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Conodonts, correlation and stratigraphy of the Plymouth Limestones

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Summary

This work embraces the study of the conodonts and the environments of the Plymouth Limestones (Devonian, South Devon).

Widespread sampling of calcareous strata in the Plymouth area has produced conodonts indicative of high Emsian to mid - Famennian levels.

The European Conodont Standard is reviewed and comparisons are made with North American and Australian successions; the South Devon faunas are examined and discussed in their light. The results indicate that, on the whole, the Upper Devonian faunas are comparable but Middle Devonian successions differ in some respects. Most of the diagnostic conodonts are treated systematically and several new form-species are introduced. Correlation based on the conodont faunas are presented for most of the disjunct sections.

The Plymouth Limestones are discussed in the context of the Variscan geosyncline and Cornubian palaeogeography. A review of the Devonian carbonate buildups, and the facial differentation therein, is followed by an assessment of the local situation in terms of possible European counterparts. It is suggested that the carbonate complex developed in an area of shallowing within the geosyncline and was unrelated to a northern shelf. Rather, a restricted environment is indicated to the east and southeast in which direction a Plymouth Schwelle may have had its maximum relief. Conodont biofacies are discussed and assessed in relation to the Plymouth distributions and the inferred environmental picture.

An appendix includes biostratigraphical detail, and diagrammatic presentation of sample location and composition and distribution of the conodont faunas in space and time. The conodonts are illustrated on thirty-six plates of stereoscan photographs.

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PART I

INTRODUCTION

General Introduction

The Plymouth Limestone of South-west Devonshire consists of a carbonate complex some six miles long (east - west) and, at its maximum, approximately one mile in breadth (see Fig. 3). The city of Plymouth and its docklands have been built on, and excavated in, the limestones, especially in the west, and consequently correlation across the area is hampered. Furthermore, the Variscan Orogeny was responsible for the upheaval and tearing of the limestone to such a degree that its present disposition and orientation bears no necessary relationship to the original. The complexity of the structure, the lack of continuous strike and dip sections, subsequent metamorphism and dolomitization, and last, but not least, the common, often subtle, facies changes, both lateral and vertical, contribute to the difficulties confronting one in any attempt to elucidate the stratigraphy and thereby gain an insight as to the nature of these limiting factors. Such an attempt has been made by the use of conodonts.

The study has mainly concentrated on the immediate area of Plymouth (see fig. 18) westward to the limestone's edge around Mutton Cove and Cremyl and eastward to the area of Plymstock; the limestones appear to be most variable within and across this area. The study has also embraced goegraphically isolated limestone developments outside the main area, in East Cornwall and (not included in this report) in central South Devon. By way of presenting some temporal parameters, the conodont faunas of calcareous horizons within the argillates below (e.g. Rum Bay) and above (e.g. Neal Point) have also been incorporated within the study (see Figs. 3 and 18). The main limestone development is herein considered to span the period from the mid Eiflian to the mid Frasnian, with some evidence of it extending into the Famennian. The earliest faunas studied indicate the late Emsian/lowest Eiflian, and the youngest - the Middle Famennian.

Apart from the Introduction and the Appendix the report is arranged in two main parts: 'The Conodonts' and 'Facies and Environments'. In the former, the Devonian conodont zonations are reviewed, and the Plymouth faunas assessed in their light. The systematic section involved a form taxonomic treatment of the stratigraphically valuable platform conodonts with an emphasis on the Middle Devonian and early Upper Devonian. The form genus Icriodus, often ignored, is treated in as much detail as the material allows, while common species of Palmatolepis on which a wealth of literature exists, are only noted.

In the third part of this work, the Plymouth environment is assessed in terms of its regional context, the carbonate environment, and the conodont biofacies. The sedimentary aspect is unavoidably treated briefly but it is hoped some pointers are included and in terms of conodont distributions there is considered to be much scope for future work on relating these to other faunal distributions.

The Appendix includes locality detail of the conodont samples and notation of the other faunal elements of the limestones within the context of the general stratigraphy. A sketch map of the structure is also included within the twenty two figures, and thirty six plates illustrate the diagnostic conodonts.

Historical Introduction

> "Another spot, affording instances of shells in primary limestones, is in Devonshire. On the seashore on the east side of Plymouth Dock, opposite to Stonehouse, I found a specimen of schistose, micaceous limestone, containing a shell of the bivalve kind: it was struck off from the solid rock, and cannot possibly be considered as an adventitious fossil."

So wrote Playfair in 1802 (p. 163) in his Illustrations of the Huttonian Theory. This affords the first record of organic remains from the Plymouth Limestone and it is notable that it comes from such an historic work. The record appears to have gone un-noticed however, for a decade later Berger (1811, p.103) wrote of the limestone "I did not discover in it any impressions of organic bodies, and I did not hear that they have ever been found in it". A debate seems to have ensued for several years on this subject and Richard Hennah (1824) must take the credit for finally settling the question with his Succinct account of the Lime Rocks of Plymouth. It is interesting to note that while Hennah found that organic remains were "nowhere common" in 1815 (p. 411), a few years later he had evidently 'got his eye in' for he writes that "these remains pervade almost every part of our limestone" (1819, p. 620).

In 1830, Prideaux wrote of the Plymouth Limestone in his survey of the area between the Rivers Plym and Tamar. His observations were essentially lithological and yet, as later noted by Lonsdale (1840, p.725), he must take some credit for relating the limestones to the Old Red Sandstone. Prideaux (1830, p.36)wrote of the limestone's "red hue" and furthermore distinguished the development from "that further east which Mr. De la Beche refers to the Carboniferous series."

The Plymouth Limestone was established in a stratigraphical context by Sedgwick and Murchison (1837-40, pl.50) when they produced their geological map of Devonshire and Cornwall and included a section from Plymouth to Bolt Head through 'Catdown' and Mount Batten (pl.51,fig.5), and from Dartmouth to the Limestone (pl.51,fig.9). They included the Limestone in the second of their five great groups- the Upper Limestone Group (1837,p.653)- on which they later based the Devonian System (1839, p.701). The Plymouth Limestone can claim to have contributed to this significant work in so much as it was a study of Hennah's collection from the Limestone that first led Lonsdale to suspect the distinct nature of the South Devon faunas. Lonsdale (1840, p.721-5) included a detailed survey of the work on these limestones in the palaeontological work which induced him".. to suggest that the South Devon limestones are of an intermediate age between the Carboniferous and Silurian Systems, and consequently the age of the Old Red Sandstone" (Lonsdale 1840, p. 727). De la Beche (1839, p. 64-5) listed J. de C. Sowerby's determinations of Hennah's material and a year later the illustrations of fossils (plates 52-55) which accompanied Sedgwick & Murchison's classic paper, again after Sowerby, were mostly from the Plymouth Limestone. Around the same time, Philips (1841) also included a synopsis of species and geographical distributions in which the Cornubian Devonian faunas were compared with those of the Carboniferous and Silurian and with European counterparts; Philips included a "Plymouth Group".

In the half century 1850-1900, the Devonian faunas were to become increasingly well known due largely to the monographs of Milne-Edwards and Haime (1850-4) on the corals, Davidson (1864-84) on the brachiopods, Salter (1864-83) on the trilobites, Nicholson (1882-92) on the stromatoporoids, and Whidborne's (1889-1907) general account of the Devonian fauna; the fauna of the Plymouth Limestone figured significantly in some of these, particularly that of Davidson. The latter author figured many brachiopods from Plymouth (1864-5, plates 1-4, 8, 11-14, 18) including many of Sowerby's types and he mentions Mount Wise as an important locality (Davidson 1864-5, p. 124-5). Davidson related the Plymouth Limestones to those of Torquay and Newton Abbot and included a probable correlation of Middle Devonian formations (p. 125- after Champernowne). Milne-Edwards and Haime (1850, p.28) cited Plymouth as one of three principal collecting areas but included only two illustrations of Plymouth corals (pl. 49, fig.5; pl.51, fig. 1a). Nicholson (1882-92) records some stromatoporoids from Plymouth but did not figure any, most of those figured originating from the Triassic conglomerates of Teignmouth. Whidborne's (1889-1907) monograph of Devonian fauna did not include any reference to the Plymouth Limestone, and though Salter (1864-83), in common with Philips and Sedgwick (1852), talked of a "Plymouth Group", no trilobites were known from Plymouth itself. McCoy 1854 also included some fauna from the Limestone.

A second controversy involving the Plymouth Limestone lasted longer than the question of the fossil content: this involved the relation of the Limestone to the slates to the north and south. Both Sedgwick and Muchison, and de la Beche considered the limestone within a normal sequence which younged southward. Sedgwick (1952, p. 17-19) went some way towards correcting this misconception when he related the Plymouth Limestone in his "eight hypothetical intervals in South-west geology" but the "Dartmouth Group" were still considered to lie above the Limestone. Doubts were apparently first raised by Jukes (1867, p.82-3) who on a "flying visit" to the area thought that the (Staddon) grits were "brought up by an anticline, accompanied by inversion as well as contortion, and that this inversion may even affect the southern borders of the Plymouth Limestones". It is noteworthy that Jukes was evidently correct in his latter hypothesis. A year later, Holl (1868, p. 443-4) briefly discussed the possibility of the sequence being inverted, but built his essay on the existence of an "Upper South Devon Group" overlying the limestones on the south, and a "Lower South Devon Group" passing under them on the north.

By 1890, Ussher was able to write on the years of uncertainty during which time both he and Champernowne had been forced to change their minds. Apparently it was Whidborne's unrevealed Lower Devonian fossils from the Cockington Beds which settled the question for him, but not, presumably, for Worth. In reply, Worth (1891), drawing on a wealth of experience and an intimate knowledge of the Plymouth Limestone, questioned the necessity and foundation of Ussher's assertion that the whole district was inverted. Worth (1891, p. 384-5) argued convincingly that the shales below the limestones to the north were in their rightful place. In particular he noted that they had the appearance of a reef-foundation and not it's crumbling superstructure, and also the volcanics associated with these levels, if later, should have altered the limestones. Worth was right but he was talking of those immediately below the Limestone and not, as Ussher was, of those further to the north.

Worth must be mentioned for adding much to our knowledge of the Plymouth Limestone. As early as 1872 (p.62-3) he discussed the growth of limestone "reefs" in terms of an initial mud bank, but here he was again thinking, incorrectly, in terms of a later arenaceous (Staddon grit) phase. Worth (1888, p. 421-3) recognised, "with very little doubt", Guppy's modern Pacific Limestone environments and he thought the Limestone was probably fringing a land mass at no great distance. Other papers by Worth include his works on Plymouth fossils (1877), igneous rock types (1885), drift deposits and bone (including human) cave remains.

W.A.E. Ussher was the author of many papers on the Plymouth Limestone in the late nineteenth century and these culminated in the Geological Survey memoirs on the Plymouth/Liskeard (1907) and Ivybridge/Modbury (1912) areas. Prior to these works, papers of note include those on the south western area (1881 - later "condemned" by Ussher 1900, p. 62), on the railway cut sections (1882), and several others which include some useful discussion on South Devon geology (1890b, 1900, 1907/8).

Previous Work

Subsequent to memoirs by Ussher, the Plymouth area received sparse attention for half a century. In 1951, P.W. Taylor published his work on the tetracorals of the Plymouth Limestone on which he based his map and his block diagram of the structure. Taylor's divisions, numbering nine, were predominantly lithological (see the legend of his map), though his correlations were essentially based on the work on corals of Wedekind and his school in Germany, which subsequently fell into disrepute as discussed by Middleton (1959, p. 138-40). The latter author worked on the coral fauna of comparable limestones in the Newton Abbot area, and his observations on the difficulty of working with the coral faunas from these limestones is equally applicable in Plymouth.

In 1951, Scott Simpson authoratively discussed the Marine Devonian of the south-west and in a way heralded the third phase of detailed stratigraphical work of which he writes. He was, perhaps, premature in accepting Taylor's findings however. Dineley (1961) similarly reviewed the Devonian strata with special emphasis on South Devon and presented a model for the reef environment of the Torbay area.

A number of contributions from Hendriks (1951, 1959, 1966) are worthy of note. Though working mainly in South Cornwall, this author first evolved the idea of a Staddon Schwelle and her detailed work on the successions south of Plymouth contributed much to the understanding of the region. Hendriks (1966) wrote of the development of four unlike facies of Middle Devonian age: the Padstow slates, the Gramscatho and Statton Grits, and the Plymouth Limestone.

Fyson (1962) worked on the structural features of the Devonian rocks near Plymouth and evolved a sequence of tectonic events for the area, as well as elucidating the regional fold and fault configurations.

House (1963) described a goniatite fauna from Warren Point on the Tamar, north west of the Limestone and reviewed the Devonian ammonoid successions in Devon and Cronwall. House (in House and Selwood 1965, p. 54-5) briefly reviewed the palaeontology of the Plymouth Limestone and presented the limestones within their regional context. At this time the Warren Point goniatite bed, or rather the green shales in which it occurs, was considered as lying above the Limestone, the carbonate environment having been superceded by the deeper water shales by the Middle Frasnian.

Braithewaite presented several papers on the subject of the Devonian limestones. In 1965, this author re-interpreted the structure of the Plymouth Limestone and generally refuted Taylor's earlier model, concluding that the Limestone was a southerly inclined sheet, locally overthrust but involving no major inversion. Braithewaite (1966) described the petrology of the limestones and a year later discussed the carbonate environments; this latter work suffers notably from the lack of a stratigraphical basis; but includes some useful observations.

More recently Scrutton (1971) has reviewed the distribution of rugose coral faunas in south west England and includes an assessment of the older faunas ("Cyathophyllum", "Petraia"), and a facies interpretation within the Torbay area.

British Devonian conodonts

Apart from the record of conodonts from Newton Abbot by Young (1880, in — —), Dineley and Rhodes (1956) were the first authors to describe Devonian conodonts from England. Their results were not outstanding insofar as three quarters of their samples were barren, but they did indicate a hitherto unrealised potential. Dineley and Rhodes (1956, p. 244) described five Devonian faunas, all of which were Upper Devonian in age and came from the Torquay, Chudleigh and East Ogwell areas. This work is also notable for the first record of 'Ordovician' conodonts in the Devonian faunas, though these authors, as it turns out, were incorrect in favouring derivation of these, rather than extended ranges. Rhodes and Dineley (1957a, p. 356) subsequently reiterated this belief in the first systematic treatment of British Devonian conodonts. These authors described, and figured a number of diagnostic forms, including Polygnathus varcus and Spathognathodus brevis, from a borehole section at Bishopsteignton; their basal fauna, at least, was probably Middle Devonian in age and thus provides the first such record. In their supplement, Rhodes and Dineley (1957b, p. 1175) include recognition of Devonian "Belodus".

Matthews (1962) described a Middle Devonian conodont fauna from Neal Point on the Tamar and another from the Lummaton Shell Bed, Torquay (1970). From South Cornwall, Harvey (1967) reported Lower Devonian conodonts, and more recently Hendriks et al. (1971) and Sadler (1973) have reported Lower, Middle and Upper Devonian faunas from this area. In the Torquay region, Austin (1967, p. 282) briefly mentioned a Middle Devonian Icriodus fauna from Hopes Nose while more recently Tucker and van Straaten (1970a, b) have reported Famennian faunas from the Saltern Cove area and from the Chudleigh region. Smythe (1973, p. 619) included a report of low Eiflian Icriodus from the Brixham Limestone.

Apart from Rhodes and Dineley's early work (1957a), Kirchgasser (1970) remains the only author to have systematically treated Devonian conodonts from Britain; his faunas came from the Padstow region of North Cornwall and straddled the Middle/Upper Devonian boundary. Orchard (1972) reported on a similar interval within the Plymouth Limestone.

An additional reference from outside the Cornubian Province comes from the work of Reynolds (1973) on the material from the Steeple Aston borehole of Oxfordshire: a fauna dominated by _Icriodus_ appears to be Famennian in age.

Introduction and Techniques

This study has involved the acid digestion of some 257 kgs. of limestones, with a resulting fauna of approximately 7500 individual conodont elements. This represents 205 samples of which 97 proved to be barren. Of the others 63 were of probable Middle Devonian age (average yield = 22/kg) and 45 of Upper Devonian age (average yield = 67 /kg.). Overall, the average yield was 22/kg., and of the productive samples it was 41/kg.

In common with other studies, the richly organic coral - stromatoporoid limestones were on the whole found to be barren, though of course there is little matrix material in which the conodont might be found. The bioclastic limestones proved to be reasonably productive and the fine detrital horizons were amongst the richest, especially the red/pink Upper Devonian crinoidal limestones. The Middle Devonian pelsparites and biomicrites usually yielded a few conodonts but large samples were usually necessary to obtain a reasonable fauna. The argillaceous limestones and calcareous shales at the base of the limestone succession proved to be variable,the best faunas coming from the detrital lenses. Limestones which were dark, argillaceous, and devoid of macrofauna or characterised by amphiporoids were invariably unproductive. Some Upper Devonian pure micrites yielded quite rich faunas. The richest of all came from red calcareous shales and argillaceous limestones.

The limestone samples were treated in a standard manner. It was found that the collection of large blocks of limestone facilitated thorough washing thus minimising the risk of contamination, and also, on the whole, yielded a less fragmented fauna, though more slowly. The blocks were digested in 10-15% acetic acid, the residue passed through 16-20 mesh (1000 microns) sieve and collected in a 140-150 mesh (100 microns) sieve. After drying, the residue was separated in tetrabromoethane or bromoform, the heavy concentrate washed in acetone and then further separated in an electromagnetic separator, The latter effectively separated the Fe-dolomite. No way has been found to separate pyrite. The remaining concentrate was then picked under a binocular microscope, all conodont fragments being separated to ensure a total appraisal of the fauna; in some samples, fragments were subsequently matched. Other elements of the fauna were also separated: pyritised ostracods, dacryoconarids, microgastropods, bryozoans. The light concentrates of the residues were also examined to appraise any additional characters of the rock, and some micro-fauna was also found therein.

Selected specimens were subsequently mounted on a half inch diameter aluminium stub for stereoscan photography. A mounting medium of Durofix was found to provide a good background and to be easily dissolved (in acetone) for recovery of the specimen. Siver-dag did not provide a good background (e.g. Pl.9, figs. 1,10) and it was subsequently very difficult to remove the specimen. The specimens were coated in carbon and then gold-palladium alloy which gave a good conductive coating for full and prolonged examination at the full range of KV and magnification. A coating of aluminium was not found to be suitable for work on higher than 7.5 KV and even at this setting, the specimens charged up badly. The advantage of aluminium is that it can be removed, in a solution of sodium hydroxide, whereas gold-palladium cannot. However, inso much as some of the Plymouth material is white and therefore difficult to examine indetail, the latter coating provides a permanent aid to examination under a normal light source.

Between six and thirty individual specimens were mounted on each stub in such a way as the view of each was not impeded by another. Icriodus, Polygnathus and Spathognathodus were spaced around the periphery of the stub anterior to posterior with the aboral surface parallel to the stub, and the sides perpendicular to it. In this way standard oral and side views can be taken systematically at zero and maximum tilt respectively. For the aboral views, the specimens needed to be remounted but the peripheral arrangement is not necessary; the same applies to photographing Palmatolepis and many of the blades (unless of course a lateral view is required). Cones are best arranged side by side, perpendicular to the stubs edge and horizontal to the stubs surface - thus lateral views are taken at zero tilt and aboral outlines can be viewed at maximum tilt.

For standard views, a magnification of 100x or 200x was normal, more rarely 50x and 500x. A KV setting of 7.5 is the one which has been used for most of the photographs. Above this the contrast is greater and a "bright edge" to the perimeter and high spots of the specimen is common, though for greater magnification a higher KV gives a better resolution. A second to maximum spot size was employed; standard film was used.

DEVONIAN CONODONT ZONATION

It was the work of Huddle (1934) and Hass (1947) which pioneered efforts to erect a Devonian conodont zonation. Their studies in the black shale sequence of central United States included the Upper Devonian in part, but it was in Europe where significant steps were taken to establish such a zonation. In the 1950's, several German workers began to apply the considerable potential of conodonts as a stratigraphic tool. Prominent amongst these are the works of Sannemann (1955a, 1955b), Bischoff (1956, 1957), Ziegler (1956-74) Müller (1956a, 1956b, 1962), Helms (1959, 1961, 1963), and Wittekindt (1965).

Elsewhere in Europe, the work of Bultynck (1965-1974) has proved valuable, and contributions from other countries have verified the widespread applicability of the schemes established by Bischoff and Ziegler (1957) and Wittekindt (1965) for the Middle Devonian, and in particular Ziegler (1962b) for the Upper Devonian (see Ziegler 1971, p.230 for list).

In North America, the work of Klapper (1970, 1971) in New York, and Orr (1971) in the Illinois Basin, have also provided separate schemes for much of the Middle Devonian. The correlation between these and with the European Standard is a continuing task.

In Australia, Pedder, Jackson and Ellenor (1969) erected a zonal scheme for the Middle Devonian Timor Limestone successions, and these too differ in some respects from the European Standard.

The Upper Devonian zonation is, for the most part, generally applicable world-wide.

Figure 1 demonstrates the present schemes and their relationships. The following is a systematic review of the conodont successions of the period covered by this study, with an emphasis on the problematical intervals.

The Conodont Zonation of the European Middle Devonian

Foreword

The Middle Devonian of Germany is divided into lower Eifel Stufe and upper Givet Stufe. The Belgian Couvinian approximates the lower division, though at its base it includes the uppermost Emsian of German usage.

The standard biochronology is based on ammonoid biozones, the Eifelian being approximately coincident with the range of Anarcestes, and the Givetian with the Stufe of Maenioceras; besides conodonts, parachronologic subdivisions are based on trilobites and brachiopods.

The base of the Couvinian, the Em_3 / Co_{1a} (sensu Mailleux) boundary, has been reviewed by Bultynck (1970) in the stratotype section, but how this relates to the German situation and the Emsian/Eifelian Boundary has been the subject of much disaccord in the past. It is here intended to review the situation only as it relates to the conodont successions.

Bultynck (1967, 1968, 1970) recognised similar conodont faunas in the basal Couvinian division, Co_{1a}, and in the Heisdorf Beds of the German Eifel, and consequently drew a parallel in the base of these two sequences, which have in common a number of fossil appearances (Bultynck 1970, fig.13).

From the work of Carls et al.(1972), it appears that the base of Co_{1a} corresponds to a level within the Wetteldorf Beds (below the Heisdorf of the Eifel. Furthermore Co_{1a} is considered to be equivalent to the Ballersbacher Kalk (in part) of the eastern Rhenish Schiefergebirge.

Definition of the base of Eifelian is complicated by the paradoxical situation in which the Heisdorfer Schichten of the Eifelian Hills, traditionally assigned to the uppermost Emsian, and the Ballersbacher Kalk of the Rhenish Schiefergebirge which has yielded Lower Eifelian ammonoids, both contain identical conodont fauna, namely an association of Icriodus corniger, Polygnathus linguiformis linguiformis and Po. costatus patulus. Carls et al. (1972) in fact show the Heisdorf and the Ballersbacher Kalk to be in part correlative, and they draw the Emsian/Eifelian boundary at the junction of the Heisdorf and Lauch Beds of the Eifel and equate this with the boundary of Co_{1a} and Co_{1b} in Belgium, and to a level within the Ballersbacher Kalk which would thus straddle the boundary.

European Middle Devonian conodonts, as such, were first described by Bischoff and Ziegler (1957) who recognised many new forms and presented extensive coverage of stratigraphical range. The subzones erected around the Middle/Upper Devonian boundary by these authors, was refined by Krebs (1959). The next contribution to a zonal scheme came from Wittekindt (1965) who erected seven Middle Devonian zones in the Harz Mountains, the uppermost one of which (the transversus Zone) was subsequently rejected by Ziegler (1965a) who further refined the zonation by introducing the hermanni-cristatus Zone. Ziegler (1971) summarised the then state of knowledge and united the two lower Givetian zones of Wittekindt as the Icriodus obliquimarginatus Zone,

Within the Belgian Couvinian, Bultynck (1966-1972)contributed significantly to the understanding of mid-Devonian conodont successions and thereby facilitated more precise intra-European correlation. In particular his work on Icriodus has produced an additional species complex for use as a zonal parameter.

The following is a systematic review of the standard European conodont zonation during the mid Devonian.

The Nonlatericrescid Icriodus-Faura of the "Upper Emsian"

The record of the late Lower Devonian non-latericrescid Icriodus-Fauna, long in need of taxonomic revision and redescription, is now better known largely due to the works of Klapper and Ziegler (1967), Carls and Gandl (1969) and Bultynck (1970, 1972). This fauna, as established by Ziegler (1971), is found in the middle and upper part of the Upper Emsian according to Ziegler (1971, p.248) and is characterised by four icriodids, namely: I. aff. corniger, I. corniger, I. aff. angustus, and I. angustus; this is not I. angustus STEWART and SWEET 1956 , in fact but rather I. culicellus BULTYNCK. These forms represent the culmination of an evolutionary trend involving the reduction, and finally the loss of the lateral processes which are typical of the earlier icriodids with which the former are linked through the forms I. sigmoidalis and I. fusiformis, according to Carls and Gandl (1969). This development began toward the top of the span of the subjacent informal division - the I. bilaticrescens - Spathognathodus steinhornensis steinhornensis - Polygnathus Fauna, in which I. aff. corniger is first recorded. The latter form appears to be restricted to the Emsian, but the other three icriodids range into the Eifelian.

In 1970 Bultynck, working in the Belgium Ardennes, recognised Zone 1 of his conodont succession in "Em$_3$". This was characterised by I. latericrescens bilatericrescens, the disappearance of which marked the top of the zone. Within this zone, (which lies toward the middle of the "Assises de Hierges") he also found I. cullicellus (an elongated variety), I. cf. corniger, and forms transitional between I. l. bilatericrescens and I. corniger (= I. aff. I. fusiformis sensu Bultynck 1972). Bultynck's Zone 2 spanned a period from the base of Co$_{1a}$ to the top of Co$_{2b}$IV and was characterised by I. corniger; the base of this zone was not fixed due to the transitional nature of the specimens which were found above the first zone (an interval which is, in any case, unsuitable for extensive sampling). Bultynck's level a (Co$_{1a}$) was furthermore characterised by the regular appearance of I. nodosus rectirostratus (= I. rectirostratus), which was confined to that level, in association with I. aff. I. fusiformis and a short variety of I. cullicellus.

More recently Bultynck (1972), has presented a study of Middle Devonian Icriodus assemblages which facilitate a more precise definition of, and delimitation within, this late Emsian and early Couvinian period. Bultynck recognises two lineages at these levels, namely the Icriodus huddlei huddlei descendents and the I. bilatericrescens bilatericrescens descendents; the former gives rise to I. cullicellus and the latter leads to the I. corniger associations (see also Ziegler and Klapper 1967, fig.2)

I. cullicellus is recorded from within Em$_3$, Co$_{1a}$ and less frequently up to a level within Co$_{1c}$.

Bultynck recognises three assemblages in which I. corniger type element occurs; an assemblage composed of I. aff. I. corniger, I. fusiformis, and I. rectirostratus (upper part of Em$_3$), an I. corniger-I. aff. I. fusiformis - I. rectirostratus assemblage (Co$_{1a}$), and an I. corniger-I. curvirostratus-I. introlevatus assemblage which he recorded through the remainder of his corniger Zone (Co$_{1b}$ - Co$_{2b}$ IV).

Bultynck (1970, pl.38) notes the occurrence of Icriodus rectirostratus and I. aff. I. fusiformis from the Heisdorf Beds of the Eifel; this is evidence for the equivalence of Co_{1a} and the Heisdorf Beds.

The Icriodus corniger Zone Wittekindt 1965

This zone was established by Wittekindt (1965) from the Ballersbacher Kalk of the eastern Rhenish Schiefergebirge. Associated ammonoids are Gyroceratites gracilis, Anarcestes lateseptatus, and Pinacites jugleri; the zone, as originally defined, is lowermost Eifelian in age, though P. jugleri is an Upper Eifelian zone fossil (Erben and Zagora 1968, p.61).

The corniger Zone, which represents the Eifelian extension of the non-latericrescid icriodid Fauna of the Upper Emsian, is recognised, according to Ziegler (1971), by the joint occurrence of Icriodus corniger, Polygnathus linguiformis linguiformis, Po. "webbi" sensu Bischoff and Ziegler (1957) and Wittekindt (1965) (= Po. costatus KLAPPER) non sensu Stauffer 1938, and Icriodus angustus (= I. cullicellus BULTYNCK) non sensu Stewart and Sweet 1956. The upper limit of this zone is drawn below the first occurrence of Spathognathus bidentatus, but the lower limit is unsatisfactorily defined.

Since the Ballersbacher Kalk is now considered to be Emsian in part (Carls et al., 1972), and because the diagnostic icriodids appear to have evolved within the uppermost Emsian, the corniger Zone, as originally conceived, clearly embraced part of the Upper Emsian.

However, according to Ziegler (1970, p.252), Po. costatus is indicative of the Eifelian part of the "corniger association" since this form has not been found in the Emsian, so the present concept of the Zone would appear to be Eifelian.

Bultynck (1970, p.60 and pl.38) noted that this polygnathid (Po. cf. "webbi") first appeared at the Co_{1a} - Co_{1b} boundary which was within his zone 2. Thus the base of the corniger Zone s.s. equates with this level within the Belgian Couvinian; he further recognises this form, albeit sporadically, from the interval Co_{1b}, Co_{1c} and Co_{2bI}. Bischoff and Ziegler (1957, taf. 5, p.135) recorded Po. costatus from the whole of the Middle Devonian but Ziegler (1971, chart 2, p.253) recorded it from throughout the Eifelian (Wittekindt's range) and only questionably in the Givetian. Two phylogenetically linked subspecies of *Po. costatus* are recognised *Po. costatus patulus* and *Po. c. costatus*, the former being the earlier.

It seems desirable to make a clear distinction between the *corniger* Zone (of Lower Eifelian age) and the *corniger* association (which appears to span the Lower/Middle Devonian boundary). The *corniger* Zone *sensu* Bultynck (1970, 1972) appears to be slightly different from Wittekindt's (1965) and Ziegler's (1970) concept of the zone, and is rather a record of the "*corniger* - association"; Bultynck records *I.* aff. *I. corniger* but not *I. corniger s.s.* below the base of Co_{1a}.

Bultynck's (1970, 1972) work on Couvinian *Icriodus* provides some refinement within the *corniger* Zone. The following assemblages have been suggested:

The *I. corniger* - *I. curvirostratus* - *I. introlevatus* assemblage ranging within Co_{1b}, Co_{1c} and Co_{2a-b} (*partim*).

The *I. curvirostratus* - *I. introlevatus* assemblage found in the topmost Co_{2b}, in Co_{2c} and Co_{2d}. (This represents the last stage in the evolution of the *I. corniger* group and is mentioned here since its first occurrence could be taken as indicative of the upper limit of that zone);

The *I. expansus* - *I. retrodepressus* assemblage - These two forms appear at a level approximating the Lower/ Upper Couvinian boundary - "level b" of Bultynck's (1970) zone 2 (the top of Co_{1c}), and range into the lower part of Co_{2b}; they thus correspond to the middle part of the *corniger* Zone. Though at these levels the two forms are end members of a morphological transition series, above the top of the Co_{2b} interval, only the *I. expansus* element is found.

The *I.* aff. *I. angustus* (= *I. cullicellus*) assemblage-as mentioned a small variety of this form is more common in the Middle Devonian, specifically within the interval Co_{1b} - Co_{1c} (*partim*).

Ziegler (1971) recorded "*I. angustus*" throughout the *corniger* Zone and questionably throughout the Eifelian. In North America (*q.v.*), *I. angustus sensu* Stewart and Sweet is the nominate species of an "Upper Eifelian" zone, but the European form is quite distinct and clearly not the same as this. In addition, Bultynck has recorded the form species *I.* "*symmetricus*" subsp. *a* from Co$_{1b}$ (rare), Co$_{1c}$ - Co$_{2b\ II}$, Co$_{2b}$ III - IV (rare), and *I.* *nodusus*" subsp. *a* from Co$_{1c}$ (rare) and Co$_{2b}$ I-II.

Bultynck (1970) distinguished three morphotypes of *Polygnathus linguiformis linguiformis* from the Belgian Couvinian, namely α, β and γ it is noteworthy that he found the former two to range within his *corniger* Zone: α morphotype - rare in Co$_{1c}$; Co$_{2b}$ I - II; β morphotype - in Co$_{2b\ II}$ only.

It was the presence of the latter that marked "level c" of Bultynck's (1970) Zone 2.

