THE CONODONT FAUNAS OF THE BAGGY AND PILTON BEDS,
NORTH DEVON

by

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Thesis submitted for the degree of *Philosophae Doctor*,

University of Wales, July 1970

ABSTRACT

The Baggy and Pilton Beds outcrop in many of the north-south trending river valleys which traverse the North Devonshire region, in the Taw estuary, and along the western coast of North Devon, north of Barnstable (Bideford) Bay. Throughout the Devonian period, the North Devon area experienced alternating periods of marine and non-marine deposition, and the marine Upper Baggy and Pilton Beds record the final episode, in Late Devonian and Early Carboniferous times, after which conditions became more uniform. The Pilton Beds are a transitional sequence which cross the Devonian - Carboniferous boundary.

Conodont faunas of Upper Devonian and Lower Carboniferous age are represented in two large coastal exposures of the Upper Baggy and Pilton Beds, at Croyde Bay and Fremington Pill. A total of 34 species, referable to 14 genera, of which three species are new, have been identified from these beds.

Three conodont assemblage zones have been established, one of which can be subdivided into an upper and lower subzone. All three assemblage zones may have only local application, and the youngest zone has been erected only tentatively. Lack of additional exposures of conodont bearing strata has made it impossible to test the regional validity of the zones.

The Upper Baggy and Lower Pilton Beds bear a fauna of Upper Famennian age and may be correlated with the Upper '*costatus*' Assemblage Zone of the German type section, established by Ziegler (1962). These North Devonshire faunas contain spathognathodids of the *costatus* group, including *Spathognathodus bischoffi*, *S. aculeatus* and *S. ziegleri*, all of which are diagnostic of Ziegler's '*costatus*' Zone. In addition *S. strigosus*, *Pseudopolygnathus dentilineata*, *Polygnathus communis* and *Polygnathus* cf. *P. nodomarginatus* are elements common to both faunas.

There are certain significant differences between the conodont faunas of North Devon and those of Germany, namely the absence of *S. costatus ultimus* and representatives of the genus *Palmatolepis* in the present succession. The absence of one or both of these forms may be the result of one or more of the following factors: inadequacy of fossiliferous samples, facies variation, geographic provincialism, or homeomorphic replacement. The relative importance of each of these possible causes is reviewed.

The *Protognathodus kockeli* Zone is also unrepresented in North Devon, however, a significant thickness of the uppermost Lower and the lowermost Upper Pilton Beds has proved unproductive and the *P. kockeli* Zone may be represented in that unfossiliferous sequence.

The Upper Pilton Beds yield conodont faunas only from the base of Goldring's (1956) local faunal division B, and these are provisionally correlated with part of the CuI Zone of Germany. The faunas are small and, in general aspect, equally representative of Upper Devonian or Lower Carboniferous. However, the presence of a single specimen of *P. pura pura* and the absence of spathognathodids of the *costatus* group tentatively suggests a Lower Carboniferous, *Gattendorfia* Stufe age.

The Pilton Beds and, to a lesser extent, the Baggy Beds of North Devonshire have been subjected to low grade metamorphism and significant deformation, with the result that conodont faunas could be recovered only from the intermittent limestone lenses found within the sequence. The sandstones and slates which dominate the succession proved impossible to disaggregate. Furthermore, the metamorphism and tectonism were responsible for the relatively poor state of preservation of the conodont faunas, many of the elements recovered being fractured and incomplete.

An Upper Devonian age is suggested for the strata which outcrop in a road-cut 1 mile east of Bampton. This is based on the occurrence of a single, broken icriodid, and the proximity of this section to rocks of known Carboniferous age.

ACKNOWLEDGEMENTS

I wish to thank Prof. F.H.T. Rhodes for his invaluable help, advice, criticism and interest throughout all stages of this work at both the University College of Swansea and the University of Michigan, Ann Arbor.

I also wish to thank Dr. Ronald Austin, University of Southampton, and Mr. Edric Druce, Bureau of Mineral Resources, Geology and Geophysics, Canberra, Australia, for their encouragement and advice in the identification of the conodont faunas recovered.

I would like to express my appreciation to Dr. Roland Goldring, University of Reading, for his most helpful and informative correspondence regarding the stratigraphy and structure of the Barnstable area, and to Mr. S. Osborne, Departmental Photographer, University College of Swansea, for his assistance and training in the production of the photographic plates.

Finally, I would like to thank my wife, Sandra, for her patience and typing skill which has made possible the production of this thesis.

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CHAPTER I

GENERAL INTRODUCTION

Although the biological affinity and function of conodonts are problems yet to be solved, there can be no argument as to the usefulness of this group of organisms in stratigraphical correlation. In the last two decades research has shown that conodonts are probably the most sensitive group of fossils available for both local and intercontinental correlation of Palaeozoic strata. European and North American micropalaeontologists have made great strides in the recent past toward the provision of a more precise zonation of the Devonian and Carboniferous type sections of their respective countries. The result has been that the conodont assemblage zones erected for rocks of this age are more refined and accurate than those established on the basis of any other fossil group.

The fact that conodonts are apparently not greatly affected by variation in facies, has allowed close correlation between the two distinct facies, the Kohlenkalk and the Kulm, found in the Upper Devonian and Dinantian of Western Europe.

The purpose of the present study is to describe conodont faunas of the Upper Devonian and Lowest Carboniferous of the North Devon area, as represented by the Upper Baggy and the Pilton Beds. A total of 209 horizons have been sampled and processed, yielding 4,296 identifiable conodont specimens.

On the basis of the conodont faunas, three Assemblage Zones have been erected for the Upper Baggy and the Pilton Beds. These Zones were established in the Croyde Bay and Fremington sections, and may or may not have local application. The more general aspect of the total fauna recovered is consistent with faunas of Upper Devonian and Lower Carboniferous age from areas in both Europe and North America.

The geological setting of the area investigated is discussed in greater detail in the succeeding chapter, (Chapter 3), which also introduces the palaeogeography of the North Devon region as a whole. The outcrops from which the bulk of the conodont faunas were obtained have been relatively highly deformed, and this has resulted in low grade metamorphism of many of the original sediments. High angled cleavage is a common feature in the slates, which are the dominant lithological type. A good working knowledge of the structural complications is essential for the accurate location of any horizon sampled within the total Baggy and Pilton succession.

The productive horizons, in terms of conodont faunas, are the lenticular, fossiliferous limestone bands which occur irregularly throughout the succession. Stratigraphically they are more abundant in the Lower Pilton Beds, and within this subdivision they are most common in the lowest 500 feet. The limestone bands are often totally or partly decalcified and their lateral occurrence is limited in all directions owing to their lenticular nature. Conodonts were not recovered from any of the lithologies represented in the Upper Baggy and the Pilton Beds, other than the fossiliferous limestone lenses. Many months and many methods of preparation (see Chapter 4) were unsuccessfully employed in an attempt to retrieve conodonts from the slate and sandstone rocks with which the limestones were associated.

Conodont specimens referable to thirteen genera have been identified from the material collected, four of which were of the platform type. The state of preservation was, in general, only fair, and in terms of numbers the fauna from individual horizons varied enormously. Of the 209 horizons sampled, only 37 yielded useful conodont faunas. Owing to the spasmodic occurrence of the productive limestone bands, the conodont record displays more continuity in some parts of the succession than in others.

The fauna of the Upper Baggy and Lower Pilton Beds is interpreted as being of uppermost Devonian age (toVI). *Spathognathodus aculeatus*, *S. bischoffi* and *S. zeigleri* are represented together with an abundant *Pseudopolygnathus dentilineata* population. The genus *Palmatolepis* is absent from all the samples examined, but, despite the fact that *S. costatus ultimus* is also unrepresented, the fauna is interpreted as being of 'upper costatus' zone age. In the upper part of the Lower Pilton Beds polygnathids of Lower Carboniferous aspect occur with the diagnostic Upper Devonian forms, which tends to substantiate the tenet that this fauna is youngest Devonian.

The faunas recovered from the Upper Pilton Beds are small by comparison with those of the underlying Pilton strata. They are smaller both in the total number of productive samples located, and in number of conodont specimens recovered. No diagnostic forms are present in these Upper Pilton beds, the fauna having few elements that are not present in the upper portion of the Lower Pilton Beds. Important differences between this fauna and that of the underlying Pilton division are the absence of spathognathodids (except for one rather dubious, incomplete specimen); the dominance of polygnathids (of the same type which are first seen in the upper portion of the Lower Pilton Beds) as the only platform elements; and the occurrence of a single specimen of *Polygnathus pura pura*. No definitive conclusions can be made regarding the precise age of the Upper Pilton Beds, but the absence of typical Devonian forms and the presence of conodonts more commonly associated with diagnostic Avonian elements, suggests a Lower Carboniferous age.

CHAPTER 2

HISTORICAL REVIEW OF PREVIOUS RESEARCH

SECTION A - CONODONT RESEARCH AND APPLICATION OF UPPER DEVONIAN AND LOWER CARBONIFEROUS CONODONT ZONATION IN THE BRITISH ISLES.

Although conodonts were reported from several localities in Britain soon after they were first described by Pander (1856), little attention was paid to them at this time. As with other countries of the world, the past 30 or 40 years has proved to be the most productive in terms of conodont research. The lowest stratigraphic occurrence of conodonts in Britain are 'paraconodonts' from the Cambrian Comley Limestone of Shropshire. This occurrence was noted by Walliser (1958).

Conodonts have been recorded from various horizons in the Ordovician of Britain, including the Lower Arenig cherts and shales of the Southern Uplands (Smith 1907: Lamont & Lindström 1957), the Lower Llandeilian, Llandeilo Limestone of the Llandeilo district (Rhodes 1953), the Upper Llandeilian and Basal Caradocian chert and shales in the Southern Uplands (Smith 1907: Lamont & Lindström 1957), the Middle Caradocian (Climacograptus wilsoni) shale of Southern Scotland (Lindström 1957), the middle and upper Caradocian Gelligrin and Pen-y-garnedd Limestones of North Wales (Rhodes 1953), the middle Upper Caradocian (Dicranograptus elingani) Crûg Limestone of Wales (Lindström 1959) and the Ashgillian Keisley Limestone of Westmorland (Rhodes 1955).

Conodonts from the Silurian of Britain have been described by several workers, and include faunas from the Pentamerus Beds of Shropshire (Whittard 1927), the Upper Silurian Bone Beds of Allenheads (Moore 1864), the Upper Silurian of Wrens Nest, Dudley Tunnel, Staffordshire and Benthall Edge etc. of Shropshire (Smith & Jones 1881), the Ludlow Bone Bed (Harley 1861), the Aymestry Limestone (Rhodes 1953: Rhodes & Newall 1963), and the Ludlovian of Shropshire and Herefordshire (Ireland 1958). Conodont faunas have also been described from a conglomeratic limestone in the Llandovery of the Malvern Hills (Brooks & Druce 1965), and from the Wenlock Limestone of the Usk Inlier (Austin & Bassett1967).

Little published research has appeared on the occurrence and distribution of conodonts in the Devonian rocks of Great Britain. Rhodes and Dineley (1957a, 1957b) reported the presence of conodonts in this system from localities in both North and South Devonshire. The publications produced by these authors were brief and intended essentially as survey reports indicating that conodont faunas could be recovered from many outcrops within the Devonian of south-west England. Conodonts from the Baggy and Pilton Beds were mentioned in a paper by Austin, Druce, Rhodes & Williams (1970). This work was an examination of the usefulness and value of conodonts in the recognition of the Devonian - Carboniferous boundary.

The present study is the first major work on the application of conodont zonation to the Upper Devonian rocks of Great Britain, but much, as yet unpublished, research into the Middle and Upper Devonian conodont faunas of South Devon is in progress.

Until the past decade, the Carboniferous Limestone of Britain had only slightly more attention, with regard to conodont zonation and general conodont research, than had the Devonian system. Moore (1863 & 1870) investigated the Carboniferous Limestone of Yorkshire and Cumberland, and Fowler (1955) worked in County Tyrone, Eire. Robbie (1955) also worked in the Lower Carboniferous rocks of County Tyrone and Rhodes and Dineley (1957a) reported the presence of conodonts in the Tournasian rocks of the Avon Gorge. In 1965, Austin completed a Ph.D. thesis on the conodonts of the Avon Gorge, Bristol. He recognised 13 conodont assemblage zones in the Carboniferous Limestone which outcrops in the Gorge. The overall conodont faunal sequence correlated favourably with that of the type sections of the Lower Carboniferous in North America and Europe, and this work marked the first major application of Lower Carboniferous conodont zonation in the British Isles. Rhodes, Austin & Druce (1969), re-examined the conodonts of the Avon Gorge and several other outcrops of Lower Carboniferous rocks in Britain, presenting their findings in a vitally important publication of the British Museum of Natural History. Conodont faunas recovered from Carboniferous outcrops in North East Devon, East Cornwall and South Devon have been described by Matthews and Thomas (1968), and Matthews (1969a, 1969b) respectively.

Austin (1968) has described the conodont faunas from two localities in Ireland in which Carboniferous Limestone rocks outcrop, namely, the Waulsortian Reef Limestone at Askeaton and from the Cork Red Marble at Midleton.

The Namurian rocks of Britain have yielded conodonts at various horizons as evidenced by the work of Fowler (1944) in the Cleveland Hills, Dunham and Stubblefield (1945) on the Millstone Grit of Yorkshire, Stevenson and Mitchell (1955) on the Millstone Grit of the Midlands, and Higgins (1961) on the Namurian of North Staffordshire. The latter work was completed as a doctoral thesis and contains systematic descriptions of the genera and species of conodonts characterising the Namurian of this area.

Austin (personal communication) is at present involved in work on conodonts of Namurian age, and the present author, with the assistance of Mr. G.T. George, has recovered conodonts of EI age from the Namurian of Pembrokeshire.

There are no systematic descriptions of post-Namurian conodonts from Great Britain, although their presence has been recorded in the Coal Measures. The following authors have noted the occurrence of conodonts in the Coal Measures of various regions of Britain: Currie, Duncan & Muir Wood (1937) in the Coal Measures of Central and West Scotland, Mitchell, Stubblefield and Crookall (1942 & 1945) in the Warwickshire and northern South Staffordshire Coal Field, Edwards & Stubblefield (1948) in the Derbyshire and Nottinghamshire Coal Field, Ramsbottom (1952) and Woodland, Archer, Evans & Calver (1957) in the South Wales Coal Field, Edwards (1954) in the Derbyshire and Nottinghamshire Coal Field, Mitchell (1954), Eden (1954), Stevenson and Mitchell (1955) and Stubblefield and Calver (1955) in the Midlands Coal Field, Earp and Magraw (1955) in the Lancashire Coal Field, Manson (1957) in the Anthraconaia modiolaris Zone in Scotland and Magraw (1957) in the Lancashire, Derbyshire and Yorkshire Coal Fields.

There are no references to post-Coal Measure conodonts in Britain.

Figure I indicates the conodont assemblage zones established by Rhodes, Austin & Druce (1969) for the British Avonian, using the Avon Gorge and North Crop of the South Wales Coal Field successions as their type sections. The table further shows the relationship of these conodont zones to the coral-brachiopod divisions of Vaughan (1905) and to the goniatite zones of Europe.

FIGURE 1

CONODONT ZONATION OF THE BRITISH AVONIAN, SHOWING THE RELATIONSHIP OF THE ZONES TO THE CORAL/BRACHIOPOD DIVISIONS OF VAUGHAN (1905), AND TO THE GONIATITE ZONES OF EUROPE (after Rhodes, Austin & Druce fig 12, 1969)

EUROPEAN ZONES		AVONIAN CONODONT ZONES	CORAL BRACHIOPOD ZONES
E1		Gnathodus girtyi collinsoni	
CuIIIγ			D$_3$
CuIIIβ		Gnathodus mononodosus	
CuIIIα		Mestognathus beckmanni—Gnathodus bilineatus	D$_2$
		Apatognathus geminus—Cavusgnathus	D$_1$
CuIIδ		Taphrognathus varians—Cavusgnathus—Apatognathus	S$_2$
		Cavusgnathus unicornis—Apatognathus	C$_2$S$_1$
		No conodonts	
		Mestognathus beckmanni—Polygnathus bischoffi	C$_1$
CuIIβ-γ		Gnathodus antetexanus—Polygnathus lacinatus	
		Polygnathus lacinatus Pseudopolygnathus cf. P longiposticus	Z
		Polygnathus lacinatus	
CuIIα		Spathognathodus costatus costatus—Gnathodus delicatus	K
	?	Spathognathodus cf. S. robustus—S. tridentatus	
		Siphonodella—Polygnathus inornatus	
CuI		Patrognathus variabilis—Spathognathodus plumulus	

SECTION B - PREVIOUS STUDIES IN THE NORTH DEVON AREA WITH PARTICULAR REFERENCE TO THE PILTON BEDS

Geological research in North Devon was initiated in 1836 when Sedgwick and Murchison produced maps and sections of the area and indicated that it constituted the northern limb of a large syncline. Weaver (1838) and Williams (1839) published short papers in the succeeding years describing and naming the rocks of the county.

In 1839, De la Beche completed a "Geological report on Cornwall, Devon and West Somerset", in which he emphasised the occurrence of two groups of shales, sandstones and calcareous rocks in North Devon. He showed the boundary between these two accumulations to run east from Fremington and through Bampton. Included in his report were excellent sketch sections across North Devon which elucidated his conclusions.

Sedgwick and Murchison (1840) described the structure and older deposits of Devonshire, referring to the Pilton Beds as the 'fifth group' of rocks of the northern region of Devon. A comprehensive description of the main Pilton Bed outcrops is included in this work. One year later, Phillips (1841) published a "Monograph of figures and Descriptions of Palaeozoic fossils from Cornwall, Devon and West Somerset". It was in this work that Phillips first introduced the name 'Pilton', and he included in the 'Pilton Group', the sandstones and slates of Woolacombe and the slates and thin limestones of Baggy Point, Croyde Bay, the Saunton foreshore and Fremington Pill. He states that this group "has yielded by far the largest proportion of the fossils of North Devon".

This timely monograph supplemented the first Geological Survey Memoir in 1846, which included in its opening chapters a report on the formation of the rocks of South Wales and South West England by De la Beche.

In this memoir, De la Beche discussed the correlation of the Pilton Group with rocks of Upper Old Red Sandstone - Lower Carboniferous age in other areas of South Wales and Southern England, including the Petherwin Beds of South Devon.

Between the years 1851 and 1865 Davidson compiled and published his work on the British Fossil Brachiopods which included a monograph of Devonian Brachiopods (Davidson 1864 - 1865).

Salter (1863) produced the next important contribution to research in this area. He noted the overall similarity between the Pembrokeshire and North Devonshire sections and looked more closely at the 'Pilton Group' of Phillips. The succession as we know it today is,

Lower Culm

Pilton Beds

Baggy Beds

Upcott Beds

Pickwell Down Sandstone

Phillips' 'Pilton Group' included within it the Upcott, Baggy and Pilton Beds. Salter subdivided Phillips' group into three, calling the two lower divisions (the Upcott & Baggy Beds of current usage) the Marwood Beds, and the upper, the upper part of the 'Pilton Group' of Phillips. Salter correlated the Marwood Beds with the Upper Old Red Sandstone and the upper part of the 'Pilton Group' of Phillips with an unknown, or very thin, accumulation of rock at the base of the Lower Limestone Shales.

In 1866 Jukes made his contribution to the explanation of the Geological structure of North Devon but added little that was not already known. Etheridge (1867) and Hall (1867) produced geological sketch maps in their respective publications. Within the Pilton Beds as we know them today, the former worker recognised three separate rock units (a) the Croydon Beds, (b) the Braunton and

Pilton Beds and (c) the Barnstable Beds, in ascending order. Etheridge also presented a well documented summary of previous work and included many faunal lists and correlation charts for rocks of Devonian and Lower Carboniferous age in Great Britain and parts of Europe. Hall's map is very close to those of the present day with regard to the Pilton Beds, and he also included detailed faunal lists from the strata of Upper Devonian age in the north of the county.

Hull (1878) agreed with Jukes that the Upper Baggy Beds and Pilton Beds were equivalent to the Lower Carboniferous Slate and the Coomhola Grits of Southern Ireland. He contributed a table of correlation between North Devon and Southern Ireland.

Ussher and Champerknowne (1879) published a series of north-south geological sections across the western part of Somerset, showing the relationship and inland occurrence of the various rock divisions of North Devon. It was these authors that were responsible for the initiation of the name 'Baggy Beds'.

In 1880, Hull, continuing his work in the area, proposed the name Upcott Beds for the slates between the Pickwell Down Sandstone and the Baggy Beds, but this division was not recognised by his contemporaries. Salter (1863) had regarded these slates as a separate unit but called them the Lower Marwood Beds.

Ussher (1881) summarised the controversy which had developed over the North Devon sequence. There were two schools of thought; the first, upheld by Sedgwick and Murchison, was that there was a conformable descending series from the Culm through the Devonian and that the Devonian marine deposits were equivalent to the Old Red Sandstone. Other followers of this theory were Etheridge, Phillips and Hall. The alternative interpretation, proposed by Jukes and partially upheld by Hull, was that the Lower Culm and Devonian of Devonshire were partly correlative with the Carboniferous Slate of Southern Ireland and partly with the Old Red Sandstone, and that the North Devon section was repeated by a huge East-West fault.

Ussher favoured the first theory and gave his own stratigraphic table for North Devon. In this table he placed the Pickwell Down Sandstone, the Baggy and the Pilton Beds as three sub-divisions of the Upper Devonian.

Hicks (1896a, 1896b) described the lithology and fauna of the North Devon deposits, publishing Whidbourne's preliminary faunal list for the Baggy and Pilton Beds. Between the years 1896 - 1907, Whidbourne wrote his monograph on the Devonian fauna of South-East England. This two volume work was of great geological value.

Ussher (1900) subsequently presented more detailed maps and endorsed his rejection of Hull's term, Upcott Beds, and Woodward (1902) produced a paper on a collection of trilobites from the Lower Culm of Devonshire.

In 1910 Hambling and Rogers conducted an excursion to North Devon, the proceedings of which were published in a short paper which was accompanied by a fine geological map of the region. These two authors, like Ussher, failed to recognise the Upcott Beds of Hull as a distinct unit, and on their map included them in the Pickwell Down Sandstone. In this same year Dewey described some of the igneous rocks to be found in the North Devon area.

Arber and Goode (1916) described the flora of the Baggy Beds, and Evans (1922) published his interpretation of the geology of North Devon. This coincided almost entirely with the interpretation of Etheridge (1867), even to the extent that Evans reproduced Etheridge's map. Evans did suggest one amendment, however, in substituting the names Lower, Middle and Upper Pilton Beds for Etheridge's terms, Croydon, Braunton & Pilton, and Barnstable Beds respectively.

Shannon (1928) provided a comprehensive petrographic analysis of the more abundant Devonian sediments to be found in Devonshire, including the sandstones and slates of the Pilton and Baggy Beds.

Reed (1943) and (1944) re-examined the Upper Devonian brachiopods and trilobites collected by Whidbourne.

In the past there has been much controversy over the precise position and age of the Pilton Beds within the Devonian and Carboniferous systems. As a result of this it has been difficult to correlate these rocks with other areas of Great Britain and Europe. A detailed discussion of the correlation of these beds can be found in Chapter 7. For the present it will surfice to say that many authors have attempted to evaluate the precise age of the Pilton Beds, and Goldring (1955, 1956) has undoubtedly been the most successful. On the basis of diagnostic brachiopod, trilobite and cephalopod species, Goldring recognised the existence of three local faunal divisions in the Pilton Beds. The youngest fauna is of Lower Carboniferous age, and the two older faunas are of Uppermost Devonian age. Furthermore, Goldring agreed with Hull that the Upcott Beds should be recognised as a separate rock group.

Prentice (1960) studies the Dinantian, Namurian and Lower Westphalian rocks south-west of Barnstable. He recognised a fourth local division of the Pilton Beds (Pilton Beds D) immediately above the youngest faunal division of Goldring and below the Chert Beds (Codden Hill Cherts).

Today, the generally accepted succession for the rocks in stratigraphical proximity to the Pilton Beds is as follows:-

After Goldring (1956) and Prentice (1960)

Lower Carboniferous	Lower Culm (Chert Beds)	D		
	Pilton Beds	C		Upper Pilton Beds
		B		
		A	3	
	Baggy Beds		2	
Upper Devonian			1	Lower Pilton Beds
	Upcott Beds			
	Pickwell Down Sandstone			

SECTION C - CEPHALOPOD ZONATION OF ROCKS OF EQUIVALENT AGE TO THE PILTON BEDS

At the First International Congress of Carboniferous Stratigraphy at Heerlen in 1927, it was agreed that cephalopods should have priority among index fossils in zoning the Upper Devonian and Lower Carboniferous. Cephalopods possessed all the necessary requirements for subdivision and correlation. It was agreed to place the Devonian - Carboniferous boundary above the Gonioclymenia stage.

As a result of studies conducted by Packelmann and Schindewolf, it was proposed that the boundary between the Wocklumeria and Gattendorfia stages be taken as the lower limit of the Carboniferous. This proposal was accepted internationally at the Second Congress of Carboniferous Stratigraphy at Heerlen in 1935. Figure 2 shows the present standard stages and cephalopod zones used in the subdivision of Upper Devonian and Lower Carboniferous rocks in western Europe. Since 1935 it has been found that more accurate and detailed subdivision can be accomplished by using other fossil groups, in particular conodonts, foraminifera and spores. The relationships between the conodont zones and the classic Upper Devonian and Lower Carboniferous cephalopod zones will be discussed in sections D & E.

Since the turn of the century it has been generally accepted that the Pilton Beds were a transition group between the Devonian and Carboniferous. Goldring (1956), confirmed the age of these beds, indicating that the Lower Pilton Beds were of Wocklumeria age and the Upper of Gattendorfia age. In the Fremington Pill section Goldring recovered a species of the genus Gattendorfia, and, although he recovered no representatives of the genus Wocklumeria in the Lower Pilton Beds, the trilobite and brachiopod fauna of this portion of the Pilton Beds indicated a Wocklumeria age. The conodont fauna of the Pilton Beds serves to endorse Goldring's general conclusions.

Eight samples of hard grey slate from various horizons in the Croyde Bay

FIGURE 2

UPPER DEVONIAN AND LOWER CARBONIFEROUS STANDARD STAGES AND CEPHALOPOD ZONES OF WESTERN EUROPE

(adapted from Collinson Scott & Rexroad 1962)

STAGES	ZONES					
VISEAN	cuII	β/γ	PERICYCLUS			
TOURNASIAN		α				
	cuI		GATTENDORFIA	γ β α	TnIb	H lepidophytus
FAMENNIAN	toVI		WOCKLUMERIA	γ β α	TnIa	
	toV		CLYMENIA			
	toIV		PRIONOCERAS			
	toIII		PROLOBITES			
	toII		CHEILOCERAS			
FRASNIAN	toI γ-δ		MANTICOCERAS			

section, (which Goldring interprets as Lower Pilton age) were sent to the University of Liège, Belgium, for the attention of the palynologist Professor M. Streel. Professor Streel, (personal communication) isolated specimens of the spore Hymenozonotriletes lepidophytus from three of these samples. This species exists in Belgium in strata of Tnlaαβ, Tnlaγ and Tnlbα age, confirming the fact that the Lower Pilton Beds generally can be equated with the late Devonian, Wocklumeria Cephalopod Stufe.

SECTION Da - UPPER DEVONIAN AND LOWER CARBONIFEROUS CONODONT ZONES OF WESTERN EUROPE

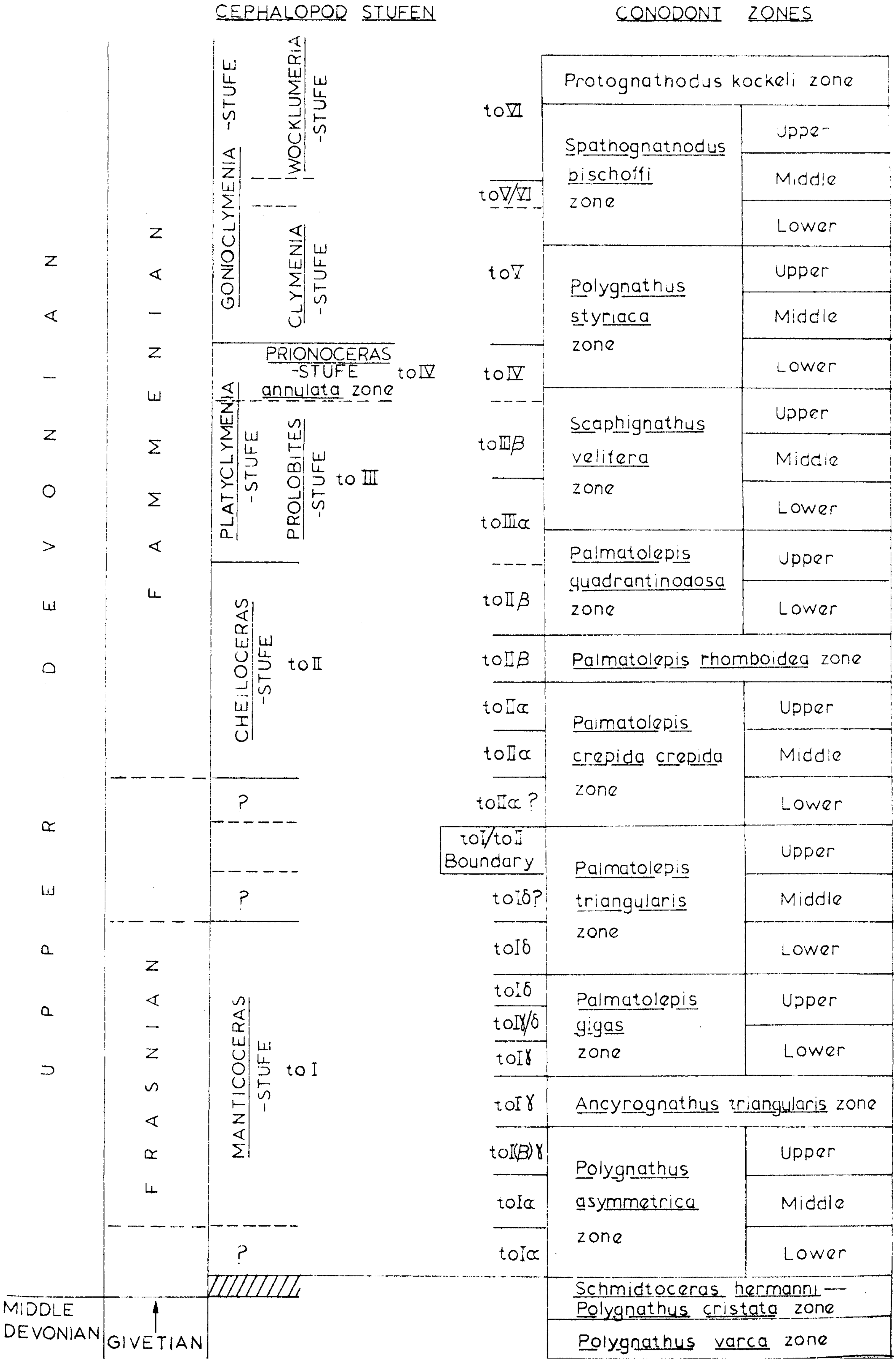
During the late 1950's and the early 1960's, three important works were published on this topic. Bischoff (1957) described the conodont stratigraphy of the rhenoherzynischen Lower Carboniferous, *Wocklumeria* - Stufe, and Devonian - Carboniferous boundary, Voges (1959) described the conodonts of the *Gattendorfia* and *Pericyclus* Stufen of Saurlandes, and Ziegler (1962) described the Upper Devonian conodonts of Germany. These studies prompted other workers to examine the conodonts of this time interval in other regions of Europe, but in many European countries it was difficult or impossible to locate complete sections ranging from Devonian into Carboniferous. Germany, for example, has no section where the Upper Devonian *Wocklumeria* Limestone is overlain directly by rocks of *Gattendorfia* age.

Figure 3 shows the conodont zones of the Upper Devonian of Germany after Ziegler (1962), as compared with the cephalopod zones. Conodont zonation affords far more detailed subdivision of the Frasnian and Fammenian strata. Ziegler recognised 10 Upper Devonian conodont assemblage zones, 8 of which could be further subdivided into upper and lower, or upper, middle and lower sub-zones. In all cases the upper and lower limits of the 10 zones correspond with the range of the particular conodont which gives its name to the zone, and consequently each zone is very well defined.

The oldest Upper Devonian zone (tolα - tol(β)γ) corresponds to the total stratigraphic range of *Polygnathus asymmetrica*, from which species it derives its name. Three sub-zones can be recognised on the absence or presence of *P. asymmetrica asymmetrica*, *P. martenburgensis* and *Ancyrodella rotundiloba*. This zone is equivalent to the lower *Manticoceras* Cephalopod Stufe. It was previously known as *P. dubia* zone.

FIGURE 3

CEPHALOPOD & CONODONT ZONATION OF THE UPPER DEVONIAN OF GERMANY (based on Ziegler 1962 with modern amendments)



The *Ancyrognathus triangularis* is limited by the range of this species, and is of toIγ age. No sub-zones are recognised and this zone is correlated with the middle part of the *Manticoceras* Stufe.

The *Palmatolepis gigas* Zone corresponds to the range of the species which gives its name to the zone, and is of toIγ to toδ age. It can be divided into Upper and Lower Subzones on the presence of *Ancyrognathus asymmetrica* and *Palmatolepis foliacea* respectively. This zone is equated with the Upper *Manticoceras* Stufe, and was previously called the *Palmatolepis rhenana* Zone.

The range of *Palmatolepis triangularis* defines the Zone to which this species gives its name. It can be subdivided into three subzones on the basis of the presence or absence of the following associated species, *P. marginata marginata*, *P. marginata clarki*, and *P. tenuipunctata*. Within this Zone occurs the boundary between toI and toII, and although it is not proven, this Zone is thought to range from toIδ to the base of toII in age. It is thus correlated with the uppermost *Manticoceras* Stufe and possibly the lowermost *Cheiloceras* Stufe.

The *Palmatolepis crepida crepida* Zone takes its name from the species whose range defines its limits, and is of toII$^{\alpha}$ age. The Zone can be subdivided into Upper, Middle and Lower Subzones on the occurrence or absence of *P. glabra glabra*, and *P. termini*, and is equivalent to the Lower *Cheiloceras* Cephalopod Stufe.

The *Palmatolepis rhomboidea* Zone is limited by the range of occurrence of this species, and has no subzones. It is correlated with the Middle *Cheiloceras* Stufe, of toIIβ age.

The *Palmatolepis quadrantinodosa* Zone (toIIβ to toIII$^{\alpha}$) is defined on the life range of this species, and subdivided into two subzones on the presence or absence of *P. quadrantinodosa inflexa*. It is correlated with the Upper *Cheiloceras* - Lower *Prolobites* Stufe.

The life span of *Scaphignathus velifera* delimits the Zone to which it gives its name, and is equivalent to the *Prolobites* and Lower *Prionoceras* Stufe, (toIIIα to lower toIV). Three Subzones can be recognised on the occurrence or absence of *Pseudopolygnathus granulosa* and *Palmatolepis rugosa trachytera*.

The *Polygnathus styriaca* Zone corresponds with the range of this species, and is of Upper to IV to Upper Middle toV age, being correlated with the upper *Prinoceras* and *Clymenia* Stufen. This Zone has three Subzones based on the presence or absence of four other conodont species. The lower Subzone is limited by the presence of *Polygnathus styriaca* and *Pseudopolygnathus granulosa*. The middle Subzone is recognised by the presence of *P. styriaca*, after the extinction of *Pseudopolygnathus granulosa* and before the introduction of *Spathognathodus jugosus*. The upper Subzone is defined on the presence of *P. styriaca* and *Pseudopolygnathus brevipennata*, *Pseudopolygnathus dentilineata* and *Spathognathodus jugosus*.

The youngest Upper Devonian Zone of Ziegler is the *Spathognathodus bischoffi* Zone, which corresponds to the life span of this species. This species was until recently called *Spathognathodus costatus costatus*, but has been renamed *Spathognathodus bischoffi* Rhodes, Austin & Druce 1969, to overcome the confusion encompassing this spathognathodid group in terms of homeomorphy, (see discussion of *Spathognathodus costatus* p.213). Three Subzones are recognised within this Zone, and they are defined on the presence or absence of *S. costatus ultimus* and *Palmatolepis gonioclymeniae*. The Zone is correlated with the Upper *Clymenia* and *Wocklumeria* Stufen, Upper toV to toVI.

Ziegler (1962) noted that the upper boundary of the Upper *Spathognathodus* bischoffi Zone was only ascertained indirectly, because the Hangenberg Shale directly overlies the uppermost sample of the Upper *S. bischoffi* Subzone, from which he had recovered no conodonts. Recent discoveries indicate that at least the lower part of this shale should be included in the S. bischoffi Zone. In 1969 Ziegler recognised and recorded a new Zone within the Hangenberg Shale. The Zone is called the Protognathodus kockeli Zone, based on Gnathodus kockeli, and it directly overlies the S. bischoffi Zone and lies immediately below the Carboniferous.

Bischoff (1957) described the conodont stratigraphy of the rhenoherzynischen Lower Carboniferous with regard to the Wocklumeria Stage and the Devonian - Carboniferous boundary. He investigated the occurrence of conodonts in the Wocklumeria - Gattendorfia - Pericyclus and Goniatites Stages, setting up Zones for these Stages where possible. He commented on the fact that if there were a section in Germany where the Gattendorfia could be found resting directly on the Wocklumeria Limestone, then Gnathodus kockeli, (whose oldest occurrence is taken as the boundary between the Devonian and Carboniferous), could possibly be found associated with Devonian forms.

In his description of the Wocklumeria - Stufe toVI, Bischoff indicated that the lower boundary was taken at the extinction of Spathognathodus tridentatus which often occurs with Spathognathodus ziegleri in the Dasburg stage. The upper boundary of this stage coincided with the upper boundary of the genus Palmatolepis, together with the youngest occurrence of S. ziegleri, S. costatus ultimus, Falcodus variabilis and Palmatodella delicatula. The fauna of the Wocklumeria Stage was distinguished by the occurrence of these two spathognathodid species and Palmatolepis gracilis, while other characteristic forms were Polygnathus communis and Pseudopolygnathus dentilineata.

The lower limit of the Gattendorfia Stage, CuI, was equated with the virtual extinction of the genus Palmatolepis and the species S. ziegleri and S. costatus ultimus. The extinction of Palmatodella delicatula, Falcodus variabilis and Spathognathodus inornatus also marked its lower limit. The genus Gnathodus (Gnathodus kockeli) first appears and becomes extinct near the upper boundary.

This species is the diagnostic conodont of this stage and other frequently occurring forms and *Pseudopolygnathus dentilineata* and *Polygnathus communis*. *Pseudopolygnathus multistriata* first appears in the *Gattendorfia* Stage.

The *Pericyclus* Stage CuII was subdivided by Bischoff into two Subzones. The Lower *Pericyclus* division was termed the *Siphonodella* Subzone, CuII$\alpha\beta$, and was characterised by the period of abundance of species of the genus *Siphonodella*. Siphonodellids were not found in the underlying *Gattendorfia* Stage, were reduced in the Upper *Pericyclus* and became extinct at the upper boundary of the Lower *Goniatites* Subzones. The lower boundary of the *Siphonodella* Subzone coincided with the first occurrence of this genus, while the upper boundary was equated with the decrease in its frequency. Other important associated forms were species of *Polygnathus* and occassional gnathodids.

The Upper Pericyclus Subzone was called the *anchoralis* - Subzone CuIIγ and was defined by the abundance of *Scaliognathus anchoralis*. Its lower boundary was equated with the marked decrease in numbers of siphonodellids and the initiation of *Scaliognathus anchoralis*, *Hindeodella segaformis* and *Gnathodus commutatus*. The upper boundary was marked by the extinction of *Scalognathus anchoralis* and *Hindeodella segaformis*. Polygnathids and gnathodids were the most important associated genera in the Subzone.

The *Goniatites* Stage CuIII was subdivided by Bischoff into three Zones, the lowermost being called the *crenistria* Zone, CuIIIα. This Zone was distinguished by the absence of *Scaliognathus anchoralis* and *Hindeodella segaformis*, (the lower boundary corresponding with the extinction of both these species), and the evolution of *Mestognathodus beckmanni* and *Hindeodella undata*. *Gnathodus bilineatus semiglaber* and *G. bilineatus bilineatus* were also found in this Zone as was *Geniculatus claviger*. No criteria were presented for the recognition of the upper boundary of this Zone. Gnathodids were still frequently found in this zone but siphonodellids and polygnathids were rare.

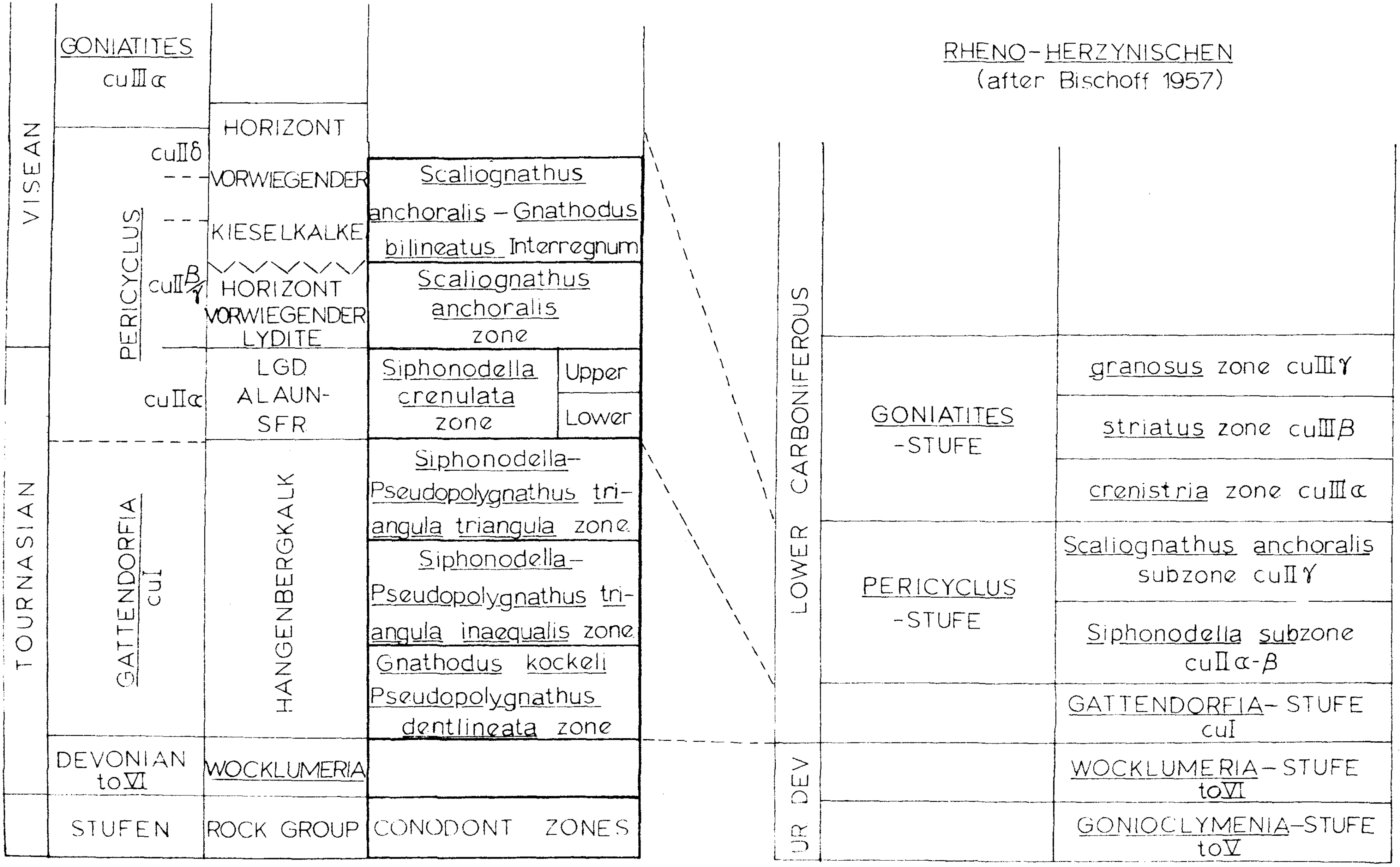
The middle Zone of the *Goniatites* Stage was called the *striatus* Zone, CuIIIβ, and was distinguished by the increasing frequency of *G. bilineatus bilineatus* and almost complete extinction of *G. bilineatus semiglaber*. The fauna was similar to that of the preceding *crenistria* Zone, but could be recognised on the relative frequency of occurrence of these two gnathodid subspecies. The former subspecies was rare and the latter frequent in the *crenistria* Zone.

The uppermost *Goniatites* Zone was termed the *granosus* Zone, CuIIIδ, and was recognised on the presence of *Gnathodus commutatus nodosus*. Further distinctive criteria were the absence of *G. bilineatus semiglaber*, the increasing frequency of *G. girtyi* and occurrence of *Ozarkodina delicatula*.

Voges (1959) described the conodonts of the *Gattendorfia* and *Pericyclus* Stufen from Sauerlandes, Western Germany. An approximate correlation between his and Bischoff's work has been included in Figure 4.

Voges' *Gattendorfia* CuI, was subdivided into three conodont zones, a lower *Gnathodus kockeli* - *Pseudopolynnathus dentilineata* Zone, a middle *Siphonodella* - *Pseudopolygnathus triangula inaequalis* Zone, and an upper *Siphonodella* - *Pseudopolygnathus triangula triangula* Zone. All three zones were found in the Hangenberg-Kalk. Voges also subdivided the Pericyclus CuII, into three conodont zones, the lower one, the *Siphonodella crenulata* Zone, corresponded to a CuIIα age, and could be further subdivided into an upper and lower portion. The middle *Pericyclus* Zone corresponded to a CuIIβ/γ age and was named the *Scaliognathus anchoralis* Zone, while the upper Zone was called the *Scaliognathus anchoralis* - *Gnathodus bilineatus* interregnum. This upper Zone is regarded as ranging in age from upper CuIIβ/γ to CuIIδ, but it does not extend to the upper limit of the *Pericyclus* Stufe, nor therefore, to upper CuIIδ age.

CORRELATION OF THE LOWER CARBONIFEROUS CONODONT AND CEPHALOPOD ZONES OF WESTERN GERMANY



SAUERLANDES
(after Voges 1959)

	STUFEN		ROCK GROUP	CONODONT ZONES	
VISEAN	GONIATITES cuIIIα				
VISEAN	PERICYCLUS	cuIIδ	HORIZONT VORWIEGENDER KIESELKALKE	Scaliognathus anchoralis – Gnathodus bilineatus Interregnum	
VISEAN	PERICYCLUS	cuIIβ/γ	HORIZONT VORWIEGENDER LYDITE	Scaliognathus anchoralis zone	
TOURNASIAN	PERICYCLUS	cuIIα	LGD ALAUN-SFR	Siphonodella crenulata zone	Upper
TOURNASIAN	PERICYCLUS	cuIIα	LGD ALAUN-SFR	Siphonodella crenulata zone	Lower
TOURNASIAN	GATTENDORFIA cuI		HANGENBERGKALK	Siphonodella–Pseudopolygnathus triangula triangula zone	
TOURNASIAN	GATTENDORFIA cuI		HANGENBERGKALK	Siphonodella–Pseudopolygnathus triangula inaequalis zone	
TOURNASIAN	GATTENDORFIA cuI		HANGENBERGKALK	Gnathodus kockeli Pseudopolygnathus dentlineata zone	
	DEVONIAN toVI		WOCKLUMERIA		

RHENO-HERZYNISCHEN
(after Bischoff 1957)

LOWER CARBONIFEROUS		
LOWER CARBONIFEROUS	GONIATITES -STUFE	granosus zone cuIIIγ
LOWER CARBONIFEROUS	GONIATITES -STUFE	striatus zone cuIIIβ
LOWER CARBONIFEROUS	GONIATITES -STUFE	crenistria zone cuIIIα
LOWER CARBONIFEROUS	PERICYCLUS -STUFE	Scaliognathus anchoralis subzone cuIIγ
LOWER CARBONIFEROUS	PERICYCLUS -STUFE	Siphonodella subzone cuIIα-β
LOWER CARBONIFEROUS		GATTENDORFIA- STUFE cuI
UR DEV		WOCKLUMERIA- STUFE toVI
UR DEV		GONIOCLYMENIA-STUFE toV

FIGURE 4

SECTION Db - APPLICATION OF UPPER DEVONIAN AND LOWER CARBONIFEROUS CONODONT ZONATION IN WESTERN EUROPE, EXCLUDING BRITAIN

The use of conodonts as biostratigraphic tools has been widely applied in western Europe in Palaeozoic rocks of all ages. A great deal of research has been directed toward zonation of the Upper Devonian and Lower Carboniferous strata which outcrop in the various countries of this region. In addition to the work of Ziegler, Bischoff and Voges, already discussed, other important descriptions of conodont faunas from rocks of Upper Devonian and Lower Carboniferous age have been provided by Helms (1959), Dvorak, Freyer & Freyer (1961), Sanneman (1955), Conil, Lys & Mauvier (1964), Muller (1962), Boogaard (1963), Bishoff & Ziegler (1956), Flugel & Ziegler (1957), Bartenstein & Bischoff (1962), Walliser (1960), Higgins, Wagner-Gentis and Wagner (1964, Ziegler (1960), Ziegler (1963), Ziegler in Kronberg, Pilger, Scherp & Ziegler (1960), Meischner (1962), Higgins (1962), Bouckaert & Ziegler (1965), Lindström and Ziegler (1965), Krebs and Ziegler (1965), Bouckaert and Thorez (1965), Klapper & Ziegler (1967), Wittekindt (1965), Helms & Wolska (1967), Boogaert (1967).

This list is by no means complete, and research continues in an effort to make the zonation of rocks of this and other ages more detailed and refined.

Figure 5 indicates the accepted Upper Devonian and Lower Carboniferous correlation between Belgium, Germany and Spain. Although conodonts play a significant role in establishing this correlation, the precise positioning of the Devonian - Carboniferous boundary is based on foraminifera and spores in Belgium and on the standard goniatite zones in Germany.

CORRELATION BETWEEN UPPER DEVONIAN AND LOWER CARBONIFEROUS ROCKS FROM THREE AREAS IN WESTERN EUROPE

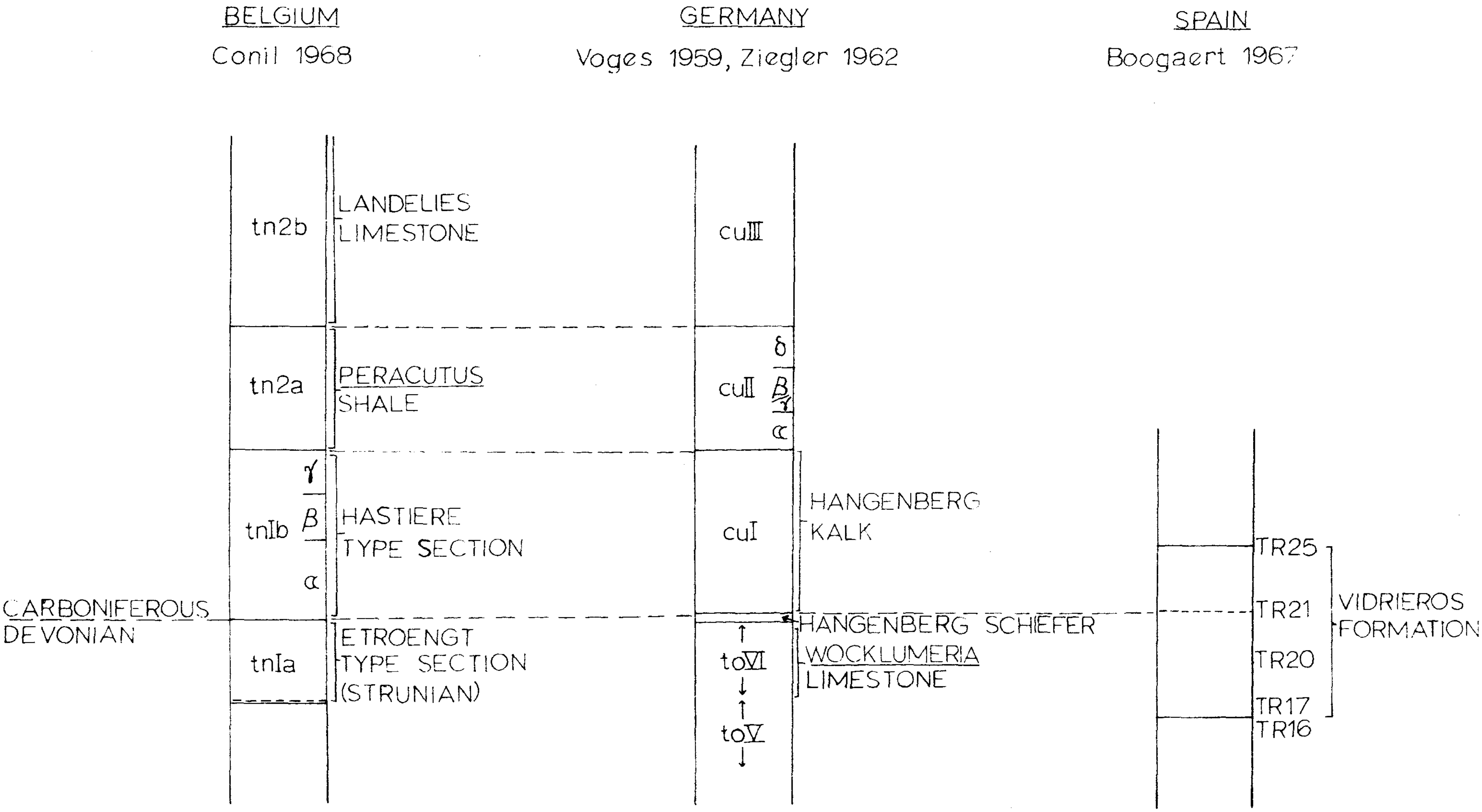


FIGURE 5

SECTION Ea - UPPER DEVONIAN AND LOWER CARBONIFEROUS CONODONT ZONES OF NORTH AMERICA

Conodont research has been intensive in the North American continent, and our present knowledge of these fossils and their occurrence is perhaps more complete in North America than in any other part of the world. In Upper Devonian and Lower Carboniferous strata, conodonts are both abundant and ubiquitous, and provide one of the most useful fossil groups for zonation of strata of this age. Collinson, Scott and Rexroad (1962) published a report summarising much of the work on the conodonts of the Upper Devonian and Mississippian of the Upper Mississippi Valley. This summary is a compilation of the original work of a number of conodont workers, and Chart 6, of the report provides an excellent summary of the zonation of the Upper Devonian and Mississippian rocks of the Mississippi Valley on the basis of conodonts. A portion of this Chart is illustrated in Figure 6 and the fifteen conodont zones, into which this portion can be divided, are briefly described. Other North American successions of a similar age, are referred to these standard Mississippian sections wherever possible in the present report.

Chart 5, from the Collinson, Scott & Rexroad publication, indicates the correlation between the standard Western European Stages and Goniatite Zones and the Mississippi Valley section, on the basis of conodonts found in rocks of Upper Devonian and Lower Carboniferous age on both sides of the Atlantic. Once again, only the portion of the original chart relevant to this thesis is illustrated (see Figure 7).

In the Mississippi Valley, the knowledge of the stratigraphic distribution of conodonts is better for the Upper Devonian and Kinderhookian, but the Valmeyeran Series can also be zoned on the basis of conodonts. In the following

UPPER DEVONIAN AND LOWER MISSISSIPPIAN CONODONT ASSEMBLAGE ZONES IN THE MISSISSIPPI VALLEY

(after Collinson Scott & Rexroad, chart 6, 1962)

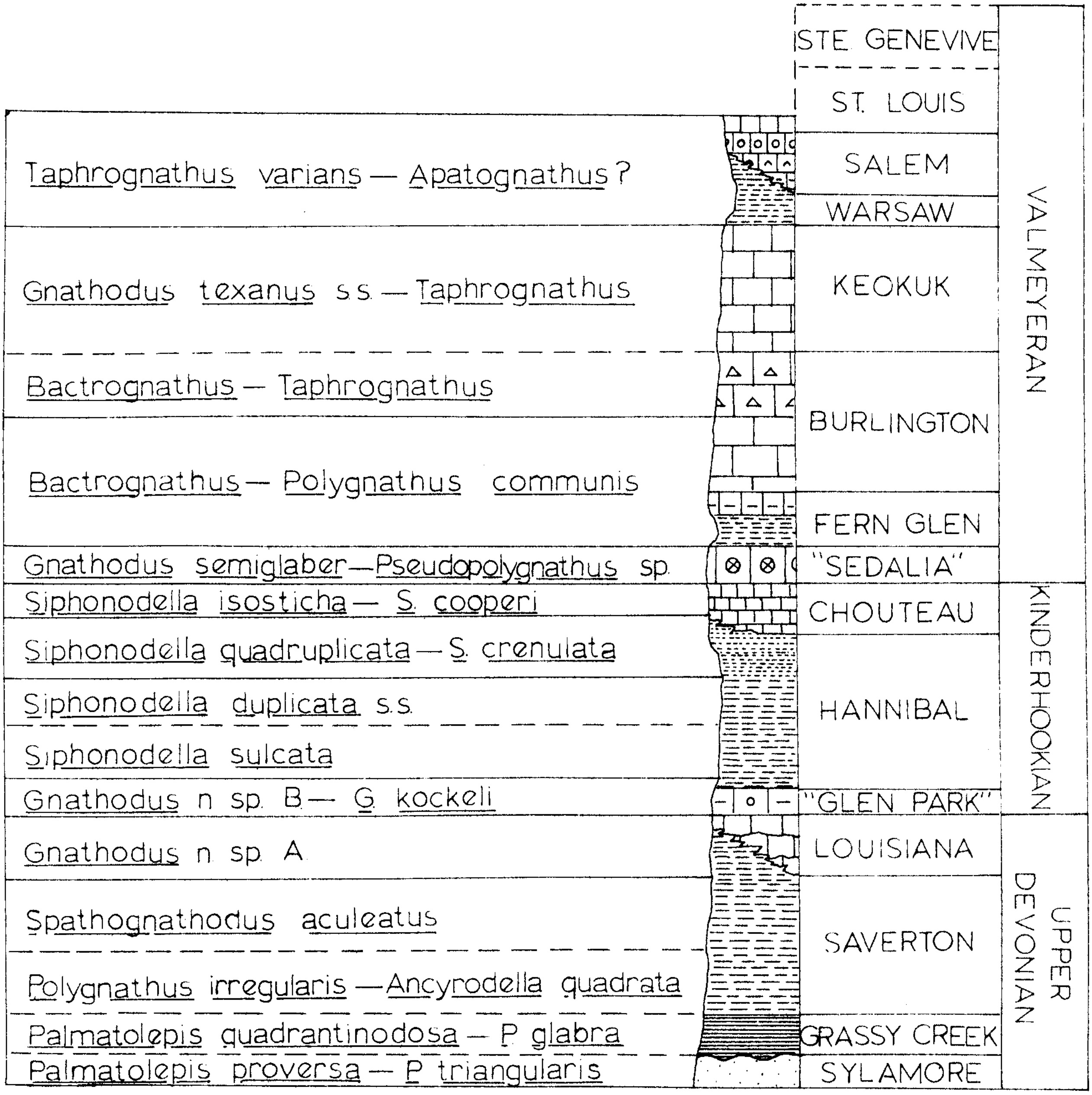
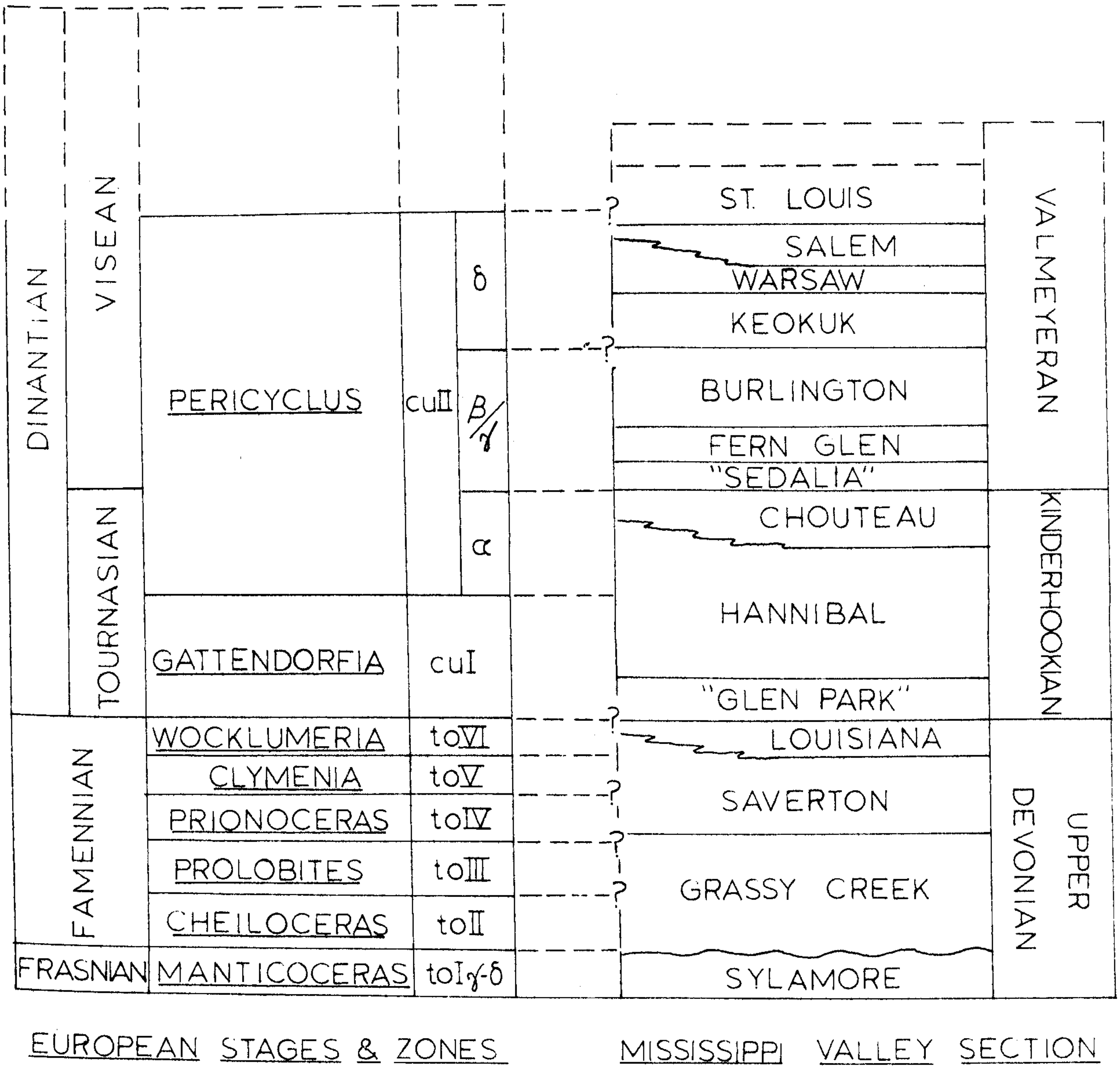


FIGURE 7

CORRELATION OF THE EUROPEAN GONIOTITE ZONES WITH UPPER DEVONIAN AND LOWER MISSISSIPPIAN SECTIONS IN THE MISSISSIPPI VALLEY (adapted from Collinson, Scott & Rexroad, chart 5 1962)



fifteen Zones, only genera or species that occur commonly to abundantly give their names to the individual Zones. In most cases the conodont that gives its name to the Zone is restricted to that Zone, but this does not apply in all instances. The Zones are described in ascending order.

In the Mississippi Valley, the oldest Upper Devonian Conodont Assemblage Zone is that of *Palmatolepis proversa* - *P. triangularis*. This Zone is apparently restricted to the Sylamore Sandstone, and is of early late Devonian age correlating with the toIβ/γ Subzones of western Europe. The limits of this Zone are the same as the ranges of the conodonts which give it its name. Other conodont species characteristic of this Zone, in addition to the zonal indices, are *Ancyrodella curvata* (Branson & Mehl), *A. lobata* Branson & Mehl, *Ancyrognathus triangularis* Youngquist, *Polygnathus foliata* Bryant, *P. normalis* Miller and Youngquist, and *Nothognathella bucristata* Youngquist and Miller. The lower limits of this Zone may be found in older rocks than shown in Figure 6.

The *Palmatolepis quadrantinodosa* - *P. glabra* Assemblage Zone is confined to the Grassy Creek Formation. The limits of this Zone may not be precise as few conodonts have been recovered in this Formation. It is correlated with the toIδ to toIIIα Zones of western Europe. Characteristic species are *Palmatolepis perlobata* Ulrich & Bassler, *P. rhomboidea* Sannemann, *P. minuta* Branson & Mehl and the conodonts which give their name to the Zone. The zonal limits correspond to the range limits of *Palmatolepis quadrantinodosa* and *P. glabra*. The species of this Zone are commonly found reworked in younger rocks.

The Saverton Formation can be divided into three conodont Zones, the oldest being the *Polygnathus irregularis* - "*Ancyrognathus*" *quadrata* Assemblage Zone. This Zone may also extend down into the upper part of the Grassy Creek Formation in certain sections in the Mississippi Valley, but the upper limit of the Zone is well defined. The Zone as a whole is limited by the range of the species which gives the Zone its name, and the other characteristic species are Palmatolepis rugosa Branson and Mehl and Spathognathodus jugosus (Branson & Mehl). These species are found in rocks of toIV and toV age in western Europe.

The middle portion of the Saverton Fromation is characterised by the Spathognathodus aculeatus Assemblage Zone, which is one of the most widespread and easily defined Zones in the Mississippi Valley. Its limits are delineated by the range of Spathognathodus aculeatus. Other characteristic species are Polygnathus triangularis (Branson & Mehl) and P. longipostica E. R. Branson. This Zone exhibits a great number of reworked specimens, but it can be correlated approximately with the uppermost toV to lowermost toVI Zones of western Europe.

The Gnathodus n.sp.A Assemblage Zone coincides with the upper part of the Saverton Formation, and its lateral equivalent, the Louisiana Formation. The upper boundary of this Zone is taken at the uppermost occurrence of abundant Apatognathus varians and representatives of the genus Palmatolepis, while the lower boundary is marked by the lowest occurrence of Gnathodus Spathognathodus anteposicornis Scott and S. collinsoni Scott. The last two species are restricted to the Zone. Other characteristic species are Spathognathodus culminidirectus Scott, Gnathodus kockeli Bischoff, and Polygnathus communis Branson & Mehl. This Assemblage Zone contains a transitional fauna between Devonian and Carboniferous, and is complicated by the presence of many reworked specimens; it is correlated with the upper toVI Zone of western Europe.

The lowest beds of the Hannibal Formation and the underlying "Glen Park" Formation as a whole, contain a fauna referred to as the Gnathodus n.sp.B-G. kockeli Assemblage Zone. It is a distinctive fauna which correlates with the lowest part of the Gattendorfia CuI Zone of Europe. The lower boundary is marked by the earliest occurrence of Gnathodus n.sp.B and the genus

Pseudopolygnathus, while the upper limit is marked by the earliest occurrence of *Siphonodella sulcata* (Huddle). The upper limit of *Gnathodus kockeli* occurs just above the upper limit of this Zone. In addition to the two gnathodid species above, other characteristic species are *Polygnathus communis* Branson and Mehl, *Polygnathus longipostica* E. R. Branson, *Spathognathodus costatus* (E.R.Branson), *Pseudopolygnathus dentilineata* E. R. Branson, and *Gnathodus* n.sp.A. This Zone represents the upper half of the general Zone of transition between Devonian and Carboniferous faunas. In some sections in the Mississippi Valley the Zone is absent.

When the previous Zone is not represented in the Mississippi Valley sections, the *Siphonodella sulcata* Assemblage Zone is the oldest Mississippian found. This Zone is confined to the Hannibal Formation and is correlated with the middle CuI Zone of Europe; it is limited by the abundant range of the conodont which lends the Zone its name. Furthermore, the upper boundary is also the lowest occurrence of abundant *Siphonodella duplicata* s.s. (Branson & Mehl). Other characteristic species include *Pseudopolygnathus prima* Branson & Mehl, *P. dentilineata* E. R. Branson, *Elictognathus* sp., *Gnathodus kockeli*, *Gnathodus* n.sp.A, *Gnathodus* n.sp.B. The conodonts of this Zone are similar to those of the underlying Zone, but can be distinguished by the presence of *P. prima* and *Elictognathus lacerata* Branson and Mehl.

The *Siphonodella duplicata* s.s. Assemblage Zone is located in the middle part of the Hannibal Formation, and is correlated with the upper CuI Zone, and possibly the lowermost CuII Zone, of western Europe. Its limits correspond to the limits of abundance of *Siphonodella duplicata* s.s. (Branson & Mehl). The upper part of the Zone exhibits abundant specimens of *Siphonodella crenulata*, and other characteristic species are *Pseudopolygnathus dentilineata* and *P. prima*.

The top of the Hannibal and Lower Chouteau Formations are characterised by the widespread and easily identifiable, *Siphonodella quadruplicata* - *S. crenulata* Assemblage Zone. This Zone probably corresponds to the lower part of the CuIIα Zone of western Europe. The upper limit is marked by the uppermost abundance of specimens of *Siphonodella crenulata* and *S. quadruplicata*, while the lower limit is marked by the lowermost common occurrence of the latter species, and the uppermost abundant occurrence of *S. duplicata* s.s. Other typical species are *Siphonodella* aff. S. *obsoleta* Hass, *S. sexplicata* (Branson & Mehl), and *S. lobata* Branson & Mehl, as well as a large number of gnathodids.

The upper part of the Chouteau Formation is represented by the *Siphonodella* n.sp.A- *S. cooperi* Assemblege Zone, which is correlated with the upper part of the CuIIα Zone of western Europe. This Zone is limited by the range of common occurrence of *Siphonodella* n.sp.A and the abundant occurrence of *S. cooperi*. The upper limit also corresponds with that of abundant *Gnathodus delicatus*. Other characteristic species are *S.* aff. *S. obsoleta*, *Polygnathus communis* Branson & Mehl, *P. inornata* E.R.Branson, *Spathognathodus curvatus* (Branson & Mehl) and *Elictognathus lacerata* (Branson & Mehl). The upper limit of this Zone corresponds with a major unconformity in the Mississippi Valley.

The *Gnathodus semiglaber* - *Pseudopolygnathus multistriata* Assemblage Zone coincides with the "Sedalia" Formation of the Mississippi Valley, and is correlated with the lowest part of the CuIIβ Zone of western Europe. The Zone corresponds with the range of abundant *Gnathodus semiglaber*, *Gnathodus* n.sp. cf. *G. girtyi* and *Pseudopolygnathus multistriata*. Additional characteristic species are *Neoprionidus oligus* (Cooper) and *Polygnathus communis*. The absence of siphonodellids and abundance of pseudopolygnathids makes the Zone easily recognisable.

The *Bactrognathus* - *Polygnathus communis* Assemblage Zone extends from the base of the Fern Glen Formation to the top of the middle part of the Burlington. In Europe this Zone corresponds to the upper CuIIβ- lower CuIIγ Zones. The lower limit of the Zone is marked by the earliest occurrence of *Bactrognathus hamata* and *B. excavata*, and the earliest abundant occurrence of *Gnathodus ceneiformis* and *Gnathodus* n.sp. aff. *Gnathodus texanus*, while the upper limit coincides with the youngest occurrence of *Polygnathus communis*. Other characteristic species include *Pseudopolygnathus triangula pinnata* Voges, *Doliognathus lata* Branson and Mehl, *Staurognathus cruciformis* Branson & Mehl, and *Pseudopolygnathus multistriata*.

The upper part of the Burlington Formation is represented by the *Bactrognathus* - *Taphrognathus* Assemblage Zone which is correlated with the upper CuIIβ/γ Zones of Europe. The upper boundary coincides with the lowest abundance of *Gnathodus texanus* s.s., and the lower boundary with the highest occurrence of *Polygnathus communis*. The new species of the two genera, which give their names to this Zone, and *Gnathodus cuneiformis* Mehl & Thomas are also characteristic. This Zone is readily subdivided into upper and lower parts.

The *Gnathodus texanus* s.s. - *Taphrognathus* Assemblage Zone coincides with the Keokuk Formation and is correlated approximately with the lower CuIIδ Zone of western Europe. The upper boundary is marked by the lowest occurrence of *Apathognathus*? and the lowest occurrence of *Taphrognathus varians*, while the lower boundary is indicated by the lowest abundant occurrence of *Gnathodus texanus* s.s. A new species of *Taphrognathus* is also characteristic of this Zone.

The Warsaw, Salem, and Lower St. Louis Formations constitute the *Taphrognathus varians* - *Apatognathus*? Assemblage Zone, whose lower limit is marked by the lowest occurrence of *Apathognathus*? and the highest common occurrence of *Taphrognathus varians*. The upper limit is distinguished by the lowest common occurrence of *Cavusagnathus* and youngest occurrence of *Taphrognathus*, together with the lower limit of the upper zone of abundance of *Apathognathus*. Other typical species of this Zone are *Gnathodus texanus* Roundy, *Neoprioniodus loxus* Rexroad, *N. tulensis* (Pander), and *Spathognathodus* n.sp. Conodonts are not abundant in this Zone, but it is distinct nevertheless, and further studies will allow its further subdivision.

SECTION Eb - UPPER DEVONIAN AND LOWER CARBONIFEROUS FAUNAS FROM AREAS OTHER THAN THE MISSISSIPPI VALLEY, AND THE APPLICATION OF CONODONT ZONATION IN ROCKS OF THIS AGE IN NORTH AMERICA

Scott and Collinson (1961) described conodonts from the Louisiana and McCraney formations in Illinois, Iowa and Missouri. They noted that where the Saverton Formation was not overlain by the Louisiana Limestone, three conodont Zones could be recognised, the Upper, Middle and Lower Zones. Where the Louisiana Limestone was present, only the Lower and Middle Saverton Zones could be recognised in the Saverton Formation itself, the Upper Zone being represented in the Louisiana Limestone. Thus the Louisiana is the lateral equivalent of the Upper Saverton Formation. Scott & Collinson have found this to be the case in western Illinois, where the Louisiana Limestone bears Upper Saverton conodonts. E.B.Branson (1944), indicated that the Louisiana and the Saverton do not have this relationship in all areas, because in Missouri the Louisiana Limestone bears conodonts characteristic of Scott and Collinson's Middle Saverton Zone. Scott and Collinson's examination of the McCraney Formation resulted in a correlation of this formation with the Upper Hannibal and Lower Chouteau of the Mississippi Valley, and the Upper *Gattendorfia* (CuI) and Lower *Pericyclus* (CuII) of Europe. The McCraney Formation bears a good siphonodellid fauna.

Huddle (1934) recognised three Zones in the New Albany Shale of southeastern Indiana. The uppermost of his Zones he equated with the Hannibal Formation, on the basis of the presence of *Elictognathus*, and his Middle Zone was equated with the Middle and Lower Saverton. Beds equivalent to the Louisiana Limestone or Upper Saverton, as the case may be, should be located at the top of Huddle's Middle Faunal Zone.

Hass (1947) published his work on the Devonian - Mississippian boundary in Ohio, and indicated the occurrence of 5 Conodont Zones. The two oldest are equivalent to the Middle and Upper Zones of the Saverton, Zone three is equated with those rocks crossing the Devonian - Mississippian boundary, while the two youngest Zones are the same age as the Hannibal Formation. Hass was able to show more detailed subdivision than has been indicated here. In 1956 Hass published a further paper on the conodonts of the Chattanooga Shale of central Tenessee, in which he showed a close correlation between the upper part of the Gassaway member of the Chattanooga Shale and the Louisiana Limestone. In the same year has described the conodonts of the Basal Maury Formation which represented a Lower Mississippian age.

Cooper (1931, 1933 & 1935) published reports on the Arkansas Novaculite of Western Arkansas, and Cloud, Barnes and Hass (1957) described conodonts from the Houy Formation of central Texas. Both areas indicated transitional Devonian - Mississippian faunas similar to those found in the Mississippi Valley.

Cooper and Sloss (1943) described the conodont fauna of the black shale member which occurs at the base of the Lower Mississippian Madison Group, and concluded that this horizon could be correlated with the Kinderhookian of the Mississippi Valley and adjacent areas. This shale can be recognised from North Dakota to South West Montana.

Younquist and Patterson (1949) indicated that the Prospect Hill Sandstone of Iowa exhibited a fauna similar to that of the Hannibal and Bushberg Formations of Missouri, which were described by E.R.Branson and Branson & Mehl respectively, in 1934. The Prospect Hill Formation is dominated by the occurrence of _Siphonodella_, as is the older English River Formation.

Youngquist & Downs (1951) described the conodonts of the Lower Mississippian Wassonville Dolomite of Iowa which overlies the Prospect Hill Sandstone. It indicated a late Kinderhookian age and was closely related to the English River and Prospect Hill of Iowa and the Bushberg and Hannibal Formations of Missouri.

Hass (1959) published a report on the Chappell Limestone of Texas, and showed this formation to contain three Conodont Zones. The lowest, *Siphonodella cooperi* Zone, correlated with the Chouteau of the Mississippi Valley, as did the *Gnathodus punctatus* Zone, while the upper *Bactrognathus communis* Zone was equated with the Fern Glen horizon of early Osage age. Hass stated that the Welden Limestone and pre-Welden Shale of Cooper (1938), from Oklahoma, were of Chouteau age. The top of the pre-Welden Shale was correlated with Hass's Middle Zone, the rest of the pre-Welden with his Lower Zone, and those shales above the pre-Welden with his Upper Zone.

Branson and Mehl (1938) and Cooper (1938) described faunas from horizons which were correlated with the *Siphonodella cooperi* Zone of Hass (1959), when they described the conodonts of the Chouteau Limestone of Missouri and the pre-Welden Shale of Oklahoma respectively.

Mehl and Thomas (1947), Branson and Mehl (1941) and Cooper (1948) described faunas from other North American horizons which correlate with the *Bactrognathus communis* zone of Hass (1959). Mehl and Thomas worked on the Fern Glen Formation of Missouri, and Cooper on the shale overlying the Rockford Limestone of Indiana.

Rexroad and Scott (1964) referred the Rockford Limestone to the *Siphonodella* n.sp. A (*S. isosticha*)- *Siphonodella cooperi* Assemblage Zone, and the *Gnathodus semiglaber* - *Pseudopolygnathus multistriata* Assemblage Zone of the Mississippi Valley. The Rockford Limestone is thus equivalent to the Upper Chouteau Limestones and Sedalia Formation. The lower part of the New Providence Shale which overlies the Rockford Limestone was found to contain two Assemblage Zones which are also recognised in the Mississippi Valley, the *Bactrognathus* - *Polygnathus communis* Zone and the *Bactrognathus* - *Taphrognathus* Zone. Thus this shale can be correlated with the Lower and Middle Burlington.

Hass (1953) discovered two Faunal Zones in the Barnett Formation of the Llano region of Texas. The lower is of Osagian age, equivalent to the Keokuk Formation of the Mississippi Valley, and the upper of Chesterian age.

Rexroad and Collinson (1963) described the St. Louis Formation of the Mississippi Valley as being transitional with the underlying Warsaw and Salem Formations. Two years later the same authors reported on the conodonts from the Keokuk, Warsaw and Salem Formations of Illinois. They established no further subdivisions to the Zones established in 1962, but explained that there was a similarity between the Warsaw - Salem fauna and the underlying Keokuk in terms of species present though not in their relative frequency of occurrence.

Huddle (1968) redescribed the Upper Devonian conodont genera and species proposed by Ulrich and Bassler (1926). Three Formations were studies, the Rhinestreet Shale member of the West Falls Formation of New York, which correlated with the *Manticoceras* Zone to Iβ/γ of Europe, the Gassaway member of the Chattanooga Shale of Alabama, which was of early - late Fammenian age, and thus equivalent to the Grassy Creek to Louisiana Formations of the Mississippi Valley, and the 'Hardin Sandstone' of Tennessee. The latter formation was correlated by Ulrich and Bassler with the Hardin Sandstone member of the Chattanooga Shale in Hardin County, Tennessee, but was regarded by Huddle as younger than the type Hardin Sandstone Member of the Chattanooga Shale (Hass 1956). This sandstone bears a mixed, reworked fauna which Hass correlated with an early Gassaway age, but, Huddle reserved his opinion, stating that it may be of Mississippian age although it also contained Ordovician and Upper Devonian conodonts from several zones.

Winder (1966) published an account of conodonts from the Upper Devonian of Ontario. He stated that he found an almost complete Upper Devonian section preserved in the Kettle Point Formation, and that 4 of the 10 Zones of Ziegler (1962) could be recognised.

Clark and Ethington (1965) described conodonts from the Devonian of the Alberta Rocky Mountains. Two of the formations sampled, the Mount Hawk and Perdrix Formations, proved to be of Upper Devonian age, and the uppermost part of the Flume Formation was of lowest Upper Devonian age.

Ethington (1965) worked on conodonts from Lower Devonian to Early Mississippian age from Arizona and New Mexico. In Arizona, the Martin and Portal Formations were found to be of early Late Devonian age. The uppermost Martin of Arizona and uppermost Percha Formation of New Mexico have a few similar forms and are suggested as age equivalents. *Siphonodella isosticha* was recovered from the Escabrosa Formation of Arizona, which was thought to be Kinderhookian even before this discovery. This would indicate a correlation between the Escabrosa Formation and the Chouteau of the Mississippi Valley.

Anderson (1966) described Upper Devonian and Lower Mississippian conodonts from North Central Iowa. He noted that five of the formations of the area were of Upper Devonian age, while two could be correlated with the Mississippian. The Lime Creek Formation was correlated with the toIγ or Lower *Palmatolepis gigas* zone of Europe, in its lower and middle part. The overlying Sheffield Formation was equated with the toIδ and toIIα zones, and the Aplington Formation, which overlies this in turn, was equated with the toIV or toV zones of Europe. The Devonian - Mississippi boundary in north central Iowa occurred between the Aplington Formation and either the English River Siltstone (which was not present everywhere) or the Hampton Formation. At one particular locality the Aplington was overlain by the "Maple Mill" formation, and here the boundary was between the "Maple Mill" and the English River Siltstone. The Hampton Formation and the

English River Siltstone, when present, were correlated with the CuI and CuII zones of Europe. On p.402, Anderson gave a correlation chart showing the relationship between the formations of north-central Iowa, southeastern Iowa, and the upper Mississippi Valley in western Illinois. This information is incorporated into the present correlation chart at the end of this section on the Upper Devonian and Lower Carboniferous zonation in North America. The "Maple Mill" of north-central Iowa is not time equivalent with the Maple Mill of southeastern Iowa.

Muller & Muller (1957) published a paper on the early Upper Devonian (Independence) conodonts of Iowa. Beautifully preserved and abundant conodont faunas of the higher portion of the early Upper Devonian were recovered from the Amana, Independence, Sweetland Creek and North Liberty Beds. The first three sequences were of the same age, as was the upper part of the North Liberty Beds. The lower part of the North Liberty Beds exhibited an older fauna than the other sequences. The Amana, Independence, Sweetland Creek, and Upper North Liberty Beds were correlated with an Upper Manticoceras age, upper toI. In North America, the Independence Formation (and equivalents) of Iowa can be correlated with the Lime Creek Formation of north-central Iowa, while the lower part of the North Liberty Bads are equivalent to the Rhinestreet Shale Member of the West Falls Formation of New York. Thus the Independence Formation may correspond to part of the Sylamore of the Mississippi Valley.

Muller and Clark (1967) described conodonts from the Squaw Bay Limestone in Michigan, concluding that this limestone equated with the upper lower or middle Polygnathus asymmetrica Zone, early Late Devonian, Lower Manticoceras (toI), of Europe. The Squaw Bay Limestone fauna was correlated with the following horizons in other parts of the United States and Canada, the lower part of the New Albany Shale of Indiana, part of the Independence Shale in Iowa, the middle part of the Martin Limestone of southern Arizona, the Upper Flume Dolomite (Maligne Formation) of Alberta, and certain Nevada Formations.

Klapper and Furnish (1962) recorded a conodont fauna from the Englewood Formation of South Dakota. The fauna indicated that this formation was in part Upper Devonian and in part Lower Mississippian. The middle part of the formation correlated with the Upper Devonian fauna from the Bighorn and Wind River Mountains, the upper few feet of the Englewood was equivalent to other horizons in South Dakota of Lower Mississippian age. Klapper (1966) also noted the presence of Upper Devonian and Lower Mississippian Conodont Zones in South Dakota, and in Montana and Wyoming. He recognised three Zones in all, one of Upper Devonian age and two of Lower Mississippian age. The former was equated with the Lower *Spathognathodus costatus* Zone (toVI) of Europe, while the two Mississippian Zones were correlated with the *Gattendorfia* Stufe (CuI) and the Lower *Siphonodella crenulata* Zone (CuIIα). Two other Upper Devonian Zones were recognised at isolated localities and were comparable with the *Scaphignathus velifera* Zone (Upper toIIIα - Lower toIV) and Upper *Polygnathus styriaca* Zone (toV).

Sandberg & Klapper (1967) described conodont faunas from the Devonian - Mississippian boundary in the northern Rocky Mountains. The boundary is located in a dark shale unit which is named by the authors as the Cottonwood Canyon Member. This Member occurs in the Madison Limestone of Wyoming and the Lodgepole Limestone of Montana and the extreme west of Wyoming. Sandberg & Klapper recorded the presence of four Conodont Zones in the Cottonwood Canyon Member, the lowest of which has been correlated with the Lower *Spathognathodus costatus* Zone (Upper toV). Above this occurred a Zone which could be equated with the *Siphonodella sulcata* Zone (Lower CuI), then a Zone corresponding to the *S. sandbergi* - *S. duplicata* Zone (Lower CuI), and finally a Zone correlating with the Lower *S. crenulata* Zone (Lower CuIIα). The last three Zones can be correlated with the Kinderhookian of the Mississippi Valley. Underlying the

Cottonwood Canyon Member in Southern Montana was the Three Forks Formation, which Sandberg and Klapper sub-divided into two Conodont Zones, a lower Zone equivalent to the *Scaphignathus velifera* Zone (Upper toIIIα - Lower toIV) and an upper Zone which correlates with the upper *Polygnathus styriaca* Zone (Lower toV). The Three Forks Formation would correlate with the Upper Grassy Creek and Lower Saverton Formations of the Mississippi Valley, (see Sandberg and Klapper 1967, p.9).

Klapper (1958) described an Upper Devonian conodont fauna from the Darby Formation of the Wind River Mountains of Wyoming. He concluded that the upper Darby Formation was contemporaneous with part of the Saverton Shale of Missouri. The Darby has been tentatively correlated with the toV Zone of the Fammenian of Germany. Ethington, Furnish and Wingert (1961) stated that the Upper Devonian conodonts from the Cottonwood Canyon member in Wyoming were the same as those reported from the Darby Formation in the Wind River Mountains of the same State.

Pollock (1968) published his work on Upper Devonian conodonts from Alberta, Canada, recording the presence of six Upper Devonian Conodont Zones of Ziegler (1962). The six zones comprised most of the *Manticoceras* Stufe of Germany (toI), including the Lower, Middle and Upper *Polygnathus asymmetrica*, the *Ancyrognathus triangularis*, and the Lower and Upper *Palmatolepis gigas* Zones.

Mound (1968) described four rock groups containing Upper Devonian conodonts from Southern Alberta. In ascending order, the Beaver Hill Formation was equated with the toI(β)γ Zone, the Woodbend Group with the toI(β)γ - toIγ Zones, the Winterburn Group with the toIγ - toI/toII Zones, and the Wabamun Group was correlated with the toIIγ - toIIβ/toIIIγ Zones of western Europe. The four groups as a whole are approximately contemporaneous with the Sylamore and Grassy Creek Formations of the Mississippi Valley.

Canis (1968) gave his interpretation of the stratigraphy of the Lower

Mississippian of Missouri, based on the conodont evidence he recorded in this region. He suggested the following correlations; In Missouri the upper Hannibal is equivalent to the Lower Chouteau (including the Bachelor Formation), the Sedalia Dolomite is equivalent to the Upper Chouteau Limestone and the Northview Shale (hence the Upper Chouteau is comtemporaneous with the Northview Shale), and finally the Chouteau Limestone of S.W. Missouri is equivalent with the Chouteau Limestone of west-central, central, east and north-east Missouri.

Thomas (1949) and Muller and Muller (1957) both correlated the Maple Mill Shale of southeastern Iowa with the Grassy Creek Shale of the Mississippi Valley, and Muller and Muller noted that these two shale horizons were also time equivalents of part of the middle New Albany Shale.

Orr and Klapper (1968) published their work on the conodont fauna from parts of Indiana and New York. They noted the occurrence of two new species of platform conodonts obtained from beds near the Middle-Upper Devonian boundary, the majority of specimens coming from a thin limestone at the base of the New Albany Shale. These authors correlated the Genundewa Limestone at Eighteen Mile Creek, New York, with the Squaw Bay Limestone in Michigan, both units being assigned an age equivalent to the upper part of the Lower <u>Polygnathus</u> <u>asymmetricus</u> Zone. The Genundewa Limestone is a physically distinct unit from the underlying North Evans Formation in western New York.

Thompson (1967) studies the conodont fauna of the lower Mississippian of south-west Missouri. He concluded that the faunas of the Mississippi Valley and south-west Missouri were similar, but important differences occurred. He combined the upper part of the <u>Gnathodus</u> <u>semiglaber</u> - <u>Pseudopolygnathus</u> <u>multistriatus</u> Zone and the <u>Bactrognathus</u> - <u>Polygnathus</u> <u>communis</u> Zone into a single Zone, the <u>Bactrognathus</u> - <u>Pseudopolygnathus</u> <u>multistriatus</u> Zone. In Missouri, Thompson recognised two Subzones within this newly erected Zone, the underlying this was the Doliognathus lata Subzone.

Many other publications, in addition to those described above, have been written on the occurrence of Upper Devonian - Lower Carboniferous conodonts in the North American continent. Special attention has here been given to those papers which have involved correlation of isolated sections with the standard Mississippi Valley section. A chart has been constructed summarising the suggested correlations of the rocks of Upper Devonian and Lower Mississippian age in North America (Figure 8). In the construction of a chart of this nature it is impossible to create a comprehensive diagram if one attempts to convey the vertical thickness relationships between the outcrops at each location. The vertical scale is not uniform, as the purpose of the chart is to indicate lateral relationships between the various localities.

CORRELATION OF UPPER DEVONIAN AND LOWER MISSISSIPPIAN SECTIONS IN NORTH AMERICA ON THE BASIS OF CONODONTS.

FIGURE 8

SECTION F - THE APPLICATION OF CONODONT ZONATION TO THE UPPER DEVONIAN AND LOWER CARBONIFEROUS ROCKS OF AREAS OTHER THAN NORTH AMERICA AND WESTERN EUROPE

In terms of volume of conodont publications, far more research has been conducted in North America and Western Europe on strata of this age than elsewhere in the world. However, many important contributions have been made as a result of work in other areas, some of which are noted below.

Glenister & Crespin (1959) described the microfauna recovered from Upper Devonian strata in the Fitzroy Basin of Western Australia, while conodont studies in the north western region of the same continent were conducted by Jones & Druce (1966). The latter authors made a preliminary investigation of the conodont palaeontology of the Boneparte Gulf Basin, and were able to correlate Upper Devonian and Lower Carboniferous successions of this basin with the classical sections of the northern hemisphere.

Ethington & Furnish (1962) recorded Upper Devonian and Silurian conodonts from the Spanish Sahara. The Devonian conodonts recovered were of Frasnian age, and the two localities at which these conodonts were found were both in the Tindouf Basin to the north of this region. The fauna compared favourably with European faunas.

Igo & Koike (1964 and 1965) described Carboniferous conodonts from the islands of Japan, while Gupta, Rhodes & Austin (1967) published a brief report on the Devonian faunas of Kashmir, some of which were of lowest Upper Devonian, Manticoceras, age.

Glenister & Klapper (1966) published a report on the Upper Devonian conodonts from the Canning Basin, Western Australia. Their work revealed the presence of an almost complete Upper Devonian series with the possible exception of the Upper Spathognathodus costatus Zone (toVI). This publication includes a chart of conodont distribution (p. 782) which shows the relationship of these conodonts with the conodont zones and ammonoid Stufen established for the Rhenish Schiefergebirge.

