn beds, Lower Eifelian. The genus *Kayseria* is very scarce below the Upper Eifelian and the true range of *K. nohnensis* is uncertain.

*Distribution.* Eifel, Germany.

*Holotype.* BMNH:BB58536.

*Diagnosis.* More globose *Kayseria* with pointed beaks, less squared outline, relatively fine ribs over the whole shell, weaker sulci on both valves.

*External.* The limited material makes the range of variation unknown. On the holotype there are 26–28 fine ribs on the shell with rib size increasing towards the sulci, but not markedly. Ribs are slightly finer in the troughs and about 4 occur there. The sulci on both valves leave the typical indentation on the anterior commissure. Poorly preserved frills are present on the brachial valve of one specimen. The shell has a pointed beak outline, but the ventral beak itself does not project more than normal for *Kayseria* (i.e. less than 1 mm).

*Internal.* No serial sections made.

*Comparison.* The diagnosis describes the difference between other species which mainly concern the more globose shell, a pointed beak, finer ribs, and narrow outline.

*Material.* Weilersbach horizon, Nohn beds, Lower Eifelian. Two specimens from type locality and also C284 C (2) MTB Dollendorf r56900:h78130. Holotype width 11.2 mm, length 13.3 mm, depth 6.0 mm (thickest of known *Kayseria* in the Eifel region).

## CONCLUSIONS

Both *Kayseria* and *Bifida* display distinctive non-atrypid characters (defining true atrypids as spire-bearers with dorsally directed spiralia). These characters are:

1. Wedge-like crural bases instead of ball-like crural bases as in atrypids.
2. Sharp deflection from the ends of the crura to the beginning of the spiralia instead of direct continuation.
3. Fused, ventrally arched jugum, instead of separate jugal processes as present in nearly all Siluro-Devonian atrypids.

4. Posterior extension of the jugum to form accessory spiral lamellae (*Kayseria*), absent in atrypids.
5. Short rudimentary accessory lamellae extending from the dorsal base of the jugum (*Bifida*), absent in atrypids.
6. Vento-laterally directed spiralia which are mirror image, 'inside-out' opposites of atrypid spiralia.
7. Plane of spiral ribbons convex inwardly, versus outwardly in atrypids.
8. True septal structures with reinforcing rods, instead of simple calcite tissue built on the shell wall as in atrypids.

These are major points of comparison with the athyridid brachiopods and are absent in true atrypids of any age known thus far.

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PAUL COPPER

Department of Geology  
Laurentian University  
Sudbury, Ontario

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# LAPWORTHELLIDS FROM THE LOWER CAMBRIAN *STRENUELLA* LIMESTONE AT COMLEY, SHROPSHIRE

by S. C. MATTHEWS

ABSTRACT. A sample of some 10 kg from the *Strenuella* Limestone (Lower Cambrian) of Comley, Shropshire, etched in 10% acetic acid, has produced over 1000 small fossils. These include 281 specimens of *Lapworthella dentata* Missarzhevsky. *L. nigra* Cobbold, already known from higher in the Comley succession, was not found in this sample. *L. dentata* typically occurs in the upper part of the Atdabanian Stage in Siberia.

CALLAWAY (1877) was first to recognize the presence of Cambrian rocks in the Comley area of Shropshire, and Lapworth (1888) first to identify the Lower Cambrian there. The major contribution on the Cambrian of Shropshire came in E. S. Cobbold's series of papers published 1909–1936. Descriptions of the succession of rocks at Comley and of the general geological setting of the area are available in Whittard *et al.* (1953) and in Greig *et al.* (1968). It would be appropriate to make special note here of two records of fossils obtained by etching limestone from Comley. Walliser (1958) collected a phosphatic problematicum, *Rhombocorniculum comleyense*, from a sample taken at Comley Quarry, and Reid (1959) found there *Chancelloria*, a heteractinellid sponge.

During 1962 the author visited Comley in the company of Dr. J. W. Cowie and Messrs. T. R. Fry and M. White, and assisted in reopening Cobbold's Excavation No. 2, situated 200 yards south of Comley Quarry (Cobbold 1909, p. 6; 1916, p. 4; 1925, pp. 371–372; 1927, p. 553; and especially 1933, pp. 473–476). At Excavation No. 2 it is possible to uncover a section which includes the *Strenuella* Limestone (Ac<sub>4</sub> in Cobbold's notation and the *Protolenus* Limestone (Ac<sub>3</sub>). According to Cobbold these two units are almost entirely faulted out of the section exposed in Comley Quarry itself. A sample (approx. 10 kg) of the reddish-grey *Strenuella* Limestone from Excavation No. 2 was placed in 10% acetic acid, and the residue washed and then screened between 10- and 125-mesh sieves. The residue consisted mainly of fossil debris, much of it phosphatized. No attempt was made to concentrate a heavy fraction by flotation since there seemed to be little reason for discarding the incompletely phosphatized (and therefore relatively light) material present. Grains of phosphate and of glauconite were fairly common and some iron-manganese mineralization is also seen.

Picking from the considerable bulk of this residue has proceeded at various times during the last 10 years and the author's collection from the *Strenuella* Limestone now includes between 1100 and 1200 small fossils. Among them are trilobites (cephala, pleura, and pygidia—254 items), brachiopods (2), gastropods (14, most as phosphatic external moulds), sponges (10), hyolithids and hyolithellids (together 551, many fragmentary), and lapworthellids (281). Cobbold's faunal list for the *Strenuella* Limestone, Ac<sub>4</sub> (Cobbold 1921, p. 371), has more specific detail of

trilobites, brachiopods, hyolithids, and hyolithellids than is offered here, but makes no mention of gastropods, sponges, nor lapworthellids. The lapworthellids now available are the subject of this paper. It is hoped to supply information on the other groups represented in the new collection at a later date.

#### THE PRESENT RECORD OF OCCURRENCE OF THE GENUS *LAPWORTHELLA*

The type of *Lapworthella* is *L. nigra* (Cobbold 1921, p. 359) from the *Lapworthella* Limestone (Ad), which Cobbold took to be the highest unit in the Lower Cambrian succession at Comley. The new finds in the *Strenuella* Limestone provide a lower record of the genus than was previously available from this particular area. However, Cobbold and Pocock (1934, p. 322) encountered *L. nigra* in Ac<sub>4</sub>, Ac<sub>5</sub>, and Ad at Rushton in the Wrekin area, and Rozanov and Missarzhevsky (1966, p. 93) mention that they obtained a *Lapworthella* cf. *nigra* from a Comley sample put at their disposal by Prof. R. Koslowski.

The recent Russian literature refers to various forms of *Lapworthella* found in successions of early Cambrian age on the Siberian Platform. Missarzhevsky (1966) produced the first report of lapworthellids from Siberia and erected two new species, *Lapworthella tortuosa* and *L. bella*. These are from the Tommotian Stage, i.e. from lower horizons than those from which Missarzhevsky (in Rozanov *et al.* 1969, p. 164) later obtained *L. dentata*. Meshkova (in Zhuravleva *et al.* 1969) described three other species (*L. lucida*, *L. marginata*, and *L. corniforma*), also from Siberia. In 1967 Rozanov published a review (in English) of the work done on the Siberian faunas that contain lapworthellids. Bengtson (1968, 1970) has described Swedish representatives of some of the elements of these faunas, and Zakowa and Jagielska (1970) have discussed Polish material; but there is as yet no published record of actual lapworthellids from Sweden or Poland.

One should mention here what may be two further records of occurrence of *Lapworthella*. First, there is the material from Bornholm in which Poulsen (1942) identified four new species of Cobbold's (1935, p. 43) genus *Stenothecopsis*. According to Missarzhevsky (1966, fig. 1) these are lapworthellids. Second, Lochman's (1956) *Stenothecopsis schodackensis* may also be a lapworthellid. Missarzhevsky (1966, fig. 1), Rozanov and Missarzhevsky (1966, p. 92), Missarzhevsky and Rozanov (1968, Table 3), Missarzhevsky (in Rozanov *et al.* 1969, pp. 163–164) are consistently (despite occasionally irregular renderings of the American specific name) of this opinion. An answer to these questions of generic identity may emerge as information accumulates on the range of variation of lapworthellids. Further guidance may come from material (at present under preparation) which the author has collected at what can be presumed to be the type locality for *Stenothecopsis*, near Ste Geniès de Varen-sal, Hérault, France.

Though Rozanov and Missarzhevsky (1966, p. 93) recorded an *L. cf. nigra* from the Kameshkov horizon in the Altai, the work in Siberia has so far produced no firm identification of *L. nigra*, and therefore no clear indication of an equivalent of Cobbold's *Lapworthella* Limestone (Ad). However, the lapworthellids from the slightly older *Strenuella* Limestone of Comley compare well with the *L. dentata*

found in the upper part of the Atdabanian Stage in Siberia, and so establish a link between the Siberian stratigraphy and a classical western European Cambrian sequence.

#### SYSTEMATIC DESCRIPTION

##### Phylum and class uncertain

##### Order TOMMOTIIDA Missarzhevsky 1970 (replacement name for CAMENIDA Missarzhevsky 1969)

*Diagnosis* (after Missarzhevsky, in Rozanov *et al.* 1969, p. 161, as Camenida Missarzhevsky ord. nov.). Small (a few mm long), phosphatic, conoidal, pyramidal shells with sloping walls, usually asymmetrical.

*Remarks.* The order contains the two families Lapworthellidae Missarzhevsky 1966 and Tommotiidae Missarzhevsky 1970 (replacement name for Camenida Missarzhevsky 1969). Bengtson (1970) offered an alternative view of the way in which these families might be allotted to orders: he found that the two families Tommotiidae and Tannuolinidae Fonin and Smirnova 1967 constitute a natural group with well-defined features, and proposed the Order Mitrosagophora to contain them. This order, he observed, would not satisfactorily accommodate the Lapworthellidae. He did not think it worth while to maintain Missarzhevsky's order Tommotiida (i.e. Camenida Missarzhevsky 1969, with the name changed as a consequence of Missarzhevsky's substitution of the generic name *Tommotia* in 1970 for *Camena* pre-occupied). The reference to the Order Tommotiida made here should not be thought to imply rejection of Bengtson's interesting and well-argued proposals. Missarzhevsky's sense of the ordinal grouping is preferred because it is the more convenient one. It makes it possible to avoid for the present any commitment to, say, an Order Lapworthellida, and it is convenient again in that using Missarzhevsky's systematic terms, one may refer without hindrance to Missarzhevsky's stratigraphic proposals.

##### Family LAPWORTHELLIDAE Missarzhevsky 1966

*Diagnosis* (after Missarzhevsky 1969). Small, multilayered shells, pyramidal or cornute in form, composed of calcium phosphate. External surface with transverse sculpture which has almost no representation on the internal surface of the shell. Aperture at right angles (or only a small angle from that) to the axis of the shell, and with an outline ranging from ovate to rounded rectangular. Initial part of the shell tends to be pointed.

*Remarks.* Missarzhevsky (1966) referred Cobbold's two genera *Lapworthella* and *Stenothecopsis* to this family. In another paper published during that year (Missarzhevsky, in Rozanov and Missarzhevsky 1966), *Camena* Miss. (now *Tommotia*), *Camenella* Miss., and *Kelanella* Miss. were also allotted to the Lapworthellidae. Meshkova (in Zhuravleva *et al.* 1969, p. 166) again referred these five genera to the Lapworthellidae, although Missarzhevsky (in Rozanov *et al.* 1969, p. 162) was by this date including only *Lapworthella*, *Stenothecopsis*, and *Fomitchella* Miss. in the family, and was of the opinion that *Camena* (now *Tommotia*), *Camenella*, and *Kelanella* were better placed in the family Camenidae.

##### Genus LAPWORTHELLA Cobbold 1921

*Type species* (by original designation). *Lapworthella nigra* Cobbold 1921.

*Diagnosis.* See Cobbold 1921, p. 359.

*Remarks.* Seven species are known. If, as Russian authors have suggested, Poulsen's (1942) and Lochman's (1956) stenothecopsids are lapworthellids, the number of species would rise to 12. In that situation, however, it would become necessary to ask whether all of Poulsen's species should stand. Lochman (1956,

p. 1395) has already remarked that Poulsen was perhaps not justified in separating species on the basis of slight changes in the shape of the assumed aperture. Poulsen's stenotheopside species, if transferred to *Lapworthella*, would need to be checked against Cobbold's *L. nigra* and also against the more recently proposed Siberian forms.

Cobbold, in his diagnosis of the genus, observed that the shell of *Lapworthella* has two layers: an inner, of 'medium' thickness, and a very much thinner chitinous outer layer. Missarzhevsky (1966) refers to a more massive outer layer and a 'platy' inner layer in *L. tortuosa*—it seems obvious that these cannot be the same two layers that Cobbold mentioned. Lochman has described *Stenotheopsis* as having a 3-layered shell. The Stereoscan work done so far on the *Strenuella* Limestone lapworthellids brings no new information to bear on these questions. The shell-structure will be understood only when fine details have been studied with due regard to the possibility that certain features of the fabric may have arisen during diagenesis. Good information on primary fabric may eventually give some guidance on the affinities of the lapworthellids. The present state of this question is seen in the treatment given to *Lapworthella* in the *Treatise of Invertebrate Paleontology (W)*, where Fisher (with a clear expression of his doubts) lists *Lapworthella* among the small conoidal shells whose affiliations are unknown at all levels up to and including phylum, and Howell (also making clear his doubts) includes *Lapworthella* among the worm order Sedentaria. The genus *Stenotheopsis*, which, it is generally agreed, may be a close relative of *Lapworthella*, has been referred tentatively to the Crustacea by Cobbold and Poulsen, and Fisher (1962) mentions phoronid, entoproctid, conulariid, and molluscan relationships as open, if not strong, possibilities. Müller (1966, 1971) has suggested that *Stenotheopsis* belongs among the paraconodonts (Müller 1962), although Müller and Nogami (1971), in an emended account of the suborder Paraconodontida, do not include *Stenotheopsis* in the list of constituent genera. An attribution to the paraconodonts would not, of course, immediately throw light on the zoological affinities of *Stenotheopsis*, nor, even indirectly, on those of its presumed relative *Lapworthella*.

### *Lapworthella dentata* Missarzhevsky 1969

Plate 8, figs. 1-16; Plate 9, figs. 1-12

v\*1969 *Lapworthella dentata* Missarzhevsky, 164, pl. 6, figs. 9, 14 (holotype), 19.

*Material.* 281 specimens. Figured specimens (numbers prefixed BU) are in the collections of the Geology Museum, University of Bristol.

*Description.* Small cornute phosphatic shells. Transverse section rounded near pointed (apical) end, may approach rectangular form near open (apertural) end. External surface regularly ribbed, each rib more or less regularly toothed (cog-like) along its apically directed free edge. Best developed teeth (seen on the most widely-developed shells) are recurved toward the apex. Internal surface relatively smooth, has low-relief bands which occur at same frequency as external ribs, and which like these are disposed at right angles to the curved axis of growth.

*Measurements* (mm). Abbreviations are: *L* = length, *Aw* = apertural width (i.e. the dimension measured left to right at the aperture of a specimen seen as in Pl. 8, fig. 13), *Ad* = apertural depth (i.e. the dimension

#### EXPLANATION OF PLATE 8

Figs. 1-16. Stereoscan micrographs of specimens of *Lapworthella dentata* Missarzhevsky. 1, BU 22182,  $\times 25$ . 2, BU 22183,  $\times 28$ . 3, BU 22181,  $\times 40$  (detail on Pl. 9, fig. 12). 4, BU 22180,  $\times 40$ . 5, BU 22177,  $\times 32$ . 6, BU 22178,  $\times 22$  (detail on Pl. 9, fig. 10). 7, BU 22179,  $\times 27$ . 8, BU 22187,  $\times 55$ . 9, BU 22188,  $\times 37$ . 10, BU 22184,  $\times 22$  (detail on Pl. 9, figs. 1, 2, 4, 7). 11, BU 22185,  $\times 24$ . 12, BU 22189,  $\times 45$ . 13, BU 22190,  $\times 30$  (detail on Pl. 9, fig. 11). 14, BU 22191,  $\times 26$  (detail on Pl. 9, figs. 3, 5, 6, 8). 15, BU 22192,  $\times 33$  (detail on Pl. 9, fig. 9). 16, BU 22186,  $\times 24$  (note banded internal surface). All from the *Strenuella* Limestone (Ac<sub>4</sub> of Cobbold), Lower Cambrian, Comley, Shropshire.



MATTHEWS, *Lapworthella dentata*

measured left to right at the aperture of a specimen seen as in Pl. 8, fig. 12), *Nr* = number of ribs, *Nt* = number of teeth on the immediately pre-apertural rib.

	Plate reference	<i>L</i>	<i>Aw</i>	<i>Ad</i>	<i>Nr</i>	<i>Nt</i>
BU 22178	Pl. 8, fig. 6	1.9	0.55	0.55	10	27
BU 22184	Pl. 8, fig. 10	1.9	0.95	0.95	12	38
BU 22190	Pl. 8, fig. 13	1.52	1.15	0.5	18	35
BU 22189	Pl. 8, fig. 12	1.15	1.15	0.5	11	39
BU 22187	Pl. 8, fig. 8	0.75	0.8	0.5	6	27
Holotype		1.10	0.45	0.35	8	*

Holotype measurements from Missarzhevsky 1969, p. 164.

\* Missarzhevsky gives a reading (20–30) for the number of teeth per millimetre. He also gives a reading for wall-thickness (0.02–0.03 mm) which can be compared with 0.05 mm (at a rib) and 0.02 mm (inter-space) for the specimen shown on Pl. 8, fig. 16.

*Remarks.* The identification is based on the fact that *Lapworthella dentata* is so far the only described species of the genus which has toothed ribs. The terms of the description above depart from the exact detail of Missarzhevsky's description (Missarzhevsky 1969, p. 164) in two relatively trivial respects only. Missarzhevsky described the internal surface merely as smooth. Here a shallow banding (Pl. 8, fig. 16) of the internal surface is noted. Missarzhevsky, referring to 30 specimens, described the curvature as weak. Here (281 specimens) it can be seen that the curved growth axis may have a cumulative redirection of more than 90°.

Missarzhevsky has suggested that *L. dentata* has more resemblance to *L. chodaca* (Loch.) (i.e. Lochman's *Stenothecopsis schodackensis*) than to any other described species. Size, general form, and the outward tapering of the ribs are said to match, but the cog-teeth on the edges of the ribs of *L. dentata* provide a clear means of distinguishing the two.

The Comley representatives of *L. dentata* all satisfy the terms of the description given above. They are, nevertheless, widely variable:

1. The axial curvature may vary from about 35° (Pl. 8, fig. 5) to about 110° (Pl. 8, fig. 15); and the apical part of this same individual shown on Pl. 9, fig. 9).
2. The ratio of shell length:apertural width (see table of measurements above) is widely variable. The specimen shown on Pl. 8, fig. 8 is the minimal case found. Shells in which this ratio is low (i.e. which have a relatively large angle of increase)

#### EXPLANATION OF PLATE 9

Figs. 1–12. *Lapworthella dentata* Missarzhevsky. Stereoscan micrographs to illustrate local details of certain of the specimens figured on Pl. 8. 1, 2, 4, 7, BU 22184 (see Pl. 8, fig. 10): 1, apertural detail,  $\times 75$ ; 2, detail of fourth rib from (broken) adapical end,  $\times 200$ ; 4, detail of seventh and eighth ribs,  $\times 100$ ; 7, detail of fourth, fifth, and sixth ribs,  $\times 100$ . 3, 5, 6, 8, BU 22191 (see Pl. 8, fig. 14): 3 ( $\times 220$ ), 6 ( $\times 290$ ), detail of curved teeth found on ribs situated near apertural end; 5 ( $\times 120$ ), detail of teeth at approximately two-thirds length from apical end; 8 ( $\times 500$ ), detail of single tooth situated immediately below centre in fig. 5. 9, apical detail ( $\times 200$ ) of BU 22192 (see Pl. 8, fig. 15). 10, apical detail ( $\times 100$ ) of BU 22178 (Pl. 8, fig. 6). 11, apical detail ( $\times 170$ ) of BU 22190 (Pl. 8, fig. 13). 12, apical detail ( $\times 160$ ) of BU 22181 (Pl. 8, fig. 3).



MATTHEWS, *Lapworthella dentata*

tend to achieve eventually a rectangular apertural outline. Their toothed ribs are more powerfully developed and the teeth found in the relatively wide, adaperturally situated part of the shell can (as Missarzhevsky observed) show an adapically directed recurvature. Shells with a large angle of increase may also show a minor rib developed under the curving teeth of the major rib (Pl. 9, figs. 5, 8).

3. The apertural margin may vary in outline from rounded to near-rectangular, and may not lie entirely within one plane (see Pl. 8, fig. 10, and note the corresponding layout of the ribs). The form of the outline of the apertural margin (near rectangular, say, or rounded) may be recognized in the (early?) adapical part of a shell, almost in the region where ribbing is first distinguishable (Pl. 9, figs. 9-12). The toothed effect is not yet evident at this point, but can be clearly seen (later?) at about half-length.

It may be noted that wide variations of form can be found among specimens whose lengths are comparable. The variation, it seems, should not be regarded as ontogenic. Variants have, at one extreme (e.g. Pl. 8, fig. 5), slim form, with a rounded aperture, relatively infrequent ribs, flat interspaces showing unelaborated interruptions of growth, ribs provided with relatively few teeth, and these teeth relatively straight, their axes disposed almost parallel to the axis of growth of the whole shell. At the other extreme (e.g. Pl. 8, figs. 13-15), the wider shells may have near-rectangular apertural outlines, have more frequent ribs, and the numerous teeth on each rib in the wider (later?) part of the shell are curved, with the axis of each tooth, in its proximal part, disposed at a relatively large angle (but less than  $90^\circ$ ) to the axis of growth of the whole shell. What are regarded as intermediate cases are figured on Pl. 8, figs. 1, 2, 10, 11. There is no evident break in the range of variation, and since all specimens show the toothed effect characteristic of *L. dentata* they are all referred to that species. *L. nigra*, it should be noted, has annular banding, and the bands may have free adapical edges; but there is no record of a denticulate free edge.

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S. C. MATTHEWS  
Geology Department  
Queen's Building  
University Walk  
Bristol BS8 1TR

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# NEW SPECIMENS OF LOWER JURASSIC HOLOSTEAN FISHES FROM INDIA

by S. L. JAIN

**ABSTRACT.** An account is given of new, well-preserved, deep-bodied holostean fishes (family Semionotidae) from the continental Lower Jurassic, India. A new genus, *Paradapedium*, has been erected with *Dapedium egertoni* Sykes 1853 as type-species. New specimens are assigned to *P. egertoni*. The validity of *Tetragonolepis oldhami* Egerton 1878 is supported but *T. analis* and *T. rugosus* are found to be indeterminable. The age and distribution of deep-bodied semionotids is discussed. The evidence from the fossil fishes is in favour of a Liassic age for the Kota Formation. Knowledge of freshwater actinopterygians is improved.

It has been pointed out by Romer (1968, p. 242) that there is a major lacuna in our knowledge of fish evolution in the Jurassic. There is a wealth of Jurassic fishes, but nearly all are marine forms, and understanding of actinopterygian evolution is, therefore, an unbalanced one. Romer also wondered whether the freshwaters of Jurassic times were relatively destitute of actinopterygians. This paper may help to restore the balance in our understanding of fish evolution during the Jurassic, for it is concerned with certain members of a freshwater fauna of actinopterygian fishes from the Lower Jurassic Kota formation of India. The Kota formation is a member of the continental Gondwana Group, and occurs in the region of the Pranhita Godavari valley. King (1881) and Pascoe (1959, p. 987) have given an account of the geology, fauna, and flora of the Kota formation, to which must be added the discovery of dinosaur remains (Jain *et al.* 1962) about 20 feet below a fish-bearing Kota limestone. The study of the Kota fish is part of a programme of research on the rocks and fossils of the Pranhita Godavari valley by the Geological Studies Unit of the Indian Statistical Institute.

Three genera of semionotids, *Dapedium*, *Tetragonolepis*, and *Lepidotes*, are known from the Kota formation. These are all well-known members of the European marine fauna of Lower Jurassic age, and the significance of their occurrence in the freshwater Kota formation will be discussed later. Neither a fresh collection nor a critical study of the fish fauna from the Kota formation has been undertaken since Sykes (1851) proposed *Lepidotes deccanensis*, and Bell (1853) reported the boring at Kota, in which Sykes proposed *Dapedium egertoni*, and the subsequent description of material (5 species of *Lepidotes*, 1 species of *Dapedium*, and 3 species of *Tetragonolepis*) by Egerton (1851, 1854, and 1878). A study of *Lepidotes* based on restudy of type material and an examination of fresh collections has been completed (Jain, S. L. and Robinson, P. L.) and is awaiting publication. This paper is confined to the deep-bodied semionotids, *Dapedium* and *Tetragonolepis*.

Woodward (1895, p. 153) cast doubt on the validity of *Dapedium egertoni* Sykes 1853 by including it in the list of species based on fragmentary material. He (1895, pp. 161–162) recognized only one species of *Tetragonolepis* (*T. oldhami*) out of three proposed by Egerton. Pascoe (1959, p. 987), while listing the fauna and flora of the Kota formation, preferred not to alter the proposals of Sykes and Egerton. Menon

(1959) compiled a catalogue of Indian fossil fishes, keeping the original nomenclature, and did not comment on the validity of any taxonomic unit. Jain (1959) reported a fresh collection of fossil fish material from the Kota formation in 1958, and new specimens have been collected by field parties of the GSU, ISI, Calcutta, from the spring of 1958 to the winter of 1969–1970. Completion of this paper was postponed in the hope that additional good material would be found. It is disappointing that a ten-year period has yielded only 6 specimens of deep-bodied semionotids which could give some reliable information on the skull. Some of these specimens also have reasonably well-preserved body and fins. The number of fragmentary specimens however, is considerable. In general, it has been noticed that there is a scarcity of material of deep-bodied semionotids as compared with the lanceolate *Lepidotes*, the latter being by far the most abundant member of the fauna, though often represented by fragments.

The new specimens described here are preserved in the Palaeontological collections of the GSU, ISI, Calcutta. The specimens in the Geological Survey of India, Calcutta, and the British Museum (Natural History), London, are referred to as GSI and BMNH, respectively. A plaster cast of ISI P. 32 (Pl. 12) and of the hinder part of ISI P. 33 (Pl. 13—the anterior fitting part shown in the plate was not found at the time when the cast was made) have been deposited with the British Museum (Natural History).

#### 'DAPEDIUM' EGERTONI Sykes

*Generic name.* In the early years of work on deep-bodied semionotids various generic names were used, as the distinguishing characters of these forms, and even their distinction from pycnodonts was still not clearly appreciated. So although the Indian form was first referred to by the name *Dapedius egertoni* Sykes (in Bell 1853) it was also termed *Tetragonolepis* or *Aechmodus* by Egerton (1851, 1854). By 1878, however, Egerton had recognized the Kota species as belonging to *Dapedius*. But he used the form of this generic name given by Agassiz in 1835, as did Sykes (in Bell 1853); however, the correct form is *Dapedium* Leach 1822 (see Gardiner, 1960, p. 299, and Woodward 1895, p. 128, for synonymy). The correct form of the generic name will be used in the next, historical, section of the paper.

*The problem of the holotype.* There is, at present, no clearly designated holotype of this species. It is necessary to review the early history of research on this fossil fish in order to make a proper choice of a specimen as lectotype.

The first mention of the species *Dapedium egertoni* is in a paper by Bell (1853). The paper gave an account of a boring near the village of Kota (spelt Kotah) put down in the Kota formation, which was situated a few miles north of the confluence of the rivers Pranhita and Godavari, on the left bank of the Pranhita. Mention is made of a specimen of a fossil fish, found in a loose mass of limestone slabs on the bank of the Pranhita River. This was a new species of *Dapedium*, differing from other species in the ornamentation of the scales, which Sykes named *Dapedium egertoni*. Neither illustration nor any proper description was given in Bell's paper, nor was the specimen referred to any collection. The specimen was, however, undoubtedly housed in the collection of the Geological Society of London, whose specimens were not individually numbered. Later in 1853 Sykes presented two more specimens of *D. egertoni* from Kota to the Geological Society of London. These two specimens were described and figured by Egerton in 1878.

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#### EXPLANATION OF PLATE 10

*Paradapedium egertoni.* a. Lectotype, BMNH P. 12147a; b. BMNH P. 12146, lower jaw and some imperfect head bones. Photographs by British Museum (Natural History).



JAIN, Jurassic fish from India

Egerton made it clear that he was describing additional specimens of the species, which he was referring to *D. egertoni*; he was not describing Sykes's original specimen, nor was he formally designating a holotype.

In 1911 the Geological Society's collection of foreign fossils was presented to the British Museum (Natural History), and the Kota specimens were given individual catalogue numbers for the first time. 4 specimens were catalogued as *Dapedium egertoni*.

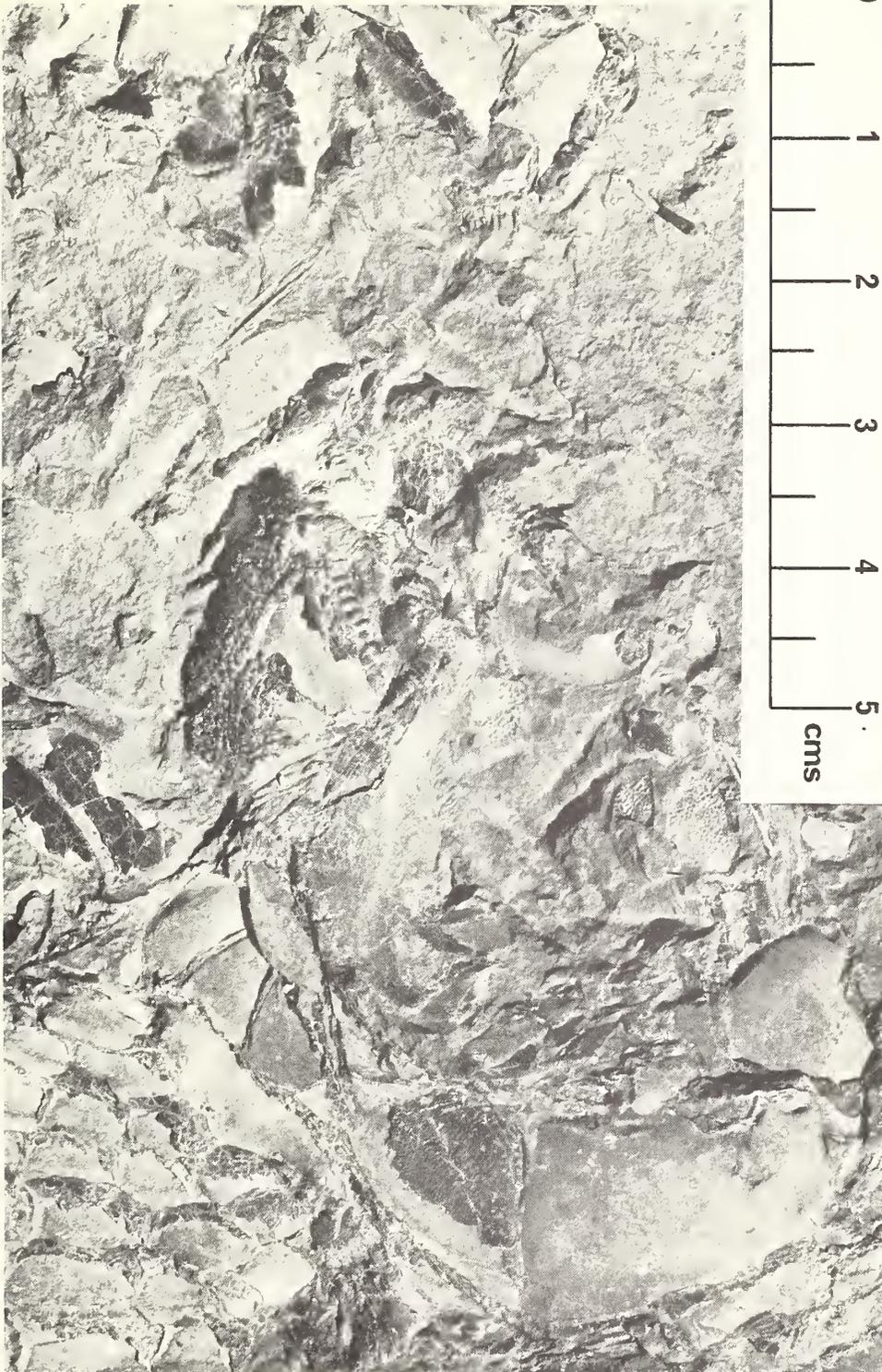
	BMNH P. 12146	not figured or described lower jaw and some imperfect cranial bones (this paper, Pl. 10).	
counterparts of the same individual	{	P. 12147	figured and described by Egerton (1878, pp. 6-8, and Pl. 11, figs. 4, 5) anterior part of the body, imperfect pectoral fin, opercular bones and one or two imperfect cranial bones.
		P. 12147a	not figured or described dorsal part of the body, and a portion of the flank, opercular bones, lower jaws and part of head (this paper, Pls. 10, 11).
		P. 12148	figured and described by Egerton (1878, pp. 6-8, and Pl. 12, fig. 3) dorsal part of the body and imperfect dorsal fin.

It remains to try to discover which of the two undescribed specimens might be the original one mentioned in Bell's paper (1853), discussed by Egerton in that paper, and proposed as *D. egertoni* by Sykes. It is unlikely that the original specimen was P. 12146, as this is only a fragment, showing a lower jaw and some fragments of head bones; it does not show body scales, and the latter were mentioned by Egerton (in Bell, 1853), as having ornament rather different from that of other species of *Dapedium*. It is likely that the original specimen was P. 12147a, as this shows part of the head, and the anterior portion of the body of the fish. It is also the best of the 4 specimens collected in the nineteenth century and listed above. Thus this specimen is chosen as a lectotype, together with its counterpart P. 12147, for *Dapedium egertoni* Sykes. P. 12146 and P. 12148 are topotypes, referred to *D. egertoni*.

*Description of the lectotype* (BMNH P. 12147 and a). P. 12147 is a fragment (Egerton 1878, pl. 11, figs. 4, 5) being part of the counterpart of BMNH P. 12147a (described next). The specimen exhibits the anterior portion of the left-hand side of the body and a portion of the opercular apparatus. The scales have the usual peg-and-socket arrangement and those below the lateral line canal are deeper dorso-ventrally than those above. The scale rows are imperfect and no count is possible. The anterior end of the lateral line canal meets the operculum at about the middle of its length. The pectoral fin is represented by a faint impression of fin rays near the posterior edge of the subopercular. Opercular and subopercular are seen mesially partly as bone and partly as impressions. The opercular is deeper than the subopercular. The opercular process for articulation with the hyomandibular is set quite high on the former bone, and is situated a little below its upper margin. No other element of the opercular apparatus can be recognized with certainty. Situated next to the opercular, dorsally, is a bone which is probably the dermopterotic, and which is exposed in mesial view, partly as an impression of the external surface and partly as bone. The impression indicates that the external surface of the bone was tuberculated and mesially smooth. BMNH P. 12147a is mostly preserved as an impression on buff limestone, of which the ventral and posterior one-third of the body and tail is missing (Pl. 10, fig. a). The left-hand side of the fish is exposed in mesial view and displays

#### EXPLANATION OF PLATE 11

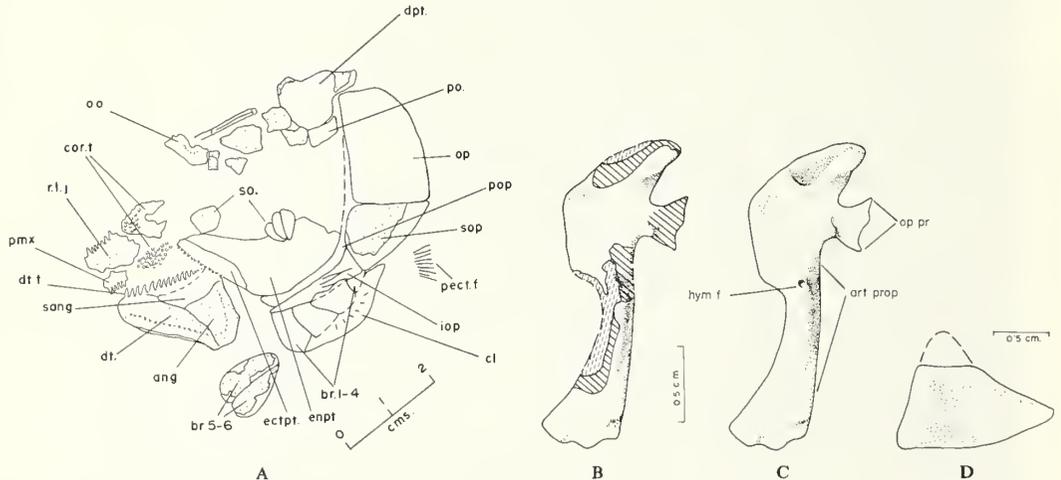
*Paradapedium egertoni*, lectotype (BMNH P. 12147a), details of the anterior portion. Photograph by British Museum (Natural History).



JAIN, Jurassic fish from India

the opercular apparatus, branchiostegal rays, jaws, a part of the cheek region, and an indication of the roof of the skull. Nearly two-thirds of the anterior dorsal part of the body is preserved, with well-marked scale rows. The specimen is about 19.5 cms long, and 9 cms deep in the region of opercular apparatus.

The only membrane bone discernible in the skull is the dermopterotic. A number of suborbitals, which are displaced from their normal position (text-fig. 1A) are also seen. The dermopterotic is large and preserved mostly as an impression of the external surface, bearing fine tuberculations. There is no clear evidence of extrascapulars. A portion of the maxilla is seen lying anterior to the lower jaw (not seen in text-fig. 1 but discernible in Pl. 11), bearing 9 stout pointed teeth. It appears that

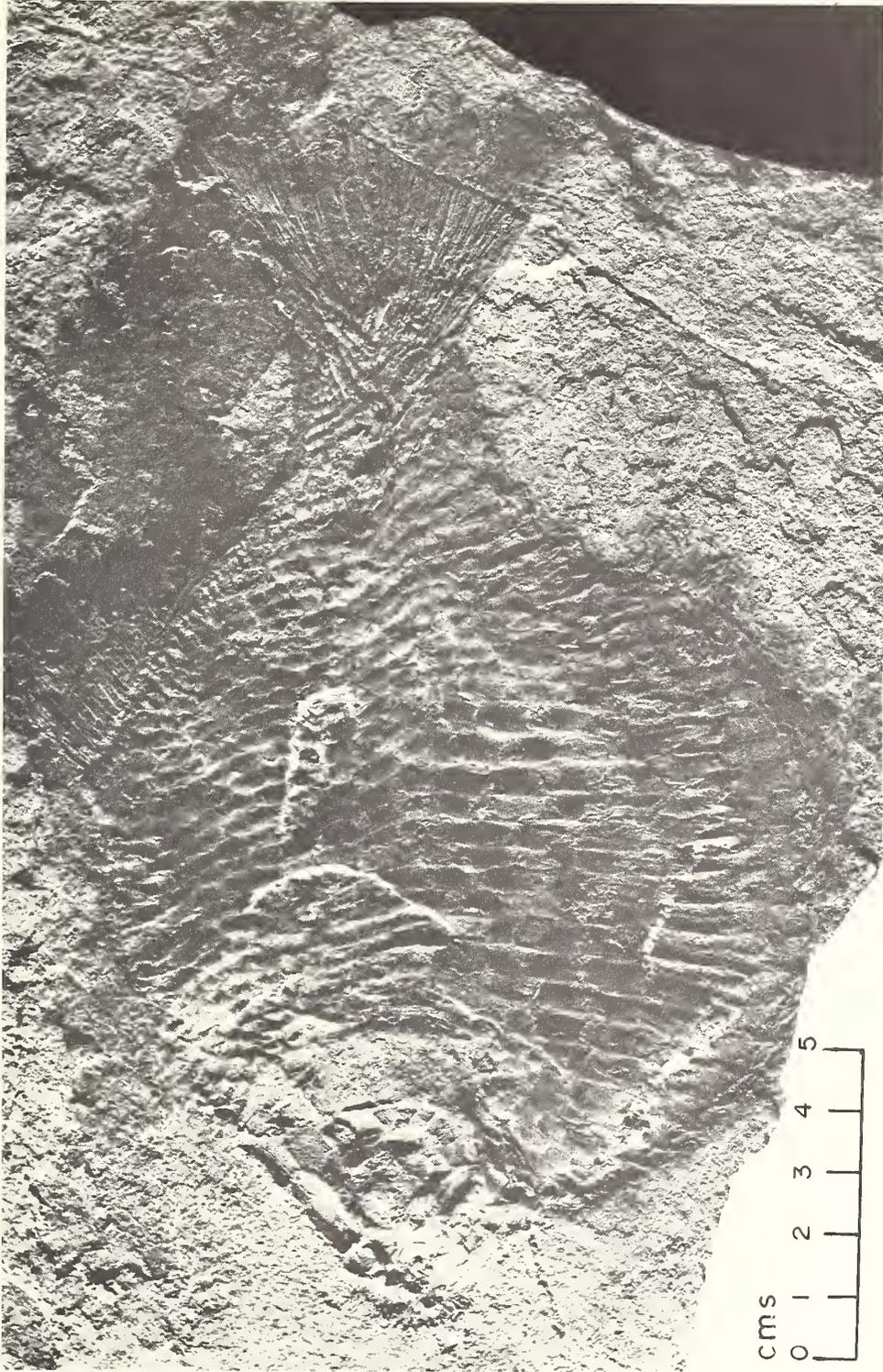


TEXT-FIG. 1. *Dapedium egertoni*, lectotype, BMNH P. 12147a. A, Anterior portion; B, hyomandibular (crushed bone hatched, impressions of bone on matrix broken hatched); C, restoration of hyomandibular; D, quadrate.

the posterior one-third of the maxilla is broken off. A disarticulated fragment bearing 5 downwardly directed teeth is probably left premaxilla (text-fig. 1A). The palatopterygoid arch is well displayed and appears to be quite stout. The ectopterygoid bears 14 fine, pointed teeth and is firmly ankylosed to the entopterygoid. The hyomandibular (text-fig. 1B and C) is displaced and is observed in one corner of the slab. It is elongated, with a slender arm ventrally and a laterally expanded portion dorsally. It is partly damaged but the impressions allow fair evidence of its shape. The bone is crushed at the site of the hyomandibular foramen, which is set obliquely, at about mid length. The edge of the hyomandibular arm is clearly demarcated by a vertical depression for the overlap of the left preopercular. The dorsal part of the hyomandibular is rather delicate and obliquely expanded with a well-defined opercular process. The quadrate (text-fig. 1D) can be recognized in the dissociated elements.

#### EXPLANATION OF PLATE 12

*Paradapedium egertoni* gen. nov., complete specimen, ISI P. 32, from Kota formation, India.



JAIN, Jurassic fish from India

It has a somewhat triangular shape, allowing for the restoration of the dorsal part which is partly crushed. The articulation facet is not pronounced.

The lower jaw (text-fig. 1A) of the left-hand side is in association. The external bones are partly preserved here, revealing fine tuberculations on dentary and angular. The mandibular sensory canal is also visible. The marginal dentary teeth are well preserved but the most anterior are probably missing. The teeth are uniformly sharp, pointed, and decrease in size posteriorly. 13 teeth are preserved. There are 2 clusters of teeth (Pl. 11 and text-fig. 1A), dorsal to the mandible, the top of most of which is gone. The cluster next to the mandible seems to be coronoid teeth, and the cluster dorsal to it is probably made up of prearticular teeth. The opercular apparatus is complete, and the shape of its various elements can be determined in P. 12147 and *a*. The opercular is deep, somewhat rectangular, narrow dorsally, and wider ventrally. The proportion of width to length is approximately 1:2. The subopercular is about half as deep as the operculum. The interopercular is partly crushed and partly hidden by the preopercular. The form of the preopercular can be worked out from impressions and is shaped like an open L. The tuberculations on the bones of the opercular apparatus seem to be very fine. Four branchiostegal rays, with damaged distal ends, are present next to the interopercular. Close to them are to be seen another 2 branchiostegal rays. Thus there are at least 6 small branchiostegal rays. The cleithrum is arched. Its upper extremity lies somewhere near the middle of the subopercular and the lower extremity lies near the last associated branchiostegal rays (text-fig. 1A).

The trunk in P. 12147*a* is imperfect and all fins, except the pectoral, are wanting. The preserved two-thirds portion of the body shows that it was laterally compressed and deeply fusiform. The scales have a broad peg-and-socket articulation, but no sharply thickened rib is present on the inner face. The scales above the lateral line canal do not appear to be as elongate as the ones below and those of the flank region are even more elongate. The dorsal and ventral ridge of the body is imperfect, which renders the number of scale rows indeterminable, but it appears that there were at least 8 to 10 horizontal rows of scales on either side of the lateral line canal. The pectoral fin is approximately as high on the body as in species of *Dapedium*. Only the bases of the fin rays are preserved, of which 10–11 can be counted.

#### SYSTEMATIC DESCRIPTION

Infraclass HOLOSTEI  
Order SEMIONOTIFORMES  
Suborder SEMIONOTOIDEI  
Family SEMIONOTIDAE

*Paradapedium* gen. nov.

*Type species: Dapedium egertoni* Sykes 1853.

*Diagnosis.* Semionotids having abdominal region protuberant ventrally; head small in relation to the body. Postrostral absent. Mandible short, deep, with coronoid elevation and anterior tooth enlarged. Teeth slender and pointed. Suborbitals, 9–10, extending beyond middle of orbit. Circumorbitals probably 15–16. Cleithrum

arched; suprascapular large, triangular. Extrascapulars, 3. Branchiostegal rays 6, small and inconspicuous. Hyomandibular slender, elongated; hyomandibular foramen at about mid length. No ossification around notochord. Neural spine fused to neural arches throughout the length of the body. Dorsal fin arising from about the middle of the back and extending to about the tail, has about 35 lepidotrichia. Anal fin shorter, opposed to hinder end of dorsal, has about 25 lepidotrichia. All lepidotrichia distally segmented and bifurcated and all fins with supporting fulcral rays. Complete squamation over trunk; flank and belly scales elongated dorso-ventrally. Dorsal ridge scales conspicuous, pectinate, or slightly denticulate. Ventral ridge scales slightly more conspicuous than dorsal, usually delicately pectinate.

*Distribution.* Lower Jurassic, India: Kota formation.

*Paradapedium egertoni* (Sykes) emended herein

Plates 10-14; text-figs. 3-6

*Synonym.* *Dapedium egertoni* Sykes 1853.

*Occurrence.* Kota Formation, India. A geological map of the Pranhita-Godavari Valley is given by King (1881). Fossil localities in the Kota formation are shown in text-fig. 2.

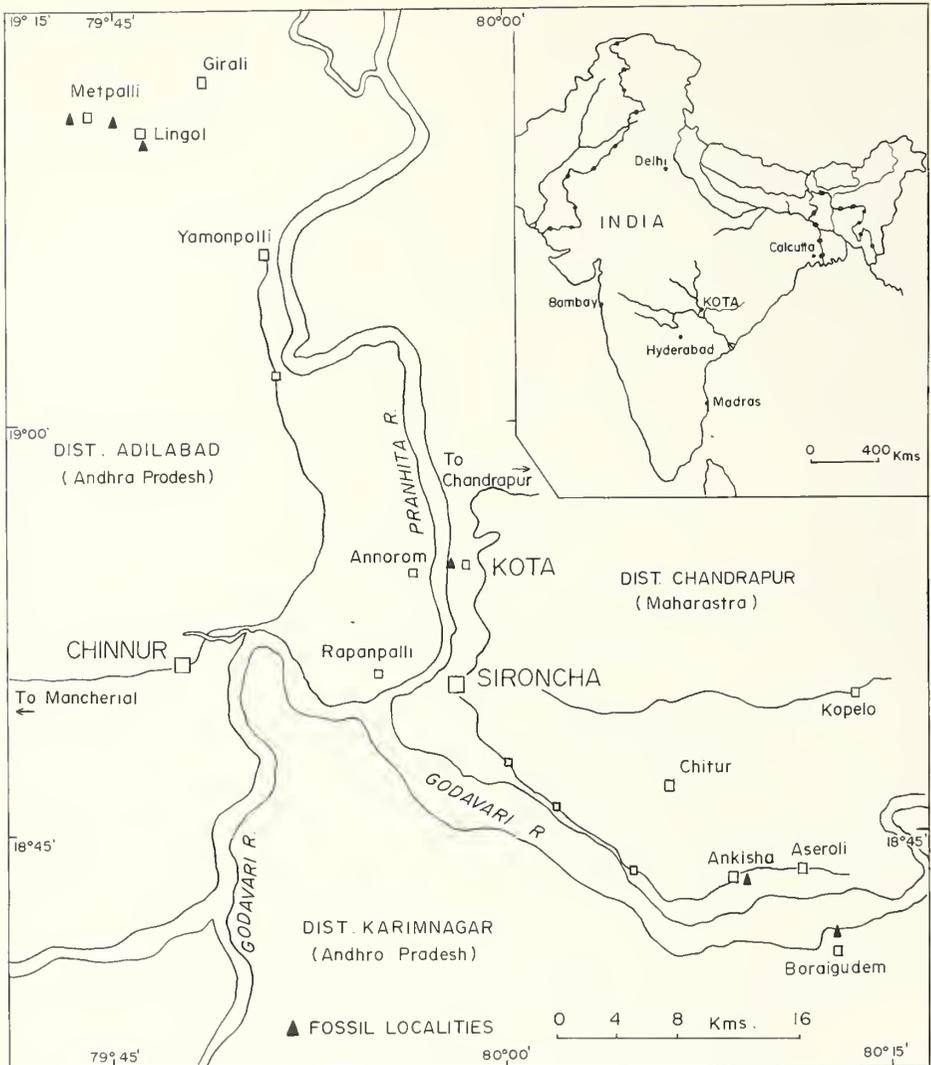
*Material.* Lectotype, in counterpart, BMNH P. 12147 and *a*, Kota formation, India, about 19.5 cm, fish wanting skull and tail.

*Other specimens.* BMNH P. 12146 and 12148, Kota formation, India; both fragmentary but the former displays left lower jaw and some imperfect head bones, mainly as impressions and the latter displays dorsal part of the body with imperfect dorsal fin.

*New specimens.* ISI P. 32, Kota ledge, Kota formation, nearly complete fish, approx. 19.5 cm long; ISI P. 33, Kota ledge, Kota formation, nearly complete fish, approx. 25.5 cm long; ISI P. 34, near village Ankisha, Kota formation, nearly complete fish, approx. 25 cm long; ISI P. 35, near village Boraigudem, Kota formation, fish wanting anterior part of head and posterior fins, approx. 14.5 cm long. All fossil localities are shown in text-fig. 2.

*Diagnosis of species.* Same as for the genus.

*Description.* *Paradapedium egertoni* is a moderately large semionotid reaching 200-320 mm in length and 120-195 mm in depth. Approximate depth/length ratio of the fish is about 1:1.6 to 1:1.7 (ISI P. 32, 34). The shape of the body is clearly hypsionomid and the whole body is covered with scales. The head region is rather small, deepened with a tendency of co-ossification of dermal roofing elements in larger specimens (ISI P. 34). The basicranial axis is not bent upwards. The frontal, parietal, and dermopterotic are differentiated by clear sutures in ISI P. 32 (text-fig. 3B). Although the course of the lateral line canals of the skull is impossible to make out, the anterior and middle pit lines on the parietal are conspicuous. The dermopterotic

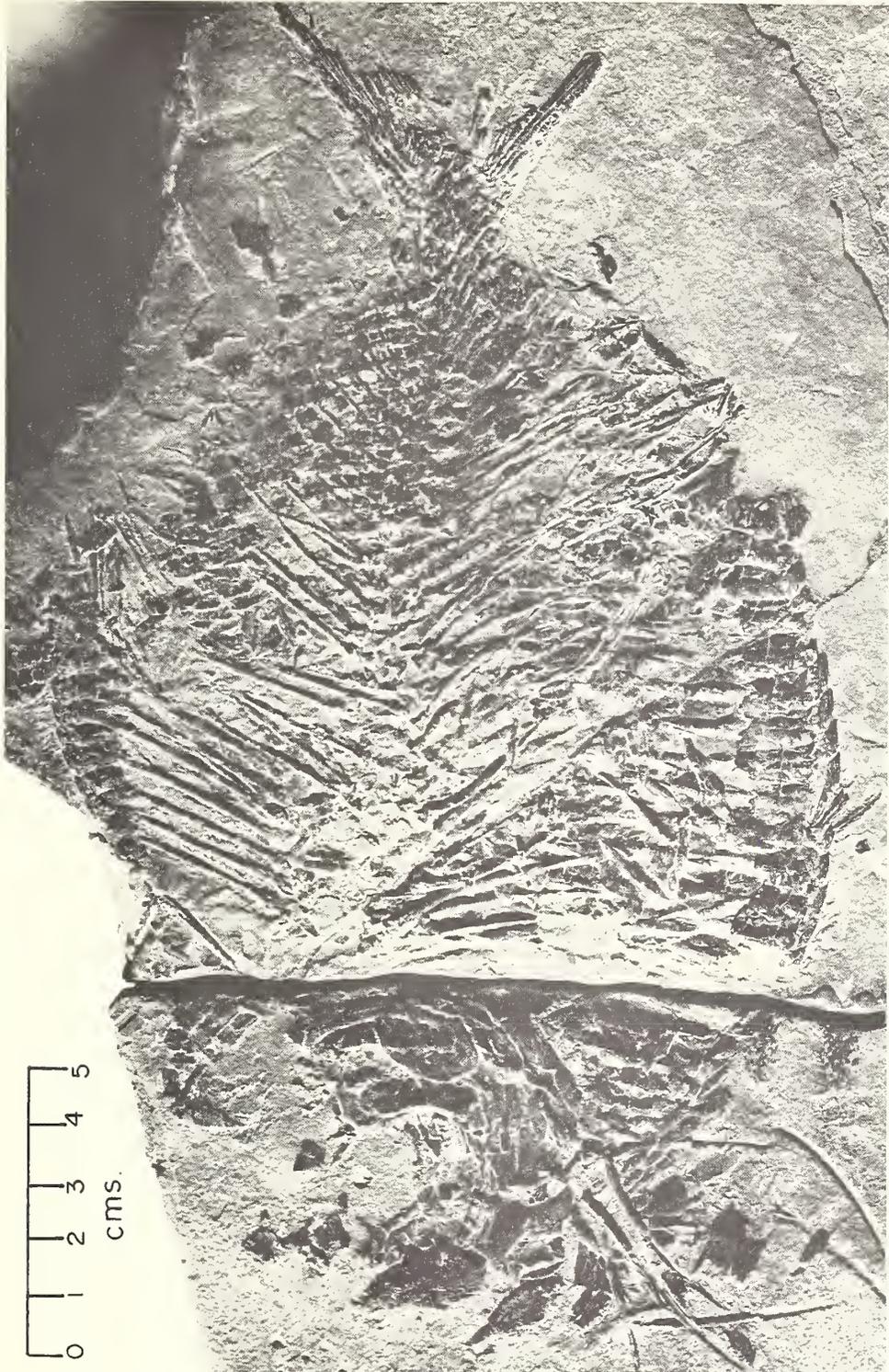


TEXT-FIG. 2. Map showing fossil localities in the Kota formation. Inset: outline map of India showing the village Kota and tributaries of the river Godavari.

is somewhat larger than the parietal. The suprascapular is large and triangular. All skull roofing bones bear fine tuberculations. There are three extrascapulars, two smaller ones adjacent to the parietal, followed by the most ventral, which is also the largest. The orbit is reasonably well defined (ISI P. 32 and 35) and is moderate in size. The circumorbital series is best observed in ISI P. 35 (text-fig. 5B) where 5 bones

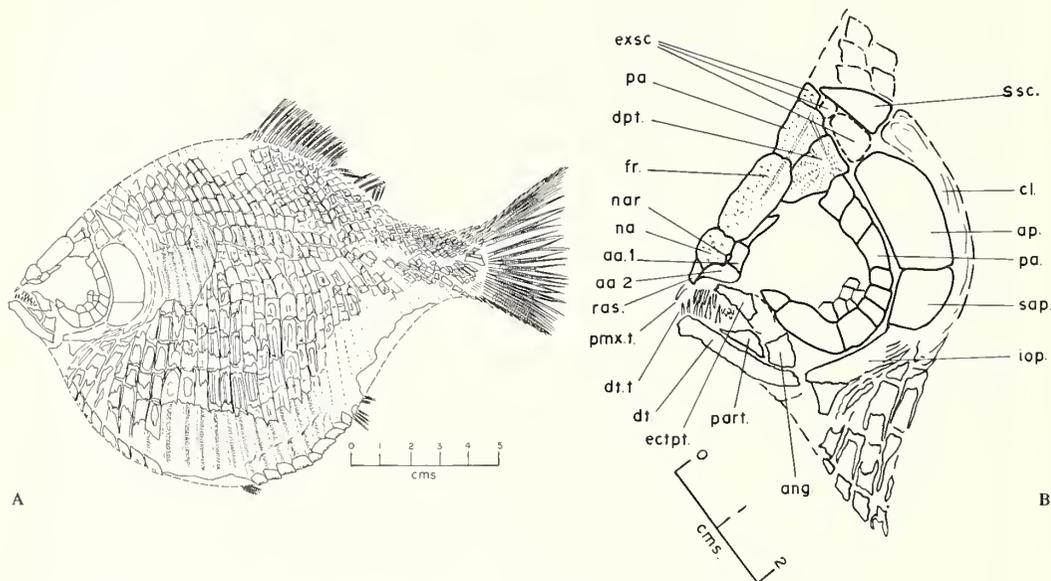
#### EXPLANATION OF PLATE 13

*Paradapedium egertoni* gen. nov., complete specimen, ISI P. 33, from Kota formation, India.



JAIN, Jurassic fish from India

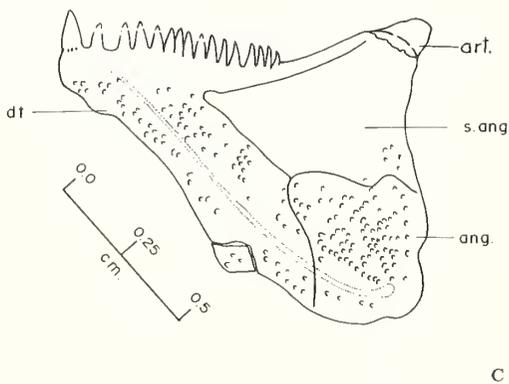
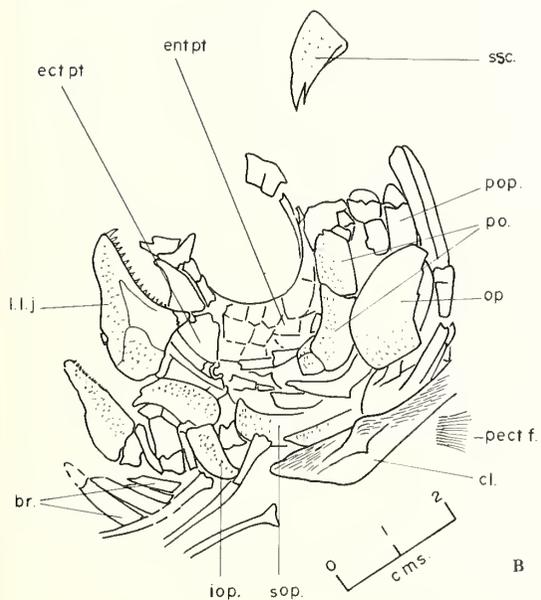
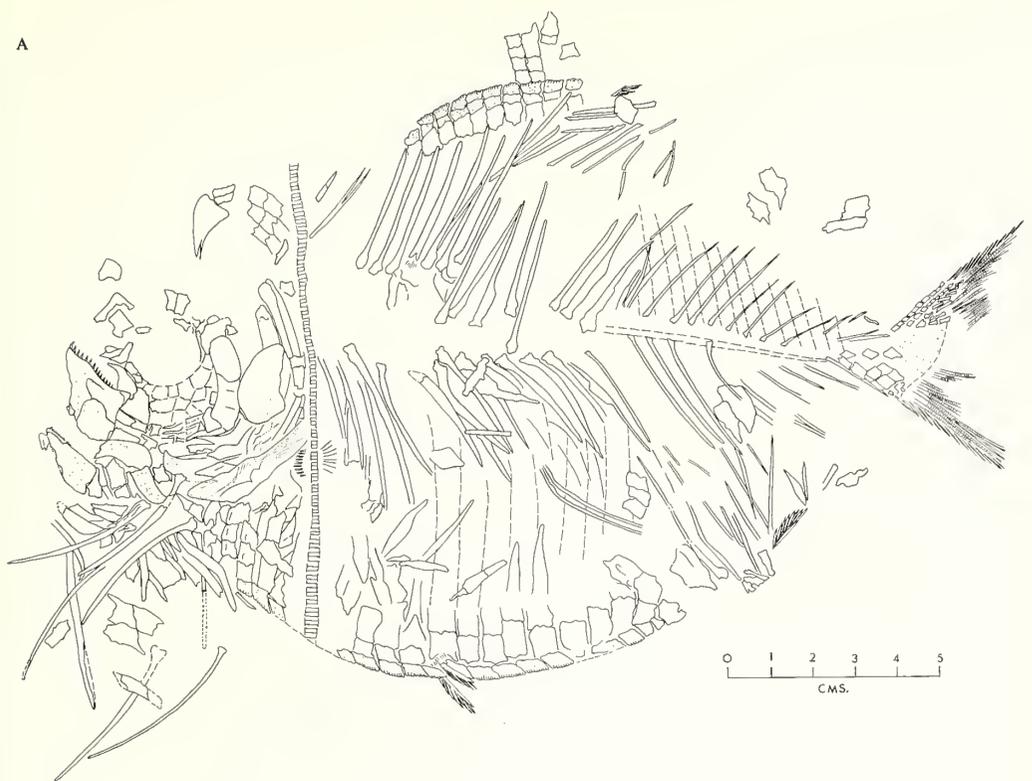
are preserved and another four are indicated by impressions. All circumorbitals are small and it seems there may have been at least 15–16 of them surrounding the orbit. The suborbitals are displayed well in ISI P. 32 (text-fig. 3B) and 35 (text-fig. 5B). These form in an arched series, varying in size, nine in ISI P. 32 and ten in ISI P. 35. The snout pattern is reasonably well defined in ISI P. 32 (text-fig. 3B). The rostral is a small element and abuts against the large nasals. The post-rostral is absent. An anterior and posterior antorbital can be recognized. The nasal aperture is single as in *Dapedium* and *Lepidotes* (Gardiner 1963). The palate is exposed in ISI P. 33 and even though the bone is crushed it is fairly easy to distinguish the arch-like entopterygoid and metapterygoid. The ectopterygoid is not preserved completely in any



TEXT-FIG. 3. *Paradapedium egertoni* gen. nov., ISI P. 32. A, complete specimen; B, anterior portion.

specimen but in ISI P. 32 it is seen to be represented by a series of teeth and fragments of bone. The premaxilla is either missing or damaged. Three slender and pointed premaxillary teeth can be recognized in ISI P. 32 of which the most anterior is enlarged. Maxilla is missing from all specimens. The hyomandibular (fig. 1B and C) is elongated, with a slender arm ventrally and a laterally expanded portion dorsally, bearing the hyomandibular foramen (VII) at about mid length (BMNH P. 12147a). The quadrate is probably triangular with poorly defined articulation facet (BMNH P. 12147a).

The lower jaw is preserved in ISI P. 32, 33, and 34, as well as in BMNH P. 12146 (Pl. 10, fig. b). It is remarkably short and deep, with coronoid elevation, comprising distinct dentary, angular, and surangular elements. All the external bones bear coarse tuberculations (text-fig. 4C). The course of the mandibular canal can be clearly traced. There are 15–16 teeth on the dentary of which the most anterior is enlarged, giving a tusk-like appearance. The opercular apparatus is partly exposed in all



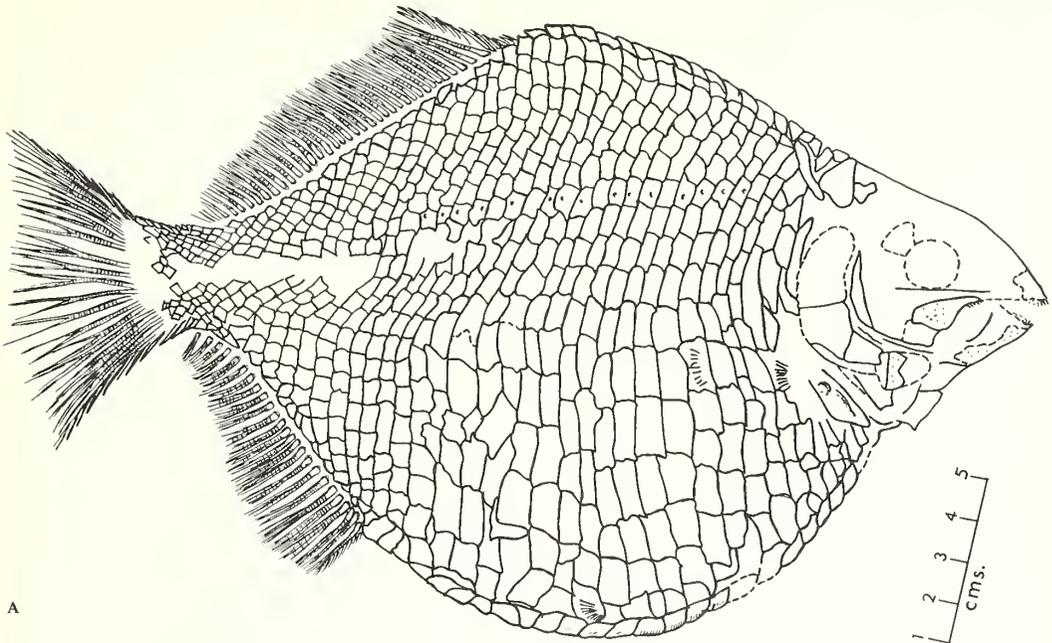
TEXT-FIG. 4. *Paradapedium egertoni* gen. nov., ISI P. 33. A, complete specimen; B, anterior portion. (Broken lines in entopterygoid are cracks in the bone, not sutures.) C, left lower jaw.

specimens but it is best displayed in ISI P. 35 (text-fig. 5B). The preopercular is partially hidden in most specimens but has a clear ascending process. The opercular is deep and maintains the approximate proportions of length/width as 2:1. It forms a well-marked arched series with subopercular and interopercular. The cleithrum is arched. Four branchiostegal rays are preserved in ISI P. 33 (text-fig. 4) and ISI P. 35 (text-fig. 5B) but the lectotype displays 6 (text-fig. 1A). The whole body of the fish is covered with scales (Pl. 14 and text-fig. 5A), though in some specimens the scales are damaged. The scales ventrally to the lateral line canal are deeper than those in the dorsal region. A rib-like thickening is evidenced in the scales preserved ventrally to the lateral line canal, but is variable in development (ISI P. 33). Post-cleithral scales are moderately enlarged (ISI P. 34). Dorsal and ventral ridge scales are a little more conspicuous than in *Dapedium*. Dorsal ridge scales are pectinate or slightly denticulate and ventral ridge scales are delicately pectinate (ISI P. 33, Pl. 13).

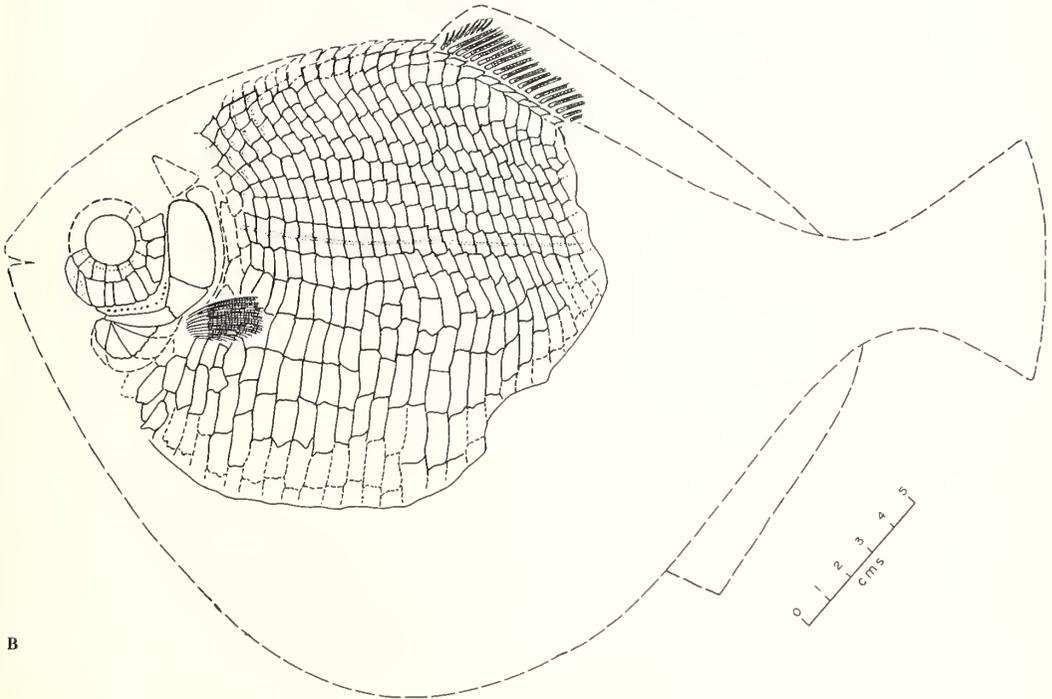
ISI P. 33 displays the axial skeleton as the scales have been leached out (text-fig. 4A and Pl. 13). The notochord must have been persistent as no traces of ossification have been detected. It occupied a position in which roughly one-third of the body lay above it and two-thirds below it. The bases of neural and haemal arches are moderately expanded and separated from each other. The neural and haemal spines are fused with their corresponding arches throughout the entire length of the body, unlike *Dapedium* where neural spines are fused only in the hinder half of the tail, but quite like *Hemicalypterus*. Median fins are best displayed in ISI P. 34 (text-fig. 5A and Pl. 14) but are partly visible in other specimens as well. The dorsal fin arises from the middle of the body and extends to nearly the end of the trunk, posteriorly. It has approximately 35 fin rays. Each fin ray is distally bifurcated and the leading fin ray has fringing fulcra. The anal fin is less extensive than the dorsal and its fin rays are more sparsely disposed. It has approximately 25 segmented and distally bifurcated rays, and the leading fin ray is provided with fringing fulcra. The caudal fin is well preserved in ISI P. 32 (Pl. 12) and ISI P. 34 (Pl. 14). It is hemiheterocercal and symmetrical and composed of about 22 segmented and distally bifurcated rays. There are fringing fulcra on both dorsal and ventral borders of the fin but these are less conspicuous ventrally than dorsally. The pectoral fin appears quite high on the flank, as in *Dapedium*. There were probably about a dozen fin rays of which nine are indicated (ISI P. 34, text-fig. 5B). The fin rays are segmented and distally bifurcated. The pelvic fin is rudimentary and is displayed in ISI P. 33 (Pl. 13). Only 2-3 fin rays can be recognized but the leading fin ray bears distinct basal fulcra.

A reconstruction of *Paradapedium egertoni* is given in text-fig. 6, based on the lectotype (BMNH P. 12147 and *a*) and ISI specimens (P. 32 to 35).

*Discussion.* All specimens assigned to *Paradapedium egertoni* have been obtained from localities in the Kota formation, India. The disposition of dermal bones, opercular apparatus, pointed non-tritoral teeth in the jaws, presence of conspicuous fulcra on all fins, and the extension of dorsal fin to not more than half the length of the trunk are some of the important characteristics shared by all specimens. The assessment of morphological uniformity is not always easy due to imperfection of some of the specimens collected in the nineteenth century, because of intraspecific

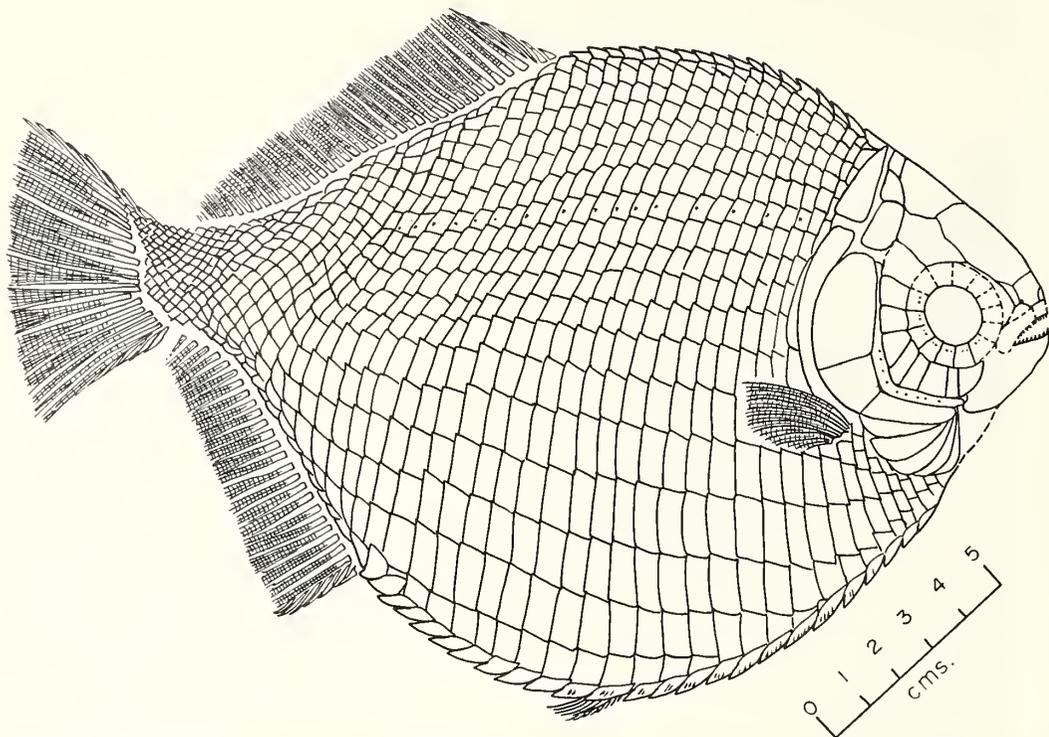


A



B

TEXT-FIG. 5. *Paradapedium egertoni* gen. nov., A, ISI P. 34, complete specimen; B, ISI P. 35, complete specimen with restored outlines.



TEXT-FIG. 6. *Paradapedium egertoni* gen. nov., reconstruction of complete fish from holotype (BMNH P. 12147 and a) and ISI specimens (P. 32 to 35).

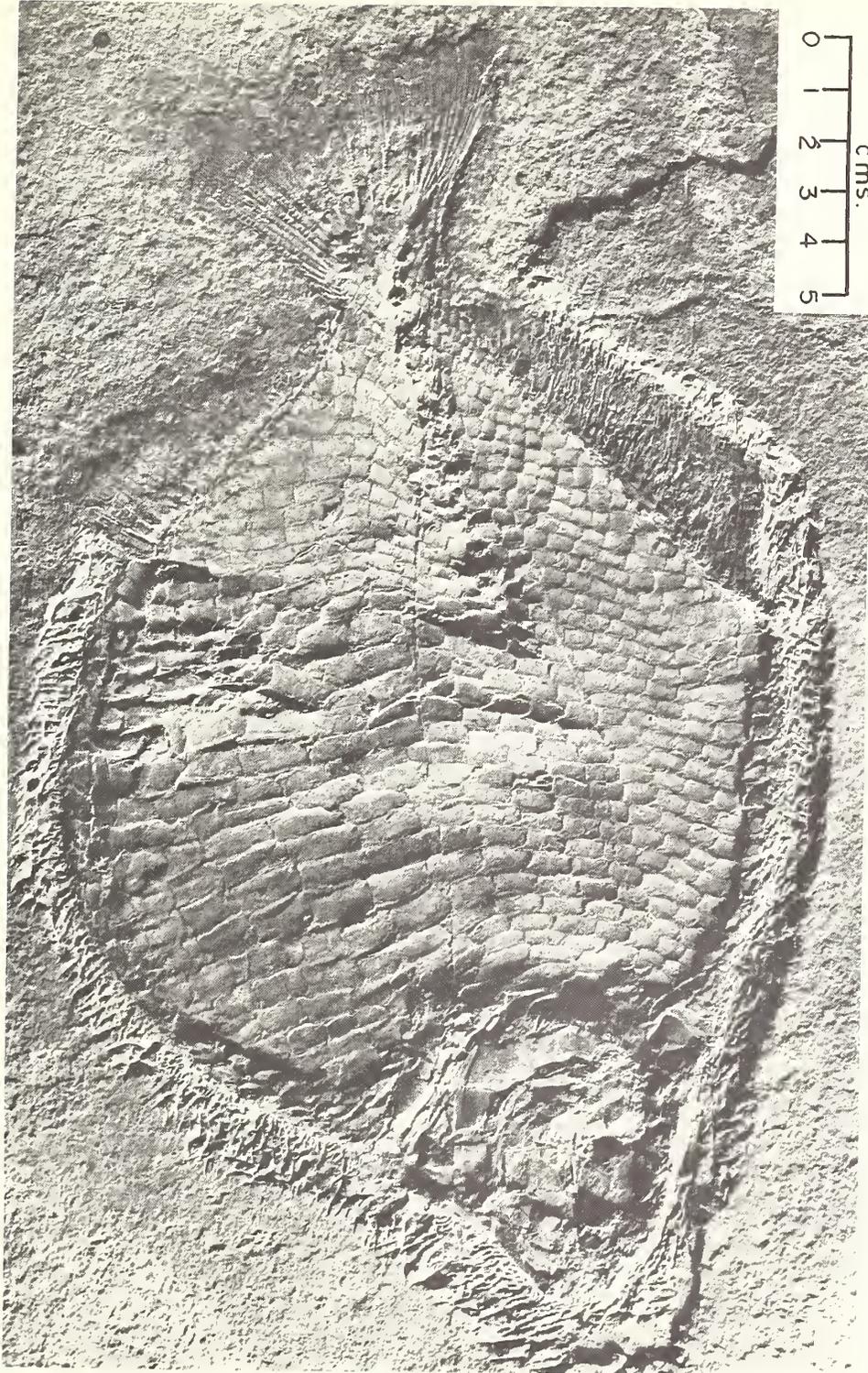
variation (e.g. number of suborbitals) and variations due to size (e.g. co-ossification of dermal bones of skull in larger specimens). A comparison shows a morphological uniformity which is consonant with their being individuals of a single species.

*Paradapedium* has closest affinities with *Dapedium*. It may, therefore, be useful to compare some important characteristics of the two. The body proportions of *Paradapedium* on 2 ISI specimens and *Dapedium* on 15 BMNH specimens were examined. Depth of the body below the lateral canal as percentage of total body depth was measured along the vertical line passing through lateral line canal at the point of maximum body depth:

	<i>Depth below lateral line canal as percentage of total body depth</i>
<i>P. egertoni</i> (ISI P. 32)	70%
<i>P. egertoni</i> (ISI P. 34)	71.9%
<i>D. politum</i> (BMNH: 6 specimens)	61-65.1%
<i>D. colei</i> (BMNH: 3 specimens)	61.9-65.5%
<i>D. punctatum</i> (BMNH: 3 specimens)	61.5-65.3%
<i>D. dorsale</i> (BMNH: 3 specimens)	60.2-64.9%

EXPLANATION OF PLATE 14

*Paradapedium egertoni* gen. nov., complete specimen, ISI P. 34, from Kota formation, India.



JAIN, Jurassic fish from India

The length of the head (from tip of the lower jaw to the posterior margin of the operculum) and depth of the head (from dorsal edge near the extrascapular to the ventral edge of the mandible) as percentage of the length of the fish (from the anterior tip of the lower jaw to the end of the body lobe) was measured on one complete specimen of *Paradapedium* (ISI) and 13 specimens of *Dapedium* (BMNH):

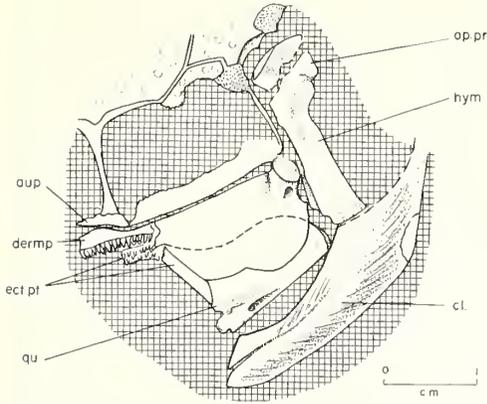
	<i>Length of the head as percentage of length of the fish</i>	<i>Depth of the head as percentage of length of the fish</i>
<i>P. egertoni</i> (ISI P. 34)	15%	16.3%
<i>D. politum</i> (BMNH: 6 specimens)	26.0-33.4%	37.0-41.0% (5 specimens)
<i>D. colei</i> (BMNH: 4 specimens)	29.5-34%	33.3-40%
<i>D. punctatum</i> (BMNH: 3 specimens)	28.6-31.8%	34.4-37.1%

The lack of well-preserved specimens of *Paradapedium* stands in the way of determining range of head and body proportions. However, *Paradapedium* probably has a deeper body and smaller head than *Dapedium*.

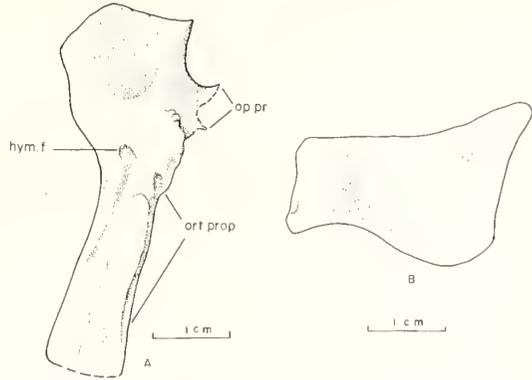
The roofing bones of the skull are heavily ossified with heavy tuberculations in *Dapedium* but in *Paradapedium* they are not heavily ossified and bear fine tuberculations. The suborbitals are variable in number in *Paradapedium* (9-10) and *Dapedium* (6-11). The suborbitals extend beyond the mid orbit in *Paradapedium* but not in *Dapedium*. The extrascapulars in *Paradapedium* are not prominent; only one specimen shows three but in *Dapedium* these are very prominent and vary in number, 4-6 (Woodward 1895, Wenz 1967).

The hyomandibular of *Dapedium* has been briefly described by Woodward (1895) but not illustrated. A specimen of *D. punctatum* (BMNH 43435) exhibits the hyomandibular particularly well (text-fig. 8A). It is elongated and laterally compressed with considerable expansion above, but contracted in its lower half with nearly parallel anterior and posterior edges. The hyomandibular foramen is situated well dorsal to the mid length of the hyomandibular. Posteriorly there is an opercular process, lying in the same plane as the body of the bone. The posterior edge of the narrow ventral stem of the bone is slightly grooved for the reception of the anterior edge of the operculum. BMNH P. 4423 also shows the hyomandibular of *Dapedium* (text-fig. 7) but the dorsal half of the bone has been broken and crushed in, and the details are not seen so well. Nevertheless the 2 specimens suggest that the shape of the hyomandibular may be rather uniform in *Dapedium*. The hyomandibular of *Paradapedium* (text-fig. 1B and C) is narrower than that of *Dapedium* and dorsally it is much more expanded. The hyomandibular foramen is set more nearly in the middle of the bone, and the opercular process is clearly marked. The hyomandibulae of *Dapedium* and *Paradapedium*, therefore, differ from each other in several ways.

Symplectic and quadrate have been mentioned as 'unknown' in *Dapedium* by Woodward (1895) and Wenz (1967) does not describe either bone of that genus. BMNH 36883 (*D. punctatum*) exhibits lower jaw, palate, and quadrate and symplectic in association in mesial view (text-fig. 9). The symplectic is somewhat displaced but has a stout, expanded, and somewhat squarish portion anteriorly and a narrower portion posteriorly. The quadrate in *D. punctatum* as exhibited by BMNH 36883 (text-figs. 8 and 9) and *Dapedium* sp., BMNH P. 4423 (text-fig. 7) is rather



TEXT-FIG. 7. *Dapedium* sp. (BMNH P. 4423), left palatal complex, quadrate and hyomandibular.



TEXT-FIG. 8. *Dapedium punctatum*. A, hyomandibular from BMNH 43435; B, quadrate from BMNH P. 36883.

stout with a pronounced articular process. In BMNH P. 4423 (text-fig. 7) the quadrate is partly overlaid by the ectopterygoid but the curved border of the quadrate can be distinguished because flakes of the ectopterygoid have been broken away. The quadrate of *Paradapedium* (text-fig. 1D) is only partly known. It is not so stout and somewhat triangular in shape. The articulation facet is not pronounced. The symplectic of *Paradapedium* is unknown.

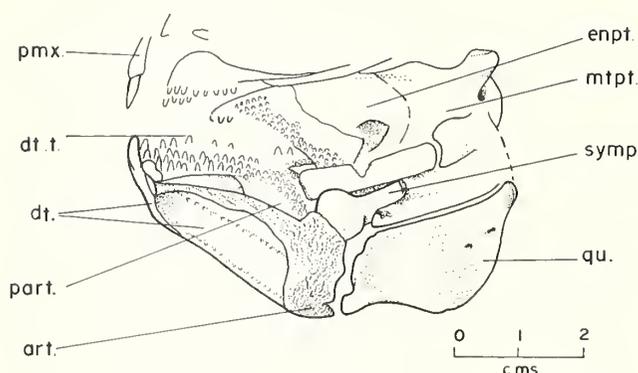
The lower jaw of *Dapedium* is well known and described by Woodward (1895) as remarkably short and deep, with coronoid elevation, comprising distinct dentary, splenial, articular, and probably coronoid elements. The mandible of *Paradapedium* is similar to *Dapedium* but the dentary in *Paradapedium* is more definitely V-shaped and in *Dapedium* it is more open V-shaped.

In *Amia* Meckel's cartilage is persistent and well chondrified, extending as an L-shaped structure, one 'arm' from the region of the jaw articulation to the symphysis, the other 'arm' from the region of the jaw articulation to the top of the coronoid process. It seems that in *Dapedium* this cartilage is ossified and can be called an 'articular' bone. The articular bone in *Dapedium* has exactly the shape of Meckel's cartilage in *Amia* (BMNH 36883: text-fig. 9; BMNH P. 4877: text-fig. 10). It extends dorsally to the coronoid process of the lower jaw. The articular is distinguishable from other dermal bones in being more 'crumpled' and less smooth. The articular is seen in external view of the lower jaw in *Dapedium* emerging to a variable degree in different specimens above and behind the surangular. In *Paradapedium* (text-fig. 4C) this feature seems to be similar.

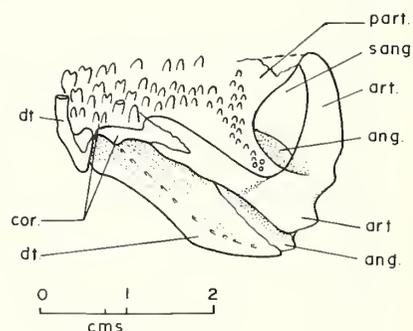
BMNH 36883 (text-fig. 9), a right lower jaw seen in mesial view, shows that the symphyseal facet in the lower jaw of *Dapedium* is contributed by three 'layers' of bone by individual subfacets. The dentary contribution is the most external with an elongate subfacet and crowned by the most anterior dentary tooth. A middle 'layer', with a distinct subfacet, lies sandwiched between dentary and coronoid. The mesio-dorsal coronoid 'layer' has its own rugose facets and well-developed teeth above. These three layers can be traced backwards along the jaw as separate

bones partly overlying one another. Reconstruction of the lower jaw of *Dapedium* has been attempted in three stages (text-fig. 11) from BMNH P. 4877. The dentition in *Dapedium* is variable. A few species have bifid or mammiliform apex and others have styliform teeth with simple apex. In *Paradapedium* the teeth are slender, elongated, and pointed and the most anterior tooth of the dentary is enlarged. The opercular apparatus and cleithrum are more or less similar in *Dapedium* and *Paradapedium*.

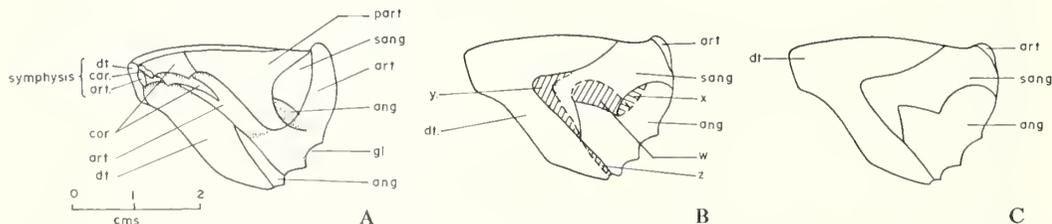
There is only a slight rib-like thickening along the row of scales on the belly in *Dapedium* and *Paradapedium*. The flank and belly scales in *Paradapedium* are, however, more elongate than *Dapedium*. The dorsal ridge scales are not very conspicuous in *Dapedium*. In *Paradapedium* there is a slight individual variation but the same are usually a little more conspicuous than *Dapedium* and are pectinate or slightly denticulate. The neural spines are fused to the respective arches throughout the length of the body in *Paradapedium* but in *Dapedium* these are fused only in the hinder part of the body. The dorsal and anal fin in *Dapedium* have been shown in Woodward's (1895) reconstruction to have 28 and 17 fin rays respectively. *Paradapedium* (ISI P. 34) has 35 and 25 fins, respectively, in dorsal and anal fins.



TEXT-FIG. 9. *Dapedium punctatum* (BMNH 36883), mesial view of right lower jaw and palate.



TEXT-FIG. 10. *Dapedium* sp. (BMNH P. 4877), mesial view of right lower jaw.



TEXT-FIG. 11. Restoration of lower jaw of *Dapedium* sp. (from BMNH P. 4877). A, internal view; B, mesial view; C, external view. (Teeth and lateral lines omitted; areas of overlap hatched.) w, surangular-angular overlap, surangular lying external to angular; x, angular-surangular overlap, angular lying external to surangular; y, surangular-dentary overlap, surangular lying external to dentary; z, dentary-angular overlap, dentary lying external to angular.

## TETRAGONOLEPIS

Three species of *Tetragonolepis* have been described from the Kota formation by Egerton (1878), namely, *T. oldhami*, *T. rugosus*, and *T. analis* on the basis of 5 specimens. Only three specimens of *Tetragonolepis* are traceable in the collections of GSI, Calcutta, in addition to the newly collected material in GSU, ISI. One specimen each of the GSI collection is assignable to the 3 species of *Tetragonolepis* on the basis of Egerton's figures, though no holotypes had been designated by Egerton. As such each of the specimens can be designated as a lectotype of the respective species: *T. oldhami*—lectotype GSI 2145 (Egerton 1878, pl. II, fig. 1); *T. rugosus*—lectotype GSI 2146 (Egerton 1878, pl. II, fig. 2); and *T. analis*—lectotype GSI 2150 (Egerton 1878, pl. III, fig. 1). Woodward (1895, p. 161) considered the Indian species of *Tetragonolepis*. He recognized *T. oldhami* and gave a diagnosis of this species but listed *T. analis* and *T. rugosus* as based upon fragmentary specimens. A re-examination of the species of *Tetragonolepis* from India was done on the basis of collections in GSI and the newly collected material in the light of a new diagnosis by Gardiner (1960).

## SYSTEMATIC DESCRIPTION

Genus *Tetragonolepis*

*Type species.* *Tetragonolepis semicineta* Bronn 1830, from the Upper Lias (Lower Jurassic), Wurtemberg and Bavaria (West Germany).

*Diagnosis of genus.* As given by Gardiner (1960, p. 305) except the number of suborbitals which may be 3 to 4.

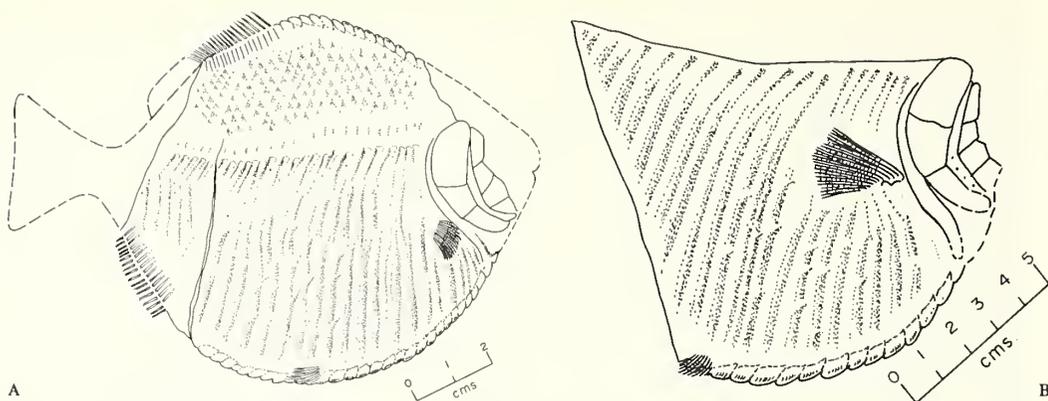
*Tetragonolepis oldhami* Egerton

Plate 15; text-figs. 12 and 13

*Diagnosis.* *Tetragonolepis* attaining an estimated length up to 180 mm, with abdominal protuberance about twice that of the portion above the lateral line canal. Branchiostegal rays, 3, elongated, progressively larger starting from the anterior one. Preopercular angulate, slightly or markedly. Suborbitals 4, asymmetric. Caudal fin has 15–16 haemal arches supporting lower lobe.