Klapper (1971) described a new subspecies of *Po. linguiformis* from the Nedrow Member of the Onondaga Limestone of New York. This form, *Po. linguiformis cooperi*, was figured by Bultynck (1970, pl.9, fig. 8-11) who called it *Po. linguiformis linguiformis* (undifferentiated); his specimens all came from Co$_{2b}$. Again, this represents a level within the *corniger* Zone.

Mirauta (1971) recorded a new species, *Polygnathus dobrogensis* from the Eifelian and lowermost Givetian of North Dobrogea.

The Spathognathodus bidentatus Zone Wittekindt 1965

This, the second of Wittekindt's zones, was first described by him from the lower part of the Günteroder Kalk of the Rhenish Schiefergebirge. Associated ammonoids are *Wernoceras ruppachense*, *Fordites occultus*, and *Pinacites jugleri*.

The *bidentatus* Zone is characterised by the occurrence of the nominate species in association with *Polygnathus angusticostatus* and *Po. eiflius*. The first occurrence of the name-giver marks the lower boundary; the upper limit is marked by the appearance of *Po. kockelianus*.

Spathognathodus bidentatus was first described from the Ballersbacher Kalk of the Harz Mountains, Germany (Bischoff and Ziegler 1957) where it is found together with *Icriodus comiger*. Although they did not record it from the Gunteroder Kalk (i.e. the upper part of the Eifel Stufe), both Wittekindt (1965) and Ziegler (1970) recorded *S. bidentatus* throughout the *bidentatus* Zone and questionably into the basal Givetian. The joint occurrence of *S. bidentatus* and *I. corniger* is evidence for the equivalence, in part, of the Ballersbacher Kalk and the Günteroder Kalk, and indeed for the extension of *I. corniger* into the zone above; this is, however, contrary to the situation within the Belgium Couvinian.

Bultynck (1970) recorded the range of *S. bidentatus* from within Co$_{2d}$ (uppermost Couvinian) through Gi$_a$ and in Gi$_b$ (partim). According to definition there appears to be a significant discrepancy between the 'base' of the zone in Belgium and in Germany. Similarly, in Belgium Bultynck (1972, p.72, fig.1) draws the top of the *corniger* Zone at the last appearance of the nominate species (top of Co$_{2b\ IV}$), whereas in Germany the latter extends into the *bidentatus* Zone *sensu* the German workers. These inconsistences remain a problem for the present.

Polygnathus angusticostatus is recorded, in Germany, from the base of the *bidentatus* Zone to the top of the Eifelian, although it is less common in the upper parts of the range. In the type section at Couvin, Bultynck (1970, pl.38) records the range from Co$_{2c\ III}$ up to the Couvinian/Givetian boundary (rare in Co$_{2cV}$ and Co$_{2d}$). It would seem that there is a fair agreement between the Belgian and German occurrences of this form and therefore it may represent a more suitable zonal index, all the more since the species range is more restricted than *S. bidentatus*.

Originally described from that part of the Eifel-Stufe above the Ballersbacher Kalk (Bischoff and Ziegler 1957, taf.. 4), *Polygnathus eiflius* has subsequently been noted as ranging from the base of this zone, well into the Givetian in Germany, but it has a very limited range in Belgium, according to Bultynck (1970) who found it only in Co$_{2c/IV}$ (*kockelianus* Zone).

A number of species occur in the *bidentatus* Zone for the first time. These are (from Wittekindt 1965 and Ziegler 1971): *Spathognathodus obliquus*, *Polygnathus angustipennatus*, *Po. pseudofoliatus*, *Po. xylus*, and *Po. robusticostatus*. The last two appeared later than the others according to Wittekindt

(1965, taf. 1) but Ziegler (1970, chart 2) notes them all making their appearance about the middle of the zone. The Couvinian ranges of these forms are more refined and apparently more limited. S. obliquus was not recorded by Bultynck (1970), though Ziegler (1971, p.255) thought that S. bidentatus transitans BULTYNCK (= Po. intermedius) may belong partly in S. obliquus. The ranges of the polygnathids, modified after Bouckaert and Streel (1974) are as follows:

Po. angustipennatus --- Co_{2c} III-IV/R; rare in Co_{2c} V and Co_{2d} ; Po. pseudofoliatus --- Co_{2c} IV/R, rare in Co_{2c} V , sporadically up to the middle of the varcus Zone (where it grades into Po. dubius) ; Po. xylus --- Co_{2d} ; Po. cf. xylus --- Co_{2c} III-IV/R; Po. cf. robusticostatus --- Co_{2c} IV/R .

Polygnathus webbi sensu Ziegler 1971 and Po. linguiformis linguiformis are long ranging forms which are encountered throughout the zone in Germany. The former species is now assigned to the forms Po. costatus patulus and Po. c. costatus but the exact ranges of each of these forms is unknown since they were not differentiated by Ziegler. This awaits clarification, but in any case there is a continuous evolutionary lineage from Po. costatus patulus through Po. costatus costatus to Po. pseudofoliatus (Klapper 1971), so differentiation is not clear cut. The γ morphotype of Po. linguiformis linguiformis is the only form which Bultynck recorded above the top of his corniger Zone. The ranges in the Couvin section are: Po. costatus costatus (= Po. webbi sensu Bultynck 1970) ---- Co_{2b} III -V (rare), Co_{2c}I, Co_{2c} III, Po. costatus costatus -> pseudofoliatus ---- rare in Co_{2c} III; Po. linguiformis linguiformis, "forma γ " ---- Co_{2c} - d (and above) .

One form which appears at these levels at Couvin, but which does not have a German parallel is Spathognathodus cf. bipennatus which is found in Co_{2b} V but not again until it appears in association with S. bidentatus in the basal Givetian. This isolated occurrence immediately above the Belgian range of I. corniger (Zone 2 of Bultynck 1970, p.63) constitutes Zone 3 of the Couvinian scheme.

That part of the section above the Co_{2b} was divided into two by Bultynck (1970, p.64). Zone 4, embraced the period Co_{2c} I -II - III (partim) and was marked, somewhat indistintively, by the relative abundance of Po. costatus costatus in association with Po. l. linguiformis. (Zone 5 is discussed in relation to the following zone).

In the remainder of the Couvinian above the vertical extension of *I. corniger*, Bultynck (1972) recognised three Icriodus assemblages two of which have been mentioned in relation to the subjacent zone; the third ranges from within Co$_{2c}$. The assemblages are:
I. curvirostratus - *I. introlevatus* assemblage - top of Co$_{2b}$, and throughout Co$_{2c-d}$; *I. expansus* assemblage - rare in uppermost Co$_{2b}$ - Co$_{2c-d}$; *I. regularicrescens* assemblage - base of Co$_{2c}$ IV/R - basal Gi$_{a}$.

The *Polygnathus kockelianus* Zone Wittekindt 1965

This Upper Eifelian zone was established by Wittekindt in, or above, the Günteroder Kalk of the German Rhenish Facies; associated goniatites are *Pinacites jugleri*, *Fordites platypleura*, and *Werneroceras ruppachense*.

The zone is characterised by the joint occurrence of the nominate species and *Polygnathus trigonicus*, both of which appear at, and thus define, the lower limit of the zone; the upper boundary is drawn at the lowest occurrence of *Icriodus obliquimarginatus*.

Both the diagnostic polygnathids were originally described from the Kalkige Zwischenschichten by Bischoff and Ziegler (1957). Wittekindt records them as being confined to this zone, which is consequently very well defined and easy to recognise, at least in Germany. In Belgium, Bultynck (1970) recorded *Po. kockelianus* from Co$_{2c}$ IV/R where it was restricted to 'level a' of his zone 5:; *Po. trigonicus* was a rare component of the fauna at this level. Bultynck (1972, fig.1) later questioned the upward extension of the top of the *kockelianus* Zone and there are two reasons why this may be warranted: firstly, he records the rare occurrence of *Po.* cf. *kockelianus* from Co$_{2d}$ beds, and secondly forms referred to as *S. bidentatus transitans* (= *S. intermedius*) were considered by Ziegler (1970, p.255) to possibly partly represent forms called *Po. kockelianus* juv. by Bischoff and Ziegler Defined as embracing the range of the name-giver, this zone may therefore be extended upward.

In Germany, the associated forms found in this zone are the same as those which first appeared in the *bidentatus* Zone with the exception of *S. obliquus* which does not range above that zone. These forms are: *Po. angusticostatus*, *Po. angustipennatus*, *Po. eiflius*, *Po. xylus*, *Po. pseudofoliatus* and *Po. robusticostatus*; the first is markedly less common toward the top of the zone, and the first two do not extend above the upper limit, but the others range into the Givetian (Ziegler 1971, chart 2). *Po. l. linguiformis* and *Po. costatus costatus* also range throughout the period, and into the Givetian (according to Ziegler 1971, chart 2), although Wittekindt did not record the latter above the top of the zone.

Zone 5 *sensu* Bultynck (1970) corresponds to the range of *Po. angustipennatus* in the Couvinian section; this is usually accompanied by *Po. angusticostatus* and approximates that time between the $Co_{2c\ II/III}$ boundary and the Couvinian/ Givetian boundary. Level a (i.e. within the *Kockelianus* Zone) also marks the first appearance of *Po. eiflius*, *Po.* cf. *xylus*, *Po. pseudofoliatus*, *Po.* cf. *robusticostatus*, *Spathognathodus intermedius* and *Icriodus regularicrescens*. Level b includes the first typical *Po. xylus* and corresponds to the base of Co_{2d} . At the top of Co_{2d} , the presence of *S. bidentatus* characterises level c.

The range of the polygnathids in Belgium have been reviewed in the previous section. *S. intermedius* was recorded by Bultynck from $Co_{2c\ IV/R}$ and (rarely) $Co_{2c\ V}$ and as such its range approximates the Belgium *kockelianus* Zone.

Three *Icriodus* assmeblages were recognised by Bultynck (1972) ranging into this Upper Couvinian zone. (see *bidentatus* Zone). *Icriodus regularicrescens* was first described by Bultynck (1970) who recorded it from the base of $Co_{2c\ IV/R}$. In 1972, it formed the basis of his *I. regularicrescens* assemblage which he noted ranged from the base of the *kockelianus* Zone in Belgium. This particular icriodid is considered by Bultynck (1972, fig.17) to be ancestral root-stock of his third, dominantly Upper Middle Devonian lineage which gave rise to *I. obliquimarginatus* and *I. eslaensis*.

The Conodont Zonation of the North American Middle Devonian

In North America, Middle Devonian conodont successions are known from New York, the Illinois Basin (Illinois and Indiana), and the Michigan Basin. Correlation between these areas and, more particularly, with the standard European zonation is hampered by the absence of critical index species in one or the other successions. For this reason, a single zonal scheme for the North American continent is precluded at present though locally the successions are well known.

The Eifelian of New York is characterised by five faunas(Klapper et al. 1971), and of these, at least two of the lower three are recognisable in the Illinois Basin. Klapper (1971) has reocgnised four conodont faunas within the lower Middle Devonian Polygnathus sequence in New York, while Orr (1971) has presented a zonation of the Michigan Basin sequence in which three zones are established in a comparable interval.

In the late Middle Devonian, Klapper et al. (1971) record three faunas in the Illinois Basin, the lower two of which are also recognised in New York and Michigan.

The North American zonation of the early Middle Devonian differs from the European Eifelian/Couvinian successions sufficiently to warrant separate treatment here, but the late Middle Devonian successions are more readily correlated and are thus considered with the European equivalents.

The lowest mid Devonian fauna recognised by Klapper et al. (1971) is characterised by Icriodus latericrescens n. sp. a = I. latericrescens robustus ORR 1971. This form characterises the Edgecliff Member of the Onondaga Limestone of New York (Klapper and Ziegler 1967, localities 1,2,3,5), the lower Grand Tower Limestone (Dutch Creek Member and overlying strata) in southern Illinois, and the lower part of the Jeffersonville Limestone of southern Indiana (Orr 1971). Orr (1971) established an I. latericrescens robustus Zone in the Illinois Basin which is defined basally by the first occurrence of the name-giver; the top is drawn below the appearance of Polygnathus "webbi", that is Po. costatus. Orr considers this zone to be Lower Eifelian in age.

Now, though the Edgecliff has been independently dated, on the basis of corals (Oliver 1960), as Lower Eifelian, *I. latericrescens robustus* is also found at lower levels e.g. in the Schoharie Formation in eastern New York and the Bois Blanc Formation of western New York (Klapper and Ziegler 1967, locs. 1,2), in association with *I. latericrescens huddlei*. This latter form, which is now called *I. huddlei huddlei*, is found in Europe below the non-latericrescid *Icriodus* Fauna, within the *Princeps* -, *Zorgensis* -, and Schönauer-Kalk (within the *I. bilatericrescens bilatericrescens*-*Spathognathodus steinhornensis* - *Polygnathus* Fauna). Unfortunately, *I. latericrescens robustus* has not been found in Europe, but it seems more likely that the top of the *robustus* Zone as recognised by the appearance of *Po. costatus* would correlate with the base of the *corniger* Zone *sensu* Ziegler 1971.

The succeeding zone recognised by Orr in the Illinois Basin, is the *Po. "webbi"* Zone, hereafter called the *Po. costatus* Zone. The base of this "mid Eifelian" Zone is defined by the first occurrence of the name-giver and and the top is drawn below the first appearance of *Icriodus angustus*. Orr further speculated on the feasibility of a lower and an upper part, the latter being characterised by the presence of *Po. robusticostatus*.

The oldest polygnathid fauna recognised by Klapper (1971) in New York is the *Po. costatus patulus* - *Po. linguiformis cooperi* fauna of the Nedrow - and (lower part of the) Moorhouse Members of the Onondaga Limestone. Associated with these two species, are rare *Po. costatus costatus*, *I. corniger*, *I. nodosus*, and *I. latericrescens robustus*. This association corresponds to the lower part of Orr's second zone and, with reference to the European zonation, it most likely corresponds to the upper part of the *corniger* zone. Klapper (1971) notes that the conodont association at the base of the *Leptathyris circula* Zone at Willow Creek, Roberts Mountains, central Nevada approximates the Nedrow fauna in age.

The upper part of the Moorhouse (for the most part) is characterised by the second of Klapper's groups, the *Po. robusticostatus* fauna, in which the name-giver is associated with *Po. l. linguiformis* α morphotype, *Po. costatus patulus* and *I. latericrescens robustus*. This fauna is almost identical to that recorded from the Detroit River Formation of northern Indiana by Orr (1971), and differs only in lacking (the rare juvenile specimens of) *Spathognathodus bidentatus* which is present in the latter. Again, with reference to the European situation, this association appears to correspond to the *bidentatus* Zone *sensu* Wittekindt, though by reference to the Couvinian section the ranges of the equivalent forms are seen to result in a discrepancy amounting to that interval from $Co_{2b\ II}$ (i.e. the last *Po.l.l.* α) to Co_{2d} (the first recorded *S. bidentatus*). Within this interval in Belgium is found Bultynck's (1970) zone 3 which is characterised by *Spathognathodus* cf. *bipennatus*, a form which has not been reported from North America. Orr included the middle part of the Grand Tower Limestone of southern Illinois and questionably the middle part of the Jefferson Limestone of southern Indiana, within his *Po. costatus* Zone.

Klapper's third polygnathid fauna, which is found in the uppermost Moorhouse and the Seneca Members of the Onondaga Limestone of New York, is the so-called *Po. costatus costatus* - *Po.* aff. *Po. trigonicus* fauna. Associated forms include *Po. intermedius* and a single specimen of *Po.l.l.* γ ; *Po. costatus patulus* and *I. latericrescens robustus* range throughout this period. This fauna is indicative of the German *kockelianus* Zone and is furthermore comparable with the same level in the Belgian Couvinian. The same is thought to be true for the overlying strata and fauna from the Cherry Valley and Union Springs (*Wernoceras* bed) Members of the Marcellus Formation in New York. The *Wernoceras* horizon was considered by House (1962, p.254) to correlate with the basal Givetian,of North African and Czechoslovakian usage. The polygnathid fauna, the youngest recognised by Klapper (1971), is the *Po. pseudofoliatus* - *Po.* aff. *Po. eiflius* fauna which is characterised by an association of the name-giver plus *Po. robusticostatus*, *Po. angusticostatus* (its highest occurrence), *Po. angustipennatus*, *Po. intermedius*, *Po. l. linguiformis* and rare specimens of *Po. kockelianus* and *I. latericrescens* subsp. indet. This fauna also appears to correspond to the *kockelianus* Zone, but a difficulty in tracing it arises from the extreme rarity of *Po. kockelianus*, and the apparent absence of *Po. trigonicus s.s.*,in New York.

A similar problem arises from the absence of *I. angustus* in the New York successions. This form lends it's name to the "Upper Eifelian" zone of Orr (1971) which, by definition, is coincident with the range of this species. The characteristic association of *I. angustus* and *I. latericrescens robustus* is found in the Dundee Limestone of western Ontario (where it is accompanied by *Po. angusticostatus*), Michigan, and northwestern Ohio. (Klapper and Ziegler 1967, p.74, locality 17 -- associated with *I. corniger*). The lower part of the Lingle Formation in southern Illinois, and the Silver Creek Member of the North

Vernon Limestone of southern Indiana, are characterised by a younger fauna, one which demonstrates the higher range of *I. angustus* compared with that of *I. latericrescens robustus* (which ranges throughout almost the entire Lower Middle Devonian in North America). Stewart and Sweet (1956) first described *I. angustus* from the Columbus and Delaware Limestones of central Nevada, and this is thus included in the *angustus* Zone. So, too, is the upper part of the Grand Tower Limestone in southern Illinois, and the upper part of the Jeffersonville Limestone of southern Indiana. Both *Po.* cf. *trigonicus* and *Po. kockelianus* are absent in the Illinois Basin, where, according to Orr (1971, p.17), *Po. eiflius* is confined to the *angustus* zone.

Because of the reciprocal absence of important index forms in New York and elsewhere in North America, Klapper *et al.* (1971) proposed a correlation based on the highest occurrences of *Po. angusticostatus*, *Po. eiflius*, and *Po. costatus costatus* (= *Po.* "*webbi*" subsp. B *sensu* Klapper *et al.* 1971). This correlates Klapper's (1971) two highest polygnathid faunas with the *I. angustus* Zone of Orr. As mentioned this appears to be equivalent with the German *Po. kockelianus* Zone.

According to Klapper *et al.* (1971, p.295), *Po. kockelianus* is also known from the *Leptathyris circula* Zone (Eifelian) of Nevada, the Bear Spring Formation of the Llano area, central Texas (associated with *Po. eiflius* and *Po. angusticostatus*) and from the subsurface of Kansas.

The *Icriodus obliquimarginatus* Zone Ziegler 1970

Ziegler (1970, p. 257) introduced this new zone to replace the *eiflius* and the *robusticostatus* Zones of Wittekindt (1965) which he considered unwisely named and inadequately defined. Wittekindt believed this period to be coincident with the lower, middle and, in part, the upper Givetian; the index goniatite for the period is *Sellagoniatites discoides*.

This zone coincides with the associated range of the nominate species and *Polygnathus klupfeli*. The lower level of the zone is recognised by the disappearance of *Polygnathus kockelianus* and *Po. trigonicus* and the appearance of *I. obliquimarginatus*; the upper boundary is drawn at the "mass appearance" of *Polygnathus varcus*.

I. obliquimarginatus was first recorded by Bischoff and Ziegler (1957) in, and restricted to, the Oderhauser Kalk (lowest Givetian) of the Rhenish Schiefergebirge. Wittekindt (1965) and Ziegler (1970) both extended its range well up into the *varcus* Zone. In the Belgian Counvinian, Bultynck (1970) recorded *I. obliquimarginatus* from Gi_a and Gi_b where, in association with *Spathognathodus* cf. *bipennatus*, it constituted his zone 6. Bultynck also recognised a similar form, *I.* cf. *obliquimarginatus* from the upper Co_{2d} beds, and more recently (1972) he records *I.* aff. *obliquimarginatus* from comparable stratigraphical levels as, but not in association with, the nominate species. Bultynck (1972) noted that his *I. obliquimarginatus* assemblage (with the nominate species as the single associated form species) is less common in the upper part of Gi_b , and is not found above this level, where its place is taken by *I. eslaensis*.

Po. klupfeli WITTEKINDT 1965 is restricted to the *obliquimarginatus* Zone, but it is rare.

The *obliquimarginatus* Zone is subdivided into a lower and an upper part, corresponding respectively, to the presence and absence of *Polygnathus latus* which appears at the base of the zone. Wittekindt recorded this form from his *eiflius* Zone in Germany, but elsewhere it is very rare, only a single specimen having hitherto been recorded, from Belgium (see Taxonomy).

Spathognathodus bipennatus, originally described from the *Sparganophyllum* Kalk by Bischoff and Ziegler (1957), has also been recovered from the Hönsel and Finnentrop beds of the Middle Devonian Rhenish development by Ziegler (1970, p.258). The latter author believed these occurrences lay in the upper part of the *obliquimarginatus* Zone. *S.* cf. *bipennatus sensu* Bultynck (1970), as mentioned, was found by him in the basal Givetian of the Couvin section (especially Gi_b), though he later (1972, fig.1, p.72) records *S. bipennatus* extending into the middle of Gi_c, which would equate with the German occurrences. Although Wittekindt did not record *S. bipennatus*, it has been recorded from a number of levels throughout the Middle Devonian as indicated by Ziegler (1971, p. 255), and hence it is not a reliable zonal indice, though Bultynck (1970, p.134) considers subdivision of the form may be possible, and valuable.

Other associated forms to be found in this zone include the following: *Polygnathus eiflius*, *Po. pseudofoliatus*, *Po. xylus*, *Po. robusticostatus*, *Po. costatus costatus*, *Po.*? *variabilis*, *Po.* cf. *varcus*, *Po. linguiformis*

linguiformis, *Spathognathodus bidentatus*, *S. planus*, and *Icriodus* spp.

Po. eiflius, despite its former status, is not a very diagnostic form, ranging through the lower part of the zone but petering out in the upper; its occurrence in the Givetian was queried by Bischoff and Ziegler (1957) in their original description. *Po. robusticostatus* ranges through the zone according to Ziegler (1971, p.253) though he has since considered the Givetian occurrences unsubstantiated (Ziegler 1973, p.379). *Po. pseudofoliatus* and *Po.l.linguiformis* range throughout, and above, the zone. *Po. xylus* was similarly recorded throughout the zone by Wittekindt but both its first given range (Bischoff and Ziegler 1957) and the latest zonal scheme indicate a paucity of specimens in the upper reaches of the zone. *Po.* "*webbi*"sensu Ziegler (1970) (? = *Po. costatus costatus*) persists sporadically throughout the zone. *S. bidentatus* is found in the lower part of the zone in Germany, and this has a parallel in the Couvinian section in horizon *a* of Bultynck's (1970, p.64) Zone 6 where it is found in a forementioned association approximating the boundary of Gi_a and Gi_b .

Among the species which make their first appearance, *S. planus* and *Po.* ? *variabilis* range from the Lower *obliquimarginatus* Zone, though neither of these were originally described from as low as this. *Po. varcus* was recorded from the *robusticostatus* Zone by Wittekindt, and by Ziegler (1970), though the latter author qualified his range chart in his statement that forms "already close to *Po. varcus*"are possibly found in the upper portion of the zone (Ziegler 1970, p.257) .

The icriodid elements of the Givetian (and indeed the Eifelian have been variously and inconsistently assigned to *I. nodosus* and *I. symmetricus* though Bultynck (1972, p.77) considers that the trends on the upper and lower surfaces of these species (particularly the latter) are clearly not the same as Middle Devonian forms and that the latter can be differentiated from the former, typically Upper Devonian, species. Besides *I. obliquimarginatus* and similar forms, Bultynck recognises an *I.* n. sp. *a* assemblage from zone Gi_c of the Ardennes (? = Upper *obliquimarginatus* Zone) and a *I. eslaensis* assemblage which ranges from the base of Gi_c into the *varcus* zone. He also records the Upper Couvinian *I. regularicrescens* assemblage ranging into the basal Givetian, although he earlier (1970) recorded the component form species throughout Gi_a and Gi_b .

In North America, the lowest Givetian Zone, as recognised by Orr (1971) in the Illinois Basin, is the *Icriodus latericrescens latericrescens* Zone.

The lower limit of this zone is drawn below the first occurrence of the name giver and the upper limit below the appearance of *Po. varcus*.

So defined, the upper boundary is equivalent to that of the *obliquimarginatus* Zone. Because of the complete absence of *I. l. latericrescens* in the lower part of the Givetian in Europe and the lack of many of the diagnostic European forms in the North American successions, there is difficulty in correlating further.

Icriodus obliquimarginatus is found in the middle limestone of the Silica Shale in northwestern Ohio and this does lend some support to the equivalence of the zones. However, *I. obliquimarginatus* has been reported from, the upper parts of the Couvinian in Belgium and from the Seneca in New York on the one hand, and from the highest Givetian in Germany (though this may be *I. eslaensis*) on the other, so it does not appear to be particularly limited stratigraphically. For the N. American occurrences of this zone see Klapper (1971, p.296) and Orr (1971, p.20).

The Polygnathus varcus Zone *Bischoff & Ziegler 1957*

Originally established as the *varcus* subzone in the Givetian "Obers *Stringocephalen* Stufe" of the Rhenish Schiefergebirge, this interval was given zonal status by Ziegler (1962) and slightly modified by him (1971), at which time he recognised it as corresponding to the Upper Givetian and coinciding with the range of *Maenioceras terebratum* and species of *Agoniatites*.

The *varcus* Zone is defined as coinciding with the range of the name-giver from its first *abundant* occurrence to the appearance of *Schmidtognathus s.s.*

The lower limit of the zone is drawn at the first abundant occurrence of the name giver, *Spathognathodus brevis* and *Polygnathus beckmanni*; the upper boundary is recognised as lying immediately below the first occurrence of *Schmidtognathus hermanni*.

As such, this zone differs somewhat from the previous concepts of its age and limits. Bischoff and Ziegler (1957) first erected the "varcus Subzone" lying between the Sparganophyllum Kalk (below) and the ordinata-dubia Subzone (above). The varcus Zone sensu Wittekindt (1965) embraced somewhat less than the current definition since Ziegler (1965b) included the uppermost part of Wittekindt's varcus(and transversus) Zone in the lower part of the hermanni-cristatus Zone, and similarly since Wittekindt recorded the nominate species ranging well down into his robusticostatus Zone, part of that zone is probably also embraced by the present definition. On the other hand, as mentioned in reference to the obliquimarginatus Zone, forms similar to, and tending toward, Po. varcus, are found in the upper part of that zone (see on).

Spathognathodus brevis was recorded by Bischoff and Ziegler (1957) extending from midway through their varca Subzone into the late Devonian, but Wittekindt (1965) recorded it ranging from the base of his zone and and Ziegler's modified definition (1971) incorporates this range in recognising it throughout the varcus Zone. Po. beckmanni occurs throughout, but not outside, the varcus Zone.

The varcus Zone is subdivided approximately equally into an upper and a lower part by a very distinctive level, the walliseri horizon which is marked by the "Terebratula pumilio" bed, which is traceable throughout the Rhenish Schiefergebirge; this is characterised by the joint occurrence of Icriodus latericrescens latericrescens and the rare Ancyrolepis walliseri.

Both these forms are restricted to this horizon within the Middle Devonian, which is especially notable in the case of the icriodid since this is the only occurrence in Europe of a latericrescid outside the Lower Devonian (but see North America zonation).

Also within the varcus Zone are found the following forms: Spathognathodus planus, Icriodus obliquimarginatus, I. n.sp. aff. obliquimarginatus, I. eslaensis, I. aff. eslaensis, Polygnathus strongi, Po. ? variabilis, Po. linguiformis linguiformis, Po. l. mucronatus, Po. xylus, Po. pseudofoliatus, Po. "webbi", Po. decorosus s. l. sensu Ziegler 1965 a, Po. latifossatus and Po. alveoliposticus.

In a recent taxonomic revision of the *Polygnathus varcus* Group, Klapper, Philip and Jackson (1970) have attempted to clarify the confusion which has arisen concerning this diagnostic but ill-defined suite. Their general morphological concept of the group embraces four form species (two of which are new): *Po. varcus s.s.*, *Po. xylus*, *Po. rhenanus*, and *Po. timorensis*. As noted by Klapper *et al.* (1970, p.651), previous descriptions and illustrations of *Po. varcus s.l.* do not allow a comprehensive synonomy nor an accurate appraisal of the ranges of the individual morphotypes: this should, however, be possible in the future, whereupon a more precise definition of the *varcus* Zone may be facilitated. The author considers that further division within the group is possible and may further aid the delimitation of the zone.

In connection with *Po. strongi*, Klapper *et al.* (1970, p. 661-2) considered some of Stauffer's (1940) forms to be identical to large forms of *Po. xylus*, though the holotype of the former clearly demonstrates the distinctiveness of the form. Klapper *et al.* (1970, p.664) also considered some Eiflian forms assigned to *Po. xylus* as better regarded as small growth stages of *Po. pseudofoliatus* or *Po. eiflius*, and this thus throws some doubt on the downward extent in the range of *Po. xylus*. Indeed, it does seem that a more thorough knowledge of the ontogenetic development of Middle Devonian polygnathids will greatly clarify and possibly significantly alter the accepted ranges of diagnostic forms. *Po. decorosus s.l.* *sensu* Ziegler differs appreciably from *Po. decorosus s.s.* which appears to be a Frasnian form, but remains inadequately defined; Ziegler (1971 p.260) featured three variants in his range chart but did not differentiate between them. He records the range of *Po. decorosus s.l.* from the topmost *obliquimarginatus* Zone, extending throughout the *varcus* Zone and well into the Upper Devonian.

Po. pseudofoliatus was recorded by Wittekindt well into the upper part of the *varcus* Zone, but Ziegler (1971) drew its range only just into the basal horizons of that zone. *Po. "webbi"* *sensu* Ziegler (1971) which is found in the lower part of the *varcus* Zone, is probably referrable to *Po. costatus costatus* Klapper, though some forms may be nearer to *Po. pseudofoliatus*.

Po. linguiformis linguiformis maintains its long range throughout the zone, but the other subspecies of this form are restricted to the interval above the "*walliseri* Horizon". *Po.* ? *variabilis* is found sporadically throughout the zone, as is *Spathognathodus planus*.

Po. latifossatus was described by Wirth (1967) from the uppermost *varcus* Zone of the western Pyrenees and although Ziegler (1971) regarded this form as a juvenile of Schmidtognathodus hermanni, he recorded it ranging from the upper part of the *varcus* Zone; this appears to be a contradiction. *Spathognathodus semialternans*, recorded by Wirth from comparable levels, was thought by Ziegler to be closely related to *Po. varcus* and/or variants of *Po. decorosus s.l.* (Ziegler 1971, p. 262).

Po. alveoliposticus was recorded in the upper part of the *varcus* Zone at Martenburg by Ziegler (in Kullman and Ziegler 1970, table 1, samples 7033 - 7037).

The icriodid elements of these levels are still in need of revision (see previous zone). Bultynck (1972) recognises two assemblages (both consisting of one form species) in the Middle Devonian of the Ardennes, namely the *I. eslaensis* assemblage (ranging from the base of Gi_{c} to upper Fi_{a}). and the *I.* aff. *eslaensis* assemblages (lower Fi_{a} only) -- founded on the form species originally described by Adrichem Boagaert (1967) from the Cantabrian Mountains (Spain). The latter author found that "the abundance of *I. eslaensis* in the *varcus* Zone *s.l.* is remarkable."

In the Belgian Ardennes, Bultynck (1972, p.72) recognised the *varcus* Zone as equivalent to the period from low to Gi_{d} to the top of Fi_{a} (and questionably higher), but does not extend the range of *I. obliquimarginatus* (see previous zone) beyond the top of Gi_{b}, i.e. not as high as the *varcus* Zone. This compares closely with the original range given by Bischoff and Ziegler (1957) for this form species (the Oderhausen Kalk), but is inconsistent with the German ranges given subsequently by Wittekindt (1965) and Ziegler (1970), both of whom recorded *I. obliquimarginatus* ranging, albeit sporadically, into the upper part of the *varcus* Zone.

In North America, the varcus Zone appears to be more or less coincident with its European namesake, though a number of forms are not common to both continents. The typical *varcus* Zone association is *Po. varcus*, *Po. l. linguiformis* and *I. latericrescens latericrescens*, though one notes that none of these forms are restricted to the Zone.