Wolska (1967) reported Upper Devonian conodonts from the south-west region of the Holy Cross Mountains, Poland. Most of the Upper Devonian Conodont Zones of the German type section are represented in Poland and in general Ziegler's succession of assemblage zones is valid for the Holy Cross Mountains. In the same year Helms & Wolska noted the occurrence of four new conodont species and one new subspecies from this region of Poland.

Druce (1969) published a detailed synthesis of the conodont faunas that he and Jones (1966) had discovered in the Upper Devonian and Lower Carboniferous strata of the Boneparte Gulf Basin of Northwestern Australia. Rocks of Frasnian. Famennian, Tournasian, Viséan and Namurian age were recognised, and in a general sense the conodont zones of the North American, British and German type sections could be correlated with the zones established in this Australian Basin. Druce concluded that the Australian assemblage zones appeared to be intermediate between the Spathognathodus-Polygnathus-Pseudopolygnathus zonation of Great Britain and the Siphonodella-Gnathodus zones of Europe and North America.

CHAPTER 3

STRATIGRAPHY AND STRUCTURE

INTRODUCTION TO PALAEOGEOGRAPHY AND GENERAL GEOLOGY

Two types of facies can be recognised in rocks of Upper Devonian and Dinantian age in Western Europe. The 'Kohlenkalk' facies represents an agitated water deposit, characterised by a dominantly limestone lithology and a benthonic fauna, while the 'Kulm' facies was deposited in relatively still waters and is characterised by a shale-sandstone lithology containing a necktonic and planktonic fauna. The former facies is considered to be indicative of sedimentation in a trough sea, while the latter is indicative of sedimentation in a shelf sea, flanking the trough.

The palaeogeography of Britain in Devonian times is well documented. The ultimate effect of the Caledonian Orogeny was to build a vast mountainous continent stretching across Northern Europe and embracing most of the British Isles. The southern shoreline of this continent can be traced from Britain in the west, through the Ardennes and the area north of the Black Sea, as far as the Caspian Sea in the east. In Britain itself, the shoreline can be traced from Ireland in the west, through the Bristol Channel, eastward to London. Although the general distribution of the continental and marine areas remained more or less constant in southwestern Britain, throughout most of the Devonian Period, there were fluctuations in the position of the shoreline, and this is reflected in the sediments deposited in North Devon. The Devonian of South Wales is dominated by continental deposits, although evidence of a temporary marine incursion has been discovered in the Upper Devonian at Skrinkle, Pembrokeshire and Craig-y-nos, in the Swansea Valley (see Fig.10). The Devonian of South Devon is composed of marine sediments while those of North Devon indicate that the shoreline was not static but subject to fluctuations and corresponding advances and retreats of the sea. This is evidenced by the alternations of marine and non-marine strata throughout the Devonian of this area (see Figure 9).

During late Devonian times, conditions became more uniform with the widespread and permanent transgression of the sea northward. The North Devon area was submerged under the transgressive sea, while in southern Devonshire fairly deep water conditions probably prevailed. Uppermost Devonian rocks of both South and Central Devon are interpreted as 'Kulm' facies, although the Baggy and Lower Pilton Beds of North Devon were probably deposited on the outermost edge of a 'shelf' sea (see Figure 10).

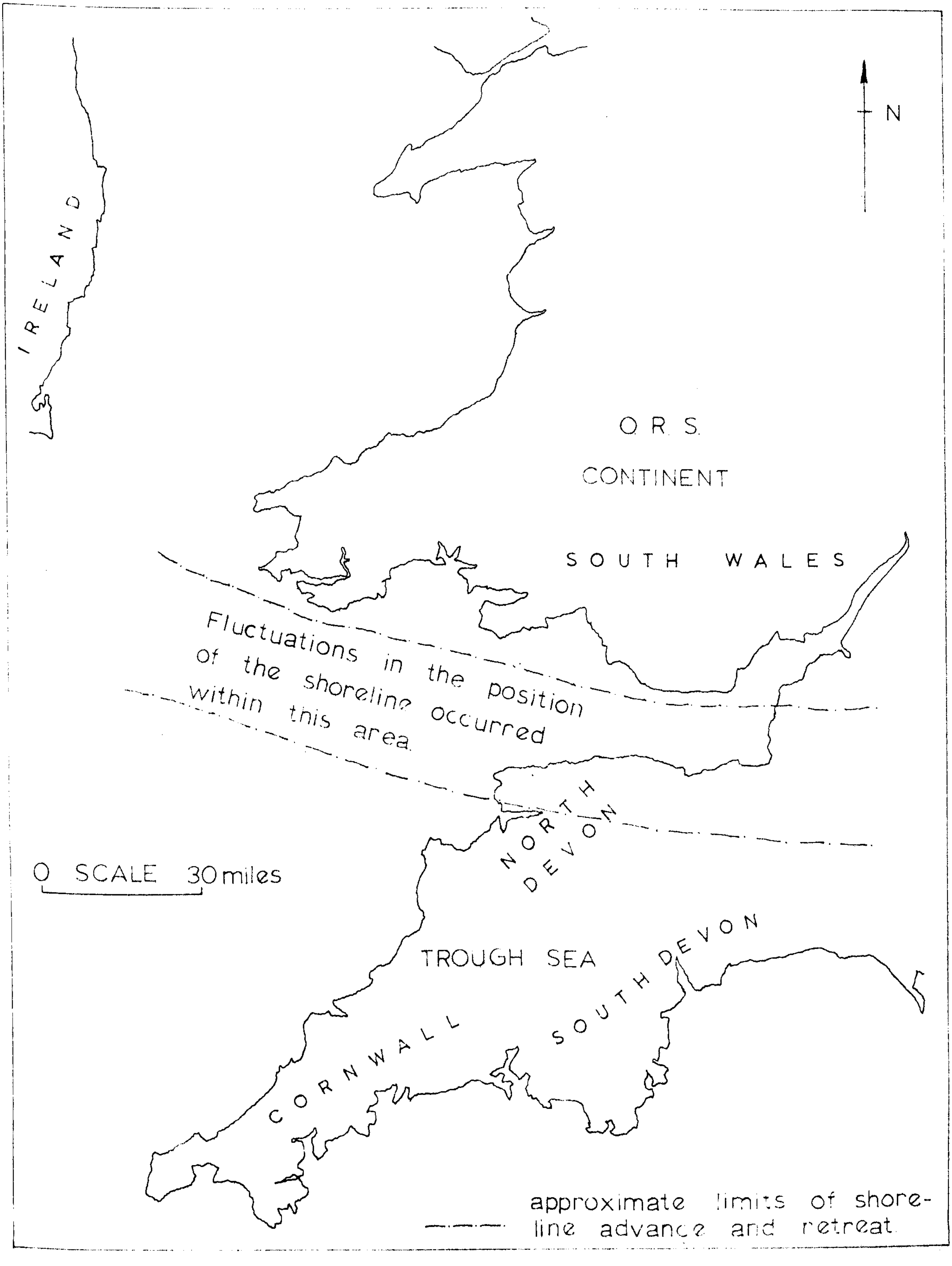
The marine transgression continued to invade northward during Lower Carboniferous times, flooding the low-lying areas between several major landmasses which had developed in central and northern Britain, and forming 'shelf seas' along their margins. The area to the south of the Leinster - Central Wales Landmass, which includes South Wales and Southwest England, is known as the South-West Province, and this merges westward into the Midland Plain Shelf which incorporated most of southern and central Ireland. The northern part of the South-West Province is represented by a 'Kohlenkalk' facies, represented by the limestone exposures of South Wales, Gloucestershire and Somerset, while the southern part of the province continues to exhibit a 'Kulm' facies, initiated in this area during late Devonian times. The Upper Pilton Beds and overlying Culm deposits of Devon and Cornwall are representative of this facies (see Figure 11).

Hercynian earth movements were responsible for the structural features which determined the present outcrop distribution of the sediments exposed in South West England, and Figure 12 illustrates the major structural elements involved.

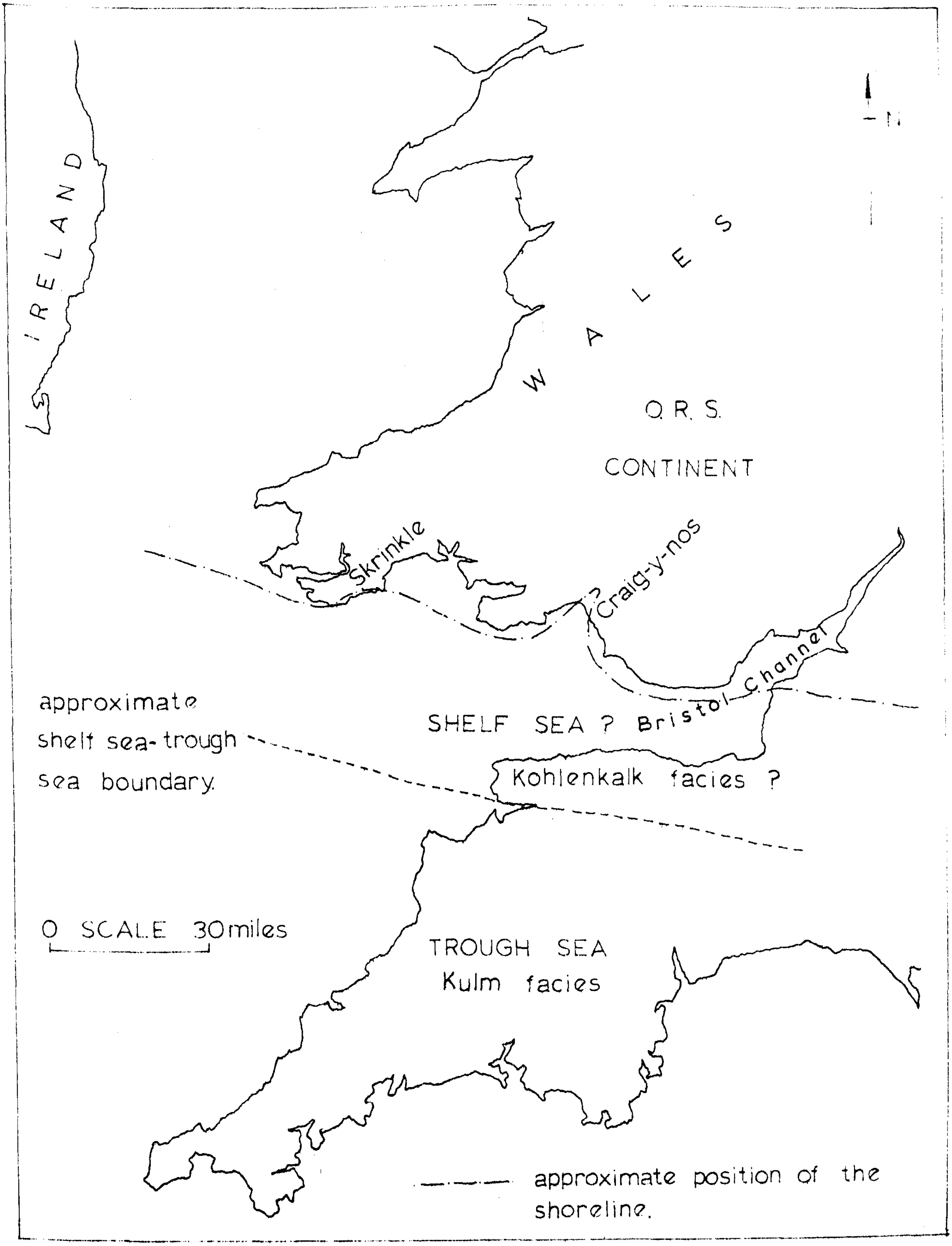
The outcrop of the Baggy and Pilton Beds over the North Devon area is shown in Figure 13, and the two sections from which useful conodont faunas were recovered

FIGURE 9

LOWER AND MIDDLE DEVONIAN PALAEOGEOGRAPHY OF SOUTH WESTERN BRITAIN



LATE DEVONIAN PALAEOGEOGRAPHY OF SOUTH WESTERN BRITAIN



LOWER CARBONIFEROUS (TOURNASIAN) PALAEOGEOGRAPHY OF SOUTH WESTERN BRITAIN (modified from Wills 1959)

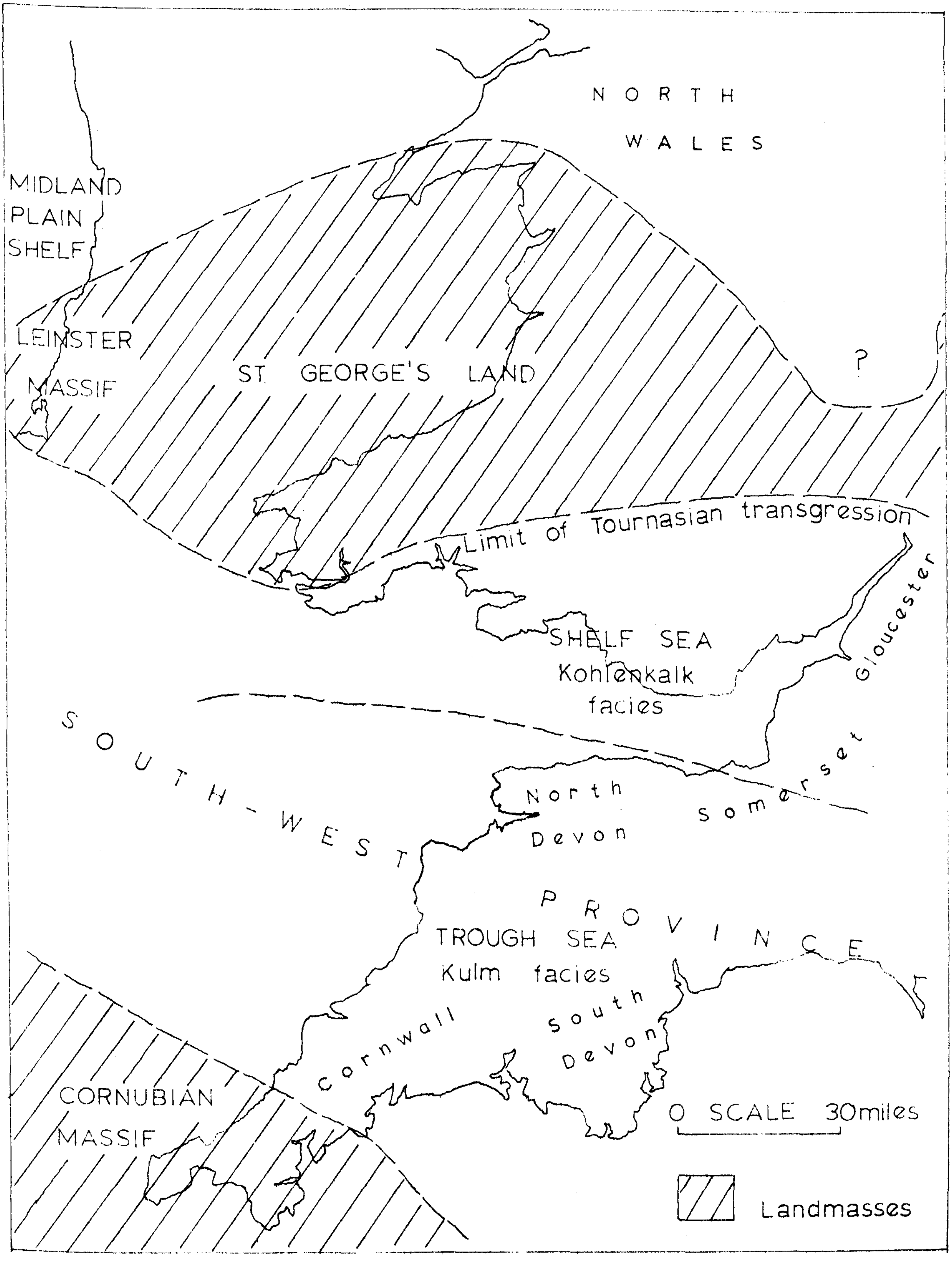
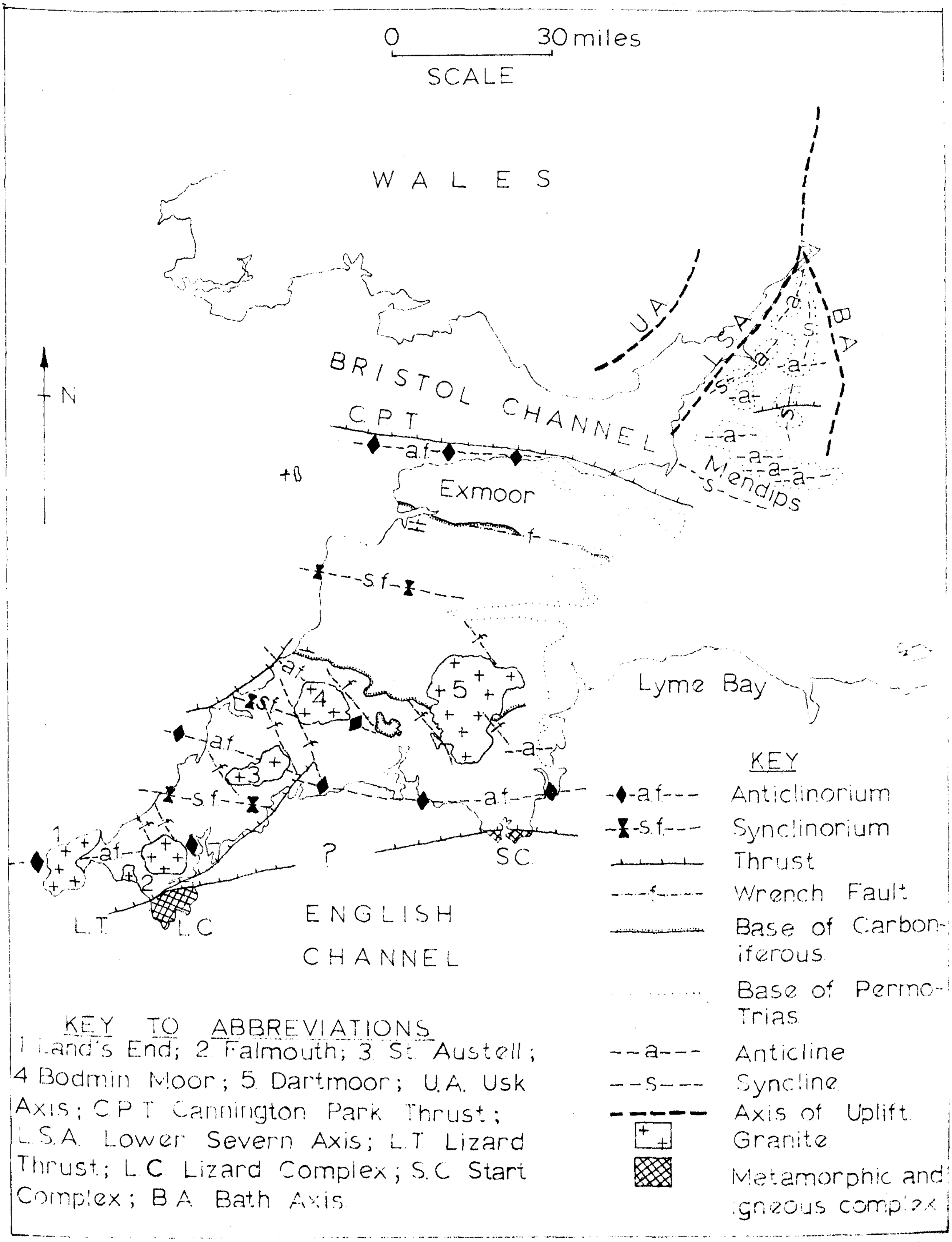


FIGURE 12

MAP SHOWING SOME OF THE MAJOR STRUCTURAL ELEMENTS IN SOUTH WEST ENGLAND

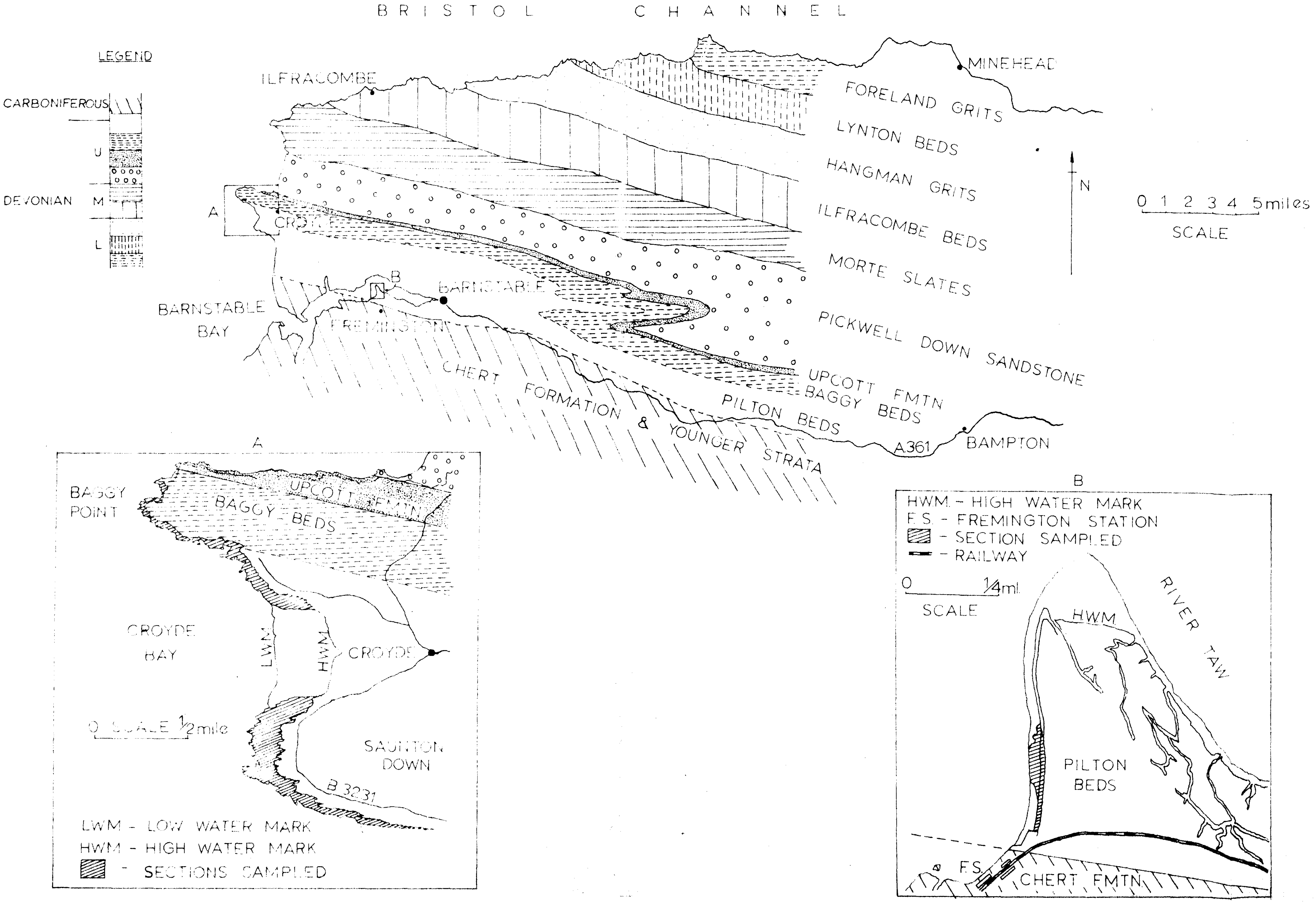
(after Anderson & Owen 1968)



KEY TO ABBREVIATIONS
1 Land's End; 2 Falmouth; 3 St Austell; 4 Bodmin Moor; 5 Dartmoor; U.A. Usk Axis; C.P.T. Cannington Park Thrust; L.S.A. Lower Severn Axis; L.T. Lizard Thrust; L.C. Lizard Complex; S.C. Start Complex; B.A. Bath Axis

FIGURE 13

GEOLOGY OF NORTH WESTERN DEVONSHIRE WITH ENLARGEMENTS OF THE CROYDE BAY AND FREMINGTON SECTIONS
(after Hambling - 1910, and Goldring - 1956)



are enlarged. The name for the Baggy Beds is derived from Baggy Point, North Devon (419.406), where a complete succession of these beds is exposed. The name was introduced by Ussher and Champerknowne, and these beds are of Upper Devonian, *Clymenia*, age, according to Goldring (1956).

The name for the Pilton Beds comes from Pilton, Barnstable, but these beds are better exposed in the proximal coastal sections at Croyde Bay and along the Taw estuary. They are of Famennian, *Wocklumeria* Zone, age in their lower portion and of Tournasian, *Gattendorfia* Zone and possibly *Pericyclus* Zone, age in their upper portion. These ages were assigned to the Pilton Beds by Goldring (1956), as a result of his study of the goniatite, brachiopod and trilobite faunas recovered from these rocks.

THE STRATIGRAPHY AND STRUCTURE OF THE BAGGY AND PILTON BEDS

I. THE STRATIGRAPHY OF THE BAGGY AND PILTON BEDS

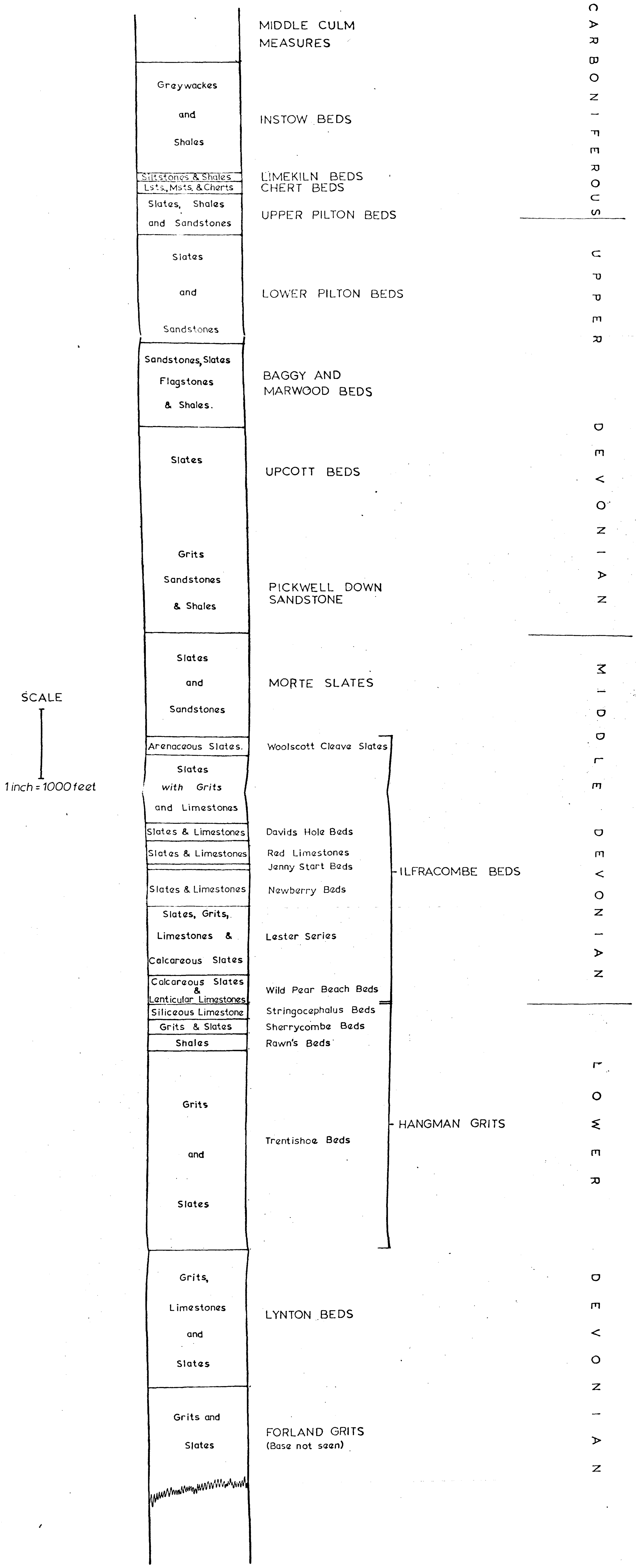
A. The Baggy and Pilton Beds Succession

i. Introduction

The general stratigraphic succession in North Devon is particularly interesting because it displays an alternation of marine and non-marine rocks. Devonian and Carboniferous strata dominate the region with younger rocks more abundant on the eastern flank of the region. The Devonian rocks outcrop north of a line which runs approximately due east from Barnstable Bay, while south of this line the Carboniferous rocks occur. The generalised Devonian - Carboniferous sequence of this area is shown diagrammatically in Figure 14.

The Foreland Beds, Lynton Beds and the Hangman Grits constitute the Lower Devonian; the Ilfracombe Beds and Morte Slates the Middle Devonian; and the Pickwell Down Sandstone, Upcott Beds, Baggy Beds, Lower Pilton Beds and Lowermost Upper Pilton Beds the Upper Devonian. The subdivisions of the Carboniferous are given in Figure 14, and this system includes the bulk of the Upper Pilton Beds. Thus the Pilton Beds as a whole are a group of rocks which are transitional in nature, crossing the Devonian - Carboniferous boundary. Within the Devonian succession there are both marine and non-marine rocks; the marine formations are the Lynton Beds, the Ilfracombe Beds, the Morte Slates, the Upper Baggy Beds, the Pilton Beds, while the non-marine rocks are represented by the Foreland Grits, the Hangman Grits, the Pickwell Down Sandstone, the Upcott Beds and the lower portion of the Baggy Beds.

The Upper Baggy and Lower Pilton Beds represent the youngest Devonian marine episode, and the transitional Upper Pilton Beds the oldest Carboniferous


MIDDLE CULM MEASURES
Greywackes and Shales
INSTOW BEDS
Siltstones & Shales
LIMEKILN BEDS
Lsts., Msts. & Cherts
CHERT BEDS
Slates, Shales and Sandstones
UPPER PILTON BEDS
Slates and Sandstones
LOWER PILTON BEDS
Sandstones, Slates Flagstones & Shales.
BAGGY AND MARWOOD BEDS
Slates
UPCOTT BEDS
Grits Sandstones & Shales
PICKWELL DOWN SANDSTONE
Slates and Sandstones
MORTE SLATES
SCALE
1 inch = 1000 feet
Arenaceous Slates.
Woolscott Cleave Slates
Slates with Grits and Limestones
Slates & Limestones
Davids Hole Beds
Slates & Limestones
Red Limestones
Jenny Start Beds
Slates & Limestones
Newberry Beds
ILFRACOMBE BEDS
Slates, Grits, Limestones & Calcareous Slates
Lester Series
Calcareous Slates & Lenticular Limestones
Wild Pear Beach Beds
Siliceous Limestone
Stringocephalus Beds
Grits & Slates
Sherrycombe Beds
Shales
Rawn's Beds
Grits and Slates
Trentishoe Beds
HANGMAN GRITS
Grits, Limestones and Slates
LYNTON BEDS
Grits and Slates
FORLAND GRITS
(Base not seen)
CARBONIFEROUS
UPPER DEVONIAN
MIDDLE DEVONIAN
LOWER DEVONIAN

sedimentation in the North Devon area.

The exposures of the Baggy and overlying Pilton Beds in this region can be conveniently divided into two types; the coastal exposures and the inland exposures. The inland outcrops are numerous but generally only reasonably exposed in sections along north-south flowing streams. Better inland exposures occur at the sites of productive and abandoned quarries or in road cuttings. The coastal outcrops are more extensive and well exposed, particularly the Croyde Bay section where an almost complete sequence of Baggy and Lower Pilton Beds can be seen. There are only two other coastal outcrops, at Fremington Pill and Asford Strand. Owing to the nature of the coastline, parts of the Croyde Bay section are inaccessible or accessible only at low tides.

The inland exposures visited by the author and the approximate age of the rocks found in them, can be listed as follows:- (see Figure 21 for location)

Road cutting 1 ml. east of Bampton on the Taunton-Barnstable road (A361)	Pilton Beds?
Plaistow Quarries at Bradiford Water (567.373)	Baggy Beds
Exposures in the Caen River valley around Braunton and Knowle	Baggy and Pilton Beds
Exposures at Lobb (470.370) and North Lobb (470.380), east of Saunton	Baggy and Pilton Beds respectively
Quarries in the Bray River valley between Brayford (680.340) and Charles (690.320) namely, Bondy's Pit (688.339), Moules' Chamber (689.338), Wilcombe Quarry (688.336), Notts Quarry and Council Quarries (693.327)	The best inland exposures of the Baggy Beds
Rumsam Road, Barnstable (570.314)	Pilton Beds and Lower Culm
Poleshill Quarry, North Barnstable (550.345)	Upper Pilton Beds

Barnstable Junction Station .... Upper Pilton Beds

Blatchford House, North Barnstable
(567.359) .... Upper Pilton Beds

The rocks exposed in the three coastal exposures are:-

Croyde Bay...........Baggy and Lower Pilton Beds. This is part of an extensive coastal exposure on the west coast of North Devon in which the underlying Devonian rock divisions can be seen as one travels north.

Fremington...........?Uppermost Lower Pilton Beds and Upper Pilton Beds.

Ashford Strand........?Uppermost Lower Pilton Beds and Lower Upper Pilton Beds.

Except in the section one mile east of Bampton, on the Barnstable-Taunton road (A361), no conodont bearing horizons were located in any of the inland exposures of the Baggy and Pilton Beds. In the coastal sections conodonts were recovered only from Croyde Bay and Fremington Pill, the Ashford Strand section proving unproductive. The present report describes the detailed stratigraphy of the three sections from which conodonts were recovered. The collecting data of the unproductive coastal and inland outcrops investigated by the author is summarised on pages 71 & 72.

ii. The succession at Croyde Bay.

Croyde Bay is located on the west coast of Devonshire, approximately sixteen miles north-west of Barnstable. The rocks exposed in the bay are naturally divided into two outcrops, north of the sandy beach Baggy and Pilton Beds are found, while south of the beach only Pilton Beds occur. The relationship between the lithological and faunal divisions of the Pilton Beds was expressed by Goldring (1956) as follows:-

CARBONIFEROUS	PILTON BEDS C		UPPER PILTON BEDS
	PILTON BEDS B		
DEVONIAN	PILTON BEDS A	1 2 3	LOWER PILTON BEDS

In Croyde Bay the rocks dip and young generally southward and the succession is continuous from the Baggy Beds through the Pilton Beds A1 and A2 to A3. No Pilton Beds B or C occur here and thus this section exhibits only Baggy and Lower Pilton Beds. A small patch of rocks in the centre of the beach, known as Cock Rock, may possibly be of Upper Pilton age.

The Baggy Beds are completely exposed along the high-cliffed, northern portion of the bay, known as Baggy Point. Just to the north of this point, the distinct junction between the Baggy Beds and the underlying Upcott Beds can be seen. The upper limit of the Baggy Beds was arbitrarily taken by Goldring within the gradational sequence to the Pilton Beds, at the top of the massive sandstone immediately overlying the local, contemporaneous slump between Pencil Rock (423.403) and Laticosta Cave (427.401). The present writer arbitrarily defines the junction of the Baggy and Pilton Beds at the upper limit of the slump itself. The slump is more easily located than the massive sandstone and is virtually concordant with the bedding. Furthermore, the conodont evidence indicates this as a more practical boundary. The slump and junction of the Baggy and Pilton Beds occur approximately half way along the north shoreline of the bay.

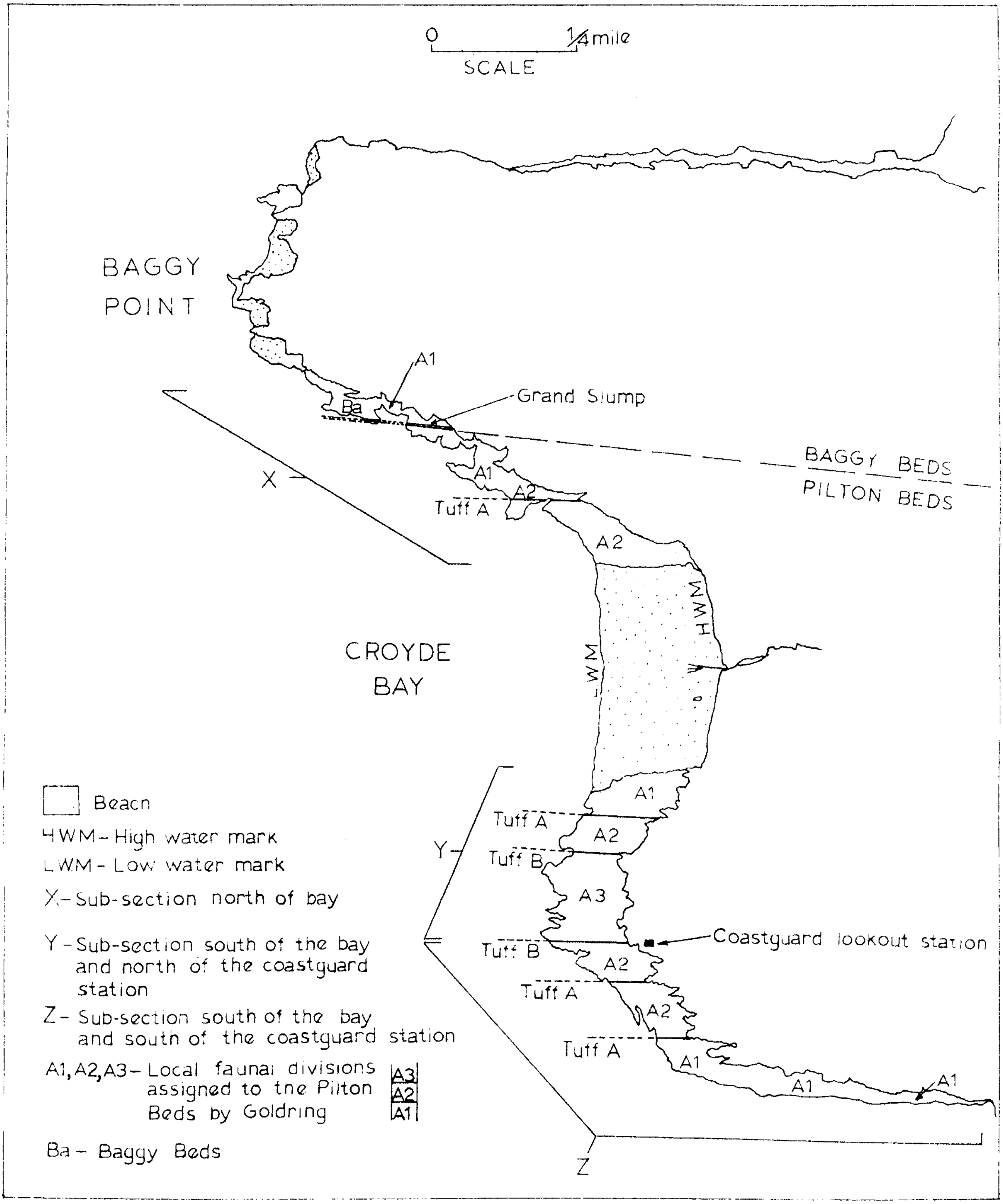
Parts of the Baggy and Upcott Beds are inaccessible owing to the precipitous nature of the cliffs, while other parts are accessible for only short periods of time at low tides. The thickness of the Baggy Beds at Croyde Bay is a little under 1400 feet.

North and South of the slump, on the north side of Croyde Bay, the oldest faunal division of the Pilton Beds is encountered, Pilton Beds A1. These rocks continue to dip and young southward and are overlain by the Pilton Beds A2, which occupy the southern part of the Pilton outcrop on the northern side of the bay. South of the bay the Pilton Beds A1 reappear due to folding, and as one continues southward they are overlain by Pilton Beds A2, which are in turn followed by Pilton Beds A3 at Downend. From Downend the section continues westward to Saunton Sands, the rocks comprising this portion of the outcrop are of A1 and A2 age which reappear due to folding (see Figure 15). The fauna characterising each of these divisions of the Pilton Beds is listed in Chapter 5.

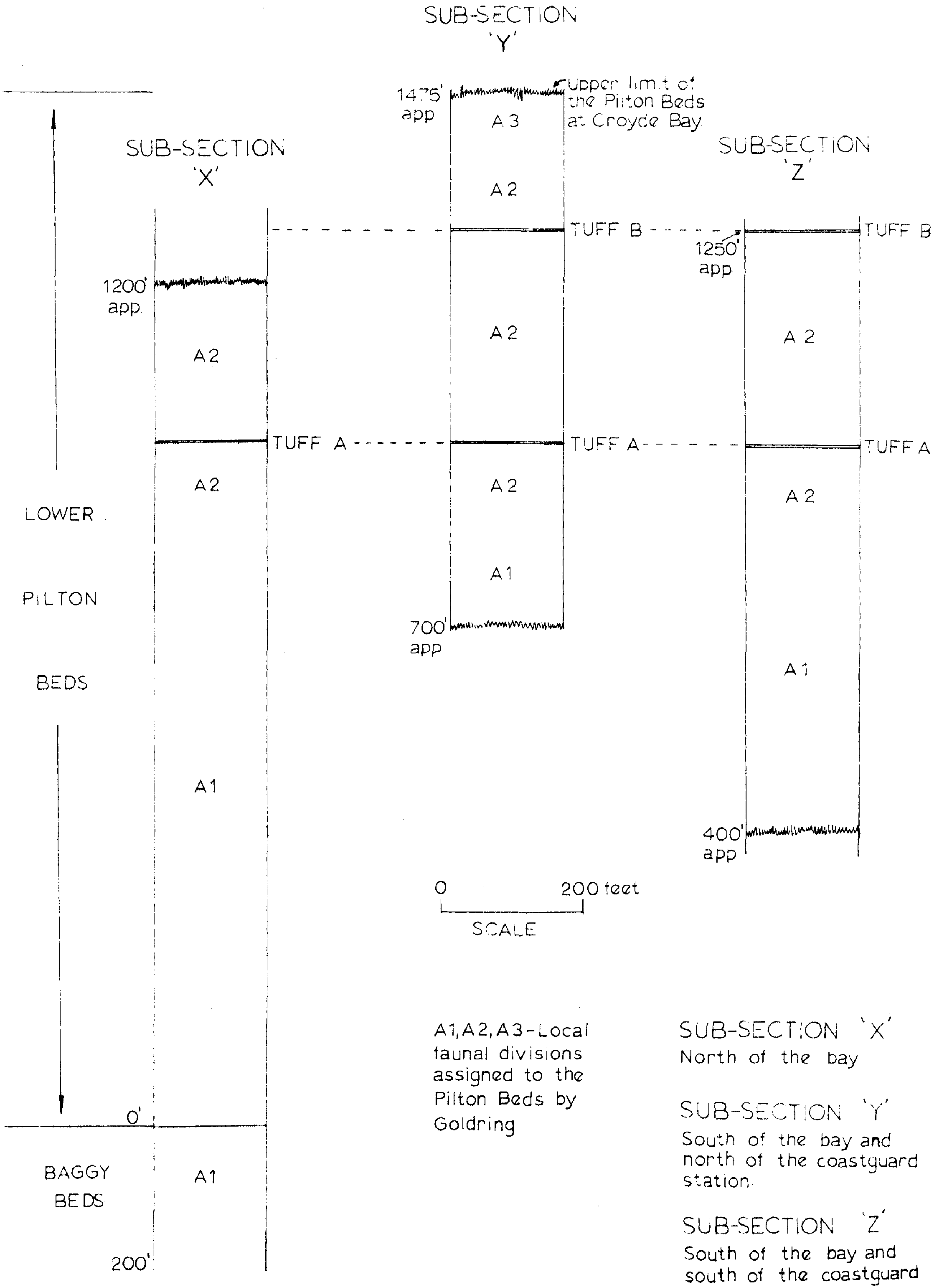
The total thickness of the Pilton Beds exposed in Croyde Bay has been measured by the present author as 1475 feet. Goldring (1956) estimated that there is a further 175 feet of rock before the junction with the Upper Pilton Beds is reached, giving the Lower Pilton Beds an estimated total thickness of 1650 feet. Goldring himself gives the total thickness of the Lower Pilton Beds as 1400 feet, as he measured only 1200 feet of Lower Pilton rocks at Croyde Bay.

The structure of this section is described in detail on page 59, but Figure 15 illustrates the stratigraphic relationship of the rocks exposed on the two sides of the bay, while Figure 16 shows the relationship of the three sub-sections (defined in Figure 15) within the complete stratigraphic range of the Upper Baggy and Lower Pilton Beds at this locality. The three sub-sections X, Y, and Z, have been arbitrarily defined in order to aid description of the outcrop as a whole. At Croyde Bay there are two 'tuff' bands which can be employed as marker horizons to correlate the rocks north and south of the beach. They are of utmost importance in the interpretation of this extensive coastal exposure.

STRATIGRAPHIC RELATIONSHIP OF THE ROCKS EXPOSED TO THE NORTH AND SOUTH OF THE BEACH AT CROYDE BAY



STRATIGRAPHIC RELATIONSHIP OF THE ROCKS EXPOSED TO THE NORTH AND SOUTH OF THE BEACH AT CROYDE BAY



A1, A2, A3 - Local faunal divisions assigned to the Pilton Beds by Goldring

SUB-SECTION 'X'
North of the bay

SUB-SECTION 'Y'
South of the bay and north of the coastguard station.

SUB-SECTION 'Z'
South of the bay and south of the coastguard station.

iii. The succession at Fremington.

Fremington Pill is located on the southern bank of the River Taw estuary, a few miles west of Barnstable. The rocks exposed at this locality occur along the narrow shoreline as reefs, and in the low, 20 foot cliffs which form the banks of the river at particularly high tides. The outcrop is approximately 1,500 feet long in a north-south direction, and has a maximum width of approximately 60 feet at low tide. Its precise location is due north of an abattoir and Fremington Station, which are both sited on the northern side of Fremington Pill.

The stratigraphy of this exposure is most intriguing, despite the extremely weathered nature of the rocks and the tidal mud which covers much of the outcrop. Three of Goldring's Pilton faunal divisions are represented, A3, B and C, and it is thus essentially an Upper Pilton locality of Carboniferous age. Only one normal junction is present, the rest of the faunal divisions being separated by thrusts or faults. Pilton Beds B occur in two distinct outcrops with Pilton Beds C thrust or faulted into the area between.

At the northern end of the section there are several small patches of rock which are exposed close to the low cliff-line. These have been identified by Goldring as being of A3 age. These beds pass through a continuous succession into the next patch or reef of rocks which yield a Pilton Bed B fauna. Beds of B age are exposed for approximately 300 feet along the shore in a southerly direction when they are faulted out and replaced by rocks bearing a Pilton C fauna. Beds yielding a C fauna continue southward for about 360 feet when they are terminated by a thrust, and B beds occur from this point to the southern end of the section.

A basic dyke, which is extremely weathered, is intruded into the beds bearing a Pilton C fauna.

The thickness of the Pilton Beds B and C is extremely difficult to determine.

Goldring admitted that his estimates of 350 feet for each of these divisions are merely educated guesses. Figure 17 shows the geographic occurrence of the three faunal subdivisions recognised in the Fremington Pill section, and also a very generalised stratigraphic succession.

iv. The succession at Bampton.

This section is located in a road cutting approximately one mile east of the village of Bampton on the main Barnstable - Taunton road (A361). The section is relatively small, its total length being about 220-250 feet, and its maximum height only 40-50 feet. It is, however, easily accessible and the rocks are well exposed. The age of the rocks occurring in this section is unknown. Goldring (personal communication) suggests an Upper Pilton age, but the present author would suggest nothing more specific than Upper Devonian. Neither suggestion can be justified by conclusive evidence. Meischner recovered some organic remains from this section but the author has been unable to obtain any record of his findings.

The total thickness of rock exposed here is between 95-100 feet, and the strata dip in a southerly direction.

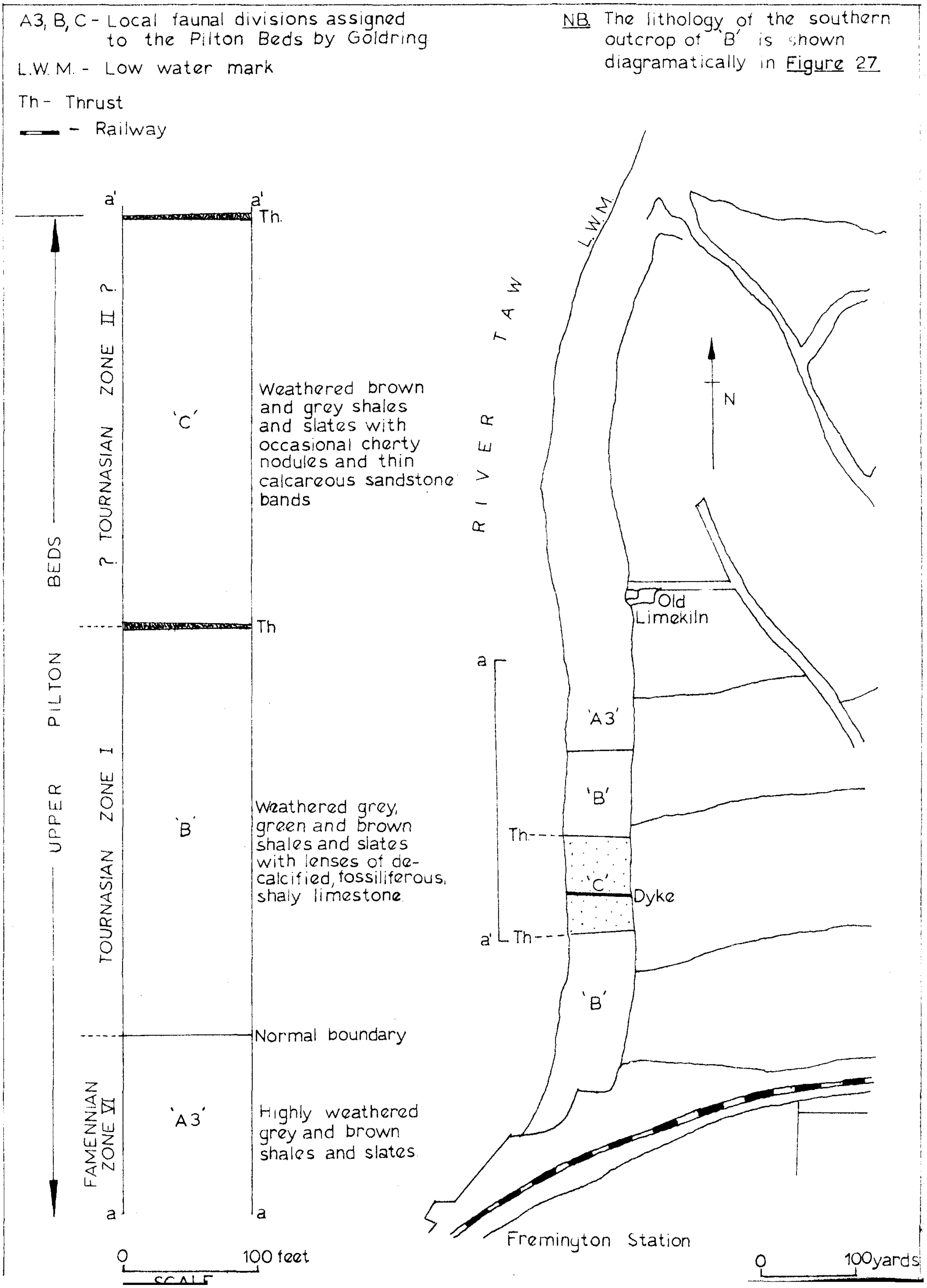
B. The Lithology of the Baggy and Pilton Beds

i. Introduction.

It has previously been pointed out that the Devonian succession of the North Devon area displays an alternation of both marine and non-marine rocks. The Pickwell Down Sandstone, which underlies the Upcott and the Baggy Beds, is a continental deposit, while the succeeding Pilton Beds are of marine origin. Whereas the lower boundary of the Baggy Beds is marked by a sharp colour change, as well as a lithological change, their upper boundary is arbitrarily chosen

FIGURE 17

STRATIGRAPHY OF THE ROCKS EXPOSED AT FREMINGTON STATION



A3, B, C - Local faunal divisions assigned to the Pilton Beds by Goldring

L.W.M. - Low water mark

Th - Thrust

▬ - Railway

NB. The lithology of the southern outcrop of 'B' is shown diagramatically in Figure 27 because of the complete lithological gradation into the Pilton Beds.

The fauna and sedimentary structures of the Baggy Beds indicate a restricted facies deposited in very shallow water conditions in which strong currents were active. Goldring (1956) has likened this facies to the near time equivalent Condroz Sandstone of Belgium. He implied that the Baggy Beds were deposited in a tidal lagoon-type environment. However, it has not been proved that the Lower Baggy Beds are definitely marine, although the nature of the Upper Baggy Beds is more clear. These rocks were probably deposited in shallow water which was becoming gradually deeper, but wave action was still important.

The Pilton Bed facies is indicative of deposition in deeper water, below the level of wave activity. The fauna is larger and more varied than that of the restricted and limited fauna of the Baggy Beds. It was generally a time of more open water conditions. When the Upper Pilton Beds were deposited the water was probably even deeper than during Lower Pilton times, the deepening of the water being associated with the marine transgression which preceded the deposition of vast thicknesses of Carboniferous Limestone further to the north.

Lithologically, the Baggy Beds consist of thick, massive sandstones with very thinly bedded sandstones and shales. The Lower Pilton Beds are distinguished by the absence of massive sandstones and the predominance of thinly bedded sandstones and slates. Although thinly bedded sandstones and slates are important in the Upper Pilton Beds, a marked decrease in the proportion of sandstones serves to distinguish these beds from the Lower Pilton Beds.

ii. The lithology of the Croyde Bay section.

At Croyde Bay the massive sandstones of the Baggy Beds form the northern promontory, called Baggy Point. In addition to the massive, medium to coarse grained, sandstones, which attain thicknesses of 10-40 feet, and display current bedding, ripple marks, and a highly micaceous composition, two other lithological types constitute the Baggy Beds. The bulk of the sediments are thinly bedded sandstones and shales, while a very minor proportion of the rocks are composed of fossiliferous limestones. The bedded sandstones and shales (or sometimes siltstones) are laminated, the laminae ranging between $\frac{1}{4}$ - 10 inches in thickness. In any portion of the Baggy Beds succession where this lithology is found, the proportion of sandstone to shale or siltstone can be equal, or completely unequal with a greater percentage of one or the other. The thicker sandstone laminae often show grading. Current bedding and ripple marks may be strongly developed and the sandstones are micaceous throughout most of the section.

The relatively uncommon limestones, which occur as thin lenses within the thinly bedded sandstones and shales are most abundant at the base and the top of the Baggy Beds. They are fossiliferous, those at the base being mainly composed of small gastropods and pelecypods, while those at the top, where the beds grade into the Lower Pilton strata, are more crinoidal. These three lithological components occur with complete irregularity, and display no rhythmical pattern.

The Lower Pilton Beds of Croyde Bay are composed predominantly of thinly bedded sandstones and slates. The colouration of these beds is dominantly brown and various shades of grey. The individual sandstones range from no more than pencil-thin partings to beds over a foot in thickness, and the thicker sandstones usually show grading. Thicker sandstone beds occur within the sandstone and slates, attaining thicknesses of 4-5 feet and often occurring in groups of 10-30 feet thick. The Lower Pilton Beds can be distinguished lithologically from the Upper Pilton Beds on the possession of these thicker sandstones, which may be of two types; (1) fossiliferous, calcareous sandstone, which usually exhibits current bedding, and which is invariably decalcified to a great depth, and (2) medium grained, brown-grey sandstone, without current bedding. This second type is rarely fossiliferous.

Relatively pure black slates up to 5 feet maximum thickness are found throughout the section. These may or may not be fossiliferous, and sandstones are absent from these groups.

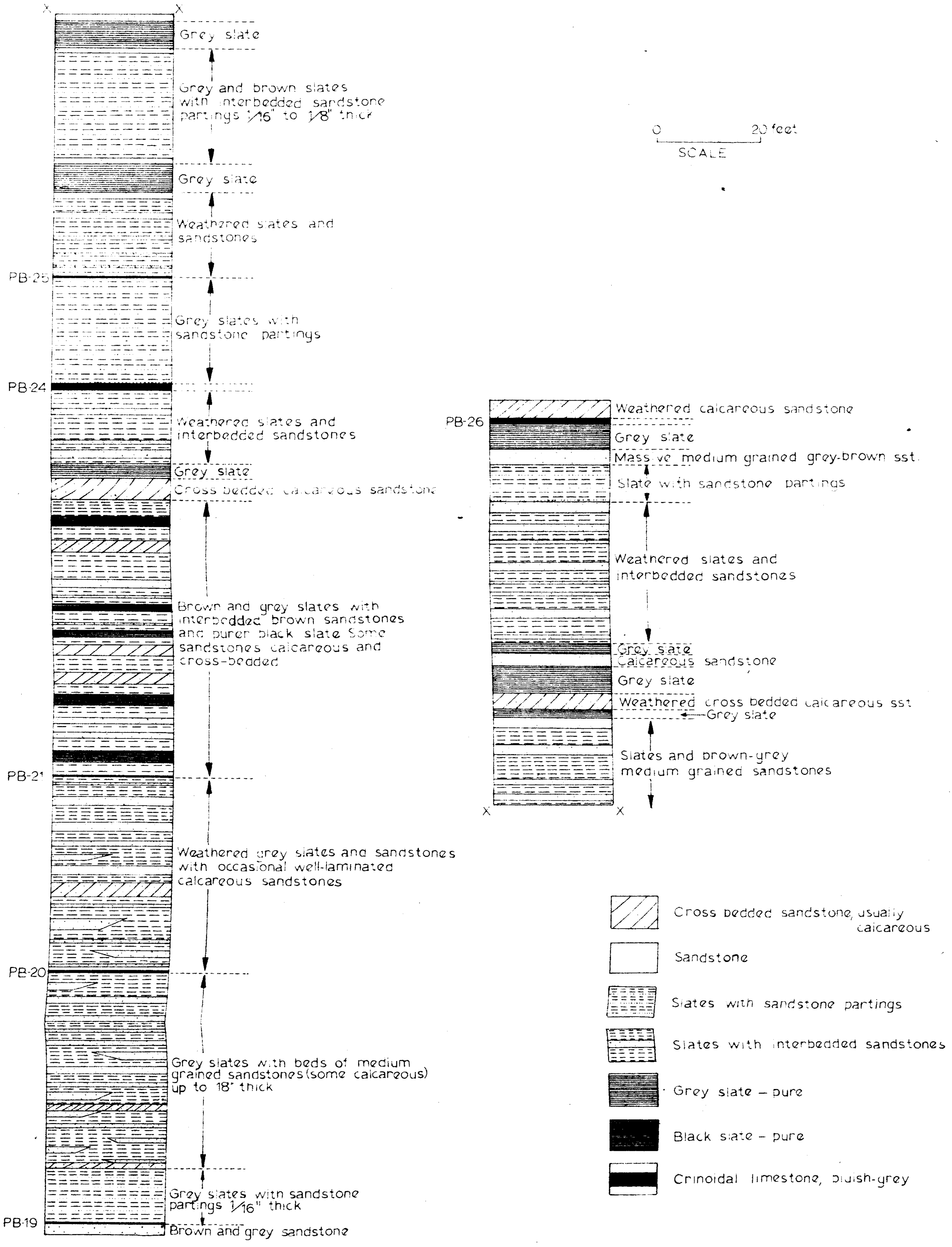
Dispersed randomly throughout the section are thin lenses of highly crinoidal limestone. These bands are not common and yet are of particular importance as they are the major conodont-bearing horizons. They range in thickness from 2 inches to 1 foot and are often partly decalcified. A more detailed description of these lenses is given on page 54.

The six lithological components of the Lower Pilton Beds at Croyde Bay, which have been mentioned above, succeed each other irregularly. The occurrence of any rock type is random, with no indication of any rhythmic or cyclic pattern of deposition. Figure 18 illustrates a representative portion of the Lower Pilton Beds lithology, north of the beach at Croyde Bay, between samples PB.19 and PB.26. The overall colouration of the rocks ranges from brown to intermediate and dark greys, while the limestones, when fresh, have a bluish-grey hue.

Within the Lower Pilton Beds at Croyde Bay two tuff bands occur, each approximately 2-6 inches thick. These bands have not been located inland. The tuffs are excellent marker horizons and have been found on both sides of the bay. The lower tuff, which Goldring called tuff A, occurs just under 1000 feet above the base of the Pilton Beds, and is separated by approximately 250 feet of overlying typical Lower Pilton strata from tuff B, (the name given to the upper tuff by Goldring). North of the beach only tuff A has been identified; tuff B is probably represented here but could not be found. Goldring believes that

FIGURE 18

PART OF THE OUTCROP TO THE NORTH OF THE BEACH AT CROYDE BAY, BETWEEN SAMPLES PB-19 AND PB-26, TO SHOW THE TYPICAL LITHOLOGICAL CHARACTERISTICS OF THE LOWER PILTON BEDS.



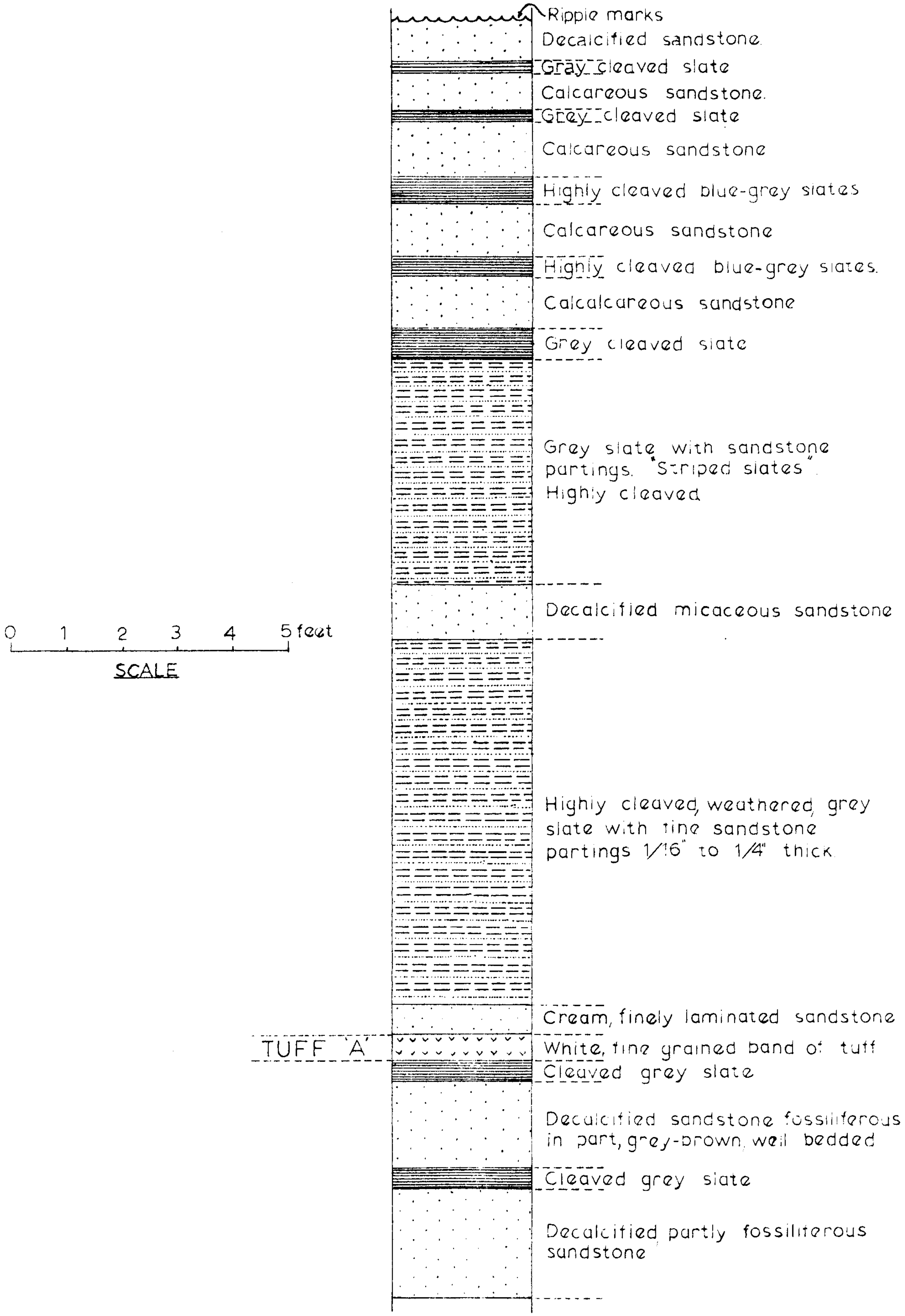
tuff B does not outcrop north of the bay because of erosion, but, in the opinion of the present author, there are more than 250 feet of strata exposed above the occurrence of tuff A in this part of the section.

South of the beach the two tuff bands are easily located; tuff A outcrops four times owing to folding and faulting, and tuff B is exposed twice. When fresh, the tuffs are a creamy-white colour and can easily be spotted against the drab browns and greys of the rest of the Lower Pilton strata. An excellent exposure of tuff A can be seen in the core of an anticline (433.382) at Downend. An equally good exposure of tuff B can be seen just north of this at Downend, due west of the coastguard lookout station. Microscopically the two tuffs are identical, but, in the field they are readily distinguished by the presence of a creamy, 6-8 inch band of thinly current laminated sandstone which, directly overlies tuff A but not tuff B. When weathered, the tuffs are dark in colour and very difficult to differentiate from the surrounding deposits. The local succession in the vicinity of the tuffs is a useful aid in locating these bands where they are more poorly exposed. Figure 19 illustrates the characteristic sequence of Lower Pilton deposits in the immediate vicinity of tuff A.

At the junction of the Baggy and Pilton Beds on the north side of the bay there occurs a contemporaneous slump. It is a prominent feature running east-west from Laticosta Cave (427.401) to Pencil Rock (423.403). The thickness of the slump is between 50 and 60 feet and while its upper margin is virtually concordant with the bedding, the lower margin is more irregular. Smaller slumps of a similar nature can be seen just to the north toward Baggy Point. The slumped beds themselves are highly contorted and show some very well-developed sedimentary structures; they consist of relatively coarse grained brown sandstone. Goldring (1956), who regards the slumps as near the Upper Baggy boundary, suggests that, together with the lithological change, they imply the

FIGURE 19

CHARACTERISTIC LOWER PILTON SUCCESSION IN THE IMMEDIATE VICINITY OF TUFF 'A'



relatively rapid development of a deeper water environment at this time.

A more detailed discussion of the fossiliferous limestone lenses is warranted because of the fact that they yielded the only significant conodont faunas recovered from the Baggy and Pilton Beds. These lenses, when fresh, are of blue-grey colouration but exhibit a brownish hue when weathered. Apart from their sporadic occurrence throughout the section as a whole, they are limited in their extent whenever they were present. They range in thickness from 2 inches to 1 foot, and are restricted laterally from a minimum of 3 feet to a maximum development of about 80 feet. At certain horizons they pinch and swell, whereas at others they attain a uniform thickness throughout their lateral extent and then lens out. In parts of the section displaying a ripple-marked bedding plane, the limestone deposits are limited to the intervening depressions between the ripple peaks. Thus the limestones are discontinuous lenses or pockets occurring within the sandstone-slate sequence. The nature of their distribution is apparently wave or current controlled.

Thin sections of these limestones were cut for microscopic study. The limestones were identified as calcarenites (Pettijohn 1957, p.401), although they are somewhat impure, and a few of the fossil fragments are of a size that would indicate a calcirudite. The groundmass is composed of calcitic mud within which small quartz sand grains, $\frac{1}{30}$ - $\frac{1}{10}$ mm. in diameter, are abundant. This quartz sand constitutes about 25% of the rock. A further 35% is occupied by large grains of recrystallized calcite, which in some cases incorporates smaller quartz grains. This recrystallized calcite often replaces fossiliferous material totally or partially. The fossil content represents the remaining 40% of the rock. The organic material is represented by crinoids, brachiopods and others, in that order of importance.

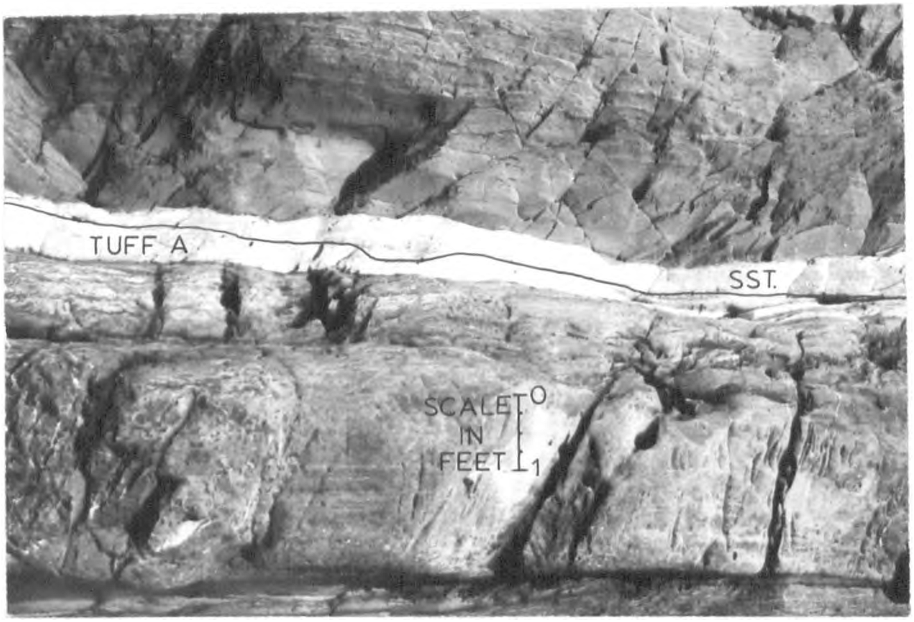


PLATE A. Outcrop of Tuff A and the overlying cream coloured sandstone in the northern limb of an anticline at Downend, south of the beach at Croyde Bay.

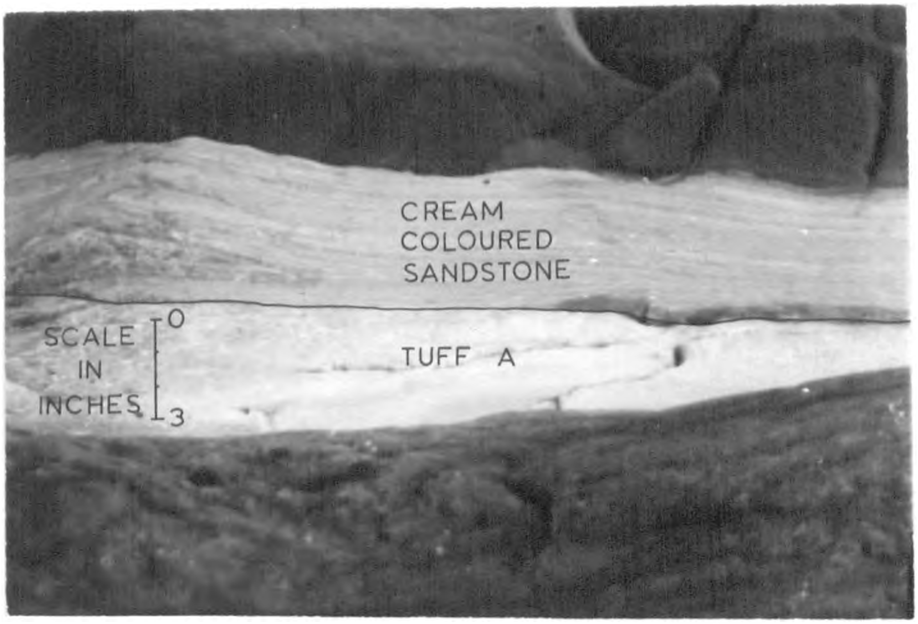


PLATE B. Enlargement of a portion of Plate A.

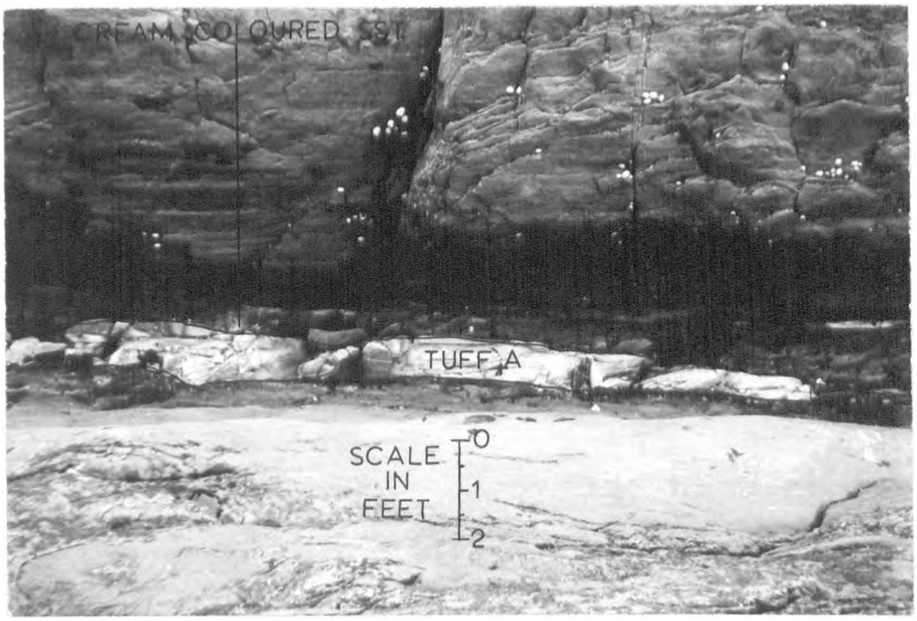


PLATE C. Outcrop of Tuff A and its associated cream coloured sandstone, due west of the Middleboro Hotel, north of the beach at Croyde Bay.

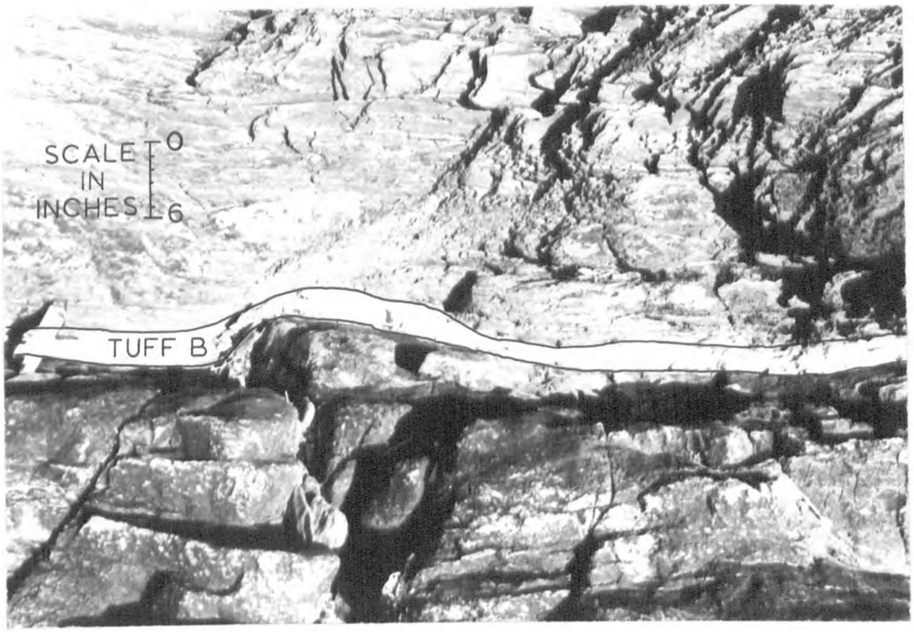


PLATE D. Outcrop of Tuff B due west of the Coast-Guard Lookout at Downend, south of the beach at Croyde Bay.

PLATE E. Deformation within the 'Grand Slump', north of the beach at Croyde Bay.

PLATE F. Deformation within the 'Grand Slump', Croyde Bay.

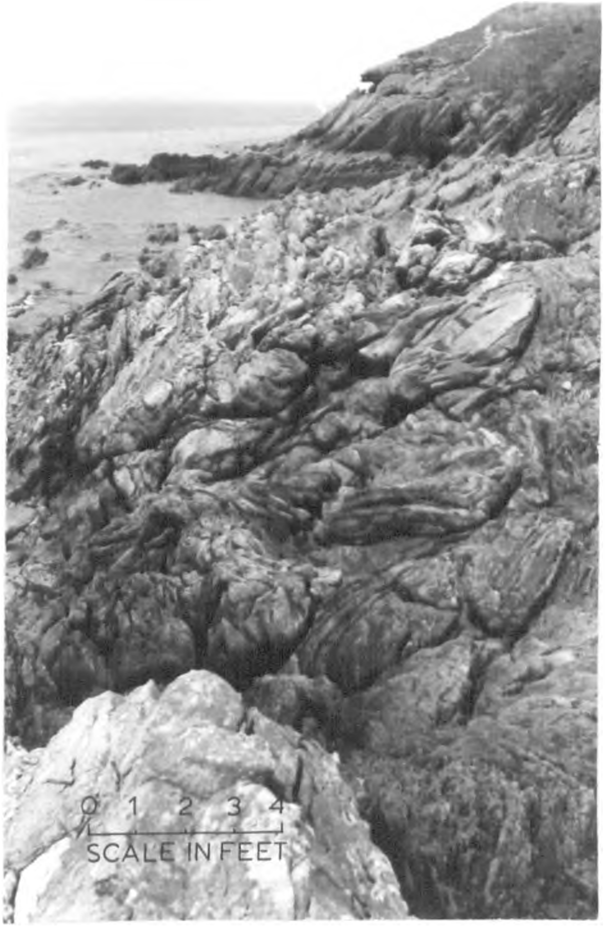


PLATE G. The 'Grand Slump' Croyde Bay, viewed from the east.

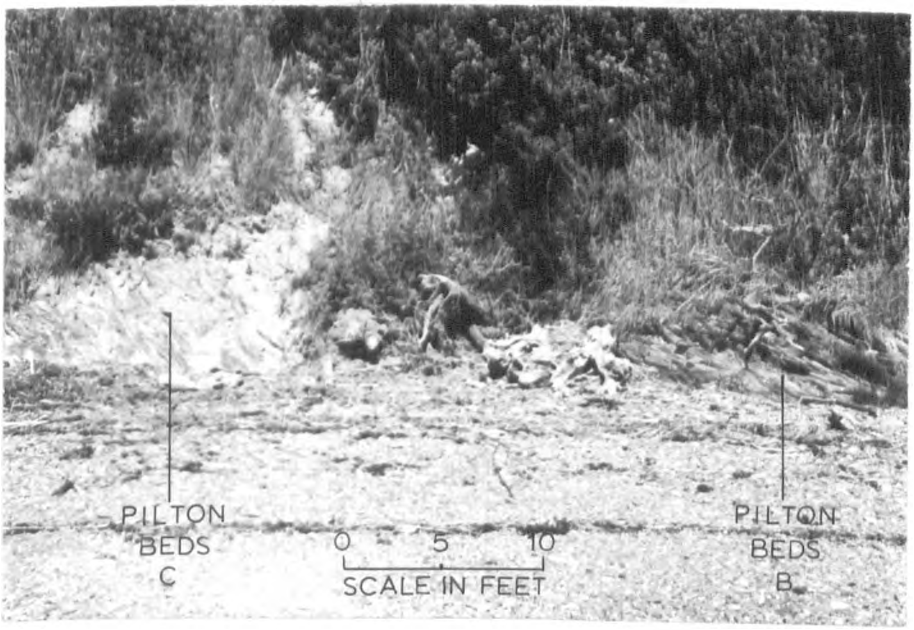


PLATE H. Fremington Pill. The change in lithology between the black muddy shales of Pilton Beds B to the right, and the brown-grey slates and shales of the Pilton Beds C. View of outcrop from the west. A thrust-fault separates the two lithological types.

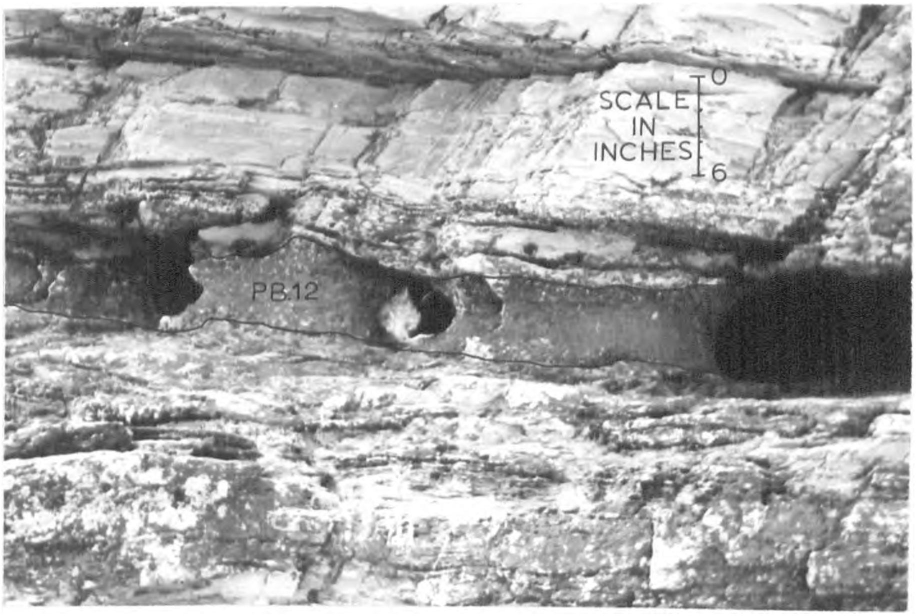


PLATE I. The occurrence of the crinoidal limestone horizon which constitutes sample PB.12, Croyde Bay.

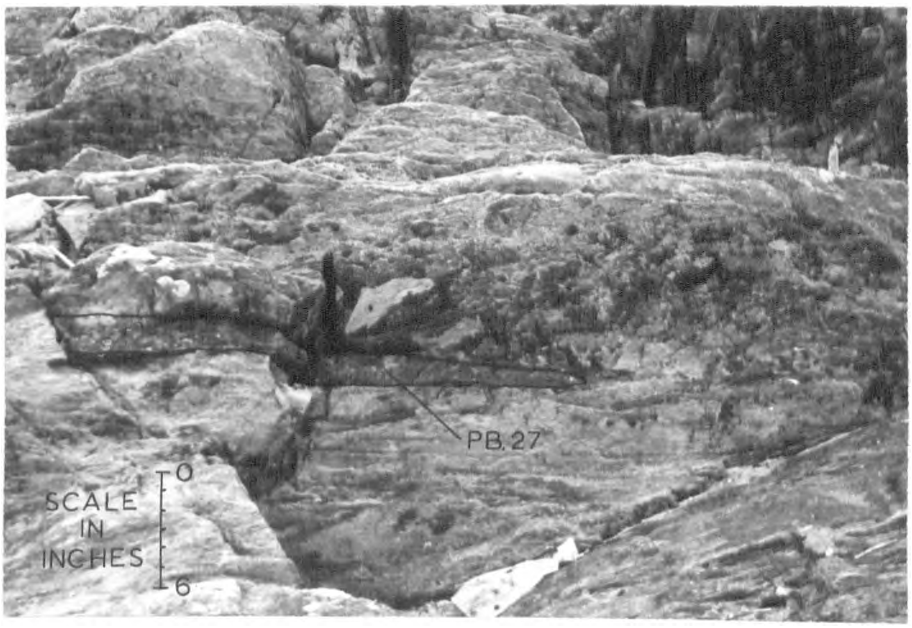


PLATE J. The occurrence of the crinoidal limestone horizon which constitutes sample PB.27, Croyde Bay.

PLATE K. The occurrence of the fossiliferous limestone horizon which constitutes sample F.5, Fremington Pill.

PLATE L. The occurrence of the fossiliferous limestone horizon which constitutes sample F.2, Fremington Pill.

According to Folk's classification (1968) these limestones would fall into the category of biosparites.

iii. <u>The lithology of the Fremington section</u>. (517.337)

The oldest rocks in this section occur at the northern end of the narrow beach (see Figure 17). They are extremely weathered and composed of lenticular sandstones and slates. These rocks are overlain with apparent conformity, by younger material consisting essentially of fine grained, brown and grey shales and slates. Within the slates thin lenses or lenticles of fossiliferous, calcareous shale occur, which are totally decalcified and badly weathered. The average size of the lenses ranges between ½ and 2 inches in thickness and 3 and 8 inches in length.

From this point southward to a thrust, which occurs approximately 450 feet from the gate at the southermost end of the section, the lithology is composed almost entirely of drab, brown and grey slates. Occasional fossil lenticles and cherty nodules are present, and calcareous sandstone bands and other paler sandstones occur infrequently. The calcareous sandstones, when present, attain a maximum thickness of 2 feet. About 600 feet north of the gate, an almost completely weathered basic dyke occurs cutting through brown and grey slates.

Immediately south of the thrust mentioned above, there is a visible change in lithology. Black, muddy shales exhibit a marked colour contrast with the browns and greys of the adjacent slates. They are indicative of a deeper water environment and intermittent, unweathered fossiliferous limestone bands occur within the shales. They reach a thickness of 45 feet before being faulted out and succeeded by 15 feet of brown and grey slates. These slates are in turn faulted out, and a further 22 feet of black shales and associated limestones occur.

Above this, faulting once more exposes the brown and grey slates, which dominate most of the section, and these continue to the southernmost end of the Fremington exposure, although here sandstones are more abundant than elsewhere in the section.

Despite the lithological changes, Goldring (1956) maintains that the rocks of the southernmost 150 years of the Fremington outcrop all yield a B fauna. Furthermore, the faults and thrusts which cut this portion of the outcrop are considered by him to have no significant throw.

The conodont bearing fresh, fossiliferous limestones which occur within the black shales were thin sectioned for microscopic study. They were found to be almost pure calcarenites, composed of 60-65% fossil material, mainly in the form of crinoid and brachiopod fragments. The fossil material is set in a matrix of fine calcitic mud, which occasionally shows larger, more consolidated masses of the same composition. There is very little quartz sand and the size of the constituent fossils ranges between $\frac{1}{16}$ and 2 mm. There are a few larger crinoid fragments but these are in the minority.

This is a purer calcarenite than the Croyde Bay limestones, with little evidence of recrystallisation. The thickness of these limestones ranges from 1 - 4 inches, and, like their Lower Pilton conterparts, they are pod-like or lenticular in their occurrence. Their lenticular nature is less obvious here owing to the size of the outcrop as a whole. They are black in colour and often accompanied by substantial secondary calcite deposits.

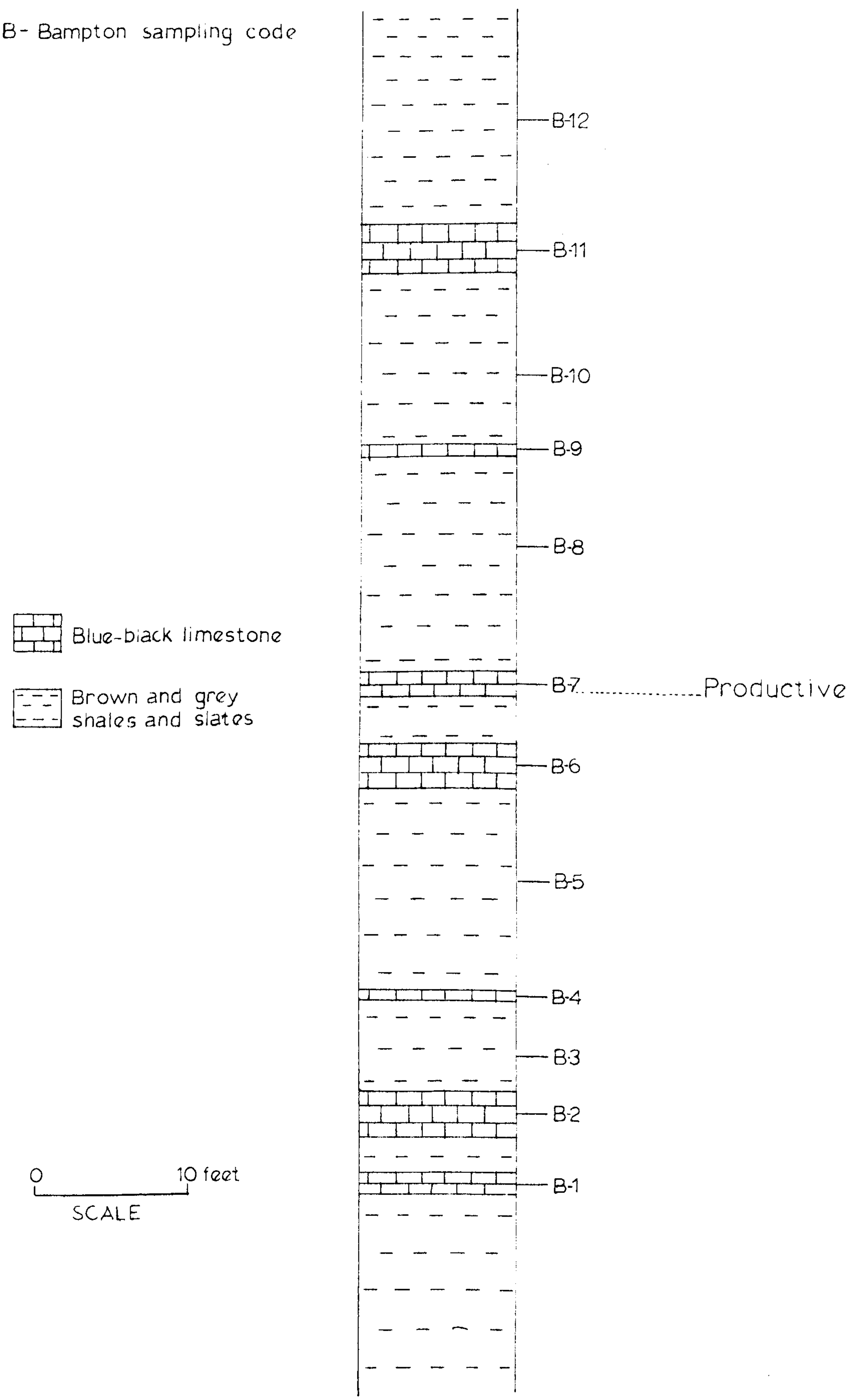
Figure 27 shows the lithology of the southern outcrop of Upper Pilton Beds B. Figure 17 illustrates the lithology of the rest of the outcrop at Fremington.

iv. <u>The lithology of the Bampton section.</u>

Only two lithological types occur within this relatively small section; brown and blue-grey shales, and fine-grained laminated blue-black limestones.

The shales are intensely weathered and form the bulk of the outcrop, while the limestones occur irregularly and are fresh and devoid of macrofossils. The limestones range in thickness from 1 to 3½ feet and seven bands are well exposed in the road cutting. Figure 20 illustrates the stratigraphic succession and the lithology of the strata occurring at this locality.

STRATIGRAPHIC DISTRIBUTION OF THE SAMPLES COLLECTED FROM A ROAD-CUT ON THE A361, ONE MILE EAST OF BAMPTON



2. THE STRUCTURE OF THE BAGGY AND PILTON BEDS

i. Introduction

The Devonian and Carboniferous rocks of the North Devon area form the southern limb of a large anticline whose axis is aligned east-west and would have been located in the Bristol Channel. These rocks also constitute the northern limb of the Devonshire synclinorium, whose axis has a similar trend. The overall regional dip is 10-20° southwards, although sections within the area usually display dips as high as 50-70° or even greater. The average strike of the North Devon strata, closely follows the trend of the major fold axes, being approximately east-west. The folds plunge at a low angle toward the west and this, together with the effect of the many large northwest-southeast trending, dextral faults which cut the region, causes the local trend of the North Devon outcrops to be WNW-ESE.

In general, the Baggy Beds are strongly folded and this is most obvious in the inland exposures such as that of the Bray Valley. The same general rule can be applied to the Lower Pilton Beds. Thrusting and faulting are the main structural features of the Upper Pilton Beds. There is an overall increase in the intensity of deformation from the older to the younger beds.

Within the region there are four main types of faults, recognised by their direction of displacement. These include (a) east-west-trending strike faults, which are encountered in both the Baggy and Pilton Beds, (b) northwest-southeast-trending tear faults, the most common of the four types, being present in both the Baggy and Pilton Beds, (c) northeast-southwest-trending tear faults and, (d) north-south faults, which are the least common type, being restricted to the Baggy Beds.

Goldring summarised the tectonic history of the area as follows:-

4. North-south normal faulting.

3. Tear faulting.

2. Thrusting and reverse faulting (the East-West strike faults).

1. Folding and imposition of cleavage.

The first three structural events he attributed to the Amorican orogeny, while the development of the north-south faulting may belong to another tectonic episode. Goldring also commented on the close association between the type of structural features and the lithology, the prime example to this being the intense cleavage developed in the Lower Pilton slates.