*Distribution.* Lower Jurassic, India; Kota formation.

*Lectotype.* GSI 2145 is preserved entirely as an impression (Egerton 1878, pl. II, fig. 1; redrawn here, text-fig. 12A). It has most of the trunk including the region of dorsal and ventral ridge scales, parts of dorsal and anal fin, but lacks the caudal fin. The anterior and dorsal portion of the skull is missing. The body is clearly hypsiform; about twice as deep below the central axis than above it. The preserved portion is about 92 mm long. It is estimated that the fish was about 128 mm long. Nothing can be ascertained about dermal skull pattern, snout, and jaws. Four suborbitals are recognizable which are asymmetric. The preopercular is somewhat angulate and the opercular is deep (approx. length/width ratio 2:1). The interopercular is slightly deeper than subopercular. The cleithrum is sigmoid. The portion of the body below



TEXT-FIG. 12. *Tetragonolepis oldhami*: A, lectotype (GSI 2145), with restored outlines; B, ISI P. 36, complete specimen, preserved as impression.

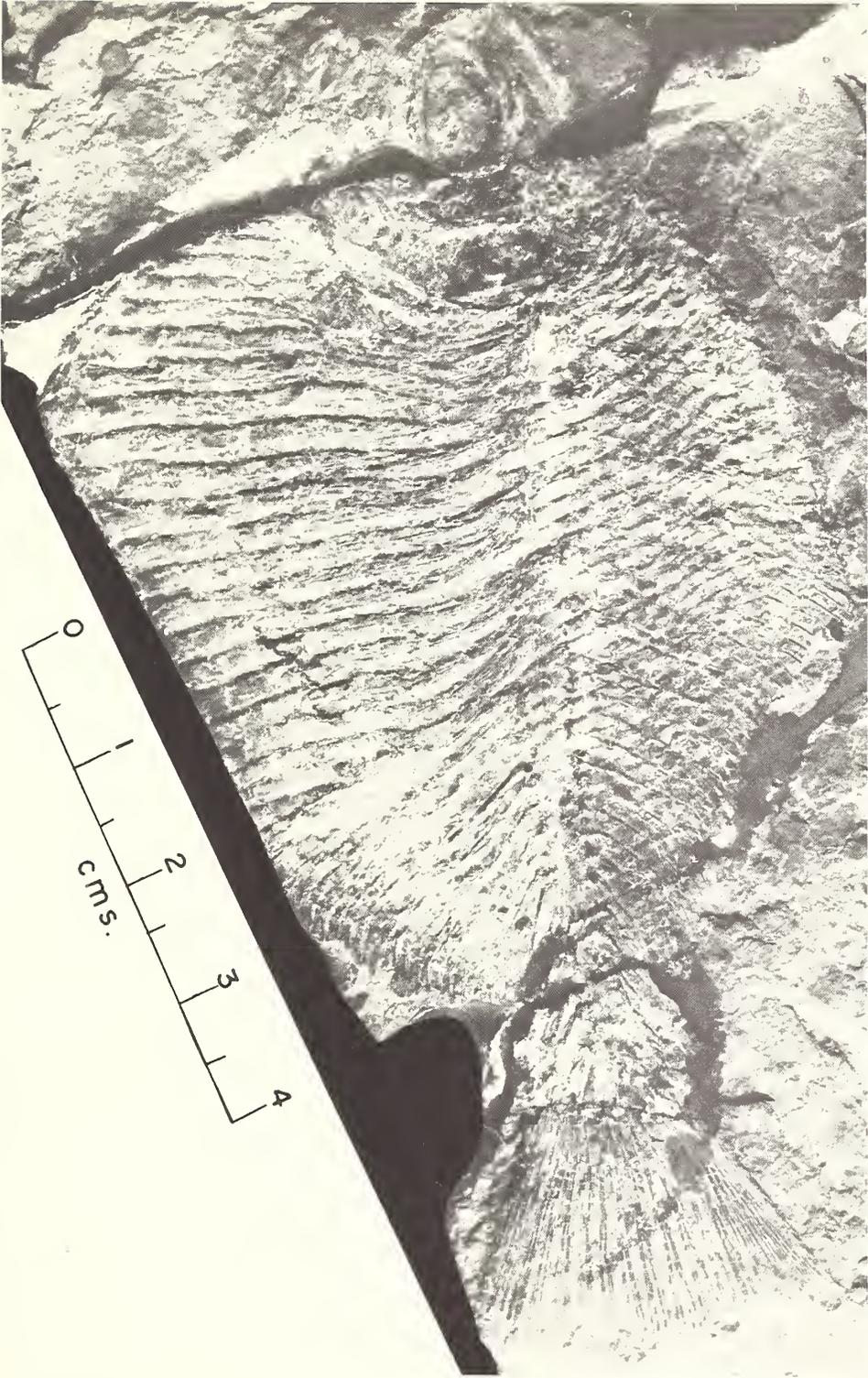
the central axis displays prominent haemal arches and ribs. There are indications of strong ribs. The scales appear to have been much deeper below the central axis than above it. The ventral ridge scales are more conspicuous than dorsal and bear fine pectinations at the ridges. The pectoral fin originates at the level of subopercular-interopercular suture and has 12-14 lepidotrichia. The pelvic fin is vestigial and has 6-7 lepidotrichia. The dorsal fin is preserved only anteriorly but has about 16 lepidotrichia, supported by an equal number of radials. The lepidotrichia were probably segmented and distally bifurcated. The anal fin is preserved anteriorly and has 17-18 close-set lepidotrichia with equal member of radials.

*Material.* Lectotype (GSI 2145), Kota formation, India, fish wanting anterior and dorsal portion of head and tail, about 92 mm long and 88 mm deep. New specimens: ISI P. 36, Kota ledge (near village Kota: text-fig. 2), Kota formation, India, fragment of ventral part of the trunk and posterior region of head preserved as an impression, 120 mm long and 90 mm deep. ISI P. 37 and 37a, Kota limestone near Lingal-Metpalli (text-fig. 2), Kota formation, India, nearly complete fish, part, and counterpart, 108 mm long and 65 mm deep.

*Description.* *Tetragonolepis oldhami* is a moderately sized semionotid reaching an estimated length of 108-180 mm and depth of 65-130 mm as seen from the lectotype and new specimens. The dermal bones of the skull in ISI P. 37 form a head shield in which the sutures are close set (Pl. 15 and text-fig. 13). The suture between frontal and parietal is obscured but the suture between dermopterotic and frontal and dermopterotic and parietal is visible. The dermopterotic is larger than the parietal. The head shield has a fine tubercular ornamentation. 4 suborbitals are seen in ISI P. 36 and 37 (text-figs. 12B and 13), similar to the lectotype. The antorbital was probably triangular and the post-rostral squarish (text-fig. 13). The nasal is uncertain.

EXPLANATION OF PLATE 15

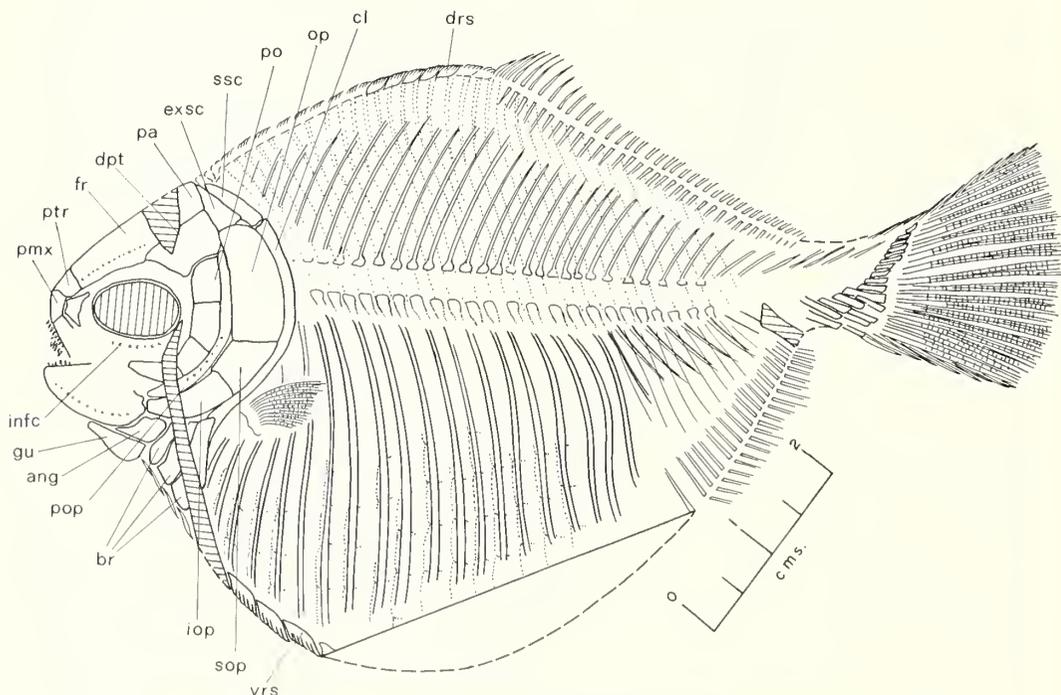
*Tetragonolepis oldhami*, complete specimen, ISI P. 37, from Kota formation, India.



JAIN, Jurassic fish from India

The premaxilla is displaced slightly and the shape of the maxilla cannot be determined posteriorly. There are fine, pointed teeth on premaxilla, maxilla, and palate. The circumorbitals could not be determined but in ISI P. 37 (text-fig. 13) the orbit seems to be surrounded by a sclerotic ring. The infraorbital sensory canal can be seen ventrally below the orbit. The lower jaw (text-fig. 13) is deep but is vague dorsally. The dentary is large, bearing fine, pointed teeth, similar to those on premaxilla and maxilla. The angular is displaced and can be seen partly behind the dentary. The mandibular sensory canal is visible. Between the rami of the lower jaw there is a gular plate. Three branchiostegal rays are seen, becoming progressively longer from the anterior. The opercular apparatus is visible in all specimens. The preopercular has a clearly ascending process and is angulate. The opercular and interopercular are both deeper than the subopercular. The cleithrum is characteristically sigmoid and an elongated suprascapular is present.

The body is covered with scales each of which has a sharply thickened rib on its anterior border. The scales are small and rhombic on the dorsal side of the notochordal axis and quadrangular and deep on the ventral side. There are 10-11 horizontal rows in the dorsal region and 8-9 in the ventral region of the body. The dorsal and ventral ridge scales bear fine pectinations and serrations but the former are only half as big as the latter (text-fig. 13). The neural spines are fused to the supporting arches along the length of the body but do not reach the body margin. The haemal spines are shorter. An 'inner' rib (text-fig. 13) is present in the flank and belly region.



TEXT-FIG. 13. *Tetragonolepis oldhami*, from ISI P. 37 and a, complete specimen.

The pectoral fin is delicate (text-figs. 12 and 13) and made up of about 10–11 lepidotrichia. The pelvic fin is vestigial (text-figs. 12A and B) and is made up of about 6–7 lepidotrichia. The dorsal fin stretches from the dorsal apex of the body almost to the tail and has the same number of radials as lepidotrichia, of which 34 can be counted in the dorsal fin of ISI P. 37 (text-fig. 13). The anal fin is not preserved completely in any specimen but it is less extensive than the dorsal fin. The anal fin has between 20 and 25 lepidotrichia and the same number of radials. The caudal fin is preserved only in ISI P. 37 (text-fig. 13) and has 15–16 haemal spines supporting the lower lobe. The lepidotrichia are segmented and distally bifurcated. There are fringing fulcra on the fin both dorsally and ventrally.

*Discussion.* The body proportions and characteristics of *T. oldhami* such as the number and disposition of suborbitals, arrangement of opercular apparatus, characteristic shape of cleithrum, presence of robust ribs in the body, and the disposition of median and paired fins are more or less identical in all specimens.

*Tetragonolepis* is essentially a European Liassic genus apart from these Indian representatives. The proportions of the body, number, and disposition of suborbitals and the shape of preoperculum are some of the important characteristics in which *T. oldhami* is distinguishable from *T. semicineta* (Upper Lias: Wurtemberg and Bavaria, W. Germany), *T. discus* (Upper Lias: Gloucestershire, England), and *T. drosera* (Upper Lias: Wurtemberg, W. Germany).

Two other species of *Tetragonolepis* from the Kota formation were proposed by Egerton (1878), *T. rugosus* and *T. analis*. *T. rugosus* is represented by a single fragmentary specimen (lectotype GSI 2146) which is about 70 mm across (Egerton 1878, pl. II, fig. 2). This shows a group of scales from the anterior region of body as impressions which suggest a 'rugged coat of ganoine, almost tubercular in aspect'. This single character of scales led Egerton to erect a new species of *Tetragonolepis*. The specimen is too fragmentary to exhibit any diagnostic characteristic of the genus *Tetragonolepis* and as such it should be regarded as *sp. indet.* *T. analis* is also represented by a single specimen (lectotype GSI 2150). The other two specimens ('portions of two other fish' mentioned by Egerton) have since been lost. The lectotype is well illustrated (Egerton 1878, pl. III, fig. 1) and is almost entirely preserved as an impression. This is clearly a deep-bodied form. Unfortunately, however, only the rear of the head is seen so that nothing is known about the dermal skull pattern nor is certain information obtainable on the opercular series. There seems to be 2–3 enlarged branchiostegal rays but their outlines cannot be clearly seen. The cleithrum is probably sigmoid. The pectoral fin is not seen. The pelvic fin is vestigial, having 7–8 lepidotrichia. The anterior part of the anal fin is preserved having lepidotrichia which are bifurcated and distally segmented. There appears to have been a complete covering of scales on the body. The scales below the notochordal axis are deeper than those above it. The proportions, however, cannot be worked out as the dorsal region of the body is missing. Thus the lectotype of *T. analis* exhibits certain characteristics suggesting a deep-bodied fish but not distinctive enough to be recognized as a species of *Tetragonolepis*. As such *T. analis* should be regarded as *sp. indet.* It may be mentioned that Woodward (1895, p. 162) classified the two species, *T. rugosus* and *T. analis*, as based upon 'fragmentary specimens'.

## AGE AND DISTRIBUTION OF THE HYPISISOMID SEMIONOTIDS

The semionotids are mostly fusiform to hypsisomid fishes with small mouths (Schaeffer 1967). There are two evolutionary trends from a basic form, typified by *Semionotus* and *Acentrophorus*, which on the one hand have given rise to hypsisomid forms such as *Dapedium* and *Tetragonolepis* and on the other hand produced the fusiform *Lepidotes*. Lehman (1966) has subdivided semionotids, on the basis of body shape, restricting the fusiform semionotids to the family Semionotidae (except *Lepisosteus*, which is placed in a new order Lepisosteiformes) and the hypsisomid forms to a new family Dapediidae. He has included *Dapedium*, *Tetragonolepis*, *Heterostrophus*, and *Dandya* in the family Dapediidae. Schaeffer (1967) has erected the genus *Hemicalypterus*, and another genus, *Paradapedium*, is proposed in this paper, both being hypsisomid. Thus 6 genera of hypsisomid semionotids are known:

1. *Hemicalypterus* Schaeffer 1967. Chinle formation, Upper Triassic, North America.
2. *Dandya* White and Moy-Thomas 1940. Upper Triassic, Hallein, Austria.
3. *Tetragonolepis* Bronn 1830. Upper Lias. Wurtemberg and Bavaria, West Germany, and Gloucestershire, England; Kota formation, Lower Jurassic, India.
4. *Dapedium* Leach 1822. Lower Lias, Lyme Regis, England, and Alsace, Germany; Upper Lias, Yonne (Vassy), Normandy, France, and Wurtemberg, Germany.
5. *Heterostrophus* Wagner 1863. Oxfordian, England, and Lower Kimmeridgian (= Solenhofen) of Germany.
6. *Paradapedium* Jain 1973. Kota formation, Lower Jurassic, Deccan, India.

Schaeffer (1967) does not support the inclusion of *Heterostrophus* and *Dandya* in the family Dapediidae. *Heterostrophus* has been restudied by Woodward (1929) and is known by a single specimen from Solenhofen, Bavaria (*H. latus*). There is also fragmentary evidence of a similar fish from the Oxford Clay of Peterborough, England (*H. phillipsi*). *Heterostrophus* has close resemblance to *Dapedium* in many features of the skull. The body is known only in *H. latus* which is not hypsisomid. *Dandya* is represented by a single neurocranium and some anterior body scales. It is not certain (Lehman 1966) that it belongs to the family Dapediidae. The present author supports Schaeffer's views in not including these genera in the family Dapediidae. The remaining four hypsisomid genera of the Semionotidae (excluding *Heterostrophus* and *Dandya*) are known by a number of well-preserved specimens. Table 1 shows a comparison of these genera.

The distribution in time and space of *Hemicalypterus*, *Dapedium*, *Tetragonolepis*, and *Paradapedium* reveals the following: *Hemicalypterus* is the earliest hypsisomid semionotid and is restricted to the Upper Triassic; *Dapedium* is known from Lower and Upper Lias; *Tetragonolepis* is restricted to the Upper Lias; *Paradapedium* is similar to *Dapedium*, and is known with *Tetragonolepis* from India. It seems, therefore, that *Paradapedium* may be an ecological substitute for *Dapedium* in Asia, and need not necessarily be younger or older than *Dapedium*.

The hypsisomid semionotids do not occur in horizons lower than Upper Triassic and higher than Liassic, i.e. Lower Jurassic. *Hemicalypterus* (Upper Triassic) is distinctive from the Liassic hypsisomid semionotids of Europe and India, but the latter show close resemblance among themselves. It seems unlikely, therefore, that the Kota formation is younger than the Lower Jurassic, and the evidence favours

TABLE 1. Comparison of characteristics of hypsisomid semionotids

	<i>Dapedium</i>	<i>Paradapedium</i>	<i>Tetragonolepis</i>	<i>Hemicalypterus</i>
Body proportions:				
a. Depth of body below lateral line canal as percentage of total body depth	60-65% (4 species; 15 specimens)	70-72% (2 specimens)	60% ( <i>T. oldhami</i> ; 1 specimen)	250% (Schaeffer's restoration)
b. Length of head as percentage of body length	26-34% (3 species; 13 specimens)	15% (1 specimen)	30% ( <i>T. oldhami</i> ; 1 specimen)	39% (Schaeffer's restoration)
c. Depth of head as percentage of body length	33-40% (3 species; 12 specimens)	16% (1 specimen)	28% ( <i>T. oldhami</i> ; 1 specimen)	30% (Schaeffer's restoration)
Body squamation	Full body; scales deeper in belly	Full body; scales deeper than <i>Dapedium</i> in belly	Full body; scales deeper in belly	Posterior half of body naked; scales deeper in mid body
Ridge scales	Dorsal, pectinate, or denticulate; ventral, more prominent than dorsal	Dorsal and ventral slightly more conspicuous than <i>Dapedium</i> ; pectinate or denticulate	Ventral larger than dorsal, both serrated	Much enlarged and prominent; strongly denticulate
Head bones	Heavily ossified; tuberculated	Not heavily ossified; delicate ornament	Thin, feebly ornamented	Thin and delicate; feeble ornamentation
Suborbitals	6-11; not extending beyond mid orbit	9-10; extending beyond mid orbit	3-4; not extending beyond mid orbit	3; slightly extending beyond mid orbit
Extrascapulars	4-6	3	1	2
Hyomandibular	Stout; foramen (VII) above mid length	Slender and delicate; foramen (VII) at about mid length	Not known	Not known
Quadrate	Squarish; stout; prominent articulation facet	? Triangular, moderate; poorly defined articulation facet	Not known	Not known
Dentary	Like open V	More definitely V-shaped	Like <i>Dapedium</i> in shape	Not completely known
Dentary teeth	Similar in size	Anterior tooth enlarged	Similar in size	Similar in size
Cleithrum	Arched	Arched	Sigmoid	? Arched
Neural spines	Fused with neural arch in hinder part of body only	Fused with neural arch throughout the length of body	Fused with neural arch throughout the length of body	? Fused with neural arch throughout the length of body

a Lower to Upper Liassic age. *Hemicalypterus* is known only from a continental formation. *Dapedium* occurs in marine sediments but a rather similar genus *Paradapedium* is found in continental beds. *Tetragonolepis* is known from marine sediments in Europe and fresh-water habitats in India. It is, therefore, likely that they were euryhaline forms. Schaeffer (1967) has suggested that these fishes probably assumed ecological roles similar to certain species of *Cyprinodon*, the centrarchids and the characins. *Tetragonolepis* and *Dapedium* are known from the northern margins of Tethys. In addition, *Tetragonolepis* also occurs in a continental area south of Tethys, i.e. India. *Paradapedium* is known from south of Tethys. *Hemicalypterus* occurs in the continental land mass of North America, presumably north-west of Tethys. The deep-bodied semionotids seem, therefore, to be enjoying a cosmopolitan distribution on both sides of Tethys over a rather limited span of time—the Later Triassic and Early Jurassic.

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## LIST OF ABBREVIATIONS USED IN TEXT-FIGURES

ang.—angular	ll.j.—left lower jaw
ao.—antorbital	m.c.—mandibular canal
art.—articular	mtpt.—metapterygoid
art. prop.—articulation facet for preopercular	mx.—maxilla
aut.—autopalatine	na.—nasal
br.—branchiostegal ray	nar.—naris
cl.—cleithrum	op.—opercular
co.—circumorbital	op. pr.—opercular process
cor.—coronoid	pa.—parietal
dermp.—dermopalatine	part.—prearticular
dpt.—dermopterotic	pect. f.—pectoral fin
drs.—dorsal ridge scales	pmx.—premaxilla
dt.—dentary	pmx. t.—premaxillary tooth
dt.t.—dentary teeth	po.—postorbital
ectpt.—ectopterygoid	pop.—preopercular
enpt.—entopterygoid	ptr.—post-rostral
exsc.—extrascapular	qu.—quadrate
fr.—frontal	r.l.j.—right lower jaw
gl.—glenoid fossa	ros.—rostral
gu.—gular	sang.—surangular
hym.—hyomandibular	so.—suborbital
hym. f.—hyomandibular foramen	sop.—subopercular
iop.—interopercular	ssc.—suprascapular
info.—infraorbital	sym.—symplectic
infc.—infraorbital sensory canal	vrs.—ventral ridge scales

S. L. JAIN

Geological Studies Unit  
 Indian Statistical Institute  
 203 Barrackpore Trunk Road  
 Calcutta-35  
 INDIA

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# ON *CRASSIGYRINUS SCOTICUS* WATSON, A PRIMITIVE AMPHIBIAN FROM THE LOWER CARBONIFEROUS OF SCOTLAND

by A. L. PANCHEN

**ABSTRACT.** The unique holotype of *Crassigyrinus scoticus* Watson is almost certainly from the Viséan Gilmerton Ironstone of Scotland, as suggested by Watson. It consists only of the right side of a large primitive amphibian skull with a very long postorbital region. The pattern of dermal bones, which includes a well-developed preopercular, is intermediate in configuration between that of a rhipidistian fish and the earliest Amphibia, the ichthyostegids. *Crassigyrinus* may also have a rhipidistian-like course of the infraorbital lateral line system, but in the amphibian form of open sulci. The configuration of bones round the nostril is probably also similar to that of osteolepiform Rhipidistia. '*Macromerium*' *scoticum* Lydekker, a lower jaw from Gilmerton, formerly attributed to *Crassigyrinus*, is more probably *Loxomma allmanni*. *Crassigyrinus* is too large and far too late to be anything but a distant relict of the ancestral tetrapod stock. A new order of labyrinthodont Amphibia, the Palaeostegalia, is proposed for *Crassigyrinus*.

*Crassigyrinus scoticus* Watson is known only from the holotype, which consists of the right side of a large amphibian skull exposed in dorsal, external view on a massive block of ironstone. Only the cheek region and the side of the snout are present: the skull table, the middle preorbital region, and the left side are completely missing and nothing is known of the braincase or palate. In his original description Watson (1929) considered that only the maxilla, lacrimal, jugal, postorbital, squamosal, quadratojugal, and quadrate were preserved.

The specimen is registered as No. 1859.33.104 in the Department of Geology, Royal Scottish Museum (originally No. 272) and is from the Hugh Miller Collection. It is labelled 'Carboniferous Limestone' and is stated by Watson to come from the Midlothian region, but there are no further data. Watson attributed it to the Gilmerton Ironstone, Lower Limestone Group (Upper Viséan) on the character of the matrix, which is a nodular ironstone consisting of concretions of siderite in a hard dark grey shaly matrix. This is one type of matrix that occurs at the Gilmerton horizon.

Thanks to the very great kindness of Dr. A. H. V. Smith of the National Coal Board I have now some corroboration of Watson's opinion. A specimen of matrix from the holotype of *Crassigyrinus* was compared with a series of matrix specimens of known horizon kindly supplied by Dr. Mahala Andrews from the Royal Scottish Museum. The control specimens were from the Loanhead No. 2 Ironstone (Limestone Coal Group: Namurian A), the Gilmerton Ironstone, and the Dunnet Shale, Straiton (Upper Oil Shale Group: Viséan). The spore assemblages from the *Crassigyrinus* matrix were of Upper Viséan or Lower Namurian age and resembled those from the Gilmerton control specimens rather than those from the other horizons.

*Crassigyrinus* was placed by Watson in the labyrinthodont superfamily Anthracosauroidae of his grade Embolomeri, but *incertae sedis* as to family. It has already

been noted (Panchen and Walker 1961) that Watson's attribution to the anthracosaurs is probably to be regarded merely as an indication that he did not consider it to be a loxomatid, the other group of his 'grade Embolomeri' and the only other common group of Carboniferous labyrinthodonts from Great Britain.

Watson noted two characters of the skull which are atypical of anthracosaurs; the great expanse of the skull immediately below the orbit and the extension of the maxillary bone to underlie the quadratojugal, thus separating the jugal from the jaw margin. They are, however, paralleled in several temnospondyl labyrinthodonts (Panchen and Walker 1961).

Romer (1947) suggested that as the preserved cheek region had apparently separated cleanly from the missing skull table there might have been a kinetic separation of table and cheek of the anthracosaur type in the complete skull. In his classification of labyrinthodonts he placed *Crassigyrinus* with *Anthracosaurus russelli* to comprise the family Anthracosauridae. This grouping is retained but with expressed doubt in the current edition of *Vertebrate Paleontology* (Romer 1966). The association was based on the common possession of an unusually long suspensorium.

It is clear, however, that *Crassigyrinus* is not a member of the Anthracosauridae because of the small, relatively uniform teeth which contrast strikingly with the massive dentition of *Anthracosaurus* with its strong canine 'peaking' (Chase 1963, Panchen 1970). The present study was undertaken in an attempt to determine the affinities of *Crassigyrinus* for my monograph on the Anthracosauria (Panchen 1970). The exposed surface was further developed with an Industrial 'Airbrasive' unit to remove all residual matrix, and, as a result, I was able to report that *Crassigyrinus scoticus* was an extremely primitive amphibian which merits the fuller redescription given here.

An amphibian lower jaw, described by Lydekker (1890) as *Macromerium scoticum*, has also been tentatively ascribed to *Crassigyrinus* by several authors and is therefore also redescribed.

#### DESCRIPTION—SKULL ROOF

The holotype of *Crassigyrinus* (text-fig. 1, Pl. 16, fig. 1) represents a skull of similar size to that of *Anthracosaurus russelli* Huxley (Panchen 1970) and because of the relationship between them suggested by Watson and by Romer the latter specimen is a useful standard of comparison. *Anthracosaurus* also represents a primitive labyrinthodont and a comparison of proportions and detailed bone pattern highlights the unique features of *Crassigyrinus*.

*Crassigyrinus* is characterized by the very long postorbital cheek region, so that the posterior border of the orbit is more than half-way forward from the back of the quadrate to the anterior end of the specimen. Preservation probably extends to the tip of the snout. The orbit is very large and, as far as preserved, is a parallelogram

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#### EXPLANATION OF PLATE 16

- Fig. 1. *Crassigyrinus scoticus*, holotype. R.S.M. 1859.33.104,  $\times \frac{1}{2}$ .  
 Fig. 2. '*Macromerium*' *scoticum*, holotype. B.M. (N.H.) R310,  $\times \frac{2}{3}$ .



PANCHEN, primitive amphibian

in outline, with the parallel anterior and posterior borders inclined backwards towards the midline and the ventro-lateral border sloping upwards towards the back of the orbit. The dorso-mesial border is missing.

Behind the orbit the long cheek region tapers towards the massive quadrate region, while anteriorly the snout is, by labyrinthodont standards, exceptionally broad and short. Significant dimensions are compared with those of *Anthracosaurus* in Table 1: all measurements in both cases are as nearly as possible in the plane of the skull roof.

TABLE 1. *Crassigyrinus scoticus* and *Anthracosaurus russelli* holotypes

	<i>Crassigyrinus</i>	<i>Anthracosaurus</i>
Overall length (centre-snout to quadrate condyle)	340 mm	420 mm
Back of orbit—quadrate	190 mm	175 mm
Ventral border of orbit—maxillary margin (minimum transverse distance)	65 mm	c. 30 mm
Length of orbit (ant.—post.)	50 mm	c. 45 mm
Depth of orbit (mesial—lateral)	c. 45 mm	35 mm
Depth of cheek immediately behind orbit	105 mm	c. 70 mm

After cleaning with the Airbrasive unit the sutures between individual dermal bones became very clear and the pattern behind the front of the orbit is established beyond reasonable doubt. There is, however, some uncertainty about the configuration of the snout region due to compression, erosion, and distortion.

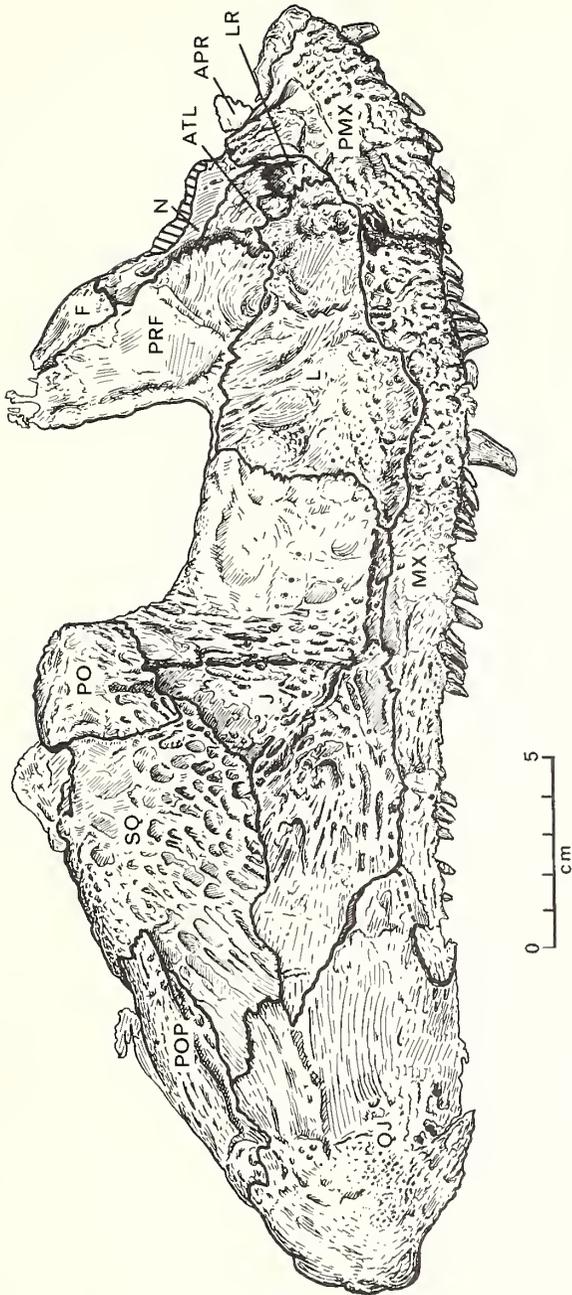
The preserved bones of the cheek region comprise the jugal and quadratojugal and above them the postorbital, squamosal, and a bone that can only be identified as preopercular. The boundary sutures of all the bones were traced throughout.

The anterior border of the jugal, formed by a long transverse suture with the lacrimal, is exceptionally far back for a labyrinthodont, being well behind the level of the front of the orbit and turning further posteriorly at its ventro-lateral end. The lacrimal thus extends behind the middle of the orbit. Ventrally the jugal is completely excluded from the jaw margin by the maxillary, as already noted, but its postero-dorsal corner, situated in the suture with the quadratojugal, extends just posteriorly to the maxillary.

The surface of the jugal is not strongly ornamented, but there is reason to think that there has been considerable erosion of the surface. The area below the orbit is certainly eroded but below the postorbital and squamosal a small irregular pit and ridge ornament is preserved. The ornament is elongated in a transverse direction below the latter bone, but is vertical below the former.

The only reasonably clear traces of the lateral line system are preserved on the jugal and then with less than absolute certainty. A series of deeper elongate pits forming a vertical line from the suture with the postorbital to that with the maxillary may mark the descending course of the infraorbital sulcus which is then reflected forward as a groove just above the maxillary suture and runs forward to continue its course more doubtfully on the lacrimal.

The course of the jugal sulcus may be marked by a line of elongate pits running



TEXT-FIG. 1. *Crassigyrinus scoticus* Watson, holotype as preserved ( $\times \frac{1}{2}$ ). APR, anterior postrostral; ATL, anterior tectal; F, frontal; J, jugal; L, lacrimal; LR, lateral rostral (septomaxillary); MX, maxillary; N, nasal; PMX, premaxillary; PO, postorbital; POP, opercular; PRF, prefrontal; QJ, quadratojugal; SQ, squamosal.

obliquely upwards and backwards from a point just above the flexion of the infra-orbital sulcus, but there is no sign of its continuation on to the squamosal.

If these sulci are correctly interpreted this course follows that of the lateral line canals of *Eusthenopteron* in that the infraorbital sulcus is inflected forwards near the ventral margin of the jugal and the jugal sulcus originates well above the flexion. In this respect the pattern is more primitive than that of *Ichthyostega* in which the flexion is more dorsal and the jugal canal originates at its angle (text-fig. 3). On the other hand *Ichthyostega* still has the fish structure of its lateral line system with canals through the bone opening only by pores to the surface and in this respect is probably more primitive than *Crassigyrinus* (Jarvik 1952).

At first I was tempted to interpret a horizontal row of pores at about half-way down the jugal as signs of a hidden fish-like canal. Three pores on the lacrimal would then continue this series, but it now seems more probable that they all represent the remnants of an eroded ornament. Ironically if the grooves represent the lateral line system they follow the fish course but are in the amphibian condition, whereas the pores would follow the amphibian course but represent the fish condition.

The quadratojugal of *Crassigyrinus* is unusually large whether compared with that of rhipidistians or labyrinthodonts. Little of the quadrate is visible and some development in its expected position indicates that most of it is probably missing. However, the massive curvature of the back of the quadratojugal suggests that the quadrate condyle was of unusually large diameter. The surface of the quadratojugal is eroded, but antero-ventrally it shows a series of fine horizontal ridges which converge slightly posteriorly suggesting a centre of ossification near the back of the bone. Posteriorly there is an area of very fine pitting.

The postorbital is a quadrilateral bone with a transverse posterior suture with the squamosal. The configuration of these bones thus have an amphibian rather than a fish-like aspect, as does the extension backward of the jugal beyond the lower border of the squamosal. The postorbital, again somewhat eroded, shows evidence of a coarse labyrinthodont pit and ridge ornament of the type better preserved on the squamosal.

The latter bone, together with the preopercular and possibly the quadratojugal, had a massive postero-dorsal exposure. This is formed by the dorsal border of the posterior half of the bone being inflected inwards through a right angle. In front of this inflected region an inset rounded piece of bone projects above the main squamosal and is apparently an overlap area for the skull table.

The ornament of the main, lateral part of the squamosal is well preserved ventrally and consists of a massive and irregular pit-and-ridge system of labyrinthodont type. The ornament converges towards a point just below the overlap area and the pits have steep proximal walls but slope up gradually distally.

The preopercular occupies exactly the same morphological position as that in the rhipidistian *Eusthenopteron* (Jarvik 1944) and that in *Ichthyostega*. It forms the posterior part of the postero-dorsal border of the cheek region and sutures with the squamosal and quadratojugal. The suture between the latter two bones thus runs perpendicularly to its ventral border. It is relatively a considerably larger bone than that of *Ichthyostega* but does not quite reach the proportions of that in *Eusthenopteron*. Because of the massive nature of its dorsal shelf compression of the specimen

has forced the dorsal part of the bone outward relative to the ventral part, but the lateral surface was probably flat in the intact skull. The preopercular runs dorsal to the squamosal for about half the length of the latter and its anterior squamosal suture is clearly marked on both lateral and dorsal surface.

The sutures bounding the lacrimal are also clear: the position of its posterior, jugal suture has already been commented on. Ventrally it has an irregular suture with the maxillary. Dorsally, as in the position of the jugal suture, its position and relationships are an accurate intermediate between those in *Eusthenopteron* and *Ichthyostega*.

The lacrimal of *Eusthenopteron* forms the major part of the ventral rim of the orbit, while that of *Ichthyostega* is excluded by the junction of jugal and prefrontal above it, as in anthracosaurs. In *Crassigyrinus* the lacrimal just fails to reach the orbit dorsally as there is a jugal-prefrontal contact along the orbital rim.

The surface of the lacrimal is deeply contoured in such a manner, which may be in part due to compression, that the form of its hidden mesial surface is impressed on the outside. Posteriorly, below the front of the orbit, there are two convex areas. The lower one is horizontally oval with an eroded ornament, the upper a vertical oval with a shallow trough in front. A concave area between them carries the pores which were thought to mark the course of the infraorbital canal while the possible sulcus runs below them.

The remaining anterior area of the bone forms two further troughs of badly eroded bone separated from one another and from the first trough by low ridges, and in front of them a raised eroded area with two deep pits.

The prefrontal forms the whole anterior border of the orbit, along which it is raised as a thickened rim, and extends along the ventral border to meet the jugal. Ventrally its suture with the lacrimal was traced throughout, as was its anterior boundary. The surface of the bone shows little ornament and is probably eroded.

The form of the maxillary is very similar to that of large anthracosaurs such as *Eogyrinus* (Panchen 1972b) and *Anthracosaurus*. It is convex in a transverse plane and is irregularly ornamented anteriorly. In the posterior half of the bone the ornament is more regular and is elongated into a series of longitudinal grooves. The bone surface is, however, considerably eroded for the final quarter of its length.

As has already been noted the maxillary completely excludes the jugal from the jaw margin and has a considerable backward extension below the quadratojugal. Anteriorly the maxillary underlies all but the extreme anterior end of the lacrimal. The suture between the maxillary and premaxillary is a transverse line. All but the dorsal half-centimetre is easily traced. Both bones curve in towards the suture so that the latter is situated along the floor of a deep but irregular groove. Dorsally this groove runs into a pit with disrupted bone in its floor and it is here that the suture cannot certainly be traced.

I was originally inclined to interpret this pit as the nostril: this would then terminate a naso-labial groove of the type common in early tetrapods (Panchen 1967, 1970). While this interpretation is still possible it is not the one I now favour.

The premaxillary is a massive bone ornamented like the front of the maxillary. Preservation apparently extends to its median edge and a possible fragment of the left premaxillary with their joint midline suture is present anteriorly.

The premaxillary is much wider from top to bottom throughout its length than the maxillary. In addition it bears a massive dorsally directed process near the front. In *Eusthenopteron* a similar but relatively smaller process of the premaxillary rises to meet the nasal series on each side and to separate the anterior tectal from the median anterior postrostral.

In *Crassigyrinus* if the process is viewed from the front it is seen to be paralleled by another more mesial to it and also apparently formed from the premaxillary. The matrix-filled groove between them was interpreted by Watson as the nostril, on the assumption that the whole bone I have called premaxillary was the anterior end of the maxillary and that the premaxillary was missing.

I have now cleaned the groove between the two processes: the bottom of the groove is marked by a line of junction which indicates that the two processes are separate and may originally have had an aperture between them. However, if the premaxillary is correctly identified and the outer process is part of it (there is a crack across the base of the process) then interpretation of the space between the processes as the nostril is very difficult.

It seems more probable that the two premaxillary processes buttressed a massively developed snout region and it is not impossible that the inner one pertains to an ossified nasal capsule. Presumably an anterior postrostral, present in both *Eusthenopteron* and *Ichthyostega*, was situated in front of the outer process. A fragment of what may be this bone is present in the specimen.

The bony area between the prefrontal and the premaxillary process is disrupted and difficult to interpret which is particularly unfortunate as, by analogy with *Eusthenopteron*, the nostril (fenestra exonarina anterior—Jarvik 1942) should be situated in that region.

The dorsal part of the suture forming the anterior boundary of the prefrontal is with a strip of bone which presumably represents the frontal. A short suture forming the antero-ventral boundary of the latter bone can be traced with reasonable certainty. Below this the nasal appears to have been twisted so that its inner, ventro-mesial surface is exposed to view with the broken posterior edge showing at the front.

However, there is a further area of bone between the nasal and the front of the lacrimal. Most of this appears to be occupied by a poorly preserved bone whose relationships are exactly those of the anterior tectal of *Eusthenopteron* and *Ichthyostega*. A small piece of raised bone bordering the front of the lacrimal may be the only part of the anterior tectal whose periosteal surface is preserved or may be an extra ossification.

The ventral edge of the anterior tectal borders what may be the nostril, although I am not entirely convinced of this. The nostril is an oval area entirely occluded by bone. This bone is presumably septomaxillary, or in fish terms the processus dermintermedius of the lateral rostral (Jarvik 1942, Panchen 1967) and, as in *Eusthenopteron*, the lateral rostral is exposed outside the cavity of the nostril as a triangle of bone between the lacrimal and the premaxillary, and bordering the nostril ventrally.

The dentition of *Crassigyrinus* is distinctive. Twenty-five small teeth are preserved on the maxillary. Those which are intact are, as Watson notes, shell or bullet-shaped but some show a slight turning back of the tip. They are fairly uniform in size with a slight but not consistent diminution towards the back. The longest is 10 mm to

the tip of the crown and has a basal diameter of 4 mm. The shortest is about half that length and has a diameter of 2.5 mm.

It is probable that a much larger number of maxillary teeth was originally present. Those preserved are in groups and are very close set, accounting for not much more than half of the maxillary length, so that an original count of about 40 including replacement pits is not improbable.

In addition to the maxillary teeth a large palatine tusk is visible below the maxillary at the level of the back of the lacrimal. The tip of the crown is broken off and presumably the whole is not visible but the maximum diameter is 9 mm and the visible length 15 mm.

Only 6 widely separated and poorly preserved premaxillary teeth are visible. The anterior one is the largest and most complete. The tip is broken off but the remainder is 9 mm long and has a diameter of 5 mm so that it is somewhat larger than the maxillary teeth. The others are comparable in size to the latter.

#### '*MACROMERIUM*' *SCOTICUM* LYDEKKER

'*Macromerium*' *scoticum*, known only from the holotype, consists of an incomplete right jaw ramus preserved with the lateral surface exposed on a block of ironstone. The specimen is from the Gilmerton Ironstone and is registered as R310 in the British Museum (Natural History).

It was briefly described by Lydekker (1890) who noted that while its shape favoured attribution to *Loxomma* the apparent poor development of the ornament was more like that of *Anthracosaurus*. He finally attributed it to Fritsch's (1889) genus *Macromerion*. The (invalid) change in the termination of the generic name represents Lydekker's policy of latinizing all genera.

He attributed the specimen to *Macromerion* on the character of the teeth but whatever the nature of the dentition the attribution is invalid. Fritsch's original genus contained a variety of unrelated species, including 2 anthracosaurs, probably 2 temnospondyls, and a pelycosaur. It may properly be used to refer to the latter (Romer 1945, Panchen 1970).

*M. scoticum* was discussed by Watson (1929), who noted the impossibility of its reference to *Macromerion* and concluded that it was 'not quite inconceivable' that it should be referred to *Crassigyrinus*. On balance, however, he considered that there was insufficient evidence even to determine its sub-ordinal position with safety and unless subsequently associated with a skull 'it had better be ignored'.

Romer (1947) noted the possibility of association with *Crassigyrinus* and more recently I noted a similarity in the teeth (Panchen 1970). I have now had the opportunity to further develop and study the holotype of *M. scoticus*.

The exposed surface of the specimen was covered with a thin film of matrix and this has been completely removed by 'Airbrasive' treatment. The surface is much eroded but the sutures can now be determined with ease. The specimen includes the whole of the jaw ramus with the exception of the articular region. Thus the articular bone and part of the surangular and angular are missing, as is the extreme posterior end of the dentary: however, preservation probably extends beyond the back of the dentary tooth row. In addition there is newly exposed a mass of badly eroded

bone behind the jaw which may include the articular region but more probably pertains to the rest of the skull (text-fig. 2, Pl. 16, fig. 2).

The shape of the jaw, as noted by Lydekker, is very reminiscent of that of a loxomatid and development shows that the pattern of dermal bones is fairly close to that of the Coal Measure loxomatid *Megalocephalus* (Watson 1926, Tilley 1971).

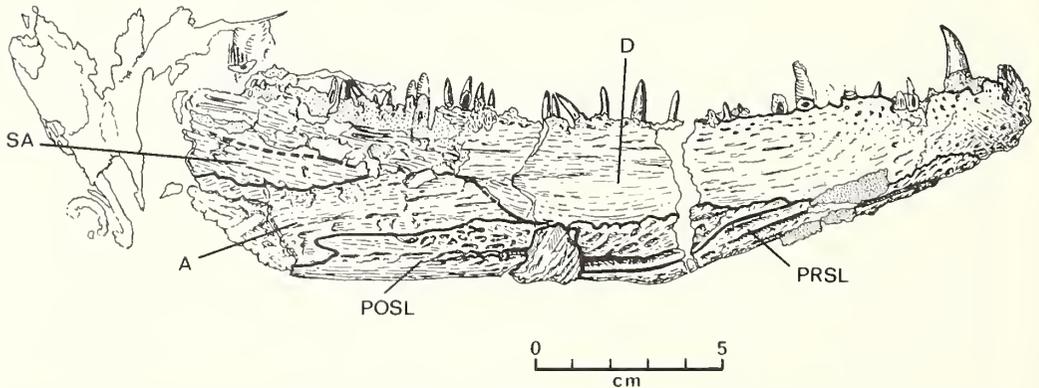
The dentary extends further ventrally, particularly in front of the anterior apex of the angular, than Watson's restoration of the jaw of *Megalocephalus* ('*Orthosaurus*') suggests, but corresponds more closely to Tilley's restoration of the Coal Measure form. The surface of the dentary appears moderately well preserved except posteriorly where it is dorsal to the angular and surangular.

Anteriorly, in the region of the symphysis, a shallow and irregular ornament is punctuated by small but deep pits. The rest of the bone is ornamented by shallow and irregular longitudinal grooves. If this appearance is not due to erosion it would appear to constitute a striking difference from the regular honeycomb ornament characteristic of the skull of *Megalocephalus* and many other temnospondyls. However, on inspection of the jaw rami of *Megalocephalus* in the Hancock Museum it is seen that the posterior part of the dentary also bears a lateral ornament of longitudinal grooves immediately below the tooth row. This may be seen in G15.46, a complete jaw ramus, and in G15.39. More anteriorly the 'Macromerium' ornament could well have been produced by erosion of the *Megalocephalus* type of dentary.

Only an anterior wedge of the surangular is preserved in 'Macromerium' between the dentary above and the angular below. Its line of junction with the dentary, which overlaps it considerably, is not preserved throughout because of the disruption of that bone. The surface of the surangular is ornamented only with fine longitudinal striae in contrast to *Megalocephalus* where the typical ornament is more or less developed in this region.

This is also the case with the angular which extends considerably further forward, as in *Megalocephalus*, but in the present specimen is underlain throughout its preserved length by the posterior splenial.

The 2 splenials form most of the ventral border of the specimen and, as in *Megalocephalus*, carry the conspicuous groove of the mandibular lateral line sulcus. The



TEXT-FIG. 2. *Macromerium scoticum* Lydekker, holotype as preserved ( $\times \frac{1}{2}$ ). A, angular; D, dentary; POSL, postsplenial; PRSL, presplenial; SA, surangular.

ornament on the splenials is most strongly developed above the groove and is not apparently of the *Megalocephalus* type but bears some resemblance to that on the jugal and squamosal of *Crassigyrinus*.

The suture between the splenials is so oblique as to be almost horizontal, beginning far forward dorsally and running back for about 6 cm until it is lost below an extraneous piece of dermal bone on the surface of the specimen. Its exact course is duplicated in the *Megalocephalus* jaw G15.39.

The greatest contrast between '*Macromerium*' and the jaw of *Megalocephalus* lies in the size of the teeth. The dentary dentition of *Megalocephalus* consists of relatively large teeth, which in the case of the parasymphysial tusk and the teeth which alternate with the tusks on the palate, reach a height of some 30 mm. The smaller teeth are between 10 and 20 mm.

In '*Macromerium*', which represents a jaw of over two-thirds of the size of that of a typical *Megalocephalus*, the majority of the teeth vary between 5 and 10 mm. This disparity is reflected in the number of teeth or tooth sites which may be estimated at nearly 50 in '*Macromerium*' but less than 35 in *Megalocephalus*.

However, '*Macromerium*' has a well-developed parasymphysial tusk with a crown height of nearly 15 mm in exactly the corresponding position to that of *Megalocephalus*. It also has an adjacent pair of large teeth both broken off at the base of the crown. The anterior one, however, is represented by a good natural cast and had a similar crown height to the parasymphysial tusk. The pair of teeth are situated at about 4 cm from the tusk in a position corresponding to that of a very large tusk in *Megalocephalus*.

The size of the small teeth is approximately the same as that of the maxillary teeth of *Crassigyrinus* and their general shape is similar, being bullet-shaped and not markedly recurved. However, they are more slender and I am not now so impressed with the resemblance. In structure they appear to be of loxommatid type with anterior and posterior keels distally. The parasymphysial tusk is less strongly lanceolate than that of *Megalocephalus* and is recurved but bears the keels.

The known amphibian fauna of Gilmerton consists of *Pholidogaster pisciformis* Huxley, an anthracosaur skull attributed to it by Watson (1929) and Romer (1964), but certainly in error (Panchen 1970), *Crassigyrinus* and *Loxomma allmanni* Huxley. There is no possibility of attributing '*Macromerium*' *scoticum* to the first two. Its minor resemblances to the skull of *Crassigyrinus* do not now, after close study, seem to warrant association with that form and it seems unlikely that such a relatively shallow jaw should be associated with such a deep skull roof.

On the other hand attribution to *Loxomma* seems quite likely. The pattern of dermal bones is loxommatid, as is the general form. The presence and position of the parasymphysial tusk also corresponds and the form, if not the size, of the teeth is suitable. Nothing is certainly known of the dentition of *Loxomma allmanni* and only the premaxillary and anterior maxillary teeth are known in the Coal Measure species *L. acutirhinus* Watson (1929, Tilley 1971). The estimated total count for the upper tooth row in this case is only about 35–38 but a larger number of smaller teeth might well be regarded as a more primitive condition likely to be found in the Lower Carboniferous *L. allmanni*.

Thus apart from the character of the ornament '*Macromerium*' *scoticum* has the

characteristics of a loxommatid jaw. It should also be noted that in *L. allmanni* the character of the ornament is known only from the posterior skull table and finally that the 'Macromerium' jaw is of exactly the right size for the reconstructed skull length (Tilley 1971) of the contemporary loxommatid. Dr. Beaumont (*née* Tilley) has kindly inspected the 'Macromerium' jaw and endorsed its attribution to *Loxomma*. It, therefore, need no longer be considered in a discussion of the anatomy of *Crassigyrinus*.

#### DISCUSSION

The size and configuration of the dermal bones present in *Crassigyrinus* together with the proportions of the skull are the most primitive recorded in any amphibian and, as far as preserved, are almost exactly intermediate between those in a typical rhipidistian, e.g. *Eusthenopteron*, and the Devonian amphibian *Ichthyostega* (text-fig. 3).

Thus the preopercular bone is intermediate in relative size as is the squamosal. The jugal increases in both anterior and posterior extent in the fish-amphibian transition and also establishes a contact with the prefrontal: again *Crassigyrinus* shows an intermediate condition in this and in the position of the jugal-lacrimal suture.

The interpretation of the bones of the snout is not absolutely certain but again it appears to be intermediate and the lateral line system, if correctly interpreted, shows a primitive course otherwise known only in fish.

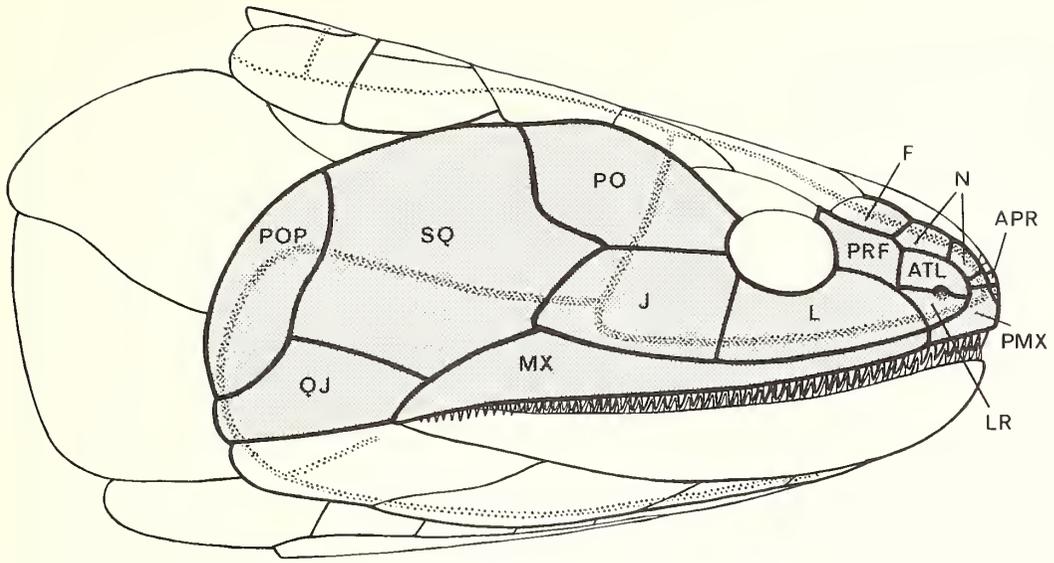
The proportions of the skull of *Crassigyrinus* as measured by the relative position of the orbit are also quite remarkable in being intermediate between those of *Eusthenopteron* and *Ichthyostega*.

There is, of course, no absolute certainty that *Crassigyrinus* is a tetrapod, but the characteristic features of massive quadratojugal and quadrate, large quadrilateral orbit, large prefrontal, and massive maxillary and premaxillary all suggest labyrinthodont affinity as does the nature of the dermal ornament and probably the lateral line sulci.

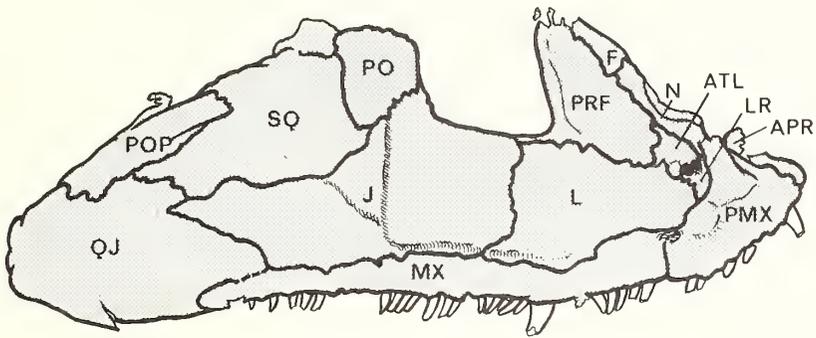
It is conceivable that the proportions of the skull of *Crassigyrinus* could have been due to a secondary migration forward of the orbits and that the interpretation given here of the fish-like snout is wrong. The presence of a preopercular bone is, however, incontestably primitive. Apart from *Ichthyostega* the only amphibian in which it is known, and then not with certainty, is the contemporary Devonian *Acanthostega* (Jarvik 1952).

In spite of these primitive characters *Crassigyrinus* is nevertheless a relatively late form and could not be more than a relict of any ancestral amphibian stock. Its large size and massive build is also in contrast to the small size to be expected in the common ancestor of reptiles and amphibians (Panchen 1972a).

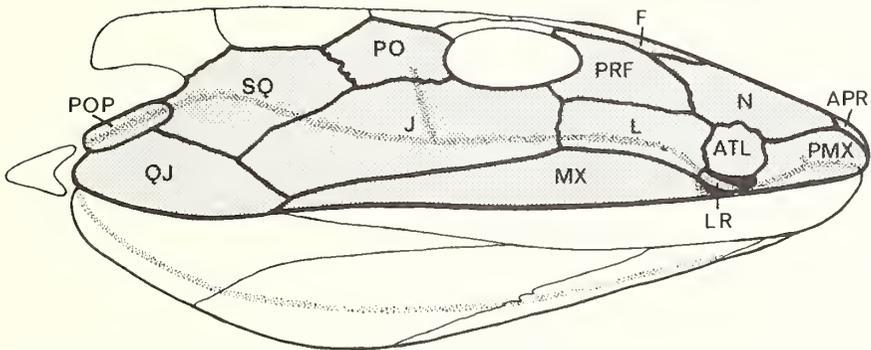
Thus the uppermost Viséan from which *Crassigyrinus* comes is dated at some 20 million years after the Devonian-Carboniferous boundary (Francis and Woodland 1964) whereas the origin of the amphibia was certainly well down in the Devonian. The age of *Ichthyostega* and *Acanthostega* is uncertain as direct correlation between the continental *Remigolepis* series from which they come and the standard marine



(a)



(b)



(c)

TEXT-FIG. 3. Skulls in right lateral view, reduced to same quadrate length. (a), *Eusthenopteron* (after Jarvik); (b), *Crassigyrinus*; (c), *Ichthyostega* (after Jarvik). (Region preserved in *Crassigyrinus* stippled.) APR, anterior postrostral; ATL, anterior tectal; F, frontal; J, jugal; L, lacrimal; LR, lateral rostral (septomaxillary), MX, maxillary; N, nasal; PMX, premaxillary; PO, postorbital; POP, preopercular; PRF, prefrontal; QJ, quadratojugal; SQ, squamosal.

section has not been achieved. Säve-Söderbergh (1932) and Jarvik (1948, 1950) favour an Upper Devonian date. The nature of the vertebrate fauna of the *Remigolepis* series, notably the placoderms including the antiarch *Remigolepis*, as well as that of the overlying *Grönlandaspis* series support this conclusion. However, Westoll (1940, 1943) bases a Lower Carboniferous date on the agreed correlation of the underlying *Phyllolepis* series with the Dura Den horizon in Scotland. This is near the summit of the British continental Devonian and passes into the base of the Carboniferous without an apparent marked unconformity.

However, limb bones from Nova Scotia awaiting description by Dr. Baird demonstrate that well-developed tetrapods were already in existence in the Tournaisian or basal Carboniferous and support a long Devonian history for amphibia.

Assigning a taxonomic position to *Crassigyrinus* is difficult. As with the ichthyostegids it is probably to be assigned to the Labyrinthodontia, but should not be included in either of the major orders of that class, the Temnospondyli and the Batrachosauria (Antracosauria of Romer). Nor can it reasonably be included in the order Ichthyostegalia. It might be regarded as premature to erect an order for *Crassigyrinus* alone: nevertheless it must be placed taxonomically and I propose a new order of labyrinthodonts, the Palaeostegalia, characterized by the fish-like proportions of the skull in lateral view and the presence of a preopercular bone: also probably diagnostic are a lateral line system with amphibian sulci but with a rhipidistian configuration on the jugal, and a snout region whose bone pattern retains features of that of the osteolepiform Rhipidistia.

The order contains only *Crassigyrinus* in the monotypic family Crassigyrinidae.

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A. L. PANCHEN

Department of Zoology  
University of Newcastle upon Tyne  
Newcastle, NE1 7RU

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# THE APTYCHI OF *SONNINIA* (AMMONITINA) FROM THE BAJOCIAN OF SCOTLAND

by N. MORTON

ABSTRACT. Aptychi found in the body chambers of four specimens of *Sonninia* (*Papilliceras*) from Skye, western Scotland, are described and figured. The aptychi do not exactly fit the aperture but it was not possible to establish conclusively whether they functioned as opercula or as part of the jaw apparatus.

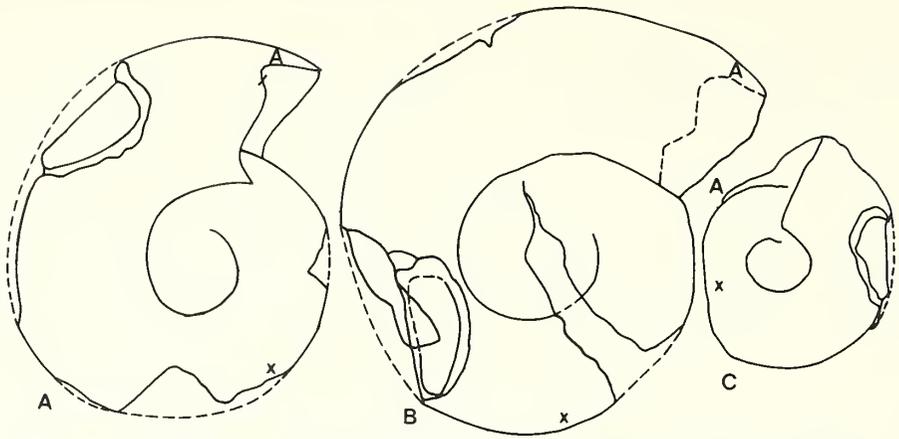
FOUR specimens of the ammonite genus *Sonninia* (*Papilliceras*) were found to have aptychi preserved within the body chamber. Three of the specimens (HMS26394, HMS26396, BkC F329) belong to the species *S. (P.) arenata* (Quenstedt) and the fourth (HMS26395) to *S. (P.) mesacantha* (Waagen). Both species are macroconchs. The specimens are from the Massive Sandstone of the Bearreraig Sandstone (Morton 1965), i.e. Sauzei Subzone, Bajocian. They were all found in loose blocks at Rudha Sughar, Bearreraig, Skye, so that details of orientation relative to bedding are not available.

The descriptive terms used are as outlined by Arkell (1957, pp. L437–439, fig. 556). This terminology is not entirely satisfactory, because it refers to relationships of the aptychi as opercula and would be inappropriate if the aptychi had a different function. It is used herein only because explanation of it is readily accessible. The specimens are in the collections of the Hunterian Museum, University of Glasgow (HM), or the Department of Geology, Birkbeck College, University of London (BkC).

## DESCRIPTION OF THE SPECIMENS

*Position.* In all four specimens under discussion the aptychi occur inside the body chambers of the ammonites. In one specimen (HMS26394, text-fig. 1B) the valves are separated and lying, one partly on top of the other, against the outer part of the whorl side near the back of the body chamber. That this side was the lower side during burial is confirmed by the partial infilling of the body chamber with sediment.

In the other three specimens (text-fig. 1A and 1C, Pl. 18, fig. 3) the aptychi are preserved with the two valves together in the ventral part of the body chamber much nearer the aperture, in a position varying from 44° to 63° from the aperture (see below for details). This is by far the most common position for the preservation of aptychi, and is the *Normalstellung* of Trauth (1927–1938). All three specimens have the apex and inner margin towards the aperture, and the harmonic margin against the ventral part of the whorl. In HMS26396 (Pl. 17, fig. 3) and HMS26395 (Pl. 17, fig. 4) the harmonic margins are in line with the middle of the venter (as defined by the keel) and the planes of bilateral symmetry coincide approximately with those of the ammonites, but in BkC F329 these are displaced slightly (1.5–3.5 mm) to one side.



TEXT-FIG. 1. Outlines of ammonites (partly restored) showing positions of aptychi. 'A' marks the position of the aperture, 'X' marks the end of the phragmocone. All specimens  $\times 0.33$ . A, *Sonninia (Papilliceras) arenata* (Quenstedt), HMS 26396; B, *Sonninia (Papilliceras) arenata* (Quenstedt), HMS 26394; C, *Sonninia (Papilliceras) mesacantha* (Waagen), HMS 26395.

*Dimensions:*

	HMS26396	BkC F329	HMS26394	HMS26395
A. aptychus				
1. maximum length	46.0	45.9	51.8	33.1
2. length of hinge line	44.6	c. 41.3	49.5	30.9
3. maximum width	20.5	19.7	21.7	14.2
4. convexity of right valve	5.9	3.8	—	5.0
5. convexity of left valve	5.2	—	4.6	—
6. thickness of pr. of valves <sup>1</sup>	16.4	—	—	c. 10.7
B. aperture <sup>2</sup>				
1. distance from keel to keel	44.9	c. 46.0	54.0	—
2. whorl height <sup>3</sup>	56.4	54.3	61.1	—
3. maximum whorl breadth	25.1	29.3	31.9	—
C. position of aptychus				
1. distance from aperture <sup>4</sup>	53°	44°	131°	63°
			152°	
2. length of body chamber <sup>4</sup>	245°	230°	235°	280°

*Notes:*

1. As preserved, not necessarily the same as in life.
2. Outside measurements, including shell.
3. From keel to umbilical seam.
4. Measured as angles subtended about protoconch (axis of coiling) by umbilical end of aperture and nearest part of aptychus, and by aperture and beginning of body chamber.

*Description.* The aptychi consist of a pair of valves showing approximate but not quite exact bilateral symmetry, with the plane of symmetry passing between the valves. In three specimens the valves are in contact along one margin (see Pl. 17, figs. 3, 4) and were presumably hinged along this margin (the harmonic margin), but no hinging structures are present and the specimens all show slight displacement

of one valve relative to the other. In the fourth specimen (HMS26394, Pl. 17, fig. 5) the two valves have been separated. The valves are not in contact along the other margins, the separation being approximately 15.8 mm at the middle of the lateral margin in HMS26396.

The shape of each valve (Pls. 17 and 18) is subtrigonal, with the angle opposite the harmonic margin broadly rounded, the apical angle a fairly sharp right angle, and the ventral angle between  $20^{\circ}$  and  $30^{\circ}$  but rounded. The harmonic margin is straight, only very slightly shorter than the maximum length of the valve, and there is a distinct harmonic facet (visible as a furrow on the internal mould, but not evident on the exterior) which becomes gradually broader from the apex to the ventral angle (Pl. 17, figs. 4 and 5). The outer margin is rounded and is not distinct from the lateral margin which is curved. Outer and lateral facets are not present or only very slightly different in attitude from the rest of the outer surface of the valve (Pl. 17, figs. 1 and 2). There is no distinct umbilical projection but a broadly rounded angle, and the inner margin is practically straight or with very slight incurvature. The maximum width of the valves is developed at about 30% of the distance from the apex to the ventral angle, and the maximum convexity of the valve is in the area between this line and the inner margin.

The exterior (i.e. where the shell is present) does not differ in appearance from the rest of the ammonite shell and there is little surface ornamentation. Faint ridges radiating from the apex are present on the adharmonic slope of the outside surface (Pl. 18, fig. 1) and are even more faint on the inside surface. More prominent are growth lines, evident on both inside and outside surfaces. The growth lines on the aptychus of *S. (P.) mesacantha* (Waagen) (HMS26395) are more prominent than those of *S. (P.) arenata* (Quenstedt). Prominent growth rugae are developed near the outer and part of the lateral margins on two specimens (Pl. 17, fig. 2; Pl. 18, fig. 1). There is no keel, and the adharmonic slope is not distinct from the flank.

The shells of the aptychi have been recrystallized to coarsely crystalline calcite, so that evidence of shell structure is limited. A thin section through the ammonite shell and the aptychus shows confirmation of the recrystallization, but the recrystallization of the aptychus is very different from that of the ammonite shell. In the aptychus large crystals of calcite with highly irregular outlines extend across the whole thickness of the shell. The ammonite shell is recrystallized so that it retains a layered structure, with smaller crystals of calcite which never extend across the whole thickness of the shell. The difference in recrystallization is presumably related to the ammonite shell having been originally composed of aragonite and the aptychus of calcite. In spite of the recrystallization the aptychus shows relict lamination with the laminae oblique (about  $20^{\circ}$ ) to the surface of the aptychus and extending from one surface to the other in just over 3 mm. It appears that growth was by adding new layers along the oblique growing edge but not over previously formed parts of the aptychus. Shell thickness varies up to approx. 0.5 mm, but generally the shell is thinner towards the apex and inner margin, so that the thickness of the calcareous layer of the aptychus increased with growth. On all specimens there is an inner layer of dark brown or black organic material which is generally dull and rather spongy in appearance.

## DISCUSSION

*Taxonomy.* The occurrence and biological affinities of aptychi have been extensively discussed, and the literature on Mesozoic occurrences is summarized by Arkell (1957, pp. L99–100, L437–440). The Skye specimens provide still more evidence of close association between specimens of aptychi and ammonites, and there can be little doubt but that they belonged to the same animal.

There then arises a taxonomic problem such as has been discussed by Arkell (1957, pp. L438–439) and Moore and Sylvester-Bradley (1957, pp. L465–470). Arkell used a taxonomic procedure in which non-Linnaean form-genera were used, but Moore and Sylvester-Bradley used full Linnaean nomenclature. According to Arkell (1957, p. L267) the sonniniid aptychus is of the *Cornaptychus* type which is described (p. L439) as having a shiny black surface with coarse folds. The Skye aptychi do not possess either of these features and so cannot belong to this type. They are more similar in ornamentation to *Laevicornaptychus*, but again do not have the shiny black surface. However, this feature may have been misinterpreted, recalling the black inner layer under the calcareous layer. Of figured specimens of aptychi the Skye aptychi are not identical with any named types, but they are almost identical with the *Somminia* aptychus figured, but not named, by Nicklès (1900).

*Function.* It has generally been assumed that aptychi were ammonite opercula, and a few specimens have been found with aptychi in a position apparently closing the aperture (e.g. a specimen figured by Arkell 1957, fig. 145, p. L99), but these are extremely rare and there is doubt as to whether Arkell's specimen is complete. Several authors have commented on the fact that many aptychi do not provide a good fit for the aperture of the ammonite with which they are associated. Many aptychi associated with lappet-bearing ammonites have been recorded and it is difficult to see how in at least some cases the aptychi could have functioned as opercula, especially with more specialized apertures such as that of *Normannites* (compare Westermann 1954, figs. 32 and 35 for example).

The length of the aptychi described herein is closely comparable with the whorl height (measured from the keel of the preceding whorl to the ventral part of the aperture), but the width of the two valves together (as preserved) is less than the whorl width (breadth) at the aperture (text-fig. 2). However, since the aptychi consist of two apparently hinged plates it is possible that by increasing the angle between the valves a better correspondence between apertural width and width of aptychus

## EXPLANATION OF PLATE 17

All stereo-pair photographs, separation 63.5 mm. Natural size unless otherwise stated.

Figs. 1A, B. Right valve of aptychus of *Somminia* (*Papilliceras*) *mesacantha* (Waagen), HMS26395. Mostly internal mould with little shell remaining.

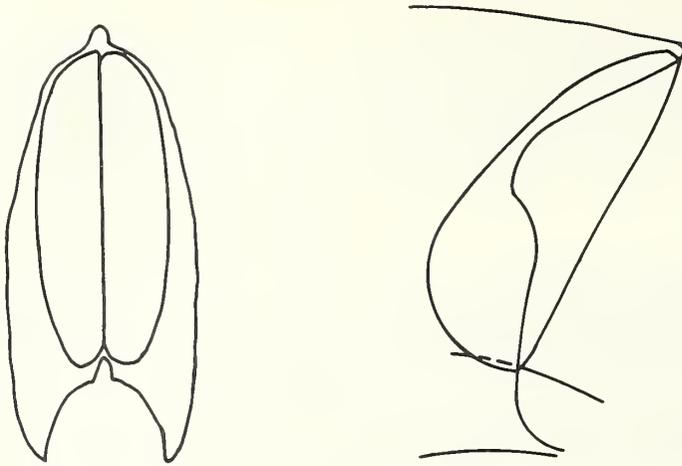
Figs. 2A, B. Right valve of aptychus of *Somminia* (*Papilliceras*) *arenata* (Quenstedt), HMS26396. Shell present except on inner part.

Figs. 3A, B. Harmonic/ventral view of fig. 2.

Figs. 4A, B. Harmonic/ventral view of fig. 1.

Figs. 5A, B. Left valve and part of right valve of aptychus of *Somminia* (*Papilliceras*) *arenata* (Quenstedt), HMS26394. Internal mould to left valve, external mould of right valve.  $\times 0.7$ .





TEXT-FIG. 2. Aperture of HMS 26396, with aptychus fitted. The two valves of the aptychus are shown hinged at the angle at which they are preserved. In the apertural view note that the aptychus appears reduced in length because of perspective of drawing.  $\times 1.0$ .

may be achieved. Even so the aptychi would not provide a perfect fit for the aperture, especially on the inner part of the whorl where it overlaps the preceding whorl. However, the hood of living *Nautilus* does not in itself completely close the aperture (see Stenzel 1964, fig. 68, p. K91), so that this does not necessarily preclude opercular function.

Change of shape with growth was investigated for one of the specimens (HMS26394) (text-fig. 3), and it was found that the width/height ratio decreases with growth in both whorl shape (measured as ratio of maximum width to height from keel of preceding whorl) and shape of aptychus (measuring one valve only at various growth lines). However, the rate of change is much less for the valve of the aptychus than for the whorl shape. This is not surprising since, even assuming opercular function, the length of the aptychus would correspond with the whorl height, but the width of the aptychus valve would correspond with approximately half of the whorl width.

Lehmann (1970, 1971) has reinterpreted some Liassic anaptychi, and later (1972) various bivalved aptychi, as the lower jaw of the ammonite, and has described the upper jaw, radula, and other structures within the body chamber. Specimen HMS26396 was sectioned through the aptychus approximately along the line of maximum convexity (see description above) and through the centre of the umbilicus. Within the aptychus various shreds of dark brown or black organic matter and some small black fragments were found. Some of the shreds appear to be derived from the

#### EXPLANATION OF PLATE 18

All figures natural size.

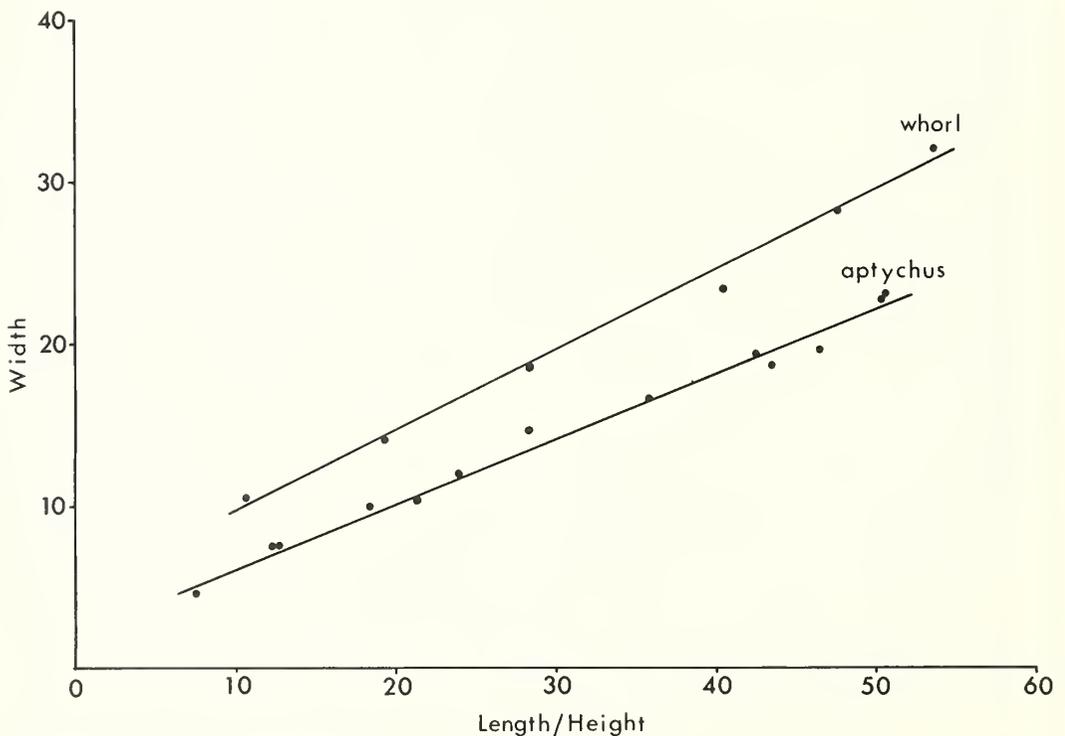
Figs. 1-3. *Sommia (Papilliceras) arenata* (Quenstedt). 1, Left valve of aptychus, HMS26394. Internal cast with shell partly replaced. 2, Left valve of aptychus, HMS26396. Internal mould with shell partly preserved. 3, Complete conch with aptychus, BkC F329.



MORTON, *Sominia aptychi*

organic layer of the aptychus, but no definitely identifiable structures such as those figured by Lehmann (1972, pl. 9, fig. 1) were found. The small black fragments may represent isolated radular teeth.

On the basis of the information available no definite conclusion can be arrived at regarding the function of the aptychi in the ammonite specimens from Skye. The possibility that they acted as rather badly fitting opercula cannot be rejected, although the fit is bad enough to suggest that this function is unlikely. The regularity in the position of the aptychi inside the body chamber in most of the Skye specimens (as in others) does suggest that this was close to their position in life. If this is so then the aptychi were situated well inside the body chamber, further away from the aperture than shown by Arkell (1957, fig. 124, p. L82). It is difficult to imagine a mechanism whereby the aptychus was pushed out of the body chamber into the aperture at the same time as the body was being retracted into the body chamber, especially if the mantle cavity (important in providing space for retraction) was between the aptychus and the aperture, a situation which would result from placing the aptychus  $50^\circ$  (see p. 196) from the aperture in Arkell's diagram. In gastropods and *Nautilus* the operculum or hood is on the part of the body which is last to be drawn into the shell—a very different situation. On the other hand the position of the aptychi does fit in well with the interpretation advanced by Lehmann that they were lower jaws, and this seems the more likely function.



TEXT-FIG. 3. Width plotted against height or length for whorl dimensions and one valve of aptychus of HMS 26394. The whorl height used is from keel to keel rather than umbilical seam to keel.

*Acknowledgements.* I am grateful to several colleagues for discussion of various aspects of the problem of aptychi, and particularly to Professor U. Lehmann (Hamburg) for helpful suggestions, and Professor D. T. Donovan (London) for comments on the manuscript. The photographs are by Mr. E. J. L. Cory of the Birkbeck College Geography/Geology Photographic Unit.

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N. MORTON

Department of Geology  
Birkbeck College  
7-15 Gresse Street  
London W1P 1PA

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## ADDENDUM

Since the above was written another sonniniid ammonite from Berreraig has been found to have the aptychus preserved within the body chamber. This is a specimen of *Euhoploceras fissilobatus* (Waagen) from the Sowerbyi Zone, Shaly Sandstones, cliff south of Berreraig. The aptychus is in the normal position with the harmonic margin exactly in line with the keel (i.e. mid venter) and the plane of symmetry corresponding with that of the ammonite. The aptychus is 51° from the aperture, a position comparable with those of the specimens described above. The dimensions for this specimen (HMS26397) corresponding with those given above are:

A:	1	2	3	4	5	6	B*:	1	2	3	C:	1	2
	60.2	54.1	30.0	5.0	5.3	30.6		c. 70.0	c. 88.0	c. 44.0		51°	217°

\* The aperture is not completely preserved and one side is crushed so that apertural dimensions are estimated.

The shape and other features of this specimen are the same as for the other specimens described above. The main difference is in the surface ornamentation. The growth lines and growth rugae are very much more pronounced on both internal and external surfaces. Other, minor, differences include a more pronounced change of slope between the adharmonic slope and the flank, and a larger harmonic facet on the *Euhoploceras* specimen.



# IN SITU CONIFEROUS (TAXODIACEOUS) TREE REMAINS IN THE UPPER EOCENE OF SOUTHERN ENGLAND

by K. FOWLER, N. EDWARDS, and D. W. BRETT

**ABSTRACT.** Coniferous tree stumps and roots attributable on evidence of wood anatomy to the form-genus *Glyptostroboxylon* Conwentz occur in Upper Bartonian (Upper Eocene) strata at two localities in the Hampshire Basin, southern England. They are the first trees found in growth position in the English Lower Tertiary. Evidence that they grew in a flooded or waterlogged habitat is given by the mode of fossilization and characteristics of the associated flora. The fossil root morphology and wood anatomy resembles that of certain living Taxodiaceae, especially *Glyptostrobus* and *Taxodium*, themselves inhabitants of waterlogged and flooded terrain. *Taxodium* type pollen occurs with the roots, but associated foliage and cones are attributable to *Sequoia couttsiae* Heer. These taxodiaceous macrofossil remains may represent a single species with the characters of more than one living genus. Similar instances are known from Tertiary deposits elsewhere.

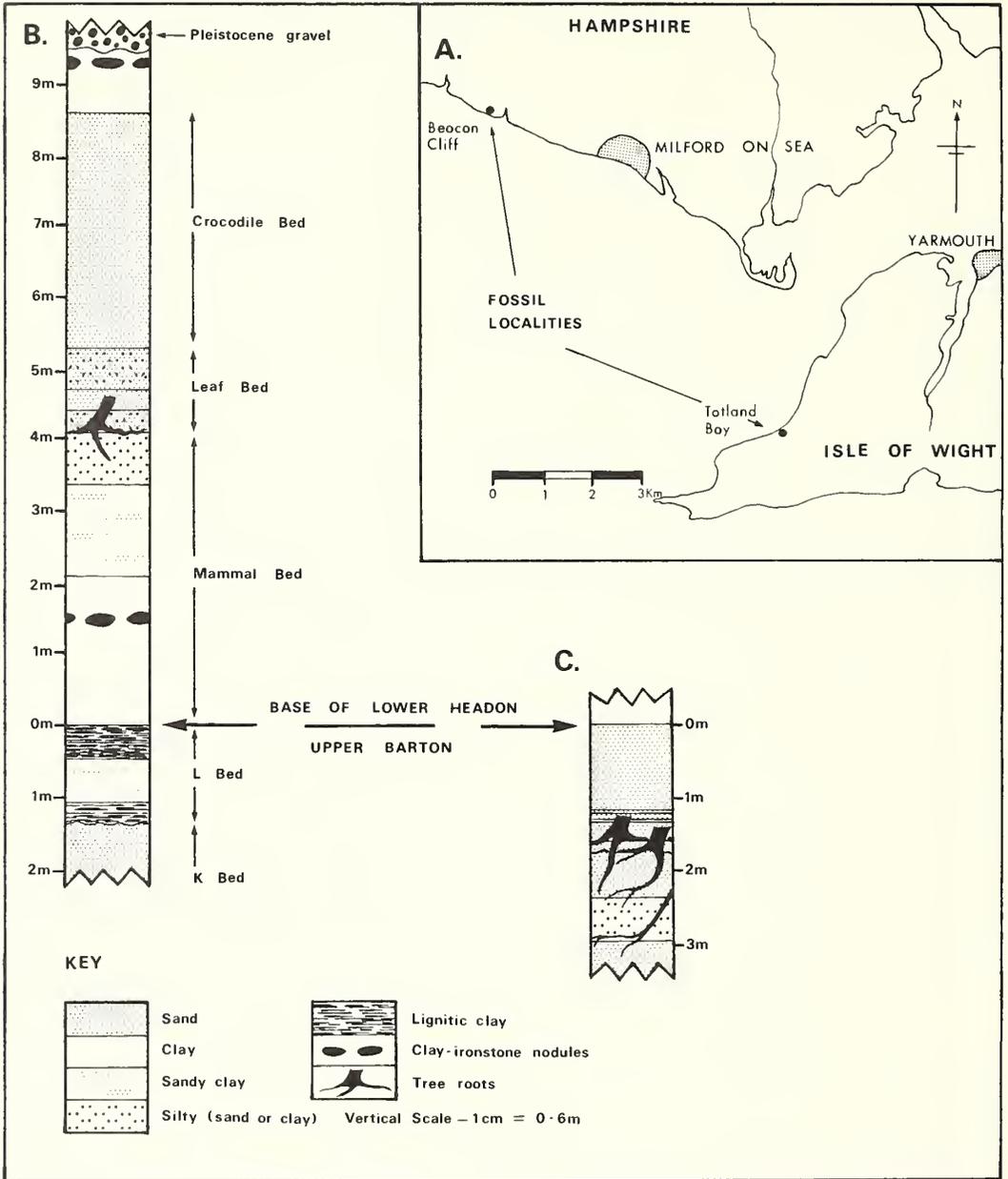
CONIFEROUS tree stumps and roots have been recognized at two localities in Upper Bartonian (Upper Eocene) strata of the Hampshire Basin (text-fig. 1A). At the eastern end of Beacon Cliff (Grid reference SZ 261923), Hampshire, the tree remains occur in the Lower Headon Beds, spaced at irregular intervals along about 400 m of the outcrop of the Leaf Bed (text-fig. 1B). In the south-eastern corner of Totland Bay (SZ 321866), Isle of Wight, similar fossils occur in strata correlated on palynological evidence with Bed L of the Barton Sands of Beacon Cliff (Fowler 1971) (text-fig. 1C), now nearly obscured by new sea defences.

The Leaf Bed at Hordle and Beacon Cliffs has yielded a rich macrofossil flora (Chandler 1925, 1926, 1961, 1964) and a rich microfossil flora (Fowler, unpublished data). Although stems and rootlets in growth position have been observed in the Leaf Bed (Hastings 1853, Tawney and Keeping 1883), tree roots were not recorded until recently (Edwards 1967). No plant macrofossils had been recorded from the Totland Bay locality prior to discovery of the tree roots.

The occurrence of *in situ* tree roots in these deposits proves that at least one element in the large contemporaneous flora grew at the fossil localities. The purpose of this paper is to establish the identity of the tree remains and the nature of their habitat, chiefly by a detailed account of the Beacon Cliff occurrence.

## OCCURRENCE AND MORPHOLOGY OF THE STUMPS AND ROOTS

The morphological features of the stumps and roots are shown in Pl. 19, fig. 1. The illustrated specimens, from the Leaf Bed at Beacon Cliff, may be matched by similar specimens from the Isle of Wight locality. The partially crushed stumps, approximately 1.00 m in length by 0.25 m in diameter, are embedded chiefly in the sandy upper unit of the Leaf Bed (text-fig. 1B). The stumps are hollow and filled with the sandy matrix; the wood is black, humified, and soft. At the base of each stump, just above the point of origin of the roots, are buttress-like flanges. The laterally spreading roots appear to fork only occasionally. The basal part of the stumps and associated roots are embedded in the clayey-silt lower unit of the bed. In this lower



TEXT-FIG. 1. Geographical and stratigraphical location of the Eocene tree roots. A, location map; B, section at eastern end of Beacon Cliff; C, section at south-eastern end of Totland Bay.

unit, which is water-saturated, the wood is similar in appearance but better preserved than that above and slightly flexible, although partially pyritized. The roots have a flattened lens-shaped cross-section and are spread out over or slightly above the undulating upper surface of the underlying Mammal Bed. The roots are very long; one lying parallel to the cliff face was uncovered for a distance of about 3.00 m without its distal end being found. Some roots penetrate downward into the silty-clay upper unit of the Mammal Bed to a depth of 1.00 m. In this the wood is often heavily pyritized and sometimes thickly coated with pyrite.

The stumps and roots examined at Totland Bay occurred at two levels, each marked by a thin lignitic clay of local extent. Here, the laterally spreading parts of the root systems form interwoven mats and, as at Beacon Cliff, the wood preservation varies according to matrix.

The extent and continuity of branching of the fossil root systems, and their penetration of more than one stratum at both localities, seems good evidence that they are in growth position.

#### ANATOMY OF THE ROOT WOOD

*Description.* Pieces of root wood from both localities and driftwood from a penecontemporaneous channel-fill deposit at Beacon Cliff were examined. As a result of compression, no useful transverse sections were possible. The following anatomical description is based on fractured surfaces and longitudinal sections. Much of the wood is badly degraded, especially near heavily pyritized areas, and fungal hyphae and rhizomorphs are frequent elsewhere. Preservation of the wood varies, only some parts being sufficiently well preserved to allow adequate examination of the finer features.

The wood is coniferous, consisting mainly of tracheids and ray parenchyma. Axial parenchyma is present but not abundant. There are no vessels or resin ducts.

The tracheids (Pl. 19, fig. 2) have circular bordered pits on the radial and tangential wall. Occasionally pitting is biseriate, but single pits usually are arranged along the tracheid, often irregularly, and never crowded. Where opposite pitting occurs, crassulae are present. The pits are approximately 10  $\mu\text{m}$  in diameter, with inner apertures of 3–5  $\mu\text{m}$ .

The rays (Pl. 19, fig. 3) range from 1–5 cells in height, but are usually low, being only 2 cells high. They are exclusively uniseriate, the cells more or less isodiametric, rounded in cross section (tangential view), somewhat bulbous, and slightly taller at the margins. The horizontal walls of the ray cells are not obviously pitted, though a few pit-like irregularities can be seen. Vertical and horizontal walls are of similar thickness and indentures were not apparent in the few entire end walls adequately observed. In the driftwood, rays of up to 7 cells in height were observed.

Cross-field pitting is taxodioid (Pl. 19, fig. 4), that is, with large, almost circular or ovoid pits having a narrow border, most commonly 1–3 pits (occasionally more) per field and typically arranged rather irregularly in 2 or 3 tiers. A few pit-pairs with a common border were seen to occur. No ray tracheids were observed.

The ray and axial parenchyma cells are often partially or completely filled with a dense material.

*Identification.* Wood of modern coniferous genera was compared with that of the fossil. The fossil wood resembles that of living genera of the Taxodiaceae and *Thuja* of the Cupressaceae. It is closely comparable to the wood of *Glyptostrobus pensilis* Koch and *Metasequoia glyptostroboides* Hu and Cheng. The arrangement of the large taxodioid cross-field pits seen in the fossil wood (Pl. 19, fig. 4) is characteristic of *Glyptostrobus*, whilst it only occasionally occurs (usually in the marginal ray cells) in other members of the Taxodiaceae.

Comparison with descriptions of wood from other Tertiary deposits suggests that the wood described above closely resembles in all important respects the wood *Glyptostroboxylon tenerum* (Kraus) Conwentz, an important element in some European brown-coals (Zalewska 1953, 1955; Grabowska 1957; Kilpper 1967). In anatomical detail the root wood differs from that of the trunk in having very low rays (Zalewska 1953). The somewhat taller rays of the driftwood from the English locality, already noted, may be thus explained.

It is proposed to use the name *Glyptostroboxylon* sp. for the fossil wood here described. Representative material has been deposited in the British Museum (Natural History), London (Catalogue numbers V57010-57014).

#### PALAEOENVIRONMENTAL INTERPRETATION

*Evidence from mode of fossilization of plant remains.* There is good evidence that the root wood at both localities has been in a waterlogged medium since death, and indeed may have lived in such an environment.

The high rate of organic accumulation in swamp environments, where woody vegetation is common, leads to arrest of decomposition at very shallow depths due to the toxic accumulation of humic derivatives (Coleman 1966*b*). In well-drained or aerated sediments wood is often destroyed by bacterial action and oxidation. The occurrence of well-preserved fossil wood suggests that it has remained under waterlogged conditions since its incorporation in these deposits. In waterlogged sediments, such wood becomes partially decayed and humified after death, ultimately collapsing during compaction of the matrix (Coleman 1966*a*) to give the lens-shaped cross-section seen in the fossil material. Corroborative evidence for these conditions is provided by the presence of abundant well-preserved macrofloral and microfloral remains in association with the fossil roots.

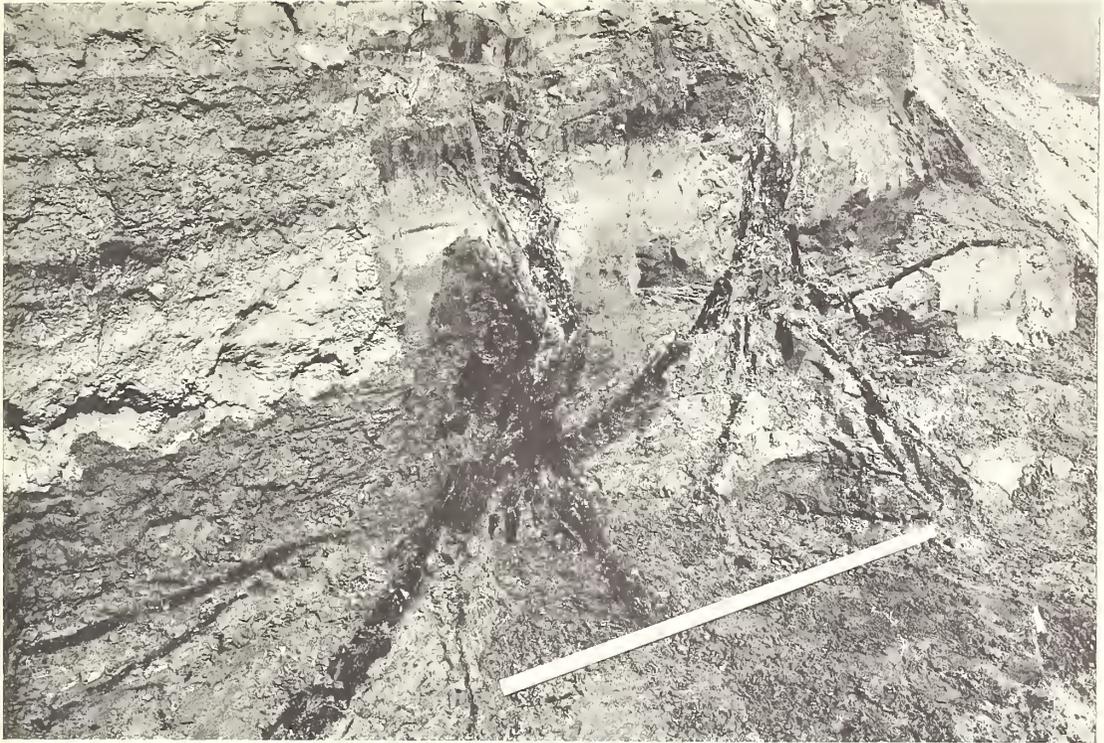
Further evidence for such an environment is presented by the occurrence of pyrite within, and forming encrustations on, the fossil roots. In modern freshwater environments, pyrite is most abundant in organic-rich, waterlogged sediments, often occurring as encrustations on dead plant rootlets (Coleman 1966*b*). It is regarded as being of early syngenetic formation under such conditions. The formation of pyrite is associated with the decay of protoplasm, and occurs commonly within plant cells (Love and Murray 1963). Crystals of pyrite in the parenchyma cells of the fossil root wood probably indicates that death of the parenchyma cells took place in the pyrite-producing medium (Brett and Edwards 1970).