According to Klapper *et al.* (1971, p.297) this association, and therefore the *varcus* Zone, is recognised in New York from the Centrefield

Member of the Hamilton Group to the top of the Tully Formation. By reference to Klapper & Ziegler (1967, p.78-9) one notes that it is only within the Tully (but not throughout it - see Middle/Upper Devonian Boundary) that one finds *Polygnathus beckmanni*, a form which is confined to the *varcus* Zone in Germany. Associated forms from the Tully also include *I. obliquimarginatus*, *I. nodosus*, *Po. pennatus*, *Spathognathodus* sp. (Klapper & Ziegler 1967, localities 14-16), *I. eslaensis* (Klapper *et al.* 1971) and *Po. alveoliposticus* (Orr & Klapper 1968, locality 8).

Elsewhere, the *varcus* Zone is recognised in all but the uppermost beds of the Solon Member of the Cedar Valley Limestone in Iowa, where the association is *Po. varcus*, *Po. decorosus* s.l., *Po. l. linguiformis*, *I. l. latericrescens*, *I. obliquimarginatus*, and *I. nodosus* (Klapper & Ziegler 1967,locs.20-21 partim).

The upper part of the Lingle Formation in southern Illinois has yielded *Po. varcus* (Orr, in Klapper *et al*.1971), though Orr (1964) recognised it as being *varcus* Zone in age before this form was found. The Beechwood Member of the North Vernon Limestone in southern Indiana has yielded a similar fauna.

Other *varcus* Zone assignments include the upper part limestone of the Silica Shale of northwestern Ohio (Klapper & Ziegler 1967, locality 17), the upper part of the Traverse Group(middle part of the Alpena Limestone through the Thunder Bay Limestone) in Michigan, the lower part of the Callaway Formation in Missouri, and the upper part of the Traverse Formation of northern Indiana.

The *transversus* Zone Wittekindt 1965

Characterised by the occurrence of *Polygnathus linguiformis transversus* and *Polygnathus bryanti* (=*Po. tuberculatus* Hinde), the interval was considered to be uppermost Middle Devonian (Wittekindt 1965, p. 628). Most of the forms present in the *varcus* Zone were also recorded from this zone (see Wittekindt 1965, table 1, p.627), the base of which was marked by the appearance of the name-giver. The presence of *Po. tuberculatus* was taken as indicative of the upper part of the interval, and the top was drawn below the first *Polygnathus cristatus* and *Po. asymmetricus*.

Wittekindt (1965, p.625) recognised the transversus Zone from three localities: the Syring Quarry, Ense, the Benner Quarry, Bicken and from Rhenert, Bonzel. Ziegler (1965a) rejected the zone since he considered that it could not be traced satisfactorily in most sections and he subsequently (1965b) included the higher horizons within his hermanni-cristatus Zone Po. l. transversus is taken to indicate the upper parts of the varcus Zone according to Ziegler (1971, p. 258).

In Ziegler 1965a, Wittekindt's guide species appear to be called Po. linguiformis subsp. and Po. sp., a designation they share with other forms.

Po. l. transversus has not been reported from outside Europe. When it is encountered, the transversus fauna may be a local facies expression of the varcus Zone in the same way as the hermanni-cristatus Zone may be, as will be discussed later.

Middle Devonian conodont successions in Australia

The Middle Devonian conodont faunas of Australia have recently been reviewed by Druce (1974, p. 5-6) who drew heavily on the work of Pedder, Jackson & Ellenor 1969.

Jackson (in Pedder et al. 1969, fig. 3, p. 248) recognised four assemblage Zones within the Timor Limestone of New South Wales and their "approximate correlation" with the German scheme is reproduced in the zonation chart. An Icriodus corniger Zone was recognised in sections 1 (unit 24), 6 (unit 23), and 7 (units 31-28). This is characterised by the name-giver in association with Po. linguiformis linguiformis, Po. webbi (= Po. costatus) and Po. cf. pseudofoliatus. Jackson equates this zone with its German namesake, though in European terms the association could conceivably date from the bidentatus Zone, particularly as regards Po. pseudofoliatus.

A little above the corniger horizons, Pedder et al. recognise a Po. kockelianus australis assemblage from sections 6 and 7. This includes the name giver, Po. angustipennatus, Po. robusticostatus, Po. cf. Po. pseudofoliatus and a few S. bidentatus and Po. intermedius. Also recorded from these levels, which these authors consider equivalent to the German bidentatus Zone, are Po. trigonicus and Po. webbi (=? Po. costatus). Po. kockelianus australis is the only form not found outside the interval.

Again, after a short break, the kockelianus - robusticostatus Zone of Pedder et al. (1969, sections 1,5,6,7) is characterised by the nominate subspecies Po. kockelianus kockelianus together with Po. robusticostatus, Po. trigonicus, and Po. eiflius. Also recorded are S. bidentatus, Po. angustipennatus, Po. intermedius, S. obliquus, Po. cf. Po. hulkus, S. bipennatus and Ozarkodina kutcheri. The last three together with the name giver and Po. eiflius appear for the first time while the latter together with Po. robusticostatus and S. bipennatus range, into the above zone. Po. kockelianus kockelianus together with occasional Ozarkodina kutcheri and forms described as Po. cf. Po. hulkus appear to be the only forms restricted to the interval. Considering the difficulty sometimes met with distinguishing the subspecies of Po. kockelianus (cf. Pedder et al. , p.252), the separation of this and the previous division must be a little difficult considering also that all the forms of the australis Zone also range up to these levels, though Pedder and others provide no numerical data nor do they note the relative abundance of the forms. Po. kockelianus kockelianus, Po. trigonicus, S. bidentatus, Po. angustipennatus range to very near the appearance of Po. varcus s.l. and for this reason Pedder et al. (p.249) considered that the interval approximated the combined kockelianus eiflius and robusticostatus Zones of Wittekindt (1965).

The Moore Creek Limestone of New South Wales has yielded a similar fauna which Philip (1966a) has considered as Late Eiflian in age, and indeed such an association does suggest, in European terms, such a designation.

The occurrence of Po. kockelianus kockelianus is somewhat different from the European occurrences, where it is restricted to the kockelianus Zone, and similarly from the N. American occurrences where it is both geographically and stratigraphically restricted. The same is true for Po. trigonicus. Po. angustipennatus is also limited to Eiflian strata in Europe and Ziegler (1974, p.379) considers that Givetian reports of Po. robusticostatus have not been substantiated. All in all, the kockelianus-robusticostatus assemblage would be better considered as older than Pedder et al. would like.

The youngest assemblage recognised by Pedder et al. (sections 1,3,5,6,7) is that of Po. varcus. Besides the name giver, S. brevis, Po. linguiformis forma nova (see Po. l. nova forma 2 in Taxonomy), Po. ? variabilis, S. planus, Po. pseudofoliatus, Po. eiflius, Po. cf. Po. webbi (=Po. costatus costatus partim, e.g. pl.15, fig.8) and S. bidentatus are also recorded. The appearance of A. walliseri in unit 5 of section 7 may equate with the walliseri horizon of the German sequence. Similarly, Pedder et al. (1970, p. 249) noted the presence of forms approaching Po. linguiformis transversus in the topmost Timor Limestone, which might also relate the two sequences. Po. varcus sensu Pedder et al. includes both Po. rhenanus and Po. timorensis, which occur together in part (e.g. section 1, unit 1). Some of the associated forms are atypical in comparison with European varcus Zone associations. Po. eiflius occurs together with Po. varcus (s.l.) in unit 10, section 6 near the base of the zone, while all the other associated forms occur high up in the zone. It might be valuable to know what expression of Po. varcus s.l. is represented at the lower levels. Certainly, forms approaching the Po. varcus group occur below the base of the varcus Zone in Europe and many of the associated forms are found already in the obliquimarginatus Zone (q.v.). It may thus be more appropriate to equate the basal parts of the varcus Zone sensu Pedder et al. with the upper parts of the European obliquimarginatus Zone. One also notes that S. brevis appears before Po. varcus s.l. in section 1, and probably in sections 3 and 5 (see on).

The Schmidtognathus hermanni-Polygnathus cristatus Zone Ziegler 1965 (a)

This zone was established by Ziegler in that interval between the (then) known ranges of the Middle Devonian ammonoid Maenioceras and the Upper Devonian Pharciceras. Therefore, this zone marked a critical interval in the Middle/Upper Devonian boundary problem (see same).

The zone is defined as the life span of Schmidtognathus in the absence of Polygnathus asymmetricus and Palmatolepis s.s. (i.e. Pa. transitans).

The lower boundary is drawn below the first occurrence of Schmidtognathus hermanni, the upper boundary below the appearance of the (aforementioned) wide-plated platform conodonts.

A lower and an upper division is recognised, the upper part being characterised by a number of forms, namely: Schmidtognathus pietzneri, S. peracutus, S. wittekindti, Polygnathus ordinatus, Po. cristatus, Po. sp. transitional to Po. cristatus, Po. rugosus, and Po. sp. Ziegler 1965a (= Po. sp. cf. tuberculatus, signata, ordinata); as noted by

Kirchgasser (1970, p.337), these do not all appear simultaneously. The last three appear to be restricted to the upper part of the *hermanni-cristatus* Zone, but the others range into the *asymmetricus* Zone, as do *Po. varcus s.l.* and *Po. decorosus s.l.* (three varieties) which range from the *varcus* Zone.

In North America, Orr and Klapper (1968) described two new forms from the boundary beds of Indiana and New York. These were *Polygnathus alveoliposticus* and *Palmatolepis* ? *disparalvea*. The first they recorded from the Tully Formation (0 to 1 foot above the base, and of *varcus* Zone age), from the lower part of the Antrim and from the limestone at the base of the New Albany Shale; the latter two localities, which have been dated as Upper *hermanni-cristatus* Zone in age, also yield *Pa.* ? *disparalvea* (which is also found in the North Evans Limestone).

In Germany, Orr and Klapper (1968, locality 9) records *Pa.* ? *disparalvea* from the Middle *asymmetricus* Zone at Martenburg. In spite of his earlier statement (Ziegler 1970, p. 263) that this form was conspecific with *Palmatolepis transitans* and was common in the lower *asymmetricus* Zone, Ziegler (in Kullman & Ziegler 1970, table 1, samples 7101, 7096, 7054) recorded *Pa.* ? *disparalvea* from the upper part of the *hermanni-cristatus* Zone. Similarly, *Po. alveoliposticus* which Ziegler notes as occurring "uncritically mixed with *Po. cristatus*" in the European *hermanni-cristatus* Zone, was later recorded by him in the *varcus* Zone (*q.v.*).

Additional associated forms from the European occurrences of the zone include *Spathognathodus sannemanni*, *Po. caelata*, and *Po. pennatus* (from Ziegler 1965a) which are found throughout the zone. From the Syring Quarry near Wildungen, Ziegler (1965a, p.656) recorded *Po.* ? *variabilis* and *Po. linguiformis* n. subsp. from throughout this period, and the latter was similarly recorded from the Martenburg profile (Kullman & Ziegler 1970, table 1).

Spathognathodus brevis was recorded from levels now considered to belong in this zone, by Bischoff & Ziegler (1957) and by Wirth (1967); both these authors also noted the occurrence, among the *Icriodus* group, of *I. nodosus*, *I. symmetricus*, *I. curvatus*, and (by Wirth only) *I. cymbiformis*. Ziegler (in Kullman & Ziegler 1970 recorded *I.* n. sp. ex gr. *obliquimarginatus* from the *varcus* Zone through the Lower *asymmetricus* Zone.

A new assemblage species ---Elsonella rhenana LINDSTROM & ZIEGLER 1965 --- consisting of four elements (Falcodus, Oulodus, Angulodus, Roundya)is also reported from the hermanni-cristatus Zone and successive levels in the asymmetricus Zone (Ziegler 1965a).

The S. hermanni - Po. cristatus Zone as defined above, has been recognised in several European sections. The zone was established from five localities in the German Rhenish Schiefgebirge, namely: Koppen, Geibringhausen Syring near Wildungen, Bicken near Dillmunde and Rhenert near Bonzel; it was also later reported from the Martenburg section, near Adorf. Muchow (1965) recorded a fauna from the Warsteiner Ridge outlier, which included Po. cristatus (sample A, p.725) which places it in the Upper hermanni-cristatus Zone.

Elsewhere in Europe, the zone has been recognised in northwestern Spain (Wirth 1967, see varcus Zone) and also from the Gustalapiedra Formation of the Cantabrian Mountains (Adrichem Boogaert 1967) (see also Ziegler 1970, p.263). In England, Kirchgasser (1970) recorded Schmidtognathus hermanni (sample 31, Trevose Slates) before the appearance of asymmetricus Zone forms, which is indicative of the lower part of the zone, though he argued that the base of the zone cannot be fixed due to the presence of transitional forms, and he consequently included these levels in the varcus Zone. The zone has not been recorded from Belgium, nor from Australia, where Druce (1974, p.6) thinks that it may be represented by a Biofacies II fauna, i.e. simple polygnathids and Icriodus, "indistinguishable" from that of the early Frasnian" .

The North American successions have also yielded the hermanni-cristatus Zone associations in a number of localities, which can be enumerated as follows:

1. The white crinoidal limestone at the base of the New Albany Shale in southern Indiana (Orr and Klapper 1968, p. 1068). The diagnostic forms are Schmidtognathus wittekindti, S. peracutus, (formerly Po. peracutus), Po. cristatus, Po. caelatus, Po. bryanti (= Po. tuberculatus), Po. ordinatus, Po. alveoliposticus, and Pa ? disparalvea; I. latericrescens latericrescens, Po. varcus, Po. l. linguiformis, Po. foliatus (= Po. dubius) and Spathognathodus sannemanni sannemanni are notable forms which range from the subjacent varcus Zone.

2. The lower calcareous part of the Antrim Shale of northern Indiana (Orr & Klapper 1968, localities 5,6) which yields *Po. cristatus*, *S. peracutus*, and *Pa. ? disparalvea*.

3. The upper part of the Alto Formation of southern Illinois (Orr 1964, p.5, samples 5-8): *Po. cristatus*, *S. peracutus*.

4. The uppermost Solon and lower Rapid Members of the Cedar Valley Limestone in southeastern Iowa (lower Rapid Member only, in the Milan area of Illinois) - Klapper & Ziegler 1967, p.80, localities 19-22; Klapper 1968) :*S.wittekindti* *S. peracutus*, *Po. ordinatus*, *Elsorella rhenana*.

5. The upper of the Denay Limestone of Red Hill, Simpson Park Range, Nevada (Klapper *et al.* 1971): *Po. cristatus*, *Po. ordinatus*, *Pa. ? disparalvea*.

6. The lower part of the Milwaukee Formation of eastern Wisconsin (Schumacher: in Klapper *et al.* 1971) : *Po. cristatus*, *Po. ordinatus*, *Elsonella rhenana.*

7. The upper part of the Callaway Formation of Missouri (Schumacher:in Klapper *et al.* 1971) : *Po. caelatus*.

8. The North Evans Limestone *partim*, Eitheenmile Creek, New York. This, the "conodont bed" of Hinde 1879 (see also Bryant 1921), contains a similar fauna to the basal limestone of the New Albany Shale (1) but differs in the presence of *Ancyrodella rotundiloba rotundiloba* which would seem to indicate a condensed succession ranging in age from the Upper *hermanni-cristatus* Zone to the Lower *asymmetricus* Zone.

All the above associations (with the exception of the limited record from Missouri) would fall within Ziegler's definition of the upper part of the *hermanni-cristatus* Zone, though Klapper appears to take the absence of *Po. cristatus* as indicative of the lower part of the Zone in the case of the Cedar Valley Limestone (4), even though the listed species of *Schmidtognathus* are not found in the lower *hermanni-cristatus* Zone.

The *Spathognathodus insitus* Fauna

This fauna, informally introduced by Klapper *et al*. (1971, p.300), is defined as that association dominated by the name-giver in strata below the first appearance of *Ancyrodella rotundiloba* (all subspecies).

It is found in the upper part of the Callaway Formation of Missouri, in the Coralville Member of the Cedar Valley Limestone and in the overlying State Quarry Limestone of southeastern Iowa, in all but the top part of the Coralville Member in Illinois, in the Firebag and basal Calumet Members of the Waterways Formation of Alberta (Uyeno 1967), and in the Point Wilkins Member and beds underlying it (above the base shale), Souris River Formation, Central Manitoba (Norris & Uyeno 1972).

Because *S. insitus* has not been found in Germany, it is not possible to say exactly how this fauna relates to Standard successions. In North America, in Missouri, Schumacher(1971c) found *S. insitus* (in association with *Schmidtognathus wittekindti* and *Po. pennatus)* occurring together with brachiopods associated elsewhere with conodonts of the Upper *hermanni-cristatus* Zone. The apparent absence of *Spathognathodus insitus* from strata in which the *hermanni-cristatus* Zone is well developed, Schumacher notes, suggests that the *S. insitus* fauna is correlative, at least in part with the former zone.

Uyeno (1967, 1974) has demonstrated a probable phylogenetic sequence from *S. insitus* through forms described as *Spathognathodus* ? sp. to *Ancyrodella rotundiloba binodosa*. This demonstrates the position of the *S. insitus* fauna immediately below the Lower *asymmetricus* Zone, as characterised by *A. rotundiloba*, in a position thus comparable with the Lowermost *asymmetricus* Zone. The occurrence of *Po. norrisi* on both the *insitus* fauna and in the Lowermost *asymmetricus* Zone of Alberta is further support for their equivalence (Uyeno 1974, p.18).

In Belgium, *S. insitus* is recorded from a level high in F_{1c} at Ny in the Dinant Basin (Coen and Coen-Aubert 1971, p.17) and from the Ave et Auffe section (in Bouckaert & Streel 1974, E, p.13, samples 21,14,13,9). The interval of F_{1c} has been considered as equivalent to the Lowermost *asymmetricus* Zone (Mouravieff & Bouckaert 1973, fig.1, p.94); *S. insitus* is found some 30 metres below the first *Ancyrodella rotundiloba* (in Bouckaert

& Streel 1974, E. p.18). In the Ave et Auffe section, a single specimen of Schmidtognathus hermanni (sample 16) is further indicative of levels comparable to the hermanni-cristatus Zone.

At the moment it is only possible to say that the S. insitus Fauna may be equivalent in age to part of, or all of the lowermost asymmetricus Zone, and possibly also to part of the Upper hermanni-cristatus Zone.

The Middle/Upper Devonian Boundary

The position of the Middle/Upper Devonian boundary has been the subject of much discussion and disagreement in recent years. Not the least reason for this is the confusion which has arisen over nomenclature and the lack of an internationally agreed definition.

A review of the present position has recently been presented by House (1973), so a brief comment will here suffice. A problem has arisen over the fact that the stratotype section of the Assise de Fromelennes (F1) in Belgium, the base of which has been traditionally taken as the base of the Frasnian, has not yielded any ammonoids, whereas in Germany the base of their Manticoceras Stufe as recognised by the first occurrence of Pharciceras lunicostata, is taken to be coincident basally (not the upper limit: House 1973, p.10), with what American workers (Klapper et al. 1970, p.300) prefer to call the "Lower Upper Devonian". The German Adorfian and North American Senecan are also names which have been used to denote this Upper Devonian interval. That these terms are all in current use to signify approximately the same time interval makes it highly desirable that a uniformity of expression is agreed upon. House argues for the retention of the Frasnian as the stage name and for the taking of the base of the Assise de Fromelennes (not the Assise de Frasnes) as the base of the Upper Devonian. This may not be very different from the lowest occurrence of Pharcicercas, House notes, but since this goniatite is not found in Belgium the use of a conodont parachronology is warrented.

Belgian workers (e.g. Coen 1972) have suggested that the Frasnian should be equated with the Ancyrodella bearing beds, and therefore that the boundary should be drawn at the base of the Lower asymmetricus Zone, i.e. at the base of the Assise de Frasnes (F_2).

In the following account, the base of the Upper Devonian has been considered as synonomous with the appearance of *Pharciceras*.

The conodont zonation about the Middle/Upper Devonian boundary

History of Work

The first attempt at a conodont zonation in relation to the Middle/ Upper Devonian boundary was that of Bischoff & Ziegler (1957). They recognised three subzones in the "Ober *Stringocephalen* Stufe" which they assigned to the Middle Devonian Givet-Stufe. These were, in ascending order, the *varca* Subzone, the *ordinata-dubia* Subzone and the *dubia-rotundiloba* Subzone. They also recognised an *asymmetrica-martenbergensis* Subzone and a *martenbergensis-triangularis* Subzone which they assigned to the Upper Devonian, *Manticoceras*-Stufe (to 1 α).

Ziegler's publication of 1958 combined the results of the classic German ammonoid stratigraphers in a detailed study of the conodont sequence of the famous Martenberg disused open Iron-mine profile (on the north eastern margin of the Rhenish Schiefergebirge), the type section of the Adorfer Kalk. At that time, he recognised a Middle/Upper Devonian "grenzschichten", amounting to a thickness of 1.30 metres, between the ranges of *Maenioceras terebratum* (tmo) and *Pharciceras lunicostata* (to 1α). From this interval (tm/to I) he recorded a conodont association which denoted the presence of the *ordinata-dubia* and the *dubia-rotundiloba* Subzones sensu Bischoff & Ziegler(1957).

In 1959, Krebs presented new goniatite evidence from the S.W. section of the Dill-Mulde (Rhenisches Schiefergebirge) and argued that this indicated that the *ordinata-dubia* Subzone and the *dubia-rotundiloba* Subzone belonged in the lowest levels of the Upper Devonian. He also considered the *asymmetricus-martenbergensis* Subzone to contain the boundary to 1α/ to 1(β) γ, and the *martenbergensis-triangularis* Subzone equivalent to a level low in to I (β) γ. Krebs (1959, p.378-381) furthermore presented a refinement of the zonation and emphasised the need to recognise characteristic combinations of different conodont species which occurred within the life-span of a leading species; the latter formed the basis of his divisions, which are as follows:-

The older *varcus* period (=*varcus* Subzone *sensu* Bischoff & Ziegler 1957), uppermost Middle Devonian in age (tmo), Krebs defined as the span of *Po. varcus* in the absence of the two subspecies of *Po. asymmetricus* (formerly *Po. dubius*) the appearance of which, in addition to *Palmatolepis transitans*, marked the upper boundary.

The younger *varcus* period was coincident with the older *dubius* period (=*ordinatus-dubius* Subzone and *dubius-rotundiloba* Subzone *sensu* Bischoff & Ziegler) which Krebs considered to date from toIα. The lower boundary was marked by the appearance of *Po. asymmetricus ovalis*, *Po. a. asymmetricus* and *Pa. transitans*, and the upper limit was drawn below the first occurrence of *Pa. punctata* (formerly *Pa. martenbergensis*).

He further speculated on the possible division of the period into an upper part with *Ancyrodella rotundiloba* in the absence of *Pa. punctata*, and a lower part characterised by *Po. ordinata* without *A. rotundiloba*. Above the older *dubius* period, Krebs, recognised a middle *dubius* period (upper toIα) a younger *dubius* period (toI(β)γ) and a *dubius-rhenanus* inter-regime (toI(β)γ).

The next significant contribution was that of Ziegler (1962b) who presented his unsurpassed zonation of the Upper Devonian. He established a *dubia* Zone at the base of the scheme with a lower, middle and upper part which corresponded to the older, middle and younger *dubia* periods (*sensu* Krebs) respectively; the *Ancyrognathus triangularis* Zone was coincident with the *dubius-rhenanus* inter-regime. Ziegler in his table 1, continued to question the Upper Devonian age of the Lower *dubia* Zone (i.e. his Grenzschichten of 1958) and it was this division which he maintained (1962b, p. 17) represented the period between proven Middle and Upper Devonian stratum (on megafaunal evidence).

In 1965, Ziegler (1965a) established the *hermanni-cristatus* Zone in that interval between the (then) known ranges of diagnostic Middle and Upper Devonian ammonoids. This interval marks a time of explosive evolution of platform conodonts, the diagnostic forms of this zone clearly demonstrating the tendency towards the palmatolepid group of the Upper Devonian, a trend which begins in the upper part of the *varcus* Zone.

Further contributions to the conodont biostratigraphy across this boundary, in the same year, include Ziegler (1965b), Lindstrom and Ziegler (1965) and Krebs and Ziegler (1965).

Discussion

In 1970, Kullman and Ziegler published an account of new ammonoid evidence from Martenberg. Layer by layer sampling of this extremely condensed sequence demonstrated the occurrence of Pharciceras and Synpharciceras in the upper part of the hermanni-cristatus Zone and of Maenioceras in the varcus Zone. The gap between known Middle/Upper Devonian stratum was reduced to 0.30m. Their subsequent contention that the boundary could be drawn at the base of the Upper hermanni-cristatus Zone does not follow, as pointed out by House (1973, p.7). Rather the boundary could lie anywhere between a level in the upper part of the varcus Zone and a level within the Upper hermanni cristatus Zone.

In North America there are two records in Klapper et al. (1971, p.299) which have a direct bearing on the boundary as it relates to the conodont zonation.

Firstly, the Denay Limestone of Nevada yields Upper hermanni-cristatus Zone conodonts in association with Leiorhynchus hippocastanea which is correlated with the Warrenella occidentalis Zone of the nearby Roberts Mountains by Johnson; this brachiopod zone is considered by him to be uppermost Givetian in age.

Secondly, the uppermost Solon and lower rapid Members of the Cedar Valley Limestone of Iowa, yields a fauna which Klapper considers is Lower hermanni-cristatus Zone in age, but strictly speaking it belongs in the upper part of that zone. The uppermost Solon with Rennselandia is dated as "Givetian" by Cooper and Phelan (1966), and even the middle Rapid contains "Givetian" corals according to Oliver.

If these opinions are correct, it appears that, in North America, the Upper hermanni-cristatus Zone is in part Middle Devonian, though one is sceptical of determinations based on corals and brachiopods.

The evidence from the Tully Limestone of New York would appear, at first, to contradict this. This formation belongs in the varcus Zone according to Huddle (in Klapper et al.1971; see also Klapper and Ziegler 1967, p.79, localities 14,15,16). A Pharciceras level described by House (1968, p.1065) bearing Pharciceras amplexum, occurs in the higher horizons. of the Tully at June's Quarry, and this was considered by House (1973, p.8) to come from approximately the same horizon as the highest fauna of conodonts described by Klapper and Ziegler (1967, p.79). This association (0 - 2.0 feet below higest exposed bed) includes Icriodus latericrescens latericrescens I. nodosus, Po. linguiformis, Po. varcus, and Spathognathodus sp., none of which are unequivocally of varcus Zone age.

The pharciceratids are associated therefore with a conodont fauna which may date from anywhere in the varcus Zone, hermanni-cristatus Zone or even from the lowest parts of the asymmetricus Zone; the absence of the diagnostic hermanni-cristatus Zone forms might be the result of facial control.

The same may be true of the unspecified conodont fauna found in association with both Pharciceras and Maenioceras by Bensaid 1973 (p.38) in the Tata region, south of the Anti-Atlas, Morocco. The absence of hermanni-cristatus forms indicates that the varcus Zone is in part Upper Devonian.

The S. insitus fauna is dated as Upper Devonian on the associated brachiopod fauna in three of the North American localities where it is recognised, namely, the Firebag and basal Calumet Members of the Waterways formation, Clearwater River, Alberta (McLaren 1962, p.15, 71), the Point Wilkins Member and underlying beds, Souris River Formation, Manitoba, and the State Quarry Limestone in Iowa, with Pugnoides and Melocrinus (Cooper et al. 1942, p.1783). These horizons are all stratigraphically higher than the others (see under S. insitus fauna)which are not dated by associated megafauna (Uyeno 1974, p.18).

In Belgium, the stratotype section at Fromelennes has yielded varcus Zone conodonts from within Gi_d to the top of F_{1a}, and questionably higher (Bultynck 1972, p.71-2) while above these levels, Ancyrodella rotundiloba binodosa marks the base of the Lower asymmetricus Zone in F_{2a}; between the two, no diagnostic forms have yet been recorded. Elsewhere in

Belgium, the Spathognathodus insitus fauna is indicated at Ny from a level high in F_{1c}, and from the Ave et Auffe section (see S. insitus fauna).

However the numbers are small and the facies is on the whole unfavourable, so it is difficult to be sure of one's position within the zonal scheme.

In summary, the appearance of Pharciceras, seems to equate with a level within the varcus Zone. Other megafaunal evidence suggests that the insitus fauna is "Upper Devonian" (N. America) or, strictly, Frasnian (Belgium) and that the Upper hermanni-cristatus Zone is "Middle Devonian". That these latter two may be in part correlative (see S. insitus fauna) would reduce the problematical interval, though again it should be stressed that these determinations are based principally on brachiopods. It seems likely that the hermanni-cristatus faunas are not everywhere developed. This may well be due to a facies control, which is also a likely explanation of the suggested equivalence of the Lowermost asymmetricus Zone and the insitus fauna, and of the latter and the Upper hermanni-cristatus Zone. It is here suggested that the transversus Zone of Wittekindt (1965) is also a (?) facies dependent, localised expression of these levels. Where the more specialised (?deeper water) platforms are not encountered the varcus zone will be indicated. All the known determinations are catered for infig. 2 which is an extremely tentative correlation of these critical intervals. In a very broad sense, deeper water faunas are to the right. A similar pattern of distributions go some way towards explaining why the Ancyro group dominate "shallow water" sequences in the higher Frasnian as opposed to the Palmatolepis sequences of the deeper areas.

Conodont Zonation of the Upper Devonian

Ziegler (1962b) proposed a detailed zonation of the Upper Devonian which has proved, on the whole, to be applicable worldwide, as demonstrated initially by Klapper and Furnish (1963) in North America, and Glenister and Klapper (1966) in Australia. (see Ziegler 1970, p.264 for full list).

Ziegler (1970, p.265-71) discussed the nomenclature changes to his original scheme and noted the taxonomic and biostratigraphic problems. To these may be added the refinement of Sandberg&Ziegler(1973) who introduced a new zone - the Lower rhomboidea Zone - and a new name - the marginifera Zone (previously the quadrantinodosa Zone). Also a recent contribution of Dreesen and Dusar (1974) provides a refinement of the palmatolepid successions in the type Famennian.

Within the Upper Devonian, the boundary between the Manticoceras and Cheiloceras Stufe has been placed at the base or within the lowermost part of the Upper Pa. triangularis Zone by Buggisch and Clausen (1972, p.165) The base of the type Famennian at Senzeille is more difficult to fix. The first limestone bed is 19 metres above the base defined by Gosselet, and has yielded a Middle triangularis Zone fauna (Bouckaert and Ziegler 1965). The 45 m. + of shales below this horizon represents the period from a level within or at the top of the Upper gigas Zone to a level within or at the base of the Middle triangularis Zone (cf. Bouckaert et al.1972; Mouravieff in Bouckaert and Streel 1974, F. p.8, sample 7).

The German standard zonation is slightly modified in Belgium since, as mentioned, the hermanni-cristatus Zone is recognised by Ancyrodella gigas rather than Pa. punctata and above the asymmetricus Zone it is only possible to recognise the A. triangularis Zone s.l. and the Upper gigas Zone s.l. (see Mouravieff and Bouckaert 1973, p.934). On the whole, the Ancyro-group provide most of the guide forms.

The North American sequence also differs slightly in the appearance of A. gigas before Pa. punctata, and the zonation chart is modified to incorporate this; essentially, recognition of, and delimitation within, the asymmetricus Zone is the same as in Belgium. Above this zone, the successions are comparable with the German ones (see Klapper 1970, p.300-5), up to the top of the marginifera Zone. The Middle crepida Zone and the rhomboidea Zone, not recognised in Klapper et al. (1970), have since been recorded by Sandberg and Ziegler (1974, p.108-9) in the Bactrian Mountains of Nevada, though Pa. crepida remains an extremely rare component (only three specimens from sample BCT - 7 B & I) of the North American faunas. The lowest Upper Devonian successions have been discussed previously (see under Middle/Upper Devonian boundary).

In Australia, Druce (1974, p. 6-9) has reviewed the present state of knowledge as regards the Upper Devonian conodont faunas. Again, up to the top of the marginifera Zone they are very similar to the German standard, above they are different. Druce (fig. 1) has Po. asymmetricus, A. rugosa, A. buckeyensis, A. gigas and A. rotundiloba appearing more or less simultaneously and prior to any species of Palmatolepis at the base of the asymmetricus Zone, which is unusual though no detail is included. On the zonation chart, the Icriodus succession of Seddon (1970a) is included in the interval of the asymmetricus, triangularis and gigas Zones.