Figure 21 illustrates the major structural features affecting the outcrop of the Baggy and Pilton Beds in the vicinity of Barnstable.

ii. The structure of the Croyde Bay section.

The location and recognition of two tuff bands is essential if the structure of the Croyde Bay section is to be interpreted correctly. The structure on each side of the bay is not difficult to determine, but the relationship between the rocks either side of the bay would be most difficult to evaluate without the occurrence of the tuffs. They are fairly easily distinguished and provide the worker with two excellent marker horizons. The overall interpretation of the structure at Croyde Bay by Goldring (1956) was fully confirmed by the work of the present author.

At Baggy Point the beds are not greatly folded, but they are frequently disturbed by faulting along a north-south line. They dip generally southward at angles of 65-75°, except in the vicinity of the slumped beds where their dips are of a lower order. South of the slump the Lower Pilton Beds continue to dip southward, with a few localised exceptions, at attitudes which range from

MAJOR STRUCTURE FEATURES AFFECTING THE OUTCROP OF THE BAGGY AND PILTON BEDS OF THE BARNSTABLE AREA

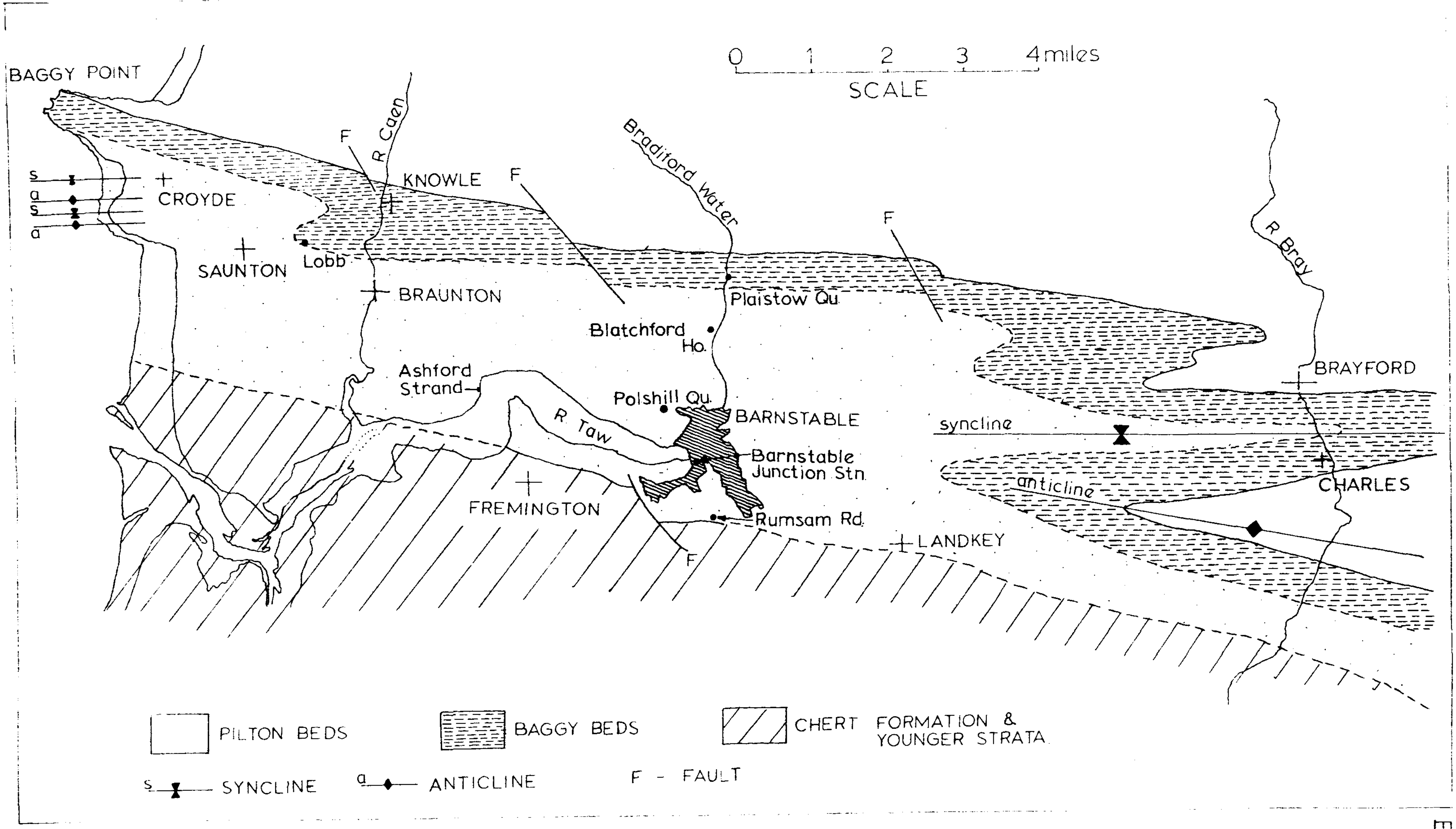


FIGURE 21

near-horizontal to near-vertical. The average dip of these beds lies between 40° and 70°. Within this part of the section, tuff A outcrops in a large and prominent gully, due west of the Middlebro Hotel, but tuff B has not been located north of the bay. East-west faults are easily recognised by the deep channels or gullies which have been eroded by the sea along these lines of weakness. Faults with this directional trend are the most abundant in this particular part of the section. Northwest-southeast tear faults are also common in this vicinity. Small-scale, localised folding occurs occasionally, the best examples being at Freshwater Gut, but in general the rocks of this area, north of the bay, dip southward.

South of the bay the structural picture is far more complex. There is some uncertainty as to what happens across the bay itself, but the presence of a large syncline has been postulated by Goldring (1956) and the present authors work confirms this as the most probable and reasonable explanation. The rocks immediately south of the beach dip northward at an angle of 25-30°. They form the north limb of an anticline whose axis can be seen at 434.388. The southern limb of the same anticline dips southward at angles of 40-45°. At Downend the rocks are folded into a large asymmetrical syncline within which numerous smaller scaled folds can be seen. The axial portion of this syncline is particularly contorted. Figure 22a indicates the major structural features affecting the Lower Pilton Beds to the south of the beach, while Figure 22b and 22c provide a more detailed picture of the complex nature of the syncline developed at Downend.

South of Downend and around the coast to Saunton, the strata are folded by a series of relatively gentle, shallow anticlines and synclines. A total of four anticlines and three intervening synclines can be identified in the Lower Pilton Beds which outcrop to the south of the beach at Croyde Bay.

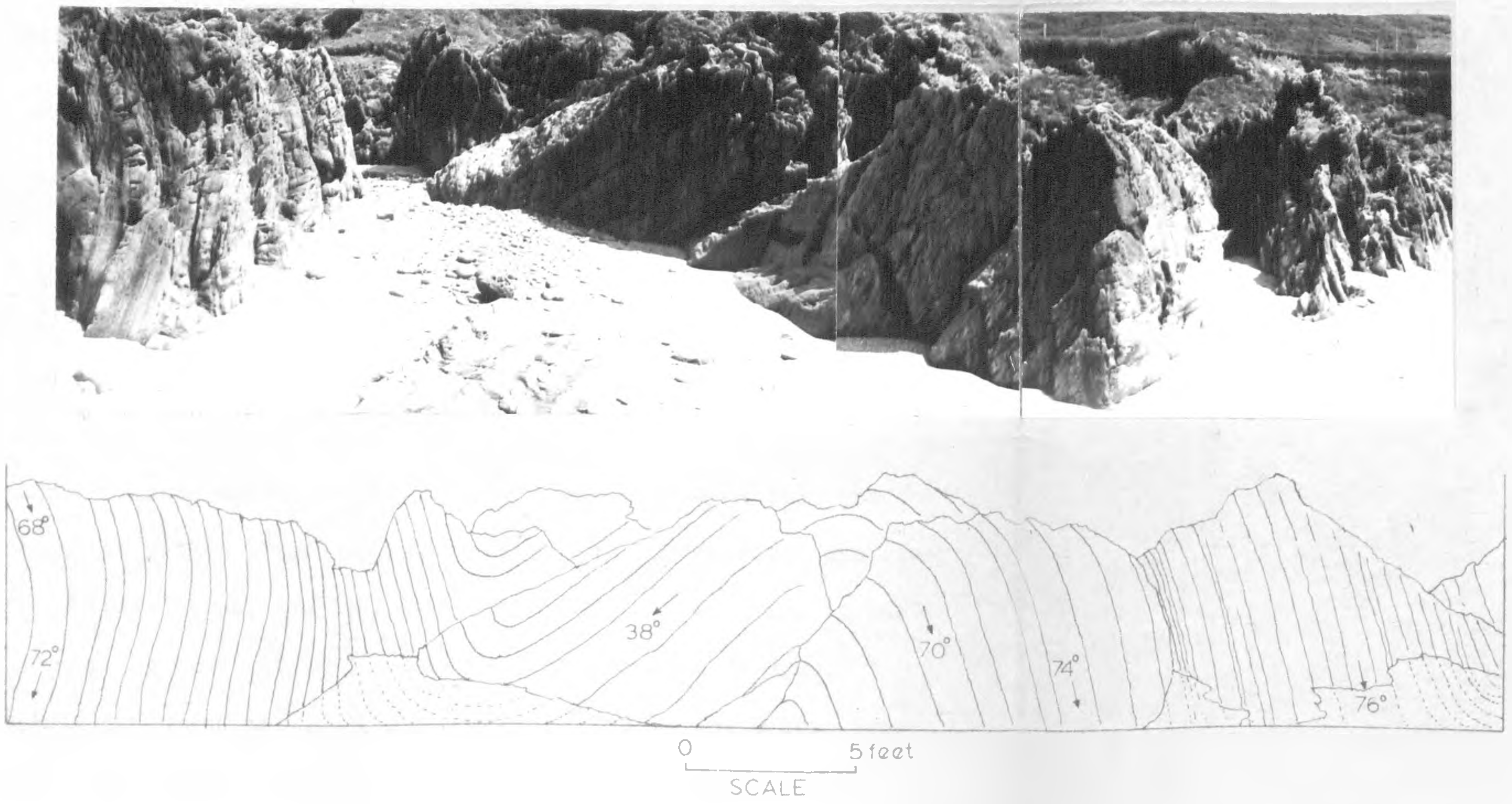
The faults affecting this part of the section are dominantly northwest-

FIGURE 22

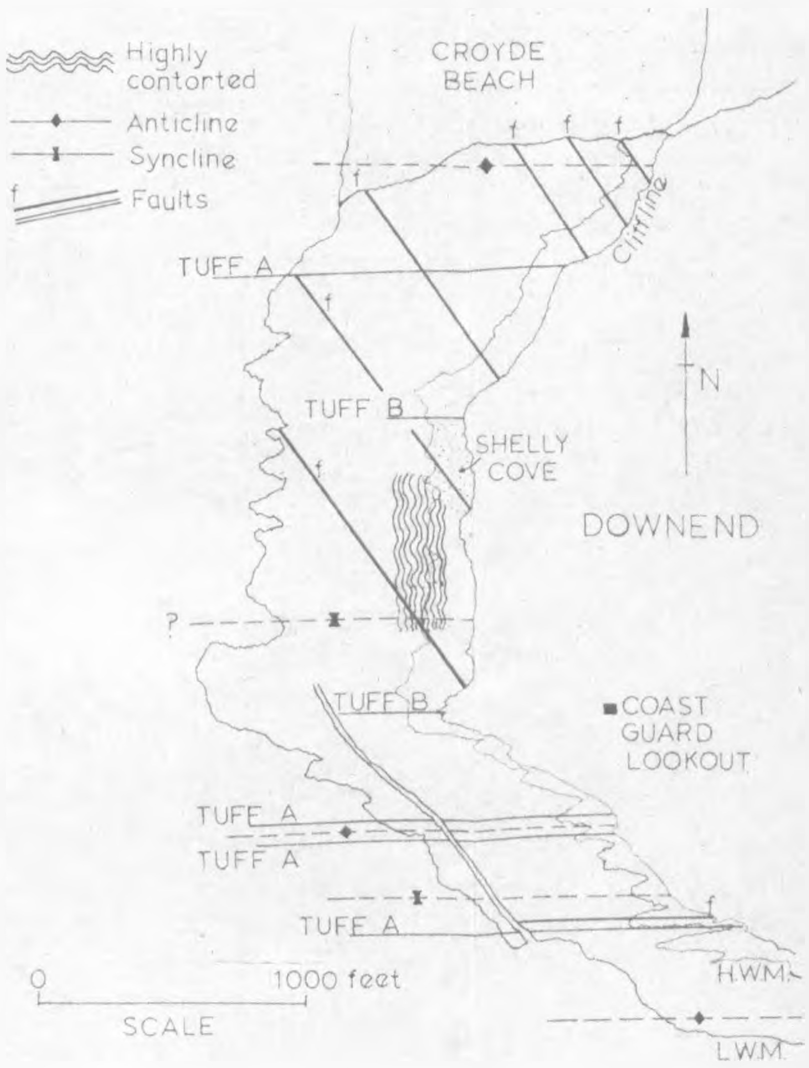
STRUCTURE OF THE LOWER PILTON BEDS TO THE SOUTH OF THE BEACH AT CROYDE BAY

C

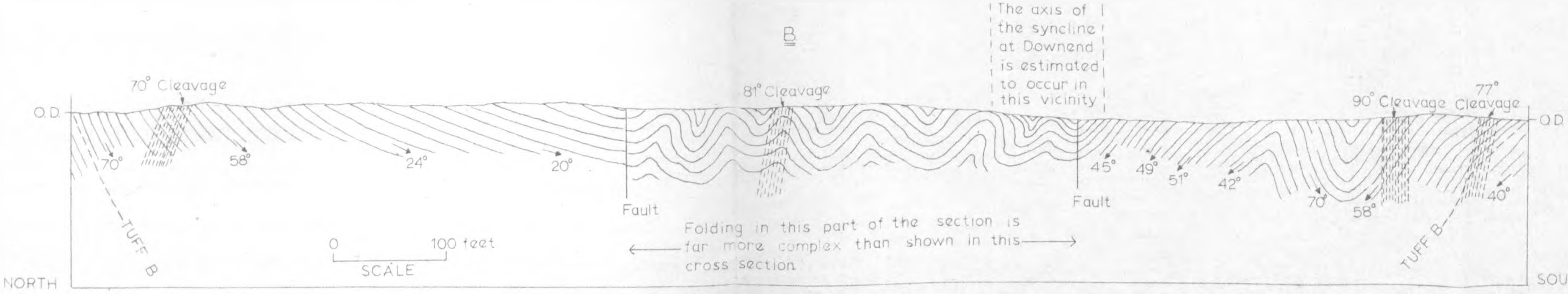
PHOTOGRAPH AND DIAGRAMATIC SECTION EXEMPLIFYING THE NATURE OF THE FOLDING WHICH COMPLICATES THE AXIAL PORTION OF THE SYNCLINE AT DOWNEND



A. MAJOR STRUCTURAL FEATURES AFFECTING THE LOWER PILTON BEDS AT DOWNEND, CROYDE BAY



B



CROSS SECTION OF THE SYNCLINE AT DOWNEND BETWEEN THE OUTCROPS OF TUFF B southeast trending tear faults, although at the Saunton end of the outcrop northeast-southwest faults are equally common.

Both north and south of the bay the slates are highly cleaved, the angle of cleavage is always high, being between 75° and vertical.

Figure 23 indicated the overall structure of the Croyde Bay section.

iii. The structure of the Fremington section.

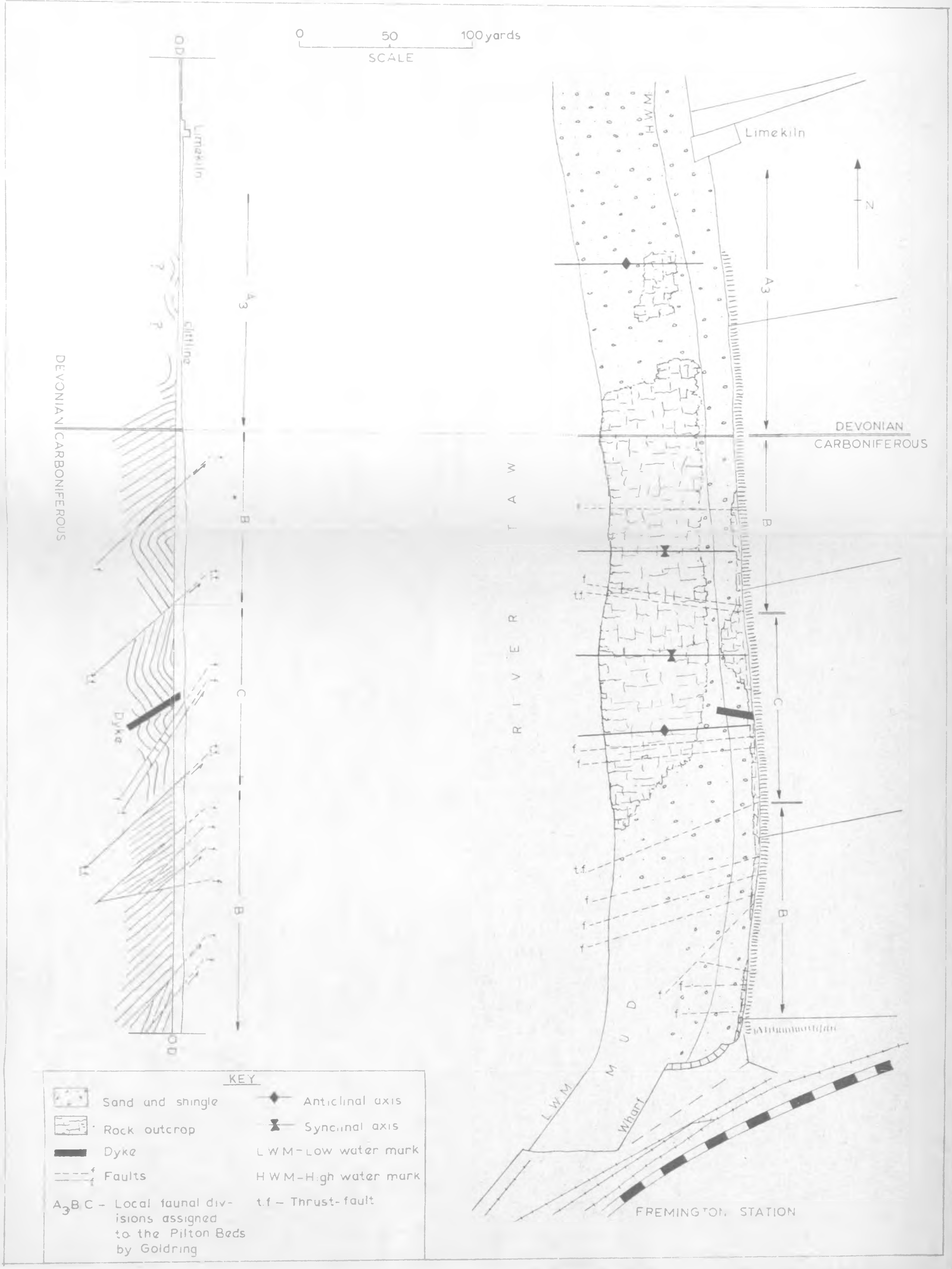
From a structural point of view, this is the most complex of the three sections described herein. The rocks are both thrust and faulted, particularly in the southern half of the outcrop. Only one normal junction occurs between the faunal divisions that can be recognised here, the rest being formed by thrust faults. The northern outcrop of Pilton Beds B exhibits dips that are generally southward, but within these beds there is a small asymmetrical syncline just to the north of their thrust junction with the Pilton Beds C. The latter occur as gently undulating beds into which has been intruded a basic dyke. Their southern margin is thrust against the southern outcrop of the Pilton Beds B. Thrusting and normal faulting are very common throughout this southern outcrop of the Pilton B beds although the fractures are not considered to have any great throws. The beds dip southward at angles of 50° - 60°. Figure 24 illustrates the structure of the Fremington section.

iv. The structure of the Bampton section.

In contrast to the coastal exposures, the strata in the road-cutting near Bampton is relatively undisturbed. The beds form a conformable sequence which dips at 27° N.187°, and there is no evidence of folding, faulting nor metamorphism is this section.

FIGURE 24

STRUCTURE OF THE FREMINGTON SECTION



CHAPTER 4

METHODS OF STUDY

In 1963 Miss J. Robinson embarked on a post-graduate study entitled, 'Conodonts from the Devonian rocks of Devonshire'. She collected samples from Middle and Upper Devonian outcrops in both North and South Devon. Her collections from South Devon were restricted to the Chudleigh area, while in North Devon she concentrated on the Croyde Bay outcrop of the Baggy and Pilton Beds, the Ilfracombe Beds at Combe Martin, and a series of isolated exposures north of Barnstable Bay, which she termed collectively, 'Goldring's Localities'.

Upon returning to the University College of Swansea, Miss Robinson processed and examined the bulk of her South Devon samples, but before starting any work on the rocks from North Devon she decided to curtail her studies in this field.

Under the supervision of Professor F.H.T.Rhodes, the writer started at the point where Miss Robinson had terminated her work. The Pilton Beds of North Devon were potentially the most interesting of her collections owing to the fact that they are a transitional group crossing the Devonian - Carboniferous boundary. These samples were duly processed, as were those from her other North Devon collections. Further sampling of the Croyde Bay section, the Fremington Pill section of the Pilton Beds, the Ashford Strand section of the Pilton Beds and the many inland exposures of the Baggy and Pilton Beds was undertaken by the author.

Of the 76 samples collected by Miss Robinson from Croyde Bay, only 6 yielded conodonts. She implemented a sample interval of 5 feet or sometimes

10 feet over much of the outcrop south of the beach, starting at the eastern end of the section, below the Saunton Sands Hotel, and working her way west and then north to Downend. It appears that she concentrated on this southerly outcrop, as 70 of her total of 76 samples were taken from here. North of the beach, where the outcrop is almost as long, and stratigraphically thicker, she collected only 6 samples. Ironically, it was these 6 samples that yielded conodonts. Miss Robinson's collection code for the Croyde Bay section was SS.

At Combe Martin Miss Robinson collected 7 samples of the Ilfracombe Beds, and here her collection code was S(CM). These samples were in no stratigraphic sequence, but merely isolated examples of the Ilfracombe Beds from various localities within the Combe Martin area. No conodonts were recovered from these grey-black limestones.

A further 7 samples were collected by Miss Robinson from various localities in the area north of Barnstable Bay, namely, Heaton Punchard 498.357 and 505.358, West Ashford 523.354, Ashford Church 533.353, Horridge 530.355, Bradiford 550.344, and Westway 562.350. No conodonts were recovered from these samples which she called 'Goldring's Localities'.

Despite the poor results obtained from the majority of Miss Robinson's samples, in terms of conodonts recovered, one important fact did emerge which was to help the writer in his own sampling. The only productive horizons in the Upper Baggy and Lower Pilton Beds were crinoidal limestone lenses, no conodonts being recovered from the black slates and shales which dominate the outcrops of these beds. Most of the slates, although treated with a variety of reagents, could not be disaggregated, while the softer and more calcareous black shales yielded no conodonts despite the fact that they could be broken down to some degree.

In view of these results, the present writer's collections within the Baggy and Pilton Beds were directed toward the location of as many crinoidal limestone horizons as possible. In many exposures such horizons could not be found, and when they were located, they were invariably uncommon and widely dispersed throughout the sections which were dominated by slate and shale. In exposures where no fresh limestone could be located the most calcareous of the shales were sampled.

Owing to the sporadic occurrence of the crinoidal limestone lenses, no systematic sample interval could be used; it was rather a case of locating limestones wherever possible and recording their stratigraphic position relative to each other and to certain marker horizons within the sections.

The exposures of the Baggy and Pilton Beds can be conveniently divided into three types:- (a) those containing fresh limestone horizons from which conodonts have been recovered, the dominant slate lithology proving unproductive; (b) those containing fresh limestones and shales, neither of which have yielded conodonts; (c) those which have no fresh limestones. The sections which may be included in type (a) are; the Croyde Bay section, the Fremington Pill section and the Bampton section. Type (b) exposures are mainly found in the Bray Valley, however, the Bampton section could almost be included in this category as only a single conodont specimen has been recovered from the limestone horizons occurring there. Type (c) includes all the other inland exposures of the Baggy and Pilton Beds together with the coastal section at Ashford Strand, and Miss Robinson's spot samples which she called 'Goldring's Localities'.

The writer proposes to give only the detailed stratigraphic distribution of the samples taken from the productive sections. Each section will be dealt with in turn.

Sampling of the Croyde Bay section.

Figure 25 indicates the stratigraphic distribution of those samples collected by Miss Robinson, and the author, from the Croyde Bay section, while Figure 26 indicates their geographic distribution.

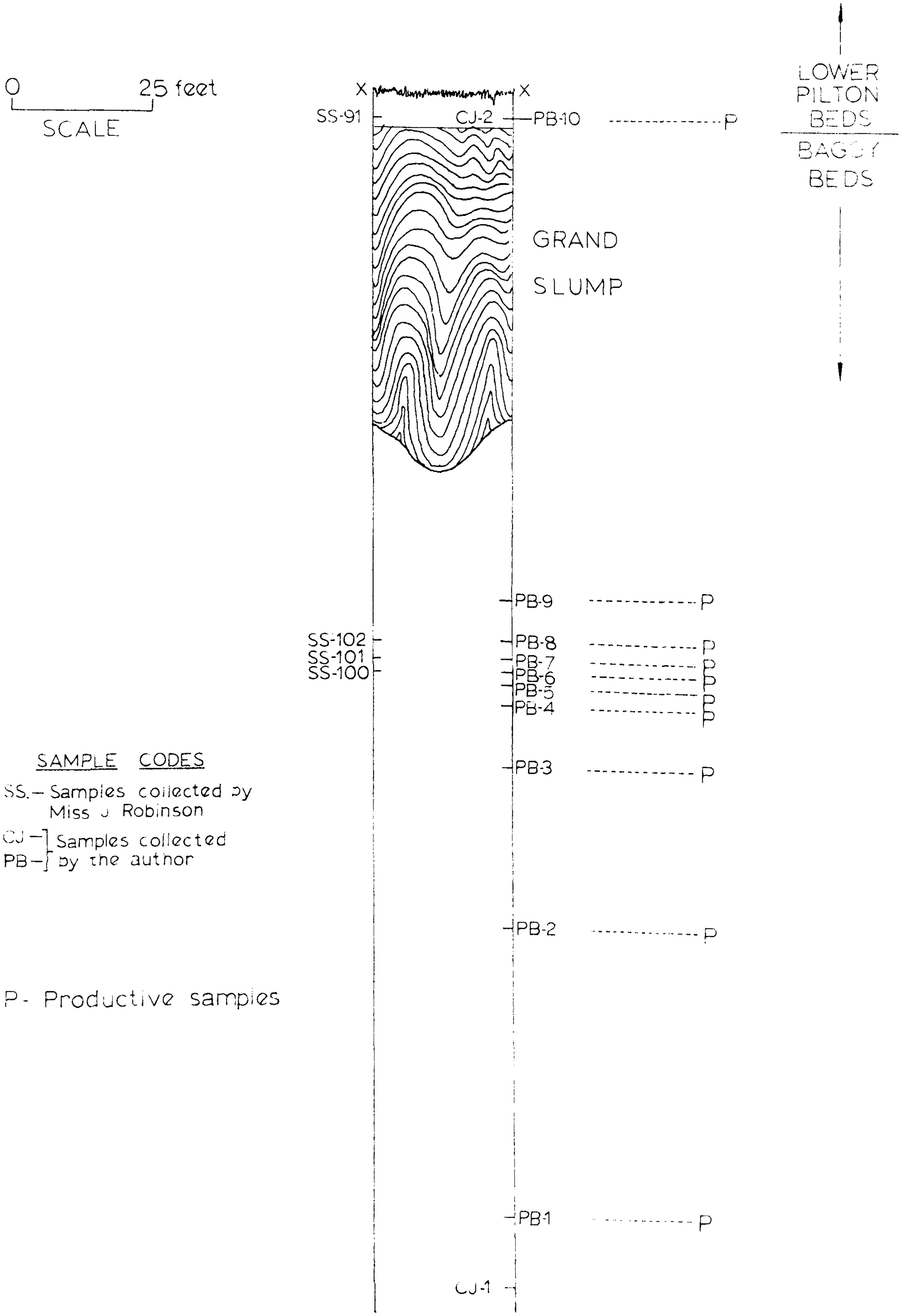
A total of 36 crinoidal limestone horizons were located in the Upper Baggy and the Lower Pilton Beds of Croyde Bay. Their distribution was completely irregular, with the result that the thickness of strata between successive samples ranged from a minimum of 10 feet to a maximum of 250 feet. The 36 samples collected by the author included recollections of the 6 productive horizons located by Miss Robinson. The crinoidal limestone lenses were relatively abundant north of the beach, but rare to the south. Initially, 5 kilograms of each sample were taken, but almost all horizons were resampled. The sample code used for these limestones was PB.

A further 32 samples of calcareous sandstone were also collected in the hope that this lithology would yield conodonts. The sample code given to these was CJ. Many of these bands were too decalcified to break down, and those that were disaggregated to some extent proved to be non-productive. Figure 25 illustrates the stratigraphic distribution of these bands.

In all, 138 samples were processed from the Croyde Bay section, of which only 34 crinoidal limestone horizons yielded conodont faunas. Figure 25 illustrates the stratigraphic distribution of these productive horizons within the Upper Baggy and the Lower Pilton Beds. As the Croyde Bay section is folded, special care in recording the precise stratigraphic position of the samples was essential. The tuff bands proved invaluable in locating the relative position of the samples from either side of the bay.

FIGURE 25

STRATIGRAPHIC DISTRIBUTION OF THE SAMPLES COLLECTED BY THE AUTHOR AND MISS J. ROBINSON FROM CROYDE BAY



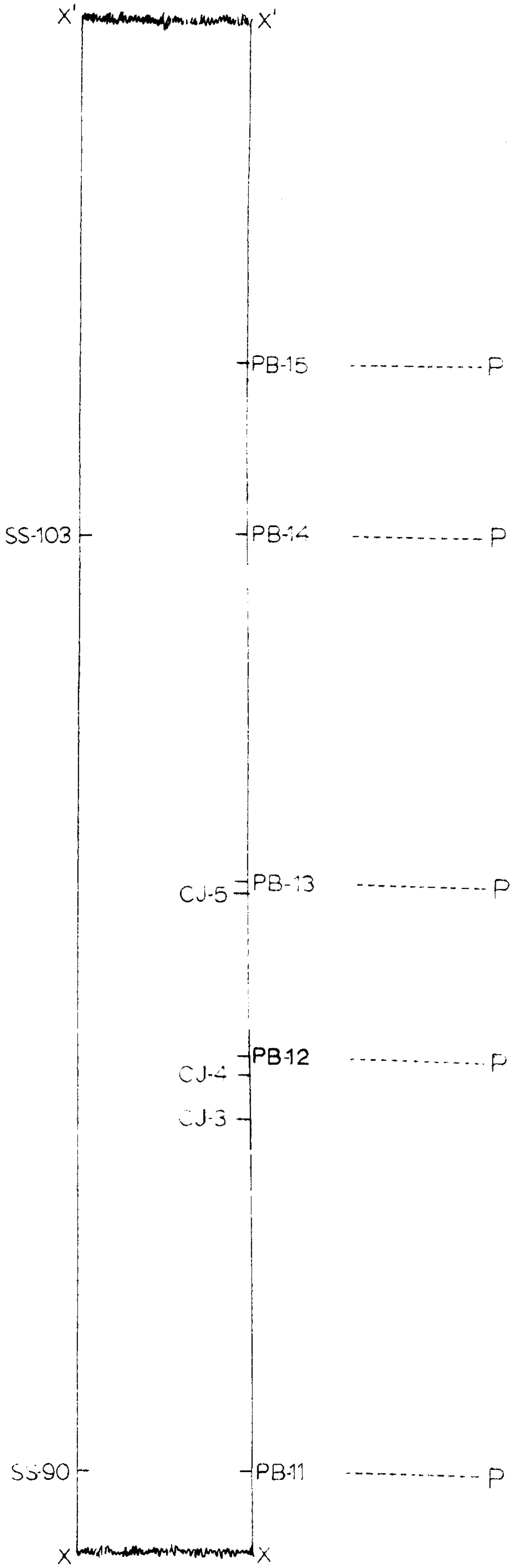

X'
X'
PB-15
P
SS-103
PB-14
P
CJ-5
PB-13
P
PB-12
P
CJ-4
CJ-3
SS-90
PB-11
P
X
X

FIGURE 25 (cont)

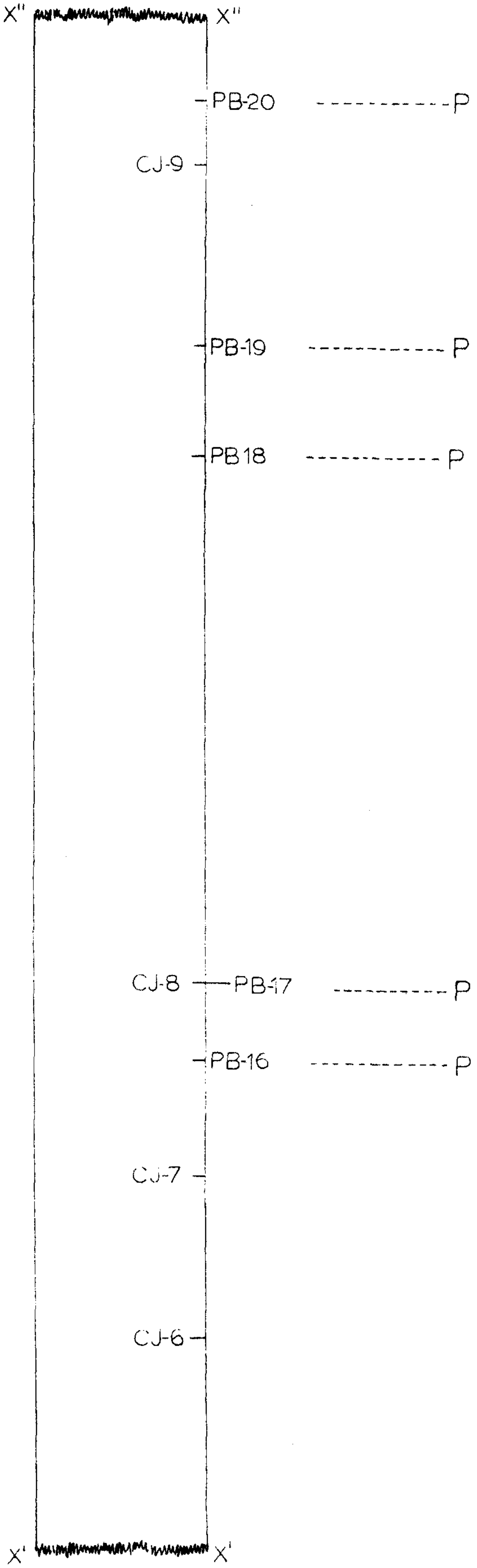


FIGURE 25(cont)

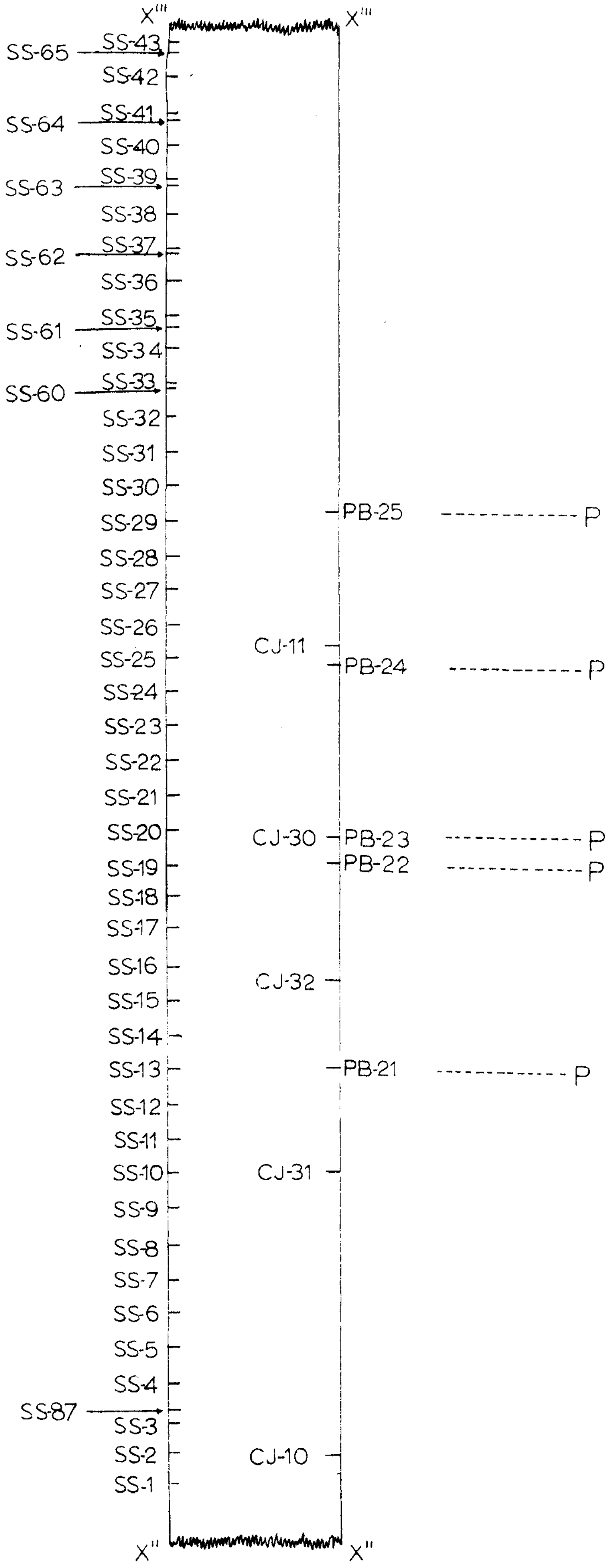


FIGURE 25 (cont)

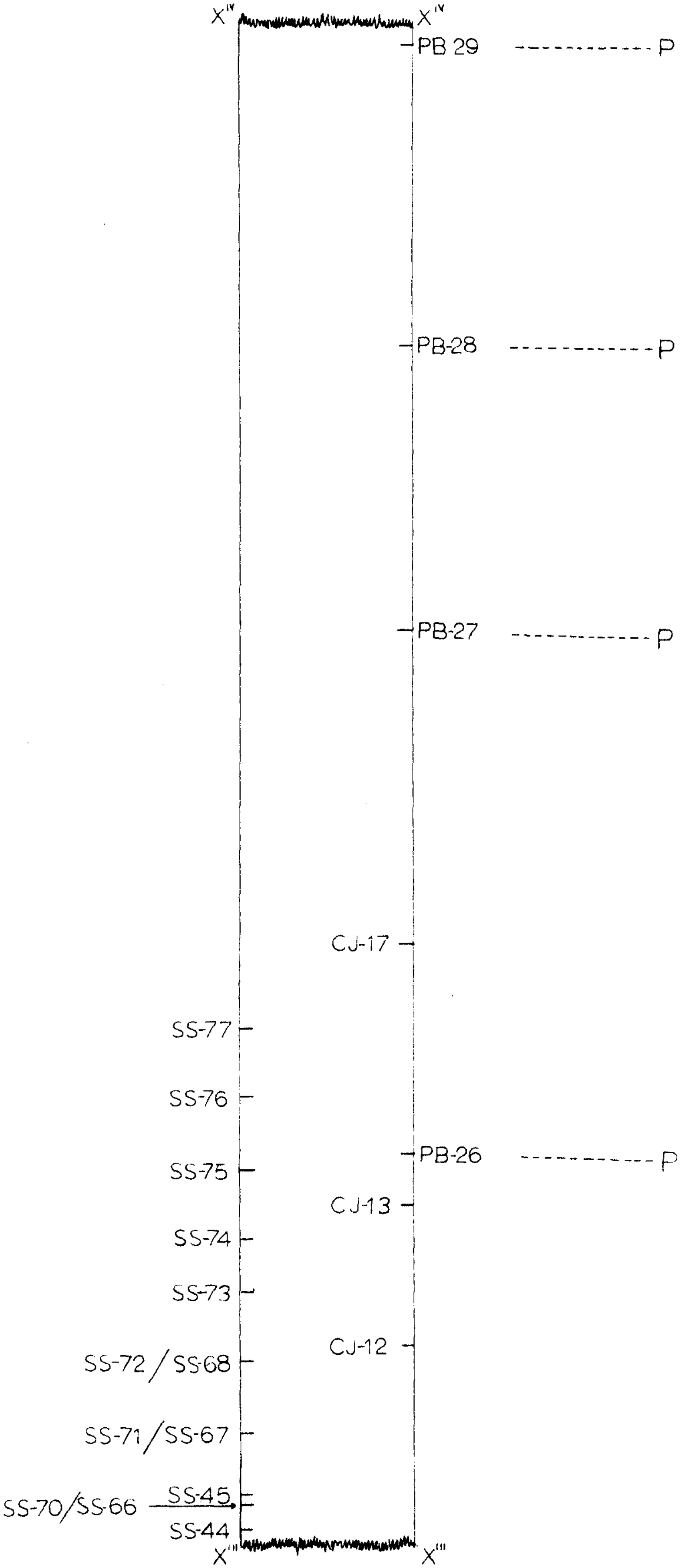


FIGURE 25 (cont)

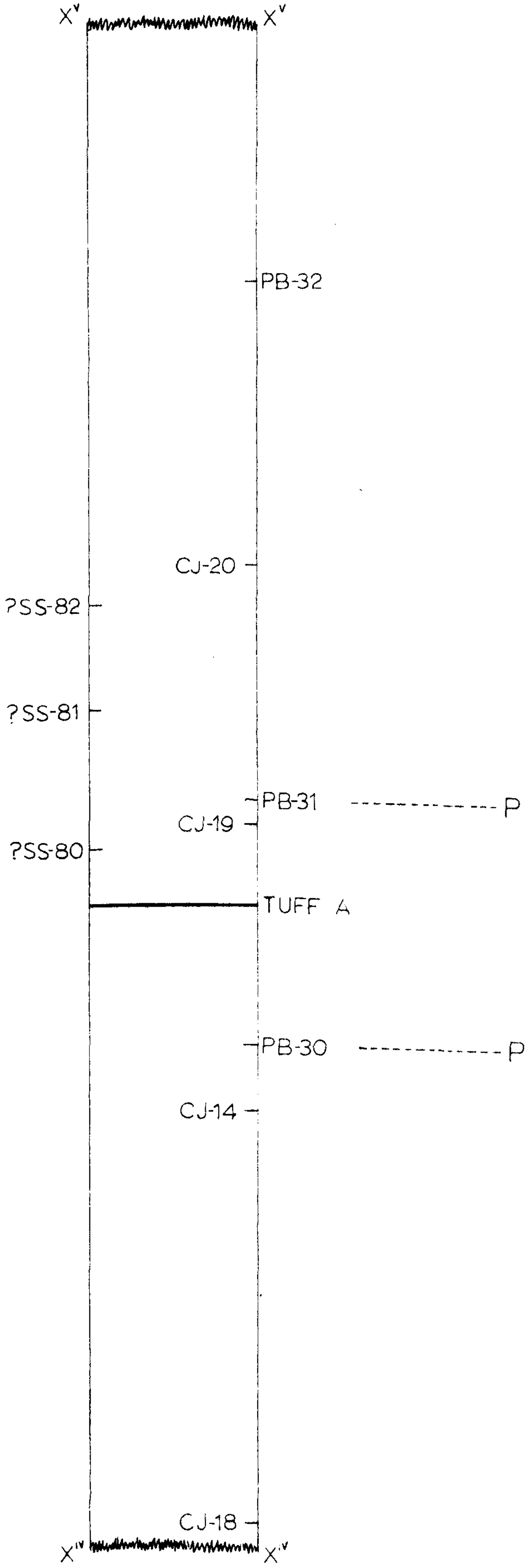


FIGURE 25 (cont.)

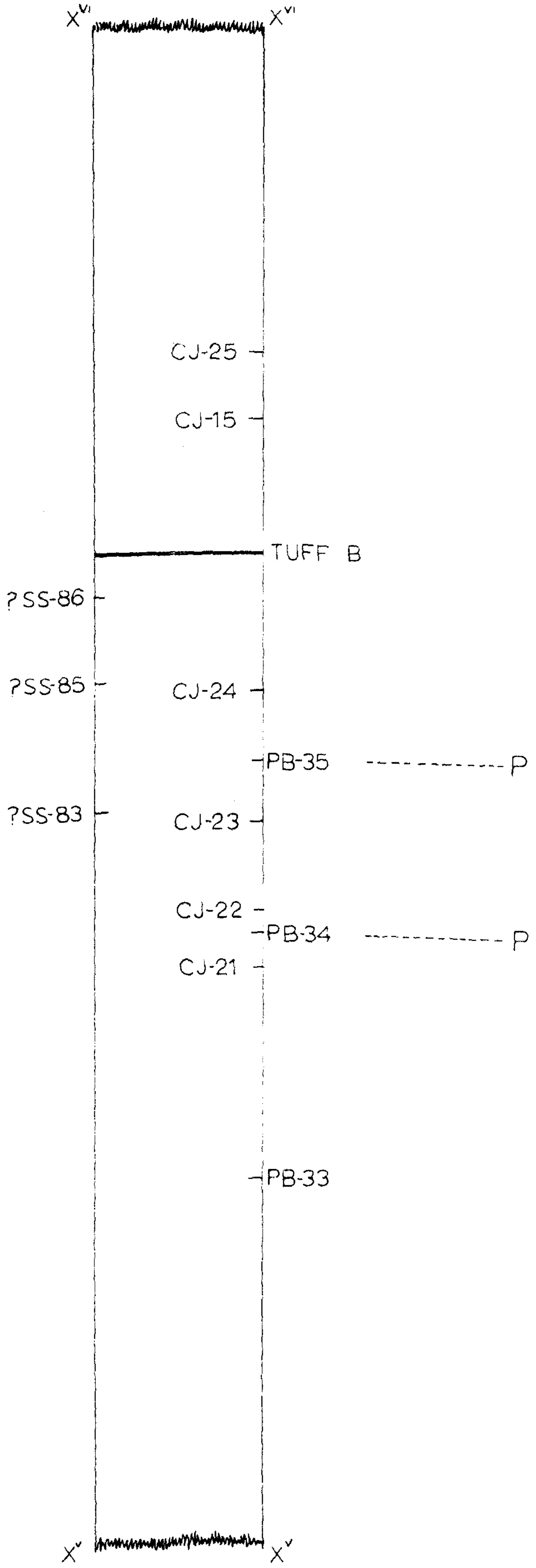


FIGURE 25 (cont)

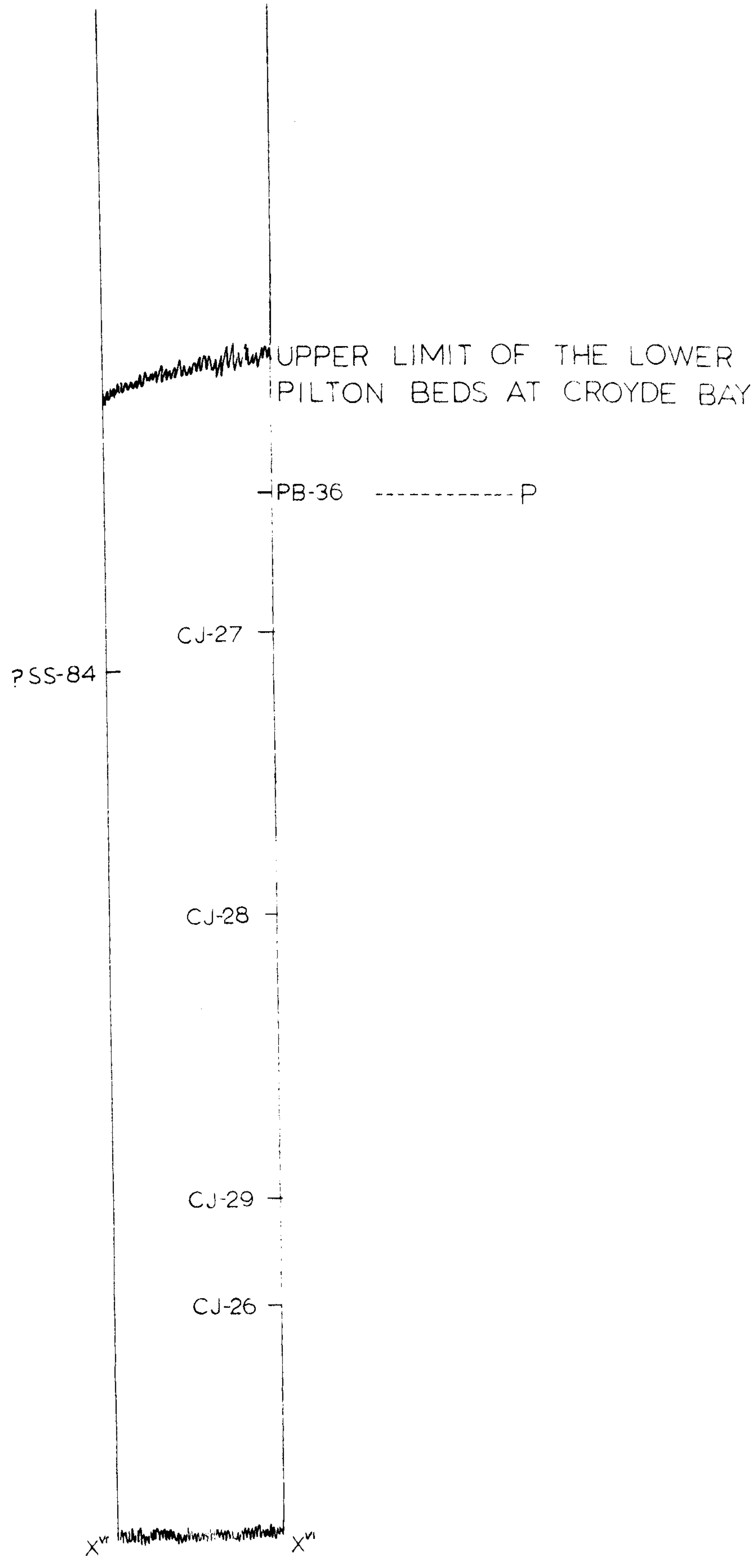
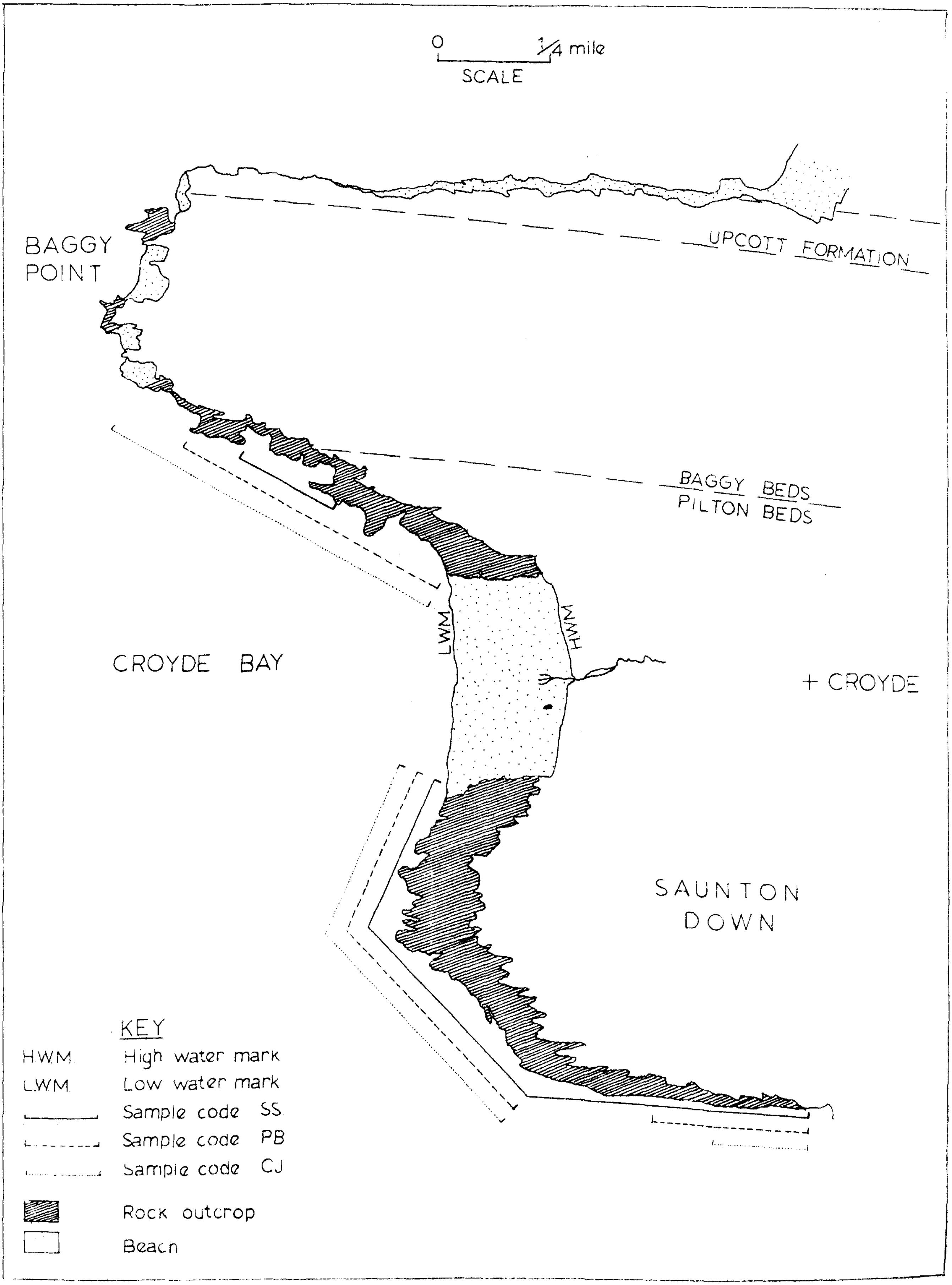


FIGURE 26

GEOGRAPHIC DISTRIBUTION OF THE SAMPLES COLLECTED BY THE AUTHOR AND MISS J ROBINSON FROM CROYDE BAY



Sampling of the Fremington Pill Section.

At Fremington, the situation was the same as at Croyde Bay. A total of 8 fresh crinoidal limestone horizons were located at this outcrop. All the horizons occurred within a vertical thickness of 70 feet in the southern third of the section. The remainder of the section was devoid of fresh material, but two further samples, which proved unproductive, were collected from the Pilton Bed C. These samples were of weathered fossiliferous shales.

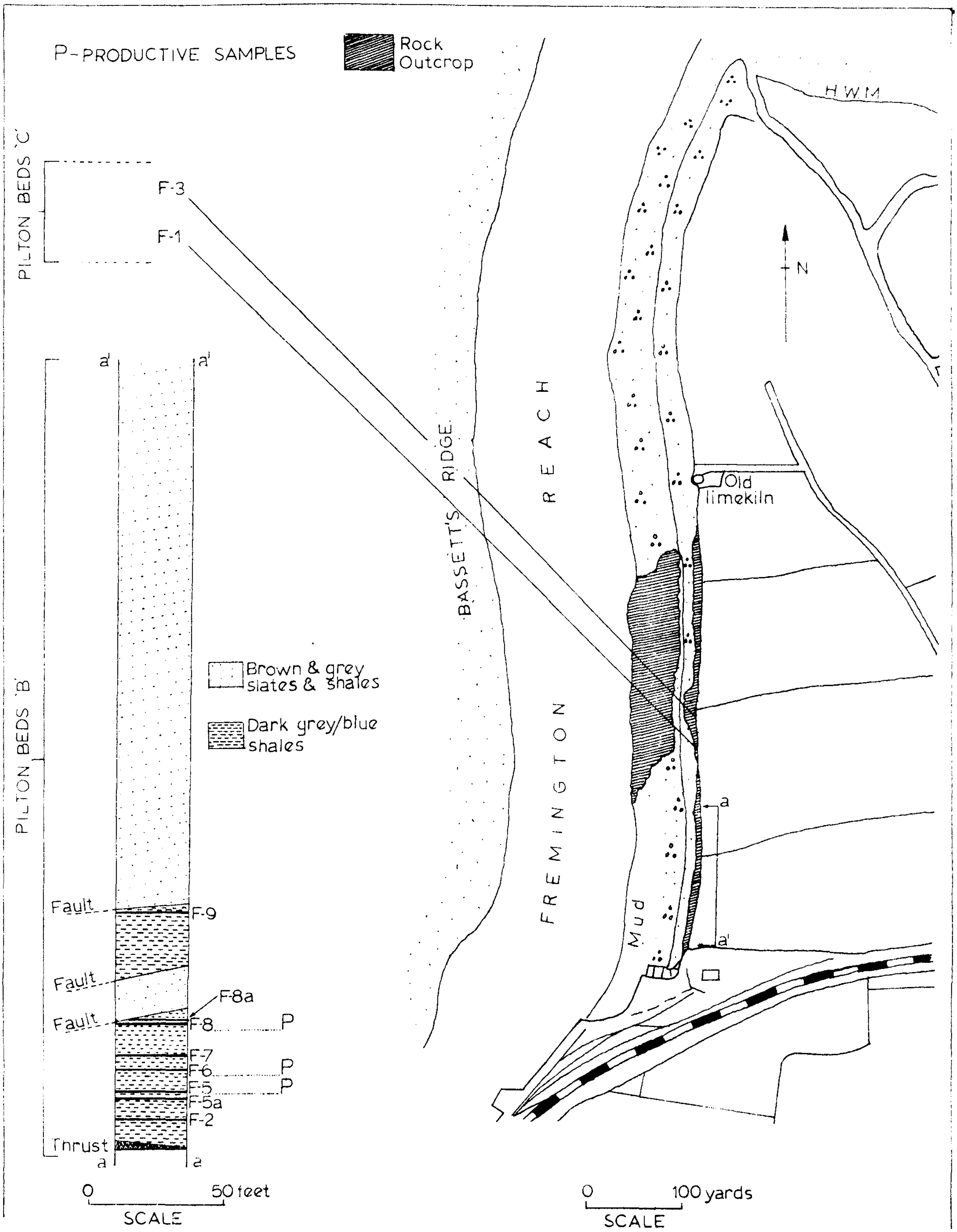
The 8 limestone samples have been recollected several times but conodont faunas were recovered from only three of them. Within the 70 feet of strata, the limestones were irregularly distributed, the thickness of rock between successive samples varies from 3 feet to 35 feet. The sample code for this locality was F, and Figure 27 shows the geographic and stratigraphic distribution of the limestones in this section.

Sampling of the Bampton Section.

At Bampton fresh limestone beds were more evenly dispersed throughout the relatively limited section. Seven limestone bands were located within the 95 feet of rock outcropping here, none of which were more than 15 feet apart stratigraphically. These seven bands, together with five samples of the interbedded slates and shales, were collected and processed. Of the twelve samples, only one yielded conodont material, and this was extensively recollected. The sample code chosen for this section was B and the stratigraphic distribution of the samples collected is indicated in Figure 20.

The age of the rocks occurring in the Bampton section has not been established precisely, although they are almost certainly uppermost Devonian or lowermost Carboniferous.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF THE SAMPLES COLLECTED FROM FREMINGTON PILL.



PROCESSING.

All the samples from the Upper Baggy and the Pilton Beds, including those collected by Miss Robinson, were processed according to the following procedure.

Five kilograms of each sample were initially collected from each horizon and this total weight was divided into two approximately equal portions of 2½ kilograms. The rock was then broken into small fragments of maximum diameter 1 inch. The fragmented portions were placed in plastic buckets and immersed in a 15% commercial acetic acid solution. Each bucket was carefully labelled and stored on wooden racks. After a period of 4 to 6 days the contents of each bucket were wet sieved and any undissolved rock was reacided with the same concentration of acetic acid. After a further 4 to 6 days the contents of the buckets were sieved once again, and if necessary further acid treatment and sieving continued until only insoluble rock material remained. Horizons which were resampled were processed in the same way, a further 3 to 4 kilograms being the average weight recollected.

The limestones collected were rapidly digested by this method, but the less calcareous samples showed little or no breakdown. A variety of other reagents were used in an effort to disaggregate the latter, including formic acid, hydrogen peroxide, sodium hydroxide and kerosene. By far the most successful was 90 volume hydrogen peroxide. Particularly durable slates were broken down to some extent by the employment of freeze-thaw techniques.

Four sieves were used in the wet sieving process, the mesh sizes being, from top to bottom, 25, 50, 100, 200. Material trapped in the first sieve was retreated with acid, while that trapped in the bottom three sieves was retained and air-dried. The residues retained on each of these three sieves were isolated. Excess moisture in each residue was removed by simple filtering in a conical funnel, and then the sieved material was spread on filter paper and allowed to dry at normal room temperatures.

When dry the samples (which were in three separate portions corresponding to the size of the sieves) were bottled and labelled. Some of the dirtier, muddy residues recovered after sieving were washed and boiled in metal saucepans to eliminate the very fine mud and silt. Immediately after the saucepan is taken from the heat and turbulence stops, the heavier conodonts sink to the bottom and the light, fine sediment, which is still in suspension, can be safely decanted.

In order to reduce the amount of material to be examined microscopically, each individual residue obtained from sieving was separated by using heavy liquids. Two methods of heavy liquid separation have been employed, one using bromoform and another using tetrabromoethane. The former method was used while the writer was working at the University College of Swansea, while the latter was introduced during his year at the Universityof Michigan.

Bromoform Method.

The dried residue is poured into a separating funnel containing clean, pure bromofrom, and stirred at frequent intervals. The specific gravity of the bromoform is 2.6 to 2.8, whereas that of conodonts is 2.84 to 3.10, consequently the conodonts, plus any other material with a density higher than that of bromoform, fall to the bottom of the separating funnel. The lighter material floats on the surface of the liquid. After one or perhaps two hours, the heavy fraction is run off and caught in filter paper. The bromoform is drained from the heavy fraction and rebottled, and then the sample itself is washed thoroughly with methanol to remove the traces of heavy liquid. After washing, the sample is rapidly dried in a furnace while the mixture of bromoform and methanol washings is set aside for later recovery of the bromoform.

The light fraction of the residue is now run off, washed and dried in a similar way, and the bromoform rebottled for further use. To recapture the bromoform from the methanol washings, the mixture is shaken in a separating funnel with clean water. The water extracts the methanol from the mixture forming a milky liquid which floats on top of the bromoform. The funnel is allowed to stand overnight and the bromoform can be run off. If clear calcite (specific gravity 2.72) floats on the heavy liquid it is then pure enough to be used once more.

Tetrabromoethane Method.

The principle is exactly the same as that of the previously described method. The use of tetrabromoethane is preferable because of its higher specific gravity of 2.89, its lower toxicity, its low volatility and relatively inoffensive odour. Furthermore, tetrabromoethane is very easily recovered from washings, an important consideration when using this relatively expensive liquid.

The residue is allowed to settle out in tetrabromoethane for one to two hours, although a longer period of time is desirable if the liquid is very pure. The dilution of such pure forms of this liquid, to a specific gravity of 2.75, is recommended to make the process more rapid. The heavy and light fractions are washed with white gasoline before being dried, and the tetrabromoethane is recovered by simply allowing the gasoline to evaporate.

Having dried the heavy and light fractions, the latter are stored and the heavy material examined microscopically, using a binocular microscope capable of magnifications of the order of at least x60. The material is scattered on a petri dish, which has been squared by some means, then systemstically searched for conodonts and other organic material. Using a fine brush, the conodonts are picked and mounted on microscope slides which are divided into 60 or 100 squares. Tragacanth is used to mount the specimens on the slides.

To aid identification the conodonts are photographed orally, aborally and laterally. The photographic prints produced for this purpose display magnifications of x40 the original size of the conodont elements. The camera used in Swansea was a Leitz Aristophot, while that used in the University of Michigan was a more sophisticated version of the same apparatus.

Preservation of the conodont faunas.

The conodonts recovered from the Croyde Bay and Fremington Pill sections were black and opaque. However, in some of the more delicate forms 'white matter' was visible at the extreme tips of the denticles. The one conodont recovered from the Bampton section was grey-brown in colour and also opaque.

A considerable number of the conodonts from the Pilton Beds were incomplete, the blades of the platform types were often missing, and few of the bar, blade and pick types were without some small fracture. However, the problem of breakages was less significant than that posed by minute quartz and calcite crystals which were often found adhering to the surface of specimens, obscuring their detailed form. Two techniques were employed in an attempt to clean specimens of these crystals, (a) using ultrasonic vibrations and (b) using hydrofluoric acid. The ultrasonic vibrator proved to be too violent and shattered the conodonts themselves, while the procedure involving the use of hyrofluoric acid is so intricate (too great a concentration of the acid attacks the conodont material) that this was also abandoned. Some cleaning was ultimately effected under the microscope, by careful and meticulous manual scraping of the specimens with a very fine needle.

There follows a list of the collecting data for the unproductive coastal and inland outcrops of the Upper Baggy and Pilton Beds investigated by the author.

Plaistow Quarries (576.373) at Bradiford Water - From this outcrop of the Baggy Beds in the Bradiford Water Valley, four spot samples were taken from the thick occasionally fossiliferous sandstones which dominated the lithology.

Exposures in the Caen River Valley - Outcrops of both the Baggy and Pilton Beds occur in this valley, but no samples were collected due to the unsuitable lithologies that were encountered at all the sections located.

Lobb (470.370), east of Saunton - No samples of the massive Baggy Beds sandstone were collected from this outcrop.

North Lobb (470.380)- Two spot samples were collected from the almost horizontally bedded fossiliferous slates and sandstones at this locality.

Quarries in the Bray River Valley between Brayford (680.340) and Charles (690.320) - Here outcrop the best inland exposures of the Baggy Beds ina series of road-side quarries. Collections were made at *Council* and *Notts* Quarries (693.327), where seven and five samples respectively were taken from the interbedded sandy limestone, massive sandstones and calcareous shales. Only the horizons which appeared to be more calcareous were sampled and hence the sample interval was inconsistent. No samples were collected from Bondy's Pit (688.339), Moule's Chamber (689.338) and Wilcombe Quarry (688.336).

Rumsam Road, Barnstable (570.314) - At this outcrop the boundary between the Upper Pilton Beds and the Codden Hill Cherts can be seen. A single sample of the bedded cherts was collected, immediately above the last occurrence of the Upper Pilton slate lithology.

Poleshill Quarry, North Barnstable (550.345) - No samples were collected at this locality.

Barnstable Junction Station, Barnstable - Here the Upper Pilton Beds outcrop to the south of the railway track in a relatively high rock face. Twelve samples of the sandstone, slate and shale lithology were collected at 5 feet intervals from the base of the exposure.

Blatchford House, North Barnstable (567.359) - No samples were collected from this outcrop.

Ashford Strand - At this locality Goldring's local faunal subdivision A3 outcrops. The exposures occur as reefs on the narrow shore, although occasional patches of rock are found in the very low cliffline of the estuary. The lithology is dominated by sandstones and slates, some of which are fossiliferous. Eleven spot samples were taken of the more fossiliferous material located within this section. The sample interval utilised was irregular in order to accommodate the irregularity of occurrence of the more fossiliferous horizons.

CHAPTER 5

FAUNA ASSOCIATED WITH THE CONODONTS OF THE UPPER BAGGY AND THE PILTON BEDS.

As has been explained in Chapters 3 and 4, the conodonts recovered from the Pilton Beds and underlying Upper Baggy Beds were restricted to the infrequently occurring crinoidal limestone lenses. These lenses were composed of shell debris and limestone and the ratio of these two constituents was highly variable. Some lenses were almost wholly made up of shell fragments, of which brachiopods, crinoids, pelecypods, gastropods, trilobites and a few corals were most abundant, while other lenses were composed primarily of crystalline limestone with only disarticulated crinoid and blastoid columnals. Owing to the nature of their deposition, the macrofossils found in the limestone lenses were invariably difficult to identify.

In the slates, shales and sandstones which constitute the bulk of the Pilton Beds, relatively well preserved macrofaunas may be collected. Goldring (1955) recovered readily identifiable macrofaunas from both the Baggy and Pilton Beds, but he made no detailed study of the fauna from the lower beds. He noted that thick-shelled pelecypods and gastropods were the main faunal elements in the Baggy Beds, together with an abundance of plant stems but a rarity of plant leaves. Fish scales were also common in these beds but the only common brachiopod was Lingula. Indications of former benthic life was present in the form of burrows and tracks of various kinds.

The fauna of the Pilton Beds is more diverse. Brachiopods are represented by productids, spiriferids, orthotetids, orthids, athyrids and rhynconellids. Pelecypods, gastropods, and trilobites are not uncommon, and goniatites, although rare, were found in the Upper Pilton Beds. Corals, echinoderms and bryozoa have also been identified from these beds.

On the basis of the characteristic macrofauna, Goldring was able to divide the Pilton Beds into three major faunal divisions, the oldest of which could be further divided into three subdivisions. Each of Goldring's divisions and its characteristic fauna are listed in ascending order:-

PILTON BEDS A: - containing *Phacops* (*P.*) *accipitrinus*.

Pilton Beds A1: type locality Laticosta Cave (427.401)
- containing *Whidbornella pauli*, *W. caperata*, *Hamlingella capillaris*, *Mesoplica praelonga*, *Cyrtospirifer verneuili*.
- absent *Hamlingella piltonensis*.

Pilton Beds A2: type locality 'Tuff' band A.
- containing *W. caperata*, *H. capillaris*, *M. praelonga*, *M. simplicoir*, *C. verneuili*.
- absent *W. pauli*, *H. piltonensis*.

Pilton Beds A3: type locality Poleshill Quarry (550.345)
- containing *W. caperata*, *H. piltonensis*, *M. simplicoir*, *Dictyoclostus* sp. 1, *C. verneuili*, *Spirifer tornacensis*.
- absent *H. capillaris*.

PILTON BEDS B: type locality Fremington Station (517.335)
- containing *Gattendorfia crassa*, *Cyrtosymbole* (*Macrobole*) *hercules*, *C.* (*M*) *duodecimae*, *C.* (*M*) *mulesi*, *C.* (*Waribole*) *porteri*, *Buxtonia paeckelmanni*, *Productina fremingtonensis*, *Spirifer tornacensis*, *Syringothyris*.

- absent *Whidbornella*, *Hamlingella*, *Cyrtospirifer verneuili*, *M. praelonga*, *M. simplicoir*.

PILTON BEDS C: type locality Ladywell Wood Quarry (517.358).

- containing *Piltonia salteri*, *P. fremingtonensis*, *Dictyoclostus porteri*, *Spirifer tornacensis*.

These then are the local faunal divisions that Goldring was able to recognise in the Pilton Beds, on the basis of the macrofossils that he identified. A complete faunal list submitted by Goldring (1956) is given in the following pages.

FAUNAL LIST FOR PILTON BEDS A1.

Phacops (*Phacops*) *accipitrinus* Rud. & E. Richter
Whidbornella caperata (Sowerby)
Whidbornella pauli Goldring
Hamlingella capillaris (Reed)
Mesoplica praelonga (Sowerby)
Pleurodictym sp.
Schizophoria resupinata (Martin)
Derbyia kayseri Gallwitz
Leptaena analoga (Phillips)
Cyrtospirifer verneuili (Murchison)
Athyris cf. *lens* (Winchell)
Nudirosta laticosta (Phillips)
Camerotoechia letiensis (Gosselet)
Aviculopecten (*A*) *nexilis* (Sowerby)
Ptychopteria damnoniensis (Sowerby)
Ctenodonta lirata (Phillips)

FAUNAL LIST FOR PILTON BEDS A2.

Phacops (*Phacops*) *accipitrinus* Rud. & E. Richter

Whidbornella caperata (Sowerby)

Hamlingella capillaris (Reed)

Mesoplica praelonga (Sowerby)

Mesoplica simplicoir (Whidbourne)

Zaphrentis omaliusi Edwards & Haime

Pleurodictym sp.

Dalmanella interlineata (Sowerby)

Dalmanella whidbornei Gallwitz

Derbyia kayseri Gallwitz

Leptaena analoga (Phillips)

?*Spirifer tornacensis* de Koninck

Cyrtospirifer verneuili (Murchison)

Cyrtospirifer julii Dehee

Athyris concentrica van Buch

Crurithyris unquiculus (Sowerby)

Camerotoechia letiensis (Gosselet)

Aviculopecten (*A*) *transversus* (Sowerby)

Aviculopecten (*A*) *nexilis* (Sowerby)

Aviculopecten (*A*) *auritus* (Whidborne)

Pterinopecten halli Whidborne

Streblopteria piltonensis (Whidborne)

Streblopteria lepis (Whidborne)

Ctenodonta lirata (Phillips)

Sanguinolites spp.

Raphistoma junius de Koninck

Capulus compressus Goldfuss

Bellerophon labyrinthoides Whidborne

Orthoynchia acuta Romer

FAUNAL LIST FOR PILTON BEDS A3

Phacops (*Phacops*) *accipitrinus* Rud. & E. Richter

Whidbornella caperata (Sowerby)

Hamlingella piltonensis (Reed)

Mesoplica simplicoir (Whidborne)

Zaphrentis sp.

Pleurodictym sp.

Dalmanella bergica (Kayser)

Cyathaxonia sp.

Lophophyllum sp.

Dalmanella interlineata (Sowerby)

Rhipidomella michelini Leveille

Derbyia kayseri Gallwitz

Streptorhynchus (*Schuchertella*) *paeckelmanni* Gallwitz

Streptorhynchus (*Schuchertella*) *portlockiani* (Von Sem)

Leptaena analoga (Phillips)

Spirifer tornacensis de Koninck

Spirifer strunianus Gosselet

Cyrtospirifer verneuili (Murchison)

Cyrtospirifer julii Dehee

Spiriferellina bouchardi (Murchison)

Athyris concentrica van Buch

Crurithyris unquiculus (Sowerby)

Aviculopecten (*A*) *transversus* (Sowerby)

Aviculopecten (*A*) *nexilis* (Sowerby)

Aviculopecten (*Girtypecten*) *austeni* (Romer)

Pterinopecten *halli* Whidborne

Streblopteria *piltonensis* (Whidborne)

Streblopteria *hicksii* (Whidborne)

Sanguinolites *porteri* Whidborne

Sanguinolites spp.

FAUNAL LIST FOR PILTON BEDS B

Streptorhynchus (*Schuchertella*) *portlockiani* (v. Sem)

Imitoceras sp.

Gattendorfia *crassa* Schindewolf

Gattendorfia sp.

Cyrtosymbole (*Macrobole*) *hercules* Rud. & E. Richter

Cyrtosymbole (*Macrobole*) *duodecimae* R. & E. Richter

Cyrtosymbole (*Macrobole*) *mulesi* R. & E. Richter

Cyrtosymbole (*Waribole*) *porteri* Goldring

Brachymetopus (*B*) *woodwardi* (Whidborne)

Productina *fremingtonensis* (Reed)

Buxtonia *paeckelmanni* Paul

Buxtonia *nigra* (Gosselet)

Linoproductus cf. *corrugatus* (McCoy)

Avonia sp. nov. 1

Spirifer *tornacensis* de Koninck

Syringothyris spp.

Brachythyris *ratingensis* Paul

Spiriferellina spp.

Cleiothyridina *roysii* (Leveille)

Derbyia *steinhagei* Paul

Derbyia kayseri Gallwitz
Streptorhynchus paeckelmanni Gallwitz
Leptaena analoga Phillips
Schizophoria resupinata (Martin)
Camerotoechia pleurodon (Phillips)
Streblopteria piltonensis (Whidborne)
Aviculopecten cf. *wasserfallensis* Paul
Leiopteria bodana Romer
Ptychomphalus cf. sp. 1 Paul
Loxonema cf. *anglicum* d'Orbigny
Pleurodictym sp.
Dalmanella bergica (Kayser)
Crurithyris unquiculus (Sowerby)
Aviculopecten (*A*) *nexilis* (Sowerby)
Pterinopecten halli (Whidborne)
Streblopteria hicksii (Whidborne)
Sanguinolites mimus Whidborne
Sanguinolites spp.
Cypricardinia scalaris Phillips
Ptychomphalus spp.
Raphistoma junius de Koninck
Bellerophon spp.
Spiriferellina perplicata North
Spiriferellina sp. nov. 1
Spiriferellina sp. nov. 2
Athyris concentrica von Buch
Athyris sp. nov. 1
Avonia schmidti Packelmann

Streptorhynchus portlockiana (von Sem)

Ptychomphalus spp.

FAUNAL LIST FOR PILTON BEDS C.

Imitoceras sp.

Piltonia salteri Goldring

Brachymetopus (*B*) *woodwardi* (Whidborne)

Productina fremingtonensis (Reed)

Avonia sp. nov. 1

Linoproductus cf. *corrugatus* (McCoy)

Spirifer tornacensis de Koninck

Cleiothyridina roysii (Leveille)

Aviculopecten nexilis (Sowerby)

Aviculopecten cf. *wasserfallensis* Paul

Cypricardinia scalaris Phillips

Bellerophon sp.

Ptychomphalus spp.

Dalmanella bergica (Kayser)

Streblopteria hicksii (Whidborne)

Capulus sp.

Sanguinolites spp.

Athyris sp. nov. 1

Spiriferellina perplicata North

Brachythyris ratingensis Paul

Streptorhynchus paeckelmanni Gallwitz

Plicatifera lamellosa Paul

Dictyoclostus porteri (Reed)

In addition to conodonts, many other types of organic remains were recovered from the limestone residues which were examined microscopically. Most abundant were fish teeth and plates, sponge spicules, and ostracod molds and casts. A small species of gastropod was particularly prolific in certain of the Lower Pilton samples, and bryozoa were well represented in several horizons. It has been mentioned in Chapter 2, Section C, that the spore Hymenozonotriletes lepidophytus, has been isolated from three horizons in the Lower Pilton Beds.

Although this chapter is essentially concerned with the fauna associated with the conodonts of the Pilton Beds, at this juncture it is convenient to include a list of conodonts prepared by D.L.Dineley. All the conodonts listed are from a horizon approximately 120 metres above the base of the Pilton Beds on the Saunton Sands foreshore.

Gnathodus texanus Roundy
Hibbardella sp. & spp.
Icriodus sp.
Ligonodina spp.
Lonchodina spp.
Lonchodina devonica n. sp.
Lonchodus distans Smith
Lonchodus spp.
Oistodus spp.
Pelekysgnathus nigrus n. sp.
Pelekysgnathus serratus n. sp.
Pelekysgnathus thomasi n. sp.
Polygnathus adola Cooper
Polygnathus cf. P. decorosus Stauffer

Polygnathus cf. *P. spicata*

Polygnathus symmetrica

Neoprioniodus cf. *P. confluens* Branson & Mehl

Neoprioniodus cf. *P. corniger* Branson

Neoprioniodus spp.

? *Ptiloconus* n. sp.

Roundya ferex n. sp.

Roundya hassi n. sp.

Spathognathodus bassleri n. sp.

Spathognathodus elongatus Branson & Mehl

Spathognathodus cf. *S. regularis* Branson & Mehl

Spathognathodus sauntonensis n. sp.

Synprioniodina forsenta Stauffer

Tripodelluoplanus n. sp.

This list differs with that of the present author in three significant respects. (1) It records no specimens of *Spathognathodus aculeatus* and its close relatives, this species is very abundant in the author's collections. (2) The genus, *Pseudopolygnathus*, does not appear on Dineley's list, a form which dominates the conodont fauna in virtually all the Lower Pilton samples examined by the author. (3) The author has noted specimens which look like *Gnathodus texanus*, but considers that such forms are juvenile pseudopolygnathids.

The two lists agree on the presence of *Icriodus*, *Pelekysgnathus* and *Polygnathus*, and the absence of *Palmatolepis*.

CHAPTER 6

DISTRIBUTION OF THE CONODONT FAUNAS WITHIN THE UPPER BAGGY AND THE PILTON BEDS

An account of the stratigraphic distribution and total number of conodont bearing horizons, located in the Upper Baggy and the Pilton Beds, has been given in Chapter 4. The present Chapter concerns the distribution of the conodont faunas themselves. A description of this nature may be conveniently accomplished under two sub-headings, (a) the numerical distribution of the conodonts within the horizons samples, and (b) the stratigraphic range of the genera, species and subspecies within the Upper Baggy and the Pilton Bed successions.

(a) The numerical distribution of the conodont faunas.

Table 1 shows the total number of identifiable conodonts recovered from each horizon sampled in the Upper Baggy and the Pilton Beds. The weight of rock initially collected at each horizon is recorded, as is the weight of any recollections that were made. A histogram has been constructed to express the number of conodonts yielded per kilogram of rock from each of the productive horizons (see Figures 28 & 29).

(b) The stratigraphic range of the important conodont taxa.

Figure 30 illustrates the range of the individual conodont genera within the Upper Baggy and the Pilton Beds. Figure 31 shows the range of the species and subspecies of the genus Spathognathodus, while Figure 32 of the genus Polygnathus. The ranges of the pseudopolygnathid, icriodid and pelekysgnathid species are included in the same Figure (Figure 33), as only two species of each genus were identified.

The 'blade' and 'bar' type conodont elements recovered from the Upper Baggy and the Pilton Beds, were present throughout the successions and consequently, they were not stratigraphically important. They have been systematically described in only a very general way.

TABLE 1

THE NUMERICAL DISTRIBUTION OF THE CONODONT FAUNAS RECOVERED FROM THE UPPER BAGGY AND THE PILTON BEDS

SAMPLE NUMBER AND CODE	WEIGHT OF INITIAL SAMPLE	WEIGHT OF SAMPLE RECOLLECTED	TOTAL NUMBER OF IDENTIFIABLE CONODONTS
F.9	5 kilograms	0 kilograms	-
F.8a	5 "	0 "	-
F.8	5 "	4 "	91
F.7	5 "	0 "	-
F.6	5 "	4 "	140
F.5	5 "	3 "	51
F.5a	5 "	0 "	-
F.3	5 "	0 "	-
F.2	5 "	0 "	-
F.1	5 "	0 "	-

F = Samples collected by the author from the Fremington coastal exposure.

PB.36	5 kilograms	2 kilograms	62
PB.35	5 "	3 "	179
PB.34	4 "	1.5 "	12
PB.33	4.5 "	0 "	0
PB.32	4 "	4 "	0
PB. 31	3 "	0.5 "	16
PB.30	5 "	3 "	15
PB.29	5 "	3 "	110

TABLE 1 (Continued)

SAMPLE NUMBER AND CODE	WEIGHT OF INITIAL SAMPLE	WEIGHT OF SAMPLE RECOLLECTED	TOTAL NUMBER OF IDENTIFIABLE CONODONTS
PB.28	5 kilograms	4 kilograms	20
PB.27	5 "	3 "	123
PB.26	5 "	0 "	12
PB.25	5 "	3 "	561
PB.24	5 "	3 "	151
PB.23	5 "	5 "	56
PB.22	5 "	0 "	10
PB.21	5 "	3 "	206
PB.20	5 "	2.5 "	322
PB.19	5 "	0 "	12
PB.18	4 "	0 "	33
PB.17	5 "	2 "	217
PB.16	5 "	4 "	478
PB.15	5 "	3 "	41
PB.14, SS.103	5 "	2 "	32
PB.13	5 "	0 "	145
PB.12	5 "	2 "	315
PB.11, SS.90	5 "	0 "	13
PB.10, SS.91	5 "	4 "	261
PB.9	5 "	1.5 "	98
PB.8, SS.102	5 "	2 "	36
PB.7, SS.101	5 "	2 "	13
PB.6, SS.100	5 "	2 "	42
PB.5	5 "	0 "	16

TABLE 1 (continued)

SAMPLE NUMBER AND CODE	WEIGHT OF INITIAL SAMPLE	WEIGHT OF SAMPLE RECOLLECTED	TOTAL NUMBER OF IDENTIFIABLE CONODONTS
PB.4	5 kilograms	3 kilograms	172
PB.3	5 "	0 "	33
PB.2	5 "	1 "	193
PB.1	5 "	2 "	8

PB = Samples of fossiliferous limestone collected by the author from Croyde Bay.

B.12	5 kilograms	0 kilograms	-
B.11	5 "	4 "	-
B.10	5 "	0 "	-
B.9	5 "	5 "	-
B.8	5 "	0 "	-
B.7	5 "	25 "	1
B.6	5 "	5 "	-
B.5	5 "	0 "	-
B.4	5 "	0 "	-
B.3	5 "	0 "	-
B.2	5 "	5 "	-
B.1	5 "	3 "	-

B = Samples of fine-grained limestone collected by the author from Bampton exposure.

N.B. In the three exposures listed above, all the sampled horizons are arranged in stratigraphic order. The samples tabulated in the remainder of Table 1 are not in stratigraphic order.

TABLE 1 (Continued)

SAMPLE NUMBER AND CODE	WEIGHT OF INITIAL SAMPLE	WEIGHT OF SAMPLE RECOLLECTED	TOTAL NUMBER OF IDENTIFIABLE CONODONTS
CJ.1	4 kilograms	0 kilograms	-
CJ.2	5 "	0 "	-
CJ.3	5 "	0 "	-
CJ.4	5 "	0 "	-
CJ.5	3.5 "	0 "	-
CJ.6	5 "	0 "	-
CJ.7	5 "	0 "	-
CJ.8	5 "	0 "	-
CJ.9	5 "	0 "	-
CJ.10	5 "	0 "	-
CJ.11	5 "	0 "	-
CJ.12	4.5 "	0 "	-
CJ.13	5 "	0 "	-
CJ.14	5 "	0 "	-
CJ.15	5 "	0 "	-
CJ.16	5 "	0 "	-
CJ.17	5 "	0 "	-
CJ.18	4 "	0 "	-
CJ.19	5 "	0 "	-
CJ.20	5 "	0 "	-
CJ.21	5 "	0 "	-
CJ.22	4.5 "	0 "	-
CJ.23	5 "	0 "	-
CJ.24	3.5 "	0 "	-
CJ.25	3.5 "	0 "	-
CJ.26	4 "	0 "	-

TABLE 1 (Continued)

SAMPLE NUMBER AND CODE	WEIGHT OF INITIAL SAMPLE	WEIGHT OF SAMPLE RECOLLECTED	TOTAL NUMBER OF IDENTIFIABLE CONODONTS
CJ.27	5 kilograms	0 kilograms	-
CJ.28	5 "	0 "	-
CJ.29	4 "	0 "	-
CJ.30	5 "	0 "	-
CJ.31	5 "	0 "	-
CJ.32	5 "	0 "	-

CJ = Samples of calcareous sandstone and sandy limestone collected by the author from Croyde Bay.

SS.1	5 kilograms	0 kilograms	-
SS.2	3 "	0 "	-
SS.3	3 "	0 "	-
SS.4	5 "	0 "	-
SS.5	5 "	0 "	-
SS.6	3 "	0 "	-
SS.7	3 "	0 "	-
SS.8	3.5 "	0 "	-
SS.9	3 "	0 "	-
SS.10	5 "	0 "	-
SS.11	3 "	0 "	-
SS.12	2.5 "	0 "	-
SS.13	3.5 "	0 "	-
SS.14	3 "	0 "	-
SS.15	5 "	0 "	-
SS.16	5 "	0 "	-

TABLE 1 (Continued)

SAMPLE NUMBER AND CODE	WEIGHT OF INITIAL SAMPLE	WEIGHT OF SAMPLE RECOLLECTED	TOTAL NUMBER OF IDENTIFIABLE CONODONTS
SS.17	3 kilograms	0 kilograms	-
SS.18	3 "	0 "	-
SS.19	5 "	0 "	-
SS.20	5 "	0 "	-
SS.21	3 "	0 "	-
SS.22	3 "	0 "	-
SS.23	3.5 "	0 "	-
SS.24	5 "	0 "	-
SS.25	5 "	0 "	-
SS.26	5 "	0 "	-
SS.27	5 "	0 "	-
SS.28	4 "	0 "	-
SS.29	3 "	0 "	-
SS.30	5 "	0 "	-
SS.31	5 "	0 "	-
SS.32	3 "	0 "	-
SS.33	3 "	0 "	-
SS.34	3 "	0 "	-
SS.35	5 "	0 "	-
SS.36	3 "	0 "	-
SS.37	3 "	0 "	-
SS.38	5 "	0 "	-
SS.39	3 "	0 "	-
SS.40	5 "	0 "	-
SS.41	3 "	0 "	-

TABLE 1 (Continued)

SAMPLE NUMBER AND CODE	WEIGHT OF INITIAL SAMPLE	WEIGHT OF SAMPLE RECOLLECTED	TOTAL NUMBER OF IDENTIFIABLE CONODONTS
SS.42	3 kilograms	0 kilograms	-
SS.43	5 "	0 "	-
SS.44	5 "	0 "	-
SS.45	5 "	0 "	-
SS.60	5 "	0 "	-
SS.61	3 "	0 "	-
SS.62	3 "	0 "	-
SS.63	3 "	0 "	-
SS.64	3 "	0 "	-
SS.65	5 "	0 "	-
SS.66	3.5 "	0 "	-
SS.67	3 "	0 "	-
SS.68	3 "	0 "	-
SS.70	5 "	0 "	-
SS.71	3 "	0 "	-
SS.72	3 "	0 "	-
SS.73	5 "	0 "	-
SS.74	2.5 "	0 "	-
SS.75	5 "	0 "	-
SS.76	3 "	0 "	-
SS.77	3 "	0 "	-
SS.80	5 "	0 "	-
SS.81	3 "	0 "	-
SS.82	3 "	0 "	-

TABLE 1 (Continued)

SAMPLE NUMBER AND CODE	WEIGHT OF INITIAL SAMPLE	WEIGHT OF SAMPLE RECOLLECTED	TOTAL NUMBER OF IDENTIFIABLE CONODONTS
SS.83	3 kilograms	0 kilograms	-
SS.84	3 "	0 "	-
SS.85	5 "	0 "	-
SS.86	3 "	0 "	-
SS.87	4 "	0 "	-
SS.90,PB.11	5 "	0 "	13
SS.91,PB.10	5 "	4 "	261
SS.100,PB.6	5 "	2 "	42
SS.101,PB.7	5 "	2 "	13
SS.102,PB.8	5 "	2 "	36
SS.103,PB.14	5 "	2 "	32

SS = Samples of slates, shales and 6 limestone horizons collected by Miss J. Robinson from Croyde Bay.

SC.2a	4 kilograms	0 kilograms	-
SC.2b	4 "	0 "	-
SB.5	4 "	0 "	-
SB.4	3 "	0 "	-
SB.3	4 "	0 "	-
S Brad	5 "	0 "	-
S (West)	5 "	0 "	-

Samples of slates and shales collected by Miss J. Robinson from several inland exposures, north of the Taw estuary.