*Palaeobotanical evidence from taxodiaceous remains.* The habitat requirements of modern taxa found to be closely related to the fossil taxa of the Leaf Bed provide

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#### EXPLANATION OF PLATE 19

Figs. 1-4. *Glyptostroboxylon* sp. from the Leaf Bed (Lower Headon Beds, Upper Eocene), Beacon Cliff, Hampshire. 1, Stumps and roots exposed at eastern end of Beacon Cliff (1.00 m rule gives scale). (Photo by D. Dore.) 2-4, Root anatomy. 2, Radial section showing the bordered pitting of the tracheids ( $\times 550$ ). 3, Tangential section showing the rays, most of which are only one or two cells high ( $\times 100$ ). 4, 'Stereoscan' view of fracture across radial surface. The cross-field pits are seen here from within the tracheid ( $\times 550$ ).



1



2



3



4

FOWLER, EDWARDS, and BRETT, Eocene conifer

evidence to suggest that the fossil trees were not only entombed, but once grew, in a waterlogged environment.

It has been shown that the fossil root wood anatomy resembles that of the modern monotypic Asiatic genus *Glyptostrobus*. Remains of this genus have been found repeatedly in Tertiary deposits of North America, Europe, and Asia, but the living species is confined to Kiangsi and Kwantung provinces, south-eastern China (Miki 1950). Its survival, at only two coastal localities, appears to be the result of cultivation since it is unknown as a wild tree (Henry and McIntyre 1926).

It has been suggested by some authors (Chaney and Axelrod 1959, Dallimore and Jackson 1966) that *Glyptostrobus* favours damp rather than swampy conditions. However, according to Henry and McIntyre (1926), *Glyptostrobus* is typically found in habitats not exceeding a few feet above sea-level, often growing near river banks in swampy soil subject to inundation. Morphological similarities between *Glyptostrobus pensilis* and *Taxodium distichum* (L.) Rich., an inhabitant of waterlogged and flooded terrain in the south-eastern United States, suggest that both genera occupy a similar ecological niche. *Metasequoia*, which also has wood similar to that of the fossil, is essentially a member of a stream bank community, preferring damp rather than waterlogged habitats (Chu and Cooper 1950).

Although considered ecologically equivalent, *Glyptostrobus* and *Taxodium* differ in their wood anatomy.

Morphologically, the fossil remains resemble the basal part of the trunk of *G. pensilis*, *M. glyptostroboides*, and *T. distichum*, species in which the bole and root systems exhibit special adaptations to waterlogged and flooded habitats (Henry and McIntyre 1926, Hu and Cheng 1948, Harrar and Harrar 1962). In such habitats, the bole becomes strongly buttressed and is often hollow, while the extensive lateral root system gives rise to downward-penetrating roots and upward-growing pneumatophores. Unlike the pneumatophore of *Taxodium* which is conical, that of *Glyptostrobus* is geniculate, a feature well illustrated by Henry and McIntyre (1926, pl. II). Buttressing of the fossil remains is apparent (Pl. 19, fig. 1), but it was not possible to confirm the presence of pneumatophores. Certain structures identified as smaller boles could have been pneumatophores, but it could not be shown that these 'boles' were in organic connection with major root systems. According to Kurz and Demaree (1934) pneumatophores of *T. distichum* do not develop in deep water or when flooding is only of short duration. Chu and Cooper (1950) suggest that the pneumatophores of *Metasequoia* develop only in deep-water swamps or during long periods of inundation. The absence of pneumatophores on *Glyptostrobus* trees up to 25 years old, growing in waterlogged habitats, may be due to their immaturity (Henry and McIntyre 1926). Therefore, the absence of pneumatophores on the fossil roots could be accounted for by the environmental conditions and age of the trees at the time of death. To the best of our knowledge no trace of pneumatophores in the fossil state has been found in Europe. This seems remarkable in view of the common occurrence in Tertiary deposits of remains of those taxodiaceous genera capable of producing such structures at the present time.

Fossil pollen attributable to the Taxodiaceae is also common in the Leaf Bed. This taxodiaceous pollen may represent more than one species, since the form-species *Inaperturopollenites hiatus* and *I. dubius*, described by Thomson and Pflug (1953),

are both recorded. Some authors, for example Zagwijn (1960), have decided fossil taxodiaceous pollen into two broad morphological groups, the *Sequoia* type (showing affinity with modern *Sequoia*, *Sequoiadendron*, *Metasequoia*, and *Cryptomeria*) and the *Taxodium* type (showing affinity with modern *Taxodium* and *Glyptostrobus*). The latter type has a smaller papilla and probably thinner exine than the former. Dispersed fossil taxodiaceous pollen which gape open, or in which the papillae cannot be readily seen, is therefore likely to belong to the *Taxodium* type. Although it is generally accepted that separation of fossil taxodiaceous pollen at modern generic level is far from reliable, comparison of pollen of modern genera has led to the conclusion that the taxodiaceous pollen found in the Leaf Bed resembles that of living *Taxodium* and *Glyptostrobus* species rather than that of *Sequoia*, *Sequoiadendron*, or *Metasequoia*.

On the basis of anatomical and morphological considerations it is evident that the fossil roots are closely comparable with modern *Glyptostrobus* and, to a lesser extent, *Metasequoia* and *Taxodium*. Although *G. pensilis* and *T. distichum* show anatomical differences, they are otherwise considered to have much in common (Dallimore and Jackson 1966). Palynological evidence suggests that *Glyptostrobus* or *Taxodium*, rather than *Metasequoia*, is represented in the Leaf Bed. Of greater significance is the fact that both *G. pensilis* and *T. distichum* inhabit waterlogged terrain.

*Evidence from the associated macro- and microfossil assemblages.* The combined plant macrofossil and microfossil assemblages of the Leaf Bed have yielded 76 families with 100 genera identifiable to modern taxa. The total fossil flora has an essentially woody aspect, with evergreen and deciduous trees and shrubs, and some climbers.

Fossil macrofloral and microfloral assemblages should complement one another in the interpretation of the whole flora. The macroflora is likely to be biased toward plants growing in swamps or close to rivers and delta distributaries, whereas many of the pollen and spores are likely to be derived from plants of more remote, and possibly very different, habitats (Chaloner 1968). However, the combined macro-microfossil floral assemblages of the Leaf Bed contain a number of taxa totalling about 40% of those identified, which, to judge from the habitats of their modern representatives, indicate very wet conditions (Table 1). Many of the other identified fossil taxa today inhabit moist lowland environments. Therefore, wet habitats seem to have occupied relatively large areas around the fossil locality. In such an environment, water transport may be more important than wind transport in carrying the plant material to the depositional site, thus increasing the likelihood of both types of fossil assemblage being derived from similar plant communities.

Palaeobotanical evidence suggests that the Leaf Bed is a freshwater deposit. The only real indication of brackish conditions is the occurrence of pinnules of *Acrostichum lanzaeanum* (Visiani) Chandler at the, now obscured, eastern end of the outcrop in Hordle Cliff (Chandler 1961). However, their association with the remains of such freshwater genera as *Salvinia*, *Brasenia*, and *Stratiotes*, together with the fact that living *Acrostichum* sp. grows in freshwater marshes (Small 1938), suggest freshwater conditions. There is no palynological evidence for the presence of *Acrostichum*. Although *Acrostichum* spores, because of their large size, are deposited in



altitudes in subtropical climates (Mirov 1967), and this genus grows in lowland wet habitats in Florida today (Monk 1965), often occupying only slightly elevated, though poorly drained areas, within or on the landward side of swamps. The effect of slight variation in the level of the water table, resulting in distinct vegetational differences has been demonstrated in southern Florida by Spackman *et al.* (1964). According to Zak (1961), water absorption by roots in saturated soil is difficult, but pines can live under such conditions because of their drought resistance. Such a distribution of *Pinus* on slightly elevated and drier areas might account for the paucity of macrofossil remains of this genus in the Leaf Bed.

#### INTERRELATIONSHIPS AND TAXONOMIC SIGNIFICANCE OF THE TAXODIACEOUS REMAINS FROM THE LEAF BED

Evidence presented by anatomical and morphological features of the fossil roots, supported by pollen morphology and habitat requirements of modern members of the Taxodiaceae, indicates affinity between the fossil roots and modern *Glyptostrobus* and *Taxodium*. Being deciduous, both genera would contribute abundant foliage, as well as cones, to the contemporary sediments. Such dispersed structures, if found in association with the fossil roots, might therefore be expected to have once belonged to the same source trees.

Taxodiaceous shoots, twigs, and female cones are locally abundant in the Leaf Bed (Chandler 1961), suggesting that the trees grew near the depositional site. However, they are all recorded as *Sequoia couttsiae* Heer (Chandler 1964).

Whilst both the *Taxodium* type and *Sequoia* type of pollen have been recorded from the Lower Tertiary of southern England (Ma Khin Sein 1961, Machin 1971), only the former has been found in abundance, the *Sequoia* type occurring in relatively insignificant amounts. *S. couttsiae* is the only taxodiaceous macrofossil occurring in the same deposits and it is therefore interesting that the above authors refer the *Sequoia* type pollen to *Sequoiadendron* and *Metasequoia*, and not to *Sequoia*.

It would be tempting to consider that the foliage and cones of *S. couttsiae* and the fossil roots here described as *Glyptostroboxylon* sp. might all belong to the same parent plant which produced *Taxodium* type pollen. An analogous situation has been reported from the Oligocene Florissant Formation of North America. Here, male cones referred to the Tertiary species *Sequoia affinis* Lesq. were found to contain pollen, also found commonly in the dispersed state, resembling that of living *Taxodium* rather than *Sequoia* (E. Leopold, quoted by Penny 1969).

In view of the palaeoecological conclusions drawn from this work, it would seem necessary to consider briefly the extent to which *S. couttsiae* resembles modern *Sequoiadendron giganteum* (Lindl.) Buchholz and *Sequoia sempervirens* Endl. This is particularly significant considering that these modern genera live in a much drier habitat than that suggested for the fossil species. At the same time, it would seem pertinent to consider the modern generic affinities of taxodiaceous macrofossil remains found in association with *Glyptostroboxylon* in some European deposits.

The morphology of *S. couttsiae*, based on foliage and cones from the Lower Tertiary of southern England, has been described by Heer (1862) and Chandler (1922, 1957), with details of cuticular structure added later (Chandler 1962). Fossil

taxodiaceous leaves and shoots are difficult to identify. According to Ferguson (1967) it is particularly difficult to assign fossil material to modern *Sequoia*, only the cuticle in conjunction with other leaf features and the female cone being sufficiently diagnostic. *S. couttsiae* has been considered by many authors (Heer 1862, Zalewska 1953) as an intermediate type between the extant genera *Sequoiadendron* and *Sequoia*. Only the seeds and female cones of the fossil species are closely comparable with the modern monotypic *S. sempervirens*, the leaves being more reminiscent of *Sequoiadendron giganteum*. However, Chandler (1964) points out that *Sequoia couttsiae* has foliage which is characteristic of neither *Sequoia* nor *Sequoiadendron*. Schwartz and Weide (1962) regard the fossil species *Sequoia reichenbachii* (Geinitz) Heer and *S. langsdorfi* (Brongn.) Heer as identical respectively with *S. gigantea* and *S. sempervirens*, but no mention was made of *S. couttsiae*. Some authors have found cuticular structure useful in the identification of fossil Taxodiaceae (Kilpper 1968) and of *Sequoia* in particular (Bandulska 1923, Chandler 1962). However, Boulter (1970) has shown that certain features of the stomatal apparatus of fossil and modern taxodiaceous cuticles may be altered by the normal maceration process, and suggests that more refined maceration techniques together with the use of the scanning electron microscope may be necessary for separating the genera. Boulter also reported that cuticular material from the Lower Pliocene of Derbyshire, attributed to *Cryptomeria* by means of various types of evidence, could not, by means of the light microscope, be distinguished from cuticles of *S. couttsiae* described by Chandler (1962). Identification to *Sequoia* of fossil foliage found in the Leaf Bed would therefore seem to be hazardous. Equally hazardous would be the identification of these remains to other modern taxodiaceous genera, and to *Glyptostrobus* in particular. Living *Glyptostrobus* is heterophyllous, the foliage varying in character with the age of the tree so that up to three distinct leaf types may be found on an individual tree at the same time (Henry and McIntyre 1926). Usually a single branchlet bears only one leaf type, but the different leaf types produced by the tree simulate those of other taxodiaceous genera. If such morphological variation existed in fossil taxodiaceous types, misidentification of such material is understandable.

It is of interest to note that, in the original description of *S. couttsiae*, Heer (1862) states 'It is however questionable if all branches belong to the same parent, because young twigs closely resemble those of *Glyptostrobus europaeus*.'

In Poland, woody assemblages have been examined from Oligo-Miocene deposits at Turów (Zalewska 1953, 1955) and Konin (Grabowska 1957). At both localities, abundant root remains of *Glyptostroboxylon tenerum* and *Taxodioxydon sequoianum* Goth. (= *T. gypsaceum* Kräusel in Zalewska 1953 and Grabowska 1957) were found, in association with abundant foliage of *S. couttsiae* and *Glyptostrobus europaeus* Heer. These authors presumed that *G. tenerum* and *G. europaeus* belonged to the same parental type. Such an alliance is supported by anatomical and morphological features which suggest affinity with modern *Glyptostrobus*. At the same time, *T. sequoianum* was regarded as being closely related to *S. couttsiae*. Again this alliance is plausible, as both types show a relationship, though tenuous, to modern *Sequoia* and *Sequoiadendron*. However, it seems equally feasible due to lack of positive evidence, that *G. tenerum* produced foliage of the *S. couttsiae* type, a situation analogous to that found in the Leaf Bed.

## CONCLUSIONS

The taxodiaceous fossil remains recovered from the Leaf Bed in the Lower Headon Beds exhibit features characteristic of a number of modern genera within the family. In general morphology and anatomy the root remains resemble *Metasequoia*, *Taxodium*, and particularly *Glyptostrobus*. In foliage and leaf cuticle features, however, there are certain similarities to modern *Sequoia*, whereas the fossil pollen is like that of modern *Glyptostrobus* and *Taxodium*. It is conceivable that more than one genus is represented here, but the association of these different plant structures in abundance suggests that only one genus is involved. Present evidence further suggests that this fossil genus had the attributes of more than one modern member of the Taxodiaceae.

The Leaf Bed plant assemblage corresponds, to some extent, with that of the deciduous and evergreen hardwood swamps of southern Florida, which characterizes wet, periodically flooded ground (Monk 1965). Previous workers on Tertiary material from Europe and North America have suggested such an analogy (Traverse 1955, Teichmüller 1958, Machin 1971).

It is suggested that the conifer trees which gave rise to the roots described as *Glyptostroboxylon* grew in a waterlogged habitat, as evidenced by their mode of fossilization, anatomical, and morphological features. It is possible that they occupied very wet, permanently flooded sites within the mixed deciduous hardwood swamp vegetation.

The occurrence of a rich terrestrial flora in the western part of the Hampshire Basin late in the Upper Bartonian accords with other evidence (Curry 1965) for the onset of extremely shallow, freshwater conditions in the area at this time. This palaeoenvironmental interpretation of the region renders unnecessary the hypothesis of long-distance river transportation of plant macrofossil remains from the west (Chandler 1963, 1964). The developing picture is of a coastal alluvial flood plain, with open water, marshes, and swamp forest.

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K. FOWLER

Department of Biological Sciences  
Portsmouth Polytechnic  
Portsmouth, Hants

N. EDWARDS

Department of Chemistry and Geology  
(Geology Division)  
Portsmouth Polytechnic  
Portsmouth, Hants

D. W. BRETT

Department of Botany  
Bedford College  
Regent's Park  
London, N.W. 1



## SHORT COMMUNICATION

# EXCEPTIONAL PRESERVATION IN CYCLOSTOME BRYOZOA FROM THE MIDDLE LIAS OF NORTHAMPTONSHIRE

by B. WALTER *and* H. P. POWELL

ABSTRACT. The genus *Cisternifera* Walford 1894 is shown to be based on a misinterpretation of *Mesenteripora wrighti* Haime 1854, with a calcified terminal membrane.

IN 1887 E. A. Walford described a small fauna of bryozoa from the Middle Lias Marlstone (Spinatum Zone, Pliensbachian) of King's Sutton, Northants. This collection which had been placed in the Oxford University Museum was thought to be lost, but recently it was rediscovered there amongst the Geological Collections, along with Walford's other type and figured bryozoa. The interest of the fauna lies in the fact that it is the oldest known from the Jurassic. Secondly it is of interest for the remarkable preservation of certain specimens, especially *Mesenteripora wrighti* Haime 1854 = *Cisternifera inconstans* (Walford 1887), as shown in Plate 20. In many of the colonies of this species the peristome is closed by a partition. This is depressed in the centre where it is pierced by a small round hole. Walford (1887, p. 633) observed this clearly, and he compared these partitions with movable opercula such as are encountered in the cyclostome suborder Salpingina. But later on (1894), comparing this partition to the frontal wall of cheilostomes, and anxious to demonstrate a relationship to the cheilostomes, he described avicularia and supra-oral ovicells, while the true ovicells, described in 1877, were now named cistern-cells, thus giving rise to the new generic name *Cisternifera*. Walter (1969) has already pointed out that *C. inconstans* shows all the characters of *Mesenteripora wrighti* Haime. Thanks to the discovery of Walford's material the original specimens have been re-examined. There are neither avicularia nor supra-oral ovicells but incompletely developed ovicells of cyclostome type and very many peristomial partitions. The partitions do not appear to show the variations (with two pores, with tubules, etc.) figured by Walford (1894). All the partitions are slightly depressed towards the centre and are pierced by a central circular pore. The study with the scanning electron microscope ( $\times 350$ ; Pl. 20, figs. 3-6) shows that each partition has a ring of smaller pores, the pseudopores. A figure very similar to ours has recently been published by K. Brood (1972, pl. 3, fig. 2) for a modern cyclostome, *Diplosolen obelia*. It shows that the 'operculum' of *Cisternifera* is a terminal diaphragm secreted by the terminal membrane. Its presence in fossils is very exceptional and it presumably indicates a very calm environment. Furthermore the very short peristomes of *M. wrighti* would

favour its preservation; the ends of long peristomes are more likely to get broken. This could explain the absence of a terminal diaphragm in the other species from the same bed.

So it appears that the genus *Cisternifera* is founded on no more than the misinterpretation of the exceptionally well-preserved terminal diaphragm of *Mesenteripora wrighti* Haime. It can therefore no longer stand.

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B. WALTER

Département des Sciences de la Terre  
Université Claude-Bernard  
Lyon

et Centre de paléontologie stratigraphique associé au C.N.R.S.

H. P. POWELL

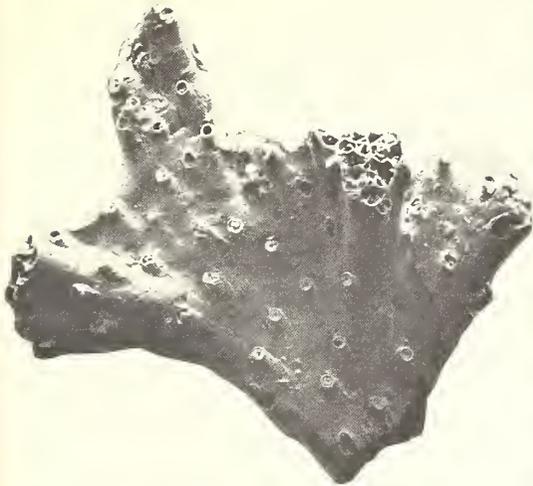
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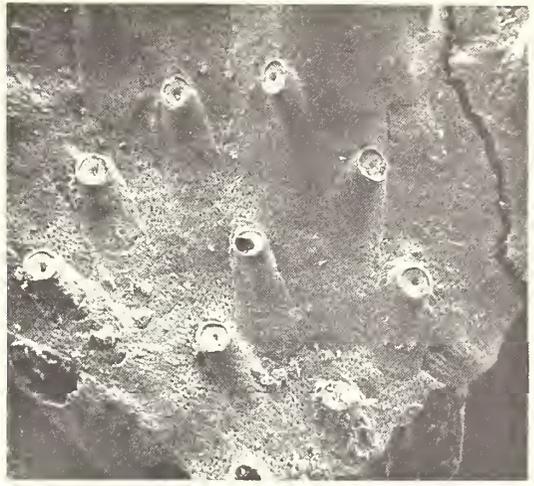
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#### EXPLANATION OF PLATE 20

Figs. 1-6. *Mesenteripora wrighti* Haime. Middle Lias, King's Sutton, Northamptonshire. Walford Collection, Oxford University Museum, No. J. 28600, Stereoscan micrographs. 1, 2, 3, and 5, using reflected electrons; 4 and 6 using secondary electrons. 1, Colony  $\times 14$ . 2, Group of peristomes  $\times 35$ . 3-6, Four peristomes showing the terminal membrane and central pore,  $\times 350$ .



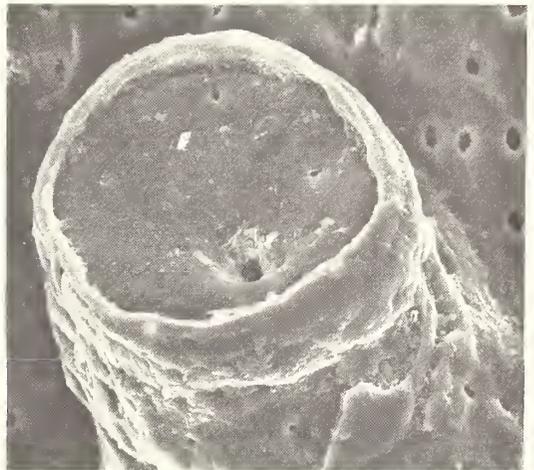
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VOLUME 16 · PART 1

---

## CONTENTS

- Use of palynologic assemblage-types in Wealden correlation  
D. J. BATTEN 1
- Upper Cretaceous staminate heads with pollen grains  
V. A. KRASSILOV 41
- Taxonomy and evolution of *Isograptus* Moberg in Australasia  
R. A. COOPER 45
- Bifida* and *Kayseria* (Brachiopoda) and their affinity  
PAUL COPPER 117
- Lapworthellids from the Lower Cambrian *Strenuella* limestone at Comley, Shropshire  
S. C. MATTHEWS 139
- New specimens of Lower Jurassic holostean fishes from India  
S. L. JAIN 149
- On *Crassygirinus scoticus* Watson, a primitive amphibian from the Lower Carboniferous of Scotland  
A. L. PANCHEN 179
- The aptychi of *Sonninia* (Ammonitina) from the Bajocian of Scotland  
N. MORTON 195
- In situ* coniferous (Taxodiaceous) tree remains in the Upper Eocene of southern England  
K. FOWLER, N. EDWARDS, and D. W. BRETT 205
- Short communication*  
Exceptional preservation in cyclostome Bryozoa from the Middle Lias of Northamptonshire  
B. WALTER and H. P. POWELL 219

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VOLUME 16 · PART 2 JUNE 1973

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Cover illustration: *Ancyrodella* element (Conodont), Cashaqua Shale, Upper Devonian, New York State, × 70.

# A MIOCENE SOLENOPOROID ALGA SHOWING REPRODUCTIVE STRUCTURES

by GRAHAM F. ELLIOTT

**ABSTRACT.** The Miocene alga *Neosolenopora armoricana* sp. nov. is described. It is most exceptional amongst Solenoporaceae in showing clear reproductive structures interpreted as similar to Corallinacean asexual sporangia, single and fused; a possible sexual structure is also described. This development came at the very end of solenoporacean evolution.

SOLENOPORACEAE are fossil calcareous algae, believed wholly extinct, which range in geological time from lower Palaeozoic to mid-Tertiary. In some ways their structure resembles that of the more familiar Corallinaceae, which especially characterize the Tertiary and of which living examples abound in present-day seas, and it seems likely that some solenoporaceans were ancestral to the corallines.

In one character the two groups differ sharply. Reproductive bodies in the Corallinaceae leave conspicuous and common structures in the fossils, so giving evidence of evolution and affording most useful morphological detail for classification. By contrast, in the Solenoporaceae, definite reproductive structures are usually missing. Those evidences interpreted as reproductive traces are usually very doubtful, so that there are very few indeed intrinsically recognizable as reproductive, and those are not found in most individuals of the relevant species. It has been supposed that reproductive structures were external and not calcified (Pia 1927, p. 97).

Many workers on fossil algae have, however, described alleged solenoporacean calcified reproductive structures and discussed the problem of their usual absence. Useful reviews of previous work are those of Wood (1944) and in Elliott (1965).

The present note describes a solenoporacean which shows definite reproductive structures with some evidence of their individual development. This is then discussed in relation to the evolution of the family. The specimens described were collected by Mr. L. J. Pitt amongst bryozoan material. The late Dr. H. D. Thomas, recognizing them as anomalous, consulted me and they were provisionally identified as a species of *Neosolenopora*, but not studied in detail until now.

Class RHODOPHYCEAE (Red Algae)  
Order CRYPTONEMIALES  
Family SOLENOPORACEAE  
Genus NEOSOLENOPORA Mastroiilli 1955

*Type-species.* *N. patrinii* Mastroiilli 1955 (*Solenopora vinassai* (Patrinii) Mastr., non *S. vinassai* Vialli 1938); Miocene of Italy.

*Diagnosis* (emend. Elliott). Solenoporaceae with rudimentary hypothallus, typical solenoporacean septate-tubular perithallus, and zonal development of reproductive cavities mostly formed by fusion of smaller reproductive elements.

*Range.* Miocene.

[Palaeontology, Vol. 16, Part 2, 1973, pp. 223-230, pls. 21-22.]

*Neosolenopora armoricana* sp. nov.

Plates 21–22

1965 *N. patrinii* Mastrorilli; Elliott, p. 699, pl. 108, figs. 1, 2.

*Diagnosis.* *Neosolenopora* with cell-columns (tubules) of about 0.09 mm diameter, cells varying in length from 0.05 to 0.20 mm. Oval reproductive bodies about 0.18 mm high and 0.11 mm diameter, typically fused into aggregates of up to 0.60 mm diameter.

*Description.* This alga is preserved as near-spherical or ovoid growths up to 20 mm high and 30 mm maximum diameter. The lower surface shows a scar or area of original attachment. The growths are often crusted with organic debris, including molluscan and echinoid fragments, and they may show surface growths of bryozoa. A clean outer surface shows a pattern of adjacent fine circular apertures, separated by gently convex calcareous skeletal material. Worn or broken surfaces show indications of the structures described below from thin-sections.

In thin-section the internal structure is seen to be typically solenoporoid. Banding or zonation is present, but is not nearly so marked as in many other solenoporoids. Fairly close-packed tubules or cell-columns, usually gently curved, radiate from the basal area to the exterior, where their terminations show as the circular apertures of the outer surface. The tubules are circular in cross-section, not usually adpressed, and divided by conspicuous wall-material which may be thickened at certain points. The diameter of the tubules, mid-wall to mid-wall, is about 0.091 mm (0.082–0.109 mm seen); the internal diameter varies from 0.073 to 0.082 mm. The thickness of the wall-material between two adjacent tube-cavities varies from 0.009 to 0.027 mm; it does not show as a double structure even under a high magnification.

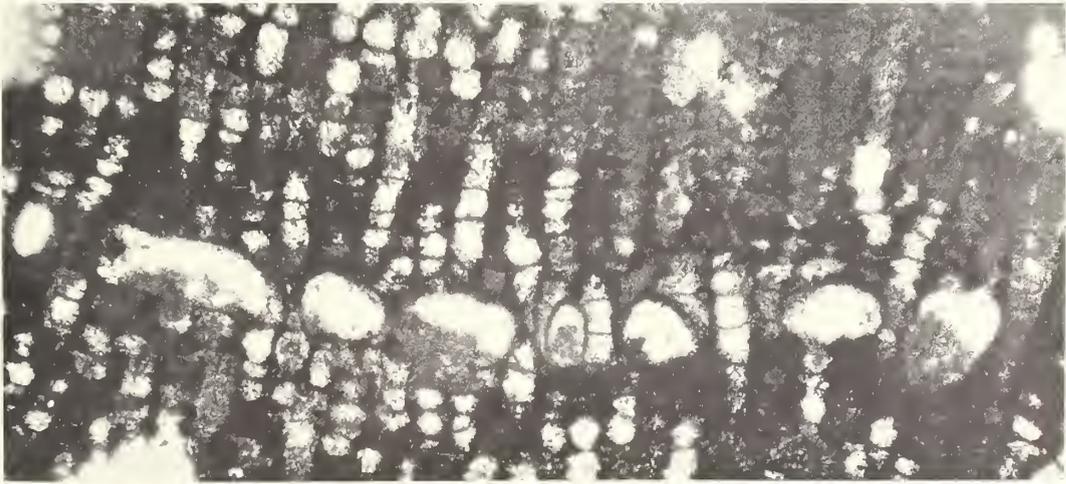
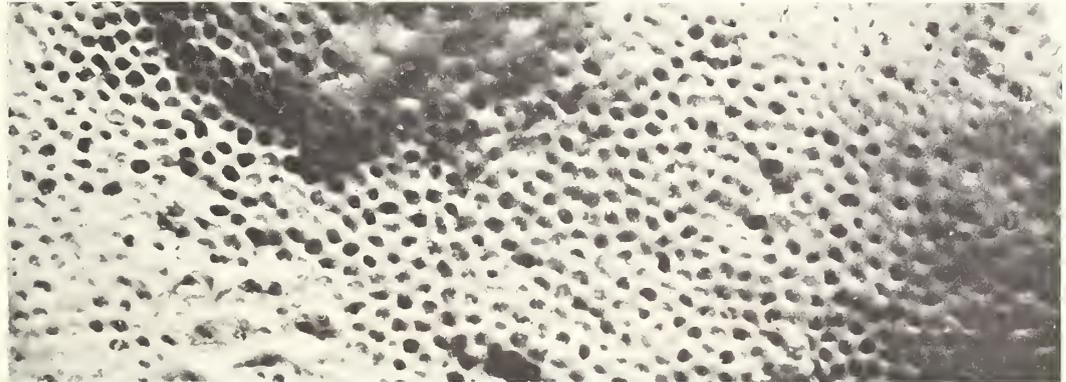
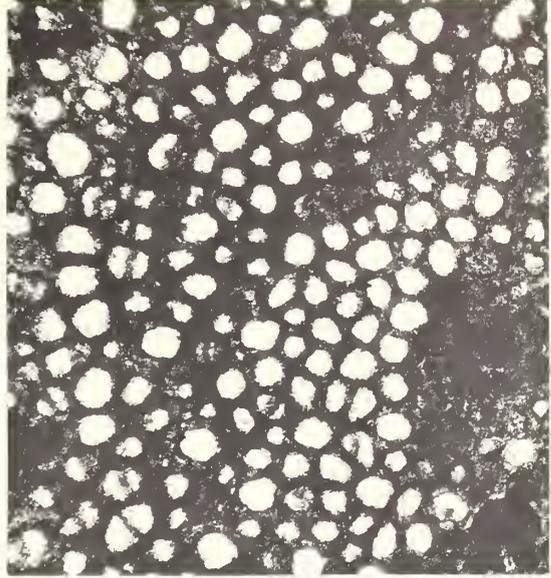
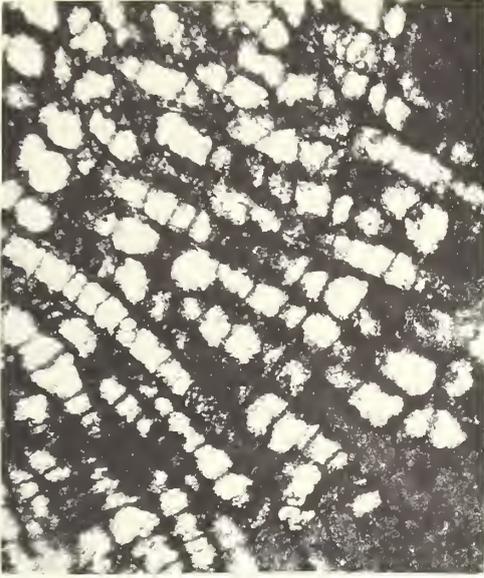
In vertical section the thickening of wall-material, apart from slight irregularity, is seen to occur mostly at changes in direction (curvature) of the tubules, often near the exterior. Mostly the tubules run adjacent and parallel, but what seems to be intercalation, and more rarely, bifurcation, occurs sparingly and randomly in the main thickness. The tubules are divided into chambers by frequent thin septa, usually gently concave with the curvature pointing inwards, i.e. away from the exterior. They may, however, be quite flat, set either at right angles to the walls or obliquely. Septa in adjacent tubules may be at the same level across several tubules, but there is no regularity at all in this occurrence, chamber-length varying from 0.054 to 0.200 mm. The septa are about 0.004–0.009 mm thick; the observed differences in this may well be mostly due to preservation.

In vertical section the tubules are seen to originate horizontally at the base of the growth, and then turn fairly sharply upwards, broadening in diameter and becoming typically septate. This basal portion is interpreted as a rudimentary hypothallus. It is not the same as the markedly distinct hypothallus (as opposed to perithallus) which occurs in many members of the Corallinaceae. Whether different preservation and different orientation of section of this rudimentary hypothallus would give a picture like the basal structures, interpreted as hypothallus, in *Cretacicrusta* (Elliott 1972) and *Solenopora* cf. *nigra* Brown (Öpik and Thomson 1933) is not known.

The main thickness of the growths contains various cavities, which are not part of the original plant structures. They are usually though not invariably irregular in outline, wholly or partly calcite-filled, and may be due to accident, borings made from the exterior, debris included during growth in life, or differential diagenesis. As well as these, however, there occur various rounded cavities, of similar calcite filling to the others, but each bounded by a definite organic wall. In vertical section they are seen to occur in curved

## EXPLANATION OF PLATE 21

Figs. 1–4. *Neosolenopora armoricana* sp. nov. Miocene, Vindobonian, Savignéan Falun; La Perchais Quarry, Tréfumal, south of Dinan, Brittany, France. 1, 2, Thin-sections; vertical and transverse sections of radiate cell-columns,  $\times 46$ . V. 53652c, V. 53652b. 3, Portion of exterior of solid algal growth,  $\times 30$ . V. 57125. 4, Thin-section, vertical cut to show row of reproductive bodies,  $\times 46$ . V. 53652c.



horizontal courses or series, like those of sporangia or conceptacles in crusting Corallinaceae, and I interpret them as evidence of definite solenoporacean reproductive structures.

The smallest of these is oval in section, 0.182 mm high by 0.109 mm diameter. It originates in one tubule and is conspicuously different to the normal rectangular, presumed vegetative, cells. It shows as a swollen structure wider than the tubule, and bounded by a dark cell-wall of 0.009–0.014 mm thickness. Within the calcite filling are several circular bodies of about 0.036 mm diameter.

To left and right of this single structure, others occur along a curved row representing an old surface or subsurface of the growing plant. Almost all these have the same height, but they vary greatly in width. From this, and from the irregularity of their upper and lower surfaces, they appear to have been formed by the fusion, in different examples, of two or of several of the single bodies described above. All are bounded by outer walls, though none show the circular bodies seen within the single example.

A second row of similar structures is seen elsewhere in the same specimen. Here a multiple example, extending across five tubule-rows, contains many circular bodies like those in the single one described, and there are traces in the contents of some other examples.

A single example is exceptional in size and form; it is heart- or shield-shaped in section, with diameter of 0.218 mm and with a minimum height of 0.300 mm measured at the indentation. The height is 0.337 mm to one side of this, and on the other, where it is prolonged into a tube-like projection, is 0.355 mm. The bottom half of the calcite-filled interior shows as an amorphous mass of the same grey as the small spherical bodies in the other examples. Although this exceptional cavity extends across two tubules, it is different from a simple 'double' example.

It seems difficult to explain these structures in any way other than that they are reproductive in origin, resembling the sporangia and conceptacles of the crusting Corallinaceae, and this is discussed in more detail below. In crusting corallines the plane of reproductive structures, at right angles to the vertical section which shows them in a curved row, usually shows them scattered irregularly. However, a similar cut in *Neosolenopora*, as interpreted by the circular tubule-sections, again showed the reproductive bodies in a row with the presumed third diameter as about 0.182 mm.

*Holotype.* A nodule from which three thin-sections have been prepared. Miocene, Vindobonian, Savignéan Falun; La Perchais Quarry, Tréfumal, south of Dinan, Brittany, France. Brit. Mus. (Nat. Hist.) Dept. Palaeont., reg. nos. V. 53652, a, b, c. Plate 21, figs. 1, 2, 4; Pl. 22, figs. 2–5.

*Paratypes.* Two thin-sections cut from another nodule, same locality and horizon. Reg. nos. V. 51237, 51238. Pl. 22, fig. 1. A third nodule, not cut, V. 57125, Pl. 21, fig. 3.

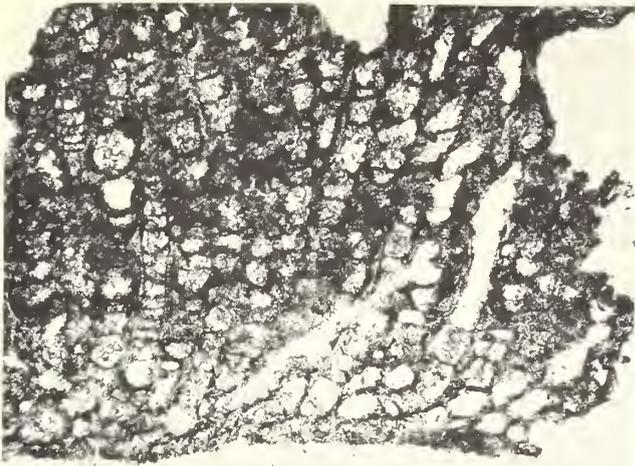
## DISCUSSION

*N. armoricana* seems similar to the type-species, *N. patrinii* from the Italian Helvetian. This was described and figured (as *Lithophyllum vinassai*) by Patrini (1932) and reviewed by Mastrorilli (1955), who emended the nomenclature. The most conspicuous difference is in the length of the ordinary cells; Mastrorilli gives dimensions for *N. patrinii* as 0.24–0.30 mm by 0.06–0.10 mm, whereas the corresponding dimensions for *N. armoricana* are 0.05–0.20 mm by 0.08–0.11 mm. Patrini's figures illustrate this clearly. They also show a hypothallial zone certainly thicker

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## EXPLANATION OF PLATE 22

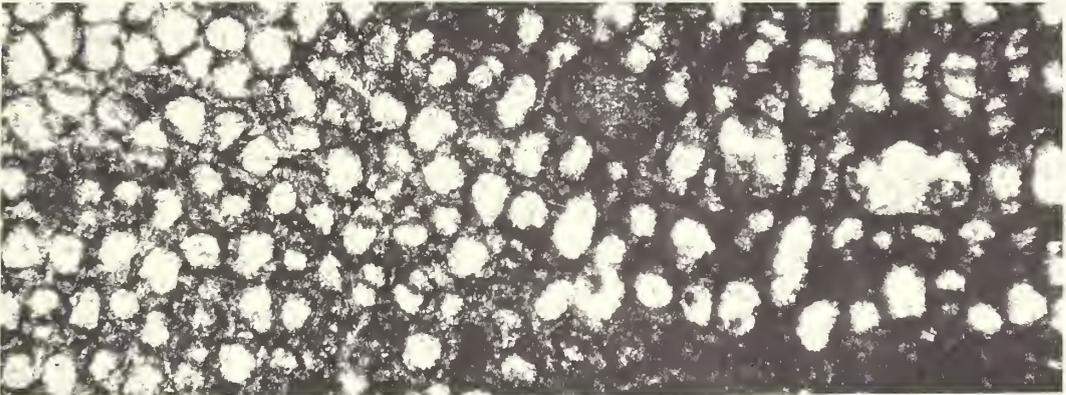
Figs. 1–5. *Neosolenopora armoricana* sp. nov. Horizon and locality as Plate 21. 1, Thin-section, vertical cut of basal growth to show rudimentary hypothallus,  $\times 46$ . V. 51238. 2, Thin-section, vertical section of single ovoid reproductive body, containing presumed tetraspore bodies,  $\times 122$ . V. 53652c. 3, Thin-section, near-horizontal (transverse) cut showing a reproductive body near right-hand margin,  $\times 46$ . V. 53652b. 4, Thin-section, vertical cut to show multiple reproductive body with presumed tetraspore bodies,  $\times 122$ . V. 53652c. 5, Thin-section, vertical cut of reproductive body, presumed sexual, ?female,  $\times 122$ . V. 53652c.



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than that in *N. armoricana*; the cell-differences seen in this may be due to a different angle of section to that figured in the present work, but this is difficult to evaluate. Clear rows of apparently calcite-filled reproductive structures, single, double, and multiple, are shown by him (op. cit., pl. 1, figs. 3, 5) but cannot be seen in as much detail as now given for *N. armoricana*.

The interpretation of the reproductive structures in *Neosolenopora* necessitates a comparison with those known in the Corallinaceae. At first sight the single bodies suggest the discrete sporangia of *Archaeolithothamnium*, and the larger bodies the conceptacles of a genus such as *Lithothamnium*. However, in living crusting corallines, conceptacles develop as structures *sui generis*, beginning as a heightening of adjacent cells over a limited area, a process facilitated by the lamellar (horizontal) cell-arrangement, and then developing to a box-structure containing the sporangial bodies. It is easy to see that this would not readily occur in *Neosolenopora* where the cell-arrangement is columnar and irregularly septate. In the single example described, the reproductive body is swollen by reference to normal tubule-diameter, encroaching on adjacent tubule-space. If, as in the crusting corallines, seasonal-physiological factors influenced the development of reproductive structures as a sporadic surface or subsurface phenomenon, then developing reproductive bodies in adjacent tubules would inevitably become modified. For this reason, the larger reproductive bodies are to be regarded not as conceptacles, but as fused sporangia, and this is indirectly confirmed by their varying width, depending entirely on the number of component merged sporangia.

The sporangia of *Archaeolithothamnium*, and the great majority of the conceptacles of *Lithothamnium*, *Lithophyllum*, and their allies, contain asexual tetraspores. The sexual structures in these genera, male and female, containing either antheridia or carposporangia are fewer, but are of general conceptacle pattern; they can sometimes be recognized in fossils (Conti 1946, 1950; Elliott 1970; Lemoine 1962, 1971; Segonzac 1970). If, as seems likely, solenoporoid reproduction was somewhat similar to that of the Corallinaceae, and also bearing in mind the necessarily different development of the sporangia already discussed for *Neosolenopora*, what form would the sexual structures take?

The solitary candidate seen for this interpretation in *Neosolenopora* is the large heart-shaped body already described. Size and shape preclude it from being an ordinary 'double sporangium', and the long neck is typical of some sexual conceptacles in Corallinaceae. It could be that the space needed for development of sexual as opposed to asexual development was in a tubular, columnal cell-arrangement only achieved by vertical development: the normal vegetative cells vary much in this dimension. It seems quite likely then, that this may have been a sexual reproductive body. The large amount of presumed organic residue in the lower part, of the same microscopic appearance as the material of the circular spore-packets in the normal asexual sporangia, suggests that it was possibly a female structure, since in my experience carpogonia leave more indication in the fossil state than antheridia. But this is speculation.

The complete absence or rare occurrence of very doubtful reproductive structures in Solenoporaceae, through Palaeozoic, Mesozoic, and Tertiary, has already been noted. If indeed comparable organs to those of the Corallinaceae were in most

Solenoporaceae external, non-calcified, and presumably deciduous, this would be in accord with the usual solenoporacean columnar cell-structure. The alleged reproductive bodies of *Solenomeris*, described by Rao and Varma (1953), and figured by Maslov (1956) and myself, were discounted by me (Elliott 1965), but some workers, e.g. Boulanger and Poignant (1969), are convinced of their sporangial nature and may well be correct in this. They are, however, not so easily reconcilable with the structures known in the Corallinaceae as are those now described for *Neosolenopora*.

I have elsewhere put forward the suggestion that the Solenoporaceae, individual species of which occasionally achieved typical corallinacean features such as calcified reproductive structures and differentiated hypothallial cell-layers, were precluded from a marked evolutionary development along these lines by cell-size and pattern, this possibly reflecting a different algal chemistry to that of the Corallinaceae (Elliott 1965). The rather different ecological behaviour of the two groups is also significant, the Corallinaceae achieving a successful exploitation of the coral-reef environment in the Tertiary never equalled by Palaeozoic or Mesozoic Solenoporaceae. *Neosolenopora* seems easily to be the most, if indeed not the only, successful solenoporoid in attaining a reproductive evolution leaving a calcified record as in Corallinaceae. It is of interest that, so far as is known, it is the very last of its kind, and evolved well after the Corallinaceae were established and dominant.

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G. F. ELLIOTT  
Department of Palaeontology  
British Museum (Natural History)  
London, SW7 5BD

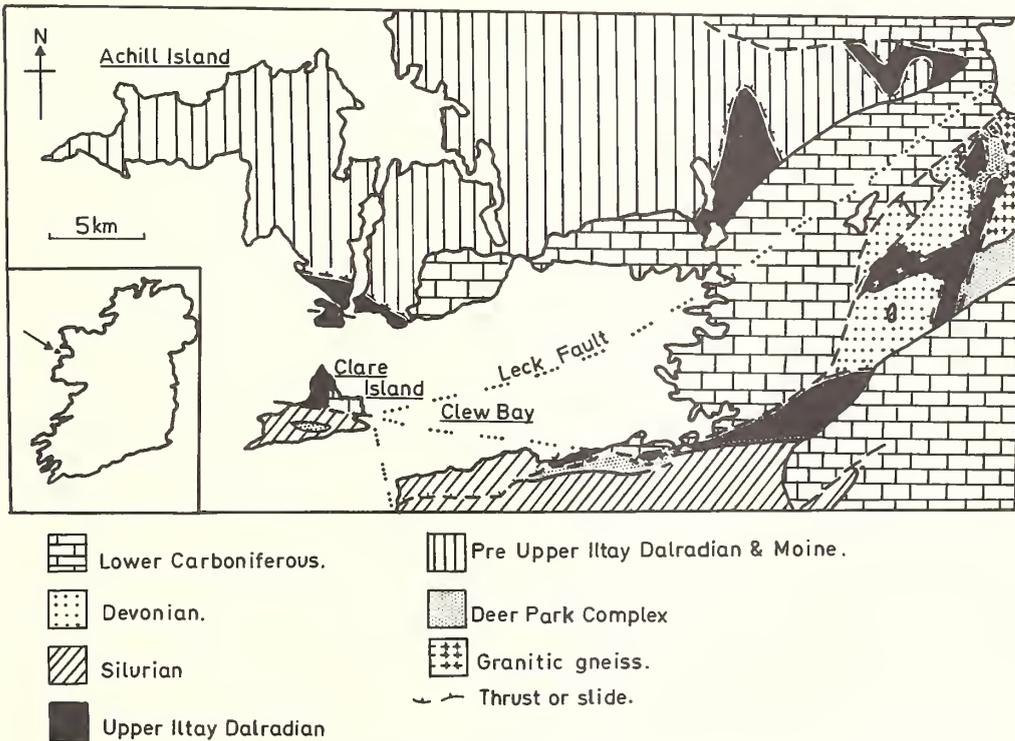
# A *PROTOSPONGIA* FROM THE DALRADIAN OF CLARE ISLAND, CO. MAYO, IRELAND

by A. W. A. RUSHTON and W. E. A. PHILLIPS

ABSTRACT. The largest specimen of *Protospongia hicksi* Hinde yet found is described from the top of the Upper Itay Dalradian succession in western Ireland. The age is uncertain but suggestive of Middle Cambrian (St. David's Series).

THE northern part of Clare Island, Co. Mayo, is underlain by a succession of graphitic pelites and cherts, coarse turbidites, and local spilitic lavas and tuffs, which are considered to be the youngest part of the Itay Dalradian succession of north Mayo (Phillips 1966; Kennedy 1969; Phillips *et al.* 1969; Kennedy *et al.* 1972). The location and stratigraphical succession are outlined in text-fig. 1 and Table 1 respectively.

During the summer of 1971 one of us (W. E. A. P.) collected a specimen of *Protospongia hicksi* Hinde on the northern promontory of Clare Island, from near the



TEXT-FIG. 1. Geological sketch-map of northern Mayo.

TABLE 1. The stratigraphy of the Iltay Dalradian in north Mayo

Group	Formation	Member	Minimum approx. thickness in metres	Lithology
Lough Feeagh Group Upper part (cf. Upper Iltay Dalradian) thickness c. 2 km	Ballytoohy Formation	Oghcorrugaun Pelitic and Psammitic Member	70	Alternating dark cherty pelite and psammitic
		Benilra Psammitic Member	390	Graded psammitic
		Tonaltatarrive Spilitic Member	36	Black pelite, grey chert, spilite, tuff and limestone
		Siorr Chert Member	24	Black-grey chert,* thin psammitic
		Carrickarrollagh Iron Member	30	Black pelite, grey chert, siderite
Lower part	(Unexposed interval) (Divisions not listed)			
West Achill Group (cf. Middle Iltay Dalradian) thickness c. 5 km	(Divisions not listed)			
Inver Group (cf. Lower Iltay Dalradian) thickness c. 1 km	(Divisions not listed)			

The horizon with *Protospongia* is indicated by the asterisk.

top of the Siorr Chert Member of the Ballytoohy Formation. The specimen was found on an interface between a band of graphitic chert and one of graphitic and pyritic pelite. The outcrop (Irish grid reference 069370 286940) is one of several on a bare hillside, and has been marked in the field by a red cross.

This specimen is the first fossil of stratigraphical significance to be found in the Dalradian of Ireland, and establishes the presence of Cambrian rocks in the northern half of Ireland. The stratigraphical and structural setting and the significance of the specimen will be discussed elsewhere (Phillips, in press).

### Genus PROTOSPONGIA Salter 1864

#### *Protospongia hicksi* Hinde

Plate 23

1887 *Protospongia Hicksi* Hinde, pl. 1, figs. 2, 2a [figured].

1888 *Protospongia Hicksi* Hinde, p. 107 [described].

1920 *Protospongia hicksi* Hinde; Walcott, p. 307, pl. 80, figs. 3, 3a, b [synonymy].

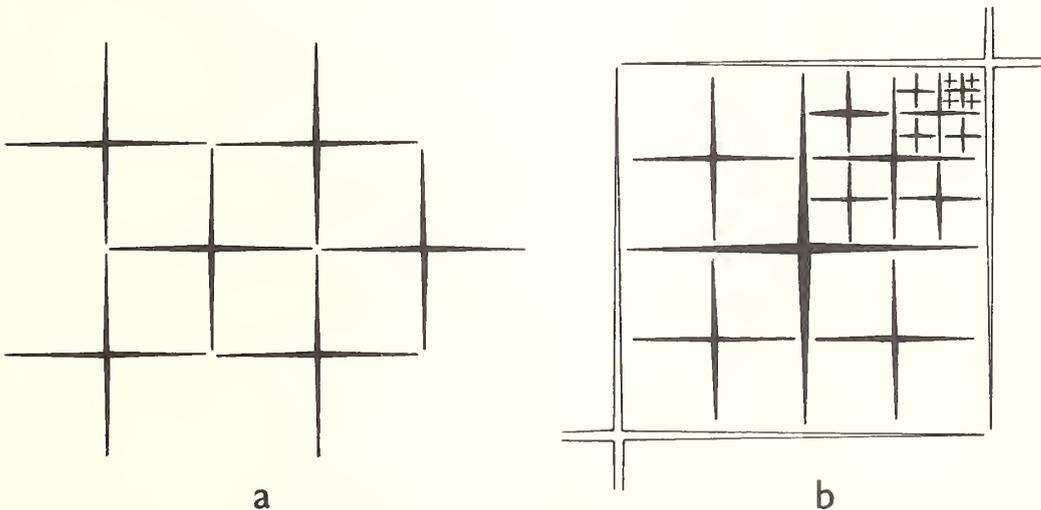
1966 *Protospongia hicksi* Hinde; Rigby, p. 550, pl. 66, figs. 1, 2 [description of American specimen].

The holotype (Sedgwick Museum A1035) is from the Menevian Beds (mid-St. David's Series), Porth-y-rhaw, near St. David's, Pembrokeshire.

*Description of the Irish specimen.* The specimen (Trinity College, Dublin, no. TCD 9834) seems to be much the largest *Protospongia* recorded. It lies on a bedding-plane cut by many joints, along some of which there has been a little tectonic movement and along others quartz crystals have grown. It was collected in several pieces. Spicules cover an area roughly 300 mm by 150 mm and originally extended well beyond the limits of the fragments collected. In places the spicules have weathered away, leaving a feeble impression on the underlying rock; in other places they are preserved in silica. These were thrown into relief by abrading the matrix with powdered dolomite in an air-blast.

The spicules are cross-shaped tetracts ('stauracts') of various sizes referable to six 'orders'. Although the spicules are partly disarranged their original disposition is seen in places (Pl. 23, fig. 1). The largest or 'first-order' spicules are arranged in a quincunx (text-fig. 2a). Each second-order spicule is centred in the squares made by the first-order spicules, and the second-order spicules make squares for the third-order spicules; this pattern is repeated on a successively smaller scale for the fourth-, fifth-, and sixth-order spicules (text-fig. 2b). The resulting lattice is not quite regular, nor square, nor truly rectangular; the general orientation of the lattice veers through about 25° across the slab, suggesting that the sponge's body, now flattened, was once conical.

The larger spicules in general overlie the smaller. The smaller spicules (third to sixth order) are domed, with the tips of all four rays sloping down into the matrix; in life the concave side probably faced internally, as in *Pleodioria* Öpik (1961, p. 50). There is no evidence of a polar ray, like those shown in '*Protospongia?* sp.' by Henningsmoen (1958, pl. 7, figs. 4-6), and in *Pleodioria tomacis* Öpik (1961, text-fig. 16B).



TEXT-FIG. 2. Idealized drawings of *Protospongia*, showing (a) first-order spicules arranged quincuncially,  $\times \frac{1}{2}$  approx. (b) arrangement of first- to sixth-order spicules: parts of two first-order spicules are shown in outline, one second-order, and four each of the third- to sixth-order spicules are shown solid black;  $\times 2$  approx.; for clarity all the rays are drawn too thick and too short; they should overlap.

There is no stump seen at the centre of the stauracts, nor was a polar ray exposed when the centre was undercut or air-blasted away.

At some places (e.g. about 2 cm below and to the left of the centre of Pl. 23, fig. 1) there are small rod-like spicules which do not appear to be parts of stauracts but which may represent dermal spicules (diacts). There is no evidence that the sponge, large as it was, had more than a single layer of spicules in its wall.

The features so far described agree with Rigby's description of a well-preserved mould of *P. hicksi*; the present specimen differs from Rigby's in having six rather than five orders of more robust and much larger spicules. Three first-order spicules have a 'radius' (centre to tip) of 20, 23, 24 mm, and other, less distinct ones appear to have exceeded 30 mm; near the centre the rays are about 0.65 mm thick. Four second-order spicules have radii of 9.8, 10.0, 12.0, 12.8 mm, and a thickness of about 0.45 mm. Third-order radius averages 5.6 mm (22 measurements), thickness about 0.35 mm. Fourth-order radius 2.5 mm (very variable), thickness about 0.28 mm. Fifth-order radius 1.3 mm, thickness a little more than 0.2 mm. Sixth-order radius 0.6 mm, thickness less than 0.2 mm. The second-order spicules compare in size with the first order of Hinde's and Rigby's descriptions. The smaller spicules are stouter than Rigby's but the sixth-order spicules compare well with Hinde's fifth-order spicules.

*Comparisons.* The present specimen can be compared only with large species of *Protospongia* with several reducing orders of spicules, namely *P. fenestrata* Salter, *P. hicksi*, and also, perhaps, *P. erixo* Walcott (1920, p. 353, pl. 79, figs. 2, 2a-c). Although the largest of the spicules are much bigger than those previously described, they have throughout their size-range the same general proportion of thickness to radius as the spicules of *P. hicksi* but not the slender ones of *P. fenestrata* (Hinde 1887, pl. 1, figs. 1, 2). The species described from Metis, Quebec, by Dawson (1889), have only three orders of spicules, those of the first order being arranged orthogonally rather than quincuncially, and are much smaller over-all.

#### IMPLICATION OF AGE

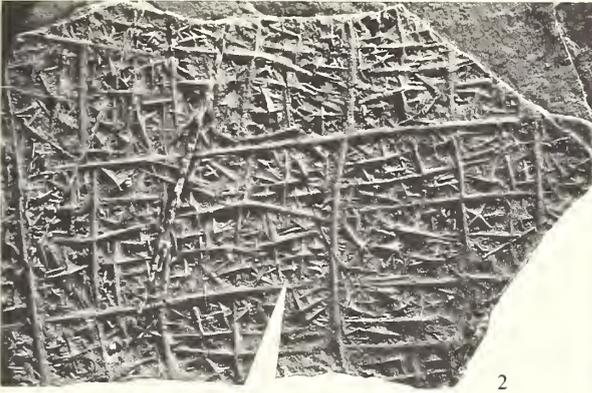
We have misgivings about assessing the age of the Ballytoohy Formation on the basis of a single fossil from a group of which the record is most imperfect; nevertheless, this fossil demands some discussion.

Species of the genus *Protospongia* are described from the Middle Cambrian to

#### EXPLANATION OF PLATE 23

Figs. 1, 2. *Protospongia hicksi* Hinde from the Siorr Chert Member of the Ballytoohy Formation, northern promontory of Clare Island, Co. Mayo, Ireland (grid ref. 069370 286940). No. TCD 9834. 1, Part of specimen (less than half is shown),  $\times 1$ . Compare the orientation of the lattice to left and right of figure. 2, Part of specimen at bottom centre of Fig. 1,  $\times 2$ . The orientation in relation to Fig. 1 is reversed; the incident light is at a low angle to show the doming of the spicules. The white pointer shows a square of four sixth-order spicules.

Fig. 3. *P. hicksi*, holotype, from the Menevian Beds, Porth-y-rhaw, Pembrokeshire (Hinde 1887, pl. 1, figs. 2, 2a).  $\times 2$ . Sedgwick Museum A1035.



2



3



1

low Ordovician (Dawson 1889). Stauract spicules referred to the genus (perhaps unjustifiably by present standards) are recorded from the Lower Cambrian by Walcott (1890, p. 597, pl. 49, fig. 2) and from the Upper Cambrian (Merioneth Series) by Westergård (1944, p. 32). *P. hicksi*, however, is known only from the Middle Cambrian (St. David's Series), and the same seems generally true for large species of *Protospongia* composed of numerous spicules of several orders of size. The present specimen, then, suggests a Middle Cambrian age for the Siorr Chert Member of the Ballytoohy Formation. It is stressed, however, that this assessment may be called in question by the discovery of new specimens of *Protospongia*; the genus existed both before and after the times of the known specimens of *P. hicksi*, represented by undescribed species. Indeed Westergård has figured (1909, pl. 2, fig. 26) a doubtful *P. fenestrata* from beds as high as the Tremadoc: it consists only of a few small spicules of two or three orders of size, the largest of 6 mm radius; the 'fenestrate' arrangement is not preserved, but that specimen clearly shows that caution is needed in interpreting the age of the present one.

The horizon in the Dalradian sequence which is most definitely fixed palaeontologically is the Leny Limestone of Leny Quarry, near Callander, Perthshire. The Leny Limestone lies within the Leny Grits and is an integral part of the Upper Itay Dalradian succession of Scotland. The age of the Leny Limestone was assessed by Cowie *et al.* (1972, p. 17) as late Lower Cambrian (Comley Series), and may therefore be older than the Siorr Chert Member of the Ballytoohy Formation. Lithologically the Ballytoohy Formation is closely comparable with the Highland Border 'Series' of Scotland which is considered to lie at a higher stratigraphical level than the Upper Itay Dalradian. The age of the rocks referred to the Highland Border Series is generally uncertain, but Downie *et al.* (1971, pp. 5, 19, 24) have obtained an assemblage of acritarchs from a sample of black mudstone within the Greenstone Division of the Highland Border Series at Edzell, Angus, to which they tentatively assign an age between the Tremadoc and Llanvirn. This is so considerably later than the age postulated for the Ballytoohy Formation as to suggest that the lithologies typical of the Highland Border Series were developed at different times, at least in eastern Scotland and western Ireland.

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A. W. A. RUSHTON  
Institute of Geological Sciences  
Exhibition Road  
London, S.W.7

W. E. A. PHILLIPS  
Department of Geology  
Trinity College  
Dublin



# OBSERVATIONS ON THE NATURE OF THE ACRITARCHS

by C. DOWNIE

*The Fifteenth Annual Address, delivered March 1972*

**ABSTRACT.** Recent studies of the acritarchs have shown that many have features in common with one or other of two major groups of planktonic algae—the prasinophyceae (tasmanitids) and the dinophyceae (dinoflagellates). However, studies of the ultrastructure, excystment mechanisms, and knowledge of their geographic and historical distribution are too incomplete at the moment to allow a worthwhile natural classification of the 300 or so acritarch genera. A rough outline of their evolution can, however, be indicated, and shows a marked diversification in the Lower Cambrian and a more rapid succession of groups through the Lower Palaeozoic.

PALYNOLOGICAL preparations, particularly of Lower Palaeozoic marine sediments, normally contain large numbers of small (10–50  $\mu\text{m}$ ) organic bodies with hollow interiors. Although these have a great variety of shape and particularly of ornament, such as spines and crests, their natural relationships are obscure beyond the general agreement that they are for the most part the reproductive stages (spores or cysts) of marine planktonic algae. To these fossils the name Acritarcha has been given and they currently include over 3000 species. Because of their abundance in the early sediments and their often characteristic appearance, they have been much studied recently in the hope of finding out more about the origin of life and in the expectation of using them for biostratigraphic correlation.

## THE GROUP ACRITARCHA

Evitt (1961) published some results of his studies of typical Cretaceous hystrichospheres, i.e. type genera of the older Hystrichosphaerida O. Wetzel, and showed them to be not of uncertain affinity as was supposed, but the resting spores or cysts of dinoflagellates. This was amply confirmed by Wall and Dale (1968 and other works), who showed the type species of *Hystrichosphaera* to belong to the dinoflagellate genus *Gonyaulax*. In this way a large number of the organic walled microfossils classed as hystrichosphaerids of unknown affinity were transferred to the dinoflagellates.

The residue of about 600 species did not possess the necessary morphological features to justify their transfer and having no other known affinities remained an *incertae sedis* group for which Evitt (1963) coined the name 'acritarch'. Realizing that this group was probably inhomogeneous, like its predecessor the hystrichospheres, he did not formally name it according to the Rules of Nomenclature but instead established an informal category, the group Acritarcha.

*The biological and stratigraphical interest of the acritarchs.* In the short time that has elapsed since the creation of the group it has been found to be of major importance as an element in the evolution of the biomass and as a contributor to biostratigraphy.

The importance of acritarchs arises from their early appearance in the Precambrian and the record they provide of the diversification of the algae and the origin of the plankton. They are evidently the major group of plankton during the Lower Palaeozoic, probably continuing as such until the Mesozoic. They therefore played an important role in the biological cycle, and were possibly the largest contributors to the biomass during this period. The scale of their contribution can be gauged from the fact that in marine sediments from about 1000 to 300 million years old they are to be found in numbers usually between 1000 and 10 000 per gramme, provided that diagenesis, metamorphism, or abrasion has not affected them.

On this basis Tappan (1971) has calculated their effect on the biological cycle and the consequences of their changing abundance on the atmosphere and the geochemistry of the oceans.

In biostratigraphy their importance also arises from this long continued abundance. In the Precambrian they are the most numerous of fossils. In many apparently unfossiliferous Palaeozoic rocks they provide the only biostratigraphic evidence and in most marine strata of Palaeozoic age they outnumber other common fossils. They have, like all microfossils, the advantages of small size making them useful in dating borehole and other small samples. These advantages would be of little significance were they not allied to distinct, or at least recognizable, differences in the morphology of acritarchs from different strata. The efforts to determine this have shown that assemblages of ten to fifty species are commonly found in samples and are characteristic of particular stratigraphic divisions. Zonal schemes have, however, not yet been established and much work remains to be done before their value in stratigraphic correlation can be accurately determined. This research so far has greatly increased the number of species named to over 3000 and with this increase has come some taxonomic confusion and many problems of systematics.

It is not intended here to review all of these difficulties but to concentrate on the larger more general problem of the affinities of the acritarchs and the possibility of discovering a way to effect a useful genetic classification.

*Distribution of the acritarchs.* As the study of the acritarchs is so recent, it is intended to give a brief review of what is known about their distribution.

It should be noted at the outset that so far the only fresh-water forms classed with the acritarchs have been found in Holocene lake deposits in Australia (Harland and Sarjeant 1970), and Pleistocene peats of England (Sarjeant and Strachan 1968). All others have been found in marine or brackish water sediments.

Among the marine environments and sedimentary rocks they are most numerous in argillites but also occur in a wide variety of carbonate and arenaceous rocks. Little work has been done on their association with particular environments and no generalizations are possible (Williams and Sarjeant 1967). In the Silurian a widespread provincial distribution, possibly climatically controlled, has been determined by Cramer (1970), affecting the continents bounding the Atlantic. There are indications, not yet confirmed, that broad provincialism of a similar kind affected Ordovician and Cambrian acritarchs as well.

Probably the most intensively studied area is that surrounding the Baltic where rocks ranging in age from the Precambrian Karelian to the Silurian have been examined, notably by Eisenack in many publications

from 1931 onwards, Timofeyev (1959, 1966, 1969), Volkova (1968), and Kjellström (1971). Assemblages from the Cambrian of the Russian platform and Poland have been described by Volkova (1969), from the Ordovician of Poland by Górka (1967, 1969), and from the Russian platform by Umnova and Vanderflit (1971). Vavrdova (1965, 1966) and Slavikova (1968) have investigated the Cambrian and Ordovician of Czechoslovakia, and Burmann (1968) has reported on some lower Ordovician forms from East Germany. In Belgium the Devonian and Carboniferous forms have been described by Stockmans and Williere in a series of papers between 1960 and 1969, Martin (1969) recorded their distribution in the Ordovician and Silurian, and Vanguetaine (1970) reported Cambrian forms. In Britain there are records of Permian acritarchs (Wall and Downie 1963), Silurian (Lister 1970), Ordovician (Rasul 1971) and Cambrian (Downie, *in press*). Mesozoic forms were described by Wall (1965). The Mesozoic acritarchs of France have been described by Valensi (1953) and Devonian and Ordovician forms by Deunff in several papers from 1951 onwards, and Silurian and Devonian forms by Rauscher (1969). In Spain the most important work is that of Cramer (1964 *et seq.*) describing Silurian and Devonian assemblages. Precambrian forms are recorded by Roblot (1964).

In Africa little is known about acritarchs from south of the Sahara, but in North Africa, Ordovician, Silurian, and Devonian forms have been repeatedly recorded notably by Deunff (1961, 1966), Combaz (1968), Magloire (1968), and Jardiné and Yapaudjian (1968).

In Asia acritarchs have been described from Cambrian and Precambrian rocks of the U.S.S.R. by several workers notably Timofeyev (1966, 1969), Lopukhin (1971), Pychova (1966). Apart from this the only records are scattered; among them, Oligocene forms from Japan (Takahashi 1964), from the Jurassic of Pakistan (Sarjeant 1967), and the Precambrian Vindhyan of India (Saluja *et al.* 1971). From Australia Combaz and Peniguel (1972) have recorded Ordovician forms but the main data from the southern hemisphere are due to the work of Brito (1967), Sommer and van Boekel (1966), and Combaz *et al.* (1967).

North American acritarchs have been studied by Cramer (1970) who reports on many Silurian occurrences in the east, and Loeblich (1970, and with various authors) has described forms from the Ordovician, Silurian, and Devonian from localities ranging from Oklahoma to New York. The Cambrian forms have been recorded by Walton (in Staplin *et al.* 1965), and Staplin (1961) has described Devonian forms from Canada.

Although this list is by no means comprehensive and indeed arbitrary to the extent that apology may be needed to authors omitted, it serves to show that, except for the southern hemisphere, a reasonably good coverage of the sedimentary rocks ranging from Precambrian to Devonian has been achieved in Europe, North America, and North Africa. Although only a few papers concerning Mesozoic and Tertiary rocks are included in the above summary these periods also have been covered, and more fully than the Palaeozoic.

#### STUDIES OF ACRITARCH MORPHOLOGY

In recent years several factors have led to an improved knowledge of the structure of various acritarchs. These include the discovery of extremely well preserved material like that from the Sylvan Shale of Oklahoma and the Lower Palaeozoic of Estonia, as well as improved methods of preparation producing cleaner and more easily examined specimens. The improved techniques of examination such as the use of the scanning electron microscope (see Loeblich 1970) and ultra-thin sections (Jux 1971) have also contributed in a major way.

This work has focused attention on wall structure and excystment mechanism as characters meriting special consideration in determining the relationships of the acritarchs to each other and to other organisms.

*Wall structure.* Too little is known about the chemistry of the substance forming the acritarchs test to help in their classification. Studies like that of Kjellström (1968)

show that some consist of condensed fatty acid derivatives, similar to the 'sporo-pollenin' material.

The wall structure does, however, show promise of being of considerable importance. The studies of Jux (1969) indicate the value of ultra-thin sections. At present these studies are limited to a very small number of genera but can be supplemented by some more obvious features visible under the ordinary microscope.

At present the following types of wall structure can be recognized:

1. *Tasmanitid*. The wall is uniform, but laminated with narrow radial pores. The wall thickness is often variable in a species, probably due to growth.

This type of wall has been shown by Jux to be present in the important Palaeozoic genera *Tasmanites* and *Baltisphaeridium*. It is also present in Mesozoic and Tertiary species attributed to *Tasmanites* and the living alga *Pachysphaera*. Optical studies suggest that the Cambrian genera *Prisogalea* and *Cymatiogalea* have a similar wall structure.

2. *Michystridian*. The wall is of a simple homogeneous nature and appears to be of a more or less constant thickness in a species, usually thin.

To this group belong *Michystridium* and *Veryhachium*, which account for a large number of acritarch species in the Palaeozoic and Mesozoic.

3. *Diacrodian*. The wall is thin and of a simple homogeneous nature. It is distinguishable from that of *Michystridium* only because of a tendency to split into angular plates when damaged (Lister 1970b). All the diacrodian genera could be placed here, although the plate structure has only been seen in *Acanthodiacrodium*, *Lophodiacrodium*, and *Dasydiacrodium*.

4. *Visbysphaerid*. The wall is thin and apparently homogeneous. It is distinguished from that of *Michystridium* because of the capacity for developing an inner body closely adpressed to the outer wall. In this way a double wall can be formed. This potentiality is nearly always realized in the genus *Visbysphaera* but only infrequently in others like *Diexallophasis*.

*Excystment mechanism*. The importance of the excystment mechanism in determining relationships in dinoflagellates was shown by Evitt (1961) and discussed at length by him later (Evitt 1967). It is possible that this is true also for the acritarchs, although, because the openings are often less distinctive and frequently unknown, the evidence is much less clear. Examples of openings are shown in Pl. 24.

The following categories of excystment mechanism are known:

1. *Archaeopyle*. A name introduced by Evitt (1961) for excystment openings formed by the loss of one or more plates from a dinoflagellate cyst.

These are of a few regular types distinguished by the number and position of the plates that open. The openings are frequently angular or sub-angular in outline.

#### EXPLANATION OF PLATE 24

All figures  $\times 1000$

Fig. 1. *Acanthodiacrodium* sp. Dictyonema Beds (Tremadoc), Leningrad. Shows the beginnings of a split in the median unornamented region.

Fig. 2. *Poikilofusa* sp. Shineton Shales (Tremadoc), England. Showing a lateral epityche.

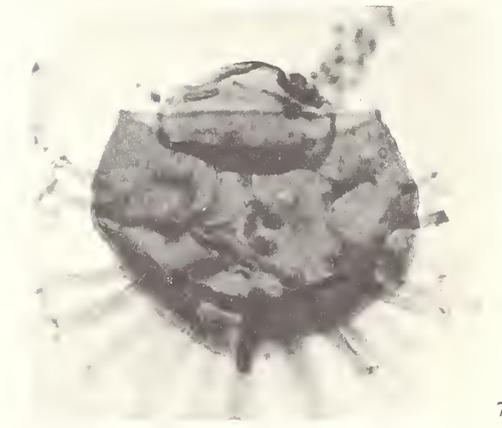
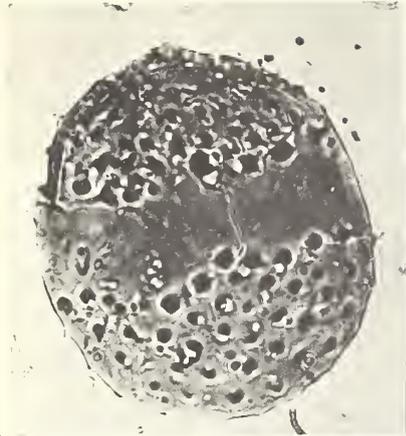
Fig. 3. *Veryhachium* sp. Shineton Shales (Tremadoc), England. Showing a lateral epityche.

Fig. 4. *Acanthodiacrodium* sp. Shineton Shales (Tremadoc), England. Shows development of split into two equal halves.

Fig. 5. *Ooidium* sp. Dictyonema Beds (Tremadoc), Leningrad.

Fig. 6. *Cymatiogalea* sp. Tremadoc, Poland. Showing thick walls, micropyle and marginal veil round operculum.

Fig. 7. *Cymatiogalea* sp. Shineton Shales (Tremadoc), England. A thinner walled specimen.



DOWNIE, Tremadocian acritarchs

These characterize dinoflagellate cysts of Mesozoic and Tertiary age, and are known in only one or two species from the Silurian and Devonian, e.g. *Arpyloris antiquus*.

2. *Cyclopyle*. This name was introduced by Eisenack (1969) for openings with a circular outline. The term pylome which had formerly been used for acritarch openings he suggested should be used as a general term for all kinds of escape apertures.

Cyclopyles are found in Palaeozoic species of *Tasmanites* and in the Ordovician genera *Baltisphaeridium*, *Peteinosphaeridium*, and *Axisphaeridium*, among others. They appear for the first time in the Cambrian, probably in the Upper Cambrian.

The openings are formed by the release of a circular operculum whose location is probably in a fixed and pre-determined position, thus allowing orientation of the cysts. This fact is not demonstrable except in a few genera, e.g. *Cymatiogalea*, which can be independently orientated by means of other characters.

Variants of the cyclopyle are found in *Priscogalea* and *Cymatiogalea* (Pl. 24, figs. 6, 7), where its diameter is unusually large, exceeding 50% of the body diameter. These large openings (macropyles) are sometimes sub-polygonal. It is also common to find the cyclopyle or macropyle surrounded by a differentiated zone, sometimes smooth, sometimes a raised rim.

3. *Epityche*. This term was introduced by Loeblich and Tappan (1969) for excystment structures formed by a curving split allowing a flap to open (Pl. 24, figs. 2, 3). These openings are commonly found in species of *Veryhachium* and *Leiofusa* where they can be shown to have a regular location.

A number of variants have been subsequently noted. Cramer (1970) distinguishes C-shaped and S-shaped splits in *Veryhachium* and Lister (1970) stresses the progressive development of a small-circle split in many genera, notably *Micrhystridium*. These are called cryptosutures and their appearance forms a large flap which may often break off.

4. *Median split*. A few forms open by splitting into two equal halves. The Ordovician genus *Orthosphaeridium* is a good example of this and it is also characteristic of many leiospheres, e.g. *Hemisphaeridium*.

Although these categories can be accepted and applied to most acritarch species, there is still difficulty arising mainly from species which have not ever been found to have natural openings. Most common among this group are the Precambrian sphaeromorphs. But *Cymatiosphaera* and *Polyedryxium*, two important Palaeozoic genera, present the same problem.

Other groups rarely show openings. Cramer (1970) reports C-shaped epityches in *Deunffia*, Rasul (1971) records a small subpolygonal opening in *Vulcanisphaera*.

In other cases the character of the opening is ambiguous. *Acanthodiacrodium*, for instance, splits along a number of planes sometimes transverse, sometimes longitudinal (Pl. 24, figs. 1, 4). In *Micrhystridium* some species, presumably with small-circle epityches, have them located very near the equator and they can only be arbitrarily separated from the median split. In *Veryhachium* and in *Leiofusa* instead of the usual epityche a split may form along one edge, and subsequent deformation of the test, particularly in *Leiofusa*, may make recognition and classification of the pylome very obscure.

*Clusters*. The overwhelming mass of acritarchs occur in preparation, and in the rock, as isolated individuals. This is true also of dinoflagellate cysts and modern representatives of the dinoflagellates and other planktonic algae. There is, however, a growing number of records of acritarchs occurring in monospecific clusters. Examples are shown in Pl. 25.

In the case of certain Precambrian and Cambrian sphaeromorph acritarchs (i.e. forms with more or less smooth surfaces) this has long been known, and in the Precambrian they are particularly common. These clusters take forms varying from

loose chains and aggregates of a few individuals to more or less compact discoid or spherical masses comprising scores of cells. Timofeyev (1966) created the subgroup Polysphaeritae to include them.

It is now known that many other kinds of acritarchs occur in similar associations although much less commonly. In the Cambrian or Tremadoc rounded clusters have been found of species belonging to *Micrhystridium*, *Prisogalea*, *Cymatiogalea*, *Tectitheca*, and *Acanthodiacrodium* (Pl. 25, fig. 1). In younger rocks records are even less common but *Leiofusa* is recorded in clusters from the Ordovician (Combaz *et al.* 1967) and possibly *Deunffia* and *Veryhachium* in the Silurian (Cramer 1970).

The significance of these clusters is not clear. The shape, size and in some cases the content is consistent with their production in sporangia like those of *Parka*, a non-vascular plant from the Lower Devonian (Challinor and Orbell 1971).

*Other morphological features used in classification.* In the sub-group created by Downie *et al.* (1963) the symmetry and shape of the body was given greatest weight, combined with the nature of the outgrowths from the body surface. These are characters that are always readily visible and can form the basis of an easily used classification. This has been extensively discussed by Cramer (1970). These features, however, probably have little significance in establishing the natural affinities of the acritarchs, the evolution of a sphere with spines being a response to very common functional requirements.

#### CLASSIFICATION OF THE ACRITARCHS

The problems of defining genera are considerable and complicated by confused concepts and irregular nomenclature. It would be inappropriate to review them partially and too large a work to be included here. It is proposed therefore to examine the question of supra-generic classification in the light of the morphological information set out above.

The earliest classification including the acritarchs was that of Wetzel (1933) which was subsequently added to by Eisenack. In 1954 the divisions were:

##### *Incertae Sedis*

##### Order HYSTRICHOSPHAERIDA Wetzel 1933

Family HYSTRICHOSPHAERIDAE Wetzel 1933

Family LEIOFUSIDAE Eisenack 1938

Family LEIOSPHAERIDAE Eisenack 1954

Family PTEROSPERMOPSIDAE Eisenack 1954

Soon after it became conventional to treat the hystrichospheres as plants, including those subsequently to become the foundation of the acritarchs. The following families were later introduced:

Family TASMANACEAE Sommer 1956

Family OOIDACEAE Timofeyev 1959

Family DIACRODIACEAE Timofeyev 1959

The last two were invalid because of legal defects.

The work of Evitt (1961) radically altered this arrangement by showing that the members of the family Hystrichosphaeridae belonged to the dinoflagellates whereas the members of the others remained *incertae sedis*. The latter formed the nucleus of the group Acritarchs.

The systematic situation was then reviewed by Downie *et al.* (1963). They suggested a number of informal subgroups to accommodate the fifty-six genera of acritarchs then named. These subgroups were based on characters easily seen, and were intended to provide a temporary classification while the data needed for a more durable and significant classification were accumulated. A somewhat similar system of groups and subgroups was later introduced by Timofeyev (1966).

These informal groups have been criticized because of their invalidity according to the 'Rules', but they have been widely adopted because many workers have recognized that a formal, valid, classification would have been, with the limited evidence available, just as arbitrary but more confusing and troublesome to discard. In fact the only subsequent formal classification, that of Mädlér (1963, 1967) cannot be used as it stands. Mädlér's classification is as follows:

- Class HYSTRICHOPHYTA Mädlér 1963
- Order TASMANALES Mädlér 1963
  - Family TASMANACEA Sommer 1956
  - Family PTEROSPHAERIDACEAE Mädlér 1963
- Order LEIOSPHAERIDALES Mädlér 1963
  - Family LEIOSPHAERIDACEAE Eisenack 1954
- Order HYSTRICHOSPHAERALES Mädlér 1963

The criticisms of this classification are that *Hystrichosphaera*, the type genus of the family, is a junior synonym of *Spiniferites* and also of *Gonyaulax*, a living dinoflagellate. *Tasmanites* and *Pterospermopsis*, the type genera of the families in the Tasmanales, most probably belong to the algal class Prasinophyceae. Some of the leiospheres may belong here too, but they appear to be a polyphyletic group.

There is therefore no acceptable legal supra-generic classification of the acritarchs available as an alternative to the subgroups of Downie *et al.* (1963). Before considering the erection of such a classification with its implications of genetic relationship, it is necessary to review the present state of knowledge and examine the evidence relevant to the nature and affinities of the acritarchs.

*The affinities of the acritarchs.* The morphological evidence, particularly that relating to the wall structure and excystment mechanism, permits a tentative subdivision of the acritarchs into related groups. The grouping is tentative because the observations

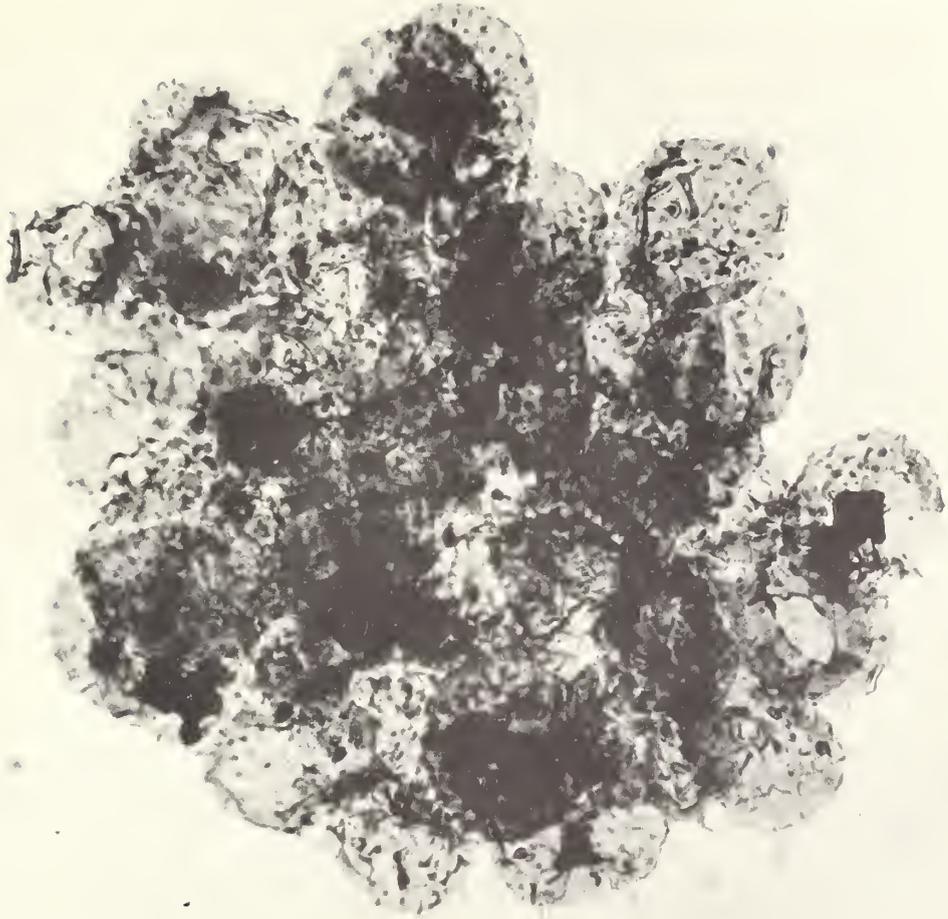
EXPLANATION OF PLATE 25

All figures  $\times 1000$

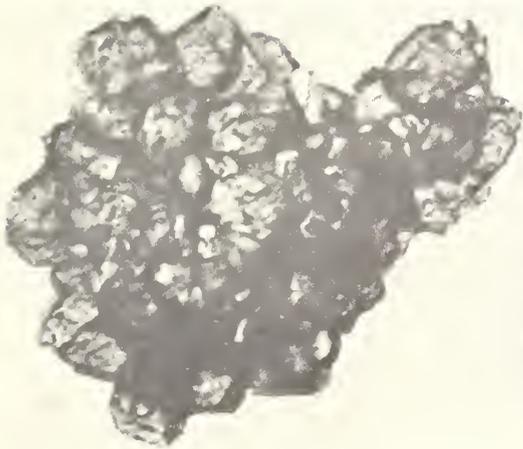
Fig. 1. Cluster of *Acanthodiacrodium* sp. Shineton Shales (Tremadoc), England.

Fig. 2. Cluster of sphaeromorphs (*Synsphaeridium* sp.). Torridonian (Precambrian), Scotland.

Fig. 3. Single sphaeromorph (?*Leiosphaeridia* sp.). Lower Cambrian, Scotland.



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are available for only a small proportion of the described species. These groups should form the basis for a more natural classification in the future.

#### 1. *Pachysphaera* group

This group is characterized among fossils by having the tasmanitid type wall, excystment by a median (great circle) split, and the absence of alae (i.e. crests or wings).

To it belong the modern genera *Pachysphaera* and *Halosphaera* and the fossil genera *Tythodiscus*, *Crassosphaera*, and *Tasmanites* (pars.) (Pl. 26, fig. 3). It appears to be confined to Mesozoic and younger periods.

The group belongs to the algal class Prasinophyceae.

#### 2. *Tasmanites* group

This group has tasmanitid wall structure, and an absence of alae. Excystment is by a cyclopyle. To it belong the Palaeozoic species of *Tasmanites*, ranging in age from Ordovician (?Cambrian) to Permian (Pl. 26, fig. 5).

Unfortunately I have been unable to determine whether or not the type species of *Tasmanites*, *T. punctatus* from the Permian of Australia, opens by a cyclopyle or a median split. The nomenclature is therefore provisional.

#### 3. *Pterospermopsis* group

This group has characteristic alae dividing the vesicle surface into fields. Living representatives excyst by splitting along the base of an ala. No excystment structures have been recorded among fossil examples. It includes the living genus *Pterosperma* and the fossils *Pterospermopsis* (Pl. 26, fig. 4) and *Cymatiosphaera*. The latter range in age from Cambrian to Tertiary. The similarity in appearance and pattern of alae to those of various species of the living *Pterosperma* (Boalch and Parke 1971) indicates that the group belongs to the Prasinophyceae.

#### 4. *Baltisphaeridium* group

Members of this group have a tasmanitid wall structure with spinose outgrowths from the vesicle surface. These outgrowths are commonly simple spines, but alae and irregular projections also are found. The excystment structures are cyclopyles, macropyles, and median splits. The group may be subdivided as follows:

(a) *Baltisphaeridium* type. This is characterized by spinose ornament (Pl. 26, fig. 7) and cyclopyles. It includes *Baltisphaeridium*, *Peteinosphaeridium*, *Asketopalla*, *Polyancistrodorus*, and *Axisphaeridium*. It is characteristically Ordovician in age (Arenig to Ashgill), but certain Cambrian species may belong here.

(b) *Priscogalea* type. This is characterized by its macropyle. It includes *Priscogalea* and *Cymatiogalea*, and is confined to the Upper Cambrian and Lower Ordovician. *Cymatiogalea* has alae and shows a field pattern very like that of some species of the living *Pterosperma* (Boalch and Parke 1971; Rasul 1971).

#### EXPLANATION OF PLATE 26

All figures  $\times 1000$

Fig. 1. *Orthosphaeridium* sp. Sylvan Shale (Ashgillian), U.S.A. Shows median equatorial split.

Fig. 2. *Orthosphaeridium* sp. Sylvan Shale (Ashgillian), U.S.A. Shows the thick wall with plugs at base of spines.

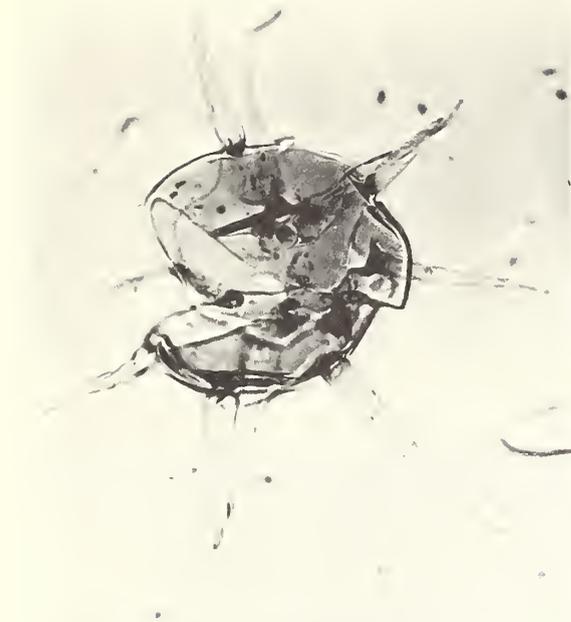
Fig. 3. *Tasmanites* sp. Bailey Formation (Lower Devonian), U.S.A. Shows thick perforated wall with split developing.

Fig. 4. *Pterospermopsis* sp. Bailey Formation (Lower Devonian), U.S.A. Shows equatorial alae.

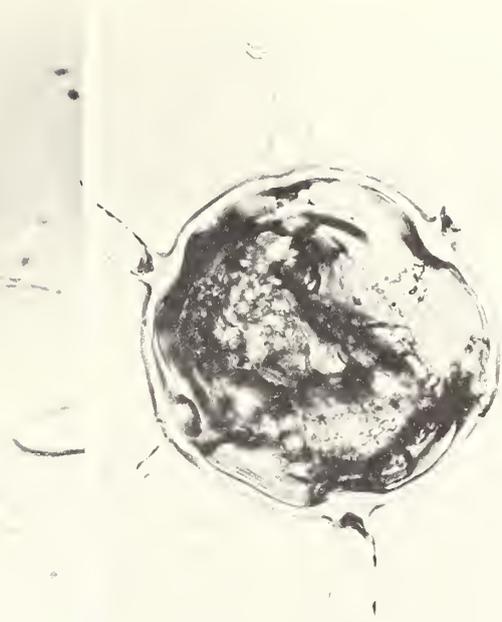
Fig. 5. ?*Tasmanites* sp. Sexton Creek Formation (Silurian), U.S.A. Shows large cyclopyle with rim.

Fig. 6. *Arenoricanicum* sp. Sylvan Shale (Ashgillian), U.S.A. Opening is through large process at the upper end.

Fig. 7. *Bacisphaeridium* sp. Caradoc, England. Single process shows constriction common in *Baltisphaeridium* group of acritarchs.



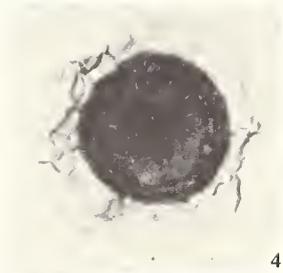
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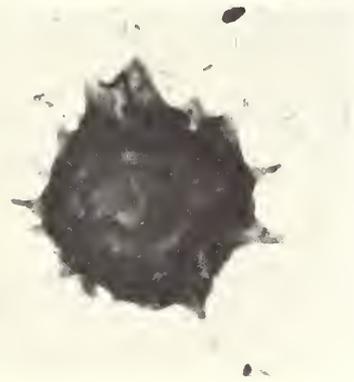
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(c) *Orthosphaeridium* type. This is characterized by its median split. Only the genera *Orthosphaeridium* (Pl. 26, figs. 1, 2) and *Actipilion* can be placed here so its range is confined to Middle and Upper Ordovician.

(d) *Goniosphaeridium* type. This is characterized by the body shape which tends to be polygonal, being formed by the fusion of the process bases. No openings are found (except possibly a cyclopyle in *Pulvinosphaeridium*). It includes the genera *Goniosphaeridium* and possibly also *Pulvinosphaeridium* and *Estiastra*. It would then range from Middle Ordovician to Ludlow.

The *Baltisphaeridium* group differs from the *Tasmanitid* group mainly by the possession of strong ornament. It is therefore probable that they both belong to the same class of algae.

#### 5. *Navifusa* group

*Navifusa* and *Leiovalia* are elongated acritarchs without spines. They rarely show excystment structures but cyclopyles are possibly present in a few species. The wall ultra-structure is unknown.

At present the only feature associating them with the other groups so far described is the presence of the cyclopyle.