The latter are recognised in the deeper water fore- and inter- reef facies by the usual index forms - the so-called Palmatolepis biofacies, but Seddon proposed the alternative scheme for the Icriodus biofacies of the reef and back-reef areas.

The correlation between the two sequences is rather tenuous but is indicated on the chart. There are three zones - I. symmetricus, "I. curvatus" and I. alternatus, the middle one including an angustulus horizon characterised by the two subspecies of I. brevis and by Pelekysgnathus planus. Seddon (1970a, p.737) found Po. dubius (formerly Po. foliatus) was often associated in the lower part of the "curvatus" Zone as was Po. decorosus s.s. in the alternatus Zone.

For definition of the zones and distributions of the index conodonts see Ziegler 1962b, 1971 and Sandberg and Ziegler 1974. For discussion of the North American situation, see Klapper and others (1971, p.300-11, figs. 3-6) and of the Australian sequences, Druce (1974, p. 6-9, fig.1).

CONODONT FAUNAS OF THE PLYMOUTH LIMESTONES

The oldest conodont faunas from the Plymouth area comes from the dominantly argillaceous succession of Rum Bay, south of Durness Point. This fauna has not been fully studied but the presence of a latericrescid and *I.* cf. *I. fusiformis* suggests a level comparable with the Belgian Em$_3$, but this requires further investigation.

The *corniger* Zone is represented by the argillaceous limestones of Durness Point. Herein *I*.. .*retrodepressus* and *I. corniger* are firmly identified. Forms which are similar to *I. curvirostratus* and *I. introlevatus* are present and may indicate the third association of Bultynck 1972; certainly the oral configuration of these forms lies nearest to these latter morphotypes. *I. expansus* has not been recovered, so its association with *I. retrodepressus* sensu Bultynck 1972 cannot be confirmed. Some of the icriodids appear to be transitional between *I. corniger* and *I. retrodepressus* in some oral features. Bultynck recorded *I. retrodepressus* from the middle part of the *corniger* Zone, specifically in the upper parts of Co$_{1c}$ into the lower part of Co$_{2b}$. The aforementioned *corniger* association corresponds with this interval. From the southern end of Richmond Walk (SX 458541), limestone with an almost identical lithology and fauna has yielded *I.* cf. *I. corniger*. Forms described as *I. expansus-nodosus* group morphotype 1 are probably new but await the collection of additional material; these show 'Eifelian' characters. In association, a single specimen of a polygnathid superficially similar to *Po. linguiformis* juv. is considered to be a new form (*Po.* n.sp. aff. *Po. porcillus*) relating the latter to *Po. angustipennatus*. The author has seen many such forms from the German Zwichenschichten (*kockelianus* Zone) and Bultynck has related similar forms in the phylogeny of Couvinian *Polygnathus* (Bultynck 1970, p. 127, fig.16, p.122). The age of this fauna from Richmond Walk may be younger than the Durness fauna but it is certainly older than Givetian.

An Eifelian age is inferred for the northern belt of thin to thick bedded limestones striking east to west through Laira, Princerock, North Cattedown and Coxside. Comparable horizons are met with in Drakes Island and probably on the Mount Batten Coast and at Hooelake. The shale - limestone transition beds are seen at Laira and Princerock, sections which need more intensive collecting to establish the age of the beginning of limestone deposition, especially as it relates to the Laira trilobites (see 'Plymouth situation').

No particularly diagnostic conodonts have been found in the Laira Bridge cutting though they would seem to correspond to horizons in Cattewater Road, Princerock and Teat's Hill Quarry, Coxside. *Icriodus* is represented by forms referred to as *I. expansus-nodosus* morphotype 2 and, from Teat's Hill, *I. regularicrescens*. The latter comes from Upper Couvinian levels in Belgium, particularly the upper part of Co_{2c} and Co_{2d}. *Po. pseudofoliatus*, *Po. linguiformis linguiformis* morphotype γ and *Po.* aff. *Po. xylus* are associated, though none of these are particularly diagnostic. The presence of a single specimen referred to as *S.* aff. *S. brevis* in a Cattewater Road fauna suggests high Givetian levels in terms of the European Standard, but the form is herein not considered to be as diagnostic as previously thought. Similarly, from these levels at Coxside comes *S. bidentatus*, an occurrence which is here equated with its occurrence in Belgium, that is during the uppermost Couvinian (Co_{2d}) and low Givetian. From Drake's Island (SX 468529)comes a single specimen of *Po. angustipennatus* from a limestone sequence at the west end of the Island, and another from a limestone raft within tuffs; this polygnathid is regarded as mid to late Eifelian in age.

Icriodus obliquimarginatus, *I.* n.sp. a, *I. expansus-nodosus* group morphotype 3, *Po. xylus*, *Po.* aff. *Po. xylus*, *Po. pseudofoliatus*, *Po. cattedowni* sp. nov., *Po. linguiformis linguiformis* γ morphotype, *Po. l.* aff. nova forma 1, *Po. latus*, *S. brevis*, and *S. bidentatus* are considered to represent a low Givetian association. These forms have been found, variously associated, in the belt of thicker bedded limestones south of and above the aforementioned Eifelian belt. The boundary may be represented in the Cattedown Quarry section (SX 493539) which is remarkably similar to the Couvinian/Givetian boundary beds of Haine Quarry, Couvin, Wellin and Marenne (Belgium). Of the above forms, *Po. latus* represents the most valuable index form but unfortunately it is very rare; the record of this form from Neal Point (NP_2) represents only the third record of the species since the original description by Wittekindt (see Taxonomy). *S. bidentatus* is here considered not to range higher than the *obliquimarginatus* Zone and is thought to be rare above the lower part of this interval. *Po. pseudofoliatus* and small forms referred to herein as *Po. xylus* and *Po.* aff. *Po. xylus* are similarly associated and are considered to have a low Givetian aspect. Later forms of *Po. pseudofoliatus*, not encountered in Plymouth have narrower platforms and tend toward *Po. dubius*. Similarly, later forms of *Po. xylus* may have larger, more robust platforms and curved axes.

Po. cattedowni n.sp. appears to be a valuable index form in Plymouth, and further collecting may prove it to be more widespread than hitherto established. Its occurrence with *I. obliquimarginatus* and I. n.sp. a (Princerock) may be significant but as yet this association represents a strictly British one. The *I. expansus-nodosus* group is the most widespread representative of *Icriodus* in the low Givetian strata of Plymouth but unfortunately the preservation of the aboral margins is such that a thorough appraisal of its stratigraphical value is limited.

Po. linguiformis linguiformis is well represented in the Plymouth Givetian. The γ morphotype appears to occur throughout but forms (*Po. l.* aff. nova forma 1) with strong marginal ornament and tongues with varying degrees of angular deflection are encountered (in Princerock and Neal Point) which may prove of stratigraphical value in the future; unfortunately numbers are few.

The presence of *S. brevis* is problematical. Rather than to consider the whole of the Plymouth Limestone, as no older than the *varcus* Zone, and the extension of most of the aforementioned forms into the latter Zone, the appearance of *S. brevis* is no longer considered to mark the base of the *varcus* Zone. This is not totally surprising in the light of its occurrence well into the Upper Devonian at the other end of its range. It may emerge that useful subspecific differentiation of this form is possible in the future.

Apart from the *I. expansus - nodosus* group and *Po. linguiformis*, conodonts are rare above the aforementioned associations in the Givetian in the east. The limestones are nearly everywhere biostromal in nature and unproductive in terms of conodont faunas. Such a facies is thought to persist in the Cattedown and in the south eastern areas until well into the Frasnian. Westwards, *varcus* Zone faunas are known from the Richmond Walk, Mount Wise and Mutton Cove areas.

The difficulty in defining the base of the *varcus* Zone has been mentioned previously. Because of the wide range of variation exhibited by forms loosely designated "*Po. varcus*" in the past, Klapper *et al.* 1970 have attempted to clarify the situation by redefining the name giver and erecting new form species. The author has introduced additional refinement and one waits to see if this proves of any stratigraphical value.

Within the *varcus* group, *Po. xylus* and associated forms certainly appear well before the late Givetian, in fact within the Eifelian. It is important that these forms are clearly recognised as such when encountered. They are not common in the material studied but one may make an observation as regards other European material: a blade in excess of half unit length is a character of some forms though not of *Po. xylus s.s.*; most of the forms have steep anterior trough margins. *Po. rhenanus*, *Po. timorensis* and *Po. biconvexus* have a more limited occurrence in Plymouth. The first named is known from the lowest horizons of Richmond Walk (North) and from near Botus Fleming, in both cases associated with forms provisionally called *Po.* aff. *rhenanus* (see Taxonomy), *S. brevis*, *Po. biconvexus*, and the long ranging *Po. linguiformis linguiformis* γ morphotype; this association is considered to be of *varcus* Zone age. Forms assigned, rather loosely, to the *Po. varcus* group also occur in the Richmond Walk section - but the difference between isolated specimens is often most pronounced, and they are quite unlike any of the "typical" representatives. Typical representatives of *Po. timorensis* have been recovered only from Mount Wise (SX 455541) where the specimens (identical to the holotype) are associated with *Po. biconvexus* sp. nov., *Po. varcus* and *Po.* aff. *Po. rhenanus*. In so much as all the members of the *varcus* group may be present (see discussion in Taxonomy), this is an exceptional fauna, and one would hope to provide more data on the variation (and its significance) within the group at a later date.

The age of the Mount Wise fauna is considered to be uppermost *varcus* Zone since *Po. mucronatus* (formerly *Po. linguiformis* subsp.) as well as the similar *Po. serratus* sp. nov. and abundant *Po. l. linguiformis* γ morphotype is encountered. In fact the presence of *Po. tuberculatus* and *Po.* aff. *Po. transversus* indicates Wittekindt's *transversus* Zone, though because *Schmidtognathodus* and other *hermanni-cristatus* Zone forms are not present, the latter zone is not represented as such; the possible partial equivalence of the *varcus*, *transversus* and *hermanni-cristatus* zones has been indicated previously. Also from Mount Wise comes *S. brevis* and *S. planus*. It is worthy of note that all the brachiopods recorded from here are also recorded from the Lummaton and Wolborough Shell beds of East Devon (Davidson 1863, p. 124; Ussher 1907, p. 53). What Mount Wise lacks in the other macrofaunal elements it appears to make up for in its rich conodont fauna (compare Matthews 1970).

A single, poorly preserved fauna from the massive limestone of West Hoe includes *Po.* cf. *Po. cristatus*, *Po. asymmetricus* group and ? *Palmatolepis*. Because of the absence of *Ancyrodella*, these horizons would appear to represent the Lowermost *asymmetricus* Zone, though the preservation is poor and they may be reworked; in any case the limestone would be younger than Middle Devonian.

The best Upper Devonian sequence of conodont faunas comes from Western King (SX461533). Closer spaced sampling is necessary here, but the results herein presented show the simultaneous appearance of *Po. asymmetricus* and *Ancyrodella rotundiloba*. *Po.* a. *ovalis* and *A.* r. *alata* are by far the most common representatives and it is debatable whether the other subspecies of these forms are present at all. Some forms are referred to *A. rugosa s.l.*, *Po. dengleri* and rare, small and smooth *Palmatolepis* (*Pa.* aff. *Pa. transitans*) are associated; the fauna is clearly indicative of the Lower *asymmetricus* Zone. *Icriodus* n.sp. aff. *I. alternatus* is an associated *icriodid* which is apparently restricted to these levels.

The Middle *asymmetricus* Zone is indicated by *A. gigas* in the southern horizons of the Barn Pool limestones (SX456532) and again in the northern outcrop of Durnford Street (SX 536464) where *A. gigas s.l.* is a preferable designation. This latter fauna (which often shows strong deformation, is white in colour and fragile) includes *Po. nismi* and *Pa.*? *durnfordi*, which are new, and *Po. asymmetricus*. The presence of a few *palmatolepids* with strong lobe development suggestive of *Pa. gigas* and/or *Pa. subperlobata* may indicate stratigraphic admixture, though typical representatives of these forms are not associated, and their occurrence is considered for the moment as due to a stratigraphic leak. *I. symmetricus*, *I. expansus-nodosus* gp., and rare *I.* aff. *I. brevis* represent the icriodids. Similar icriodids come from southern horizons of Radford Quarry (SX 505530) with *A.* aff. *A. rotundiloba* and *Po. asymmetricus*. These horizons are considered to be late Lower *asymmetricus* Zone in age.

With few exceptions, the whole of this eastern region, apart from Radford Quarry, is barren in terms of conodonts and to a relatively large extent in macrofauna too. Such faunas that have been retrieved indicate an Upper Devonian history but are probably fortuitous and may result, at least at these levels, from occasional 'insweepings' into this 'restricted' environment.

The Upper Devonian sequences above the Middle *asymmetricus* Zone are mostly characterised by occasional polygnathids in Radford Quarry. The northern beds have yielded *Pa.* aff. *Pa. subrecta* and *Ancyrognathus* cf. *A triangularis* indicating the *A. triangularis* Zone, but again the faunas are poor and in the absence of continuous successions it is not possible to rule out a younger age, since both form range higher than the latter Zone. The same is true for the isolated fauna of the Fisons Quarry (SX 493538) red argillaceous shale and conglomerate matrix in which numerous *Pa. subrecta* are associated with *Ancyrodella curvata, Ancyrognathus triangularis* and morphotype 2 of *I. symmetricus.* A comparable though much sparser fauna comes from the red and pink limestones at the southern end of Durnford Street. The latter appears to be in sequence but one must take great care to distinguish between these red limestones many of which are stratigraphic leaks (see Plymouth environments).

Faunas definitely older than Middle Frasnian are sporadic. The red argillaceous limestone and shales of Western King (South), often discordant, sometimes with brecciated grey limestone inclusions and occasionally infilling what have been interpreted as solution hollows (Orchard 1975) have yielded an abundant Upper Frasnian/Lower Famennian fauna (see appendix for details). Similar features can be seen in Durnford Street too. In Radford Quarry a single specimen of *Pa. termini* in addition to other indeterminate palmatolepid fragments from the highest horizons, suggests that the Middle *crepida* Zone is represented. The limestone is not thought to be condensed here, though on the other hand there is no evidence of solution of the limestone. The latter is, however, thought to be responsible for the presence of these Famennian forms at the top of the sequence. Not far away, in Langshill Quarry (SX 499532), the top of the limestone is seen in contact with green shales (in the core of the syncline). The contact here appears to be concordant, allowing for some degree of differential movement, but bulk sampling has not produced a single conodont, so the age of this event is not known; this is the only locality where the contact is seen. Elsewhere red shales, still undated, appear to lie above the massive limestones in the Turnchapel area (SX 496531) and they appear again in Bedford Quarry (SX 540538). Their presence may be due to differential subsidence and/or later tectonics but no clear uniform termination of limestone deposition is indicated.

The green and purple shales north of the limestone are thought to be in faulted contact, though the contact is nowhere seen; the nearest point of outcrop to the limestone is north east of Saltram Quarry (SX 518547). The age of the shales is indicated in Fig. 3 (Ostracod ages after Gooday 1975). A conodont fauna from Neal Point indicates the lower part of the Upper *marginifera* Zone (see Appendix for details).

SYSTEMATIC PALAEONTOLOGY

Foreword

The current trend in conodont systematics is toward a unified multi-element taxonomy. Such an approach is well established in some parts of the Palaeozoic and conodont zonations are consequently more 'natural' in being based on phylogenies into which the mozaic nature of multi-element evolution is incorporated. As has been discussed by Klapper and Philip (1971, p.439), form taxonomy obscures important differences between similar elements which occur in very different assemblages, obscures homologies and has led to a confused excess of synonomous form-generic names. Furthermore there are many form species based on minor and perhaps insignificant morphological variation. The major difficulty is, of course, that since we do not know the nature of the conodont animal nor the function of the conodont apparatus, it is impossible to be sure of the characters which are of taxonomic importance, and so such variation as is due to ecological differences or dimorphism (see e.g. Jeppsson 1972, Merrill and Merrill 1974) is extremely difficult to evaluate. There is also an urgent need for ontogenetic studies, since these have often been overlooked. A biometric approach (e.g. Barnett 1971) will perhaps be a great help in sorting out the meaning and significance of these variations, but meanwhile a more natural approach to conodont taxonomy must inevitably lead to a fuller understanding of the subject.

Within the Devonian the problems are underlined simply by the great diversity of the conodonts. Devonian natural assemblages are known only from the Upper Devonian Kellwasserkalk of Germany, and all these occur in coprolites (Lange 1968). Fortunately because there appears to have been relatively few 'structural plans' within the conodont apparatus, by means of structural homology it seems possible to indicate assemblages compositions in some instances. Klapper and Philip 1971 introduced a system of symbols (1971) and recognised four basic apparatus types which they (1972) related to a familial classification (1972):

Type 1 apparatus = Polygnathidae Bassler, 1925 –
consists of P,O_1,N,A_1-A_2-A_3 elements
(see Klapper and Philip 1971, p.432-3; 1972, p.99-100).
Type 2 apparatus = Cryptotaxidae - consists of P,O_2,N,B_1-B_2-B_3 elements.
Type 3 apparatus = Hibbardellidae Muller, 1956 –
consists of O_2, N,B_1-B_2-B_3 elements
(see Klapper and Philip 1971, p.435-7; 1972, p.100-01).
Type 4 apparatus = Icriodontidae Muller and Muller, 1957 -
consists of I,S ± M elements
(see Klapper and Philip 1971, p.438-9; 1972, p.101-03).

A fifth family, the Panderodontidae, may include intergradational series of simple cones (see Klapper and Philip 1972, p.103-4).

It is premature to say whether Klapper and Philip's scheme is correct. There has subsequently been some support for some of their assemblages (e.g. Savage, 1973; Chatterton 1974) though Fahraeus (1974) considers that the element composition of the earliest *Polygnathus* apparatus (i.e. *Polygnathus berbonus* - see Klapper and Philip 1971, fig. 11, p.449) remains unknown. Ziegler and Lindstrom (1972) have presented alternative views on Devonian assemblages, notably considering the association of different platforms in apparatus devoid of ramiform elements.

Bultynck (1972, p.72) has considered that the Belgian Middle Devonian *Icriodus* associations do not support the suggested association of Philip and Klapper (1971, fig. 8, p.446), that is an icriodonton plus an acodinan element. Rather, Bultynck groups one to three form species of *Icriodus* together within an assemblage. The results from this work support the approach of Bultynck as regards the icriodids, though the poor preservation of the aboral surfaces presents a difficulty.

Insofar as a general multi-element approach is concerned, there are a number of difficulties. For the most part, the depositional environment of the Plymouth Limestones was a high energy situation. Because of this, associations, particularly those from the often enriched bioclastic horizons, will rarely reflect original assemblage compositions due to the effects of spatial and perhaps temporal mixing, due to differential current sorting and to preferential breakage of particular elements. Though this is true for the most part, elemental distributions throughout the limestones do reflect what are thought to be primary distributional patterns to an extent (see conodont biofacies). Of course, there are inevitable difficulties arising from the often identical nature of fragmented ramiform elements. Whenever it has been possible, the "bars and blades" have been identified in multielement terms and some are illustrated, but it is felt impracticable to attempt a multielement approach. Hence the main systematic part is predominantly a single element, form-taxonomy, for reasons mentioned, and because the main thrust of the thesis is biostratigraphi The latter reason is presented as a justification for such a dual nomenclature and also for the recognition of 'morphotypes'.

Such distinctions are used because they allow observations on the morphological variation of specimens to be stressed without defining the nature or the significance of such variation. Thus, morphotype "1", "2" and "3" may prove to have a stratigraphical application and therefore be biologically meaningful, and hence subspecific/specific status can be later effected. Such may now be warranted for the morphotypes of Polygnathus linguiformis linguiformis (see Polygnathus linguiformis group) On the other hand, morphotypes may reflect only different ontogenetic stages, different positions within a single conodont apparatus, dimorphism or ecologic variation. Such may be revealed on further collecting.

Further emendation of taxonomic status has been necessitated by the nonsensical situation of subspecies occurring in the same fauna (see Sylvester Bradley 1956, p.3; Aldridge 1972, p.160). Of course one must be wary of stratigraphic mixing, but this practice is not uncommon in the Devonian, especially the late Devonian (e.g. the Palmatolepis glabra group). Complete revision is outside the scope of this work, so some distinctions such as these are evident in the faunal lists. As Seddon (1970a, p.737) has noted, 'artificial' (specific) distinctions are worth making if they clarify morphology, articulate evolutionary patterns and/or permit stratigraphic discriminations.

Lindstrom and Ziegler (1972) and Huddle (1972) have written authorative statements on the subject of conodont taxonomy.

The Ancyro Group

The group is distinctive and of short stratigraphical range, being restricted to the lower Upper Devonian. *Ancyrodella* is the most common representative, *Ancyrognathus* is less common and appears later.

Form genus *Ancyrodella* ULRICH AND BASSLER

Type species *Ancyrodella nodosa* ULRICH & BASSLER 1926.
1926 *Ancyrodella* ULRICH AND BASSLER, p.48.
1957 *Ancyropenta* MULLER AND MULLER, p.1092-3.
Description: See Huddle 1968, p.6, Ziegler 1973, p.21.
Remarks: Within this form genus, the general outline of the platform and, aborally, the development of secondary keels, have been considered as the most important characters for specific differentiation.

The stratigraphical valve of *Ancyrodella* was demonstrated by Ziegler (1962, fig. 2) who outlined the plylogenetic development of the group. This author considered that *Ancyrodella rotundiloba*, the earliest representative, evolved from a polygnathid ancestor, probably *Polygnathus asymmetricus asymmetricus* through progressive restrictions of the anterior platform to produce distinct lobes, by thickening of the platform and through the strong attenuation of radial undulations aborally to form keels.

Ethington and Furnish (1962, p.1260) considered a complete sequence of *A. curvata* and noted the close similarity of the juvenile specimens to *Spathognathodus insitus* (STAUFFER), the former differing in the development of "denticulate lateral processes on the upper surfaces of the flared lips of the escutcheon". As pointed out by Glenister and Klapper (1966, p.798) the stratigraphical succession of *Ancyrodella* suggests that *A.curvata* was derived from *A. lobata*, but nevertheless the ontogeny of the former would seem to be recapitulating its phylogeny in view of more recent work.

Uyeno (1967 and 1974, p.23, 26, 43, 44) has indicated a phylogentic sequence from *Spathognathodus insitus*, through *Spathognathodus*? sp. to *Ancyrodella rotundiloba binodosa*, and *A. rotundiloba* subsp.A.

Uyeno considers that the succession within the Waterways Formation "suggests a possible phylogeny and origin of *Ancyrodella*, relating it with *Spathognathodus*". Walliser (1957, p.34) has reported a similar series relating *Spathognathodus* = *Ozarkodina fundamentata* to the homeomorph *Kockella* in the Silurian.

The multielement *Ancyrodella* is of type 1 apparatus according to Klapper and Philip (1972, p.99). Ziegler 1972, suggested it may be represented by a single pair of ancyrodellids or be associated with *Ancyrognathus*.

Range: By definition, *Ancyrodella* ranges from the base of the Lower *Polygnathus asymmetricus* Zone (Ziegler 1971). According to Ziegler (1958) *A. buckeyensis* is the last to disappear - within the Middle *Pa. triangularis* Zone. Ziegler 1974 (p.22) gives the upper limit of its range as the top of the Lower *Pa. triangularis* Zone.

Ancyrodella curvata (BRANSON & MEHL)

Plate 26, figs.10,11,13; Plate 27, fig. 6

*1934 *Ancyrognathus curvata* n.sp. - BRANSON & MEHL, p.241,pl.19, figs.6,11.
.1938 *Ancyrognathus asteroideus* n.sp. - STAUFFER, p. 418,pl.52, figs.8,9.
.1955 *Ancyrognathus curvata* BRANSON & MEHL - SANNEMANN, p.331, pl.24, fig.11.
.1956 *Ancyrodella curvata* (BRANSON & MEHL) -BISCHOFF, p.118-9,pl.8, figs.9-11.
?1956 *Ancyrodella* sp.A - HASS, p.20, pl.4, fig. 18.
.1956 *Ancyrodella* sp.B - HASS, p.18, pl.4, fig. 20.
.1957 *Ancyropenta asteroideus* (STAUFFER) -MULLER & MULLER, p.1093,pl.136,figs,7,8.
.1957 *Ancyrodella curvata* (BRANSON & MEHL)-FLÜGEL & ZIEGLER, pl.1,fig.8.
.1958 *Ancyrodella curvata* (BRANSON & MEHL)-ZIEGLER, p.40-1, pl.11,fig.5.
.1962 *Ancyrodella curvata* (BRANSON & MEHL)-ETHINGTON & FURNISH, p. 1261-2, pl. 172, figs. 12 - 20.
.1966 *Ancyrodella curvata* (BRANSON & MEHL) - GLENISTER & KLAPPER, p. 798, pl. 86, figs. 13-15.
.1966 *Ancyrodella curvata* (BRANSON & MEHL) - ANDERSON, p.403, pl.48, figs. 2,4,6,9,11,13.
.1967 *Ancyrodella curvata* (BRANSON & MEHL) - WOLSKA, p.373, pl.1,figs.12,13.
.1967 *Ancyrodella curvata* (BRANSON & MEHL) -VAN ADRICHEN BOOGAERD, p. 177-8, pl. 1, fig. 1.
.1968 *Ancyrodella curvatus* (BRANSON & MEHL) - MOUND, p. 469-70, pl.65, figs. 5,6, 13-16.
.1968 *Ancyrodella lobata* (BRANSON & MEHL) - MOUND, p. 470-1, pl.65,figs.7-12.

. 1970 Ancyrodella curvata (BRANSON & MEHL) - SEDDON (a), pl.16, figs.3,4.

. 1971 Ancyrodella curvata (BRANSON & MEHL) - SCHUMACHER(b), p 100-1, pl.12, figs. 4-6.

. 1971 Ancyrodella curvata (BRANSON & MEHL) - SCULSZEWSKI, p.11-12, pl.3 fig. 5; pl.4, figs. 4-5.

Diagnosis: Ancyrodella with a distinct postero-lateral lobe which bears a well developed secondary carina and keel, making a total of three in all. The posterior process is typically very narrow. Besides the strong carina, the platform surface bears a nodose ornament, which may be regularly aligned.
Remarks: This form lies close to A. lobata which is not clearly established. A. curvata differs in having a clearly differentiated postero-lateral process bearing both a carina and keel. The latter, in particular, is apparent even in very small specimens (e.g. pl. 26, fig.11), and thereafter, growth involves the greater differentiation of this lobe. See also Ethington and Furnish p.1261-2.

One notes that A. lobata sensu Sculczewski fills nicely the "morphological gap" between his A.gigas (pl.4, fig.1) and his A. curvata; from the former to the latter we have the specimens figured on his pl.4, fig.3 → pl.3, figs.3 → 4 → 1 and hence to his A. curvata (Sculczewski 1971, pl.4, fig.4).

Occurrence: Samples 77, 77c Fisons Quarry, Cattedown; WK 6a, WKb$_1$, Western King ; 115, Radford Quarry.
In Germany: base of the Upper asymmetricus Zone - low Middle Pa. triangularis Zone.

Ancyrodella gigas YOUNGQUIST *sensu lato*

Plate 26, figs. 1,3,4,9,12; Pl.27, figs.3,8.

* 1947 *Ancyrodella gigas* n.sp. - YOUNGQUIST, p.96-7, pl.25, fig.23.
1947 *Ancyrodella sp.* - MILLER & YOUNGQUIST, p.503-4, pl.74, fig. 13.
1947 *Polygnathus rotundiloba* BRYANT - YOUNGQUIST, p.110, pl. 26, fig. 6.
. 1957 *Ancyrodella gigas* - YOUNGQUIST - MULLER & MULLER, p.1091,pl.141,fig.8 pl. 142, fig. 1.
. 1958 *Ancyrodella gigas* YOUNGQUIST-ZIEGLER, p.41-2, pl.11,figs.8,10,17.
1965 *Ancyrodella gigas* YOUNGQUIST - KREBS & ZIEGLER, pl.2, fig.7.
1965(a) *Ancyrodella gigas* MILLER & YOUNGQUIST (sic) -ZIEGLER, pl.1, fig.1.
. 1966 *Ancyrodella gigas* YOUNGQUIST - ANDERSON, p.403, pl.48,figs.10,14.
. 1968 *Ancyrodella gigas* YOUNGQUIST - MOUND, p.470, pl.65, figs. 17,18.
1971 *Ancyrodella gigas* YOUNGQUIST - SCULCZEWSKI, p.12, pl.2, fig.3; pl.4, fig.1.
. 1974 *Ancyrodella gigas* YOUNGQUIST - UYENO, p.23, pl.1, figs. 1,8,9.

Diagnosis: *Ancyrodella* with an elongate, triangular platform with well developed secondary carinae and keels which extend to the pointed anterior lobe tips. Platform ornament consists of stout 'semi-regular' nodes.

Remarks: Youngquist's holotype is rather atypical in comparison with forms subsequently designated *A. gigas*. The former is characterised by a platform which is distinctly and abruptly narrowed at about its midlength to produce an extremely long and narrow posterior process. In this respect the form approaches *A. nodosa* ULRICH & BASSLER which differs in being even more strongly constricted posteriorly, in its equi-triangular and often reduced platform, and its more subdued ornament. Sometimes, *A. nodosa* also has an ornament of transverse ridges and this relates it to *A. buckeyensis* STAUFFER, the platform outline of which often approaches that of *A. gigas*. The shorter, more equitriangular platform and ornament of transverse ridges distinguishes *A. buckeyensis* from *A. gigas*.

A. rugosa also has strongly developed secondary keels but, in the holotype (Branson & Mehl 1934, pl.19, figs.15,17), these do not extend to the lobe tips, which are rounded and not pointed as in *A. gigas*. The characteristic ornament of numerous rounded nodes of *A. rugosa* is also a feature of some specimens referred to *A. gigas* (e.g. Uyeno 1974, pl.1, figs. 1,8).

The specimen illustrated on plate 26, fig. 1 appears to be closest to the type of A. gigas in possessing a long platform. Others included here are characterised by a shorter, broader platform with an ornament of large random nodes. (pl.26, figs. 3,4,9,12; pl.27, figs. 2,8); the specimen figured by Miller and Youngquist is very similar. It is thought that these latter may represent a new form species, since similar forms can be distinguished in the Belgian Frasnian (personal communication, Mouravieff 1974). However, they do fall within a broad concept of A. gigas, together with the very different specimens of Uyeno, and with others such as those illustrated by Sculczewski 1971 which have a platform shape tending toward A. curvata. For these reasons, the suffix sensu lato is here used until the stratigraphical meaning of these various forms is clarified.

Occurrence: Sample 135, Barn Pool, nr. Cremyl; Sample DS1, Durnford Street; (cf.) HL11, Hooelake Quarry. In Germany: from the base of the Middle asymmetricus Zone to the top of the Lower gigas Zone.

Ancyrodella nodosa ULRICH & BASSLER

Plate 27, fig. 7

* 1926 Ancyrodella nodosa n.sp. - ULRICH & BASSLER, p.48,pl.1, figs.10-13.

. 1926 Ancyrodella hamata n.sp. - ULRICH & BASSLER, p.48,pl.7, fig.7.

. 1948 Ancyrodella nodosa ULRICH & BASSLER - YOUNGQUIST & MILLER, p.441, pl.68, figs. 13,14.

. 1956 Ancyrodella nodosa ULRICH & BASSLER - BISCHOFF, p.119, pl.8, fig.15 (non fig.12 = A. buckeyensis).

. 1957 Ancyrodella hamata ULRICH & BASSLER - MULLER & MULLER, p.1091-2, pl.136, fig. 4.

. 1958 Ancyrodella nodosa ULRICH & BASSLER - ZIEGLER, p.44, pl.11,fig.1.

. 1962 Ancyrodella nodosa ULRICH & BASSLER - REICHSTEIN, p.1 fig.14,15 (fig.14 transitional from A. buckeyensis).

. 1966 Ancyrodella nodosa ULRICH & BASSLER - GLENISTER & KLAPPER, p.798-9 pl.86, figs. 5-12.

. 1968 Ancyrodella nodosa ULRICH & BASSLER - HUDDLE, p.6 - 7, pl.13, figs.1-4, 7-10 (cop. ULRICH & BASSLER).

. 1969 Ancyrodella nodosa ULRICH & BASSLER - CHALYMBADSCHA & TSCHERNUSHEVA pl. 2, figs. 10-13.

. 1970 Ancyrodella nodosa ULRICH & BASSLER - SEDDON (a), pl.16,fig.5.

. 1971 Ancyrodella nodosa ULRICH & BASSLER - SCHÖNLAUB, pl.4, fig.14.