HISTOGRAM INDICATING THE NUMBER OF CONODONTS YIELDED, PER KILOGRAM OF ROCK, FROM THE PRODUCTIVE HORIZONS WITHIN THE UPPER BAGGY AND THE PILTON BEDS

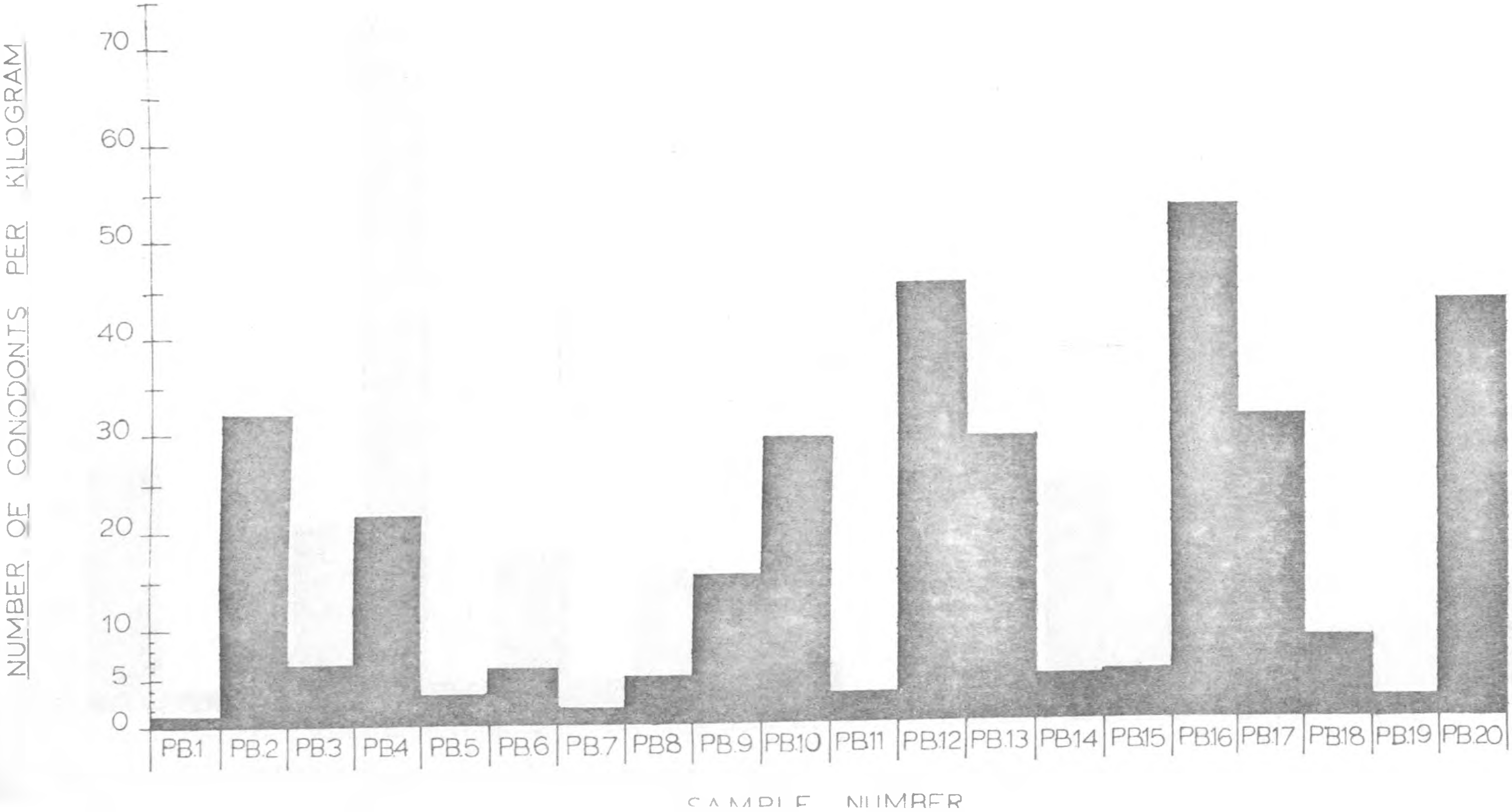


FIGURE 28

HISTOGRAM INDICATING THE NUMBER OF CONODONTS YIELDED, PER KILOGRAM OF ROCK, FROM THE PRODUCTIVE HORIZONS WITHIN THE UPPER BAGGY AND THE PILTON BEDS

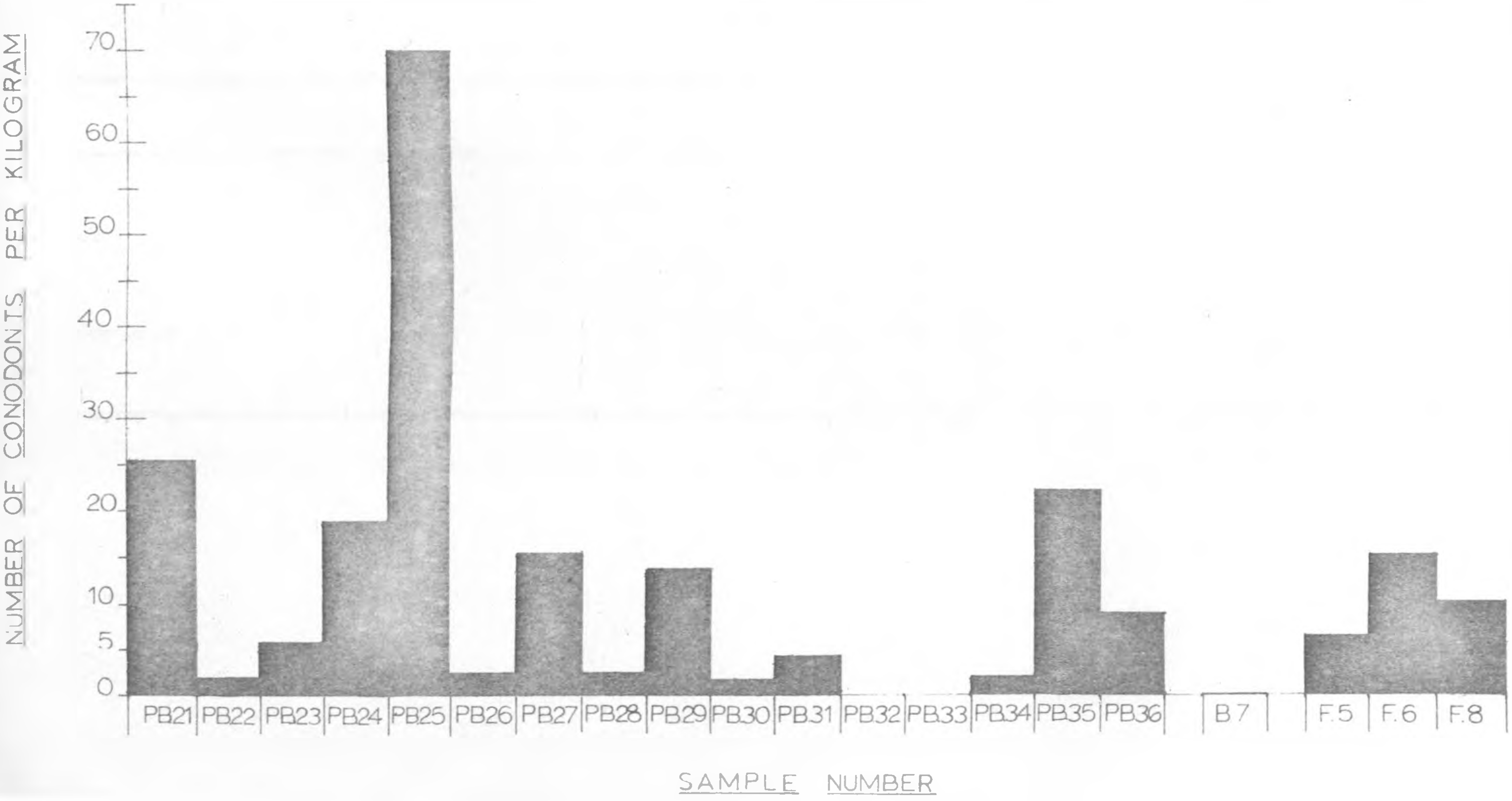


FIGURE 29

FIGURE 30

STRATIGRAPIC RANGES OF THE CONODONT GENERA IDENTIFIED FROM THE UPPER BAGGY AND THE PILTON BEDS

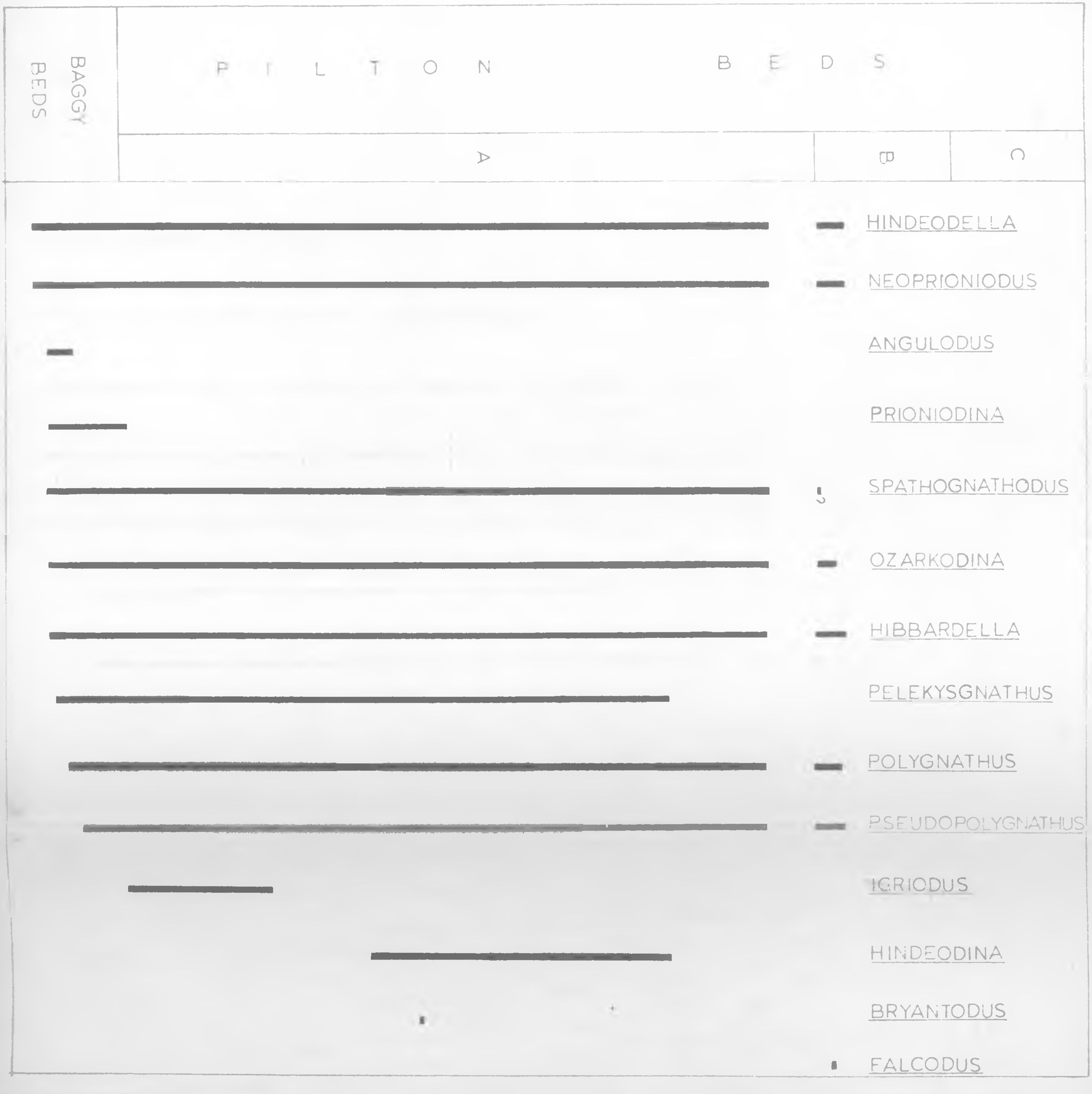


FIGURE 31

STRATIGRAPHIC RANGES OF THE SPECIES AND SUBSPECIES OF THE GENUS SPATHOGNATHODUS IN THE UPPER BAGGY AND THE PILTON BEDS

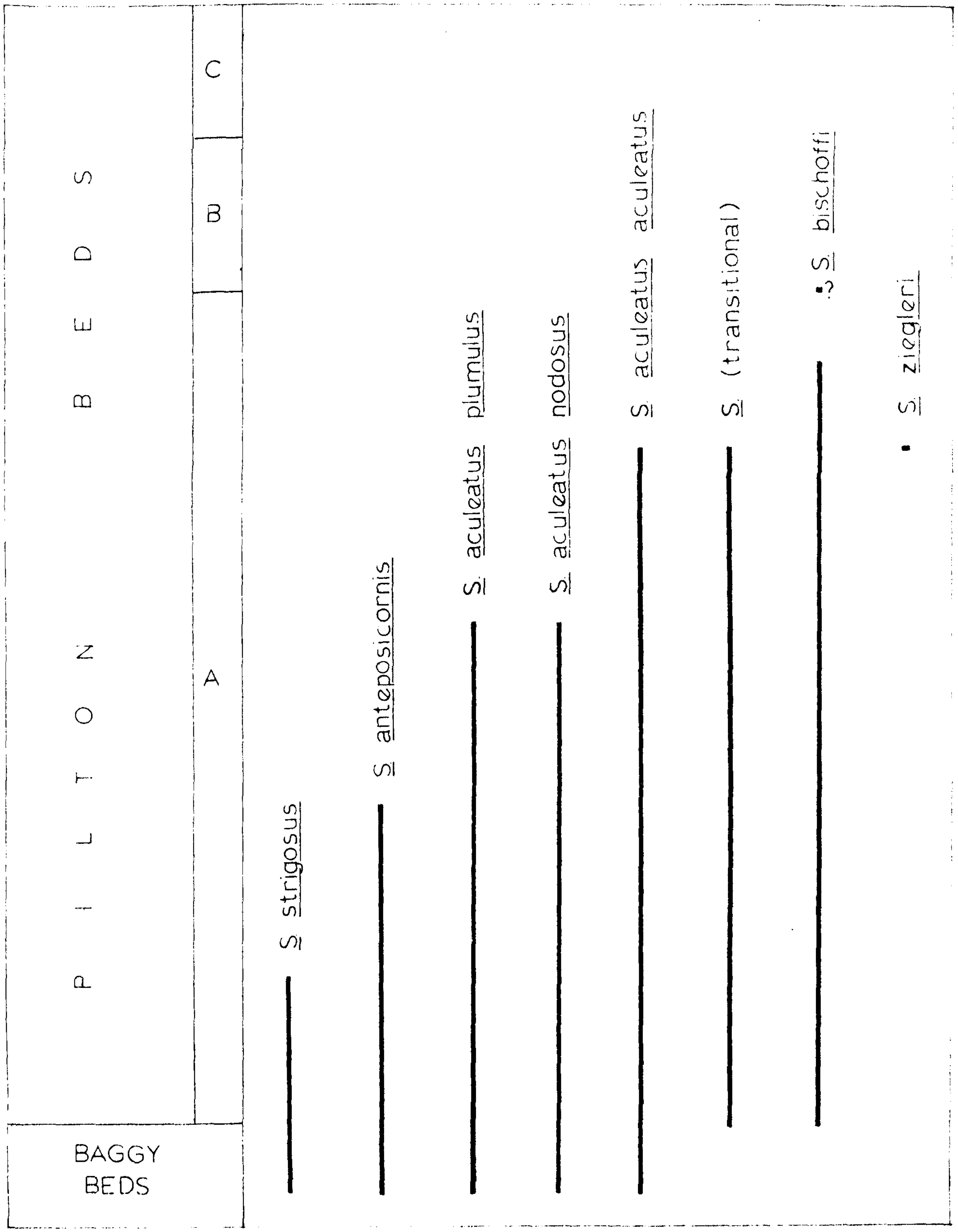


FIGURE 32

STRATIGRAPHIC RANGES OF THE SPECIES AND SUBSPECIES OF THE GENUS POLYGNATHUS IN THE UPPER BAGGY AND THE PILTON BEDS

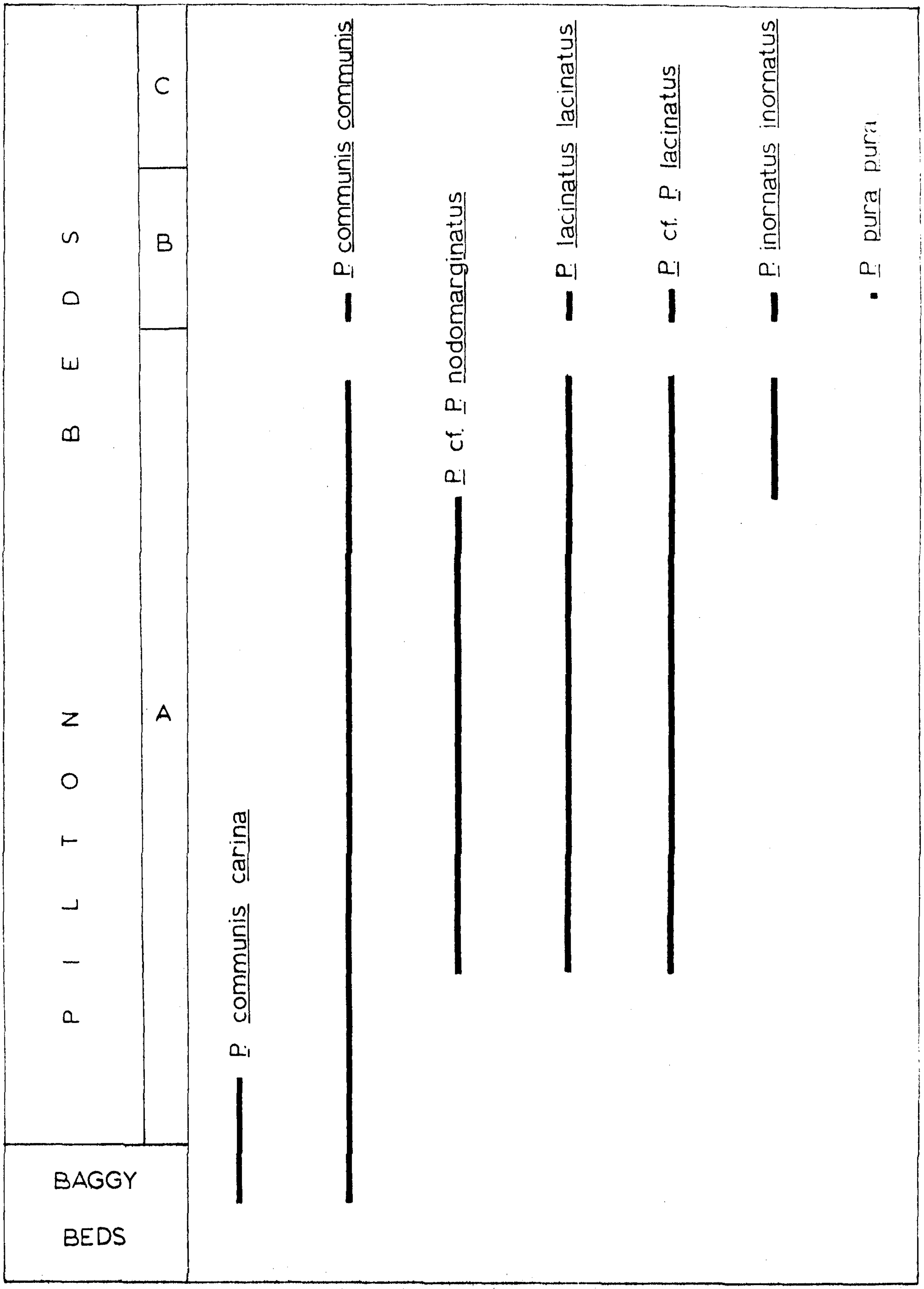
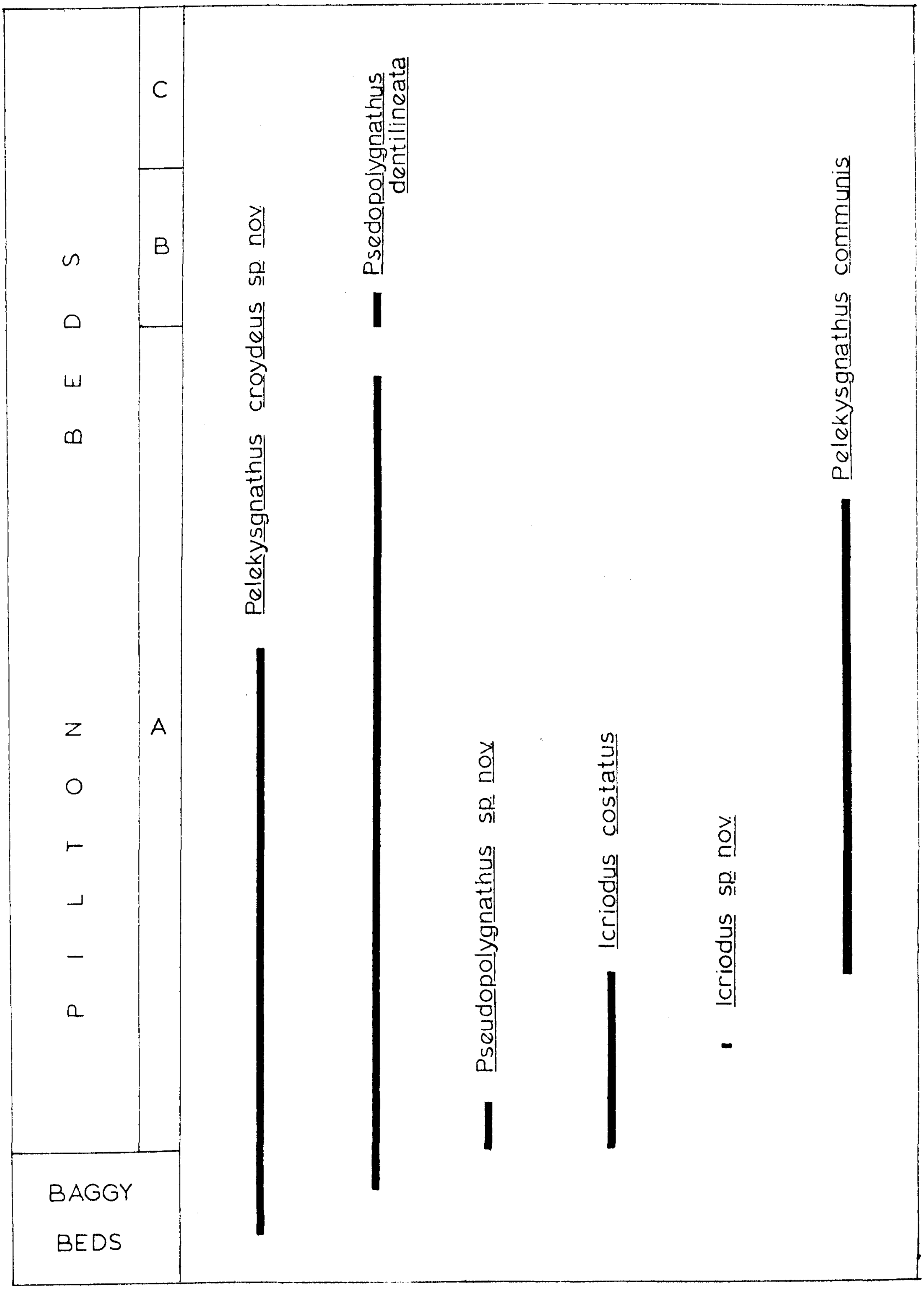


FIGURE 33

STRATIGRAPHIC RANGE OF THE SPECIES OF THE GENERA PSEUDOPOLYGNATHUS, ICRIODUS AND PELEKYSGNATHUS IN THE UPPER BAGGY AND THE PILTON BEDS.



CHAPTER 7

CORRELATION OF THE UPPER BAGGY AND PILTON BEDS WITH OTHER AREAS OF THE WORLD

As has been mentioned in earlier chapters, the Pilton Beds have been assessed by Goldring (1956) to be of Devonian age in their lower part and Carboniferous age in their upper part. Goldring studied the brachiopod, trilobite and goniatite faunas of the Baggy and Pilton Beds, establishing three local faunal divisions, A, B & C, the lowest of which, A, can be further subdivided into three subdivisions. The Devonian - Carboniferous boundary occurs at the junction of Beds A & B, but, the junction of the Lower and Upper lithological divisions of the Pilton Beds falls within the A3 faunal division (see Figure 34).

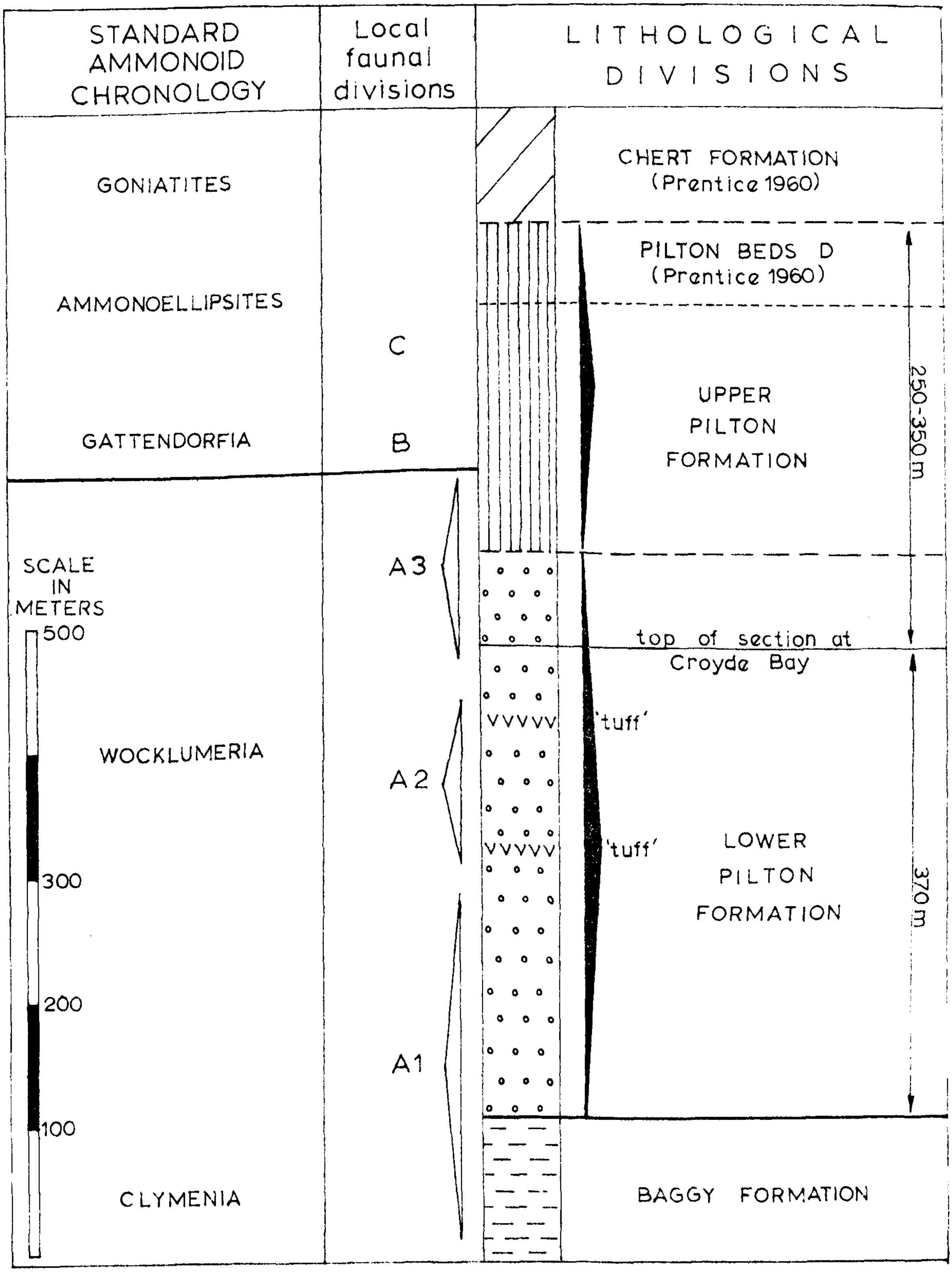
The conodont faunas of the Baggy and Pilton Beds are relatively poorly preserved and one less continuous stratigraphically than the macrofaunas utilised by Goldring, by virtue of the fact that they may be recovered only from sporadically occurring, crinoidal limestone bands. Nevertheless, the conodonts serve to verify the conclusions and results of Goldring, particularly in the Lower Pilton Beds where they are most abundant.

For ease of description, the conodont faunas of the Upper Baggy and the Pilton Beds can be considered in two separate groups according to their geographic localities. The first group includes the faunas located at Croyde Bay, where the Baggy and Lower Pilton Beds outcrop, and local

FIGURE 34

THE LITHOLOGICAL AND LOCAL FAUNAL DIVISIONS OF THE PILTON BEDS AND THEIR CORRELATION WITH THE STANDARD AMMONOID CHRONOLOGY

(after Goldring 1956 with modern amendments)



faunal divisions A1, A2 and lower A3 are found. The second group includes the faunas located at Fremington Pill, where the Upper Pilton Beds outcrop and local faunal divisions upper A3, B and C are located.

In general aspect the conodont faunas recovered from the Croyde Bay section are clearly Upper Devonian. Prominent members of the fauna are spathognathodids typical of the Spathognathodus costatus Zone, established in the German type section by Ziegler (1962), representatives of the genera Icriodus and Pelekysgnathus, which suggest a Devonian and Upper Devonian age respectively, and pseudopolygnathids typical of Upper Devonian and/or Lower Carboniferous rocks elsewhere in Britain, Europe and North America. However, in detail the age determination of these beds is a little more perplexing. The absence of representatives of the genus Palmatolepis from this Upper Devonian sequence suggests either a very late Devonian age, younger than the last occurrence of Palmatolepis within the Upper costatus Zone of Germany, or a Baggy and Pilton Bed facies that was not conducive to palmatolepid elements, indicating that Palmatolepis is facies controlled. (Many areas of the world exhibit youngest Upper Devonian faunas in which this genus is absent.)

The discovery of Palmatolepis in Lower Carboniferous rocks of East Cornwall by Matthews (1969a), supports one or other of these interpretations depending on whether or not these palmatolepids are indigenous or reworked. If they are reworked (as was suggested for the palmatolepids recovered by Voges (1959) from the Scaliognathus anchoralis in Germany), then Palmatolepis does not range from the Devonian through to the Carboniferous and thus the possibility that the Baggy and Lower Pilton Beds are of Upper costatus Zone age, after the last occurrence of Palmatolepis, is still valid. However, if they are indigenous to the Lower Carboniferous, then the only explanation for the absence of *Palmatolepis* from the Baggy and Lower Pilton sediments is that the facies was inhospitable.

In 1969, Ziegler announced the recognition of the *Protognathodus kockeli* Zone, which occurs in the Hangenberg Schiefer, immediately above the Upper *costatus* Zone, and is also of Upper Devonian age. No forms similar to *Protognathodus* have been recorded from the Baggy and Lower Pilton Beds, and this implies that the latter are either younger or older than this new Zone. *Spathognathodus costatus* is not represented in the German *Protognathodus kockeli* Zone. It becomes extinct at the top of the Upper *costatus* Zone, and the Baggy and Lower Pilton Beds must, therefore, be considered as older than the *P. kockeli* Zone. This conclusion is based on the fact that the present state of knowledge indicates that *S. costatus* had a ubiquitous occurrence and its absence from any section cannot be explained by facies variation. Ziegler's designation of the age of the *P. kockeli* Zone as Upper Devonian is based on the occurrence, in this Zone, of the goniatite genera *Prionoceras* (*Imitoceras*) *carinatum* and *Prinonoceras* (*Imitoceras*) *prorsum prorsum*.

The species of the genus *Spathognathodus* from the Baggy and Lower Pilton Beds are identical to those which characterise the German *costatus* Zone. Specimens of *S. aculeatus*, *S. bischoffi* (*S. costatus costatus*), and *S. zeigleri* (*S. costatus spinulicostatus*) have been recovered although no specimens of *S. costatus ultimus* have been found. The latter subspecies is diagnostic of the Upper *costatus* Zone. Other conodont elements that are common to both the *costatus* Zone and the Baggy and Lower Pilton Beds are:- *Pseudopolygnathus dentilineata*, *Polygnathus communis*, *Polygnathus* cf. *P. nodomarginatus* and *Spathognathodus strigosus*.

Further evidence in support of the assignment of a late Upper Devonian age to these Croyde Bay Beds, is the influx of polygnathids, similar to those more characteristic of Lower Avonian faunas, in the upper portion of the Lower Pilton sequence. They occur side by side with spathognathodids of the *costatus* group and therefore the fauna must still be considered as Upper Devonian, but the presence of these polygnathids indicates a close proximity to the Lower Carboniferous and confirms the late Upper Devonian age of this strata.

Thus two interpretations remain open for consideration with regard to the precise age of the Baggy and Lower Pilton Beds. (1) That they are equivalent to the uppermost part of the Upper *costatus* Zone, after the last occurrence of *Palmatolepis* and before the first occurrence of *Protognathodus*. (2) That they are equivalent to all or part of the *costatus* Zone, and that the absence of *Palmatolepis* can be explained by facies variation.

At present it is impossible to say which interpretation is correct, but certainly these Croye Bay Beds must be of *costatus* Zone age. If the first interpretation is accepted then *S. costatus ultimus* should be present in the fauna, and *Protognathodus* might be expected to occur in younger Pilton Beds. Spathognathodids generally make up no more than 20-25% of any given sample, and their average percent abundance is only 5-6%. It may therefore be that the absence of *S. costatus ultimus* is a result of insufficient recovery and/or inadequacy of fossiliferous samples. Other explanations for the absence of this subspecies are facies variation, geographic provincialism and homeomorphic replacement and substitution. Both facies variation and geographic provincialism are possibilities but not probabilites, as all other representatives of the *S. costatus* group had an apparently ubiquitous distribution in the Upper Devonian and there is no evidence to suggest that *S. costatus ultimus* was an exception. Homeomorphic replacement may have been responsible for the absence of S. costatus ultimus in the Pilton Beds, in that spathognathodids refered to as *Spathognathodus* transitional and *S. zeiglcri* in this study, are morphologically very similar to *S. costatus ultimus* and possibly served the same functional purpose as this element, causing its development to be unnecessary.

The absence of *Protognathodus* may be explained in one of two ways, (a) this Zone occurs within the unproductive rocks between the Croyde Bay and the Fremington Pill sections, or (b) that this genus was facies controlled, or perhaps geographically provincial, and found the North Devon area unfavourable.

If the second interpretation is accepted, the absence of *S. costatus ultimus* would require no explanation, as the Baggy and Lower Pilton Beds could be older than the first occurrence of this subspecies. However, the occurrence of polygnathids of Lower Avonian aspect in this part of the Lower Pilton Beds suggests that these beds at least are of late *costatus* Zone age. By regarding them as equivalent to the uppermost Upper *costatus* Zone, then the absence of *S. costatus ultimus* and *Protognathodus* must again be accounted for. This second interpretation is based on the premise that the absence of *Palmatolepis* can be explained by facies variation, but all the possibilities reviewed above for the absence of *S. costatus ultimus* can be advanced for the absence of *Palmatolepis*. Nevertheless, present evidence from other areas of the world indicate that *Palmatolepis* is susceptible to facies variation and thus this explanation is probably the best for the absence of this genus in North Devonshire.

There is evidence to suggest that this North Devon fauna was facies controlled, however, regardless of which of the two possible interpretations is correct, both point to a fairly late *costatus* Zone age for the Upper

Baggy and the Lower Pilton Beds.

Goldring (1956) correlated the Lower Pilton Beds with the *Wocklumeria* Stufe, and suggested that the upper portion of the Baggy Beds were of *Clymenia* Stufe age (see Figure 34). The present author does not consider the Upper Baggy Beds to be appreciably older than the succeeding Lower Pilton Beds, and would suggest a *Wocklumeria* rather than a *Clymenia* age for the former, based on the correlation of conodont zones with goniatite Stufen in the standard German sequence. However, the macrofaunas collected by Goldring (1956), and the microfaunas collected in this study, from the Upper Baggy Beds, were both relatively meagre and any interpretation based on these faunas must be somewhat tentative.

The conodont faunas gained from the Fremington Pill section provide only inconclusive evidence with regard to the age of these rocks. The faunas are small and no diagnostic forms have been found to suggest either an Upper Devonian or Lower Carboniferous age. Three horizons, at the base of Goldring's Upper Pilton faunal division B, have yielded conodonts, and inferences as to the age of these horizons can be based only on rather negative evidence.

The fauna is dominated by *Polygnathus communis communis* and two or three species of larger polygnathids identical to those found in the upper portion of the Lower Pilton Beds, namely, *P. lacinatus lacinatus*, *P.* cf. *P. lacinatus*, and *P. inornatus*. Another prominent feature of the fauna is the presence of numberous bars and blades, of a very delicate nature, less robust than the same species in the Lower Pilton Beds. From these discoveries alone no objective conclusions can be drawn. However, the absence of spathognathodids of the '*costatus*' group, except for one dubious specimen, and the absence of any other diagnostic Devonian forms, suggests that these rocks are younger than the Lower Pilton Beds. By the same token, no siphonodellids, patrognathids, or clydagnathids, indicative of the lowest Carboniferous, have been recovered from these faunas. A single specimen of *Polygnathus pura pura* was located from one of the horizons sampled at Fremington, and this sub-species has been recorded by Voges (1959) in the *Gattendorfia* Stufe (CuI) of the Hangenberg Kalk of Sauerlandes. It ranges from the upper portion of the *kockeli*-*dentilineata* Zone to the top of the *Siphonodella* - *triangula triangula* Zone in Germany. In the Hangenberg Kalk it is found associated with *Polygnathus communis* and *P. pura subplana*, in addition to *Gnathodus kockeli*, *Pseudopolygnathus dentilineata*, *Pseudopolygnathus triangula triangula* and representatives of the genus *Siphonodella*. Most of these associated forms are absent from the Fremington samples and although the occurrence of one specimen of *P. pura pura* is but scant evidence, it is the only positive indication of the age of these beds. If this interpretation is valid it suggests a *Gattendorfia Stufe* (CuI) age for the Upper Pilton Beds B, which confirms Goldring's estimation of the age of these beds (see Figure 34).

Unfortunately, no productive horizons were located within that part of the stratigraphic sequence between the uppermost Croyde Bay and the lowermost Fremington strata, nor within the Pilton Beds C at Fremington.

The ranges of all the conodont species and subspecies identified from the Upper Baggy and the Pilton Beds, together with the Conodont Assemblage Zones erected on the basis of the distribution of the faunal elements, are shown in Figure 35.

A single conodont specimen has been found in the rocks which outcrop in the Bampton section. The specimen is very poorly preserved in that it

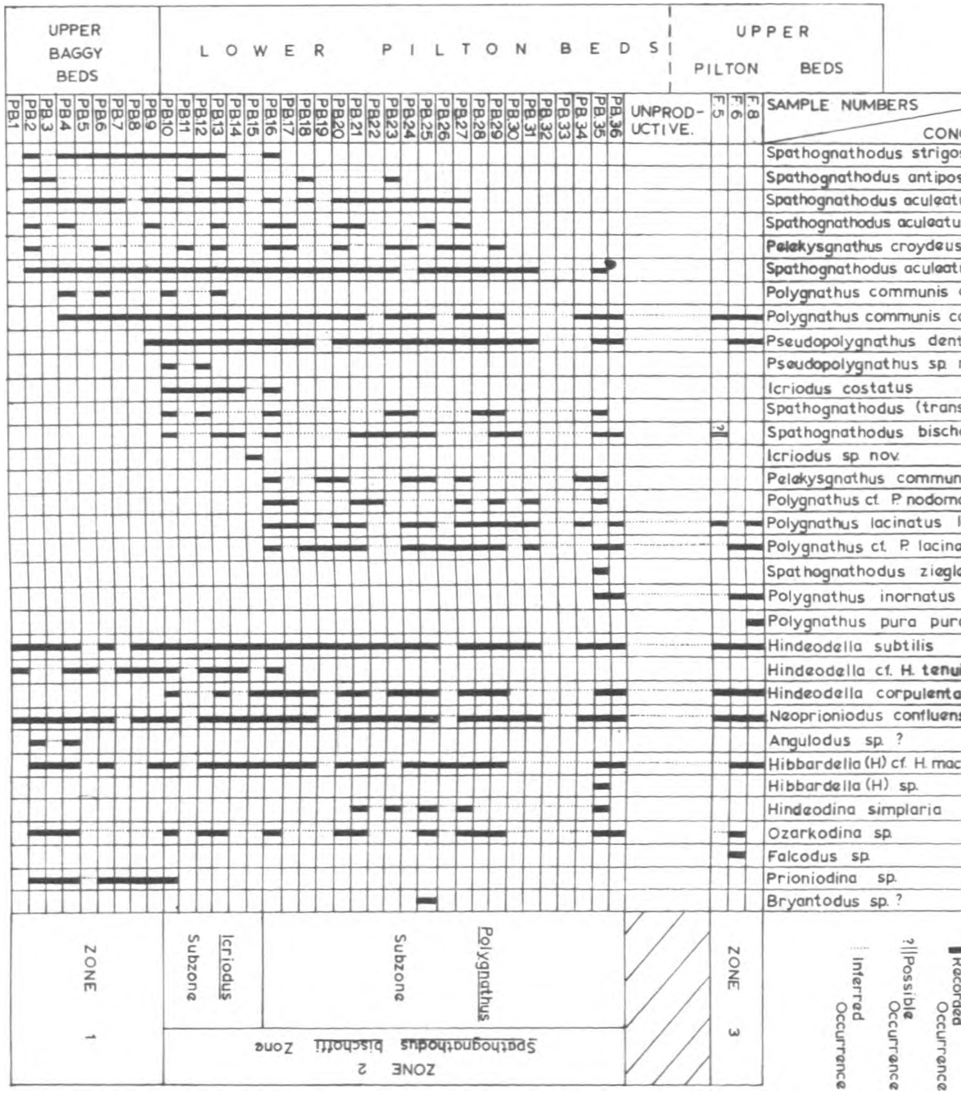


FIGURE 35

STRATIGRAPHIC RANGES OF THE CONODONT SPECIES AND SUBSPECIES IDENTIFIED FROM THE UPPER BAGGY AND THE PILTON BEDS, AND THE CONODONT ASSEMBLAGE ZONES ERECTED ON THE BASIS OF THEIR DISTRIBUTION.

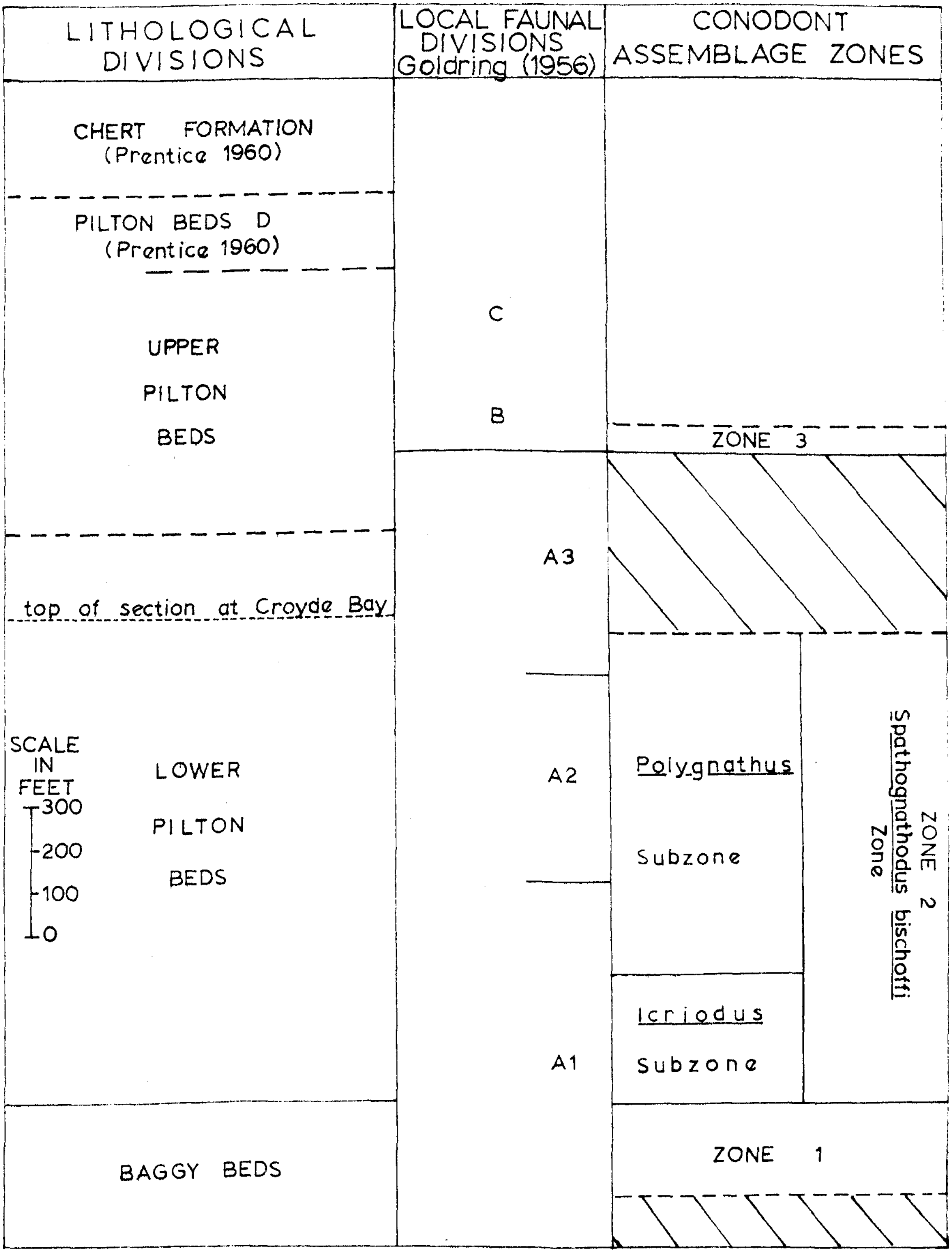
is partially broken and the basal cavity is infilled with sedimentary material. Nevertheless, the conodont can be identified as an icriodid although no specific designation is possible. If the conodont is indigenous to these rocks, and not reworked, then this indicates an Upper Devonian age for the rocks of this section. However, the possibility that this specimen has been reworked cannot be ruled out. Goldring (personal communication) has suggested a younger age for this outcrop, but he stressed that this was merely a suggestion based on the lithology, and the proximity to rocks of definite Carboniferous age.

Three Conodont Assemblage Zones, one of which can be divided into two Subzones, have been erected on the basis of the stratigraphic distribution of the faunas recovered from the Baggy and Pilton Beds. The Zones were established for the Croyde Bay and Fremington outcrops, and although they may have local application within the North Devon area, as do the faunal divisions of Goldring (1956), lack of additional exposures of conodont bearing strata has made it impossible to test their regional validity. The Zones erected are shown in Figure 36, where they are correlated with the faunal divisions of Goldring.

The oldest Zone (Zone I) is characterised by an abundance of *Spathognathodus aculeatus aculeatus*, *S. aculeatus nodosus* and *S. aculeatus plumulus*. No representatives of the genus *Icriodus*, or of the species *S. bischoffi* have been found in this Zone. Other elements present are *S. anteposicornis*, *S. strigosus*, *Polygnathus communis* and *Pelekysgnathus croydeus* sp. nov. The Zone is correlated with the first two hundred feet of Goldring's Pilton Beds faunal division AI, immediately below the arbitrarily defined boundary between the Baggy and Pilton Beds. The boundary itself forms the upper limit of Zone I.

FIGURE 36

CORRELATION OF CONODONT ASSEMBLAGE ZONES, ERECTED FOR THE BAGGY AND PILTON BEDS IN THIS STUDY, WITH THE FAUNAL DIVISIONS ESTABLISHED BY GOLDRING (1956).



Zone 2, the *Spathognathodus bischoffi* Assemblage Zone, has a lower limit which is marked by the first occurrence of the species which gives the Zone its name. The upper zonal boundary is taken at the last productive horizon in the Croyde Bay section, which is located approximately 1,410 feet above the boundary between the Baggy and Pilton Beds. Two Subzones can be identified within this Zone, the *Icriodus* Subzone and the *Polygnathus* Subzone. The lower limit of the *Icriodus* Subzone coincides with the lower limit of the *S. bischoffi* Zone and is marked by the first occurrence of *S. bischoffi* and *Icriodus*. The upper limit of this Subzone is marked by the extinction of icriodids and the first appearance of polygnathid species other than *Polygnathus communis*. Other forms found in this Subzone are *Pseudopolygnathus dentilineata*, *Spathognathodus aculeatus aculeatus*, *S. aculeatus plumulus*, *S. aculeatus nodosus*, *S. anteposicornis*, *Spathognathodus* (transitional)between *S. bischoffi* and *S. zeigleri*), *S. strigosus*, *Polygnathus communis* and *Pelekysgnathus croydeus* sp. nov. This Subzone is correlated with the first 295-300 feet of Pilton Beds AI immediately above the Baggy - Pilton boundary.

The younger Subzone of the *S. bischoffi* Zone is the *Polygnathus* Subzone, and is less clearly defined than the underlying Subzone. The lower limit coincides with the first appearance of polygnathids other than *P. communis* group; these include *P. lacinatus lacinatus*, *P.* cf. *P. lacinatus* and *P.* cf. *P. nodomarginatus*. This point also marks the extinction of icriodids in the Pilton Bed succession. Conodonts present in this Subzone, in addition to those mentioned above, include *Polygnathus communis communis*, *Pelekysgnathus communis*, *Spathognathodus* (transitional), *S. aculeatus aculeatus*, *S. aculeatus plumulus* and *Pseudopolygnathus dentilineata*. This Subzone is correlated with the upper 175 feet of Goldring's Pilton Beds AI, the total thickness of A2, and approximately the lower 85 feet of A3.

Zone 3 is tentatively suggested to include the conodont bearing Fremington Pill strata which occupy the lower 40 feet of the southern outcrop of Goldring's Upper Pilton Beds B faunal division. There is only meagre evidence for the erection of this Zone, owing to the absence of both diagnositc Devonian and Carboniferous elements other than a single specimen of *Polygnathus pura pura*. The zonal boundaries are limited by the occurrence of the oldest and youngest productive samples in the Fremington Pill section. Other conodont species found in this Zone, in addition to *P. pura pura*, are *P. lacinatus lacinatus*, *P. inornatus* and *Pseudopolygnathus dentilineata*.

As has been shown with the German type section, a comparison of the faunas from the Baggy and Pilton Beds with those of European sections of a comparable age is strikingly close, and nowhere are the North Devon faunas matched more closely than at Huy in Belgium.

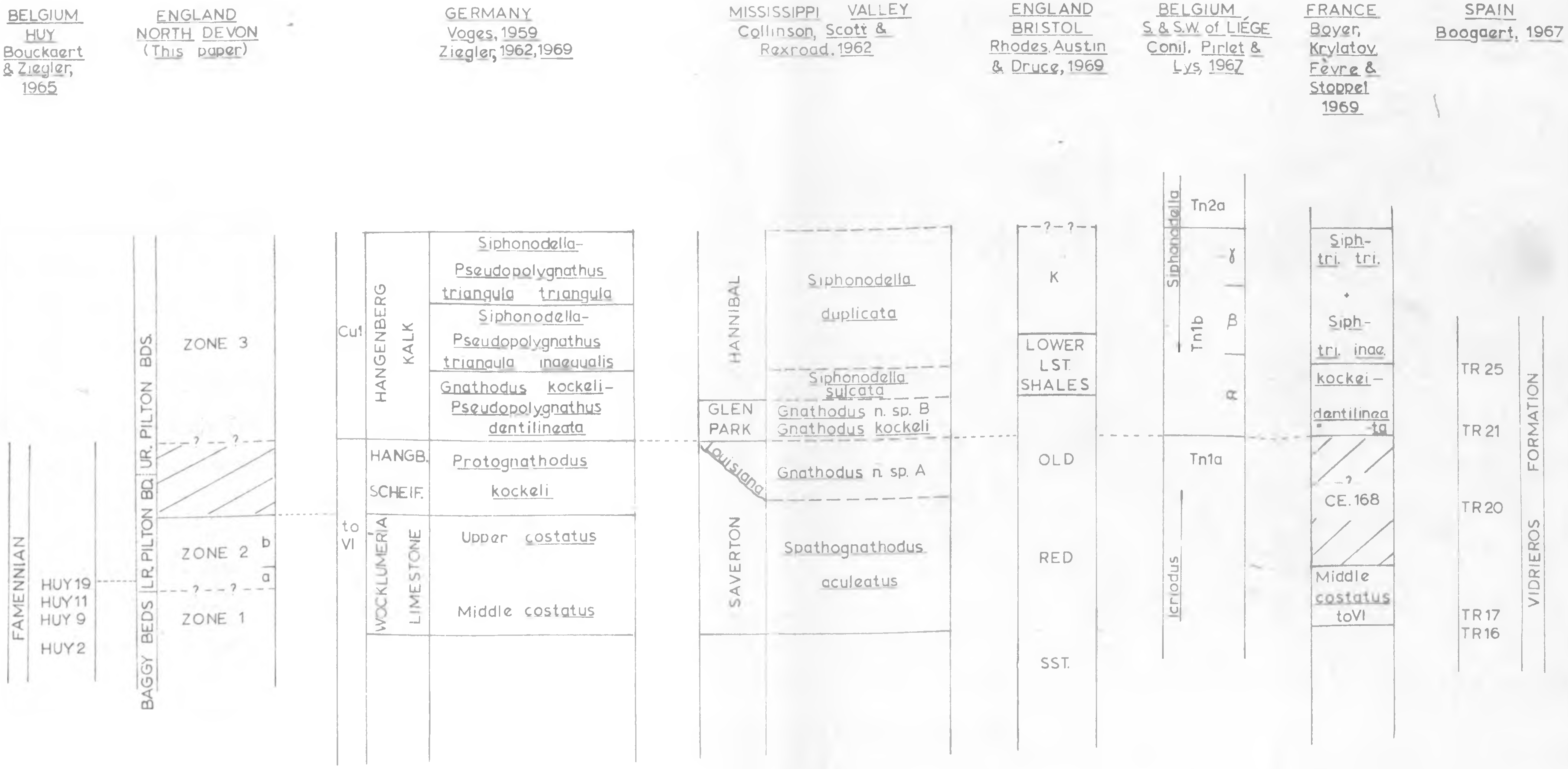
Bouckaert and Ziegler (1965) collected small faunas from a section at Huy, Belgium which indicated a *costatus* Zone age. They claimed that a more precise age determination could not be derived from the Huy conodonts, and thus they correlated this section with the upper part of the *Clymenia* Stufe and/or part of the *Wocklumeria* Stufe. Bouckaert and Ziegler recorded specimens of *Spathognathodus costatus spinulicostatus* (*Spathognathodus zeigleri*), *S. costatus costatus* (*S. bischoffi*), *S. aculeatus*, *Pseudopolygnathus dentilineata*, and a new genus. All these elements are found in the Lower Pilton Beds including a species of *Icriodus* (*Icriodus* sp.nov.) which is similar to the new genus described by Bouckaert and Ziegler. The Huy fauna as a whole bears a closer resemblance to that of the older portion of the Lower Pilton Beds (the *Icriodus* Subzone of the *S. bischoffi* Zone) than any other investigated. If the two faunas could be correlated this would imply that the Huy fauna was equivalent to the upper part of the Wocklumeria Stufe, rather than the Clymenia Stufe or any other part of the Wocklumeria Stufe. Conil (1964) studied the foraminifera of this section and assigned it a TnIa age (Lower Tournaisian - Lower Étroeungt and Comblain-au-Pont Beds).

Correlation of the Baggy and Pilton Beds fauna with faunas from North America is difficult, as there are few elements which are common to both sections. In most outcrops of this age in North America, Palmatolepis occurs in the Upper Devonian and Siphonodella in the Lower Mississippian. There are no faunas such as those exhibited by the Upper Baggy and the Pilton Beds. However, in the Mississippi Valley, two Zones at the Devonian - Carboniferous boundary bear some elements which are characteristic of the North Devon beds, although there are many important differences also. If a correlation were attempted, the Upper Baggy and Pilton Beds would be tentatively equated with all or part of the Conodont Zones of the Middle and Upper Saverton and its lateral equivalent the Louisiana Limestone Formation (Upper toVI). The Spathognathodus aculeatus Assemblage Zone is confined to the Middle Saverton, and the Gnathodus new sp. A. Assemblage Zone to the Upper Saverton and Louisiana Formation. Figure 37 shows the suggested correlation of the Baggy and Pilton Beds with sections in Europe and North America, on the basis of conodonts.

Goldring (1956) correlated the Baggy and Pilton Beds of North Devon with several other localities in Western Europe. His correlation table shows a comparison of time-equivalence between the North Devon area, the Velbert region of Germany, the Sauerland region of Germany, North France, Belgium and Aachèn and the Bristol and South Wales area.

FIGURE 37

CORRELATION OF THE BAGGY AND PILTON BEDS WITH SECTIONS IN NORTH AMERICA AND EUROPE, ON THE BASIS OF CONODONTS.



Goldring concluded that the Pilton Beds A can be equated with the Etroeungt Beds of Velbert, Germany, although the correlation of the bases of these two groups of beds was only tentative. The Étroeungt Beds of Germany were subdivided by Paul (1937) into three faunal divisions α, β, and γ. The oldest, α, division is correlated with the Wocklumeria Limestone of Sauerland, Germany, while the two younger divisions can be equated with the Hangenberg Slates. Thus according to Goldring, the Pilton Beds A are equivalent to the Wocklumeria Limestone and overlying Hangenberg Slates of Sauerland and also to the Étroeungt Beds of France and their lateral equivalents, the Comblain-au-Pont Beds of Aachèn and Dinant.

If this correlation is correct then the Baggy Beds of North Devon may be tentatively equated, at least in part, with the Angertal and Veberter Beds of Germany, which underlie the Étroeungt Beds, and with the Condroz Sandstone which underlies the Étroeungt and Comblain-au-Pont Beds of Belgium, France and Aachèn. There is a close lithological similarity between the Condroz Sandstone and the Baggy Beds, although Goldring states that the fauna of the Baggy Beds is too meagre and poorly preserved to permit any direct correlation with any of its postulated equivalents in Europe.

The Pilton Beds B display disinct faunal similarities with both the Tournasian Limestone of Germany, which is equivalent in part to the Hangenberg Limestone of Sauerland, and to the Hastiére Limestone of Belgium and France.

Thus correlation of the Baggy and Pilton Beds with many of the European sections is not overly difficult, but by contrast correlation of these North Devon beds with the Avonian type section and other outcrops in

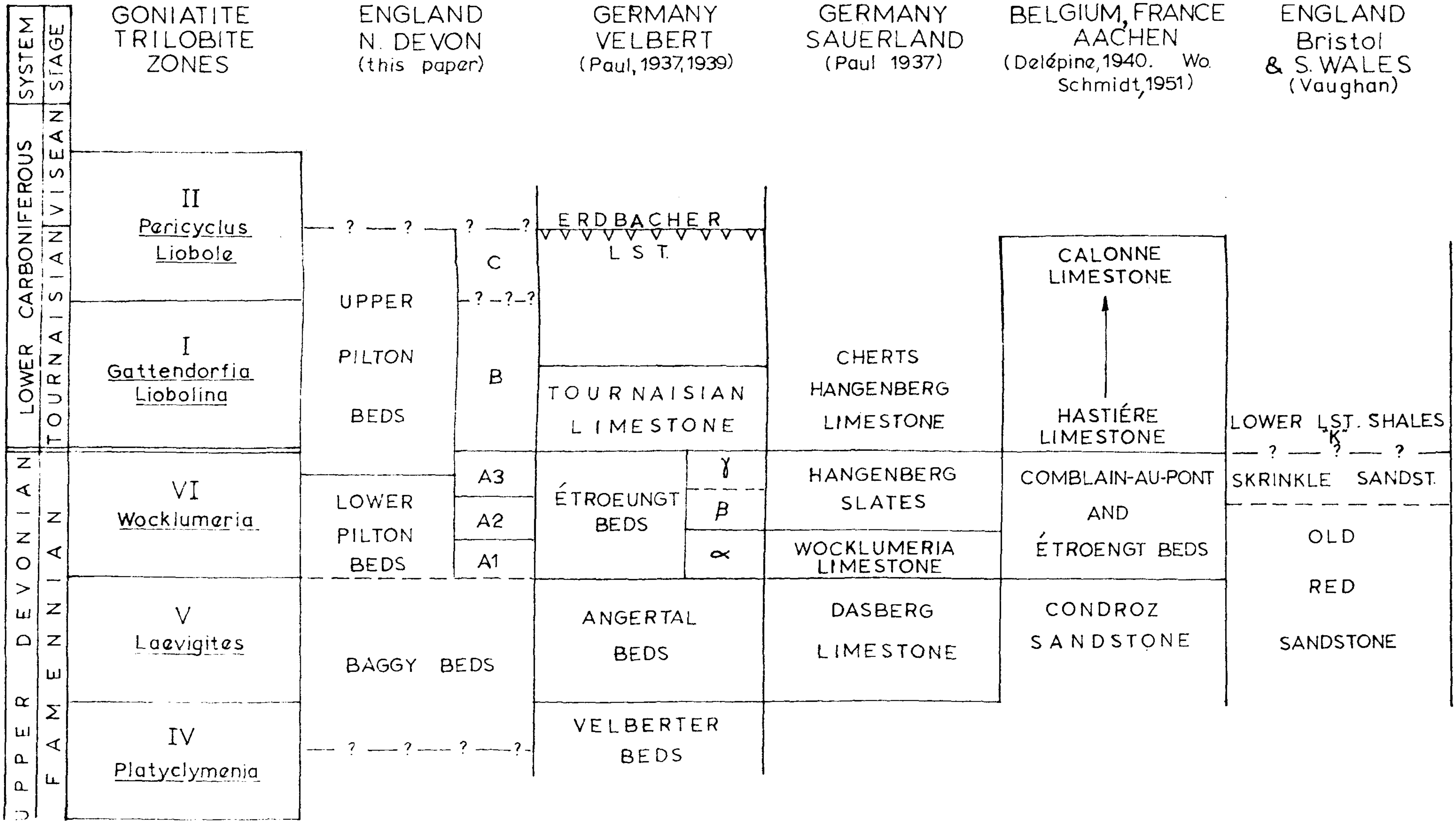
South Wales is more complex. The problem lies in attempting to equate the coral - brachiopod Zones of the 'Kohlenkalk' facies with the cephalopod Zones of the 'Kulm'. Goldring concluded that the 'K' Zone of the Avonian could not be correlated with the Wocklumeria Zone and thus with the Pilton Beds A or Étroeungt Beds. However, the presence of Liobolina in KI Zone is evidence for equating this Zone at least with part of the Gattendorfia Zone.

Dixon (1921) contends that the fauna of the Skrinkle Sandstones of Pembrokeshire may be closely compared with that of the Baggy Beds, but Goldring (1956) noted that the Lower Limestone Shales of Pembrokeshire, which succeed the Skrinkle Sandstones, exhibit a fauna which suggests a correlation with the Pilton Beds B and beds higher than the Étroeungt. This observation implies that the Skrinkle Sandstones are probably better equated with the Pilton Beds A than the Baggy Beds. Goldring, therefore, correlates the Baggy Beds with part of the Old Red Sandstone of areas to the north and west of the Bristol Channel, and the Pilton Beds B with the lowest Carboniferous deposits of K age (see Figure 38).

In general, the conodont faunas of the Baggy and Pilton Beds substantiate the conclusions drawn by Goldring. The Upper Baggy and Lower Pilton Beds can be compared with the upper or uppermost Wocklumeria Zone of the Devonian type section in Germany. In terms of Conodont Assemblage Zones erected by Ziegler (1962) for this type section, these North Devon sediments can probably best be equated with the Upper costatus Zone (Upper toVI).

The Upper Pilton Beds may be correlated only provisionally with part of the CuI Zone of the Hangenberg Kalk. The paucity of the faunas recovered from these beds allows no more precision than this.

CORRELATION OF THE BAGGY AND PILTON BEDS WITH OTHER AREAS IN BRITAIN AND WESTERN EUROPE (after Goldring 1956)



SYSTEM	STAGE	GONIATITE TRILOBITE ZONES	ENGLAND N. DEVON (this paper)		GERMANY VELBERT (Paul, 1937, 1939)		GERMANY SAUERLAND (Paul 1937)	BELGIUM, FRANCE AACHEN (Delépine, 1940. Wo. Schmidt, 1951)	ENGLAND Bristol & S. WALES (Vaughan)
LOWER CARBONIFEROUS	VISEAN								
	TOURNAISIAN	II *Pericyclus* *Liobole*	— ? — ? —	? — ? C — ? — ? — ?	ERDBACHER LST.			CALONNE LIMESTONE	
		I *Gattendorfia* *Liobolina*	UPPER PILTON BEDS	B	TOURNAISIAN LIMESTONE		CHERTS HANGENBERG LIMESTONE	↑ HASTIÉRE LIMESTONE	LOWER LST. SHALES "K" — ? — ? — ?
UPPER DEVONIAN	FAMENNIAN	VI *Wocklumeria*	LOWER PILTON BEDS	A3	ÉTROEUNGT BEDS	γ	HANGENBERG SLATES	COMBLAIN-AU-PONT AND ÉTROEUNGT BEDS	SKRINKLE SANDST.
				A2		β			OLD RED SANDSTONE
				A1		∝	WOCKLUMERIA LIMESTONE		
		V *Laevigites*	BAGGY BEDS		ANGERTAL BEDS		DASBERG LIMESTONE	CONDROZ SANDSTONE	
		IV *Platyclymenia*	— ? — ? — ? — ?		VELBERTER BEDS				

FIGURE 38

CHAPTER 8

THE VALUE OF CONODONTS IN THE RECOGNITION OF THE DEVONIAN-CARBONIFEROUS BOUNDARY, WITH PARTICULAR REFERENCE TO GREAT BRITAIN

The typescript of a publication bearing the same title as that of this chapter is included in Appendix I of this thesis. The paper, written by Austin, Druce, Rhodes and Williams, was read at the International Carboniferous Congress at Sheffield in 1967, and was published in 1970.

Included in the first half of this work is a brief history of the placement of the Devonian-Carboniferous boundary and a discussion of the problems in correlation between the cephalopod-bearing rocks of Devon and Cornwall and the coral-brachiopod carbonate facies of the type section for the British Lower Carboniferous. In addition, the difficulties in correlation of the British, Belgian and German Lower Carboniferous type sections are reviewed, as are the lithological criteria for the recognition of the Lower Carboniferous in Western Europe.

The latter half of the paper is devoted to an evaluation of microfossils and in particular conodonts, in the recognition of the Devonian - Carboniferous boundary. It outlines the advantages of using conodonts as zonal tools, and describes a number of significant faunas from North America, Australia, Europe and Great Britain, where it is now possible to recognise an almost ubiquitous sequence of Upper Devonian-Lower Carboniferous Conodont Assemblage Zones.

Since 1967, continuing studies have brought to light new evidence which allows refinement of that part of the text which describes the conodonts recovered from the Baggy and Pilton Beds of North Devon. Specimens of the genus Icriodus and of the spathognathodid species S. bischoffi and S. zeigleri (including transitional forms between these two species) have been recovered from the Lower Pilton Beds. However, no representatives of Palmatolepis have been found in these beds, nor in the Upper Baggy Beds. Pseudopolygnathus dentilineata is an abundant faunal component, and in the upper part of the lower Pilton Beds, polygnathids, similar in character to those of the lower Avonian faunas, become prominent faunal members.

The absence of such diagnostic Carboniferous elements as Patrognathus and Clydagnathus, and the presence of S. costatus group forms, indicates that the Lower Pilton Beds must be regarded as Devonian.

No additional specimens of the reported new genus (similar to that figured by Bouckart and Ziegler (1965, pl.5, figs.9-11)) were recovered, and hence no definitive assumptions regarding an Icriodus-Pseudopolygnathus transition can be made. However, very recently, a fauna from the base of Tn 1b in Belgium has shown such a transition (Austin, personal communication).

Several publications on this general topic of conodonts and the Devonian - Carboniferous boundary have appeared in the past two years, two of which deserve particular attention:-

Conil, Pirlet & Lys (1967) described the biostratigraphy of the Dinantian of Belgium. They showed the distribution of species of six individual fossil groups (cephalopods, corals, brachiopods, spores, conodonts and foraminifera) in the uppermost Devonian and the Dinantian of this country. Their collections were made from four localities to the south and southwest of Liege, namely Dinant, Comblain, Modave and Dolhain. Plate 1 of their publication is a chart summarising the findings of these authors, and part of this chart, recording the faunal distribution in the immediate vicinity of the Devonian - Carboniferous boundary, has been reproduced in Figure 39.

BIO-STRATIGRAPHY OF SIX FOSSIL GROUPS OVER THE DEVONIAN-CARBONIFEROUS BOUNDARY IN BELGIUM (after Conil, Pirlet & Lys 1967)

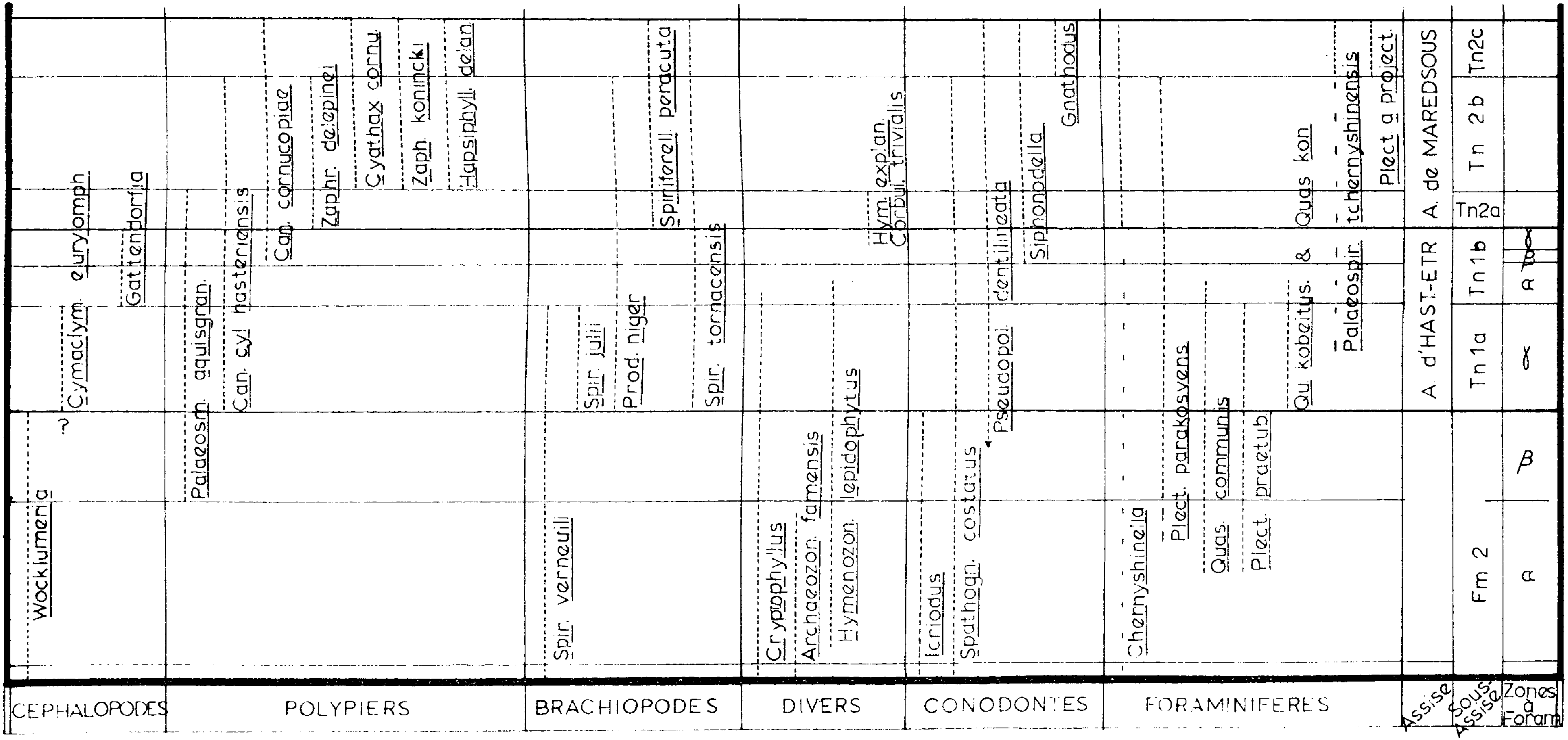


FIGURE 39

On the evidence of goniatites and spores, the boundary in Belgium is probably best taken to be the base of Tn1bα. However, on the basis of conodonts the boundary would be most conveniently located at the first occurrence of Siphonodella, at the base of Tn1bβ. Recent work indicates that the stratigraphic range of Siphonodella in Belgium may be different to that shown in Figure 39.

Boyer, Krylatov, Fevre and Stoppel (1968) described conodonts from the Upper Devonian and the Devonian - Carboniferous boundary of the Black Mountains of France, where there is an uninterrupted transition in a carbonate sequence, from one system to the other. The conodont assemblage zones recognised by these authors are illustrated in fig.4, pg.19 and in fig.8 of their publication, and they compare closely with those of the German type section.

CHAPTER 9

SYSTEMATIC PALAEONTOLOGY

Genus ANGULODUS? Huddle, 1934

(Fig.40)

1934 Angulodus Huddle, p.76.

Type species. Angulodus walrathi (Hibbard, 1927)

Angulodus sp. ?
(Pl. 13, figs. 3a-5c)

Diagnosis.

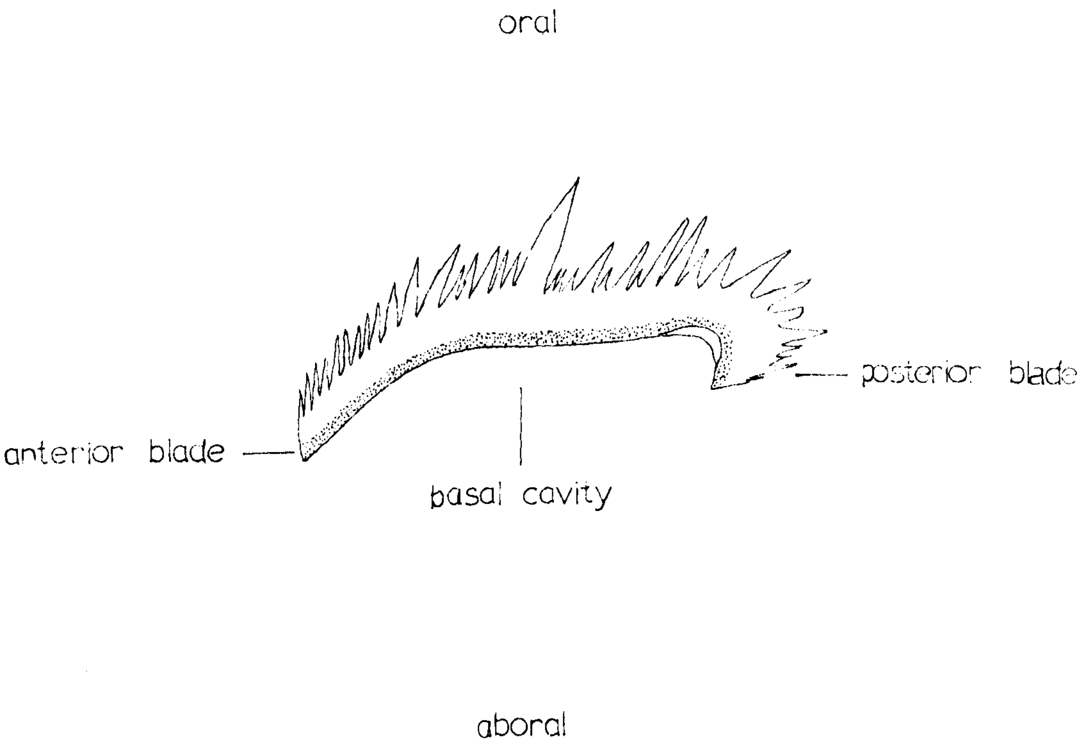
Laterally compressed, arched blade with a large basal cavity occupying the mid-third of the unit. The cavity bears lips. The denticles of the mid-third are small, of uniform height, and are bounded anteriorly and posteriorly by larger denticles. Beyond the larger denticles developed on the anterior blade, smaller, partially fused denticles occur, and beyond those on the posterior blade, smaller discrete denticles are developed.

Description.

Orally the unit is straight or the posterior and anterior blades are curved gently inward. Laterally the mid-third of the conodont is straight but the anterior and posterior thirds are deflected downward at angles of between 30 - 45° from the horizontal. This gives the form an arched outline.

The anterior third of this conodont bears 6-8 denticles, the first 3-5 denticles from the anterior end are small and partially fused, only their tips being discrete. The following three denticles are extremely large and curved slightly toward the posterior. These denticles are also discrete only at their tips.

GENUS ANGULODUS



The mid-third of the blade consists of 6-8 denticles, all of which are small and almost entirely fused. These denticles all attain approximately equal height.

The beginning of the posterior third is marked by 2 or 3 large denticles, while the rest of this fraction of the conodont bears 3 or 4 slightly smaller but strong discrete denticles.

Aborally there is a fairly large basal cavity, which is located in the central third of the unit. The cavity bears lips and is tapered anteriorly and posteriorly; it is bilaterally symmetrical. Keels are present at the anterior and posterior ends of the unit, their length being dependent on the longitudinal extension of the cavity and its lips.

Remarks.

These forms do not compare exactly with the description of Angulodus Huddle. They appear to possess some characteristics of this genus and some of the genus Falcodus. Angulodus and Falcodus are closely related, if not synonymous, and an intermediate form such as this would tend to lend weight to this consideration.

The figured specimens of this genus are represented by a single species.

Material studied. 3 specimens

Occurrence. PB.2 - PB.4

Catalogue numbers of the figured specimens. JW.239 - JW.241

Genus BRYANTODUS? Bassler, 1925
(Pl.13, figs. 14a,b.)
(Text fig.41)

1925 *Bryantodus* Bassler, p.219

1926 *Bryantodus* Ulrich & Bassler, p.21.

Type species. *Bryantodus typicus* Ulrich & Bassler, 1926.

A blade or bar-like genus which has a basal cavity (which may display lips) in the mid third of the unit, a centrally located main cusp, (which is considerably larger than the other denticles of the blade) immediately above the cavity, and an approximately equal number of denticles on the anterior and posterior portions of the blade. This genus resembles *Ozarkodina* but is distinguished by a triangular outline to the blade or bar in transverse section, the oral side being broad and the aboral side sharp-edged. There is also a tendency for the main cusp to develop a short downward projection which is not a feature of *Ozarkodina*.

A single broken specimen of this genus was recovered from the Lower Pilton Beds.

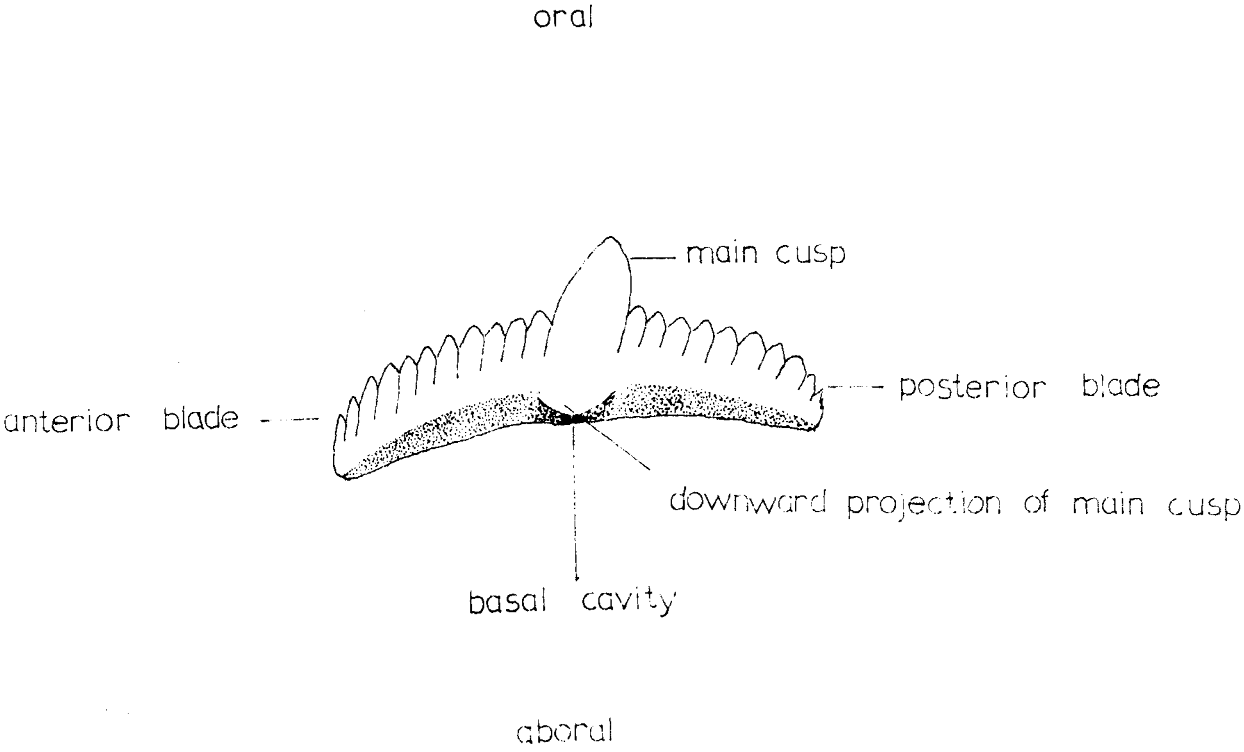
Material studied. I specimen

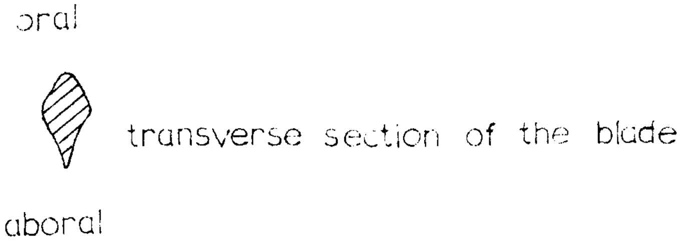
Occurrence. PB.25

Catalogue numbers of the figured specimen. JW.250

FIGURE 41

GENUS BRYANTODUS





Genus FALCODUS Huddle, 1934
(Pl. 13, figs. 6a,b.)
(Text fig.42)

1934 Falcodus Huddle, p.87

Type species. Falcodus angulatus Huddle, 1934

One partially broken specimen has been assigned to this genus, which is characterised by a posterior bar which exhibits a marked downward deflection through an angle of abour 90°. The denticles of the bar at the point of deflection are commonly larger than those immediately adjacent. The basal cavity is extremely small and there is no distinct main cusp developed above it. The shorter anterior bar usually bears one or two very large denticles. The unit is laterally compressed and has a distinctive outline.

Material studied. I specimen

Occurrence. F.6

Catalogue number of the figured specimen. JW.247

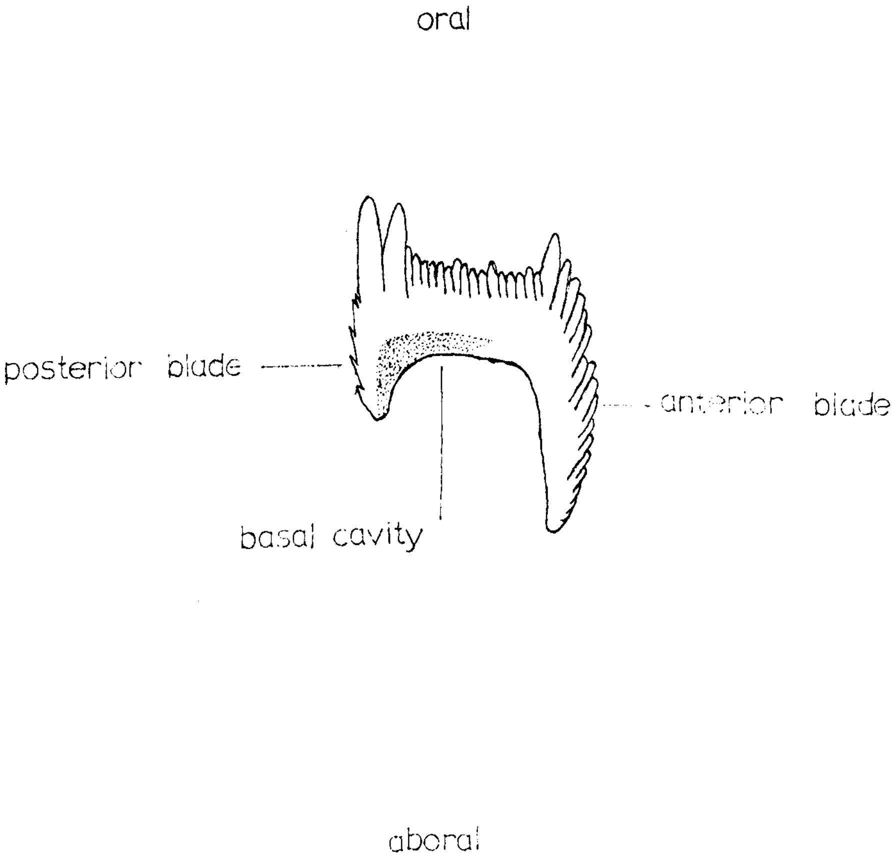
Genus HIBBARDELLA Bassler, 1925
(Fig.43)

1925 Hibbardella Bassler, p.219

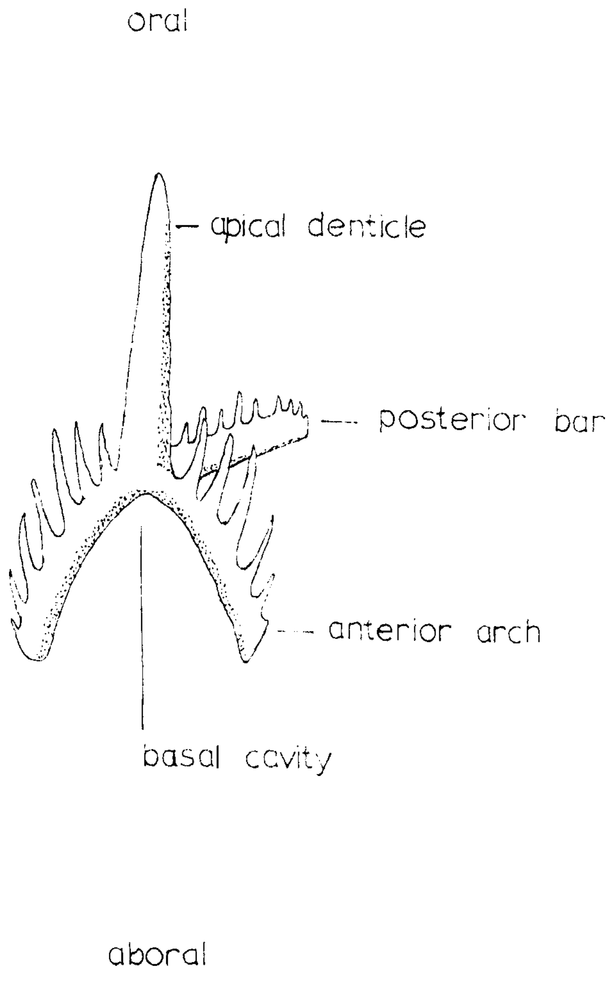
1926 Hibbardella Ulrich and Bassler, p.37

FIGURE 42

GENUS FALCODUS



GENUS HIBBARDELLA



Type species. *Prioniodus angulatus* Hinde, 1879

The genus *Hibbardella* was established by Ulrich and Bassler (1926) for a group of arched, blade-like conodonts which bore a very large apical denticle. The denticles of the anterior arch were discrete, slightly curved inward and usually few in number. These authors did not mention the groove-like nature of the basal cavity nor the development of the posterior, denticulated bar, but later work revealed these features as further characters of the genus.

Rhodes, Austin and Druce (1969) argued that various authors had erected several new genera which differed in only minor morphological respects from the genus *Hibbardella*. These included *Roundya* Hass (1953), *Ellisonia* Muller (1956) and possibly *Diplododella* Bassler (1925). The solution proposed by Rhodes et al (1969) for this situation was to divide the genus *Hibbardella* into three subgenera:-

(a) *Hibbardella* (*Hibbardella*)
(b) *Hibbardella* (*Roundya*)
(c) *Hibbardella* (*Hassognathus*)

These three forms can be distinguished by the nature of the basal cavity and apical denticle.

(a) *Hibbardella* (*Hibbardella*) is characterised by an apical denticle which is compressed antero-posteriorly, the lateral edges being sharp, and by a small basal cavity which is restricted to the aboral surface of the apical denticle. However, aboral grooves are present on the anterior and posterior bars.

(b) *Hibbardella* (*Roundya*) is characterised by a large basal cavity and the whole aboral surface of the apical denticle is hollowed out. The apical denticle itself is sub-circular in cross-section in its lower half, becoming compressed

(c) Hibbardella (Hassognathus) is characterised by a conspicuous basal cavity which is largely developed below the posterior bar, although it is also present below the apical denticle which is sub-circular in cross-section, and unornamented.

Hibbardella (Hibbardella) cf. H. microdentata Thomas, 1949

(Pl.12, figs.1a-1c,3,4a-4c,6a-7b)

cf. 1949 Hibbardella macrodentata Thomas; p.422, pl.4, fig.25.

1969 Hibbardella (Hibbardella) cf. H. macrodentata Thomas: Rhodes, Austin & Druce; p.115, pl.25, figs.16a-18c.

1969 Hibbardella (Hibbardella) cf. H. macrodentata Thomas: Druce; p.64, pl.9, figs.4a-6.

Description.

The anterior arch is symmetrical, compressed laterally and bears a keel on its aboral surface. The oral surface of the arch exhibits 5 to 7 strong, discrete, peg-like denticles on either side of the apical denticle. These denticles are slightly inclined posteriorly and are sub-circular in cross-section.

The apical denticle is tall, posteriorly inclined and also sub-circular in cross-section. The posterior bar is strongly developed, subcircular in cross-section and bears small, discrete, peg-like denticles, but in all the figured specimens the posterior bar is broken.

The basal cavity is small, sub-rounded and occurs directly beneath the apical denticle.

One specimen (Pl.12, fig.7a-b) possesses an anterior arch typical of *H. macrodentata* except that it bears no obvious apical denticle. This may possibly be interpreted as a pathological variant of *H. macrodentata*.

Material studied. 43 specimens

Occurrence. PB.2 - F.8

Catalogue number of the figured specimens. JW.224, JW.226, JW.228, JW.229.

Hibbardella (*Hibbardella*) sp.

(Pl.12, fig.5a-b)

Description.

These are small elements with a symmetrical anterior arch which is laterally compressed. The angle between the two limbs of the arch varies between 45° to 60°, and each limb bears 5 to 7 small but discrete denticles on its oral surface. The posterior bar is laterally compressed and bears very small, closely set denticles at its anterior end, the rest of the bar being broken off in the two specimens recovered.

The apical denticle is sub-oval in cross section, two to three times the size of the largest arch denticle, and surmounts a tiny aboral cavity from which short keels radiate along the anterior arch and posterior bar.

Remarks.

Only two specimens of this type were recovered from the Pilton section and both were incomplete.

Material studied. 2 specimens

Occurrence. PB.35

Catalogue number of the figured specimen. JW.227

Genus HINDEODELLA Bassler, 1925
(Fig.44)

1925 Hindeodella Bassler, p.219

1926 Hindeodella Ulrich & Bassler, p.38

Type species. Hindeodella subtilis Ulrich & Bassler, 1926

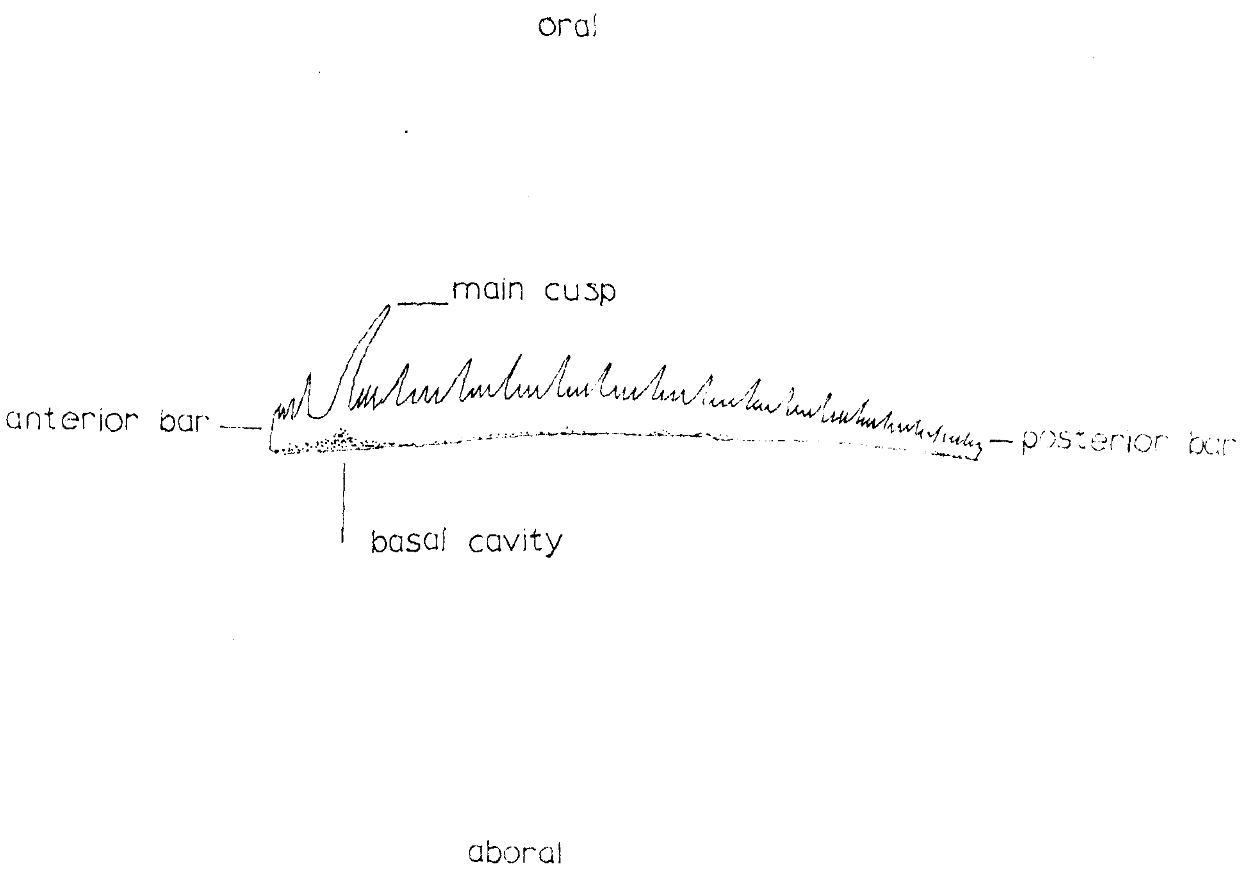
This genus is a member of the subfamily Hindeodellinae Hass 1959, which is characterised by the presence of a distinct main cusp, which usually separates a long posterior bar or blade from a shorter anterior bar or blade. Ulrich and Bassler (1926) erected this genus for those long, straight, bar-like conodonts which bore up to 10 small denticles on the anterior bar and numerous small denticles, which often alternate in size, on the posterior bar. The main cusp was larger and stronger than the other bar denticles. The basal cavity, although not described by Ulrich and Bassler, is small, often occurring as a narrow groove on the aboral surface. The anterior bar was commonly curved in oral view.