#### 6. *Sphaeromorph* acritarchs

The previous five groups have features indicating relationship to the class Prasinophyceae. The only other acritarchs having such characters are a few species included in the smooth, round genus *Leiosphaeridia*. This genus was defined by Eisenack (1954) who distinguished it from *Tasmanites* by its simple wall structure. Both have cyclopyles.

Several species in which the excystment opening is rarely or not at all developed have been put in *Leiosphaeridia*, although there is no evidence of the way in which they open. The affinities of such forms poses a difficult problem since the structure is featureless, consisting solely of a more or less smooth round pellicle.

At the present time it is not possible to constructively review the content of the sphaeromorph group, which includes about 120 generic names. However, it is clear on the basis of excystment mechanism that some are related to the Prasinophyceae; others, like *Chytroesphaeridium*, have been classed with the dinoflagellates. A great number remains, some of which have been compared with Chlorophyceae and other algal classes, but the grounds for doing so are slender.

The sphaeromorphs appear in the Precambrian where they are extremely abundant, particularly in the Upper Proterozoic. Their widespread occurrence suggests they are marine, their morphology that they are spores. Beyond this there is little positive evidence about their nature. They have been classified into genera mainly on slight differences of surface ornament (some of which may have been diagenetically introduced), on size which ranges from 5 to 500  $\mu$  and on various obscure structures like rims, folds, and openings.

Many are found in associations, the most complete being compressed spherical groups of hundreds of individuals.

The openings are unknown until the Lower Cambrian where several uniporate and multiporate forms have been recorded (Pychova 1969). These openings appear to be irregular in shape and size and their biological meaning is not clear.

The sphaeromorphs decline in numbers from the Lower Cambrian onwards. By the Ordovician they have become a minor element in most palynological assemblages but occasionally dominate in certain facies. The decline continues until by the Devonian there are relatively few forms that need to be placed in the biologically unclassifiable sphaeromorphs.

Here the group is treated as primitive and polyphyletic, probably including ancestral forms of other algal groups represented among the acritarchs. The cluster habit supports this view. It is a habit persisting in the microhystria, diacrodians, baltisphaerids, and leiofusids as late as the Tremadoc or Arenig and in the leiospheres to the Upper Silurian.

#### 7. The *Micrhystridium-Veryhachium* group

This group characteristically has a spinose body with a simple wall structure: excystment is by epityche or cryptosuture (small circle epityche). Additional features are the size of the body, which is usually small, and the free extension of the body cavity into the processes.

Some members of the group are very similar to the cysts of the living *Peridinium* and naked dinoflagel-

lates (Wall and Dale 1968). It is quite possible that the affinity of the group is with the dinoflagellates (Lister 1970b).

The group ranges in time from the Cambrian possibly to Recent sediments. Its abundance in favourable facies of the Mesozoic equals that in the Palaeozoic.

#### 8. The *Leiofusa* group

This group is in many ways similar to the *Micrhystridium-Verhachium* group, differing in its elongate body shape. Opening is by splitting (lateral or median) or flap-epityche (C-shape). Deformation of the body sometimes makes recognition of the type of opening difficult.

Included in the group are several genera of somewhat disparate morphology, e.g. *Deunffia*. The range is from Cambrian to Tertiary with a clear acme in the Silurian-Devonian.

There is no direct evidence of their affinity but structurally they are similar to the *Micrhystridium-Verhachium* group with which they are often associated. Relationship to this group is likely in several instances at least.

#### 9. The *Acanthodiacrodian* group

This group is characterized by its simple wall structure, its elongate body shape, and the polarity of its ornament. There does not appear to be a consistent method of opening, but splitting does occur along clear lines and there are indications of a wall structure of plates bounded by sutures (Lister 1970a).

The possession of a tabular wall structure is reminiscent of the cysts of tabulate dinoflagellates.

The group ranges in age from Lower Cambrian to Llanvirn and possibly later. There is a clear acme around the Cambro-Ordovician boundary.

#### 10. The *Visbysphaera* group

Members of this group open by a cryptosuture (small-circle epityche) and have a greater or less tendency to develop an inner cyst.

It is convenient (although not perhaps justifiable on biological grounds) to subdivide them.

(a) *Visbysphaera* type. This type is rarely found without an inner cyst. The wall is therefore nearly always double (Pl. 27, fig. 5), the inner layer being relatively thick with a smooth surface, the outer layer thinner and extending outwards to form processes (usually hollow). Some individuals closely resemble dinoflagellate cysts particularly of the chorate group (mostly gonyaulacid types), e.g. *Hystrichosphaeridium*, *Cleistosphaeridium*.

Included here are the genera *Daillydium*, *Dilatissphaera*, and *Cymbosphaeridium*. Its range in time is restricted from the Silurian to the Carboniferous with a clear acme in the Upper Silurian/Lower Devonian.

(b) *Triangulina* type. This type is similar to the above, but has a triangular body (Pl. 27, fig. 4). It includes also *Ozotobrachion* and *Onondagella*.

(c) *Diexallophasis* type. In this type (Pl. 27, fig. 6) an inner cyst is only infrequently developed. In addition the processes are inclined to have small excrescences and a peculiar type of digitate terminal branching. It includes also *Florisphaeridium* and *Evittia*. Its range is confined to the Silurian and Lower Devonian.

The similarity of some species to dinoflagellate cysts indicates the possibility of a relationship. The evidence is as yet rather superficial and inconclusive.

#### *Other acritarchs*

The above groups include over 90% of the described acritarch species and genera. The remainder are not included either because there is not enough evidence about wall structure and opening, e.g. *Polyedryxium*, or because they do not fit into any of the categories established, e.g. *Duvernaysphaera* and *Quadraditum*.

### THE ACRITARCH SUCCESSION

The tentative relationships expressed in the groups described above, when considered against the background of the geological time scale, permit the consideration of possible evolutionary trends. This is displayed on text-fig. 1. Several stages can

be recognized, each in succession being marked by assemblages characteristic of the period.

*Period 1.* This is in the Precambrian where, following an early phase of very fragmentary records, there is from about 1000 million years to the base of the Cambrian an abundant record of sphaeromorphs. These simple types cannot be assigned to any particular algal group because they have not yet evolved any differentiation of wall structure or developed any distinctive ornament. They tend to occur in clusters, and are probably spores of larger marine algae. This basic, primitive, and probably heterogeneous stock begins to show pronounced ornament near the Cambrian base and in the next period clear differentiation is possible.

*Period 2.* In the Lower Cambrian four innovations are found. There is the development of short spines with the appearance of *Micrhystridium*, the appearance of crests (?alae) in *Cymatiosphaera* (their structure needs closer investigation), the development of processes with a closed base in species currently classified as *Baltisphaeridium* (these Lower Cambrian species also require detailed investigation to determine their relationship to typical Ordovician *Baltisphaeridium*), and there is the development of polarity in *Leiofusa* and *Lophodiacrodium*. Thus from the Cambrian onwards the acritarchs include both prasinophycean and possible dinoflagellate groups.

The tendency to occur in clusters persists, but no opening styles have yet been clearly developed, although *Uniporata-Polyporata* are present.

*Period 3.* The Upper Cambrian is marked by the flourishing of the *Acanthodiacrodium* and *Priscogalea* groups. *Tasmanites* also appears and the macropyle opening is a common feature.

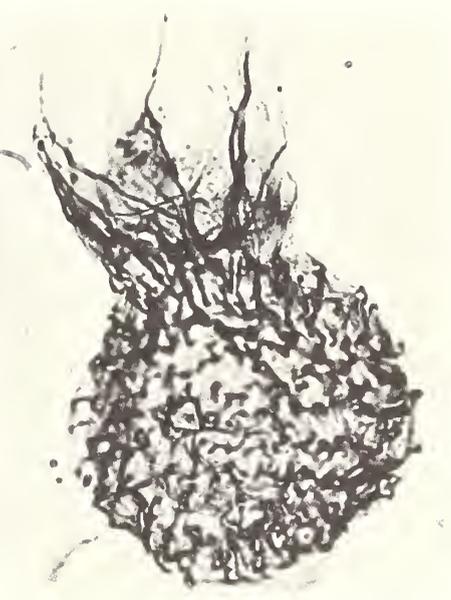
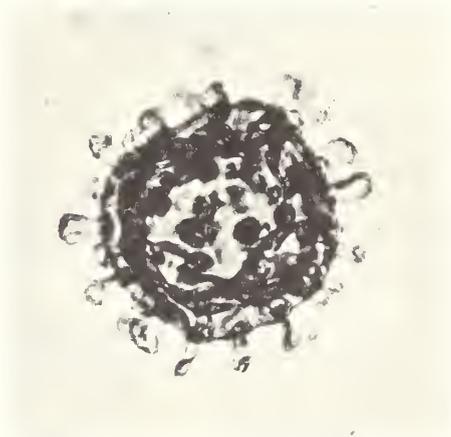
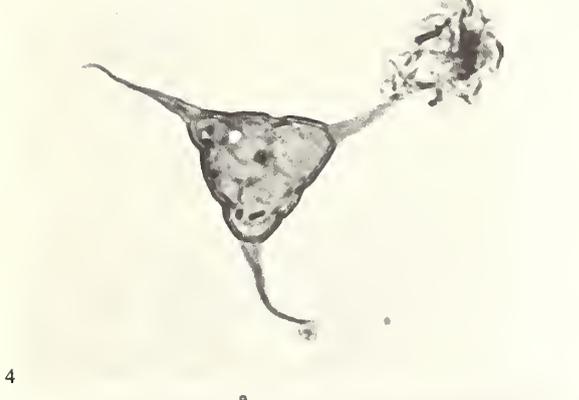
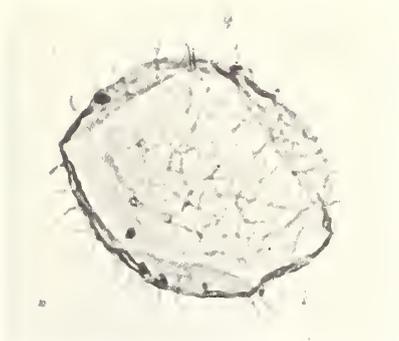
*Period 4.* In the Arenig the most striking feature is the increase of typical *Baltisphaeridium* types and the development of differentiates of the *Acanthodiacrodium* group which is now waning. *Veryhachium* appears in force in a rather simple form. The Upper Ordovician is distinguished by the abundance of *Baltisphaeridium* and its derivatives.

*Period 5.* In the Silurian the Baltisphaerids die out, and are replaced after a short interval by the *Diexallophasis* type. During the Lower Silurian, which is dominated

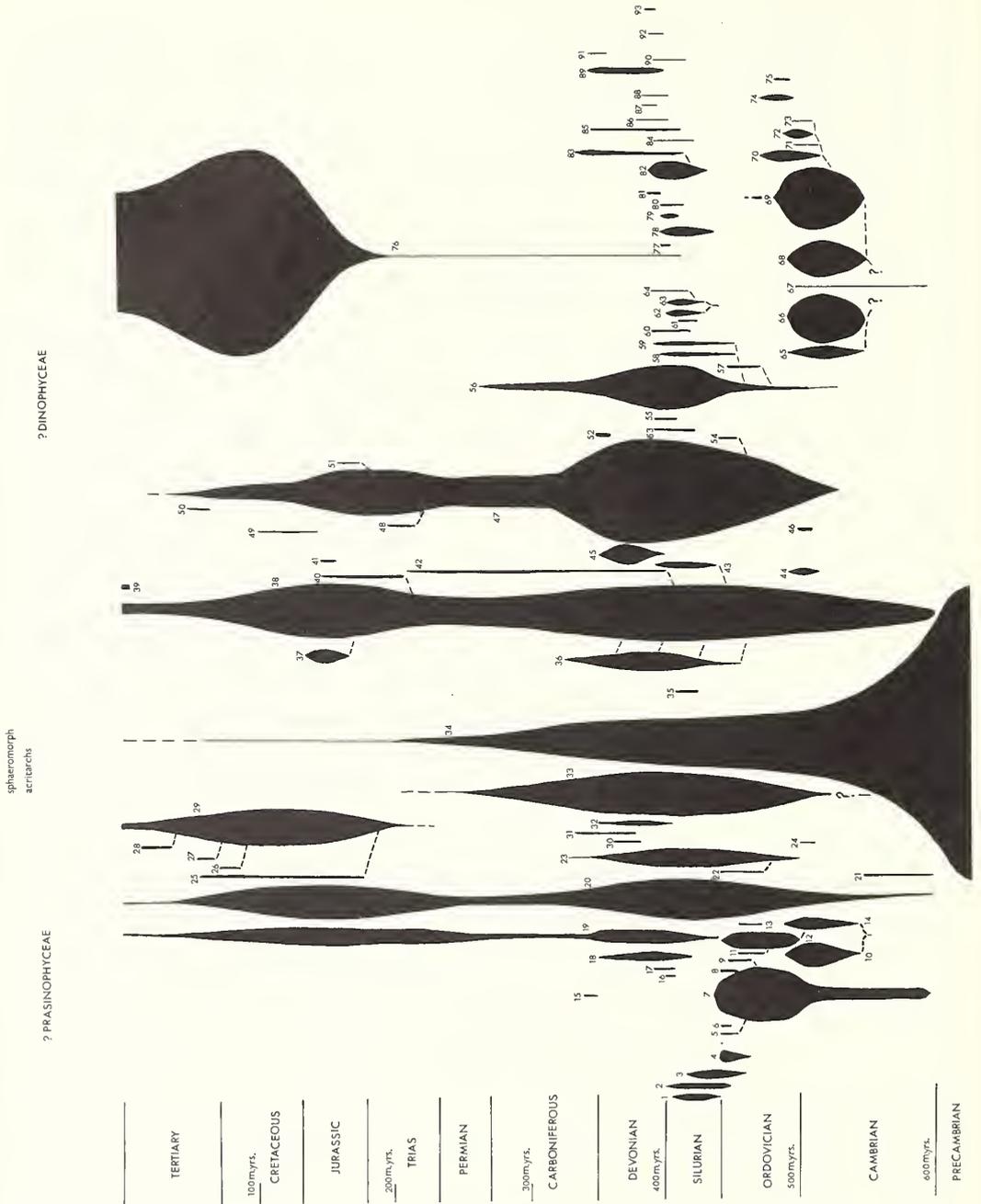
EXPLANATION OF PLATE 27

All figures  $\times 1000$

- Fig. 1. *Multiplicisphaeridium* sp. Bailey Formation (Devonian), U.S.A. Single walled acritarch.  
 Fig. 2. *Domasia* sp. Buildwas Beds (Silurian), England. Single walled acritarch.  
 Fig. 3. *Ammonidium* sp. Bailey Formation (Devonian), U.S.A. Shows complete sub-equatorial epitache development.  
 Fig. 4. ?*Triangulina* sp. Bailey Formation (Devonian), U.S.A. Shows double walled structure.  
 Fig. 5. *Visbysphaera* sp. Wenlock Shales (Silurian), England. Shows double walled structure.  
 Fig. 6. *Diexallophasis* sp. Neahga Shales (Silurian), U.S.A. A form with no inner body.  
 Fig. 7. ?*Geron* sp. Neahga Shales (Silurian), U.S.A. A form related to *Tunisphaeridium* and *Carminella*, but difficult to classify.



DOWNIE, Silurian and Devonian acritarchs



TEXT-FIG. 1. Possible relationships among the acritarchs.

The width of the columns is approximately proportional to the number of species described from a given period. The horizontal arrangement is indicative of possible relationship. Not all genera are included partly because of synonymy problems and partly because of classification difficulties. The numbers refer to generic names as follows:

- Baltisphaerid group:  
 1, *Estiastra* 2, *Pulvinosphaeridium* 3, *Gontosphaeridium* 4, *Orthosphaeridium* 5, *Axisphaeridium* 6, *Actipilion* 7, *Baltisphaeridium* 8, *Bacisphaeridium* 9, *Arenoricanicum* 10, *Priscogalea* 11, *Asketopalla* 12, *Peteinosphaeridium* 13, *Polyaucystrodorus* 14, *Cymatiogalea*.
- Pterospermopsis group:  
 15, *Tornacia* 16, *Sol* 17, *Helios* 18, *Duvernaysphaera* 19, *Pterospermopsis* 20, *Cymatiosphaera* and *Dictyotidium* 21, *Retisphaeridium*.
- Navifusa group:  
 22, *Leiovalia* 23, *Navifusa* 24, *Lunulida* 25, *Crassosphaera* 26, *Pleurozonaria* 27, *Noremia* 28, *Cooksoniella* 29, *Tasmanites-Pachysphaera* 30, *Quisquelites* 31, *Tapajonites* 32, *Maranhites* 33, *Tasmanites*.
- Sphaeromorph group:  
 34, *Sphaeromorph acritarchs*.
- Microstridium-Veryhachium group:  
 35, *Piliferosphaera* 36, *Multiplicisphaeridium* 37, *Solisphaeridium* 38, *Microhystridium* 39, *Creberlumectum* 40, *Filisphaeridium* 41, *Comasphaeridium* 42, *Buedingsphaeridium* 43, *Elektroriskos* 44, *Vulcanisphaera* 45, *Polyedrixium* 46, *Impluviculus* 47, *Veryhachium* 48, *Staplinium* 49, *Prismatocysta* 50, *Hidasia* 51, *Metaleiofusa* 52, *Unellium* 53, *Neoveveryhachium* 54, *Sylvanidium*.
- Leiofusa group:  
 55, *Anthractacus* 56, *Leiofusa* 57, *Disparifusa* 58, *Poikilofusa* 59, *Eupoikilofusa* 60, *Dactylofusa* 61, *Baiomeniscus* and *Holothurodiagna* 62, *Deumiffia* 63, *Domasia* 64, *Hemibaltisphaeridium*.
- Diacrobian group:  
 65, *Trachydiacrodium* 66, *Lophodiacrodium* 67, *Ooidium* 68, *Dasydiocrodium* 69, *Acanthodiacrodium* 70, *Tectitheca* 71, *Polygonium* 72, *Priscotheca* 73, *Arbusculidium* 74, *Dicrodiacrodium* 75, *Schizodiacrodium*.
- Dinoflagellate group:  
 76, Dinoflagellate cysts.
- Visbysphaera group:  
 77, *Percultisphaera* 78, *Diexallophasis* 79, *Florisphaeridium* 80, *Helosphaeridium* 81, *Evittia* 82, *Visbysphaera* 83, *Gorgonisphaeridium* 84, *Cymbosphaeridium* 85, *Ammonidium* 86, *Triangulina* 87, *Ozotobracion* 88, *Onodagella* 89, *Eisenackia* and *Crameria* 90, *Dilatitsphaera* 91, *Daillyidium* 92, *Leoniella* 93, *Fimbrialogmerella*.

Connecting lines indicate close relationship.  
 The width of the columns roughly represents the number of species recorded from the appropriate period.

by the *Micrhystridium-Verhachium* group, there is a progressive enrichment of the assemblages by the appearance of many new forms belonging to the *Visbysphaera*, *Leiofusa*, and *Micrhystridium-Verhachium* groups. This enrichment continues into the Upper Silurian and Lower Devonian. *Arpylorus*, an Upper Silurian form with an archaeopyle, is commonly considered to be a dinoflagellate.

*Period 6.* The Devonian begins with rich assemblages, but there is considerable change in this period. The *Visbysphaera* group declines, but is represented by a few forms very like dinoflagellates, e.g. *Dilatisphaera* and '*Hystrichosphaeridium*'. *Leiofusa* types become rarer and are reduced mainly to simple forms. The *Verhachium-Micrhystridium* group becomes dominant by Middle Devonian and produces novel forms like the spinose *V. rosendae* group. The Middle and Upper Devonian assemblages are also enriched by *Polyeduxium* and *Senziella*, possibly derivatives from a *Verhachium* stock.

*Period 7.* This period begins with the Carboniferous and continues into the Triassic. It is marked by a great paucity of all organic walled plankton, following a rapid decline in the Carboniferous. In the Permian a few species of the *Verhachium-Micrhystridium* group account for nearly everything so far known.

*Period 8.* The period from the Upper Triassic onwards can be treated as a unit because dinoflagellates clearly of the peridinoid and gonyaulacoid stocks dominate the marine organic-walled microplankton. The acritarchs, however, persist and during the Middle Jurassic there is even a late flourishing of *Micrhystridium*. The *Pachysphaera* group appears in the Lias and several new derivatives are known in the Cretaceous and Tertiary. *Pterospermopsis* and *Cymatiosphaera* are commonly found.

The first fresh water forms appear in the Quaternary.

#### CONCLUSIONS

Although some idea of the natural affinities and evolution of the acritarchs can be gained by a review of the evidence currently available, it is not enough to obviate radical errors in classification such as have occurred in the past. For this reason the informal groupings should be retained, if found useful, while more data are gathered.

Already, however, it is evident that there are two main divisions of the acritarchs, both arising from primitive Precambrian stocks. One of these is related to the prasinophycean algae, the other possibly to dinoflagellates.

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C. DOWNIE  
Department of Geology  
The University  
Sheffield



# THE PALAEOENVIRONMENT OF THE ABBOTSBURY IRONSTONE (UPPER JURASSIC) OF DORSET

by M. E. BROOKFIELD

**ABSTRACT.** The Abbotsbury Ironstone represents a rare sandy facies of the Lower Kimmeridgian in Britain. Palaeoecological studies show that it consists of three facies deposited in an offshore beach or barrier bar environment. The main control on the fauna is thought to be the degree of water agitation.

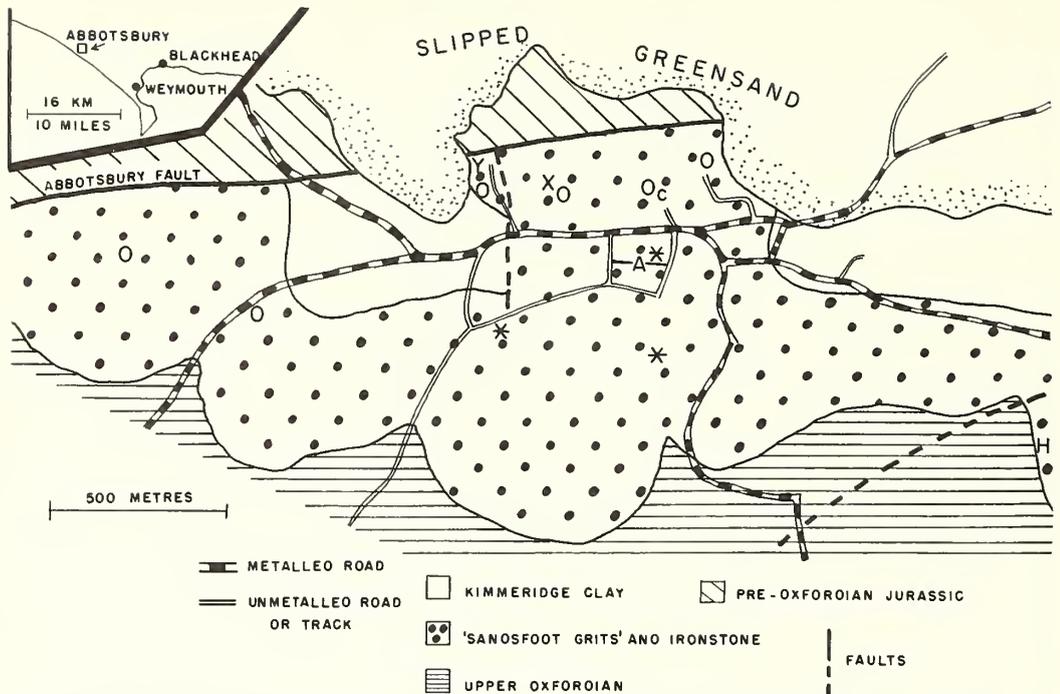
THE Abbotsbury Ironstone consists of a sequence of limonite-oolitic sandstones, about 8 m thick. It is restricted to a small area around the village of Abbotsbury, Dorset (text-fig. 1), and apparently passes rapidly into clays less than one mile east of Abbotsbury. The outcrop is bounded on the north and west by a fault, and to the south by a seaward-facing scarp. It is the most westerly outcrop (on land) of Kimmeridgian in England, being 13 km west of the nearest known outcrop at Weymouth.

The Abbotsbury Ironstone is underlain by a 7-m-thick sequence of ferruginous sandstones (Sandsfoot Grits of Arkell, 1936). The junction of these with the ironstone is transitional. Neither the upper boundary of the ironstone, nor the lower boundary of the sandstones have ever been recorded at Abbotsbury. However, 4 miles NNW. of Abbotsbury, at Litton Cheney, Cope (1971) recorded 6-7 ft of limonite oolite, lithologically identical to the Abbotsbury Ironstone. This was overlain by 'yellowish clayey glauconitic sand' containing a large nodule which yielded a rich bivalve, gastropod, brachiopod, and ammonite fauna. The ammonites, as at Abbotsbury, were *Rasenia* sp. and *Prorasenia* sp. indicative of the Cymodoce Zone (Cope *in litt.*, 1971). The nodule is lithologically identical to the ironstone below, suggesting that the 'glauconitic sand' is merely leached ironstone. The fauna suggests facies C<sub>1</sub> of the ironstone (see below) though containing a more diversified bivalve and gastropod assemblage.

The ironstone was initially considered to be Upper Oxfordian (Corallian) in age (Strahan 1898), but later work showed it to be Kimmeridgian (Arkell 1933, 1936). It represents a rare exposure in Britain of a sandy facies of the Lower Kimmeridgian. Ammonites, *Rasenia* spp. and *Prorasenia* sp., indicate that the ironstone is confined to the Cymodoce Zone.

The natural exposures are poor and few; but in late 1966 a sewer-pipe trench exposed an almost complete section of the ironstone (loc. A, text-figs. 1, 2). This and other shallower excavations provided fresher and more fossiliferous material than now available from the natural exposures. All fossils in the natural exposures, and most in the excavations are leached. Collections of material are at present deposited in the Sedimentology Research Laboratory, Reading.

The ironstone has formerly been described from a stratigraphic and economic aspect by Blake and Hudleston (1877), Strahan (1898), Arkell (1933, 1936, 1947),



TEXT-FIG. 1. Geological map of the Abbotsbury area. Inset shows location and other exposures of Lower Kimmeridgian sediments. Letters, A, C, H, X, Y, are localities cited in text. Loc. A is in the centre of Abbotsbury village.

Open circles: areas with subfacies  $C_2$ .

Asterisks: areas with subfacies  $C_1$ .

Lamplugh *et al.* (1920), and Wilson *et al.* (1958). The purpose of this paper is to show the contribution that palaeoecological studies can make to the understanding of the depositional environment of oolitic ironstones; despite the wealth of sedimentological investigations on ironstones their faunas have been relatively neglected.

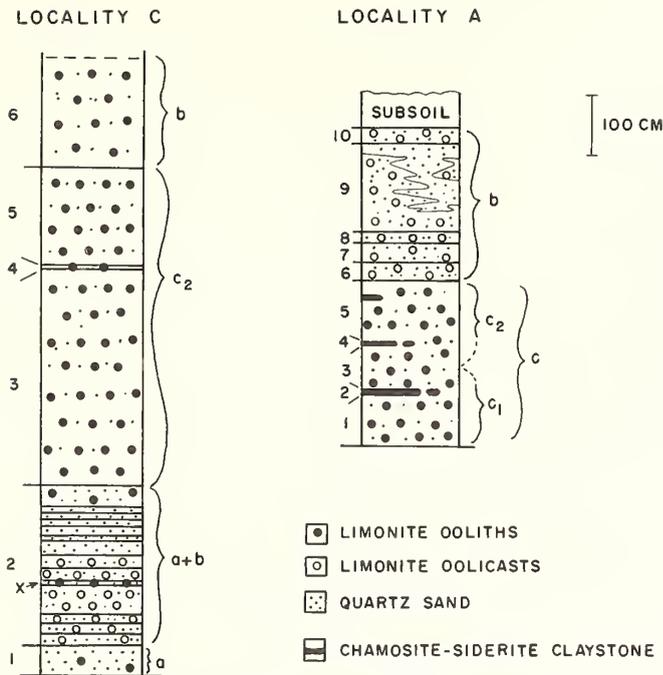
#### SEDIMENTS

The Abbotsbury Ironstone and associated Sandsfoot Grits can be divided into three main lithofacies, which are discussed in detail below.

- A. Medium-bedded, moderately well sorted, bioturbated, fine-grained quartz sandstone.
- B. Thin-bedded, poorly sorted to moderately well sorted, fine-grained quartz sandstone.
- C. Massive, poorly sorted, limonite-oolitic fine-grained quartz sandstone.

The vertical distribution of these facies in the main exposures is shown on text-fig. 2.

The ironstone and underlying Sandsfoot Grits consist essentially of three constituents; chamosite clay, medium- to fine-grained quartz sand, and limonite oolites. The differences in lithofacies are mainly due to differences in proportion of these



TEXT-FIG. 2. Sections of the Abbotsbury Ironstone. Bed nos. on left of columns, facies on right.

Loc. C

1. Reddish-purple, sparsely limonite-oolitic fine-grained quartz sandstone.
2. Irregularly thin-bedded, oolitic fine-medium-grained quartz sandstone. At X is the lowest stratigraphic occurrence of ammonites; *Rasenia* spp. and *Prorasenia* sp. of lower Cymodoce zone.
3. Massive, limonite oolitic fine-grained sandstone.
4. Thin parting as 3, with abundant *Aulacothyris dorsetensis*.
5. As 3, but getting less oolitic towards top.
6. Limonite-oolitic fine-grained quartz sandstone (less oolitic than 3) passing up into non-oolitic leached sand.

Loc. A

1. Reddish-purple limonite oolitic fine-grained sandstone.
2. Hard concretionary chamosite-siderite mudstone with sparse limonite oololiths.
3. As 1.
4. As 2.
5. As 1, oolith content variable.
6. Limonite-oolitic fine-grained sandstone, with concretionary limonite veins.
7. Limonite oolitic fine-grained sandstone, with abundant fossils.
8. As 7, with abundant ammonites.
9. Sparsely oolitic sandstone and leached, non-oolitic sand.
10. Limonite oolitic, fine-grained sandstone. Highest stratigraphic occurrence of ammonites, *Rasenia* spp. (transitional to *Aulacostephanus*), of upper Cymodoce zone.

three constituents. The sand grains are dominantly of sub-angular to sub-rounded strained quartz (always greater than 80% of the quartz sand fraction). A few sand grains show sutured grain contacts characteristic of metamorphic textures. Silt-sized particles are rare.

The most obvious diagenetic change is oxidation and leaching of the ironstone, probably at outcrop. This, however, has not altered the relative proportion of the major primary sedimentary constituents, quartz sand, clay, and limonite oolites. The preservation of fossil moulds and uncrushed empty inner whorls of ammonites with their lappets preserved show that little if any compaction of the sediment has occurred. Even in the rare chamositic sideritic mudstone bands of facies C uncrushed shells indicate little compaction, and thus early growth of siderite and ferroan calcite cements in these bands is indicated.

Heavy mineral analysis, after hot hydrochloric acid treatment, of five samples from the base to the top of the composite Sandsfoot Grit-Abbotsbury Ironstone sequence showed the following in order of abundance: zoned zircon, tourmaline, staurolite, and garnet; with minor amounts of rutile, epidote, tremolite, and kyanite. Only zircon, a brown variety of tourmaline and epidote showed much rounding. All others were distinctly angular. There is no obvious variation in the heavy minerals between samples.

Both light and heavy minerals suggest that the sediments have not been extensively recycled, and can hence be used as indicators of the original source of the sediments. The light minerals show derivation from a tectonically deformed area. The heavy minerals indicate a source including metamorphic rocks. The most likely source is north-west France (Boswell 1924; Neaverson 1925), the sediments being carried from this area by a river occupying the western approaches of the English Channel (cf. Davies 1969; Wilson 1968). Despite the evidence from clay mineral studies (Cosgrove and Salter 1966), there is no evidence from the light and heavy minerals of derivation from south-west England (and the clay mineral distributions, at least in the Upper Oxfordian-Lower Kimmeridgian, are not as simple as Cosgrove and Salter indicate). This could either be due to lack of drainage from south-west England, or more likely, in view of the occurrence of Oxfordian and Kimmeridgian sediments in the Bristol Channel (Donovan 1971), the south-west England area was covered by a shallow sea. If the interpretation of the Abbotsbury sediments as subtidal barrier bar deposits is correct, they would separate a deeper basin towards the south-east from a hypothetical lagoonal area to the north-west.

#### FAUNA

The Abbotsbury Ironstone fauna (Table 1) is taxonomically dominated by bivalves, though in facies C brachiopods are numerically more abundant. The fauna can be closely compared ecologically with that of the Frodingham Ironstone (Hallam 1963).

Arkell (1936) stated that the Abbotsbury Ironstone had a specialized fauna. However, most of the bivalves and gastropod species are the same as those found in the equivalent Cymodoce Zone strata at Weymouth, and are either identical or allied to species of the underlying Upper Oxfordian. The brachiopods *Aulacothyris*

TABLE 1. Invertebrate fauna of Abbotsbury Ironstone, inferred feeding and ecological type, and facies distribution.

SPECIES	ECOLOGY	FACIES
<b>Brachiopoda</b>		
? <i>Septaliphoria hudlestoni</i> (Rollier)	ATTACHED EPIFAUNAL	c
' <i>Terebratula</i> ' <i>subsella</i> (Leymerie)	SUSPENSION	c
<i>Ornithella lampas</i> (J. Sowerby)	"	c
<i>Aulacothyris dorsetensis</i> (Davidson)	"	bc
<i>Lingula</i> sp.	INFAUNAL SUSPENSION (1)	abc
<b>Echinodermata</b>		
<i>Nucleolites scutatus</i> (Lamarck)	SHALLOW INFAUNAL (2)	b
<b>Bivalvia (3)</b>		
<i>Ostrea grypheata</i> De Loriol	ATTACHED EPIFAUNAL (4)	b
<i>Exogyra nana</i> (J. Sowerby)	SUSPENSION	bc
<i>Modiolus</i> sp.	"	b
<i>Gervillia</i> ? <i>aviculoides</i> (J. Sowerby)	"	bc
<i>Trigonia reticulata</i> Agassiz	"	b
<i>Anisocardia globosa</i> (Roemer)	SHALLOW INFAUNAL SUSPENSION	ab
<i>Astarte ovata</i> (Wm. Smith)	"	b
<i>Pholadidea abbreviatus</i> (Blake and Hudleston) (5)	"	b
<i>Isodonta triangularis</i> (Phillips)	?	b
<i>Opis</i> ( <i>Trigonopsis</i> ) <i>corallina</i> Damon	?	b
<i>Pleuromya uniformis</i> (J. Sowerby)	DEEP INFAUNAL SUSPENSION	abc
<i>Goniomya literata</i> (J. Sowerby)	"	a
<i>Pholadomya canaliculata</i> Roemer	"	b
<i>Entolium corneolum</i> (Young and Bird)	SWIMMING EPIFAUNAL SUSPENSION	bc
<i>Camptonectes auritus</i> (Schlotheim)	"	bc
<i>Chlamys</i> aff. <i>midas</i> Damon	"	ab
<i>Velata</i> sp.	EPIFAUNAL SUSPENSION	bc
<b>Gastropoda</b>		
<i>Bathrotomaria</i> spp.	EPIFAUNAL ?HERBIVOROUS (6)	bc
<i>Dicroloma</i> sp.	?	bc
<i>Chemnitzia</i> sp.	?	bc
' <i>Natica</i> ' sp.	?	bc
<i>Amberlya</i> sp.	?	bc
<b>Cephalopoda</b>		
<i>Rasenia</i> spp.	NEKTONIC ?CARNIVORE	bc
<i>Paracenoceras calloviense</i> (Oppel)	"	b
<b>Annelida</b>		
<i>Serpula</i> spp.	ATTACHED EPIFAUNAL SUSPENSION (7)	bc

References are as follows: (1) Craig 1966, (2) Durham 1966, (3) Purchon 1968, (4) Yonge 1960, (5) Turner 1954, (6) Morton 1967, (7) Dales 1967.

*dorsetensis* and *Ornithella lampas* have been recorded in a Cymodoce Zone limestone at Cambridge, as has '*Terebratula*' *subsella* under the genus *Loboidothyris* (uncatalogued material in Sedgwick Museum, Cambridge). The only species that is unique to the ironstone is ?*Septaliphoria hudlestoni*, whose asymmetric variants have often been mistakenly recorded as *Torquirhynchia* [*Rhactorhynchia*] *inconstans*.

No microfauna was detected, probably due to the post-depositional leaching, and trace fossils are mainly confined to vague mottlings seen in some mudstone beds.

Each facies has its own faunal assemblage, with little sign of intergradation.

Fossils are generally rare, except in certain beds of facies B and lenses in facies C (see p. 269). The individual facies faunas are considered to be dominantly life assemblages because:

1. Few shells are broken: those that are belong to fragile types, e.g. occasional *Entolium*, *Nucleolites*, tall-spined gastropods.
2. Most of the bivalves are still articulated.
3. None of the shells show signs of wear.
4. Many of the burrowing forms are in life position (e.g. *Pleuromya*) and in some cases even the epifauna is in place (brachiopod 'nests', serpulids, and oysters in facies C).
5. Individual facies faunas pass very rapidly laterally into each other, e.g. facies C into B over a distance of less than 30 m.

The above points indicate very little disturbance of the fauna. The main exception is the breakage of *Chlamys* valves in facies A, which is considered to represent the most turbulent environment.

The inferred mode of life of each member of the ironstone invertebrate fauna is shown in Table 1. The percentage distribution of types in each facies is shown in text-fig. 3.

#### DEPOSITIONAL ENVIRONMENT

All the facies accumulated in a somewhat restricted range of environments, in which the wave turbulence was sufficient to move fine- to medium-grained quartz sand and generally keep clay in suspension, but insufficient to move or wear shells much, and incompetent to move sediment coarser than medium-grained sand. This is shown by the general absence of penecontemporaneous pebbles, which are frequently common in ironstones. Small clay pebbles are confined to rare occurrences in facies A.

Within this environmental framework, several higher and lower energy environments can be distinguished. These are based mainly on the fauna, but in part on the proportion of clay to sand, and the sorting characteristics of the sediment. The differences between environments is ascribed to differences in mean turbulence, and

FACIES		(a)	(b)	(c)	
SUBFACIES				2.	1.
NUMBER OF PRESERVED BENTHIC SPECIES		5	21	12	6
%	EPIFAUNA	20	42	50	100
%	INFAUNA	80	29	17	0
%	UNKNOWN	0	29	33	0

TEXT-FIG. 3. Percentage of each ecological type in each facies.

thus by implication, depth. Variations in salinity and temperature as environmental controls are unlikely in view of the rapid lateral facies transitions. At least in facies C faunal differences cannot be attributed to substrate differences, and the range in grain size is insufficient to account for the pronounced faunal differences between facies.

*Facies A.* Medium-bedded, moderately well-sorted, bioturbated, fine-grained quartz sandstone.

This forms the major part of the ferruginous sandstones (Sandsfoot Grits) below the ironstone at localities H and C (text-fig. 1). The bedding units are of the order of 1 m. The sandstones are fine- to medium-grained and contain up to 5% of limonite ooliths, from which the iron is usually leached forming oolitic casts (Pettijohn 1957: although oolimoulds would be a more accurate term). Where the sparse interstitial matrix has survived leaching and oxidation it is a chloritic, chamositic, and/or sideritic clay. Extensive bioturbation is present in most beds.

Considering the evidence for a turbulent environment (see below), much of the clay may have been introduced by bioturbation after relatively rare periods of clay deposition.

The macrofauna is sparse, consisting of deep and shallow burrowing suspension feeders and epifaunal suspension feeders (Table 1). In some beds the bioturbation takes the form of indistinct mottling indicating extensive biogenic reworking by deposit feeders. No recognizable ichnogenera occur. This bioturbation does not disturb the deep burrowing macrofauna, nor a few  $\frac{1}{2}$ -cm-diameter tubes which, in one bed, penetrate to 25 cm from the top of the bed: this possibly represents an additional non-preserved suspension feeder. Thus deposit feeding apparently predated suspension feeding in these beds. No adjustment of the burrowers to erosion and deposition can be traced, due to the lack of any preserved primary sedimentary structures (though this was not confirmed with X-ray studies).

The thick sedimentary units of this facies (average 1 m) appear to have been deposited fairly rapidly; there are no identifiable fossil fragments in the lower parts of the beds; bioturbation is often extensive throughout with no sign of internal partings; identifiable trace fossils all extend down from the tops of the beds; and the deep-burrowing bivalves (*Pleuromya*) are *in situ* and at a constant horizon below the tops of the beds. The shallow burrowing and surface-living species (*Chlamys*, *Anisocardia*) are disarticulated, but only *Chlamys* is usually damaged: this indicates merely reworking of the top few centimetres of the bed, with little transport. The presence of epifaunal bivalves possibly capable of swimming (*Chlamys*) in the tops of the beds shows that these were the only forms capable of surviving the movement of sand at the sediment-water interface, probably by migration from one temporarily stable area to another. Simple washing in is unlikely as one would then expect them to be scattered through the beds and not consistently recur at the top of each bed.

The faunal characteristics of this facies are those of beaches or shallow subtidal areas (Rhoads 1967), where attached surface living is impossible and animals form deep burrows, both to avoid reworking and on beaches to avoid desiccation. In its grain size, heavy bioturbation, and fauna of dominantly deep burrowers this facies closely resembles the tidal sand flats of the Solway estuary, Scotland (personal

observations; see also Wilson 1967). They differ from them in the intensity of bioturbation—usually some lamination survives in the Solway, and in the type of deep burrower—the Solway species consist of motile deep burrowers, whereas the Abbotsbury species (*Pleuromya*) is a sessile deep burrower. These differences may be related to slower rate of deposition of facies A. Facies A also lacks evidence for tidal channels: however, east of the map area (text-fig. 1) an isolated exposure at Rodden (Grid. Ref. SY 590846) shows a fragmental shelly sand with reworked *Pinna* sp. which may possibly represent a basal channel lag. A possibly closer analogy is with the middle shoreface sands of Galveston Island, Texas (Davies *et al.* 1971; Bernard *et al.* 1962), which consist of fine grained, structureless, bioturbated sands deposited in 5–30 ft (1.7–9 m) of water. Thus facies A could represent either tidal or subtidal sands: a decision between these is not possible. The absence of evidence of exposure is not significant, as the Solway sediments, although continuously exposed at each low tide, also show no evidence of exposure in sections.

*Facies B.* Thin-bedded, poor- to moderately well-sorted, fine-grained quartz sandstone.

This forms the upper beds of the ironstone in all exposures, and also some of the upper beds of the Sandsfoot Grits at locality C (text-fig. 2). Individual bed units are less than 5 cm thick and contain up to 5% of limonite oolite casts. The sparse matrix is oxidized chamosite-siderite clay. No bioturbation can usually be seen.

This facies contains the most diversified fauna, both in terms of species abundance and ecological type (Table 1). The fauna consists dominantly of abundant bivalves, gastropods, and ammonites: none of these show signs of wear and the ammonites have their lappets preserved. The ecological types include deep and shallow burrowing suspension feeders, epifaunal suspension feeders and nektonic forms. Carnivores and scavengers, not recorded in Table 1, are represented by rare ichthyosaur fragments and arthropods (*Eryma* sp.).

This facies represents a quieter water environment than facies A. This is indicated by the presence of a large diverse fauna, including all the major feeding types except deposit feeders, and by the abundance of shallow burrowing and epifaunal forms. The fauna is, however, still dominated by suspension feeders. The sedimentary units are thinner, and the deep burrowers in life position are scattered vertically throughout this facies, indicating that thick units were not deposited rapidly, but that sedimentation was slow enough to allow adjustment of the burrowers to erosion and deposition, or to allow renewed colonization. Some beds show features, such as impoverished fauna and thicker bedding, transitional to facies A.

The presence of common attached epifaunal suspension feeders (*Exogyra*, *Serpula*) and motile surface feeders (? some of the gastropods) indicate a greater stability of the sediment surface than facies A. The presence of oysters and serpulids also indicate periods of non-deposition and absence of movement of the sediment surface, in order to allow colonization by these forms; although the oysters are of the cupped type enabling them to cope with a certain amount of sedimentation on reaching maturity.

It is uncertain whether the increased stability of the sediment surface was due to decreased turbulence or whether the surface was stabilized by a vegetation cover.

Some of the attachment areas of the oysters seem to indicate attachment to vegetation. The type of vegetation indicated is round, whip-like stems, approximately 2–3 mm in diameter, probably algae. Marine grasses had not evolved by the Jurassic.

The physical conditions of this facies can be summarized as: turbulence sufficient to keep clay in suspension, but insufficient to move the sand surface continually and insufficient to move shells much; deposition of thin units of sand separated by periods of non-deposition. This fits in with the poorer sorting of the sediments relative to facies A. Modern analogues of this facies are those of shallow shelf regions (Newell *et al.* 1959; Parker 1964; Purdy 1964). In view of the vertical alternation (text-fig. 2), facies B may be considered as a deeper equivalent of facies A.

*Facies C.* Massive, poorly sorted, limonite-oolitic, fine-grained quartz sandstone.

This forms the main ironstone beds. Limonite oololiths make up 40–50% of the rock by volume, with fine- to medium-grained quartz sand about 40%. The matrix is chamosite-siderite clay, up to 20%, but in several beds in the trench (loc. A, text-fig. 2) the percentage rises to 60%, and the consequent decreased porosity has preserved the clay in its original unoxidized state. Bedding is apparently absent, except for the intercalation of the clay bands.

The macrofauna is sparse and confined to a few species of brachiopods and bivalves, and occasional gastropods and serpulids (Table 1). The brachiopods tend to be concentrated in 'nests' or lenticles. 'Nests' are globose clusters of brachiopod shells, usually monotypic, and thought to be original colonial associations (Hallam 1962; Ager 1967). The Abbotsbury 'nests' consist of only one species, *Aulacothyris dorsetensis*. 'Nests' indicate that attachment areas were rare and utilized to their full potential (cf. brachiopods on New Zealand boulders, Rudwick 1962). The lack of preserved growth rings on the brachiopods, due to cast preservation, makes stunting difficult to detect: but other species, such as *?Septaliphoria huddlestoni* and '*Terebratula*' *subsella* have typically mature commissures. (Perhaps it should be noted here that *Ornithella lampas* and '*Terebratula*' *subsella* could be simply different growth stages of the same species, as the characteristic commissure of '*T.*' *subsella* does not develop until about 2 cm size, and below this their range of variation is very similar to *O. lampas*.) The reason for the small size of brachiopods forming 'nests' is probably the low food supply in a given volume of water. A large colony of small brachiopods could live in an area whose food supply was insufficient for even a small colony of large brachiopods. This correlation of size with 'nests' also disproves the idea that 'nests' are storm accumulates, as there is no reason why storm accumulates should consist only of small species.

Lenticles can be divided into two types: monotypic lenticles, and lenticles with several invertebrate species. Monotypic lenticles may represent either collapsed 'nests' or original colonial associations on the sediment surface. The latter is probably the mode of life of the curious species *?S. huddlestoni*. This never forms 'nests' but occurs in monotypic lenticles. It is much larger than *A. dorsetensis* and shows a curious variation in symmetry of the commissure. This varies from asymmetrical to the left, through symmetrical, to asymmetrical to the right. This may be a direct phenotypic response to interference with the inhalent currents consequent on a colonial mode of life. It can be contrasted with genotypic asymmetrical brachiopods,

such as *Torquirhynchia inconstans*, which is always asymmetrical either to left or right but shows no intermediate stages (cf. Ager 1967).

Lenticles with several species may either represent original colonial associations with a few exotic species, or more likely current accumulations of shells in irregularities in the sediment surface. 'Nests' and lenticles with several species are characteristic of different sub-environments of facies C.

All other faunal elements of facies C occur randomly, and are rare, except where they occur in lenticles. However, they are rarely damaged or worn and Pectinids are frequently articulated. The fauna can be used to distinguish two sub-facies.

Sub-facies 1. This occurs at the base of the ironstone in the trench (loc. A, text-figs. 1, 2) and elsewhere is restricted to the exposures shown on text-fig. 1. It passes very rapidly laterally into the second sub-facies.

The fauna consists of the brachiopods '*Terebratula*' *subsella*, *A. dorsetensis*, *O. lampas*, and ?*S. huddlestoni*; the bivalves *Entolium corneolum*, and *Exogyra* sp., and several species of serpulid worms (Table 1). The brachiopods are distributed in 'nests' (*A. dorsetensis*), monotypic lenticles (*A. dorsetensis*, ?*S. huddlestoni*), or isolated (all). Disarticulated shells are very rare. The serpulids grew on the brachiopod shells, or used them as initial attachment points. The bivalves are frequently articulated with both valves closed: the oysters, *Exogyra* sp., always have both valves together and closed. All the fossils, except where they occur in 'nests' and lenticles are rare. All forms are epifaunal suspension feeders and most are attached forms indicating breaks in sedimentation and cessation of movement of the sediment surface during which the fauna could colonize the sea floor.

This represents the environment of quietest conditions, as shown by the dominance of attached epifauna on a soft bottom. It is abnormal in that it contains no preserved infauna (even traces of burrowers) or any epifauna that contacted the sediment with their soft parts (e.g. gastropods). This is in direct contrast to the usual case in recent deposits, where an increase in mud content, related to the organic content of the sediments, allows an increase in the number of infaunal and deposit feeders. The absence of infauna could be attributed to removal of aragonitic forms by solution. This would bias the preserved fauna in favour of calcitic forms, and certainly the forms found are all calcitic, with the exception of the ammonites. But aragonitic forms are found in the lithologically identical sub-facies 2, and aragonitic forms should be detectable in sub-facies 1, if originally present, since sediment compaction is virtually absent.

The lack of infauna is associated with the presence of the brachiopod 'nests', whose formation has been ascribed to attachment of brachiopods to seaweed or sponges (Rudwick 1961; Ager 1965). The epifauna indicates normal oxidizing conditions at and above the sediment-water interface, so the infaunal absence must be due to chemical or mechanical factors within the sediment, or to faunal interactions with the epifauna. Chemical control seems unlikely, as the only signs of reducing conditions within the sediment is post-depositional pyrite within shell material; none is developed outside in the matrix, and limonite oolites have not been altered to a more reduced form or replaced by siderite or pyrite. This also does not explain the absence of such epifauna as gastropods.

Faunal interactions are possible. Zenkevitch (1963) found that in certain cases bottom deposits were suitable for colonization by infauna but that the epifauna had taken all the food supplied.

Another possibility is that mechanical factors made the bottom unfit for colonization by infauna. In view of the absence of gastropods, this is more likely. If the brachiopod 'nests' were formed by attachment to sponges, the absence of infauna can be explained. Ager and Evamy (1964, p. 334) commented on the common association of the rhyconellid *Lacunosella* and sponges in the Upper Jurassic of the French Jura (confirmed by Childs 1966). Ager (1967) figured a sponge (from Ijima 1902) with no less than sixty-nine individual brachiopods attached. Zenkevitch (1963) noted that in the Barents Sea, the bottom may contain large amounts of sponge spicules and owing to mechanical factors may become unfit for benthos. This occurs on the Kildin bank, where finely cartilaginous and sufficiently silted floors give refuge to a rich epifauna, and are almost devoid of infauna. Sponges and brachiopods are predominant in these regions. The development of other members of the epifauna are also restricted by the mass growth of sponges, since these powerful filters take all the nutrients out of the water.

This would explain the dominance of brachiopods in this sub-facies, with only a few other forms. It can also explain the curious lack of lamination without evidence for bioturbation, as decay of cartilaginous sponge spicules could cause loss of any lamination prior to shell solution. The absence of sponge spicules in the sediments is against this interpretation, but the spicules may have been leached out together with the microfauna, or the sponges may have been entirely cartilaginous.

Sub-facies 2. This lies to the north and west of sub-facies 1 and vertically above it in the trench (loc. A, text-fig. 2). It is lithologically identical to sub-facies 1. It forms the main ironstone where sub-facies 1 is absent. Faunally it is distinguished by the presence of gastropods and rarity of all brachiopods with the exception of *A. dorsetensis*. Ecologically the fauna shows an increase compared to sub-facies 1 of motile epifaunal feeders, the gastropod *Bathrotomaria*, and perhaps some of the other gastropods. In this sub-facies all the brachiopods are spread out into lenticles of the predominantly mixed type and there are no 'nests'. Gastropods of the genera *Bathrotomaria* and *Nerinea* are common. In most exposures the bivalve fauna is restricted to *Exogyra* and Pectinids (*Chlamys*, *Entolium*) with occasional *Pleuromya*, but there is a slight increase in diversity of the bivalves towards the north-west (locs. X and Y, text-fig. 1), where *Trigonia* and *Astarte* are found in this sub-facies. This may indicate a gradation in that direction into facies B.

The spreading out of the brachiopod *A. dorsetensis* together with other shells into lenticles indicates greater turbulence than sub-facies 1. This species forms the 'nests' in sub-facies 1 and the lenticles may represent shells removed from sub-facies 1 and concentrated in depressions in sub-facies 2. The occurrence of mixed lenticles tends to confirm this. The three other larger brachiopods of sub-facies 1 are absent. This is rather surprising in view of the ease with which brachiopod shells are transported (Boucot *et al.* 1958). Though others (Middlemiss 1962) have shown that brachiopods are not likely to be transported far without comminution, the absence of transport over as short a distance as 30 m indicates some sort of baffle preventing

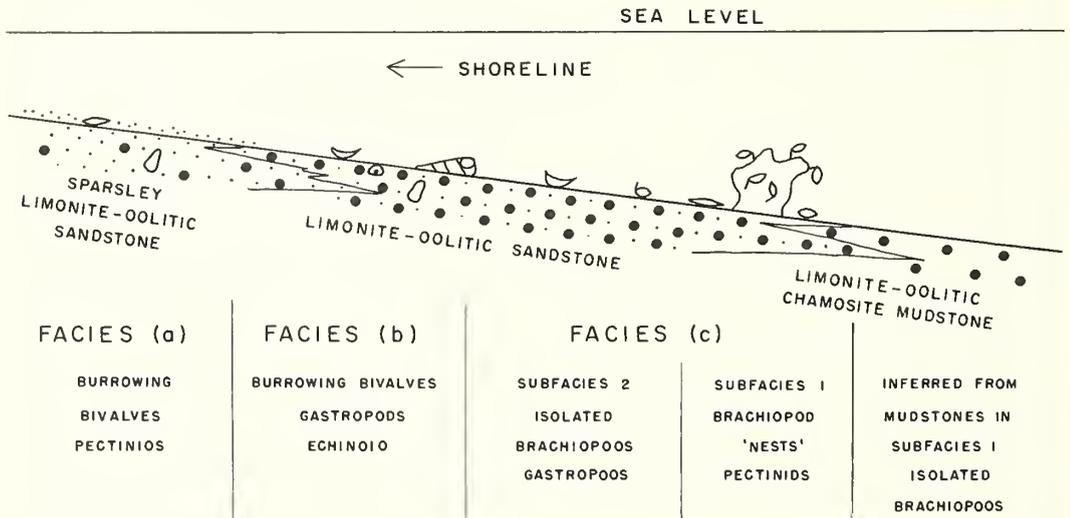
transport—such as the sponges mentioned in sub-facies 1. *A. dorsetensis* could be transported, as it lived attached to the sponges, and thus could be lifted off them.

The mode of deposition of the two sub-facies can be treated together. Both were apparently formed in an environment transitional between sand and clay deposition, thus probably at greater depth than either of the other facies.

Conditions envisaged are fairly rapid periods of deposition separated by periods of non-deposition. There was little movement of the surface after deposition, and these stable substrates were colonized by a variety of attached epifauna, intolerant of surface movement. This colonization could not occur in an environment of continual deposition: slow deposition could not account for the burial of whole colonies and lenticles of brachiopods in life position. Thicknesses of up to 30 cm of sediment must have been rapidly deposited in order to preserve the brachiopod 'nests'.

Recent analogues of such a specialized environment are difficult to find. The poor sorting, presence of clay bands, and evidence of lateral passage into facies B indicates a quieter water equivalent for facies C. Whether this was due to increased depth, or to baffling by organisms such as sponges or algae is not known.

*Environmental summary.* As noted above, the faunal and lithological characteristics of the Abbotsbury Ironstone seem to fit best a nearshore environment, or one marginal to an offshore (barrier) bar (text-fig. 4). An offshore (barrier) bar is preferred, due to the absence of any shoreline or strand indications, such as shell hashes, and strand line shell and fish accumulations; and the lack of any sediment derived from south-west England. The reconstruction indicated is of a barrier bar, facing south-east. This is similar to the reconstruction of Davies (1969) for the Upper Lias sands, with the difference that no land is thought to have existed in south-west England.



TEXT-FIG. 4. Reconstruction of the facies distributions of the Abbotsbury Ironstone, with characteristic faunal elements. 'Shoreline' refers to beach or top of bar.

The vertical sequence and indications of lateral passage between environments suggests a gradual deepening during the course of deposition, until facies C<sub>1</sub>, with shallowing again above this. The nearest analogue of the Abbotsbury environment appears to be the barrier bar environments of the Gulf of Mexico, discussed by Bernard *et al.* (1962). If the Cymodoce Zone sediments on the Dorset coast at Weymouth are considered, the comparison can be strengthened. These consist of a series of clays, siltstones, and fine-grained sandstones (Blake's, 1875, Transition Beds). Palaeoenvironmental studies (unpublished) indicate that these sediments can be interpreted as open bay, topset, prodelta deposits comparable to those of the Gulf of Mexico region (Shepard 1956; Parker 1956), with marine fining upward cycles interpreted as distal barrier bar inlet deposits. The Recent sediments of the northern Gulf of Mexico are the result of a Holocene transgression, punctuated by periods of stillstand (Bernard and Leblanc 1965): the Lower Kimmeridgian sediments in Dorset also show transgressive sedimentation, with evidence for stillstand in the Cymodoce Zone. The depositional episode of the Abbotsbury Ironstone was apparently terminated by a marine transgression bringing the relatively quiet water black clays of the Mutabilis Zone westwards over the former barrier bar environment.

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M. E. BROOKFIELD  
 Dept. of Land Resources  
 University of Guelph  
 Guelph  
 Ontario  
 Canada

# A LOWER MIOCENE MAMMALIAN FAUNA FROM SIWA, EGYPT

by W. R. HAMILTON

ABSTRACT. A small collection of fossil vertebrates from the Siwa area of Egypt is described. This fauna includes five mammalian genera—a creodont, a cetacean—*Schizodelphis aff. sulcatus*, a proboscidean—*Gomphotherium angustidens*, a rhinoceros—*Brachyotherium snowi*, and an anthracothere—*Brachyodus africanus*; fish and reptiles are also present. This fauna is important as it agrees with the mammalian faunas of Moghara, Egypt, and Gebel Zelten, Libya, which are both early Miocene in age.

IN 1920 the British Museum (Natural History) purchased from Lady Moon a small collection of fossil vertebrates which had been collected near Siwa Oasis (29° 13' N. 25° 40' E.), Egypt. More accurate geographical details are not available but the nearest known fossil mammal localities to Siwa which could have yielded a similar fauna are Moghara (30° 15' N. 28° 56' E.) and Wadi Faregh (30° 15' N. 30° 22' E.) in Egypt, and Gebel Zelten (28° 30' N. 20° E.) in Libya. In each case the distances involved are great; it therefore seems likely that a previously undescribed fossil mammal site is located at Siwa. The rediscovery of this small fauna is important as it lies approximately mid-way between Moghara and Gebel Zelten and these two sites are the subject of much study at present as a result of their large and important mammalian faunas. It is likely that Moghara and Gebel Zelten were part of the same faunal unit during early Miocene times and the presence of this small fauna between them provides additional support for this theory. The vertebrate fauna is small consisting of a reptile—*Tomistoma dowsoni* Fourtau, a fish—*Pristis* sp., and five mammalian genera, three of which are represented by teeth.

## DESCRIPTIONS

### Creodonta indet.

Plate 28, fig. 2

An axis vertebra (M. 11970) is carnivore-like with a strong odontoid process and posteriorly sloping lateral faces of the anterior centrum face. The centrum, which is depressed anteriorly, is much longer than in *Apterodon macrognathus* from the Fayum (Andrews 1906, p. 228). The neural spine is strong and its distal edge is parallel to the centrum whereas in *Apterodon* the neural spine rises steeply and projects behind the rest of the vertebra. The vertebra is large, having a maximum height of 72 mm and length of 127 mm; its size suggests an animal rather larger than a lion.

Fourtau (1920) described an isolated upper premolar from Moghara which he identified as '*Hyaena* sp. indet.'. This was redescribed by von Koenigswald (1947) as *Hyaenaehurus fourtaui* which becomes *Hyainailouros fourtaui* as a result of Simpson's (1945) correction of the generic name. *H. fourtaui* is larger than a lion but far smaller than the large creodont from Gebel Zelten (Savage pers. comm.).

Carnivores of comparable age and size from Africa are *Afrocyon burrolleti* and *Afrocyon* sp. from Gebel Zelten (Savage 1967) and *Pterodon* from East Africa (Savage 1965). The axis from Siwa cannot be identified with any of the African carnivores but its size suggests *H. fourtaui* rather than *A. burrolleti*.

### Cetacea

#### SCHIZODELPHIS Gervais

#### *Schizodelphis* aff. *sulcatus* Gervais

Plate 28, fig. 1

A mandibular fragment (M. 11971) comprising the posterior part of the symphyseal region compares in size with a specimen described by Fourtau (1920) from Moghara. This was named *Cyrtodelphis* aff. *sulcatus* by Fourtau but the generic name *Schizodelphis* has precedence (Pia 1937) and should therefore be applied. The fragment (M. 11971) is less complete than Fourtau's, consisting of the posterior edge of the symphysis and the left and right rows of alveoli separated by a shallow antero-posterior channel. The specimen has a maximum length of 110 mm and carries ten alveoli on each side in a distance of 90 mm. The ventral surface has a sharp median groove and shallow, paired lateral channels.

*Schizodelphis* aff. *sulcatus* was first described from North Africa by Stromer (1907) on the basis of a mandibular fragment from Wadi Faregh. The specimen described by Fourtau (1920) is similar to that of Stromer but specific identification was not made. The cross-sections of the Wadi Faregh specimen are similar to those of the Siwa specimen and those from the three areas agree in size and regularity of the alveoli and in over-all size (Table 1).

TABLE 1. A mandibular fragment of *Schizodelphis* aff. *sulcatus*

	Siwa M. 11971	Wadi Faregh (from Stromer 1907)	Moghara (from Fourtau 1920)
Width across posterior end of symphysis	45 mm	48 mm	52 mm
Depth at posterior end of symphysis	16 mm	18 mm	—
No. of alveoli in 100 mm	12	11	10

### Proboscidea

#### *Gomphotherium angustidens* (Cuvier)

Plate 28, fig. 3

A right  $M_3$  (M. 11964) agrees with *Gomphotherium*; the tooth lacks the lingual and antero-lingual regions and exhibits medium wear. Fourtau (1920) described upper molars of an adult and lower molars of a juvenile gomphothere which he identified as *Mastodon* (*Gomphotherium*) *angustidens* var. *libyca*. These specimens were discussed by Osborn (1936) who questioned the identity with *G. angustidens*, mainly on a size basis. Further revision of the Moghara material has not been attempted. Fourtau also described a new species of gomphothere from Moghara which he named *Mastodon* (*Gomphotherium*) *spenceri* and which was distinguished from *G. angustidens* by features of the mandible and the greater development of

the talonid in  $M_2$ . This species was identified as *Rhynchotherium spenceri* by Osborn (1936) but he indicated some uncertainty in this identification. An isolated  $M_3$  and mandibular fragment from Moghara (M. 14075) is very similar to the *G. angustidens* from Europe and East Africa and also to the Siwa specimen which is therefore identified with this species.

TABLE 2. The  $M_3$  of *Gomphotherium angustidens* (M. 11964)

	Siwa (M. 11964)	Moghara (M. 14075)
Length	120 mm	142 mm
Width of posterior lobe	60 mm (approx.)	65 mm
Length of talonid	30 mm	42 mm

## Rhinocerotidae

*Brachypotherium snowi* Fourtau

Plate 28, fig. 4

North African Miocene rhinoceroses are known from Moghara and Gebel Zelten with two genera, *Brachypotherium* and *Aceratherium*, described from each site. A rhinocerotid  $M^3$  from Siwa (M. 11966) differs greatly in size and anatomy from the only known upper third molars of *Aceratherium* from North Africa (Hamilton 1973) but agrees closely with the  $M^3$  of *B. snowi* (Fourtau 1920, p. 38, fig. 26). *B. heinzeli* from the Congo (Hooijer 1963) and East Africa (Andrews 1914) is of similar size but differs in features of the metaloph, and cingula from M. 11966 and in these features the Siwa specimen agrees with *B. snowi* from Moghara. *B. snowi* is also known from Gebel Zelten but unfortunately this site has not yielded any third upper molars.

TABLE 3. The  $M^3$  of *Brachypotherium snowi* (M. 11966)

	Moghara	Siwa	<i>B. heinzeli</i>	<i>Aceratherium</i> (Zelten)
Length of lingual region	61 mm	57 mm	56 mm	46 mm

## Anthracotheriidae

*Brachyodus africanus* Andrews

Plate 28, fig. 5

Of the three anthracotheres known from Moghara, published information on two—*B. africanus* and *B. moneyi*—deals with the lower dentitions only and *Masritherium* is known mainly from lower dentitions. The three forms represent three size groups as demonstrated by the lengths of the lower cheek tooth rows (Table 4).

TABLE 4. Anthracothere dentitions (from Fourtau 1920)

	<i>Brachyodus moneyi</i>	<i>B. africanus</i>	<i>Masritherium depereti</i>
$M^1$ - $M^3$	59	112	127
	59	114	140

A right maxilla with P<sup>1</sup>-M<sup>3</sup> from Moghara (M. 15020) is from an animal larger than *B. moneyi* and smaller than *Masritherium* and is identified with *B. africanus* although it is smaller than lower dentitions identified with this species. The right maxillary fragment (M. 11967) from Siwa is larger than M. 15020 but the M<sup>1</sup>-M<sup>3</sup> length agrees closely with the corresponding length in *B. africanus* and is smaller than that length in *Masritherium*. Specimens M. 11967 and M. 15020 also agree in several anatomical features in which they contrast with *Masritherium*. As a result of these similarities the Siwa anthracothere (M. 11967, Pl. 28, fig. 5) is identified with *B. africanus*. The teeth are similar in size to those of *B. aequatorialis* from East Africa (Table 5) but are distinguished from this species by features of the second and third upper premolars.

TABLE 5. The upper dentition of *Brachyodus africanus* (in mm)

	<i>M. 15020</i> (Moghara)	<i>M. 11967</i> (Siwa)	<i>Masritherium</i> (from Fourtau 1920)	<i>B. aequatorialis</i> (from MacInnes 1951)
P <sup>1</sup> length	14	—	18	17
width	12	—	19	17
P <sup>2</sup> length	17	—	—	22
width	14	—	—	22
P <sup>3</sup> length	17	—	—	23
width	17	—	—	24
P <sup>4</sup> length	16	22	27	21
width	19	28	31	26
M <sup>1</sup> length	23	24	30	31
width	28	34	44	—
M <sup>2</sup> length	32	34	34	32
width	37	45	46	36
M <sup>3</sup> length	36	43	53	35
width	40	48	54	38
P <sup>4</sup> -P <sup>1</sup>	65	—	100	83
M <sup>3</sup> -M <sup>1</sup>	89	102	—	92

#### Mammalia indet.

A caudal vertebra (M. 11969) and a sacrum (M. 11968) are also mammalian but cannot be identified with any group. Both specimens are large and probably in the size range of *Brachyodus africanus* or *Brachypotherium snowi*.

#### Other vertebrates

Part of the rostrum of a large *Pristis* sp. and two skull fragments identified with *Tomistoma dowsoni* are also known from Siwa. *T. dowsoni* was described from

#### EXPLANATION OF PLATE 28

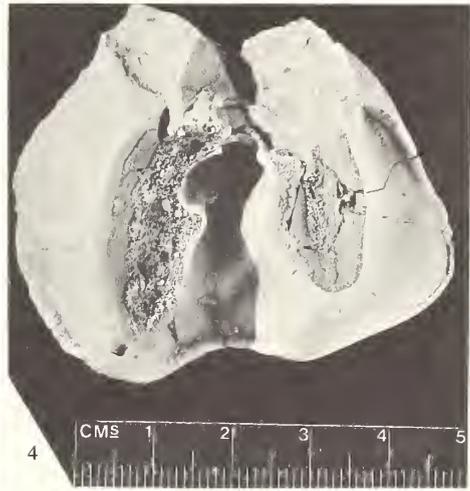
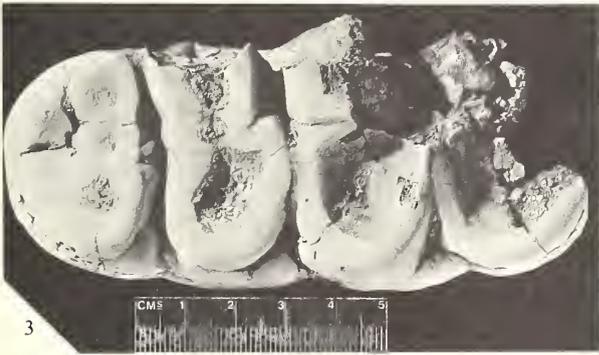
Fig. 1. *Schizodelphis aff. sulcatus* Gervais M. 11971, mandibular fragment.

Fig. 2. Creodont indet. M. 11970, axis vertebra, left lateral aspect.

Fig. 3. *Gomphotherium angustidens* (Cuvier) M. 11964, right M<sub>3</sub>, occlusal aspect.

Fig. 4. *Brachypotherium snowi* Fourtau M. 11966, right M<sup>3</sup>, occlusal aspect.

Fig. 5. *Brachyodus africanus* Andrews M. 11967, right maxilla with cheek teeth P<sup>4</sup> to M<sup>3</sup>, occlusal aspect.



HAMILTON, Miocene mammals from Siwa

Moghara by Fourtau and *Tomistoma* from Gebel Zelten may also belong with this species.

#### DISCUSSION

The Siwa fauna agrees with the large faunas from Zelten and Moghara and the smaller fauna from Wadi Faregh. *Schizodelphis aff. sulcatus* and *Brachypotherium snowi* are characteristic of the North African sites and the latter is otherwise known only from Zelten and Moghara. *Brachyodus africanus* and *Gomphotherium angustidens* are known from Miocene sites in North and East Africa but the latter is of little use in dating. Their mammalian faunas suggest the contemporary nature of the sediments at Zelten, Moghara, Siwa, and Wadi Faregh. The Moghara Formation occurs throughout north-western Egypt and an exposure at Siwa is mentioned by Said (1962); it is therefore likely that the vertebrate remains of Moghara and Siwa were derived from rocks of the same formation. Selley (1969) suggests that the Moghara Formation of Egypt may represent the eastern extremity of the Marada Formation (Desio 1935) which includes the Zelten deposits; if this is so then the localities of Zelten, Moghara, and Siwa are all in the same formation and may be expected to agree closely in age.

The presence in the Siwa fauna of a cetacean suggests deposition in marine conditions but Savage (1967) states: 'Localities which contain sirenians and cetaceans are probably not far from the coast.' The presence of cetacean, fish, and aquatic reptile remains in association with those of terrestrial vertebrates suggests near-shore deposition and the Siwa remains are not water-worn. The existence of large, northward-flowing rivers at Zelten (Selley 1969) and Moghara (Said 1962) has been suggested and another large river may have existed in the Siwa area.

The age of the Siwa fauna depends upon the age of the Zelten and Moghara faunas, these have been consistently identified as early Miocene (Desio 1935; Arambourg 1961, 1963; Savage 1967) and Savage (in Selley 1969) refined this to early Burdigalian or late Aquitanian.

*Acknowledgements.* I would like to thank Dr. R. J. G. Savage of Bristol University who read the manuscript of this paper and provided several useful suggestions; and Mr. P. A. Richens of the British Museum (Natural History), Photographic Unit, who prepared the plate.

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W. R. HAMILTON  
Department of Palaeontology  
British Museum (Nat. Hist.)  
London SW7 5BD

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# A NEW CRAB FROM THE MIDDLE EOCENE OF LIBYA

by J. S. H. COLLINS and S. F. MORRIS

**ABSTRACT.** A new species of carpiliid crab, *Palaeocarpilius aquilinus*, is described from the Lutetian of Central Libya and comparisons are made with other members of the genus. The posterior margin of *P. aquilinus* is wider in the female than the male. This finding is compared with four species of xanthid crabs.

*Palaeocarpilius* is known to have ranged from the Lutetian (Middle Eocene) to the Lower Miocene and species have been described from north-west Africa to Saipan and from the Paris Basin to Zanzibar (Perrin Island). It is represented in north-east Africa (Egypt and the Somali Republic) by *P. macrochelus* (Desmarest) (Stubblefield 1946), which has a widespread distribution and ranges from the Lutetian to the Oligocene; by *P. simplex* Stoliczka from the Upper Eocene of Egypt (Glaessner 1929) and *P. straeleni* Remy from the lower Lutetian of Senegal.

The material described here forms part of the collection made by the 1964 Bristol University Expedition led by Dr. R. J. G. Savage from the area of Bu el Haderait; and collections made by oil-pipeline engineers from Beda Oilfield, Central Libya. The presence of *Nummulites laevigatus*, *Nonion* sp., *Elphidium* sp. in the accompanying fauna of corals, bryozoans, gastropods, lamellibranchs, nautiloids, echinoids, and marine mammals (Savage and White 1965, p. 91) indicates a late Lutetian age for the deposits, which consist of alternating micrites and shelly limestones. Goudarzi (1970, p. 38) assigns these beds to the two lower units of the Wadi Thamit Group, the Al Gata and T'med al K'sour Chalks. The Wadi Thamit Group is underlain by the *Orbitolites* Limestone of the Jabal Waddan Group, which is considered to be of Ypresian age, and is overlain by the Dur al Abd Formation of Upper Eocene to Oligocene age (Goudarzi 1970, p. 38).

The specimens from Bu el Haderait have been rolled and damaged, the outer layer of the dorsal carapace being lost; whereas the specimens from south-west of Beda were collected *in situ* and still retain the outer layer of shell. They are, however, sometimes covered by a dendritic encrustation which may possibly have been leached from the shell itself.

## SYSTEMATICS

Section BRACHYRHYNCHA Borradaile, 1907

Superfamily XANTHOIDEA Dana, 1851

Family CARPILIIDAE Ortmann, 1894

*Remarks.* On the basis that *Palaeocarpilius* and some closely allied genera were derived from the Cretaceous *Caloxanthus* which had its origins in a different dynomenid stock from xanthid crabs *sensu stricto*, Wright and Collins (1972, p. 103) raised Ortmann's subfamily to family status.

## Genus PALAEOCARPILIUS A. Milne-Edwards, 1862

*Type species. Cancer macrochelus* Desmarest, 1822, subsequently designated by Glaessner (1929, p. 291).

*P. aquilinus* sp. nov.

Plate 29, figs. 1-8, Plate 30, figs. 1-8

*Derivation of name.* The trivial name, eagle-like, is suggested by the resemblance of the median ornament to a Roman standard-eagle (Pl. 30, fig. 1).

*Diagnosis.* A *Palaeocarpilius* with the front slightly produced; four almost coalescing bosses forming a low ridge, with a steep depression behind, across the posterior part of the mesogastric lobe.

*Material.* Thirty-three imperfectly preserved carapaces, some with parts of limbs associated, of which fifteen are males, six females, and the remainder indeterminate. Specimen In. 60890 from the Beda oilfield is designated holotype, which with paratypes In. 60891-In. 60899 is in the Department of Palaeontology, British Museum (Natural History). The other paratypes are: BU20286-BU20306 Department of Geology, Bristol University and 1691 JSHC Coll.

*Occurrence.* Middle Eocene, late Lutetian.

*Localities.* 1. Bu el Haderait, 28° 30' N. 18° 40' E.  
2. 40 miles SW. of Beda oilfield, lat. 28° 10' N. long., 18° 47' E.

*Description.* The carapace is sub-ovate in outline, the length being about two-thirds of the width; it is strongly arched transversely and more steeply rounded anteriorly in longitudinal section. There are nine (including the external orbital) sharp, triangular, slightly upturned spines increasing in size posteriorly on the rather thin antero-lateral margins. At the antero-lateral angle a rounded ridge extends on to and delimits the epibranchial lobe on a level with the rear of the urogastric; there is an upturned spine on the outer third of this ridge. The postero-lateral margins are short and deeply concave and lead by a broadly rounded angle and notches for the fifth coxae into the almost straight posterior margin which is bounded by a narrow marginal groove and is about a quarter of the maximum width. The posterior margin is delimited by two small processes. The orbito-frontal margin occupies half the carapace width. The orbits are large and open to the front. The upper orbital margin is thickened by a rounded ridge, which becoming sharper continues across the front.

## EXPLANATION OF PLATE 29

*Palaeocarpilius aquilinus* sp. nov.

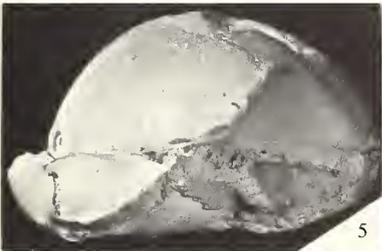
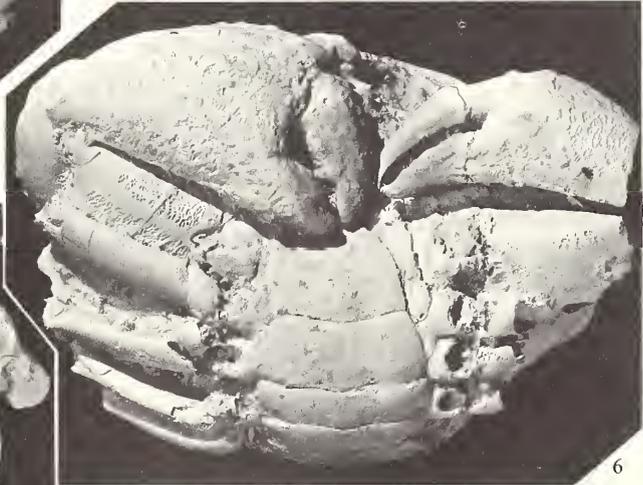
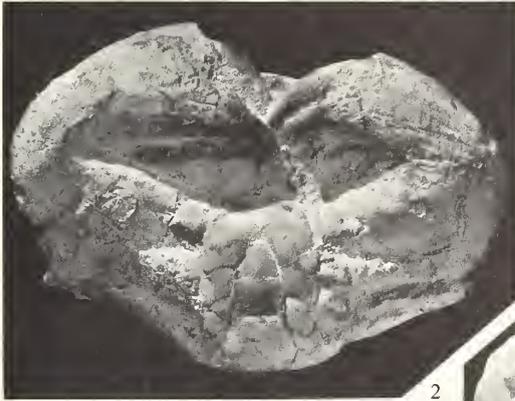
Figs. 1-3. Paratype BM. In. 60893 Lutetian, Bu el Haderait, Libya. Male  $\times 1$ . 1, Dorsal. 2, Ventral. 3, Anterior showing 2 rows of spines on chelae.

Figs. 4-5. Paratype BM. In. 60894. 4, Flattened male abdomen. 5, Left lateral view showing epibranchial ridge spine.

Fig. 6. Paratype BM. In. 60895, ventral view of female abdomen.

Fig. 7. Paratype BM. In. 60896, ventral view.

Fig. 8. Holotype BM. In. 60890 Lutetian, 40 miles SW. of Beda Oilfield, Central Libya. Anterior view showing orbit, notched front and sculpture. Male  $\times 1$ .



COLLINS and MORRIS, Eocene crab

The inner supra-orbital spine is broadly triangular and somewhat larger than the external one. The lower orbital margin is thin, with a sharp sub-orbital spine (Pl. 29, fig. 8) and the second segment of the antenna completes the lower orbital margin. The front is set a little in advance of the general curve produced by the antero-lateral margins so that it can be seen when viewed directly from above; it is divided into three nearly equal parts. The central portion is produced, slightly upturned and notched medially; the portion on either side is concave.

The lobes are barely differentiated on the anterior part of the carapace. A gently curving ridge, formed by four transversely elongated, almost coalescing bosses extends across the posterior part of the mesogastric lobe and adjacent portion of the protogastrics; anteriorly this ridge is barely raised above the general surface of the carapace, but posteriorly it is steeply depressed. The urogastric lobe is quadrate and tumid, but not higher than the ridge before it; the cardiac lobe is pentagonal with concave lateral margins and rounded base. The small intestinal region is rounded and hardly differentiated from the metabranchial lobes. The lateral portion of the metabranchials is deeply deflected under the epibranchial ridge.

A V-shaped mass of 'wedge-shaped' pits scarifies the mesogastric anterior to the bosses and a single row of similar pits curves back, round and under the bosses to the centre of the epimeral adductor muscle scars, immediately above which the posterior gastric pits are generally prominent. A row of circular pits extends in a broad semicircle from near the mesogastric pits back to the epibranchial ridge, and other pits of several diameters are scattered within the area enclosed. A further row begins below the epibranchial ridge and extends ventrally close to the pleural suture to a small kidney-shaped mass of pits marking the attachment of the adductor testis muscle. The sculpture of the carapace anterior to the epibranchial ridges (Pl. 29, fig. 8, Pl. 30, fig. 5), is composed of regular even-sized pits. Postero-lateral, metabranchial, and intestinal areas are mostly smooth with sporadic pits. As with many carpilliids the pits are deepest and densest nearest to the margins. The pits continue, but much less densely, on to the sub-orbital and sporadically over the sub-hepatic regions (Pl. 30, fig. 6). A lower shell layer is composed of numerous flattened, somewhat reticulate nodes, many overlapping one another.

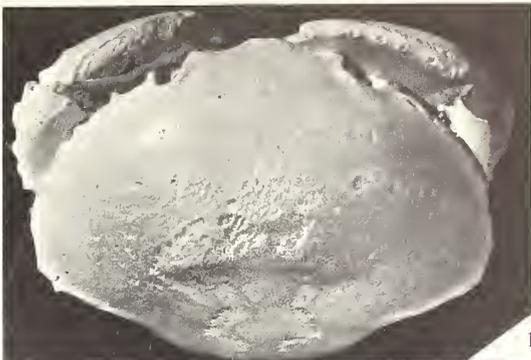
On the ventral surface the front curves downward and backward to meet the head of the rather narrow epistome, which has a thickened margin round a median pit. The basal segment of the antennules is half-moon shaped with the distal margin

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EXPLANATION OF PLATE 30

*Palaecarpilius aquilinus* sp. nov.

- Figs. 1-4. Lutetian, Bu el Haderait, Central Libya. 1, Dorsal view, Paratype BM. In. 60894 male  $\times 1$ . 2, Enlarged view of branchial and cardiac areas to show sculpture  $\times 2$ . 3, Paratype BM. In. 60897 immature juvenile male showing main characters of adults,  $\times 1$ . 4, Lateral view of paratype BM. In. 60893,  $\times 1$ .
- Figs. 5-8. Lutetian, 40 miles SW. of Beda Oilfield, Central Libya. 5, Dorsal view of holotype BM. In. 60890 to show surface sculpture,  $\times 1$ . 6, Ventral view of holotype with right chela removed at wrist joint to show buccal cavity and antennular areas,  $\times 1$ . 7, Lateral view of holotype showing outer marginal spines of carpus and upper distal spines of merus,  $\times 1$ . 8, Anterior view of paratype BM. In. 60892.



COLLINS and MORRIS, Eocene crab

ridged. The second segment of the antenna is of moderate length, shaped like an arrow-head at its base with the 'shaft' parallel sided, terminating in the orbit. A moderate ridge extends across the endostome. The buccal margins converge a little posteriorly and the distal angles are broadly rounded. The pterygostomial region is finely pitted; a fine groove bounds the buccal margin and, becoming broader, continues round the anterior and lateral border of that part of the process enclosing the chelipeds. The ischial endognath of the third maxillipeds is rhomboidal and medially depressed; the exognath is about two-thirds of the width of the endognath and rounded transversely; both members are pitted.

The part of the sternum corresponding to the third thoracic sternite is flattened and ridged at the postero-lateral angle where a deep marginal cleft separates it from the fourth sternite. The cleft continues as a broad groove towards the midline where there is a small pit. The lateral edge of the fourth sternite is raised and the posterior part is tumid; the anterior part of the abdominal 'trough' is densely pitted and a few fine pits extend on to the tumid area. The remaining sternites are flattened, with a few scattered pits, particularly round the edges.

The 1st and 2nd abdominal somites of the male (Pl. 29, figs. 2, 4) are of about equal length; the 3rd-5th are fused, but their positions are marked by short notches on the lateral margins and a few pits extend further towards the centre; the lateral thirds of the '3rd' and '4th' are tumid, the '5th' is almost flat; the 6th is quadrate and about as long as the triangular telson; a shallow groove extends round the lateral margin leaving a broad median portion. In the female abdomen the lower margin of the 1st somite is deeply concave and medially about half the length of the 2nd; the 3rd-5th become slightly longer, the 6th is triangular, about twice the length of the 5th and somewhat shorter than the more or less sub-oval telson; the median and almost equal-sized lateral portions are separated by shallow depressions.

The chelipeds are robust and the larger claw, where preserved, is on the right. The merus is triangular with fairly sharp angles; there are two spines in line on the upper distal angle; on the inner distal angle is a large quadrate node with a pit behind into which fits a node on the proximal end of the palm. The carpus is half the length of the merus, sub-triangular in section; dorsally it is triangular with a sharp tooth on the inner distal angle and a carinated tubercle between it and the rounded articulating knob; there are generally four sharp, carinated spines on the rim-like outer margin. The palm of the right claw is heavy, about half the carapace width in length, and increasing in width from the proximal to the distal end. The fixed finger is half the length of the palm, squat, and with the lower margin almost in line with that of the palm; the opposing margin has a single broad cusp and a lower terminal 'pad'. The movable finger is broadly curved with three evenly spaced cusps on the opposing margin. The palm of the left claw is shorter and much less tapered from distal to proximal end; the fixed finger is longer, more slender, and inclined downwards forming a distinct curve with the basal margin of the palm. The movable finger is straighter. Both the opposing margins are sharper, with fine, almost granular cusps.

Both the claws share the same character of a row of strong, almost conical spines increasing in size distally on the upper margin of the palm; the number on the larger claw varies from nine to seven, while on the smaller there may be only six or seven. The spines are separated by a shallow groove from a prominent node-lined ridge

extending nearly the whole length of the upper outer margin. The lower margin of the palm is lined with a thin ridge (beginning at the node which fits into the meral pit) which becomes thickened at the junction with the fixed finger and extends a short way along it, tapering rapidly. There is a large tubercle, with a smaller one beside it, on the proximal upper margin of the movable finger and a shallow groove extends about half the length of the upper outer margin. The lower articulating knob is protected by a short process and above this is a prominent tubercle, sometimes forming part of a short rounded ridge.

The walking legs are long and stout; the meri are elliptical in section and a strong ridge lines the upper (and possibly lateral) margin of the slender dactylus. The fingers on both hands are markedly dark coloured, a feature which, according to Stoliczka (1871, p. 9) is typical of this group.

*Measurements in mm.*

	<i>Carapace length</i>	<i>Width*</i>	<i>Orbito-frontal width</i>
Holotype In. 60890	61	82	40
Paratype In. 60893	41	57	29
Paratype In. 60898	66	86	46
Paratype In. 60894	45	64	32
Paratype In. 60897	28	38	20

\* Between 8th/9th antero-lateral spines.

*Discussion.* While most of the specimens are to some degree damaged or rolled, the diagnostic characters are generally sufficiently well preserved, although the antero-lateral spines often appear rounded and almost globular, and the additional spine on the epibranchial ridge is much reduced, as is the ornament on the upper margin of the hand. Traces of the endophragmal skeleton are preserved on specimen BU. 20297.

The new species has affinities with *P. macrochelus* (Desmarest), but may at once be distinguished by its slightly produced front, the arrangement of the bosses and the depression caused by them, and the presence of the additional spine on the epibranchial ridge. The nature of the tubercles on the upper margin of the hand of *P. aquilinus* is of solid individuals rising directly from the margin and not fringed like *P. macrochelus* as stated and figured by Stubblefield (1946, pl. 8, fig. 5); also the carina on the upper outer margin is nodose and does not extend the whole length of the hand. The strong ridge figured by Stubblefield (1946, pl. 8, figs. 2b, 6) extending the length of the movable finger (and to some extent on to the immovable finger) is not developed in *P. aquilinus*. One of the specimens (C11,113 Sedgwick Museum) described by Stubblefield from British Somaliland, is a juvenile which nearly corresponds in size with paratype BM. In. 60897 of *P. aquilinus*; each shows the distinctive specific characters of the adult which do not appear to alter to any great extent during ontogeny. On Bittner's subspecies, *P. m. coronata* (1886, pl. 1), from the Priabonian of Verona, the bosses are prominent, individual, and arranged in a distinct semicircle. Bittner also stated that a second row of tubercles is developed near the 'upper hump' of a chela of one large male. The specimens from the Upper Eocene of Rumania (Ghiurca and Givulescu 1964, figs. 2-5) appear to belong to this subspecies. Milne-Edwards figured (1862, pl. 6, figs. 2, 2a) a specimen from the

neighbourhood of Verona; this compares favourably with Bittner's description and figure (1886, pl. 1) and evidently belongs to *P. m. coronata*, as does the specimen BM. 39355, formerly considered by Stubblefield (1946, p. 516) to be *P. macrochelus*. In this specimen, however, the bosses are somewhat more subdued than Bittner's figure (op. cit.) would indicate. The front is produced in *P. stenurus* (Reuss) (vide Milne-Edwards 1862, pl. 1, fig. 3) from the 'terrine nummulitique' near Verona, but in this form only two bosses are present and the epibranchial ridge extends much further towards the midline of the carapace. Milne-Edwards (1862) and Glaessner (1929) consider *P. stenurus* is a juvenile of *P. macrochelus*. The unique specimen of *P. stenurus* is an internal mould and appears to differ in certain aspects from small specimens assigned to *P. macrochelus* in the British Museum (Natural History). The nature of the preservation of *P. stenurus* may account for these differences, but more material may show it to be a valid species. Antero-lateral spines are reduced to nodes on *P. straeleni* and are not developed on *P. simplex* Stoliczka which is also recorded from the Upper Eocene of Egypt. There is a close similarity between the antero-lateral spines of *P. aquilinus* and *P. rugifer* Stoliczka, and some specimens of the former show a similar rugose ornament of the cheliped on a subsurface shell layer, but among other differences the bosses are lacking and the orbito-frontal width is much greater on *P. rugifer*.

Six female specimens were determined from their broader abdominal somites. Further to distinguish male and female forms two parameters were measured; the dorsal carapace width (trs.) and posterior margin width (trs.). The dorsal carapace width measurement was taken from between the 8th-9th antero-lateral spines. The posterior margin width was taken between the tips of the two spiny processes that delimit the posterior margin. These processes form the lateral extent of the 1st abdominal somite. The percentage ratios of the two measured parameters of the small population (only six females) of *P. aquilinus* indicated a substantially wider abdomen in the female of 14.4% as compared with the male. Hu (1971, p. 36) has indicated similar but unquantified results from the ocypodid *Uca pugilator* (Bosc.).

For comparison four Recent species belonging to genera related to *Palaecarpilius* were studied. Six specimens of each sex of *Carpilius corallinus* (Herbst), *C. maculatus* (Linn.), *C. convexus* (Forskål), and *Atergatis floridus* (Linn.) were used. In all the species the female abdomens are wider than the males. The increase in size ranged from 8.5% in *C. convexus* to 15.8% in *C. maculatus*. The ratios do not overlap but in *C. convexus* the upper limit of the male range just coincides with the lower limit of the range of the females. Their average ratios are quite dissimilar. One male specimen of *A. floridus* had the unusually low ratio of 14.7%. The ratio was so low that it has been excluded from the average rather than produce an abnormally low figure. Generally, but by no means uniformly, the larger the specimens the greater difference between the ratios of the sexes.

Using the measurements of Ghiurca and Givelescu (1964, table 1) from an unknown population, the ratios fall into two groups 23.2-24.3%, average 23.9% (specimens 1-4) and 26.0-27.5%, average 26.6% (specimens 5-8, 10). One specimen, 9, had a ratio of 25% and cannot be assigned to either group. We can now assume that specimens 1-4 are males and specimens 5-8 and 10 are females. Specimens 1 and 3 are in fact figured as males.

Thus, by using the method described above it is possible to determine with some degree of accuracy the sex of an individual when no abdominal somites are present, provided that the carapace width and posterior margin are entire.

#### *Habits and ecology*

The family Carpiliidae is common around the shores of tropical countries and especially the Indo-Pacific islands. They are free-living, bottom-crawling inhabitants of the fringes of coral reefs. Early workers considered that they were the inhabitants of the fringes of coral reefs. Recent work by Macnae and Kalk (1958), Taylor (1968, 1971) suggests that in fact larger members of the family are mostly found in the sublittoral zone or the algal ridge of the eulittoral zone of wave-cut platforms. These wave-cut platforms are frequently associated with pre-existing coral colonies. Tweedie (1950) and Guinot (1967) observe that carpiliids are normally nocturnal and Macnae and Kalk state that the large carpiliids are to be found under large stones during daylight. But Taylor (1968, p. 174) has observed them to move about during daylight, when their bright yellow and orange spots make them difficult to see.

To date nobody has studied the habits and ecology of these crabs in any detail and it has been assumed that they are general scavengers as well as possibly preying on molluscs and worms that inhabit the same environment. In the Seychelles the swimming crab *Thalamita* has been seen to prey upon *Carpilius* (Taylor 1968). Abundant molluscs have been found in association with *Palaeocarpilius*, but without more work on the recent genera it is impossible to give any idea of the prey of *Palaeocarpilius*.