. 1971 Ancyrodella nodosa ULRICH & BASSLER - SZULCZEWSKI, p.14-15, pl.2 fig.2; pl. 5, figs. 2 - 5.

Diagnosis: *Ancyrodella* with a strongly constricted posterior platform produced into a narrow posterior lobe. The two anterior lobes are equally narrow, and on their underside bear fully developed secondary keels which extend to the sharp anterior lobe tips.

Description: See Huddle 1968, p. 6-7.

Remarks: A single specimen from Plymouth conforms exactly to *A. nodosa* in the strongly constricted posterior platform, in this case very short. *A. buckeyensis* differs in having a less constricted platform whereas that of *A. ioides* is more so.

Occurrence: Sample 56, Western King, Plymouth. In Germany the form ranges from the base of the *A. triangularis* Zone to a level within the Upper *gigas* Zone.

Ancyrodella rotundiloba (BRYANT)

1921 *Polygnathus rotundilobus*, spec. nov.- BRYANT, p.26-7, pl.12, figs. 1-6 ; p.26, tx. fig.7 (Ziegler designated fig. 1 as lectotype in 1958, p.44).
1967 *Ancyrodella rotundiloba* (BRYANT) - MULLER & CLARK, p.908, pl. 115, fig.8; pl. 116, figs. 1-5; p. 908-10, tx. figs. 5-7.

Diagnosis: *Ancyrodella* with a basal cavity of variable size from which up to two keels may be developed, though neither extends to the platform margins which are rounded anteriorly.

Remarks: Four subspecies have been distinguished and all appear to have staggered ranges and distributional anomalies. *A.r.binodosa* is the earliest representative and is followed by *A.r.* subsp.A. sensu Uyeno 1967, *A.r. rotundiloba* and *A.r. alata*. There is some uncertainty as to the validity of *A.r.* subsp.A. In the Waterways Formation of Canada, this form closely follows *A.r. binodosa* but appears well before *A.r. alata* (Uyeno 1974, p.5, 1 7); *A.r. rotundiloba* is not recorded. In Belgium, from the zone F2a at Fromlennes, Mouravieff (in Bouckaert and Street 1974, F, p.1) has recorded forms transitional between *A.r. binodosa* and *A.r. rotundiloba* above the lowest level of the former. These are characterised by a coarser platform ornament than is typical of the later forms, and in this respect would seem to correspond to *A.r.* subsp.A.

However, Mouravieff (personal communication) has posed the critical question of whether such forms are truly an evolutionary development or rather due to an ecological response. Chalymbadscha & Tschernusheva 1969 (fig.1, p.82) recorded *A. prima* and *A. pristina* from strata below the first *A.r. rotundiloba*; these are thought to be synonomous with *A.r. binodosa*.

A. rotundiloba lies closest to *A. rugosa*. The differences are dealt with under each.

Ancyrodella rotundiloba alata GLENISTER & KLAPPER

Plate 25, figs. 2,3, 5-10; Pl.26, figs.5,6; Pl.27,figs.2,9

. 1957 *Ancyrodella rotundiloba* (BRYANT) - BISCHOFF & ZIEGLER, p.42, pl.16, figs. 6,9,11,12,16,17 (only).

1958 *Ancyrodella rotundiloba* (BRYANT) - ZIEGLER, p.44-5, pl.11, fig.12 (only).

1965 *Ancyrodella rotundiloba* (BRYANT) n.subsp. - KREBS & ZIEGLER, pl.1, figs. 8,9 (only).

. 1966 *Ancyrodella rotundiloba alata* n.subsp.- GLENISTER & KLAPPER, p.799-800, pl. 85, figs. 1-8, pl.86, figs. 1-4.

. 1967 *Ancyrodella rotundiloba* (BRYANT)- CLARK & ETHINGTON p. 29-30, pl.2, figs. 4,8-10, 13 (non fig.7 = *A.r. binodosa*, non fig. 15 = *A.r. rotundiloba*.

. 1968 *Ancyrodella rotundiloba alata* GLENISTER & KLAPPER - POLLOCK, p. 424, pl. 61, figs. 2,3.

. 1969 *Ancyrodella rotundiloba alata* GLENISTER & KLAPPER - POLSLER, p.404, pl.4, figs. 1-4.

. 1969 *Ancyrodella rotundiloba alata* GLENISTER & KLAPPER- CHALYMBADSCHA & TSCHERNUSHEVA, pl. 2, figs. 1-9.

. 1971 *Ancyrodella rotundiloba alata* GLENISTER & KLAPPER - SZULCZEWSKI, p.15 - 16, pl.1, figs. 1,2.

. 1974 *Ancyrodella rotundiloba alata* GLENISTER & KLAPPER - UYENO, p.24, pl.1, figs. 3,7.

Diagnosis: A subspecies of *A. rotundiloba* with an alate platform outline with two secondary keels, the inner one generally extending anteriorly to the crimp and the outer one a lesser distance in a lateral or even posterior direction.

Remarks: The keel development is the most advanced within the form-species and provides the best criterion for distinction. In addition, according to Glenister & Klapper, the platform often bears a finer ornament than the nominate subspecies and the blade is generally composed of a larger number of lower denticles.

In Plymouth, this subspecies is the most common and perhaps the only representative of the form species. Some of the material is strongly deformed and the state of preservation is generally poor, but two degrees of keel development is apparent amongst the 'alate' group. Some specimens have a very small keel development and yet lack a triangular platform outline (e.g. pl. 25, figs. 2,3,5,8) as in typical *A.r. rotundiloba*. Although they are not as strongly alate as other, associated, specimens (e.g. pl. 25, figs. 9,10), they are included here with them. The keel development is not ontogenetic, as the small specimens on plate 25, figs. 6 and 7 demonstrate; the former is very similar to the 'uncommon' juvenile form illustrated by Muller and Clark (1967, text fig. 7).

Occurrence: Samples WK1, WK2, WK3, Western King, Plymouth.
In Germany, the form ranges from the base of the Lower *asymmetricus* Zone to the top of the Middle *asymmetricus* Zone.
Chalymbadscha & Tschernusheva 1969 (fig. 1, p.82) recorded *A.r. alata* from strata above the appearance of *A.r. rotundiloba* and *A. rugosa* in the Volga-Kama region.

Ancyrodella rotundiloba rotundiloba (BRYANT)

1921 *Polygnathus rotundilobus* n.sp. - BRYANT, p.26-7,pl.12, figs. 1-6.
1933 *Polygnathus tuberculata* HINDE - BRANSON & MEHL, p.148, pl.11,fig.9(only).
1934 *Polygnathus rotundiloba* BRYANT - HUDDLE, p.102-3, pl.8, figs. 36-7.
non1947 *Polygnathus rotundiloba* BRYANT - YOUNGQUIST, p.110, pl.26, fig.6(=*A.gigas*).
? 1957 *Ancyrodella rotundiloba* (BRYANT) - BISCHOFF & ZIEGLER, p.42,pl.16, figs. 5,7,8,10 (only).
. 1958 *Ancyrodella rotundiloba* (BRYANT) - ZIEGLER, p.44-5, pl.11, fig.11 (only).
. 1966 *Ancyrodella rotundiloba rotundiloba* (BRYANT)- GLENISTER & KLAPPER, p. 799, pl. 85, figs. 9-13.
. 1967 *Ancyrodella rotundiloba* (BRYANT) - CLARK & ETHINGTON, p.29-30, pl.2, figs.15 (only).
. 1967 *Ancyrodella rotundiloba* (BRYANT) - MULLER & CLARK, p.908, pl.115, fig.8, pl. 116, figs. 1-5.
1969 *Ancyrodella rotundiloba rotundiloba* (BRYANT) - POLSLER, p.404, pl. 4, figs. 5 - 8.
1969 *Ancyrodella rotundiloba rotundiloba* (BRYANT) - CHALYMBADSCHA & TSCHERNUSHEVA, pl.1, figs. 9 - 12.
. 1970 *Ancyrodella rotundiloba* (BRYANT) - SEDDON (b), pl. 7, fig. 1.

v. 1970 *Ancyrodella rotundiloba* (BRYANT) - KIRCHGASSER, pl.65, figs.5,6,8,9.
1971 *Ancyrodella rotundiloba rotundiloba* (BRYANT) - SCULCZEWSKI, p. 15, pl. 1, fig. 3 (only).
1971 *Ancyrodella sinecarina* n.sp. - SCULCZEWSKI , p.16-17, pl.1, figs. 5,6.
1972 *Ancyrodella rotundiloba rotundiloba* (BRYANT) - KLAPPER & PHILIP, p. 99, pl.2, figs. 7-13 (not fig. 6).

Diagnosis: A subspecies of *A. rotundiloba* with a triangular platform and a secondary keel development which is only incipient, with neither keel, if present, extending to the crimp.

Remarks: *A.r. rotundiloba* differs from *A.r. alata* particularly in the form of the keel development, which is never pronounced and often absent in the former. Furthermore, the ornamentation is coarser, the blade composed of fewer, and higher, denticles; the anterior lobes are also directed anteriorly rather than laterally. The form is similar to *A. rugosa* which differs in having strong keel development. Plymouth forms with triangular platforms and relatively coarse ornament all have a fairly strong keel development and are therefore related to *A. rugosa*.

In Germany, *A.r. rotundiloba* ranges from the base of the Lower *asymmetricus* Zone to the top of the Middle *asymmetricus* Zone.

Ancyrodella rugosa BRANSON & MEHL *sensu lato*

Plate 25, figs.1,4; Plate 26, fig.2 aff.7

aff. * 1934 *Ancyrodella rugosa* n.sp. BRANSON & MEHL, p.239, pl.19, figs. 15.17.
1949 *Ancyrodella rugosa* BRANSON & MEHL - BECKMAN, p.155, pl.1, fig.1; pl. 4, fig. 2.
1965 *Ancyrodella rotundiloba rotundiloba* (BRYANT) - KREBS & ZIEGLER, pl. 1, figs. 10-13.
non 1968 *Ancyrodella rugosa* BRANSON & MEHL - POLLOCK, p.428, pl.61, fig.1.
. 1971 *Ancyrodella rugosa* BRANSON & MEHL - SCULCZEWSKI, p.16,pl.2,fig.5 (see synonomy).

Diagnosis: An ancyrodellid with a triangular platform, bluntly terminated anteriorly directed lobes and secondary keels which extend near to the lobe tips.

Remarks: Several specimens from Plymouth have strongly developed secondary keels which do not, however, reach the anterior lobe tips. They lack the alate outline of *A. rotundaloba alata* yet have a much stronger secondary keel development than is typical of *A.r. rotundiloba*. In this respect they can be considered as being intermediate between *A. rotundiloba* and *A. gigas*. Such a position is represented by *A. rugosa* according to Ziegler (1962b, fig.2).

The paratype of *A. rugosa* figured by Branson & Mehl (1934) has an arrow shaped platform set with closely spaced coarse nodes. Forms with similar platforms and ornament but with sharply terminated anterior lobes and completely developed secondary keels are excluded. (e.g. cf. Pollock 1968). Forms, here included, share a similar keel development, though orally they have less in common both with the type and with each other. Plate 26, fig. 2 is similar to *A. gigas s.l.* but has secondary keels which do not extend to the rounded lobe tips, as well as a very much enlarged basal cavity. Krebs & Ziegler 1965 (pl.1, figs. 10-13) illustrated similar forms. Plate 27, fig. 1, has a very large, evenly tapered platform and a similar keel development, though the asymmetry of the lobes suggest affinities with *A. rotundiloba alata*. Because of this variety, such forms as do not clearly belong to *A. rotundiloba* subspp.nor to *A. gigas* but which lie between them in keel development, are referred to *A. rugosa s.l.* See also Remarks in Sculczewski (1971, p.16).

Occurrence: Samples WK2, 54d, Western King; DS1 (aff.), Durnford Street.

In Germany, from the base of the Lower *asymmetricus* Zone to the lower part of the Upper *asymmetricus* Zone.

Ancyrognathus BRANSON & MEHL

Type species : *Ancyrognathus symmetrica* BRANSON & MEHL 1934, p.240.

1934 *Ancyrognathus* BRANSON & MEHL, p.240.
1947 *Ancyroides* MILLER & YOUNGQUIST, p.504.

Diagnosis: A plate-like conodont consisting of one anterior lobe and two posterior lobes. Secondary carinae and keels are well developed and a triangular basal cavity is located near the junction of the latter. The oral surface bears nodes or ridges.

Remarks: see Ziegler 1962 (fig. 5 - phylogeny) and Glenister & Klapper 1966.

Ancyrognathus triangularis YOUNGQUIST

Plate 27, fig. 10

* 1945 *Ancyrognathus triangularis* n.sp. - YOUNGQUIST, p. 356-7, pl.54,fig.7.
1957 *Ancyrognathus triangularis* YOUNGQUIST - MULLER & MULLER, p.1097, pl. 137, figs. 3,6.
1965 *Ancyrognathus triangularis* YOUNGQUIST - ETHINGTON, p.570-1, pl.68, fig. 10.
. 1966 *Ancyrognathus triangularis* YOUNGQUIST - GLENISTER & KLAPPER, p.802-3, pl. 87, figs. 10-13 (see synonomy).
. 1966 *Ancyrognathus triangularis* YOUNGQUIST - ANDERSON, p.404, pl.48,figs.1,5.
. 1967 *Ancyrognathus triangularis* YOUNGQUIST - van ADRICHEM BOOGAERD, p.178, pl. 1, fig. 7.
. 1968 *Ancyrognathus triangularis* YOUNGQUIST - MOUND, p.471-2, pl.65,figs.19-22.
. 1970 *Ancyrognathus triangularis* YOUNGQUIST - SEDDON(a), pl.16, fig.10.
. 1971 *Ancyrognathus triangularis* YOUNGQUIST - SCHUMACHER(b), pl. 12, fig.7.
. 1971 *Ancyrognathus triangularis* YOUNGQUIST - SCULCZEWSKI, p.19-20, pl.6,figs.3-5.
. 1972 *Ancyrognathus triangularis triangularis* YOUNGQUIST-COEN, pl.1,figs.3-5.

Diagnosis: Platform more or less triangular with straight or concave margins. The angle between the posterior keels is 90^{o} degrees or more, and the blade is short, and progressively and gradually lower posteriorly.

Remarks: Two specimens from Plymouth show the variation described by Ethington and Furnish (1962, p.1263) as ontogenetic, i.e. a small specimen has narrowed tapered lobes whereas the larger (pl.27, fig.10) has broader, more rounded lobe tips. See also Glenister and Klapper (1966, p.802-3). Coen (1972) discussed the stratigraphical integrity of the form and recognised two subspecies. *A.r. euglypheus* STAUFFER differs from *A.t. triangularis* in the angle between the posterior keels, that is less than 90^{o}. The former appears earlier than the nominate subspecies in the Belgian Frasnian.

Occurrence: Sample 77a, Fisons Quarry conglomerate matrix. In Germany: from the base of the *A. triangularis* Zone to the lower part of the Upper Pa. *gigas* Zone.

Ancyrognathus cryptus ZIEGLER

Plate 27, figs. 4,5.

1957 Polygnathus ? sp. - LYS & SERRE, pl.6 fig. 2.
* 1962 Ancyrognathus cryptus n.sp. - ZIEGLER, p.49-50, pl.9, figs. 2-6.
1972 Ancyrognathus cryptus ZIEGLER - BUGGISCH & CLAUSEN, p.147 tbl. 1; p.151, tbl. 2.

Diagnosis: Ancyrognathus with a slender, strongly incurved platform which is flexed sharply downward posteriorly. The blade is very short, the ornament is coarsely nodose, the outer lobe is only vestigial and the pit is situated a little posterior of platform mid-length.

Remarks: Ziegler included this atypical species in Ancyrognathus because he considered it to have evolved from A. asymmetricus by reduction of the outer lobe. It lies nearest to A. sinelamina (BRANSON & MEHL) from which it differs in the stronger lateral and vertical deflections of the unit. Po. deformis ANDERSON is similar in some respects, but differs in its twisted bar-like posterior end.

Occurrence: Sample WK6a, Western King. According to Ziegler (1970), the form has a restricted range within the Middle Pa. triangularis Zone.

Form genus Icriodus BRANSON & MEHL

Type species : Icriodus expansus BRANSON & MEHL 1938

As noted by Schumacher(1971b, p.90) this genus is in dire need of monographic revision. Many of the described species are open to question having been based on inadequate material and/or inadequate study. Furthermore, there is a difference of opinion about the morphological features which are of taxonomic importance. Bultynck (1972) considers that a sound classification, and phylogeny, can be deduced by using the sum total of the features both oral and aboral. However, the opinion of Druce (see conodont facies) is that the nature of the denticulation (degree of alignment and fusion) and the overall ratio of length to breadth are variable and facies dependent.

As far as a multielement taxonomy is concerned there is also disagreement. Klapper & Philip (1971, 1972) included an icriodontan(I) element with an acodinan (S_2) element in their type 4 apparatus (= Icriodontidae). The validity of this association has been questioned by Bultynck (1972) who grouped one or more form species of *Icriodus* together in his natural assemblages.

In the Plymouth material, *Icriodus* is rarely associated with *Acodina*, though when the latter is present the former is common. Chatterton (1974 p.1467-8, 1478) has presented similar results and I agree with him that the natural association remains to be proven. Bultynck has discussed this problem (1972, p.72).

It is noteworthy that the type material of long established *Icriodus* species is invariably poor. Suffice it to say that the holotype of *I. nodosus* was broken aborally and is now lost, the three illustrated co-types of *I. alternatus* have abraded aboral margins (Ethington 1965,p.573), and the syntypes of *I. curvatus* are also incomplete aborally (Glenister & KLapper 1966, p.805). As a consequence, different authors have variously placed *I. nodosus* and *I. expansus*, and *I. symmetricus* and *I. curvatus* in synonomy (see separate discussions). Furthermore, the different growth stages of the same form are often very different in appearance and undoubtedly insufficient ontogenetic knowledge has resulted in many misidentifications and dubious new species. *Icriodus cymbiformis* is a form which continues to appear in the literature though Bischoff & Ziegler (1957, p.62) considered the concept to embrace juvenile specimens of various species. Schumacher (1971, fig. 18, p.96) considered such forms to be young growth stages of *I. alternatus* though it is recorded in profusion from much lower levels (e.g. Orr 1972, p.33). Such forms as *I. incrassatus*, *I. spicatus*, and *I. parvus* described by Youngquist and Peterson (1947) are typical of species of doubtful validity, based on somewhat unusual (?pathological) characters.

Intergradation between *Icriodus* form species is common. The literature is full of records of "morphologically intermediate specimens" and different authors have felt it necessary to remark on the distinctions between various, not necessarily the same, forms. In the ensuing morass of taxonomic confusion, one finds it difficult to make dogmatic designations. Of course, it is far more difficult with the quality of the Plymouth icriodid material which rarely have complete aboral margins.

As discussed under conodont biofacies, it seems likely that the nature of Icriodus-bearing animal was such that the elements may demonstrate more plasticity than most other conodonts. Thus, a form taxonomic approach may be even more artificial in its application to Icriodus. Nevertheless, it must be of some value to distinguish morphotypes since some degree of biostratigraphic integrity clearly does exist.

Bultynck (1970, p.101-2) has listed five principal diagnostic characters for from-species differentiation, namely:-

1. Form of the basal cavity, especially the posterior part
2. Presence and number of lateral processes
3. Platform outline (oral plan)
4. Denticle shape, and relative position of the median and lateral denticles
5. Form of blade

Bultynck noted that characters 4 and 5 varied during ontogeny, viz. isolated, round and pointed denticles in young forms, and fused, oval and blunt denticles in large, adult and sessile specimens.

Latericrescids (Muller 1962), that is icriodids with one or more lateral processes (character 2), do not form part of this study, though this character (2) provides the clearest distinction between forms.

The form of the basal cavity (1) has perhaps provided the most important basis for distinction more recently. Bultynck (1970) erected several new forms in which this character was of paramount importance in differentiation. As mentioned, the lack of total aboral preservation in the Plymouth icriodids, excludes a thorough appraisal of the material. This is particularly true with respect to the distinction between I. expansus and I. nodosus (see remarks under former), but also between the different elements of the Icriodus assemblages, as described by Bultynck 1972. The latter author, considered several forms of similar oral configurations but differing aboral outlines to be associated within some assemblages, hence the oral characters provide the most constant plan (e.g. the I. corniger associations).

The platform outline (3) seems to provide a fairly constant feature within some species, but is still a highly variable character within some single populations. The form of the blade (s) has gained favour in many recent works, this character forming the distinguishing feature between a number of species.

The intergradation of form-species is in denticulation (*I.expansus* - *I. retrodepressus*),form of blade (*I. regularicrescens* - *I. obliquimarginatus*), (*I. alternatus* - *I. cornutus*), denticle alignment (*I. costatus* - *I. cornutus*), basal outline (*I. expansus* - *I. nodosus*) *et al.*

In the following study, the Middle and Upper Devonian icriodids are treated separately since they differ quite appreciably and the lack of forms from around the boundary also separates them naturally, no clear phylogeny being apparent.

A number of forms recognised in the Belgian Couvinian are included but in addition a number of new forms occur, though nowhere in abundant numbers, so it is considered premature to formally introduce them; further collecting may well produce stratigraphically useful results. The North American Middle Devonian is quite different in a number of respects as regards the *Icriodus* successions, the abundance of *I. latericrescens latericrescens* being particularly notable (see Zonation review). However, the occurrence of the *I. retrodepressus* - *I. expansus* association in Michigan at comparable levels to the Belgian counterparts (Bultynck 1975, personal communication) indicates the stratigraphical value of *Icriodus*.

In the following descriptions, the terminology introduced by Bultynck (1972, p.74) has been followed.

Icriodus corniger WITTEKINDT

Plate 1,cf. figs.3,4; Pl.2, fig.1,cf.2,3,8

* 1965 *Icriodus corniger* n.sp. - WITTEKINDT, p.629, pl.1, figs 9-12.

1967 *Icriodus nodosus* (HUDDLE) - WIRTH, p.218, pl.20, fig. 24.

• 1967 *Icriodus* cf. *I. corniger* WITTEKINDT - van ADRICHEM BOOGAERT, p.180, pl. 1, figs. 5,6.

• 1967 *Icriodus corniger* WITTEKINDT - van ADRICHEM BOOGAERT, p.180, pl.1, figs. 7,8.

non 1969 *Icriodus corniger* WITTEKINDT - CARLS & GANDL, p.187, pl.17, figs. 20-22 pl.18, fig. 1 (fig. 22, fig. 1 = *I. rectirostratus*).

1969 *Icriodus* aff. *I. corniger* WITTEKINDT - CARLS & GANDL, p.187, pl.18, figs. 3,4 (only).

. 1969 *Icriodus corniger* WITTEKINDT - PEDDER, JACKSON & ELLENOR, p.271, pl. 17, figs. 1,2.

. 1970 *Icriodus corniger* WITTEKINDT - BULTYNCK, p.103, pl.1, fig. 8; pl. 2, figs. 1-6, 8-10 (non fig. 7 - *I. retrodepressus*).

. 1972 *Icriodus nodosus* (HUDDLE) - MCGREGOR & UYENO, pl. 5, figs. 33-5 ("form approaching *I. corniger*").

Diagnosis: Icriodid characterised by a distinct posterio-lateral fringe on the outer side. There is an anterior directed spur on the inner side. The platform is broad and flat and the axis curved. The growth point is usually differentiated from the middle platform. Transverse and longitudinal bridges are commonly developed, connecting round denticles of equal size. The laterals and medians may or may not be alignated. The blade is composed of two or three, often fused, denticles.

Remarks: The concept of *Icriodus corniger* has been given a broad meaning since Wittekindt first described it from the Ballersbach Limestone in Germany. The types demonstrate an oral configuration of rounded median and lateral denticles which are subparallel and joined by ridges.

Bultynck (1972, p.76-8) recognised three *Icriodus* assemblages which involved a distinct morphotype of *I. corniger*, each with a characteristic stratigraphical range which thus gives a certain degree of refinement to the *corniger* Zone *sensu* Wittekindt (1965,taf..1, p.627). Bultynck recognised an assemblage involving *I.* aff. *corniger*, *I. fusiformis*, and *I. rectirostratus* a second involving *I. corniger*, *I.* aff. *fusiformis* and *I. rectirostratus* and a third composed of *I. corniger*, *I. curvirostratus* and *I. introlevatus*.

The first morphotype, *I.* aff. *corniger*, has a broad, flat, biconvex platform, with a slightly curved axis. The growth point is slightly delimited from the middle platform which bears six to fifteen well-aligned denticles connected by strong transverse and longitudinal ridges; the blade itself bears transverse ridges. Aborally the gully to bowl expansion is broad.

The second morphotype differs from the first in the lack of biconvexity, the greater differentiation of the growth point, the fewer number of denticles in the middle platform ($\leqslant$ six), the weaker development of connecting ridges and the relative simplicity of the blade.

A third morphotype is characterised by a concavo-convex, curved platform with a clearly differentiated growth point, four to five discrete denticles in the middle platform, and medians which are slightly displaced towards the anterior tip.

In the Plymouth material, several specimens have the characteristic posterior-lateral expansion, best seen in aboral view, though some are incomplete.

The specimen illustrated on pl. 2, fig. 1 corresponds closely to the third morphotype of Bultynck, though it has a longer and somewhat more sinuous blade than is typical, a feature of the specimens figures on pl. 2, figs. 2,3 and 8 (which have incomplete aboral outlines) also.

A sinuous blade ("a short but pronounced lateral flexture") was a diagnostic character of I. postiflexus BRANSON & MEHL (1934, p.163, pl.26, figs. 10-13), but appears to be a feature of several otherwise very different species (see I.n.sp. a).

The anteriormost denticle of the blade in these small forms is broken, but would appear to be the largest and to lie higher than the others,as is true for some (larger) associated specimens (e.g. pl.1, figs. 1,3,4,6), though not all (e.g. pl. 1, figs. 7,8).

Considering the whole population, the smaller specimens are characterised by more biconvex platforms, though the anterior tips and the main axis is curved. The larger are more concavo-convex. Transverse bridges are variably developed but are stronger in large specimens, which similarly have more transversely elongate lateral denticles. All the specimens have well differentiated growth points.

Icriodus retrodepressus is present in the same fauna as the above forms. The specimen illustrated on pl. 1, fig. 5, is typical in having strongly expanded posterior laterals and suppression of the posterior medians. These characters, supplemented by high posterior blade denticles, transverse bridge development and a biconvex platform serve to differentiate the form from the third morphotype of I. corniger. The illustrated specimen of I. retrodepressus differs from the types in not having a strongly biconvex platform outline. As mentioned, high posterior blade denticles and transverse ridge development is also a character of associated forms.

Because of the poor preservation of the aboral surfaces, on which firm identification of I. introlovatus and I. curvirostratus must be based, it is not possible to be sure that Bultynck's assemblage is represented here. The oral configuration of the specimen illustrated on plate 1, fig. 6 is similar to I. introlevatus and I. curvirostratus (e.g. Bultynck 1970, pl.4) as is the aboral outline of fig. 7, plate 1. A study of topotype material of the I. corniger-I. curvirostratus - I. introlevatus assemblage shows that there is some variation in transverse bridge development, and the overall assemblage resembles the Plymouth association to a degree which warrants some acknowledgement here, though it is premature to be certain of any natural association.

Furthermore, Bultynck (1972, fig. 17, p.84) considered the I. retrodepressus - I. expansus intergrading couple to have originated from his third I. corniger assemblage. In the characters mentioned, the majority of these Plymouth forms would appear to be transitional. Consequently all those forms other than those which have the essential characters of I. retrodepressus (i.e. pl.1, fig.5) are kept together under the designation I. aff. (I. corniger - I. curvirostratus-I. introlevatus assemblage).

Occurrence: Sample MB23, Durness Point, near Plymouth.
In Germany, I. corniger is recorded from near the base of the corniger Zone to within the bidentatus Zone (Ziegler 1971, chart 2). In Belgium, the first morphotype, I. aff. I. corniger is confined to levels below the base, the second and third morphotypes (with their respective associates) appear at and above the base of the Zone, respectively. The first is confined to Co_{1a}, the second ranges from the base of Co_{1b} to within Co_{2b} (Bultynck 1972, p.76, 78). See also Devonian conodont zonations.

Icriodus expansus BRANSON & MEHL *sensu lato*

1934 *Icriodus expansus* n.sp. (nomen nudum) - BRANSON & MEHL, p.225.

* 1938 *Icriodus expansus* n.sp. BRANSON & MEHL, p.160-1, pl.26, fig.18-21.

1938 *Icriodus expansus* BRANSON & MEHL - STAUFFER, 1938, p.430, pl.52, figs. 12,14,16,19,20,25,33,35.

1938 *Icriodus arkonensis* n.sp. - STAUFFER , p. 429, pl. 52, figs.10,15.

1940 *Icriodus expansus* BRANSON & MEHL - STAUFFER, p.425, pl.60, figs. 40 47,48 (only).

1947 *Icriodus expansus* BRANSON & MEHL - YOUNGQUIST & PETERSON, p.246-7, pl.37, figs. 5-7 (non figs. 10,20 = *I. nodosus s.l.*).

1947 *Icriodus iowaensis* n.sp.- YOUNGQUIST & PETERSON, p. 247, pl. 37, fig. 22-4, 27-9.

1950 *Icriodus alternatus* BRANSON & MEHL - DOWNS & YOUNGQUIST, p.669, pl. 87, figs. 8,11,12.

1956 *Icriodus expansus* BRANSON & MEHL - STEWART & SWEET, p.267-8, pl.33, figs. 1,9,13 (non fig. 3, = *I. nodosus s.l.*, fig. 12,14 = *I. corniger*).

non1966 *Icriodus expansus* BRANSON & MEHL - CLARK & ETHINGTON, p.680, pl. 83 fig. 9.

non1967 *Icriodus expansus* BRANSON & MEHL _ WIRTH, p.215-6, pl.20, figs.20,21.

1970 *Icriodus expansus* BRANSON & MEHL - SEDDON (a), p.736, pl. 11, fig.30-32 pl. 12, figs. 1,2.

1970 *Icriodus expansus* BRANSON & MEHL - BULTYNCK, p.105-6, pl. 6, figs. 3-5, 7, 8, 10 (non figs. 6,9 - *I. nodosus s.l.*).

1972 *Icriodus expansus* BRANSON & MEHL - ORR, p.34, pl. 3, figs. 14-17.

1974 *Icriodus expansus* BRANSON & MEHL - UYENO, p.30, pl.6, figs. 1,2,5.

non1967 *Icriodus expansus* BRANSON & MEHL - CLARK & ETHINGTON, p.39, pl.3, fig. 2 (= *I. cornutus*).

Description: Icriodid with a biconvex platform being broadest at mid-length and tapering to sharp anterior and posterior ends. The axis is straight to very slightly incurved near the anterior end. The growth point is in the line of the main axis and consists of about two denticles series, the laterals appearing together.

The middle platform bears three rows of about six denticles. The medians are discrete, round-tipped to slightly pointed, and of uniform size. Anteriorly they are round in cross section but posteriorly they tend to become laterally compressed. The medians also tend to be higher than the laterals which are also discrete and blunt to slightly pointed. In plan, the laterals are transversely oval to elongate elliptical, and are broadest at the platform midlength; transverse bridges may be developed. The median denticles are displaced anteriorly with respect to the laterals.

The blade is composed of about two denticles, partially fused and inclined posteriorly, so as to project beyond the basal cavity.

The aboral configuration is marked by a gully and bowl of comparable length. The expansion is quite broad and though it is abrupt on the inner side, a spur is not developed. The posterior edge is evenly rounded.

Discussion: (see later).