Numerous fragments of bars and blades were found throughout the Baggy and Pilton sequence, and although many could be identified as belonging to this genus, specific identification was impossible.

Hindeodella subtilis Ulrich & Bassler, 1926
(Pl.12, figs.8a-c, 10a-c, 14a-c)

1926 Hindeodella subtilis Ulrich & Bassler; p.39, pl.8, figs.17-19.

GENUS HINDEODELLA



1931 *Hindeodella subtilis* Ulrich & Bassler: Cooper; p.147, pl.20, fig.9.

? 1931 *Hindeodella pumilla* Cooper; p.236, pl.28, fig.18.

? 1931 *Hindeodella subtilita* Cooper; p.236, pl.28, fig.17.

1934 *Hindeodella delicatula* Branson & Mehl; p.280, pl.22, fig.30.

1934 *Hindeodella alternidens* Huddle; p.44, pl.5, fig.13(*non* Pl.5, fig.12 = *Hindeodella* sp.).

1934 *Hindeodella angulus* Huddle; p.44, pl.5, fig.15.

1934 *Hindeodella grandis* Huddle; p.41, pl.4, fig.22.

? 1934 *Hindeodella laticlavis* Huddle; p.43, pl.5, figs.9,10.

1938 *Hindeodella delicatula* Branson & Mehl: Branson & Mehl; pl.33, fig.34.

1943 *Hindeodella subtilis* Ulrich & Bassler: Cooper & Sloss; p.170, pl.28, figs.22,32,33.

1943 *Hindeodella atteridens* Huddle: Cooper & Sloss; p.170, pl.28, fig.23.

1943 *Hindeodella petila* Cooper: Cooper & Sloss; p.170, pl.28, figs.26,35.

1943 *Hindeodella deflecta* Hibbard: Cooper & Sloss; p.170, pl.28, figs.27, 34.

1943 *Hindeodella germana* Holmes: Cooper & Sloss; p.170, pl.28, fig.28.

1943 *Hindeodella grandis* Huddle: Cooper & Sloss; p.170, pl.28, figs.31,37,39.

1943 *Hindeodella laticlavis* Huddle: Cooper & Sloss; p.170, pl.28, fig.38.

1955 *Hindeodella germana* Holmes: Sannemann; p.130, pl.2, fig.45.

1955 *Hindeodella deflecta* Hibbard: Sannemann; p.129, pl.5, fig.8.

1959 *Hindeodella deflecta* Hibbard: Helms; pl.4, fig.32, pl.1, fig.17.

1960 *Hindeodella germana* Holmes: Zimmermann; pl.1, fig.16.

1961 *Hindeodella germana* Holmes: Budurov; p.262, pl.3, fig.11.

1962 *Hindeodella* sp. Winder; p.91, fig.1,6.

1965 *Hindeodella germana* Holmes: Spasov; p.86,87, pl.1, fig.10.

1965 *Hindeodella similis* Ulrich & Bassler; Spasov; p.87, pl.1, fig.11.

1969 Hindeodella subtilis Ulrich & Bassler: Rhodes, Austin & Druce; p.125, pl.29, figs.6a-7b, 9-10b.

1969 Hindeodella subtilis Ulrich & Bassler: Druce; p.69, pl.10, figs.3,4.

Description.

The apical denticle is tall, laterally compressed, biconvex in cross-section and inclined posteriorly. The anterior bar is deflected laterally through 90°, or deflected only slightly in a lateral sense. The anterior bar is also laterally compressed, bearing 4 or 5 small denticles.

The posterior bar is thin, and often comparitively deep, bearing numerous discrete denticles. There is some variety in the pattern of the posteriorly inclined dentition of this bar, as it may be cyclic or the denticles may be of relatively uniform dimensions. Toward the posterior end of the bar the denticles become flat lying or inclined at a very low angle to the horizontal.

The basal cavity is small and situated beneath the apical denticle.

Remarks.

This group was by far the most abundant identifiable form of hindeodellid in the Baggy Pilton Beds, occurring in all the samples collected from Croyde Bay and Fremington. Many of these specimens were broken, the anterior bar or part of the posterior bar being missing in most cases.

Material studied. 83 specimens

Occurrence. PB.1 - F.8

Catalogue numbers of the figured specimens. JW.230, JW.232, JW.236

Hindeodella cf. H. tenuis Clarke, 1960

(Pl.12, figs.12a-13b)

1960 Hindeodella tenuis Clarke; p.8,9, pl.1, fig.10,11.

1969 Hindeodella tenuis Clarke: Rhodes, Austin & Druce; p.126, pl.28, fig.27.

Description.

The posterior bar is long, straight in its anterior two thirds and gently down-curved in its posterior third. The denticles increase in size posteriorly and are discrete though relatively closely set along the oral surface of the bar. The denticles are inclined posteriorly, the degree of inclination being greatest in the posterior third of the bar.

The apical denticle is recurved, massive and tall, its basal width being 2 to 3 times that of the largest posterior bar denticle.

The anterior bar is relatively short and only gently inflexed. The basal cavity occurs directly beneath the apical denticle and is small and slit-like with a prominent keel extending from it along the aboral side of the posterior bar.

Remarks.

The present specimens are similar to those described by Rhodes, Austin & Druce, except for one morphologic feature that the Pilton specimens do not share with those described from the Dibunophyllum Zone of the Lower Carboniferous of the North Crop of the South Wales coalfield. The Pilton forms lack the presence of smaller denticles between each of the larger denticles of the posterior bar.

Material studied. 17 specimens

Occurrence. PB.1 - PB.16

Catalogue numbers of the figured specimens. JW.234, JW.235

Hindeodella corpulenta Branson & Mehl, 1934

(Pl.12, figs.9a-c, 11a-c)

1934 *Hindeodella corpulenta* Branson & Mehl; p.281, pl.22, figs.32,33.
1934 *Metaprioniodus fractus* Huddle; p.11, figs.14,15.
1934 *Ligonodina conidens* Huddle; p.63, pl.12, figs.18,19.
1938 *Ligonodina angulata* Branson & Mehl; p.142, pl.34, fig.43.
1939 *Ligonodina conidens* Huddle: Cooper; p.390, pl.45, fig.45.
1944 *Ligonodina angulata* Branson & Mehl: E.B. Branson; pl.39, fig.43.
? 1947 *Hindeodella millerella* Youngquist & Peterson; p.245, pl.38, fig.1-5.
1949 *Hindeodella* cf. *Hindeodella corpulenta* Branson & Mehl: Thomas; p.408, pl.1, fig.4.
1969 *Hindeodella corpulenta* Branson & Mehl: Rhodes, Austin & Druce; p.120, pl.29, figs.16a-17c.
1969 *Hindeodella corpulenta* Branson & Mehl: Druce; p.68, pl.10, figs.5-7.

Description.

The anterior lateral bar is deflected laterally through 90° and depressed downward through 60° to 90°. It bears between 4 to 6 discrete subcircular denticles which may be vertical, anteriorly or posteriorly inclined. These denticles are commonly inclined posteriorly.

The apical denticle is tall, ovate at its base becoming semicircular toward its tip. It is gently recurved and inclined posteriorly.

The posterior bar is straight or gently bowed in lateral view, bearing 5 to 6 large, isolated, posteriorly inclined denticles which increase in size and inclination toward the posterior end of the bar.

The basal cavity is large and expanded beneath the apical denticle and extends approximately two thirds of the way along the aboral surface of the posterior bar before tapering to a point.

Material studied. 38 specimens

Occurrence. PB.10 - F.8

Catalogue numbers of the figured specimens. JW.231, JW.233

Genus HINDEODINA Hass, 1959
(Fig.45)

1959 Hindeodina Hass, p.382

Type species. Hindeodina simplaria Hass, 1959

Hass's diagnosis of this genus is as follows:-

> "Elongate blade-like or bar-like unit; anterior bar may be flexed inward. Main cusp aborted, indistinct, distinguished from bar denticles only through its position above the pulp cavity. Bar denticles may be of more than one size. Greater part of aboral side sharp edged. Lips of pulp cavity either absent or extremely small."

This genus is distinguished from Hindeodella and Cervicornoides by the absence of a large, well developed main cusp. It is distinguished from Branmehla and Coleodus by its more elongate nature, and from Bactrognathus by the possession of a sharp-edged aboral side and only small lips to its basal cavity, if it has lips at all.

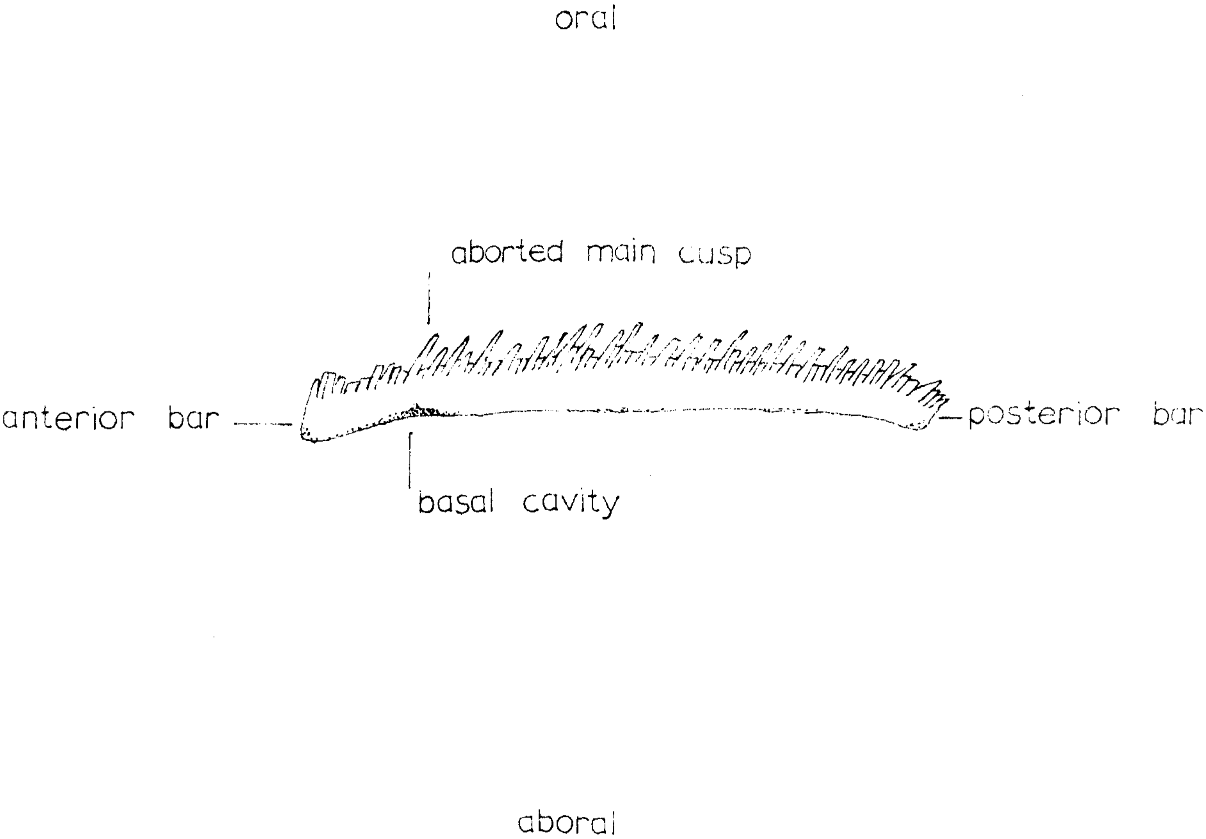
Hindeodina simplaria Hass, 1959
(Pl. 13, figs. 1a-2b)

1959 Hindeodina simplaria Hass, p.382, pl.48, fig.17

Three specimens of this species were recovered from the Lower Pilton Beds. They compare closely with Hass's (1959, p.382) original description. Many of the broken conodont bars and blades recovered in this study are probably fragments of this genus, but in most cases, it is impossible to distinguish such fragments from broken hindeodellids.

FIGURE 45

GENUS HINDEODINA



Material studied. 5 specimens

Occurrence. PB.21 - PB.35

Catalogue numbers of the figured specimens. JW.237 - JW.238

Genus ICRIODUS (Branson & Mehl, 1934)
(Fig.46)

1934 Icriodus Branson & Mehl, p.225 (nomen nudum)

1938 Icriodus Branson & Mehl, p.159

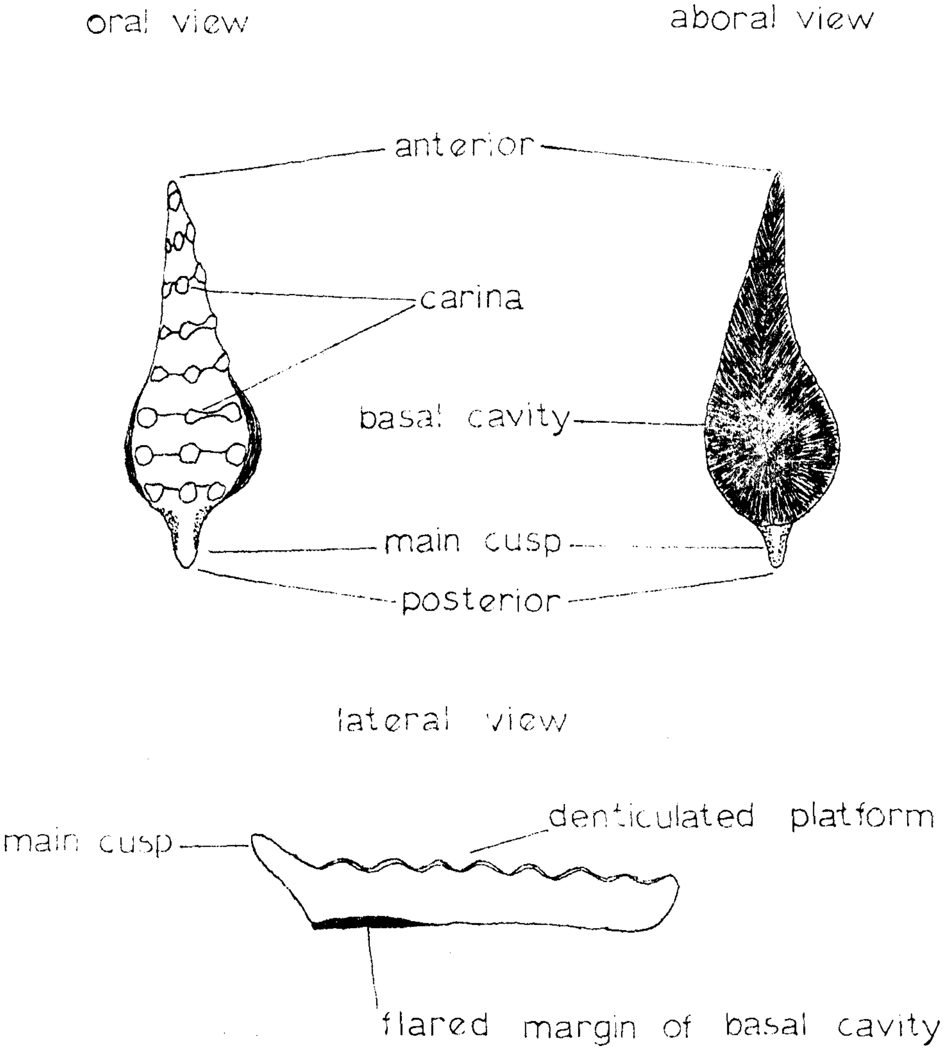
Type species. Icriodus expansus Branson & Mehl (1938) p.160-161, pl.2 figs. 18-21, by original designation.

Branson and Mehl's original description of this genus was as follows; "Platform-like teeth with high sides either straight or flaring near the lower margin, of more or less spindle-shaped or lachrymiform outline in superior view and without a distinct anterior blade as in polygnathids. The aboral side is deeply excavated its entire length and the oral surface consists of two or more longtitudinal rows of low, sharp cusps."

These authors noted that this genus seemed closely related to Gnathodus but could be distinguished in that the aboral cavity of Gnathodus consisted of a circular cup at the posterior end of a long blade, and the oral surface posterior to the blade was convex rather than platform-like.

Thomas (1949) described a new genus which he called Pelekysgnathus. He commented that its generic relationships were doubtful but the morphology of of one of his specimens suggested an affinity with Icriodus. It is true that

GENUS ICRIODUS



the genera Icriodus and Pelekysgnathus are closely related, and since 1949 opinions have varied with regard to the criteria that should be employed to distinguish them. Klapper (1966) summarised the problems which have arisen, and the present author proposes to follow his arguments and conclusions.

The present interpretation is that Pelekysgnathus differs from Icriodus in possessing only one row of oral denticles. Icriodus normally has three such rows, although forms with two rows of oral denticles have been recorded (e.g. Voges 1959, Taf.33, fig.44; Voges calls his two rowed forms, Pelekysgnathus sp.A). Muller & Muller (1957) diagnosed forms with two rows of denticles as belonging to Icriodus, but they emphasised that such forms were a rarity. Klapper (1966) expressed his agreement with Muller & Muller's interpretation.

According to this interpretation, Pelekysgnathus costata Thomas 1949, should be assigned to the genus Icriodus, because of the presence of two lateral rows of denticles which have become fused transversely. Similarly, Voges (1959, pl.33, fig.44) illustrated a conodont with two rows of nodes, which he called Pelekysgnathus sp., and this too should be included in the genus Icriodus.

Ethington et al (1961) decided that the best criteria for distinguishing the two genera in question were the more prominent inclined main cusp and the greater degree of arching of Pelekysgnathus. However, evidence that icriodids have developed long inclined cusps at various stages in their evolution is substantiated by the icriodids from the Lower Pilton Beds, all of which display prominent main cusps. In a number of cases the main cusps of the icriodids are more prominent than those of the associated pelekysgnathids. Thus, the possession of a long inclined main cusp is not a feature which is unique to Pelekysgnathus, and, as suggested by Klapper (1966), "the degree of arching does not seem to be character of sufficient value for generic differentiation in platform conodonts".

According to the criteria of Ethington et al (1961), *Icriodus costatus*, which can be arched and which does possess an inclined main cusp, should be assigned to the genus *Pelekysgnathus* despite the fact that it has three rows of denticles.

Another point of conjecture, during the past thirty years or so, has been the orientation of *Icriodus*. Branson & Mehl (1934c) and Thomas (1949) orientated the genus with the main cusp when present, and greatest width of the aboral cavity, as posterior. The same orientation is used by Hass (1962) in the Treatise on Invertebrate Palaeontology (Part W Misscellanea). Muller & Muller (1957) interpreted the main cusp as a reduced blade, and thus orientated the genus with this cusp and the maximum width of the basal cavity as anterior. Ethington & Furnish (1962) also orientated *Icriodus* in this way, as did Anderson (1966). However, Ziegler (1960), Klapper (1966), Sannemann (1955), Lindstrom (1944) and Glenister and Klapper (1966) advocate the former method of orientation for icriodids, because of the inclination of the main cusp when it is present. In all other conodont elements the posterior end is indicated by the direction of inclination of the denticles, and these authors note that it would be wrong to make *Icriodus* the exception. The writer proposes to follow this argument and orient the members of the genus with the main cusp as posterior; the maximum width of the large excavated basal cavity is thus also posterior.

Icriodus costatus (Thomas, 1949)
(Pl.7, figs.9a - 10c, Pl.8, figs.1a-c, 3a-c)

1949 *Pelekysgnathus costata* Thomas; p.424, pl.2, fig.9

1949 *Icriodus* cf. *I. rectus* (Youngquist & Peterson): Thomas; p.434, pl.1, figs.17,18.

non 1955 *Icriodus cornutus* Sannemann; p.130, taf.4, figs.19a-c, 20, 21.

1958 *Icriodus darbyensis* Kalpper; p.1086, pl.141, figs.9,11,12.

1961 *Pelekysgnathus darbyensis* (Klapper): Ethington, Furnish & Wingert; p.765, pl.90, figs.12-17.

1964 *Pelekysgnathus darbyensis* (Klapper): Lindstrom; p.53 & 161, text fig. 17A, 56h.

non 1966 *Icriodus cornutus* (Sannemann): Glenister & Klapper; p.804-805, pl.95, figs.2,3.

1966 *Icriodus costatus* (Thomas): Anderson; p.406, pl.52, figs.1-6,10.

1966 *Icriodus costatus* (Thomas): Klapper; p.30, pl.6, figs.19-22.

? 1967 *Icriodus cornutus* (Sannemann): Wolska; p.380, pl.11, fig.5a-b.

Diagnosis.

Prominent main cusp inclined posteriorly, three sub-paralled rows of denticles ornament the oral surface. The denticles of the lateral rows are aligned with those of the carina. In mature forms, transverse ridges may develop connecting the denticles of the three rows. Basal cavity widest posteriorly, often displaying flared margins.

Description.

Disregarding the prominent main cusp, the overall shape of these units, in oral view, can vary from those with sub-parallel sides to those (more mature forms) with platforms which taper gradually toward the anterior. The aboral cavity in both juvenile and mature forms alike, is widest posteriorly, tapering to a sharp point anteriorly.

Orally these elements are dominated by the large, posterior cusp which projects out beyond the platform of the conodont unit. On the platform itself the ornamentation consists of three rows of denticles, a carinal or central row and two lateral rows. The three rows run sub-parallel for the greater part of the platform length, but the denticles of the lateral rows become markedly smaller toward the anterior end, owing to the tapered nature of the platform. In some cases the most anterior carinal denticle is unaccompanied by lateral denticles, but often minute lateral denticles are visible, budding off the sides of this carinal denticle. The nodes of the lateral rows are aligned opposite those of the carina and in mature forms all or most of the carinal nodes are connected by transverse ridges to the adjacent lateral nodes. The number of denticles composing the carina ranges from 6 to 8, excluding the main cusp. Both lateral rows of any one specimen invariably consist of one fewer denticle than the carinal row.

Individual units are bilaterally asymmetrical, the outer side being convex while the inner side is straight or slightly concave. This is true of both right and left forms and consequently right and left forms are mirror images of each other with regard to oral ornamentation.

Aborally the basal cavity of right and left forms is also bilaterally symmetrical, but the cavity of an individual unit is bilaterally asymmetrical. The maximum width of the large excavated cavity, which occupies the whole of the aboral surface, is located at the posterior end of the unit. The cavity is rounded posteriorly and tapers gradually toward the anterior end where it terminates in a point. The outer edge of the aboral cavity of an individual element is convex, while the inner edge is convex in the posterior third becoming concave in the middle and anterior thirds, after curving sharply. The margin of the cavity may be flared, particularly in the posterior half of the unit.

In aboral view the prominent, inclined main cusp on the oral surface can be seen projecting beyond the posterior limit of the basal excavation.

Laterally the units are slightly arched to straight; the main posteriorly inclined cusp dominates the lateral profile. It projects from the platform at an angle of 45° to 65°, and often it is curved gently upwards, having a hook-like appearance. The denticles of the three oral rows all attain approximately the same height but are considerably lower than the posterior cusp. In laterally arched forms, the denticles of the anteriormost portion of the carina are not as high as the rest of the platform denticles, but this is due solely to the arching. With the exception of the main cusp the oral and aboral edges are parallel, whether or not the unit is arched or straight.

Remarks.

Klapper (1966) diagnosed this species, stating that the lateral and median rows of denticles were always connected by transverse ridges. This was apparent only in mature specimens of this species, from the Lower Pilton Beds, smaller forms usually displaying three distinct rows of nodes with no connecting ridges. However, in every case the lateral and median rows of nodes were aligned, if not connected, transversely.

Icriodus costatus is similar to *Icriodus symmetricus* in that they both possess aligned rows of denticles, but *Icriodus symmetricus* lacks a prominent, horn-like, posteriorly inclined main cusp. Anderson (1966) noted that specimens which he called *Icriodus costatus* generally did not develop transverse ridges and he concluded that his specimens were transitional forms between *Icriodus cornutus* Sannemann and *Icriodus costatus*, as illustrated by Thomas (1949), Klapper (1958 & 1966) and Ethington et al (1961). The author has considered all the forms from the Pilton Beds with prominent posterior cusps and aligned lateral and median denticles (with or without connecting transverse ridges) as Icriodus costatus, those without ridges being interpreted as immature forms. However, Anderson's conclusions that those forms without ridges are transitional may well be valid.

Icriodus cornutus Sannemann has alternating lateral and median nodes and is distinguished from Icriodus alternatus Branson & Mehl by the possession of a prominent main cusp, which is strongly inclined posteriorly. Although the photographs are not perfectly clear, Icriodus cornutus illustrated by Wolska pl.2, fig.5a-b, apparently has aligned denticles characteristic of Icriodus costatus.

Material studied. 23 specimens

Occurrence. PB.10 - PB.16

Catalogue numbers of the figured specimens. JW.178 - JW.180, JW.182

Icriodus sp. nov.

(Pl.8, fig.2a-c)

Diagnosis.

Prominent, curved main cusp, two lateral rows of seven denticles which can be nodose or ridge-like. Central or carinal row of denticles fused for the greater part of their length, occurring as a longtitudinal ridge. Basal cavity extremely large and the edges prominently flared; it is as wide as long. Maximum width of the basal cavity is much greater than the maximum width of the oral platform. In lateral view the platform is boat-shaped.

Description.

Orally the ornamentation shows no precise symmetry. The platform sides are bi-convex, approximately twice as long as broad. Two distinct lateral rows, each consisting of seven denticles, are visible, some of the denticles comprising these rows are restricted to the platform margins and are nodose; others are ridge-like and connected transversely to the median or carinal ridge. The nodes of the carina are fused for the greater part of their length, occurring as a low continuous ridge, but three distinct nodes belonging to the carina can be seen, two at the anterior end of the ridge and one at the posterior end (other than the main posterior cusp). These three nodes and the ridge, which compose the carina, do not run in a straight or gently curved line but have an angular distribution, and thus the oral surface is markedly asymmetrical. The main cusp at the posterior end of the unit is prominent and curved.

This specimen is apparently a right form; this is based on the overall curvature of the unit, and if this designation is correct then there is a shallow trough developed on the outer side of the platform between the carina and the outer lateral row of nodes.

Aborally the anterior tip of the basal cavity is missing, but, the rest of the cavity is well preserved. The cavity is extremely large and widely flared, the length and width being approximately equidimensional. The outer edge is convex while the inner edge is convex in the posterior half and then sharply curved to become concave in the anterior half of the unit. The posterior margin of the cavity is rounded and, although the extreme anterior portion of the cavity is missing, the nature of the sides leading to this region suggest a pointed anterior margin. The maximum width of the aboral cavity is considerably larger than the maximum width of the oral platform; this is due to the flared nature of the margins of the excavation.

Laterally the unit has a boat-like profile. The flared margins of the basal cavity form a sturdy base, and the platform, including the main cusp, resembles a boat sitting on this base. The posterior edge of the unit curves backward anteriorly meeting the flared posterior margin of the basal cavity at an angle of just under 90°. The anterior margin curves back posteriorly, but, because the anteriormost portion of the basal cavity is missing, it is impossible to ascertain the angle of the junction between the anterior margin of the platform and the basal cavity.

The posterior main cusp is by far the largest denticle, but, the platform rises gradually from the base of the main cusp to the anterior extremity and the height of the main cusp is thus equated by the anteriormost denticle of the carina. The carinal ridge of the platform is obscured by the larger denticles of the lateral rows in this view. The main cusp itself is curved or hook-like and although its base is inclined posteriorly, the tip of the cusp is inclined vertically if not slightly anteriorly.

Remarks.

Only one specimen of this type was recovered despite extensive resampling of the horizon from which it came. This specimen could be cited as an argument against the orientation of Icriodus with the main cusp as posterior. This orientation is recommended by many authors based on the direction of inclination of the cusp, but in the present specimen the main cusp is directed vertically, if not slightly anteriorly.

Only two other forms have been located in the literature which show any resemblance to this specimen. This resemblance is merely in overall shape, and in detail there are significant differences. The two forms in question are N. g. and n. sp. Bouckaert & Ziegler (1965, pl.5, figs.9,10,11) and Icriodus constrictus Thomas, as illustrated by Anderson (1966, p.405, pl.52, figs.14-16). Only a few specimens of both of these forms have been recovered and described as yet, and hence the range of intraspecific variation is not yet established. The multitude of complex transverse ridges serves to distinguish Bouckaert and Ziegler's specimen from that of the Pilton Beds, together with a differently shaped basal cavity. Anderson's illustration of Icriodus constrictus resembles this Pilton form in general shape, but possesses characteristic bifurcating transverse ridges and no prominent main cusp. Klapper's (1966) illustration of this species (pl.6, fig.18) does not even resemble the Pilton form in overall shape.

Until more is known with regard to the limits of intraspecific variation within forms such as these, the author prefers to regard this as a separate and new species.

Material studied. 1 (one) specimen

Occurrence. PB.15

Catalogue number of the figured specimen. JW.181

N.B. One specimen of Icriodus from the Lower Pilton Beds had a very flared cavity developed conspicuously on just one side of the unit. However, this specimen was only partially preserved and consequently no valid assumptions could be made as to its specific affinities. Despite this, the nature of the cavity is unique in the Lower Pilton Beds and this incomplete specimen is apparently not a member of either of the species described.

Icriodus sp.
(Pl.7, fig.8a-c)

Description.

Orally, what appears to be the posterior third of the unit has been partially removed. Nevertheless, three distinct rows of platform denticles are visible and the platform itself is bi-convex in outline, tapering gradually toward the anterior. The denticles are peg-like and discrete, no transverse ridges being evident. In the anterior half of the platform the nodes of the lateral rows alternate with those of the carina, while in the posterior half they become aligned with the carinal nodes.

The flared margin of the basal cavity projects prominently beyond the edge of the platform. Whatever the nature of the aboral cavity (it is totally obscured) it is far wider than the maximum width of the oral platform.

In lateral view the nodes of the anterior half of the platform are visibly larger than those of the posterior half. The oral edge is straight, but no conclusions can be reached with regard to the aboral edge, owing to fracturing.

Aborally no features are visible, owing to the sedimentary material which coats this surface, and totally infills the basal cavity.

Remarks.

This specimen was the only conodont retrieved from the Pilton Bed outcrop on the main Barnstable-Taunton road, one mile east of the village of Bampton. This conodont has been assigned to the genus Icriodus, although the specimen is incomplete and the aboral surface is completely hidden by adhering sedimentary material which cannot be removed without further damaging the specimen.

Despite this, the oral ornamentation displays three rows of nodose denticles typical of icriodids, and, although incomplete the specimen, has a characteristic icriodid outline in oral view. The aboral side of the unit has a flared margin, typical of many species of this genus.

This specimen is not a member of either of the icriodid species described from Croyde Bay. The oral ornamentation, which is a combination of both alternating and aligned lateral and median denticles, is unlike that of the other Pilton icriodids.

If the present identification is correct, this would indicate that the Pilton Beds at Bampton are of Upper Devonian age (Lower Pilton age). Naturally the evidence of a single, broken specimen is far from conclusive, and furthermore one cannot rule out the possibility that this specimen has been reworked.

Despite extensive resampling no other conodonts were found in any of the Bampton horizons.

Material studied. 1 (one) specimen

Occurrence. B.7

Catalogue number of the figured specimen. JW.177

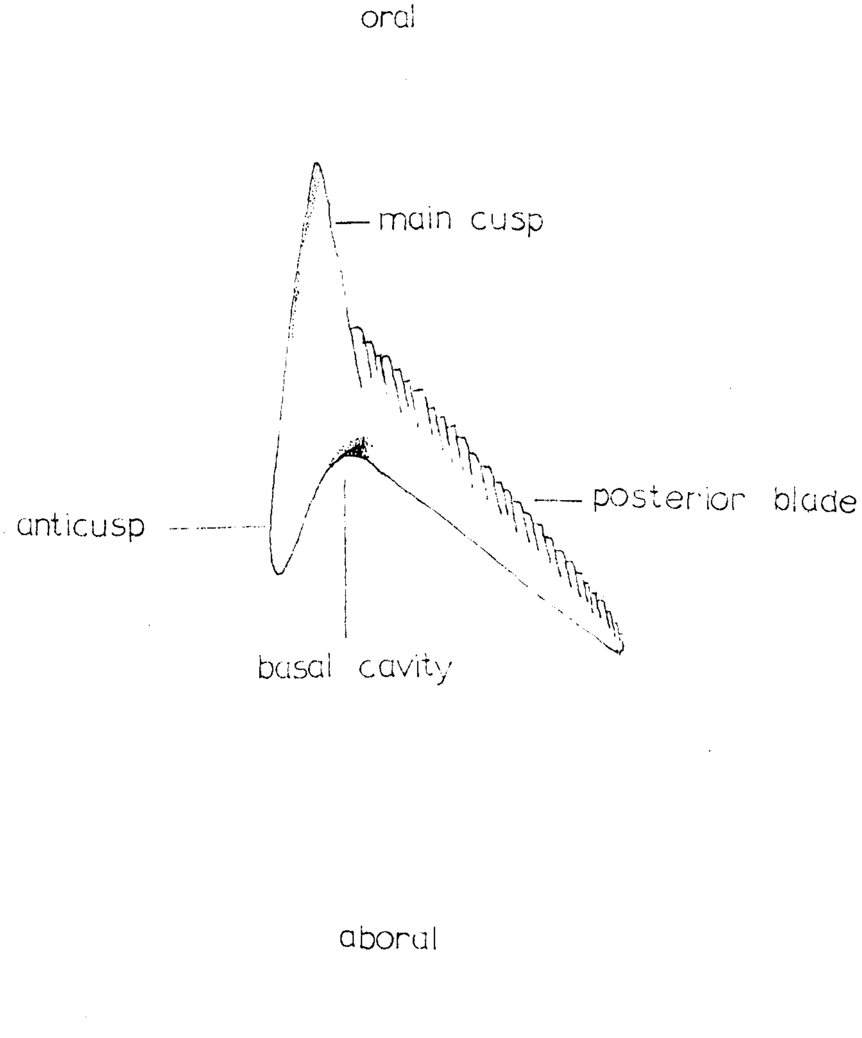
Genus NEOPRIONIODUS Rhodes & Muller, 1956
(Fig.47)

1956 Neoprioniodus Rhodes & Muller, p.698.

Type species. Prioniodus conjunctus Gunnell, 1931

FIGURE 47

GENUS NEOPRIONIODUS



Pander's (1856, p.29) original definition of the genus *Prioniodus* was very broad in nature, encompassing all forms which displayed a large fang, a posterior and possibly an anterior bar or blade, and a long narrow basal cavity. Rhodes & Muller (1956) refined Pander's genus into five genera namely,

Prioniodus s.s.
Neoprioniodus Rhodes & Muller
Ligonodina Ulrich & Bassler
Genus indet a
Genus indet b

Their diagnosis of the genus *Neoprioniodus* was as follows:-

> "Compound conodonts consisting of a denticulated posterior bar, at the anterior end of which a large fang (main cusp) is developed. The base of this fang may or may not extend downward below the level of the bar to form an 'anticusp', the anterior edge of which may or may not be denticulated. There is usually a basal cavity below the fang, which may be extended as a shallow groove on the aboral surface of the posterior bar."

Neoprioniodus *confluens* (Branson & Mehl, 1934)

(Pl.13, figs.7a-9b)

1934 *Prioniodus* *confluens* Branson & Mehl; p.206, pl.15, fig.7 (non pl.15, fig.17 = *N.* *alatus*)

1934 *Euprioniodina* *prona* Huddle; p.52, pl.6, fig.19, (non pl.11, fig.8 = *E.* *alternata*)

1939 *Prioniodus* *alatus* Hinde; Cooper: p.404, pl.46, figs.6,8.

1949 *Prioniodus aphanes* (Cooper); Thomas: p.411, pl.4, figs.20, 34.

1949 *Prioniodus obtusus* Branson & Mehl; Thomas: p.408, pl.1, figs.1,7.

1955 *Prioniodus prona* (Huddle); Sannemann: p.152, pl.3, fig.1.

1957 *Prioniodus prona* (Huddle); Ziegler in Flugel & Ziegler; p.49, pl.4, fig.6.

1961 *Neoprioniodus armata* (Hinde); Scott & Collinson; p.127, pl.2, fig.24 (non pl.2, fig.22 = *N. armata*).

1969 *Neoprioniodus confluens* (Branson & Mehl): Rhodes, Austin & Druce; p.158, pl.21, figs.2,8.

1969 *Neoprioniodus confluens* (Branson & Mehl): Druce; p.76, pl.14, figs.11a-12.

Description.

The anterior denticle is tall, laterally compressed, ovate in cross-section, and extended aborally to form a prominent anticusp. The basal cavity, which commonly displays a flared margin, is located at the junction of the anticusp and the posterior bar. The position bar is very long and straight or gently bowed in lateral view. Several specimens display a bar which is straight in its anterior two-thirds and gently deflected upward, through an angle of approximately 45° , in its posterior third. The posterior bar possesses at least 10 and in some specimens as many as 35 denticles which are discrete only at their tips.

Material studied. 73 specimens

Occurrence. PB.1 - F.8

Catalogue numbers of the figured specimens. JW.242 - JW.244

Genus <u>OZARKODINA</u> Branson & Mehl, 1934

(pl.13, figs.10a-11c)
(Text fig.48)

1934 <u>Ozarkodina</u> Branson & Mehl, p.51

<u>Type species.</u> <u>Ozarkodina typica</u> Branson & Mehl, 1934

Branson & Mehl erected the genus <u>Ozarkodina</u> for those conodonts which consisted of thin, denticulated, arched blades or bars with a large main cusp near mid-length, and an approximately equal number of smaller denticles on either side of this cusp. The denticles were compressed laterally and the basal cavity was located beneath the main cusp.

The figured specimens of this genus are represented by a single species.

<u>Material studied.</u> 18 specimens

<u>Occurrence.</u> PB.2 - F.6

<u>Catalogue numbers of the figured specimens.</u> JW.245 - JW.246

Genus <u>PELEKYSGNATHUS</u> (Thomas, 1949)

(Fig.49)

1949 <u>Pelekysgnathus</u> Thomas, p.424, 425

1961 <u>Pelekysgnathus</u> Thomas: Ethington, Furnish & Wingert, p.764, 765

<u>Type species.</u> <u>Pelekysgnathus inclinata</u> Thomas 1949, p.425 by original designation.

FIGURE 48

GENUS OZARKODINA

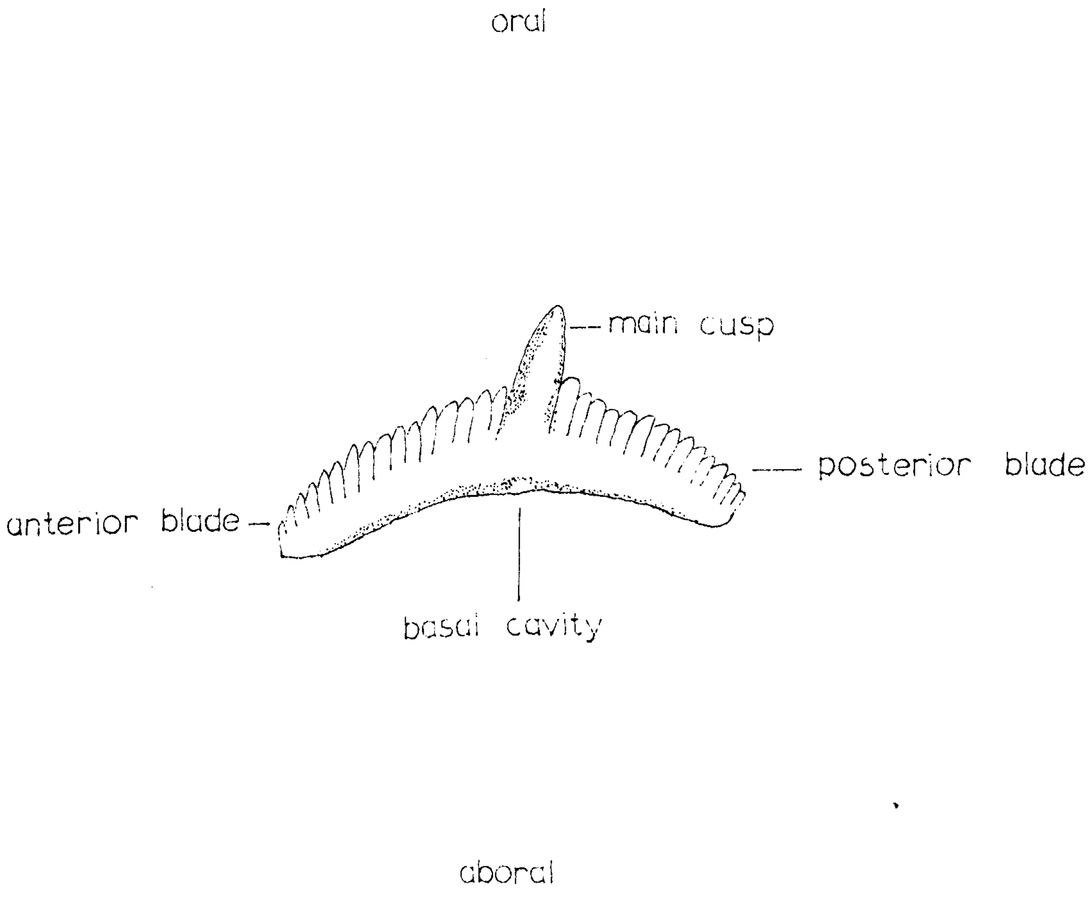
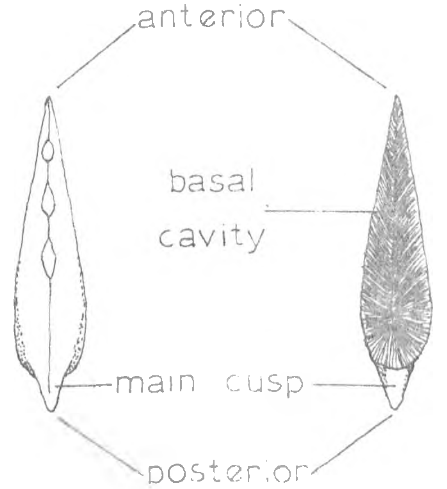


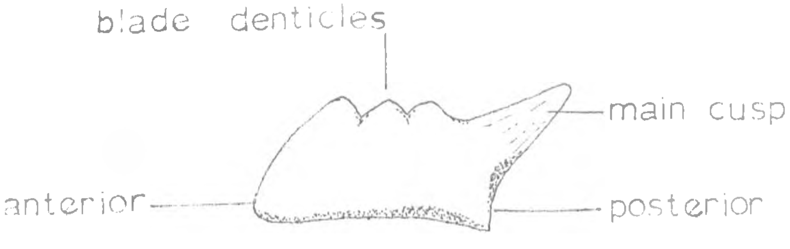
FIGURE 49

GENUS PELEKYSGNATHUS


oral view

aboral view

lateral view



This genus was designated for a series of forms from the Maple Mill Shale of South-east Iowa. The problems of differentiating *Pelekysgnathus* from *Icriodus* have been discussed in the systematic description of the latter genus.

Thomas's original description of *Pelekysgnathus* was as follows:-

> "Dental unit composed of a thin, moderately deep blade that is straight to slightly arched in lateral view. Oral surface of the blade marked by low, discrete or fused, node or ridge denticles that are not evident as germ denticles within the blade. Posterior end of the blade consists of a major thorn-like denticle that is directed posteriorly at varying degrees. Aboral surface symmetrically throughout its entire length; pit deepest beneath major fang. Thin lips project downward to cover aboral excavation."

Thomas noted that the generic relations of this group were doubtful, but that the nature of the basal cavity and sometimes ridge-like oral denticles suggested an icriodid relationship, whereas the main thorn-like fang suggested a prioniodid relationship. Klapper (1966) stated that the reference of *Pelekysgnathus* to the prioniodidae by Hass was doubtful.

The apparent restriction of *Pelekysgnathus* to the Upper Devonian, makes it possible that this genus represents a descendant of *Icriodus*. Anderson (1966) considers that the two rowed forms of *Icriodus*, which are rare, represent the transitional stage from *Icriodus* to *Pelekysgnathus*. The evolution of *Pelekysgnathus* from *Icriodus* would be effected by a reduction in the number of oral denticle rows from three to one (those with two rows are regarded as icriodids). Some authors include the development of a prominent posterior fang as a second trend although several species of *Icriodus* exhibit this feature.

The orientation of *Pelekysgnathus* is similar to that of *Icriodus*, the position of the main cusp indicating the posterior end. This orientation is followed in the present paper for the same reasons cited in the systematic description of the genus *Icriodus*.

The diagnostic features of the genus *Pelekysgnathus* are:-

(a) The possession of a prominent posterior cusp.
(b) A unit which is arched or straight in lateral view.
(c) A symmetrically tapered basal cavity.
(d) A single row of oral denticles which may be nodose or ridge-like.

Pelekysgnathus communis Thomas, 1949

(Pl.8, figs.4a-c, 5a-c, 6a-c)

1949 *Pelekysgnathus communis* Thomas;p.424, pl.2, figs.6,7,8
1966 *Pelekysgnathus inclinata* Thomas: Anderson, p.409
1966 *Pelekysgnathus* sp. Glenister & Klapper;p.826, pl.95, fig.10
1966 *Pelekysgnathus communis* Thomas: Glenister & Klapper; p.826

Diagnosis.

Prominent posterior cusp; three nodose denticles comprising the blade which are discrete only at their tips. Aboral and oral edges straight or only gently arched in lateral view. Basal cavity tapers symmetrically toward anterior and displays flared edges, this being particularly obvious at the posterior of the unit.

Description.

Orally the unit can be subdivided into two distinct parts, the large posterior cusp and the short thin blade. The blade is straight and in all five specimens, is composed of three nodose denticles which are fused for the greater part of their length and discrete only at their tips. The main cusp is markedly inclined toward the posterior and may be slightly curved toward the inner or outer side of the unit. The expanded margins of the basal cavity flare out prominently below the main cusp and less prominently below the blade.

The basal cavity occupies the whole of the aboral surface and is deeply excavated throughout. It is widest posteriorly, tapering gradually and symmetrically toward the anterior. The posterior edge of the cavity is rounded and the anterior edge bluntly pointed. The margins of the cavity are flared in the posterior half, and here the deepest excavation occurs, corresponding to a point directly below the main cusp. In its anterior half the cavity shows little or no flaring.

In lateral view the aboral edge is straight or only gently arched, but, the oral edge is a little more complex. The three denticles comprising the blade, which point vertically or almost so, increase in height very gradually from anterior to posterior. There is then a substantial gap where the blade is undenticulated and finally the prominent Posterior cusp is encountered, inclined at an angle varying between 45° and 65° posteriorly. The maximum height of the cusp is approximately twice that of the maximum height of the blade. The angle made by the junction of the aboral and anterior margins is variable but generally around 90°. The ratio of the height to width of the blade is 2:3 or smaller.

Remarks.

Anderson (1966) recommends that three of Thomas's original species of this genus should be considered as belonging to a single species. He states that Pelekysgnathus nodosa Thomas and P. communis Thomas are distinguished from P. inclinata Thomas by only minor details such as inclination of the main cusp and fusion of the denticles of the blade. Anderson considers that these minor differences do not warrant the erection of three individual species and suggests that such variation can be attributed to infraspecific variability within a single species. He selects P. inclinata, the type species of the genus, as the valid name.

Anderson's assumptions are probably well founded, but, the pelekysgnathid specimens from the Pilton Beds are not numerous enough either to substantiate or refute them. The reason why these Pilton specimens have been included in what is possibly an invalid species, is that they comply very closely with Thomas's original description of Pelekysgnathus communis.

Material studied. 11 specimens

Occurrence. PB.16 - PB.35

Catalogue numbers of the figured specimens. JW.183, JW.184, JW.186

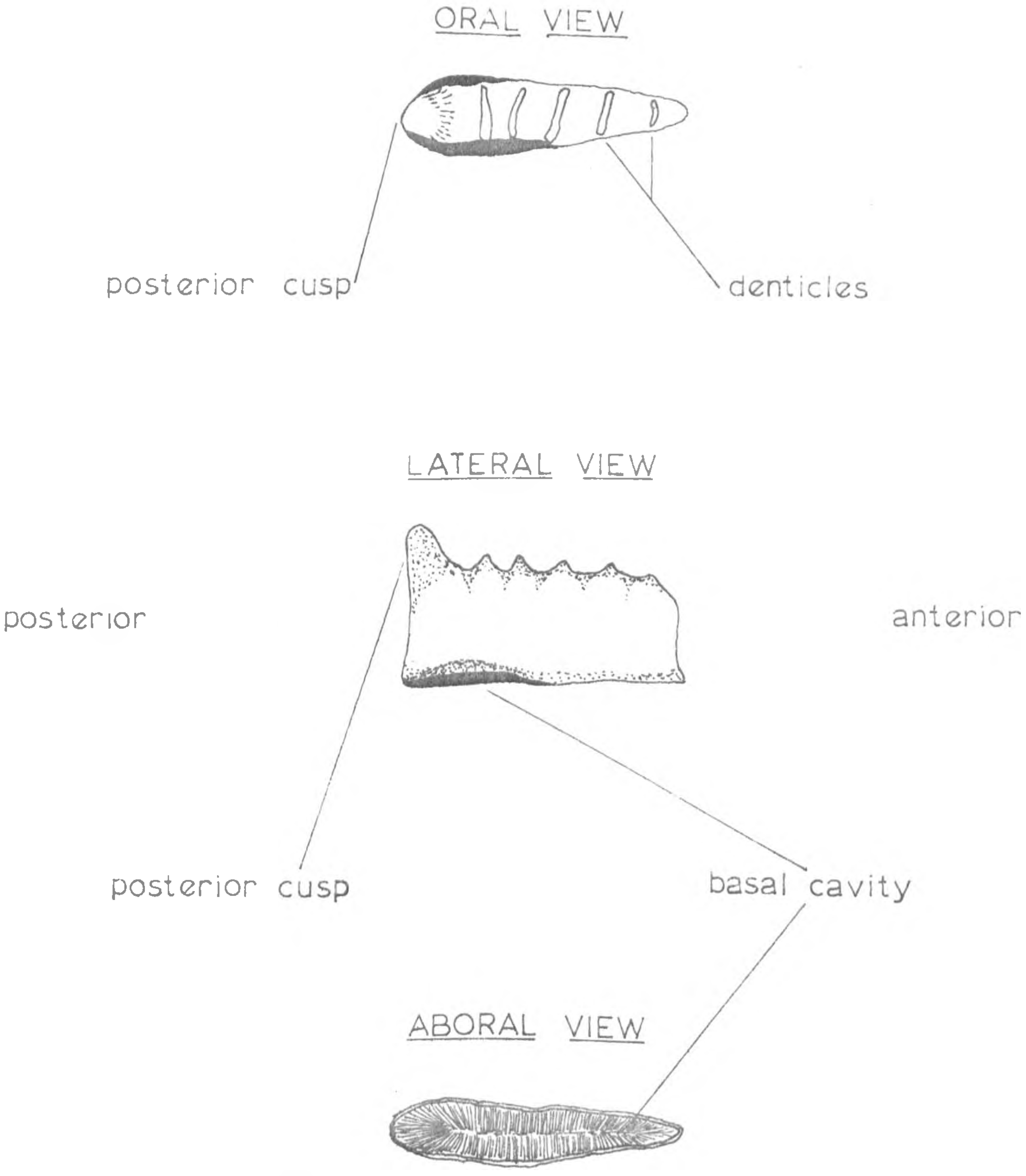
Pelekysgnathus croydeus sp. nov.

(Pl.8, figs.7a-10c, Text fig.50)

Derivation of name. From its occurrence in the Pilton Beds exposed at Croyde Bay.

Type specimen. Holotype JW.185, Pl.8, fig.7a-c.
Paratypes JW.187, JW.188, JW.189, Pl.8, figs.8a-10c.

FIGURE 50



ORAL VIEW

LATERAL VIEW

ABORAL VIEW

Pelekysgnathus croydeus sp. nov.

Diagnosis.

Small conodonts with blade composed of a single row of four to six denticles which are compressed transversely and as a result wedge-shaped. Posterior cusp large by comparison with the blade denticles. Basal cavity tapers very slightly from posterior to anterior.

Description.

In oral view the unit is slender, the blade being composed of 4-6 transversely compressed, ridge-like denticles. The overall shape of each denticle is wedge-like, similar to an inverted triangle, they become wider upward and are discrete for only half their total length. Orally the main posterior cusp is distinguished from the blade denticles by its nodose nature and its posterior inclination. The flared margins of the basal cavity make this feature obvious, even in oral view.

The basal cavity occupies the whole of the aboral surface and its sides are sub-parallel. The cavity tapers very slightly anteriorly from its widest development beneath the main cusp. Both anterior and posterior margins of the cavity are rounded. The inner and outer margins of the basal cavity are flared, particularly in the posterior half of the unit.

In lateral view the unit is lowest anteriorly, the three most anterior denticles of the blade increase gradually in height toward the posterior. At this point the outline of the blade becomes straight, the rest of the blade denticles attaining an equal elevation. At the posterior end of the blade the profile of the unit is marked by the thicker, posteriorly inclined, main cusp. The cusp, when complete, reaches a height which is approximately twice that of the larger blade denticles. The posterior inclination of the cusp varies between 60° and 90° from the horizontal. However, the cusp does not dominate the profile of this species to the extent that it does in other species of this genus.

The aboral edge of the unit is straight or only gently arched in lateral view. The angle made by the junction of the aboral and posterior edges is approximately a right angle.

Remarks.

These specimens are regarded as pelekysgnathids because of the single row of denticles on the oral surface, and the presence of a large, posteriorly inclined main cusp. However, careful examination of two specimens revealed that one or two of the blade denticles, in both cases, have two peaks. These peaks are imperceptible in oral view but visible, though indistinct, in lateral view. The presence of two peaks on these ridge-like denticles may indicate that the ridges were formed by the fusion of two previously discrete nodes. If all the ridges were formed in this way then this would indicate the fusion of two previously discrete rows of nodes. As stated in the systematic description of the icriodids, such forms with two rows of oral nodes are considered as members of the genus Icriodus.

This provides further possible evidence of Pelekysgnathus and Icriodus having close genetic ties with possibly the former developing from the latter through a reduction in the number of rows of oral denticles. However, the pelekysgnathids recovered from the Pilton Beds were extremely small both in size and number, and no definitive conclusions could be drawn from the results of this study.

The two specimens from the Pilton Beds which have dual peaks to one or two of their ridges are still regarded as pelekysgnathids however, because, (a) the peaks are indistinct, and if fusion has occurred it is at a most advanced stage; and (b) most of the ridges of the blade are flat topped, showing no evidence of their ever having been the result of fusion of two distinct nodes.

Material studied. 20 specimens

Occurrence. PB.2 - PB.29

Catalogue numbers of the figured specimens. JW.185, JW.187 - JW.189

Genus POLYGNATHUS Hinde, 1879

(Fig.51)

1879	Polygnathus Hinde; p.362-364
1889	Polygnathus Hinde: Miller; p.520
1926	Polygnathus Hinde: Roundy; p.13
1926	Polygnathus Hinde: Ulrich and Bassler; p.43
1957	Ctenopolygnathus Muller and Muller; p.1084
1964	Polygnathus Hinde: Ziegler, Klapper and Lindstrom; p.421-423
1968	Polygnathus Hinde: Huddle; p.37-38

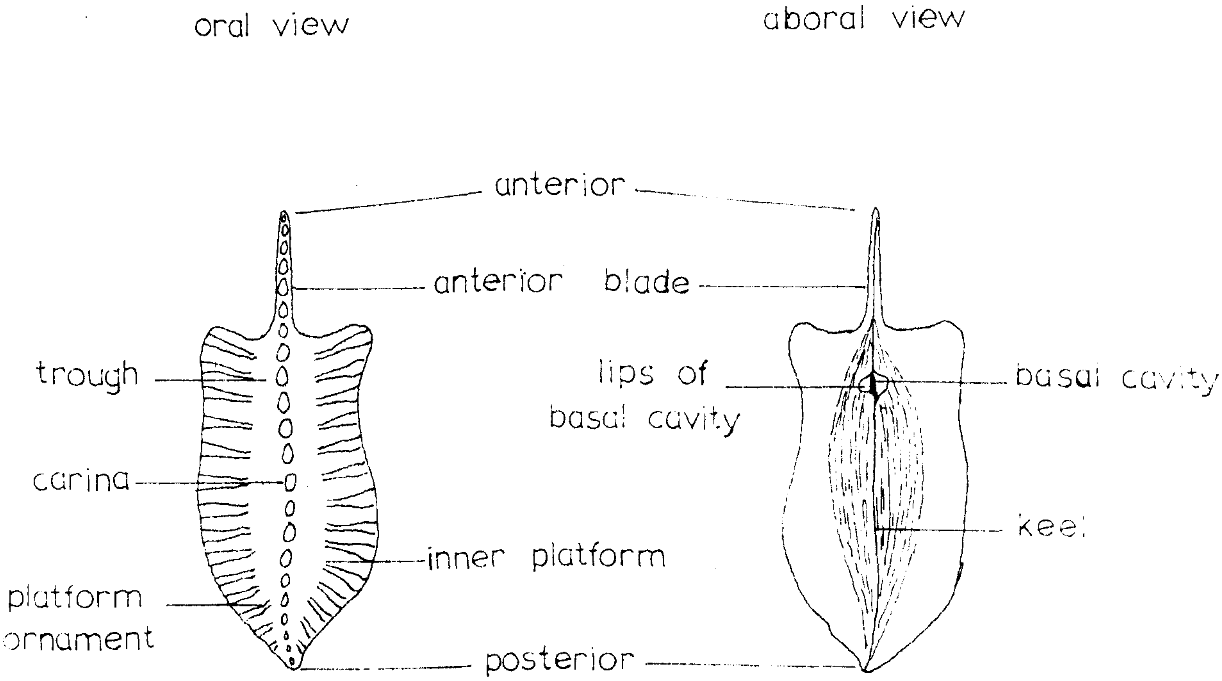
Type species: Polygnathus dubia Hinde, 1879, by original designation Miller, 1889.

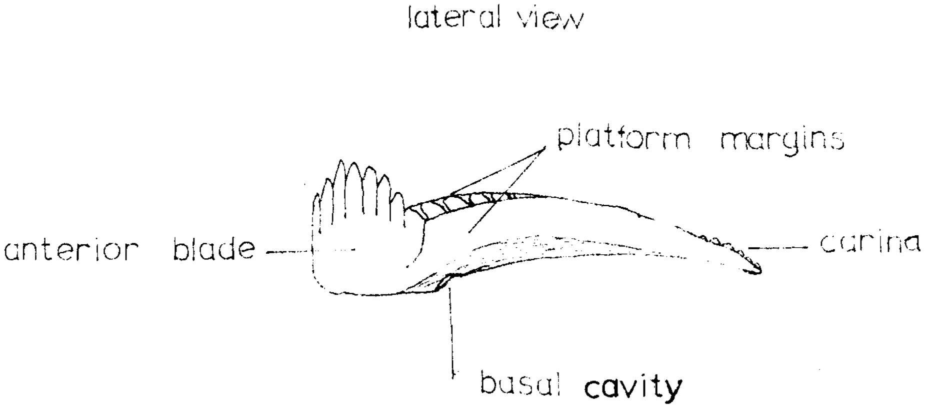
Polygnathus robusticostata Ziegler, Klapper and Lindstrom, 1964.

The validity of the name Polygnathus has been a point of conjecture for many years. The arguments and theories which have arisen over this topic, have been summarised in a short note published by Ziegler, Klapper and

FIGURE 51

GENUS POLYGNATHUS





Lindström (1964). The problem arose, when Hinde (1879) neglected to designate a type species for his newly erected genus, Polygnathus. This genus was proposed for 20 species of conodonts recovered from the Upper Devonian of New York. One of the species, Polygnathus dubia, recognised by Hinde was supposed to represent a natural assemblage, composed of 30 discrete conodonts preserved on a single slab of rock, and thus he selected no holotype.

Miller (1889) subsequently designated Polygnathus dubia as the type species, and Roundy (1926) selected Hinde's specimen pl.XVI, fig.17, as the lectotype of this species, although he had not seen Hinde's material. Only the lateral view of the lectotype is exposed, as it is partially embedded in shale.

Several authors, including Ulrich and Bassler (1926), noted that Bryant (1921) designated Polygnathus pennata as the type species of this genus, although no statement to this effect can be found in his work. Nevertheless, Miller was first to revise Polygnathus and thus his type species should have priority.

Ziegler, Klapper and Lindstrom (1964) regarded the type species, Polygnathus dubia, as a nomen dubium, and they stated also, that if the genus, Polygnathus, was regarded as a nomen dubium then one must accept the earliest junior synonym as the name bearer of those forms previously called Polygnathus. The genus Macropolygnathus Cooper (1939) is considered by some as a subjective junior synonym of Polygnathus, (herein it is considered to be a subjective junior synonym of Pseudopolygnathus) as is Ctenopolygnathus Muller and Muller (1957). However, Ziegler, Klapper and Lindstrom (1964) recommended that the name Polygnathus be retained, in the interests of nomenclatorial stability, but they requested that the type species be changed to *Polygnathus robusticostata* Bischoff and Ziegler (1957 p.95-96). They further proposed new subspecific names for *Polygnathus dubia dubia*, and *Polygnathus dubia asymmetrica* which were, *Polygnathus asymmetrica ovalis* Ziegler and Klapper, and *Polygnathus asymmetrica asymmetrica* respectively. The proposals of these authors have been generally accepted, and as a result, the *Polygnathus dubia* zone of the Upper Devonian of Germany has been renamed, the *Polygnathus asymmetrica* zone, although, the designation of *Polygnathus robusticostata* as the new type species for the genus has yet to be accepted.

Huddle (1968) redescribed the conodont genera and species recognised by Ulrich and Bassler (1926), and his description of Polygnathus is as follows:-

> "Lanceolate conodonts with a nearly symmetrical thick plate divided by a carina which continues anteriorly into a free blade. Oral surface marked by nodes or ridges; or, rarely, smooth. Aboral side has a continuous keel corresponding to the carina, a small basal cavity, growth lines and a narrow crimp".

This genus developed from *Spathognathodus*, and specimens from the Saverton Shale of North America show this development. *Polygnathus* gave rise to several other genera including *Ancyrodella*, *Polylophodonta*, *Siphonodella* and *Palmatolepis*. *Polygnathus* differs from *Ancyrodella* in having a differently shaped plate, and no secondary keels or carinae. *Siphonodella* is distinguished from *Polygnathus* by a strong rostrum and rostral ridges, a sharp deflection of the axis immediately posterior to the rostrum and by the presence of both nodes and ridges in oral ornamentation. *Palmatolepis* differs from *Polygnathus* in having a central node, sigmoidal curve of the carina and a generally thinner plate. *Polylophodonta* has an oral surface ornamented with nodes and ridges commonly arranged concentrically around the apex of the basal cavity, and a suppressed carina.

Polygnathids can be subdivided into three basic groups, on the nature of the platform ornament.

a. Those species with transverse ridges - Found in the Devonian and very common in the Lower Mississippian.

b. Those species with nodose platforms - Common in the Upper Devonian.

c. Those species with smooth platforms - Typically Devonian, but not very important stratigraphically.

Rexroad and Scott (1964) stated that the most important morphological features that can be used for specific differentiation of polygnathids are:-

a. Overall shape of the platform.

b. Type and pattern of oral ornamentation.

c. Length and outline of the anterior free blade.

d. Nature of the aboral side, including the size, position and shape of the basal cavity.

Furthermore, Rexroad and Scott remark that polygnathids are extremely variable in form and many species have been erected. Minor differences in the four categories listed above should not be considered taxonomically significant, but study should rather be made of the stratigraphic distribution and changes which occur in the faunal succession.

The '*Polygnathus communis*' group

Polygnathus communis was originally described by Branson & Mehl (1934b) from the Bushberg Sandstone of North America. Hass (1959 p.390-391) distinguished two subspecies of *Polygnathus communis*, in addition to *P. communis* s.s., which he named *Polygnathus communis bifurcata* and *Polygnathus communis carina*. The diagnostic feature of *P. communis bifurcata* was the development of a secondary carina at the posterior end of the outer platform and a corresponding secondary keel on the aboral surface. The diagnostic feature of *P. communis carina* was the development of a noded ridge on either side of the anterior platform, running from the point where the anterior blade met the carina, to the anterior margin of the platform.

Hass (1959) orientated polygnathids with the blade as posterior, however, most workers orientate this genus in the opposite direction.

Rexroad and Scott (1964) renamed *Polygnathus communis* s.s. Branson and Mehl, *Polygnathus communis communis*, in order to clarify its taxonomic status. Their diagnosis of the subspecies *Polygnathus communis carina* is more flexible than that of Hass, as they include forms which display nodose ornamentation on the anterior portion of the platform regardless of precise trend of the nodes.

Bischoff (1956) distinguished *Polygnathus glabra* from *Polygnathus communis* on the basis of the shape of the platform and the thick-lipped, rounded, basal cavity in *Polygnathus communis*. Freyer (1961) reported transitional stages in the basal cavity between *P. glabra* and *P. communis*. The only reliable distinction between these two species is considered to be the presence of a depressed area immediately posterior to the basal cavity in *P. communis*.

Polygnathus adola Cooper, was reported from the Pilton Beds by Dineley, however, this is considered as synonymous with *Polygnathus communis communis*.

Diagnosis.

The species *Polygnathus communis* Branson & Mehl is characterised by a small lanceolate platform and a nodose carina which may bifurcate posteriorly. The platform is either smooth or ornamented only at the anterior end by short ridges. The aboral surface has a raised keel which bifurcates posteriorly when the carina bifurcates on the oral surface. The basal cavity is small and subcircular, and that portion of the keel immediately posterior to the cavity is depressed and flattened.

Polygnathus communis carina Hass, 1959

(Pl.9, figs.1a-c)

1956 *Polygnathus communis* Branson & Mehl: Hass; pl.2, figs.4,5, (non pl.2, figs.2,3, = *P. communis communis*).

1959 *Polygnathus communis* Branson & Mehl; *carnia* Hass, n.var. p.391, pl.47, figs.8,9.

1959 *Polygnathus* cf. *styriaca* (Ziegler): Voges; p.294, pl.34, figs.36-39.

1964 *Polygnathus communis carina* Hass: Rexroad & Scott; p.34, pl.2, figs.24-25.

1967 *Polygnathus communis carina* Hass: Boogaert; pl.2, figs.3,4.

1969 *Polygnathus communis carinus* Hass: Druce; p.95, pl.18, figs.12a-c

Diagnosis.

A polygnathid with the development of a ridge, which may or may not be nodose, on one or both sides of the platform at the anterior end. Platform otherwise smooth, apart from a nodose carina.

Description.

Orally the platform is unornamented except for a nodose carina and the development of a short, but well defined, ridge at the anterior end. In all specimens the ridge is only obvious on one side of the platform. It is developed on the inner side of the platform of right forms and on the outer side of left forms, and in this sence the subspecies is bilaterally asymmetrical. The length of the ridge is approximately $\frac{1}{4}$ of the total length of the platform and runs diagonally toward the carina from the anterior edge of the platform. A corresponding diagonal trough occurs between the ridge and the carina.

The overall shape of the platform is lanceolate, tapering anteriorly and posteriorly, the posterior margin may be sharply pointed or bluntly rounded. The carina may run the whole length of the platform or stop abruptly, just short of the posterior tip. It is composed of 6-11 nodes which become smaller posteriorly. Invariably the carina curved and this feature is used to distinguish right and left forms. Either side of the carina, throughout its entire length, there is a distinct trough, and on that side of the platform which bears the anterior ridge, the trough opens out at the anterior end of the platform where it coalesces with the diagonal trough on the inside of the ridge.

The anterior blade which projects from the platform was completely or partially broken in all specimens of this subspecies recovered from the Pilton Beds. Posteriorly the blade merges into the carina.

Aborally the unit bears a keel which corresponds to the anterior blade and carina of the oral surface. A small subcircular basal cavity is located just posterior to the junction of the blade and the platform. Immediately posterior to the cavity the keel is depressed and flattened, and this depression is a more prominent aboral feature than the cavity itself.

Laterally the carina is hidden from view by the higher lateral platforms.

The anterior ridge is the highest topographic point on the platform, and the anterior blade attains approximately twice the height of this ridge. The aboral edge of these forms is distinctly arched to almost straight in lateral view, but the oral edge is always straight, increasing very gradually in elevation from posterior to anterior. Specimens displaying an arched margin are concave beneath the platform and slightly convex beneath the anterior blade.

Remarks.

Hass's (1959) original diagnosis of this subspecies stated that it had a noded ridge developed on each side of the platform, Rexroad and Scott (1964) stated that it was characterised by nodose ornamentation, while Boogaert (1967) diagnosed two or more nodose ridges. Thus over the years the diagnosis of P. communis carina has been expanded to incorporate those forms with more than two nodose ridges, those with a distinct nodose ridge on only one side of the platform, and those with irregularly arranged nodes. The specimens from the Lower Pilton Beds, which have been included in this subspecies, bear ridges which are not nodose but smooth, yet in all other respects they are identical to P. communis carina. In the present study the diagnosis has been expanded once again to include forms which develop ridges, which may or may not be nodose.

Material studied. 9 specimens

Occurrence. PB.4 - PB.13

Catalogue numbers of figured specimens. JW.191 - 193

Polygnathus communis communis Branson & Mehl, 1934

(Pl.9, figs.4a-12c, pl.10, figs.1a-2c)

1934 *Polygnathus communis* Branson & Mehl; p.293, pl.24, figs.1-4.

1934 *Polygnathus communis* Branson & Mehl: E.R. Branson; p.308, pl.25, fig.5,6.

1938 *Polygnathus communis* Branson & Mehl: Branson & Mehl; p.145, pl.34, figs.39-41.

1939 *Polygnathus communis* Branson & Mehl: Cooper; p.399, pl.39, figs.1,2,9,10,23,24.

1947 *Polygnathus communis* Branson & Mehl: Mehl & Thomas; p.15, pl.I, fig.36.

1949 *Polygnathus communis* Branson & Mehl: Youngquist & Patterson; p.62, pl.15, figs.7,8.

1949 *Polygnathus communis* Branson & Mehl: Thomas; p.60, pl.3, fig.37.

1951 *Polygnathus communis* Branson & Mehl: Youngquist & Downs; p.787, pl.3, figs.4,5,19,20.

1951 *Polygnathus communis* Branson & Mehl: Hass; p.35, pl.I, fig.10.

1956 *Polygnathus communis* Branson & Mehl: Bischoff & Ziegler; p.156, pl.12, figs.1-3.

1956 *Polygnathus communis* Branson & Mehl: Hass; p.286, pl.2, figs.2-3, (non Pl.2, figs.4-5, = *P. communis carina*)

1957 *Polygnathus communis* Branson & Mehl: Bischoff; p.42, pl.2, figs.23-27.

1957 *Polygnathus communis* Branson & Mehl: Flugel & Ziegler; p.46, pl.2, fig.15.

1959 *Polygnathus communis* Branson & Mehl: Hass; p.390, pl.49, figs.9-11,13.

1959 *Polygnathus communis* Branson & Mehl: Voges; p.288, pl34, figs.1-7.

1960 *Polygnathus communis* Branson & Mehl: Ziegler; pl.I, fig.9.

1961 *Polygnathus communis* Branson & Mehl: Scott & Collinson; p.130, pl.I, figs.6-10, pl.2, fig.30.

1962 *Polygnathus communis* Branson & Mehl: Ziegler; p.87.

1964 *Polygnathus communis* Branson & Mehl: Higgins, Wagner-Gentis and Wagner; pl.5, fig.30.

1966 Polygnathus communis Branson & Mehl; Klapper; p.21, pl.6, figs.6-11.

1966 Polygnathus communis Branson & Mehl: Anderson; p.411.

1967 Polygnathus communis Branson & Mehl; Wolska; p.411, pl.14, figs. 1,2a-b.

1939 Polygnathus adola Cooper, p.399, pl.39, figs.33-36.

1964 Polygnathus communis communis Branson & Mehl: Rexroad & Scott; p.33, pl.2, figs.17,18.

1967 Polygnathus communis communis Branson & Mehl: Boogaert; p.183, pl.2, fig.37.

Diagnosis.

The oral surface of this subspecies displays a central nodose carina and is otherwise unornamented.

Description.

The platform is lanceolate, tapered posteriorly, and ornamented by a medial carina. In some specimens the carina is distinctly nodose throughout its length, but the majority of specimens display a carina which is nodose only in its mid-third, the nodes of the anterior and posterior thirds being fused forming an uneven ridge. The carina becomes lower and thinner toward the posterior margin of the platform, which may be sharply pointed or bluntly rounded. The carina itself may or may not reach the posterior extremity. The anterior end of the carina merges featurelessly into the anterior blade which is as long as the platform. A few specimens exhibit an even longer blade. The 9-12 denticles of the blade are discrete only at their tips. The smooth lateral margins of the platform are upturned with the result that there are 2 distinct furrows running either side of the carina. Aborally this subspecies is identical to Polygnathus communis carina. Laterally these specimens are also identical to Polygnathus communis carina, except that there are no ridges on the anterior portion of the platform.

Remarks.

This subspecies is by far the most common form of Polygnathus in the Pilton Beds. The shape of the platform has been described in general terms as lanceolate, but, the platform outline shows certain variations such as indentations and thickened margins. Some specimens display posterior margins which are sharply pointed, whereas others are bluntly rounded in this region. Rexroad & Scott (1964) have suggested that future studies on the posterior platform outline may be useful in further taxonomic refinement. Polygnathus communis communis specimens, displaying both sharply pointed and bluntly rounded posterior platform margins, are common in all horizons bearing this subspecies in the Upper Baggy and Pilton Beds. A plot of the ratio of both variations, from eleven horizons where P. communis communis was particularly abundant, was made to determine whether or not the ratios themselves might be utilized as zonal tools. The ratios are expressed as a percentage of the total P. communis communis population in each horizon, (see Figure 52). The results of this plot did not prove to be particularly useful. In the lower horizons those forms with pointed posterior platforms were more abundant. Higher in the succession the distribution of the two variations becomes more or less equal while higher in the succession the dominance of pointed forms recurs.

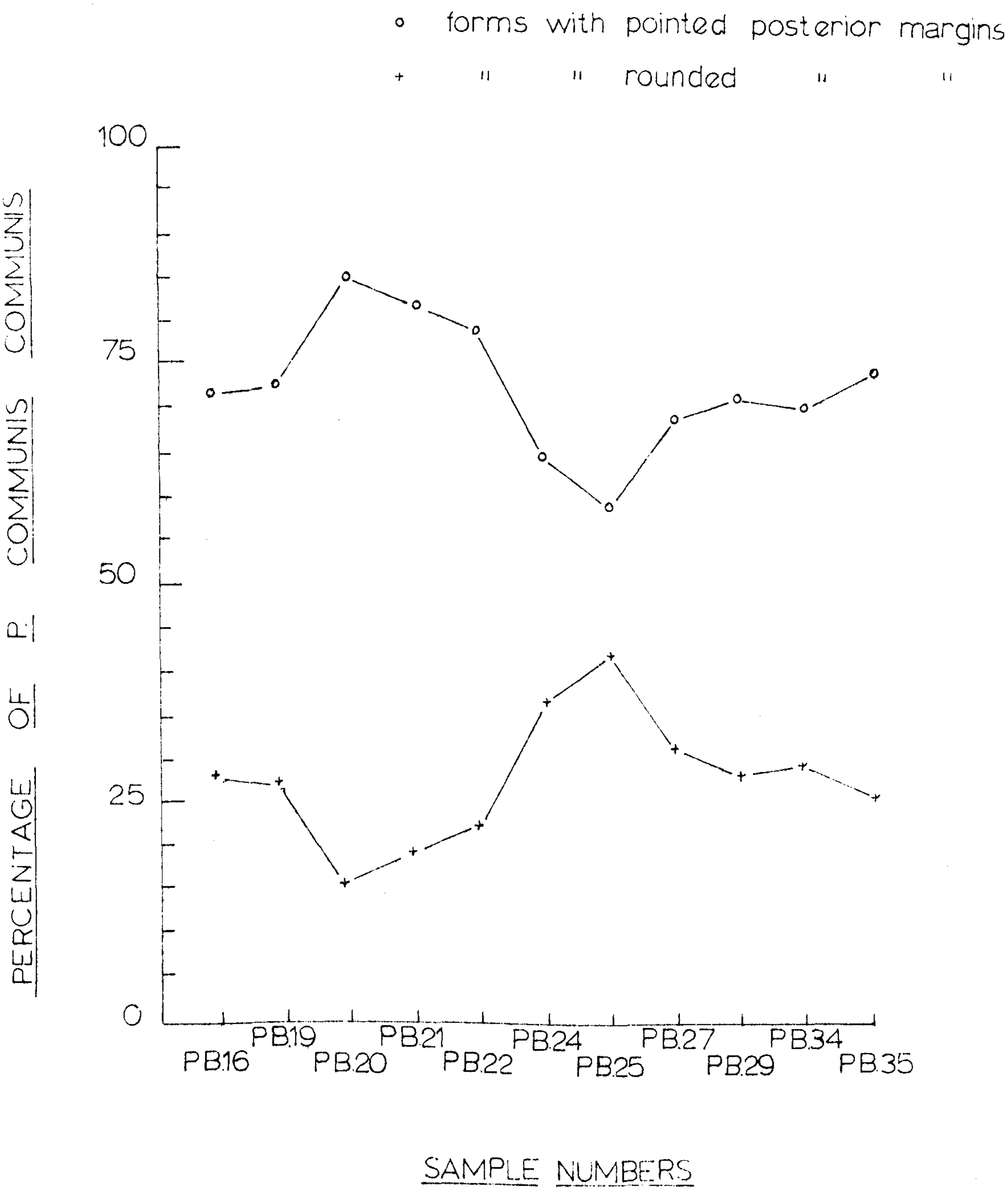
Material studied. 384 specimens

Occurrence. PB.4 - F.8

Catalogue numbers of the figured specimens. JW.194 - JW.204

FIGURE 52

A PLOT OF THE RATIO OF POSTERIORLY POINTED AND POSTERIORLY ROUNDED FORMS OF POLYGNATHUS COMMUNIS COMMUNIS FROM ELEVEN PILTON BED HORIZONS.



The "*Polygnathus inornata*" group

Rexroad and Scott (1964) reported that *Polygnathus inornatus* was a remarkably varied species and that some of their specimens were transitional with *P. lobatus*. The transition between these two species was also noted by Rhodes, Austin & Druce (1969). Both *P. inornatus* and *P. lobatus* are considered valid species by most workers, and neither of the publications, cited above, recommend the suppression of *P. lobatus* on the grounds that it may be based on an artificial distinction.

Rhodes, Austin & Druce erected two new subspecies in addition to *P. inornatus* s.s., namely, *P. inornatus rostratus* and *P. inornatus vexatus*. The former is distinguished by the development of a rostral ridge at the anterior end of the inner platform margin. This results from a tendency for this part of the platform margin to move toward the anterior blade, the posterior part of the same side of the platform becoming lobate. *P. inornatus vexatus* is characterised by a more lanceolate platform and a longer free blade.

Polygnathus inornatus inornatus Branson & Mehl, 1934

(Pl.11, figs.6a-8c)

1934 *Polygnathus inornata* Branson & Mehl; p.293, pl.24, figs.5-7.

1934 *Polygnathus inornata* Branson & Mehl: E.R. Branson; p.309, pl.25, figs.6,26.

1938 *Polygnathus inornata* Branson & Mehl: Branson & Mehl; p.132,146, pl.34, fig.37.

non 1939 *Polygnathus inornata* Branson & Mehl: Cooper; p.400, pl.39, figs. 11,12.(=*P. inornata rostrata*).

1944 *Polygnathus inornata* Branson & Mehl: E.B. Branson; pl.39, fig.37.

1949 *Polygnathus inornata* Branson & Mehl: Youngquist & Patterson; p.64, pl.17, figs.4,5,9,13.

1949 *Polygnathus inornata* Branson & Mehl: Thomas; pl.3, fig.36.

1951 *Polygnathus inornata* Branson & Mehl: Youngquist & Downs: pl.3, figs.17,18.

non 1956 *Polygnathus inornata* Branson & Mehl: Bischoff and Ziegler; p.157, pl.12, figs.4,5. (=*P. flabella*)

1956 *Polygnathus inornata* Branson & Mehl: Hass; pl.2, figs.14,15.

non 1957 *Polygnathus inornata* Branson & Mehl: Bischoff; p.42, pl.2, figs.17, 18,20,21. (=*P. lacinata lacinata*).

1957 *Polygnathus inornata* Branson & Mehl: Cloud, Barnes & Hass; pl.5, fig.6.

non 1958 *Polygnathus inornata* Branson & Mehl: Klapper; p.1089, pl.142, figs.2,3.

1959 *Polygnathus inornata* Branson & Mehl: Voges; p.291, pl.34, figs.12-16. (non Pl.34, figs.17-20 = *P. lacinata lacinata*).

non 1964 *Polygnathus inornata* Branson & Mehl: Higgins, Wagner-Gentis & Wagner; pl.5, fig.29. (=*P. lacinata lacinata*).

1964 *Polygnathus inornata* Branson & Mehl: Rexroad & Scott; p.35, pl.2, figs.19,20.

1966 *Polygnathus inornata* Branson & Mehl: Klapper; p.19, pl.1, figs.7,8 9,10; pl.4, figs.2,4. (non pl.1, figs.11-14; pl.4, fig.3 = *P.* cf. *inornata rostrata*).

1967 *Polygnathus inornata* Branson & Mehl; Boogaert; p.184, pl.2, figs. 39,40.

1969 *Polygnathus inornatus inornatus* Branson & Mehl: Rhodes, Austin & Druce; p.186, pl.10, figs.4a-6c.

Diagnosis.

Lanceolate, displaying a short high blade and a straight to strongly curved carina. The posterior part of the platform is fairly flat, but anteriorly it bears deep troughs because the platform margins are strongly upturned. The amount of upturning on either side of the platform is typically unequal. The platform ornamentation and outline are extremely variable, and the basal cavity is small, subcircular, and may have prominent lips.

Description.

The anterior third of the platform bears deep troughs on either side of the carina, due to the marked upturning of the margins of the platform in this vicinity. In the mid-third the elevation of the upturned margins becomes less pronounced until the platform is almost flat in the posterior third. Oral ornamentation consists of transverse ribs which terminate on the platform edge as low nodes. The strength of the ribbing is extremely variable. The carina is nodose and may be straight to strongly curved. It passes anteriorly into the short free blade, and terminates as a point at the posterior end of the platform. The whole unit is sub-symmetrical and is commonly arched in lateral view.

Aborally the subspecies is keeled and bears a small, subcircular basal cavity which is located just posterior to the junction of the anterior blade and the carina. The cavity may display thickened lips.

Remarks.

Only a very limited number of forms, assigned to this subspecies, were recovered from the Pilton Beds, and the specimens involved exhibited a great deal of variation in both platform ornament and outline. One specimen (Pl.11, fig.6a,b.) is more elongate than the rest and probably should be considered as an example of the subspecies *P. inornatus vexatus.* Another specimen (Pl.11, fig.7a-c.) displays a carina which bifurcates at the posterior end of the platform. This may be considered by many authors as representative of another new subspecies of *P. inornatus* however, no conclusions may be drawn from the present study as only a single specimen shows this feature.

Material studied. 6 specimens

Occurrence. PB.35 - F.8

Catalogue numbers of the figured specimens. JW.218 - JW.220

Polygnathus lacinatus Huddle, 1934

Rhodes, Austin & Druce (1969, p.365) stated that they regarded P. lacinatus Huddle as a separate and variable species in its own right. They maintained that the nature of the basal cavity of P. lacinatus served to distinguish it in this respect. Prior to this, Rexroad & Scott (1964, p.35) had included P. sagittaria Youngquist & Patterson, a junior synonym of P. lacinatus within the species P. inornatus Branson & Mehl.

Huddle (1934) initiated the species P. lacinatus for certain polygnathids with a lanceolate platform and an elongate, excavated basal cavity. This species was identified by Cooper (1939) but Youngquist and various co-authors (1949m 1950 & 1951) referred these forms to a new species P. sagittarius Youngquist & Patterson.

In addition to Rexroad & Scott (1964), German workers have included P. lacinatus synonymy with P. inornatus.

The identification of P. lacinatus in the Pilton Beds, involves the downward extension of the range of this species, which was thought previously to be restricted to beds of CuIIβ/γ age in Europe.

Rhodes, Austin & Druce (1969) recognised four subspecies of *P. lacinatus* including *P. lacinatus* s.s. The species displays a basal cavity which is quite different from that which typifies this genus as a whole. It is reminiscent of the cavity of *Pseudopolygnathus*, but its symmetrical and posteriorly tapered outline, together with the polygnathid nature of the oral surface, serve to distinguish this form from *Pseudopolygnathus*.

The three subspecies erected, in addition to *P. lacinatus lacinatus* are:- *P. lacinatus asymmetricus* Rhodes, Austin & Druce (1969, Pl.XI, figs. 1a-4c) which is characterised by a reduction of the posterior part of the inner platform which, as a result, does not extend to the posterior end of the unit.

P. lacinatus circaperipherus Rhodes, Austin & Druce (1969, Pl.XI, figs. 12a-15c) displays a posterior platform edge which is wrapped around the carina, the carina not reaching the posterior end of the unit.

P. lacinatus prelobatus Rhodes, Austin & Druce (1969, Pl.XI, figs.5a-7b, 11a-c) is characterised by a modification of the inner posterior platform margin which tends to be produced as a lobe, narrowing rapidly toward the posterior termination.

From the Pilton fauna, only specimens of *P. lacinatus lacinatus* were recovered, although a few forms showed a tendency toward the development of the features characteristic of *P. lacinatus asymmetricus*.

Polygnathus lacinatus lacinatus Huddle, 1934

(pl.10, figs.3a - 8c)

1934 *Polygnathus lacinata* Huddle; p.95, pl.8, figs.1-3.

1939 *Polygnathus lacinata* Huddle: Cooper; p.401, pl.40, figs.3,4.

1949 *Polygnathus sagittaria* Youngquist & Patterson; p.66, pl.15, figs.9,10.

1950 *Polygnathus* aff. *Polygnathus sagittaria* Youngquist & Patterson: Youngquist, Miller & Downs; p.527, pl.67, figs.2-4.

1951 *Polygnathus sagittaria* Youngquist & Patterson: Youngquist & Downs; p.788, pl.3, figs.7-9.

1959 *Polygnathus inornata* Branson & Mehl: Voges; p.291, pl.34, figs.17-20, (non pl.34, figs.12-16 = *P. inornata*)

1969 *Polygnathus lacinatus lacinatus* Huddle: Rhodes, Austin & Druce; p.189, pl.XI, figs.8a-10c.

Diagnosis.

Lanceolate polygnathids with a marked longtitudinal extention of the lips of the basal cavity, which is often over half the length of the platform.

Description.

The platform is lanceolate, two to three times as long as wide, narrowing toward the posterior. The free blade is approximately one third of the length of the platform.

Orally, the platform is ornamented by a strong carina, which may be almost straight to strongly curved. Often the carina extends beyond the platform as a short posterior blade; the carinal nodes are slightly larger in this region. An unornamented trough runs on either side of the carina, and is accentuated, particularly at the anterior end of the platform, by the strongly upturned platform margins. The outer margin of the platform commonly attains a higher elevation than the inner. The platform itself is ornamented by transverse ridges which terminate in denticles on the platform margins, giving the unit a crenulate lateral outline. The nature of the platform ornament varies considerably, as does the outline of the platform as a whole. The outline may be almost straight, convex, slightly lobed or nearly concave.

Laterally, the aboral edge of the anterior blade is straight, while the platform is arched. The anterior blade is high, consisting of six to eight denticles which are discrete only at their tips. They are highest just anterior of mid-length, decreasing regularly in height toward their junction with the platform and the anterior edge. The carinal nodes are almost totally fused, forming an irregular ridge, but, those forms with a short posterior blade display larger, more discrete denticles in this region.

Aborally, the unit is very distinctive, the basal cavity being large and elongate. It is widest anteriorly, gradually narrowing posteriorly. In addition to the length of the basal cavity itself, the lips around the cavity are even more conspicuous, being strongly extended both laterally and longitudinally. The lips extend further posteriorly than the cavity, terminating within the posterior third of the platform. They narrow posteriorly from their maximum development at the mid-point of the cavity. There is a sharp angular junction between the lateral margins of the cavity lips and the sloping aboral surface of the platform. The overall length of this aboral feature is approximately three-quarters of the total length of the platform, and its development is bilaterally symmetrical.

A short grooved keel is present at the anterior and posterior ends of the aboral surface.

Remarks.

This subspecies is distinguished by the large basal cavity. Rhodes, Austin & Druce (1969) remarked that forms described as P. marginata Branson & Mehl, by Rexroad & Scott (1947, p.37) are recorded as having large basal cavities and may be referable to P. lacinatus s.s. However, the absence of an aboral illustration deterred Rhodes et al from including P. marginata in synonymy.

Orally P. lacinatus s.s. is highly variable and often difficult to distinguish from P. inornatus. The nature of the basal cavity is the most distinctive feature, together with the narrower, more elongate, platform outline.

A few specimens show a tendency toward the reduction of the inner posterior platform, which is the diagnostic feature of the subspecies, P. lacinatus asymmetricus. However, this feature is not as obviously developed as in specimens figured by Rhodes, Austin & Druce (1969), and for this reason have been retained in the subspecies P. lacinatus lacinatus.

Material studied. 51 specimens

Occurrence. PB.16 - F.8

Catalogue numbers of the figured specimens. JW.205 - JW.210

Polygnathus cf. P. lacinatus Huddle, 1934

(Pl.10, figs.9a-c, Pl.11, figs.1a-5b)

1934 Polygnathus lacinata Huddle; p.95, pl.8, figs.1-3.

Description.

The morphology of these forms is closely comparable with P. lacinatus s.s. with one minor exception. The large, elongate basal cavity, which is diagnostic of *P. lacinatus* s.s., is present in these forms but not as fully developed posteriorly. The lips surrounding the cavity taper posteriorly, from their widest development adjacent to the basal pit, but they extend to about the mid-point of the platform. The result of this is an elongate, symmetrical, but more oval basal cavity outline, and a longer grooved posterior keel than in *P. lacinatus* s.s. The longitudinal extension of the cavity lips is less than half the total length of the platform.

Orally and laterally there are no significant differences between these forms and *P. lacinatus* s.s.

Remarks.

Polygnathus cf. *P. lacinatus* has the same stratigraphic range as *Polygnathus lacinatus lacinatus* in the Pilton Beds, and should probably be included as an infraspecific variant of the latter. It is possible, however, that these forms represent a transitional stage between *P. inornatus* and *P. lacinatus* s.s.