In his work on shoreline sedimentation in the Miocene of Libya, Selley (1966, p. 3) points out that the Miocene deposition is the continuation of a facies that started in the Cretaceous. The facies consists of an alternation of shallow-water limestones and shales and the limestones are generally of detrital organic origin. It would seem that *Palaeocarpilius* occupied an environment not very different from the recent *Carpilius*. No swimming crabs have been found in association with *Palaeocarpilius* in Libya, but the portunids are thin-shelled animals and are not often preserved.

None of the characteristic coloured spots of the dorsal carapace of the recent genera have been found on the fossil material, but the spots usually fade fairly rapidly after death in *Carpilius*. It would seem that the strong spinosity of the antero-lateral margins of *Palaeocarpilius* similar to that on portunid crabs, although less exaggerated, would act as a defence mechanism against predators.

It seems likely that *Palaeocarpilius* lived in the high-energy environment of a shallow water hard bottom, probably at the seaward edge of a wave-cut platform, living by scavenging at night and sheltering under rocks by day.

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*Repositories.* BM., British Museum (Natural History), London; BU., Geology Department, Bristol University; J.S.H.C. Collection.

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J. S. H. COLLINS  
63 Oakhurst Grove  
East Dulwich  
London, SE 22

S. F. MORRIS  
Department of Palaeontology  
British Museum (Nat. Hist.)  
London, SW 7

# FISH OTOLITHS FROM THE ENGLISH CRETACEOUS

*by* FREDERICK C. STINTON

**ABSTRACT.** Fish otoliths including the representatives of one new genus and four new species are described from the Neocomian, Albian, and Upper Cenomanian. Their possible affinities with earlier and later teleost groups are discussed.

ALTHOUGH teleost remains have been well known from the Upper Cretaceous Chalk for many years little is known of the fish fauna of the Lower Greensand, Gault, and Upper Greensand. Most of the literature has been concerned with skeletal remains; but teleost otoliths, which occur frequently in the English Albian, have been largely neglected, despite the fact that they are to be found in the collections of the British Museum (Natural History) dating from 1861. Koken (1891) described a single otolith from the Gault of Folkestone and Shepherd (1916) described two further otoliths from the same area. Apart from a mention by Milbourne (1956, p. 239) of the occurrence of otoliths in Bed 3 of the Gault exposed at Greatness Lane, Sevenoaks, Kent, no other work has been done on the subject.

In recent years detailed collecting at inland exposures of the Gault of Kent has produced many more otoliths, mainly fragmentary but occasionally in an excellent state of preservation. The remaining Cretaceous strata are notable for the paucity of otoliths, largely due to the decalcification of much of their thickness. Apart from the Albian (Gault) otoliths only three other sacculiths are known to date, two from the Neocomian (Speeton Clay) and one from the Upper Cenomanian (Lower Chalk). This latter specimen is largely in the form of an impression. It is probable that other otoliths occur in the Speeton Clay but they may well have been overlooked by workers who were unfamiliar with these objects.

A very few otoliths have been recorded from the Cretaceous of continental Europe and America. Priem (1908) described one species from the Neocomian of Attancourt (Haute-Marne), France, and Weiler (1969) subsequently recorded the same species from the Neocomian in the vicinity of Hanover, Germany. It is of interest to note that these forms appear to be conspecific with those described herein from the Speeton Clay and that the German specimens are recorded from the same stage as the English ones.

Strata containing an abundance of fish otoliths often appear to contain few osseous remains. The accumulation of otoliths may have originated from faecal concentrates derived from marine mammals or birds which would create a false impression of the relative numbers of teleosts occurring at that time.

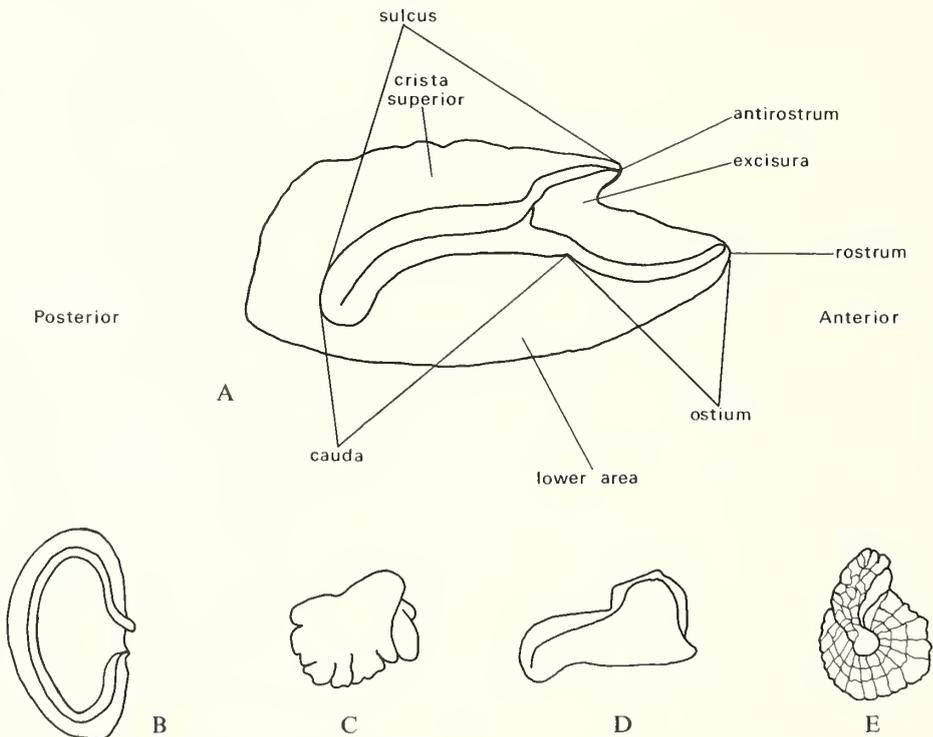
The otoliths to be described are mainly quite distinct from those of Tertiary and Recent fishes so that, in the absence of associated skeletons or suitable comparative material, a certain amount of conjecture as to their relationship is inevitable. However, certain morphological features are perpetuated from Jurassic forms through

to the present day and these offer good indicators to the possible affinities of the forms under consideration.

### TERMINOLOGY

The terminology is that proposed by Koken (1884, p. 525) whose original names for the morphological features of the otolith are still applicable. Chaîne and Duvergier (1934) described further specialized features which appear in a few teleost groups. The original names for the different types of otoliths were revised by Adams (1940). He suggested terms which directly related the otoliths to their sites within the labyrinth and these are adopted here in preference to the original terms.

The generalized percoid features of the three otolith types are shown in text-fig. 1A, B, D, while the utriculiths of two primitive teleosts, *Notopterus notopterus* Pallas (text-fig. 1C) and *Esox lucius* Linnaeus (text-fig. 1E) show the variable sculpture of this type of otolith. The characters of the lagenalith are relatively constant in all teleost groups and are insufficiently variable to be of use for generic determination. Similarly, among the many percoid groups, the utriculith shows little variation in detail and is of little use in generic determination. Among the more primitive fishes



TEXT-FIG. 1. A, Schematic percoid left sacculith, medial view. B, Generalized features of a percoid lagenalith approximately,  $\times 12$ . C, Utriculith of *Notopterus notopterus* Pallas,  $\times 12$ . D, Percoid utriculith (*Gaterin gaterinus* Forskål),  $\times 21$ . E, Utriculith of *Esox lucius* Linnaeus,  $\times 10$ .

and among the siluroids the utriculiths are very variable, and those of the Ariidae are characteristic of the various genera. They are large, biconvex, circular to oval objects occurring frequently in the Upper Eocene and, because of their size, are well known to palaeontologists who work in the English Bartonian.

#### SYSTEMATIC DESCRIPTIONS

Subclass TELEOSTEI

Order ELOPIFORMES

Family MEGALOPIDAE

Genus MEGALOPS Lacépède 1803, p. 289

*Type species. Megalops filamentosus* Lacépède = *Chupea cyprinoides* Broussonet, monotypic.

*Megalops bicrenulatus* sp. nov.

Plate 31, figs. 1-3

*Holotype.* P. 51770/1. Paired sacculiths, one utriculith and associated scales and bones, the remains of a single individual.

*Dimensions.* P. 51770 (pl. 31, figs. 1*a*, *b*), length 5.68 mm, width 3.38 mm  
P. 51770 (pl. 31, figs. 2*a*, *b*), length 5.74 mm, width 3.48 mm  
P. 51771, utriculith (pl. 31, figs. 3*a*, *b*), length 1.38 mm, width 0.96 mm

*Description.* The sacculiths (pl. 31, figs. 1*a*, *b*, 2*a*, *b*) are rather thick, biconvex, rounded posteriorly, and bluntly pointed anteriorly. Dorsal rims bicrenulate anteriorly and very slightly rounded posteriorly, coalescing completely with the rounded posterior rim which in turn coalesces with the regularly rounded ventral rim; slightly undulant anterior rims. Outer faces smooth, somewhat undulant, and depressed in the postero-dorsal area. Inner faces smooth. Sulcus opening obliquely on the anterior rim and not reaching the posterior rim. It consists of a short, wide, triangular ostium with a concave lower rim and a long, slightly arcuate, rather narrow cauda expanding slightly towards its pointed extremity. A depression above the crista superior, accentuating it. A very slight lower angle and a marked upper angle at the junction of ostium and cauda, the upper angle being formed by the crista superior recurving nearly vertically to the junction of the anterior and dorsal rims. Blunt rostrum, slight excisura, but no antirostrum or collicula present.

The utriculith (pl. 31, figs. 3*a*, *b*) is a rather triangular, biconvex right otolith. The ventral rim is finely crenulated while the smooth anterior and posterior rims form a dorsal point. Outer face smoothly rugose with a central concavity in the ventral area producing a keeled ventral rim. No characters of specific value are present.

*Discussion.* The sacculiths have a distinct resemblance to the Jurassic forms described as *Pholidophorus* by Stinton and Torrens (1968), both in the character of the sulcus and in peripheral details, but lack the denticulated ventral rims of the Jurassic forms besides being thicker. It was suggested that the otolith described as *Pholidophorus paradoxicus* Stinton and Torrens, might be a precursor of *Megalops* and the present form has a distinct resemblance to sacculiths of *Megalops cyprinoides*

(Broussonet) which today inhabits the Indo-Pacific. Both forms have a similar sulcus and peripheral characters but the fossil form has a shorter rostrum while the smooth ventral rim also differs from the serrated one of the Recent species. Dr. C. Patterson has examined the accompanying scales and states (pers. comm.) that they bear some resemblance to those of the Recent genus *Megalops* but cannot be definitely identified with it.

*Locality of holotype.* Albian (Gault), Folkestone, Kent. Exact horizon unknown.

*Other material.* P. 47558/9 Lower Gault, *niobe* subzone, B.P.C.M. Pit, Small Dole, Sussex. H. A. Toombs Colln. P. 51772 Gault, *varicosum* zone, Folkestone, Kent. A. Gale Colln. P. 51783 Gault, Trottscliffe, Kent. G. Freeman Colln.

Family ELOPIDAE  
Genus *Elops* Linnaeus 1766

*Type species.* *Elops saurus* Linnaeus.

‘*Elops*’ *neocomiensis* (Priem)

Plate 31, figs. 4-5

- 1908 *Otolithus (Clupeidarum) neocomiensis* Priem, p. 37, text-figs. 11-14.  
1965 *Palealbula neocomiensis* Frizzell, p. 97, pl. 4, fig. 8.  
1969 *Palealbula neocomiensis* Weiler, pp. 358-361, text-figs. 2, 3, 5, 7, 8.

*Material and locality.* Left sacculith (P. 15954) and right sacculith (P. 15953), Lower Cretaceous (Neocomian), Hauterivian zone D1, Speeton Clay, Yorkshire. G. W. Lamplugh Colln.

*Dimensions.* Right sacculith (pl. 31, fig. 4a, b), length 13.94 mm, width 8.90 mm.  
Left sacculith (pl. 31, fig. 5a, b), length 14.30 mm, width 8.05 mm.

*Description.* Both otoliths are eroded, rather thick, with convex inner faces and concave outer faces. Dorsal rims probably somewhat eroded but show an irregular, slightly rounded periphery; posterior rim of the right specimen is nearly vertical and smoothly rounded; ventral rims of both specimens smoothly rounded; anterior rims eroded but probably rather oblique. Outer faces rugose with compressed peripheries to form keeled rims. The sulcus is arcuate, evidently opening widely on the anterior rim and terminating on or near the posterior rim. It consists of a short obtusely triangular ostium with a steeply descending lower rim and a long, arcuate cauda

EXPLANATION OF PLATE 31

- Figs. 1-3. *Megalops bicrenulatus* sp. nov. 1a, b, Syntype P. 51770, right sacculith, inner and outer faces,  $\times 4$ . 2a, b, Syntype P. 51770, left sacculith, inner and outer faces,  $\times 4$ . 3a, b, Syntype P. 51771, utriculith, inner and outer faces,  $\times 16$ .  
Figs. 4-5. ‘*Elops*’ *neocomiensis* (Priem). 4a, b, P. 15953, right sacculith, inner and outer faces,  $\times 1.6$ . 5a, b, P. 15954, left sacculith, inner and outer faces,  $\times 1.6$ .  
Fig. 6a, b, *Pteralbula cantiana* (Shepherd). Syntype P. 17, left sacculith, inner and outer faces,  $\times 1.6$ .  
Fig. 7a, b, *Albula obesa* sp. nov. Holotype P. 51773, right sacculith, inner and outer faces,  $\times 2$ .  
Fig. 8a, b, *Pterothrissus galtinus* (Koken). P. 51767, right sacculith, inner and outer faces,  $\times 4.8$ .  
Fig. 9a, b, ‘*Osmerus*’ *lobatus* sp. nov. Holotype P. 23274, left sacculith, inner and outer faces,  $\times 10.4$ .  
Fig. 10. *Sphaeronchus rotundus* sp. nov. Holotype P. 51766, right sacculith, inner face,  $\times 2.4$ .  
Fig. 11. Fragment of sacculith, P. 51769, simulating the utriculith of a Recent Ariid. Inner face,  $\times 4$ .



1a



1b



3a



2a



2b



3b



4a



4b



6a



5a



5b



6b



7a



7b



8a



8b



10



9a



9b



11

which is deep and widens somewhat towards the posterior end before narrowing to a rounded point. Crista superior raised and there is a very narrow excavation between it and the dorsal rim. A rounded lower angle and an oblique upper angle produced by a recurving of the crista superior, at the junction of ostium and cauda. A rostrum probably present but no evidence of an antirostrum or excisura. No collicula.

*Discussion.* These otoliths show an obvious affinity to sacculiths of the modern Elopidae in the character of the dorsal periphery, the arcuate sulcus, and the very short, triangular ostium with its position on the anterior rim. Erosion has shortened the rostrum so that it is impossible to ascertain whether it was comparable in length with that of the Recent forms.

It has not been possible to compare these specimens directly with those from the French and German Cretaceous but illustrations indicate that they are identical. The origin of the French holotype from the Lower Cretaceous and the German specimens from the contemporaneous Hauterivian stage of the Lower Cretaceous near Hanover further confirms the identity of the English and continental specimens.

Frizzell (1965) related these forms to an albulid complex, suggesting that Priem's species was a precursor of *Albula*. He also ascribed two forms from the Upper Cretaceous of the United States—*Prealbula weileri* Frizzell and *Protalbula sohli* Frizzell to this same complex. However, none of these forms shows the ostium opening in the characteristic position of the albulids nor do they have the almost continuous anterior and dorsal rims. Furthermore, they lack the produced posterior area which appears to be an established character of albulid sacculiths.

Family ALBULIDAE  
Genus *Pteralbula* gen. nov.

*Type species.* (*Atherina*) *cantiana* Shepherd 1916, p. 203.

Rectangular sacculiths with a prominent vertical extension of the postero-dorsal area. They are biconvex. Sulcus occupying the dorsal half of the otolith, opening on the antero-dorsal corner and running diagonally towards the postero-ventral corner but terminating before reaching the periphery. Sulcus consisting of a very short, angular ostium and an almost straight cauda. Undulant dorsal rim and all other rims regularly rounded. Osteological details unknown at present.

*Pteralbula cantiana* (Shepherd)

Plate 31, fig. 6

1916 *Otolithus* (*Atherina*) *cantiana* Shepherd, p. 203, text-fig. 157.

*Syntype.* P. 17, Albian (Gault), Folkestone, Kent. Gardner Colln.

*Dimensions.* Length 12.86 mm, width 10.83 mm.

*Description.* An adult left sacculith, somewhat eroded. Morphological characters as for the genus. Smooth, irregularly undulant outer face with depressed antero-dorsal and postero-dorsal areas. Dorsal area of inner face compressed, accentuating the crista superior. A rounded lower angle and upper right angle at the junction of ostium and cauda. No rostrum, antirostrum, excisura, or collicula. A wide, smooth, semicircular lower area.

*Discussion.* The salient feature of this otolith is the marked vertical projection of the postero-dorsal area, a character previously only seen in typical albulid sacculiths. Also, the sulcus occupies a similar position on the inner face with the ostium opening on the antero-dorsal edge. On the other hand, the rather rectangular outline and the diagonal course of the sulcus resemble pterothrissid sacculiths and it is considered that this fish was ancestral to both *Albula* and *Pterothrissus*. One might expect to find the genus represented in the Jurassic and it seems probable that it extended into the Cretaceous before becoming replaced by modern forms of *Albula* and *Pterothrissus*.

A realignment of the postero-dorsal extension to a horizontal posterior extension, the rounding and narrowing of the otolith with the necessary realignment of the sulcus to conform with these morphological changes would result in a typical albulid sacculith. Similarly, the entire loss of the posterior extension would result in a relatively typical otolith of *Pterothrissus* without any further morphological changes. Such changes would also require modifications of the cranial structures in the area of the auditory bullae to accommodate these alterations in the design.

Shepherd (1916) suggested that this form compared with that described as *Otolithus (Atherina) austriacus* Schubert because of a supposed similarity between the sulcus of each species. However, atherine sacculiths have a median, narrow sulcus quite dissimilar from the present form.

*Other material and localities.* P. 51774 Gault, *intermedius/subdelaruei* zone, Folkestone, Kent. A. Gale Colln. 41358 Gault, Folkestone, Kent. Horizon unknown. B. N. Wright Colln. 47213 Gault, Folkestone, Kent. Horizon unknown. Gardner Colln. P. 15727 Gault, Bed VIII, Copt Point, Folkestone, Kent. W. A. McFadyen Colln. 36115 Gault, Folkestone, Kent. Horizon unknown. W. Griffiths Colln. 36321 Gault, Folkestone, Kent. Horizon unknown. W. Griffiths Colln. P. 47710-47716 Gault, level 2, ?*E. latus* zone, B.P.C.M. Old Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 47587-47588 Gault, basal level below nodule bed, B.P.C.M. Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 49805 Gault, A.P.C.M. Pit, Small Dole, Sussex. S. Cragg Colln.

Two examples (Nos. 112229, 112230), Gault, Folkestone, Price Colln., are contained in the museum collections of the Institute of Geological Sciences.

### Genus ALBULA Scopoli 1777

*Type species.* *Esox vulpes* Linnaeus.

#### *Albula obesa* sp. nov.

Plate 31, fig. 7

*Holotype.* P. 51773.

*Dimensions.* Length 10.67 mm, width 6.23 mm.

*Description.* A thick, eroded, biconvex right sacculith. Slightly rounded dorsal rim; rounded, slightly produced posterior rim; fairly deeply rounded ventral rim; rounded anterior rim. Smooth convex outer face with a slight depression at the postero-dorsal corner. Convex inner face with an indistinct sulcus, due to erosion, apparently opening on the antero-dorsal corner of the otolith and extending somewhat diagonally to parallel the dorsal and posterior rims. It terminates near the postero-ventral corner of the otolith. Details of sulcus obscure but it appears to consist of a short, wide ostium and a long, slightly undulant, relatively wide cauda. A very

slight depression on the dorsal rim. No apparent rostrum, antirostrum, excisura, or collicula. A wide, smooth lower area.

*Discussion.* Despite the very worn condition of this specimen it shows a marked similarity to sacculiths of Tertiary and Recent albulids in its peripheral contours, position, and alignment of the sulcus and especially in the characteristic extension of the posterior rim. It appears that this may well have come from a true *Albula*.

In the Cenozoic the first typical albulid otolith recorded is that figured by Priem (1908, p. 84, text-figs. 45, 46) from the Palaeocene, Thanétien, Sables de Châlons-sur-Vesles (Marnes) which he named *Otolithus (Trachini ?) bellevoiyii*, a species which is very similar to, if not synonymous with, the English species *Albula eppsi* Frost, from the Ypresian, Blackheath Beds. This more rounded outline persists throughout the Eocene and Oligocene eventually becoming further modified to the more elongate and narrower sacculith seen in the Recent forms.

*Locality.* Gault, *varicosum* subzone, Small Dole, Sussex. D. Ward Colln.

Family PTEROTHRISSIDAE  
Genus PTEROTHRISSUS Hilgendorf 1877

*Type species.* *Pterothrissus gissu* Hilgendorf.

*Pterothrissus galtinus* (Koken)

Plate 31, fig. 8

1891 *Otolithus galtinus* Koken, p. 138, text-fig. 27.

*Material and locality.* Right sacculith P. 51767 Gault, Bed 11, *intermedius* zone, B.P.C.M. Pit, Small Dole, Sussex. G. Freeman Colln.

*Dimensions.* Length 4.33 mm, width 2.50 mm.

*Description.* A beautifully preserved right sacculith. Nearly horizontal, crenulated dorsal rim; rounded, crenulate posterior rim; long, rounded denticulate ventral rim; short, irregularly denticulate anterior rim. Convex outer face prominently umbonated on the dorsal area. Compressed posterior and ventral areas peripherally ornamented with short, tuberoso ribs. Almost flat inner face with a somewhat diagonal sulcus which opens very slightly on the upper part of the anterior rim and terminates near the postero-ventral corner. Sulcus consisting of an almost enclosed, rather wide, oval ostium and a long, narrow, straight cauda which turns down slightly near its pointed extremity. An indistinct sulculus extends vertically from the end of the cauda to the postero-dorsal corner of the otolith. Slightly rounded lower angle and an acute upper angle, produced by the recurved upper ostial rim, present at the junction of ostium and cauda. A shallow depression above the crista superior, accentuating it. No rostrum, antirostrum or collicula but an excisura present. Lower area finely latticed.

*Discussion.* The present species was originally established by Koken on a somewhat eroded specimen from the Folkestone Gault and he assigned it to his 'umbonatus' (= *Pterothrissus*) group. However, this sacculith is so similar to those of the living species that it can only be referred to the Recent *Pterothrissus*. It suggests that the Pterothrissidae evolved fully during the Cretaceous at least as far as the otoliths

are concerned. Many adult sacculiths up to 15 mm length have been found at various Gault exposures indicating that this fairly common fish grew to a large size. The adult otoliths usually show evidence of erosion and it is frequently difficult to separate them from similarly affected otoliths of other species which accompany them.

*Other material and localities.* P. 23274 Gault, zone VI, Copt Point, Folkestone, Kent. W. A. Macfadyen Colln. 36105 Gault, Folkestone, Kent. Horizon unknown. W. Griffiths Colln. P. 23275 Gault, zone VIII, Copt Point, Folkestone, Kent. W. A. Macfadyen Colln. 35879 Gault, Folkestone, Kent. Horizon unknown. W. Griffiths Colln. 41358 Gault, Folkestone, Kent. Horizon unknown. B. N. Wright Colln. 47213 Gault, Folkestone, Kent. Horizon unknown. Gardner Colln. P. 10818 Gault, Folkestone, Kent. Horizon unknown. Hilton Price Colln. P. 47717-47719 Gault, level 2 (?*E. latus* zone), B.P.C.M. Old Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 47680-47681 Gault, level 1, base of old pit, B.P.C.M. Pit, Small Dole, Sussex. Macdonald Colln. P. 47620-47662 Gault, basal level (below nodule bed), B.P.C.M. Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 47587-47588 Gault, basal level (below nodule bed), B.P.C.M. Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 48669 Lower Gault, *bennettianus* zone, Bed 1, top shell seam, A.P.C.M. Pit, Small Dole, Sussex. H. Owen Colln. P. 51784 Gault, Leighton Buzzard, Bedfordshire. Horizon unknown. Buteux Colln.

### Order SALMONIFORMES

#### Family OSMERIDAE

#### Genus OSMERUS Lacépède 1803

*Type species.* *Salmo eperlanus* Linnaeus.

#### '*Osmerus*' *lobatus* sp. nov.

Plate 31, fig. 9

*Holotype.* P. 23274 Gault, zone VI, Copt Point, Folkestone, Kent. W. A. Macfadyen Colln.

*Dimensions.* Length 2.42 mm, width 1.59 mm.

*Description.* A rather thin, oval left sacculith which is slightly eroded. Crenulated, nearly horizontal dorsal rim; short, nearly vertical posterior rim with a small central point and a notch above it; a moderately rounded ventral rim, indistinctly crenulated on the posterior half; oblique anterior rim. Slightly convex outer face with indistinct tuberculations on the dorsal area and very faint radial ribbing on the ventral area. Inner face very slightly convex with a slightly diagonal sulcus opening obliquely on the anterior rim and terminating almost on the postero-ventral point. Sulcus consisting of a short, wide, triangular ostium and a long, rather narrow cauda which is open-ended. A depression above the crista superior, accentuating it. A rounded upper angle and a slight, rounded lower angle at the junction of ostium and cauda. A very blunt rostrum and a slight excisura but no antirostrum or collicula present. A smooth, semicircular lower area.

*Discussion.* This otolith resembles those of the Recent subspecies *Osmerus eperlanus mordax* (Mitchill) in its outline and in the over-all characters of the sulcus. It lacks the serrated anterior part of the ventral rim but this characteristic osmeroid feature might be present in unworn specimens in view of the faint ribbing on the outer face. In the absence of corroborative osteological remains and considering the evident affinity of this sacculith to modern osmeroid forms it is probable that this represents an ancestral type of *Osmerus*.

*Other material and localities.* P. 51768 Gault, Lower Bed XI, Ford Place, Kent. G. Freeman Colln. P.47663 Gault, basal level below nodule bed, B. P.C.M. Pit, Small Dole, Sussex. Bernard Cooper Colln.

Order BERYCIFORMES  
Family BERYCIDAE *sensu lato*  
Genus *Sphaeronchus* Stinton and Torrens 1968

*Type species.* *Sphaeronchus dorsetensis* Stinton and Torrens, 1968, p. 250.

Further consideration of the sacculiths of *Sphaeronchus* assigned by Stinton and Torrens (1968, p. 50) to the Pycnodontidae suggests that they are more likely to have been derived from fishes related to the Berycoidei. The circular outline of the otolith together with the short, oval, wide ostium and nearly straight cauda could be interpreted as berycoid features and could logically be expected to evolve into the sacculiths seen today in the genera *Beryx*, *Gephyroberyx*, *Cleidopus*, *Mono-centris*, *Hoplostethus*, *Trachichthodes*, *Trachichthys*, and *Antigonia*. The Antigoniidae were assigned to the Berycoidei by myself (Stinton 1967) on the evidence of the sacculiths, which are remarkably similar to those of the Recent Australian berycoid *Trachichthys australis* Shaw and Nodder.

*Sphaeronchus rotundus* sp. nov.

Plate 31, fig. 10

*Holotype.* P. 51766 Lower Chalk (Upper Cenomanian), *subglobosus* zone, Gayton, Norfolk. A. Gale Colln.

*Dimensions.* Length 6.50 mm, width 5.67 mm.

*Description.* A partial impression of the inner face of a right sacculith, the original substance of the otolith having been decalcified. It is circular in outline and the rims appear to be continuous. The inner face is slightly convex. The median sulcus opens widely on the anterior rim and just reaches the posterior rim. It consists of a short, wide, somewhat semicircular ostium and a long, rather narrow, slightly arcuate cauda. A slightly rounded lower angle and a near right-angled upper angle at the junction of ostium and cauda. A depression above the crista superior, accentuating it. A blunt rostrum present but no apparent antirostrum. An excisura is probably present but there are no collicula.

*Discussion.* This otolith has the characters of the genus *Sphaeronchus* Stinton, described from the Inferior Oolite, but it differs from the Jurassic form in its ostial characters and more circular periphery. It is the only known otolith from the Chalk at present.

It is common to find objects simulating utriculiths of modern ariids at all Gault horizons where determinable otoliths occur. One such specimen (P. 51769, Pl. 31, fig. 11), demonstrates this similarity when examined cursorily. However, a closer inspection reveals that a trace of a sulcus still remains (seen as a straight line at the top of fig. 11 on Pl. 31). When a large series of these objects is examined it will be seen that they are the remains of large otoliths, probably mostly pterothrissids, which have suffered fracture and/or erosion of the dorsal area, the weakest part of

the sacculith. This results in a truncated, conic object which further erosion by rolling rounds off the fractured edges. It also removes the patina of the inner face to show the underlying laminated structure of the otolith. Many specimens have the remnants of the sulcus reduced to a small, spheroid central depression. The outer face usually retains the patina so that one may be easily misled into supposing that these were utriculiths of ariids.

### CONCLUSIONS

The frequently occurring sacculiths of *Pterothrissus* associated with elopid-like otoliths, *Albula* and a probable precursor of *Megalops* in the Gault, offer reasonable evidence of the geographical and climatic conditions pertaining at that time. Today the Pterothrissidae are restricted to two comparatively narrow areas, one off the west coast of Africa between latitudes 16° N. and 20° S. (Poll 1951-1959, p. 16) and the second around the 42° N. parallel in the Tsugare Straits, Japan (Jordan and Herre 1906, p. 619). The West African species *P. bellocci* Cadenat is commonest off the Congo region at depths of 120-250 m. It becomes rarer northwards but occurs fairly frequently off the coast of Senegal (Cadenat 1950) where the pelagic/littoral genera *Megalops*, *Elops*, and *Albula* are not uncommon. Thus the conditions prevailing during the deposition of the Gault may well have been comparable with those now obtaining in West African seas. The presence of the Japanese pterothrissid in more temperate waters beyond the range of the tropical *Elops*, *Megalops*, and *Albula* suggests an anachronism but in the depths at which both *Pterothrissus* species live it is probable that temperatures and habitats are similar.

The common occurrence of rolled fragments of otoliths suggests inshore wave and current action although it has been proved that currents of considerable strength may be encountered at all depths. The absence of otoliths comparable with those of other modern teleost groups in the Gault is noteworthy but this may be due to collecting methods so far used as these may tend to miss the smaller otoliths which often make up the bulk of the specimens in Tertiary and Recent deposits. There is no reason to suppose that the same situation did not obtain during the Cretaceous era.

The record of the two otoliths from the Speeton Clay suggests that intense collecting would bring to light other forms for it is evident that this clay is a suitable medium for their preservation. It may be mentioned here that while '*Elops*' *neocomiensis* (Priem) has predominantly elopid features the over-all shape of the otolith and the ostium have certain resemblances to percoid sacculiths and it is possible that this particular species could have evolved into certain of the modern percoids. The true elopid otoliths are relatively thin and small and the denseness of this fossil form suggests that the fish lived at some depth, rather than being pelagic. Frost (1925, p. 153) in his work on Recent otoliths makes the statement that 'Clupeoidea exhibit . . . primitive simplicity unapproached in other groups and that we may take these as the basic form from which the otoliths of later and more specialized fishes have been derived.' While this is undoubtedly true for some groups of modern teleosts this premiss is unacceptable for some of the groups mentioned below.

The osmeroid type of otolith exhibits some characteristics of modern osmeroids. Again, Frost (1925, p. 158) suggests that the sacculiths of the living *Osmerus eperlanus* Linnaeus, indicate an affinity with the berycoids and other unnamed groups.

In the absence of any comparable morphological features between the sacculiths this statement is also untenable. The Gault osmeroid sacculith does show a distinct affinity to the salmonid fishes and may well be related to the Salmoniformes. Patterson (*in* Harland *et al.* 1967, p. 658) listed a number of suborders under the order Salmoniformes of which only the Salmonoidei, Argentinoidei, and Galaxioidei have sacculiths of a type which could have evolved from the fossil '*Osmerus*' *lobatus* sp. nov. Patterson (1970) later described in detail two salmoniform Cenomanian species (*Gaudreyella audryi* and *Humbertia operata*) suggesting that they showed an affinity to the Recent genus *Hypomesus* and to the argentinoid/osmeroid fishes generally. It might well be that the sacculiths of '*Osmerus*' *lobatus* represent a fish referable to this group. The sub-orders listed by Gosline (1960, p. 361) and McAllister (1968, p. 52) also include these salmonoid groups.

One might reasonably expect to find berycoid otoliths in the Chalk in view of the typical berycoid skeletons which are a feature in some areas, especially as the Chalk forms appear to differ little from the Recent ones. However, the very nature of the Chalk deposits precludes the likelihood of any otoliths being found apart from casts similar to those described herein.

Patterson (1964) in his studies on Mesozoic acanthopterygians postulated three sub-orders, Polymixioidei, Dinopterygoidei, and Berycoidei, which together had evolved from a polymixiid stock. He included the genera *Beryx*, *Gephyroberyx*, *Cleidopus*, *Monocentris*, *Hoplostethus*, *Trachichthodes*, and *Trachichthys* within the Berycoidei together with certain other families including the Holocentridae. However, the sacculiths of Recent species of *Polymixia* are quite distinct from the true berycoids in their characters, as are the holocentrids and myripristids which appear to have some affinity with the polymixiids as far as the sulcus characters are concerned. Rosen and Patterson (1969, p. 460) divorced the Polymixioidei entirely from the Beryciformes, including them in the superorder Paracanthopterygii while the Beryciformes were transferred to the series Percomorpha within the superorder Acanthopterygii. This regrouping is consistent with the evidence of the otoliths of *Sphaeronchus* for these could well have evolved into the true berycoids of today and also certain modern deep-bodied percoids such as the Scorpidae, Monodactylidae, Sparidae, Lactariidae, and perhaps the Chandidae. In discussing the possible origin of the Perciformes Patterson (1964, p. 467) lists the Scorpidae, Monodactylidae, and Sparidae, together with some other groups including the Kyphosidae as being possible relatives of the berycoids. However, the sacculiths of *Kyphosus* bear no resemblance to typical berycoid sacculiths but have a distinct relationship to certain carangid otoliths. The characters of carangid sacculiths indicate that they probably evolved from an ancestral stock distinct from the berycoids.

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All of the described specimens are lodged in the collections of the Department of Palaeontology, British Museum (Natural History), and bear the registration numbers of the museum.

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FREDERICK C. STINTON  
51 Craigmoor Avenue  
Strouden Park  
Bournemouth  
Hants BH8 9LP



# LOWER DEVONIAN CONODONTS FROM NEW SOUTH WALES

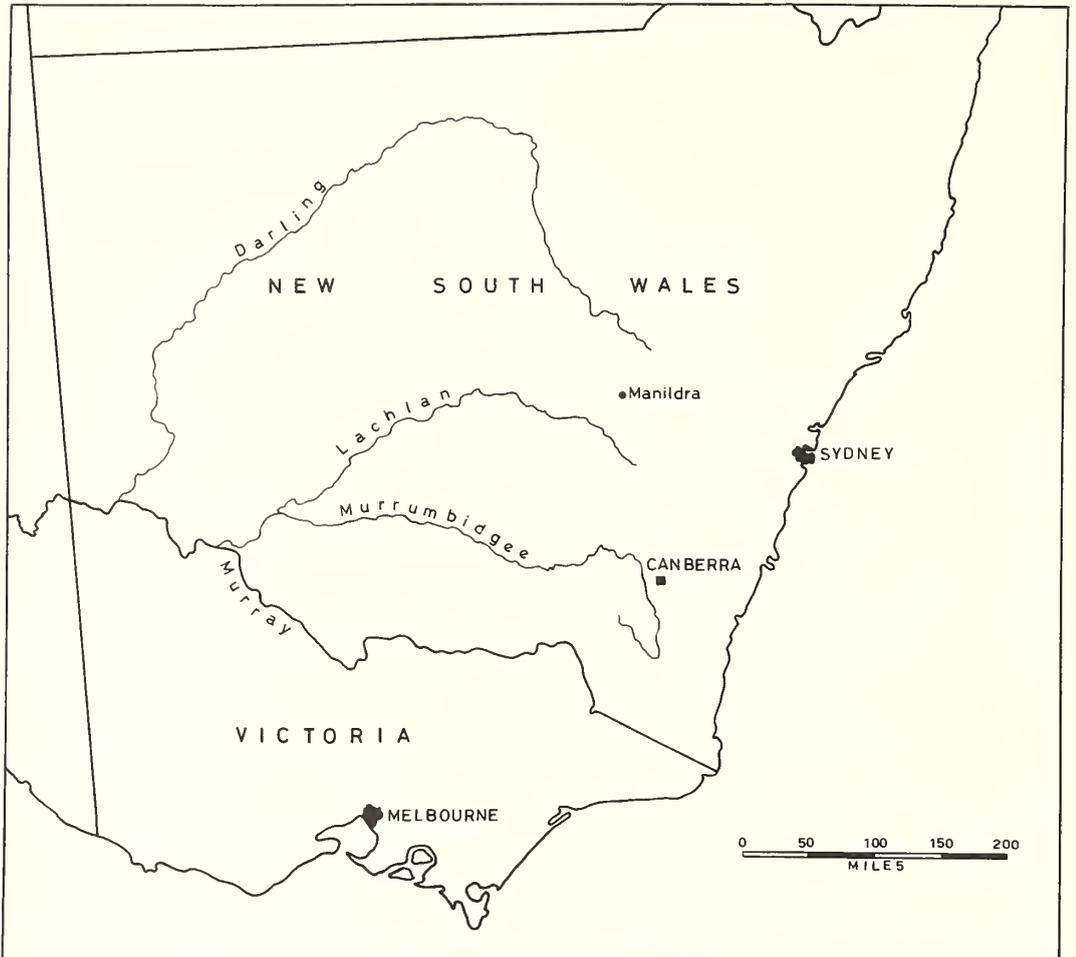
by NORMAN M. SAVAGE

**ABSTRACT.** Recent examination of the conodonts from the basal limestone of the Mandagery Park Formation suggests a middle to late Lochkovian (late Lower Gedinnian) age for this richly fossiliferous horizon. The fauna includes numerous early Lower Devonian conodonts but the characteristic early to late Praguian species *Spathognathodus sulcatus* and *S. optimus* are absent and this is significant in indicating a pre-Praguian upper age limit. A post-middle Lochkovian lower age limit is suggested by the presence of the conodonts *Belodella devonica*, *B. triangularis*, *S. inclinatus wurmi*, and *S. remscheidensis* in association with a brachiopod fauna which includes the genus *Quadrithyrus* and several other *Quadrithyrus* Zone brachiopods. Further, indirect, evidence of a late Lochkovian age is the association of *Quadrithyrus* Zone brachiopods with *Monograptus hercynicus* in western North America. A table of correlation is given for some important Lower Devonian sequences in eastern Australia and western North America.

THE Mandagery Park Formation, exposed in the vicinity of Manildra, New South Wales (text-fig. 1), consists largely of interbedded limestone and tuffaceous sandstone. Most of the formation is unfossiliferous but the basal limestone at Locality 1 of Savage (1968*a*, fig. 1) has yielded a rich fauna of brachiopods and corals with some gastropods, bryozoans, and conodonts. The brachiopod fauna has been described in several papers (Savage 1968*a, b, c*, 1969, 1970, 1971) in which the age of the fossiliferous basal horizon has been given as early Siegenian. The evidence of the conodonts described herein, together with new information relating to the age of brachiopod assemblages assigned to the *Quadrithyrus* Zone in northern Canada, suggests that the Mandagery Park Formation is older than Siegenian.

One of the difficulties in assessing the age of the eastern Australian deposits relative to the western European type sections is the facies difference. Traditionally, Rhenish stage names have been used for Lower Devonian deposits but it is becoming increasingly evident that the early Devonian faunas of eastern Australia can be more readily compared with those of the Bohemian facies of central and eastern Europe. The better knowledge of Lower Devonian graptolites in central and eastern Europe which has accumulated in the past decade and the growing record of Lower Devonian graptolites in eastern Australia are further factors making the Bohemian stage names more convenient. Correlation with the Rhenish stages is increasingly secondary via correlation with the Bohemian stages. Whether the base of the Mandagery Park Formation is considered to be of Gedinnian or Siegenian age will depend on where the Gedinnian-Siegenian boundary is drawn relative to the Bohemian stages. This vital correlation is still variously interpreted (Churkin and Brabb 1967; Carls 1969; Jaeger 1970; Fåhraeus 1971; Koreň 1971). In the absence of graptolites from the Rhenish area, conodont information from both the Siegenian type section and the Praguian sections would greatly aid correlation. Unfortunately conodonts are apparently absent from the Siegenian section and represented by only restricted faunas in the Praguian sections. Recent evidence from northern Canada discussed below suggests that this area might provide important mixtures of facies elements permitting more precise correlation of the Rhenish and Bohemian

stages. What is known to date indicates that the correlation of Carls (1969) was probably more accurate than most Rhenish-Bohemian correlations.



TEXT-FIG. 1. Locality map for Manildra.

Several of the species occurring in the Manildra fauna are long-ranging forms which do not at present appear to have precise stratigraphic value apart from indicating a general late Silurian or early Devonian age. Others are much more useful as age indicators and the presence of the forms *Belodella devonica*, *B. triangularis*, *Spathognathodus inclinatus wurmi*, and *S. remscheidensis* suggests a post-Pridolian age. The characteristic early to late Praguian form *S. sulcatus* and late Lochkovian to early Zlichovian form *S. optimus* are absent and this is significant in indicating a pre-Praguian age. These two species are known from several localities in eastern Australia (Philip 1965, 1966; Philip and Pedder 1967; Philip and Jackson 1970) and from Praguian age sediments in the Royal Creek and Solo Creek sections, Yukon Territory (Klapper 1969; Fåhræus 1971). Their absence from the Manildra fauna

suggests that the base of the Mandagery Park Formation is older than the Coopers Creek Formation in Victoria and the upper part of the *Spirigerina* Unit at Royal Creek where both species occur (Philip 1965; Klapper 1969). The Mandagery Park Formation brachiopod-conodont fauna is therefore most likely of middle to late Lochkovian age, being young enough to include the four post-Pridolian conodonts mentioned above together with the brachiopod *Quadrithyrus* and other *Quadrithyrus* Zone brachiopods such as are associated with *Monograptus hercynicus* in Nevada and Yukon Territory, and old enough to pre-date the appearance of the Praguian conodonts *S. sulcatus* and *S. optimus*.

The conodont faunas of the Tyers and Buchan areas, Victoria (Philip 1965, 1966) were among the first eastern Australian conodont faunas described and these have subsequently become important reference horizons within the Lower Devonian sequences of southeast Australia. The Coopers Creek Formation at Tyers contains *S. sulcatus* and *Icriodus bilatericrescens* which indicates an age younger than the *Quadrithyrus* Zone assemblages in Nevada and Yukon Territory. Philip and Pedder (1967) consider this fauna to be of early Siegenian age and this correlation is accepted herein (text-fig. 2). The underlying Boola Beds contain a brachiopod fauna very

STAGES		GRAPTOLITE ZONES	CONODONT RANGES	MANILDRA N.S.W. AUSTRALIA	TYERS VICTORIA AUSTRALIA	BUCHAN VICTORIA AUSTRALIA	CENTRAL NEVADA U.S.A.	ROYAL CREEK YUKON CANADA
BOHEMIAN	RHENISH							
EIFELIAN								
ZLICHOVIAN	EMSIAN	<i>M. pacificus</i>	<i>S. exiguus</i>			MURRINDAL LIMESTONE		
				<i>P. foveolatus</i>			BUCHAN CAVES LST	
PRAGUIAN	SIEGENIAN	<i>M. yukonensis</i>	<i>P. dehiscens</i>				TREMATOSPIRA ZONE	GYPIDULA SPI— BICONOSTROPHIA UNIT
		<i>M. thomasi</i>	<i>S. sulcatus</i>	<i>S. optimus</i>		COOPERS CREEK FORMATION	SPINOPLASIA ZONE	
LOCHKOVIAN	GEDINNIAN	<i>M. hercynicus</i>	<i>I. pesovis</i>		MANDAGERY PARK FORMATION		QUADRITHYRIS ZONE	SPIRIGERINA UNIT
		<i>M. praehercynicus</i>	<i>I. woschmidti</i>	<i>S. remscheidensis</i>	MARADANA SHALE	BOOLA BEOS		GYPIDULA PELAGICA ZONE
PRIDOLIAN		<i>M. uniformis</i> <i>M. angustidens</i> <i>M. transgrediens</i>			FAIRHILL FORMATION			

TEXT-FIG. 2. Correlation chart for selected Lower Devonian sequences in south-east Australia and western North America.

close to that of the Maradana Shale at Manildra and both deposits are here assigned an early Lochkovian age. The Buchan Group limestones in Victoria are younger than the Coopers Creek Formation. The presence of *S. exiguus*, *Polygnathus foveolatus*, and *P. deshiscens* indicates a late Praguian to early Zlichovian (early to middle Emsian) age for these Buchan deposits.

Of considerable help in tying together the Bohemian and Rhenish stages is a recent discovery on Prince of Wales Island, northern Canada. R. Thorsteinsson has found a primitive pteraspid, very similar to *P. gosseleti*, associated with brachiopods which J. G. Johnson and A. J. Boucot have identified and assigned to the *Quadrithyris* Zone (pers. comm., R. Thorsteinsson 1971). This association points to a late Lower Gedinnian ('middle' Gedinnian) age for the *Quadrithyris* assemblage in that instance, assuming the 'Psammites de Lievin' of northern France are of late Lower Gedinnian age. As the *Quadrithyris* assemblage has been found associated with *M. hercynicus* in Nevada and Yukon Territory, these recent developments suggest that the middle Lochkovian *M. hercynicus* Zone of the Bohemian facies may be equivalent to the early Dittonian (late Lower Gedinnian) *P. gosseleti* horizon of the Old Red Sandstone and Rhenish facies. In terms of the Rhenish stages the *Quadrithyris* Zone of Nevada and Yukon Territory thus seems to be older than hitherto shown. The overlying Spinoplasia Zone is also affected by this correlation readjustment and is probably no younger than Upper Gedinnian in age. Similarly the *Gypidula pelagica* fauna in Nevada and Yukon Territory is probably of early Lower Gedinnian age rather than of late Lower Gedinnian age as commonly suggested in recent years (see Klapper 1969; Johnson 1970; Klapper *et al.* 1971).

#### TAXONOMIC PROCEDURES

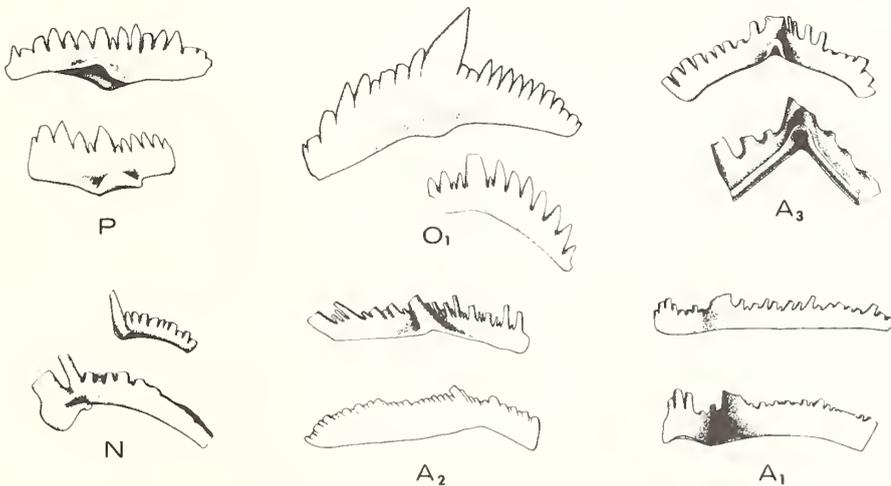
For a number of years attempts have been made to construct a biological conodont taxonomy based on actual clusters of elements (Scott 1934; Rhodes 1962) or based on logical and numerical analysis of large collections of conodont elements occurring at certain horizons (Walliser 1964; Bergström and Sweet 1966; Kohut 1969; Jeppsson 1969, 1971; Klapper and Philip 1971). From a biological point of view a multi-element classification is manifestly more satisfactory than a taxonomy based on form species, and recent progress in defining multi-element species suggests that this type of conodont taxonomy will progressively replace the single-element taxonomy during the next few years.

The conodonts recovered from the Mandagery Park Formation are few in numbers and do not lend themselves to statistical analysis nor to logical analysis at a time when very few reference multi-element species from Lower Devonian horizons are on record for comparison. Even with such meagre faunas, one might expect to be able to recognize certain recurring associations indicative of multi-element species by comparing enough assemblages of isolated elements from different localities. However, such groupings do not fall into place as smoothly as one might hope and there is evidence that the same form species may occur in more than one multi-element species (Klapper and Philip 1971). That individual elements within any apparatus have evolved independently is indicated by the great variety of ranges known for conodont elements. Branson and Mehl (1936) used the evidence of these

range differences to argue that natural assemblages do not exist, but a more acceptable explanation is that individual elements within a multi-element organism have evolved at different speeds. Thus there are problems resulting from both differential evolution of elements in a single apparatus and parallel evolution of elements in distinct apparatuses.

Klapper and Philip (1971) have described a method of reconstruction of Devonian apparatuses in which a system of symbols is used for the individual elements. Their concept of what might comprise a natural assemblage is founded on known clusters of elements. Recognition of assemblage species with elements different from those in known clusters depends on logical deduction from recurring sets of elements and numerical analysis.

The Manildra material appears to include evidence of two multi-element species of a group classified as Type 1 by Klapper and Philip (1971, pp. 431–432). Their Type 1 apparatuses comprise a platform element (P) such as *Spathognathodus* or *Polygnathus*, an ozarkodinan element ( $O_1$ ) such as *Ozarkodina*, a neoprioniodontan element (N) such as *Neoprioniodus*, a hindeodellan element ( $A_1$ ) such as *Hindeodella*, a plectospathodontan element ( $A_2$ ) such as *Plectospathodus*, and a symmetrical element ( $A_3$ ) such as *Trichonodella*; the last three elements forming a symmetry transition series. Although there are apparently two Type 1 species present in the Manildra material it is not possible at present to determine how these elements are combined. Several associations of the elements are possible to result in two apparatuses with the Type 1 diagnosis P,  $O_1$ , N,  $A_1$ ,  $A_2$ ,  $A_3$  (text-fig. 3). Other elements in the Manildra material are suggestive of the Type 3 apparatus *Delotaxis* Klapper and Philip. The form species *Lonchodina walliseri* is thought by Klapper and Philip to represent the  $O_2$  element in their *Delotaxis* apparatus. Presumably the Manildra form species *Ligonodina* aff. *salopia* and *Ligonodina* sp. also belong in this apparatus. The abundant *Belodella* and *Pauderodus* elements in the Manildra fauna may be



TEXT-FIG. 3. Elements of two apparatuses of a group classified as Type 1 by Klapper and Philip (1971) with the diagnosis P,  $O_1$ , N,  $A_1$ ,  $A_2$ ,  $A_3$ . It is not possible at present to determine how these elements are combined. Scale of elements  $\times 40$ .

tentatively included in the Group 1 apparatuses of Jeppsson (1971). The work of Lange (1968) on *Belodella* clusters indicates that the total apparatus probably comprised at least six pairs of these simple elements.

Apart from the general observations above, the systematic treatment in this paper is based on the older taxonomy of isolated elements. A number of elements are described which cannot at present be even tentatively referred to multi-element apparatuses but by describing such occurrences the evidence necessary to build a more complete multi-element taxonomy will eventually become available.

In the systematic descriptions below the specimen numbers are those of the Palaeontology Collection, Department of Geology and Geophysics, University of Sydney.

#### SYSTEMATIC DESCRIPTIONS

##### Genus BELODELLA Ethington 1959

*Type species.* *Belodus devonicus* Stauffer 1940, by original designation of Ethington 1959, p. 272.

##### *Belodella devonica* (Stauffer 1940)

Plate 32, figs. 19, 20, 25, 26; text-fig. 4A, B, C

Differences in the cross-section of the base have been used by several workers in diagnosing various forms of *Belodella*. However, Serpagli (1967) has suggested that there is a continuous gradation between forms with a symmetrically biconvex cross-section, usually referred to *B. devonica*, and forms with a strongly triangular cross-section, usually referred to *B. triangularis*. The specimens available in the present study exhibit very different cross-sectional profiles. Three distinct types occur (text-figs. 4B, 5B, 6B) and the gradation reported by Serpagli is not evident. With so few specimens available in this Manildra fauna it is not possible to comment on the advisability of adopting Serpagli's synonymy and the division into separate forms is tentatively followed herein.

*B. devonica* has been described previously from Minnesota (Stauffer 1940), Nevada (Clark and Ethington 1966), Pakistan (Barnett *et al.* 1966), Turkestan (Moskolenko 1966), and England (Rhodes and Dineley 1957) in deposits of early Lower Devonian to possible Upper Devonian age.

*Material.* Figured specimens SU11921 and SU11922 plus one other.

##### *Belodella resima* (Philip 1965)

Plate 32, figs. 9, 10; text-fig. 5A, B, C

This form appears to be characteristic of early Devonian limestones in eastern Australia but also has been recorded from the Upper Silurian Bainbridge Limestone of Missouri (Rexroad and Craig 1971) and may be present in the early Lower Devonian fauna described from Pakistan by Barnett *et al.* (1966). Fåhraeus (1971) has placed *B. resima* and *B. triangularis* in synonymy with *B. devonica* in his treatment of the Lower Devonian conodonts from the Yukon Territory and it is possible that forms with a *B. resima* cross-section also occur in that fauna.

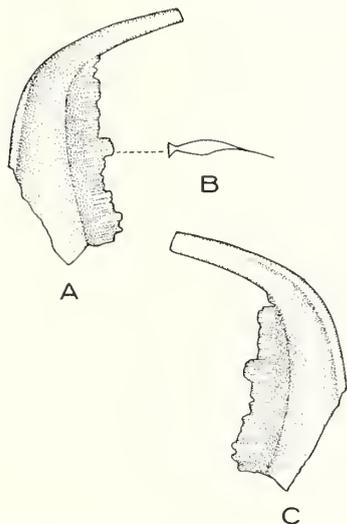
*Material.* Figured specimen SU11919 plus 2 others.

*Belodella triangularis* (Stauffer 1940)

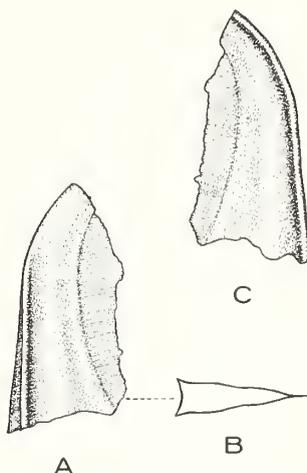
Plate 32, figs. 21, 22; text-fig. 6A, B, C

Only two specimens are available but these clearly belong to *B. triangularis*. In cross-section the cusp is strongly triangular and this is accentuated by the prominent carinae projecting from the anterior face. This element has been recorded previously in the Lower Devonian Tyers and Buchan faunas from Victoria (Philip 1965, 1966) in addition to several Devonian occurrences in America and elsewhere. It appears to range through the Devonian.

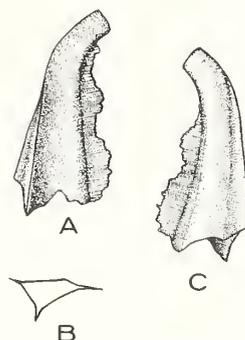
*Material.* Figured specimen SU11923 plus one other.



TEXT-FIG. 4. *Belodella devonica* (Stauffer 1940). A, C, Lateral views of SU11922. B, Cross-section at mid-height.  $\times 60$ .



TEXT-FIG. 5. *Belodella resima* (Philip 1965). A, C, Lateral views of SU11919. B, Cross-section at base.  $\times 60$ .



TEXT-FIG. 6. *Belodella triangularis* (Stauffer 1940). A, C, Lateral views of SU11923. B, Cross-section at base.  $\times 60$ .

## Genus HINDEODELLA Bassler 1925

*Type species.* *Hindeodella subtilis* Bassler 1925, by original designation of Bassler 1925, p. 219.

*Hindeodella equidentata* Rhodes 1953

Plate 33, fig. 22; plate 34, figs. 4-6; text-fig. 7A, B, C

This element appears to be restricted to late Silurian and early Devonian deposits. The earliest recorded occurrence is that of the type material in the Aymestry Limestone (Rhodes 1953) of Lower Ludlow age and the latest occurrence is in the Murrindal Limestone in eastern Australia (Philip 1966) which is of late Praguian or early Zlichovian age. The element occurs in numerous faunas described from continental Europe (Ziegler 1960; Walliser 1964; Schulze 1968) and has also been recorded from Morocco (Ethington and Furnish 1962) and northern Canada (Walliser 1960).

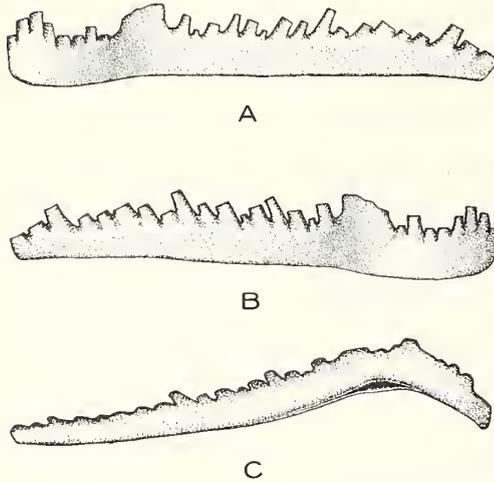
*Material.* Figured specimens SU11945 and SU11955 plus one other.

*Hindeodella* sp. A.

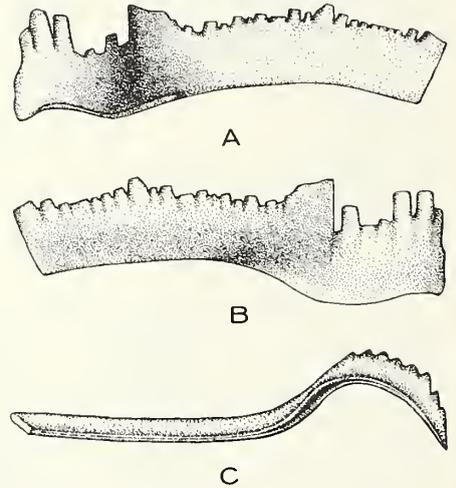
Plate 34, figs. 1-3; text-fig. 8A, B, C

Only a single specimen is available but this is very distinctive. It is characterized by the hook-like curvature of the bars, the depth of the bars, and the flattened to concave outer face of the main cusp near its base. The posterior denticles are considerably smaller than those of *H. equidentata* and *Hindeodella* sp. B.

*Material.* Figured specimen SU11954.



TEXT-FIG. 7. *Hindeodella equidentata* Rhodes 1953. A-C, Inner lateral, outer lateral, and aboral views of SU11955.  $\times 60$ .



TEXT-FIG. 8. *Hindeodella* sp. A. A-C, Inner lateral, outer lateral, and aboral views of SU11954.  $\times 60$ .

## EXPLANATION OF PLATE 32

All figures  $\times 40$ .

Figs. 1, 2. *Ligonodina* aff. *salopia* Rhodes 1953. Lateral views of SU11912.

Figs. 3, 4. *Paltodus* sp. Lateral views of SU11913.

Figs. 5, 6. *Panderodus unicostatus* (Branson and Mehl 1933). Lateral views of SU11914.

Figs. 7, 8. *Panderodus simplex* (Branson and Mehl 1933). Lateral views of SU11918.

Figs. 9, 10. *Belodella resima* (Philip 1965). Lateral views of SU11919.

Figs. 11, 12. Gen. et sp. indet. Lateral views of SU11920.

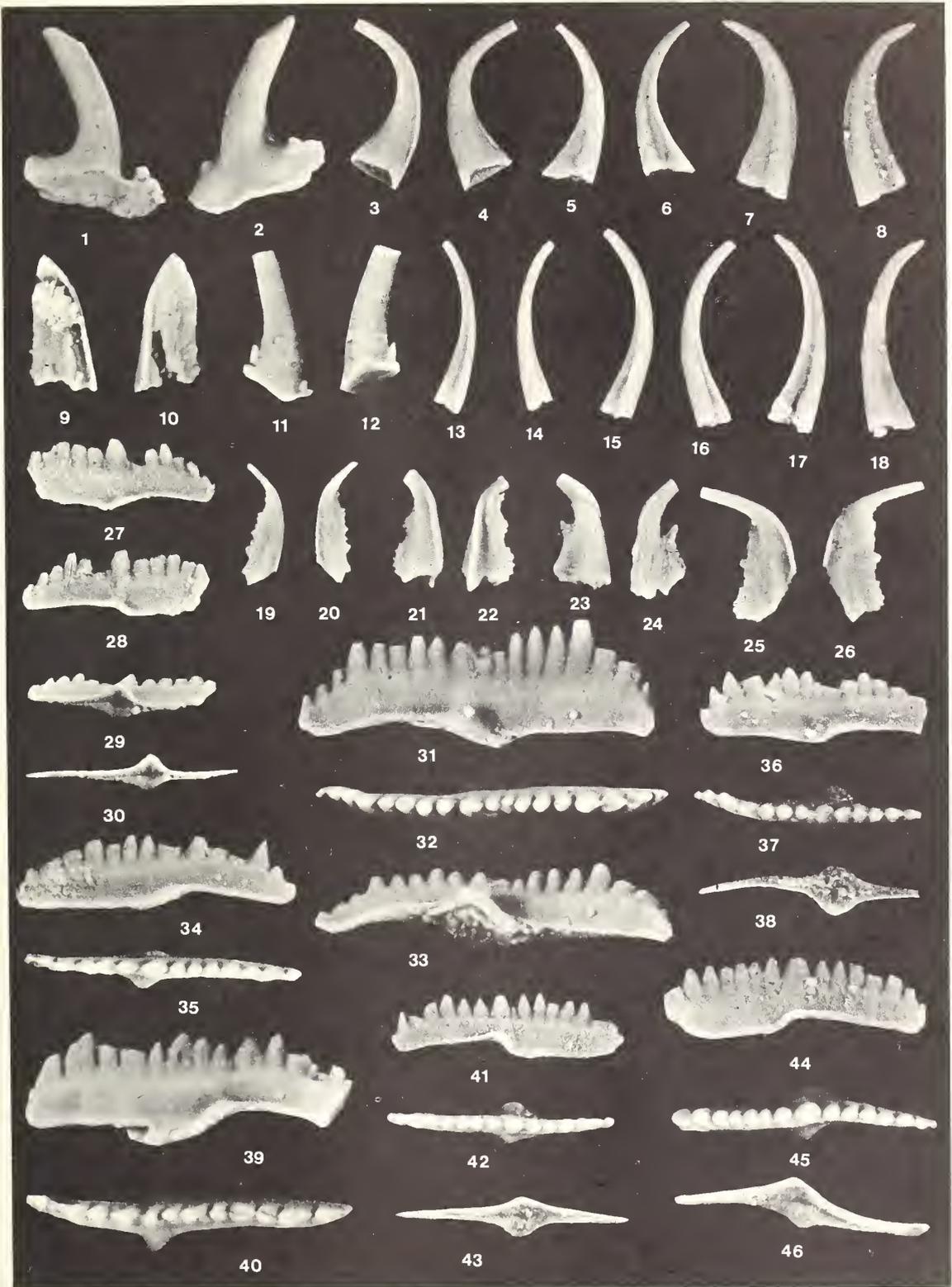
Figs. 13-18. *Panderodus gracilis* (Branson and Mehl 1933). 13, 14, Lateral views of SU11915. 15, 16, Lateral views of SU11916. 17, 18, Lateral views of SU11917.

Figs. 19, 20, 25, 26. *Belodella devonica* (Stauffer 1940). 19, 20, Lateral views of SU11921. 25, 26, Lateral views of SU11922.

Figs. 21, 22. *Belodella triangularis* (Stauffer 1940). Lateral views of SU11923.

Figs. 23, 24. *Rotundacodina dubia* (Rhodes 1953). Lateral views of SU11924.

Figs. 27-46. *Spathognathodus inclinatus wurmi* Bischoff and Sannemann 1958. 27-29, Lateral and aboral views of SU11925. 30, Aboral view of SU11926. 31-33, Lateral, oral, and aboral views of SU11927. 34, 35, Lateral and oral views of SU11928. 36-38, Lateral, oral, and aboral views of SU11929. 39, 40, Lateral and oral views of SU11930. 41-43, Lateral, oral, and aboral views of SU11931. 44-46, Lateral, oral, and aboral views of SU11932.

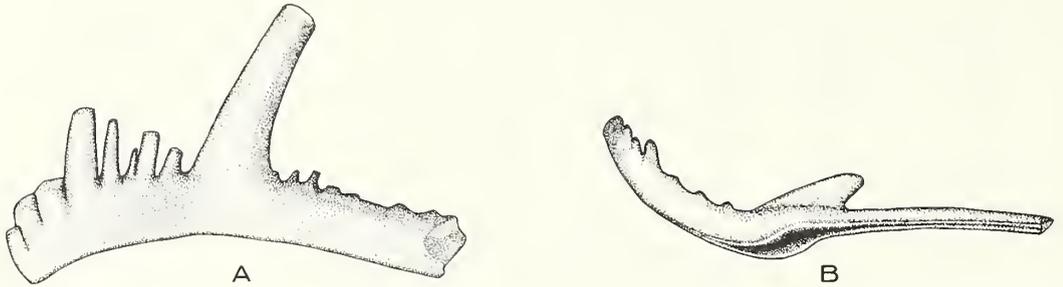


SAVAGE, Lower Devonian conodonts

*Hindeodella* sp. B.

Plate 33, figs. 2, 3, 11, 12; text-fig. 9A, B

This material bears some resemblance to *H. equidentata* but it is stouter than the type material of that element and has a larger, more tapering main cusp. There is also a more pronounced downward flexure of the anterior bar in the Manildra form.



TEXT-FIG. 9. *Hindeodella* sp. B. A, B, Inner lateral and aboral views of SU11934.  $\times 60$ .

Rexroad and Craig (1971) have restudied the type material of *H. confluens* and according to their description this Manildra material could belong to that form. Klapper (pers. comm., 1971) assures me that the denticles of *H. confluens* are characteristically fused.

*Material.* Figured specimens SU11934 and SU11935 plus one other.

*?Hindeodella* sp.

Plate 34, figs. 12, 13

Several fragments of these bars are present in the collection. They may belong to a species of *Hindeodella*.

*Material.* Figured specimens SU11959 and SU11960 plus four others.

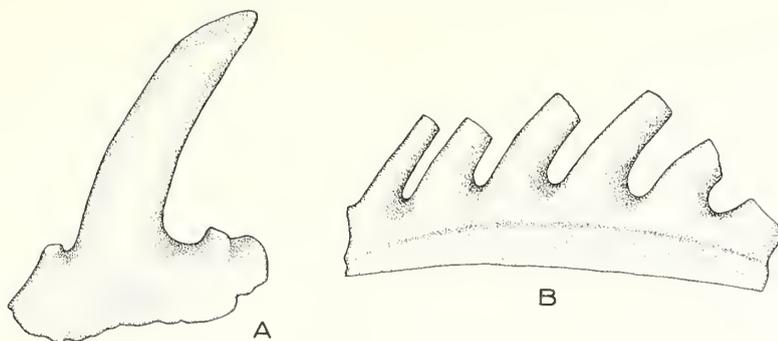
## Genus LIGONODINA Bassler 1925

*Type species.* *Ligonodina pectinata* Bassler 1925, by original designation of Bassler 1925, p. 218.

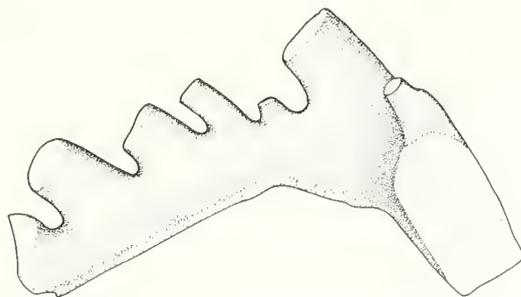
*Ligonodina* aff. *salopia* Rhodes 1953

Plate 32, figs. 1, 2; plate 33, fig. 36; plate 34, figs. 14, 15; text-figs. 10A, B; 11

This material resembles the type material from the Aymestry Limestone and several of the specimens from the Rheinisches Schiefergebirge described by Ziegler (1960). However, the Manildra specimens are unusually large and may be more mature than the type material. A detailed comparison is difficult with so few specimens available.



TEXT-FIG. 10. *Ligonodina* aff. *salopia* Rhodes 1953. A, Lateral view of main cusp fragment SU11912. B, Lateral view of posterior bar fragment SU11961.  $\times 60$ .



TEXT-FIG. 11. *Ligonodina* aff. *salopia* Rhodes 1953. Inner view of fragment SU11952.  $\times 60$ .

*L. salopina* appears to be restricted to deposits of Upper Silurian and Gedinnian age. It has been recorded mostly in continental Europe (Ziegler 1960; Walliser 1964) and England (Rhodes 1953).

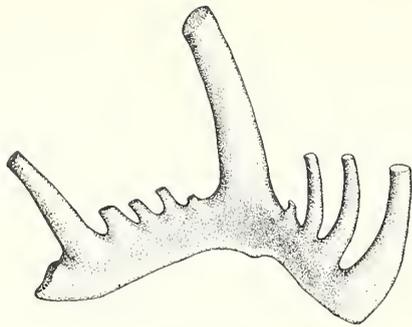
*Material.* Figured specimens SU11912, SU11952, and SU11961.

#### *Ligonodina* sp.

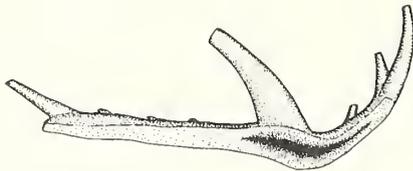
Plate 33, figs. 4-6, 37, 38; text-fig. 12A, B

This appears to be a new form of *Ligonodina* but is represented by only a single relatively complete specimen plus one fragment. It shows some resemblance to *L. silurica* Branson and Mehl but differs in possessing posterior denticles which are fewer and which become progressively larger away from the main cusp. Forms of *Ligonodina* are not prominent in the conodont literature of eastern Australia. Philip (1967) described two elements from the Middle Devonian deposits of New South Wales. The Manildra form is easily distinguished from both *Ligonodina* sp. A and *Ligonodina* sp. B of Philip (1967, pl. 3, figs. 6-8, 13, 14) in having denticles more closely set and in being less sharply geniculate. Furthermore, the processes are relatively deeper and there is no sign of the interposed denticles visible in some of the younger material.

*Material.* Figured specimen SU11936 and SU11948.

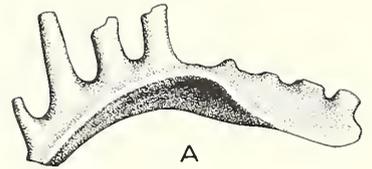


A

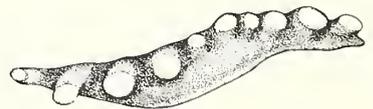


B

TEXT-FIG. 12. *Ligonodina* sp. A, B, Inner lateral and aboral views of SU11936.  $\times 60$ .



A



B

TEXT-FIG. 13. *Lonchodina walliseri* Ziegler 1960. A, B, Lateral and oral views of SU11947.  $\times 60$ .

### Genus LONCHODINA Bassler 1925

*Type species.* *Lonchodina typicalis* Bassler 1925, by original designation of Bassler 1925, p. 219.

#### *Lonchodina walliseri* Ziegler 1960

Plate 33, figs. 26-28; text-fig. 13A, B

This form lies well within the variation of Ziegler's illustrated specimens (Ziegler 1960, pl. 14, figs. 2, 6, 7). An error in Walliser's 1964 synonymy (p. 44) is in need of comment as it has been followed by several later workers. Walliser refers figs. 1, 3, and 7 of Ziegler 1960, pl. 14, to *L. walliseri*, but on the preceding page he refers figs. 1 and 3 of the same plate to *Lonchodina cristagalli*. Walliser evidently intended to include Ziegler's original figures of *Lonchodina walliseri* in his 1964 synonymy, viz. Ziegler 1960, pl. 14, figs. 2, 6, and 7.

*Lonchodina* sp. of Rexroad (1967, p. 38, pl. 3, fig. 5) was excluded from *L. walliseri* because the basal cavity did not lie below the main cusp. However, this is not unusual in *L. walliseri* and is visible in some of the specimens figured by Walliser (1964, pl. 30, figs. 26, 30, 33) in addition to the material described herein. The basal cavity is commonly displaced posteriorly to underlie the proximal posterior denticles (text-fig. 13B).

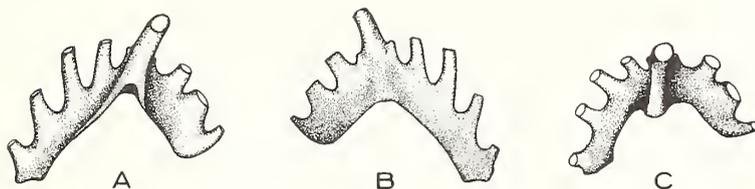
*L. walliseri* has previously been described from the Lower Silurian of North

America (Rexroad 1967), from the Upper Silurian of Europe (Walliser 1957, 1964), and from the Lower Devonian of eastern Australia (Philip 1965) and Europe (Ziegler 1960).

*Material.* Figured specimens SU11947 and SU11948 plus one other.

*Lonchodina greilingi* Walliser 1957

Plate 33, figs. 23, 24; text-fig. 14A, B, C



TEXT-FIG. 14. *Lonchodina greilingi* Walliser 1957. A-C, Inner lateral, outer lateral, and aboral views of SU11946.  $\times 60$ .

This specimen of *L. greilingi* appears to be a juvenile form. It bears some resemblance to *Trichonodella asymmetrica* Nicoll and Rexroad 1969 but differs in having more widely spaced denticles and less deep bars. *L. greilingi* is characteristically a Silurian and early Lower Devonian element. It has been described previously from Silurian beds in Morocco (Ethington and Furnish 1962), Spain (Kockel 1958), and Algeria (Müller 1962), and from Lower Devonian beds in Germany (Ziegler 1960, Walliser 1957, 1964), and eastern Australia (Philip 1965).

*Material.* Figured specimen SU11946.

Genus NEOPRIONIODUS Rhodes and Müller 1956

*Type species.* *Prioniodus conjunctus* Gunnell 1933, by original designation of Rhodes and Müller 1956, p. 698.

*Neoprioniodus excavatus* (Branson and Mehl 1933)

Plate 33, figs. 18, 19, 21, 25; text-fig. 15A, B, C

The review of this element by Rexroad and Craig (1971) has helped clarify the range of variation which occurs in toptype material. They have excluded many occurrences previously assigned to the form. Their restricted diagnosis is followed here. *N. excavatus* is known previously from deposits of Upper Silurian age in North America (Branson and Mehl 1933a; Rexroad and Craig 1971) and Europe (Walliser 1964; Jeppsson 1969), and from Lower Devonian deposits in Morocco (Ethington and Furnish 1962), Europe (Bischoff and Sannemann 1958), and eastern Australia (Philip 1965).

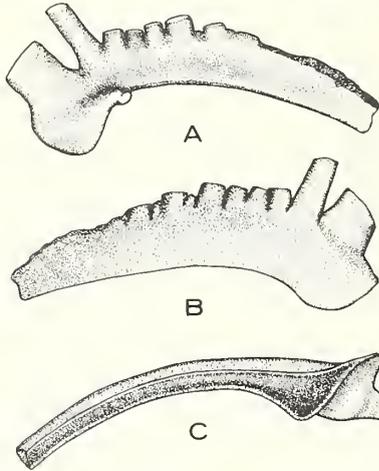
*Material.* Figured specimens SU11943 and SU11944 plus one other.

*Neoprioniodus* sp.

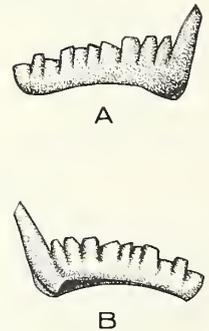
Plate 33, figs. 34, 35; text-fig. 16A, B

This form bears some resemblance to *N. planus* Walliser 1964 but differs in having a main cusp which is erect or slightly inclined anteriorly instead of being inclined posteriorly and in having a gently arched lower margin to the posterior bar.

*Material.* Figured specimen SU11951 plus six others.



TEXT-FIG. 15. *Neoprioniodus excavatus* (Branson and Mehl 1933). A-C, Inner lateral, outer lateral, and aboral views of SU11944.  $\times 60$ .



TEXT-FIG. 16. *Neoprioniodus* sp. A, B, Outer lateral and inner lateral views of SU11951.  $\times 60$ .

## EXPLANATION OF PLATE 33

All figures  $\times 40$ .

- Figs. 1, 7-10. *Ozarkodina typica denckmanni* Ziegler 1956. 1, Lateral view of SU11933. 7, 9, Lateral and aboral views of SU11937. 8, 10, Lateral and oral views of SU11938.
- Figs. 2, 3, 11, 12. *Hindeodella* sp. B. 2, 3, Outer lateral and inner lateral views of SU11934. 11, 12, Outer lateral and inner lateral views of fragment SU11935.
- Figs. 4-6, 37, 38. *Ligonodina* sp. 4-6, Outer lateral, inner lateral, and oral views of SU11936. 37, 38, Aboral and oral views of fragment SU11948.
- Figs. 13-17. *Ozarkodina media* Walliser 1957. 13, Lateral view of SU11939. 14, Lateral view of SU11940. 15, Lateral view of SU11941. 16, 17, Lateral and aboral views of SU11942.
- Figs. 18, 19, 21, 25. *Neoprioniodus excavatus* (Branson and Mehl 1933). 18, 19, 21, Inner lateral and outer lateral views of SU11943. 25, Lateral view of SU11944.
- Figs. 20, 29-33. *Plectospathodus extensus* Rhodes 1953. 20, 32, 33, Aboral, inner lateral, and outer lateral views of SU11949. 29, 30, 31, Outer lateral, oral, and inner lateral views of SU11950.
- Fig. 22. *Hindeodella equidentata* Rhodes 1953. Inner lateral view of SU11945.
- Figs. 23, 24. *Lonchodina greilingi* Walliser 1957. Lateral views of SU11946.
- Figs. 26-28. *Lonchodina walliseri* Ziegler 1960. Lateral and oral views of SU11947.
- Figs. 34, 35. *Neoprioniodus* sp. Oral and outer lateral views of SU11951.
- Fig. 36. *Ligonodina* aff. *salopia* Rhodes 1953. Inner lateral view of fragment SU11952.
- Figs. 39-41. *Trichonodella inconstans* Walliser 1957. Oral, anterior, and aboral views of fragment SU11953.



SAVAGE, Lower Devonian conodonts

Genus *OZARKODINA* Branson and Mehl 1933

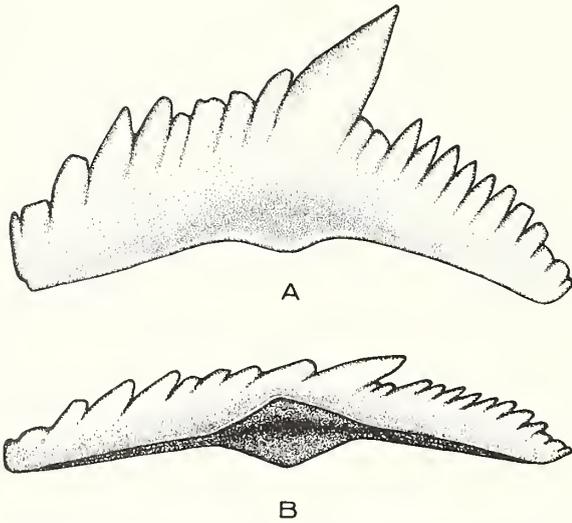
*Type species. Ozarkodina typica* Branson and Mehl 1933, by original designation of Branson and Mehl 1933a, p. 51.

*Ozarkodina typica denckmanni* Ziegler 1956

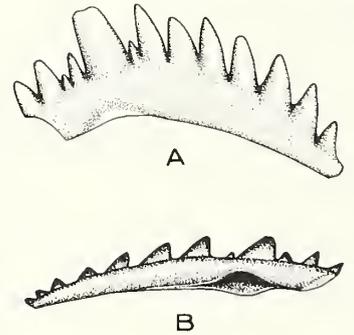
Plate 33, figs. 1, 7-10; text-fig. 17A, B

Only one mature and two immature specimens have been recovered. *O. typica denckmanni* has previously been described in eastern Australia from the Tyers, Lilydale, Buchan Caves, and Murrindal Limestones in Victoria, and from the Wee Jasper Limestone and Lick Hole Limestone in New South Wales. It is known to range from late Upper Silurian to at least Emsian age deposits in Europe (Walliser 1964).

*Material.* Figured specimens SU11933, SU11937, and SU11938.



TEXT-FIG. 17. *Ozarkodina typica denckmanni* Ziegler 1956.  
A, B, Lateral and aboral views of SU11933.  $\times 60$ .



TEXT-FIG. 18. *Ozarkodina media* Walliser 1957. A, B, Lateral and aboral views of SU11941.  $\times 60$ .

*Ozarkodina media* Walliser 1957

Plate 33, figs. 13-17; text-fig. 18A, B

*Ozarkodina* has commonly been interpreted to include a wide range of variation. Some forms assigned to that genus could equally well be referred to *Bryodontus*. Reference to *Bryodontus* may be appropriate when the denticles are not in contact for most of their height and arise from bars with well-developed oral shoulders as in some of the Manildra material (pl. 32, figs. 15, 16). In this present study insufficient material is available for a critical review of these problems and the popular interpretation of *O. media* has been followed.

The form is common in Upper Silurian and Lower Devonian assemblages and

has been described previously from England (Rhodes 1953), North Africa (Ethington and Furnish 1962), Spain (Kockel 1958), Germany (Walliser 1957, 1964; Bischoff and Sannemann 1958), North America (Rexroad and Craig 1971; Fåhraeus 1971) and eastern Australia (Philip 1965, 1966). These occurrences indicate a range extending into Zlichovian age (Upper Emsian) deposits.

*Material.* Figured specimens SU11939, SU11940, SU11941, and SU11942 plus eight others.

#### Genus PALTODUS Pander 1856

*Type species.* *Paltodus subaequalis* Pander 1856, by subsequent designation of Ulrich and Bassler 1926, p. 7.

#### *Paltodus* sp.

Plate 32, figs. 3, 4; text-fig. 19A, B, C, D

This material is closely related to the form described by Philip (1965, p. 109, pl. 8, figs. 36, 37) from the Tyers area in Victoria but may differ in possessing a more lenticular cross-section. It appears to be close to *Paltodus* n. sp. A from the Lower Silurian Brassfield Limestone described by Nicoll and Rexroad (1969, p. 52, pl. 7, figs. 21, 22).

*Material.* Figured specimen SU11913 plus five others.

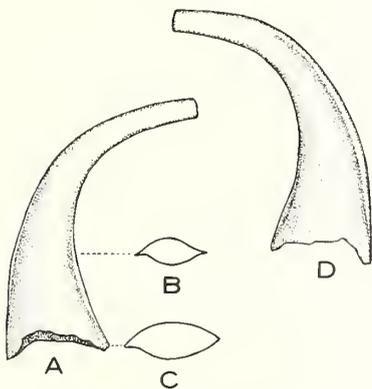
#### Genus PANDERODUS Ethington 1959

*Type species.* *Paltodus unicastatus* Branson and Mehl 1933, by original designation of Ethington 1959, p. 284.

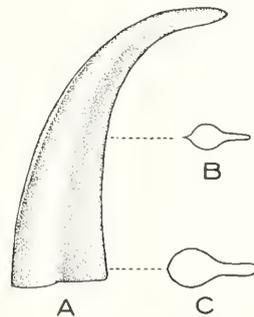
#### *Panderodus simplex* (Branson and Mehl 1933)

Plate 32, figs. 7, 8; text-fig. 20A, B, C

Rexroad and Craig have re-examined and re-figured the type material of this element and extensively revised the synonymy (Rexroad and Craig 1971, p. 697).



TEXT-FIG. 19. *Paltodus* sp. A, D, Lateral views of SU11913. B, Cross-section at mid-height. C, Cross-section at base.  $\times 60$ .



TEXT-FIG. 20. *Panderodus simplex* (Branson and Mehl 1933). A, Lateral view of SU11918. B, Cross-section at mid-height. C, Cross-section at base.  $\times 60$ .

These *Manildra* specimens differ from most descriptions of material referred to *P. simplex* in possessing a small carina developed along part of the anterior margin. However, such a carina is clearly visible in the re-figured type material (Rexroad and Craig 1971, pl. 81, figs. 35–40), and there seems little doubt that the *Manildra* specimens are the same element.

As diagnosed by Rexroad and Craig this form ranges from the Ordovician (Bergström 1961) to the late Lower Devonian (Philip 1966).

*Material.* Figured specimen SU11918 plus twenty-six others.

*Panderodus unicostatus* (Branson and Mehl 1933)

Plate 32, figs. 5, 6; text-fig. 21A, B, C

Many occurrences of *P. unicostatus* have been recorded and the diagnosis varies considerably with different authors. The problem has recently been discussed by Rexroad and Craig (1971, pp. 697, 698) who conclude that the material of many authors is not well enough figured for the precise nature of the carina or carinae to be assessed. Only a detailed examination of all material previously referred to this element would lead to a reliable synonymy.

*Material.* Figured specimen SU11914 plus twelve others.

*Panderodus gracilis* (Branson and Mehl 1933)

Plate 32, figs. 13–18; text-fig. 22A, B

There are some differences between specimens in the *Manildra* assemblage. All are slender and evenly recurved but the position and sharpness of the angles vary so that a considerable range of cross-section profiles results. Nevertheless, the stout opposed ridges and deep re-entrant excavations on each side are common to all specimens. Rexroad and Craig (1971, pp. 695, 696) recognize two variants in their collection but a clear distinction is not evident in the *Manildra* material. The records of the form indicate a range from Ordovician to Devonian.

*Material.* Figured specimens SU11915, SU11916, and SU11917 plus twenty-four others.

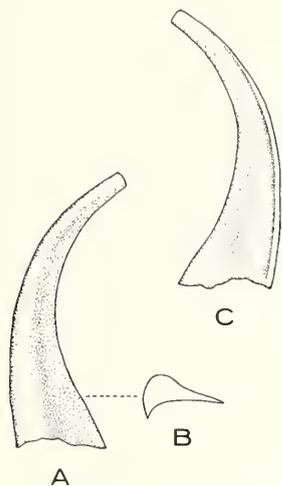
GENUS PLECTOSPETHODUS Branson and Mehl 1933

*Type species.* *Plectospathodus flexuosus* Branson and Mehl 1933, by original designation of Branson and Mehl 1933a, p. 47.

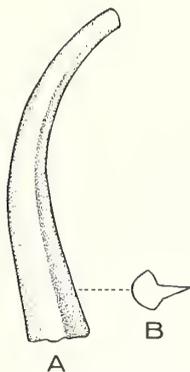
*Plectospathodus extensus* Rhodes 1953

Plate 33, figs. 20, 29–33; text-fig. 23A, B, C

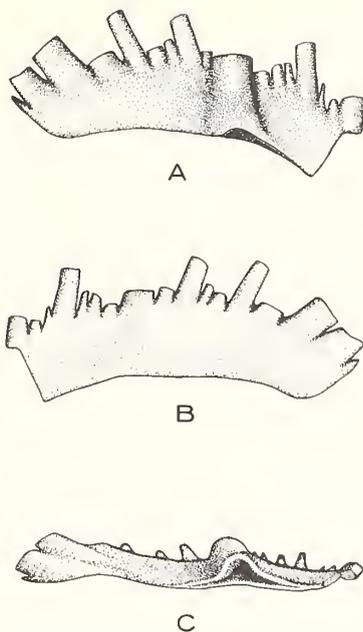
This *Manildra* material is less arched than the type material but falls within the range of variation of forms referred to the element elsewhere. The form has been described from widespread deposits ranging in age from Upper Silurian (Rhodes



TEXT-FIG. 21. *Panderodus unicosatus* (Branson and Mehl 1933). A, C, Lateral views of SU11914. B, Cross-section near base.  $\times 60$ .



TEXT-FIG. 22. *Panderodus gracilis* (Branson and Mehl 1933). A, Lateral view of SU11916. B, Cross-section near base.  $\times 60$ .



TEXT-FIG. 23. *Plectospathodus extensus* Rhodes 1953. A-C, Inner lateral, outer lateral, and aboral views of SU11949.  $\times 60$ .

1953; Jeppsson 1969; Walliser 1964; Rexroad and Craig 1971) to Lower Devonian (Philip 1965; Jentsch 1962; Bischoff and Sannemann 1958).

*Material.* Figured specimens SU11949 and SU11950 plus four others.

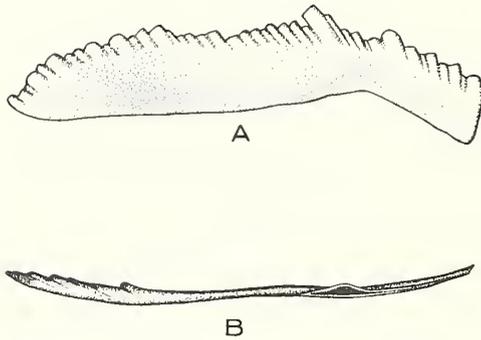
*Plectospathodus* aff. *alternatus* Walliser 1964

Plate 34, figs. 16-18; text-fig. 24A, B

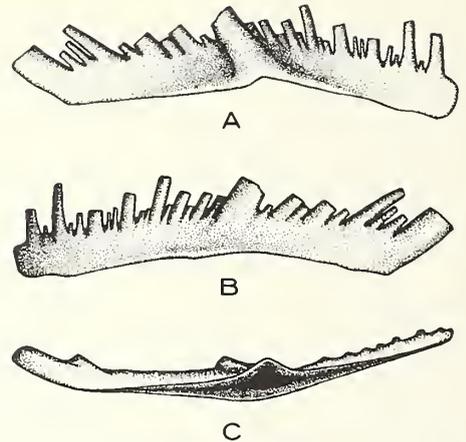
This is a *Hindeodella*-like form with finer denticles and deeper bars than in the type material of *P. alternatus*. It is close to material described as *P. alternatus* by Philip (1965, 1966) from the Tyers and Buchan Caves Limestones in Victoria. The variation noted by Philip suggests that a similar variation could occur in the Manildra material if more specimens were available.

*P. alternatus* appears to range from the very latest Silurian (Walliser 1964) to the late Lower Devonian (Philip and Jackson 1970). It is known from several localities in Europe (Ziegler 1960; Walliser 1964), eastern Australia (Philip 1965, 1966; Philip and Jackson 1970) and northern Canada (Walliser 1960).

*Material.* Figured specimens SU11962 and SU11963.



TEXT-FIG. 24. *Plectospathodus* aff. *alternatus* Walliser 1964. A, B, Inner lateral and aboral views of SU11963.  $\times 60$ .



TEXT-FIG. 25. *Plectospathodus* sp. A-C, Inner lateral, outer lateral, and aboral views of SU11955.  $\times 60$ .

*Plectospathodus* sp.

Plate 34, figs. 7, 8; text-fig. 25A, B, C

This form resembles *P. extensus* in lateral view but lacks the upcurved extension of the basal cavity which characterizes that element. Furthermore, there is a prominent basal groove present for much of the length of the unit. Thus it is very different from *P. extensus* aborally. It is probably conspecific with material illustrated by Walliser as *Plectospathodus* sp. (Walliser 1964, pl. 30, figs. 18, 20, 22). There is evidently some gradation from *Plectospathodus* sp. to *P. alternatus* and then through to deep, finely denticulate forms of the latter element such as illustrated herein.

*Material.* Figured specimen SU11955 plus one other.

EXPLANATION OF PLATE 34

All figures  $\times 40$ .

Figs. 1-3. *Hindeodella* sp. A. Inner lateral, outer lateral, and oral views of SU11954.

Figs. 4-6. *Hindeodella equidentata* Rhodes 1953. Inner lateral, outer lateral, and oral views of SU11955.

Figs. 7, 8. *Plectospathodus* sp. Inner lateral and outer lateral views of SU11955.

Fig. 9. *Trichonodella excavata* (Branson and Mehl 1933). Posterior view of SU11956.