Icriodus nodosus (HUDDLE) *sensu lato*

* 1934 *Gondolella ? nodosa* n.sp. - HUDDLE, p.94, pl.8, figs. 24,25.
1938 *Icriodus nodosus* (HUDDLE) - BRANSON & MEHL, p.160, pl. 26, figs.14-17,22.
1947 *Icriodus expansus* BRANSON & MEHL - YOUNGQUIST & PETERSON, pl. 37, figs. 10,20 (only).
1950 *Icriodus nodosus* (HUDDLE) - DOWNS & YOUNGQUIST, p.670, pl. 87 figs. 17,18,21,22.
1956 *Icriodus nodosus* (HUDDLE) -STEWART & SWEET, p.269, pl. 33, fig.10(only).
1956 *Icriodus nodosus* (HUDDLE) - ZIEGLER, p.102, pl. 6, figs. 18-21.
1956 *Icriodus expansus* BRANSON & MEHL - STEWART & SWEET, pl.33, fig. 3(only).
1957 *Icriodus nodosus* (HUDDLE) - BISCHOFF & ZIEGLER, p.62, pl. 6, figs.2,3,5; pl. 19, figs. 1-5.
1957 *Icriodus symmetricus* BRANSON & MEHL - BISCHOFF & ZIEGLER, p. 64, pl.6, figs. 1,4.
non1967 *Icriodus nodosus* (HUDDLE) - NEHRING, p.131-2, pl.3, fig.2(=*I. alternatus*).
non1967 *Icriodus nodosus* (HUDDLE) - WIRTH p.218, pl.20, fig.24 (= *I. corniger*).
1970 *Icriodus expansus* BRANSON & MEHL - BULTYNCK, pl.6, figs.6,9 (only).
1970 *Icriodus nodosus* (HUDDLE) - SEDDON(b), p.27, pl.7, figs. 4,6.
. 1971 *Icriodus nodosus* (HUDDLE) *s.l.* - SCULCZEWSKI, p.22-3, pl.7, fig.1.
1971 *Icriodus nodosus* (HUDDLE) - SCHUMACHER(b), p. 93-5, pl.9, figs.1-29.
1972 *Icriodus nodosus* (HUDDLE) - ORR, p.38, pl. 2, figs. 20-23.
. 1974 *Icriodus nodosus* (HUDDLE) *s.l.* - UYENO, p.30, pl.6, figs. 4,10.

The Icriodus expansus - Icriodus nodosus plexus

Discussion: Branson & Mehl introduced their genotype in 1934, but it was not until 1938 that they described and figured the form;no lateral view was included. The above description is based on these. Huddle described Gondodella (?) nodosa in 1934 but the only illustration is an oral view. The former authors included an additional description of Icriodus nodosus and included an oral and aboral view of Huddle's holotype, which is now lost.

The types of Icriodus expansus and Icriodus nodosus figured by Branson and Mehl differ in the relative length and breadth, in the platform outline and in the aboral configuration; i.e. I. expansus has a shorter, more biconvex platform and lacks a spur development. The holotype of I. nodosus was broken aborally and Huddle's description includes no reference to a spur, but subsequent authors have followed Branson & Mehl's lead in this respect.

However, it is clear from the literature that a spur development is variable in otherwise similar forms and thus I. expansus and I. nodosus appear to be end members of an intergradational series (e.g. Stewart & Sweet 1956, p.269; Muller and Clark 1967, p. 914; Orr 1972, p.39).

The studied material from Plymouth includes numerous forms which conform to a generalised concept of I. expansus - I. nodosus. Aboral outlines are rarely intact and prevent a full assessment of the variability of this character. However, it is clear from detailed study (greatly facilitated by the stereoscan) that Middle and Upper Devonian representatives are at least different in other respects and can be separated on the basis of a number of characters; furthermore there appears to be distinct differences between Lower and Upper Middle Devonian forms. Branson & Mehl designated two syntypes of I. expansus, both from the Middle Devonian Mineola Limestone of Missouri (1938, pl.26, figs. 18,19); they also recorded the form from Upper Devonian strata. Huddle's holotype and Branson & Mehl's hypotypes of I. nodosus came from Upper Devonian levels and the latter authors did not record it from older rocks (1938, p.156, table).

The author considers that a revision of the group involving analysis of topotype material may confirm at least some of the observations enumerated below and result in a stratigraphically useful refinement of the group.

Until such time as this is done, and in view of the generally poor aboral surfaces, the Plymouth material is here considered under a generalised I. expansus - I. nodosus group. Time will tell whether forms grouped according to the overall plan and the oral denticulation are meaningful.

In the literature there is a great deal of difference in forms brought together on the basis of their biconvex platforms, transversely elongated lateral nodes and characteristic basal outlines. Some such variation may stem from ecological differences (see Conodont Biofacies)and there is certainly a good deal of morphological change during ontogeny, not to mention the possible vicarious nature of some. Consequently the separate synonomy lists should be considered as possibly embracing different forms; for this reason the suffix sensu lato has been used.

Seddon (1970 (a), p.737, fig. 7) noted the existence of "at least three variants" of I. nodosus - an Eifelian form (= I. corniger), a Givetian and a Frasnian form. This is perhaps an over-simplification of the situation, but such differences clearly do exist. Bultynck (1970, p.106-7) recognised an Icriodus nodosus group, noting that the spur is not only typical for a species but for a group. He distinguished four subspecies: I. nodosus rectirostratus, I.n.curvirostratus, I.n.subsp. a, and I.n.subsp.b. Subsequently, Bultynck (1972, p.77) raised the former two to form specific status since he felt that I. nodosus was typically an Upper Devonian species. Though he considered that the trends on the upper and lower surface were "partially" different, he did not elaborate on this view.

I. iowaensis YOUNGQUIST & PETERSON was originally described from the Sheffield Formation of Iowa. The types differ from I. expansus only in the greater, and sometimes, complete fusion of the laterals and medians. It should be appreciated that all the types are large and in fact exhibit this feature increasingly with growth, whereas thos forms designated I. expansus are invariably smaller. Anderson 1966 maintained this species though the criticism may be equally applicable to his fauna.

Icriodus expansus - Icriodus nodosus group

Description: Icriodids with generally biconvex platforms. The axis may be straight, inwardly curved at the anterior end or less commonly evenly curved throughout. The median denticles tend to be round and those of the lateral rows oval and transversely elongate; longitudinal bridges are only rarely developed and never conspicious; transverse bridges are common and often strong. The blade is relatively short and the posterior border is often inclined posteriorly. The aboral expansion is one third to one half the total length, rounded on the outer side, with or without a spur on the inner side and the posterior edge is straight.

Remarks: The following variation has been noted.

Early Middle Devonian - the growth point is well differentiated and the denticles are not in line with those of the middle platform. The platform is strongly biconvex and the axis more commonly straight. Transverse bridges are strongly developed and the denticles of the growth point are often completely fused by them. Lateral denticles strongly elongate transversely, and frequently joined to the medians. The blade is frequently composed of two denticles fused so as to form a large robust "cusp". The bowl is equal to about one third total unit length.

Late Middle Devonian - the growth point is not strongly differentiated from the middle platform, and the median row can be traced to nearer the anterior tip. The platform is often strongly biconvex but does not taper so rapidly away from the broadest (mid) point. Transverse bridges are commonly developed but tend to be strongest posteriorly and disappear anteriorward. A gradational series is recognised (in oral view) from well aligned to (sub) alternate denticles (see on).

Upper Devonian - the character of the growth point and its relationship to the middle platform is similar to Late Middle Devonian representatives, though generally the two are even less differentiated. The platform outline tends to be only weakly biconvex and is more commonly plano-convex or concavo-convex. The units are relatively elongate and narrow, and the denticulation is of a less "coarse" aspect in specimens of comparable size. Transverse ridges are not so commonly developed but are generally more constant when they are. Similarly, the tendency for variation in denticle alignment within a single unit is not as pronounced in the studied material, indeed the extreme of near alternation of the denticles has been rarely observed, The horn-like cusp of Middle Devonian forms has not been observed, rather they have a somewhat shorter blade of equal height and are composed of two fairly descrete denticles. The bowl is usually at least one half the total unit length.

Thus, these trends appear to involve a lessening in growth point differentiation, longitudinal growth rather than transverse elongation, the loss of a distinct horn-like, strongly inclined blade, greater uniformity in platform denticulation and (possibly) relatively greater aboral expansion. Overall, there appears to be a trend toward greater uniformity of the total oral surface.

In the Lowest Middle Devonian, Icriodus expansus in involved in an inter-gradational series with I. retrodepressus according to Bultynck (1972, p.80) who has suggested the two form species belong together in an assemblage. Material from these levels does not form a large part of this study so it may be premature to judge the truth of such an hypothesis. (See I. retrodepressus).

Within the Plymouth Limestone, high Eifelian and low Givetian levels have produced a large number of forms corresponding to a generalised concept of I. expansus - I. nodosus. Three distinct forms are here described as morphotypes 1,2 and 3 pending the collection of more, aborally complete, material and the clarificarion of the group taxonomy.

The Upper Devonian representatives are described separately (see on).

Morphotype 1

Plate 2, figs.4, 6

Description: Platform biconvex, axis straight, broadest near midpoint, and pointed at each end. Growth point is well differentiated and composed of two to three denticle series which are not in line with those of mid-platform.

The middle platform bears three rows of five denticles. The medians are round in cross section, the central one being the largest and the others decreasing in size (in both directions). The laterals are mostly oval and transversely elongate and also are largest at platform mid-length. In some specimens the two posterior most lateral denticles are distinctly reduced in size. The median denticles are mostly slightly displaced towards the anterior end. Transverse ridges are well developed in the posterior platform, progressively less so anteriorward. The blade is composed of 2 - 3 partially fused denticles which are set higher than the middle platform and sometimes bear a median crest. The posterior border is inclined. The basal outline is unknown in detail. The expansion is quite broad and begins about, or in front of, unit midlength. In one specimen an inner spur is indicated.

Remarks: This form differs from all others in the character of the high blade. The blade of Icriodus retrodepressus may be similar but the development of the posterior laterals is quite the reverse.

Occurrence: Sample 39, Richmond Walk (Eifelian).

Morphotype 2

Plate 4, figs. 1,2,4,5,8,10,11,12; Pl.6, figs.1-6, 8-10

Description: Platform axis generally curved throughout or straight and incurved at the anterior end. Platform outline varies from biconvex to concavo-convex, often the former posteriorly and the latter anteriorly. Broadest point at the second or third lateral denticle from the posterior end.

Growth point fairly well differentiated and about two denticles long; laterals appear together. Middle platforms bear 5 - 7 denticle rows. The medians are round in cross section and of uniform size, except perhaps the posteriormost one or two which may be slightly smaller. The laterals are mostly oval in cross section, the posterior ones being more transversely elongate than the anteriorward laterals. The latter become more rounded towards the anterior end of the platform. Concurrent with this is a decline in the development of transverse bridges and an increase in the degree of lateral and median denticle alternation. The denticles approach alignment in the posterior part of the platform.

The blade is relatively short, usually composed of two,mostly fused denticles which form a strong "horn"-like cusp which is often strongly inclined posteriorly. The cusp lies in the same plane as the denticles of the middle platform and does not rise above them.

On the aboral side, the expansion continues progressively from the anterior end but broadens rapidly in the posterior third to half. Where seen, the expansion appears to be symmetrical and the posterior edge straight; an inner spur is sometimes indicated.

Remarks: Included here are the majority of M. Devonian forms studied. There appears to be a similar variation in both the individual elements and within a single population. Thus in some forms, transverse bridges are well developed throughout and the medians are only slightly displaced anteriorward with respect to the laterals (pl. 4, fig. 5). In others, transverse bridges are restricted to the posterior platform and the denticles(sub)alternate (pl.4, fig. 12); other forms are intermediate (pl.4, fig. 10 - 11). The platform outline appears to be somewhat independent of these variations; the form of the blade is particularly constant.

Ontogenic development also seems to involve a similar variation. Juvenile forms, included herein, are characterised by sharp, fairly discrete, round and alternating denticles throughout (pl. 6, figs. 10 , 9). Large (?gerontic) specimens are strongly biconvex, often asymmetrically so, and have broad, blunt laterals and strong transverse bridges. Variation in the degree of alignment persists throughout growth.

Morphotype 3

Plate 5, figs. 4,5,7,8,12.

Description: Platform biconvex, axis more or less straight except for the posterior tip which may be turned inward. Growth point generally not well differentiated, the medians being traceable to near the anterior tip.

The middle platform is broadest about mid-point and tapers slowly but progressively to each,pointed,end. There are about 6 -7 denticle rows, mostly well aligned throughout. Median denticles round, mostly larger centrally and perhaps showing some lateral compression posteriorly - low longitudinal bridges may be developed.

The lateral denticles are oval and become increasingly elongate transversely during growth; transverse bridges are developed throughout, though they are more distinct posteriorly. The posteriormost laterals may be somewhat reduced in common with the medians.

The blade is composed of 2 - 4 partially fused denticles which do not rise above the denticles of the middle platform. The posterior border is inclined posteriorly. The aboral expansion is a little less than one half of the total unit length and apparently symmetrical.

Remarks: Included here are specimens from a sample from Cattedown (20) in which the icriodids are fairly uniform and demonstrate a similar form in various growth stages, particularly in platform outline and denticle alignment (plate 5, figs. 4,7,12). The extremes of denticle alternation as seen in the populations of morphotype 2 have not been observed. The posterior reduction in the size of the lateral denticles is also a constant feature, and in this respect they are similar to morphotype 1. The blade, though fused, does not have the "horn"-like character of morphotype 2, and it is often longer than the latter.

Occurrence: Samples 20, Cattedown; 44/3 ,Teat's Hill Quarry, Coxside;
NP 15 , Neal Point.

Icriodus fusiformis CARLS & GANDL
cf. Plate 1, fig. 2.

* 1969 Icriodus fusiformis n.sp. - CARLS & GANDL, p. 186-7, pl.17, fig.17-19.
1972 Icriodus fusiformis CARLS & GANDLE - BULTYNCK, p.76-7, figs. 6A, 7A.

Remarks: Bultynck (1972, p.76-7) distinguished I. fusiformis and I. aff. fusiformis, two forms which were associated in different assemblages with the I. corniger group. A single specimen from calcareous shales south of Durness Point corresponds to I. aff. I. fusiformis in its oral configuration, though the aboral outline is not preserved. It shares the oral characteristics of the second morphotype of I. corniger of Bultynck (see I. corniger).

Occurrence: Sample JB 19, South of Durness Point.
In Belgium, I. aff. I. fusiformis is found in zone Co_{1a}.

Icriodus obliquimarginatus BISCHOFF & ZIEGLER

Plate 3, figs.10 aff. 7

* 1957 Icriodus obliquimarginatus n.sp. - BISCHOFF & ZIEGLER, p. 62, pl. 6, fig. 14.
. 1965 Icriodus obliquimarginatus BISCHOFF & ZIEGLER - WITTEKINDT, p. 630, pl. 1, fig. 13.
. 1970 Icriodus obliquimarginatus BISCHOFF & ZIEGLER - BULTYNCK, p. 109-10, pl. 8, figs. 1,3,5.
1970 Icriodus regularicrescens n.sp. - BULTYNCK, pl. 8, fig. 6 (only).
1972 Icriodus obliquimarginatus BISCHOFF & ZIEGLER - BULTYNCK,p.81, fig.13.

Diagnosis: Icriodid characterised by a blade which is clearly higher than the rest of the unit in profile, and which forms a convex crest. The posterior border is clearly inclined backwards.

Description: see Bultynck 1972 (p.181).

Remarks: This is a quite distinctive form in its typical development though it grades morphologically into I. regularicrescens which it succeeds stratigraphically, and into I. eslaensis which replaces it in the higher Givetian. Typical is the high posterior blade and inclined border. An additional characteristic is the tendency for the intercalation of smaller denticles in the median row.

Bultynck (1972, p.181) distinguished I. aff. I. obliquimarginatus which was characterised by a broader platform, by more denticles in the middle platform, by a shorter blade and by a more abrupt gully-bowl transition aborally with a prominent spur develcpment on the inner side. The specimen figures on pl. 3, fig. 7 seem to be nearer this form.

Occurrence: Sample 20, Gasworks Quarry, Cattedown; 44/3 (aff.) Teat's Hill Quarry, Coxside.

In Germany, *I. obliquimarginatus* is found in the zone of that name and also in the *varcus* Zone (Wittekindt 1965, tbl. 1, p.627)
In Belgium, it is found in zones Gi_a and Gi_b.

Icriodus regularicrescens BULTYNCK
Plate 3, figs. 1-6, 8, 9.

1965 *Icriodus* n.sp. - BULTYNCK, p. 370-1, fig. 1.
1967 *Icriodus* n.sp. - BULTYNCK, p. 426.
v* 1970 *Icriodus regularicrescens* n.sp. BULTYNCK,p. 111-2, pl. 7, figs. 1-7; pl. 8, figs. 2,4,7,8.
1972 *Icriodus regularicrescens* BULTYNCK - BULTYNCK, p. 80-1, fig. 12.

Diagnosis: Relatively long, slender icriodid with pointed anterior and posterior extremities and a large,regularly crescentic outer basal expansion.

Description: See Bultynck 1970 (p.111-2) and also Bultynck 1972 (p.80-1).

Remarks: The Plymouth material includes specimens which demonstrate variation in the degree of alignment of the median and lateral rows, in the development of transverse bridges, and in the regularity of the denticulation (unpaired laterals and intercalated medians occur). Furthermore although aboral surfaces are rarely intact, there certainly appears to be some variation in this character. For example, the specimen illustrated on pl. 4, fig. 7 shows a tendency towards *I. corniger* in the development of a slightly posterior lateral projection which may suggest an origin for the form; Bultynck 1972 (fig. 17, p.84) did not relate it ancestrally. Some specimens (pl. 4, figs. 5,9) show transitional tendencies toward *I. obliquimarginatus* in the relative height and convexity of their blades and in the inclination of their posterior borders, but are retained here on the basis of their other characters. Bultynck (1970, p.112) considered the possibility that *I. obliquimarginatus* developed from this form.

Occurrence: Sample 44 (2), 44 (3), Teat's Hill Quarry, Coxside.
In Belgium, Bultynck records the range of *I. regularicrescens* from the upper part of Co_{2c} to just into Gi_a.

Icriodus retrodepressus BULTYNCK

Plate 1, fig. 5.

* 1970 *Icriodus retrodepressus* n.sp. - BULTYNCK, p.110-1, pl.30 figs.1-6.
. 1970 *Icriodus corniger* WITTEKINDT - BULTYNCK, pl.2, fig. 7 (only).
. 1972 *Icriodus retrodepressus* BULTYNCK - BULTYNCK, p.80, fig. 10 A,B,F.

Diagnosis: Icriodid characterised by a convex platform bearing well aligned laterals and median denticles, the latter tending to become completely suppressed posteriorly where they lie in a central depression. The posterior (most) denticles of the (outer) lateral rows generally show a strong lateral development. The blade is represented by a completely fused "horn" which bears a median crest and increases rapidly in height posteriorly, in which direction it is strongly inclined. The aboral side is characterised by an expansion in the posterior one third of the unit, which is rounded on the outer side and is marked by a spur on the inner side.

Description: For full description, see Bultynck 1970, p.110-1.

Remarks: *I. retrodepressus* differs from *I. expansus*, with which it forms an intergradational series according to Bultynck (1972, p.80) in the lateral development of the posterior denticles of the (usually outer) lateral rows. According to Bultynck, the median depression of the posterior middle platform is sometimes seen in *I. expansus*, though not in its extreme form. Forms which are more strongly biconvex and more reduced medially than the figured specimen have been found, but *I. expansus* has not been found in association.

The form is quite distinctive though in the sometimes oblique nature of the posterior border it may approach *I. corniger*. The latter, however, does not have the posterior median depression nor, in typical forms, a cusp-like blade. Furthermore, *I. corniger* from comparable levels in the Belgian Couvinian have rounded lateral denticles and there are no prominent transverse ridges (but see under *I. corniger*). For these reasons, the specimen illustrated by Bultynck (1970, pl. 2, fig. 7) is considered to be better assigned to *I. retrodepressus*.

See also under *I. corniger*.

Occurrence: Sample MB 23, Durness Point. In Belgium, the form is known from the middle part of the <u>corniger</u> Zone, i.e. top of Co_{1c}- lower part of Zone Co_{2b}.

<u>Icriodus</u> n.sp. a

Plate 2, figs.5,7,9,10

Description: Long, relatively slim icriodid with subparallel margins and a straight axis. The growth point is variable, but generally well differentiated from the middle platform; the laterals may or may not appear together. The middle platform bears 3 - 5 denticle rows. The medians are equal in size, laterally compressed and connected by low longitudinal bridges. The laterals are oval in cross section and, especially in larger specimens, strongly elongate transversely. The lateral denticles are of a comparable size throughout the unit and in some specimens exhibit extreme irregularity, being unpaired and developed further posteriorly on the outer side and sometimes appearing on the side of "blade" (e.g. plate 2, figs. 5,9). The medians and laterals are subalternate and joined by transverse ridges (also irregular sometimes).

The blade is long, up to nearly one half of the unit length, and bears 5 - 7 denticles, mostly fused and increasing in height to the posterior end. The posteriormost blade denticle is the highest and largest, and the posterior border is upright, inclined or distinctly concavo-convex (e.g. plate 2, fig. 5). In oral view the blade may show a distinct sinuosity, the posterior tip being turned outward.

Aborally, the gully and bowl appear to be of equal length, and the expansion is apparently symmetrical.

Remarks: The specimen illustrated on pl. 2, fig. 5 is remarkably similar in profile to the "small form" of <u>I. culicellus</u> figured by Bultynck (e.g. 1972, fig. 3C) particularly with respect to the large posteriormost "cusp". It differs from this latter, Lower Couvinian, form, in possessing strong transverse bridges connecting subalternate denticles, a blade which is not laterally compressed, and a growth point which may be clearly differentiated from the middle platform; it is also much longer and narrower. Furthermore the blade axis is sinuous, very similar in fact to those specimens of Icriodus corniger illustrated on pl. 2, figs. 1-3. In the suppression of the lateral denticles, the (only) two specimens from sample PS4 (plate 2, figs. 5,9) are identical though the profile of the blade of the smaller specimen reminds one rather of I. obliquimarginatus. pl. 2, fig. 7 illustrates yet another unique specimen. This has a similar blade profile to fig. 5, though it displays a unique transverse bridge arrangement, clearly exaggerated by deformation, but apparently connecting the same median row denticles to 2 laterals.

Each of the four specimens included together here differ in some respect, but in the absence of more material it seems impractical to separate them.

Wirth 1967 (pl.20, figs. 18,19) illustrated two specimens of "I. cymbiformis" which are similar in some respects.

Occurrence: Samples PS3 and PS4, Plymouth Power Station, Princerock Quarry.

Icriodus n.sp. c
Plate 6, fig. 11

Description: Very long, slim icriodid. Axis straight, margins subparallel. Growth point two denticles long, not well differentiated from the mid-platform. The middle platform bears seven rows of denticles. The medians are of equal size, laterally compressed and joined by longitudinal bridges. The laterals are larger, of equal size, round in cross section, and joined to the medians by low transverse bridges. The alignment is good in the posterior two rows, thereafter the medians become progressively displaced anteriorward.

The blade is composed of four mostly fused denticles which are not higher than the platform denticles. The posteriormost denticle is more discrete than the others and is inclined backward. Gully and bowl of equal length. Outline of expansion incomplete, but apparently subquadrate; posterior edge straight.

Remarks: This unique specimen is unlike any other from Plymouth, or as appears in the literature. It is also thought to be the youngest Middle

Devonian icriodid retrieved. Further collecting from comparable levels may prove its value.

Occurrence: Sample 50, Coxside. Late Givetian (?).

Icriodus sp. a
Plate 4, fig.3

Description: Slim, biconvex platform, axis more or less straight. Growth point as long as the middle platform and clearly differentiated from it. The former is composed of five denticle series which are not in prolongation of those of the middle platform. The latter consists of five rounded medians and five round to oval laterals. Transverse bridges small and restricted to the posterior platform. Blade composed of two fused denticles which do not rise above the level of the middle platform. Posterior border slightly inclined. Bowl about half the length of the gully. Aboral outline unknown.

Remarks: This unique specimen differs from all others studied in the strongly differentiated growth point. It shows some affinities to the Icriodus expansus-nodosus group.

Occurrence: Sample 10, Princerock Quarry.

Icriodus n.sp. a sensu BULTYNCK
cf. Plate 4, fig. 9

1972 Icriodus n.sp.a - BULTYNCK, p.83, figs. 16A-E.

Description: Short, biconvex platform pointed at both ends. Axis straight. Denticles round in cross-section, discrete, of equal size and subalternate. Blade composed of two fused denticles, strongly inclined posteriorly. Bowl longer than gully. Aboral expansion broad but outline unknown.

Remarks: This unique specimen resembles Icriodus n.sp.a. BULTYNCK 1972 which was recorded from the zone Gi_c in Belgium.

Occurrence: Sample 16, Gasworks Quarry, Cattedown.

Icriodus n.sp.b

Plate 5, figs.1-3,6,13 cf.9

Description: Slender icriodids with generally concavo-convex platforms. The growth point is not usually strongly delimited from the middle platform, though rarely it may be (fig. 6), and the median denticles can be traced to within one or two denticle series from the anterior tip. The middle platform consists of 5 - 7 denticle series, the medians being displaced slightly anteriorward. The median denticles are round to elongate oval longitudinally and may be connected by low bridges. Lateral denticles are round (anteriorly) to elongate transversely (posteriorly) and are often connected to the medians by bridges. The blade is quite long, being composed of four partially fused denticles which may rise slightly above the level of the middle platform. The posterior border is upright or inclined. Aborally, the expansion of the bowl appears to be about ½ total unit length.

Remarks: Forms included here differ from other icriodids with similar platform developments (i.e. I.expansus - nodosus group) in the long blade development, which is not particularly conspicuous in the same way as those of I. obliquimarginatus and I. eslaensis are.

Occurrence: NP 15, Neal Point; 44 (3), Teat's Hill Quarry, Coxside.

Upper Devonian Icriodus from Plymouth

The U. Devonian icriodids studied come from strata ranging in age from the Lower asymmetricus Zone to the triangularis/crepida Zones, though continuous sequences are lacking from the whole of this interval. On the whole, these faunas differ significantly from the Middle Devonian counterparts. The only immediate point for comparison is the forms which belong to that termed the I. expansus - I. nodosus group, but here too, the total fauna differs in some notable respects (see M. Devonian Icriodus).

For reasons previously expounded, one is hesitant to ascribe specimens to established taxon, on the one hand because of the unspecified nature of aboral configurations of the types of the latter and, on the other hand, because of the invariably poor preservation of this character in the studied material.

Icriodus aff. *I. alternatus*

Plate 33, figs.1-7,11,12

aff.*1934 *Icriodus alternatus* n.sp.BRANSON & MEHL, p.225-6, pl.13, figs.4-6.
1938 *Icriodus alternatus* BRANSON & MEHL - BRANSON & MEHL p.161, pl. 26, figs. 4-6.
1938 *Icriodus elegantulus* n.sp. - STAUFFER, p.430, pl.52, figs. 26-7.
1959 *Icriodus* sp. - HESS (a), pl.50, fig. 2.
non 1964 *Icriodus alternatus* BRANSON & MEHL - ORR, p.9, pl.2, figs.11,12 (= *I.* aff. *I. expansus*).
1965 *Icriodus alternatus* BRANSON & MEHL - ETHINGTON, p.573, pl.67,fig.8.
. 1966 *Icriodus alternatus* BRANSON & MEHL-ANDERSON,p.405,pl.52,figs.11,12.
1966 *Icriodus alternatus* BRANSON & MEHL - GLENISTER & KLAPPER, p.804.
1967 *Icriodus nodosus* (HUDDLE) - NEHRING, p.131-2, pl.3 figs.1-2.
1967 *Icriodus alternatus* BRANSON & MEHL - WIRTH, pl.20, figs. 15,16.
p. 1967 *Icriodus alternatus* BRANSON & MEHL - WOLSKA,p.379-80,pl.2,fig.6(only).
. 1967 *Icriodus nodosus* (HUDDLE)- WOLSKA,p.380-1,pl.2, figs. 1-3.
1970 *Icriodus alternatus* BRANSON & MEHL -SEDDON(a), p.743,pl.12,figs.3,4.
1971 *Icriodus alternatus* BRANSON & MEHL-SCHUMACHER,p.102,pl.13,figs.1-7.
. 1971 *Icriodus alternatus* BRANSON & MEHL - SCULCZEWSKI, p.21, pl.7,fig.2.

Description: A typically slim icriodid with subparallel mid-platform margins and a straight to slightly curved long axis. The denticles are in all cases small, discrete and pointed, those of the median rown, tending to be perfectly alternate posteriorly and subalternate anteriorly.

The denticles of the growth point are usually in prolongation of those of the middle platform:the former is generally short and not well differentiated.

The middle platform bears 3 - 5 denticles in both the lateral and median rows. The laterals appear together and are typically of equal size and round in cross section, though, in some large, somewhat atypical specimens (e.g. pl.33, fig. 6), they are transversely elongate; occasionally they may lie in from the margins and join across the midline (e.g. pl.33, fig. 7,11). The medians are of a comparable size in smaller specimens though they are often laterally compressed and oval in cross section. In larger specimens the tendency is for the medians to become strongly reduced.

The blade is commonly composed of three denticles, the posteriormost of which is the largest (of all denticles).The latter is inclined backwards in such a way as to produce an arcuate posterior border (seen in side view) which is exaggerated by the posterior basal flare extending beyond the denticle row. Though larger, the blade denticles do not lie conspicuously higher than those of the middle platform in all specimens, due to the strong backward inclination. This character is very exaggerated in the largest specimens which have a fused horn-like blade.

From the pointed anterior end of the unit, the basal cavity becomes progressively and evenly enlarged on the outer side. In oral view, this flare is seen to extend beyond the sides of the platform as far forward as the beginning of the middle platform; its maximum width lies on a level with the beginning of the blade. On the inner side, the expansion is not always so pronounced initially and in some specimens is seen to turn abruptly at a point near the last or penultimate platform denticle; the resulting spur is directed somewhat anteriorly. The rounded posterior edge is flexed slightly downward, though this is exaggerated by the strongly raised inner bowl edge (e.g. pl.33, fig. 7).

Remarks: The Plymouth specimens differ from the types of I. alternatus in the form of the lateral denticles, the blade and the basal outline. Branson & Mehl (1934,38) figured three views of three syntypes in which the lateral denticles were "somewhat ridge-like with a slight diagonal trend back from the median line". Such a development is not typical of the studied specimens, nor of the majority of forms subsequently called I. alternatus. The same applies with respect to the blade which is only one denticle long in the types compared with three in this material, as in others (e.g. Ethington 1965 p. 573; Schumacher 1971 b , p.102). In side view, Branson & Mehl's specimens show the blade denticle to be slightly enlarged and slightly inclined posteriorly, and the posterior end to be slightly arched downward. These trends lead to I. cornutus SANNEMANN. The Plymouth material shows an intermediate development of these characters mostly. However, the large specimens have an extremely enlarged and inclined blade cusp, though the posterior end is rarely as strongly downarched as in Sannemann's types. A main point of difference between these specimens and both I. alternatus and I. cornutus is the basal outline. In I. cornutus, the basal cavity is symmetrical and lachrymiform, and though the types of I. alternatus are clearly broken aborally, an essentially similar basal outline appears in the subsequent literature, i.e. no spur development. However, Schumacher (1971 b , p. 102) has noted that the aboral outline of *I. alternatus* shows gradations between circular forms and those with a spur development. No record of a similar variability exists for *I. cornutus* though such does not seem unreasonable. The Plymouth material may include both extremes of aboral outline, though it is difficult to be sure.

Overall, it seems that the smaller specimens fall within the range of variability of *I. alternatus* while the larger ones lie closer to *I. cornutus*. It is considered improper to divide the specimens between these two simply on the basis of size. Glenister & Klapper (1966, p.805) thought that *I. alternatus* may have given rise to *I. cornutus*. It seems reasonable to suppose that these specimens, which occur in strata equivalent to the lowest recorded range of *I. cornutus* (Ziegler 1971, chart 5), are truly intermediate between the two forms.

Anderson 1966 (p.407) considered *I. cornutus* to be a junior synonym of *I. rectus* YOUNGQUIST & PETERSON since topotype material of the latter shared all the variations in the degree of denticle alignment from perfectly alternate (= *I. cornutus*) to nearly aligned, as in the types of *I. rectus*. Figures of the latter do not display clearly the diagnostic features of *I. cornutus* SANNEMANN, rather there may be grounds for placing *I. rectus* in synonomy with *I. expansus*. Since Anderson did not illustrate *I. rectus* it is thought best to retain *I. cornutus* for the present.

As Glenister & Klapper have noted, the median row of denticles in *I. alternatus* are often suppressed whereas in those specimens of *I. expansus* (and *I. nodosus*), in which the denticles alternate,they are not. For this reason Wolska's specimens of *I. nodosus* are included herein whereas one of the *I. alternatus* is not.

Occurrence: Samples WK6a, WKb2, Western King.
In Germany, *I. alternatus* appears at the base of the Upper *Pa. triangularis* Zone according to Ziegler 1971.