Material studied. 44 specimens

Occurrence. PB.16 - F.8

Catalogue numbers of the figured specimens. JW.212 - JW.217

Polygnathus cf. *P. nodomarginatus* E.R.Branson, 1934

(Pl.11, figs.9a-10c; Pl.12, figs.2a-c)

1934 *Polygnathus nodomarginata* E.R.Branson; p.310, pl.25, fig.10.

Diagnosis.

A nearly bilaterally symmetrical platform which is lanceolate in outline. The oral surface is ornamented by a nodose carina and lateral nodes which are restricted to the upturned margins of the platform. The basal cavity is exceptionally large, and bears prominently flared lips. The cavity has an asymmetrical outline and is closely comparable with that of *Pseudopolygnathus*.

Description.

The platform is lanceolate in outline and nearly bilaterally symmetrical. The margins of the anterior portion of the platform are subparallel, at approximately mid-length there is an expansion in the width of the platform and from here it tapers rapidly to a sharp point at the posterior tip of the unit.

The carina is a prominent feature, composed of parially fused, rounded nodes, which tapers gradually from anterior to posterior. It is low, nearly straight or only gently curved, and sometimes extends beyond the limit of the platform forming a short posterior blade. Anteriorly the carina meets the high anterior blade and the junction is marked by a considerable change in elevation. The anterior blade is composed of 4-6 denticles which are laterally compressed and discrete only at their tips. It is highest at about mid-length from which point it drops sharply to the level of the carina. The blade is about one third of the total length of the unit, and is as high as it is long.

The platform margins are strongly upturned, particularly at the anterior end of the unit, and unornamented troughs parallel the carina from anterior to posterior. The upturned edges of the platform are ornamented by low, short, transverse ridges which terminate in blunt nodes on the lateral margins.

Laterally the units are straight or gently arched. The upturned margin of one side of the platform attains a greater height than the carina, while the other equals the carina in elevation.

Aborally these forms bear prominent grooved keels running anteriorly and posteriorly from the basal cavity. The cavity itself, which is located at the anterior end of the platform, is large, elongate and displays thick, prominently flared lips which are strongly developed both laterally and longitudinally. The outline of the cavity is asymmetrical and the aboral surface, as a whole, is typical of Pseudopolygnathus.

Remarks.

Aborally this species closely resembles Pseudopolygnathus, but the oral morphology is more typically polygnathid in nature. Thus, there are valid reasons for assigning such forms as these to either of these genera. In the past, it has been the practice of most workers to refer these forms to the genus Polygnathus, and this philosophy has been followed herein. This indicates a close relationship between Polygnathus and Pseudopolygnathus, which may be of genetic or merely functional significance.

These Pilton forms, and polygnathids from other Upper Devonian sections which have been referred to this species, are considered to be homeomorphs of the Polygnathus nodomarginatus development in the Hannibal of the Mississippi Valley and the Avonian of Bristol.

Rhodes, Austin & Druce (1969) prefer to consider these forms as pseudopolygnathids rather than polygnathids, thus in their publication these elements are systematically described under Pseudopolygnathus nodomarginatus (pp.212-213, pl.9, figs.1-4, pl.12, figs.6a-8c, 10a-c).

Material studied. 12 specimens

Occurrence. PB.16 - PB.35

Catalogue numbers of the figured specimens. JW.221 - JW.223

Polygnathus pura pura Voges, 1959

(Pl.10, fig.10a-c.)

1959 *Polygnathus pura pura* Voges, p.291-292, pl.34, figs.21-26.

Diagnosis.

Voges's original description of this subspecies may be translated as follows:-

> "A species of the genus *Polygnathus* which has a platform which is flat or only gently arched. The oral surface of the platform is smooth even when it is finely grained. The platform outline is asymmetrical and leaf-like, pointed posteriorly. The platform is a half to two-thirds of the total length of the unit. The carina is composed of broad, fused nodes, but the individual nodes are nevertheless discernable. A small basal cavity is located in the anterior third of the platform, on the aboral surface".

Description.

The platform is flat to very gently arched, and except for the carina it is smooth and unornamented. The maximum width of the platform is developed anteriorly, and it tapers asymmetrically to a point at the posterior end. The outline of the platform as a whole is pear-shaped. The carina and the anterior blade merge together and consist of many fused nodes, which are only discrete at their tips. The carina curves over the oral surface of the platform, terminating just short of the posterior extremity.

The anterior blade is highest anteriorly, gradually becoming smaller toward the posterior, where it merges with the carina. The carina continues to gradually decrease in height posteriorly.

Aborally, a small basal cavity is visible, corresponding to a point just posterior to the junction of the anterior blade and the platform on the oral surface. A fine, thin keel runs from the cavity to the posterior and anterior extremities of the unit.

Remarks.

This subspecies is distinguished from *P. pura subplana* Voges, by its flat or gently convex platform. The platform of *P. pura subplana* displays unturned margins, particularly in the anterior and central thirds. Members of this subspecies, and those of *P. pura subplana*, are very similar to to *P. communis* in oral view, but may be distinguished by a less slender platform, and the absence of a depressed, flattened area immediately posterior to the basal cavity.

Voges includes three specimens of *P. communis* illustrated by Bischoff (1957, pl.2, figs.23,25,26.) in synonymy, but the author is reluctant to do this because two of these figured specimens are of the oral surface, while the one that does show an aboral view is obscure in the critical region. Furthermore, Bischoff (1959, p.42) mentions, in his description of *P. communis*, that all the forms that he assigned to this species possessed the characteristic depression immediately posterior to the basal cavity.

Material studied. 1 (one) specimen

Occurrence. F.8

Catalogue number of the figured specimen. JW.211

Genus PRIONIODINA Bassler, 1925

(Pl.13, figs.12a-13b)
(Text fig.53)

1925 Prioniodina Bassler, p.219

1926 Prioniodina Ulrich & Bassler, p.18

1934 Subbryantodus Branson & Mehl, p.285

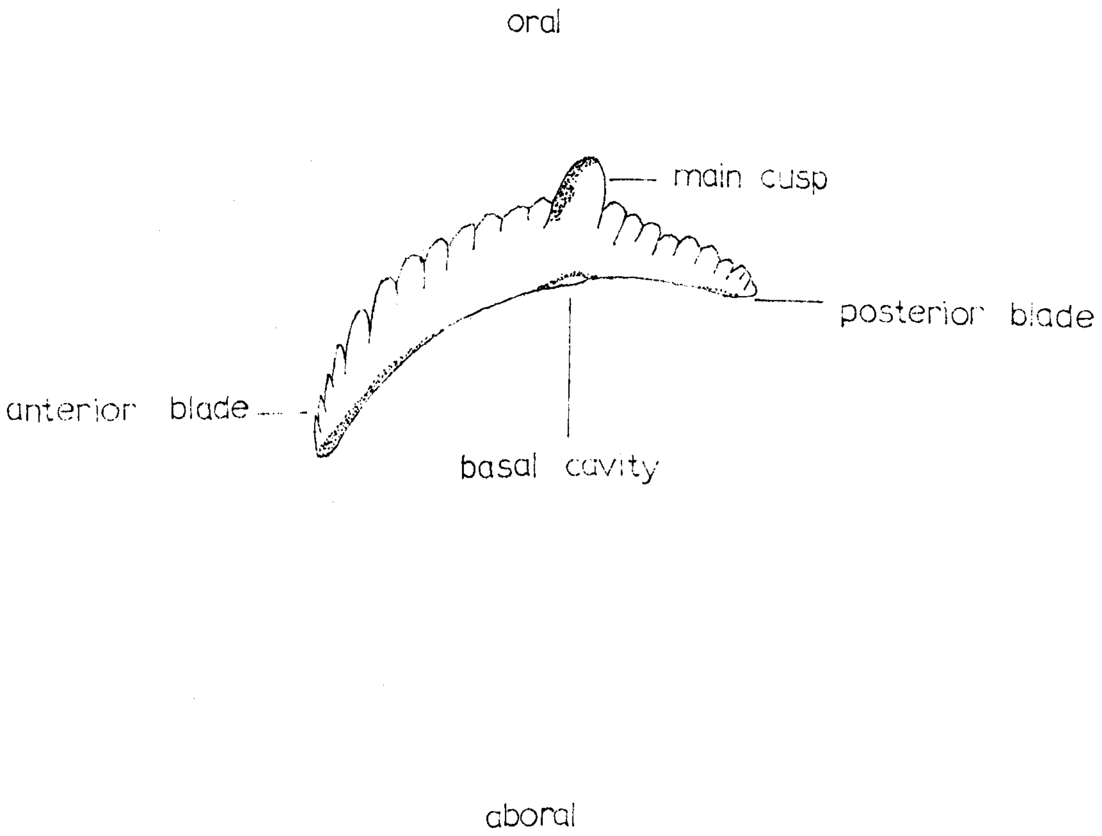
Type species. Prioniodina subcurvata Ulrich & Bassler, 1926.

Bassler (1925) erected the genus Prioniodina, and one year later, he and Ulrich published the following description of this group of conodonts.

> "Base of tooth more or less curved, crowned with numerous, subparallel, rounded, discrete denticles all inclined in one direction, one of which, located in the median third, is considerably larger than the others".

Branson & Mehl (1934b) erected the genus Subbryantodus for essentially similar forms, which differed from Prioniodina in possessing fused oral denticles and a tendency toward a split aboral edge. Rhodes, Austin & Druce (1969) consider that the differences cited by Branson & Mehl (1934b) do not warrant the erection of a separate genus, and they consider Subbryantodus as a junior subjective synonym of Prioniodina. The suppression of the genus Subbryantodus has been followed herein.

GENUS PRIONIODINA



The modern diagnosis of Prioniodina is essentially the same as that initiated by Ulrich & Bassler (1926) except that the basal cavity of this genus, and other members of the Family Prioniodinidae Bassler, is considered to be typically developed at or near the posterior end of the blade or bar. Diagnosed thus, they can be readily distinguished from the members of the Family Prioniodontidae Bassler, (e.g. Ozarkodina) which are characterised by a basal cavity which is located in the middle third of the unit.

The figured specimens of the genus Prioniodina are represented by a single species.

Material studied. 22 specimens

Occurrence. PB.2 - PB.10

Catalogue numbers of the figured specimens. JW.248 - JW.249

Genus PSEUDOPOLYGNATHUS Branson & Mehl, 1934

(Fig.54)

1934 Pseudopolygnathus Branson & Mehl, p.297

1939 Macropolygnathus Cooper, p.392

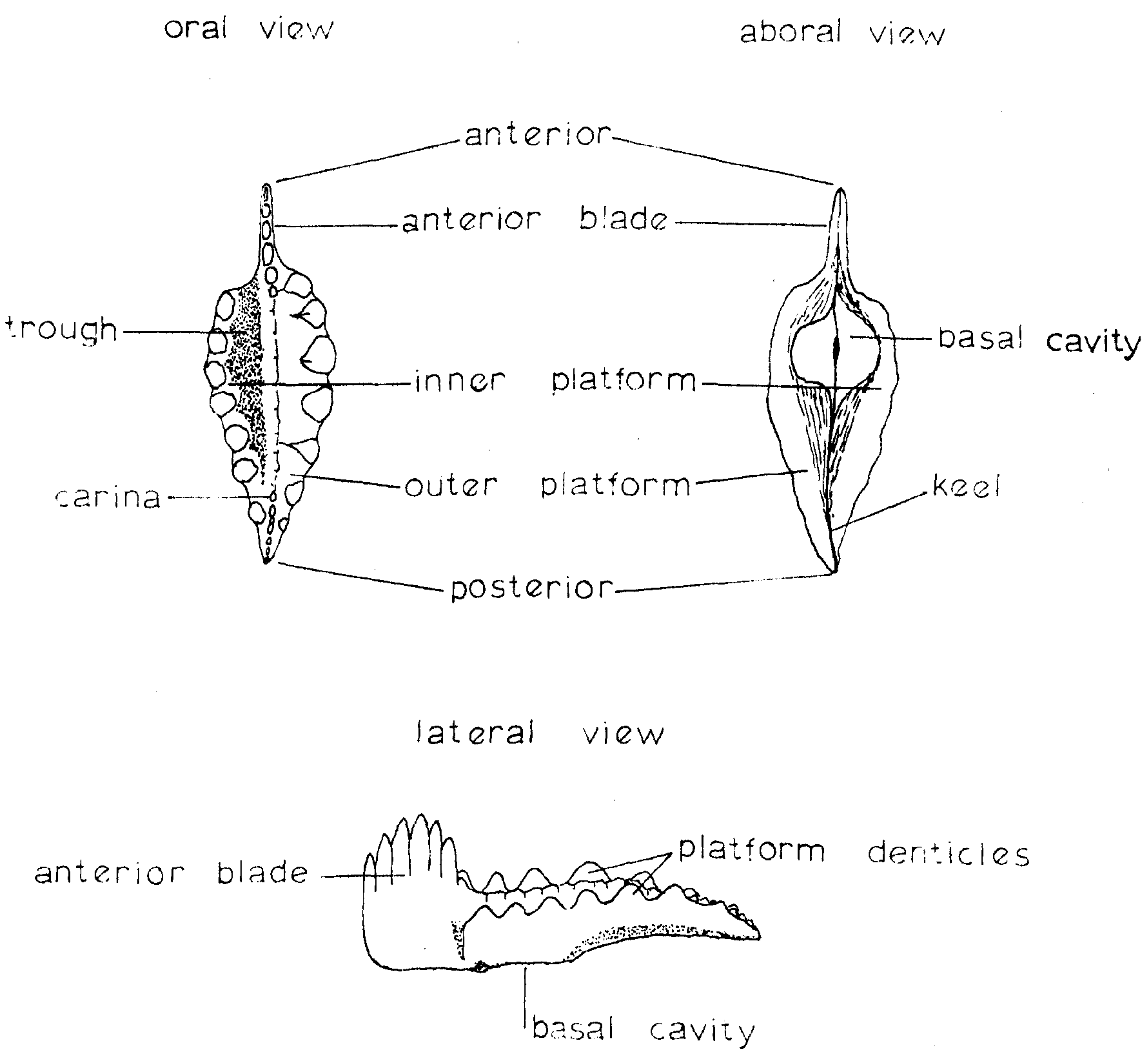
Type species. Pseudopolygnathus prima Branson & Mehl, 1934, p.298

This genus was first identified by Branson & Mehl (1934b), from the Bushberg Sandstone of North America. Their description was as follows:-

> "Teeth consisting of a thick plate, lanceolate and arrow-shaped, pointed posteriorly with a free, wide, vertical blade which extends

FIGURE 54

GENUS PSEUDOPOLYGNATHUS


oral view

aboral view

lateral view

considerably in front of the plate margin. Blade grading into a distinct carina which divides the oral side of the plate into two lateral areas or platforms of unequal lateral and anterior extent. Oral surface of each platform traversed by coarse sharp transverse ridges and deep intervening valleys, most of which extend from the margin of the plate to the carina. Aboral side smooth save for an exceptionally large navel at the anterior end of the plate and a pronounced keel that extends from the navel to the posterior end of the plate. In most specimens the navel is wider than long and is more or less set off from the plate surface by a raised margin".

Pseudopolygnathus, although showing a certain oral resemblance to *Polygnathus* Pander, is developed from the genus *Spathognathodus* Branson & Mehl. Specimens have been found which show a complete gradation between *Spathognathodus* and *Pseudopolygnathus*. The latter is easily distinguished from *Polygnathus* by the anterior position, and greater size of the basal cavity. The cavity of *Polygnathus* is located at mid-length and is slit-like in appearance. Branson & Mehl further maintain that orally the sharp transverse ridges, at about the level of the carina, and the deep intervening valleys, also serve to distinguish *Polygnathus* from *Pseudopolygnathus*. However, specimens from the Avon Gorge and Croyde Bay have aboral cavities which are either typically polygnathid or pseudopolygnathid in nature, and yet their oral morphology is identical.

Cooper (1939), described a prolific conodont fauna from a Bushberg-Hannibal horizon in Oklahoma. From this fauna he identified a new genus which he named *Macropolygnathus* (p.392), and 19 species of this genus. Hass (1959), and others, considered that *Macropolygnathus* (Cooper) was a junior subjective synonym of *Polygnathus* Hinde (1879), and Hass has referred the former genus its type species, *Macropolygnathus* itha, and the other

18 species of this genus to the species Polygnathus allocata (Cooper).

Rexroad & Scott (1964) stated that the nature of the basal cavity of Macropolygnathus itha suggested that this form was more closely related to Pseudopolygnathus than Polygnathus, and the location of forms transitional between Macropolygnathus itha and Pseudopolygnathus fusiformis substantiated this theory. Many authors have expressed their agreement with this line of thought and in this thesis Macropolygnathus is included in synonymy with Pseudopolygnathus.

THE DEVELOPMENT OF PSEUDOPOLYGNATHUS

Much has been published on this topic and in general most authors agree that his genus has been derived from the spathognathodids. Branson & Mehl (1934b) observed this development, and reported a series of transitional forms between the two genera.

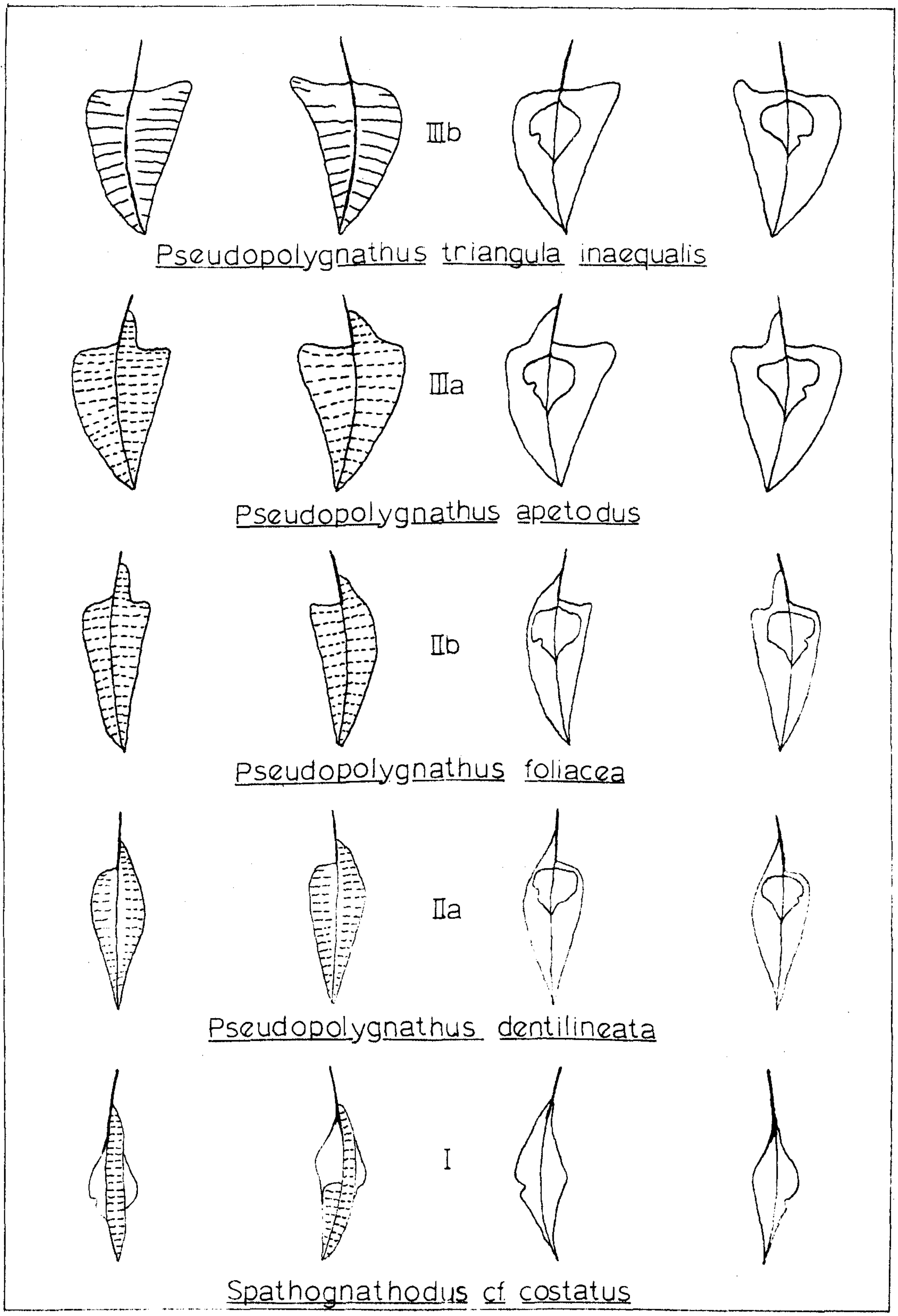
Hass (1959) figured a sequence of paratypes of Pseudopolygnathus lanceolata Hass (Pl.47, figs.19-26). The smaller paratypes, figs. 20 & 21, which Hass calls juveniles of P. lanceolata, are spathognathodid elements, fig.21 being a straight-bladed spathognathodid with three lateral denticles.

Voges (1959) pp.295-301 examined the derivation of Pseudopolygnathus from Spathognathodus in his study of conodonts from the Gattendorfia and and Pericyclus Stufen. He subdivided the Gattendorfia Stufe, CuI, of the Hangenburg-Kalk at the Honnetal Railway Cutting into three zones with the aid of pseudopolygnathid species. His studies led him to conclude that Pseudopolygnathus prima and certain other pseudopolygnathids which were bilaterally asymmetrical were developed initially from Spathognathodus c.f. costatus sensu Bischoff & Ziegler, by the addition of denticles on the inner side of the platform of right forms and the outer side of left forms. Voges recognised two forms within the *Spathognathodus costatus* group, a right and a left form, whose basal cavities were bilaterally symmetrical. Both forms were bilaterally asymmetrical in that the outer margin of the platform of right forms and the inner margin of the left forms were convex. In the right forms there was a row of nodes or ridges on the outer side of the platform which extended for three-quarters of the length of the unit, and in left forms this row of nodes and ridges occurred on the inner side of the platform. Small left forms usually showed no nodes on the outer side of the platform, although one or two may be present in larger specimens. Voges further recognised two variations of right forms which today are considered as two separate species, *Spathognathodus spinulicostatus ultimus* Ziegler, and *Spathognathodus spinulicostatus spinulicostatus* (renamed *Spathognathodus zeigleri* Rhodes, Austin & Druce 1969. Both variations showed a secondary row of nodes on the inner side of the platform extending posteriorly from the middle of the basal cavity. The form now called *Spathognathodus costatus ultimus* showed more strongly developed secondary nodes with a furrow replacing the blade nodes in the posterior third of the unit. Thus Voges interpreted *Spathognathodus ziegleri* and *S. costatus ultimus* as the right forms and *S. costatus* as the left form of the same species. It was Ziegler (1962) who found left forms of *S. ziegleri* and *S. costatus ultimus* and right forms of *S. costatus costatus*, (renamed *Sp. bischoffi*, Rhodes, Austin & Druce 1968).

The following is a summary of the development of *Pseudopolygnathus prima* from *Spathognathodus* cf. *costatus* as documented by Voges (1959, p.296, fig.4). Voges identified three stages of development (see Figure55); Stage I was represented by the *Spathognathodus* cf. *costatus* group, and from this Stage IIa was derived, represented by *Pseudopolygnathus dentilineata*, by the addition of

FIGURE 55

THE DEVELOPMENT OF PSEUDOPOLYGNATHUS PRIMA
FROM SPATHOGNATHODUS cf. COSTATUS GROUP
(after Voges diagram 4, 1959)



denticles on the outer side of left forms and the inner side of right forms. The basal cavities of right and left forms were bilaterally symmetrical, but the two halves of the basal cavity of individual elements were bilaterally asymmetrical. This nature of the basal cavity was retained during the further development of the oral surface of the *P. prima* group. Stages 11b and 111a were represented hypothetically by *P. foliacea* E.R. Branson and *P. apetodus* Cooper. According to Voges, these stages developed by the extension of nodes and ridges, towards the anterior on the outer side of the platform in left forms and on the inner side in right forms, and also the extension of the nodes and ridges of the opposite side of the platform to a point nearer the anterior extremity. A symmetrical element was present in the platform ornament when the inner anterior angle of the platform of right forms and/or the outer anterior angle of left forms was accentuated. Stage 111b is represented by *P. triangula inaequalis* from which developed *P. triangula triangula*, both these subspecies were symmetrical elements in terms of oral denticulation.

Klapper (1966) expressed his agreement with Voges that *P. dentilineata* probably developed from double-rowed forms of *Spathognathodus* (see Voges 1959, p.296, Tagel 5). He qualified his remarks by noting that this development at least applied to the Lower Carboniferous forms of *P. dentilineata*. In his discussion of Voges's interpretation, Klapper suggested that Stages 11b and 111a, said to be hypothetical, *were* possibly equivalent to *P. foliacea* and *P. apetodus* respectively. He considered both these species to be junior synonyms of *Pseudopolygnathus prima*, Stage 11b (*P. foliacea*) corresponding to an early representative of *P. prima*, still transitional with *P. dentilineata*, and Stage 111a (*P. apetodus*) corresponding to a more advanced form of *P. prima*. Klapper regarded specimens such as *P. irregularis* Branson (1934) pl.26, figs. 25 & 26, as being transitional between *P. prima* and *P. dentilineata*.

He stated that the distinction between these two species was purely arbitrary, based on the size of the basal cavity relative to the width of the platform. Klapper further noted that if it was accepted that *P. apetodus* (Voges Stage llla) was equivalent to *P. prima*, then *P. triangula inequalis* (Voges Stage lllb) probably developed from *P. prima* in the manner suggested by Voges. Another point of interest recorded by Klapper was that the basal cavity of *P. triangula triangula* was referable to the genus *Polygnathus* in a strict morphological sense. However, *P. triangula inaequalis* had a typical pseudopolygnathid cavity and Voges's lineage (Abb.5, p.297, 1959) showed a consistent trend toward the reduction of the basal cavity. Klapper stated that this phylogenetic evidence should be given precedence over morphological similarities and thus *P. triangula triangula* should be retained in the genus *Pseudopolygnathus*.

Rhodes, Austin & Druce (1969) concluded that there had been three separate developments of the genus *Pseudopolygnathus* in the type Avonian of Great Britain. One in the Lower and Middle part of the K zone, a second at the base of the Z1 zone and a third in the Middle and Upper part of the Z1 zone. He stated that all three developments had been along similar lines, the starting point of each being a straight-bladed Spathognathodid with lateral denticles. Austin compared specimens of his *Pseudopolygnathus vogesi* development, from the Lower and Middle K zone, with specimens from the *Pseudopolygnathus dentilineata* development of Voges (1959). Similarly he compared *Pseudopolygnathus prima*, from the Lower Z1 zone, with forms from the stage Voges referred to as "having specimens similar to *P. foliacea* and *P. apetodus*".

Rhodes, Austin & Druce (1969), in their report on the Avonian conodont faunas of Great Britain, remarked that "since the laterally nodose spathognathodids, which gave rise to the pseudopolygnathids, are homeomorphic and at least three chronologically distinct evolutionary lines have been demonstrated, it follows that the genus *Pseudopolygnathus* is polyphyletic". The authors stated that the forms from the Lower K zone arose from the platform evolution of Upper Devonian toV1 nodose spathognathodids, while those from the Upper Z zone can been seen to have evolved directly from forms which the authors have renamed *Spathognathodus costatus costatus* (previously *Spathognathodus costatus* Branson). The latter form of *Spathognathodus* is restricted to the Lower and Middle Zone. The two youngest pseudopolygnathid developments in the Avon Gorge of Great Britain are referred to the same phylogeny as that described by Branson from the Hannibal of Missouri. The third and oldest development, *P. vogesi* n.sp. Rhodes, Austin & Druce, is regarded as a separate phylogeny and a homeomorph of the younger pseudopolygnathid forms. The stage of development in Voges's fauna represented by *P. triangula inaequalis* and *P. triangula triangula* is not represented in the Avon Gorge, where *P. multistriata* developed from *P. prima*.

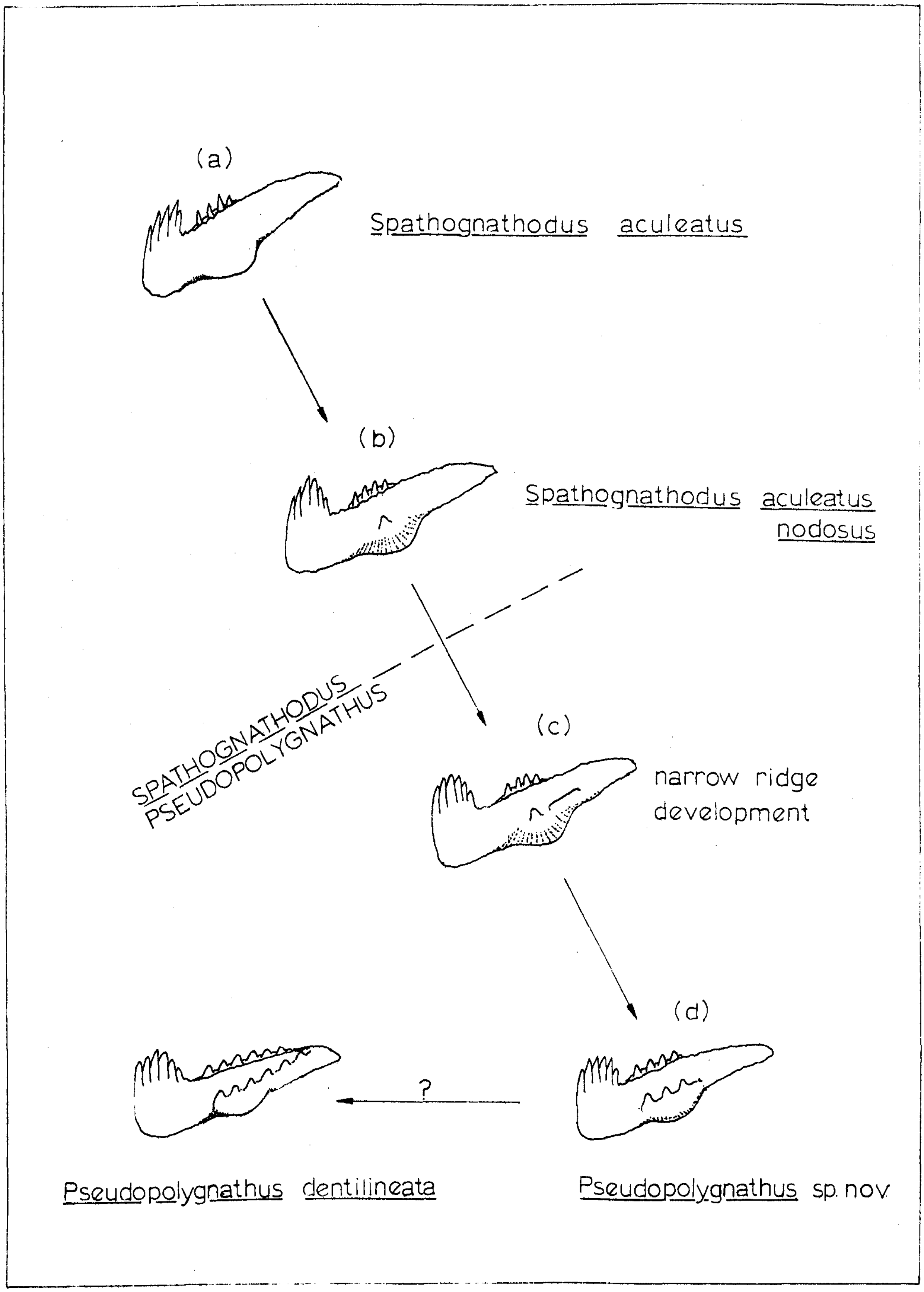
Rexroad and Scott (1964) suggested *Spathognathodus aculeatus* (Branson & Mehl) and *Spathognathodus anteposicornis* Scott, as possible ancestors of the genus *Pseudopolygnathus*. They also included *P. striata* Mehl & Thomas in synonymy with *P. multistriata* Mehl & Thomas.

In the Pilton Beds of North Devon, the two most abundant genera are *Spathognathodus* and *Pseudopolygnathus*. The former is present throughout the succession and the latter restricted to the upper two-third. Although the faunal evidence does not afford complete gradation along similar lines to that documented by some of the authors quoted above, the mere existence and stratigraphic location of *S. aculeatus*, *S. bischoffi*, *S. ziegleri* and *P. dentilineata* in the Pilton succession, tend to endorse the supposition that *Pseudopolygnathus* was developed from *Spathognathodus*. However, the evidence from the Pilton Beds suggests that the derivation of *Pseudopolygnathus dentilineata* may have been twofold: firstly, through the *Spathognathodus costatus* group, as documented by Voges (1959), and secondly, directly through *Spathognathodus aculeatus*, as postulated by Rexroad & Scott (1964). This second alternative trend of development is briefly mentioned in the remarks on *Spathognathodus aculeatus nodosus* (p. 209). This sub-species is considered as the last stage in the development of *Spathognathodus aculeatus* before it gave rise to a pseudopolygnathid form similar to that described later as *Pseudopolygnathus* sp.nov.(p. 196). Evidence of this path of development is further substantiated in the Lower Pilton Beds by the presence of several specimens which are identical to *S. aculeatus nodosus* except for the presence of a fine narrow ridge on the inner side of right forms and the outer side of left forms. This ridge is developed posterior to the single node which characterises the sub-species *S. aculeatus nodosus*. Theoretically, such forms still have only one node on this subspecies. However, this ridge is obviously the precursor of other denticles, which if developed would define the specimen as a pseudopolygnathid. Whether or not these forms with ridges are considered to be one genus or the other is of little importance, as they are truly transitional. The stages of development from *Spathognathodus aculeatus* through *S. aculeatus nodosus* to *Pseudopolygnathus* are shown diagramatically in Figure 56.

Whether or not this trend ultimately gave rise to *P. dentilineata* in the Lower Pilton Beds cannot be stated with any certainty, it may have ended with forms like *Pseudopolygnathus* sp. nov. However, it is possible that the latter forms did give rise to *P. dentilineata* and consequently this alternative development of *Pseudopolygnathus* may be of more significance than implied herein.

FIGURE 56

AN ALTERNATIVE EVOLUTIONARY DEVELOPMENT OF PSEUDOPOLYGNATHUS FROM SPATHOGNATHODUS



Orientation.

Taking Pseudopolygnathus dentilineata as the example, the curvature of the longtitudinal axis is a bilaterally symmetrical element. The ornamentation of the oral surface, the shape of the basal cavity and cross-section through the blade near the platform are bilaterally asymmetrical elements. The two sides of the basal cavity and of the platform of an individual right or left form are also bilaterally asymmetrical, although some specimens show the former feature to be almost symmetrical. The inner and outer platform margins of these conodonts are convex in both right and left forms. Individuals are designated as being right or left by orientating them with the anterior blade placed forward and then noting the curvature of the longtitudinal axis.

Identification of the Pseudopolygnathids in the Pilton Beds.

Some of the most recent ideas on pseudopolygnathid taxonomy were forwarded by Klapper (1966), in which he expressed his agreement with Voges (1959) that P. dentilineata was transitional with Pseudopolygnathus prima. Klapper considered the arbitrary distinction between these two species to be that the basal cavity of P. dentilineata was as wide as the platform whereas that of P. prima was more restricted. Furthermore, the margins of the basal cavity were more flared in P. dentilineata. Thus, Klapper disregarded specific identification on the basis of variation in the oral ornament, for these species. The author is in agreement with this approach in the light of the vast variety of platform ornamentation possible.

Rhodes, Austin & Druce (1969) considered P. vogesi from the Avon Gorge to be homeomorph of P. dentilineata Branson, and similar but not identical to P. dentilineata Voges. Klapper's diagnosis of P. dentilineata would include P. vogesi Rhodes, Austin & Druce (1969), and it is also interesting to note that Klapper placed a great many named pseudopolygnathid species in synonmy with *P. prima*. He stated that "They were proposed primarily on the basis of details of the upper surface ornamentation, here regarded as within the range of intraspecific variability".

At any one horizon in the Pilton Beds, containing pseudopolygnathids of sufficient number, the variety of platform shape, denticle number and arrangement is found to be diverse. However, it was readily recognised that many of the elements could be referred to the species *Pseudopolygnathus dentilineata* Branson. Forms similar to *Pseudopolygnathus vogesi* were found in association with *P. dentilineata* at all horizons where the latter was present, as were forms which orally resembled *Pseudopolygnathus multistriata*. The author considers that the forms similar to *P. vogesi* are infra-specific variants of *P. dentilineata* and that the fact that the former shows ridge-like denticles does not warrant the erection of a separate species in the Pilton Beds. Both forms have identical basal cavities and there are a variety of intermediates between them. However, in the Lower and Middle K zone of the Avon Gorge, there may be a valid case for isolating this particular variant of *P. dentilineata* and designating it as a separate species, as here it is not associated with any other pseudopolygnathids. Klapper's diagnosis of *P. dentilineata* includes several of the morphological features regarded as characteristic of *P. vogesi*.

No forms identical with *Pseudopolygnathus prima* have been located in the Pilton Beds, but there are forms in which the nodes have become either thickened and ridge-like or else, simply more numerous on both sides of the platform. Such specimens are treated as varieties of *P. dentilineata*, since the basal cavity is not restricted but is typical of that described for *P. dentilineata* by Klapper (1966). Like the forms similar to *P. vogesi* and those which resembled *P. multistriata*, these forms are always found wherever *P. dentilineata* is found.

The specimens which orally are similar to *P. multistriata* are aborally dissimilar, in that they also have basal cavities which are not restricted but the same width as the platform. On this basis they are included as further variants of the species *P. dentilineata*. Klapper (1966) calls *P. multistriata* and *P. dentilineata* homeomorphs, distinguished only by the difference in their basal cavity dimensions. Because they can be distinguished in this way they are not true homeomorphs, but rather near homeomorphs. Thus, according to Klapper's classification, the present author's use of the phrase 'forms which orally resemble *P. multistriata*' is invalid, because the oral surface cannot be used as a criteria for distinguishing *P. dentilineata*, *P. multistriata* and *P. prima*. Klapper's diagnosis serves to describe all the pseudopolygnathids recovered from the Pilton Beds. His diagnosis is:-

> "Right side of the platform more fully developed anteriorly along blade. Single row of large nodes or ridges on each side of the platform. Basal cavity covers entire width of platform in mature specimens and has flaring margins".

For the reasons cited, the pseudopolygnathid population of the Pilton Beds is considered to be represented by a single species, *P. dentilineata*, with the exception of only a few specimens. Although variation in oral ornamentation is diverse, this is regarded as infraspecific variation. The basal cavity of all the pseudopolygnathids studied is consistently large and flared, with no evidence of restriction.

A few mature specimens from three of the lowest horizons at which pseudopolygnathids have been found in the Pilton Beds, still possessed a large flared cavity, but were of particular interest for three reasons. (a) The platform was restricted to the mid-third of the unit, usually overlapping slightly into the anterior third. (b) The platform supported only 3 or 4 denticles on either side of the carina even in mature forms. (c) These forms were restricted to the three horizons mentioned, and at one of these horizons were the only pseudopolygnathid representatives found. Such forms could be interpreted as further variants of P. dentilineata, but the position and shape of their platform, and more important their restriction in terms of stratigraphic occurrence, has prompted the author to treat them as a separate species, Pseudopolygnathus sp. nov.

INFRASPECIFIC VARIABILITY IN PSEUDOPOLYGNATHUS DENTILINEATA E.R.BRANSON IN THE PILTON BEDS OF NORTH DEVON.

Scott and Collinson (1959) stated that:-

> "Conodonts lend themselves to studies of variability because (1) specimens are exceedingly abundant; (2) the stratigraphic occurrence of conodonts in Paleozoic rocks, despite the gaps apparent in the literature, is one of the most nearly complete in the fossil realm; (3) each specimen carries a record of its ontogenetic history; (4) preparation and examination of great numbers of specimens is both easy and rapid; and (5) conodonts are resistant to weathering and to abrasion so that specimens are commonly perfectly preserved and are suitable for detailed study".

The authors further noted that variation had received only scant attention and that it was common to find 10-20 subjective synonyms for a single species.

In their publication, Scott & Collinson (1959), described the infraspecific variation that they recognised within the species Palmatolepis glabra Ulrich & Bassler. They interpreted groups of infrapopulation variants, not as separate species, but as 'morphotypes', which were each distinguished by a Greek letter. The authors pointed out that further studies of P. glabra populations may indicate that one or more of the morphotypes differ sufficiently from other palmatolepids to warrant individual specific names. However, until thattime occurs, the conodont worker is not "burdened with a lot of arbitrarily defined species which are gradational and may be without stratigraphic value". Given the correct circumstances, all species could probably be seen to be time gradational.

In the present study of P. dentilineata, the author adhered closely to the methods of Scott & Collinson, as this approach was considered to be the most suitable in the interpretation of the pseudopolygnathid population of the Pilton Beds. The preceding quotation from the work of these authors is considered to be most relevant to the problem at hand, in that the variants of Pseudopolygnathus, in the Pilton Beds, have no individual stratigraphic value with the exception of Pseudopolygnathus sp. nov.

CONSTRUCTION AND INTERPRETATION OF THE INFRASPECIFIC VARIATION DIAGRAMS (FIGS. 57 & 58)

Variability within a population was just one of three types of infraspecific variation summarized by Muller (1956, p.1330 & 1331). The two other types he noted were (b) variation within a single natural assemblage and (c) ontogenetic transfromation. To these three categories Scott & Collinson (1959) added (d) the effect of injury and regeneration and (e) variation produced by genetic trends and natural selection.

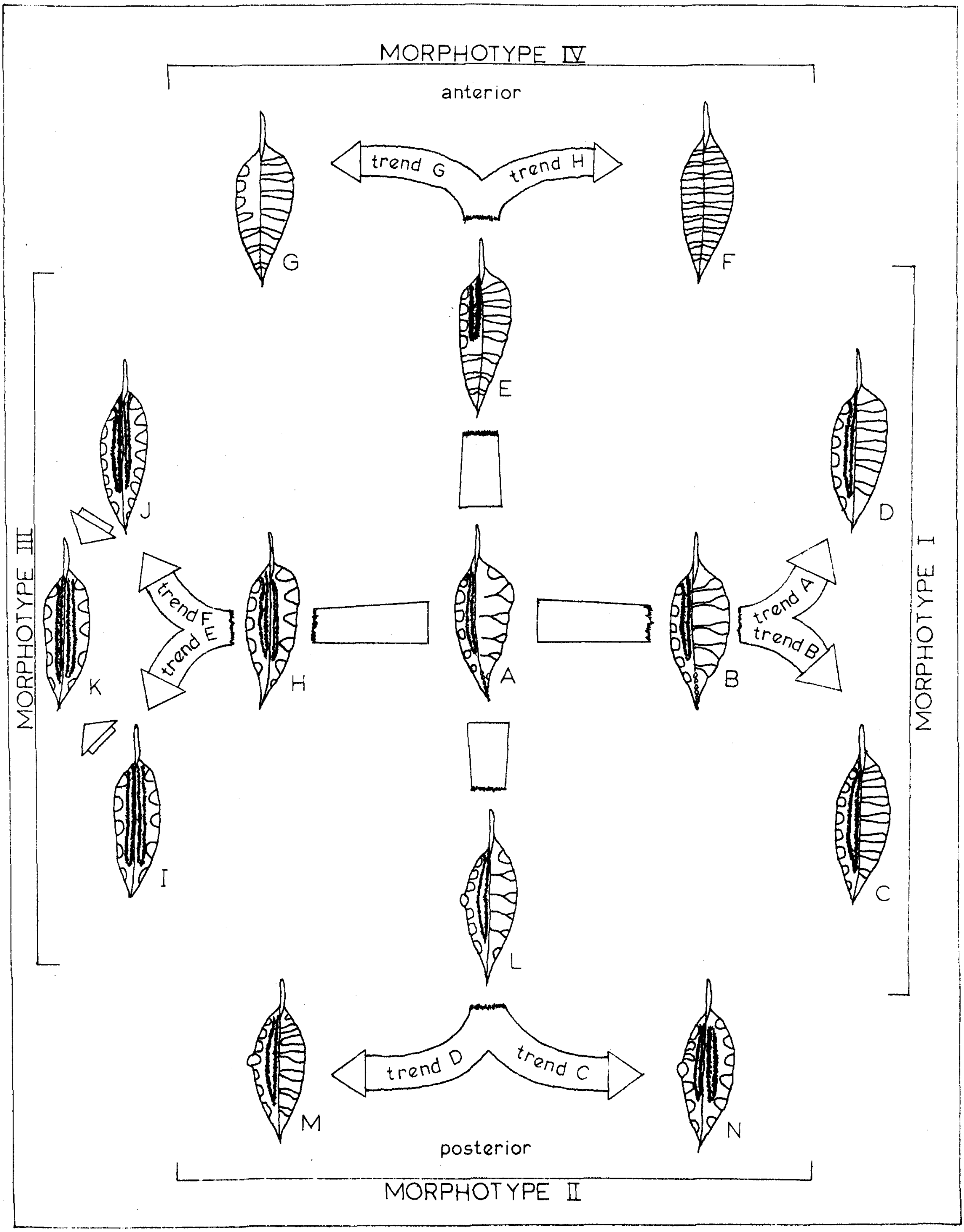
In the following discussion the present author is dealing with normal infraspecific variation, or variation within a population. The term population is used loosely. The principal morphologic variants found in the Pilton Beds are illustrated in Figure 57, and the frequency distribution of these variants recorded graphically in Figure 58. Trueman et al, (in Imbrie, 1957) devised a similar technique to that of Scott and Collinson, with one major difference. Whereas Trueman et al interpreted the infrapopulation variants as separate species, Scott & Collinson chose to use the term 'morphotypes', as applied by Sylvester-Bradley (1958), for their major groups of variants.

At this juncture it is convenient to repeat that the nature of the aboral cavity is a non-variable feature, the variability dealt with herein being only that which occurs in the oral ornamentation.

Figure 57 was constructed as follows:- Two hundred mature specimens of Pseudopolygnathus were isolated from a single horizon, PB.16. The only criteria used in choosing these specimens was that they were mature and essentially unbroken (the anterior blade was missing in a great number of specimens). No attention was paid to the oral ornamentation at this stage. With the aid of photographs the variants were sorted into groups with morphological similarities, and a total of four groups were recognised by the author. As stated by Scott & Collinson, "this division is somewhat arbitrary and other workers might recognise fewer or more groups. It is doubtful, however, that such differences would significantly affect the conclusions drawn herein". The figure was then constructed placing one specimen, representing the most common form present in the population, in the centre. This centrally illustrated specimen is similar, but does not conform precisely to the original description of P. dentilineata by Branson (1934).

Thirteen other specimens are illustrated in Figure 57 to show the type and range of variability found. These specimens are arranged concentrically around the central specimen, those furthest from the centre are thought to show the greatest degree of variation from the 'normal' form. The trends of divergence are indicated by the arrows e.g. trend 1 is considered to

INFRASPECIFIC VARIATION IN THE ORAL ORNAMENTATION OF SPECIMENS OF PSEUDOPOLYGNATHUS DENTILINEATA FROM SAMPLE NUMBER PB.16 OF THE PILTON BEDS.



represent the development of ridge-like denticles and intervening furrows on one side of the platform, with or without an increase in the number of denticles.

In the construction of Figure 58 the present author preferred to deviate from the methods of Scott & Collinson. The frequency distribution diagram used by these authors gave only a very generalised picture of the density statistics, whereas the plot used herein represents the figures more lucidly and simply. Figure 58 indicates graphically the frequency distribution of the individual variants recognised within each morphotype. Furthermore it readily shows the relative frequency of each morphotype as a group.

The maximum length of the platform of the outer side of right forms, and the inner side of left forms, is considered to be satisfactory criterion for indicating the ontogenetic stage of development of *P. dentilineata*. The platform length of all 200 specimens used in the construction of Figures 57 & 58 was greater than 0.64 mm.

DESCRIPTIONS OF THE MAIN GROUPS OF VARIANTS OF *P. DENTILINEATA*.

Theoretically each variant in Figure 57 should be described individually, but as four arbitrary groups have been recognised, it is more practical to restrict descriptions to these well defined collective units, which are based solely on the 200 specimens used in the construction of the variation diagrams. It must be remembered that the descriptions of these four groups of 'morphotypes' are generalisations expressing only the major variations in the *P. dentilineata* population. There are an infinite number of other minute variations, in denticle number and shape, which are unspecified in Figure 57 To clarify this let us consider a hypothetical trend showing an increase in denticle number from five to nine; apart from the end members of this trend,

FREQUENCY DISTRIBUTION OF INFRASPECIFIC VARIANTS OF PSEUDOPOLYGNATHUS DENTILINEATA FROM PB-16.

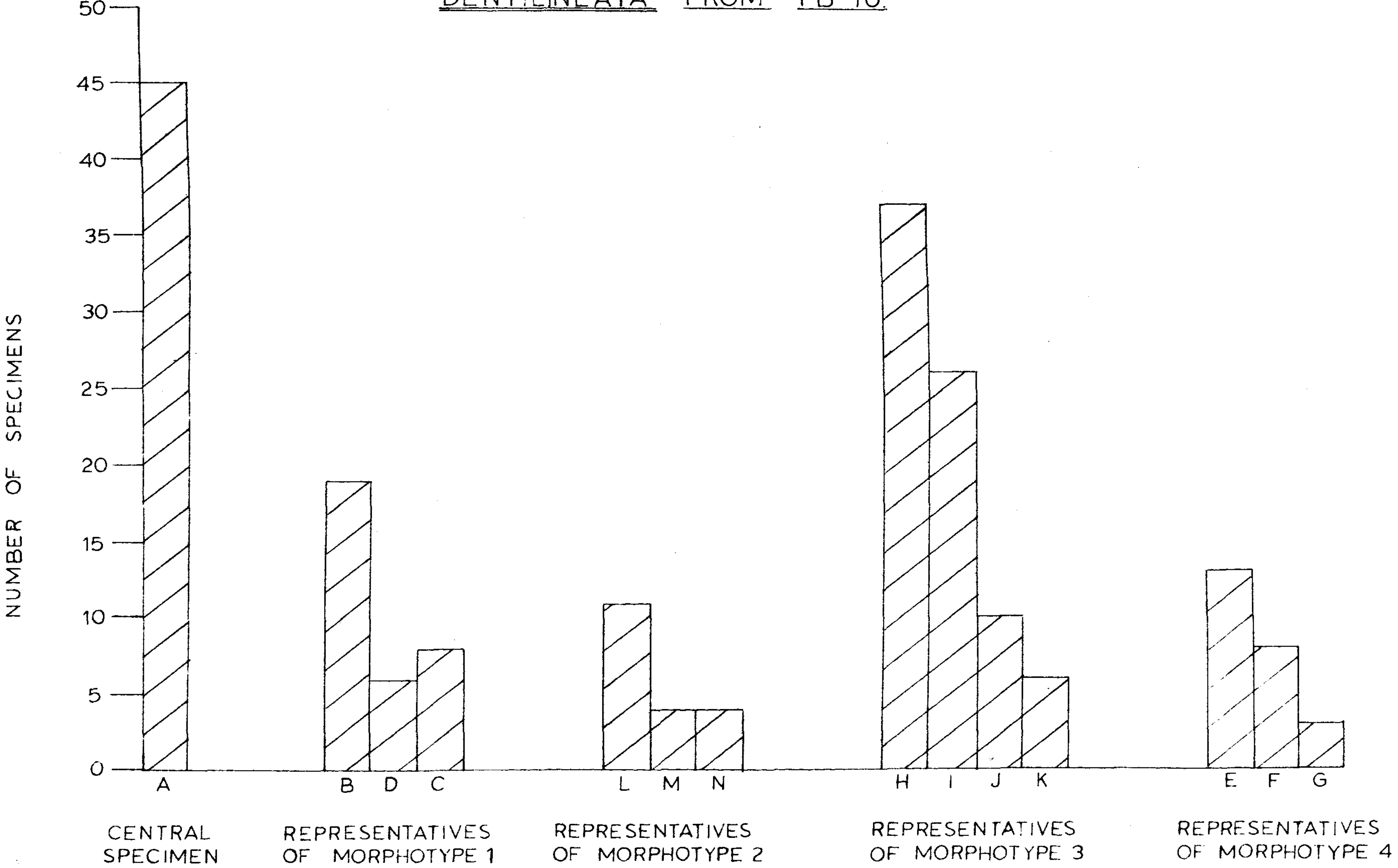


FIGURE 58

forms with six, seven and eight denticles would have been observed but they would not have been recorded in the diagram.

The bilateral asymmetry of the units means that the descriptive terms 'outer side of the platform of right forms' and 'inner side of the platform of right forms' used in the following paragraphs, also imply a corresponding development of the 'inner side of the platform of left forms' and 'outer side of the platform of left forms' respectively.

MORPHOTYPE I (Pl.4, figs.9a-10c; Pl.5, figs.1a-2c)

This group is characterised by a marked thickening of the denticles, (5 or 6 in number), of the outer side of the platform of right forms. The net result is the production of prominent ridges and alternating furrows, which traverse this side of the platform and are in contact with the carina. The denticles of the inner side of the platform of right forms show no change, remaining the same size, shape (nodose) and number (usually one more than the opposite side of the platform) and furthermore they remain restricted to the margin of the platform. Of the 200 specimens studied, 33 are members of this morphotype.

Within this group, two trends are recognisable, the first, trend a, shows even further thickening of the 5 or 6 ridge-like denticles on the outer side of the platform of right forms, without any other significant change in the conodont platform. The second trend, trend b, shows the development of more numerous ridge-like denticles (maximum number 8) on the outer side of the platform of right forms, while the opposite side of the platform undergoes no change other than corresponding increases in the number of nodose denticles. There may or may not be further thickening of the denticles of the outer side of right forms. A further result of both trends a and b is to lose the discrete denticulation of the posterior third of the carina.

Trend a results in forms which are similar to P. vogesi, from the Avonian of the Avon Gorge. Austin (personal communication) has encouraged the present author in his consideration of these forms as variants of P. dentilineata, and it would seem that Austin now thinks that he was incorrect in establishing a new species, looking upon the first development of pseudopolygnathids in the Avon Gorge as a P. dentilineata development. However, as explained earlier, these are the only pseudopolygnathids found in the Lower and Middle K zone of the Gorge, and the present author contends that there may be a case for isolating this particular variant of P. dentilineata, and elevating it to a species.

MORPHOTYPE II (Pl.5, figs.3a-7c)

This group is represented by only a small number of specimens, 19 in all, and is characterised primarily by the development of an offset, accessory denticle on the inner side of the platform of right forms. This denticle is located between the third and fourth platform denticle from the anterior end of the unit. Once again two trends can be recognised namely, trend c and trend d. Trend c is toward the development of a platform bearing denticles which are all nodose and restricted to the margins. The number of denticles on each side of the carina is either 6 or 7. Trend d variants show the denticles of the outer side of the platform of right forms to become ridge-like, crossing the platform to meet the carina. Those denticles on the opposite side of the platform are restricted to the margin. The end products of trends c and d are very similar in overall appearance to those of trend f, Morphotype III and trend b, Morphotype I respectively, but are differentiated by the presence of the accessory lateral node. Both trends c and d are equally common with regard to numbers of specimens.

Having pointed out that specimens of Morphotype II can be referred to both Morphotypes I and III, this emphasises that these groups are purely arbitrary and often based on the presence of just one common character, in this case the development of an accessory lateral denticle.

MORPHOTYPE III (Pl. 5, figs.8a-9c; Pl. 6, figs.1a-4c)

This group is characteristed by the restriction of the 5 or 6 platform denticles, on both sides of the carina, to the margins of the platform. A well marked trough occurs between the denticles and the carina, on both sides of the platform. The denticles are nodose, and two trends of variation are recognised within this group. Representatives of this Morphotype are twice as numerous as the next largest group. Many of the forms of this Morphotype, which show only a small degree of divergence, are very similar to the original description of P. dentilineata Branson (1934). Trend e indicates further regression of the denticles toward the platform margin, where they become rounded in shape. The denticles are still 5 or 6 in number on either side of the platform. This is the most prominent trend.

Trend f is toward a unit in which the denticles are restricted to the margin but are more numerous on both sides of the platform. The maximum number of denticles increases from 5 or 6 to 9 or in rare cases 10. The denticles retain their triangular shape as opposed to becoming rounded. In Figures 57 & 58 there is one illustration which is not directly included in either trend. A few specimens achieve the ultimate development of both trends e and f, having rounded denticles restricted to the margin and more numerous denticles. Such specimens may be derived from either or both trends.

The result of trend f is not unlike representatives of the species, P. prima Branson & Mehl, but differs in that the basal cavity is unrestricted and it bears no lateral lobe on one side of the platform. It is considered that these variants are homeomorphs of P. prima from the Avon Gorge, and from the CuI of Germany.

MORPHOTYPE IV (Pl.6, figs.5a-7c)

Specimens displaying an increase in the number of denticles, of the order of one to three, on each side of the platform, together with a tendency for these denticles to become ridge-like on the outer and inner posterior side of the platform of right forms, are ascribed to this group. The anterior portion of the inner side of the platform of right forms bears a prominent unornamented trough between the marginal nodes and the carina. As a result of this the inner anterior portion of the platform is lower on the carina than the outer anterior portion in right forms. Two trends can be recognised, the most important being trend h, in which, the ridge-like nature of the denticles extends over the whole platform on both sides of the carina. In a few specimens the most anterior denticle on the inner side of the platform of right forms may be the only exception, in that it fails to extend to the carina. There is no prominent trough present and these forms are identical, orally, to P. multistriata Mehl & Thomas, although, aborally, the basal cavity is as wide as the platform, and is not restricted. (Klapper (1966) considers P. multistriata Mehl & Thomas to be a Lower Osage homeomorph of P. dentilineata). The present author considers P. multistriata Mehl & Thomas to be a homeomorph of this variant of P. dentilineata.

Trend g shows that the ridge-like denticles remain restricted to the outer and inner posterior portion of the platform; in right forms, however, the inner anterior trough is lost. The inner side of the platform of right forms becomes elevated to a position higher on the carina, so that the platform on both sides of the carina is of equal height. The result of this is to suppress the trough, and this, together with the elevation of the platform, constitutes trend g.

CENTRAL SPECIMEN (Pl.7, figs.1a-7)

This type of specimen represents over 25% of the total number of conodonts used in this variation analysis. It is characterised by the presence, on the outer and inner sides of the platform of right forms, of 5 and 6 denticles respectively. The denticles of the outer side of right forms are intermediate between nodose and ridge-like, in two senses. Firstly, they are intermediate in their actual shape, many of the individual denticles being tear-shaped in outline, tapering toward the carina. Secondly, forms are found in which a few of the 5 denticles are ridge-like, almost reaching the carina, while the rest are nodose and rounded, restricted to the margins of the platform.

THE NATURE OF THE BASAL CAVITY

Figure 59 was constructed to show the basal cavities of the specimens used to illustrate oral variation in Figure 57. As can be seen from Figure 59 the aboral similarity of all the specimens is most striking.

To further illustrate the consistent nature of the basal cavity of the pseudopolygnathids in the Pilton Beds, a series of graphs has been constructed. The graphs in Figures 60 & 61 express the maximum width of the basal cavity as a plot against the maximum width of the platform. A separate graph is constructed for each of the Morphotypes outlined in the previous pages. All the graphs plotted as straight lines indicating a constant relationship between the basal cavity and platform width, and furthermore the lines were all at an angle of 45° indicating that the widths of these two morphological

BASAL CAVITIES OF THE PSEUDOPOLYGNATHUS DENTILINEATA VARIANTS ILLUSTRATED IN FIG. 57

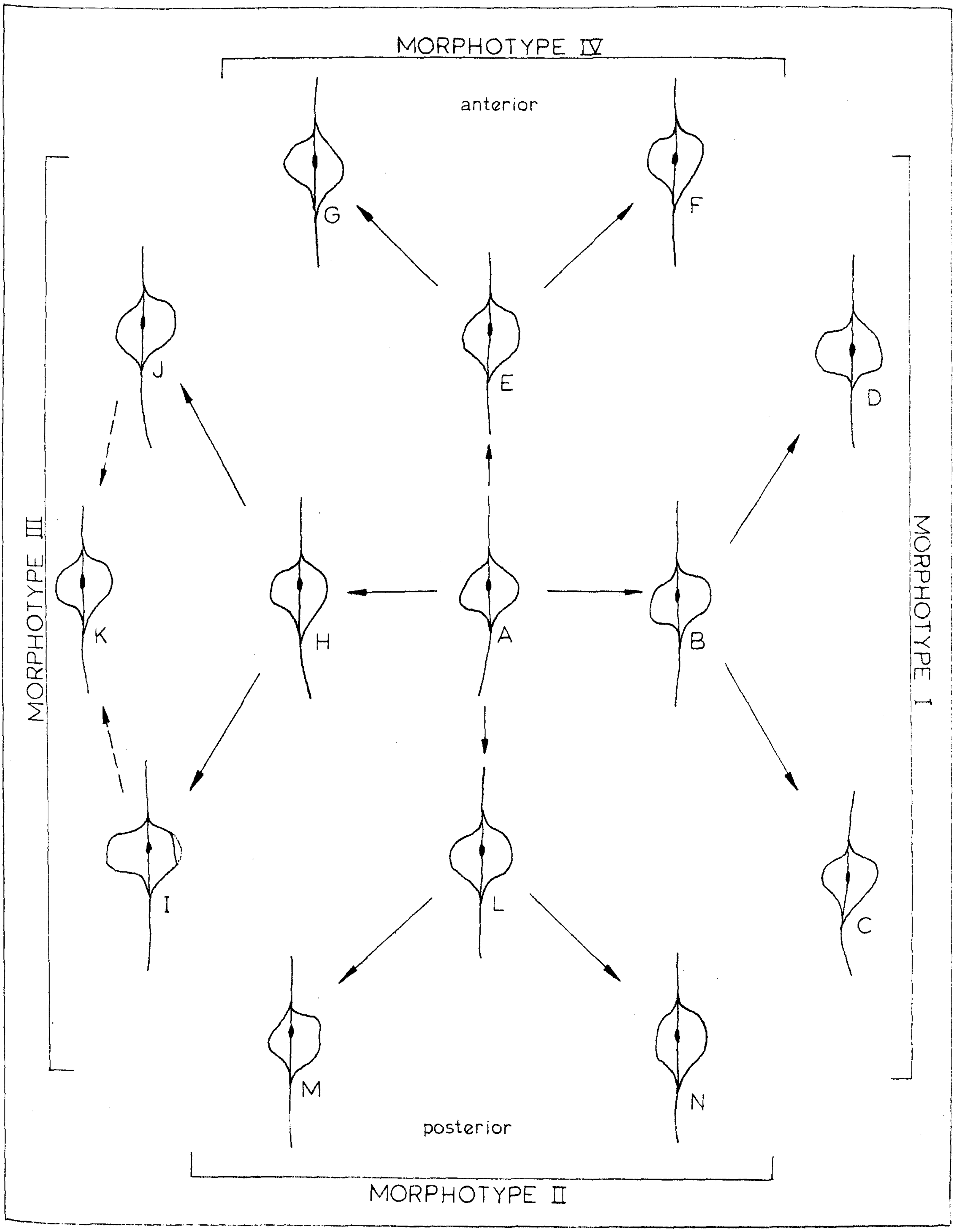
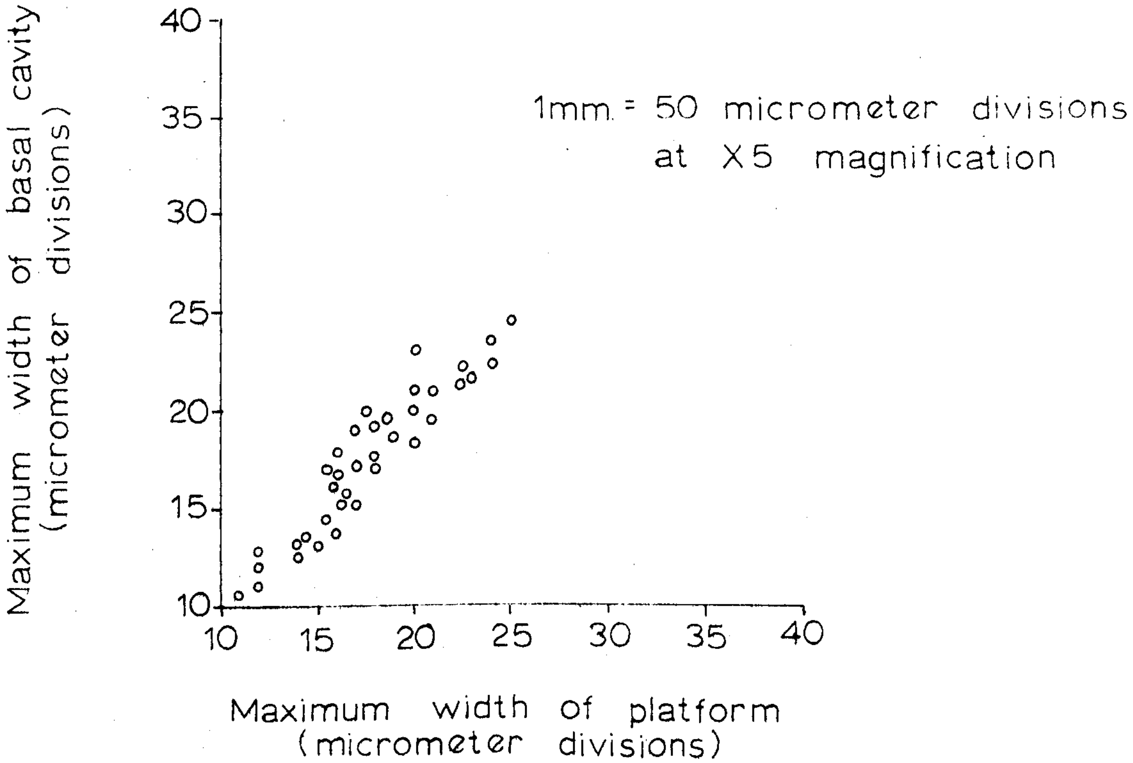
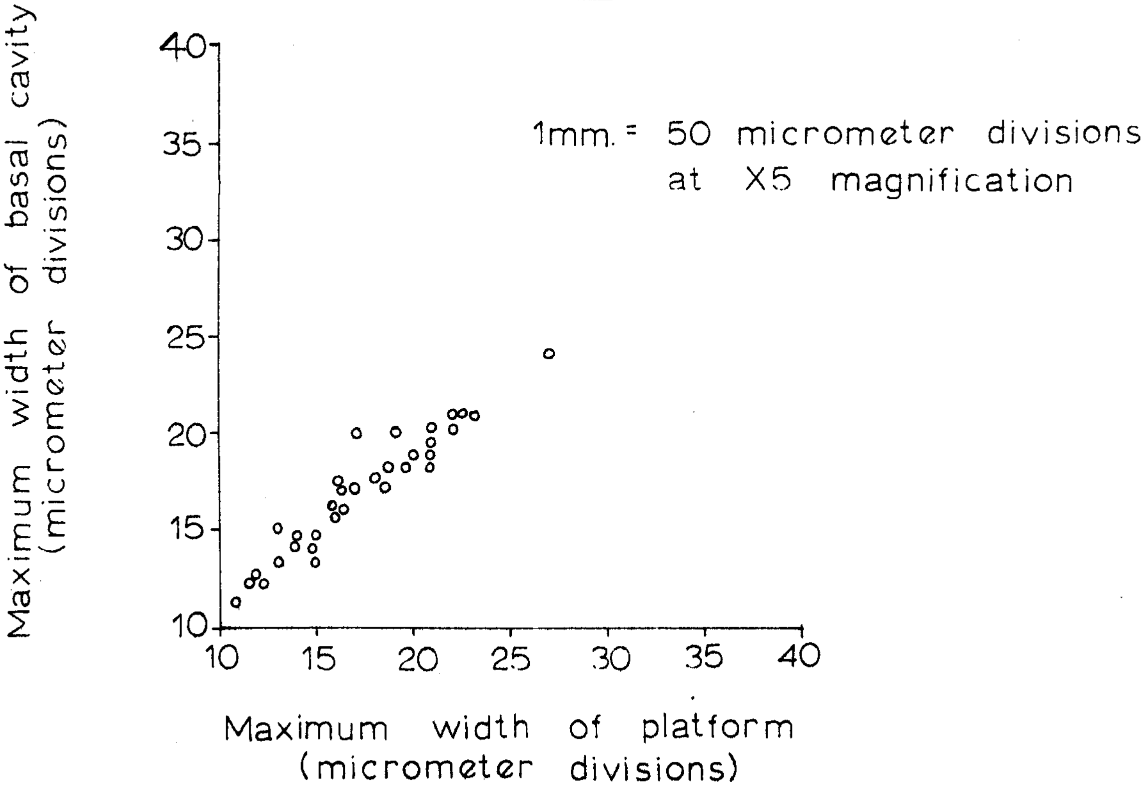


FIGURE 60

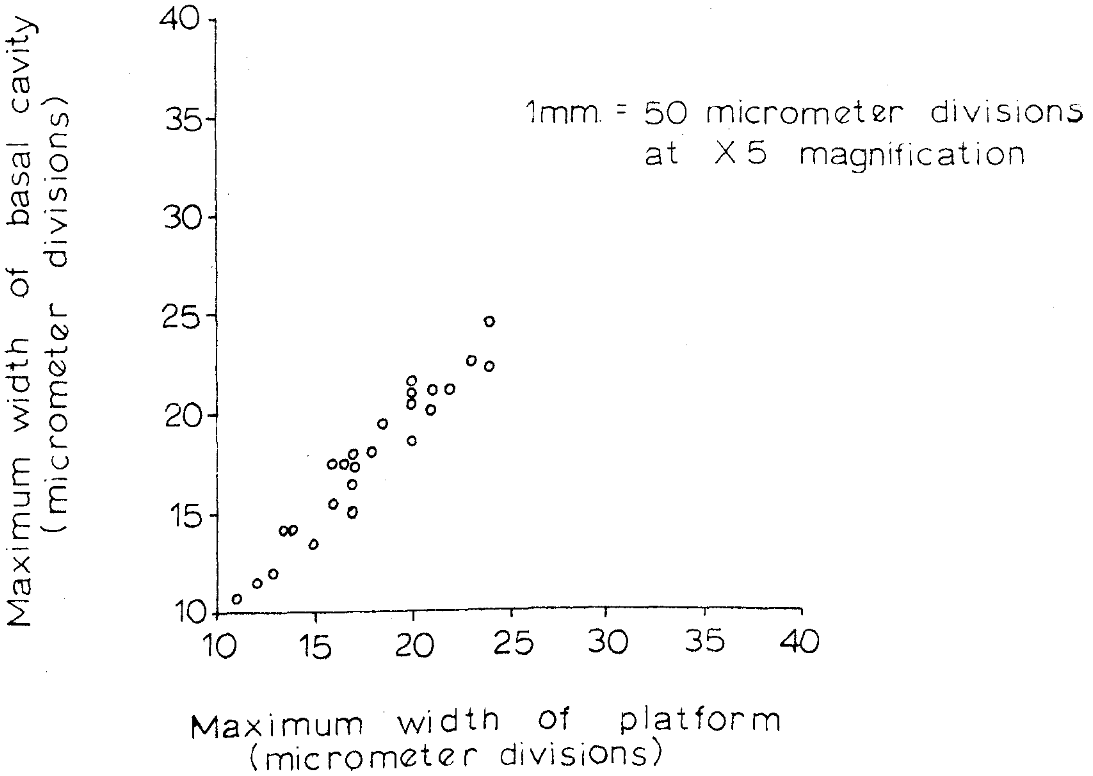
COMPARISON OF THE WIDTH OF THE BASAL CAVITY WITH THE WIDTH OF THE PLATFORM IN SPECIMENS OF MORPHOTYPE I



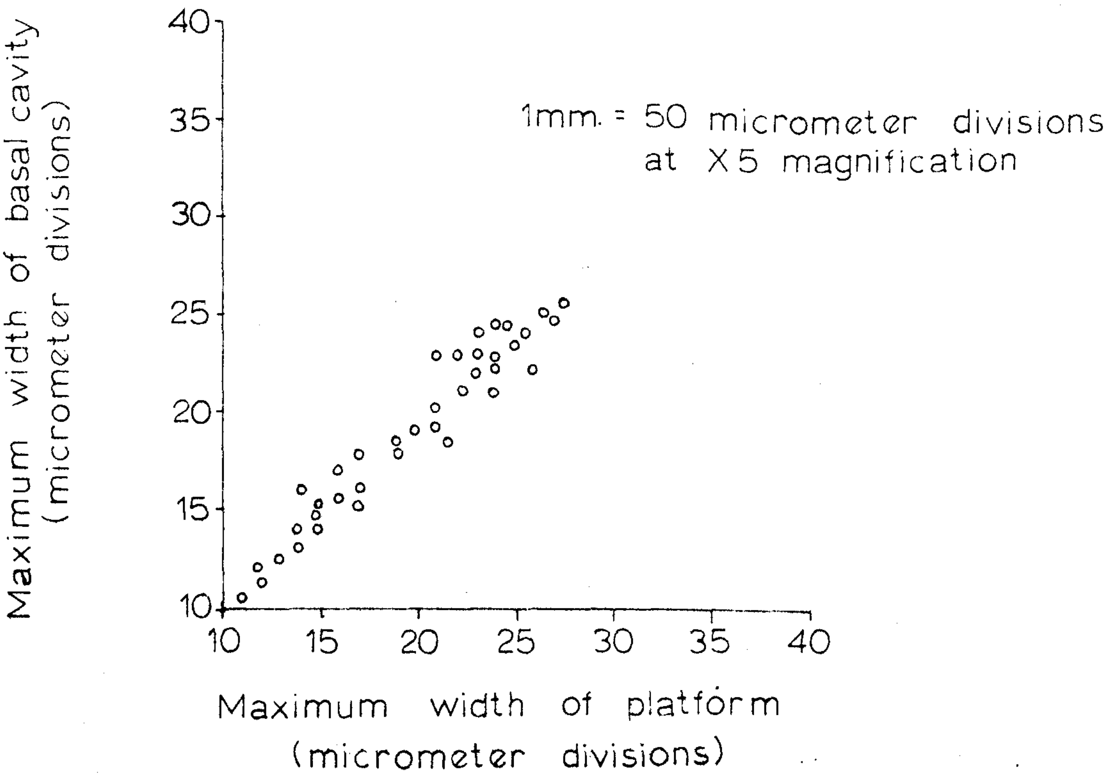
COMPARISON OF THE WIDTH OF THE BASAL CAVITY WITH THE WIDTH OF THE PLATFORM IN SPECIMENS OF MORPHOTYPE II



COMPARISON OF THE WIDTH OF THE BASAL CAVITY WITH THE WIDTH OF THE PLATFORM IN SPECIMENS OF MORPHOTYPE IV



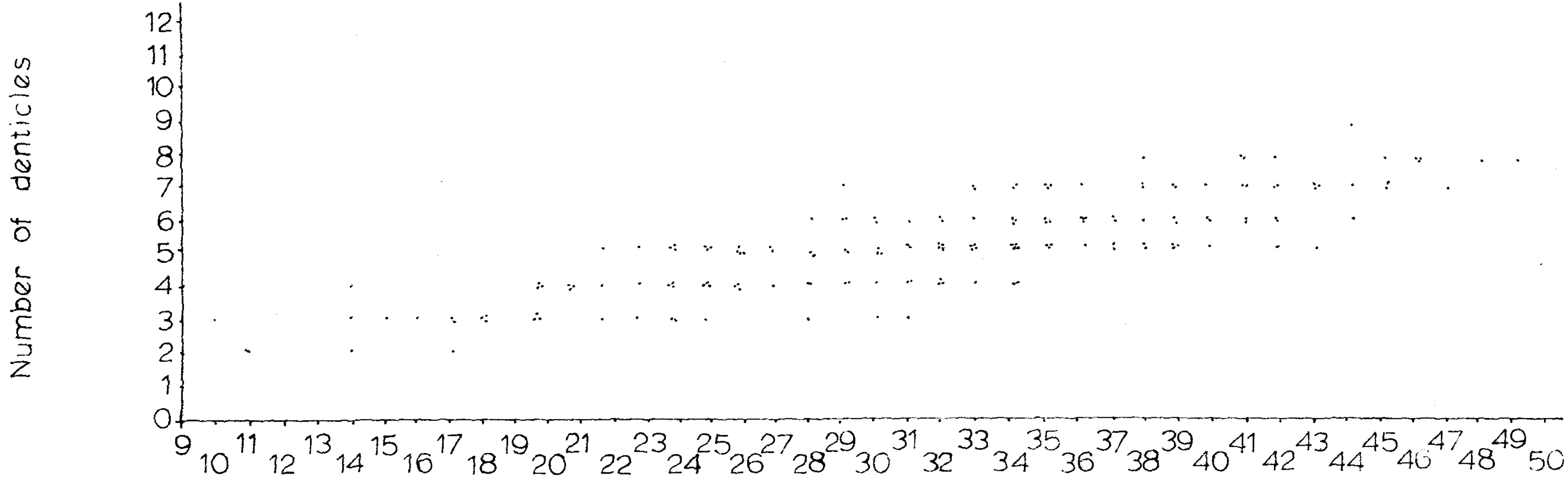
COMPARISON OF THE WIDTH OF THE BASAL CAVITY WITH THE WIDTH OF THE PLATFORM IN SPECIMENS OF MORPHOTYPE III



features was essentially the same for any one individual. A comparison of the 4 graphs indicates that none of the major groups of variants has restricted basal cavities, but rather cavities which are as wide as the oral platforms. Specimens from horizons throughout the Lower Pilton Beds were used in plotting this data.

Two other graphs were constructed in order to ascertain the relationship between the rate of growth of the conodont unit and the increase in the number of denticles on the platform. Figure 62 compared the number of denticles on the inner side of the platform of right forms, or the outer side of the platform of left forms, with the length of those sides of the platform, while Figure 63 compared the number of denticles on the outer side of the platform of right forms, or the inner side of the platform of left forms, with the length of the corresponding sides of the platform in this case. Specimens from sample PB.20 were used in the construction of both graphs. The data indicate that there are two patterns of growth, the first, and dominant trend, is simply the increase in length of the platform on both sides of the carina. Both sides of the platform increase in length at approximately the same rate, and as the denticle number remains constant then the denticles are increasing in size as the platform grows. This trend is apparent throughout the ontogeny, and particularly apparent in the juvenile members of the species. The second trend does not become obvious until maturity, when there appears to be an increase in the number of denticles on the platform without an increase in the platform length. The two trends are most apparent when expressed graphically and despite determined efforts, the author has been unable to show these two trends convincingly in diagrammatic form. The probable reason for this is that the patterns of growth are very closely allied.

COMPARISON OF THE NUMBER OF DENTICLES BORNE ON THE INNER SIDE OF THE PLATFORM OF RIGHT FORMS (OUTER SIDE OF LEFT FORMS) WITH THE LENGTH OF THAT SIDE OF THE PLATFORM IN PSEUDOPOLYGNATHID SPECIMENS FROM SAMPLE PB-20

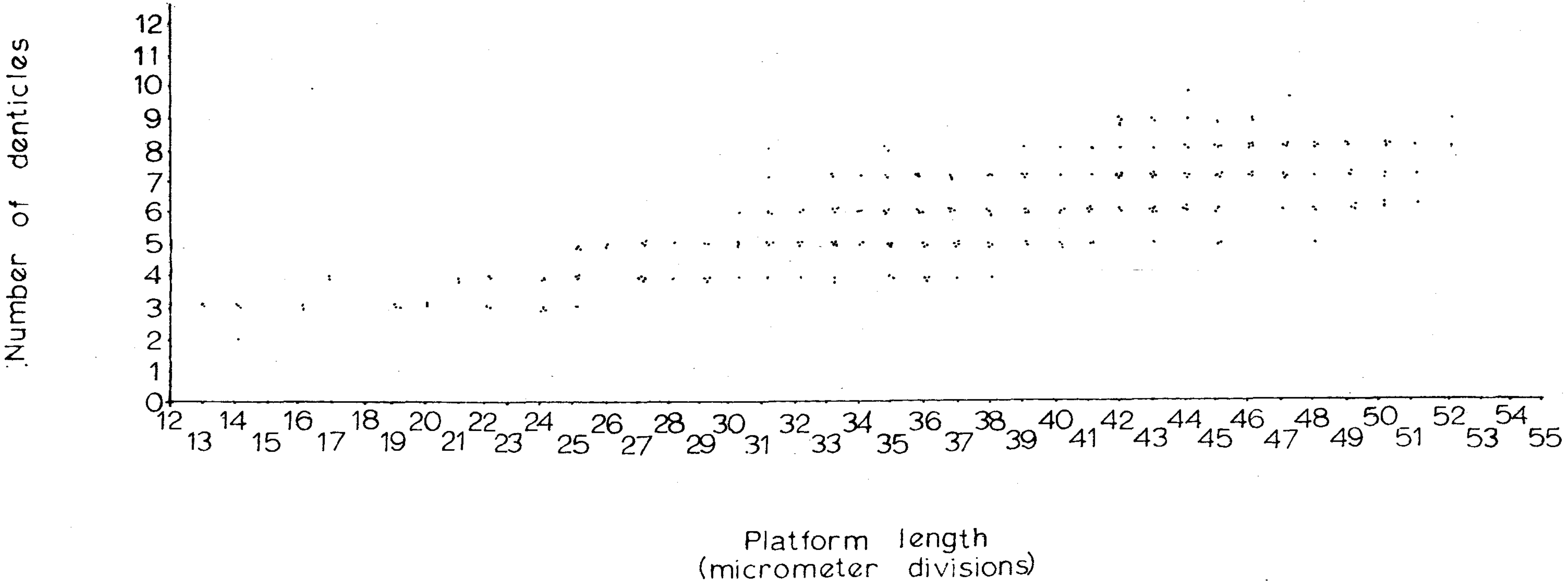


Platform length
(micrometer divisions)

1mm = 50 micrometer divisions at X5 magnification

FIGURE 62

COMPARISON OF THE NUMBER OF DENTICLES BORNE ON THE OUTER SIDE OF THE PLATFORM OF RIGHT FORMS (INNER SIDE OF LEFT FORMS) WITH THE LENGTH OF THAT SIDE OF THE PLATFORM, IN PSEUDOPOLYGNATHID SPECIMENS FROM SAMPLE PB-20.



1mm = 50 micrometer divisions at X5 magnification

FIGURE 63

In an effort to understand the relative rates of growth of different parts of the same individual, Figure 64 was constructed. This shows a comparison of the length of the outer side of the platform of right forms (inner side of left forms) with the total length of the conodont, from anterior to posterior extremity. The graph indicated that the length of the platform of any one individual increases at a greater rate than the overall length of that conodont. A juvenile form may have a platform which is half the overall length of the unit, whereas the mature form will exhibit a platform which is three-quarters the overall length.

At all the horizons in the Pilton Beds in which pseudopolygnathids were abundant, the four morphotypes were always evident and hence no zonal scheme could be produced based on their stratigraphic distribution. A chart was constructed (Figure 65) to show the relative percentage of each morphotype, and the central specimen, at these horizons which contain numerous pseudopolygnathids.

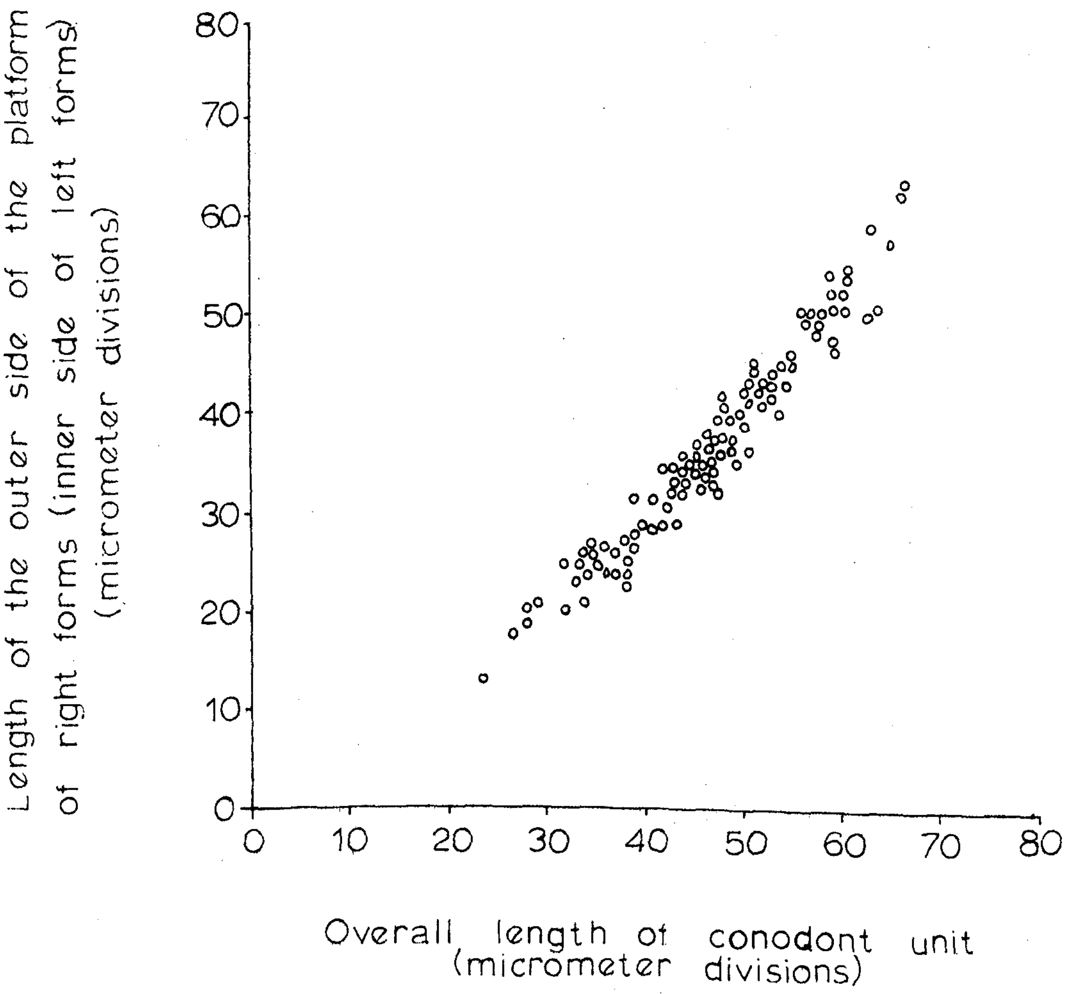
As can be seen from Figure 65, the percentage of each morphotype and the central specimen is variable throughout that part of the succession from which pseudopolygnathids were recovered. However, there are no significant fluctuations in the relative percentages that could be utilised for zonal purposes. The morphologic variation is therefore interpreted as infraspecific.

Pseudopolygnathus dentilineata E.R. Branson, 1934

(Pl.4, figs.9a-10c; Pl.5, figs.1a-9c; Pl.6, figs.1a-7c;
Pl.7, figs.1a-7)

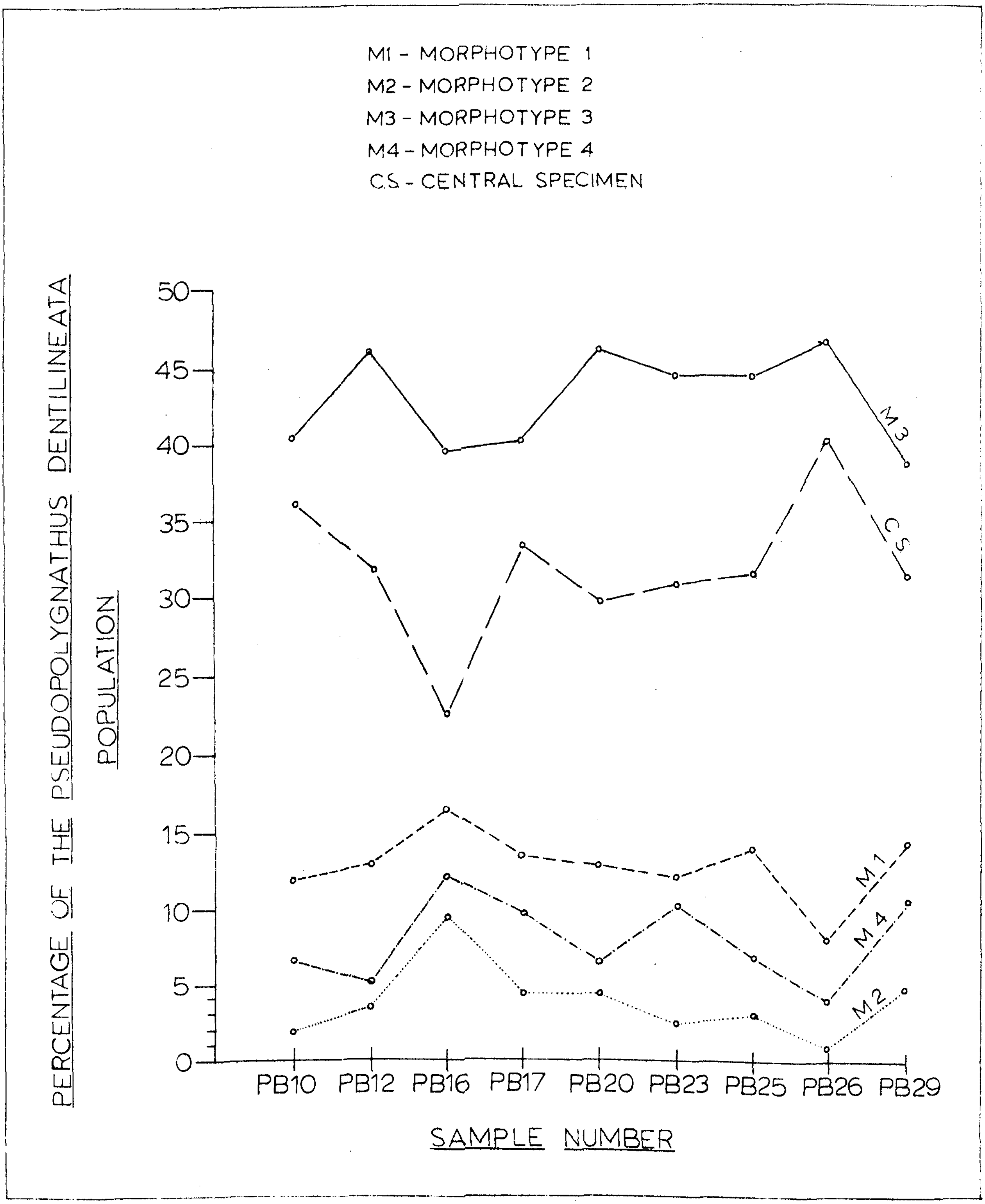
non 1947 Pseudopolygnathus multistriata Mehl & Thomas; p.16, pl.1, fig.36.

A COMPARISON OF THE RELATIVE RATES OF GROWTH OF DIFFERENT PARTS OF THE CONODONT UNIT, AS OBSERVED IN SPECIMENS OF PSEUDO-POLYGNATHUS.



1mm.=50 micrometer divisions at X5 magnification

TO SHOW THE PERCENTAGE OF THE PSEUDOPOLYGNATHUS DENTILINEATA POPULATION REPRESENTED BY EACH MORPHOTYPE AND THE CENTRAL SPECIMEN, AT HORIZONS IN THE LOWER PILTON BEDS WHERE THIS SPECIES WAS ABUNDANT



non 1966 *Pseudopolygnathus prima* (Branson & Mehl): Klapper; p.14, pl.4, fig.8.

1934 ?*Pseudopolygnathus dentilineata* E.R. Branson; p.317, pl.26, fig.22.

1957 *Pseudopolygnathus dentilineata* (E.R. Branson): Bischoff; p.50-51, pl.4, figs.29-32,34.

1959 *Pseudopolygnathus dentilineata* (E.R. Branson): Voges; p.300-301, pl.34, figs.49,50, text-fig.5, fig.2.

1962 *Pseudopolygnathus dentilineata* (E.R. Branson): Ziegler; p.99.

1934 *Pseudopolygnathus varicostata* E.R. Branson; p.318, pl.26, figs.19,20.

1939 *Pseudopolygnathus varicostata* (E.R. Branson): Cooper; p.408,409, pl.40, figs.44,45.

1934 *Pseudopolygnathus subrugosa* E.R. Branson; p.318, pl.26, fig.18.

1934 *Pseudopolygnathus projecta* E.R. Branson; p.320, pl.26, fig.10,11.

1934 *Pseudopolygnathus brevimarginata* E.R. Branson; p.322, pl.26, fig.3.

1956 *Pseudopolygnathus striata* (Mehl & Thomas): Bischoff & Ziegler; p.164, pl.11, fig.20.

1966 *Pseudopolygnathus dentilineata* (E.R. Branson): Klapper; p.14, pl.5, figs.10,11.