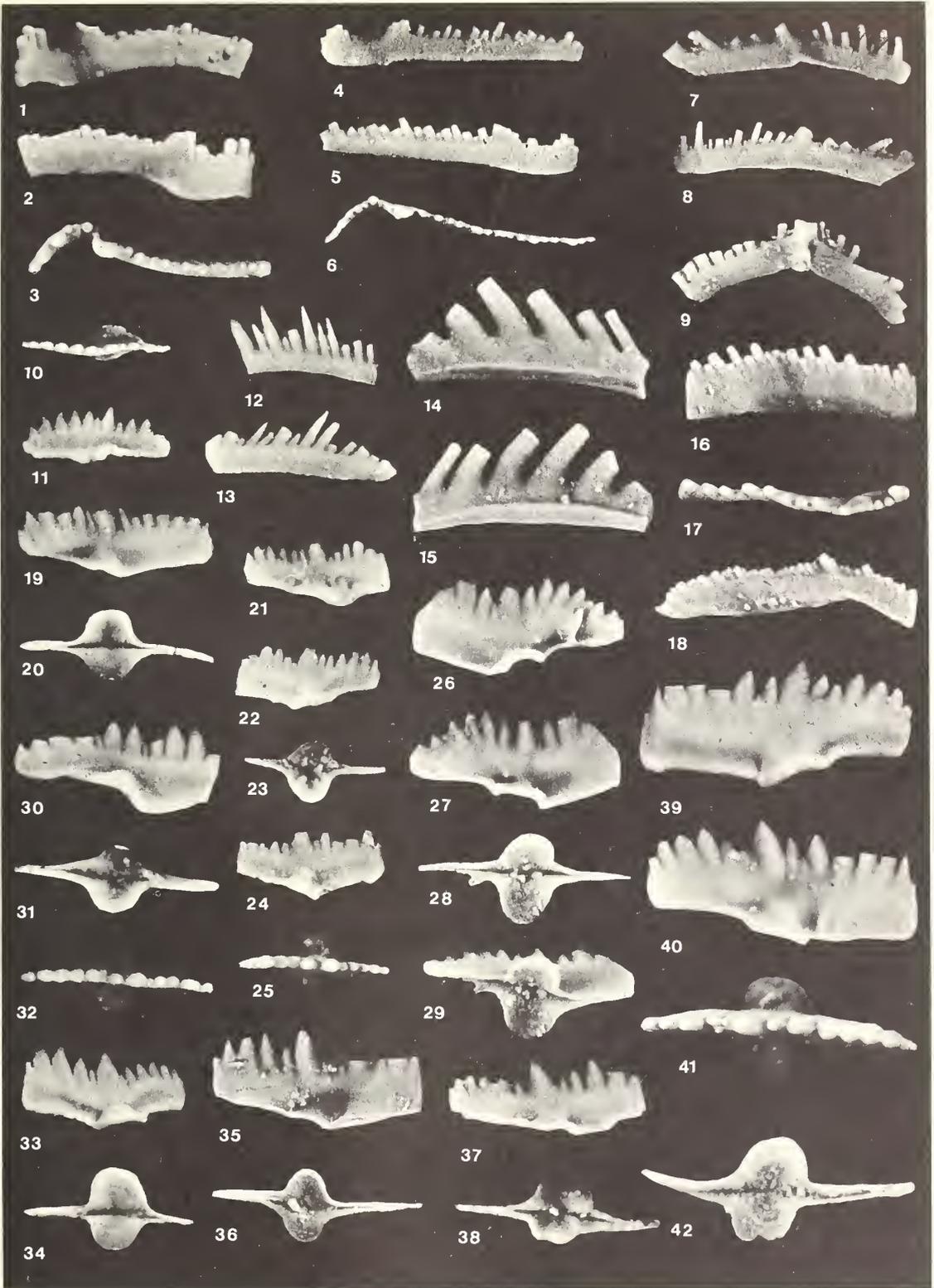
Figs. 10, 11, 30-32. *Spathognathodus inclinatus wurmi* Bischoff and Sannemann 1958. 10, 11, Oral and lateral views of SU11957. 30, 31, Lateral and aboral views of SU11958.

Figs. 12, 13. ?*Hindeodella* sp. 12, Lateral view of fragment SU11959. 13, Lateral view of fragment SU11960.

Figs. 14, 15. *Ligonodina* aff. *salopina* Rhodes 1953. Lateral views of posterior bar fragment SU11961.

Figs. 16-18. *Plectospathodus* aff. *alternatus* Walliser 1964. 16, 17, Lateral and oral views of SU11962. 18, Lateral view of SU11963.

Figs. 19-29, 33-42. *Spathognathodus remscheidensis* Ziegler 1960. 19, 20, Lateral and aboral views of SU11964. 21-23, Lateral and aboral views of SU11965. 24, 25, Lateral and oral views of SU11966. 26-29, Lateral and aboral views of SU11967. 33, 34, Lateral and aboral views of SU11968. 35, 36, Lateral and aboral views of SU11969. 37, 38, Lateral and aboral views of SU11970. 39-42, Lateral, oral, and aboral views of SU11971.



SAVAGE, Lower Devonian conodonts

## Genus ROTUNDACODINA Carls and Gandl 1969

*Type species. Rotundacodina noguerensis* Carls and Gandl 1969, by original designation of Carls and Gandl 1969, p. 206.

*Rotundacodina dubia* (Rhodes 1953)

Plate 32, figs. 23, 24; text-fig. 26A, B, C

Rhodes (1953) clearly had doubts about referring his material to *Cordylodus*, particularly as there was no evidence of a posterior bar. The genus *Rotundacodina*, recently proposed by Carls and Gandl (1969), encompasses Rhodes's species although the type species lacks the posterior denticle.

The Manildra occurrence in beds of late Lochkovian age (middle Gedinnian) extends the known range of the element. The type material is from the Upper Silurian of England (Rhodes 1953) and the Spanish material is of early Gedinnian age (Carls and Gandl 1969).

*Material.* Figured specimen SU11924.

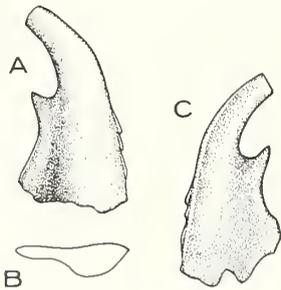
## Genus SPATHOGNATHODUS Branson and Mehl 1941

*Type species. Spathodus primus* Branson and Mehl 1933, by original designation of Branson and Mehl 1941, p. 98.

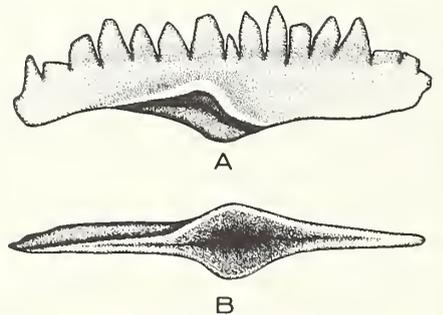
*Spathognathodus inclinatus wurmi* Bischoff and Sannemann 1958

Plate 32, figs. 27-46; plate 34, figs. 10, 11, 30-32; text-fig. 27A, B

In placing *S. wurmi* in synonymy with *S. inclinatus*, Walliser (1964, p. 76) reasoned that a continuous gradation was evident between these forms. A comparison of the illustrations of the type specimens shows that, at the very least, there are extreme end members which are easily distinguishable. It may be argued that Rhodes's specimens, which are relatively short and have denticles which are backwardly inclined, are immature forms of *S. inclinatus*, and that the specimens described by Bischoff and Sannemann, which are long and have upright denticles, particularly large at the anterior end of the specimens, are mature or even gerontic forms of



TEXT-FIG. 26. *Rotundacodina dubia* (Rhodes 1953). A, C, Lateral views of SU11924. B, Cross-section of base.  $\times 60$ .



TEXT-FIG. 27. *Spathognathodus inclinatus wurmi* Bischoff and Sannemann 1958. A, B, Lateral and aboral views of SU11931.  $\times 60$ .

*S. inclinatus*. However, if this is the case there is a surprising tendency for the different growth stages to occur in distinct faunas and even to assume some stratigraphic significance, with the larger, upright forms having larger anterior denticles occurring most commonly in Lower Devonian deposits. For these reasons the latter are herein treated as the distinct subspecies *S. inclinatus wurmi*.

This Manildra material is close to the type material of Bischoff and Sannemann (1958, pl. 14, figs. 4-9) but is conspicuously less elongate with proportionally fewer denticles. The Frankenwald material generally grew to a larger size and several of the illustrated specimens are almost twice the length of the larger Manildra specimens. Nevertheless, if specimens of the same size are compared there is very little difference in the blade proportions and the number of denticles developed (cf. Bischoff and Sannemann, pl. 14, fig. 4 and pl. 31, fig. 41 herein). An important feature of the subspecies is the development of distinct shoulders along the upper surfaces of the bars below the denticle bases. One specimen figured herein (pl. 33, figs. 10, 11) is probably a juvenile form of *S. inclinatus wurmi* but could be interpreted as *S. inclinatus inclinatus*.

*S. inclinatus wurmi* has been described from Europe (Bischoff and Sannemann 1958; Ziegler 1960; Walliser 1964; Spasov and Veselinović 1963), eastern Australia (Philip 1965; Philip and Jackson 1970) and North America (Klapper 1969; Fåhraeus 1971) in beds of Upper Silurian to late Lower Devonian age.

*Material.* Figured specimens SU11925-SU11932.

#### *Spathognathodus remscheidensis* Ziegler 1960

Plate 34, figs. 19-29, 33-42; text-fig. 28A, B

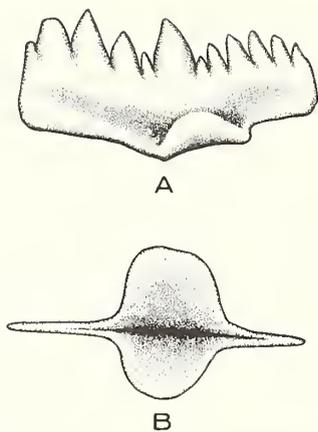
There is a close resemblance between this Manildra form and the material described as *S. canadensis* from the Upper Silurian (?) of Arctic Canada (Walliser 1960). Walliser (1964, p. 87) placed *S. canadensis* in synonymy with *S. remscheidensis*, together with the material described as *Spathognathodus* cf. *canadensis* by Ziegler from the Rheinisches Schiefergebirge. The recent work of Barnett (1971) suggests that much of the variation previously recorded for this element may be ecological.

*S. remscheidensis* is known from Europe (Ziegler 1960; Walliser 1964; Mashkova 1967; Fåhraeus 1969), eastern Australia (herein), North America (Walliser 1960; Klapper 1969; Barnett 1971) and Pakistan (Barnett *et al.* 1966). All these occurrences are in Gedinian age deposits. However, it may be reasoned that the forms described as *S. steinhornensis buchaneensis* from the Buchan Caves Limestone by Philip (1966) should be referred to *S. remscheidensis*, in which case the range of the element would extend to the late Siegenian.

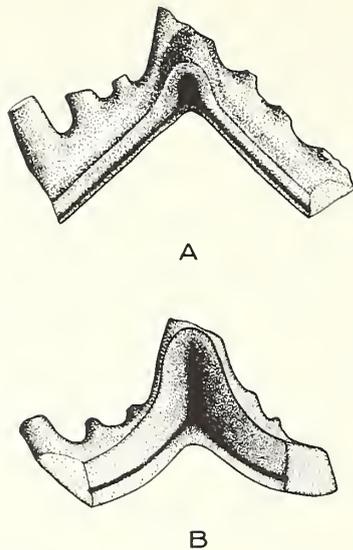
*Material.* Figured specimens SU11964-SU11971 plus five others.

#### Genus TRICHONODELLA Branson and Mehl 1948

*Type species.* *Trichognathus prima* Branson and Mehl 1933, by original designation of Branson and Mehl 1948, p. 527.



TEXT-FIG. 28. *Spathognathodus remscheidensis* Ziegler 1960. A, B, Lateral and aboral views of SU11968.  $\times 60$ .



TEXT-FIG. 29. *Trichonodella inconstans* Walliser 1957. A, B, Posterior and aboral views of SU11953.  $\times 60$ .

### *Trichonodella inconstans* Walliser 1957

Plate 33, figs. 39–41; text-fig. 29A, B

Only two fragmentary specimens are available but they undoubtedly fall within the range of variation of *T. inconstans* as defined by Walliser (1964). This element is of widespread distribution and its recorded range extends from the Upper Silurian (Rexroad and Craig 1971; Walliser 1964) to the late Lower Devonian (Philip 1966).

*Material.* Figured specimen SU11953 plus one other.

### *Trichonodella excavata* (Branson and Mehl 1933)

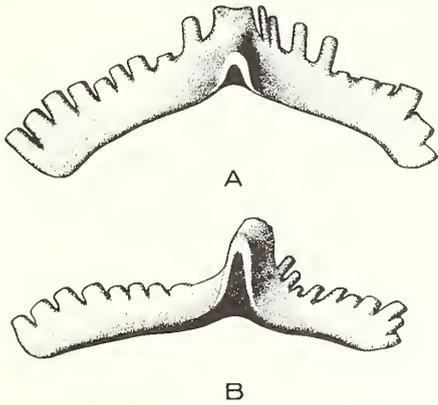
Plate 34, fig. 9; text-fig. 30A, B

This Manildra material agrees closely with the lectotype and topotype material recently figured by Rexroad and Craig (1971, pl. 79, figs. 43–46). The basal cavity of the Bainbridge material is more strongly flexed upwards but this may be a function of growth. The specimens described by Philip (1966) are only doubtfully included in this form. They are characterized by ridges running from the basal cavity along the posterior sides of the lateral bars, a feature not apparent in the illustrations of the topotype material.

*T. excavata* is a common element in assemblages ranging in age from Upper Silurian (Rhodes 1953; Rexroad and Craig 1971; Walliser 1964) to Gedinian (Bischoff and Sannemann 1958; Schulze 1968; Ethington and Furnish 1962). The

inclusion of the Buchan material (Philip 1966) would extend this range to the late Siegenian or early Emsian.

*Material.* Figured specimen SU11956 plus one other.



TEXT-FIG. 30. *Trichonodella excavata* (Branson and Mehl 1933). A, B, Posterior and aboral views of SU11956.  $\times 60$ .

*Acknowledgements.* I wish to thank Dr. F. H. T. Rhodes and Dr. G. Klapper for reading an early draft of the manuscript and making several helpful suggestions. Dr. R. Thorsteinsson and Dr. J. G. Johnson provided valuable information concerning unpublished faunal occurrences in northern Canada and central Nevada, respectively.

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NORMAN M. SAVAGE  
 Department of Geology  
 University of Oregon  
 Eugene  
 Oregon 97403



# LOWER CARBONIFEROUS CONODONT FAUNAS FROM SOUTH-WEST IRELAND

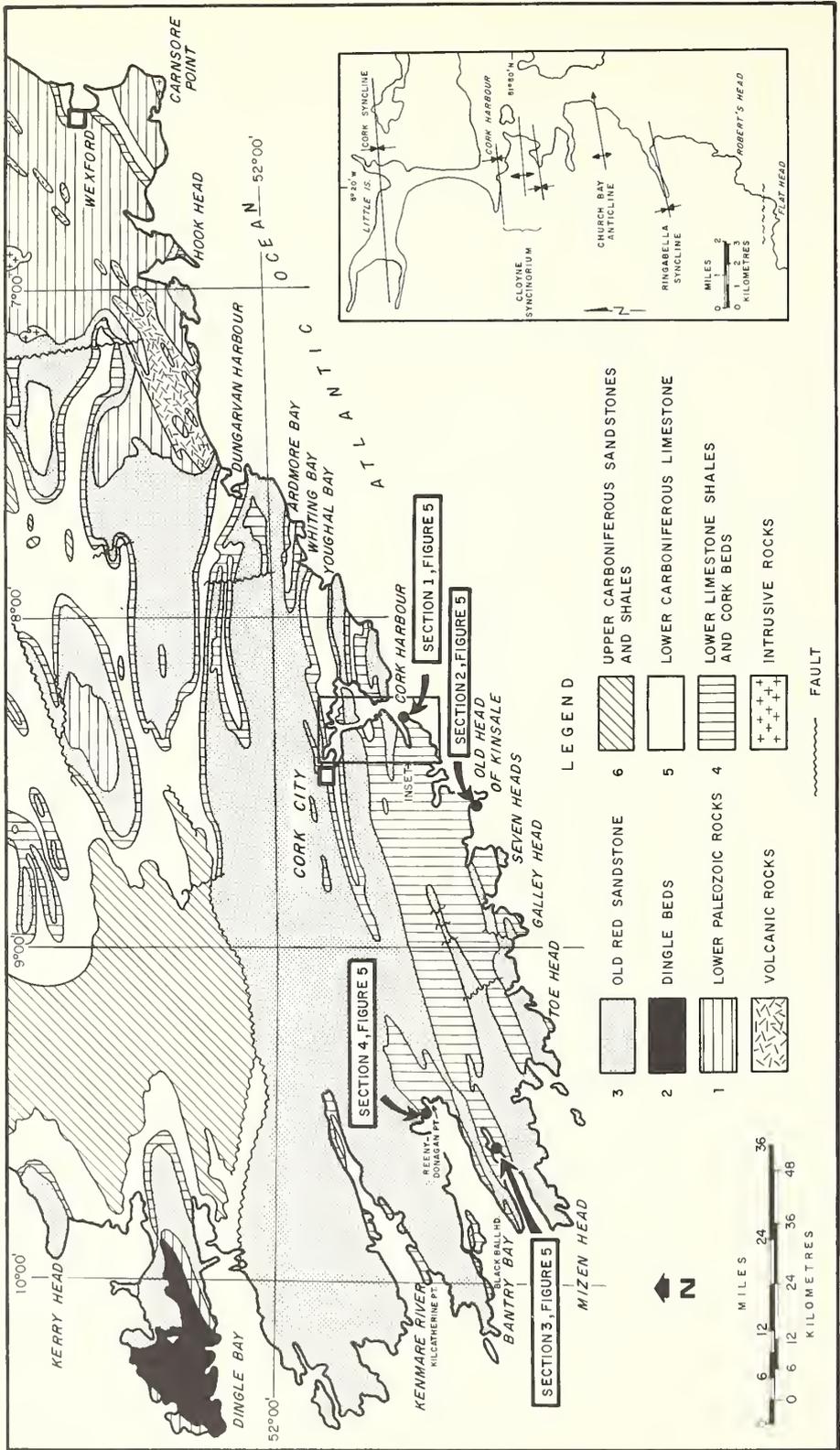
by S. C. MATTHEWS and D. NAYLOR

ABSTRACT. Lower Carboniferous conodonts have been recovered from the Cork Beds at several localities situated between Cork and Bantry Bay in south-west Ireland. They are all of Tournaisian age. Faunas with siphonodellids and gnathodids suggest comparison with the late Kinderhookian and early Osagean of the U.S.A., and with the upper *Siphonodella crenulata* Zone of Germany. Some small faunas from lower in the Cork Beds succession are tentatively referred to the neighbourhood of the Devonian–Carboniferous boundary.

A criticism of Rhodes, Austin, and Druce's work on the Avonian conodonts shows that there is, as yet, no good basis for detailed correlations with the Lower Carboniferous of the Bristol–South Wales region. A previous suggestion that the Cork Beds resemble the Pilton Beds of Devonshire receives support from the new Irish evidence. The Lower Carboniferous portion of the Cork Beds can be shown to be much thicker in south Cork than at Bantry Bay. It can also be shown that this Cork Beds wedge is in general older than the major development of carbonates (including bank-limestone facies) found to the north of the Cork–Kenmare line.

TEXT-FIG. 1 shows the general run of Old Red Sandstone and Lower Carboniferous outcrop in southern Ireland. A line drawn from the Kenmare River to Cork Harbour separates two distinct geological provinces. To the north of the line the Old Red Sandstone is overlain by a relatively thin Lower Limestone Shale unit, which is followed by a thick carbonate succession dominated by shelf and bank limestones. To the south, the red beds referred to the Old Red Sandstone are succeeded by a thick marine sequence which has relatively little carbonate and which is known to range into early Namurian age. Naylor (1966) introduced the name Cork Beds for the succession of rocks that follows above the Old Red Sandstone in this southerly region. Naylor and Jones (1967) used the term 'Cork Facies' for the whole southern facies-complex, contrasting it with the Waulsortian Bank Limestone facies to the north. Naylor *et al.* (1969) attempted correlations of individual rock units distinguished within the Cork Facies, and they reviewed the existing state of information on the age of particular parts of the sequence. Some further palaeontological information (including Matthews's tentative identifications of some small collections of conodonts) was produced by Coe and Selwood (1968). Naylor (1969) has offered an interpretation of facies-relationships across the Cork–Kenmare line.

It has become evident that the Cork Beds are broadly divisible into four gross lithostratigraphical units. The first of these, following above the red and purple strata of the Old Red Sandstone, is a thick arenaceous development, the Old Head Sandstone Group of Naylor (1966). This is overlain by a predominantly argillaceous unit, the Kinsale Group. There follows the relatively calcareous Courtmacsherry Group, and this is overlain by the black goniatic mudstones of the Lispatrick Group. It should be noted that although thin calcareous lenses are found in the Kinsale Group, the base of the Courtmacsherry Group is clearly marked by the incoming of thick beds of crinoid debris with associated soft calcareous mudstones. It was suggested by Naylor *et al.* (1969) that the character of these broad stratigraphic subdivisions was maintained through to sections in Dunmanus Bay and



TEXT-FIG. 1. Geological map of south and south-west Ireland to show location of sections studied.

Bantry Bay on the west coast, although the units were given locally based names in these sections. Stratigraphic nomenclature has inadvertently been brought into some confusion on the west coast because of proposals of names made independently by Coe and Selwood (1968), Naylor *et al.* (1969), and Gardiner (1970). It is hoped to unravel these problems in a later paper. The nomenclature of Naylor *et al.* (1969) is used here.

We describe now the results of a study of conodont faunas obtained from several sites in the Cork Beds stratigraphy. The objectives of the work have been, first, to provide for a more precise scheme of correlations within the Cork Beds and, secondly, to suggest how this interesting southern Irish facies-complex may be related to Lower Carboniferous successions of other kinds elsewhere. Naylor undertook the entire task of sampling, and has responsibility here for statements on stratigraphic relationships within the Cork Beds. Matthews, who did most of the work of preparation, takes responsibility for the identifications of conodonts, and for comments on comparisons to be made with conodont faunas described from places outside south-west Ireland.

Most of the samples were collected from four sections through the Courtmacsherry Group or its equivalents (text-fig. 1). These sections are situated, respectively, in the Ringabella Syncline (text-fig. 5, section 1: samples prefixed F and R), on the west coast of the Old Head of Kinsale (text-fig. 5, section 2: samples prefixed OH), in the core of the Dunmanus Bay Syncline (text-fig. 5, section 3: samples prefixed D) and on the northern limb of the Bantry Bay Syncline at Ardnamanagh Point (text-fig. 5, section 4: samples prefixed B). Details of the individual localities are supplied in the Appendix. Some further samples were taken from isolated lenses within the Kinsale Group (see their stratigraphic location in text-fig. 4). A separate study is at present in progress on the Lower Carboniferous rocks of the Ardmore-Whiting Bay area of south-east Ireland (text-fig. 1), described by Smyth (1939), and some mention of relevant results is included here.

The yield of conodonts was in general small. Those sites which proved to be relatively productive were sampled a second time in order to check the first indication of age. In some cases (especially among the higher Ringabella samples) the rock would not readily come apart in 10% acetic acid, although it was often possible to disaggregate rock fragments manually after they had lain for a few weeks in acid and had lost some carbonate from their fabric. Many of the conodonts obtained are deformed, and most specimens carry impacted quartz grains. Some specimens have pyrite overgrowths (especially those from the OH1 sample, a case in which almost the whole of the acid residue sank in tetrabromoethane). In spite of these occasional deficiencies of the specimens, some useful results have been obtained. The following list identifies the most productive cases (the majority of them sampled a second time, in 1971—see suffix '71 here and elsewhere in the text) upon which the scheme of correlations suggested below for the Cork Beds principally depends. Faunal lists for all productive samples are given in the Appendix.

Ringabella:

F1 *Polygnathus inornatus* (3 specimens), *P. inornatus?* (4), *P. cf. communis* (1), *Pseudopolygnathus dentilineatus* (3), *Ps. multistriatus* (1), *Ps. primus* (1), *Ps. sp.* (1), bar (1). Total 15. Collection number: GSL SAD33.

- F1 '71 *Polygnathus inornatus* (5), *P. sp.* (1), *Pseudopolygnathus dentilineatus* (6), *Siphonodella sp.* (5), *Spathognathodus sp.* indet. (1). Total 18. GSL SAD34.
- R2 *Gnathodus delicatus* (7), *G. semiglaber* (2), *G. sp.* (1), *Spathognathodus crassidentatus* (1), *Sp. stabilis* (2), *Sp.* indet. (1), *Sp. sp.* (9), bars (8). Total 31. GSL SAD22.
- R4 *Gnathodus delicatus* (5), *G. semiglaber* (3), *Polygnathus communis carina* (20), *P. cf. communis* (4), *Spathognathodus stabilis* (5), *Sp. sp.* (1), bars (13). Total 51. GSL SAD24.
- R4a '71 *Gnathodus delicatus* (4), *Polygnathus communis carina* (11), *P. inornatus* (1), *Spathognathodus sp.* (3), indet. (1), bars (6). Total 26. GSL SAD25.
- R4b '71 *Gnathodus delicatus* (11), *G. punctatus* (1), *Polygnathus communis communis* (6), *P. communis carina* (9), *P. communis subsp.* (7), *Spathognathodus* indet. (1), *Spathognathodus cf. stabilis* (2), indet. (1). Total 38. GSL SAD26.

Old Head of Kinsale:

- OH1 *Patrognathus variabilis* (1), *Pa. cf. variabilis* (1), *Polygnathus communis communis* (8), *P. cf. communis* (1), *Spathognathodus aculeatus* (4), *Sp. cf. aculeatus* (1), *Sp. anteposicornis* (1), *Sp. stabilis* (11), *Sp. sp.* (2), bars (8). Total 38. GSL SAD47.
- OH1 '71 Bar (1). Total 1. GSL SAD48.
- OH4 *Polygnathus sp. juv.* (1), *Siphonodella isosticha* (3), *S. obsoleta* (2), *Spathognathodus cf. costatus* (1), *Sp.?* sp. (1), bars (6). Total 14. GSL SAD50.
- OH4 '71 *Siphonodella isosticha* (3), *S. obsoleta* (1), *S. sp. indet.* (1), bars (9). Total 14. GSL SAD41.

Bantry Bay:

- B8 *Polygnathus symmetricus* (1), *P. sp. indet.* (1), *P. sp.* (3), *Spathognathodus aculeatus/Clydagnathus* transition (2), *Spathognathodus stabilis* (1), indet. (1), bars (7). Total 16. GSL SAD43.
- B2 *Gnathodus aff. semiglaber* (1), *Polygnathus symmetricus* (1), *Pseudopolygnathus multistriatus* (1), *Ps. cf. multistriatus* (1), *Siphonodella cooperi* (6), *S. cf. cooperi* (1), *S. cf. S. isosticha* (2), *S. sp.* (17), bar (1). Total 31. GSL SAD36.
- B2 '71 *Elictognathus cf. laceratus* (1), *Gnathodus punctatus* (3), *G. aff. semiglaber* (2), *G. sp.* (1), *Polygnathus inornatus* (3), *P. longiposticus* (1), *P. symmetricus* (1), *P. cf. symmetricus* (1), *P. sp.* (4), *Pseudopolygnathus multistriatus* (1), *Siphonodella cooperi* (10), *S. cf. cooperi* (1), *S. isosticha* (5), *S. obsoleta* (3), *S. sp. indet.* (1), *S. sp.* (7), bars (7). Total 52. GSL SAD37.

Whiting Bay:

- WB2 *Elictognathus laceratus* (1), *E. cf. laceratus* (1), *Polygnathus communis communis* (7), *P. inornatus* (5), *P. symmetricus* (4), *P. sp.* (3), *Siphonodella cooperi* (8), *S. spp. juv.* (4), *S. sp.* (4), bars (4). Total 41. GSL SAD57.

It will be recognized that the presence of siphonodellids and gnathodids (and the occasional coincidence of the two) provides a particularly interesting feature of the results. Before embarking on a discussion of whatever relationships within the Cork Beds this new information would suggest, it is useful first to consider the 'external' relations of the Cork Beds and to recognize a frame of reference by which the relative ages of these associations of conodonts might be judged.

#### CORRELATION WITH REGIONS OUTSIDE IRELAND

The Cork Beds conodonts described here can all be taken to be of Tournaisian age. It is not possible at present to justify this statement by direct reference to the type Tournaisian of Belgium, for although a certain amount of information has been published on the conodonts of the lower (Conil *et al.* 1964; Austin, Conil *et al.* 1970) and of the higher (Conil *et al.* 1969; Groessens 1971) parts of the Belgian Tournaisian, there is, as yet, only relatively meagre information on the middle range, where the siphonodellids give out (in the lowest reaches of Tn 3 according to Groes-

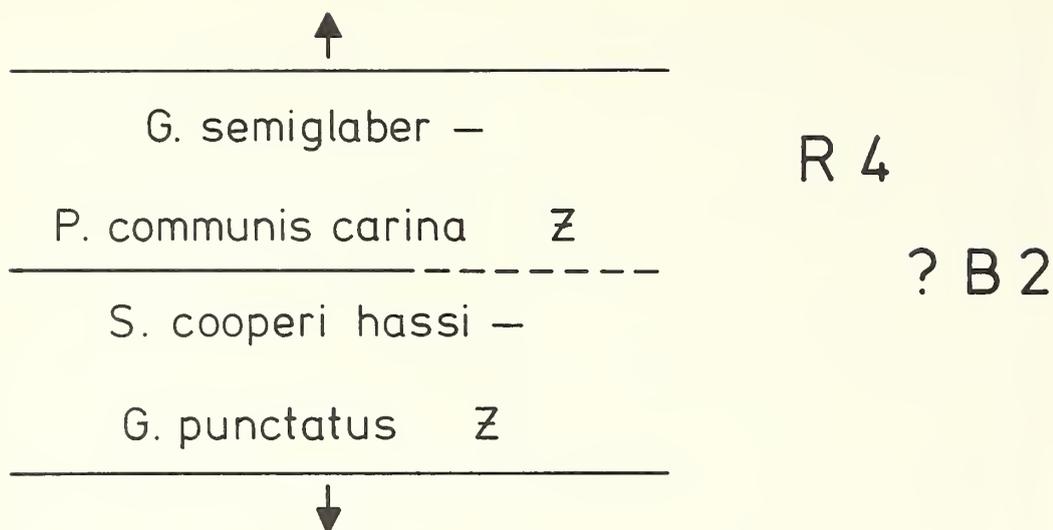
sens) and the first representatives of the main suite of gnathodids emerge. Belgian work, therefore, cannot yet supply precise guidance on the relative ages of the Cork Beds faunas. Nor is German work particularly helpful in the present case. The German succession has yielded good information on the conodont faunas of horizons close to the Devonian–Carboniferous boundary (treated most recently in Ziegler 1969, and Koch *et al.* 1970), and this has made it possible (see Paproth 1964 and later commentators) to recognize an equivalent of the earliest Carboniferous of Germany in Tn 1b of Belgium. Again, it was German evidence (Bischoff 1957; Voges 1959, 1960) which first showed that faunas with siphonodellids are followed in the Lower Carboniferous succession by faunas which have *Scaliognathus anchoralis* and its associates, and it is a representation of this latter association that Groessens (1971) records in the Belgian Tn 3c. However, the thin German stratigraphy supplies relatively little information on siphonodellid–gnathodid associations (i.e. from the carbonate-poor Liegende Alaunschiefer and the lower part of the Horizont vorwiegender Lydite, where the upper part of Voges's *Siphonodella crenulata*-Zone is followed by his *anchoralis*-Zone). One must therefore look elsewhere for guidance on the relative ages of the Cork Beds faunas. It is American evidence that serves this purpose best at the present time. Taking American information together with Groessens's results from Tn 3c, one can establish a sense of the age of the highest Cork Beds conodont faunas, and can proceed from there to make comparisons between southern Ireland and south-west England. The discussion of age-relationships includes also some fairly detailed references to the record of conodonts from the 'Avonian' succession: since much of the earlier information on the age of the Cork Beds has been rendered in terms of Vaughan's coral–brachiopod zonal scheme, one compares the Cork Beds conodont faunas with those reported from the Avon Gorge by Rhodes *et al.* (1969) and hopes to make some test of the consistency of two different lines of information on age.

#### *Correlation with North America*

Thompson and Fellows's (1970) work on conodont faunas from the Kinderhook and Osage in south-west Missouri and adjacent parts of Arkansas and Oklahoma has done much to improve our knowledge of the sequence of conodonts in the lower part of the Mississippian. They have been able to show that the rock succession is fuller in the area where they worked than in the upper Mississippi Valley states further to the north. The succession of zones they propose makes reference to certain faunas that were not accounted for in, for example, Collinson, Scott, and Rexroad's (1962) or Rexroad and Scott's (1964) work. It happens that some of the conodonts present in the newly revealed Mississippian zones are found in the Cork Beds faunas also. Cork Beds faunas can be associated with Thompson and Fellows's zones as in text-fig. 2.

Three necessary comments on text-fig. 2 are:

1. Systematic practice in this paper is not absolutely consistent with that of Thompson and Fellows. The Cork Beds siphonodellids are identified in accordance with Klapper's (1971) revision of certain of Thompson and Fellows's proposals.



TEXT-FIG. 2. Two Cork Beds samples related to units in Thompson and Fellows's (1970) zonal scheme for the Kinderhookian-Osagean.

Gnathodids too (especially *Gnathodus punctatus* and *G. delicatus*) are treated slightly differently here. These adjustments are dealt with in the systematic section below.

2. A more substantial departure from the Mississippian arrangement of things is shown by the case of sample B2 (full list above), which has siphonodellids, *Gnathodus punctatus* and *Pseudopolygnathus multistriatus*. According to Thompson and Fellows (1970, table 1) these should not coincide. The possibility of reworking (i.e. 'Kinderhookian' conodonts—the siphonodellids and gnathodids of B2—admixed among 'Osagean' forms—*Ps. multistriatus*) suggests itself. But in that case one would expect to find other conodont species supporting *Ps. multistriatus* in the suggestion of Osagean age. None have been found, neither in the first B2 sample, nor in the second (B2 '71 above). An alternative explanation of this apparent anomaly is possible:

3. Matthews *et al.* (1972) have pointed to certain records of coincidence of *Gnathodus punctatus* and *Polygnathus communis carina*. These suggest the existence of an association of conodonts that is not treated in Thompson and Fellows's (1970) zonal scheme. The chief implication of the suggestion is that Thompson and Fellows have perhaps not yet entirely succeeded in closing the gap which they show to exist in Mississippian sections further north (see fig. 27 of their paper, and also, in their table 1, the decided break of faunal character evident at their Kinderhook-Osage boundary). The suggestion cannot be advanced with any great firmness here, considering the scattered nature of the sampling and the small numbers of the Cork Beds conodonts; but the possibility is indicated in text-fig. 2 by inserting B2, with a query, at the boundary separating the *G. punctatus* subzone from the *G. semiglaber*-*P. communis carinus* (properly: *carina*) Zone in Thompson and Fellows's scheme.

*P. communis carina*, which is taken to mark a later position in the stratigraphy

than is indicated by the B2 association of forms, is abundantly represented in R4, where it occurs with (among others) *G. semiglaber*. R4 is tentatively allotted to Thompson and Fellows's *G. semiglaber*-*P. communis carina* Zone in text-fig. 2. The qualifications expressed in comment 3 above would apply again here: one should perhaps not regard Thompson and Fellows's definition of the lower limit of the *G. semiglaber*-*P. communis carina* Zone as entirely firm.

The productive samples from the Cork Beds have nowhere supplied any hint of horizons higher than those represented in the Ringabella (R) faunas. No bactrognathids, doliognathids, nor scaliognathids were found, although the presence of *P. communis carina* may be taken to indicate that the Ringabella section ranges up to make a close approach to horizons at which these distinctive forms might appear. Groessens's (1971) results from Belgium would lend some support to this suggestion. He has shown that relatively abundant occurrence of *P. communis carina* precedes fairly closely the emergence (in Tn 3c) of such forms as *Scaliognathus anchoralis*. Given this indication of the age of the highest faunas recovered from the Cork Beds, it is possible to attempt some brief proposals on the way in which the Cork Beds stratigraphy might relate to stratigraphic successions further east in the Variscan fold-belt.

#### *Correlation with south-west England*

The higher conodont faunas obtained from the Cork Beds provide a basis for sketching out some relationships with south-west England. At Chudleigh, in south-east Devon, for example, the lower of two conodont faunas described by Matthews (1969*b*) is an approximate equivalent of the WB2, OH4, and B2 faunas described here. The higher Chudleigh fauna described by Matthews (1969*b*) has *Scaliognathus anchoralis* and would therefore appear to be later than anything discovered in the present work. In east Cornwall a detached sheet of Lower Carboniferous rock again has a fauna with *Sc. anchoralis* in a higher, siliceous part of its stratigraphy (Matthews 1969*a*) and a goniatite fauna in a shaly succession below (Matthews 1970). A further occurrence of conodonts in siliceous rocks, at Chillaton, north-east of Tavistock, is approximately of *anchoralis*-Zone age (Matthews *et al.* 1972). A small fauna with a siphonodellid and a gnathodid in association has been found high in the Pilton Beds in north-east Devon (Matthews and Thomas, in preparation) and would seem to be once more an approximate equivalent of the highest Cork Beds faunas. Two interesting points follow from these observations. The first is that siliceous rocks enter the stratigraphy fairly consistently at horizons near the base of the *anchoralis*-Zone. An exceptional case exists at Chudleigh, where silicification is already evident high in the Upper Devonian and continues through the lower part of the Lower Carboniferous (House 1963; Tucker and van Straaten 1970). The implication for the Cork Beds is that the equivalent of the *anchoralis*-Zone might be sought somewhat above the highest conodont faunas so far obtained (e.g. above R4: note the character of the gnathodids and the relative abundance of *Polygnathus communis carina*) in siliceous rocks such as occur in the Lispatrick Group at Minanebridge (Naylor 1969, p. 317). It should, however, be mentioned that at Minanebridge itself the goniatite-lamelibranch fauna reported by Turner (1939, p. 323) would indicate a horizon that is perhaps already slightly higher than the (poorly defined)

upper limit of the *anchoralis*-Zone. The second point is that the increasing amount of evidence of Tournaisian age now available from the Cork Beds does much to reinforce Coe and Selwood's (1968, p. 129) suggestion that the stratigraphic sequence in south-west Ireland has a parallel in the Pilton Beds and immediately succeeding stratigraphy of north Devon.

*Correlation with the Lower Carboniferous in 'Avonian' facies*

It was noted above that, so far, most of the attempts to set dates on the Cork Beds stratigraphy have depended on the evidence of corals and brachiopods, with the section in the Avon Gorge at Bristol taken as the eventual standard. It should therefore be of some interest to compare the Cork Beds conodont faunas with the zonal units Rhodes *et al.* (1969) proposed on the basis of the conodonts they had collected from the Avon section and from a composite of sections on the North Crop of the South Wales coalfield. Certain of the 'Avonian' conodonts occur again in the Irish faunas. But it is soon clear that the associations of forms found in the Cork Beds do not readily fall into particular positions in Rhodes, Austin, and Druce's scheme of zones. A brief examination of what Rhodes, Austin, and Druce proposed will show that their scheme was not particularly well founded. The following comments refer to that range of the Avonian stratigraphy which has produced individual conodonts of kinds now encountered in the Cork Beds:

1. The lowest Avonian zone, the *Patrognathus variabilis*-*Spathognathodus plumulus plumulus* Assemblage Zone, was recognized in both the Avon Gorge and the North Crop. There was, necessarily, no clear definition of its base. Two subzones were recognized on the North Crop, but these could not be distinguished in the Avon Gorge.

2. Only the Avon Gorge allowed continuous exposure into the rocks allotted to the second zone, the *Siphonodella*-*Polygnathus inornatus* Assemblage Zone. A lower subzone, proposed from the Avon Gorge, was thought to occupy an unexposed interval in the North Crop succession. A higher subzone, proposed from the stratigraphy immediately above the concealed interval on the North Crop, was thought to occupy an unexposed interval in the Avon Gorge. Rhodes *et al.* (1969, p. 39), having suggested this, observed lower on the same page of their paper that that concealed interval in the Avon Gorge probably includes the lower part of their third zone. It should be understood that Rhodes *et al.* (1969, pp. 220-221) recovered only two siphonodellid specimens from the Avon section, from K12 (above the Bryozoa Bed—see Rhodes *et al.* 1969, fig. 59) and K17. A stratigraphic column for the Avon Gorge published by Austin, Conil *et al.* (1971), and said to be based on Rhodes *et al.* (1969), nevertheless shows a range for the genus *Siphonodella* which beings below the Bryozoa Bed.

3. The sequence from the top of the *Siphonodella*-*P. inornatus* Assemblage Zone, through the *Spathognathodus cf. robustus*-*Spathognathodus tridentatus* Assemblage Zone and into the *Spathognathodus costatus costatus*-*Gnathodus delicatus* Assemblage Zone, is apparently relatively well represented on the North Crop, although presumably (it is difficult to unravel the evidence from Rhodes *et al.* 1969, figs. 7, 70, and 71) a transfer from one stratigraphic section to another is involved. The

*Sp. costatus costatus*-*G. delicatus* Assemblage Zone had three subzones valid for the North Crop and two different subzones valid for the Avon Gorge. Neither set of subzones was confirmed in any other section. In the Avon Gorge the *Sp. costatus costatus*-*G. delicatus* Assemblage Zone had no *G. delicatus*. This form, it was reported, first appeared rather higher in the section there—a situation which Rhodes *et al.* (1969, p. 56) interpreted as meaning that the apparently lower North Crop occurrence could be compared with the first North American occurrence of the species in the *Siphonodella quadruplicata*-*S. crenulata* Zone, whereas the apparently higher Avon Gorge occurrence could be compared with the abundant occurrence of the species in what was then called the *S. isosticha*-*S. cooperi* Zone of North America. It should be realized that Rhodes *et al.* (1969, p. 97) had collected, in all, eleven specimens of *G. delicatus*.

4. The *Polygnathus lacinatus* Assemblage Zone, which followed the *Sp. costatus costatus*-*G. delicatus* Assemblage Zone, had no *P. lacinatus* in the Avon Gorge. The three zones following were described from the Avon Gorge (high in the Black Rock Group) only. Apparently there is no stratigraphy of this range of age on the North Crop.

These comments bring attention to certain deficiencies of Rhodes, Austin, and Druce's scheme—to the thinness of their evidence, and to their failure to produce confirmation of the zonal arrangements they proposed. There are cases where proposals based on Avon Gorge evidence could not be confirmed in the North Crop sections, and vice versa. Rhodes *et al.* (1969) mention only one attempt to seek confirmation of the proposals they made for the range of the stratigraphy discussed here. That dealt with sections in Shropshire (Rhodes *et al.* 1969, pp. 25, 48) and some further inconsistencies emerged. Another deficiency of Rhodes, Austin, and Druce's work lies in the fact that they nowhere made allowance for the possibility that conodonts might have been to any extent reworked in the thick Avonian carbonate sequence. They attached a certain amount of significance to upper limits of occurrence, e.g. where they remarked (Rhodes *et al.* 1969, p. 40) that the top of the *Gnathodus simplicatus* assemblage subzone of the *Spathognathodus costatus costatus* Assemblage Zone on the North Crop is marked by the final occurrence of, among others, *Polygnathus communis*—compare Rhodes *et al.* 1969, p. 42, where they remark that the youngest stratigraphic occurrence of *P. communis communis* in the Avon Gorge lies within their *G. antetexanus*-*P. lacinatus* Assemblage Zone. They attached significance also to maximum abundance of particular forms (see an example below) thus again ignoring the risk that sedimentary processes might have had any effect on the observed distribution of conodonts.

Yet another shortcoming of Rhodes, Austin, and Druce's zonal scheme is found in the fact that many of the conodonts involved were given highly idiosyncratic systematic treatment. In the discussion of their scheme above, it has been convenient to retain the generic and specific names they themselves used. The systematic section below will show that in their determinations of genera and species, they departed, in many instances, from opinions generally accepted among conodont workers.

Rhodes, Austin, and Druce's proposals on correlations with the U.S.A. and with

Germany may appear (as in their fig. 12, for example) to be in some cases different from, and in any case more elaborate than, proposals of the kind made for the Cork Beds faunas. Their suggestions involve, here and there, conodonts of kinds now discovered in the Cork Beds, and so it is necessary to examine the essentials of the suggestions they made. They offered a choice between two alternative schemes of correlation with North America. Both schemes were hung on an equation of the Avonian *Polygnathus lacinatus* Assemblage Zone with the *Gnathodus semiglaber*-*Pseudopolygnathus multistriatus* Zone of the Mississippian. The case for this correlation rested on Rhodes, Austin, and Druce's (1969, p. 57) suggestion that gnathodids occur in the Avon Gorge succession in a pattern which could be compared with Rexroad and Scott's (1964) record of a shift of maximum abundance from *G. delicatus* in the *S. isosticha*-*S. cooperi* Zone, to *G. semiglaber* in the *G. semiglaber*-*Ps. multistriatus* Zone and then to *G. antetexanus* in the *Bactrognathus*-*P. communis* Zone. Rhodes, Austin, and Druce claimed to match this with *G. delicatus* at the base of Z<sub>2</sub> (note Rhodes *et al.* 1969, p. 97, where they record that they recovered a total of eleven specimens of this species, and that the range of those found in the Avon Gorge was Z 28-Z 37), with *G. semiglaber* in the upper part of Z<sub>2</sub> (cf. Rhodes *et al.* 1969, p. 106: a total of three specimens, recovered from the range Z 28-Z 30) and with *G. antetexanus*, first appearing in the upper part of Z<sub>2</sub> and ranging into C<sub>1</sub> (cf. Rhodes *et al.* 1969, p. 93: in all ten specimens, Avon Gorge range Z 33-C 9). Nothing of this justifies the suggestion that the Avon Gorge gnathodids show a shift of maximum abundance to be compared with what Rexroad and Scott had observed, nor is there anything to enforce a correlation of the *P. lacinatus* Assemblage Zone (Z 26-Z 32 in the Avon Gorge, according to Rhodes *et al.* 1969, p. 41, i.e. a range which has no *P. lacinatus*; or ZLA 29-ZL 19 on the North Crop, a range which has no *G. semiglaber*) with the *G. semiglaber*-*Ps. multistriatus* Zone of North America. Rhodes, Austin, and Druce's two alternative schemes for correlation with the Mississippian therefore fail at their single common point.

There are numerous shortcomings in Rhodes, Austin, and Druce's (1969) references to the German evidence. Some, such as their mention of 'the Hartz Mountains of the Sauerland' (p. 64 of their paper) should confuse no one. Other references to the German evidence are potentially misleading, and ought to be corrected. For example, their text mentions subdivisions of German zonal units, such as 'basal Cu II $\alpha$ ' (p. 39) as distinct from (i.e. they were correlated with two different Avonian zones) 'Lower Cu II $\alpha$ ' (p. 39), 'Middle and Upper Cu II $\alpha$ ' (p. 40), 'lowest Cu II $\beta$ - $\gamma$ ' (p. 41), 'Middle Cu II $\beta$ - $\gamma$ ', as well as 'Upper Cu II $\beta$ - $\gamma$ ' (p. 42), 'lowest Cu II $\delta$ ' (p. 42), and 'the middle and upper part of Cu II $\delta$ ' (p. 43). The use of a capital letter in some of these adjectives may be thought to imply that such subdivisions of the zonal units have some established standing. This is not so. In fact the examples quoted above would in every case involve finer distinctions than the Germans themselves have ever attempted. Comments on the ammonoid zones (to which symbols such as cu II $\alpha$  refer), and on the possibility and indeed advisability of rendering conodont dates in ammonoid terms, are available in Matthews (1966, 1970, 1971).

Rhodes, Austin, and Druce's claim to have identified equivalents of the German cu I cannot be substantiated, as Ziegler (1971*a*) has already pointed out. The claim, which is repeated in Rhodes and Austin (1971), involves reference to a specimen

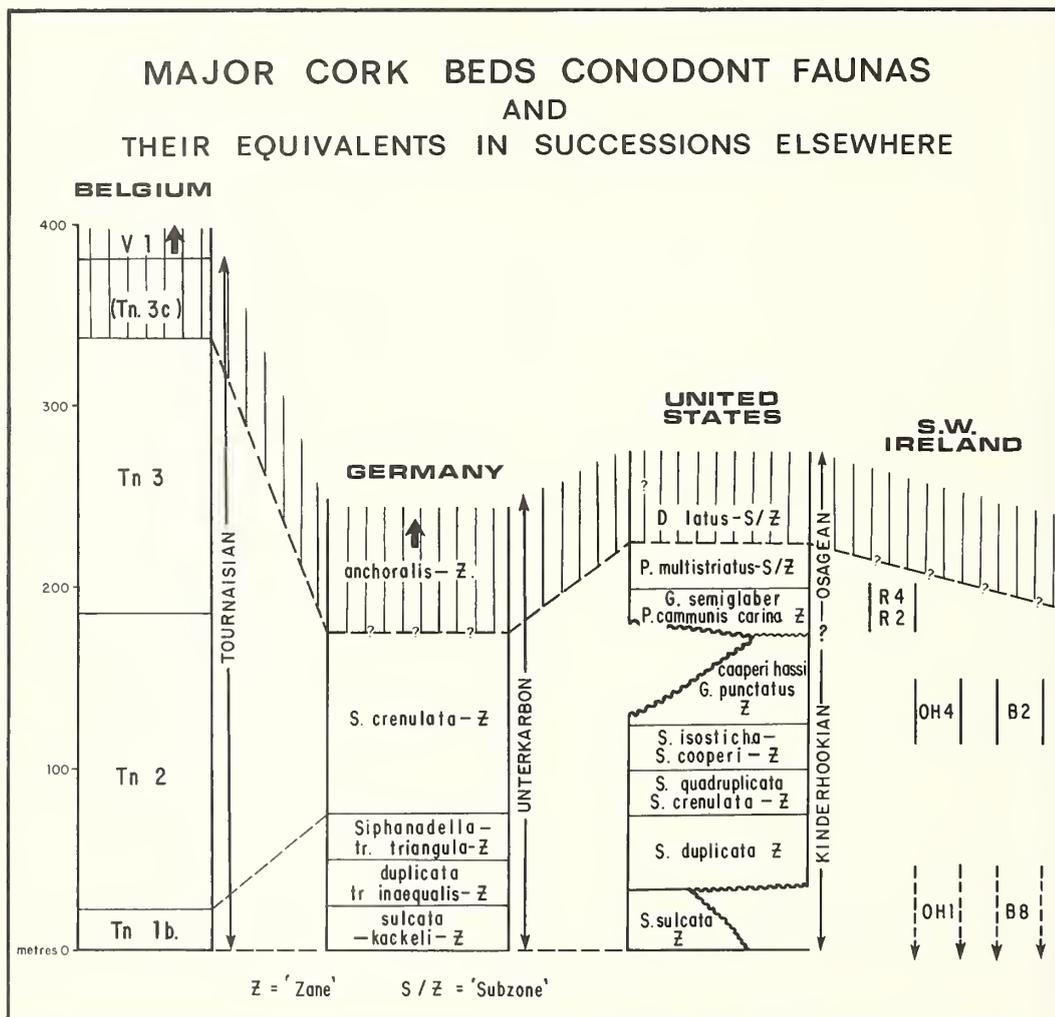
of *Elictognathus*, which Rhodes *et al.* (1969) did not describe nor figure. The genus *Elictognathus*, which is represented in the Irish faunas, need not be thought to specify earliest Carboniferous age (see Voges 1959; Collinson *et al.* 1962; Rexroad and Scott 1964; and later American authors). Rhodes, Austin, and Druce's suggestions on Avonian equivalents of the German *anchoralis*-Zone should also be examined here, for their arguments involved gnathodids of kinds found in the Cork Beds. They twice referred to gnathodids in this connection. On p. 57 of their paper they suggested that 'Ziegler (1960, 1963) has described gnathodids identical to those of the middle *Polygnathus lacinatus* Zone of the Avonian (samples Z 28-Z 30)'. If one refers to Rhodes, Austin, and Druce's systematic treatment of the gnathodids for information on ranges, one finds that only *Gnathodus delicatus* and *G. semiglaber* occur in that range. If one refers to their list of works cited (p. 292 of Rhodes *et al.* 1969) one discovers that 'Ziegler 1960' is a paper on Lower Devonian conodonts. 'Ziegler 1960a' there is a paper in which Ziegler described *G. commutatus homopunctatus* but no other gnathodid. One is left to presume that Rhodes, Austin, and Druce intended to refer to Ziegler's contribution to Kronberg *et al.* (1960) where Ziegler figured a number of gnathodids, *G. delicatus* and *G. semiglaber* among them, found in *anchoralis*-Zone faunas. Ziegler (1963) again figured gnathodids (including *G. delicatus*) from *anchoralis*-Zone faunas and mentioned one specimen of *G. semiglaber* in a faunal list. But he made no extensive descriptive reference to the gnathodids in 1963 since he was awaiting the outcome of American work in progress at that time. In a second reference to the age-significance (in German terms) of their gnathodids, Rhodes *et al.* (1969, p. 60) mentioned that Ziegler had communicated to them his belief that the gnathodid fauna of samples Z 34-Z 38 'is identical to that found in Western Europe in beds equivalent to the *Siphonodella crenulata* Zone . . .'. These two references to comparisons with Germany, taken together, would appear to show that the gnathodids of Z 28-Z 30 are 'identical' to some found in *anchoralis*-Zone faunas, whereas those of Z 34-Z 38 (higher) are 'identical' to gnathodids found in the (earlier) *S. crenulata*-Zone. It might also be noted here that Ziegler's communication, referring to *S. crenulata*-Zone gnathodids, would clash with Rhodes, Austin, and Druce's (1969, p. 57) own observation that the '*anchoralis* fauna of Germany, as at present understood, contains the simultaneous first appearance of several species of *Gnathodus* . . .'. Rhodes and Austin (1971, fig. 4) have repeated this view of the German situation. But Ziegler, in the 1963 paper mentioned above, explicitly denied any such suggestion, citing evidence from Voges (1960), and from Ziegler (in Kronberg *et al.* 1960), in favour of possible earlier, i.e. pre-*anchoralis*-Zone, occurrence of gnathodids in Germany (Ziegler 1963, p. 323).

The conclusion is that Rhodes, Austin, and Druce's paper gives no better guidance on correlation with the German conodont sequence than it does on correlation with the American. Criticisms of further features of Rhodes, Austin, and Druce's work are possible (see Ziegler 1971a; and Matthews and Butler, in press). The remarks made here should be sufficient to show that no purpose is served by attempting to refer the Cork Beds faunas to Rhodes, Austin, and Druce's set of Avonian zones. The comparisons that can be made between the southern Irish and the Bristol-Mendip stratigraphy will be clearer when work now in progress on the conodont faunas of the latter area has been published (Butler, in preparation). For the present,

there is no more to be suggested than that the higher Cork Beds faunas include conodonts which can be compared with specimens recovered from the Black Rock Group by Rhodes, Austin, and Druce—a modest proposal, which is consistent with Turner's (1952) suggestions based on the corals and brachiopods.

These various observations on the relationships of stratigraphic successions that produce conodonts of the kind found in the Cork Beds are brought together in text-fig. 3, to which the following considerations apply:

1. Belgium: if Tn 1b is accepted as an equivalent of the Hangenbergkalk, and the occurrence of *Scaliognathus anchoralis* and *Hindeodella segaformis* reported in Tn 3c by Groessens accepted as an equivalent of the beginning of the *anchoralis*-Zone of Germany, then it is permissible to treat the intervening range (Tn 2a-Tn 3b



TEXT-FIG. 3. Major Cork Beds conodont faunas related to successions in the U.S.A., Germany, and Belgium.

inclusive) of the Belgian succession as an equivalent of the *Siphonodella crenulata*-Zone (defined in Voges 1960, p. 210, as extending from the point of entry of *S. crenulata*, i.e. close above the Hangenbergkalk in Germany, up to the point of entry of *Sc. anchoralis*, *H. segaformis*, and *D. latus*). Belgian thicknesses in text-fig. 3 are taken from Legrand *et al.* (1966).

2. No attempt is made to show the thickness of the German succession to the same scale (see Voges 1960, fig. 2, for an indication of German thicknesses). Lowest Carboniferous zones are shown as in Ziegler (1969).

3. Thicknesses of the American succession can be read from a fence-diagram in Thompson and Fellows (1970, plate 9). The zones shown in text-fig. 3 would occur in some 20–30 m of beds. Thompson and Fellows's figs. 25 and 26 serve as a source of information on breaks in the American succession (left side of the American column in text-fig. 3: Collinson, Scott, and Rexroad's findings; right: Thompson and Fellows's). The interval between Thompson and Fellows's *Pseudopolygnathus multistriatus* subzone and their *D. latus* subzone is taken here as an approximate equivalent of the beginning of the German *anchoralis*-Zone.

4. Some of the Cork Beds faunas are shown on the right of the figure. The placing of OH1 and B8 are by no means certain. For more detailed information on Cork Beds correlations and thicknesses text-fig. 4 should be consulted.

5. Vertical lines indicate the lower part of the *anchoralis*-Zone. None of the Cork Beds conodont faunas are as young as this.

The above discussion provides for the following comments on the ages of the major Cork Beds conodont faunas (see faunal lists on pp. 337 and 338):

OH1: The age of this collection of conodonts involves some rather indirect arguments. The fauna is dominated by spathognathodids, and has *Polygnathus communis communis* and *Patrognathus variabilis*. *Pa. variabilis* is characteristic of Rhodes, Austin, and Druce's lowest Avonian zone, but, as Ziegler (1971) has already pointed out, there was no evidence to justify Rhodes, Austin, and Druce's suggestion that their lowest zone was an equivalent of the earliest Carboniferous of Germany. More recently, Austin, Conil *et al.* (1970) have recovered a fauna (Huy 15/111 in their paper) from Tn 1b in Belgium which includes, notably, several spathognathodids, a patrognathodid, and a specimen of *Siphonodella cooperi*. This fauna, whose evidence is supported by that of spores, gives a clearer indication of very early Carboniferous age. There is a close resemblance between the Huy 15/111 spathognathodids and those of OH1. The resemblance is masked by different use of names (note remarks in the systematic section below, where it will appear that usage here has much in common with, for example, that of Sandberg and Klapper 1967; and note too that the Huy 15/111 conodonts, as identified in Austin, Conil *et al.* (1970), include indices to more than one of Rhodes, Austin, and Druce's Avonian zones), but it exists, and is taken to indicate that OH1 belongs in the neighbourhood of the Devonian/Carboniferous boundary. OH1 was resampled in the hope of obtaining siphonodellids, or protognathodids, which might have provided for a more precise estimate of age. Unfortunately, this is the one case in which the second sampling proved unfruitful. Some support for this estimate of the age of OH1 can

be found in Kuijpers (1972), who refers to palynological evidence of very early Carboniferous age obtained from the lowest part of the Kinsale Group. B8 and the Black Ball Head fauna are tentatively regarded as equivalents of OH1, a suggestion which will be firmer when the range of the clydagnathoid variants of *Spathognathodus aculeatus* is better understood.

B2: In the discussion of American evidence above it was suggested that B2 is an approximate equivalent of the late Kinderhook-early Osage conodont faunas of the U.S.A. *Siphonodella cooperi* is the dominant siphonodellid. The presence of *Pseudopolygnathus multistriatus* is something of an anomaly, in that the American zonal scheme would have it emerge at a higher level. In dealing with relations within the Cork Beds (see text-fig. 4 below), WB2 is treated as an equivalent of B2. OH4 has some similar conodonts, although the specimens are all of relatively small size, and this fauna too is taken to be of much the same age as B2. It is clear that F1 is older than the faunas found higher in the Ringabella succession (R4 for example), but it is difficult to judge its age relative to the B2, OH4, WB2 faunas (note that it includes, again, *Ps. multistriatus*). However, there need be no doubt that it should be interpreted, within the Cork Beds, as representing a horizon distinctly higher than that recorded in OH1.

R4: The R4 fauna has been mentioned above. The presence of abundant *Polygnathus communis carina* is taken to indicate a horizon close below the point at which *Scalio-gnathus anchoralis* and its associates might be expected to emerge.

These suggestions on age are built into the discussion of stratigraphical relationships within the Cork Beds which now follows. References to conodont faunas already reported from southern Ireland have been reserved for this part of the paper.

#### CORRELATION WITHIN SOUTHERN IRELAND

The four main sections sampled for this study (text-fig. 5) are in the Courtmacsherry Group and its lithological equivalents, at Ringabella, Old Head of Kinsale, Dunmanus, and Bantry (text-fig. 1). Some results are available from the Kinsale Group also.

The new information may be used first to make comments on age-relationships between the Cork Beds and the 'Waulsortian' and associated carbonate rocks found to the north. This more northerly facies includes the 4000 ft (approx. 1300 m) of bank limestone known in the Cork Syncline at Little Island. These limestones are underlain by a thin Lower Limestone Shale succession, and below that there is the Old Red Sandstone. The middle part of the limestone sequence includes the distinctive reddened horizon known as the Cork Red Marble (Nevill 1962). Quarrying provides good access to the stratigraphy at and above the Red Marble horizon, but the lower part of the limestone succession is poorly exposed. Macrofossils from the upper part of the sequence give no exact information on age. Naylor (1969) has reviewed the evidence available and has suggested that Viséan age is probable. Foraminiferids (reported in Naylor 1964, unpublished Ph.D. thesis, University of Dublin) from the upper part of the succession—the lowest sample was taken from a position 50 ft below the Red Marble—again indicate Viséan (S-D<sub>1</sub>) age. Austin

(1968) has recorded a Viséan conodont fauna from the Red Marble (it should be noted that his sample was collected 10 miles along strike at Middleton: see Nevill 1962, locality 10). Further to the north in Co. Cork, Hudson and Philcox (1965) were able to distinguish two Lower Carboniferous 'reef' developments. They regarded the lower, a Waulsortian carbonate mud-bank complex, as being of Tournaisian age. It is followed by a thin pyroclastic development, then by well-bedded argillaceous limestones ( $C_2S_1$ ) and then by the higher reef-complex, of Cracoean character, which was given dates in the range  $S_2-D_1$ . This differentiation between two complexes is not possible at Little Island. It may be that the Cracoean complex here succeeds the Waulsortian bank limestones at some point within the poorly exposed succession lying below the Cork Red Marble. Alternatively, the Waulsortian carbonates may be very thin, and much of the Tournaisian represented in the Lower Limestone Shale facies.

Comparing these northerly successions with that in the Ringabella Syncline, the first point to be considered is the Tournaisian age of the Ringabella Limestone Formation (see especially samples R2, R3, R4). A poor coral fauna from these beds was considered to be of Viséan age by Naylor *et al.* (1969). If the Tournaisian date is now accepted, it would follow that the Ringabella Limestone Formation must predate a considerable part of the thick carbonate succession found to the north. Samples from the base of the bank limestone in the Cloyne Syncline have proved unproductive, and there is no information on whatever might be the correlative of the Ringabella Limestone in the poorly exposed lower part of the stratigraphy at Little Island. But it is clear that the Ringabella conodonts are older than those reported from the Cork Red Marble by Austin (1968). One implication of these suggestions is that much of the thick carbonate succession found at Little Island should correlate with whatever stratigraphy is present along the axis of the Ringabella Syncline in the ground between the coast and the Minanebridge quarries. There is no direct information on the nature of this stratigraphy, nor its age (a possibility discussed above is that it might be to some extent siliceous, and might include the equivalent of the *anchoralis*-Zone), but its thickness can be estimated. It would be reasonable to suggest that this concealed interval is unlikely to contain more than 500 ft (approx. 160 m) of beds. A regional southward thinning is therefore indicated.

The west-coast evidence also suggests southward thinning of the Lower Carboniferous. The northern limit of Cork Beds outcrop is at Kenmare River. North of Kenmare, the Lower Carboniferous includes a Lower Limestone Shale unit and a major thickness of carbonate rocks. There is no published information on the age of the limestones that crop out of the northern limb of the Kenmare Syncline; but somewhat further north, in the Castleisland area at the eastern end of the Dingle Peninsula, Hudson *et al.* (1966) have recognized a lower, Waulsortian ( $C_1$ ) complex and a higher, Cracoean ( $S_2-D_1$ ) complex within a Lower Carboniferous succession which totals 4750 ft (approx. 1500 m) in thickness. A similar succession exists in north-west Co. Limerick, where Shepard-Thorn (1963) referred the Waulsortian stratigraphy to the C Zone. Information on conodonts is available here. Austin, Husri, and Conil's (1971) faunas include one from the base of the Waulsortian reef which would appear to be younger than any of the Cork Beds faunas. Hill's (1971) fauna, recovered from 'within the Waulsortian reef bank complex' of this same

general area, has *Scaliognathus anchoralis* and should also be adjudged younger than anything available from the Cork Beds. Comparing these Limerick successions now with that on Bantry Bay, one should first take note of the suggestion that the B8 and B9 faunas are of early Tournaisian age. They come from the northern limb of the Bantry Syncline, where the total thickness of the calcareous succession (which has been regarded as the west-coast equivalent of the Courtmacsherry Group) is unlikely to exceed 800 ft (P. C. Jones, pers. comm.). It is difficult to unravel the structures in the core of the Bantry Syncline, but present opinion is that the succession runs without a break from the Courtmacsherry Group to the goniatite bearing (P-Zone and E-Zone) mudstones on Whiddy Island. The Bantry succession appears then to represent most of the Lower Carboniferous, and is considerably thinner than the Limerick succession.

A second major feature of the results is that they suggest considerable variations of thickness within the Cork Beds themselves. OH4, collected near the base of the Courtmacsherry Group on the Old Head of Kinsale, is regarded as a near correlative of B2 from Bantry Bay. The implication here is that the Kinsale Group, 2500 ft (approximately 750 m) thick at the Old Head of Kinsale, is equivalent to less than 350 ft (approximately 105 m) of the calcareous succession at Bantry Bay. This correlation involves the most surprising result obtained, namely the suggestion that OH1 might be compared with B8 and B9. OH1 comes from the Castle Slate Formation, at the base of the Kinsale Group on the Old Head of Kinsale. B8 and B9 come from near the base of the Reenydonagan Group, which was earlier (Naylor *et al.* 1969) taken to be a Bantry Bay equivalent of the Courtmacsherry Group. The Reenydonagan Group is available again in west Cork, in the Dunmanus section, but samples from there have proved unproductive and, so far, supply no confirmation of the Bantry results. However, P. C. Jones (paper in preparation) finds that there are detailed similarities between the occurrences of the Reenydonagan Group in the Dunmanus and the Bantry successions, and this, together with their close proximity to one another, suggests that they are quite possibly time-equivalent.

The evidence of age in these lowest Bantry samples is weak at present. It may nevertheless be useful to offer it here for consideration along with results emerging from other researches in progress in south-west Ireland. The B8 and B9 conodonts imply that calcareous sediment entered the west-coast succession relatively early. Later in the Tournaisian, sedimentary material of this kind was accumulating both in the west (Bantry) and in the east (Old Head of Kinsale, Ringabella). One possibility is that two separate sub-basins were in existence for a time. Work in progress on the Toe Head to Seven Heads area may help to clarify the picture. Reilly (pers. comm.) finds that in the Glandore area the Kinsale Group is particularly thin, and is overlain directly by beds containing *Posidonia becheri*. There is no calcareous development in the succession, and this appears to be the case at Galley Head also. These preliminary findings may indicate that a positive feature existed in the Glandore-Galley Head area and separated two sub-basins, each of which received calcareous sediment, but it should be recognized that any such proposal will have more weight when further palaeontological work has been done.

Further palaeontological information is needed in the lowest parts of the Cork Beds succession too. References to the early Carboniferous, and to thin Lower

Carboniferous successions, should not obscure the fact that more than 5000 ft (approximately 1500 m) of beds belonging to the Cork Beds lie below sample B9. Two attempts have been made to recover conodonts from this lower part of the succession. In the first case, a limestone sample from Kilcatherine Point was processed. This horizon had been sampled earlier by R. O. Ducharme (then of the University of Reading), who kindly offered his conodonts to Matthews for study (see text-fig. 4, 1966 sample: Columnar Section 8). They include *Polygnathus communis communis*, *Spathognathus* cf. *aculeatus*, and *Sp. stabilis*, so that fauna is hardly to be distinguished, in terms of age-significance, from OH1. The Kilcatherine Point locality was resampled by Naylor, in the hope of providing for a more precise estimate of age, but no further conodonts were found. The second case involved a sample from the Ardaturrish Group, on the north flank of the Bantry Syncline, but this unfortunately proved unproductive. Possibly palynological work may achieve more in this part of the succession.

Summarizing information available on the Lower Carboniferous part of the Cork Beds, one can suggest first that the succession is distinctly thicker in south Cork than on the west coast. Secondly, it seems to be the case that most of this Cork Beds clastic wedge was already developed before the Waulsortian Bank Limestone and associated carbonates began to accumulate in the area north of the Cork-Kenmare line. The equivalent of the thick Viséan successions found to the north should be sought in the fine-grained upper parts of the Cork Beds, which have a few goniatites, but so far have produced no conodonts. The Cork Beds show a general upward sequence from alluvial, deltaic (Naylor 1966), or tidal (Kuijpers 1971, 1972) sandstones through prodelta siltstones (Kinsale Group) and shallow marine carbonates (Courtmacsherry Group) to restricted basin sediments at the top (Lispatrick Mudstone Group). This sedimentary progression indicates the existence of a gradually deepening basin. Earlier suggestions of a break (P-E zone goniatite-bearing mudstones resting unconformably on Tournaisian) find little support in the evidence now available.

Correlations within the Cork Beds are shown in text-fig. 4.

#### SYSTEMATIC PALAEOONTOLOGY

The Cork Beds faunas have been deposited in the collections of the Institute of Geological Sciences (Leeds Office). Two-figure numbers prefixed GSL SAD identify 32-cavity microslides. A suffix identifies each cavity.

The synonymy lists carry annotations according to the system proposed by Richter (1948). A brief explanation of the system is available in Matthews *et al.* (1972), Matthews (in press).

#### Genus ELICTOGNATHUS Cooper, 1939 *Elictognathus laceratus* (Branson and Mehl, 1934)

Plate 37, fig. 19

- \*1934 *Solenognathus lacerata* Branson and Mehl, p. 271, pl. 22, figs. 5, 6.
- 1959 *Elictognathus lacerata* (Branson and Mehl); Hass, pp. 386-387, pl. 49, figs. 1-8, 12.
- 1968 *Elictognathus lacerata* (Branson and Mehl 1934); Manzoni, p. 659.



- 1969 *Elictognathus laceratus* (Branson and Mehl); Rexroad, pp. 15-17, pl. 1, figs. 15-19.  
 1969 *Elictognathus costatus* (E. R. Branson); Rexroad, pp. 14-15, pl. 1, figs. 6-8.  
 1969 *Elictognathus tylus* (Cooper); Rexroad, p. 17, pl. 1, fig. 14.  
 1969 *Elictognathus lacerata* (Branson and Mehl 1934); Schönlaub, p. 329, pl. 3, fig. 1.  
 1970 *Elictognathus laceratus* (Branson and Mehl); Thompson and Fellows, pp. 81-83, pl. 5, figs. 20, 21 (with synonymy).

*Material.* *E. laceratus* (1), *E. cf. laceratus* (2): 3 specimens from 2 samples. Figured: GSL SAD5717.

*Remarks.* Thompson and Fellows's (1970) synonymy differs from Klapper's (1966) in only two respects: first, in updating Klapper's list (some further updating is done in the list above) and secondly in placing *Solenognathus fulcrata* Branson and Mehl 1934—and also the *So. fulcrata* (*sic*) Branson and Mehl of Cooper 1939—in synonymy with *E. laceratus*. Thompson and Fellows (1970) are consistent with Klapper (1966), and also with Hass (1959), whose example was followed by Voges (1959), in putting *E. costatus* (Branson and Mehl) in synonymy with *E. laceratus*. Straka (1968) and Rexroad (1969) have suggested that the crestal profile of the blade serves to separate these two, and that the separation is stratigraphically useful in that although the two species have much the same stratigraphic range, *E. laceratus* is the more abundant form in the higher part of the range. Because of the small number of specimens available here, and their immature form, it is not possible to follow Straka's and Rexroad's practice. The synonymy list above adjusts Rexroad's findings, treating *E. costatus* as Thompson and Fellows did, and suggesting that Rexroad, who put the relatively elaborate *So. fulcrata* into synonymy with *E. laceratus*, should not have treated *So. tyla* differently.

It may be useful to note here a record of *E. laceratus* in the Caballero Formation of New Mexico (Burton, pers. comm.) and further records of the species given in Klapper (1971, table 1).

#### Genus GNATHODUS Pander, 1856

*Remarks.* The literature of the last ten years carries numerous references to the difficult problem of reconciling Voges's (1959) and Collinson, Scott, and Rexroad's (1962) proposals on species of the genus *Gnathodus*. Thompson and Fellows's (1970) work has now made it possible to see that the range of the *anchoralis*-Zone from which Voges obtained the bulk of his *Gnathodus* material is at best only poorly represented in the broken Upper Mississippi Valley sections from which Collinson, Scott, and Rexroad collected their Chouteau, 'Sedalia', Lower Burlington, and Fern Glen gnathodids (Collinson *et al.* 1962, chart 3). There has, as yet, been no comprehensive treatment of the gnathodids (American, European) available from this range of the Lower Carboniferous. Rhodes and Austin's (1971) attempt to supply the need does not suffice. For one thing, it is stratigraphically uninformed. Also, it arbitrarily reassigns specimens described and figured by other authors to particular categories of the genus, some of which are new, and none of which are given adequate definition, neither in respect of their basic characteristics, nor in respect of their range of variation. The effect of this latter shortcoming is that other authors, even if convinced that Rhodes and Austin's phylogenetic proposals were worthwhile, would not find it possible themselves to attempt the identifications Rhodes and Austin recommend.

*Gnathodus delicatus* Branson and Mehl, 1938

Plate 35, figs. 14-17, 23-26

- \*1938 *Gnathodus delicatus* Branson and Mehl, p. 145, pl. 34, figs. 25-27.  
 ?1967 *Gnathodus delicatus* Branson and Mehl 1938; Wirth, pp. 209-210, pl. 19, fig. 21 (? = *G. semiglaber*).  
 v1972 *Gnathodus delicatus* Branson and Mehl; Matthews, Sadler, and Selwood, pp. 559-560, pl. 110, figs. 5, 7-9 (with synonymy).

*Material.* 29 specimens (including 1 'cf.' determination) from 5 samples. Figured specimens: GSL SAD22/18, 19, SAD24/6, 14, 15, 16, SAD26/6, 7.

*Remarks.* The species is interpreted here on the basis described in Matthews *et al.* (1972). It is seen that the parapet on the inner side of the carina tends to be broader in an anterior part of its course. Certain forms are relatively slim, but usually appear to have better-developed ornament (particularly in the posterior parts of the upper surface of the cup) than would be found in *G. cuneiformis* or *G. typicus* (Pl. 35, figs. 17, 26). Some specimens show an arrow-like arrangement of the inner and outer parapet (Pl. 35, figs. 15, 16) but are broader and have more ornament on the anterior part of the outer oral surface than would be found in *G. cuneiformis*.

*Gnathodus punctatus* (Cooper, 1939)

Plate 35, fig. 11; Plate 36, figs. 7, 8

- \*1939 *Dryphenotus punctatus* Cooper, p. 386, pl. 41, figs. 42, 43; pl. 42, figs. 10, 11.  
 ?1962 *Gnathodus semiglaber* Bischoff 1957; Müller, p. 1388, pl. 1, figs. 1a, b, c.  
 v1972 *Gnathodus punctatus* (Cooper 1939); Matthews, Sadler, and Selwood, pp. 560-562, pl. 109, figs. 5, 13; pl. 110, figs. 1-4, 11-15 (with synonymy).

*Material.* 4 specimens from 2 samples. Figured specimens: GSL SAD26/15, SAD 37/1, 2.

## EXPLANATION OF PLATE 35

Specimens dusted with ammonium chloride. All  $\times 30$ .

Figs. 1, 10, 21, 27. *Spathognathodus stabilis* (Branson and Mehl). 1, GSL SAD47/2 (OH1). 10, GSL SAD43/20 (B8). 21, GSL SAD22/4 (R2). 27, GSL SAD24/4 (R4).

Fig. 2. *Spathognathodus anteposicornis* Scott. GSL SAD47/11 (OH1).

Figs. 3-9. *Spathognathodus aculeatus* (Branson and Mehl). 3, 8, 9, Lateral, aboral, and oral views of GSL SAD47/8 (OH1). 4, 5, 6, Aboral, oral, and lateral views of GSL SAD47/6 (OH1). 7, GSL SAD47/13 (OH1).

Fig. 11. *Gnathodus punctatus* (Cooper). GSL SAD26/15 (R4b '71).

Figs. 12, 13. *Patrognathus variabilis* Rhodes, Austin, and Druce. Oral and lateral views of GSL SAD47/15 (OH1).

Figs. 14-17, 23-26. *Gnathodus delicatus* Branson and Mehl. 14, GSL SAD24/6 (R4). 15, GSL SAD24/14 (R4). 16, GSL SAD24/15 (R4). 17, GSL SAD24/16 (R4). 23, GSL SAD26/7 (R4b '71). 24, GSL SAD26/6 (R4b '71). 25, GSL SAD22/18 (R2). 26, GSL SAD22/19 (R2).

Figs. 18-20. *Spathognathodus* sp. Lateral, aboral, and oral views of GSL SAD26/11 (R4b '71).

Fig. 22. *Gnathodus semiglaber* Bischoff. GSL SAD24/5 (R4).



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15



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*Remarks.* Matthews *et al.* (1972) have referred to *G. punctatus* specimens which have on the inner side of their upper surface a short curved parapet arranged convex to the carina. They recognized a variant of the species (variant 2: Matthews *et al.* 1972, p. 561) which would include a form attributed to *G. delicatus* by Thompson and Fellows (1970). A further variant recognized by Matthews *et al.* (1972: variant 3), and regarded by them as showing some resemblance to *G. semiglaber*, occurs again in the Cork Beds (Pl. 35, fig. 11).

*Gnathodus semiglaber* Bischoff, 1957

Plate 35, fig. 22

- v\*1957 *Gnathodus bilineatus semiglaber* Bischoff, p. 22, pl. 3, figs. 1-10, 12-14.
- ?non 1962 *Gnathodus semiglaber* Bischoff 1957; Müller, p. 1388, pl. 1, figs. 1a, b, c (? = *G. punctatus*; see above).
- v1972 *Gnathodus semiglaber* Bischoff 1957; Matthews, Sadler, and Selwood, p. 562, pl. 110, fig. 10 (with synonymy).

*Material.* 14 specimens (including 3 'aff.' determinations) from 5 samples. Figured specimen: GSL SAD24/5.

*Remarks.* The R4 fauna has clear examples of this species. B2 contains slimmer forms which resemble the *G. aff. semiglaber* of Matthews (1969b). Matthews there suggested a resemblance to Thompson's (1967) *Gnathodus* sp. C, which was later referred to *Gnathodus* n. sp. B by Thompson and Fellows (1970). Rexroad's (1969) *Gnathodus* n. sp. includes forms that are again comparable.

Genus PATROGNATHUS Rhodes, Austin, and Druce, 1969

*Patrognathus variabilis* Rhodes, Austin, and Druce, 1969

Plate 35, figs. 12, 13

- 1967 N. gen. n. sp. Rhodes, Austin, and Druce; Sandberg and Klapper, p. B 52 (*vide* Klapper 1971).
- v\*1969 *Patrognathus variabilis* Rhodes, Austin, and Druce, pp. 179-180, pl. 2, figs. 8-11. (N.B.: The specimen shown on figs. 10a, b, c appears again on pl. 1, figs. 15b, a, c of Rhodes and Austin 1971.)

*Material.* 2 specimens (of which 1 'cf.') from 1 sample. Figured specimens: GSL SAD47/15.

*Remarks.* Klapper (1971), introducing *Pa. andersoni*, a second species of this genus, suggested that *Pa. andersoni* should receive certain specimens (Anderson 1969; Austin, Conil *et al.* 1970) formerly attributed to *Pa. variabilis*. Further records of *Pa. variabilis* (without illustration) are found in Austin, Husri, and Conil (1971) and Austin and Rhodes (1971).

Genus POLYGNATHUS Hinde, 1879

*Remarks.* The difference between *Polygnathus* and *Pseudopolygnathus* is not clear in Rhodes, Austin, and Druce's (1969) work. For example, they made much reference to *P. lacinatus*, proposing four subspecies, but failed to take account of Rexroad and Scott's (1964) opinion that *P. lacinata* Huddle 1934 is a synonym of

*Ps. fusiformis* Branson and Mehl 1934. This view is confirmed by Thompson and Fellows (1970) and in part, by Rexroad (1969), who refers only the specimen shown in fig. 3 of Huddle (1934, pl. 8)—i.e. the only one of Huddle's specimens whose basal cavity is figured—to *Ps. fusiformis*. *P. lacinata* Huddle of Cooper (1939, pl. 40, figs. 3, 4), which Rhodes, Austin, and Druce included in their *P. lacinatus lacinatus* synonymy, had already been referred to *Ps. marginata* Branson and Mehl 1934 by Klapper, an opinion confirmed by Rexroad (1969) and Thompson and Fellows (1970). Rhodes, Austin, and Druce's (1969) treatment of *P. longiposticus* Branson and Mehl also deserves attention here. On p. 210 of their paper they dealt with *Ps. cf. longiposticus* Branson and Mehl (*sic*). The sole item in their synonymy list was *P. longipostica* Branson and Mehl 1934. On p. 212 they remarked that 'the Avonian *P. multistriatus* pseudopolygnathids gave rise to *P. cf. longiposticus*'. Rhodes, Austin, and Druce's (1969) *Ps. nodomarginatus* (E. R. Branson) is again an example of a case in which *Pseudopolygnathus* and *Polygnathus* are confused. Other authors have been consistent in referring this species to *Polygnathus*. The only pseudopolygnathid in Rhodes, Austin, and Druce's synonymy list for this species is *Ps. brevimarginata* E. R. Branson 1934, which appears again in their synonymy list for *Ps. dentilineata*, with the same plate and figure reference but a different page reference. The page reference under *nodomarginatus* is the correct one, but it is the attribution to *dentilineatus* that matches other authors' opinions (e.g. Voges 1959; Klapper 1966). Rhodes, Austin, and Druce's synonymy list for '*Pseudopolygnathus*' *nodomarginatus* (p. 212 of their paper) also includes *P. cf. flabella* of Voges (1959, p. 290, pl. 34, figs. 8–11). One finds that the synonymy list for Rhodes, Austin, and Druce's own *P. bischoffi* (p. 184 of their paper) includes *P. cf. flabella* of Voges (1959, pl. 34, fig. 11 only).

It is possible to identify a worthwhile systematic problem among these confusions. Certain polygnathid conodonts have relatively large basal cavities whose lips extend some way toward the posterior end. Klapper (1966) recognized such a case in *P. delicatula*. A similar condition appears to exist in Thompson's (1967) *P. mehli* (which resembles *P. delicatula*, as Thompson noted, and may be an immature form of that species). The question is whether these polygnathoid conodonts that have relatively robustly featured, attenuate basal cavities should be excluded from *Polygnathus*. If this were to be done, it would not necessarily follow that they should be placed in *Pseudopolygnathus*, a genus whose basal cavity normally gives a clear indication of asymmetry and is relatively well developed in the lateral sense. Any attempt to produce such a reinterpretation of the polygnathoid conodonts might take account of the fact that *Siphonodella* is distinguished from *Polygnathus* on the evidence of basal features (Klapper 1966), and might also touch on the problem of the status of those late pseudopolygnathids (e.g. *Ps. triangulus pinnatus*) whose basal cavity is relatively small (see Ziegler 1963, footnote on p. 324).

*Polygnathus communis* Branson and Mehl, 1934

*Polygnathus communis communis* Branson and Mehl, 1934

*Material.* 49 specimens (including 14 *P. cf. communis*) from 5 samples.

*Polygnathus communis carina* Hass, 1959

Plate 37, figs. 2-5, 10

- \*1959 *Polygnathus communis* Branson and Mehl *carina* Hass n. var., Hass, p. 391, pl. 47, figs. 8, 9.  
 v1972 *Polygnathus communis carina* Hass; Matthews, Sadler, and Selwood, pp. 563-564, pl. 111, figs. 6, 7, 13 (with synonymy).

*Material.* 43 specimens from 4 samples. Figured specimens: GSL SAD24/2, 7, 8, SAD26/21.

*Remarks.* Matthews *et al.* (1972) have remarked that *carina* is the proper form of the subspecies name. The form '*carinus*' is unnecessary and the form '*carinatus*' (as given in Austin and Rhodes 1971, p. 194, and in Austin, Husri, and Conil 1971, p. 187: *P. communis carinatus* Hass) is wrong.

Details of ornament are seen to vary in specimens attributed to this subspecies. Matthews *et al.* (1972) refer to one variant which has up to three ridges on the anterior part of the platform on the inner side. That arrangement has been found again here (Pl. 37, fig. 5). Another variant (Pl. 37, fig. 10) has a longitudinal row of fine nodes on the inner platform surface. A similar form, but with larger nodes, is noted in Matthews *et al.* (1972).

*Polygnathus flabellus* Branson and Mehl, 1938

Plate 37, figs. 16, 24

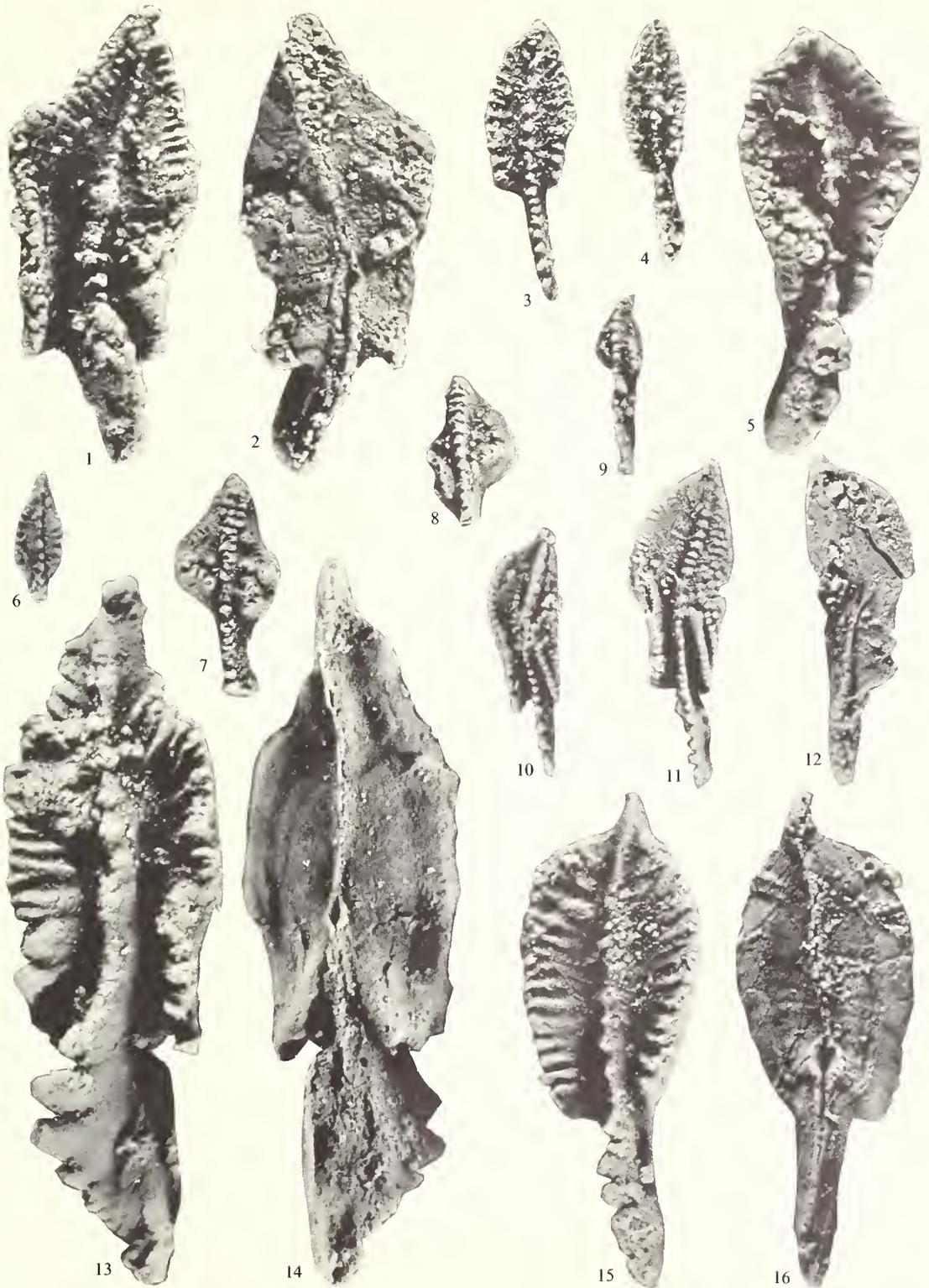
- \*1939 *Polygnathus flabella* Branson and Mehl, p. 147, pl. 34, fig. 48.  
 non 1939 *Polygnathus flabellum* Branson and Mehl; Cooper, p. 400, pl. 39, figs. 13, 14 (= *P. symmetricus*, *fide* Klapper 1966).  
 v?1959 *Polygnathus cf. flabella* Branson and Mehl; Voges, p. 290, pl. 34, figs. 8-11.  
 1968 *Polygnathus flabella* (Branson and Mehl 1938); Manzoni, p. 667, pl. 62, fig. 16 only (fig. 17 = ?).  
 ?1968 *Polygnathus inornata*; Manzoni, pl. 61, figs. 6, 9.  
 ?1968 *Siphonodella cf. sulcata*; Manzoni, pl. 61, fig. 10 only.  
 1969 *Polygnathus flabella* Branson and Mehl 1938; Schönlaub, pp. 333-334, pl. 2, fig. 25.  
 ?1969 *Siphonodella sulcata* (Huddle 1934); Schönlaub, pl. 2, figs. 16, 17 (figured as an 'adult example'; 'juvenile forms' on figs. 18-20 = ?).

*Material.* 2 specimens from 2 samples. Figured specimen: GSL SAD27/20.

## EXPLANATION OF PLATE 36

Specimens dusted with ammonium chloride. All  $\times 30$ .

- Figs. 1, 2, 5, 15, 16. *Polygnathus inornatus* E. R. Branson. 1, 2, Oral and aboral views of GSL SAD37/23 (B2 '71). 5, GSL SAD37/20 (B2 '71). 15, 16, Oral and aboral views of GSL SAD37/21 (B2 '71).  
 Figs. 3, 4. *Polygnathus symmetricus* E. R. Branson. 3, GSL SAD36/10 (B2). 4, GSL SAD37/19 (B2 '71).  
 Fig. 6. *Polygnathus* sp. GSL SAD37/32 (B2 '71).  
 Figs. 7, 8. *Gnathodus punctatus* (Cooper). 7, GSL SAD37/1 (B2 '71). 8, GSL SAD37/2 (B2 '71).  
 Fig. 9. *Gnathodus* aff. *semiglaber* Bischoff. GSL SAD36/20 (B2).  
 Figs. 10-12. *Siphonodella cooperi* Hass. 10, GSL SAD37/3 (B2 '71). 11, 12, Oral and aboral views of GSL SAD36/4 (B2).  
 Figs. 13, 14. *Polygnathus longiposticus* Branson and Mehl. Oral and aboral views of GSL SAD37/24 (B2 '71).



MATTHEWS and NAYLOR, Carboniferous conodonts

*Remarks.* The large specimen figured on Pl. 37, figs. 16, 24, agrees well with Branson and Mehl's holotype (which, it might be noted, is figured on plate 34 of their paper along with the conodonts among which it occurred at Branson and Mehl's Danville locality). The posterior end of the platform is better preserved in the present specimen (and seen to be broadly rounded), and the blade is complete. The convex outward lateral margins of the platform are slightly upturned as they converge at the relatively narrow anterior end, but the general appearance of the platform is one of broad flatness, as compared with forms referred to either of the two *P. inornatus* groups. Voges (1959) used the name '*Polygnathus cf. flabella*' for one of the two groups of ribbed polygnathids he encountered in his Sauerland faunas, the other being '*Polygnathus inornata* s.l.'. He noted a superficial resemblance to siphonodellid form. Manzoni (1968) and Schönlaub (1969) were also aware of this resemblance, but appear to have confused polygnathids of this type with siphonodellids of the type of *S. sulcata* (Huddle). The difference should be clear from the characters of the aboral surface: note here (and in Schönlaub's pl. 2, fig. 17) the relatively large, polygnathid-type basal cavity, and also the presence of a well-developed keel extending from the basal cavity to the posterior end, and compare, for example, the aboral features of the specimen of *S. sulcata* figured in Canis (1968, pl. 72, figs. 22, 23).

Voges (1959, pl. 34, figs. 8, 9) included in *P. cf. flabella* one variant which has a pair of specially well-developed radial ridges near the anterior end of the platform. Manzoni (1968, pl. 62, fig. 17) has figured a specimen whose platform ribs are breaking down into runs of nodes and in which the posterior part of the carina fails. It is not at all clear that this interesting specimen deserves to be referred to *P. flabellus*.