Icriodus brevis STAUFFER

aff. Plate 33, figs. 8, 9

1940 *Icriodus brevis* n.sp.- STAUFFER, p.424, pl.60, figs.35, 43, 44, 52.

1970 *Icriodus brevis brevis* STAUFFER - SEDDON(a), p.735-6, pl.12, figs. 12-15.

1970 *Icriodus brevis angustulus* subsp. nov.-SEDDON(a), p.736, pl.11,figs.16-24.

1974 *Icriodus brevis brevis* STAUFFER -UYENO, p.29-30, pl.6, figs.3,11,12.

Remarks: Stauffer originally described *I. brevis* from the clay above the Cedar Valley Limestone in S. Minnesota. The form is characterised by two blade denticles which rise much higher than the other denticles. Subsequent to its introduction, *I. brevis* was placed in synonomy with *I. cymbiformis* STAUFFER (Anderson 1966, p.406), which, like *I. brevis*,was based on small, probably juvenile, specimens. Seddon (1970(a), p.735-6) however, maintained the form species since he was able to recognise the diagnostic characters in all growth stages. The latter author distinguished two subspecies: *I. brevis angustulus* and *I. brevis brevis*, the former differing in the complete fusion of the blade denticles. Seddon found the distribution of *I. brevis brevis* to be more widespread, though both were restricted to the "*angustulus*-horizon" of the Sadler Limestone (Canning Basin, W. Australia). (See Zonations).

In Plymouth a few specimens have a high free blade of this sort, though they differ in other respects. Seddon noted that the species was part of an intergrading Icriodus complex (p.729, 735) and that specimens intermediate between *I. brevis* and *I. symmetricus* were common. The specimen illustrated on plate 33, fig. 9 seems to be such a form, and it is worthy of note that it comes from a stratigraphical position (M. *asymmetricus* Zone) in keeping with its gradational nature between the two (see Zonation chart, *I. angustulus* ~ U. *asymmetricus* Zone). Figure 8, plate 33, seems to lie nearer *I. brevis angustulus* in the greater fusion of the blade. The same is true for the single specimen of *Icriodus* n.sp.aff.*I. alternatus* (pl.33, fig.14) which seems to demonstrate the "brevis" tendency.

Many form species of *Icriodus* are characterised by a distinctly high blade development, and it seems desirable to distinguish them here. In the Middle (M) and Upper (U) Devonian these include:

Icriodus brevis brevis STAUFFER 1940	(U)
Icriodus costatus (THOMAS 1949)	(U)
Icriodus cornutus SANNEMANN 1955	(U)
Icriodus angustus STEWART & SWEET 1956	(M)
Icriodus obliquimarginatus BISCHOFF & ZIEGLER 1957	(M)
Icriodus eslaensis eslaensis van ADRICHEM BOOGAERT 1967	(M)
Icriodus brevis angustulus SEDDON 1970(a)	(U)
Icriodus culicellus BULTYNCK 1974	(M)
Icriodus n.sp. a (described herein)	(M)
Icriodus eslaensis laticarinatus BULTYNCK (in press)	(M)

I. brevis STAUFFER (1940, p.424, pl.60, figs. 36, 43, 44, 52) is characterised by discrete denticles, medians and laterals which are subalternate, a straight posterior border and a symmetrically ovoid basal outline. The two posterior blade denticles are much higher than the others.

I. darbyensis KLAPPER(1958, p.1086, pl. 141, figs. 9,11,12) is a junior synonym of *I. costatus*. The latter lies closest to *I. cornutus*, both being characterised by a downarched posterior platform and a large horn-like blade. They are distinguished by the relative position of the median and lateral denticles. In *I. cornutus* they are perfectly alternating, in *I. costatus* they are aligned and connected by transverse bridges. Ethington (1965, p. 574) described a specimen of *I. cornutus* in which the denticles were subalternate. The cusp of *I. cornutus* may be differentiated into two or three denticles (Glenister & Klapper 1966, p.805). *I. angustus* has aligned denticles posteriorly which are connected by transverse bridges. The basal outline tends to be pointed at both ends due to the development of a posterior-lateral projection. The blade is much higher, consisting of several mostly fused denticles inclined posteriorly. *I. angustus* differs from other icriodids with high blades in the aboral outline. Orr (1972, p. 32, pl.2, figs.7-9) described *I.* cf. *I. angustus* from the Michigan Basin. This form has two high,discrete blade denticles and subalternate denticles and is thus very similar to *I. brevis* from which it differs in its subtriangular aboral outline. *I. culicellus* (= *I.* aff. *I. angustus* sensu Bultynck 1970, p.102, pl. 1, figs. 1-6, 9; 1972, p.73-4, fig. 3) differs from *I. angustus* in the absence of transverse bridge development, in the form of the growth tip, and in the less angular posterior aboral outline. This form approaches *I. obliquimarginatus* which differs in the aboral configuration. In the latter, the transition from gully to bowl on the outer side is gradual, a spur may be present on the inner side and the posterior border is straight - all in contrast to I. culicellus.

I. eslaensis is probably related to I. obliquimarginatus from which it differs in it's broader platform, usually less inclined posterior border and lower, less strongly convex blade, and, in profile, a lesser arched outer lower rim. Bultynck (1972, p.82, fig.15) described I. aff. eslaensis = I.e. laticarinatus, which differed in the greater differentiation of the growth tip, the more common development of transverse bridges, the laterally enlarged and fused blade, the inclined posterior border, and the more abrupt transition from gully to bowl.

The intergradation of some of these forms should be noted. Thus I. brevis brevis and I. brevis angustulus form end members of a transitional series and similarly, intermediate forms occur between I. brevis angustulus and I. cornutus in the degree of down-arching of the posterior end of the unit. The latter and I. costatus are connected by forms in which the platform denticles are subalternate (or subparallel). Thus these four forms appear to represent an intergrading complex in the Upper Devonian. The other forms are Middle Devonian. Orr suggested that his I. cf. I. angustus may have been the precurser of I. angustus STEWART & SWEET, though according to Klapper and Ziegler (1967) the latter diverged from I. latericrescens robustus. These latter three are essentially North American forms.

Bultynck has recognised a long Upper Emsian form and a short Lower Couvinian form of I. culicellus in Belgium. I.n.sp.a, herein described, may be a late Eifelian relation.

I. eslaensis follows I. obliquimarginatus stratigraphically and is itself followed by I.aff. I. eslaensis, the morphological distinction being somewhat arbitary.

In the same way all these aforementioned forms tend to grade into form species in which a high blade is not a diagnostic character. Thus, I. regularicrescens is thought to have given rise to I. obliquimarginatus, and I. alternatus to I. cornutus.

Icriodus expansus - Icriodus nodosus group

Plate 33, figs.13,18,21; Plate 34, figs.14-19,21

Description:(see also Middle Devonian Icriodus) Forms with a regularly convex outer margin and a weakly convex to weakly concave inner margin. The unit is pointed at both extremities and is broadest at about the third transverse denticle row from the posterior end, from which point the oral outline tapers in each direction.

The growth point is not well differentiated from the middle platform, though the denticles do not appear in prolongation of those of the former. The denticles of the middle platform number about 6 - 8, the medians and laterals are commonly well aligned, more rarely subalternate. The medians are round and discrete the laterals are on the whole a little larger and, in the broadest part of the platform, transversely elongate. Low transverse bridges may be developed and in large specimens are strong. The denticulation is generally regular, though laterals may be unpaired posteriorly.

The blade is typically composed of two fairly discrete denticles which are the same height as the denticles of the platform, themselves of equal height. The posterior border is inclined posteriorly or is upright.

The basal expansion of the bowl is a half or more of the total length, and begins more anteriorward on the outer side. Where preserved, the posterior basal outline is evenly curved.and rounded.

Remarks: This group includes forms in which the overall oral outline, the form of the denticulation and the character of the blade provide the most constant features for group identity. Within the group, variation is sometimes extreme. in a large part due to the very different configurations of the different growth stages. Such a variation has been demonstrated within the Middle Devonian I. expansus - nodosus group.

Middle and Upper Devonian representatives share a similar overall shape and denticle arrangement; the maximum width of the platform and the greatest development of lateral denticles is in a similar position and transverse bridges are often well developed.in both. Furthermore there is a similar ontogenetic development, and within both an individual element and a population, a gradation from alignment throughout to an anteriorward migration of the median denticle row in the anterior platform, can be observed (e.g. pl.34, figs. 15-17-14; see also Middle Devonian Icriodus). The essential differences have been discussed previously.

Occurrence: WK5, Western King; DS1, Durnford Street; C4 , Barn Pool; R9, Radford Quarry.

Icriodus symmetricus BRANSON & MEHL group

* 1934 Icriodus symmetricus n.sp. - BRANSON & MEHL, p.226, pl. 13, figs.1-3.

Discussion: Branson & Mehl (1934) erected this species to include forms characterised by mostly parallel sides, a medium denticle row somewhat higher than the lateral rows and a broadly flared posterior basal cavity. These authors (1938) recorded species only from Upper Devonian strata. Subsequently several workers recorded it from Middle Devonian strata but Bultynck (1970, p.112-3) has noted the differing aspect of such forms and enumerated the essential differences between these and I. symmetricus s.s.

In the latter, the bowl is situated relatively posteriorly and is not more than half the total unit length, and is also clearly rounded. Furthermore, the general form is very slender, never massive, and, as mentioned, the median denticles are higher than the laterals. Middle Devonian representatives, according to Bultynck, differ in these respects. Thus, with Bultynck (1972) having raised to specific status I. introlevatus, I. symmetricus can be considered as typically Upper Devonian.

In 1938, Branson & Mehl also erected I. curvatus (p. 162-3, pl.26, figs. 23-6). The oral expression of this species was almost identical to that of I. symmetricus and as these authors noted in the description, the median denticle row lay distinctly above the laterals; I. curvatus was also confined to U. Devonian strata according to their chart (p.156). Glenister and Klapper (1966, p.805) considered I. curvatus to be a junior synonym of I. symmetricus because the diagnostic asymmetrical basal cavity of the former resulted "from lack of preservation of part of the cavity margin". This is not fully evident from the figured types, which also differ from I. symmetricus in their relatively long blade (three to four denticles as opposed to two.) Because forms with truly asymmetrical cavities do occur in the literature, Glenister & Klapper chose to place such forms in open nomenclature, calling them *I.* sp.A (see their synonomy list).

Icriodus symmetricus BRANSON & MEHL

Plate 34, figs. 1-13, 20

* 1934 *Icriodus symmetricus* n.sp. - BRANSON & MEHL, p.226, pl.13,figs.1-3.

. 1938 *Icriodus symmetricus* BRANSON & MEHL - BRANSON & MEHL, p.161, pl. 26, figs. 1-3.

1951 *Icriodus* sp.- HASS, pl. 1, fig. 17.

. 1957 *Icriodus symmetricus* BRANSON & MEHL - MULLER & MULLER, p.1106, pl. 138, figs. 1-3; pl. 142, fig. 8.

. 1967 *Icriodus symmetricus* BRANSON & MEHL - GLENISTER & KLAPPER,p.805, pl. 95, figs. 4,5.

? 1967 *Icriodus cornutus* SANNEMANN - CLARK & ETHINGTON,p. 37-8, pl. 3 figs.3,4.

. 1967 *Icriodus curvatus* BRANSON & MEHL - CLARK & ETHINGTON,p. 38, pl. 3, fig.13.

. 1971 *Icriodus symmetricus* BRANSON & MEHL - SCULCZEWSKI,p.23, pl. 7, fig 5 ,?4.

Diagnosis: Slender icriodids with subparallel platform margins, well aligned median and lateral denticles joined by transverse bridges, and a median denticle row connected by longitudinal bridges and clearly higher than the lateral rows. The aboral flare is rounded and asymmetrical, being greater on the outer side; it is between a third and a half total unit length.

Remarks: The single cotype illustrated in aboral view by Branson & Mehl (1934, pl.13, fig.3) has a symmetrical basal flare though this is apparently broken. Their cotype figured in oral view (fig. 1) is in accord with their description "..one side usually more conspicuously flared than the other". As with other species of *Icriodus*, *I. symmetricus* has been given wide interpretation in the past, though the above diagnosis provides a distinct set of diagnostic characters. The diagnosis also embraces *I. curvatus* sensu Branson & Mehl. I agree with Glenister & Klapper (1966) in considering *I. curvatus* as a junior synonym. *I. curvatus sensu* other authors (e.g. see Bultynck 1970, p.103-4) is not considered to be the same.

The studies material from Plymouth includes specimens from several different stratigraphical horizons which have the following characteristics in common:-

1. Well aligned denticles connected by both transverse and longitudinal bridges.
2. Median denticles clearly rising above the lateral rows.
3. Rounded aboral expansion which begins further anteriorly on the outer side and which commonly extends further laterally on the inner side.

These specimens, which are considered to constitute a coherent group, differ in the following respects:-

1. Curvature of axis.
2. Number of denticles per unit length.
3. Relative height of median and lateral denticles.
4. Relative length of blade.

These variations are manifest in at least two morphotypes. The first, herein called morphotype 1, corresponds to I. symmetricus sensu most authors. In Plymouth this appears to be more common at a lower stratigraphic level, i.e. in the M. asymmetricus Zone. Morphotype 2 corresponds to what many authors have called I. curvatus. This is associated with the first morphotype in the A. triangularis Zone; it is possible that the two are naturally associated in the latter as a class III symmetry pair sensu Lane (1968,p. 1259-60).

Morphotype 1
Plate 34, figs.1-5, 11-13,20

This form is characterised by a straight to curved longitudinal axis and usually subparallel platform margins; more rarely the latter are biconvex. The lateral and median denticles are well aligned and are connected by both well developed transverse and longitudinal bridges. A growth point is not well differentiated, the denticles of the anterior platform lying in prolongation of those of the middle platform. There may be some variation in the spacing of the transverse denticle rows, but generally they are close and number about 5 - 7. The laterals may be occasionally unpaired posteriorly.

The blade is composed of about two denticles mostly fused and lying on a level with the median denticle row. The latter bears longitudinally elongate denticles partially fused into a high crest which clearly rises above the smaller, more discrete laterals in a posterior direction. The posterior border is straight or slightly inclined posteriorly. The basal expansion is typical of the group.

Specimens from the supposed restricted area of Radford Quarry are small and generally have a straight axis and relatively lower median denticle row. Occurrence: Samples 117, Radford Quarry; DS1, Durnford Street; 77c, Fisons Quarry, Cattedown; C4, Barn Pool, near Cremyl.

Morphotype 2
Plate 34, figs.6-10

This form tends to be more slender than morphotype 1 and is always curved, sometimes strongly so, so as to be distinctly concavo-convex in oral view. Two important points of difference are the fewer number of denticles (4-5 as opposed to 7-8), and the distinctly longer blade which is composed of at least three fairly discrete denticles and is commonly at least equal in length to half the platform. Transverse bridges are not always so clearly developed as in morphotype 1. Rare specimens have irregular denticle arrangement near the posterior and/or anterior ends of the unit (e.g. fig.8). The height of the median denticle row is comparable in the two forms.

This form is comparable to many forms designated _I. curvatus_ in the past. It should be stressed however, that the aboral configuration is identical to morphotype 1.

Occurrence: Sample 77a, 77c, Fisons Quarry, Cattedown; DS1 (?), Durnford Street.

Icriodus n.sp.aff._I. alternatus_
Plate 33, figs.10,14-16,22, 23

Diagnosis: _Icriodus_ characterised by a very short growth point and round, discrete (sub-) alternate denticles.

Description: The axis is straight but may be incurved at the anterior end. Margins slightly biconvex to subparallel. The growth point is very short and composed of only a single denticle, in continuation of the median denticle row. The middle platform consists of 4 - 5 discrete denticles in each row. The medians in the central part of the platform are large and round in cross-section, and those in both directions, smaller and laterally compressed. The lateral denticles are generally round in cross section and of equal size; the posteriormost one or two may be slightly elongate transversely and directed slightly anteriorward. In small specimens the denticles are alternate but tend to become subalternate in later growth stages. Occasionally, the spacing of the denticle rows is irregular, the anterior denticles being further apart than the posterior ones.

The blade is composed of three denticles, partially fused and increasing in size posteriorly. They are higher than the platform denticles in some specimens.

Aborally, the gully expands progressively posteriorly to a point a little behind the unit midlength, beyond which the basal expansion is apparently symmetrical.

Remarks: The form is distinctive and unlike any established form species. It appears to be restricted to the Lower asymmetricus Zone.

Occurrence: Samples WK1, WK2, Western King.

Form genus: Palmatolepis ULRICH & BASSLER·

Type species:Palmatolepis perlobata ULRICH & BASSLER 1926

Remarks: Palmatolepis is restricted to the Upper Devonian. It evolved from Polygnathus at the base of the interval and thereafter went through rapid and varied evolution giving rise to quite different morphological expressions. Detailed phylogenies have been worked out by Ziegler (1962a,b), Helms (1963) and Muller (1956, 1962) and the first named author zoned the Upper Devonian of Germany (1962a) by means of the genus (predominantly) though this work continues (e.g. Sandberg and Ziegler 1973).

Palmatolepis is very well known and it is not felt necessary to deal with the taxonomy of the group herein, except for those forms which appear to be new. Suffice it to say that six characters have been considered of taxonomic value in differentiating between species:

1. Platform outline
2. Oral ornament
3. Position and character of outer lobe
4. Character of blade carina
5. Position and character of parapet if developed
6. Profile of the posterior platform

It should be noted that the lobe, when developed (or the concave side of the carina anterior of the azygous node), is outer (Orr and Klapper 1968, p.1071); much of the literature contains descriptions using the converse.

The multielement Palmatolepis is believed to involve a type 1 apparatus (A_1 = smithiform, A_2 = angulodiform, A_3 = scutuliform; O_1 = nothognathelliform. N =palmatodelliform by Klapper and Philip (1972, p.100) whereas Ziegler (1972, p.94) prefers the platform element (s) on its own.

Palmatolepis aff. Pa. transitans MULLER
Plate 29, fig. 8

* 1956 Palmatolepis transitans n.sp. MULLER, p.18-19, pl. 1, figs. 1,2.

v non 1970 Palmatolepis transitans MULLER - KIRCHGASSER, p. 344-5, pl. 63, figs. 1,8 (= Pa.? disparalvea).

. 1974 Palmatolepis transitans MULLER - ZIEGLER, p.309-10, pl.1, figs. 1-3 (see synonomy).

Diagnosis: see Ziegler 1973, p.309-10.

Remarks: A single specimen from Western King may be a juvenile of this form-species. The straight carina, and not well differentiated lobe are characteristic, though the absence of a carina development posterior of the azygous node is not.

See also Ziegler 1973, p.309.

Occurrence: Sample WK 5, Western King. Palmatolepis cf. Pa.transitans (one specimen)from sample 135, Barn Pool, nr. Cremyl.

In Germany, Pa. transitans ranges from the base of the L. asymmetricus Zone into the A. triangularis Zone.

Palmatolepis n.sp.a

Plate 29, fig. 10

Remarks: A single specimen from the Plymouth Limestone is peculiar in several respects. The elongate-oval and apparently symmetrical platform bears a central azygous node which also marks the posterior termination of a fairly high carina. The platform surface bears transverse ridges and, occasionally, aligned nodes. Aborally, at the midpoint of the platform, the keel is interrupted by the abruptly expanded anterior edge of a parallelogram- shaped basal cavity. The posterior edge of the cavity meets the keel abruptly nearly one quarter of the platform length from the posterior platform tip. The outer edge parallels the keel and lies between one third and one half of the distance from the latter to the platform margin.

The specimen is not well preserved but clearly differs from any previously described. The platform shape is polygnathoid, the position and asymmetry of the basal cavity is suggestive of Schmidtognathus, while an azygous node is a diagnostic character of Palmatolepis.

Occurrence: Sample H1, West Hoe, Plymouth. ?Lowermost asymmetricus Zone.

Palmatolepis? durnfordi n.sp.

Plate 29, figs.1,2,5,cf.17; aff.Pl.30, fig.4

Diagnosis: A form which differs from other species of Palmatolepis in lacking an azygous node and in possessing an asymmetrical basal cavity. The platform is broad, thick and bears coarse nodes. A lobe is indicated but not always well differentiated; the carina may be distinctly sinous.

Description: The platform is about as broad as it is long and is usually strongly asymmetric, being broader on the outer side where a lobe is indicated. The latter is not always well differentiated. The inner platform margin is regularly curved and meets the blade at the same position as the outer margin. The platform is arched in profile, more strongly so anteriorly, and bears an ornament of quite coarse nodes which may be transversely elongate or aligned.

The (rarely preserved) blade is short and composed of numerous, mostly fused denticles of equal height. Posteriorly, the platform rises to meet the carina which is progressively lower in that direction. At, or a little in front of, the platform midlength, the denticles of the fixed blade are replaced by low, broad, fused nodes which become increasingly discrete in the posterior half of the platform and disappear before the posterior tip. The blade is distinctly sinuous in some specimens.

Aborally, a large basal cavity is situated at mid-platform. This is strongly expanded laterally on one side (the outer) and attains its maximum width near the anterior end of the cavity.

Remarks: This new form is questionably placed in Palmatolepis on the basis of the incipient lobe development and blade sinuosity. Unlike other palmatolepids, it lacks an azygous node and a distinct lobe development. These latter characters are also variable in the early palmatolepid representatives.Palmatolepis transitans and Pa. punctata, though in their aboral configurations these two species are typical of the form-genus, i.e. bearing a minute pit. Pa.? disparalvea was also questionably assigned to Palmatolepis because of its unusual basal cavity. In Pa.? disparalvea the lobe is well differentiated and the cavity lies further posteriorly (see also Remarks under Polygnathus nismi).

A single large specimen (pl.30, fig. 4) from the same sample as those figured appears to have an azygous node and also has a clearly developed lobe. The ornament of this form consists of strong radial ridges and aligned nodes and as such is similar, though, perhaps predictably, more extreme than in the small specimens. The basal cavity of this specimen is obscured by a basal attachment so its nature is not known. If the latter is asymmetrical and thus if this form does represent a late growth stage of the same species, then the inclusion of Pa.? durnfordi in Palmatolepis s.s. may be more justified.

Occurrence: Sample DS1, Durnford Street, Plymouth.

Form genus: Polygnathus HINDE

Type species: Polygnathus dubius HINDE 1879 (subsequent designation, MILLER 1889, p.520).

The neotype of Polygnathus dubius is the lectotype of Polygnathus foliatus figured by Bryant 1921, pl. 10, fig. 16. See Huddle 1970, p.1030-3 for comprehensive discussion of the genus, Huddle 1968, p.37 for synonomy.

In multielement terms, Klapper and Philip (1971, 1972) considered Polygnathus to be involved in two of their multielement families, the Polygnathidae and Cryptiotaxidae (see Foreword). Within the former, two genera were distinguished - Polygnathus and the Upper Devonian Mesotaxis, these differing in their O_1, A, and N elements. This distinction separates some of the widely differing forms assigned to the form-genus, though further separation must still be possible (see Remarks under the "linguiformid" group).

Ziegler 1972 (p.93, 96) suggested that Polygnathus may have been associated in an apparatus devoid of ramiform elements. The symmetry transition demonstrated by some polygnathids may support this conjecture since it seems reasonable to include together some such forms (e.g. See Po. mucronatus, Po. serratus) though this is not to say that ramiform elements are not associated.

Polygnathus aff. Po. aspera HUDDLE. 1934
Plate 24, fig. 2

aff.*1934 Polygnathus aspera n.sp. - HUDDLE, p.104, pl.8, figs. 45-6.

Description: Large, broad, massive, flat and flexed platform. Outer margin is mostly regularly convex, the inner margin is nearly straight. The posterior one seventh of the platform is somewhat pinched and twisted laterally. A carina is represented by a thick, fused, irregular ridge more or less straight and central in the anterior half but turning inward and lying nearer to the inner margin in the posterior half. In the posteriormost part of the platform the carina breaks up into nodes and cannot be clearly traced, but appears to be turned outwards. On its inner side, and at the posterior tip of the platform, there is a smooth, shallow depression.

The oral surface of the platform is ornamented by strong perpendicular ridges which tend to be divided posteriorly into laterally elongate nodes. They are generally separated from the carina by narrow, shallow adcarinal grooves, though some do meet it. The anterior platform margins are turned strongly downwards in front of the first divergent ridges which make an angle of about 45° - 50° with the fixed blade. The free blade is not preserved.

Aborally there is a diamond shaped pit situated a third of the platform length in from the anterior end. A keel extends to near the blunt posterior end where, reflecting the carina, it is lost. Anteriorly, a wide-flared furrow equal in width to the pit is developed.

Remarks: This form differs from Po. aspera HUDDLE insomuch as the latter tends to be somewhat more elongate. Also the difference in the height of the posterior platform on either side of the carina, as described by Huddle, is not clearly a feature of the unit, though the depression is thought to be analogous.

In common with the holotype, this specimen is (relatively) very large and is associated with Po. tuberculatus with which a relationship is strongly suggested by the general form of the platform (compare aboral views too). The specimen may represent a late stage, gerontic development of Po. tuberculatus, but it is retained here for the present.

Polygnathus aspera was found to be very rare in the Lower New Albany Shale. The single specimen from Plymouth comes from the upper part of the varcus Zone.

Occurrence: Sample 36, Mount Wise.

The Polygnathus asymmetricus group

Diagnosis: Polygnathids with long, often broad, platforms covered with numerous small nodes. A short free blade continues on the underside of the platform as a sharp keel which is interrupted by a basal cavity situated in the anterior half of the platform.

Remarks: Ziegler et al. (1964, p.422) considered the lectotype of Polygnathus dubia to be an indeterminate fragment and that therefore the first available name for Bischoff and Ziegler's concept of this form species was Polygnathus asymmetrica. Huddle (1972, p.5) discussed Hinde's (1879, p.362-4, pl.16, figs. 6-17) type of the multielement Polygnathus dubius which he considers to be a food-ball. The lectotype of Polygnathus dubius chosen by Roundy (1926, p.13) was judged by Huddle (1970, p. 1031) to be suggestive pf Polygnathus foliatus BRYANT, the lectotype of which (Bryant 1921, pl.10, fig. 16) was designated by Huddle (1970, p.1032) as the neotype of Polygnathus dubius.

Bischoff and Ziegler (1957) recognised two subspecies - (now called) Polygnathus asymmetricus ovalis and P. asymmetricus asymmetricus. These are differentiated mainly on their platform outlines which may be gradational. There appears to be some difference in the stratigraphic and geographical ranges of the subspecies but there are discrepancies in range charts (compare Bischoff and Ziegler 1957, p.135, table 5; Ziegler 1962b, table 2). Po. dengleri seems to be a related form.

A study of material from S.W. England, Belgium and Germany and an appraisal of published illustrations indicated further division of this group is desirable and biostratigraphically useful. Distinction is primarily based on the form of the basal cavity.

The holotype of Polygnathus asymmetricus has been illustrated in oral view only (Bischoff and Ziegler 1957, pl.16, fig. 20). In the only syntype shown in aboral aspect (pl.16, fig.18) the basal cavity appears to be minute and situated at a point two thirds of the total length of the platform from the posterior tip. This development is typified in the specimen illustrated by Ziegler 1958, pl. 1, fig.10a.

The holotype of *Polygnathus asymmetricus ovalis* is figured in Ziegler 1958, pl.1, fig. 2 a-b (by subsequent designation of Ziegler and Klapper 1964, p.422). This has a relatively large, slightly asymmetrical based cavity situated somewhat further posteriorly than in the nominate subspecies, though still anterior of the platform midlength. Other specimens assigned to *Polygnathus asymmetricus ovalis* (e.g. Ziegler 1958, pl.1, fig. 3), on the basis of a relatively symmetrical platform outline, have a pit development characteristic of *P. asymmetricus asymmetricus.* Such specimens have a more quadrate outline and a more robust appearance and are here included in the latter taxon. It is thought that the character of the aboral surface provides a meaningful distinction between the two subspecies. Most illustrated specimens of *P. asymmetricus ovalis* have a symmetrical tear-shaped cavity.

Many illustrated specimens are not shown in aboral view and are questionably placed in synonomy on the basis of their overall shape and oral configuration.

Polygnathus nismi sp.nov. is a related member of this platform complex. This is characterised by a large, strongly asymmetrical basal cavity situated at mid-platform length. The shape of the units tends to reflect that of the laterally expanded cavity and thus one side of the platform is larger; especially in juveniles. This tendency for the platform outline to reflect the shape of the basal cavity is seen in the holotype of *Polygnathus asymmetricus ovalis*, which is, in some respects, transitional towards *Polygnathus nismi* and thus atypical of the species (*sensu* most authors).

Po.dengleri is quite distinct in its typical form, but Sculczewski(1971) has figured some specimens which have a much broader platform and are thus very similar to *Po. asymmetricus.* The asymmetrical basal cavity of these forms do in fact suggest rather *Po. nismi.* Some of Kirchgasser's (1970) specimens of *Po.dengleri* have broader than usual platforms.

There appears to be inter-gradation between all these aforementioned forms.

Polygnathus asymmetricus asymmetricus BISCHOFF & ZIEGLER 1957
Plate 28, fig. 16, cf.13

* 1957 *Polygnathus dubia asymmetrica* n.sp. - BISCHOFF & ZIEGLER p.88-9, pl.16, figs.18,20-22; pl.21, fig.3.

. 1957 *Polygnathus dubia dubia* HINDE - BISCHOFF & ZIEGLER, pl.21, fig.2 (only).

1958 *Polygnathus dubia asymmetrica* BISCHOFF & ZIEGLER - ZIEGLER, pl.1, figs. 4,5,6,8,10a-b.

. 1958 *Polygnathus dubia dubia* HINDE - ZIEGLER, pl.1, fig.3a-b (only). fig.3.

1959 *Polygnathus dubia asymmetrica* BISCHOFF & ZIEGLER - KREBS, p.384, pl.1,

1963 *Polygnathus dubia asymmetrica* BISCHOFF & ZIEGLER-HELMS,text fig.2,fig.2.

. 1966 *Polygnathus asymmetrica asymmetrica* BISCHOFF & ZIEGLER - GLENISTER & KLAPPER, p. 828, pl. 88, figs. 6, 7.

? 1966 *Polygnathus asymmetrica asymmetrica* BISCHOFF & ZIEGLER - FLAJS, p.230-2 pl. 26, figs. 1-3, 8,9 (non figs. 4-6= *Polygnathus nismi* sp. nov.).

. 1967 *Polygnathus dubia asymmetrica* BISCHOFF & ZIEGLER - CLARK & ETHINGTON, p.61, pl.7, fig.18.

. 1967 *Polygnathus dubia dubia* HINDE - CLARK & ETHINGTON, p.60-1, pl. 82, fig.14, (non-fig. 15 = *Polygnathus dengleri*)

. 1970 *Polygnathus asymmetrica asymmetrica* BISCHOFF & ZIEGLER - SEDDON(b), pl. 10, fig. 2.

. 1970 *Polygnathus asymmetricus ovalis* BISCHOFF & ZIEGLER - SEDDON (a), pl.13, figs. 16,17 (only).

v. 1970 *Polygnathus asymmetricus asymmetricus* BISCHOFF & ZIEGLER- KIRCHGASSER, p.345-6, pl.63, fig. 9.

. 1971 *Polygnathus asymmetricus asymmetricus* BISCHOFF & ZIEGLER - SCULCZEWSKI, p.45, pl.16, figs. 3,5 (non fig.4).

. 1971 *Polygnathus asymmetricus asymmetricus* BISCHOFF & ZIEGLER - KLAPPER & PHILIP, p. 434, 449, fig. 3P (only).

. 1972 *Mesotaxis asymmetricus asymmetricus* BISCHOFF & ZIEGLER - KLAPPER & PHILIP, p.100, pl.1, fig. 20 (only).

. 1974 *Polygnathus asymmetricus asymmetricus* BISCHOFF & ZIEGLER - UYENO, p.37, pl.3, figs. 1,4,6 (?3).

Diagnosis: A subspecies of *Polygnathus asymmetricus* with a broad, asymmetrical and often subquadrate platform and a very small basal cavity.

Occurrence: Sample 117, Radford Quarry;
cf. Sample DS1, Durnford Street.
Ziegler 1971 (chart 5) records *Po. a. asymmetricus* from throughout and restricted to, the *asymmetricus* Zone.

Polygnathus asymmetricus ovalis ZIEGLER AND KLAPPER 1964
Plate 28, figs. 1-5, 7-10, 12-14, aff. 15

. 1957 *Polygnathus dubia dubia* HINDE - BISCHOFF & ZIEGLER, p.88, pl.16, fig.19; pl.21, fig.1 (non.fig.2=? Po. *asymmetricus asymmetricus*).