1967 *Pseudopolygnathus dentilineata* (E.R. Branson): Boogaert; p.185, pl.3, fig.8.

Diagnosis.

The outer side of the platform of right forms, and the inner side of the platform of left forms, are developed further anteriorly along the blade than the opposite side of the platform. The oral ornamentation consists of a row of nodes or ridges on each side of the carina. The basal cavity covers the entire width of the platform in mature specimens and has flared margins. This diagnosis is almost identical to that given by Klapper (1966), for the same species. It is used in preference to the original description of this species, from the Hannibal Formation of North America, by E.R. Branson (1934), as Branson's description does not cover the range of variation recognised in this species in the Pilton Beds. Furthermore, if it is assumed that *Spathognathodus costatus* group gave rise to *P. dentilineata* in the Hannibal Formation, and that same group produced *P. dentilineata* in the Pilton Beds, then we must consider *P. dentilineata* from these two horizons as homeomorphs. The reason for this is that their immediate ancestors are considered to be homeomorphs, (see the discussion of *Spathognathodus costatus*).

Description.

A comprehensive description of the variety of oral ornamentation which can occur within this species, has been presented in the foregoing pages. The nature of the basal cavity has also received attention with regard to its relationship in size with the maximum width of the conodont element.

The aboral surface as a whole is dominated by the large, flared, basal cavity which is located just anterior of mid-length. A prominent keel runs from the basal cavity to the anterior and posterior extremities of the unit. Owing to the position of the cavity, the anterior keel is the shorter of the two. The outer and inner sides of the basal cavity of any individual of this species are asymmetrical, but in many specimens only slightly so. The cavity edges may be smooth and sub-circular in outline, or they may show shallow folds in the cavity edge, and consequently all manner of outlines. These folds can occur on the anterior, posterior or lateral edges of the basal cavity. The second possibility occurs most frequently. In all specimens, one side of the cavity reaches fractionally further anteriorly than the other, and hence it is an asymmetrical feature. Without exception, it is the inner side of the cavity of right forms, outer side of left forms, that exhibits this anterior extension. Thus, the basal cavity of both right and left forms and individual specimens are bilaterally asymmetrical.

The junction of the basal cavity and the posterior keel is more tapered than that of the anterior junction. In juvenile forms and also a few mature specimens, the cavities are almost symmetrical and very prominently tapered to the posterior; the result is a tear-shaped basal cavity. The fact that one side of the cavity extends slightly further anteriorly is not obvious in juvenile forms.

Laterally, the element is arched in the posterior half and in the majority of specimens, (with the exception of Morphotype V, trend h) the outer side of the platform of right forms, and inner side of left, is higher relative to the carina than the opposite side of the platform. The latter feature is most obvious at the anterior end of the platform.

The anterior blade, when not disattached, marks the highest elevated in lateral view, and the blade itself has a variable outline. It ranges from triangular, through plume-like to a shape where its highest denticles occur at the anterior or posterior end of the blade with the rest of the denticles gradually falling off in height in one direction or the other. The anterior blade consists of 5 or 6 denticles which are discrete only at their tips.

The members of this species have an average ratio of 3:1 times as long as wide, and the posterior blade extends just beyond the platform in the majority of cases.

Remarks.

In the Pilton Beds, the pseudopolygnathids are not important stratigraphic zonal tools, as they occur at most horizons with no significant change.

A series of photographs indicating the growth stages and ontogenetic variability of P. dentilineata, as represented by the central specimen in

Figure 57 can be found on Plate 7 figures 4,5,6,7. Problems of identification which arise due to ontogenetic development can usually be overcome by intensive scrutiny of the juvenile individuals. A great number of specimens recovered from the Pilton Beds were incomplete in that the anterior blade was broken off. This is not considered to be any great handicap in identification.

Material studied. 1,853 specimens

Occurrence. PB.9 - F.8

Catalogue numbers of figured specimens. JW.150 - JW.171, JW.174 - JW.176

Pseudopolygnathus sp. nov.

(Pl.6, figs.8a-9c)

Diagnosis.

This species is characterised by the presence of a very small platform which is restricted to the mid-third of the unit, and by a very long posterior blade. The platform denticles attain a maximum number of 5 on the outer side of the platform of right forms, (inner side of left), while there is commonly one less denticle on the opposite side of the platform.

Description.

Orally the platform is restricted, occupying a position in the mid-third of the unit. It is as wide as long, having a sub-rounded outline. The outer side of the platform of right forms, (and the inner side of left forms), bears 3-5 large strong nodes which are restricted to the margin of the platform, a distinct furrow runs between them and the carina. The opposite side of the platform usually bears one less node, varying in number from 2-4. The latter are also restricted to the platform margin and separated from the carina by a furrow, and they are smaller in comparison to those of the opposite side.

Aborally the unit is dominated by a large basal cavity equal in width to the platform and centred just anterior of the mid-point of the conodont. The basal cavity is open and flared, and the inner side of the cavity of right forms (outer side of left forms), extends fractionally further anteriorly than the opposite side. The cavity of individuals is therefore bilaterally asymmetrical. There are prominent posterior and anterior keels running from the basal cavity, the former being the longer, and the junction of the posterior keel and the cavity is more tapered than that of the cavity and the anterior keel.

In lateral view the unit is bowed in the posterior half, and the anterior blade exhibits the greatest elevation. The anterior blade is composed of 6 denticles which are discrete only at their tips, and the blade itself is highest at mid-point, (denticles 3 & 4), falling away rapidly to the anterior, and more gradually to the posterior. There is a distinct drop in elevation where the anterior blade meets the carina. The carina rises gradually throughout its length and is virtually smooth, showing no denticulation. The nodes of the outer side of the platform of right forms (inner side of left forms), rise high above the carina, whereas those of the opposite of the platform are low on the carina. The carina itself occupies only the mid-third of the unit and then merges with the long posterior blade, which falls away in height to the posterior extremity. The posterior blade is composed of 11 or 12 denticles which are discrete only at their tips.

The unit as a whole is nearly four times as long as broad. The junction between the anterior blade and the aboral edge is approximately 90° or slightly less, and that of the posterior blade and the aboral edge is tapered.

Remarks.

This group is treated as a different species because of its restricted platform and its stratigraphic significance in the Pilton Beds. Furthermore this species is the "perfect" form of pseudopolygnathid in the suggested development this genus from *Spathognathodus aculeatus* through *Spathognathodus aculeatus nodosus*. By removing the denticles from the inner side of the platform of a right form (outer side of a left form) a 'parental' *Spathognathodus aculeatus* could be obtained.

Material studied. 18 specimens

Occurrence. PB.10 - PB.12

Catalogue numbers of the figured specimens. JW.172 - JW.173

Genus *SPATHOGNATHODUS* (Branson & Mehl, 1941)

(Fig. 66)

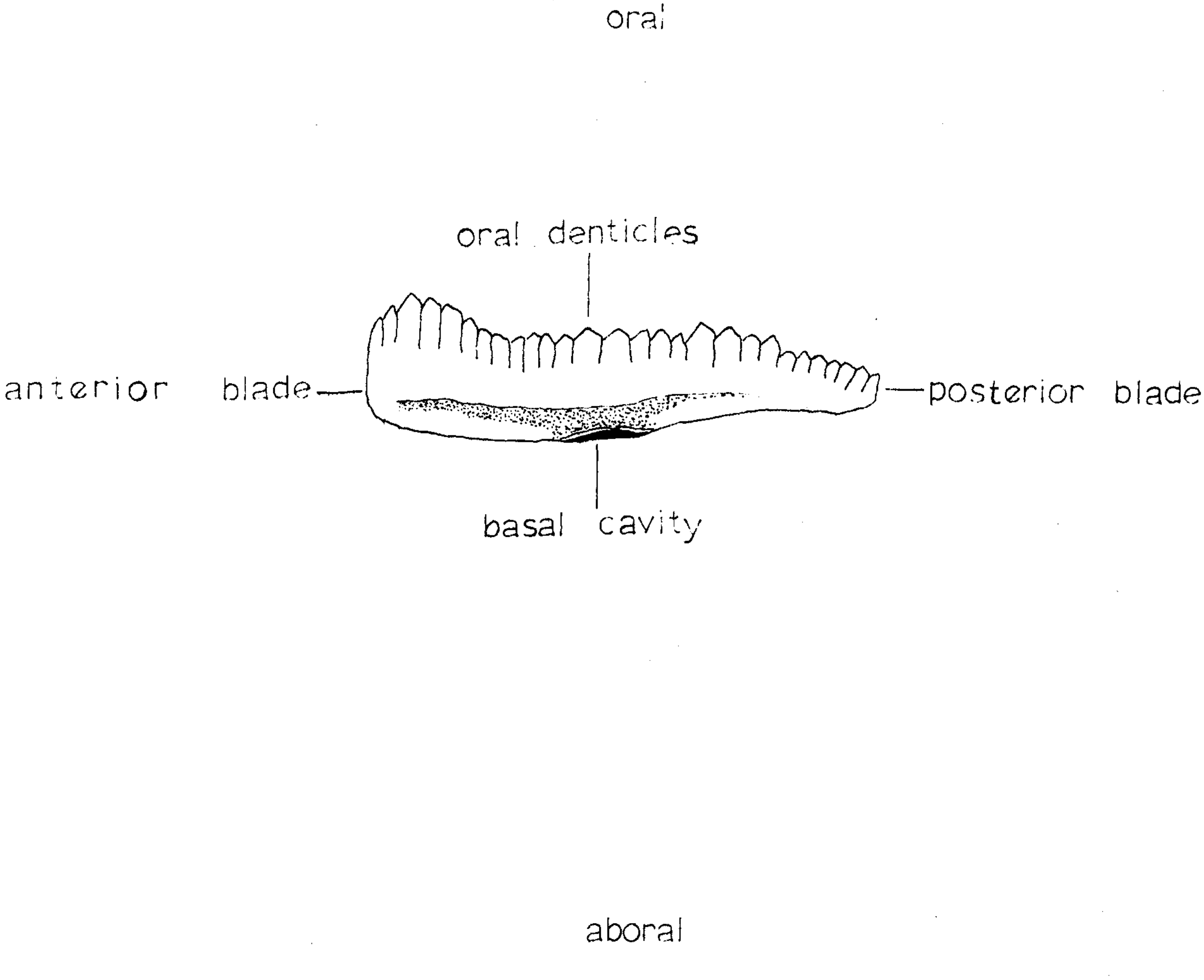
1856 *Ctenognathus* Pander, p.32 (non. Fairmaire, 1843, Soc. entomol. de France, Annales ser.2, v.1, p.13.

non 1900 *Spathodus* Boulenger, p.152.

1934 *Spathodus* Branson & Mehl, p.46.

1940 *Pandorina* Stauffer, p.428.

GENUS SPATHOGNATHODUS



1941 Spathognathodus Branson & Mehl, p.98.

1945 Mehlina Youngquist, p.363.

1959 Branmehla Hass, p.381.

1959 Ctenognathus Fay, p.195.(pro. Ctenognathus Pander).

1959 Pandorinella Hass, p.378-379.(pro. Pandorina Stauffer).

1962 Spathognathus (Bispathodus) Muller, p.114.

Type species by subsequent designation, Ctenognathus murchisoni Pander, 1856. Klapper (1966), named Spathodus primus (Branson & Mehl, 1934a as the type species.

Diagnosis.

Branson & Mehl's (1934a) original description is as follows:-

> "Compound, straight, blade-like dental units with nearly straight aboral margin, and oral margin curved or straight, but highest at or neat the anterior end. A short lateral expansion near mid-length produces on the otherwise comparitively sharp aboral edge, a cup-like expansion or navel, which ranges in shape from slightly elongate antero-posteriorly through circular to laterally elongate, either bilaterally symmetrical or asymmetrical in relation to the blade. Oral edge or crest consisting of a single row of 'germ denticles' evident in transmitted light completely sheathed to form a continuous crenulate oral edge. Oral surface of mid-length, basal expansion, or navel typically smooth, but in some species bearing one or a few separate denticles".

This genus was originally named and described by Branson & Mehl in 1934 when it was called Spathodus. However, this generic name had already been given to a group of African fish (Boulenger 1900) and consequently these conodonts were renamed Spathognathodus by Branson & Mehl in 1941. In the past there has been much confusion over the genus Spathognathodus. Stauffer (1940), introduced the genus Pandorina, but did not mention its striking similarity with Spathognathodus. Youngquist (1945), stated that his new genus Mehlina, "...resembles Spathognathodus Branson & Mehl but differs in the absence of an escutcheon ...... Also the oral surface is made up of projecting non-sheathed denticles rather than germ denticles completely sheathed...".

Some authors, notable Muller & Muller (1957), have considered Spathognathodus a junior synonym of Ctenognathus Pander (1856). These authors state also that certain species of Ctenognathus are synonymous with Mehlina sp. and Pandorina sp. (later called Pandorinellina Hass 1959). The name Ctenognathus was proposed by Pander (1856) for blade-like conodonts with a flaring sub-central cavity situated on the aboral edge. Hass (1959) and Fay (1959) noted that Ctenognathus was used in 1843 by Fairmaire for a species of Coleoptera and that this usage has priority over Pander. The name Ctenognathodus was suggested by Fay, but it was argued that Spathognathodus was now a more valid name. Now, owing to the influence and example of Rexroad (1958), Rexroad & Scott (1964), Bischoff and Ziegler (1957), and Ziegler (1961, 1962), the name Spathognathodus has been retained and is followed by most authors.

Hass (1959) proposed a new genus, Branmehla, for several species assigned to Spathognathodus and designated Spathognathodus inornata as the type species. Hass also stated that Branmehla and Spathognathodus differ in that the former has an aboral cavity toward the posterior end of the unit, and not in a sub-central position. Scott and Collinson

(1961), have included *Branmehla* in the genus *Spathognathodus* for the following reason ... "*Gnathodus* Pander has the escutcheon located at the extreme posterior end of the unit. We do not think this criterion alone is sufficient for the erection of a new genus for forms intermediate between *Spathognathodus* and *Gnathodus* and we therefore consider *Branmehla* a junior synonym of *Spathognathodus*". Rexorad & Scott (1964) confirm their agreement with Ziegler over the validity of *Spathognathodus*, and also the inclusion of *Branmehla* as one of its synonyms.

That *Spathognathodus* had given rise to many other genera was pointed out by Branson & Mehl (1934a and 1941), who stated that at more than one stage in the history of the genus there was a tendency for the migration of the aboral cavity to the posterior end of the blade. Muller (1962), also indicated that many platform genera developed from *Spathognathodus* as a result of several distinct morphological trends. The chief genera thought to be derived from *Spathognathodus* are:-

1. *Gnathodus*, derived by an increase in size, and a posterior migration, of the basal cavity.
2. *Polygnathus*, by the development of a posterior platform, illustrated by faunas from the Saverton of North America.
3. *Bactrognathus*, Rexroad & Scott (1964), suggest that *Spathognathodus* is the precursor of this genus.
4. *Pseudopolygnathus*, by the addition of denticles either side of the carina. The development can be seen in the Upper Devonian of Germany and Britain, including the Pilton fauna. (In the present study *Spathognathodus* and *Pseudopolygnathus* are distinguished by the number of denticles on the inner side of right forms or the outer side of left forms. If there is only a single node in this position the specimen is called *Spathognathodus aculeatus nodosa* (new subspecies),

if more than one, then it is called a pseudopolygnathid.

5. *Scaphignathus*, possibly developed from *Spathognathodus* (Austin 1965).
6. New genus B, developed from *Spathognathodus* (Austin 1965).
7. *Icriodus*, *Taphrognathus*, *Idiognathus* & *Ctenopolygnathus* are all suggested by Hass (1959) as probable descendents of *Spathognathodus*.

Spathognathodus aculeatus aculeatus Branson & Mehl, 1934

(Pl.1, figs.1a-3c; Pl.4, figs.7a-7c)

1934 *Spathodus aculeatus* Branson & Mehl; p.186, pl.17, figs.11,14.

non 1934 *Spathodus sulciferus* Branson & Mehl; p.274, pl.22, figs.12,13

non 1934 *Spathodus sulciferus* Branson & Mehl: E.R. Branson; p.304, pl.27, figs.15,20,22.

1934 *Spathodus duplidens* Huddle; p.91, pl.12, figs.1-4.

non 1934 *Spathodus tridentatus* E.R. Branson; p.307, pl.27, fig.26.

1947 *Spathognathodus aculeatus* (Branson & Mehl): Hass; p.134,135,140.

non 1955 *Spathognathodus tridentatus* (Branson E.R.): Sannemann; p.331, pl.24, fig.13.

1956 *Spathognathodus aculeatus* (Branson & Mehl): Hass; p.17,22,24.

non 1956 *Spathognathodus tridentatus* (E.R. Branson): Bischoff & Ziegler; p.167, pl.13, figs.1,2.

1958 *Spathognathodus aculeatus* (Branson & Mehl): Klapper; p.1091, pl.141, fig.13.

1959 *Spathognathodus aculeatus* (Branson & Mehl): Helms; p.657, pl.3, Fig.8.

non 1959 *Spathognathodus tridentatus* (E.R. Branson): Helms; p.658, pl.3, fig.7.

1961 *Spathognathodus aculeatus* (Branson & Mehl): Ethington, Furnish & Wingert; p.766-767, pl.90, figs.5,9.

non 1961 *Spathognathodus tridentatus* (Branson E.R.): Freyer; p.89, pl.6, fig.150.

1962 *Spathognathodus aculeatus* (Branson & Mehl): Ziegler; p.105-106, pl.13, figs.27-36.

non 1962 Spathognathodus tridentatus (E.R. Branson): Ziegler; p.3, pl.3, fig.8,9 (preprint 1960).

non 1962 Spathognathodus sulciferus (Branson & Mehl): Ziegler; p.3, pl.3, fig.7, (preprint 1960).

? 1962 Spathodus (Bispathodus) aculeatus (Branson & Mehl): Muller; p.114.

1965 Spathognathodus aculeatus (Branson & Mehl): Bouckaert & Ziegler; p.17, pl.5, figs.1-4.

1966 Spathognathodus aculeatus (Branson & Mehl): Klapper; p.24, pl.6, figs.15-17.

1967 Spathognathodus aculeatus (Branson & Mehl): Boogaert; p.186, pl.3, figs.15-17.

1967 Spathognathodus aculeatus (Branson & Mehl): Wolska; p.425, pl.19, figs.4-8.

non 1969 Spathognathodus plumulus plumulus Rhodes, Austin & Druce; p.229, pl.1, figs.1a-2c,5,6.

Klapper (1966), states that forms referred to as Spathognathodus tridentatus E.R. Branson do not differ sufficiently from Spathognathodus aculeatus to warrant recognition as a separate species. The present author agrees that forms called Spathognathodus tridentatus which occur in the Upper Devonian with Spathognathodus aculeatus, are indeed very similar to the latter. However, the forms which E.R. Branson originally called Spathognathodus tridentatus from the Hannibal Formation (Lower Carboniferous) must remain as a separate species, as present day evidence indicates that these forms are homeomorphs of Spathognathodus aculeatus.

Diagnosis.

Straight or gently curved unit with 2-5 lateral denticles in the anterior part of the mid-third of the element, which are incorporated into the oral surface. (Klapper (1966) states, that some specimens of S. aculeatus may have as many as seven lateral denticles.) The outline of the anterior blade is variable in shape. The bilaterally symmetrical aboral cavity is tear-shaped or sub-circular and is situated in the mid-third of the element.

Description.

In oral view the unit is straight or only gently curved, the curvature of the blade being diagnostic of whether the unit is a right or left form.

The anterior blade can have a variable outline and is composed of 4-6 denticles. The blade is high relative to the rest of the unit; the highest denticle may occur in several positions, (see Figures 67 a,b,c.).

(a) It may be central and vertical with the rest of the blade sloping away anteriorly and posteriorly, thus giving the blade a triangular outline.

(b) The highest denticle may be the most posterior of those of the anterior blade, in which case the denticles are nearly verticle, making an angle of 90° with the oral surface (as in type (a)).
The angle between the anterior margin of the anterior blade, and the margin of the aboral surface is variable in all types, (a), (b) & (c).)

(c) A few specimens show an anterior blade which has its most anterior denticles as the highest, and the remainder of the denticles of the blade slope away posteriorly, merging into the middle blade. Here the angle between the anterior edge of the anterior blade and the aboral edge of the unit as a whole is a right angle.

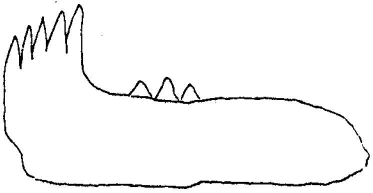
The posterior blade is composed of 8-10 denticles which are discrete only at their tips, and which are smaller than the denticles of the anterior blade. Invariably these posterior denticles are highest anteriorly,

FIGURE 67

VARIATION IN THE OUTLINE OF THE ANTERIOR BLADE OF SPATHOGNATHODUS ACULEATUS

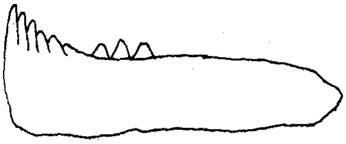
(a)

Spathognathodus aculeatus aculeatus



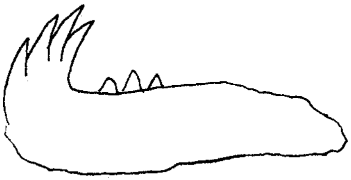
(b)

Spathognathodus aculeatus aculeatus



(c)

Spathognathodus aculeatus aculeatus



(d)

Spathognathodus aculeatus plumulus

becoming lower and smaller posteriorly.

The mid-third of the unit incorporates 2-5 lateral denticles into the oral surface. The blade or carinal denticles in this region are all fused, except in one or two specimens, but the lateral denticles are usually discrete. In some cases the lateral denticles are more ridge-like, in that they reach the carina and form a definate lateral platform. Other specimens show a distinct furrow between the carina and the lateral denticles, and, as a result a lateral platform is not such an obvious feature. If there are only two or three lateral denticles they occur parallel to the carina; if there are five they occur in a semi-circular or bow shaped pattern against the carina; if there are four, then they may occur in either of these two ways.

In lateral view the unit may be straight, although it is more often bowed in the posterior half. This bowing explains in part the way in which the denticles of the posterior blade slope down posteriorly.

In aboral view, the basal cavity occurs in the mid-third of the unit and is large and flared. Most of the specimens have a cavity which is widest at its mid-point, rounded anteriorly and slightly tapered posteriorly. A few mature specimens show a more tear-shaped cavity as a result of antero-posterior elongation. The juvenile forms of this species all have large flared cavities which are more open than those of their descendents, and which embrace a greater postion of the aboral surface. The aboral pit itself occurs in the anterior region of the flared cavity in mature specimens, and is small and slit-like. The pit of the juveline forms is much larger relative to the cavity.

This species is bilaterally asymmetrical, as the lateral denticles of right forms occur on the outer side, and those of left forms occur on the inner side. Thus a right form is not a mirror image of a left form. Right and left forms are recognised by the curvature of the axis of the individual specimen.

Remarks.

This species is distinguished by the presence of 2-5 lateral denticles on one side of the axis in the central third of the unit. However, as has been shown, the remainder of the element can show slight variation especially in the region of the anterior blade and basal cavity. Klapper (1958), states that Branson & Mehl compared *Spathognathodus aculeatus* with *Spathognathodus sulciferus*, but they noted that *Spathognathodus sulciferus* had a thicker blade and longer navel. The author agrees and acknowledges that these two forms are not conspecific for the same reason that *Spathognathodus aculeatus* and *Spathognathodus tridentatus* (from the Hannibal Formation) cannot be conspecific, but are homeomorphs (see p.203). There is also some further confusion concerning *Spathognathodus sulciferus*, in that two photographs (Branson & Mehl 1934b, pl.22, fig.13 and Branson E.R. 1934, pl.27, fig.20) designated as *Spathognathodus sulciferus* are more similar to *S. costatus spinulicostatus* than to *S. aculeatus*.

Certain specimens from the Pilton Beds exhibit a plume-like anterior blade and are identical to specimens from the Avon Gorge, illustrated by Rhodes, Austin & Druce 1969, which they named *S. plumulus plumulus*. All the spathognathodids recovered from the Avon Gorge displayed this feature, and Rhodes, Austin and Druce cited the plume-like blade and more elongate tear-shaped cavity as the morphologic features which distinguished *S. plumulus* from *S. aculeatus* (Branson & Mehl). Specimens from the Pilton Beds, which have this anterior plume, can display either type of cavity, tear-shaped or the more typical sub-circular cavity of *S. aculeatus*.

It is difficult to agree that the Avon Gorge spathognathodids should warrant a new specific name on the basis of these small differences, but maybe there is a case for sub-specific distinction. The specimens of *S. aculeatus*, from the Pilton Beds and the Avon Gorge, which have a plume-like anterior blade should be called *Spathognathodus aculeatus plumulus*, and those from the Pilton Beds without this characteristic, *Spathognathodus aculeatus aculeatus*. The one problem that does arise is that *S. aculeatus* aculeatus of the Pilton Beds would become synonymous with *S. aculeatus* of of Europe and the North American continent. It is believed that *S. aculeatus* plumulus developed from *S. aculeatus aculeatus* in the uppermost Devonian.

Material studied. 139 specimens.

Occurrence. PB.2 - PB.35

Catalogue numbers of the figured specimens. JW.100, JW.101, JW.102, JW.145

Spathognathodus aculeatus nodosus (Rhodes, Austin & Druce, 1969)
(Pl.2, figs.8a-11c; Pl.3, figs.1a-c)

1969 *Spathognathodus plumulus nodosus* Rhodes, Austin & Druce, p.230, pl.1, figs.3a-4c.

Diagnosis.

This subspecies is identical to *Spathognathodus aculeatus* except that it possesses a single node on the opposite side of the blade to the main group of denticles.

Description.

In lateral view the unit is straight or slightly curved. If curved, it is the posterior half of the aboral edge which shows this curvature, the anterior half being straight. The oral edge is denticulate with twenty or more fused denticles, discrete only at their tips. The anterior third of the blade is higher than the rest and the denticles are larger, but still almost entirely fused. The mid-third of the blade is lower and straight, while the posterior third slopes down gradually to the posterior extremity. The anterior blade can assume a variety of shapes from triangular to plume-like.

Orally the element is straight or only gently curved, so that in most cases it is difficult to determine right and left forms. However, this sub-species appears to be bilaterally asymmetrical, the single node occurring on the inner side in right forms and on the outer side in left forms. The number of lateral denticles on the opposite side of the blade is usually 3-5, although one specimen has 6. The single node occurs centrally on the oral expansion of the basal cavity, although an exception to this is seen when it is found on the posterior edge of this expansion. Relative to the row of lateral denticles on the other side of the blade, the node occurs approximately opposite the mid-point. A few or all of the lateral denticles attain the same height as the blade denticles, but the single node is always much lower than the blade. Smaller forms, assumed to be juveniles, show only a very small projection on the side of the blade, whereas mature specimens have a distinct gap between the blade and the node.

The basal cavity is situated in the mid-third of the unit and is sub-circular, rounded anteriorly and tapered posteriorly. In more mature forms with a well developed node, that side of the cavity aboral to the node is expanded, so that the usually sub-circular outline is distorted.

Remarks.

This sub-species is believed to have enolved from *S. aculeatus* s.s. by the addition of a single node on the opposite side of the blade from the main group of lateral denticles. It is particularly significant in the Lower Pilton fauna as it appears to be the intermediate form through which the genus *Pseudopolygnathus* developed from *Spathognathodus* *S. aculeatus nodosus* is taken as the penultimate stage in the development of *Spathognathodus* before it gave rise to *Pseudopolygnathus*, and thus all those forms with more than one denticle on this side of the blade are considered as members of the latter genus. The ultimate stage is represented by *S. aculeatus nodosus* which bears a ridge posterior to the single node. It is of course a point of conjecture as to whether or not such forms as these should in fact be called spathognathodids or pseudopolygnathids. A more detailed description of this possible transition is included in the description of the genus *Pseudopolygnathus* (p. 178).

The majority of these specimens from the Pilton Beds were incomplete, lacking the anterior and/or posterior blades.

Material studied. 15 specimens

Occurrence. PB.2 - PB.27

Catalogue numbers of the figured specimens. JW.115, 116, 117, 146, 137

Spathognathodus aculeatus plumulus (Rhodes, Austin & Druce, 1969)

(Pl.1, figs.4a-8c)

non 1934 *Spathodus irregularis* E.R. Branson; p.307, pl.27, fig.25

non 1934 *Spathodus aculeatus* Branson & Mehl; p.186, pl.17, figs.11,14

?non 1949 *Spathognathodus irregularis* (E.R. Branson); Thomas; p.412, pl.2, fig.32.

non 1962 *Spathognathodus sulciferus* (E.R. Branson); Ziegler; p.3, pl.3, fig.7.

non 1962 *Spathognathodus tridentatus* (E.R. Branson): Ziegler; p.3, pl.3, figs. 8,9.

non 1962 *Spathognathodus aculeatus* (Branson & Mehl): Ziegler; p.105-106, pl.13, figs.27-36.

1965 *Spathognathodus plumula* Austin; p.358, pl.1, figs.14-23,26,27.

1969 *Spathognathodus plumulus plumulus* Rhodes, Austin & Druce; p.229, pl.1, figs.1a-2c,5,6.

Diagnosis.

Straight or gently curved unit with 2-5 lateral denticles in the mid-third of the element. The outline of the anterior blade in lateral view is plume-like. The aboral cavity is tear-shaped or sub-circular in outline and is situated in the mid-third of the element also.

Description.

The description ofthis sub-species is identical to that of *S. aculeatus aculeatus* except for the nature of the anterior blade. Figure 67d illustrates the plume-like anterior blade which characterises these forms. The highest denticle of the blade is commonly the second from the posterior end, and all the denticles are inclined posteriorly, making an angle of 70°-80° with the oral edge of the middle blade; this gives a plume-like outline typical of forms such as *Scaphignathus*. The blade denticles to the anterior of the highest denticle decrease fairly rapidly in height toward the anterior margin.

Remarks.

These specimens are identical to S. plumulus plumulus Rhodes, Austin & Druce (1969). For reasons cited earlier it is suggested that the name S. aculeatus plumulus be used in preference to the name given to these forms by Rhodes et al. S. aculeatus plumulus is distinguished from S. aculeatus aculeatus by the shape of the anterior blade. This subspecific distinction preserves the stratigraphic usefulness of both groups and yet also indicates their genetic affinities and morphologic similarities.

Material studied. 44 specimens

Occurrence. PB.2 - PB.27

Catalogue numbers of the figured specimens. JW.103-JW.106, JW.136

Spathognathodus anteposicornis Scott, 1961

(Pl.1, figs.9a-9c; Pl.2, figs.1a-3c)

1961	Spathognathodus n.sp. A. Scott & Collinson; p.132, pl.1, figs.12-15.
1961	Spathognathodus anteposicornis Scott; p.1224, fig.2h-k.
1965	Spathognathodus anteposicornis (Scott); Austin; p.339, pl.4, figs.22a,b.
1969	Spathognathodus anteposicornis (Scott): Rhodes, Austin & Druce; p.442, pl.3, figs.5a-8b.

Diagnosis.

Scott & Collinson's (1961) original description was as follows; "This distinctive species of Spathognathodus is characterised by the presence of a single, well-developed lateral denticle on the inner side of the unit immediately anterior to the escutcheon." Later Scott (1961) named the species Spathognathodus anteposicornis.

Description.

The unit is 2 to 2.5 times as long as high and straight or only slightly bowed laterally. In lateral view the oral surface in the mid-third is straight, rising abruptly to the anterior and falling away gradually to the posterior. The denticles of the oral surface are fused for the greater part of their length, only their tips being discrete. The anterior third of the blade is the highest, bearing 4 denticles, the third from the anterior edge being the largest. A single horn-like lateral denticle is developed on the inner side of the blade, immediately anterior to the basal cavity. The basal cavity is situated in the mid-third of the unit and is widely flared, (relative to the thickness of the blade itself), slightly longer than wide, and the lips of the cavity are also flared. The only difference observed between the Pilton specimens and those from the Louisiana Limestone Formation, (Scott, 1961; Scott & Collinson, 1961), is that the denticles comprising the anterior blade of the Pilton forms are higher and more acutely curved posteriorly, giving a plume-like outline.

Orally the unit is straight or only gently bowed, and therefore it is difficult to differentiate right and left forms.

Remarks.

This species is characteristic of the Gnathodus n.sp.A Assemblage Zone of North America, and common in the conodont faunas of the Louisiana Limestone Formation, (Collinson, Scott & Rexroad, 1962, p.17-19). Scott (1961) noted that faunas from the overlying Glen Park and Hannibal, and the underlying Saverton Formations contain spathognathodids with one lateral denticle, but these forms do not have the denticle to the anterior of the basal cavity. Austin (1965), first recorded the occurrence of *Spathognathodus anteposicornis* in Western Europe, in the Carboniferous rocks of the Avon Gorge. However, in the Avon Gorge, the species is not confined to the horizons equivalent to the *Gnathodus* n.sp.A Assemblage Zone of North America. This is explained by the belief that a number of straight bladed spathognathodids developed a lateral denticle, anterior to the basal cavity, and that this development took place at many stratigraphical horizons. The Pilton and Avon Gorge specimens of this species also differ slightly in that the anterior blades of the former are more plume-like.

Material studied. 6 specimens

Occurrence. PB.2 & PB.23

Catalogue numbers of the figured specimens. JW.107 - JW.109, JW.140

Spathognathodus costatus group

Spathognathodus costatus was first described by E. R. Branson (1934) from the Hannibal Formation where it was originally called *Spathodus costatus*. The species was diagnosed thus:

> "On the inner side of the blade there is a row of about 8 denticles, some short and peg-like, others broad and formed by the union of two peg-like ones to give the blade, in superior view, a cross-ridged rather than a denticulate appearance".

EVOLUTION OF SPATHOGNATHODUS COSTATUS

To fully understand the development of this species, a resumé of its position in the evolutionary pattern of the spathognathodids is required. Throughout the Upper Devonian and Lower Carboniferous, Spathognathodus costatus has been identified at several horizons. In West Germany, Ziegler (1962) noted the occurrence of Spathognathodus costatus in the toVI Wocklumeria Zone of the Upper Devonian. In this zone he described an evolutionary sequence from Spathognathodus aculeatus to Spathognathodus costatus by the development of more lateral denticles, on the same side of the blade. Ziegler also subdivided Spathognathodus costatus into three sub-species; Spathognathodus costatus costatus, (renamed Spathognathodus bischoffi Rhodes, Austin & Druce, 1969), Spathognathodus costatus spinulicostatus, (renamed Spathognathodus ziegleri Rhodes, Austin & Druce, 1969), and Spathognathodus costatus ultimus, and showed that the evolutionary sequence was continued through these sub-species terminating in Spathognathodus costatus ultimus.

In North America, E.R. Branson (1934) described Spathognathodus costatus from the Hannibal Formation (Lower Mississippian) and Austin (person communication) reports seeing forms identical to Spathognathodus costatus costatus Ziegler (Spathognathodus bischoffi), from the Saverton Formation at Atlas South, North America, Upper Devonian. Austin (1965), also describes Spathognathodus costatus from the Upper K and Lower Z Zones of the Lower Carboniferous of the Avon Gorge. Spathognathodus costatus is also recorded from the Lower Pilton Beds and these beds are interpreted as youngest Wocklumeria Zone age, equivalent to the Upper costatus Zone of Germany. Therefore, Spathognathodus costatus occurs at two stratigraphic levels; in the Wocklumeria Zone of the Upper Devonian, and in the Lower Mississippian (see Figure 68).

Like Ziegler, Austin (1965) saw an evolutionary sequence in the spathognathodids from the Avon Gorge. The sequence ran from a straight bladed spathognathodid through *Spathognathodus plumula* (herein renamed *Spathognathodus aculeatus plumulus*) to *Spathognathodus costatus*.

In the Hannibal Formation of North America, an evolutionary sequence can also be identified, from a straight bladed spathognathodid through *Spathognathodus tridentatus* and/or *Spathognathodus sulciferus*, to *Spathognathodus costatus*. (Two published photographs of *Spathognathodus sulciferus* (Branson & Mehl, 1934b, pl.22, fig.13; and E.R. Branson, 1934 pl.27, fig.20), are identical to *Spathognathodus spinulicostatus* (E.R. Branson).) The latter species has now been renamed *Spathognathodus costatus sulciferus* Rhodes, Austin & Druce, 1969.

By the addition of lateral denticles on the opposite side of the blade these sequences can be carried a stage further.

(a) In the Lower Z of the Avonian, *Spathognathodus spinulicostatus* (*Spathognathodus costatus sulciferus*) developed from *Spathognathodus costatus*.

(b) In the Hannibal Formation of North America, the *Spathognathodus spinulicostatus* of E.R. Branson (*Spathognathodus costatus sulciferus*), developed from *Spathognathodus costatus*. Unfortunately, Branson (1934) does not give the stratigraphic ranges for these species in his publication.

(c) Ziegler noted the development of *Spathognathodus costatus spinulicostatus* (*Spathognathodus ziegleri*) from *Spathognathodus costatus costatus* (*Spathognathodus bischoffi*) in the toVI *Wocklumeria* Zone of West Germany.

THE EVOLUTION OF SPATHOGNATHODUS COSTATUS GROUP IN THE UPPER DEVONIAN AND LOWER CARBONIFEROUS OF WESTERN EUROPE AND NORTH AMERICA

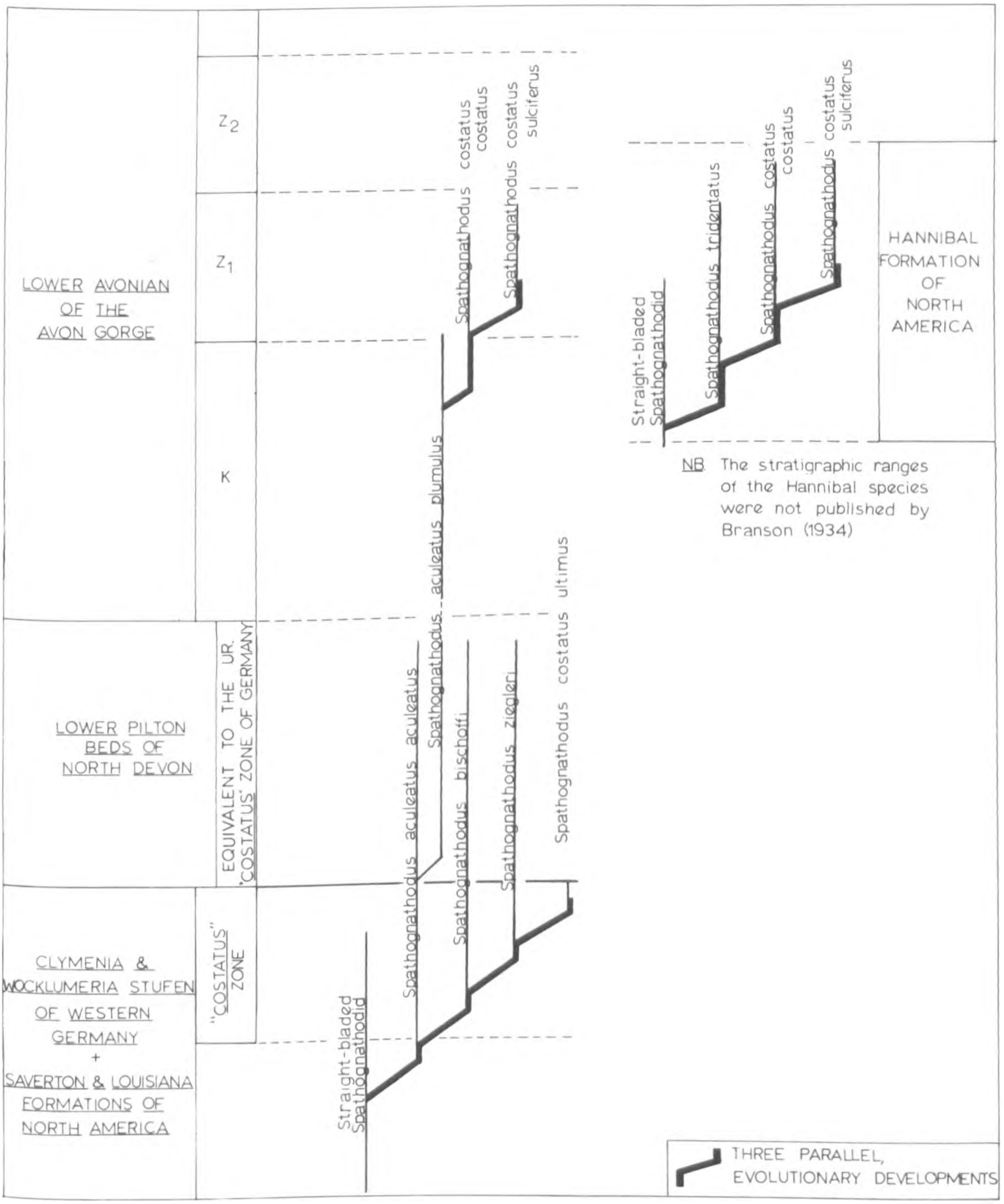


FIGURE 68

In the Lower Pilton Beds, *Spathognathodus aculeatus*, *Spathognathodus bischoffi* and *Spathognathodus ziegleri* have been identified, although here all three forms occur at the same horizons and hence there is no obvious evolutionary sequence observed.

Voges (1959, p.296, fig.4; p.297, fig.5), considered there to be a second evolutionary trend whereby *Pseudopolygnathus dentilineata* developed from *Spathognathodus costatus*, in the lower CuI Zone of the Carboniferous of Saurland. Branson & Mehl (1934), also considered a series of their specimens from the Bushberg Sandstone to be transitional between *Spathognathodus* and *Pseudopolygnathus*. Austin (1965), recorded three developments of *Pseudopolygnathus* in the Avon Gorge, and stated that all three originated from straight bladed spathognathodids with lateral denticles.

A similar development between *Spathognathodus* and *Pseudopolygnathus* is found in the Pilton Beds of North Devon, but once again it is less obvious than in the localities mentioned above. Nevertheless, a new subspecies, *S. aculeatus nodosus*, has been erected as an intermediate between *Spathognathodus aculeatus* and *Pseudopolygnathus dentiliniata*.

It has been shown the *Spathognathodus costatus* has developed at several periods during the Upper Devonian and Lower Carboniferous, and the results of these developments are recognised as homeomorphs. It has been concluded that the *Spathognathodus costatus* of the Hannibal, Avon Gorge and *Wocklumeria* Zone are similar but unrelated, as they have different ancestries. This also implies that *Spathognathodus tridentatus*, *Spathognathodus aculeatus* and *Spathognathodus plumula* are homeomorphs.

Straight bladed spathognathodids developed lateral denticles at many stratigraphic levels, e.g.

(a) *Spathognathodus aculeatus* in the Upper Devonian of North America (Grassy Creek Shale-Branson & Mehl, 1934c; Saverton Formation - Collinson, Scott & Rexroad, 1962).

(b) *Spathognathodus aculeatus* in the Upper Devonian of West Germany (*Wocklumeria* toVI-Ziegler, 1962; Bischoff,1957), and in the Upper Devonian of Great Britain (Pilton Beds - Present Study).

(c) *Spathognathodus plumula* in the Lower Carboniferous of Great Britain (Avon Gorge - Austin,1965).

(d) *Spathognathodus tridentatus* & *Spathognathodus sulciferus* in the Lower Mississippian of North America. (Hannibal Formation - Branson, 1934).

(e) *Spathognathodus tridentatus* & *Spathognathodus sulciferus* in the Upper Devonian of Germany (Ziegler, 1962c (preprint 1960); Helms, 1959).

In the Pilton Beds both the *Spathognathodus aculeatus plumulus* and *Spathognathodus aculeatus aculeatus* development occurs. The result of the investigation conducted in the Lower Pilton Beds indicate that these two forms are very similar but simply distinguished. The fact that both occur together suggests that *Spathognathodus aculeatus plumulus* evolved from *Spathognathodus aculeatus aculeatus* and hence is not its homeomorph but its direct descendent. Since the range of *Spathognathodus aculeatus plumulus* must be extended down into the Upper Devonian, there is now no gap between the extinction of *Spathognathodus aculeatus* Branson & Mehl and development of *Spathognathodus plumula* Austin and consequently no grounds to consider them as products of two isolated developments. The recognition of the two forms as subspecies, acknowledges the slight differences between the two and preserves their stratigraphic significance.

Klapper (1966) considers *Spathognathodus aculeatus* as a synonym of *Spathognathodus tridentatus*. However, the present author believes *Spathognathodus tridentatus* from the Hannibal formation to be a near-homeomorph of *Spathognathodus aculeatus*.

The slight differences which occur between the forms discussed above can be summarised as follows:

(a) *Spathognathodus plumula* (*Spathognathodus aculeatus plumulus*) has a plume-like anterior blade.

(b) *Spathognathodus tridentatus* has a narrower basal cavity than *S. aculeatus* (*S. aculeatus aculeatus*).

The same discussion that was applied to *Spathognathodus aculeatus* applies to *S. costatus* and *S. spinulicostatus* (*S. costatus sulciferus*).

S. bischoffi and *S. ziegleri* from the Pilton Beds are the same as those found by Ziegler in West Germany. The fact that these two species are not found in the Lowermost K of the Avon Gorge may be due to one of two factors. Firstly, this may be due to the fact that only a few individuals of these species represented the lineage in the Lower K, before they became more common in the Upper K and Lower Z, and that sampling has not revealed them. Secondly, the representatives of these species are not the same stock as the forms similar to them in the Upper K, and that the forms in the Upper K developed independently from *Spathognathodus plumula* (*S. aculeatus plumulus*) after the extinction of *S. bishoffi* and *S. ziegleri*, as was suggested by Austin (1965).

The second hypothesis is prefered, the names *S. costatus* and *S. costatus sulciferus* being attributed to the Upper K forms, which are considered homeomorphs of *S. bischoffi* and *S. ziegleri*. There are morphological differences between these forms and consequently they are not homeomorphs in the true sense of the word, but rather near-homeomorphs. However, it is further proposed that the *S. costatus* development in the Hannibal Formation origninated from yet another independent source, *S. tridentatus*, and the resultant forms, which are identical to the Upper K forms, are true homeomorphs of the *Spathognathodus* development in the Avon Gorge.

All three independent developments of forms previously all called *S. costatus* has caused some confusion for the simple reason that they had the same specific name. This problem has been remedied in part by Rhodes, Austin & Druce (1969) in that they have proposed the new specific name *S. bischoffi* for the Upper Devonian forms.

Spathognathodids which may have initiated these evolutionary developments include *S. crassidentatus*, *Spathognathodus aciedentatus* and *S. strigosus*. *S. anteposicornis*, which is common in the Louisiana Limestone and is also found in the Pilton Beds and the Avon Gorge, is believed to be a further intermediate form (in the Upper Devonian evolutionary sequence) between the original straight bladed spathognathodid and *S. aculeatus*.

Spathognathodus bischoffi Rhodes, Austin & Druce, 1969

(Pl.2, figs.4a-7c)

non 1934 *Spathodus costatus* E.R. Branson; p.303, pl.27, fig.13.
? 1938 *Spathodus costatus* (E.R. Branson): Branson & Mehl; pl.33, fig.1.
non 1949 *Spathognathodus costatus* (E.R. Branson): Thomas; pl.4, fig.10.
1956 *Spathognathodus costatus* (E.R. Branson): Bischoff & Ziegler; p.166, pl.13, fig.3.

1957 *Spathognathodus costatus* (E.R. Branson): Bischoff; p.56, pl.4, fig. 28.

1957 *Spathognathodus costatus* (E.R. Branson): Flugel & Ziegler; pl.1, figs.15,18.

1959 *Spathognathodus costatus* (E.R. Branson): Helms; pl.3, figs.2-4.

? 1959 *Spathognathodus* cf. *S. costatus* (E. R. Branson): Voges; p.296,297, pl.34, figs.47,48.

1962 *Spathognathodus costatus costatus* Ziegler; p.107, pl.4, figs.1-6,8-10.

? 1964 *Spathognathodus costatus costatus* (Ziegler): Higgins, Wagner-Gentis & Wagner; pl.5, fig.21.

non 1965 *Spathognathodus costatus* (E.R. Branson): Austin; p.350, pl.1, fig.11; pl.2, fig.6,7,9; pl.4, figs.10a,b,15, 16,23.

1967 *Spathognathodus costatus costatus* (E.R. Branson): Wolska; p.426, pl.19, figs.9-12.

1967 *Spathognathodus costatus* (E.R. Branson); *S. costatus costatus* (Ziegler); van Adrichem Boogaert; p.186, pl.3, figs.20,22a.

1969 *Spathognathodus bischoffi* Rhodes, Austin & Druce; p.223, pl.4, figs.1a-4c.

Diagnosis.

This spathognathodid has a parallel row of lateral denticles, developed one one side of the blade, from the middle of the anterior half to the posterior extremity. These denticles may occur as transverse ridges, uniting with the blade. The basal cavity is elongate and usually subcircular; it is rounded anteriorly and pointed posteriorly. The cavity is located in the posterior two-thirds of the unit.

Description.

In lateral view this spathognathodid is straight or only gently bowed, and if bowed then it is the posterior portion of the unit which shows this feature, the anterior portion being straight. The anterior blade is the highest part of the specimen, comprising 3-4 distinct denticles. From the anterior, the unit slopes down to the mid-third, where it is straight, and then slopes down again to the posterior tip.

In oral view the blade is seen to be curved and it consists of 12 to 20 denticles (depending on the size of the specimen), all of which are fused except for those 3 or 4 comprising the anterior blade, and these are discrete only at their tips. A row of lateral denticles is developed on one side of the blade (outer side of right forms, inner side in left forms) running parallel with the blade for approximately three-quarters of its length. The denticles occur from a point coinciding with the posterior end of the anterior blade, to the posterior extremity of the unit. The number of lateral denticles ranges from 8 to 15, and they can occur as isolated nodes, transverse ridges, or a combination of both. Transverse ridges are most common in the larger specimens, giving a rib-like effect to the unit. When this ribbing is developed, the individual ribs are longest at mid-length.

The basal cavity is large and elongate, rounded anteriorly and pointed posteriorly. It is asymmetrical, the outer edge of the cavity showing a distinct fold, whereas the inner edge tapers gradually from the anterior to the posterior. One exception to this general rule is seen, and in this specimen the cavity is subrounded, and restricted to the mid-third. Juvenile forms do not show clearly, this characteristic basal cavity.

Remarks.

A detailed discussion of S. costatus has been given earlier (p.213). S. costatus costatus Ziegler, has been renamed S. bischoffi by Rhodes, Austin & Druce, and this underlines the slight differences between S. costatus Branson, and the near-homeomorphic S. costatus costatus Ziegler.

Material studied. 27 specimens

Occurrence. PB.10 - PB.36

Catalogue numbers of the figured specimens. JW.111-JW.113, JW.149

Spathognathodus strigosus (Branson & Mehl, 1934)

(Pl.3, figs.2a-7c)

1934 *Spathodus strigosus* Branson & Mehl; p.187, pl.17, fig.17.

1949 *Spathognathodus strigosus* (Branson & Mehl): Thomas; pl.4, fig.15, pl.2, fig.19.

non 1949 *Spathognathodus strigosus* (Branson & Mehl): Thomas; pl.2, fig.21.

1956 *Spathognathodus strigosus* (Branson & Mehl): Bischoff & Ziegler; p.167, pl.13, fig.15.

1962 *Spathognathodus strigosus* (Branson & Mehl): Ziegler; p.111-112, pl.12, figs.21-23.

1965 *Spathognathodus strigosus* (Branson & Mehl): Austin; p.376-377, pl.2, fig.10.

1965 *Spathognathodus strigosus* (Branson & Mehl): Bouckaert & Ziegler; pl.5, fig.8.

1967 *Spathognathodus strigosus* (Branson & Mehl): Wolska; p.428, pl.XVIII, figs.9-15

Diagnosis.

A straight-bladed spathognathodid with oral denticles of the same height for approximately half its length, but lower at the posterior end and distinctly higher at the anterior end of the blade. The posterior half of the aboral edge is prominently arched. The basal cavity is long and narrow centred on a point just anterior of mid-length.

Description.

Laterally the blade (which is 2 to 2.5 times as long as high) has a distinctive outline. The oral margin is dominated by three or sometimes four high anterior denticles. The oral denticles of the blade posterior to these are lower and attain an approximately equal elevation, apart from those in the posterior quarter which slope downward to the posterior extremity. The number of oral denticles ranges from sixteen to twenty-four, and all, including those of the high anterior postion, are fused for the greater part of their length, only their tips being discrete.

The aboral edge is straight from the anterior margin to a point just anterior of mid-length, it then arches to the posterior tip. The anterior margin and aboral margin meet at right angles.

In oral view the blade is thin and straight but occasionally it is gently curved.

The basal cavity is long, narrow and symmetrical, more tapered posteriorly than anteriorly. It is centered on a point just anterior of the mid-length of the unit, and occupies one third of the length of the aboral margin. The edge of the basal cavity has small lateral lips.

Remarks.

This species is very similar to Spathognathodus aciedentatus E.R. Branson, and Spathognathodus denticulatus E.R. Branson, but Spathognathodus aciedentatus does not have the characteristic aboral outline of Spathognathodus strigosus. The original descriptions of Spathognathodus denticulatus E.R. Branson and Spathognathodus strigosus Branson & Mehl are almost identical. The main distinction which arises from these descriptions is that Spathognathodus denticulatus has denticles in the anterior third which are much longer than those of the rest of the unit, and which are slightly pointed and discrete to near their bases, whereas Spathognathodus strigosus has only a gradual ascent of oral denticles toward the anterior end.

The Pilton forms have much higher and larger denticles at the anterior end, but they are not discrete. Ziegler (1962) and Bouckaert and Ziegler (1965) name forms identical to those from the Pilton Beds as Spathognathodus strigosus, and the interpretation of these authors has been followed in this thesis.

Material studied. 31 specimens

Occurrence. PB.2 - PB.16

Catalogue numbers of the figured specimens. JW.128 - JW.130, JW.133, JW.134, JW.139

Spathognathodus ziegleri Rhodes, Austin & Druce, 1969
(Pl.3, figs.8a-8c)

non 1934	Spathodus spinulicostatus E.R. Branson; p.305, pl.27, fig.19 (= S. sulciferus)
1956	Spathognathodus spinulicostatus (E.R. Branson): Bischoff & Ziegler; p.167, pl.13, fig.7.
1957	Spathognathodus spinulicostatus spinulicostatus (E.R. Branson): Ziegler, in Flugel & Ziegler; p.1, fig.14.
1959	Spathognathodus spinulicostatus spinulicostatus (E.R. Branson): Helms; pl.3, figs.12a & b.
1961	Spathognathodus spinulicostatus spinulicostatus (E.R. Branson): Freyer; p.87,88, pl.6, fig.145, text fig.146.

1962 *Spathognathodus costatus spinulicostatus* (E.R. Branson): Ziegler; p.108, pl.14, figs.11-18.

non 1965 *Spathognathodus spinulicostatus* (E.R. Branson): Austin; pl.1, figs.10,12.

1967 *Spathognathodus costatus spinulicostatus* (E.R. Branson): Wolska; p.427, pl.19, figs.13-16.

1967 *Spathognathodus costatus spinulicostatus* (E.R. Branson): Boogaert; pl.3, figs.23,24.

1969 *Spathognathodus ziegleri* Rhodes, Austin & Druce; p.238, pl.4, figs.5a-8d.

non 1969 *Spathognathodus costatus sulciferus* Rhodes, Austin & Druce, p.266, pl.3, figs.16a-18c.

Diagnosis.

This species has a row of lateral denticles running parallel to the blade for over three-quarters of its length, as does its related species *Spathognathodus bischoffi*. However, in addition there is a shorter second row of denticles on the opposite side of the blade in the posterior quarter of the unit. The lateral denticles occur as ribs, the majority of which reach the main blade, giving the species a ladder-like oral appearance. The basal cavity is large and asymmetrical, occupying the posterior half of the element.

Description.

Laterally, the element is seen to be four times as long as high. The oral edge is highest at the anterior, where three small triangular denticles are visable. The oral outline falls away very gently, and the denticles are completely fused to the mid-point. At mid-point the outline rises gently and denticulation is visible once more. The second highest point of the oral edge is found in the middle of the posterior third, and then it falls away to the posterior extremity. From the middle of the posterior third to the posterior tip the denticles of the main blade are surpassed in height by the lateral denticles. The anterior edge is three times as high as the posterior edge. The aboral outline in lateral view is straight and the angles made between the anterior and aboral edges, and the posterior and aboral edges, are approximately 90° in both cases.

Orally, the element appears flat. The free anterior blade is a quarter of the total length of the unit. On one side of the blade a row of lateral denticles occurs, running from a point immediately behind the anterior blade to the posterior extremity. These denticles are rib-like, the majority of them reaching the blade. The ribs are longest in the mid-third of the unit. In the posterior quarter of the element, the denticles of the blade are smaller and less uniform in distribution, and a second row of lateral denticles is initiated on the opposite side of the blade. Hence, the posterior quarter shows three rows of denticles, the middle half shows two, and the anterior quarter one row of denticles (the free anterior blade). The element is widest in the posterior third, as here the flared lips of the basal cavity are to be found. The unit is 3.5 times as long as broad.

Aborally the conodont is gently curved. The basal cavity is wide and flared, occurring in the posterior half of the unit. The cavity is asymmetrical, the inner half being sub-semicircular and the outer half showing a distinct fold. It is pointed anteriorly and posteriorly, but the cavity is more tapered posteriorly where it extends to the posterior extremity.

Only a single right form of this species was recovered from the Pilton fauna.

Remarks.

This species was previously called *Spathognathodus costatus spinulicostatus* by Ziegler (1962), and has recently been renamed *Spathognathodus ziegleri* by Rhodes, Austin & Druce (1969), the name being in honour of Dr. W. Ziegler. The new name aids in distinguishing this species from Carboniferous forms which are very similar in appearance, but are near-homeomorphs of *Spathognathodus ziegleri*. (See discussion of *Spathognathodus costatus*.)

Forms previously called *Spathognathodus* (*costatus*) *spinulicostatus* had been named incorrectly for many years. Branson & Mehl and E.R. Branson (1934) both figured specimens which they named *Spathognathodus sulciferus* which are identical to *Spathognathodus* (*costatus*) *spinulicostatus*, and hence, the name *Spathognathodus* (*costatus*) *sulciferus* should have had priority, and now has. This name applies only to the Carboniferous forms. Thus the completely new terminology proposed by Rhodes, Austin & Druce 1968, clarifies the problem.

Material studied. 1 (one) specimen.

Occurrence. PB.35

Catalogue number of the figured specimen. JW.121

Spathognathodus (transitional)

Forms transitional between *Spathognathodus bischoffi* and *Spathognathodus ziegleri*

(Pl.3, figs.9a-10c; Pl.4, figs.1a-6c, 8a,b)

1959 Spathognathodus jugosus (Branson & Mehl): Hass; pl.50, fig.15

Diagnosis.

These forms are considered to be intermediate between Spathognathodus bischoffi Rhodes, Austin & Druce and Spathognathodus ziegleri Rhodes, Austin & Druce. In oral view they show the initiation of a third row of denticles in the posterior third, but the alignment of the three rows differs from that of S. zeigleri, in that they are offset.

Description.

Laterally these forms have an almost straight oral outline for the greater part of their length, but in the posterior third this outline falls gradually to the posterior tip. Denticulation is most prominent in the posterior half of the oral edge in most specimens. The aboral edge is also generally straight or sometimes gently undulating.

Aborally these forms have a large basal cavity which is situated in the mid-third of the unit. The shape of the cavity varies from sub-circular, through tear-shaped to sub-triangular, also the cavity can be bilaterally symmetrical or asymmetrical. All the cavities are more rounded anteriorly and more tapered posteriorly.

In oral view these forms expost two rows of denticles running sub-parallel for almost the entire length of the unit, as does S. bischoffi. However, at a point approximately corresponding to the beginning of the posterior third of the element, a third row of denticles is initiated. Unlike S. zeigleri this third row of denticles may or may not extend to the posterior tip of the unit, if it does so, however, the other two rows will fail to reach the posterior extremity. In most cases this third row of denticles is developed between the blade and the main lateral row, and not on the opposite side of the blade from the main lateral row, as in S. zeigleri. In other forms the three rows develop and immediately the blade becomes sharply kinked, with the result that the main lateral row dies out before it reaches the posterior tip, its position occupied by the realignment of the blade denticles.

Remarks.

Of the specimens found which have been allocated to this group, no two are the same. They vary in the number of denticles and in the pattern of their denticle rows. The basal cavities also vary considerably. The one feature that they all have in common is that three rows of denticles occur somewhere in the posterior third. In no case do the denticles of these forms attain the typical alignment characteristic of S. zeigleri, nor can the forms be assigned to S. bischoffi because of the presence of a third row of denticles. In the position of intermediate forms it would be expected that a great deal of variation would be shown in the elements assigned to this group.

The anterior blades of the members of this group were missing in most cases, but they are similar to those of S. zeigleri.

Material studied. 11 specimens

Occurrence. PB.10 - PB.35

Catalogue numbers of the figured specimens. JW.119, JW.122 - JW.127, JW.143, JW.144

It was hoped that these spathognathodids would show an increasing similarity with Spathognathodus zeigleri from the older to the younger Pilton Beds, but no such trend was observed in either the denticulation or position and shape of the basal cavity.

EXPLANATION OF PLATE 1

(all figures x 27.1)

Spathognathodus aculeatus aculeatus Branson & Mehl

Fig. 1a	Lateral view of specimen JW.100	
b	Oral view of specimen JW.100	
c	Aboral view of specimen JW.100	Sample PB.4
Fig. 2a	Lateral view of specimen JW.101	
b	Oral view of specimen JW.101	
c	Aboral view of specimen JW.101	Sample PB.25
Fig. 3a	Lateral view of specimen JW.102	
b	Oral view of specimen JW.102	
c	Aboral view of specimen JW.102	Sample PB.9

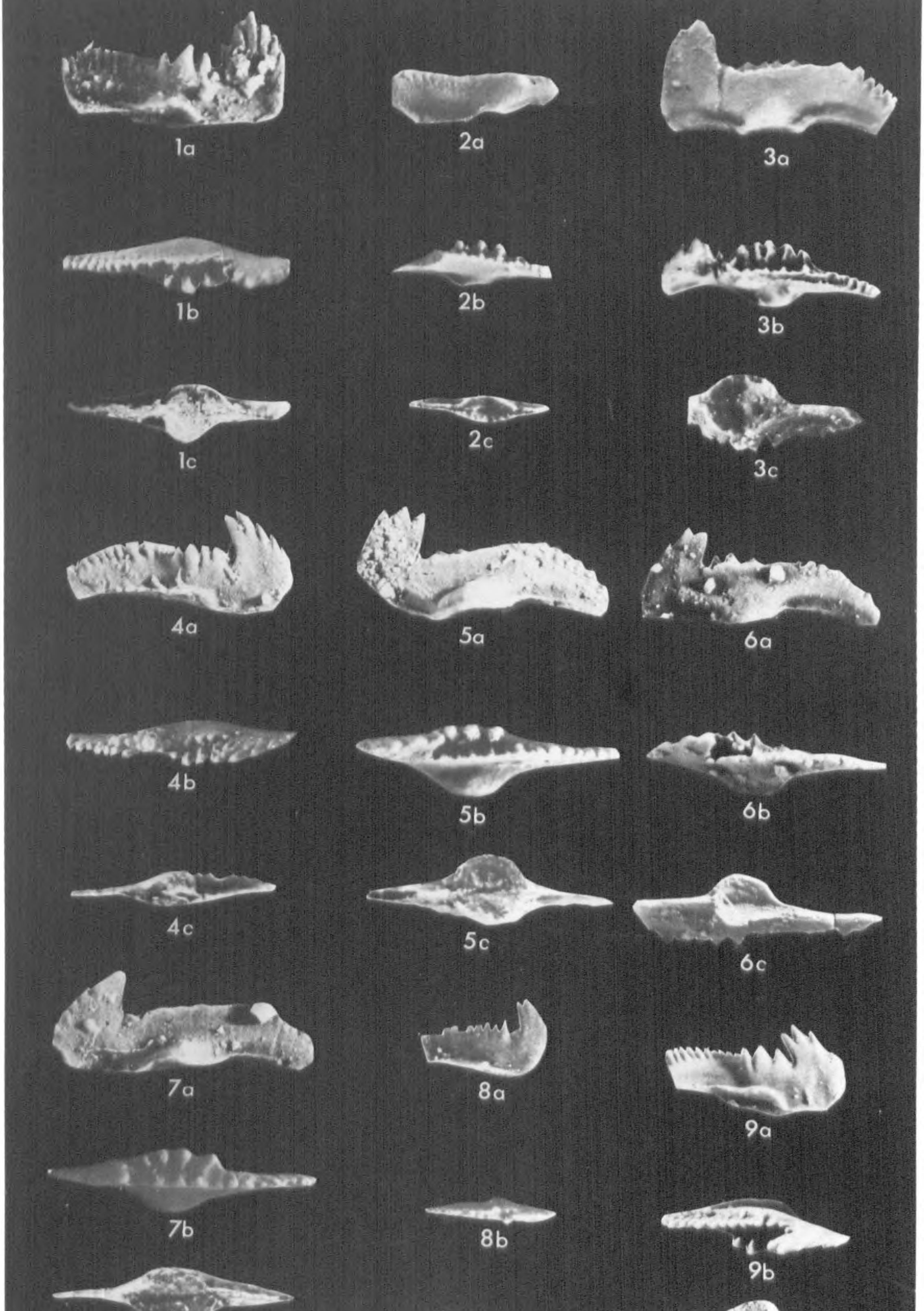
Spathognathodus aculeatus plumulus (Rhodes, Austin & Druce)

Fig. 4a	Lateral view of specimen JW.103	
b	Oral view of specimen JW.103	
c	Aboral view of specimen JW.103	Sample PB.4
Fig. 5a	Lateral view of specimen JW.104	
b	Oral view of specimen JW.104	
c	Aboral view of specimen JW.104	Sample PB.4
Fig. 6a	Lateral view of specimen JW.105	
b	Oral view of specimen JW.105	
c	Aboral view of specimen JW.105	Sample PB.4
Fig. 7a	Lateral view of specimen JW.106	
b	Oral view of specimen JW.106	
c	Aboral view of specimen JW.106	Sample PB.4
Fig. 8a	Lateral view of specimen JW.136	
b	Oral view of specimen JW.136	
c	Aboral view of specimen JW.136	Sample PB.4

Spathognathodus anteposicornis Scott

Fig. 9a	Lateral view of specimen JW.107	
b	Oral view of specimen JW.107	
c	Aboral view of specimen JW.107	Sample PB.2

PLATE 1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7c
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9c

EXPLANATION OF PLATE 2

(all figures x 27.1)

Spathognathodus anteposicornis Scott

Fig. 1a	Lateral view of specimen JW.108	
b	Oral view of specimen JW.108	
c	Aboral view of specimen JW.108	Sample PB.23
Fig. 2a	Lateral view of specimen JW.109	
b	Oral view of specimen JW.109	
c	Aboral view of specimen JW.109	Sample PB.13
Fig. 3a	Lateral view of specimen JW.140	
b	Oral view of specimen JW.140	
c	Aboral view of specimen JW.140	Sample PB.13

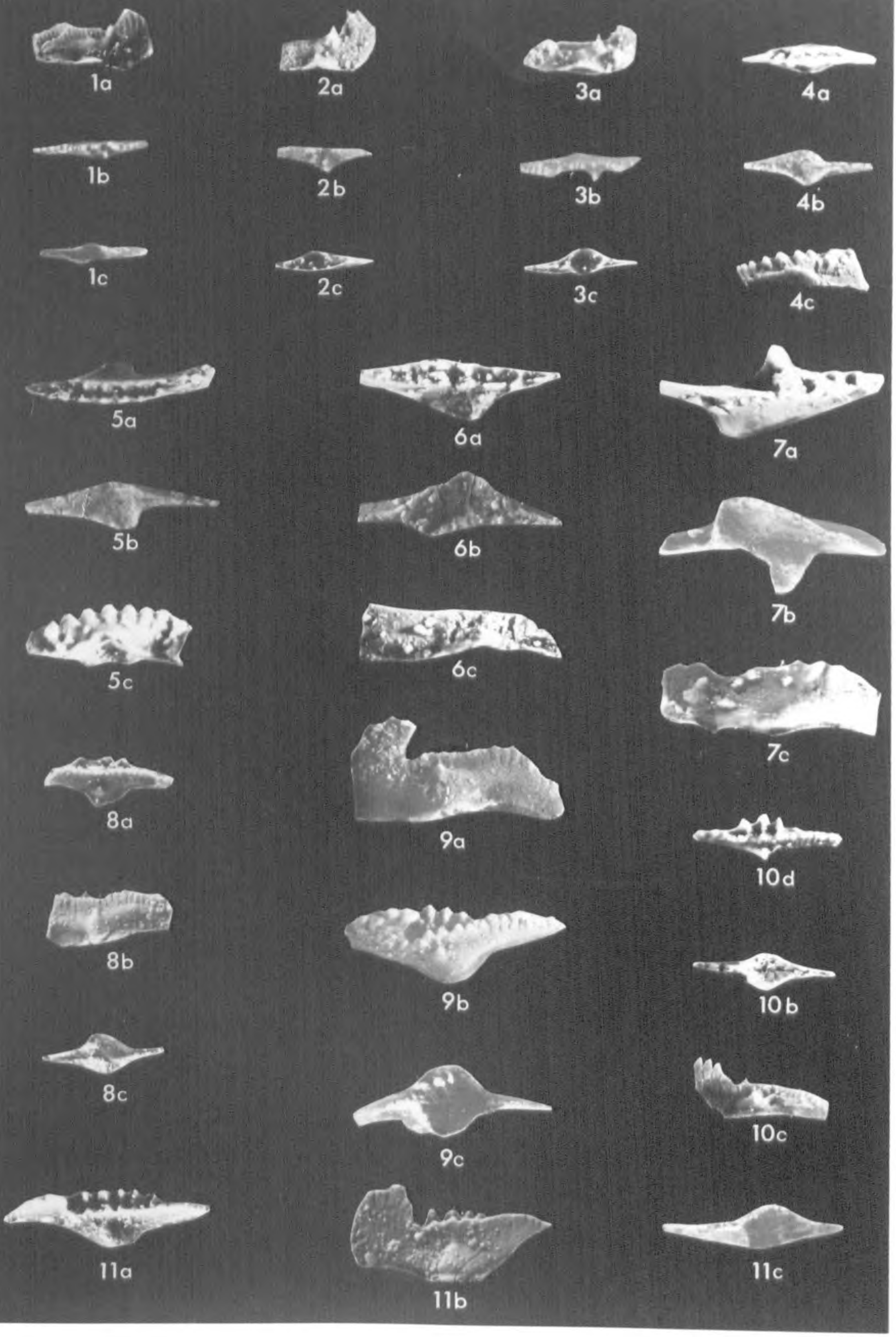
Spathognathodus bischoffi Rhodes, Austin & Druce

Fig. 4a	Oral view of specimen JW.111	
b	Aboral view of specimen JW.111	
c	Lateral view of specimen JW.111	Sample PB.35
Fig. 5a	Oral view of specimen JW.112	
b	Aboral view of specimen JW.112	
c	Lateral view of specimen JW.112	Sample PB.35
Fig. 6a	Oral view of specimen JW.113	
b	Aboral view of specimen JW.113	
c	Lateral view of specimen JW.113	Sample PB.30
Fig. 7a	Oral view of specimen JW.149	
b	Aboral view of specimen JW.149	
c	Lateral view of specimen JW.149	Sample PB.14

Spathognathodus aculeatus nodosus (Rhodes, Austin & Druce)

Fig. 8a	Oral view of specimen JW.115	
b	Lateral view of specimen JW.115	
c	Aboral view of specimen JW.115	Sample PB.20
Fig. 9a	Lateral view of specimen JW.116	
b	Oral view of specimen JW.116	
c	Aboral view of specimen JW.116	Sample PB.4
Fig.10a	Oral view of specimen JW.117	
b	Aboral view of specimen JW.117	
c	Lateral view of specimen JW.117	Sample PB.16
Fig.11a	Oral view of specimen JW.146	
b	Lateral view of specimen JW.146	
c	Aboral view of specimen JW.146	Sample PB.9

PLATE 2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7b
5c
6c
7c
8a
9a
10d
8b
9b
10b
8c
9c
10c
11a
11b
11c

EXPLANATION OF PLATE 3

(all figures x 27.1)

Spathognathodus aculeatus nodosus (Rhodes, Austin & Druce)

Fig. 1a	Oral view of specimen JW.137	
b	Aboral view of specimen JW.137	
c	Lateral view of specimen JW.137	Sample PB.2

Spathognathodus strigosus (Branson & Mehl)

Fig. 2a	Lateral view of specimen JW.128	
b	Oral view of specimen JW.128	Sample PB.4
Fig. 3	Lateral view of specimen JW.129	Sample PB.2
Fig. 4a	Lateral view of specimen JW.130	
b	Oral view of specimen JW.130	
c	Aboral view of specimen JW.130	Sample PB.9
Fig. 5a	Lateral view of specimen JW.133	
b	Oral view of specimen JW.133	
c	Aboral view of specimen JW.133	Sample PB.2
Fig. 6a	Lateral view of specimen JW.134	
b	Oral view of specimen JW.134	
c	Aboral view of specimen JW.134	Sample PB.4
Fig. 7a	Lateral view of specimen JW.139	
b	Oral view of specimen JW.139	
c	Aboral view of specimen JW.139	Sample PB.4

Spathognathodus ziegleri Rhodes, Austin & Druce

Fig. 8a	Oral view of specimen JW.121	
b	Lateral view of specimen JW.121	
c	Aboral view of specimen JW.121	Sample PB.35

Spathognathodus (transitional)

Fig. 9a	Oral view of specimen JW.119	
b	Aboral view of specimen JW.119	
c	Lateral view of specimen JW.119	Sample PB.35
Fig. 10a	Oral view of specimen JW.122	
b	Aboral view of specimen JW.122	
c	Lateral view of specimen JW.122	Sample PB.12

PLATE 3


1a


2a


4a


1b


2b


4b


1c


3


4c


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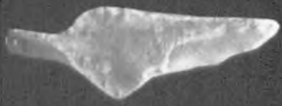
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EXPLANATION OF PLATE 4

(all figures x 27.1)

Spathognathodus (transitional).

Fig. 1a	Oral view of specimen JW.123	
b	Aboral view of specimen JW.123	
c	Lateral view of specimen JW.123	Sample PB.10
Fig. 2a	Oral view of specimen JW.124	
b	Aboral view of specimen JW.124	
c	Lateral view of specimen JW.124	Sample PB.16
Fig. 3a	Oral view of specimen JW.125	
b	Aboral view of specimen JW.125	
c	Lateral view of specimen JW.125	Sample PB.23
Fig. 4a	Oral view of specimen JW.126	
b	Aboral view of specimen JW.126	
c	Lateral view of specimen JW.126	Sample PB.24
Fig. 5a	Oral view of specimen JW.127	
b	Aboral view of specimen JW.127	Sample PB.28
Fig. 6a	Oral view of specimen JW.143	
b	Aboral view of specimen JW.143	
c	Lateral view of specimen JW.143	Sample PB.16
Fig. 8a	Oral view of specimen JW.144	
b	Aboral view of specimen JW.144	Sample PB.16

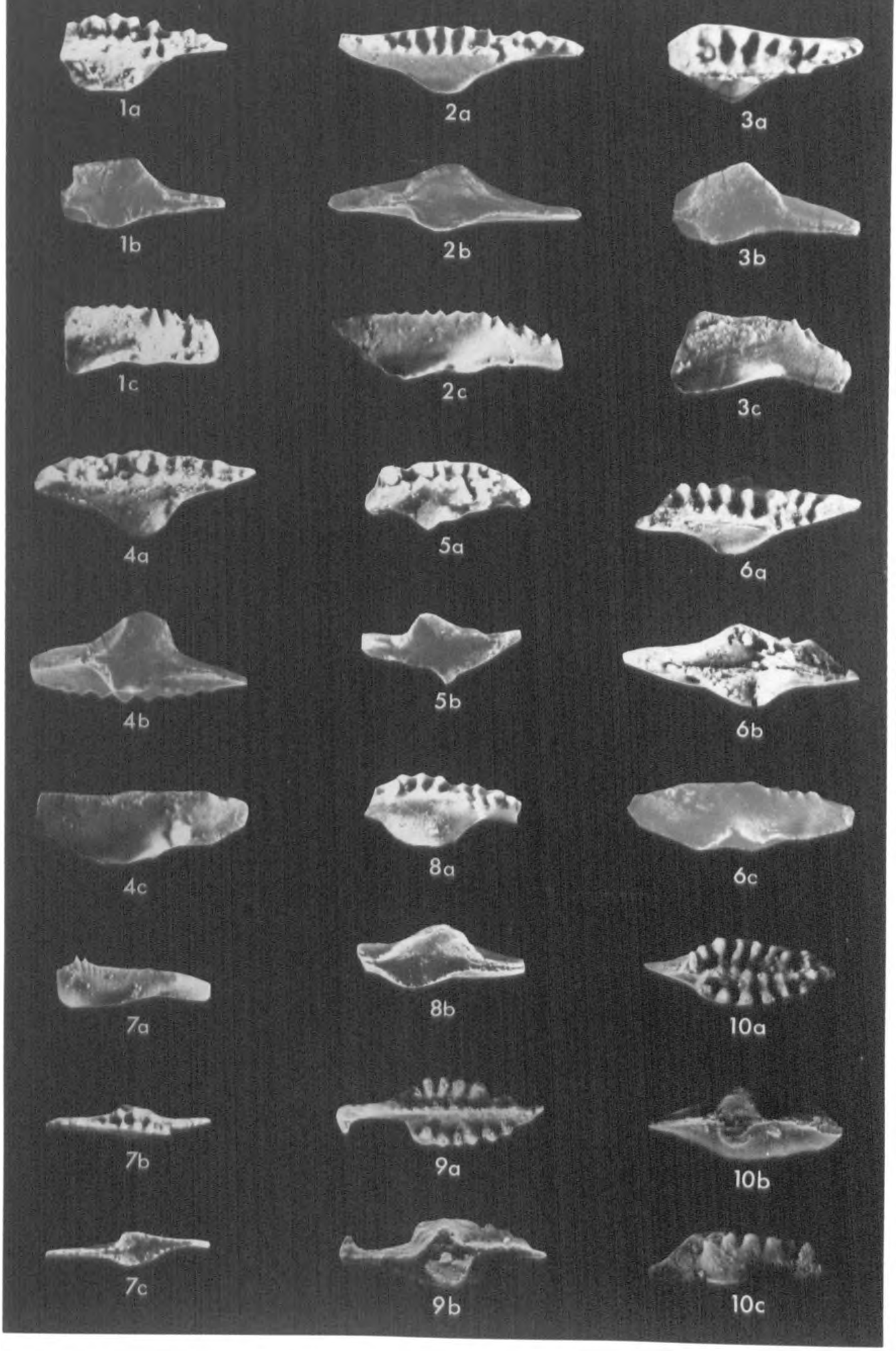
Spathognathodus aculeatus aculeatus Branson & Mehl

Fig. 7a	Lateral view of specimen JW.145	
b	Oral view of specimen JW.145	
c	Aboral view of specimen JW.145	Sample PB.16

Pseudopolygnathus dentilineata E.R. Branson (MORPHOTYPE I)

Fig. 9a	Oral view of specimen JW.154	
b	Aboral view of specimen JW.154	Sample PB.16
Fig.10a	Oral view of specimen JW.155	
b	Aboral view of specimen JW.155	
c	Lateral view of specimen JW.155	Sample PB.16

PLATE 4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EXPLANATION OF PLATE 5

(all figures x 27.1)

Pseudopolygnathus dentilineata E.R. Branson (MORPHOTYPE I)

Fig. 1a	Oral view of specimen JW.156	
b	Aboral view of specimen JW.156	
c	Lateral view of specimen JW.156	Sample PB.16
Fig. 2a	Oral view of specimen JW.157	
b	Aboral view of specimen JW.157	
c	Lateral view of specimen JW.157	Sample PB.16

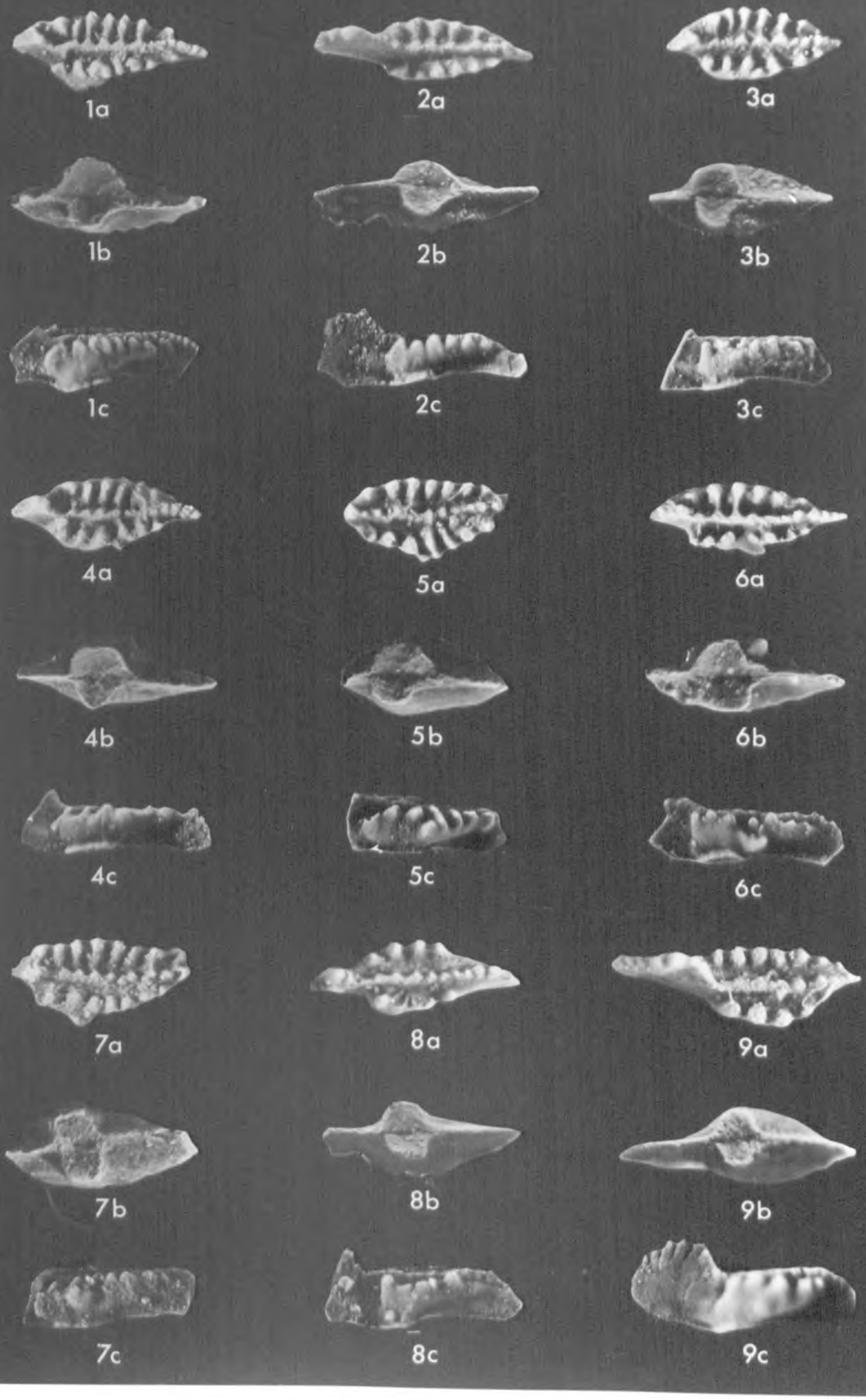
Pseudopolygnathus dentilineata E.R. Branson (MORPHOTYPE II)

Fig. 3a	Oral view of specimen JW.158	
b	Aboral view of specimen JW.158	
c	Lateral view of specimen JW.158	Sample PB.16
Fig. 4a	Oral view of specimen JW.159	
b	Aboral view of specimen JW.159	
c	Lateral view of specimen JW.159	Sample PB.16
Fig. 5a	Oral view of specimen JW.160	
b	Aboral view of specimen JW.160	
c	Lateral view of specimen JW.160	Sample PB.16
Fig. 6a	Oral view of specimen JW.161	
b	Aboral view of specimen JW.161	
c	Lateral view of specimen JW.161	Sample PB.16
Fig. 7a	Oral view of specimen JW.162	
b	Aboral view of specimen JW.162	
c	Lateral view of specimen JW.162	Sample PB.16

Pseudopolygnathus dentilineata E.R. Branson (MORPHOTYPE III)

Fig. 8a	Oral view of specimen JW.163	
b	Aboral view of specimen JW.163	
c	Lateral view of specimen JW.163	Sample PB.16
Fig. 9a	Oral view of specimen JW.164	
b	Aboral view of specimen JW.164	
c	Lateral view of specimen JW.164	Sample PB.16

PLATE 5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EXPLANATION OF PLATE 6

(all figures x 27.1)

Pseudopolygnathus dentilineata E.R. Branson (MORPHOTYPE III)

Fig. 1a Oral view of specimen JW.165
b Aboral view of specimen JW.165
c Lateral view of specimen JW.165 Sample PB.16

Fig. 2a Oral view of specimen JW.166
b Aboral view of specimen JW.166
c Lateral view of specimen JW.166 Sample PB.16

Fig. 3a Oral view of specimen JW.167
b Aboral view of specimen JW.167
c Lateral view of specimen JW.167 Sample PB.16

Fig. 4a Oral view of specimen JW.168
b Aboral view of specimen JW.168
c Lateral view of specimen JW.168 Sample PB.16

Pseudopolygnathus dentilineata E.R. Branson (MORPHOTYPE IV)

Fig. 5a Oral view of specimen JW.169
b Aboral view of specimen JW.169
c Lateral view of specimen JW.169 Sample PB.16

Fig. 6a Oral view of specimen JW.170
b Aboral view of specimen JW.170
c Lateral view of specimen JW.170 Sample PB.16

Fig. 7a Oral view of specimen JW.171
b Aboral view of specimen JW.171
c Lateral view of specimen JW.171 Sample PB.16

Pseudopolygnathus sp. nov.

Fig. 8a Oral view of specimen JW.172
b Aboral view of specimen JW.172
c Lateral view of specimen JW.172 Sample PB.10

Fig. 9a Oral view of specimen JW.173
b Aboral view of specimen JW.173
c Lateral view of specimen JW.173 Sample PB.10

PLATE 6


1a


2a


3a


1b


2b


3b


1c


2c


3c


4a


5a


6a


4b


5b


6b


4c


5c


6c


7a


8a


9a


7b


8b


9b


7c


8c


9c

EXPLANATION OF PLATE 7

(all figures x 27.1)

Pseudopolygnathus dentilineata E.R. Branson (CENTRAL SPECIMEN)

Fig. 1a	Oral view of specimen JW.174	
b	Aboral view of specimen JW.174	
c	Lateral view of specimen JW.174	Sample PB.12
Fig. 2a	Oral view of specimen JW.175	
b	Lateral view of specimen JW.175	Sample PB.12
Fig. 3a	Oral view of specimen JW.176	
b	Aboral view of specimen JW.176	
c	Lateral view of specimen JW.176	Sample PB.20
Fig. 4	Oral and Aboral views of a	
5	series of specimens showing	
6	growth stages of *P. dentilineata*	
7	E.R. Branson. Specimens JW.150-153	Sample PB.16

Icriodus sp.

Fig. 8a	Oral view of specimen JW.177	
b	Aboral view of specimen JW.177	
c	Lateral view of specimen JW.177	Sample B.7

Icriodus costatus (Thomas)

Fig. 9a	Oral view of specimen JW.179	
b	Aboral view of specimen JW.179	
c	Lateral view of specimen JW.179	Sample PB.12
Fig.10a	Oral view of specimen JW.178 (Juvenile)	
b	Aboral view of specimen JW.178	
c	Lateral view of specimen JW.178	Sample PB.12

PLATE 7


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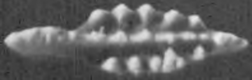
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8c


9c


10c

EXPLANATION OF PLATE 8

(all figures x 27.1)

Icriodus costatus (Thomas)

Fig. 1a	Oral view of specimen JW.180	
b	Aboral view of specimen JW.180	
c	Lateral view of specimen JW.180	Sample PB.16
Fig. 3a	Oral view of specimen JW.182	
b	Aboral view of specimen JW.182	
c	Lateral view of specimen JW.182	Sample PB.16

Icriodus sp. nov.

Fig. 2a	Oral view of specimen JW.181	
b	Aboral view of specimen JW.181	
c	Lateral view of specimen JW.181	Sample PB.15

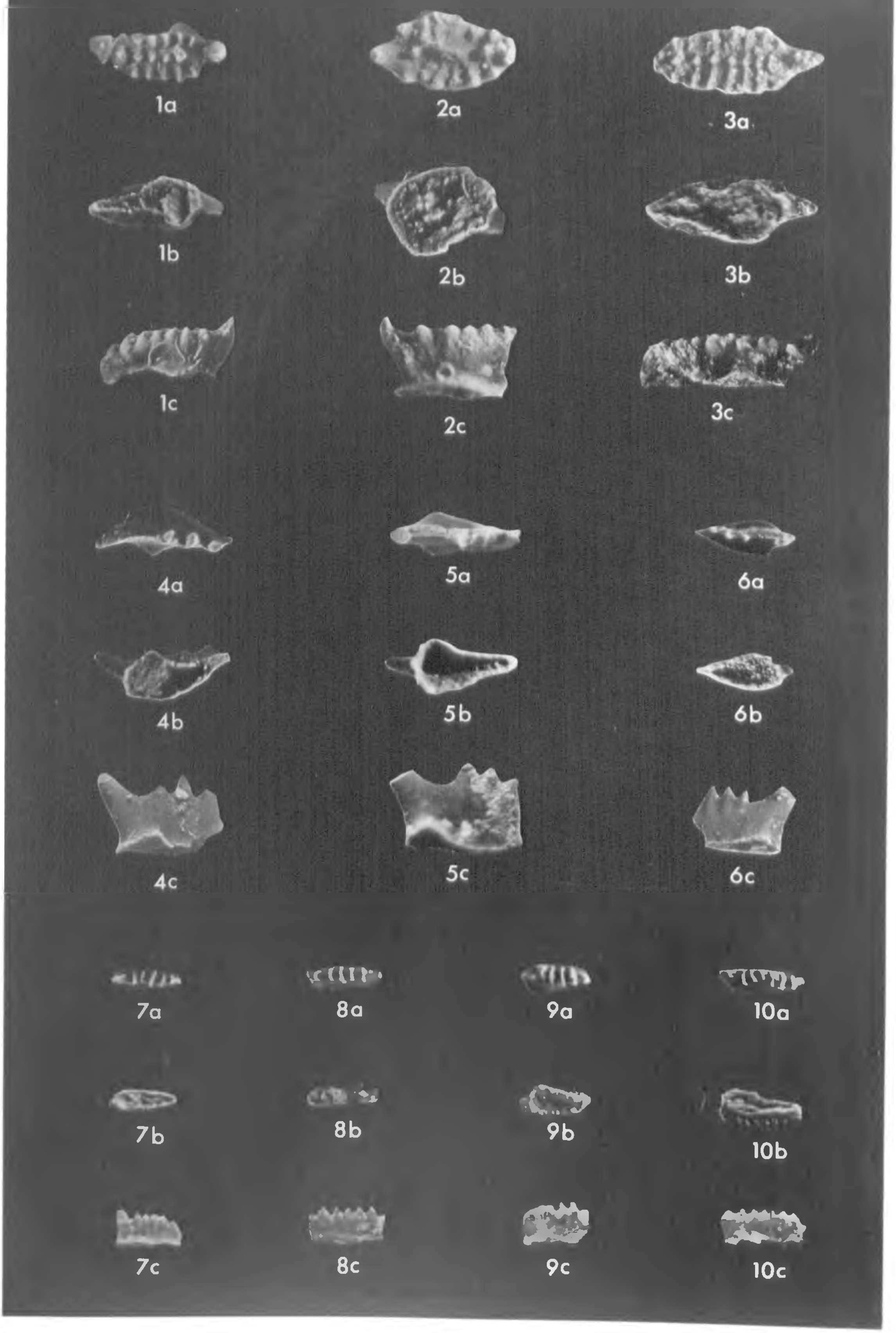
Pelekysgnathus communis Thomas

Fig. 4a	Oral view of specimen JW.183	
b	Aboral view of specimen JW.183	
c	Lateral view of specimen JW.183	Sample PB.24
Fig. 5a	Oral view of specimen JW.184	
b	Aboral view of specimen JW.184	
c	Lateral view of specimen JW.184	Sample PB.24
Fig. 6a	Oral view of specimen JW.186	
b	Aboral view of specimen JW.186	
c	Lateral view of specimen JW.186	Sample PB.16

Pelekysgnathus croydeus sp. nov.