### *Polygnathus inornatus* E. R. Branson, 1934

Plate 36, figs. 1, 2, 5, 15, 16; Plate 37, figs. 17, 18

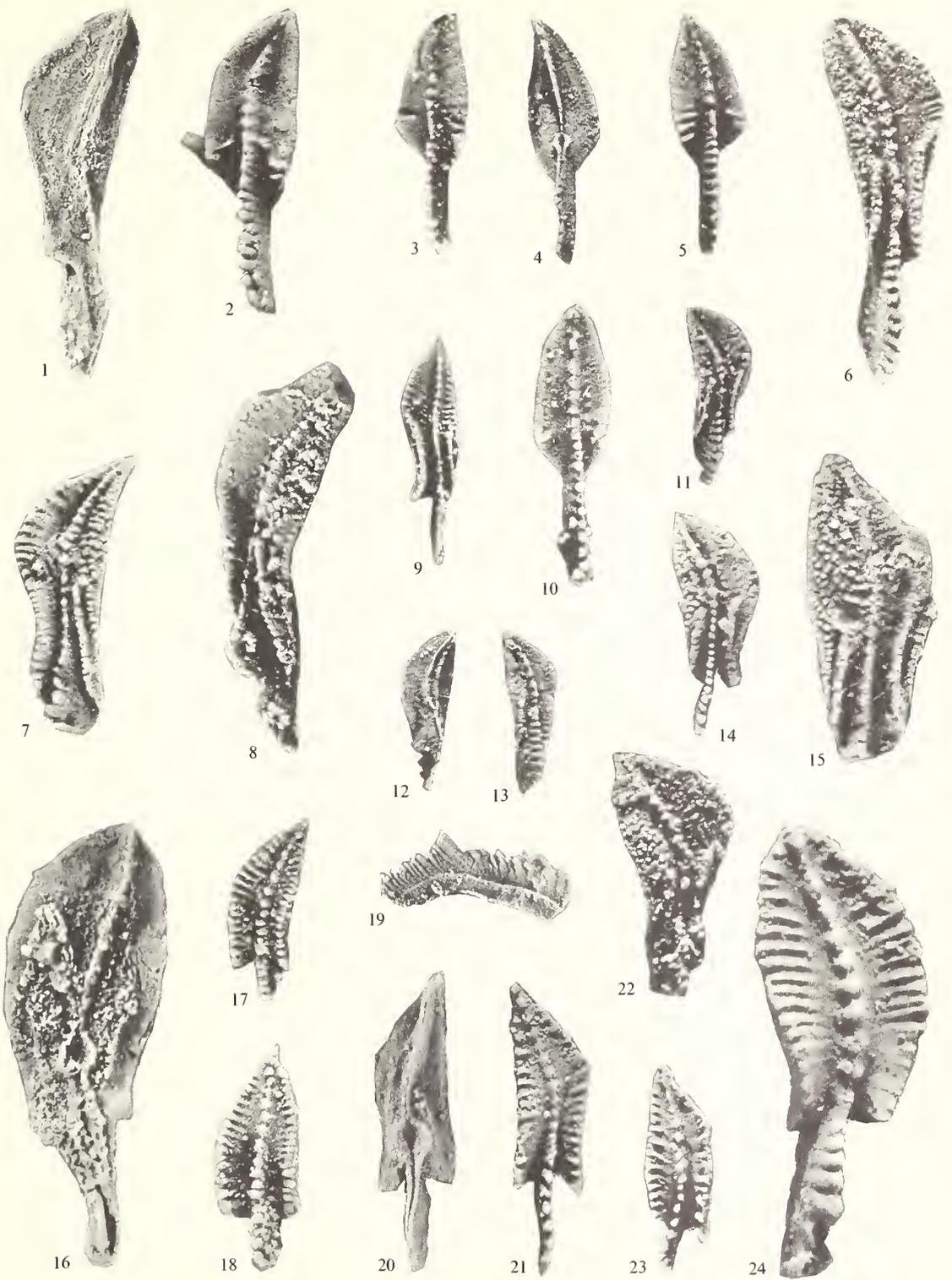
\*1934 *Polygnathus inornata* E. R. Branson, p. 309, pl. 25, figs. 8, 26.

v1969 *Polygnathus bischoffi* Rhodes, Austin, and Druce, pp. 184-185, pl. 13, figs. 7a-11c. (N.B.: The specimen shown on fig. 10 appears again on pl. 2, fig. 13 of Rhodes and Austin 1971.)

#### EXPLANATION OF PLATE 37

Specimens dusted with ammonium chloride. All  $\times 30$ .

- Figs. 1, 6, 7, 9, 14. *Siphonodella cooperi* Hass. 1, 6, Aboral and oral views of GSL SAD57/6 (WB2). 7, GSL SAD57/3 (WB2). 9, GSL SAD57/4 (WB2). 14, GSL SAD37/6 (B2 '71).  
 Figs. 2-5, 10. *Polygnathus communis carina* Hass. 2, GSL SAD24/8 (R4). 3, 4, Oral and aboral views of GSL SAD24/2 (R4). 5, GSL SAD 24/7 (R4). 10, GSL SAD26/21 (R4b '71).  
 Figs. 8, 15. *Siphonodella cf. cooperi* Hass. 8, GSL SAD 37/4 (B2 '71). 15, GSL SAD36/5 (B2).  
 Fig. 11. *Siphonodella isosticha* (Cooper). GSL SAD37/25 (B2 '71).  
 Figs. 12, 13. *Siphonodella cf. S. isosticha* (Cooper). Aboral and oral views of GSL SAD36/3 (B2).  
 Figs. 16, 24. *Polygnathus flabellus* Branson and Mehl. Aboral and oral views of GSL SAD27/20 (R6).  
 Figs. 17, 18. *Polygnathus inornatus* E. R. Branson. 17, GSL SAD33/6 (F1). 18, GSL SAD27/11 (R6).  
 Fig. 19. *Elictognathus laceratus* (Branson and Mehl). GSL SAD57/7 (WB2).  
 Figs. 20, 21, 23. *Polygnathus symmetricus* E. R. Branson. 20, 21, Aboral and oral views of GSL SAD57/18 (WB2). 23, GSL SAD57/20 (WB2).  
 Fig. 22. *Siphonodella* sp. GSL SAD36/6 (B2).



- . 1969 *Polygnathus inornatus* E. R. Branson; Rexroad, p. 34, pl. 5, figs. 13–15.
- 1969 *Polygnathus lobatus* Branson and Mehl; Rexroad, p. 35, pl. 5, figs. 16–18.
- 1971 *Polygnathus inornatus* Branson; Klapper, pp. 6–7 (with synonymy).
- ?1971 *Polygnathus inornatus* E. R. Branson; Austin, Husri, and Conil, pl. 1, figs. 12a, b.
- 1971 *Polygnathus lobatus lobatus* Branson and Mehl; Rhodes and Austin, pl. 1, fig. 8. (N.B.: The same figure appears in Rhodes, Austin, and Druce 1969, pl. 9, fig. 8a, and has been referred to *P. inornatus* E. R. Branson by Klapper 1971.)
- 1971 *Polygnathus inornatus vexatus* Rhodes, Austin, and Druce; Rhodes and Austin, pl. 1, fig. 10 (= Rhodes, Austin, and Druce 1969, pl. 10, fig. 3a, see Klapper 1971).
- 1971 *Polygnathus inornatus rostratus* Rhodes, Austin, and Druce; Rhodes and Austin, pl. 1, fig. 13 (= Rhodes, Austin, and Druce 1969, pl. 10, fig. 9b, see Klapper 1971).

*Material.* 35 specimens (of which 4 are 'cf.' determinations) from 10 samples. Figured specimens: GSL SAD27/11, SAD33/6, SAD37/20, 21, 23.

*Remarks.* The treatment given to these polygnathids here follows Klapper's (1971) paper, which separates *P. inornatus* E. R. Branson from *P. inornatus* sensu Branson and Mehl. Klapper does not yet offer a proposal on the name which *P. inornatus* sensu Branson and Mehl should finally receive. He unfortunately omits to point out what should now be the proper identity of the specimen figured in Klapper (1966, pl. 1, figs. 7, 8). Also, he gives no explicit instruction on the status of a form which has a bent carina but lacks any clear development of a sinus in the posterior margin. There is some guidance on this latter point in the treatment given by Klapper (1971) to one of the specimens he figured in 1966 (Klapper 1966, p. 1, figs. 9, 10, attributed to *P. inornatus* E. R. Branson in 1971). In the light of this example, it seems probable that *P. bischoffi* Rhodes, Austin, and Druce should be referred to *P. inornatus* E. R. Branson. It was remarked above that there is a common element in Rhodes, Austin, and Druce's synonymy lists for *P. bischoffi* and '*Pseudopolygnathus*' *nodomarginatus*. One might also note that these authors' synonymy list for *P. bischoffi* includes '*Polygnathus inornata* E. R. Branson; Bischoff: 42, pl. 2, figs. 17, 18, 20, 21' and that in their synonymy list for *P. inornatus inornatus* Branson and Mehl (*sic*), specimens listed as '*Polygnathus inornata* Branson and Mehl; Bischoff: 42, pl. 2, figs. 17, 18, 20, 21' are specifically excluded and referred to *P. lacinatus lacinatus*. Bischoff's specimens (described and figured as *P. inornata* E. R. Branson 1934) should probably go to *P. inornatus* E. R. Branson. So, too, should his *P. lobata* Branson and Mehl 1934 (Bischoff 1957, pl. 2, fig. 19).

Klapper's (1971) synonymy lists make no mention of Voges's (1959) specimens. Voges, who treated *P. lobata* as falling within the group that he called *P. inornatus* E. R. Branson 1934 s.l., figured (Voges 1959, pl. 34, figs. 12–20) five specimens under this name. All save the specimen shown in his figs. 15 and 16 should probably go to *P. inornatus* E. R. Branson as interpreted by Klapper. Rhodes *et al.* (1969, p. 188) have remarked that 'German workers, describing collections from condensed sequences of strata, included *P. lacinatus* within the species *P. inornatus* E. R. Branson, thus extending both the stratigraphic range and concept of that species'. In their synonymy list for *P. lacinatus lacinatus*, Rhodes, Austin, and Druce refer the specimens shown in Voges's figs. 17–20 to *P. lacinatus lacinatus*. These specimens come from the Hangenbergkalk (Voges 1959, explanation of pl. 34). The specimens which remain in *P. inornatus* according to Rhodes, Austin, and Druce (figs. 12–16 on

Voges's pl. 34) include one (fig. 12) which comes from the Erdbacherkalk equivalent at Borkewehr.

The specimen shown on Pl. 36, figs. 15, 16, is relatively straight, hinting at *P. inornatus* sensu Branson and Mehl, and has an attenuate posterior end, hinting at *P. longiposticus*, but is included here because of the sinus in the posterior part of its outer margin. Müller's (1962a) *Pseudopolygnathus?* cf. *P. triangula* Voges, which Klapper (1966) referred to *P. inornatus*, is comparable in many respects.

*Polygnathus longiposticus* Branson and Mehl, 1934

Plate 36, figs. 13, 14

- \*1934 *Polygnathus longipostica* Branson and Mehl, p. 294, pl. 24, figs. 8-11, 13.
- 1969 *Polygnathus longiposticus* Branson and Mehl; Rexroad, pp. 35-36, pl. 5, figs. 11, 12.
- 1969 *Polygnathus* cf. *P. longiposticus* Branson and Mehl 1934; Druce, pp. 100-101, pl. 21, figs. 4a, b only (fig. 5 = ?).
- ?1969 *Polygnathus toxophorus* Cooper, 1939; Druce, pp. 105-106, pl. 25, figs. 4a, b, 7a-9c.
- 1970 *Polygnathus longiposticus* Branson and Mehl; Thompson and Fellows, pp. 95-96, pl. 4, figs. 4, 16, 19 (with synonymy).
- ?1971 *Pseudopolygnathus longiposticus* Branson and Mehl; Austin, Husri, and Conil, pl. 1, fig. 10 (lateral view only).

*Material.* 1 specimen, GSL SAD37/24, figured.

*Remarks.* A particularly large specimen (Pl. 36, figs. 13, 14: length 3.5 mm) has all of the oral characteristics of the species, including the relatively poor development of carinal nodes near mid length (as observed by Klapper 1966). The blade has the character seen in the holotype. On the aboral surface, however, the basal cavity is small. The sample which produced this large conodont (B2 '71) produced also the large specimens of *P. inornatus* E. R. Branson illustrated on Pl. 36. These four conodonts vary in terms of the amount of marginal upturn developed at the anterior end of the platform, of the shape developed at the posterior end, and of the approach to straightness of the carina. However, there is a sense of common character in their ribbing (arranged everywhere at right angles to the margin, and fading toward the carina), and they may be more closely related to one another than the use of two different specific names would suggest. Klapper (1966) has some remarks on forms which mediate between *P. longiposticus* and *P. inornatus* (presumably *P. inornatus* in the sense of Branson and Mehl, since *P. longiposticus* has a relatively straight blade-carina arrangement) and he has observed, too, that *P. longiposticus* itself mediates between *P. inornatus* and *P. symmetricus*. An occurrence of *P. symmetricus* in the B2 fauna is noted below.

Reference has been made above to the question of the generic status of the specimens described as *Pseudopolygnathus* cf. *P. longiposticus* Branson and Mehl by Rhodes, Austin, and Druce. The question of their specific status also arises. They are omitted from the synonymy list here because the writer (S. C. M.) is not satisfied that the specimens figured by Rhodes, Austin, and Druce deserve to be included in this species. They would in most cases seem to have more in common with *P. nodomarginatus*. One specimen (Rhodes *et al.* 1969, pl. 30, fig. 11) resembles the holotype of their *Ps. postinodosus* (Rhodes *et al.* 1969, pl. 6, figs. 6a-c).

*Polygnathus symmetricus* E. R. Branson, 1934

Plate 36, figs. 3, 4; Plate 37, figs. 20, 21, 23

- \*1934 *Polygnathus symmetrica* E. R. Branson, p. 310, pl. 25, fig. 11.  
 v. 1969 *Polygnathus lacinatus asymmetricus* Rhodes, Austin, and Druce, pp. 188-189, pl. 11, figs. 1a-3c only (figs. 4a-c = ?).  
 1969 *Polygnathus symmetrica* E. R. Branson 1934; Schönlaub, p. 337, pl. 1, fig. 27; pl. 2, fig. 23.  
 1969 *Polygnathus anidus* Cooper, 1939; Druce, pp. 91-92, pl. 22, figs. 1a-4c.  
 1970 *Polygnathus symmetricus* Branson; Thompson and Fellows, p. 97, pl. 4, figs. 17-18 (with synonymy).  
 1970 *Polygnathus symmetricus* E. R. Branson; Austin, Conil, Rhodes, and Strel, pl. 1, figs. 20a, b, 21a, b.  
 ?1971 *Polygnathus* cf. *symmetricus* Branson; Philip and Jackson, pp. 70-71, pl. 5, figs. 17-18.

*Material.* 10 (1 'cf.') specimens from 6 samples. Figured specimens: GSL SAD36/10, SAD37/19, SAD57/18, 20.

*Remarks.* Klapper (1966) and Thompson and Fellows (1970) have commented on the similarities this species shows to *P. inornatus* and *P. longiposticus*. Thompson and Fellows's (1970) diagnosis and description mentions that maximum width of this narrow conodont is to be found in the posterior half of the platform. This involves a departure from what is typical of Branson's species. The character of the holotype is well represented by the specimen shown in Klapper (1966, pl. 6, figs. 1, 5). The features specified by Thompson and Fellows are evident in the specimen shown in Klapper (1966, pl. 4, figs. 7, 8). The specimens referred to *P. anidus* by Druce appear to be of this latter type. Rhodes, Austin, and Druce's (1969) *P. lacinatus asymmetricus* has the same character. It seems possible that this relatively slim *P. symmetricus* variant might be simply an immature form (relatively large basal cavity, relatively poorly developed marginal upturn at the anterior end of the platform) of the *P. inornatus* type of polygnathid.

Philip and Jackson (1971), like Bischoff (1957), have suggested that *P. symmetricus* might be represented in the late Devonian.

## Genus PSEUDOPOLYGNATHUS Branson and Mehl, 1934

*Remarks.* Some attention was given above to the problem of the *Polygnathus-Pseudopolygnathus* distinction. Identification of pseudopolygnathid species also involves problems. Klapper's (1966) procedure is followed here. It is not entirely satisfactory in that it depends to some extent on the width of the basal cavity relative to that of the platform, a ratio which may vary during ontogeny. His procedure is nevertheless clearly preferable to that of Rhodes *et al.* (1969), which relies heavily on numbers of nodes and ridges, and which, as Ziegler (1971a) has observed, attempts too many and too fine distinctions. A number of internal inconsistencies can be discovered in Rhodes, Austin, and Druce's treatment of the pseudopolygnathid species, and could serve to illustrate the essential impracticability of their proposals. Given the present state of pseudopolygnathid systematics, and the low numbers of specimens available as a basis for judgement here, it seems best to make only a brief record of the species found, with no suggestions on synonymies.

*Pseudopolygnathus dentilineatus* E. R. Branson, 1934

Plate 38, figs. 14, 15

*Material.* 15 specimens from 6 samples. Figured specimen: GSL SAD34/5.

*Remarks.* The species has an Upper Devonian range (recent information in Ziegler 1971*b* and Klapper *et al.* 1971), and possibly continues as high as the *anchoralis*-Zone (Ziegler 1963). In the Cork Beds faunas the highest occurrence appears to be in F1; but many of these relatively high records may involve immature representatives of other species of the genus.

*Pseudopolygnathus multistriatus* Mehl and Thomas, 1947

Plate 38, figs. 12, 13, 16-18, 20

*Material.* 7 specimens (2 'cf.') from 6 samples. Figured specimens: GSL SAD3/11, SAD36/9, SAD37/8; 'cf.' specimens figured SAD27/5, SAD36/18.

*Remarks.* Specimens of *Ps. multistriatus* have relatively small basal cavities. All save one of the conodonts referred to this species here have ribs which maintain their character toward the carina. The exception is the individual figured on Pl. 38, figs. 16-18. This has marginal nodes which are in many cases linked to the carina by low fine ridges. It also has a relatively narrow, more elongate, basal cavity. It resembles in some respects *Ps. lanceolata* Hass, a species which most authors place in synonymy with *Ps. multistriatus*.

*Pseudopolygnathus primus* Branson and Mehl, 1934

Plate 38, figs. 5, 6, 21-23

*Material.* 2 specimens from 2 samples. Figured specimens: GSL SAD33/12, SAD44/20.

*Remarks.* Specimens referred to *Ps. primus* here have a less wide basal cavity than is found in *Ps. dentilineatus* and have ridges rather than marginal nodes on the upper surface. *Ps. multistriatus* also has ridges, but has a smaller basal cavity again. The specimen figured on Pl. 38, figs. 5, 6, has a relatively small basal cavity, but is referred to *Ps. primus* because of its relatively broad platform. None of the Cork Beds pseudopolygnathids show any hint of a transition to *Ps. triangulus*.

## Genus SIPHONODELLA Branson and Mehl, 1944

*Remarks.* Klapper's (1971) proposals on the systematics of this genus are accepted here.

*Siphonodella cooperi* Hass, 1959

Plate 36, figs. 10-12; Plate 37, figs. 1, 6, 7, 9, 11, 14

\*1959 *Siphonodella cooperi* Hass, pp. 392-393, pl. 48, figs. 35, 36.

1971 *Siphonodella cooperi* Hass; Klapper, p. 10, pl. 1, figs. 13-15, 21; pl. 2, figs. 1-3 (with synonymy).

*Material.* 26 specimens (2 'cf.') from 3 samples. Figured specimens: GSL SAD36/4, SAD37/3, 6, SAD57/3, 4, 6; 'cf.' specimens figured: SAD36/5, SAD37/4.

*Siphonodella isosticha* (Cooper, 1939)

Plate 37, fig. 11

- \*1939 *Siphonognathus isosticha* Cooper, p. 409, pl. 41, figs. 9, 10 (refigured in Klapper 1971, pl. 1, fig. 16).
- v1971 *Siphonodella isosticha* (Cooper); Rhodes and Austin, pl. 1, fig. 6 (= pl. 12, figs. 11a, b of Rhodes, Austin, and Druce 1969).
- 1971 *Siphonodella isosticha* (Cooper); Klapper, p. 10, pl. 1, fig. 16 (with synonymy).

*Material.* 11 specimens from 3 samples. Figured specimen: GSL SAD37/25.

*Siphonodella* cf. *S. isosticha* (Cooper)

Plate 37, figs. 12, 13

- 1971 *Siphonodella* cf. *S. isosticha* (Cooper); Klapper, p. 12, pl. 1, figs. 17-20 (with synonymy).

*Material.* 2 specimens from 1 sample. Figured specimen: GSL SAD36/3.

*Remarks.* Klapper (1971) applies this name to certain specimens which would formerly have been referred to *S. isosticha*. Their longer outer rostral ridge terminates on the platform rather than at its outer margin.

*Siphonodella obsoleta* Hass, 1959

- \*1959 *Siphonodella obsoleta* Hass, pp. 392-393, pl. 47, figs. 1, 2.
- v1969 *Siphonodella obsoleta* Hass 1959; Matthews (1969a), pp. 273-274, pl. 46, fig. 1.
- 1971 *Siphonodella obsoleta* Hass; Klapper, p. 12, pl. 1, fig. 25 (with synonymy).
- v1972 *Siphonodella obsoleta* Hass 1959; Matthews, Sadler, and Selwood, p. 565, pl. 111, figs. 4, 5.

*Material.* 6 specimens from 3 samples.

EXPLANATION OF PLATE 38

Specimens dusted with ammonium chloride. All  $\times 30$ .

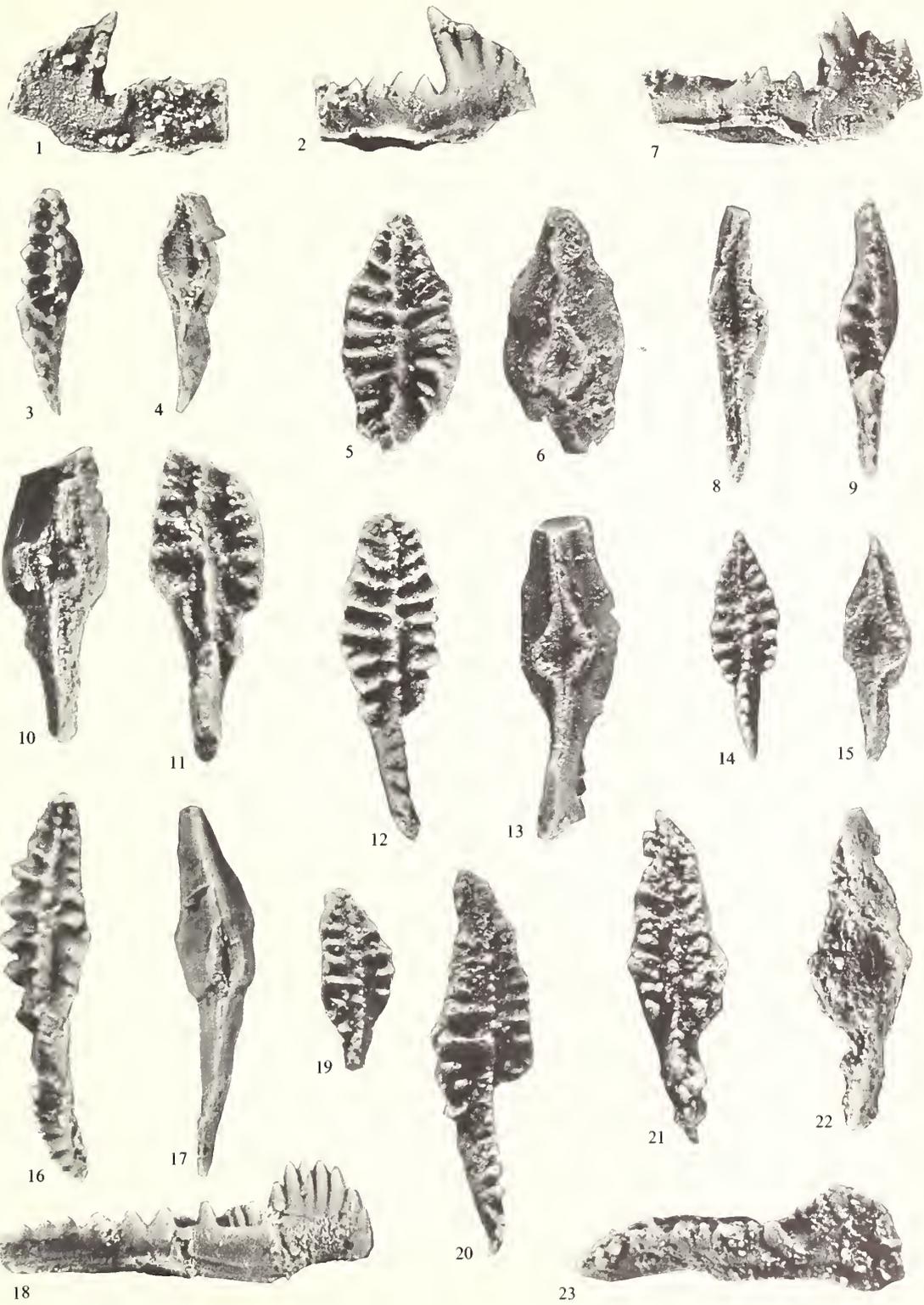
Figs. 1-4, 7-9. *Spathognathodus aculeatus*-*Clydagnathus* transition. 1-4, Left and right lateral, oral, and aboral views of GSL SAD46/12 (BBH). 7-9, Right lateral, aboral, and oral views of GSL SAD43/22 (B8).

Figs. 5, 6, 21-23. *Pseudopolygnathus primus* Branson and Mehl. 5, 6, Oral and aboral views of GSL SAD33/12 (F1). 21-23, Oral, aboral, and right lateral views of GSL SAD44/20 (B9).

Figs. 10, 11, 19. *Pseudopolygnathus* cf. *multistriatus* Mehl and Thomas. 10, 11, Aboral and oral views of GSL SAD36/18 (B2). 19, GSL SAD27/5 (R6).

Figs. 12, 13, 16-18, 20. *Pseudopolygnathus multistriatus* Mehl and Thomas. 12, 13, Oral and aboral views of GSL SAD33/11 (F1). 16-18, Oral, aboral, and right lateral views of GSL SAD37/8 (B2 '71). 20, GSL SAD36/19 (B2).

Figs. 14, 15. *Pseudopolygnathus dentilineatus* E. R. Branson. Oral and aboral views of GSL SAD34/5 (F2 '71).



MATTHEWS and NAYLOR, Carboniferous conodonts

Genus SPATHOGNATHODUS Branson and Mehl, 1941  
*Spathognathodus aculeatus* (Branson and Mehl, 1934)

Plate 35, figs. 3-9

- \*1934 *Spathodus aculeatus* Branson and Mehl, pp. 186-187, pl. 17, figs. 11, 14.
- 1962 *Spathognathodus aculeatus* Branson and Mehl; Ziegler 1962, pp. 105-106, pl. 13, figs. 27-36 (with synonymy).
- 1962 *Spathodus (Bispathodus) aculeatus* (Branson and Mehl); Müller (1962a), p. 114.
- 1966 *Spathognathodus aculeatus* (Branson and Mehl) 1934; Klapper, p. 24, pl. 6, figs. 16-17 (with further synonymy).
- v. 1969 *Spathognathodus tridentatus* (E. R. Branson); Rhodes, Austin, and Druce, p. 237, pl. 3, figs. 9a-12c.
- 1969 *Spathognathodus* cf. *S. aculeatus* (Branson and Mehl 1934); Druce, p. 124, pl. 27, figs. 5a-c.
- ?1969 *Spathognathodus cyrius nodus* n. subsp., Druce, pp. 129-130, pl. 28, figs. 6a-c, text-fig. 27.
- . 1969 *Spathognathodus sculderus* n. sp., Druce, p. 135, pl. 43, figs. 1a-5.
- 1969 *Spathognathodus aculeatus* (Branson and Mehl 1934); Schönlaub, p. 347, pl. 3, fig. 17.
- 1970 *Spathognathodus tridentatus* (E. R. Branson); Conil, Austin, Rhodes, and Streel, pl. 1, figs. 3, 6a, b.
- 1971 *Spathognathodus aculeatus* (Branson and Mehl); Philip and Jackson, pp. 72-73, figs. 12, 20 (with recent synonymy).

*Material.* 5 specimens from 1 sample. Figured specimens: GSL SAD47/6, 8, 13.

*Remarks.* Ziegler (1962) and Klapper (1966) have given detailed descriptions of this species. Ziegler (1962) referred to the presence of one to three, often four, or rarely five lateral (accessory) denticles. They arise from the area where the basal cavity has its maximum lateral extent, often reach the same height as the blade denticles and are occasionally bound to these by weak ridges. At all ontogenetic stages they are more powerfully developed than the blade denticles. Ziegler also observed that the crestal profile of the blade becomes lower posteriorly, and that the highest blade denticles arise either abruptly or gradually out of the series of blade denticles in the anteriormost parts of the conodont. Klapper's (1966) treatment of the species is consistent with Ziegler's (1962) in most essentials, but points out that most of his (Klapper's) specimens have three to five lateral denticles and some may have as many as seven. The series of lateral denticles in no case reaches the posterior end of the conodont.

The present specimens can be referred confidently to *Sp. aculeatus*. The variable profile of the anterior blade is evident in the figures, and the number of lateral denticles is found to vary from one to seven. The basal cavity is in some cases (i.e. in relatively small specimens, e.g. Pl. 35, fig. 4) long-elliptical rather than circular. Klapper (1966) observed that *Sp. anteposicornis* Scott is a case in which a single lateral denticle is situated anterior to the basal cavity. Such a specimen is available here (Pl. 35, fig. 4).

Both Ziegler (1962) and Klapper (1966) regard *Sp. tridentatus* (E. R. Branson) as a synonym of *Sp. aculeatus*. Rhodes *et al.* (1969) appear to have taken too little account of Ziegler's and Klapper's opinions on this matter. Their synonymy list for *Sp. tridentatus* (see Rhodes *et al.* 1969, p. 237) contains no entry dated later than 1961. Their suggestion (same page) that *Sp. aculeatus* has a more expanded (laterally) basal cavity than *Sp. tridentatus* does not seem to be borne out by the evidence

of their own and others' published figures. Philip and Jackson (1971) have already pointed out that there was no basis for Rhodes, Austin, and Druce's (1969, p. 236) querying of Ziegler's (1961) (*sic*) and other authors' identifications of German examples of *Sp. aculeatus*.

Rhodes *et al.* (1969) have proposed a species, *Sp. plumulus*, which is characterized by a plume-like blade, whose crestal profile descends rapidly from maximum height seen in the posteriormost denticle of the series. In other respects it bears comparison with *Sp. aculeatus* (whose variable blade profile was mentioned by Ziegler 1962—see above) although Rhodes *et al.* (1969) specify that the lateral nodes are developed on the outer side only, whereas Ziegler (1962) noted that the lateral denticles of *Sp. aculeatus* may appear on either the inner or the outer side. The present material, like Klapper's of 1966, shows inner side development only. The holotype of *Sp. plumulus plumulus* has denticles on its inner side (Rhodes *et al.* 1969, pl. 1, fig. 1*b*) and thus fails to match the terms of Rhodes, Austin, and Druce's diagnosis of the species. Rhodes, Austin, and Druce also proposed the subspecies *Sp. plumulus nodosus*, which has one or more nodes developed on the inner side. Two specimens in the present collection resemble the forms Rhodes, Austin, and Druce attributed to *Sp. plumulus*. In view of the confused state of the definition of that species, and in view of the fact that one of the specimens here (Pl. 38, figs. 7–9) does not exactly match the form of the blade specified for *Sp. plumulus* (the holotype of *Sp. plumulus nodosus* may also fail to do this) the two are figured as *Sp. aculeatus-Clydagnathus* transitions. One (Pl. 38, figs. 7–9) shows continuity from the blade into the relatively short run of accessory denticles. The other (Pl. 38, figs. 1–4) has a more plumose blade and appears to make a closer approach to *Clydagnathus*. Again, the blade runs into the series of accessory denticles, which are more numerous here, and which are each bound to the relatively featureless carina by a low ridge. The inner side (i.e. left side as seen in oral view, posterior end down) has a single peg-like denticle. Druce (1969, pl. 30, figs. 1*a*–2*c*: *Spathognathodus* cf. *S. plumulus*) has figured a specimen which bears some resemblance to the two discussed here. Beinert *et al.* (1971) have described *Clydagnathus? ormistoni* from the Upper Devonian, and remark that the generic assignment is tentative because of the lack of a complete lineage linking their conodont to early Carboniferous clydagnathids.

The majority of recorded occurrences of *Sp. aculeatus* are from the Upper Devonian. Lower Carboniferous records can be found in Sandberg and Klapper (1967) and in Canis (1968).

*Spathognathodus crassidentatus* (Branson and Mehl 1934)

- \*1934 *Spathodus crassidentatus* Branson and Mehl, p. 276, pl. 22, fig. 17.
- 1966 *Spathognathodus crassidentatus* (Branson and Mehl), 1934; Klapper, p. 23, pl. 5, figs. 15–17 (with synonymy).
- ?1969 *Spathognathodus crassidentatus* (Branson and Mehl); Rhodes, Austin, and Druce, pp. 227–228, pl. 3, figs. 1–4 (fig. 2*a* repeated in 1971).
- 1969 *Spathognathodus crassidentatus* (Branson and Mehl, 1934); Druce, pp. 127–128, pl. 27, figs. 2*a*–3*b*.
- 1969 *Spathognathodus crassidentatus* (Branson and Mehl); Rexroad, p. 46, pls. 6, 7, 8.
- 1970 *Spathognathodus crassidentatus* (Branson and Mehl); Thompson and Fellows, pp. 111–112, pl. 7, figs. 8, 14.

- 1970 *Spathognathodus crassidentatus* (Branson and Mehl); Austin, Conil, Rhodes, and Streeb, pl. 1, fig. 4.  
 1971 *Spathognathodus crassidentatus* (Branson and Mehl); Philip and Jackson, p. 73, pl. 6, fig. 1.

*Material.* 1 specimen.

*Remarks.* Klapper's (1966) revision of the species restricts *Sp. crassidentatus* to forms which have two distinctly well-developed anterior denticles. Rhodes, Austin, and Druce's (1969) representatives of this species would, therefore, not match entirely the specifications given by Klapper. Philip and Jackson (1971) have observed that their own specimens agree with paucidentate forms of *Sp. crassidentatus* rather than with forms of the kind illustrated by Rhodes *et al.* (see further remarks under *Sp. stabilis*, below).

*Spathognathodus* sp. indet.

Plate 35, figs. 18–20

*Material.* 4 specimens from 4 samples. Figured specimen: GSL SAD26/11.

*Spathognathodus stabilis* (Branson and Mehl, 1934)

Plate 35, figs. 1, 10, 21, 27

- \*1934 *Spathodus stabilis* Branson and Mehl, pp. 188–189, pl. 17, fig. 20.  
 1962 *Spathognathodus stabilis* (Branson and Mehl); Ziegler, pp. 112–114, pl. 13, figs. 1–10 (with synonymy).  
 1966 *Spathognathodus stabilis* (Branson and Mehl); Klapper, p. 23, pl. 5, figs. 6, 7 (with further synonymy).  
 ?1968 *Spathognathodus* cf. *S. stabilis* (Branson and Mehl, 1934); Straka, pp. 49–50, pl. 6, fig. 3.  
 1968 *Spathognathodus macer* (Branson and Mehl); Canis, p. 553, pl. 74, fig. 32.  
 1968 *Spathognathodus stabilis* (Branson and Mehl 1934); Schulze, p. 228, pl. 20, fig. 19.  
 ?1969 *Spathognathodus stabilis* (Branson and Mehl); Anderson, p. 925, pl. 109, figs. 2, 5, 8, 19.  
 1969 *Spathognathodus macer* (Branson and Mehl); Rexroad, pp. 47–48, pl. 6, figs. 9–11.  
 v. 1969 *Spathognathodus coaptus* (Branson and Mehl); Rhodes, Austin, and Druce, pp. 224–225, pl. 7, figs. 9a–11c.  
 v. 1969 *Spathognathodus elongatus* (Branson and Mehl); Rhodes, Austin, and Druce, pp. 228–229, pl. 7, figs. 1a–5b.  
 v. 1969 *Spathognathodus pulcher* (Branson and Mehl); Rhodes, Austin, and Druce, p. 231, pl. 4, figs. 9a–11c.  
 v. 1969 *Spathognathodus* cf. *cyrius* (Cooper); Rhodes, Austin, and Druce, pp. 234–235, pl. 7, figs. 12a–14c.  
 . 1969 *Spathognathodus cyrius cyrius* (Cooper, 1939); Druce, p. 129, pl. 28, figs. 4a–5c.  
 . 1969 *Spathognathodus quintidentatus* Thomas, 1949; Druce, p. 132, pl. 31, figs. 2a, b.  
 1969 *Spathognathodus stabilis* (Branson and Mehl, 1934); Druce, p. 136, pl. 31, figs. 6a, b.  
 1969 *Spathognathodus stabilis* (Branson and Mehl 1934); Schönlaub, p. 349, pl. 3, figs. 14, 15.  
 1970 *Spathognathodus stabilis* (Branson and Mehl); Thompson and Fellows, p. 113, pl. 4, figs. 1–3.  
 v. 1972 *Spathognathodus* cf. *stabilis* (Branson and Mehl); Matthews, Sadler, and Selwood, pp. 565–566, pl. 109, fig. 11.

*Material.* 22 specimens from 6 samples. Figured specimens: GSL SAD22/4, SAD24/4, SAD43/20, SAD47/2.

*Remarks.* Rhodes *et al.* (1969) and Druce (1969) failed to take note of Klapper's (1966) revision of *Sp. crassidentatus*. One consequence of Klapper's proposal is

that many forms earlier attributed to *Sp. crassidentatus* are now switched to *Sp. stabilis*. Klapper's (1966) synonymy list for *Sp. stabilis* includes species—*Sp. elongatus*, *Sp. pulcher*—which Rhodes *et al.* (1969) continued to treat as having independent standing. *Sp. cf. cyrius*, which Rhodes *et al.* (1969) regarded as distinct from *Sp. crassidentatus* because of the large number of its denticles, would not be excluded for that reason from *Sp. stabilis*. Rhodes, Austin, and Druce's synonymy lists for *Sp. crassidentatus* and *Sp. coaptus* have numerous items in common, which becomes reasonable if they are regarded as close to (their *Sp. crassidentatus*—see remarks above) or synonymous with (their *Sp. coaptus*) *Sp. stabilis*.

Ziegler (1962) has supplied a detailed description of *Sp. stabilis*. The species ranges from the Upper Devonian into the Lower Carboniferous (as high as the *anchoralis*-Zone) and it has been regarded as the root from which protognathodid form was derived (Ziegler 1969; Collinson *et al.* 1971).

Canis (1968) and Thompson and Fellows (1970) propose that the name *Sp. stabilis* be reserved for forms whose basal cavity extends to the posterior end. They would refer forms whose basal cavity is confined to the middle third of the conodont to *Sp. macer*. Thompson and Fellows's figures (cf. their pl. 4, fig. 3, with their pl. 4, fig. 7) do not seem to justify this view.

*Spathognathus cf. costatus* (E. R. Branson, 1934)

*Material.* 3 specimens from 3 samples.

*Remarks.* These conodonts are identified here in keeping with Voges's (1959) practice. Ziegler (1971a) has emphatically rejected Rhodes, Austin, and Druce's (1969) view of such forms.

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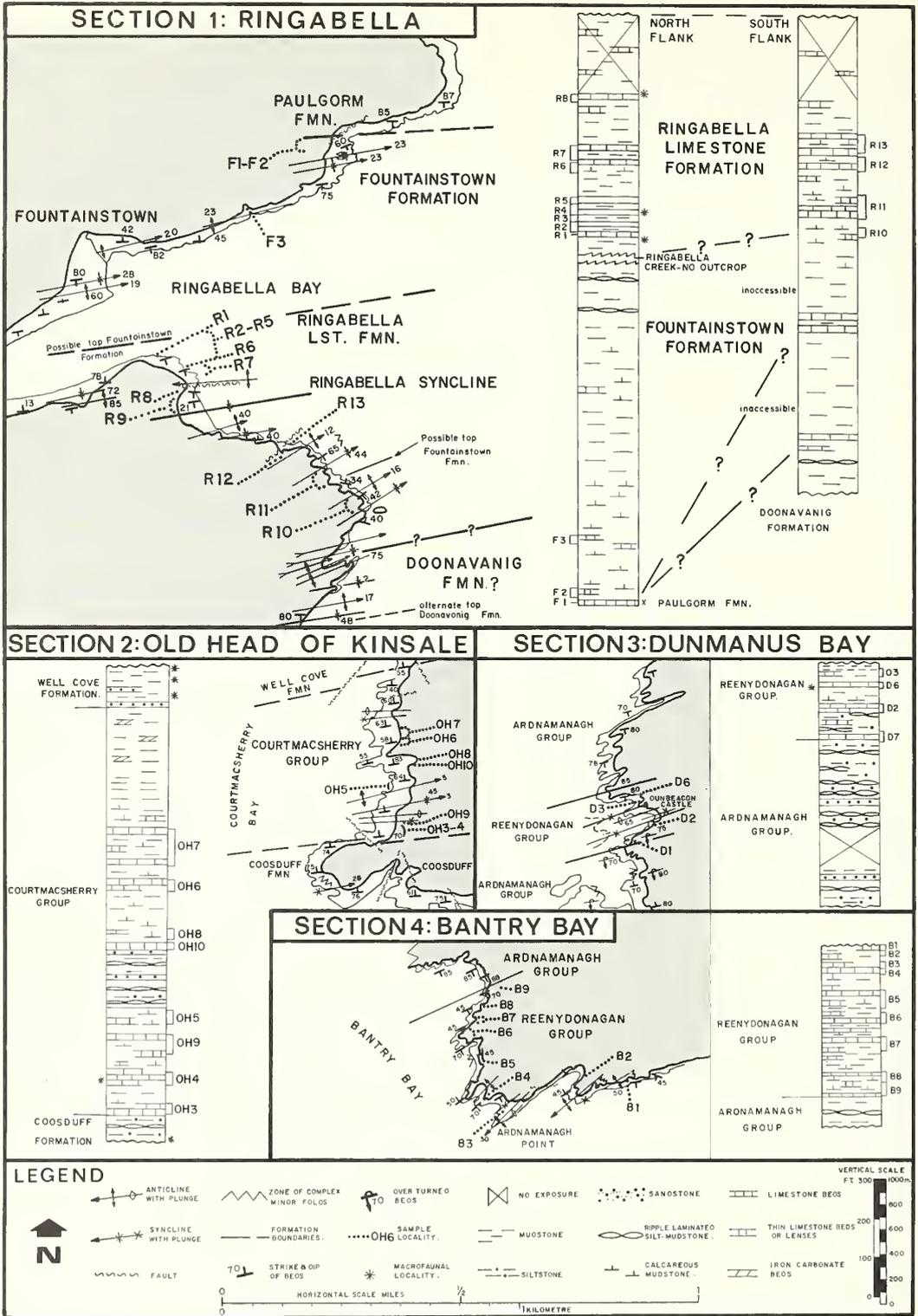
#### APPENDIX

The Courtmacsherry Group, which has provided the majority of the conodonts described here, consists typically of calcareous or non-calcareous mudstones interbedded with crinoid-rich limestone beds and lenses. Initial conodont samples were bulked from several limestone lenses. Productive or otherwise interesting horizons were resampled with greater precision.

Text-fig. 5 gives sample locations and details of the stratigraphic sequence in each of the four main sections. The main sections may be briefly described as follows:

*Ringabella Syncline*

The Courtmacsherry Group crops out on each flank of the Ringabella Syncline. Exposure is interrupted at Ringabella Creek and Fountainstown beach. On the south limb of the major syncline exposure is almost continuous, but the lower part of the succession is almost inaccessible because of the height of the cliffs. The base



TEXT-FIG. 5. Location of sampling-points in the four major sections studied.

of the Courtmacsherry Group (Fountainstown Formation plus Ringabella Limestone Formation) has been taken at a siliceous limestone bed with corals (Naylor *et al.* 1969) and this interpretation of the boundary is used in text-fig. 5. More recent examination of the high cliff section southward from this marker has revealed a further limestone (at the southern limit of the map in text-fig. 5) and the base of the group should probably be taken at this lower limestone. The laminated calcareous mudstones immediately to the north strongly resemble those attributed to the Fountainstown Formation on the north limb of the fold and are probably their equivalent. The possibility of a representation of the Fountainstown Formation on this south flank of the fold was not recognized in Naylor *et al.* (1969). The laminated beds are overlain by a sequence of calcareous and non-calcareous mudstones which include beds and lenses of crinoidal debris. A sequence of irregularly bedded limestones (R12 and R13) to the south of the synclinal axis is very similar to the limestones at Ringabella Point to the north. The highest beds seen are calcareous grey mudstones.

The succession on the north limb of the Ringabella Syncline has been described by Naylor (1969). The Fountainstown Formation as defined in that paper is 840 ft (approximately 250 m) thick. The well-exposed upper bedding plane of a bioclastic limestone with rolled fossils and phosphatic pebbles was taken to define the base of the formation. This limestone has corals of Tournaisian aspect and is the site of sample F1. The Fountainstown Formation consists of calcareous and non-calcareous mudstone with a delicate lamination. Near the base there is some crinoid debris (F2). Naylor (1969) referred the formation to the Kinsale Group, but because of the calcareous material present it would be more reasonable to regard it as the lowest formation of the Courtmacsherry Group. Ringabella Creek obscures the Fountainstown Formation–Ringabella Limestone Formation contact. The covered stratigraphic interval may be only a small one because of the amount of repetition produced by small folds hereabouts. The Ringabella Limestone Formation is excellently exposed on Ringabella Point, where some 350 ft of beds are seen. Dark grey, non-calcareous pyritic mudstones at the base of the sequence have goniatites (including some which Dr. W. H. C. Ramsbottom proposes to refer to a new species of the genus *Kazakhstania*, and which he will describe elsewhere). The succession above has calcareous and non-calcareous mudstones, with inter-bedded bioclastic limestones which contribute approximately 40% of the total thickness. Many of the limestones (R1 to R8 are representative samples) contain simple corals and black phosphatic pebbles. Their bases cut down into the sediment below. Limestones become less abundant in the upper part of the exposed section. R9 was bulked from lenses poorly exposed on the north flank of the syncline. The sample ranges through much of the succession from R8 up toward the presumed position of the main synclinal axis.

Text-fig. 5 shows different thicknesses on the north and south limbs of the Ringabella Syncline. Three considerations to be borne in mind are:

1. The base of the Courtmacsherry Group should perhaps be placed rather lower in the southern sequence, as mentioned above.
2. Complex folding makes it difficult to effect exact correlation.

3. Exposure is poor in the axial zone of the Ringabella Syncline and the position of the main synclinal axis itself is not precisely known.

*Old Head of Kinsale (west side)*

The type-locality of the Courtmacsherry Group (1116 ft—approximately 330 m—thick: Naylor 1966) is here. There are many minor folds and faults in the section on the west side of the headland, and these make it difficult to estimate thickness. The upper part of the sequence is especially affected by these difficulties. A number of units can be recognized in the Courtmacsherry Group. They are, in upward sequence:

*Unit 1.* 273 ft thick. The abrupt entry of calcareous beds clearly identifies the base of the group on the north side of Ringalurisky Point. Crinoidal debris in beds and lenses is inserted into a calcareous and non-calcareous grey nodular mudstone succession. Samples OH3–OH5 were collected from this unit.

*Unit 2.* 118 ft thick. A non-calcareous unit consisting of siltstones with fine sand cross laminae and rare thin shale-flake breccias.

*Unit 3.* 385 ft thick. Interbedded calcareous and non-calcareous mudstones with fewer thick limestone beds than in Unit 1, although parallel-sided and lensing laminae of crinoidal debris are still available.

*Unit 4.* 340 ft thick. Dark-grey mudstones containing rhombs of ferroan dolomite form the uppermost part of the group. The iron carbonate in places forms 20% of the rock. It occurs as rhombs in the groundmass or as occasional large concretions but never as discrete beds. The top of the Courtmacsherry Group is taken at the base of an unusual 7-ft-thick fine sandstone.

The overlying Lispatrick Mudstone Group contains a P-Zone lamellibranch-goniatite fauna near its base. Pyritic black mudstones are interbedded with evenly bedded fine sandstone and ferroan dolomite beds. There is also an intercalation of crinoidal limestones. These have been sampled, but no conodonts have been obtained.

It is difficult to associate the units of the Old Head succession with any in the Ringabella succession. The Old Head sequence has nothing that compares with the parallel-laminated, partly calcareous Fountainstown succession. F1, according to the conodont faunas, might be an equivalent of OH4, but fuller evidence is desirable before reaching any firm conclusion. On the other hand, it is already clear that the faunas of Unit 1 at the Old Head (see OH4) are older than those of the Ringabella Limestone Formation (see R2 to R4).

*Dunmanus Bay (Dunbeacon Castle)*

The samples from this sequence have produced only a single conodont. It may be useful to provide for any resampling (for conodonts or any other fossils) by making a record here of the character of the stratigraphy. Over 200–250 ft (60–75 m) of beds are available in the tightly folded axial part of the Dunmanus Bay Syncline. On each flank of the fold there are four units to be recognized:

*Unit 1.* 80–90 ft thick. Limestone beds and lenses usually 1–2 ft thick, interbedded with cleaved non-calcareous or slightly calcareous mudstones. The base of the unit is taken at the first bed of limestone (9 in thick) in the sequence. The underlying beds

of the Kinsale Group are massive ripple-banded non-calcareous siltstones with common horizontal burrows. Unit 1 becomes more calcareous upwards, with perhaps 30% of the sequence in the middle of the unit consisting of thin brown decalcified limestone beds and lenses, whilst the uppermost 8 ft are decalcified limestone.

*Unit 2.* 30 ft (may be 45 ft on north flank). Dark-grey brittle cleaved mudstones, rarely nodular. The uppermost 10 ft of this unit contains very thin (less than 3 in) bands and lenses of brown carbonate.

*Unit 3.* Approximately 35 ft. Non-calcareous and calcareous brittle grey mudstones with interbeds (40%) of evenly bedded brown decalcified limestones and possibly ferroan dolomite. Thin, grey carbonate stringers are also present. Sections through isolate corals are sometimes seen on joint surfaces. The uppermost bed of the unit is a 1-ft-thick bed of ferroan carbonate.

*Unit 4.* ?50 ft, top not seen. The grey non-calcareous mudstones of the previous unit grade upwards into the pyritic, black, highly organic massive mudstones of Unit 4. Concretions and bands of pyrite are common throughout and occasional large non-calcareous bullions also occur.

The Dunmanus sequence is less calcareous than at Bantry. P. C. Jones (pers. comm. and paper in preparation) recognizes four units similar to these discussed above in the Reenydonagan Group of the Bantry Syncline. The calcareous basal beds of this group at Ardnamanagh Point on the north flank of the Bantry Syncline, described below, constitute the lowest member of Jones's sequence. Whether they are equivalent to Unit 1, or Units 1 to 3 of the Dunmanus sequence is not yet known. However, the Ardnamanagh Beds are lithologically similar to Unit 1 at Dunmanus and the latter may be an attenuated and less calcareous equivalent. Certainly, no pyritic shales (Unit 4) occur at Ardnamanagh Point itself, although they are known in the core of the Bantry Syncline (Coe and Selwood 1968; P. C. Jones, pers. comm.).

#### *Bantry Bay (Ardnamanagh Point)*

The stratigraphy of the Cork Beds on the north flank of the Bantry Bay Syncline has been outlined by Naylor *et al.* (1969). Calcareous strata of the Reenydonagan Group are well exposed on Ardnamanagh Point (text-fig. 5). A coastal section, with complex folding and faulting, at the head of the bay in the neighbourhood of Reenydonagan Point exposes higher beds of the group (text-fig. 1). Since these will be described by P. C. Jones (in preparation), no attempt has been made to sample or map from this portion of the coastline. The thickness of the Reenydonagan Group shown in text-fig. 4 for the Bantry section is based on work by P. C. Jones and is included with his kind permission.

The base of the Reenydonagan Group in the Ardnamanagh section is clearly defined. Ripple-laminated non-calcareous siltstones on Ardnamanagh beach are abruptly succeeded southwards (up sequence) by crinoidal limestones set in calcareous and non-calcareous mudstones. The limestones (2 in to 1 ft thick) increase in number upwards and constitute up to 20% of the sequence. Channelled bases can be seen on some beds. For the remainder of the Ardnamanagh section non-calcareous medium-grey mudstone is dominant and contains variable amounts of

limestone. Light-grey limestone occurs as thin lenses of comminuted crinoid debris, in thin (1-ft) beds or occasionally as massive beds (more than 50% of the succession in places). There is severe folding on Ardnamanagh Point itself and correlation through these folds is difficult. The stratigraphic thickness shown on the section (text-fig. 5) should be regarded as a maximum figure: the upper part of the section may be too expanded. However, the Ardnamanagh sequence is strikingly calcareous and quite unlike any underlying part of the Cork Beds. The limestones are characteristically of variable thickness and often exhibit downcutting relationships at their bases and some internal cross bedding.

Text-fig. 5 shows all horizons sampled in the four major sections. These should be put on record in order to provide for any resampling or for any attempt to integrate, say, palynological studies with this conodont work. Only the productive samples are treated in the faunal lists that follow.

#### Faunal lists

- R1 *Gnathodus delicatus* (1), *G. delicatus* juv.? (1), *Polygnathus communis communis* (8). Total 10. GSL SAD21.
- R2 (GSL SAD22): see list on p. 338, above.
- R3 *Gnathodus semiglaber* (6), *G. sp.* (1), *Polygnathus communis communis* (2), *P. communis carina* (3), *Spathognathodus stabilis* (1), *Sp. cf. costatus* (1), *Sp. sp.* (2), bars (7). Total 23. GSL SAD23.
- R4 (GSL SAD24), R4a '71 (GSL SAD25), R4b '71 (GSL SAD26): see lists on p. 338, above.
- R6 *Polygnathus communis communis* (3), *P. flabellus* (1), *P. symmetricus* (1), *P. sp.* (4), *Pseudopolygnathus dentilineatus* (1), *Ps. multistriatus* (1), *Ps. cf. multistriatus* (1), *Ps. sp.* (1), *Siphonodella sp.* (1), indet. (2). Total 16. GSL SAD27.
- R7 *Polygnathus symmetricus* (1), *P. sp.* (2). Total 3. GSL SAD28.
- R8 *Polygnathus sp.* (1). Total 1. GSL SAD29.
- R9 *Polygnathus inornatus* (6), *P. sp.* (1), *Pseudopolygnathus dentilineatus* (1), *Ps. multistriatus* (1). Total 9. GSL SAD30.
- R11 *Polygnathus sp.* (3), *Pseudopolygnathus sp.* (1). Total 4. GSL SAD31.
- R13 *Polygnathus cf. inornatus* (3), *P. sp.* (1), *Ps. dentilineatus* (1). Total 5. GSL SAD32.
- F1 (GSL SAD33), F1 '71 (GSL SAD34): see lists on pp. 337, 338, above.
- B1 *Polygnathus cf. communis* (1). Total 1. GSL SAD35.
- B2 (GSL SAD36), B2 '71 (GSL SAD37): see lists on p. 338, above.
- B3 *Polygnathus communis communis* (1). Total 1. GSL SAD38.
- B4 *Polygnathus flabellus* (1), *P. inornatus* (1), *Siphonodella sp.* (2). Total 4. GSL SAD39.
- B5 *Polygnathus inornatus* (2), *Siphonodella sp.* (1). Total 3. GSL SAD40.
- B6 *Polygnathus inornatus* (2), *P.?* sp. (2), *Pseudopolygnathus multistriatus* (1), bar (1). Total 6. GSL SAD41.
- B7 *Polygnathus symmetricus* (1), *Pseudopolygnathus?* sp. (1), *Spathognathodus cf. costatus* (1), indet. (1), bars (2). Total 6. GSL SAD42.
- B8 (GSL SAD43): see list on p. 338, above.
- B9 *Polygnathus symmetricus* (1), *Pseudopolygnathus dentilineatus* (3), *Ps. primus* (1), bars (3). Total 8. GSL SAD4.
- BBH *Spathognathodus aculeatus/Clydagnathus* transition (1), gen. et sp. indet. (2). Total 3. GSL SAD46. (Sampled by E. B. Selwood—location: V 60/40 intersection on Bantry sheet, at a point 1 mile west of Black Ball Head.)
- OH1 (GSL SAD47), OH1 '71 (GSL SAD48), OH4 (GSL SAD50), OH4 '71. (GSL SAD51): see lists on p. 338, above. (Note that OH1 and OH1 '71, which are not located on text-fig. 5, were taken from the middle of the Castle Slate Formation at the northern end of Holcopen Bay West—see Naylor 1966, pl. 21.)
- D6 Bar (1). Total 1. GSL SAD54.
- WB2 (GSL SAD57): see list on p. 338, above.

Many of the samples produced small (< mesh no. 10) specimens of molluscs, brachiopods, ostracodes (internal casts), echinoderms (plates and spines of echinoids and, more frequently, crinoid ossicles), and fish denticles. These have been retained in the collections, but are not treated in the lists. This explains the omission of, for example, GSL SAD49 (i.e. sample OH3) from the sequence of collection-numbers in the faunal lists above.

In one case (sample R3), two partially silicified brachiopods were recovered from the acid residue before sieving. Both specimens have been deposited in the collections of the Institute of Geological Sciences, Leeds. Mr. Murray Mitchell has kindly provided the following identifications and comments:

LZA 522 *Antiquatonia molarum* Turner.

LZA 523 Orthotetoid, juv., encrusted with a bryozoan identified as cf. *Fistulipora*.

The holotype of *A. molarum* is from the *Productus globosus* Band of Fawcett Mill, Ravenstonedale. The horizon of this band is currently correlated with low Viséan (very low) but the full range of the species is not known as the *P. globosus* Band is underlain by algal beds with very little macrofauna.

The evidence of the conodonts in R3 would suggest that in southern Ireland, at least, *A. molarum* was extant during the late Tournaisian.

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S. C. MATTHEWS

Department of Geology  
University of Bristol  
Queen's Building  
University Walk  
Bristol, BS8 1TR

D. NAYLOR

Exploration Consultants Limited  
31-33 Grosvenor Hill  
London, W1X 9HG

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# PALAEOECOLOGY OF APPALACHIAN GYPIDULID BRACHIOPODS

by E. J. ANDERSON and J. H. MAKURATH

**ABSTRACT.** Gypidulid brachiopods lived unattached, oriented in a beak-down position aided by weighting of the posterior end of the pedicle valve. This adaptation evolved as a specialization for occupying well reworked and occasionally shifting sand substrates. This sedimentary environment characterizes the open shelf, near wave base in transgressing epeiric seas. The occurrence of *Gypidula* and its associated faunal community suggest a substrate-salinity control for the analogous *Pentamerus* Community of Ziegler.

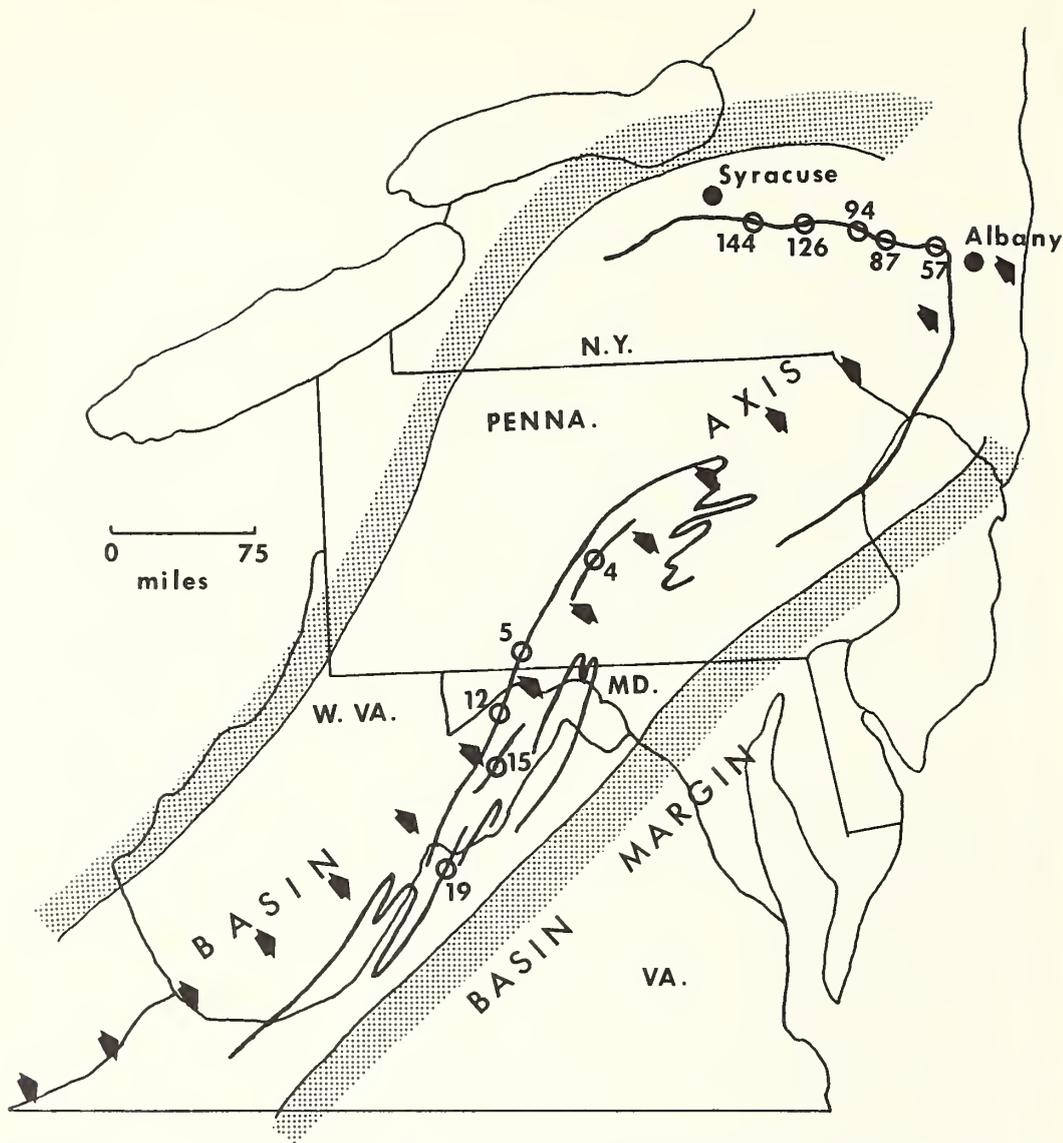
**ASSEMBLAGES** of articulated gypidulid brachiopods in life position have been found in the Keyser and Coeymans Formations (Pridolian and Gedinnian) in the Appalachian Basin (text-fig. 1). These brachiopods lived in a specific orientation, on a specific substrate, and within narrowly prescribed geographical limits in Late Silurian and Early Devonian epeiric seas. This interpretation is based on two distinct kinds of evidence: (1) biologic evidence including analysis of gypidulid functional morphology and gypidulid biofacies associations, and (2) sedimentary evidence including thin-section analyses of the rocks entombing the gypidulid assemblages and mapping of vertical and lateral lithofacies patterns.

## PALAEOBIOLOGIC EVIDENCE

*Life position.* A large slab containing *Gypidula coeymanensis* in life position was found in the Lower Devonian Coeymans Formation at Sharon Springs, New York (Pl. 39). The rock and fossil specimens were separated with a hydraulic rock splitter. The lower half of the slab and the gypidulids were then reconstructed and cemented in their original positions. Pl. 40, figs. 1-3, show views of the bottom surface of a rock slab from the Upper Silurian Keyser Formation at Hyndman, Pennsylvania. The posterior ends (beaks) of silicified specimens of *G. prognostica* are seen projecting from the naturally weathered lower bedding surface.

Two observations can be made on both the Silurian and Devonian samples: all of the obviously articulated specimens are preserved in a beak-down orientation and there is no indication of a pedicle opening in any specimen. The beak region of gypidulid pedicle valves is several times thicker than the anterior part of the pedicle valve or the brachial valve (Pl. 40, figs. 4-6). This weighting of the posterior parts of the valves served to orientate the living brachiopods all in a similar way (Ziegler *et al.* 1966), with the anterior commissure as high as possible above the substrate.

*Substrate.* Thin sections of the slabs containing articulated gypidulids indicate that the gypidulids lived on a substrate consisting of poorly sorted sand-sized to clay-sized skeletal fragments and relatively unbroken shells interpreted as organisms that lived at or near the sample collection point (Pl. 40, figs. 4-6). This sediment indicates an unconsolidated substrate which may have been occasionally reworked by currents, but in which most of the reworking was probably biogenic. Crude bedding and remnants of cross-stratification disrupted by burrows and mottled



TEXT-FIG. 1. Outcrop map of the Upper Silurian and Lower Devonian in the central Appalachians. Sample localities and general configuration of the depositional basin are indicated. Arrows marking the basin axis show the general transgressive trend. New York localities are those of Rickard (1962, p. 120); other localities are described in Bowen (1967, p. 65).

EXPLANATION OF PLATE 39

Lower Devonian, Sharon Springs, N.Y. (loc. 87).

Figs. 1, 3. Front and back views of a slab showing *G. coeymanensis* in life position on its original substrate.

1,  $\times 1.2$ , 3,  $\times 1.5$ .

Figs. 2, 4. Front and back views of a second slab showing *G. coeymanensis* in life position,  $\times 1$ .

2



4



1



3



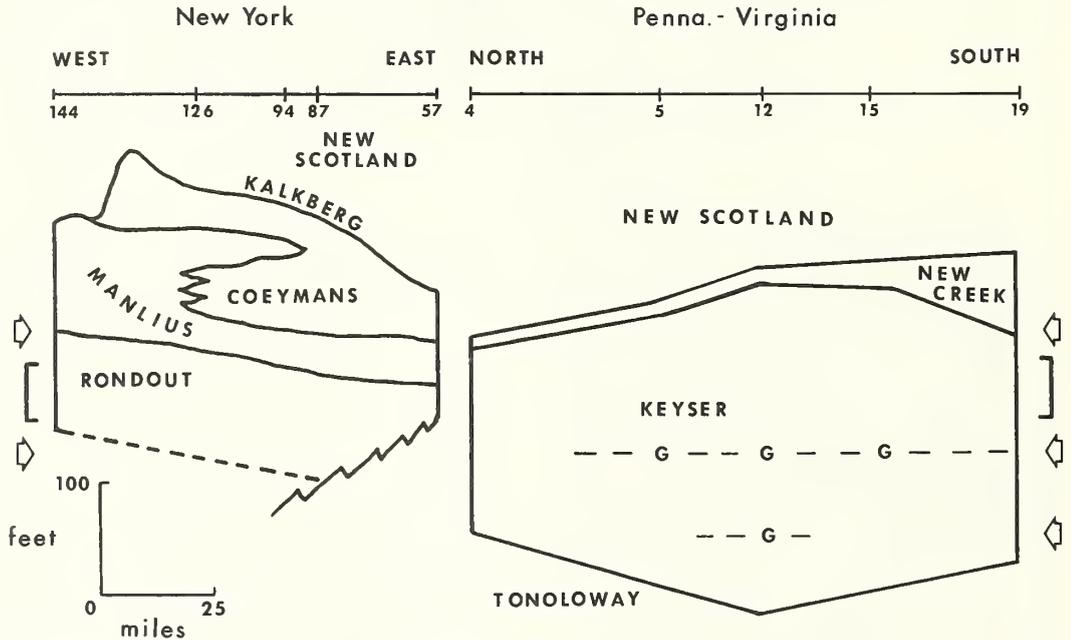
ANDERSON and MAKURATH, gypidulid brachiopods

zones substantiate this interpretation. The weighted pedicle beak is an ideal orienting and stabilizing mechanism for a substrate that occasionally shifts with ripple migration. Brachiopods with fixed pedicle attachments would have less chance of survival when the sediment occasionally moved.

*Faunal association.* Gypidulids occur with a limited brachiopod fauna dominated by robust globose forms, the most common of which are atrypids and uncinulids. Ramose ectoprocts, cystoids, and crinoids are the other common faunal elements. Faunas may be expected to become more restricted in higher-energy zones nearer shore, whereas more diverse brachiopod faunas dominated by a mixture of large flat and small angular forms are more characteristic of silt and clay substrates further offshore (Epstein 1971).

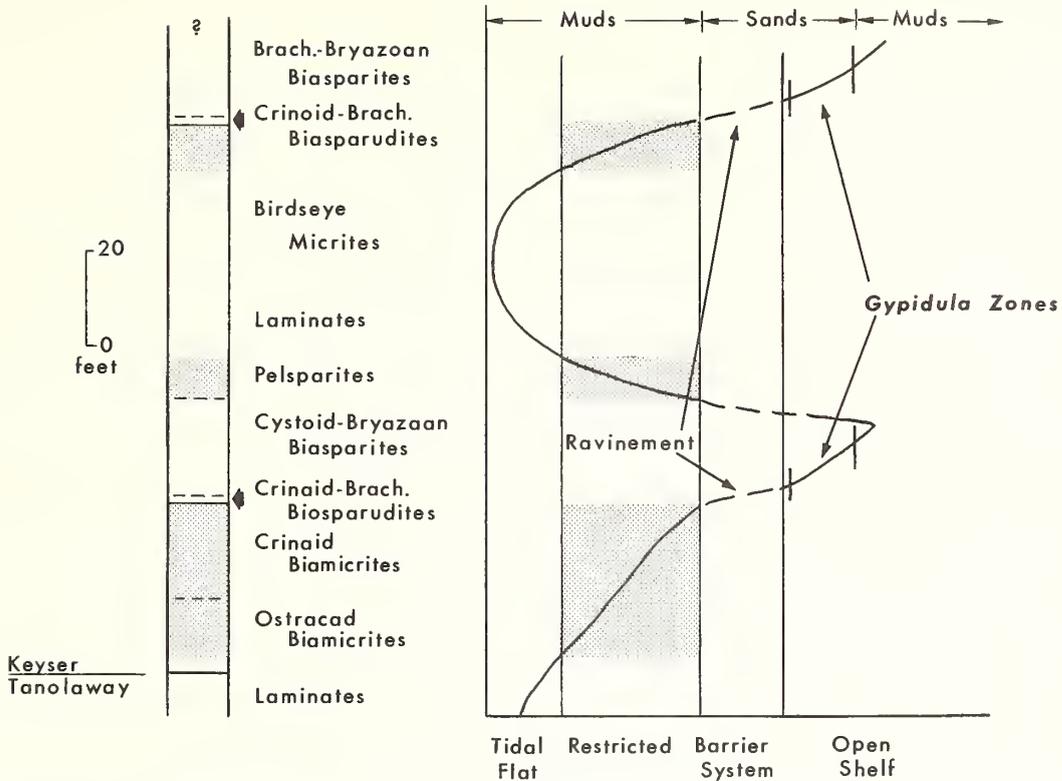
#### PALAEOENVIRONMENTAL EVIDENCE

*Vertical sequences (Upper Silurian).* Gypidulid brachiopods occur only at one position in vertical and lateral facies sequences in the Appalachian Basin. General stratigraphic relationships are depicted in text-fig. 2. In the Pennsylvania-Virginia



TEXT-FIG. 2. Stratigraphic cross-sections of Upper Silurian and Lower Devonian formations in the Appalachian Basin keyed to locality numbers in text-fig. 1. The section on the left extends from Syracuse (near-shore) to Albany (basin axis). Thicknesses are measured from a time datum in the upper Manlius (Rickard 1962).

The section on the right approximately parallels the basin axis from central Pennsylvania to Monterey, Virginia. Thicknesses are measured from a time datum in the middle Keyser (Head 1969) approximately coincident with the *Gypidula prognostica* epibole (the upper gypidulid occurrence). Sedimentation is continuous across the Silurian-Devonian boundary which is placed within the bracketed interval (Head 1969; Bowen 1967; Rickard 1962). Correlative transgressive events are marked by arrows. The gypidulid-bearing slabs (Pls. 39, 40) came from locality 87 (Sharon Springs, N.Y.) and locality 5 (Hyndman, Pa.).



TEXT-FIG. 3. Detailed columnar section and environmental interpretation of the lower half of the Keyser Formation at locality 5, Hyndman, Pa. Gypidulids are narrowly restricted to transgressive sand-grade open-shelf environments.

area the sequence of formations, Tonoloway–Keyser–New Creek–New Scotland, represents basinal transgression from tidal flats to fossiliferous shelf muds (Head 1969).

Within the Upper Silurian Keyser Formation, a more specific environmental sequence can be detailed. Two transgressions each terminated by progradation are recorded at widely separated localities. Gypidulid brachiopods occur at two specific horizons within these environmental sequences. This is well illustrated in the Keyser Formation at Hyndman, Pennsylvania (text-fig. 3).

The vertical sequence of lithologies (facies) at Hyndman is depicted in the measured column in text-fig. 3. The sequence: laminites, ostracod-crinoid biomicrite, brachiopod-crinoid calcarenite, to brachiopod-bryozoan-cystoid calcisiltite represents the first transgressive sequence. An erosional loss of high-energy barrier deposits may occur at the centre of the sequence which is interpreted as a ravinement (Swift 1968).

The above sequence is followed in order by: brachiopod-pelletal calcisiltites, laminites, and birdseye filled micrites representing the infilling of onshore subtidal zones and tidal flat progradation. Gypidulids are not present in this sequence. The transgressive sequence is then repeated with preservation of a massive bed of

gypidulids in the brachiopod-crinoid calcarenite position (Pl. 40, figs. 1-3, 6). At Hyndman *G. prognostica* occurs only at this one level. In the Keyser Formation at nearby localities the species also occurs in the lower brachiopod-crinoid facies. The upper Keyser again progrades to tidal flats before transgression is re-established with the New Creek Formation, a brachiopod-crinoid calcarenite, which again contains gypidulids (*G. coeymanensis*).

*Lateral sequences (Lower Devonian)*. The stratigraphic sequence in New York State is analogous to that in the Pennsylvania-Virginia region. It begins with deposition of very restricted sediments in the Rondout Formation and proceeds to deposition of offshore fossiliferous sediments, the New Scotland Formation. The sequence includes several episodes of progradation and it is possible to match some of these cyclic events with those occurring to the south (text-fig. 2).

Anderson (1971*a*) has established a lateral sequence of environments within the Coeymans Formation, a brachiopod-crinoid calcarenite. During transgressive or stable shoreline periods the lateral sequence is: 1, barrier deposits; 2, shallow stratified bar calcarenites; 3, bioturbated calcarenites deposited a little above wave base (Anderson 1972). These occur within the general sequence outlined above (text-fig. 4). *G. coeymanensis* occurs only offshore from the barriers, a little above wave base. Samples oriented in life position have been found at this position in the lateral facies sequence at several localities in the Coeymans Formation.

At most localities gypidulid-bearing, biogenically disrupted shelf sands overlie onshore restricted sediments (Manlius Formation) with a ravinement contact in vertical section. As in the Hyndman section, barrier deposits are removed by the ravinement process (Anderson 1972). During progradation of the Manlius tongue gypidulids disappear in adjacent Coeymans facies.

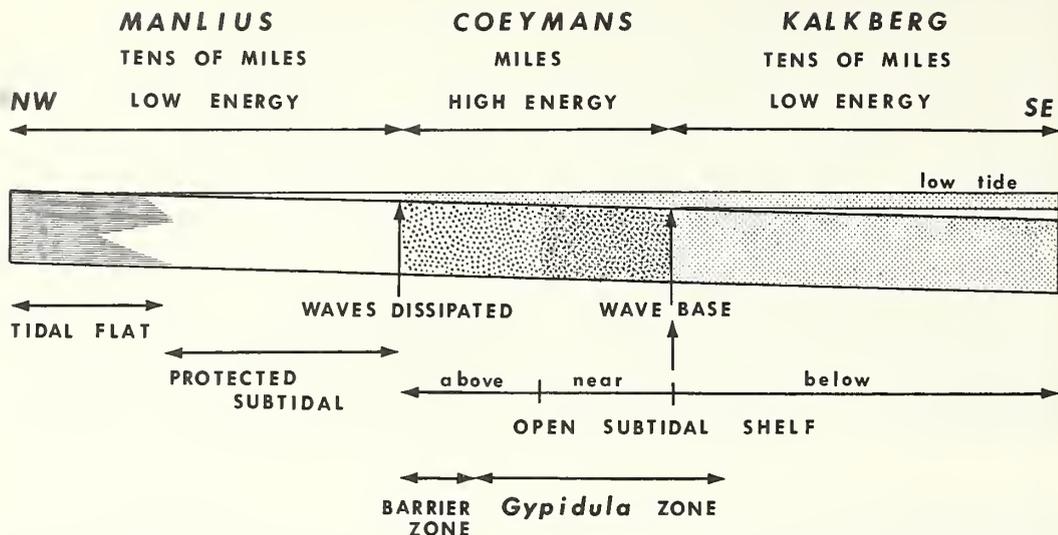
*Community patterns*. Ziegler (1965) has identified a recurrent pattern of communities (*Lingula* through *Clorinda* Communities) which sequentially occupy zones parallel to shore. Ziegler's central community, the *Pentamerus* Community, is directly analogous to *Gypidula* and its associated faunal assemblage. *Gypidula* has a similar shape and orientation mechanism to *Pentamerus* (Ziegler *et al.* 1966) and is associated with a limited brachiopod assemblage of similar robust forms. It also occupies an analogous position in an onshore to offshore sequence of communities based on form, diversity, and key related genera (Anderson 1971*b*). The evidence from gypidulids indicates that the distribution of the '*Pentamerus* Community' is controlled by sedimentary environment, specifically substrate type, and salinity.

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#### EXPLANATION OF PLATE 40

- Figs. 1-3. Upper Silurian, Hyndman, Pa. (loc. 5). Three views of the bottom surface of a large slab containing *G. prognostica* in life position. 1,  $\times 2$ , 2,  $\times 1.5$ , 3,  $\times 1.8$ .
- Figs. 4, 5. Negative prints of thin sections. Gypidulids in a poorly sorted sand to mud-size substrate, the Coeymans Formation, Sharon Springs, N.Y. (loc. 87), bar scale 3 mm. 4, Longitudinal cross-section through both valves of an articulated gypidulid in life orientation on its original substrate.  $\times 2.5$ . 5, Transverse cross-section of a pedicle valve near the beak showing thick shell and median septum.  $\times 3$ .
- Fig. 6. Negative print of thin section, bar scale 3 mm. Disarticulated but unbroken gypidulid pedicle valve in association with a typical substrate, the Keyser Formation, Hyndman, Pa. (loc. 5). The inner prismatic layer thickens the posterior end of all pedicle valves.  $\times 3$ .





TEXT-FIG. 4. Idealized cross-section relating contemporaneous lower Helderberg formations to depositional environments from the basin margin to the basin axis. The distribution of kinetic energy, barrier development, and gypidulids are indicated. The zone of sand-grade deposition is narrow relative to onshore and offshore zones of mud deposition.

*Environment.* Gypidulids are adapted by their weighting mechanism for slowly shifting sand-grade substrates, an environment in which fixed attachment points are not available. Sediments which average in the sand-size range are interpreted as wave or current reworked deposits. However, biogenic disruption and abundant silt and clay-sized particles in the sand suggest a non-persistent physical reworking. In addition most brachiopods are adapted for life in water with good circulation, normal salinity, and low rates of sediment accumulation. All the above conditions probably prevailed on the open shelf, a little above wave base, in middle Palaeozoic epeiric seas.

The occurrence of gypidulids at two stratigraphic levels in the Keyser Formation and two levels in the Coeymans Formation, each occurrence corresponding to this one environmental position on the open shelf, confirms this interpretation. This environmental position can be identified in both vertical and lateral facies sequences. The lateral facies evidence places the gypidulid fauna offshore from a high-energy or barrier zone. The vertical facies evidence places the fauna in a transgressive sequence offshore from an interpreted barrier indicated by a ravinement.

The transgressive setting, although not necessary, provides an optimum environment for the gypidulid fauna. A landward migrating barrier system, believed to be typical of a transgressing epeiric sea, leaves behind a well reworked shelf sand (Anderson 1972). Shelf sedimentation rates would be relatively low and the barrier system would protect nearshore shelf communities from fluctuating salinities and influxes of mud from restricted onshore zones. Progradation in the Keyser and Coeymans Formations is correlated with the disappearance of gypidulids, apparent loss of barrier systems, more rapid sediment accumulation, and less reworking.

## CONCLUSIONS

Gypidulid brachiopods discovered in their life orientation indicate that they are specialized for extensively reworked yet poorly sorted sand substrates. Recurrent appearance at one position in vertical and lateral facies sequences, that is in open shelf sediments near wave base, indicates that gypidulids were specific to this environment. Identification of the *Gypidula* fauna as equivalent to a *Pentamerus* Community suggests similar environmental controls (primarily substrate and salinity for Ziegler's community). A gypidulid fauna is most likely to develop in a transgressing epeiric sea where optimum substrate and salinity conditions occur in the shallow near wave base zone.

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E. J. ANDERSON

Department of Geology  
Temple University  
Philadelphia, Pennsylvania 19122

J. H. MAKURATH

Department of Earth and Planetary Sciences  
The John Hopkins University  
Baltimore, Maryland 21218  
U.S.A.



# LOWER VISÉAN TRILOBITES FROM FELTRIM, IRELAND

by G. HAHN and C. BRAUCKMANN

ABSTRACT. *Archegonus (Weania) feltrimensis* sp. nov. is described from the Lower Viséan of Feltrim, Co. Dublin, Ireland. This species combines characteristics of *A. (Weania)* with those of *A. (Waribole)* and *A. (Angustibole)* and shows that *A. (Weania)* evolved from the *A. (Waribole)* stock and not from *Cyrtosymbole (Pseudowaribole)* as supposed by Osmólska.

HUDSON *et al.* (1966*a, b*) described an outcrop of richly fossiliferous Lower Viséan pyritic mudstones at Feltrim, Co. Dublin, Ireland, lying above an Upper Tournaisian reef-knoll complex. More than 400 trilobite specimens were collected and most of these were assigned by Hudson *et al.* to *Cyrtosymbole (Waribole)* cf. *colei* (M'Coy 1844). Five specimens were identified as *Brachymetopus* sp.

Comparison of the material from Feltrim with the lectotype of '*P.*' *colei* figured by Osmólska (1970, pl. 1, fig. 13) shows that the Feltrim material is specifically distinct. The Feltrim material may be assigned to *Archegonus (Weania)* Campbell and Engel 1963 though it has some of the features diagnostic of *A. (Waribole)* R. and E. Richter 1926, *A. (Belgibole)* G. Hahn 1963, and *A. (Angustibole)* G. Hahn 1965. '*P.*' *colei* shows a combination of features which makes it distinct from *A. (Weania)* and other described subgenera of *Archegonus*. Probably '*P.*' *colei* is best assigned to a new subgenus (G. and R. Hahn 1972, p. 428). The Feltrim material provides some indication of the relationships between the subgenera of *Archegonus*.

*Acknowledgements.* The Feltrim trilobites have been kindly loaned to us by Mrs. V. Burns (Trinity College, Dublin). We are also grateful to Mr. J. Miller (University of Manchester) and to Dr. G. D. Sevastopulo (Trinity College, Dublin) for advice. The described material is deposited in the Museum of the Department of Geology, Trinity College, Dublin.

Family PROETIDAE Hawle and Corda 1847

Subfamily CYRTOSYMBOLINAE Hupé 1953

Genus ARCHEGONUS Burmeister 1843

Subgenus ARCHEGONUS (WEANIA) Campbell and Engel 1963

*Type species.* *Weania goldringi* Campbell and Engel 1963.

*Diagnosis.* Campbell and Engel (1963, p. 108) revised by Osmólska (1970, p. 117).

*Archegonus (Weania) feltrimensis* sp. nov.

Text-figs. 1-3, 6, 10

*Holotype.* Cranidium no. 9513, text-figs. 1, 10*b*.

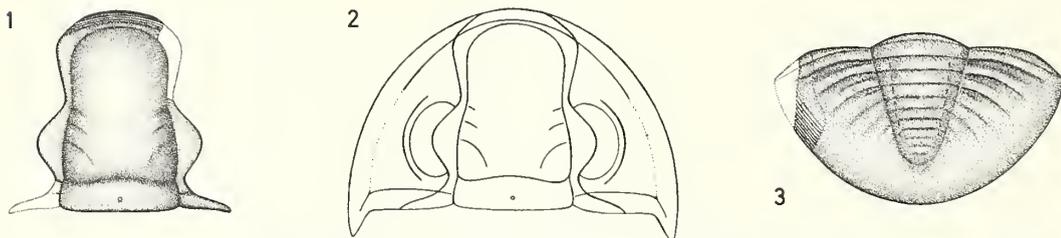
*Type locality.* Feltrim Hill, Co. Dublin, Ireland. For locality details see Hudson *et al.* (1966, pp. 253, 257 and Pl. 23).

[*Palaeontology*, Vol. 16, Part 2, 1973, pp. 391-397.]

*Type horizon.* Black mudstone of the Lower Viséan ( $C_2S_1$  subzone, *Ammonellites* stage, cu II $\beta$ ). Known only from type locality. Material, 403 specimens as listed in Hudson *et al.* (1966, pp. 276–277).

*Diagnosis.* As for subgenus with the following: Glabella subrectangular, relatively long, region posterior to  $\gamma$  only slighter broader than region anterior to  $\gamma$ . Anterior border prominent, elevated. Anterior part of fixed cheek very narrow; palpebral lobe long and wide (tr.); posterior part of fixed cheek short. Free cheek with very large eye and short genal spine. Pygidium short, 9–11 rings, 4–7 ribs. Anterior branch of the ribs somewhat elevated. Ribs fading on outer part of pleurae; no border furrow.

*Description.* All specimens are internal moulds, therefore the furrows of the cephalon and pygidia are relatively broad and shallow. On the exterior of the exoskeleton they may have been narrower and deeper.



TEXT-FIGS. 1–3. *Archegonus (Weania) feltrimensis* sp. nov. *Ammonellites* stage,  $C_2S_1$ , Feltrim, Co. Dublin, Ireland. See also text-fig. 10. 1, Cranidium, holotype, no. 9513. 2, Reconstruction of cephalon. 3, Pygidium, no. 9503.

*Cranidium.* Glabella relatively massive, outline subrectangular, incised by  $\gamma$ , depressed vertically; posterior part (between palpebral lobes) broader than anterior. Glabellar furrows 1p impressed, curved, nearly extending to occipital furrow; preglabellar lobes (L1) partially separated from rest of glabella. Glabellar furrows (2p–3p) short and shallow on holotype, but more strongly impressed on other specimens. Occipital furrow incised, slightly curved, projecting forward at sagittal line, curving back behind preoccipital glabellar lobes, projecting forward again near axial furrow. Occipital node near to posterior border of cranidium; central part of ring wider (sag.) than laterally. Preglabellar region relatively broad (sag.), divided into a narrow, deepened preglabellar field and a broad, elevated, anterior border equipped with 3–4 parallel lines. Axial furrows well marked. Anterior branch of facial suture long, scarcely diverging; anterior part of fixed cheek narrow, similar to *Archegonus (Angustibole)*.  $\beta$  rounded, situated within the projection of  $\delta$ .  $\alpha$  marked by a slight knick. Palpebral lobe long and wide (tr.), projecting laterally;  $\gamma$ ,  $\delta$ , and  $\epsilon$  gently curved. Posterior branch short, initially running sub-parallel to axial furrow, then (at  $\zeta$ ) curving outward, forming the long (tr.) and narrow (exsag.) posterior portion of fixed cheek. Posterior border furrow indistinct, shallow. Ornamentation of glabella and occipital ring weakly granular (not shown in text-fig. 1). Length of cranidium 5.6 mm; length of glabella 4.2 mm; length of  $\beta$ – $\beta$  1.5 mm; length of palpebral lobe ( $\gamma$ – $\epsilon$ ) 1.9 mm; length of  $\epsilon$ – $\omega$  0.9 mm; breadth of cranidium at  $\beta$ – $\beta$  3.5 mm; breadth of cranidium at  $\delta$ – $\delta$  4.75 mm; breadth of glabella at  $\delta$ – $\delta$  3.2 mm.

*Free cheek* (text-fig. 10a). Cheek area plane, not rising against eye (diagenetic compaction?). Border region narrow, slightly elevated (less elevated than anterior border of cranidium). Eye large, strongly curved, slightly raised above the cheek area; eye furrow weak. Number of lenses in no. 9506 (length of eye 1.6 mm) about 250–300, in no. 9515 (length of eye 2.5 mm, text-fig. 10f) about 500–600. (This is high for a cyrtosymbolinid trilobite.) Posterior border furrow deeply incised, vanishing against lateral border, not continuing in lateral border furrow. Genal spine blunt and short in no. 9506, longer in no. 9510 (text-fig. 10c). Surface of free cheek nearly smooth. Length of free cheek 3.5 mm; breadth of free cheek (at  $\epsilon$ ) 2.3 mm.

*Cephalon* (text-fig. 2). Shape rounded, characterized by relatively slender glabella and large eyes. Border elevated in front of glabella, descending on the anterior part of free cheeks, disappearing against genal spines. Cephalon less vaulted than in other species of *A. (Weania)*.

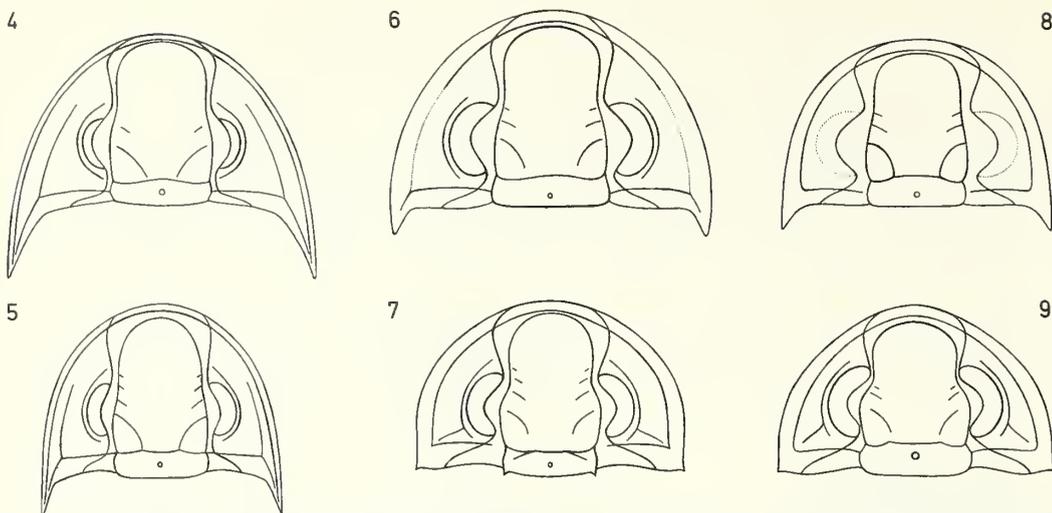
*Pygidium*. Shape rounded, broader than long (breadth to length ratio 1:1.63). Axis massive, broader than one pleura, tapering rapidly, terminating in a blunt curve; short in comparison with total length of pygidium. Axis completely subdivided into eleven rings; ring furrows straight (tr.), clearly incised. Appendage muscle scars, oval, shallow, near to the axial furrows which are well pronounced. 6–7 ribs on each pleura. Ribs 1–4 distinct; anterior branch slightly elevated, slowly ascending from pleural furrow, quickly descending to the following rib furrow; posterior branch low. Remaining ribs (5–7) vaguely indicated by somewhat raised anterior branch. Pleural furrows broad and shallow, rib furrows deeply incised. Ribs not reaching to outer border of pygidium; border region smooth, no border furrow. Axis arched, but pleurae planar. Connecting half-ring and connecting half-ribs slightly projecting anteriorly. Doublure (seen on anterior part of left pleura) relatively broad, ornament of faint parallel lines. Surface of pygidium smooth. Length of pygidium 4.6 mm; length of axis 3.5 mm; breadth of pygidium 7.5 mm; breadth of axis 2.75 mm.

*Variation*. In most features the pygidia are very uniform. The most important difference is in the expression of rings and ribs. In pygidium no. 9502 and no. 9508 only nine rings are clearly discernible, in no. 9502, no. 9504, and no. 9507 only 3–4 ribs are well defined.

#### DISCUSSION

The characteristic features of *A. (Weania)* are: (i) the massive glabella, broadened between the palpebral lobes; (ii) the elevation of the prominent cephalic border, both on the cranidium and free cheeks; (iii) the reduction of the genal spines; (iv) the large size of the eyes; (v) a short pygidium with relatively few rings and ribs; and (vi) the elevation of the anterior branch of the pygidial ribs. The most important features are the shape of the glabella and the size of the eyes, characteristics which are confined to *A. (Weania)*, occurring in all known species of the subgenus.

We include the following species in *A. (Weania)*: *A. (Weania) goldringi* (Campbell and Engel 1963), the type species, *A. (Weania) librovitchi* (Weber 1937), and *A. (Weania) osmolskae* G. and R. Hahn 1972 [= *A. (Weania) anglica* (Osmólska 1970)].

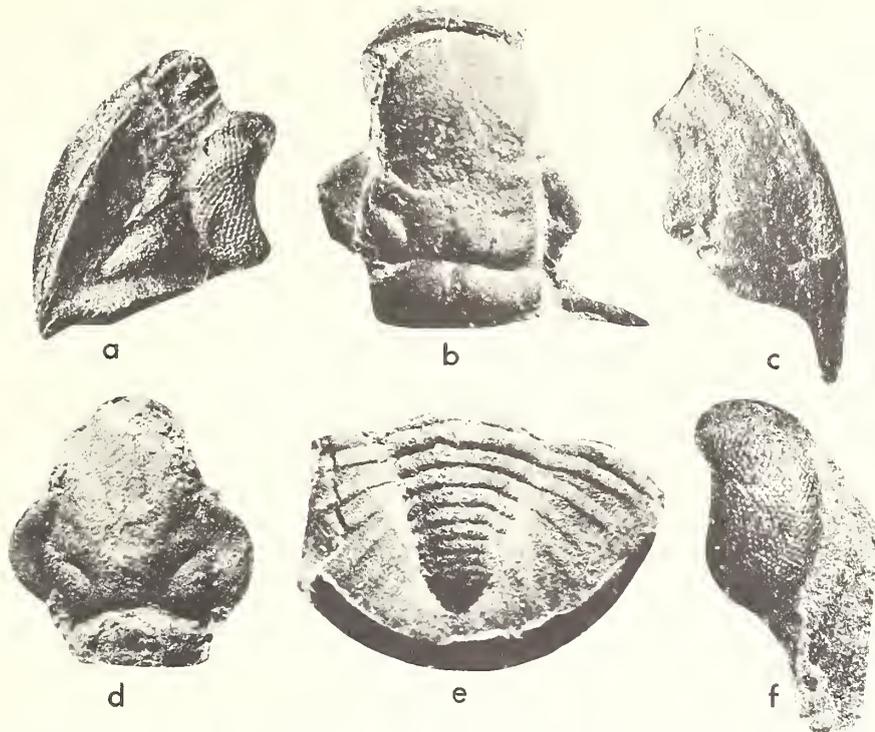


TEXT-FIGS. 4-9. Comparison of cephala of *Archegonus* (*Weania*) and relatives. 4, *Archegonus* (*Angustibole*) *winterbergensis* G. Hahn 1965. Lower Viséan, *Ammonellipsites* stage, cu II $\gamma$ , Winterberg, Harz-Mountains, Germany. After G. Hahn 1965. 5, *Archegonus* (*Belgibole*) *belgicus* (G. Hahn 1963). Upper Tournaisian, *Ammonellipsites* stage, cu II $\beta$ , Modave, Belgium. After G. Hahn 1963. 6, *Archegonus* (*Weania*) *feltrimensis* sp. nov. Lower Viséan, *Ammonellipsites* stage, C<sub>2</sub>S<sub>1</sub>, Feltrim, Co. Dublin, Ireland. 7, *Archegonus* (*Weania*) *librovitchi* (Weber 1937). Upper Viséan, *Goniatites* stage, Kizil river, S-Urals, U.S.S.R. After Weber 1937 and Osmólska 1970. 8, *Archegonus* (*Weania*) *goldringi* (Campbell and Engel 1963), *type species*. Lower Tournaisian, Tulcumba Sandstone, New South Wales, Australia. After Campbell and Engel 1963. 9, *Archegonus* (*Weania*) *osmolskae* G. and R. Hahn 1972 [= *Archegonus* (*Weania*) *anglica* (Osmólska 1970)]. Viséan, D<sub>1</sub>, Narrowdale, Staffordshire, England. After Osmólska 1970.

*Proetus zarecznyi* Jarosz 1914, assigned to *A.* (*Weania*) by Osmólska (1970), is included by us with *A.* (*Belgibole*); *Phillipsia colei* M'Coy 1844, also assigned to *A.* (*Weania*) by Osmólska (1970) may represent a new subgenus of *Archegonus*; see also G. and R. Hahn (1969, p. 118; 1972, p. 428).

The elevation of the cephalic border is prominent in *A.* (*Weania*) *osmolskae*, and to a lesser degree in *A.* (*Weania*) *librovitchi*, but is only slightly indicated in the type species; and is therefore less important taxonomically than the shape of the glabella and the size of the eyes. The remaining features (iii), (v), and (vi) are characteristic of all species of *A.* (*Weania*), but they also occur in other subgenera of *Archegonus*. Reduction of the genal spines occurs in *A.* (*Belgibole*) and *A.* (*Waribole*); the elevation of the anterior branches of the pygidial ribs occurs in *A.* (*Belgibole*) and *A.* (*Waribole*) *abruptirhachis* (R. and E. Richter 1951). In contrast to *A.* (*Weania*) the pygidium of *A.* (*Belgibole*) is much more vaulted and the elevation of the anterior branches of the pygidial ribs is much more prominent.

*A.* *feltrimensis* sp. nov. combines the characteristics of several subgenera of *Archegonus*. The shape of the glabella is unlike that in *A.* (*Weania*), *A.* (*Waribole*), and *A.* (*Belgibole*). It is too slender for *A.* (*Weania*), especially between the palpebral lobes; but in comparison with the other subgenera it is too massive anteriorly. Thus the glabella of *A.* *feltrimensis* is intermediate between *A.* (*Waribole*) and *A.* (*Weania*), so that *A.* (*Weania*) may be interpreted as a descendant of *A.* (*Waribole*) in this



TEXT-FIG. 10. *Archegonus (Weania) feltrimensis* sp. nov., internal moulds. Lower Viséan, *Ammonellipsites* stage, C<sub>2</sub>S<sub>1</sub>, Feltrim, Co. Dublin, Ireland. *a*, Free cheek, negative impression, reversed by photographic effect, with eye well preserved and a short genal spine,  $\times 11.4$  (No. 9506). *b*, Cranidium, holotype,  $\times 6.9$  (No. 9513). *c*, Free cheek, with genal spine longer than in text-fig. 10*a*,  $\times 12.3$  (No. 9510). *d*, Cranidium, with anterior glabella furrows (p<sub>2</sub>-p<sub>3</sub>) better preserved than the holotype,  $\times 10.1$  (No. 9514). *e*, Pygidium, with well-marked rings and ribs,  $\times 7.0$  (No. 9503). *f*, Part of free cheek, with eye well preserved,  $\times 10.0$  (No. 9515).

respect. A glabella similar to the new species occurs in *A. (Angustibole) winterbergensis* G. Hahn 1965 (text-fig. 4), also a descendant of *A. (Waribole)*.

The cephalic border of the new species is moderately elevated, more than in *A. (Weania) goldringi* but less than in *A. (Weania) osmolskae*, and fits into our concept of *A. (Weania)*. The degree of reduction of the genal spines is similar to other species of *A. (Weania)* and *A. (Belgibole)* (text-fig. 5), and also to *A. (Waribole) abruptirhachis*. This is only significant at the species level. The eyes of the new species are very large, agreeing with all other species of *A. (Weania)*. The anterior part of the fixed cheeks, however, differs from *A. (Weania) goldringi* and *A. (Weania) librovitchi* in being narrower, as in *A. (Weania) osmolskae* and *A. (Angustibole) winterbergensis* (compare text-figs. 4 and 6-9). Over-all the cranidium agrees more with *A. (Angustibole) winterbergensis* than with *A. (Weania) osmolskae*.

The pygidium of the new species is characterized by its shortness, a few rings (9-11) and ribs (7), the slightly elevated anterior branches of the ribs, and the manner

in which the ribs fade against the border. A similar short pygidium is seen in *A. (Weania) goldringi* (8 rings, 5–6 ribs) and in most species of *A. (Waribole)*, whereas in *A. (Weania) librovitchi* and *A. (Weania) osmolskae* the pygidia are longer, with 11–12 rings and 9–10 ribs. The ribs of the new species are intermediate between *A. (Waribole)* and *A. (Weania)*: whereas the ribs terminate against the border as in *A. (Waribole)*, the elevation of the anterior branches agrees with *A. (Weania)*. The pygidium of *A. (Angustibole)* differs from the new species: the ribs are not elevated and the axis and pleurae are only slightly vaulted.

Thus the features of the new species may be summarized: (1) Features characteristic of *A. (Weania)*: the elevation of the cephalic border, the large size of the eyes, the shape of the pygidium, and the elevation of the anterior branches of the ribs. (2) Features intermediate between *A. (Waribole)* and *A. (Weania)*: the shape of the glabella and the termination of the pygidial ribs against the border. (3) Features distinct from *A. (Waribole)* and most species of *A. (Weania)*: the narrow anterior fixed cheeks. Therefore 'progressive' features of *A. (Weania)* occur in the new species, with some 'primitive' features of *A. (Waribole)*. We prefer to include the species in *A. (Weania)*, because the features of that subgenus are predominant.

This discussion sheds light on the systematic position of *A. (Weania)*. It shows that it is a member of the *Archegonus*-group among the *Cyrtosymbolinae*, descending from *A. (Waribole)*, not from *Cyrtosymbole (Pseudowaribole)* as concluded by Osmólska (1970). In all known species of *Cyrtosymbole (Pseudowaribole)* the glabella is long and slender, never as short and massive as in *A. (Weania)*. *A. (Waribole)* and *A. (Belgibole)* are the subgenera closest to *A. (Weania)*; the first, the common ancestor; the second, as the most similar evolutionarily parallel branch. The close relationship is shown best by the structure of the pygidia. The elevation of the anterior branches of the ribs and the strongly differentiated relief on the axis and pleurae first occurs in *A. (Waribole) abruptirhachis*, as well as in *A. (Weania)*, and reaches its maximum in *A. (Belgibole)*. On the other hand, the structure of the *A. (Waribole)* type of glabella persists in *A. (Belgibole)*, whereas *A. (Weania)* evolves a new shape. Palaeoecologically *A. (Weania)* and *A. (Belgibole)* both occur in Carboniferous Limestone facies, whereas the other subgenera of *Archegonus* are only found in the Culm facies. The *Archegonus*-subgenera are very closely related, with several transitional species, and it would be unwise to elevate the subgenera to genera.

The four described species of *A. (Weania)* may be divided into two groups. The stratigraphically older and morphologically more primitive species are *A. (Weania) feltrimensis* (text-fig. 6) and *A. (Weania) goldringi* (text-fig. 8); the stratigraphically younger and morphologically more advanced species are *A. (Weania) osmolskae* (text-fig. 9) and *A. (Weania) librovitchi* (text-fig. 7). The two pairs are separated by the broadening of the glabella between the palpebral lobes, the degree of elevation of the cephalic border, the reduction of the genal spines, and the length of the pygidium. The first pair are characterized by their slightly broadened glabella; weakly to moderately elevated cephalic border; short, pointed genal spines and short pygidium with relatively few segments (8–11 rings, 5–7 ribs). The second pair show a broadened glabella, the cephalic border strongly elevated, the genal spines completely reduced, and the pygidium longer, resembling *A. (Belgibole)* rather than

*A. (Waribole)* with 11–12 rings and 9–10 ribs. Of the first pair, *A. (Weania) feltrimensis* is the more primitive, though not the older stratigraphically, since it preserves features transitional between *A. (Waribole)* and *A. (Weania)*. *A. (Weania) goldringi* has lost these transitional features, but without evolving the characteristic features of the second pair of species. *A. (Weania) osmolskae* differs from *A. (Weania) librovitchi* in its narrower anterior fixed cheeks, its more elevated cephalic border, its broader glabella, and its larger eyes. *A. (Weania) osmolskae* is the most evolved species in the subgenus, though somewhat older stratigraphically than *A. (Weania) librovitchi*. The pygidia of both species do not differ markedly (see Osmólska 1970, pl. 1, figs. 3 and 4). It is likely that the second pair evolved from the first, perhaps directly from *A. (Weania) goldringi*. In contrast, *A. (Weania) feltrimensis*, despite its primitive features, cannot be the ancestor of the other species of *A. (Weania)*, since it is stratigraphically younger than *A. (Weania) goldringi*. However, it suggests a model of the form representing the root species of the subgenus which existed about the end of the Devonian.

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GERHARD HAHN

CARSTEN BRAUCKMANN

Geol.-Paläontol. Institut, Freie Universität  
 Altensteinstrasse 34a  
 1 Berlin 33, Germany

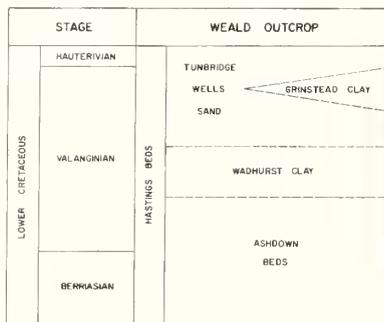


# PALYNOLOGY OF EARLY CRETACEOUS SOIL BEDS AND ASSOCIATED STRATA

by D. J. BATTEN

**ABSTRACT.** A distinctive palynologic assemblage is associated with *Equisetites* soil beds and fragment partings in the Wadhurst Clay of south-east England. Some of the components are probably the products of a local flora which grew in or near the *Equisetites* communities. Palynologic and palaeobotanic data suggest that the communities were isolated from the 'homogeneous Wealden delta flora', probably offshore from the delta complex. New taxa have been recorded from the assemblages. *Converrucosporites venitus*, *Regresporites lophus*, *Retitriletes* sp., *Triobosporites ivanovae*, and *Admolia amphidoxa* are described.

*Equisetites* ('horsetail') soil beds are common in the Wadhurst Clay (Lower Cretaceous; text-fig. 1) of south-east England. They constitute combinations of roots, rhizomes, and stems of the plant preserved *in situ*, generally in a matrix of inter-laminated clays and fine-medium silts. They are the only truly autochthonous plant beds of botanic value in the Wealden. Some of the *Equisetites* fragment partings which occur above and occasionally within the soil beds are probably para-autochthonous. The majority of the rootlet beds in the succession have, however, been truncated and there is nothing to indicate to which plants the roots were attached (although in the Wadhurst Clay they may frequently belong to *Equisetites*). It has proved difficult to determine both the environments of deposition in which *Equisetites* thrived and the factors which controlled its distribution. The Hastings Beds succession accumulated in an essentially non-marine basin (the Anglo-Paris Basin) with the result that similar aquatic faunas and floras lived both on the delta complex and offshore (Allen 1959, 1967). Although the properties of many of the sediment types are probably characteristic for special areas of formation, these areas are difficult to delimit. Four possible interpretations of the standard Hastings Beds megacyclothem, in which *Equisetites* soil beds play an important part, have been proposed by Allen (summarized 1967, text-fig. 1). The distribution of palynomorphs in samples from horizons within and adjacent to some of the Wadhurst Clay soil beds is considered here both in the light of these interpretations and with regard to the distribution of local flora.



TEXT-FIG. 1. Correlation of the Hastings Beds in south-east England (after Harland *et al.* 1967, and latest published information). Lithological boundaries are indicated by broken lines. Thickness of Wadhurst Clay varies from 30 to 70 m.

## MATERIAL

The samples came from the Wadhurst Clay in the Cuckfield No. 1 Borehole, Sidnye Farm, Sussex (TQ 2962 2729, first redrilling, and TQ 2961 2731, second redrilling); Warlingham Borehole, Surrey

(TQ 3476 5719); Railway Brickyard, Sharpthorne, Sussex (TQ 3740 2729); and Freshfield Lane Brickworks, Danehill, Sussex (TQ 3813 2659). Most of the sampling horizons are figured in Batten (1968, text-figs. 1 and 2). Approximately 15 g of each sample from not more than 2 cm stratigraphic thickness were subjected to a standard preparation procedure (see Batten 1973) employing 50% hydrochloric acid, HF, nitric acid (< 30 minutes) or Schulze solution (< 10 minutes), ammonium hydroxide (5 minutes), and zinc bromide (sp. gr. c. 2.2). Strew slides were made with Clearcol; Euparal sealed the cover-slips to the slides.

#### WADHURST CLAY *EQUISETITES*

Rootlets preserved as casts and infilled rhizomes are usually all that remain of Wadhurst *Equisetites* communities. Infilled stems in position of growth occur less often and rhizomes preserved as carbonaceous compressions are rare. The species preserved in the soil beds examined is *Equisetites lyellii* (Mantell) (1833). Since the species was erected, it has been consistently referred to as *lyelli*. Mantell's spelling is correct and is here reverted to (see Lanjouw *et al.* 1966, Recommendation 73C). *E. lyellii* is the only common plant megafossil in the Wadhurst Clay. *E. burchardti* Dunker and *E. yokoyamae* Seward, both tuber-bearing forms, were not encountered; they tend to occur in the more arenaceous facies of the succession (cf. Allen 1962).

The scarcity of other plants in the Wadhurst Clay suggests: (1) that most of the plant material derived from the lowland flora bordering the basin of deposition was deposited or comminuted before it reached the Wadhurst zone of deposition, (2) that the horsetail communities were isolated in some way from the bulk of the lowland flora. In addition, the preservation of *E. lyellii* may have been enhanced by two factors: (1) it was not dependent on chance deposition in an aqueous environment conducive to preservation because it probably grew in the shallow waters of the Wadhurst Clay, (2) although there is no direct evidence, the plants may have accumulated silica in their tissues as do species of extant *Equisetum* (e.g. *E. hyemale*; Lovering and Engel 1967).

Stem fragments of *E. lyellii* may be scattered through the clays and silts above or within the soil beds or concentrated in thin bands separated by more or less fragment-free horizons. The concentrations represent periods when deposition of waterlogged plant debris was more rapid than that of sediment deposition, and are probably the product of destruction of *E. lyellii* communities by water disturbance (Allen 1941; Batten 1968). The preservation state varies, but the accumulations which are well preserved may be nearly autochthonous. The absence of any large accumulations of *Equisetites* suggests that the communities were short lived (Allen 1941, 1960) and that *E. lyellii* was a pioneer coloniser (Hughes and Moody-Stuart 1967a); their existence was probably terminated by deepening water. Had the communities existed for many more than a few years, thin coal seams like those in the Yorkshire Jurassic (Harris 1953) might have been formed.

#### SOIL BED AND FRAGMENT PARTING PALYNOLOGY

Soil beds and fragment partings often yield a distinctive palynologic assemblage. This assemblage is here designated as the SF (soil bed/fragment parting) type. During a routine examination of Wadhurst preparations most were assigned (at

the specific level) to assemblage-types 8 and/or 16 (Table 1 and Batten 1973). Important characters are: (1) the miospore *Pilasporites allenii* (described from a Wadhurst Clay soil bed preparation (CUC 792) and attributed by Batten 1968 to *Equisetites*) is abundant (V or F on Table 1), (2) there is usually a large amount of plant debris comprising brown 'wood' (probably mostly degraded *Equisetites* material) and *Equisetites* cuticle, (3) the general state of preservation of the miospores is usually fair to good.

Certain miospore taxa, viz. *Retitriletes* sp., *Regresporites lophus* gen. et sp. nov., *Ischyosporites arkellii* (Pocock 1970) comb. nov., and *Admolia amphidoxa* gen. et sp. nov. appear to be significantly associated. *I. arkellii* and *A. amphidoxa* occur more often and in greater abundances in SF assemblages than elsewhere, and *Retitriletes* sp. and *Regresporites lophus* have only been recorded from the SF type. *Trilobosporites ivanovae* sp. nov. and *Patellasporites* spp. occur more frequently associated with *Equisetites* than elsewhere in the Wadhurst Clay (although the former is more numerous and better preserved in the described Grinstead Clay sample). The frequency of occurrence of *Pilosisorites* spp., *Converrucosisorites venitus* sp. nov., *Staplinisorites* spp., *Classopollis* spp., and most of the other taxa recorded from soil beds and associated strata differs little from their frequency in the rest of the Wadhurst. However, megaspores have not been recovered, and the following are notably less common: *Inapertisorites* sp., *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958, *Couperisorites* spp., *Vitreisorites pallidus* (Reissinger 1938) Nilsson 1958, *Ceratosporites* spp., and *Celyphus rallus* Batten 1973. Some soil bed and fragment parting samples do not yield an SF kind of assemblage (Table 1). Instead, the assemblages show little diversity and poor preservation and have (see below) a typical 'Wadhurst aspect' (assemblage-types 1, 4, 7, 9, 10, and 12 in Batten 1973).

#### NUMERICAL COMPARISON OF ASSEMBLAGES

The relationships between forty-two selected assemblages recovered from soil beds and adjacent strata were determined by using both cluster analysis and non-metric multidimensional scaling (see Kruskal 1964*a, b*). For cluster analysis both weighted and unweighted pair-group linkage methods were used (Sokal and Michener 1958; Sokal and Sneath 1963). The cluster program operated on matrices of coefficients of association derived by comparing data from counts of both 500 (Table 1) and 200 miospores, with and without other data (on preservation, abundance of wood, cuticle, etc.). The coefficients of association used were those of proportional similarity ( $\text{Cos } \theta$ ) of Imbrie and Purdy (1962), the Jaccard, and Sokal and Michener (see Cheetham and Hazel 1969). The multivariate data were converted to binary form to use the Sokal and Jaccard coefficients. The nonmetric multidimensional scaling program employed  $\text{Cos } \theta$  converted to a distance coefficient. Both procedures yielded similar results but those from the cluster analysis were more clear cut than the multidimensional scaling. Assemblages with an SF aspect formed one grouping and those identified as 'typical Wadhurst type' formed another. 'Borderline' assemblages which show only some of the characters of the SF type (i.e. those from samples CUC 792/1, CUC 792/4, CUC 792/6, DJB 329, and DJB 368;

Table 1) tended not to be well linked with either group. The records of *Regresporites lophus*, *Ischyosporites arkellii*, *Admolia amphidoxa*, *Pilasporites allenii*, *Classopollis* spp., *Ceratosporites* spp., and *Gleicheniidites* spp. were important in determining the grouping of the assemblages. The state of preservation and the abundance of brown wood and cuticle fragments were also important when all the data, not just the miospore content, were taken into account.

#### PALAEOECOLOGY

Both onshore and offshore habitats have been postulated for the *Equisetites* communities (Allen 1959, 1967, text-fig. 1). On the delta top they could have thrived on levées and in backswamps and shallow ponds (Allen 1949, 1959, megacyclothem interpretations 1 and 2); offshore they could have become established in a band along much of the length of the delta shore-face and in other areas of shallow water (shoals) (Allen 1959, 1967, interpretations 3 and 4). Most Wadhurst Clay palynologic assemblages reflect the homogeneous delta flora in their composition. They are composed mainly of pteropsid and coniferopsid elements. Fern spores, especially the families Schizaeaceae and Gleicheniaceae, are prominent and, in the former, diverse. The miospores are, however, generally in a poor state of preservation, and when compared with the whole Wealden succession, show below average diversity. The general aspect of the assemblages, and the scarcity of both megaspores (Batten 1969) and determinable megascopic plant remains, apart from those of *Equisetites*, in the Wadhurst suggest that deposition took place far from source. The poor preservation of the palynomorphs can be accounted for by prolonged aerobic decay and reworking. All but the more resistant spores and plant fragments (fusain) would have been destroyed by the alternations of erosion and deposition on the delta complex.

The SF kind of assemblage has, however, a different aspect. The homogeneous delta flora forms only a background component. The better preservation suggests that some of the elements were not transported over long distances but were deposited in an environment where water transport was restricted to some extent, and where the duration of their exposure to aerobic decay depended on the rate at which they

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TABLE 1. Plant megafossil and miospore content of 42 selected samples from *Equisetites* soil beds and associated strata. Sample numbers on left-hand side of table: prefix DJB = field sample, CUC = core sample from Cuckfield No. 1 Borehole, WM = core sample from Warlingham Borehole. On extreme right, record of assemblage-type assignments (see Batten 1973) noted during routine examination of Wadhurst Clay preparations (before counts of 500 miospores), and of SF kinds of assemblages (B = 'borderline' type).

Miospore taxa: P = present (< 3% after count of 500), C = common (3-14.5%), V = very common (15-29.5%), F = frequent (30% or more). Taxa grouped within suprageneric categories except where indicated by solid line. Elements recorded subsequent to completion of count not included. Rootlets, rhizomes, and stems, X if recorded. Megascopic fragments of *Equisetites*: C = common, F = frequent. 1. *Cyclogranisporites* Pot. and Kr./*Granulatisporites* Ibr. emend. Pot. and Kr. 2. *Corrugatisporites* Th. and Pfl. ex Wey. and Greif./*Rugulatisporites* Th. and Pfl. 3. *Foveosporites* Balme/*Foveotrilletes* v.d. Hammen ex Pot./*Sestrosporites* Dett. 4. *Lycopodiumsporites* Thiery. ex Del. and Spr./*Reticulisporites* Pot. and Kr. in Wey. and Krieg. 5. *Tauocusporites* Stover emend. Play. and Dett./*Polycingulatisporites* Simonc. and Kedv. emend. Play. and Dett.

SAMPLES		TAXA	
CUC	78B	<i>Aurilinasporites</i> NILSSON	LAEVIGATI
CUC	78B/6-9	<i>Concavosporites jurienensis</i> BALME	
CUC	78B/10-11A	<i>Stereisporites</i> PFL. in TH and PFL.	
CUC	78B/10-11B	<i>P</i> <i>Stereisporites</i> sp. (undescribed)	
CUC	791/11	<i>Undulatisporites</i> PFL. in TH and PFL.	
CUC	792/1	TOTAL SMOOTH WALLED TRILETES	
CUC	792/2	<i>Acanthotriletes</i> NAUM emend. POT. and KR.	APICULATI
CUC	792/3	<i>Apiculatisporis</i> POT. and KR	
CUC	792/4	<i>Baculatisporites</i> TH. and PFL.	
CUC	792/5	<i>Cerataspites</i> COOK and OETT.	
CUC	792/6	<i>Concovissimisporites</i> OEL and SPR emend. OEL. et al.	
CUC	794	<i>Converrucosporites</i> POT. and KR.	
CUC	794/3	<i>C. venustus</i> SP NOV	
CUC	865/3	<i>Cyclogranisporites/Granulatisporites</i> 1.	
CUC	866	<i>Foraminisporis</i> KRUTZSCH	
CUC	866/3	<i>Osmundacidites</i> COUPER	
WM	1774/6	<i>Pilasporites</i> OEL. and SPR	
D/8	320	<i>Verrucosporites</i> IBR emend SMITH and B'WORTH	
D/8	321	<i>Verrucosporites</i> sp. (undescribed)	
D/8	324	<i>Cicatricosporites</i> POT and GELL	MURORNATI
D/8	325	<i>Corrugatisporites/Rugulatisporites</i> 2	
D/8	326	<i>Foveosporites/Foveatrilletes/Sestrasporites</i> 3.	
D/8	327	<i>Kluksporites</i> COUPER	
D/8	328	<i>Lycopodiumsporites/Trelliculispores</i> 4	
D/8	329	<i>Lycopodiumsporites austroavoidites</i> (COOK) POCKOCK	
D/8	330	<i>Microsciculatisporites</i> KNOX emend. POT and KR.	
D/8	331	<i>Retliculispores semireticulatus</i> (BURGER) NORRIS	
D/8	332	<i>Retitrilletes</i> vd. HAMMEN ex PIERCE	
D/8	333	<i>Retitrilletes</i> sp.	
D/8	334	<i>Regesporites laphus</i> GEN and SP NOV	
D/8	335	<i>Staplinisporites</i> POCKOCK/Caranatispora OETT.	
D/8	336	<i>Tourcosporites/Polycingulatisporites</i> 5.	
D/8	337	<i>Tripartita</i> MALJ. ex POT.	
D/8	338	<i>Ischyasporites</i> BALME	AURICULATI
D/8	339	<i>Larkella</i> (POCKOCK) comb. nov.	
D/8	340	<i>Matanisporites</i> COUPER emend OETT.	
D/8	341	<i>Trilobosporites</i> PANT ex POT	
D/8	342	<i>T. ivanavae</i> SP NOV	
D/8	343	<i>Gleicheniidites</i> ROSS ex OEL. B. SPR. emend. OETT	TRICRASSATI
D/8	344	<i>Gleicheniidites aplobatus</i> BRENNER	
D/8	345	<i>Cingulitrites</i> PIERCE emend OETT	CINGULATI
D/8	346	<i>Contignisporites</i> OETT.	
D/8	347	<i>Oenosisporites</i> WETZ and KRIEG emend OETT.	
D/8	348	<i>Patellisporites</i> GROOT and GROOT emend. KEMP	PATINATI
D/8	349	<i>Patellisporites</i> sp. (undescribed)	
D/8	350	INDET. SCULPTURED TRILETES	
D/8	351	<i>Aequitriletes</i> OEL and SPR emend. COOK and OETT.	HILATES
D/8	352	<i>Coaxosporites</i> POCKOCK emend OETT.	
D/8	353	<i>Couperisporites complexus</i> (COUPER) POCKOCK	
D/8	354	<i>Couperisporites</i> sp. (undescribed)	
D/8	355	<i>Rouseisporites</i> POCKOCK	
D/8	356	<i>Marattisporites</i> COUPER	MONOLETES
D/8	357	<i>Peramanites</i> EROT ex COUPER	
D/8	358	<i>Araucariacites</i> COOK ex COUPER	ALETES
D/8	359	<i>Inapertisporites</i> vd. HAMMEN ex ROUSE	
D/8	360	<i>Inaperturopollenites</i> PFL ex TH and PFL. emend. POT.	
D/8	361	<i>Pilasporites allenii</i> BATTEN	
D/8	362	<i>Retliculatisporites</i> IBR emend. POT and KR	
D/8	363	<i>Taxodiaceepollenites</i> KR.	
D/8	364	<i>Cerapollenites mesozoicus</i> (COUPER) NILSSON	SACCITES
D/8	365	<i>Tsugapollenites</i> POT and VEN. emend. POT	
D/8	366	<i>BISACCATES</i> excluding <i>Vitreisporites</i>	
D/8	367	<i>Vitreisporites</i> LESCHM emend. JANSONIUS	
D/8	368	<i>Eucosmidites</i> EROT emend. HUGHES	PLICATES
D/8	369	<i>Coccolpites</i> WOODW. ex WILS. and WEBST.	
D/8	370	<i>Classopollis</i> PFL emend. REYRE	POROSIS
D/8	371	<i>Classopollis</i> sp. (undescribed)	
D/8	372	<i>Evesipollenites</i> BALME	
D/8	373	<i>Perinapollenites</i> COUPER	
D/8	374	<i>Spheripollenites</i> COUPER	INCERTAE SEOSIS
D/8	375	<i>S. subgranulatus</i> COUPER	
D/8	376	<i>Admia amphidax</i> GEN. and SP NOV	
D/8	377	<i>Schizosporis</i> COOK and OETT	
D/8	378	<i>Calyphus rollus</i> BATTEN	
D/8	379	ROOTLETS	
D/8	380	RHIZOMES (AND STEMS)	
D/8	381	MEGASCOPIC FRAGMENTS (Cor F)	
D/8	382	SF TYPE	
D/8	383	ASSEMBLAGE - TYPE RECORD	

For explanation of Table 1 see opposite.

were buried. The relative abundance of *Pilasporites allenii* and to a lesser extent of *Ischyosporites arkellii*, *Admolia amphidoxa*, and *Regresporites lophus* suggests both local production and some kind of ecological association between the parent plants. *R. lophus*, a relatively large thick-walled spore, and *A. amphidoxa*, another thick-walled palynomorph, could not have been produced by plant species constituting part of the homogeneous delta flora. If they had been, they would have been recovered from sediments deposited closer to this source, particularly in medium and coarse siltstones of near-shore and back-delta facies. Thus *Equisetites* appears not to have been an important component of the onshore flora but probably thrived offshore in the pro-delta. This supports interpretations 3 and 4 of Allen (1959, 1967).

The local flora may be poorly represented in the soil beds and fragment partings. Possible reasons for the fluctuations in abundances include depositional environments unfavourable for preservation, winnowing, low rate of spore production, seasonal production, and variable rate of sedimentation (Batten 1968). Fragment partings yield *P. allenii* abundances more consistently than soil beds, probably because they contain a greater number of dispersed *E. lyellii* sporangia. Allen has suggested (*Pal. Ass. Circ.* 64, 1971, unpublished) that the larger Hastings Beds *Equisetites* (i.e. *E. lyellii*) may have flourished during periods of low salinity (cf. Anderson *et al.* 1967), that low salinity transgressions might have been followed by offshore *Equisetites*, and that brackish transgressions might not. The lack of dinoflagellates and acritarchs in soil beds and adjacent strata suggests that *Equisetites* flourished in fresh or only weakly saline waters. However, disagreement over the salinity ranges of several of the fossils of the Wadhurst Clay confuses the picture.

The *Classopollis* group of species is an important component of many Wadhurst assemblages. Hughes and Moody-Stuart (1967a) proposed that the group was not available for deposition in back-delta environments but that the parent plants were favourably placed for their pollen to be preserved in offshore deposits; they suggested a coastal swamp habitat comparable with the Tertiary and Recent mangroves. There is, however, no direct (megafossil) evidence for this and by contrast, Vakhrameev (1970) has suggested that the parent plants of *Classopollis* were psammophilic, preferring upland slopes, and able to tolerate drought conditions. An attempt to determine the relationship between *Classopollis* producers and *Equisetites* using palynology has merely shown that the *Classopollis* parent plants are not significantly associated with *Equisetites*, nor do they show an antipathetic relationship. There are some roots of unknown origin, which are larger than those of *Equisetites*, preserved in the coarse-grained Ashdown and Tunbridge Wells Sand facies (e.g. at Hastings, East Grinstead, and Pembury; White 1928, Allen 1959); Hughes and Moody-Stuart (1967a) suggested that *Classopollis* plants might have borne them, but attempts to prove this by palynologic association have been unsuccessful.

The affinities of the palynomorph taxa associated with *Pilasporites allenii* are uncertain because it is hazardous to compare them either with the spores of modern plants or with modern plant associations. It is probable that *Ischyosporites arkellii* is a filicalean spore (produced by a member of the Schizaeaceae?). *Regresporites lophus* is probably a fern spore, but *Retriletes* sp. could have been produced by a member of the Lycopodiaceae or of the Bryophyta, and the affinities of *Admolia*

*amphidoxa* can only be guessed at (Thallophyta (Algae)?, Bryophyta?). However, the palynologic record does suggest that other plants grew, if not amongst the *Equisetites*, at least near by. That remains of the parent plants have not been recorded may be due either to non-preservation or lack of recognition. The only other record of plants suggested as being ecologically associated with *Equisetites* is that of 'doubtful leafy liverworts' (Allen 1959, p. 295).

TABLE 2A. Records of miospores tentatively attributed to the Equisetaceae (*Equisetites*/*Equisetum*) or compared with the spores of *Equisetum* (see *Pilasporites allenii* discussion). The spores that Rogalska (1962) attributed to cf. *Equisetum* differ from her earlier assignments (1954, 1956) in lacking a 'perisporium'. She noted that the earlier records may represent another genus.

Author	Record	Age
Rogalska 1956	<i>Equisetum</i> sp.	Lower Jurassic
Rogalska 1962	Cf. <i>Equisetum</i>	Jurassic
Góczán 1956	<i>Calamospora</i> cf. 'cf. <i>C. pallida</i> Schemel'	Lower Jurassic
Nagy 1958	Cf. <i>Equisetum</i>	Pliocene
Kara-Murza 1960	<i>Leiotriletes</i> spp.	Mesozoic
Chun'-Bin Chzhan 1962	<i>Equisetum</i> sp.	Lower Cretaceous
Verbitskaja 1962	<i>Leiotriletes</i> spp.	Cretaceous
Simoncsics 1964	<i>Perinosporites sphaericus</i> Simoncsics 1964	Miocene
Voevodova (in Pokrovskaja and Stel'mak) 1964	<i>Equisetum chassynense</i> Voevodova 1964	Lower Cretaceous
Piel 1971	? <i>Equisetum</i> sp.	Oligocene

TABLE 2B. Dispersed spores which bear some resemblance to *Pilasporites allenii*.

Author	Record	Age
Nakoman 1964	<i>Inaperturopollenites problematicus</i> Nakoman 1964	Oligocene
Wall 1965	<i>Concentrisporites hallei</i> (Nilsson 1958) Wall 1965	Lower Jurassic
Goubin 1965	<i>Inaperturopollenites</i> cf. <i>orbicularis</i> Nilsson 1958	Middle Jurassic
Goubin 1965	<i>Laricoidites desquamatus</i> Goubin 1965	Upper Triassic
Volkheimer 1968	<i>Inaperturopollenites velatus</i> Volkheimer 1968	Jurassic

## SYSTEMATIC PALAEOLOGY

*Ischyosporites arkelii* (Pocock 1970) comb. nov., recorded in graded comparison form (see Hughes and Moody-Stuart 1967b, p. 355), *Retitriletes* sp., and the four new taxa referred to in the text are here described and compared. *Pilasporites allenii* Batten 1968 is also discussed. Assemblage-type identifications (see Batten 1972, 1973) are given for the assemblages from which the taxa are described. The age/stage from which a compared species was described is given if it came from outside the Cretaceous period.

Miospores examined with the scanning electron microscope were individually mounted on 'Durofix' or double-sided 'Sellotape' on 12-mm diameter stubs, or strew mounted on stubs without adhesive. Most mounts were coated with carbon but gold-palladium was also used. The assemblage slides are labelled with the preparation number prefixed by 'T'. A holotype specimen is present with topotypes on a strew slide of a single preparation. The slides containing the figured specimens are in the Sedgwick Museum, Cambridge. Representative specimens of the new species are in the Institute of Geological Sciences, Leeds. Stage co-ordinates given refer to Leitz Laborlux (LI) microscope, number 557187, Sedgwick Museum.

Turma TRILETES Reinsch emend. Dettmann 1963

Infraturma APICULATI Bennie and Kidston emend. Potonié 1956

Genus CONVERRUCOSISPORITES Potonié and Kremp 1954

*Converrucosisporites venitus* sp. nov.

Plate 41, figs. 1-9; Plate 42, figs. 1-5

*Type sample.* CUC 924, Cuckfield No. 1 Borehole, Sidnye Farm, Sussex (TQ 2961 2731), depth 924 ft (281.6 m); upper Ashdown Sand, Valanginian? Grey (N5-N7) laminated fine siltstone, sedimentary mica, bedding disturbed, rootlets *in situ*. Preparation T206; ten minutes Schulze solution, cleared in dilute  $\text{NH}_4\text{OH}$ , mineral separation, strew slides with Clearcol. AT1.

*Holotype.* Slide T206/3, L1 48.4 125.2; Pl. 41, fig. 3.

*Diagnosis.* Miospore, trilete, mean maximum diameter  $41.5 \mu\text{m}$ , standard deviation  $4.1 \mu\text{m}$  (100 specimens). Amb triangular; concave, straight or slightly convex sides, rounded angles. Proximal face slightly convex, may be raised up along margins of laesurae; distal surface convex. Laesurae distinct,  $> \frac{3}{4}$  radius. Exine two-layered, total thickness  $1-2 \mu\text{m}$ . Inner layer smooth  $0.75-1.5 \mu\text{m}$  thick. Outer layer  $0.5-1 \mu\text{m}$  thick, carries sculpture on both proximal and distal surfaces. Sculpture, which may be only weakly developed on proximal face, generally consists of grana and verrucae of low elevations ( $< 1-2 \mu\text{m}$  high) and variable maximum diameter (up to  $6 \mu\text{m}$ ). Elements spaced  $< 1-2 \mu\text{m}$  (sometimes up to  $4 \mu\text{m}$ ) apart; bases rounded to irregular in outline, distinct or (more usually) partially fused, leading to the formation of irregular rugulae.

*Description.* The observed limits of the maximum diameter of the spores are  $33-53 \mu\text{m}$  (coefficient of variation 9.8%). Fifty per cent of the specimens are in polar aspect; none are in equatorial view. Proximal arcuate folds resulting from compression of the raised up area of the proximal face may be present (Pl. 41, fig. 5). The sculptural elements are sparsely distributed on four specimens (Pl. 41, fig. 6), and predominantly dome shaped on seven (Pl. 41, fig. 3). Four show isolated clavae or dome shaped verrucae up to  $6 \mu\text{m}$  high (Pl. 41, fig. 1) and two have almost smooth proximal

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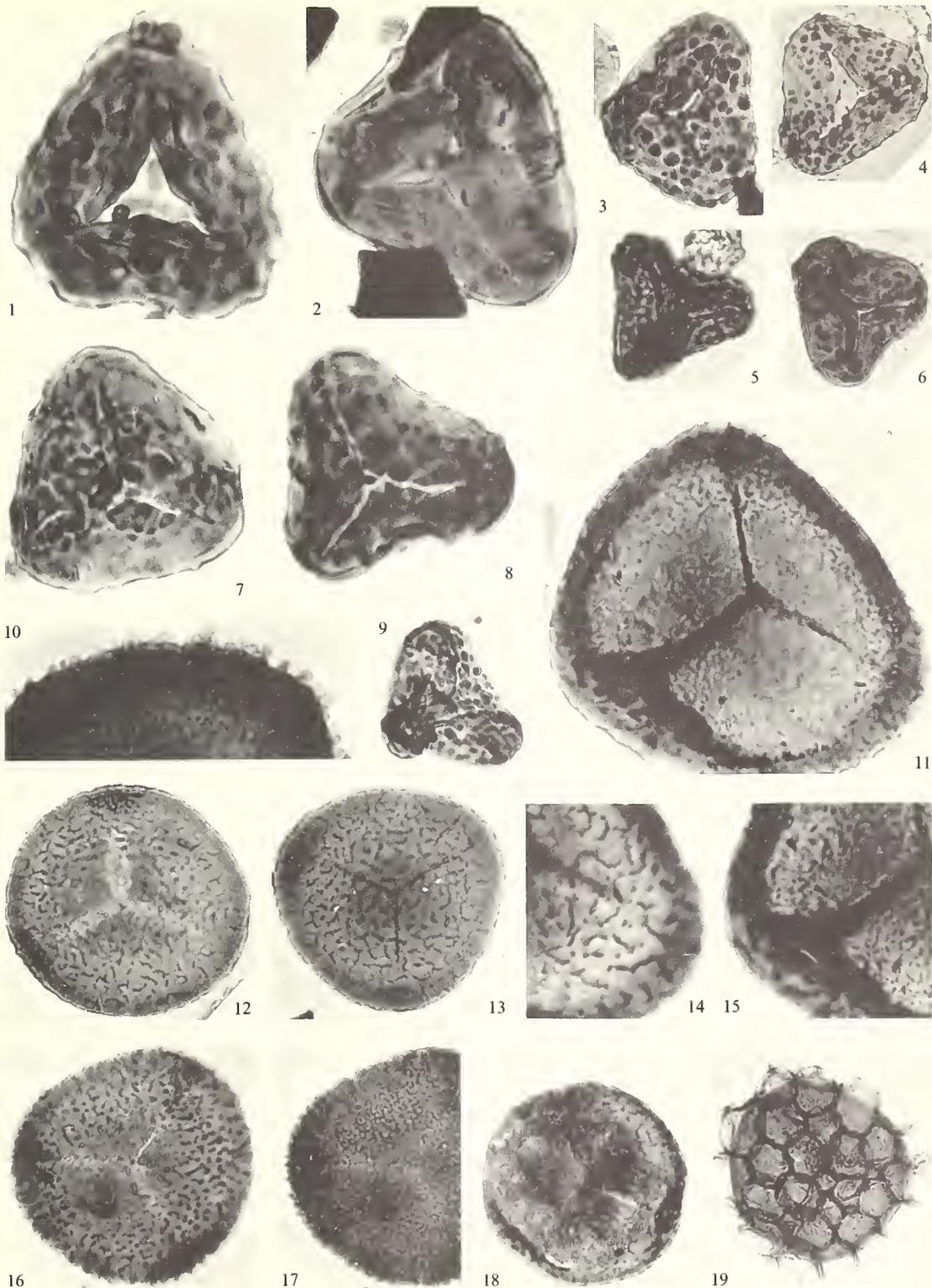
EXPLANATION OF PLATE 41

Figs. 1-9. *Converrucosisporites venitus* sp. nov. Preparation T206. 1, Showing variable shape and distribution of sculptural elements and two layered exine, T206/1, L1 54.1 123.2,  $\times 1000$ . 2, Proximal surface almost smooth, T206/1, L1 58.7 116.6,  $\times 1000$ . 3, Holotype, T206/3, L1 48.4 125.2,  $\times 500$ . 4, T206/3, L1 42.9 118.2,  $\times 500$ . 5, Proximal kyrtomes, T206/1, L1 38.7 120.2,  $\times 500$ . 6, Sparsely distributed sculptural elements, T206/2, L1 40.3 118.7,  $\times 500$ . 7, T206/1, L1 53.3 118.2,  $\times 1000$ . 8, T206/1, L1 43.3 118.1,  $\times 1000$ . 9, T206/3, L1 41.6 118.8,  $\times 500$ .

Figs. 10-17. *Regresporites lophus* gen. et sp. nov. Preparation T209. 10, Equatorial sculpture, T209/1, L1 57.0 129.1,  $\times 1000$ . 11, 14, 15, Same specimen. 11, Raised lips; 14, distal sculpture; 15, proximal sculpture; T209/1, L1 61.7 129.1,  $\times 1000$ . 12, T209/1, L1 63.3 125.7,  $\times 500$ . 13, T209/3, L1 58.4 126.0,  $\times 1000$ . 16, 17, Same specimen, holotype. 16, Distal focus; 17, equatorial focus; T209/1, L1 41.5 126.4,  $\times 500$ .

Fig. 18. cfA. *Regresporites lophus* gen. et sp. nov. Specimen corroded, preparation T210/13, L1 58.7 123.2,  $\times 500$ .

Fig. 19. *Retitriletes* sp. Preparation T210/13, L1 54.3 115.7,  $\times 500$ .



BATTEN, Cretaceous spores

surfaces (Pl. 41, fig. 2). Predepositional and diagenetic corrosion is shown by tearing and pitting of the exine of some specimens.

*Discussion.* The sculptural elements of *Converrucosisporites cameroni* (de Jersey 1962) Playford and Dettmann 1965 (Triassic) rarely coalesce, and although they consist mostly of verrucae, they may also comprise some bacula, spinae, coni, and grana. The closely spaced verrucae on the exine of *C. geniculatus* Deák and Combaz 1967 are more rounded and more strongly developed. '*Trilitisporites*' *rariverrucatus* Danzé-Corsin and Laveine 1963 (lower Lias) has more or less rounded verrucae 1–3  $\mu\text{m}$  high scattered widely over its surface. *Concavissimisporites southeyensis* Pocock 1970 (lower Bajocian) is larger and has a sexine which is thicker in equatorial radial regions than interradially. *Concavisporites variverrucatus* Couper 1958 is somewhat larger and has a thicker exine. *Converrucosisporites venitus* resembles some Carboniferous species of the genera *Pustulatisporites* Potonié and Kremp 1954 and *Converrucosisporites*. The specimens ascribed by Lantz (1958, pl. 1, fig. 12) to *Leptolepidites* cf. *verrucatus* Couper 1953 are similar. Forms recorded as *Converrucosisporites venitus* have been recovered from the Ashdown Beds, Wadhurst Clay, Lower Tunbridge Wells Sand, and Grinstead Clay (Berriasian–Valanginian?).

Infraturma MURORNATI Potonié and Kremp 1954

REGRESPORITES gen. nov.

*Type species.* *R. lophus* sp. nov.

*Diagnosis.* Miospore, trilete, rounded triangular to subcircular in equatorial outline. Extremities of laesurae usually merge with equatorial or proximal subequatorial exine thickening. Distal sculpture of irregular, occasionally anastomosing rugulae  $\pm$  scattered grana, verrucae, clavae, or bacula. Proximal sculpture similar but reduced, may consist only of grana, rarely scabrate.

*Discussion.* Spores which structurally resemble *Regresporites* include *Retusotriletes* Naumova 1953 emend. Strel 1964 and related genera (e.g. *Apiculiretusispora* Strel 1964) described from the Palaeozoic. *Rugulatisporites* Thomson and Pflug 1953 is used for rugulate Mesozoic spores but the diagnosis of the genus does not allow for the inclusion of forms which show modifications of the exine in equatorial

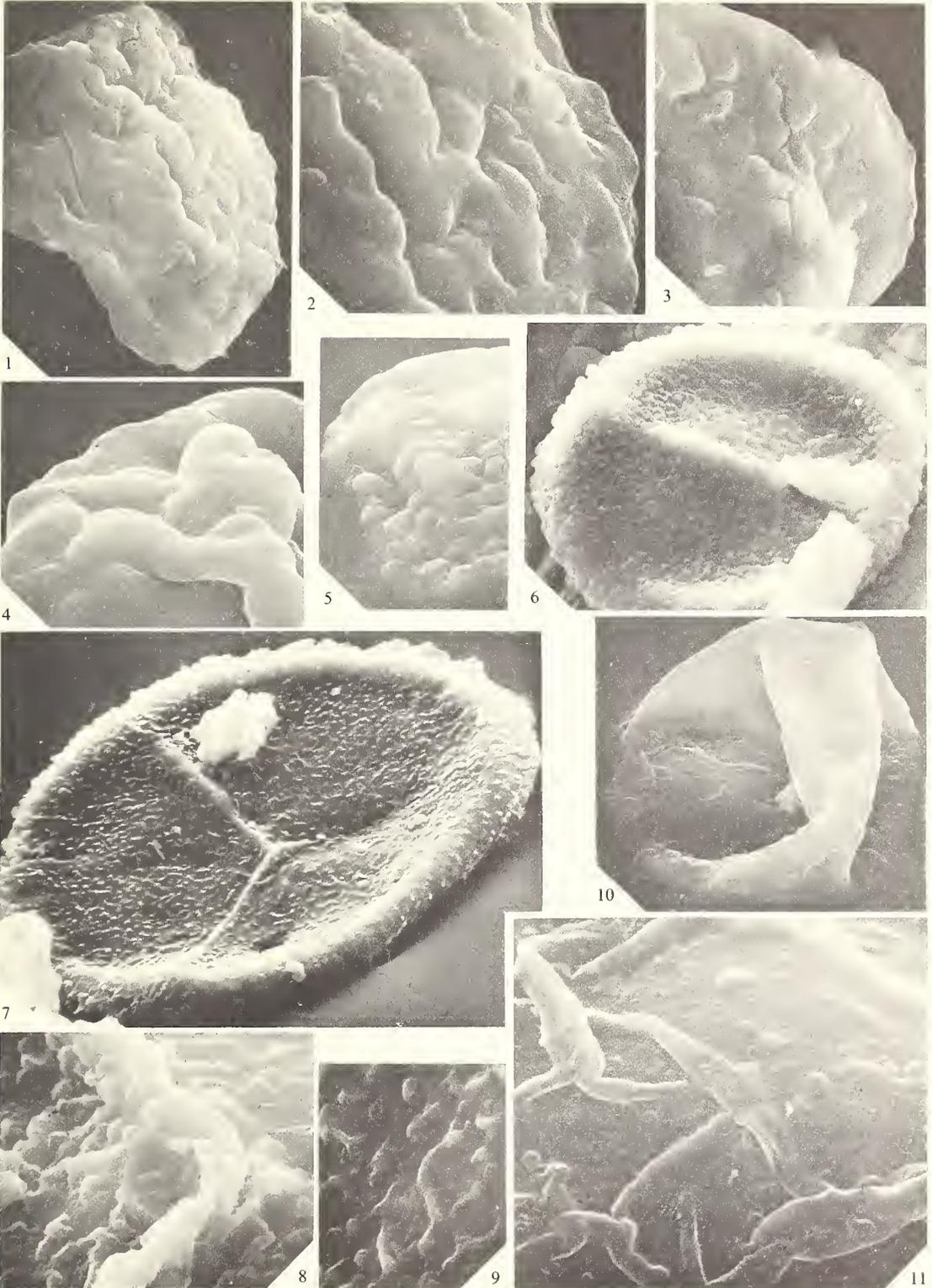
EXPLANATION OF PLATE 42

All scanning electron micrographs.

Figs. 1–5. *Converrucosisporites venitus* sp. nov. Preparation T206. 1, 2, Specimen on stub (SH) DB 44. 1, Specimen obliquely compressed,  $\times 1500$ . 2, Detail of distal sculpture,  $\times 3500$ . 3, Second specimen, distal view,  $\times 1500$ , (SH) DB 50. 4, Third specimen, detail of proximal radial region,  $\times 3500$ , (SH) DB 44. 5, Part of distal surface of fourth specimen,  $\times 1500$ , (SH) DB 44.

Figs. 6–9. *Regresporites lophus* gen. et sp. nov. Preparation T209. 6, Slightly oblique compression,  $\times 1000$ , (SH) DB 36. 7, Second specimen showing raised lips and thickened proximal equatorial regions,  $\times 1000$ , (SH) DB 1a. 8, Third specimen, detail of proximal pole,  $\times 4000$ , (SH) DB 34. 9, Distal sculpture detail of fourth specimen,  $\times 2000$ , (SH) DB 36.

Figs. 10–11. *Pilasporites allenii* Batten 1968. Preparation T210. Specimen on (SH) DB 47. 10,  $\times 1500$ . 11, Detail of loosened ?ektexine showing crinkling and attached globules,  $\times 7500$ .



BATTEN, Cretaceous spores

or subequatorial regions. *Lycopodiacidites* Couper 1953 emend. Potonié 1956 is generally used for azonate miospores which are verrucate to rugulate on their distal surface. *Hamulatisporis* Krutzsch 1959, erected from the Tertiary, is a subtriangular spore with hamulate sculpture.

*Regresporites lophus* sp. nov.

Plate 41, figs. 10–17; Plate 42, figs. 6–9; Plate 44, figs. 1–6

*Type sample.* CUC 791/11, Cuckfield No. 1 Borehole, Sidnye Farm, Sussex (TQ 2962 2729), depth 791 ft 11 in (241.4 m), Wadhurst Clay, Valanginian? Medium grey (N5) clay, thin fine silt laminations, *Equisetites in situ* and fragments of same. Preparation T209; 10 minutes Schulze solution, cleared in dilute  $\text{NH}_4\text{OH}$ , mineral separation, strew slides with Clearcol. AT8. Holotype slide T209/1, LI 41.5 126.4; Pl. 41, figs. 16, 17.

*Diagnosis.* Miospore, trilete, mean maximum diameter  $62.6 \mu\text{m}$ , standard deviation  $5.5 \mu\text{m}$  (100 specimens). Amb rounded triangular to subcircular. Distal surface (when uncompressed) more strongly convex than proximal. Laesurae length  $\frac{3}{4}$  spore radius or more, straight or (rarely) slightly sinuous. Lips may be raised,  $0.5\text{--}2 \mu\text{m}$  wide at base on each side of laesurae and up to  $5 \mu\text{m}$  high (measured on thirty-eight specimens). Extremities of laesurae usually merge with equatorial or subequatorial exinal thickening which appears as a dark zone in transmitted light. Width of this zone usually  $5\text{--}7 \mu\text{m}$  interradially and  $6\text{--}11 \mu\text{m}$  radially; inner margin usually indistinct.

Exine  $2\text{--}3 \mu\text{m}$  thick except near equator where it may be up to  $4.5 \mu\text{m}$  thick in interradial regions and up to  $5 \mu\text{m}$  thick at angles, probably two-layered; outer layer thin (*c.*  $1 \mu\text{m}$ ?), carries sculpture. A subcircular area (outline indistinct) at proximal pole may be slightly darkened in transmitted light (= slight thickening of exine); observed limits of maximum diameter  $19\text{--}36 \mu\text{m}$ , mean  $26.3 \mu\text{m}$  (sixty-six specimens).

Proximal sculpture usually of small grana and/or occasionally anastomosing irregular rugulae (up to  $1 \mu\text{m}$  high,  $< 4 \mu\text{m}$  in length, up to  $3 \mu\text{m}$  apart). Distal and equatorial sculpture of rugulae  $\pm$  scattered grana, verrucae, clavae, and baculae; rugulae irregular, occasionally anastomosing, up to  $4 \mu\text{m}$  apart,  $4\text{--}10 \mu\text{m}$  long, usually  $0.5\text{--}2 \mu\text{m}$  (rarely up to  $3.5 \mu\text{m}$ ) wide, and  $< 2 \mu\text{m}$  (rarely up to  $4 \mu\text{m}$ ) high.

*Description.* The observed limits of the maximum diameter of these spores are  $51\text{--}80 \mu\text{m}$  (coefficient of variation  $8.7\%$ ). Seventy-five of the specimens are in polar aspect but none are in equatorial view. The laesurae are sometimes only weakly developed (Pl. 42, fig. 6 in part; Pl. 44, fig. 4). The dimensions of the sculptural elements on the proximal face tend to increase towards the equator. Eighty-two specimens have both grana and rugulae proximally (Pl. 41, fig. 15; Pl. 42, fig. 7). Most specimens are very compressed, usually in polar orientation or slightly obliquely. The proximal face is often concave (Pl. 42, figs. 6, 7; Pl. 44, fig. 4). The sculptured layer of the exine has been loosened on, and partially removed from, some specimens. Twenty-four specimens show a single fold which in most cases is developed subparallel to the equator.

*Discussion.* Forms identified as *Regresporites lophus* have only been recorded from the Wadhurst and Grinstead Clays (Valanginian?).

Genus RETITRILETES van der Hammen *ex* Pierce 1961*Retitriletes* sp.

Plate 41, fig. 19; Plate 43, fig. 1

*Description.* The observed limits of the maximum diameter of this miospore, excluding sculpture, are 40–75  $\mu\text{m}$  (twenty specimens). The amb is circular or subcircular in outline. An irregular weakly developed (discontinuous) triradiate ridge may be present on the proximal face extending to the equator of the spore body. The exine is 2–3  $\mu\text{m}$  thick and sculptured with a reticulum both on the distal face and equatorially. On the proximal face the sculpture is reduced, sometimes to a low reticulum, but more often to irregular grana, and muri < 3  $\mu\text{m}$  high. Near the trilete mark the exine may be scabrate. The distal and equatorial muri are 0.5–1.5  $\mu\text{m}$  wide at their bases but rapidly become membraneous above and are up to 12  $\mu\text{m}$  high. The lumina are 4–21  $\mu\text{m}$  in maximum diameter and circular to polygonal in outline.

*Discussion.* Species of *Januasporites* Pocock 1962 emend. Singh 1964 are alete miospores possessing a two-layered exine. The outer layer is absent over a more or less circular area on the distal face. The muri of *Reticulatisporites arcuatus* Brenner 1963 are thicker and more irregular in width. The proximal sculpture of *Hymenoreticulispores altimuronatus* Döring 1964 (Jurassic; Upper Malm) is not reduced. The laesurae of *R. castellatus* Pocock 1962 are not visible and the proximal sculpture is not reduced. *Woodsia reticulata* Bolkhovitina 1953 appears to possess a clearly defined triradiate mark. *R. incomptus* Manum 1962 (Tertiary) has muri of lower elevations and is clearly triradiate. *Zlivisporis blanensis* Pačtová 1961 is clearly trilete, lacks sculpture on the proximal face, and the arrangement of the muri is different. *Lycopodiumsporites marginatus* Singh 1964 differs chiefly in having a stronger trilete mark. *Retitriletes* sp. bears some resemblance to palynomorphs which have been referred to species of the acritarch genus *Cymatiosphaera* (cf. Wall 1965, pl. 9, fig. 8). *Retitriletes* sp. has only been recorded from the Wadhurst Clay (Valanginian?).

Infraturma AURICULATI Schopf emend. Dettmann 1963

*Ischyosporites arkellii* (Pocock 1970) comb. nov.1970 *Dictyotriletes arkelli* Pocock, p. 52, pl. 9, fig. 16A; *D. arkellii*, p. 119.Pocock's species is included here in *Ischyosporites* because it has a valvate exine.Cf. B. *Ischyosporites arkellii*

Plate 43, figs. 2–14; Plate 44, figs. 7–11; Plate 46, fig. 2

*Sample.* CUC 792, Cuckfield No. 1 Borehole, Sidnye Farm, Sussex (TQ 2962 2729), depth 792 ft (241.4 m); Wadhurst clay, Valanginian? Medium dark grey (N4) clay, thin fine silt laminations. *Equisetites in situ* and fragments of same. Preparation T210; 10 minutes Schulze solution, cleared in dilute  $\text{NH}_4\text{OH}$ , mineral separation, strew slides with Clearcol. AT8/16.

*Description.* A trilete miospore with a mean maximum equatorial diameter of 43.6  $\mu\text{m}$

(standard deviation  $5.1 \mu\text{m}$ , observed limits  $32\text{--}57 \mu\text{m}$ , coefficient of variation  $11.7\%$  (100 specimens)) and a mean maximum polar diameter (including membraneous lips of trilete mark) of  $45 \mu\text{m}$  (twenty-two specimens). The amb has straight to slightly convex sides and rounded angles. The proximal face is slightly, and the distal face markedly, convex. The laesurae are straight or slightly sinuous and are longer than three-quarters of the spore radius. The membraneous lips of the trilete mark are up to  $5 \mu\text{m}$  high and have a basal width of  $1.5\text{--}2 \mu\text{m}$ . The (perfect or imperfect) distal reticulum encroaches on to the otherwise smooth proximal face at the angles. The muri are rounded or (sometimes) flat-topped,  $0.5\text{--}3.5 \mu\text{m}$  (usually  $1\text{--}2.5 \mu\text{m}$ ) high, highest where they join and at the angles. They are  $1\text{--}2.5 \mu\text{m}$  wide except at intersections where the width may increase to  $4 \mu\text{m}$ . The lumina are generally subcircular to polygonal and  $2\text{--}7 \mu\text{m}$  in diameter but may be larger and irregular if the reticulum is imperfect. They tend to be smallest in equatorial radial regions.

Thirty-two specimens are in polar and twenty-two in equatorial aspect. One weakly sculptured specimen has unusually convex sides (Pl. 43, fig. 9) but this is probably because the triradiate lips have parted. The compression of the specimens varies from relatively uncompressed to very compressed. A few show signs of corrosion in the form of pitting of the exine.

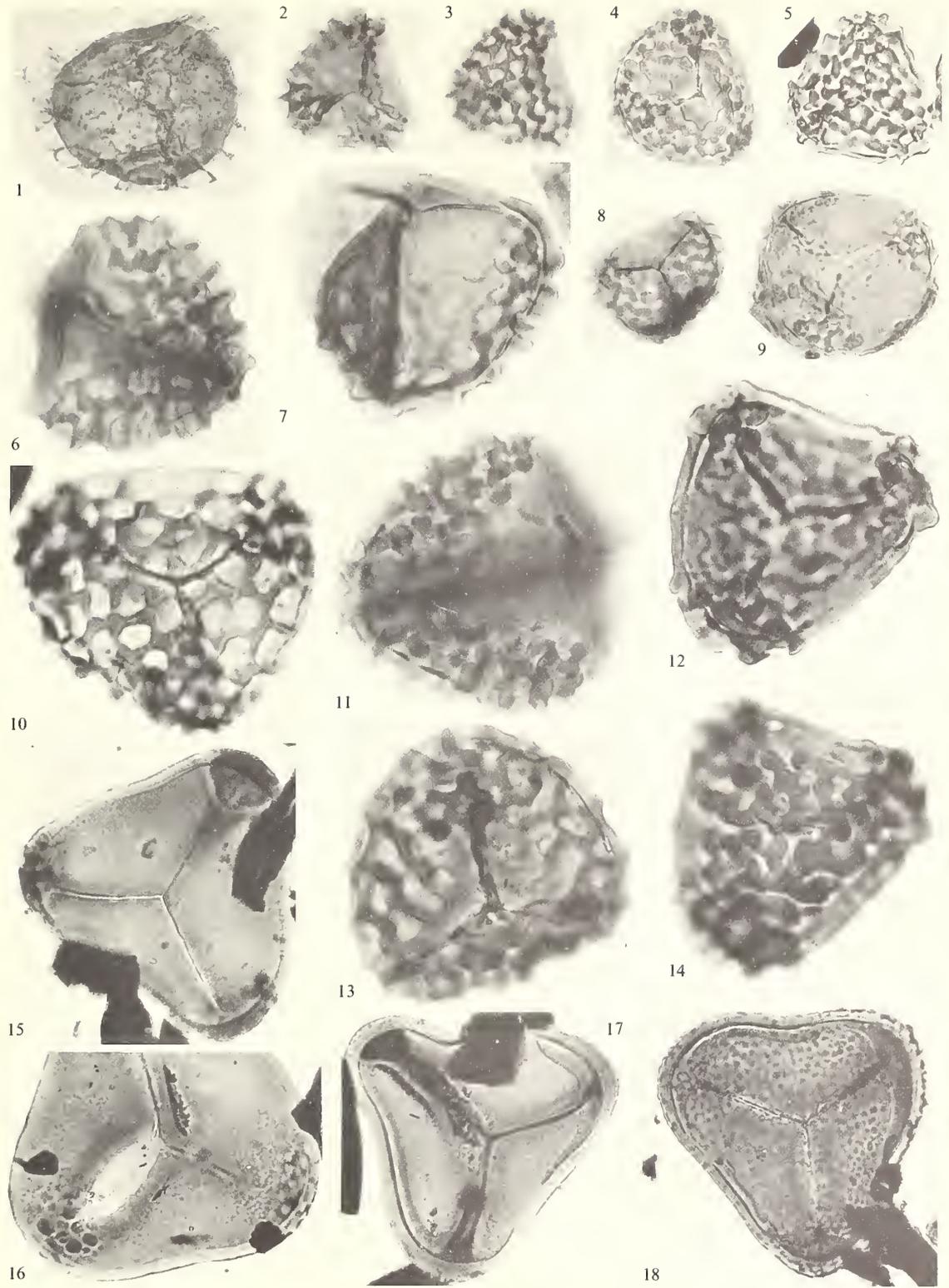
*Discussion.* The lumina of *Ischyosporites crateris* Balme 1957 are larger and the exine is thicker. *I. punctatus* Cookson and Dettmann 1958 has a thicker exine, foveoreticulate sculpture and wider muri. *I. marburgensis* de Jersey 1963 (Jurassic) has a different sculpture and a thicker exine. '*Lycopodiacidisporites*' *cerniidites* (Ross 1949; Delcourt and Sprumont 1955) Danzé-Corsin and Laveine 1963 (*in Briche et al.* 1963; Lower Lias), has cristate sculpture disposed more or less concentrically and not forming a true reticulum. *Lycopodiumsporites crassimacerius* Hedlund 1966 has a thicker exine, is sculptured with a polygonal reticulum, and has higher muri. The distal sculpture of '*Ischyisporites*' *puzzlei* Levet-Carette 1966 consists of little cavities, rounded or more often vermiform in shape, separated by muri  $3\text{--}5 \mu\text{m}$  wide. *Ischyosporites disjunctus* Singh 1971 is larger, and the muri are wider and the exine thicker. The nature of the murornate sculpture and/or other features distinguishes *I. arkellii* from the following: *L. dentimuratus* Brenner 1963, '*Ischyisporites*' *surangulus* Levet-Carette 1964 (Bajocian), *Foveasporis microfovearis* Krutzsch 1959 (Tertiary), *Ischyosporites asolidus* (Krutzsch 1959) Krutzsch 1967 (Tertiary), *I. foveasolidus*

#### EXPLANATION OF PLATE 43

Fig. 1. *Retitriletes* sp. Preparation T210/14, L1 47.9 123.0,  $\times 500$ .

Figs. 2-14. cfB. *Ischyosporites arkellii* (Pocock 1970) comb. nov. Preparation T210. 2, 3, Same specimen. 2, Proximal focus; 3, distal focus; T210/14, L1 30.3 121.6,  $\times 500$ . 4, T210/11, L1 35.6 121.2,  $\times 500$ . 5, T210/2, L1 42.7 118.0,  $\times 500$ . 6, Lateral view, T210/2, L1 28.7 118.7,  $\times 1000$ . 7, Oblique view, T210/1, L1 48.3 115.8,  $\times 1000$ . 8, T210/14, L1 25.2 119.7,  $\times 500$ . 9, Specimen weakly sculptured, unusually convex sides, T210/2, L1 46.0 122.8,  $\times 500$ . 10, Distal focus, T210/13, L1 60.7 123.7,  $\times 1000$ . 11, Lateral view, T210/14, L1 48.6 123.0,  $\times 1000$ . 12, 14, Same specimen. 12, Proximal focus; 14, distal focus; T210/3, L1 48.0 122.2,  $\times 1000$ . 13, Oblique view, T210/14, L1 47.5 122.0,  $\times 1000$ .

Figs. 15-18. *Trilobosporites ivanovae* sp. nov. Preparation T061. 15, Holotype T061/1, L1 43.6 109.8,  $\times 500$ . 16, T061/1, L1 37.3 111.8,  $\times 500$ . 17, Margins of laesurae thickened, T061/1 L1 52.7 113.0,  $\times 500$ . 18, T061/1, L1 27.0 113.8,  $\times 500$ .



BATTEN, Cretaceous spores

Krutzsch 1967 (Tertiary), *I. tuberosus* Döring 1965, and *F. triangulus* Stanley 1965 (Paleocene).

The spores *Dictyotriletes arkellii* Pocock 1970 from the lower Bajocian of western Canada (not recorded from younger strata) are similar to those described here. Some characters differ slightly, but there are not sufficient criteria for the erection of a new species for the Wealden spores. The illustrations of *Klukisporites pseudoreticulatus* Couper 1958 in Agasie (1969) resemble some of those of *I. arkellii* shown here. Forms comparable with *I. arkellii* have been recorded from the Ashdown Beds, Wadhurst Clay, Lower Tunbridge Wells Sand, and Grinstead Clay (Berriasian-Valanginian?).

*Trilobosporites ivanovae* sp. nov.

Plate 43, figs. 15-18; Plate 45, figs. 1-8; Plate 46, figs. 1, 5-9

*Type sample.* DJB 18, Philpots Quarry, West Hoathly, Sussex (TQ 3592 3221), 5.4 m above base of Grinstead Clay, Valanginian? Light brown (5YR 6/4) medium silt, plant fragments. Preparation T061; 20 minutes HNO<sub>3</sub>, cleared in dilute NH<sub>4</sub>OH, mineral separation, strew slides with Clearcol. AT13/14; S4, 5. Holotype slide T061/1, Ll. 43.6 109.8; Pl. 43, fig. 15.

*Diagnosis.* Miospore, trilete, mean maximum diameter 92  $\mu\text{m}$ , standard deviation 8.3  $\mu\text{m}$  (100 specimens). Amb triangular with slightly concave, straight or slightly convex sides and rounded angles. Distal surface more convex than proximal. Laesurae about  $\frac{3}{4}$  spore radius, may divide near extremities, bordered by simple membraneous lips 1-2.5  $\mu\text{m}$  high. Exine may be slightly thickened for 4-7  $\mu\text{m}$  on each side of laesurae (forty-four specimens). Width of thickened zone may increase slightly near equatorial radial regions and merge with equatorial radial thickenings.

Exine mainly 3-5  $\mu\text{m}$  thick but generally thicker (up to 8  $\mu\text{m}$ ) in equatorial radial regions; increase in thickness varies from 0.5 to 4  $\mu\text{m}$ . Thickened areas extend from 14 to 25  $\mu\text{m}$  over proximal and distal faces; boundaries usually indistinct. Exine scabrate, maculate, or sculptured with closely spaced (0.25  $\mu\text{m}$  or less apart) grana and/or verrucae. Verrucae subcircular, polygonal, or somewhat irregular in shape, usually < 1  $\mu\text{m}$  high and with a diameter of < 3  $\mu\text{m}$  interradially and < 5  $\mu\text{m}$  at the angles, may form a negative reticulum. Sculpture often more strongly developed on distal face and/or near equatorial radial regions. Forms with verrucate distal exines are usually maculate or scabrate in vicinity of proximal pole and in proximal interradial regions.

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EXPLANATION OF PLATE 44

All scanning electron micrographs.

Figs. 1-6. *Regresporites lophus* gen. et sp. nov. 1, 2, 3, Fifth specimen, on stub (SH) DB 36. 1, Part of distal surface,  $\times 1000$ . 2, Sculpture detail,  $\times 1500$ . 3, Sculpture detail,  $\times 4000$ . 4, 5, 6, Sixth specimen, (SH) DB 36. 4, Proximal surface, trilete mark weakly developed,  $\times 1000$ . 5, Sculpture detail,  $\times 2000$ . 6, Sculpture detail,  $\times 5000$ .

Figs. 7-11. cfB. *Ischyosporites arkellii* (Pocock 1970) comb. nov. Preparation T210. 7, 8, Specimen laterally compressed, (SH) DB 46. 7,  $\times 1500$ . 8, Sculpture detail,  $\times 3500$ . 9, Second specimen, proximal surface,  $\times 1500$ , (SH) DB 44. 10, Third specimen, lateral view,  $\times 1500$ , (SH) DB 46. 11, Fourth specimen,  $\times 1500$ , (SH) DB 44.



*Description.* The observed limits of the maximum equatorial diameter of this microspore are 75–126  $\mu\text{m}$  (coefficient of variation 9%) and of the maximum polar diameter are 62–80  $\mu\text{m}$  (seven specimens). Although the increase in thickness of the exine from interradial to radial regions is usually about the same at each angle, differences of up to 3.5  $\mu\text{m}$  have been noted. There is no increase in thickness at one or two of the angles of three specimens (Pl. 45, fig. 6). Three specimens which are sculptured with a few verrucae up to 7  $\mu\text{m}$  in diameter and 3  $\mu\text{m}$  in height (Pl. 45, figs. 10–12) are considered to be extreme variants.

*Discussion.* *Trilobosporites (Trilobosporites) tenuiparietalis* Döring 1965 has a thinner exine and more strongly concave sides. *Maculatisporites microverrucatus* Döring 1964 and *M. undulatus* Döring 1964, both from the Wealden A of Westmecklenburg, lack thickening of the exine in equatorial radial regions and are somewhat smaller; the exine of *M. microverrucatus* is also thinner. Rare specimens of *T. ivanovae* resemble *Lygodium (Tuberculata) triangulatum* E. Ivanova 1961 but the latter has a thinner exine.

The descriptions and illustrations of both *Lygodium (Cavernosotriangulata) cavernosum* E. Ivanova 1961 and *L. (C.) cavernosum* var. *tuberculatum* E. Ivanova 1961 (in Samoilovitch *et al.* 1961; Cenomanian) suggest that these taxa may fall within *T. ivanovae*, but in Ivanova's descriptions are insufficient to confirm this. Some of the weakly sculptured specimens of *T. ivanovae* resemble both *T. (Trilobosporites) aornatus* Döring 1965 (Upper Malm) and *T. (T.) crassiangularis* Döring 1965 (German Wealden A).

Forms comparable with *T. ivanovae* have been recorded from the Wadhurst Clay, Lower Tunbridge Wells Sand, and Grinstead Clay (Berriasian–Valanginian?).

Turma ALETES Ibrahim 1933

Subturma AZONALETES Lubert emend. Potonié and Kremp 1954

GENUS PILASPORITES Balme and Hennelly 1956

*Pilasporites allenii* Batten 1968

Plate 42, figs. 10, 11

A specimen of *Pilasporites allenii* from the type sample (CUC 792) was illustrated in Batten (1968, pl. 123, fig. 11) and described as having granules and small verrucate

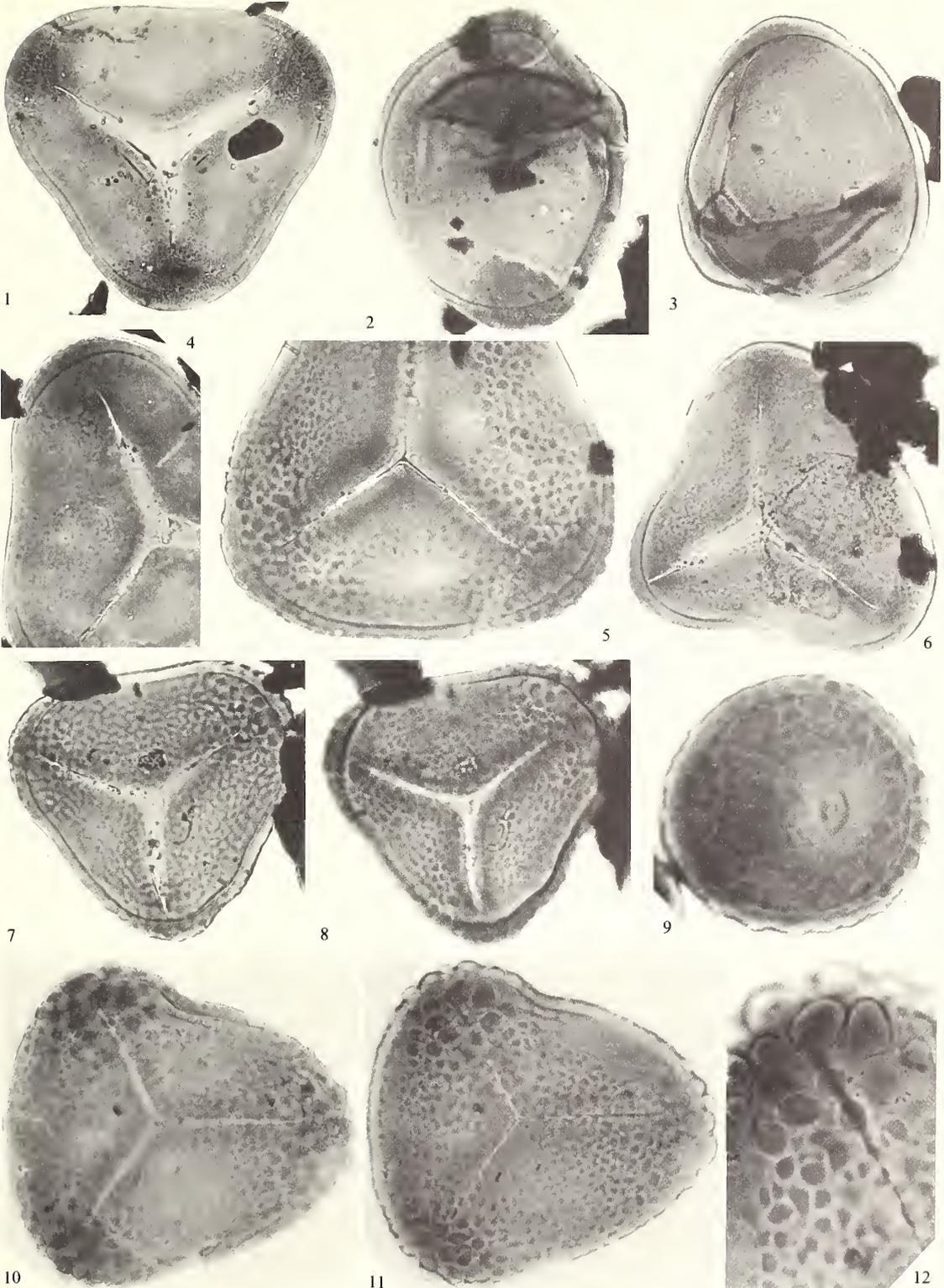
EXPLANATION OF PLATE 45

All figures  $\times 500$  unless otherwise specified.

Figs. 1–8. *Trilobosporites ivanovae* sp. nov. Preparation T061. 1, Specimen with scabrate exine and scattered corrosion pits, T061/1, LI 35.1 112.2. 2, Lateral view showing equatorial radial thickenings, T061/1, LI 57.1 111.1. 3, Oblique orientation, T061/1, LI 35.7 114.3. 4, Small verrucae on distal face near equatorial radial thickening, T061/1, LI 43.0 111.1. 5, Unusually large specimen, T061/1, LI 44.9 114.2. 6, Exine weakly thickened in equatorial radial regions, T061/1, LI 35.3 113.7. 7, 8, Same specimen, strongly sculptured. 7, Equatorial focus; 8, distal focus; T061/1, LI 41.9 121.0.

Fig. 9. *Admolia amphidoxa* gen. et sp. nov. Preparation T209/2, LI 39.9 124.2,  $\times 1000$ .

Figs. 10–12. cfA. *Trilobosporites ivanovae* sp. nov., showing strongly developed sculpture in equatorial radial regions. 10, Equatorial focus; 11, proximal focus; 12, detail,  $\times 1000$ ; preparation T053/2, LI 36.0 114.3.



BATTEN, Cretaceous spores

elements attached to a closely adhering perine. These elements (Pl. 42, fig. 11) are similar to the 'resin droplets' observed by Smith and Butterworth (1967, p. 145) on the Carboniferous miospore *Cadiospora magna* Kosanke 1950, and to the 'globules of ?tapetal material' (Evans 1970, p. 65) characteristically attached to the 'exoexine' of species of *Diaphanospora* Balme and Hassell 1962 emend. Evans 1970. They may also be comparable with Ubisch bodies (cf. Rowley 1963; Pettitt 1966). Lugardon (1969) showed similar bodies adhering to the perispore of spores of *Equisetum maximum* Lamk. Abnormal spores (not Ubisch bodies) attached to *P. allenii* exines occasionally occur in Wealden dispersed spore preparations. They are comparable with those of Gould (1968, pl. 2, fig. 11). Specimens of *P. allenii* may pseudomorph *Cycadopites* or *Taxodiaceapollenites* and resemble probable algal bodies, e.g. *Halosphaeropsis liassica* Mädlar 1963 (Lias) and *Leiosphaeridia pusilla* Mädlar 1963 (Lias). Species of *Inaperturopollenites* generally have thinner exines containing many more secondary folds than is usual in *P. allenii*.

*P. allenii* was compared by Batten (1968) with other miospore species, some attributed to the Equisetaceae (*Equisetites*/*Equisetum*). Additional records of dispersed miospores which have been (tentatively) attributed to the family or genera or compared with the spores of *Equisetum* are listed on Table 2. Other dispersed spore species resembling *P. allenii* are also listed. Perhaps most closely comparable with *P. allenii* is *P. marcidus* Balme 1957 (Batten 1968, p. 641), from the Lower Jurassic of Western Australia, and recorded from both the Jurassic and Cretaceous. It may have affinities with the Equisetaceae (Balme 1957, p. 28) but other species of *Pilasporites* (including the type species *P. calculus* Balme and Hennelly 1956, *P. plurigenus* Balme and Hennelly 1956, and others) are unlikely to be so related.

#### INCERTAE SEDIS

#### ADMOLIA gen. nov.

*Type species. A. amphidoxa* sp. nov.

*Diagnosis.* Spherical or subspherical body in uncompressed state. Exine differentially thickened, smooth or sculptured, may show a circular or subcircular perforation (rarely a pore) on thinnest part.

*Discussion.* Forms referable to *Exesipollenites* have a circular depression, which probably represents a pore, surrounded by exine thickening. The wall of *Discoperulina* Phillips 1971 is thickest by the operculum; this palynomorph also has a thin-

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#### EXPLANATION OF PLATE 46

All scanning electron micrographs.

Figs. 1, 5-9. *Trilobosporites ivanovae* sp. nov. Preparation T061. 1, 5, Specimen on stub (SH) DB 33. 1, Proximal view,  $\times 400$ . 5, Detail of radial equatorial region,  $\times 2000$ . 6, Second specimen,  $\times 1000$ , (SH) DB 33. 7, Third specimen, part of proximal exine,  $\times 1000$ , (SH) DB 8. 8, Fourth specimen, detail of proximal pole,  $\times 2000$ , (SH) DB 33. 9, Fifth specimen, distal surface,  $\times 500$ , (SH) DB 8.  
 Fig. 2. cfB. *Ischyosporites arkellii* (Pocock 1970) comb. nov. Fifth specimen,  $\times 750$ , (SH) DB 46.  
 Figs. 3-4. *Admolia amphidoxa* gen. et sp. nov. Preparation T209. 3, Specimen with pore,  $\times 2000$ , (SH) DB 34. 4, Second specimen,  $\times 1500$ , (SH) DB 36.



BATTEN, Cretaceous spores

walled inner body. *O. carbonis*, of the monotypic genus *Operculites* Newman 1965 is smaller than *A. amphidoxa*, bears a rounded or helicoidal operculum of width about  $\frac{1}{3}$ – $\frac{2}{3}$  grain diameter attached at one side when in place, and the exine is thinner and not differentially thickened.

*Admolia amphidoxa* sp. nov.

Plate 45, fig. 9; Plate 46, figs. 3, 4; Plate 47, figs. 1–14

*Type sample.* CUC 791/11, preparation T209; details under *Regresporites lophus* sp. nov. Holotype slide T209/2, L1 27·4 115·1; Pl. 47, fig. 5.

*Diagnosis.* Mean maximum diameter of grain 42·5  $\mu\text{m}$ , standard deviation 4·7  $\mu\text{m}$  (200 specimens). Amb circular or subcircular. A circular or subcircular perforation of exine (rarely a pore or tear) 5–8  $\mu\text{m}$  in diameter, may be present on thinnest part of differentially thickened exine. Perforation frequently only partially separates (sub)circular area of exine (operculum) from surrounding exine, but separation may be as much as 3  $\mu\text{m}$ . Thickness of exine mainly between 2 and 4·5  $\mu\text{m}$ ; difference between thinnest and thickest parts varies considerably (from < 0·5 to 3  $\mu\text{m}$ ), thickest on face opposite perforation. Exine smooth, gently undulating, or scabrate, or sculptured with micrograna, grana, or dome-shaped verrucae or combinations of these. Sculpture often more weakly developed on thinnest part of wall. Height of verrucae usually 1  $\mu\text{m}$  or less, but may be as much as 3  $\mu\text{m}$ . Elements sometimes separated by distances greater than their diameter but usually closely spaced and partially coalescent, may form a negative reticulum.

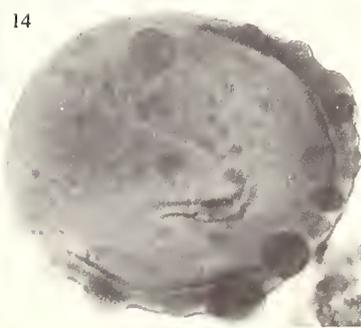
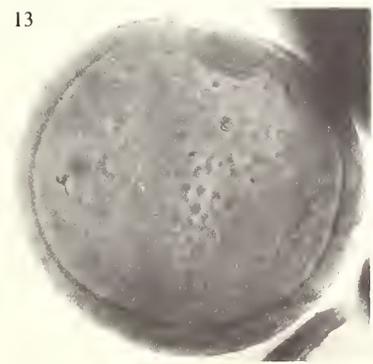
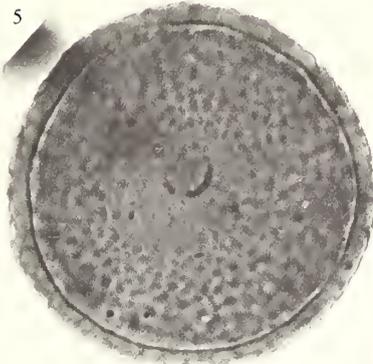
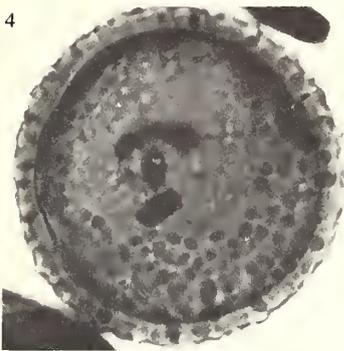
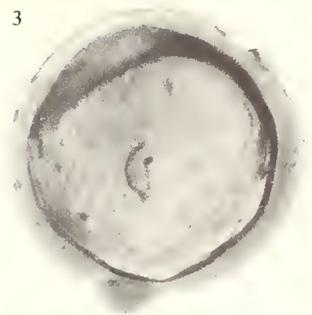
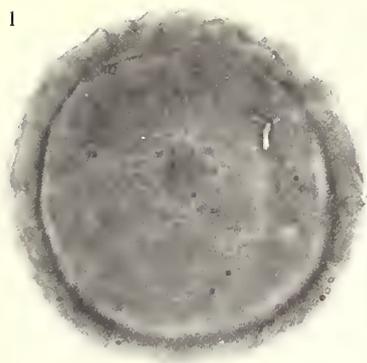
*Description.* The observed limits of the maximum diameter of the body of this palynomorph are 33–57  $\mu\text{m}$  (coefficient of variation 11·1%). The exine of seven specimens is *c.* 1·5  $\mu\text{m}$  around the perforation. One-hundred-and-two specimens show a small circular or subcircular perforation in the exine (Pl. 47, fig. 8), eight show a pore or tear (Pl. 46, fig. 3). The perforation may be obscured by a small fold developed on the thin area, and it is invisible in some compression states or orientations. Discrete grana, bacula, or verrucae may be superimposed on low verrucae. The specimens are compressed but generally well preserved.

*Discussion.* *Foveoinaperturites paucipunctatus* Pierce 1961 is larger and has an infra-punctate, sparsely foveolate exine. Some phytoplankton show a naturally constituted exit hole. Forms probably comparable with *A. amphidoxa* have been seen in the Tertiary (A. E. González Guzmán, pers. comm.). The relatively small size variation

EXPLANATION OF PLATE 47

All figures  $\times 1000$  unless otherwise specified.

Figs. 1–14. *Admolia amphidoxa* gen. et sp. nov. Preparation T209. 1, T209/2, L1 37·7 109·3. 2, Showing perforation of thinnest part of differentially thickened exine, T209/2, L1 52·1 113·0. 3, T209/2, L1 25·3 117·8. 4, T209/1, L1 54·6 116·7. 5, Holotype, T209/2, L1 27·4 115·1. 6, T209/2, L1 29·0 123·8. 7, Perforated area of exine on fold, T209/2, L1 38·3 119·6. 8, T209/2, L1 42·2 124·2. 9, Smooth exine, T209/2, L1 28·8 114·1,  $\times 500$ . 10, Partial separation of circular area from surrounding exine, T209/2, L1 25·8 118·9,  $\times 500$ . 11, Large verrucae, T209/2, L1 33·6 115·3. 12, T209/2, L1 34·7 124·7. 13, T209/2, L1 51·1 118·0. 14, Large dome-shaped verrucae, T209/1, L1 47·2 129·6.



and the variety of sculpture observed in this population is usual. DJB 294, a sample from the Wadhurst Clay of the High Brooms Brick and Tile Company's pit at Southborough, Kent (TQ 5948 4189), however, yielded an assemblage composed almost entirely of smooth forms. The High Brooms assemblages are mostly smaller and darker in colour than the population on which this species is based. Specimens identified as *A. amphidoxa* have so far only been recorded from the Wadhurst and Grinstead Clays (Valanginian?).

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D. J. BATTEN  
Robertson Research International Ltd.  
'Ty'n-y-Coed'  
Llanrhos, Llandudno  
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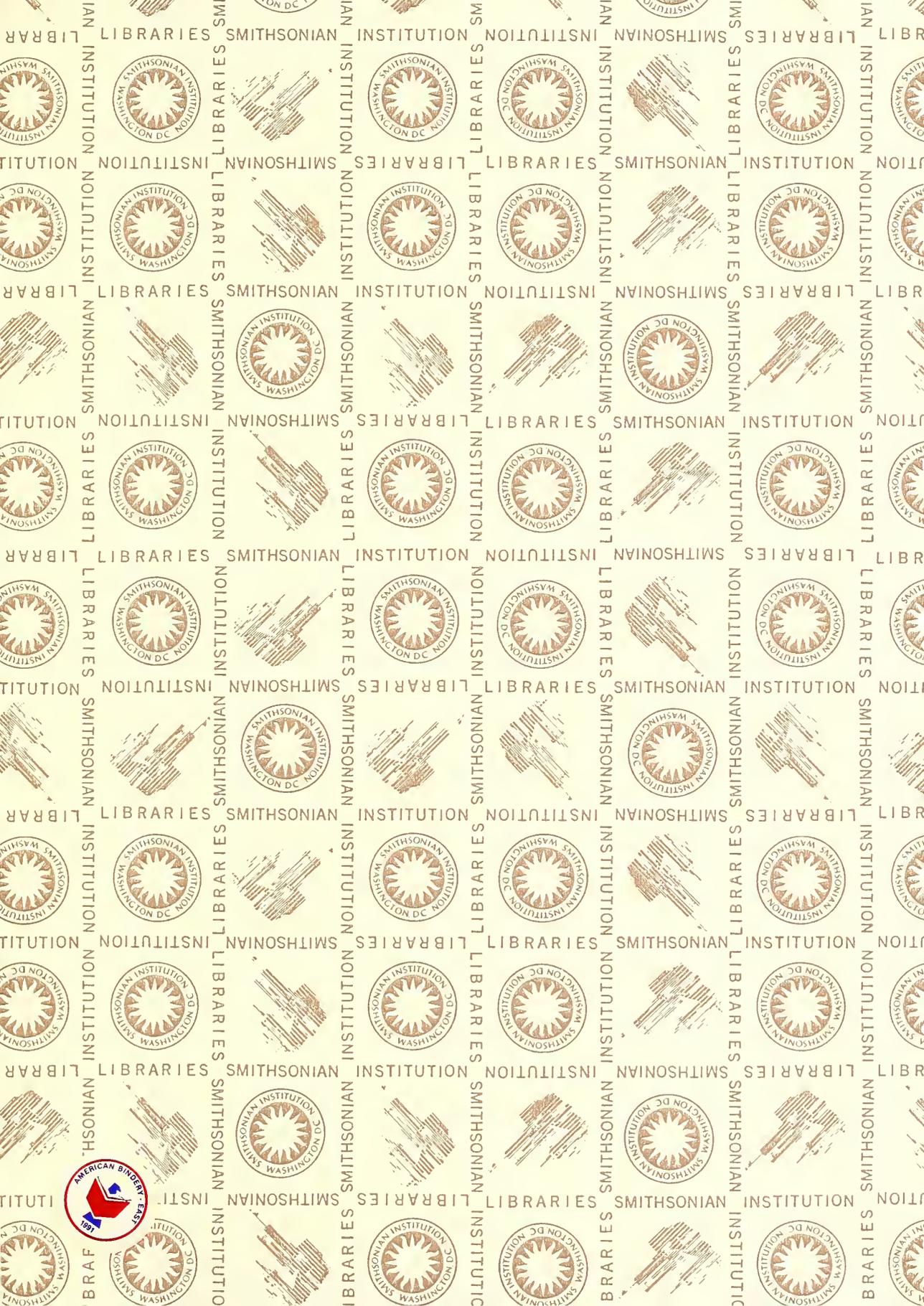
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## CONTENTS

- A Miocene solenoporoid alga showing reproductive structures  
G. F. ELLIOTT 223
- A *Protospongia* from the Dalradian of Clare Island, Co. Mayo, Ireland  
A. W. A. RUSHTON and W. E. A. PHILLIPS 231
- Observations on the nature of the acritarchs  
C. DOWNIE 239
- The palaeoenvironment of the Abbotsbury Ironstone (Upper Jurassic) of Dorset  
M. E. BROOKFIELD 261
- A Lower Miocene mammalian fauna from Siwa, Egypt  
W. R. HAMILTON 275
- A new crab from the Middle Eocene of Libya  
J. S. H. COLLINS and S. F. MORRIS 283
- Fish otoliths from the English Cretaceous  
F. C. STINTON 293
- Lower Devonian conodonts from New South Wales  
N. M. SAVAGE 307
- Lower Carboniferous conodont faunas from south-west Ireland  
S. C. MATTHEWS and D. NAYLOR 335
- Palaeoecology of Appalachian gypidulid brachiopods  
E. J. ANDERSON and J. H. MAKURATH 381
- Lower Viséan trilobites from Feltrim, Ireland  
G. HAHN and C. BRAUCKMANN 391
- Palynology of early Cretaceous soil beds and associated strata  
D. J. BATTEN 399







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