Fig. 7a	Oral view of Holotype JW.185	
b	Aboral view of Holotype JW.185	
c	Lateral view of Holotype JW.185	Sample PB.24
Fig. 8a	Oral view of Paratype JW.189	
b	Aboral view of Paratype JW.189	
c	Lateral view of Paratype JW.189	Sample PB.29
Fig. 9a	Oral view of Paratype JW.188	
b	Aboral view of Paratype JW.188	
c	Lateral view of Paratype JW.188	Sample PB.2
Fig.10a	Oral view of Paratype JW.187	
b	Aboral view of Paratype JW.187	
c	Lateral view of Paratype JW.187	Sample PB.2

PLATE 8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EXPLANATION OF PLATE 9

(all figures x 27.1)

Polygnathus communis carina Hass

Fig. 1a	Oral view of specimen JW.191	
b	Aboral view of specimen JW.191	
c	Lateral view of specimen JW.191	Sample PB.4
Fig. 2a	Oral view of specimen JW.192	
b	Aboral view of specimen JW.192	
c	Lateral view of specimen JW.192	Sample PB.4
Fig. 3a	Oral view of specimen JW.193	
b	Aboral view of specimen JW.193	
c	Lateral view of specimen JW.193	Sample PB.13

Polygnathus communis communis Branson & Mehl

Fig. 4a	Oral view of specimen JW.194	
b	Aboral view of specimen JW.194	
c	Lateral view of specimen JW.194	Sample PB.24
Fig. 5a	Oral view of specimen JW.195	
b	Aboral view of specimen JW.195	
c	Lateral view of specimen JW.195	Sample PB.24
Fig. 6a	Oral view of specimen JW.196	
b	Aboral view of specimen JW.196	
c	Lateral view of specimen JW.196	Sample PB.17
Fig. 7a	Oral view of specimen JW.197	
b	Aboral view of specimen JW.197	
c	Lateral view of specimen JW.197	Sample PB.20
Fig. 8a	Oral view of specimen JW.198	
b	Aboral view of specimen JW.198	
c	Lateral view of specimen JW.198	Sample PB.27
Fig. 9a	Oral view of specimen JW.199	
b	Aboral view of specimen JW.199	
c	Lateral view of specimen JW.199	Sample PB.27
Fig. 10a	Oral view of specimen JW.200	
b	Aboral view of specimen JW.200	
c	Lateral view of specimen JW.200	Sample PB.25

Polygnathus communis comminis Branson & Mehl

Fig.11a	Oral view of specimen JW.201	
b	Aboral view of specimen JW.201	
c	Lateral view of specimen JW.201	Sample PB.25
Fig.12a	Oral view of specimen JW.202	
b	Aboral view of specimen JW.202	
c	Lateral view of specimen JW.202	Sample PB.25

PLATE 9


1a


2a


3a


4a


1b


2b


3b


4b


1c


2c


3c


4c


5a


6a


7a


8a


5b


6b


7b


8b


5c


6c


7c


8c


9a


10a


11a


12a


9b


10b


11b


12b


9c


10c


11c


12c

EXPLANATION OF PLATE 10

(all figures x 27.1)

Polygnathus communis communis Branson & Mehl

Fig. 1a	Oral view of specimen JW.203	
b	Lateral view of specimen JW.203	Sample PB.25
Fig. 2a	Oral view of specimen JW.204	
b	Aboral view of specimen JW.204	
c	Lateral view of specimen JW.204	Sample PB.24

Polygnathus lacinatus lacinatus Huddle

Fig. 3a	Oral view of specimen JW.205	
b	Aboral view of specimen JW.205	
c	Lateral view of specimen JW.205	Sample PB.21
Fig. 4a	Oral view of specimen JW.206	
b	Aboral view of specimen JW.206	
c	Lateral view of specimen JW.206	Sample PB.25
Fig. 5a	Oral view of specimen JW.207	
b	Aboral view of specimen JW.207	
c	Lateral view of specimen JW.207	Sample PB.24
Fig. 6a	Oral view of specimen JW.208	
b	Aboral view of specimen JW.208	
c	Lateral view of specimen JW.208	Sample PB.36
Fig. 7a	Oral view of specimen JW.209	
b	Aboral view of specimen JW.209	
c	Lateral view of specimen JW.209	Sample PB.34
Fig. 8a	Oral view of specimen JW.210	
b	Aboral view of specimen JW.210	
c	Lateral view of specimen JW.210	Sample PB.24

Polygnathus cf. *P. lacinatus* Huddle

Fig. 9a	Oral view of specimen JW.212	
b	Aboral view of specimen JW.212	
c	Lateral view of specimen JW.212	Sample PB.20

Polygnathus pura pura Voges

Fig.10a	Oral view of specimen JW.211	
b	Aboral view of specimen JW.211	
c	Lateral view of specimen JW.211	Sample F.8

PLATE 10


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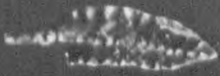
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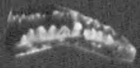
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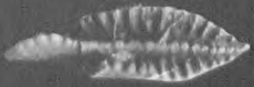
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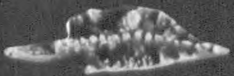
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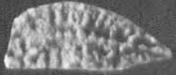
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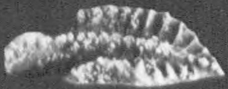
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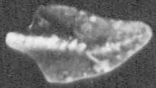
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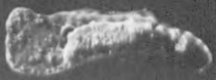
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EXPLANATION OF PLATE 11

(all figures x 27.1)

Polygnathus cf. *P. lacinatus* Huddle

Fig. 1a	Oral view of specimen JW.213	
b	Aboral view of specimen JW.213	
c	Lateral view of specimen JW.213	Sample PB.24
Fig. 2a	Oral view of specimen JW.214	
b	Aboral view of specimen JW.214	
c	Lateral view of specimen JW.214	Sample PB.24
Fig. 3a	Oral view of specimen JW.215	
b	Aboral view of specimen JW.215	
c	Lateral view of specimen JW.215	Sample PB.36
Fig. 4a	Oral view of specimen JW.216	
b	Aboral view of specimen JW.216	
c	Lateral view of specimen JW.216	Sample PB.36
Fig. 5a	Oral view of specimen JW.217	
b	Aboral view of specimen JW.217	Sample PB.35

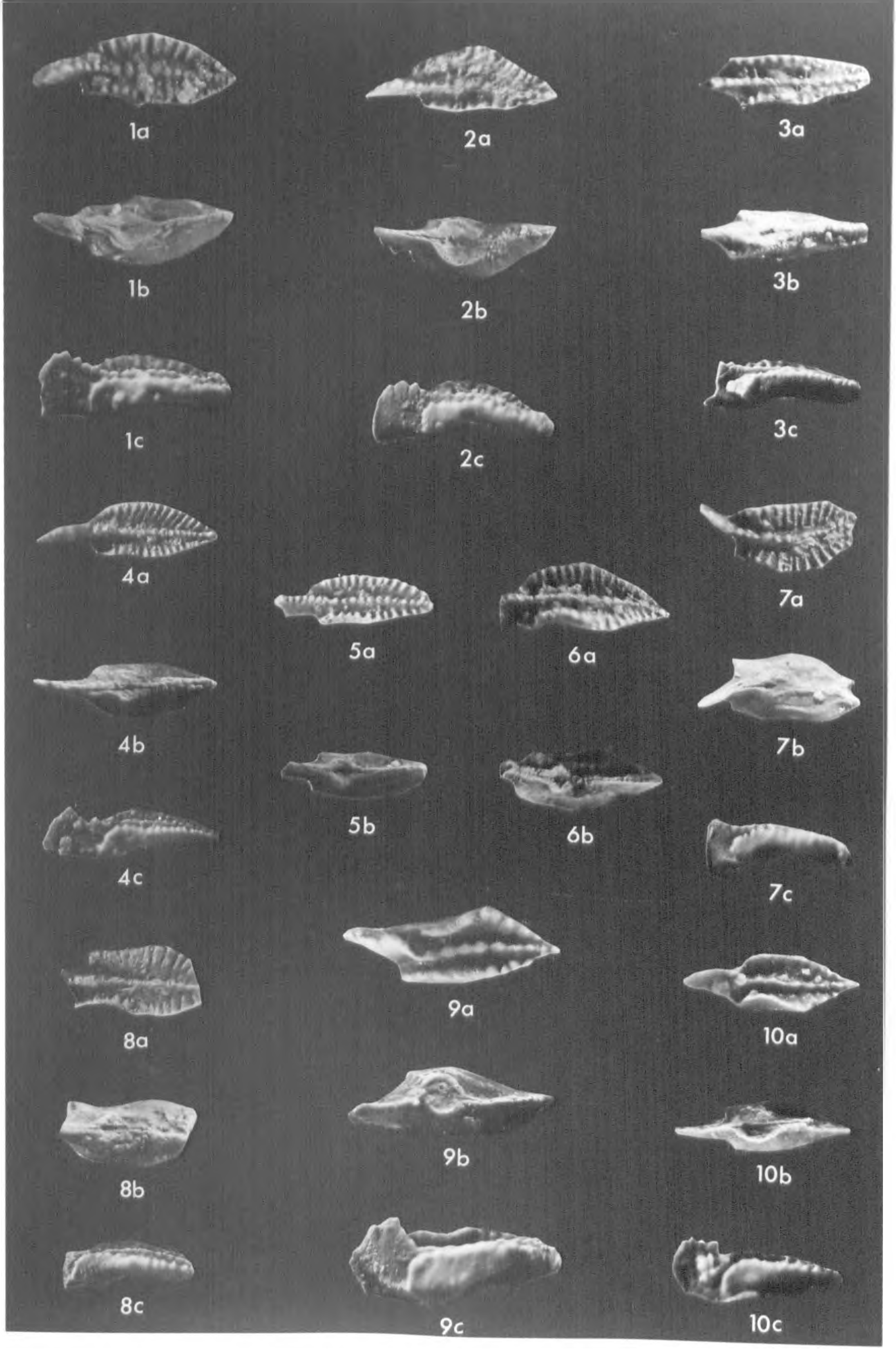
Polygnathus inornatus inornatus Branson & Mehl

Fig. 6a	Oral view of specimen JW.218	
b	Aboral view of specimen JW.218	Sample PB.36
Fig. 7a	Oral view of specimen JW.219	
b	Aboral view of specimen JW.219	
c	Lateral view of specimen JW.219	Sample PB.35
Fig. 8a	Oral view of specimen JW.220	
b	Aboral view of specimen JW.220	
c	Lateral view of specimen JW.220	Sample PB.36

Polygnathus cf. *P. nodomarginatus* E.R. Branson

Fig. 9a	Oral view of specimen JW.222	
b	Aboral view of specimen JW.222	
c	Lateral view of specimen JW.222	Sample PB.16
Fig.10a	Oral view of specimen JW.221	
b	Aboral view of specimen JW.221	
c	Lateral view of specimen JW.221	Sample PB.35

PLATE 11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EXPLANATION OF PLATE 12

(all figures x 27.1)

Hibbardella (*Hibbardella*) cf. *H. macrodentata* Thomas

Fig. 1a	Anterior view of specimen JW.224	
b	Posterior view of specimen JW.224	
c	Aboral view of specimen JW.224	Sample PB.2
Fig. 3	Posterior view of specimen JW.225	Sample PB.12
Fig. 4a	Posterior view of specimen JW.226	
b	Aboral view of specimen JW.226	Sample PB.25
Fig. 6a	Posterior view of specimen JW.228	
b	Aboral view of specimen JW.228	Sample PB.21
Fig. 7a	Anterior view of specimen JW.229	
b	Aboral view of specimen JW.229	Sample PB.9

Polygnathus cf. *P. nodomarginatus* E.R. Branson

Fig. 2a	Oral view of specimen JW.223	
b	Aboral view of specimen JW.223	
c	Lateral view of specimen JW.223	Sample PB.29

Hibbardella (*Hibbardella*) sp.

Fig. 5a	Posterior view of specimen JW.227	
b	Lateral view of specimen JW.227	Sample PB.35

Hindeodella subtilis Ulrich & Bassler

Fig. 8a	Oral view of specimen JW.230	
b	Aboral view of specimen JW.230	
c	Lateral view of specimen JW.230	Sample PB.25
Fig.10a	Oral view of specimen JW.232	
b	Aboral view of specimen JW.232	
c	Lateral view of specimen JW.232	Sample PB.35
Fig.14a	Oral view of specimen JW.236	
b	Aboral view of specimen JW.236	
c	Lateral view of specimen JW.236	Sample PB.25

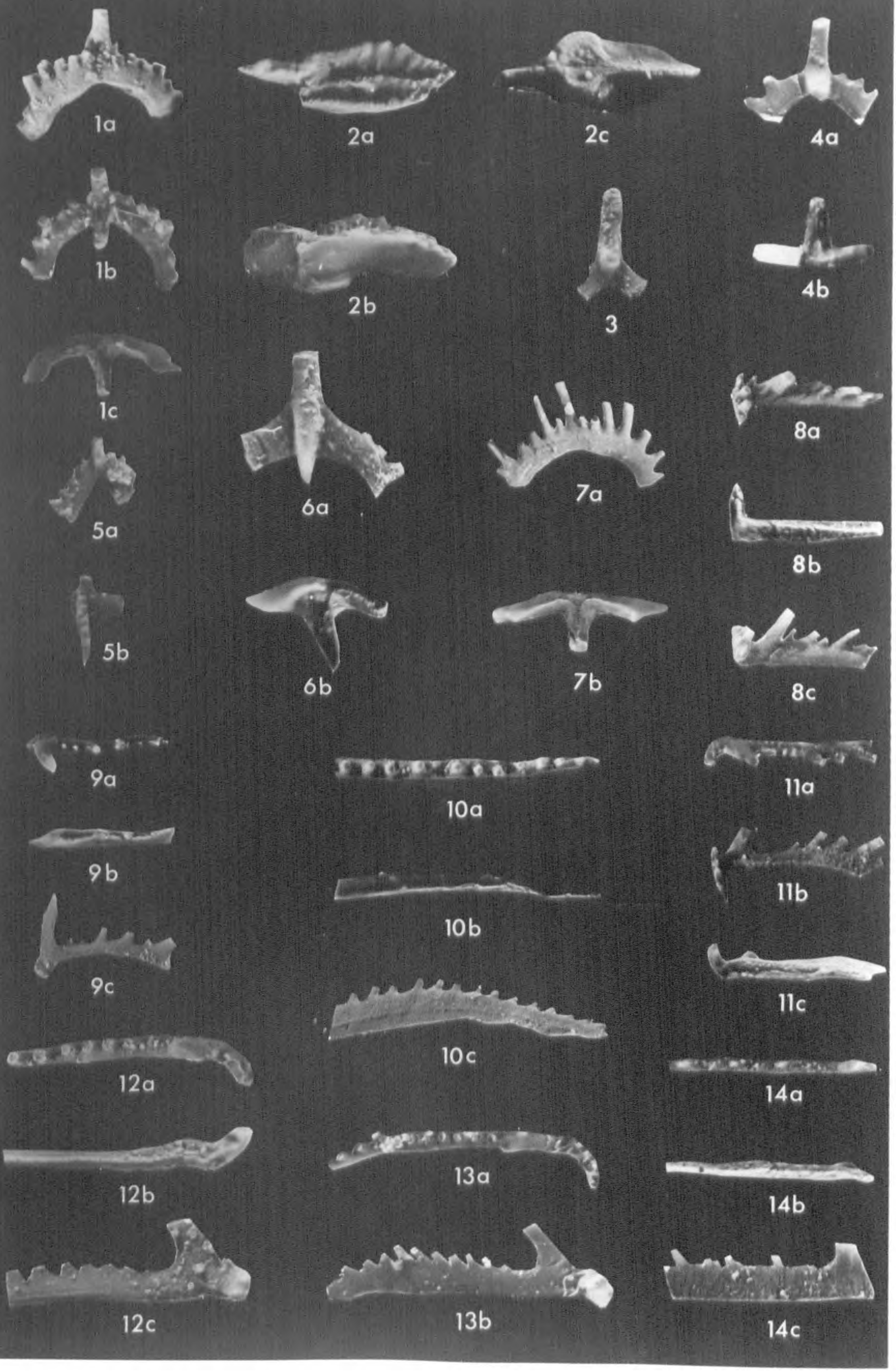
Hindeodella corpulenta Branson & Mehl

Fig. 9a	Oral view of specimen JW.231	
b	Aboral view of specimen JW.231	
c	Lateral view of specimen JW.231	Sample PB.35
Fig.11a	Oral view of specimen JW.233	
b	Aboral view of specimen JW.233	
c	Lateral view of specimen JW.233	Sample PB.36

Hindeodella cf. *H. tenuis* Clarke

Fig.12a	Oral view of specimen JW.234	
b	Aboral view of specimen JW.234	
c	Lateral view of specimen JW.234	Sample PB.4
Fig.13a	Oral view of specimen JW.235	
b	Lateral view of specimen JW.235	Sample PB.4

PLATE 12



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EXPLANATION OF PLATE 13

(all figures x 27.1)

Hindeodina simplaria Hass

Fig. 1a	Oral view of specimen JW.237	
b	Aboral view of specimen JW.237	
c	Lateral view of specimen JW.237	Sample PB.27
Fig. 2a	Oral view of specimen JW.238	
b	Aboral view of specimen JW.238	Sample PB.35

? *Angulodus* sp.

Fig. 3a	Oral view of specimen JW.239	
b	Aboral view of specimen JW.239	
c	Lateral view of specimen JW.239	Sample PB.2
Fig. 4a	Lateral view of specimen JW.240	
b	Aboral view of specimen JW.240	Sample PB.4
Fig. 5a	Oral view of specimen JW.241	
b	Aboral view of specimen JW.241	
c	Lateral view of specimen JW.241	Sample PB.4

Falcodus sp.

Fig. 6a	Lateral view of specimen JW.247	
b	Lateral view of specimen JW.247	Sample F.6

Neoprioniodus confluens (Branson & Mehl)

Fig. 7a	Lateral view of specimen JW.243	
b	Lateral view of specimen JW.243	Sample PB.4
Fig. 8a	Lateral view of specimen JW.244	
b	Lateral view of specimen JW.244	Sample PB.36
Fig. 9a	Lateral view of specimen JW.242	
b	Lateral view of specimen JW.242	Sample PB.2

Ozarkodina sp.

Fig. 10a	Lateral view of specimen JW.246	
b	Aboral view of specimen JW.246	Sample PB.2

Ozarkodina sp.

Fig.11a	Oral view of specimen JW.245	
b	Aboral view of specimen JW.245	
c	Lateral view of specimen JW.245	Sample PB.12

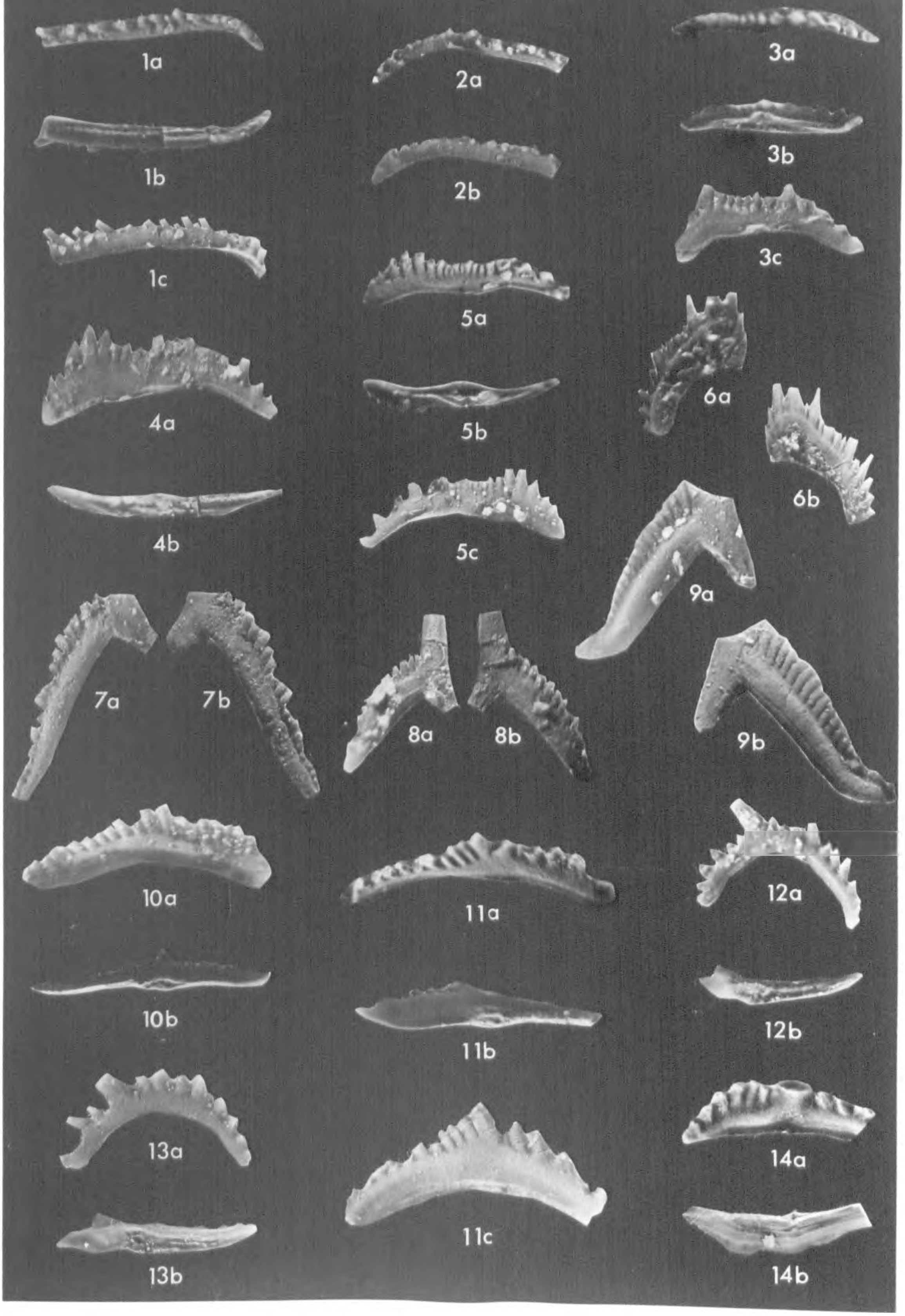
Prioniodina sp.

Fig.12a	Lateral view of specimen JW.248	
b	Aboral view of specimen JW.248	Sample PB.2
Fig.13a	Lateral view of specimen JW.249	
b	Aboral view of specimen JW.249	Sample PB.4

? *Bryantodus* sp.

Fig.14a	Lateral view of specimen JW.250	
b	Aboral view of specimen JW.250	Sample PB.25

PLATE 13


1a
2a
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7b
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11c
13b
14b

CONCLUSIONS

The conodont faunas of the Upper Baggy and the Pilton Beds serve to confirm Goldring's (1956) interpretation of the age of these beds on the basis of the macrofauna. The Upper Baggy and Lower Pilton Formations are of _Wocklumeria_ Stufe age, while those Upper Pilton Beds which proved productive are tentatively correlated with rocks of _Gattendorfia_ Stufe age.

The absence of productive conodont horizons in the many inland exposures of the Baggy and Pilton Beds has restricted this study to the well exposed coastal section at Croyde Bay and Fremington Pill. It is unfortunate that between the youngest productive horizons exposed at Croyde Bay and the oldest productive horizons exposed at Fremington, there is a substantial thickness of unproductive strata which occur in a most critical stratigraphical position. The oldest Croyde Bay faunas are Upper Devonian, while the youngest Fremington faunas are probably Lower Carboniferous. The transition in the faunas from the top of one system to the base of the other is thus interrupted.

Despite this interruption, the conodont faunas of the Baggy and Pilton Beds show basic similarities to those of the German type section, although, in the upper portion of the Lower Pilton Beds, forms more typical of the British Avonian type section are also well represented. In this sense these rocks can be considered to bear a mixed fauna, perhaps a response to a facies type intermediate between those of the 'shelf' and 'trough' seas.

BIBLIOGRAPHY

ANDERSON, W.I. 1966 Upper Devonian conodonts and the Devonian - Mississippian boundary of North Central Iowa. *J. Paleont.*, Chicago, v.40, pp.395-415, pls.48-52.

ANDERSON, J.G.C. and OWEN, T.R. 1968 *The Structure of the British Isles*. Pergamon Press, London.

ARBER, E.A.N. and GOODE, R.H. 1916 On some fossil plants from the Devonian rocks of North Devon. *Proc. Camb. phil. Soc.*, v.18, pp.89-104.

ASH, S.R. 1961 Bibliography and index of conodonts, 1949-1958, *Micropaleontology*, New York, v.7, no.2, pp.213-244.

AUSTIN, R.L. 1965 Conodonts from the Avon Gorge, Bristol. Ph.D. Thesis. University of Wales, Swansea.

——————— 1968 Conodont faunas from the Waulsortian Reef Limestone at Askeaton and from the Cork Red Marble at Midleton. *Sci. Proc. R. Dublin Soc.*, Series A, v.3, no.9, pp.107-114.

AUSTIN, R.L. and BASSETT, M.G. 1967 A *sagitta* Zone conodont fauna - from the Wenlockian of the Usk Inlier, Monmouthshire. *Geol Mag.*, London, v.104, pp.274-283, pl.14.

AUSTIN, R.L. DRUCE, E.C. RHODES, F.H.T. and WILLIAMS, J.A. 1970 The value of conodonts in the recognition of the Devonian - Carboniferous boundary, with particular reference to Great Britain. (In the press.)

BARTENSTEIN, H. and BISCHOFF, G. 1962 Conodonten - Stratigraphic im Devon and Unterkarbon Deutschland. *Leitfossilien der Mikropalaeontologie*, Gubruder Borntraeger. Berlin, pp.43-66, figs.3-6.

BASSLER, R.S. 1925 Classification and stratigraphic use of conodonts (abst). *Bull. geol. Soc. Am.*, New York, v.36, pp.218-220.

BERGSTROM, S.M. and SWEET, W.C. 1966 Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky and its lateral equivalent in Ohio and Indiana. *Bull. Am. Paleont.*, v.50, no.229, pp.271-433, pls.28-35

BISCHOFF, G. 1956 Oberdevonische Conodonten (told) aus dem Rheinischen Schiefergebirge. Notizbl. hess Landesamt. Bodenforsch. Wiesbaden., bd.84, pp.115-137, taf.8-10.

———— 1957 Die Conodonten - stratigraphie des rhenoherzynischen Unterkarbons mit Berucktsichtigung der Wocklumeria - Stufe und der Devon - Karbon Grenze. Notizbl. hess Landesamt. Bodenforsch. Weisbaden., Bd.19, pp.1-64, taf.1-6.

BISCHOFF, G. and SANNEMANN, D. 1958 Unterdevonische Conodonten aus dem Frankenwald. Notizbl. hess Landesamt. Bodenforsch. Weisbaden., Bd.86, pp.87-110, taf.12-15.

BISCHOFF, G. and ZIEGLER, W. 1956 Das Alter der "Urfer Schichten" in Marburger Hinterland nach Conodonten. Notizbl. hess Landesamt. Bodenforsch. Weisbaden., Bd.84, pp.138-169, taf.11-14.

———— 1957 Die Conodontenchronologie des Mitteldevons und des tiefsten Oberdevons. Notizbl. hess Landesamt. Bodenforsch. Weisbaden., Bd.22, pp.1-136, taf.1-21.

BOOGAARD, M. 1963 Conodonts of Upper Devonian and Lower Carboniferous age from Southern Portugal. Geologie Mijnb. The Hague, 42e Jaargang, pp.248-259.

BOOGAERT, H.A. van Adrichem 1967 Devonian and Lower Carboniferous conodonts of the Cantabrian Mountains (Spain) and their stratigraphic application. Leidse Geologische Mededelingen, v.39, pp.129-192, pls.1-3.

BOUCKAERT, J. and HIGGINS, A.C. 1963 La base du Namurien dan le Bassin de Dinant. Bull. Soc. Belge de Geol., v.72(2), pp.1-17

BOUCKAERT, J. and THOREZ, J. 1965 Contribution a l'etude du Devonien superieur dans la region d'Esneux. Bull. Soc. Belge Geol., Pal., Hydr.

BOUCKAERT, J. and ZIEGLER, W. 1965 Conodont stratigraphy of the Famennian Stage (Upper Devonian) in Belgium. Mem. Expl. Cartes geol. et Minieres de la Belgique., v.5, pp.1-62, pls.1-10.

BOULENGER, G.A. 1900 Annales du Musee du Congo, v.1, f.6, p.152

BOYER, F., KRYLATOV, S., LE FÈVRE, J. and STOPPEL, D. 1968 Le Devonien Superieur et la Limite Devono - Carbonifere en Montange Noire (France) Lithostratigraphie - Biostratigraphie (Conodontes). *Bull. Centre Rech. Pau - SNPA*, v.2(1), pp.5-33.

BRANSON, C.C. 1934 Age of the shale series at Bedford, Illinois (abst.). *Proc. geol Soc. Am.*, New York, (for 1933) p.365.

BRANSON, E.B. 1937 Review of conodont studies nembers 1,2,3,4. *Univ. Mo. Stud.*, v.8, pp.1-349, pls.1-28.

———— 1938 Stratigraphy and paleontology of the Lower Mississippian of Missouri, Part 1. *Univ. Mo. Stud.*, v.13, no.3, pp.1-208

———— 1944 The Geology of Missouri. *Univ. Mo. Stud.*, v.19, no.3, pp.1-535, pls.1-49.

BRANSON, E.B. and MEHL, M.G. 1934a Conodonts from the Bainbridge (Silurian) of Missouri. *Univ. Mo. Stud.*, v.8, pp.39-52, pl.3.

———— 1934b Conodonts from the Bushberg Sandstone and equivalent formations of Missouri. *Univ. Mo. Stud.*, v.8, pp.265-300, pls.22-24.

———— 1934c Conodonts from the Grassy Creek shale of Missouri. *Univ. Mo. Stud.*, v.8, pp.171-259, pls.13-21.

———— 1935a Value of conodonts in stratigraphic determinations (abst.). *Proc. geol. Soc. Am.*, New York, (for 1934), p.375.

———— 1935b Methods, problems and results of conodont studies (abst.). *Proc. geol. Soc. Am.*, New York, (for 1934), p.441.

———— 1938 Conodonts from the Lower Mississippian of Missouri. *Univ. Mo. Stud.*, v.13, pp.128-148, pls. 33-34.

———— 1940a Conodonts from the Keokuk formation. *J. scient. Labs. Denison Univ.*, v.40, no.14, pp.179-188, pl.6.

———— 1940b The recognition and interpretation of mixed conodont faunas. *J. Scient. Labs. Denison Univ.*, v.40, no.14, pp.195-209.

BRANSON, E.B. and MEHL, M.G.	1940c	A record of typical American conodont genera in various parts of Europe. J. scient. Labs. Denison Univ., v.40, no.14, pp.189-194, pl.7.
————	1941	New and little known Carboniferous conodont genera. J. Paleont., Chicago. v.15, pp.97-106, pl.19.
————	1944	Conodonts, in Shimer, H.W. & Schrock, R.R., Index Fossils of North America. pp.1-837, (pp.235-246, pls.93,94). John Wiley & Sons, New York.
————	1946	Geological and Geographical distribution of conodonts in the Mississippi Valley (abst.). Bull. geol. Soc. Am., New York, v.57, pp.1263-1264.
————	1948	Conodont homonyms and names to replace them J. Paleont., Chicago, v.22, pp.527-528.
BRANSON, E.B. MEHL, M.G. and BRANSON, C.C.	1951	Richmond conodonts of Kentucky and Indiana. J. Paleont., Chicago, v.25, pp.1-17, pls.1-4.
BRANSON, E.R.	1934	Conodonts from the Hannibal Formation of Missouri. Univ. Mo. Stud., v.8, pp.301-343, pls.25-28.
BROOKS, M. and DRUCE, E.C.	1965	A Llandovery Conglomeratic Limestone in Gullet Quarry, Malvern Hills, and its conodont fauna. Geol. Mag., London, v.102, pp.370-382.
BRYANT, W.L.	1921	The Genessee conodonts. Bull. Buffalo Soc. nat. Sci., v.13, no.2, pp.1-59, pls.1-16.
BUCKLAND, W. and CONYBEARE, W.D.	1824	Observations on the South Western Coal district of England. Trans. geol. Soc. Lond., ser.2, v.1, pp.210-316.
BUDINGER, P. and KULLMANN, J.	1964	Zur frange van Sedimentation - sunterbrech - ungen im Goniatiten und Conodonten -- fuhrenden Oberdevon und Karbon des Kantabrischen Gebirges (Nordspanien). Neues. Jb. Geol. Palaont. Mh., Stuttgart, v.7, pp.414-419.
BUDUROV, K.	1961	Conodonten aus dem Devon Nordostbulgariens. Spis. bulg. geol. Druzh., Sofia, v.22, pp.259-273.
BUDUROV, K. and TSCHURNER, D.	1964	Conodonten fauna und petrographie Charakteristik der Gerollen aus den devonische und unterkarbonischen Kalksteinen in derm jungen Paleozoi Nord west bulgariens (in Bulgarian). Bull. Inst. Scientifique de Recherche Geol., v.1, pp.247-267, pls.1-5.

BUTCHER, N.E. 1959 Culm Measure stratigraphy. *Geol. Mag.*, London, v.96, pp.418-419.

BUTCHER, N.E. and HODSON, F. 1960 A review of the Carboniferous Goniatite zones in Devon and Cornwall, *Palaeontology*, London, v.3, pp.75-81, pls.17-19.

CAMBELL, G. 1946 New Albany Shale. *Bull. geol. Soc. Am.*, New York, v.57, pp.829-908, pls.1-3.

CANIS, W.F. 1968 Conodonts and biostratigraphy of the Lower Mississippian of Missouri. *J. Paleont.*, Chicago, v.42, no.2, pp.525-555.

CLARK, D.L. and ETHINGTON, R.L. 1965 Conodont biostratigraphy of part of the Devonian of the Alberta Rocky Mountains. *Bull. Can. Pet. Geol.*, v.13, no.13, no.3, pp.382-388.

——————— 1966 Conodonts and biostratigraphy of the Lower and Middle Devonian of Nevada and Utah. *J. Paleont.*, Chicago, v.40, no.3, pp.659-689, pls.82-84.

CLARK, D.L. and MOSHER, C.M. 1966 Stratigraphic, geographic and evolutionary development of the conodont genus *Gondolella*. *J. Paleont.*, Chicago, v.40, no.2, pp.376-394, pls.45-47.

CLARKE, W.J. 1960 Scottish Carboniferous conodonts. *Trans. Edinb. geol. Soc.*, v.18, pp.1-31, pls.1-5.

CLOUD, P.E. BARNES, V.E. and HASS, W.H. 1957 Devonian-Mississippian transition in central Texas. *Bull. geol. Soc. Am.*, New York, v.68, pp.807-816, pls.1-6.

COLLINSON, C.W. 1961 The Kinderhookian series in the Mississippi Valley. *Fld. Conf. Guidebk. Kansas geol. Soc.*, v.26, pp.100-109.

——————— 1963 Collection and preparation of conodonts through mass production techniques. *Circ. Ill. St. geol. Surv.*, 343, pp.1-16.

COLLINSON, C.W. REXROAD, C.B. and SCOTT, A.J. 1959 Abundance and stratigraphic distribution of Devonian and Mississippian conodonts in the upper Mississippi Valley. *J. Paleont.*, Chicago, v.33, pp.692-696.

——————— 1962 Six charts showing biostratigraphic zones and correlations based on conodonts from Devonian and Mississippian rocks of the upper Mississippi Valley. *Circ. Ill. St. geol. Surv.* 328, pp. 1-32.

CONIL, R. 1964 Localites et coupes types pour l'etude du Tournasien inferieur (Revision des limites sous l'aspect Micropaleontologique). *Mem. Acad. Roy. Belgique, Mem.* 4°, 2e serie, v.14, 4.

CONIL, R. AUSTIN, R.L. LYS, M. and RHODES, F.H.T. 1969 La limite des etages tournasien et viseen au stratotype de l'assise de Dinant. *Bull. Soc. Belge. Geol.*, Tome. LXXVII, fas.1, pp.40-69, pls.1,2.

CONIL, R. LYS, M. and MAUVIER, A. 1964 Criteres micropaleontologiques essentiels des formations - types du Carbonifere (Dinantien) du Bassin Franco-Belge. *C.R. Congr. Avanc. Etud. stratigr. carb.* (Paris 1963), v.1, pp.325-332.

CONIL, R. PIRLÉT, H. and LYS, M. 1967 Echelle Biostratigraphique du Dinantien de la Belgique. *Prof. paper*. no.13, pp.1-56.

CONYBEARE, W.D. and PHILLIPS, W. 1822 *Outlines of the Geology of England and Wales.* Part 1. William Phillips, London.

COOPER, C.L. 1931 Conodonts from the Arkansas novaculite, Woodford formation, Ohio shale, and Sunbury shale. *J. Paleont.*, Chicago, v.5, pp.143-151 pl. 20

________ 1931a New conodonts from the Woodford formation of Oklahoma. *J. Paleont.*, Chicago, v.5, pp.230-243, pl.28.

________ 1933 Revision of *Ligonodina* Ulrich & Bassler 1926, and *Prioniodus* Pander 1856 (abst.). *Bull. goel. Soc. Am.*, New York, v.44, pp.210

________ 1935 Conodonts from the upper and middle Arkansas novaculite, Mississippian, at Caddo Gap, Arkansas. *J. Paleont.*, Chicago, v.9, pp.307-315, pl.27.

________ 1938 Conodonts from a pre-Welden post-Woodford horizon in Oklahoma (abst.). *Proc. Geol. Soc. Am.*, New York, (for 1937), p.272.

________ 1939 Conodonts from a Bushberg-Hannibal horizon in Oklahoma. *J. Paleont.*, Chicago, v.13, pp.379-422, pls. 39-47.

________ 1939a Erratum to "Conodonts from a Bushberg-Hannibal horizon in Oklahoma". *J. Paleont.*, Chicago, v.13, p.626.

________ 1945 Devonian conodonts from North-western Montana. *J. Paleont.*, Chicago, v.19, pp.612-615, pl.84.

________ 1948 Kinderhook micropaleontology. *J. Geol.*, Chicago, v.56, pp.353-366.

COOPER, C.L. and SLOSS, L.L.	1943	Conodont fauna and distribution of a Lower Mississippian black shale in Montana and Alberta. *J. Paleont.*, Chicago, v.17, pp.168-172, pls.28-29.
CURRIE, E.D. DUNCAN, C. and MUIR-WOOD, H.M.	1937	The fauna of Skipsey's Marine Band. *Trans. geol. Soc. Glsg.*, v.19, pp.413-451.
DAVIDSON, T.	1864-1865	British Fossil Brachiopoda, 3, Pt.6, Devonian Brachiopoda. *Palaeo. Soc.*, London, v.16-17, pp.1-131, pls.1-20.
DEARMAN, W.R.	1959	The structure of the Culm Measures at Meldon, near Okehampton, North Devon. *Q. Jl. geol. Soc. Lond.*, v.115, pp.65-106.
DEARMAN, W.R. and BUTCHER, N.E.	1959	The geology of the Devonian and Carboniferous rocks on the north-west border of the Dartmoor Granite, Devonshire. *Proc. geol. Ass.*, London, v.70, pp.51-92.
DE LA BECHE, H.T.	1839	Report on the Geology of Cornwall, Devon and West Somerset. *Geol. Surv. Gt. Bt.*, London, pp.1-648.
———	1846	On the formation of the rocks of South Wales and South Western England. *Mem. geol. Surv. U.K.*, London, v.1, pp.1-296.
DELEPINE, G.	1951	Studies of the Devonian and Carboniferous of Western Europe and North Africa. *Proc. geol. Ass.*, London, v.62, pp.140-166.
———	1958	Les goniatites du Dinantien de la Belgique. *Mem. Mus. r. Hist. nat. Belg.*, Brussels, no.91.
DEMANET, F.	1956	*Le Dinantien de la Belgique*. pp.1-240, Brussels.
DEWEY, H.	1948	British Regional Geology, South-West England (2nd. Edition). His Majesty's Stationary Office, London. 73pp.
DINELEY, D.L.	1961	The Devonian system in South Devonshire. *Fld. Stud.*, v.1, pp.1-20.
DINELEY, D.L. and RHODES, F.H.T.	1956	Conodont horizons in the west and south-west of England. *Geol. Mag.*, London, v.93, pp.242-248.
DIXON, E.E.L.	1921	The country around Pembroke and Tenby. *Mem. geol. Surv. U.K.*, London, 220pp.

DOW, V.E. 1960 Magnetic separation of Conodonts. *J. Paleont.*, Chicago, v.34, pp.738-743.

DOWNS, H.R. and YOUNGQUIST, W.L. 1950 Conodonts from the Cedar Valley Limestone of Iowa. *J. Paleont.*, Chicago, v.24, pp.667-679, pl.87.

DRUCE, E.C. 1969 Devonian and Carboniferous conodonts from the Boneparte Gulf Basin, Northern Australia. *Dept. Nat. Devel. Bur. Min. Res. Geol. Geophys.*, Bull.98, pp.1-242, pls.1-43.

DUNHAM, K.C. and STUBBLEFIELD, C.J. 1945 The stratigraphy, structure and mineralisation of the Greenhow mining area, Yorkshire. *Q. Jl. geol. Soc. Lond.*, v.100, pp.209-268 (p.240).

DUNN, D.L. 1965 Late Mississippian conodonts from the Bird Spring Formation in Nevada. *J. Paleont.*, Chicago, v.39, pp.1145-1150, pl.140.

DVORAK, J. FREYER, B. and FREYER, G. 1961 Die Devon/Karbon Grenze im Mahrischen Karst (Sudteil des Marischen Sedimentationsbeckens) auf der Grundlage von Conodontenfaunen. *Geologie*, Berlin, v.10, pp.881-895.

EARP, J.R. and MAGRAW, D. 1955 Tongue's Marine Band in Lancashire. *Bull. geol. Surv. Gt. Bt.*, London, v.9, pp.22-32.

EDEN, R.A. 1954 The Coal Measures of Anthraconaia lenisulcata Zone in the East Midlands coalfield. *Bull. geol. Surv. Gt. Br.*, London, v.5, pp.82-84,94,105,106.

EDWARDS, W. 1954 The Yorkshire - Nottinghamshire coalfield, *in* Trueman, A.E., '*The coalfields of Great Britain*', 187pp., Edward Arnold, Lnd.

EDWARDS, W. and STUBBLEFIELD, C.J. 1948 Marine bands and other faunal marker-horizons in relation to the sedimentary cycles of the Middle Coal Measures of Nottinghamshire and Derbyshire. *Q. Jl. geol. Soc. Lond.*, v.103, pp.219,222-223.

EICHENBERG, W. 1930 Conodonten aus dem Culm des Harzes. *Paläont. Z.*, Berlin, v.12, pp.177-182, pl.1

ELLISON, S.P. 1962 Annotated bibliography and index of conodonts. *Univ. Texas* (*Bur. Econ. Geol.*) Pub. no. 6210, 128pp., 6 charts.

——————— 1963 Supplement to annotated bibliography and index of conodonts. *Texas. Jour. Sci.*, v.15, pp.50-67.

ETHERIDGE, R.	1867	On the Physical Structure of West Somerset and North Devon, and on the Palacontological value of the Devonian fossils. *Q. Jl. geol. Soc. Lond.*, v.23, pp.568-698.
ETHINGTON, R.L.	1965	Late Devonian and early Mississippian conodonts from Arizona and New Mexico. *J. Paleont.*, Chicago, v.39, pp.566-589, *pls.67,68.*
ETHINGTON, R.L. and FURNISH, W.M.	1959	Ordovician conodonts from northern Manitoba. *J. Paleont.*, Chicago, v.33, pp.540-546, pl.73.
———	1962	Silurian and Devonian conodonts from Spanish Sahara. *J. Paleont.*, Chicago, v.36, pp.1253-1290, pls.172-173.
ETHINGTON, R.L. FURNISH, W.M. and WINGERT, J.R.	1961	Upper Devonian conodonts from Bighorn Mountains, Wyoming. *J. Paleont.*, Chicago, v.35, pp.759-768, pl.90.
EVANS, J.W.	1922	Geological structure of the country around Combe Martin, North Devon. *Proc. Geol. Ass.*, London, v.33, pp.201-234, pls.6,7.
EVANS, J.W. and STUBBLEFIELD, C.J.	1929	*Handbook of the Geology of Great Britain.* (A compilative work). Thomas Murby & Co., London.
FAIRMAIRE, L.	1843	Trois nouvelles especes d'Insectes de l'Oceanie. *Societe entomologique de France, Annales*, ser.2, v.1, p.13.
FAY, R.O.	1952	Catalogue of conodonts. *Univ. Kansas Paleont. Contrib. Vertebrata*, Art.3, pp.1-206.
———	1958	A key to conodont genera and subgenera. *Oklahoma Geol. Surv. Nts.*, v.18, nos.6,7, pp.103-120.
———	1958a	A key to conodont genera and subgenera - addenda. *Oklahoma Geol. Surv. Nts.*, v.18, p.178.
———	1959	Generic and subgeneric homonyms of conodonts. *J. Paleont.*, Chicago, v.33, pp.195-196.
———	1961	Bibliography and index of conodonts, 1949-1958, a review. *Oklahoma Geol. Surv. Nts.*, v.21, pp.202-203.
FLUGEL, H. and ZIEGLER, W.	1957	Dies Gliederung des Oberdevons und Unterkarbons am Steinberg Westlich Graz mit Conodonten. *Mitt. naturw. Ver. Steierm.*, v.87, pp.25-60, pls.1-5.

FOLK, R.L. 1968 *Petrology of Sedimentary Rocks.* Hemhill's, Austin, Texas, pp. 170.

FOWLER, A. 1944 A deep bore in the Cleveland Hills. *Geol. Mag.*, London, v.81, pp.193-206.

———————— 1955 The zonal sequence in the Carboniferous rocks of Southwest Tyrone. *Bull. geol. Surv. Gt. Br.*, London, v.5, pp.38-43.

FREYER, G. 1961 Zur Taxionomie und Biostratigraphie der Conodonten aus dem Oberdevon des Vogtlandes unter besonderer Berucksichtigung des toV/VI. *Freiberger Forschrungsh.*, Berlin, v.95, pp.1-96, pls.I-VI.

GEORGE, T.N. 1927 The Carboniferous Limestone (Avonian) succession of a portion of the North Crop of the South Wales Coalfield. *Q. Jl. geol. Soc. London.*, v.83, pp.83-95.

GEORGE, T.N. 1940 The structure of the Gower. *Q. Jl. geol. Soc.* Lond., v.96, pp.131-198.

———————— 1952 Tournasian facies in Britain. *Int. geol. Cong.*, v.18, G.B., (10), pp.34-41.

———————— 1955 British Carboniferous Stratigraphy. *Sci. Prog.*, London, v.43, 169, pp.87-103.

———————— 1958 Lower Carboniferous Palaeogeography of the British Isles. *Proc. Yorks. geol. Soc.*, Leeds, v.31, pp.227-318.

GLENISTER, B.F. and CRESPIN, I. 1959 Upper Devonian microfaunas from the Fitzroy Basin, Western Australia. *Aust. J. Sci.*, Sydney, v.21, pp.222-223.

GLENISTER, B.F. and KLAPPER, G. 1966 Upper Devonian conodonts from the Canning Basin, Western Australia. *J. Paleont.*, Chicago, v.40, pp.777-842, pls.85-96.

GLOBENSKY, Y. 1967 Middle and Upper Mississippian conodonts from the Winsor Group of the Atlantic Provinces of Canada. *J. Paleont.* v.41, pp.432-448, pls.55-58.

GOLDRING, R. 1955 The Upper Devonian and Lower Carboniferous trilobites of the Pilton Beds in North Devon. *Senckenberg. leth.*, Frankfurt, v.36, pp.27-48.

———————— 1956 The Upper Devonian & Lower Carboniferous in the Barnstable area of North Devon. Ph.D. Thesis, University of Bristol, Bristol.

GOLDRING, R.	1958	Lower Tournasian trilobites of the Carboniferous Limestone facies of the South West Province of Great Britain and Belgium. *Palaeontology*, London, v.1, pp.231-244.
GRAVES, R.W., Jr.	1952	Devonian Conodonts from the Caballos novaculite. *J. Paleont.*, Chicago, v.26, pp.610-612.
GUPTA, V.J. RHODES, F.H.T. and AUSTIN, R.L.	1967	Devonian conodonts from Kashmir, Nature, v. 216, pp.468-469.
HALL, T.M.	1867	On the relative distribution of fossils throughout the North Devon Series. *Q. Jl. geol. Soc. Lond.*, v.23, pp.371-380.
HAMBLING, J.G. and ROGERS, I.	1910	Excursion to North Devon. *Proc. Geol. Assn.*, London, v.21, pp.457-472.
HARLEY, J.	1861	On the Ludlow bone-bed and its crustacean remains. *Q. Jl. geol. Soc. Lond.*, v.17, pp.542-552, pl.17.
HASS, W.H.	1947	Conodont zone-s in Upper Devonian and Lower Mississippian formations of Ohio. *J. Paleont.*, Chicago, v.21, pp.131-141.
————————	1951	Age of Arkansas novaculite. *Bull. Am. Assoc. Petrol. Geol.*, v.35, pp.2526-2541.
————————	1953	Conodonts of Barnett formation of Texas. *Prof. Pap. U.S. geol. Surv.*, Washington D.C., 243F, pp.69-94, pls.14-16.
————————	1956	Age and correlation of the Chattanooga shale and the Maury formation. *Prof. Pap. U.S. geol. Surv.*, Washington D.C., 286, pp.1-47, pls. 1-5.
————————	1959	Conodonts from the Chappell limestone of Texas. *Prof. Pap. U.S. geol Surv.*, Washington D.C., 294J, pp.365-399, pls.46-50.
————————	1962	Conodonts, in Moore, R.C. Treatise on Invertebrate Paleontology. Pt. W, pp.W3-W69, New York.
HELMS, J.	1959	Conodonten aus dem Saalfelder-Oberdevon (Thuringen). *Geologie*, Berlin, v.8, pp.634-677, pls.1-6.
————————	1961	Die Bedeutung der Conodonten fur die Stratigraphie. *Geologie*, v.10, pp.973-995.

HELMS, J. and WOLSKA, Z.	1967	New Upper Devonian conodonts from Poland and Germany. Acta. Palaeont. Polon., v.12, pp.227-237.
HENDRICKS, E.M.L.	1966	Correlation of South and North Cornwall. Proc. Ussher Soc., v.1, pp.225-227.
HIBBARD, R.R.	1927	Conodonts from the Prtage group of western New York. Am. J. Sct., New Haven, (5), v.13, pp.189-208.
HICKS, H.	1896a	On the Morte Slates and associated beds in North Devon and West Somerset. Part 1, Q. Jl. geol. Soc. Lond., v.52, pp.254-272.
————	1896b	The Palaeozoic rocks of West Somerset and North Devon. Proc. Geol. Ass., London, v.14, pp.357-370.
————	1897	On the Morte Slates and associated beds in North Devon and West Somerset. Part 2, Q. Jl. geol. Soc. Lond., v.53, pp.438-462.
HIGGINS, A.C.	1961	Some Namurian conodonts from North Staffordshire. Geol. Mag., London, v.48, pp.210-224, pls.10-12.
————	1962	Conodonts from the "Griotte" Limestone of north-west Spain. Notas. Comun. Inst. geol. min. Esp., Madrid, No.65, pp.5-22, pls.1-3.
HIGGINS, A.C. WAGNER-GENTIS, C.H.T. WAGNER, R.H.	1964	Basal Carboniferous strata in part of Northern Leon, N.W. Spain. Stratigraphy, Conodont and Goniatite faunas. Bull. Soc. belge Geol. Paleont. Hydrol., Brussels, LXXII, pp.206-248, pls.I-V.
HINDE, G.J.	1879	On annelid jaws from the Cambro-Silurian and Devonian formation in Canada and from the Lower Carboniferous in Scotland. Q. Jl. geol. Soc. Lond., v.35, pp.370-389.
————	1879a	On conodonts from the Chazy and Cincinnati group of the Cambro-Silurian and from the Hamilton and Genesee shale division of the Devonian in Canada and the United States. Q. Jl. geol. Soc. Lond., v.35, pp.351-369, pls. 15, 17.
————	1900	Notes and descriptions of new species of Scottish Carboniferous conodonts. Trans. nat. Hist. Soc. Glasgow, v.5, pp.338-346, pls. 9,10.

HOLMES, G.B. 1928 A bibliography of the conodonts with descriptions of early Mississippian species. *Proc. U.S. natn. Mus.*, Washington, v.72, pp.1-38, pls. 1-11.

HOUSE, M.R. 1963 Devonian ammonoid successions and facies in Devon and Cornwall. *Q.Jl. geol. Soc. Lond.*, v.119, pp.1-27, pls. 1-4.

HOUSE, M.R. and SELWOOD, E.B. 1964 Palaeozoic palaeontology in Cornwall. In: Present views of some aspects of the geology of Cornwall and Devon. *Trans. R. geol. Soc. Corn.*, pp.45-86, pls.1-4.

HUDDLE, J.W. 1934 Conodonts from the New Albany shale of Indiana. *Bull. Am. Paleont.*, Ithaca, v.21, no.72, pp.1-136, pls.1-12.

———— 1968 Redescription of Upper Devonian conodont genera and species proposed by Ulrich and Bassler in 1926. *Prof. Pap. U.S. geol. Surv.* Washington, 578, pp.1-55, pls.1-17.

HULL, E. 1878 A possible explanation of the North Devon section. *Geol. Mag.*, London, v.5, pp.529-532.

———— 1880 On the Geological Relations of the Rocks of the South of Ireland to those of North Devon ... and other British and Continental Districts. *Q. Jl. geol. Soc. Lond.*, v.36, pp.255-276.

IGO, H. and KOIKE, T. 1964 Carboniferous conodonts from the Omi Limestone, Central Japan. *Trans. Proc. Paleont. Soc. Japan*, no.53, pp.179-193.

———— 1965 Carboniferous conodonts from Yabara, Akiyoshi Limestone, Japan. *Trans. Proc. Paleont. Soc. Japan*, no.59, pp.83-91.

IMBRIE, J. 1957 The species problem with fossil animals. The Species Problem, *Amer. Assoc. Advanc. Sci. Pub.*, pp.125-153.

IRELAND, H.A. 1958 Microfauna of Wenlockian and Ludlovian, Silurian beds, in western England (abst.). *Bull. geol. Soc. Am.*, New York, v.69, p.1592.

———— 1962 Microfossils of Wenlockian and Ludlovian Beds of Shropshire, England (Abst.). *Micropaleontology*, v.8, p.284.

JONES, P.J. and DRUCE, E.C. 1966 Intercontinental conodont correlation of the Palaeozoic sediments of the Boneparte Gulf Basin, N.W. Australia. *Nature*, London, v.211, pp.357-359.

KELLAWAY, G.A. and WELCH, F.B.A. 1948 *Bristol and Gloucester District*: British Regional Geology. 91pp. Geol. Surv. and Mus., London.

——— 1955 The Upper Old Red Sandstone and Lower Carboniferous rocks of Bristol and the Mendips compared with those of Chepstow and the Forest of Dean. *Bull. geol. Surv.* Gt. Br., London. no.9, pp.1-21.

KLAPPER, G. 1958 An Upper Devonian conodont fauna from the Darby formation of the Wind River Mountains, Wyoming. *J. Paleont.*, Chicago, v.32, pp.1082-1093, pls.141-142.

——— 1966 Upper Devonian and Lower Mississippian Conodont zones in Montana, Wyoming, and South Dakota. *Paleont. Contr. Univ. Kans.*, Lawrence, Paper 3, pp.1-43, pls.1-6.

KLAPPER, G. and FURNISH, W.M. 1962 Devonian-Mississippian Englewood Formation in the Black Hills, South Dakota. *Bull. Am. Ass. Petrol. Geol.*, Chicago, v.46, pp.2071-2078.

KLAPPER, G. and ZIEGLER, W. 1967 Evolutionary Development of the *Icriodus latericrescens* Group (Conodonta) in the Devonian of Europe and North America. Sonder-Abdruck aus Palaeontographica Beitrage Zur. Naturgeschichte Der Vorzeit, Band 127, Abt. A, pp.69-83.

KOUCKY, F.E. CYGAN, N.E. and RHODES, F.H.T. 1961 Conodonts from the eastern flank of the central part of the Bighorn Mountains, Wyoming. *J. Paleont.*, Chicago, v.35, pp.877-879.

KREBS, W. and ZIEGLER, W. 1965 Uber die Mitteldevon/Oberdevon - Grenze in der Riffazies bei Aachen. *Fortschr. Geol. Rheinld Westf.*, Krefeld, 9, pp.731-754, pls.1,2.

KRONBERG, P. PILGER, A. SCHERP, A. and ZIEGLER, W. 1960 Zu den altvarischenischen Bewegungen an der Wende Devon/Karbon. *Fortschr. Geol. Rheinld. Westf.*, Krefeld, 3, pp.1-46.

LAMONT, A. and LINDSTROM, M. 1957 Arenigian and Llandeilian cherts identified in the Southern Uplands of Scotland by means of conodonts. *Trans. Edinb. geol. Soc.*, v.17, pp.60-70, pl.5.

LANE, H.R. 1967 Uppermost Mississippian and Lower Pennsylvanian conodonts from the type Morrowan region, Arkansas. *J. Paleont.*, Chicago, v.41, pp.920-942, pls.119-123.

LEES, G.M. and COX, P.T. 1937 The geological basis of the present search for oil in Great Britain by the D'Arcy Exploration Company, Limited (with discussion) *Q. Jl. Geol. Soc. Lond.*, no.370, v.93, pp.156 -194, 3 pls.

LIBROVITCH, L.S. 1960 The lower boundary of the Carboniferous system and criteria for its determination. *Congr. Avanc. Etud. Stratigr. carb.*, 1958, pp.375-379.

LINDSTRÖM, M. 1957 Two Ordovician conodont faunas fround with zonal graptolites. *Geol. For. Stockh. Forh.*, Stockholm, v.79, pp.161-178, pls.1-2.

——— 1959 Conodonts from the Crug limestone (Ordovician Wales). *Micropaleontology*, New York, v.5, pp.427-452, pls.1-4.

——— 1960 Conodonts from the Crug limestone (Ordovician Wales) (Comments and Errata). *Micropaleontology*, New York, v.6, p.446.

——— 1964 Conodonts. 196pp. Amsterdam.

LINDSTRÖM, M. and ZIEGLER, W. 1965 Ein Conodontentaxon aus vier morphologisch verschiedenen Typen., *Fortschr. Geol. Rheinld Westf.*, Krefeld, 9, pp.209-218, pls.1,2.

LYS, M. and SERRE, B. 1957 Etude de conodontes du Devonien et du Carbonifere de la region d'Adrar - Tanezrouft (Sahara). *Revue. Inst. fr. Petrole*, v.12, pp.1035-1066, pls.1-7.

——— 1958 Contributions con microfaunas Paleozoique etudes Micropaleontologie dans le Carbonifere des Asturies (Espagne). *Revue. Inst. fr. Petrole*, v.13, pp.881-892, pl.9.

MAGRAW, D. 1957 New boreholes into the Lower Coal Measures below the Arley mines of Lancashire and adjacent areas. *Bull. geol Surv. Gt. Br.*, London, v.13, pp.21-23, 37-38.

MANSON, W. 1957 On the occurrence of a marine band in *Anthraconaia modiolaris* zone of the Scottish Coal Measures with notes on certain marine fossils. *Bull. geol. Surv. Gt. Br.*, London, v.12, pp.66-86.

MANZONI, M. 1966 Conodonti, Neodevonici ed Eocarboniferi al Monte Zermula., *G. Geol.*, v.33, pp.461-488, pls.59,60.

MASON, R.	1881	On sponge spicules, conodonts and fish remains in Specimens Exhibited. Proc. later Trans. Nat. Hist. Soc. Glasg., v.4, pp.190-192.
MATTHEWS, S.C.	1961	A Carboniferous conodont fauna from Callington, East Cornwall, R. geol. Soc. Corn., Proc. 4th Conf. Geol. and Geomorph. Working in the southwest of England, pp.13-15.
————	1962	A Middle Devonian conodont fauna from the Tamar Valley. Proc. Ussher Soc., Redruth, v.1, pp.27-28.
————	1966	Lower Carboniferous Stratigraphy in the St. Mellion area. Proc. Ussher Soc., Redruth, v.1, pp.227-229.
————	1969a	A lower Carboniferous conodont fauna from East Cornwall, Palaeontology, London, v.12, pp.262-275.
————	1969b	Two conodont faunas from the Lower Carboniferous of Chudleigh, South Devon, Palaeontology, London. v.12, pp.276-280.
MATTHEWS, S.C. and THOMAS, J.M.	1968	Conodonts from the Dinantian of North East Devon - Ussher. Soc. Proc., v.2, pt.1, pp.27-28.
MEHL, M.G.	1960	The relations of the base of the Mississippian system in Missouri. J. scient. Labs Denison Univ., v.45, pp.58-107.
MEHL, M.G. and THOMAS, L.A.	1947	Conodonts from the Fern Glen of Missouri. J. scient. Labs Denison Univ., v.47, pp.3-19, pl.1.
MEISCHNER, K.D.	1962	Rhenaer Kalk und Posidonienkalk im Kulm des nordoctlichen Rheinischen Schiefergebirges und der Kohlenkalk von Schreufa (Eder). Abh. hess. Landesamt. Bodenforsch., Weisbaden, no.39, pp.1-47, pls.1-7.
MILLER, S.A.	1889	North American geology and palaeontology for the use of amateurs, students and scientists. Cincinnati, Western Methodist Book Concern. 718 p.
MITCHELL, G.H.	1954	The Whittington Heath borehole. Bull. geol. Surv. Gt. Br., London, v.5, pp.1-60.
MITCHELL, G.H. and STUBBLEFIELD, C.J.	1941	The geology of the Leicestershire and South Derbyshire coalfield. Mem. geol. Surv. U.K., Wartime Pamphlet, No.22.

MITCHELL, G.H. STUBBLEFIELD, C.J. and CROOKALL, R.	1942	The geology of the Warwickshire coalfield. *Mem. geol. Surv. U.K., Wartime Pamphlet*, No.25.
———	1945	The geology of the northern part of the south Staffordshire coalfield. (Cannock Chase region). *Mem. geol. Surv. U.K.*, *Wartime Pamphlet*, No.43.
MOORE, C.	1863	On the Palaeontology of mineral veins; and on the secondary age of some mineral veins in the Carboniferous limestone. *Rep. Br. Ass. Advmt. Sci.*, 32nd. meet., Oct. 1862, pp.82-83.
———	1864	On the organic contents of the lead veins of Allenheads, and other lead veins of Yorkshire. *Rep. Br. Ass. Advmt. Sci.*, 33rd. meet., Aug. 1863, 83.
———	1870	Report on mineral veins in Carboniferous limestone and their organic contents. *Rep. Br. Ass. Advmt. Sci.*, 39th meet., pp.360-380.
MOUND, M.C.	1965	*Kladognathus* Rexroad 1958, not *Clydagnathus* Rexroad and Collinson 1961. *Micropaleontology*, New York, v.11, pp.372-373.
———	1968	Upper Devonian conodonts from southern Alberta. *J. Paleont.*, Chicago. v.42, pp.444-524.
MULLER, K.J.	1956	Triassic conodonts from Nevada. *J. Paleont.*, Chicago, v.30, pp.818-830. pls.95,96.
———	1962	A conodont fauna from the Banff Formation, western Canada. *J. Paleont.*, Chicago, v.36, pp.1387-1391.
MULLER, K.J. and CLARK, D.L.	1967	Early late Devonian conodonts from the Squaw Bay Limestone in Michigan. *J. Paleont.*, Chicago, v.41, pp.902-919, pls.115-118.
MULLER, K.J. and MULLER, E.M.	1957	Early Upper Devonian (Independence) conodonts from Iowa, Part 1. *J. Paleont.*, Chicago, v.31, pp.1069-1108, pls.135-142.
NICHOLSON, H.A.	1888	On certain anomalous organisms which are concerned in the formation of some of the Palaeozoic limestones. *Geol. Mag.*, London, pp.15-24.
ORR, R.W.	1964	Conodonts from the Devonian Lingle and Alto formations of Southern Illinois. *Circ. Ill. St. geol. Surv.*, circ. 361, pp.1-28, pls.1-4.

ORR, R.W. and KLAPPER, G. 1968 Two new conodont species from Middle-Upper Devonian boundary beds of Indiana and New York. *J. Paleont.*, Chicago, v.42, pp.1066-1075, pls. 139,140.

PAECKELMANN, W. and SCHINDEWOLF, O.H. 1935 Die Devon-Karbon-Grenze. *Congr. Avanc. Etud. Stratigr. carb.*, 2nd., pp.703-714.

PANDER, C.H. 1856 *Monographie der fossilen Fische des silurischen Systems der russischbaltischen Gouvernements.* St. Petersburg, pp.1-91, pls. 1-9, (pp.5-34, 80, pls.1-4).

PAPROTH, E. 1960 Der Kulm und die floz leere Fazies des Namurs Stand der Untersuchungen und offene Fragen. Fortschr. *Geo. Rheinld. Westf.*, Krefeld, No.1, pp.385-422.

——— 1964 The lower limit of the Carboniferous. *Congr. Avanc. Etud. Stratigr. carb.*, 1958, pp.611-618.

PAUL, H. 1937 The relationships of the Pilton Beds in North Devon to their equivalents on the Continent. Geol. Mag., London, v.74, pp.433-442.

——— 1937a Die Transgression der Vise Stufe am Nordrande des Rheinischen Schiefergebirges. *Abh. preuss. geol. Landesanst.*, Berlin, 179, pp.1-117.

——— 1939 Die Etroeungt Schichten des Bergischen Landes. *Jb. preuss. Geol. Landesanst.*, Berlin, 59, pp.647-726, pls.39-42.

PETTIJOHN, F.J. 1957 *Sedimentary Rocks*, 2nd. Edn., Harper and Bros. New York, pp.1-718.

PHILIP, G.M. 1966 Lower Devonian conodonts from the Buchan Group, E. Victoria, Australia, *Micropaeontology*, New York, v.12, pp.441-460, pls.1-4.

PHILLIPS, J. 1841 Figures and descriptions of the Palaeozoic Fossils of Cornwall, Devon and West Somerset. London. pp.1-231, 60pls.

POLLOCK, C.A. 1968 Lower Upper Devonian conodonts from Alberta, Canada. *J. Paleont.*, Chicago, v.42, pp.415-443, pls. 61-64.

PRENTICE, J.E. 1960 The Dinantian, Namurian and Lower Westphalian rocks of the region of South West Barnstable, North Devon. *Q. Jl. geol. Soc. Lond.*, v.115, pp.261-289.

PRENTICE, J.E. 1962 The sedimentation history of the Carboniferous in Devon, in A.J. Cox and Scott Simpson, '*Some Aspects of the Variscan Fold Belt*'. pp.93-108, Manchester.

PRENTICE, J.E. and THOMAS, J.M. 1965 *Prolecanitina* from the Carboniferous rocks of North Devon. *Proc. Yorks. geol. Soc.*, v.35, Pt.1, No.2, pp.33-46, pls.1,2.

PRINGLE, J. and GEORGE, T.N. 1961 *South Wales British Regional Geology*. 2nd Edn. 100pp., London.

RAMSBOTTOM, W.H.C. 1952 The fauna of the Cefn Coed Marine Band in the Coal Measures of Aberbaiden near Tondu, Glamorgan. *Bull. geol. Surv. Gt. Br.* 4, pp.8-32.

REED, F.R.C. 1942 Some new Carboniferous trilobites. *Ann. Mag. Nat. Hist.* (II), v.9, pp.649-672.

———— 1943 Notes on certain Upper Devonian Brachiopods figured by Whidbourne. *Geol. Mag.*, London, v.80, pp.69-78, 95-106, 132-138.

———— 1944 Notes on the Upper Devonian trilobites in the Whidborne collection in the Sedgewick Museum. *Geol. Mag.*, London, v.81, pp.121-126.

REXROAD, C.B. 1957 Conodonts from the Chester series in the type area of south-western Illinois. *Rep. Invest. Ill. St. geol. Surv.*, no.199, pp.1-43, pls.1-4.

———— 1958 Conodonts from the Glen Dean formation (Chester) of the Illinois Basin. *Rep. Invest. Ill. St.* geol. Surv., no.209, pp.1-27, pls.1-6.

REXROAD, C.B. and BURTON, R.C. 1961 Conodonts from the Kinkaid Formation (Chester) in Illinois. *J. Paleont.*, Chicago, v.35, pp.1143-1158, pls.138-141.

REXROAD, C.B. and CLARKE, C.E. 1960 Conodonts from the Glen Dean Formation of Kentucky and equivalent formations of Virginia and West Virginia. *J. Paleont.*, Chicago, v.34, pp.1201-1206.

REXROAD, C.B. and COLLINSON, C.W. 1961 Preliminary range chart of conodonts from the Chester Series (Mississippian) in the Illinois Basin. *Circ. Ill. St. Geol. Surv.*, circ. 319, pp.1-11.

———— 1963 Conodonts from the St. Louis Formation (Valmeyeran series) of Illinois, Indiana and Missouri. *Circ. Ill. St. geol. Surv.*, circ.355, pp.1-28, pl.2.

REXROAD, C.B. and COLLINSON, C.W. 1965 Conodonts from the Keokuk, Warsaw and Salem formations (Mississippian) of Illinois. *Circ. Ill. St. geol. Surv.*, circ. 388, pp.1-26, pl.1.

REXROAD, C.B. and FURNISH, W.M. 1964 Conodonts from the Pella Formation (Mississippian), South Central Iowa. *J. Paleont.*, Chicago, v.38, pp.667-676, pl.III.

REXROAD, C.B. and LIEBE, R.M. 1962 Conodonts from the Paoli and equivalent formations in the Illinois Basin. *Micropaleontology*, New York, v.8, pp.509-514.

REXROAD, C.B. and SCOTT, A.J. 1964 Conodont zones in the Rockford Limestone and the Lower part of the New Providence Shale (Mississippian) in Indiana. *Bull. Indiana Dep. Conserv. geol. Surv.*, 30, pp.1-54, pls.2,3.

REYNOLDS, S.H. and SMITH, S. 1925 The Old Red Sandstone and Avonian succession at Westbury-on-Trym. *Geol. Mag.*, London, v.62, pp.464-473.

REYNOLDS, S.H. and VAUGHAN, A. 1911 The faunal and lithological succession in the Carboniferous Limestone series (Avonian) of Burrington Combe, Somerset. *Q. Jl. geol. Soc. Lond.*, v.67, pp.342-392.

RHODES, F.H.T. 1952 A classification of Pennsylvanian conodont assemblages. *J. Paleont.*, Chicago, v.26, pp.886-901, pls.126-129.

——————— 1953 Some British Lower Palaeozoic conodont faunas. *Phil. Trans. R. Soc.*, ser.(B), no.647, v.237, pp.261-334, pls.20-23.

——————— 1954 The zoological affinites of conodonts. *Biological Reviews*, v.29, pp.419-452.

——————— 1955 The conodont fauna of the Keisley Limestone. *Q. Jl. geol. Soc. Lond.*, v.111, pp.117-142, pls.7-10.

RHODES, F.H.T. AUSTIN, R.L. and DRUCE, E.C. 1969 British Avonian (Carboniferous) conodont faunas, and their value in local and intercontinental correlation. *Bull. Br. Mus. (Nat. Hist.), Geol.* Supp.5, London, pp.1-313, pls.1-31.

RHODES, F.H.T. and DINELEY, D.L. 1957a Devonian conodont faunas from southwest England. *J. Paleont.*, Chicago, v.31, pp.353-369, pls.37,38.

——————— 1957b Supplementary notes on Devonian conodont faunas from southwest England. *J. Paleont.*, Chicago, v.31, pp.1175.

RHODES, F.H.T. and MULLER, K.J. 1956 The conodont genus *Prioniodus* and related forms. *J. Paleont.*, Chicago, v.30, pp.695-699.

RHODES, F.H.T. and NEWALL, G. 1963 Occurrence of *Kockelella variabilis*, Walliser in the Aymestry Limestone of Shropshire, *Nature*, v.199, pp.166-167.

RICHTER, RUD. 1951 Der Beginn des Karbons im Wechsel der Trilobiten. *Senckenbergiana*, v.32, pp.219-266, pl.1-5.

ROBBIE, J.A. 1955 The Carboniferous rocks of Edenork County, Tyrone. *Bull. geol. Surv. Gt. Br.*, Bull.8, pp.21-37.

ROUNDY, P.V. 1926 The micro-fauna in Mississippian formations of San Saba County, Texas. *Prof. pap. U.S. Geol. Surv.*, Washington. Pap.146, pp.1-63, pls.1-4.

SALTER, J.W. 1863 On the Upper Old Red Sandstone and Upper Devonian Rocks. *Q. Jl. geol. Soc. Lond.*, v.19, pp.474-496.

SANDBERG, C.A. and KLAPPER, G. 1967 Stratigraphy, Age and Paleotectonic significance of the Cottonwood Canyon Member of the Madison Limestone in Wyoming and Montana. *Bull. U.S. Geol. Surv.*, Washington, 1251-B, pp.B1-B70.

SANNEMANN, D. 1955 Oberdevonische Conodonten. *Senckenbergiana*, Frankfurt, Bd.36, pp.123-156.

——————— 1955a Beitrag zu Untergliederung des Oberdevons nach Conodonten. *Neues. Jb. Geol. Palaont.*, Stuttgart, Bd.100, pp.324-330, pl.24.

——————— 1955b Ordovicium und Oberdevon der Bayerischen Fazies des Frankenwaldes nach Conodonten - funden. *Neus. Jb. Geol. Palaont.*, Stuttgart, Bd.102, pp.1-36, pls.1-3.

SAVAGE, T.E. and SUTTON, A.H. 1931 Age of the black shale in south-central Kentucky. *Am. J. Sci.*, New Haven, 5th ser., v.22, pp.441-448.

SCHINDEWOLF, O.H. 1927 Zur Kenntnis der Devon-Karbon-Grenze in Deutschland. *Z. Dt. geol. Ges.*, Berlin, Bd.78, pp.88-133.

——————— 1928 Die Liegendgrenze des Karbons im Lichte biostratigraphischer Kritik. *Congr. Avanc. Etud. Stratigr. carb.*, 1927, pp.651-661.

SCHINDEWOLF, O.H. 1935 Probleme der Devon-Karbon-Grenze, 16th Int. geol. Congr. 1933, pp.505-514.

——— 1939 Bemerkungen zur stratigraphic des oberfrankisch-ostthuringischen Unterkarbons. Jb. preuss. geol. Landesanst. Berg. Akad., Berlin, Bd.59, pp.456-475.

SCHMIDT, H. 1924 Zwei Cephalopoden fauna an der Devon-Karbon-Grenze in Sauerland. Jb. preuss. geol. Landesanst. Berg. Akad., Berlin, Bd.44, pp.1923-1924.

——— 1925 Die Carbonischen Goniatiten Deutschlands. Jb. press. geol. Landesanst. Berg. Akad., Berlin, Bd.45, pp.489-609.

——— 1928 Biostratigraphie des Carbon in Deutschland. Congr. Avanc. Etud. Stratigr. carb. 1927, pp.663-673.

SCOTT, A.J. 1961 Three new conodonts from the Louisiana Limestone (Upper Devonian) of western Illinois. J. Paleont., Chicago, v.35, pp.1223-1227.

SCOTT, A.J. and COLLINSON, C.W. 1959 Intraspecific variability in Conodonts: Palmatolepis glabra - Ulrich & Bassler. (Late Devonian of Illinois). J. Paleont., v.33, pp.550-565, pls.75-76.

——— 1961 Conodont faunas from the Louisiana and McCraney formations of Illinois, Iowa and Missouri. Fld. Conf. Guidebk. Kansas geol. Soc., (26th), pp.110-142.

SEDGEWICK, A. and MURCHISON, R.I. 1836 Classification of the slate rocks of the North of Devonshire and on the true position of the Culm Deposits in the central portion of the county. Br. Ass. Rep., 5, 95.

——— 1840 On the physical structure of Devonshire, and on the subdivisions and geological relations of its older startified deposits, etc. Trans. Geol. Soc. Lond., London, v.5, pp.633-705, pls.50-57.

SELWOOD, E.B. 1960 Ammonoids and Trilobites from the Upper Devonian and Lower Carboniferous of the Launceston area, Cornwall. Palaeontology, London, v.3, pp.153-185, pls.26-29.

——— 1961 The Upper Devonian and Lower Carboniferous Stratigraphy of Boscastle and Tintagel, Cornwall. Geol. Mag., London, v.98, pp.161-167.

SELWOOD, E.B. 1965 Dichenellid trilobites from Britain's Middle Devonian. Bull. Br. Mus. (Nat. Hist.). v.10, pp.319-333, pl.1.

SERRE, B. and LYS, M. 1959 Apercu sur les Conodontes des calcaires devoniens de l'Anjou. Bull. Soc. Etud. scient. Angers, Tome. II, v.89, pp.105-106.

——— 1960 Repartition de quelques conodontes dans le Devonien et le Carbonifere inferieur de France et de Belgique. Int. geol. Congr. 21, Rept. part. 6, Proc. of sec. 6, Pre-Quaternary micropaleontology, pp.35-40.

SHANNON, W.G. 1928 The geology of the Tourquay District. Proc. Geol. Ass., London, v.39, pp.103-156.

SIMPSON, S. 1951 Some solved and unsolved problems of stratigraphy of the marine Devonian in Great Britain. Abhandlungen Senckenberg. Nat. Gesell. 485, pp.53-66.

——— 1959 Culm stratigraphy and the age of the main orogenic phase in Devon and Cornwall. Geol. Mag., London, v.96, pp.201-208.

——— 1962 The Devonian-Carboniferous boundary and the problem of the British and Ardennes-Rhineland successions from the Upper Famennian to the Namurian. Congr. Avanc. Etud. Stratigr. carb., (4th.). pp.629-633.

SMITH, J. 1900 Conodonts from the Carboniferous Limestone strata of the west of Scotland. Trans. nat. Hist. Soc. Glasg., v.5, pp.336-338.

——— 1907 On the occurrence of conodonts in the Arenig-Llandeilo formation of the Southern Uplands of Scotland. Trans. nat. Hist. Soc. Glasg., v.7, pp.235-252, pls.5-9.

——— 1907a Conodonts in Coal Measure Strata. Geol. Mag., London, v.4, pp.239.

SMITH, J. and JONES, T.R. 1881 Notes on a collection of bivalved Entomostraca and other Microzoa from the Upper Silurian strata of the Shropshire District. Geol. Mag., London, v.8, pp.70-75.

SPASOV, C. 1965 Das Karbonatische Oberdevon im Kraiste und seine Conodontenfauna (in Bulgarian). Trud. Geol. Bulg., Sofia, v.7, pp.71-113, pls.1-3.

STAUFFER, C.R. 1938 Conodonts from the Olentangy Shale, *J. Paleont.*, Chicago, v.12, pp.411-443, pls.48-53.

——— 1940 Conodonts from the Devonian and associated clays of Minnesota. *J. Paleont.*, Chicago, v.14, pp.417-435, pls.58-60.

STEFANOV, S.A. and OTHERS 1962 The Carboniferous system and its main stratigraphic subdivisions. *Congr. Avanc. Etud. Stratigr. carb.*, (4th), pp.645-656.

STEVENSON, I.P. and MITCHELL, G.H. 1955 Geology of the country between Burton, Trent, Rugeley and Uttoxeter. *Mem. geol. Surv. Gt. Br.*, London, (11), pp.10-19.

STOPPEL, D. 1961 Geologie des sudlichen Kellerwaldgebirges. *Abh. hess. Landesamt.* Bodenforsch, Berlin, H.34, pp.1-114.

STREEL, M. 1966 Criteres palynologiques pour une stratigraphie deaillee du inla dans les bassins ardenno-rhenans. *Annls. Soc. geol. Belg.*, 89, pp.65-95.

STUBBLEFIELD, C.J. and CALVER, M.A. 1955 Palaeontology of the Coal Measures in Stevenson, I.P. and Mitchell, G.H., and others; Geology of the country between Burton, Trent, Rugeley and Uttoxeter. *Mem. geol. Surv. Gt. Br.*, pp.20-30.

SYLVESTER-BRADLEY, P.C. 1958 The description of fossil populations. *J. Paleont.*, Chicago, v.32, pp.214-235.

THOMAS, L.A. 1949 Devonian-Mississippian formations of southwest Iowa. *Bull. geol. Soc. Am.*, New York, v.60, pp.403-407, pls.1-4.

——— 1950 Sweetland Creek (Devonian) conodonts. *J. Paleont.*, Chicago, v.24, pp.497-498.

THOMPSON, T.L. 1967 Conodont zonation of Lower Osageon rocks (Lower Mississippian) of southwestern Missouri, *Rep. Inv. Mo. geol. Surv.*, v.39, pp.1-88, pls.1-6.

ULRICH, E.O. and BASSLER, R.S. 1926 A classification of tooth-like fossils, conodonts, with descriptions of American Devonian and Mississippian species. *Proc. U.S. natn. Mus.*, Washington, v.68, pp.1-63, pls.1-11.

USSHER, W.A.E. 1881 On the Palaeozoic rocks of North Devon and West Somerset. *Geol. Mag.*, London, v.8, pp.441-449.

USSHER, W.A.E.	1900	The Devonian, Carboniferous and New Red rocks of West Somerset, Devon, and Cornwall. Proc. Somerset Arch. N.H. Soc., v.46, pp.1-64.
USSHER, W.A.E. and CHAMPERKNOWNE, A.	1879	Notes on the Structure of the Palaeozoic Districts of West Somerset. Q. Jl. geol. Soc. Lond., v.35, pp.532-548.
VARKER, W.J.	1967	Conodonts of the genus Apatognathus Branson & Mehl from the Yoredale Series of England. Palaeontology, London, v.10, pp.124-141, pls.17-18.
VAUGHAN, A.	1905	The palaeontological sequence in the Carboniferous Limestone of the Bristol area. Q. Jl. geol. Soc. Lond., v.61, pp.181-305.
————————	1906	The Carboniferous Limestone series (Avonian) of the Avon Gorge, Proc. Bristol Nat. Soc., v.1, pp.74-168.
————————	1909	The faunal succession of the Lower Carboniferous (Avonian) of the British Isles. Rep. 79th Br. Ass. Advmt. Sci. (Winnipeg).
————————	1915	Correlation of Dinantian and Avonian. Q. Jl. geol. Soc. Lond., v.71, pp.1-52.
VOGES, A.	1959	Conodonten aus dem Unterkarbon I & II (Gattendorfia - und Pericyclus - stufe) des Sauerlandes. Palaont. Z., Berlin, Bd.33, pp.266-314, pls.33-35.
————————	1960	Die Bedeutung der Conodonten fur die Stratigraphie des Unterkarbon I and II (Gattendorfia - und Pericyclus - stufe) in Sauerlandes. Fortschr. Geol. Rheinld. Westf., Krefeld, v.3, pp.1-33.
WALLISER, O.H.	1957	Conodonten aus dem overen Gotlandium Deutschlands und der Karnischen Alpen. Notizbl. hess. Landesamt. Bodenforsch Weisbaden, Bd.35, pp.28-52, pls.6,7.
————————	1958	Rhombocorniculum comleyense. n. gen. n. sp. Palaont. Z., Berlin, Bd.32, pp.176-186.
————————	1960	Zum Alter des kimgstem Diadasvalkanismus in der Lahn und Dilt Mulde. Fortschr. Geol. Rheinld. Westf., Krefeld, v.3, pp.229-242.
————————	1964	Conodonten des Silurs. Abh. hess. Landesamt Bodenforsch., Bd.41, pp.1-106.

WEAVER, T. 1838 Geological relations of North Devon. Proc. Geol. Soc., London, v.2, pp.589-590.

——— 1839 On the older stratified rocks of North Devon. Phil. Mag., v.15, pp.109-129.

WEBBY, B.D. 1965 The stratigraphy and structure of the Devonian rocks in the Brendon Hills, West Somerset. Proc. Geol. Ass., London, v.76, pp.39-61.

——— 1966a The stratigraphy and structure of the Devonian rocks in the Quantock Hills, West Somerset, Proc. Geol. Ass., London, v.76, pp.321-345.

——— 1966b Middle-Upper Devonian Palaeogeography of North Devon and West Somerset, England. Palaeogeog. Palaeoclim. Palaeoecol., Amsterdam, v.2, no.1, pp.27-46.

WEBBY, B.D. and THOMAS J.M. 1965 Whitsun Field Meeting: Devonian of West Somerset and Carboniferous of North-East Devon. Proc. Geol. Ass., London, v.76, pp.179-195.

WEBERS, G.F. 1966 The Middle and Upper Ordovician Conodont faunas of Minnesota. Minn. Geol. Surv. SP-4, pgs.1-123, pls.1-15.

WHIDBOURNE, G.F. 1896 A preliminary synopsis of the fauna of the Pickwell Down, Baggy & Pilton Beds. Proc. Geol. Ass., London, v.14, pp.371-377.

——— 1896-1907 A monograph of the Devonian fauna of the South of England: 3. The fauna of the Marwood and Pilton Beds. Palaeont. Soc. Lond., v.50, pp.1-247.

——— 1901 Devonian fossils from Devonshire. Geol. Mag., London, v.8, pp.529-540.

WHITTARD, F.W. 1927 The stratigraphy of the Valentian rocks of Shropshire, the main outcrop. Q. Jl. geol. Soc. Lond., pp.737-759.

WILLIAMS, D. 1839 On the classification of certain geological formations in Devonshire. Phil. Mag., v.14, pp.358-359.

——— 1839a On as much of the Transition or Greywacke System as is exposed in the counties of Somerset, Devon and Cornwall. Proc. Geol. Soc., London, v.3, pp.115-117.

WINDER, C.G. 1962 Upper Devonian age of the Kettle Point Shale. *Trans. R. Soc. Can.*, Ottawa, v.56, pp.85-95.

——— 1966 Conodont zones and stratigraphic variability in Upper Devonian rocks, Ontario, *J. Paleont.*, Chicago, v.40, pp.1275-1293, pl.156.

WITTEKINDT, H. 1965 Zur Conodontenchronologie des Mitteldevons. *Fortschr. Geol. Rheinld.* Westf., v.9, pp.621-645, pls.1-3.

WOLSKA, Z. 1967 Upper Devonian conodonts from the south-west region of the Holy Cross Mountains, Poland, *Acta Palaeont. Polon.* v.12, pp.363-435, pls.1-19.

WOODLAND, A.W. ARCHER, A.A. EVANS, W.B. and CALVER, M.A. 1957 Recent boreholes into the Lower Coal Measures below the Gellideg-Lower Pumpquart coal horizon in South Wales. *Bull. geol. Surv. Gt. Br.*, London, Bull. 13, pp.39-60.

WOODWARD, H. 1902 On a collection of trilobites from the Codden Hill Beds, Lower Culm Measurers, near Barnstable, North Devon, and one from Glamorganshire. *Geol. Mag.*, London, v.9, pp.481-487.

YOUNG, J. 1880 Notes on Scottish Carboniferous Microzoa and the methods by which they may be collected and mounted. *Trans. Edinb. geol. Soc.*, v.3, pp.299-303.

——— 1880a On a group of fossil organisms termed conodonts. Proc. later *Trans. Nat. Hist. Soc. Glasg.*, v.4, pp.5-7,10,78,79.

YOUNGQUIST, W.L. 1945 Upper Devonian conodonts from the Independence shale of Iowa. *J. Paleont.*, Chicago, v.19, pp.355-367, pls.54-56.

——— 1947 A new Upper Devonian conodont fauna from Iowa. *J. Paleont.*, Chicago, v.21, pp.95-112, pls.24-26.

YOUNGQUIST, W.L. and DOWNS, R.H. 1951 Conodonts from the Lower Mississippian Wassonville dolomite of Iowa. *J. Paleont.*, Chicago, v.25, pp.785-792, pl.3.

YOUNGQUIST, W.L. HIBBARD, R.R. and REIMANN, I.G. 1948 Additions to the Devonian conodont faunas of western New York. *J. Paleont.*, Chicago, v.22, pp.48-59, pls.14,15.

YOUNGQUIST, W.L. and MILLER, A.K. 1948 Additional conodonts from the Sweetland Creek shale of Iowa. *J. Paleont.*, Chicago, v.22, pp.440-450, pls.67-68.

YOUNGQUIST, W.L. and MILLER, A.K. 1949 Conodonts from the late Mississippian Pella beds of south-central Iowa. J. Paleont., Chicago, v.23, pp.617-622, pl.101.

YOUNGQUIST, W.L. MILLER, A.K. and DOWNS, H.R. 1950 Burlington conodonts from Iowa. J. Paleont., Chicago, v.24, pp.525-530, pl.67.

YOUNGQUIST, W.L. and PATTERSON, S.H. 1949 Conodonts from the Lower Mississippian Prospect Hill Sandstone of Iowa. J. Paleont., Chicago, v.23, pp.57-73, pls.15-17.

YOUNGQUIST, W.L. and PETERSON, R.F. 1947 Conodonts from the Sheffield formation of north-central Iowa. J. Paleont., Chicago, v.21, pp.242-253, pls.36-38.

ZIEGLER, W. 1958 Conodontenfeinstratigraphische Untersuchungen an der Grenze-Mittel-devon/Oberdevon und in der Adorfstufe. Notizbl. hess Landesamt. Bodenforsch. Weisbaden, Bd.84, pp.7-77, pls.1-12.

——— 1959 Conodonten aus Devon und Karbon Sudwesteuropas und Bemerkungen zur Bretonischen Faltung. Neues. Jb. Geol. Palaont. Mh., Stuttgart, 289-309.

——— 1960 Conodonten aus dem Rheinischen Unterdevon (Gedinnium) des Remscheider Sattels (Rheinischen Schiefergebirges) Palaont. Z., Berlin, Bd.34, pp.169-201, pls.13-15.

——— 1960a Die Conodonten aus den Gerollen des Zechsteinkonglomerates von Rossensay (sudwestlich Rheinberg/Neiderrhein). Fortschr. Geol. Rheinld. Westf., Krefeld, Bd.6, pp.1-15, pls.1-4.

——— 1961 Ctenognathodus Fay 1959, or Spathognathodus Branson & Mehl 1941? J. Paleont., Chicago, v.35, pp.1236-1238.

——— 1962 Taxonomie und Phylogenie Oberdevonischer Conodonten und ihre stratigraphische Bedeutung. Abh. hess. Landesamt. Bodenforsch. Weisbaden, Heft.38, pp.1-166, pls.1-14.

——— 1962a Conodonten aus den Huinhauser Schichten (Gedinnium) des Remscheider Sattels: International Arbeitstagung uber die Silur-Devon-Grenze und die Stratigraphie von Silur und Devon, Bonn-Bruzelles, 1960. Symposium Band, E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart, pp.296-303.

ZIEGLER, W. 1963 Conodonten aus dem Unterkarbon der Behrung Munsterland I. *Fortschr. Geol. Rheinld. Westf.*, Krefeld, pp.319-328, pls.1,2.

—————— 1969 Eine neue Conodontenfauna aus dem hochsten Oberdevon. *Fortschr. Geol. Rheinld. Westf.*, Krefeld, 17, pp.343-360, pls.1,2.

ZIEGLER, W. KLAPPER G. and LINDSTROM, M. 1964 The validity of the name *Polygnathus* (Conodonta, Devonian and Lower Carboniferous). *J. Paleont.*, Chicago, v.38, pp.421-422

ZIMMERMANN, E. 1960 Conodonten aus dem Oberdevon von Wildenfels (Sachsen). *Freiberger Forschrungsh.*, Berlin, (c), pp.177-299.

ADDITIONAL REFERENCES

WILLS, L.J. 1959 *Palaeogeographical Atlas*, Blackie & Son, Glasgow, pp.1-64.