. 1958 *Polygnathus dubia dubia* HINDE - ZIEGLER, pl.1, fig.1, 2a-b, 7a-b.

1963 *Polygnathus dubia dubia* HINDE - HELMS, text fig.2, fig.1.

? 1965 *Polygnathus asymmetricus ovalis* ZIEGLER & KLAPPER - ETHINGTON, p. 581, pl.68, fig.1 (oral-view only).

. 1966 *Polygnathus asymmetricus ovalis* ZIEGLER & KLAPPER - GLENISTER & KLAPPER, p.828, pl.87, figs. 8,9.

. 1966 *Polygnathus asymmetricus ovalis* ZIEGLER & KLAPPER - FLAJS, p.239, pl.25, figs. 1-3.

. 1965 *Polygnathus asymmetrica ovalis* ZIEGLER & KLAPPER - ZIEGLER (b), p.671. pl. 5, fig. 6.

. 1967 *Polygnathus dubia dubia* HINDE - CLARK & ETHINGTON, p.60-1, pl.7, figs.14,15; pl.8, fig. 9 (non fig.8= *Polygnathus dengleri*).

. 1967 *Polygnathus dubius* HINDE - MULLER & CLARK, p.916, pl.115,figs.5a-c, 6.

. 1969 *Polygnathus asymmetricus* ovalis ZIEGLER & KLAPPER - POLSLER, p.420, pl.4, figs. 17,18.

1970 *Polygnathus asymmetricus ovalis* ZIEGLER & KLAPPER - SEDDON (b), pl.10, fig.1.

. 1971 *Polygnathus asymmetricus ovalis* ZIEGLER & KLAPPER - SCULCZEWSKI, p.45-6, pl.17, figs. 1a-b, 2.

. 1974 *Polygnathus asymmetricus ovalis* ZIEGLER & KLAPPER - UYENO, p.37, pl.3, figs. 2,5,7; pl.4, fig.1 (non fig.3 = *Polygnathus* sp.nov.).

Diagnosis: A subspecies of *Polygnathus asymmetricus* with a symmetrically lanceolate platform and a small tear shaped basal cavity.

Description: The platform is typically symmetrically lanceolate, evenly and gently arched, and tapers to a point. The blade is very short (about one seventh total unit length), low and deep and continues posteriorly as a carina, the individual nodes of which are relatively large and discrete. The oral surface bears small nodes or granules which tend to become transversely aligned. Aborally, a small basal cavity is located a little anterior of the platform midlength. There is a sharp keel and a broad crimp.

Remarks: Most of the specimens of *Polygnathus asymmetricus* from Plymouth are considered to belong to this subspecies. Much of the material is fragmentary, all of it is very fragile and most is also tectonically deformed. The variety in platform symmetry is judged to be the result of this deformation and dislocation. Aboral configurations, the form of the carina and the ornament, provide a fairly constant criterion for group identity. The course of the carina, though often obviously affected by tectonics, occasionally shows a sinuosity or even a lateral displacement (e.g. pl.28, fig.12) which suggests a tendency toward *Palmotolepis*, though an azygous node is never developed. The platform ornament usually shows a good transverse alignment, especially anteriorly, and this is sometimes pronounced enough to produce an irregular platform margin (e.g. pl.28, fig.7). Sometimes the ornament is completely random as in fig. 9, pl.28, a specimen which also has a downarched and twisted posterior tip. This is probably due to deformation though to what degree this is responsible for the trough shaped platform of the specimen figured on pl.28, fig. 15, is debatable; this latter specimen also differs in the pronounced extension of the carina posteriorly, a festure which characterised *Polygnathus* n.sp. D *sensu* Pollock 1968. The specimen figured by Seddon 1970 (a) (pl.13, figs. 14,15) appears to be transitional to *Po. nismi* sp.nov.

Occurrence: Samples WK1, WK2 Western King; Sample DS1, Durnford Street; Sample 117, Radford Quarry. In Germany, Ziegler 1971 records *Polygnathus asymmtricus ovalis* from the base of the Lowermost *asymmetricus* Zone up to a level near the top of the Upper *asymmetricus* Zone.

Polygnathus dengleri BISCHOFF & ZIEGLER

Plate 28, figs. 6, 11, 19

* 1957 *Polygnathus dengleri* n.sp.-BISCHOFF & ZIEGLER,p.87-8, pl.15,
figs. 14,15,17-24; pl.16, figs. 1-4.
. 1965 *Polygnathus dengleri* BISCHOFF & ZIEGLER - ZIEGLER (b),p.671-2,pl.6,
figs. 1 - 6.
. 1967 *Polygnathus dengleri* BISCHOFF & ZIEGLER - CLARK & ETHINGTON,
p. 60, pl.7, figs. 3,8. /figs.3,7.
. 1967 *Polygnathus dengleri* BISCHOFF & ZIEGLER - MULLER & CLARK,p.916,pl.115
. 1968 *Polygnathus dengleri* BISCHOFF & ZIEGLER-ORR & KLAPPER,pl.139,figs.5-7.
. 1969 *Polygnathus dengleri* BISCHOFF & ZIEGLER- POLSLER, p.421, pl.4;
figs.13, 14.
v. 1970 *Polygnathus dengleri* BISCHOFF & ZIEGLER - SEDDON(a),p.739,pl.13,figs.20-3.
v. 1970 *Polygnathus dengleri* BISCHOFF & ZIEGLER - KIRCHGASSER, p. 348-9,
pl. 63, fig.2;pl.65, fig.4; pl. 66, fig.2.
non1971 *Polygnathus dengleri* BISCHOFF & ZIEGLER - SCULCZEWSKI, p.48,pl.16
figs. 1,2,6,7.

Diagnosis: A species of *Polygnathus* with a long, narrowly ovoid platform with upturned margins. An often strong platform ornament of transverse ridges is separated from a high carina by shallow adcarinal grooves. A free blade is relatively short and high. Aborally, an oval basal cavity is situated in the anterior half of the platform.

Remarks: *Polygnathus dengleri* differs from *Po. asymmetricus* in its narrower, trough-shaped platform, high blade and carina and adcarinal grooves. Plymouth specimens have rather longitudinally elongated basal cavities. Some small specimens here assigned to *Po. asymmetricus*, have similar platform outlines and upturned margins (e.g. plate 28, figs. 14,15), but the latter character is judged to be due to tectonic deformation; the posterior carinae of the latter specimens are typical of *Polygnathus asymmetricus*. The specimens illustrated by Sculczewski, as noted by him, are much broader than is typical. Some also have an asymmetrical basal cavity (see *Po. nismi*).

Occurrence: Samples WK1, WK2, Western King. In Germany, Ziegler (1971) records *Po. dengleri* from within the Lowermost to the top of the Lower *asymmetricus* Zone.

Polygnathus nismi n.sp.

Plate 29, figs. 3,4,6,11-15, cf. 16

P . 1949 Polygnathus dubia HINDE - BECKMANN, p.154-5, pl.4, fig.4
(Pl.1, fig.3 appears to be transitional from Po. a. ovalis).
. 1966 Polygnathus asymmetrica asymmetrica BISCHOFF & ZIEGLER - FLAJS,
p.230-2, pl.26, figs. 4-6 (only; fig.7 appears to be transitional).
. 1968 Polygnathus n.sp.c - POLLOCK, p.438, pl.62, figs.28,29,35.
aff. 1968 Polygnathus asymmetricus ovalis ZIEGLER & KLAPPER - MOUND,
p. 504, pl.69, figs. 4,5.
1971 Polygnathus dengleri BISCHOFF & ZIEGLER - SCULCZEWSKI, p.48, pl.16
fig. 2 (only).
p. 1973 Polygnathus asymmetricus - MOURAVIEFF & BOUCKAERT, p.94-5.
p. 1974 Polygnathus asymmetricus - MOURAVIEFF, in BOUCKAERT & STREEL,F, p.2.

Diagnosis: An atypical polygnathid with a broad, flat, slightly asymmetrical platform, a low, occasionally slightly sinuous carina, and a relatively large asymmetrical basal cavity.

Description: The unit is slightly to strongly asymmetrical in plan view and slightly to moderately arched in lateral view. The blade is fairly deep and short, about one fifth of the total unit length, and consists of 3 - 5 mostly fused denticles which tend to increase in height anteriorly. The carina becomes progressively lower posteriorly in conjunction with the broadening of the denticles into fused nodes which attain their maximum development just posterior of mid-platform, where there are two nodes invariably larger than all others. Posterior of that point, two or three discrete, smaller denticles, increasingly separated, mark the discontinuous prolongation of the carina. In some (about half) the specimens the carina is slightly sigmoidal and has an arcuate curvature (the concave side being outward) a little anterior of platform midlength. Adjacent to and opposite this arc, the outer platform is slightly depressed, and/or lies lower than the inner side. This point also marks the greatest width of the unit and may be marked by strong lateral growth. Thus the outer platform is invariably broader than the inner, the difference being especially pronounced in juveniles. Posteriorly, the platform tapers evenly to a point, while anteriorly the platform margins are smoothly rounded and stretched downward to meet the blade at more or less opposite points.

The ornament consists of fine granules which may become fused into ridges marginally and anteriorly, especially in larger specimens. The ornament on the inner and outer sides is not necessarily the same. Aborally, the unit has a large asymmetrical basal cavity, the centre of which is situated at mid-length. The shape of the cavity is approximately triangular. It is strongly expanded laterally at its anterior end, extending toward the maximum development of the outer platform. Posteriorly, the expanded side of the cavity tapers irregularly towards a point one quarter, or less of the total platform length from the posterior tip, in such a way as a fold is often developed. The inner margin of the cavity is evenly arcuate. The depression on the oral surface of the outer platform corresponds to a position immediately anterior of the basal cavity. The keel is grooved anteriorly under the blade.

Remarks: *Po. nismi* lies closest to *Po. asymmetricus* from which it differs most obviously in its larger and strongly asymmetrical basal cavity. (see also Remarks under *Po. a. ovalis*). The platform shape varies from ones very similar to *Po. asymmetricus ovalis* to others comparable to *Po. asymmetricus asymmetricus* and even to *Palmatolepis transitans*. The lack of a well differentiated azygous node excludes the new species from *Palmatolepis* and yet the cavity is not dissimilar to *Palmatolepis ? disparalvea* ORR and KLAPPER 1968, a species which was questionably assigned to the latter genus also because of its large asymmetrical basal cavity. Although *Pa? disparalvea* does not always possess a well developed azygous node, it is characterised further by a well developed lobe, coarser ornamentation and the extreme development of the basal cavity which also lies relatively further posteriorly than in *Polygnathus nismi*.

The genus *Schmidtognathus* ZIEGLER is by definition (Ziegler 1965, p. 661), characterised by an asymmetrical basal cavity, though in fact only in the type species *S. hermanni* and to a lesser extent in *S. pietzneri*, is such a cavity well exhibited. These differ from *Polygnathus nismi* in their slimmer, symmetrical platforms and longer free blades as well as in the relative shape and position of the basal cavity. Furthermore, in *Schmidtognathus*, the lateral expansion of the cavity is central relative to the whole cavity rather than anterior and it is not related to platform asymmetry.

An asymmetrical basal cavity is also a character of *Po. dissimilis* HELMS & WOLSKA. This Famennian polygnathid is much slimmer and has upturned platform margins. *Palmatolepis? durnfordi* sp. nov. has a cavity very similar though often more pronounced, than *Polygnathus nismi* but differs in possessing a usually markedly sigmoidal carina, outer lobe and a coarser ornament; the former unit is also thicker and more robust.

Specimens designated *Po. dengleri* by Sculczewski have a much broader platform than is typical of the species and some also have an asymmetrical basal cavity. They differ from most representatives of *Po. nismi* in the anteriorly upturned platform margins and also in the coarser ornament. They may also be slightly older than the former.

Occurrence: Sample DS1, Durnford Street Plymouth.
Elsewhere: - Sample 8, section II, Saskatchewan Gap - the Maligne Formation (Some discrepancy exists here : Pollock 1968, pl. 62, figs. 28,29,35 + U.A. Dv.1844, cites the Perdrix Formation, whereas on p.438 the two specimens are noted as coming from the Maligne Formation. Since Section II does not appear elsewhere other than in relation to the Maligne Formation, this is assumed correct.)

Samples 4,5,7,9,28,29,31,33 (=51, 52, 54, 56, 23, 24, 26, 28 *sensu* Mouravieff, personal communication) Nismes, Belgium.

Samples H15, H33, Hon,Belgium; MRZ 7 Martouzin - Neuville, Belgium
Probes 9' and 11' Kansel profile, Graz, Austria (Flajs)

All these occurrences appear to be in the Middle *asymmetricus* Zone.

Sculczewski's specimens appear to come in part from the Lower *asymmetricus* Zone - Wietrznia I (28, 52), and in part from the Upper *asymmetricus* Zone - Słuchowice (15). These are not,however,necessarily referable to *Po.*aff.*Po.nismi*.

Mound's figured specimen clearly has an asymmetrical basal cavity, though it may be considered as transitional since this is relatively small. No.1 well, Calstan Winterburn, Duvernay Fm. (*A. triangularis* Zone)

The Polygnathus costatus Group

In 1971, Klapper erected this group to include several forms characterised by a regularly curved outer margin, and a platform narrower than the radius of this curve. Additionally, the posterior platform bears an ornament of nodes (which may become transversely aligned or partially fused) or ridges, which are separated by adcarinal grooves from a carina which extends at least into the posterior third of the platform. The aboral surface of these forms is characterised by a small pit located about halfway between platform midlength and the anterior end of the platform. Thus conceived, the group embraces the following:

Polygnathus costatus patulus KLAPPER 1971
Polygnathus costatus costatus KLAPPER 1971
Polygnathus pseudofoliatus WITTEKINDT 1965
Polygnathus eiflius BISCHOFF & ZIEGLER 1957

The first three forms are considered to form a phylogenetic series, the gradation being reflected both morphologically and stratigraphically. The last two also grade into each other and are connected by Polygnathus aff. Po. eiflius described by Klapper (1971, p. 63) from the New York Lower Middle Devonian.

The Polygnathus costatus group differs from the Polygnathus linguiformis group in the lack of transverse ridge development on the posterior platform. As noted by Klapper (1971, p.62) it is not possible to distinguish all forms of Polygnathus linguiformis on the basis of the platform outline (see also discussion of Polygnathus linguiformis group). Polygnathus linguiformis cooperi has a similar outline and forms transitional from Po. costatus patulus are known.

Polygnathus costatus costatus KLAPPER
aff. Plate 9, figs. 11,12,15; Plate 14, fig.9

* 1971 Polygnathus costatus costatus subsp. nov. - KLAPPER, p.63, pl.1 figs. 30-36; plate 2, figs. 1-7 (includes synonomy).

Diagnosis: A polygnathid of the *Po. costatus* group in which the carina is continuous to the posterior end. The platform is widest in the posterior third and tends to be somewhat constricted near the anterior end.

Remarks: Several, mostly fragmentry, specimens from a sample at Neal Point may be related to *Po. costatus costatus*. This subspecies differs from *Po. c. patulus* in having an overall narrower platform, a larger carina, narrower adcarinal grooves, a more constricted anterior platform, and closer spaced, more numerous ridges on the platform margins. The Plymouth specimens differ in having a narrower platform and relatively little outer lateral expansion of the posterior platform. A small form (pl. 9, fig.11) shows no curvature of the outer margin whereas in larger forms this characteristic feature of the group is demonstrated. A complete specimen (pl. 14, fig.9) has a blade with anteriorly inclined denticles; this is also longer than in *Po. costatus*.

Occurrence: Sample NP15, Neal Point, nr. Landulph.

Polygnathus pseudofoliatus WITTEKINDT

Plate 10, figs. 1-10, 14, 17

. 1957 *Polygnathus foliata* BRYANT - BISCHOFF & ZIEGLER,p.90, pl.4, figs.1-4.
p 1957 *Polygnathus xylus* STAUFFER - BISCHOFF & ZIEGLER, p.101,pl.5,fig.11.
. 1965 *Polygnathus* n.sp. - BULTYNCK, p. B70, pl. fig. 6a-b.
* 1965 *Polygnathus pseudofoliata* n.sp. - WITTEKINDT, p.637-8, pl.2, figs. 20-23 (fig. 19 is transitional to *Po. eiflius*).
. 1966 *Polygnathus* sp. nov. B - PHILIP, p.158-9, pl.2, figs. 4-9.
. 1966 *Polygnathus xylus* STAUFFER - BULTYNCK, pl.2, figs. 3a-c.
. 1970 *Polygnathus pseudofoliata* WITTEKINDT-BULTYNCK, p.127-8, pl.14, figs. 1,2,5,7,8 (non fig.3 = *Polygnathus eiflius*).
. 1970 *Polygnathus pseudofoliatus* WITTEKINDT - KLAPPER, PHILIP & JACKSON, p. 664, pl.3 figs. 7-19.
. 1970 *Polygnathus xyla* STAUFFER-BULTYNCK, pl.15, fig.5 (only).
. 1971 *Polygnathus pseudofoliatus* WITTEKINDT-KLAPPER, p. 63-4,pl.2, figs.8-13.
. 1971 *Polygnathus pseudofoliatus* WITTEKINDT - ORR, p.52-3, pl.4, figs. 18-22.

Diagnosis: Polygnathid of the *Polygnathus costatus* group with a free blade a third to a half of the total unit length and a platform which is constricted anteriorly and bears transverse ridges or nodes.

Remarks: The Plymouth material includes a variation in platform outline. This involves a moderate (pl.10,fig.8) to a strong (pl.10,figs. 3,7) outer platform flare, and a variation in the anterior platform margins from steep and opposed (pl.10, figs.1,3) to strongly asymmetrical with the outer margin less sharply inclined downward (pl.10, figs. 4,10). Some forms have strongly denticulate anterior platform margins bordering the deep adcarinal grooves (e.g. pl.10, figs. 1,9). These latter two variations are comparable with those found in the stratigraphically younger *Po. varcus* group. All the studied specimens have a nodose ornament on the flattened posterior platforms but the tendency to alignment is oblique (pl.10,fig.6) or longitudinal (pl.10, fig.4), if at all, rather than transverse, as Klapper (1971, p.63) has indicated. More often the nodes are randomly distributed, but this is a relatively unimportant character of the form.

All the specimens share adcarinal grooves which extend the full length of the platform but which are clearly shallower posteriorly, the deeper anterior grooves being due to the constricted, upturned platform margins. This character distinguishes even small specimens of *Polygnathus xylus* (see remarks under same). The ontogeny of *Po. pseudofoliatus* appears to involve the lateral enlargement of the posterior platform, the establishment of a continuous posterior carina and slight anteriorward platform growth resulting in a pit which lies relatively further posteriorly (pl.10,figs. 14-8-3). The pit in all the studied material lies further anteriorly than is typical of the *costatus* group *sensu* Klapper (1971) (see diagnosis).

In the specimens preserved with blades intact, the latter are about ½ of the total unit length and the blade denticles are highest a little posterior of the anterior end.

Po. pseudofoliatus lies closest to *Po. costatus costatus* which it succeeds stratigraphically both in New York and in Belgium.

The two are distinguished, according to Klapper (1971, p.63-4), by the relatively longer blade and greater anterior platform constriction in *Po. pseudofoliatus*.

As discussed by Klapper (1971, p. 63) Po. eiflius can only be maintained if one uses the combination of both platform outline and rostral ridge development in order to distinguish this form from the related Po. pseudofoliatus.

Polygnathus strongi STAUFFER differs from Po. pseudofoliatus in the symmetrical biconvexity of the posterior platform.

Po. pseudofoliatus differs from the Late Devonian Po. dubius (formerly Po. foliatus) in it's wider platform, greater anterior constriction and relatively longer free blade.

The distinction of Polygnathus xylus is discussed under that form.

Occurrence: Sample CR3, Cattewater Road, Princerock; Samples PS3, PS4, Plymouth Power Station, Princerock; Samples 44 (1), 44 (3), Teat's Hill Quarry, Coxside. The form has been considered indicative of the late Eifelian to early Givetian (e.g. Ziegler 1973, p. 375). In Belgium it has been recorded mainly from Upper Couvinian levels and sporadically up to the varcus Zone (in Bouckaert & Steel, 1974).

Polygnathus cristatus HINDE
cf. Plate 29, fig. 9

* 1879 Polygnathus cristatus n.sp. - HINDE, p.366, pl.17, fig. 11.
. 1947 Polygnathus cristatus HINDE - YOUNGQUIST AND PETERSON, p.251, pl.38, fig.11.

. 1957 Polygnathus cristatus HINDE - BISCHOFF & ZIEGLER, p.86-7, pl.15, figs. 1-13, 16; pl. 17, figs. 12,13.
. 1964 Polygnathus cristata HINDE - ORR, p.13-14, text.fig.4, pl. 3, figs.4-8,10.
1965 Polygnathus cristata HINDE - ZIEGLER (b), p.670-1, pl.4, figs.17-23; pl. 5, figs. 1,2,5.
1967 Polygnathus cristata HINDE - ADRICHEM BOOGAERD, p.184, pl.2, fig.41.
. 1968 Polygnathus cristatus HINDE - ORR & KLAPPER, pl.139, figs.1-4, 8,9.
v. 1970 Polygnathus cristatus HINDE - KIRCHGASSER, p.346-7, pl.63, figs. 3,7,10.
. 1971 Polygnathus cristatus HINDE - ORR, p.48, pl.6, figs. 1-2.

Remarks: A single fragment of a broad platform conodont corresponds closely to Polygnathus cristatus in the presence of longitudinally aligned, coarse nodes.

Occurrence: In Plymouth, sample H1, West Hoe. In Germany, the form is known from the base of the Upper hermanni-cristatus Zone to the top of the Middle asymmetricus Zone according to Ziegler 1971 (chart 3).

The "linguiformid" Group

Considered together here are the mainly Middle Devonian suite of polygnathids characterised by a posterior process which is flexed downward and inward and which commonly bears transverse ridges.

Apart from Polygnathus linguiformis subspp., one may include the early Devonian forms Po. dehiscens and Po. foveolatus and the Upper Devonian Po. semicostatus and Po. brevis. Po. cattedowni is newly described from the Middle Devonian.

The description of these forms utilises the distinction made by Bultynck (1970, p.126, footnote 1). This involves the distinction between the posterior process - the tongue, and the anterior platform. Distinction is not in all cases simple since the one sometimes passes imperceptibly into the other, and transverse ridge development is also variable. However, unless qualified, the following descriptions use this distinction.

Polygnathus dobrogensis MIRAUTA 1970, described from North Dobrogea, Hungary, may be a related form. This is very similar to Po. linguiformis but differs in lacking a tongue development. Mirauta's line diagrams (1970, pl.3, figs. 6-11) are very similar to juvenile specimens of Po. linguiformis which also lack a tongue, but because there is no indication of scale, it is not possible to be sure that the form is a synonym.

Polygnathus parawebbi CHATTERTON 1974 has a very similar platform outline but is characterised by a carina which extends (always) to the posterior tip. Po. webbi STAUFFER, and Po. costatus KLAPPER, may have a comparable shape to some forms, but these lack the tongue development.

Polygnathus cattedowni n.sp.

Plate 17, figs.1-5

Diagnosis: A polygnathid with a linguiformid tongue, a high carina which rises well above the flat platform, and a large, anteriorly situated pit with broad and thickened margins.

Description: The platform is almost completely flat and has more or less straight, parallel margins. The anterior inner platform margin is less sharply turned toward the free blade and meets it further anteriorly than the outer. The outer platform tends to be broader than the inner, but both demonstrate a large degree of variation both in width and in ornament. The latter may be absent or consist of marginal nodes, sometimes large and pointed. There are shallow, relatively wide adcarinal grooves. Posteriorly, the tongue is constricted and flexed downward and inward (all to a variable degree).

The tongue is nearly as wide as the platform and tapers to a point in narrow (juvenile ?) specimens but is bluntly rounded in larger forms. A few specimens are laterally twisted terminally. The ornament of the tongue is variable but appears to always involve transverse ridges which are curved so as to be convex posteriorward. The ridges may connect marginal nodes and may be interrupted by an incipient or discontinuous carina; short intercalated ridges and nodes are common marginally.

The free blade is between one third and one half of the total unit length and is deepest at the downward arched anterior end. It bears 7-9 long, pointed denticles, highest and widest at the anterior end (except the anteriormost one) and progressively smaller and lower posteriorly. The denticles tend to be inclined posteriorward. Traced onto the platform, the denticles become increasingly fused and lie lower, but nevertheless remain well above the platform. In the smaller forms, the denticles of the carina are relatively large and tend to persist further posteriorward, whereas the carina of the large forms diminishes progressively and disappears near the beginning of the tongue.

Aborally, a pit is situated a little behind the anterior end of the platform. This has wide and slightly raised lips which extend half the platform width on either side, and posteriorly to platform midlength or beyond. A sharp keel is developed in the posterior part of the unit while anterior of the pit, a furrow extends beneath the blade.

Remarks: The studied material includes two forms: narrow specimens with strong tongue ornament and relatively large carina denticles, and broad forms with a relatively subdued carina. These are thought to be, respectively, juvenile and adult forms, though a gradational series is lacking, and so additional material may indicate otherwise.

This form-species is quite distinctive and confusion with other species is unlikely. *Polygnathus linguiformis* is clearly distinguished by its aboral configuration. *Polygnathus variabilis* BISCHOFF & ZIEGLER is similar in some respects but usually has a strongly reduced platform and no tongue development. One specimen in particular (pl.17, fig.5) puts one in mind of *Polygnathus Kockelianus* BISCHOFF & ZIEGLER with its twisted aspect (possibly exaggerated in this case by deformation), but the two are otherwise quite different. One notes however that Bultynck (1970, fig.16, p.122) considered *Po. linguiformis* to have given rise to *Po.* kockelianus (during Co_{2c} times) and records transitional forms from the later Couvinian. The relative height of the fixed blade / carina is similar to *Po. angustipennatus* (e.g. Bischoff & Ziegler 1957, pl.2.,fig.16).

Occurrence: Samples PS4, Plymouth Power Station, Princerock; Sample 20, Gasworks Quarry, Cattedown. *Polygnathus cattedowni* is found in what is considered to be an *obliquimarginatus* Zone association.

Polygnathus linguiformis HINDE 1879
Plates 18-24 *(partim)*

* 1879 *Polygnathus linguiformis* n.sp.-HINDE, p.367, pl.17, fig. 15.

Original description (cf. Hinde 1879, p.367)-

"Plate elongate, one extremity produced into a tongue-like projection, bending downwards; the sides of the plate curving upwards forming a central trough, from the bottom of which the keel (read carina) rises beyond the sides of the plate and has an expanded crenulated crest (= blade). The anterior tongue-like projection has several strongly marked transverse ridges; the lateral surfaces have a few scattered tubercles."

Discussion: Hitherto, four subspecies of *Polygnathus linguiformis* have been recognised.

In 1965, Wittekindt erected two subspecies (herein given form-specific status - see on). *Po. l. mucronatus* was characterised by the lack of transverse ridge development on a strongly reduced tongue and *Po.l.transversus* was unique in possessing diagonal rows of nodes on the anterior platform. *Po.l.linguiformis* was maintained as corresponding to Hinde's original concept. Philip and Jackson (1967) recognised three subspecies, including the nominate subspecies, and stressed the differing aboral configurations and the mid-platform cross-sections. Because of the very different nature of the former character in the two new forms, Klapper (1969, p. 13,15) elevated *Po. fovealatus* and *Po. dehiscens* to specific level. The trough shaped outer platform noted by Philip and Jackson (text, fig. 3c) remained an essential character of *Po.l. linguiformis*.

In 1970, Bultynck distinguished three morphotypes of *Po.l.linguiformis*: α, β, and γ. These differed in a number of respects, including the degree of curvature of the outer border and relative flatness of the platform.

Po.l.cooperi was established by Klapper (1971) for forms with much flattened platforms, curved outer margins and tongues with relatively irregular transverse ridge development.

The morphological variation of "*Polygnathus linguiformis*" has been repeatedly noted in the literature. Stauffer (1940, p.430) mentioned that the "plate varies in depth and steepness of the sides" and Stewart and Sweet (1956, p.271) wrote of the "considerable variation in length, degree of aboral deflection, and amount of twisting of the posterior process". More recently Polster (1969, p.423-4, text fig.1) demonstrated the variability in the oral configuration of the tongue. Consequently it is to be expected that some subdivision is possible and, as Bultynck (1970) has shown, stratigraphically valuable. However, an analysis of the current form taxonomy of this large group reveals an unsatisfactory situation involving inconsistencies and contradictions, partly unavoidable and inherent in the nature of form taxonomy, but capable of clarification and improvement.

The difficulties stem in part from Wittekindt's original division. The illustrations of his three subspecies indicate that they have very little in common, sharing only a downward and inward deflected posterior portion and a similar aboral pit development. Fortunately the latter character can be used to rule out from further discussion forms which belong to the larger grouping of linguiformids - i.e. *Po. fovealatus*, *Po. dehiscens*, *Po. cattedown* and *Po. semicostatus*. However, given that a carina is developed in some forms of *Po. linguiformis* there is an immediate difficulty in excluding from this concept, forms with similar aboral configurations and platform outlines, e.g. *Po. parawebbi*. In possessing a posterior carina, *Po. l. mucronatus sensu* Wittekindt is perhaps the most atypical subspecies, but to exclude from *Po. linguiformis* forms with carina development would also involve, in part, *Po.l.cooperi*.

Since a flange-like outer platform margin is typical only of the nominate subspecies (and not even all the morphotypes), there remains little general criterion for the group identity in Hinde's original concept. To exclude all forms other than *Po. l. linguiformis* from the species would appear to be rather negative as it doesn't provide for any of the relationships which clearly exist. The Plymouth material includes forms which are considered to be clearly related to *Po. l. mucronatus* sense Wittekindt but which do display distinct transverse ridge development. Consequently, group identity can be maintained by a diagnosis (see on) embracing subspecies which *involve* transverse ridge development.

Within *Po. l. linguiformis*, a similar difficulty is met with. A diagnosis involving flange-like development of the outer platform margin excludes the α morphotype of Bultynck. There appears to be no other character of the present three morphotypes which hold them together and distinguish them from the other forms of *Po. linguiformis*. *Po. l. cooperi* in common with the α morphotype, has a relatively flattened platform and a curved outer border. Having noted this similarity, the author has considered that these two forms should, perhaps, be related, perhaps as separate subspecies. Thus *Po.l. linguiformis* would also have a more precise meaning and, in fact, correspond exactly to Hinde's original diagnosis. Until an examination of further material is possible, one has decided to leave this for the moment. In any case, it would seem appropriate to give *Polygnathus linguiformis* a high taxonomic status in order to provide for the wide range of stratigraphically meaningful variations without resorting to morphotype differentiation of subspecies. A higher taxon relating the "linguiformid" group might also be desirable. For the moment, besides clarifying the relationships within the group, a preliminary step in this direction is necessitated by the concurrence of "subspecies" of *Po. linguiformis* in the same fauna (see Foreword on Taxonomy).

The *Polygnathus linguiformis* Group

This group includes relatively elongated polygnathids with the posterior part of the platform bent downwards and inwards. This part, the tongue, typically bears transverse ridges, though some species embrace forms with carina development. The aboral surface is characterised by a small pit situated in the anterior half of the platform.

Thus defined, the concept embraces the following forms:

Polygnathus linguiformis cooperi KLAPPER 1971
Polygnathus linguiformis linguiformis HINDE 1879
α morphotype BULTYNCK 1970
β morphotype BULTYNCK 1970
γ morphotype BULTYNCK 1970
Polygnathus linguiformis group *nova forma* 1
Polygnathus linguiformis group *nova forma* 2
Polygnathus mucronatus WITTEKINDT 1965
Polygnathus serratus n.sp.
Polygnathus transversus WITTEKINDT 1965

Polygnathus dehiscens PHILIP & JACKSON and *Polygnathus fovealatus* PHILIP & JACKSON are distinguished by their much enlarged basal cavities and, in the latter, the more posterior position of the pit. *Polygnathus cattedowni* n. sp. also has a very different aboral development with a large "swollen" pit near the anterior platform margin. The Famennian homeomorph *Polygnathus semicostatus* BRANSON & MEHL is very similar to some forms of the *Polygnathus linguiformis* group from which it is distinguished most readily in the form of it's basal cavity, this appearing as a slight depression in a thickened part of the keel.

Forms with a sometimes comparable platform outline - *Polygnathus parawebbi* CHATTERTON, *Polygnathus costatus* KLAPPER, *Polygnathus webbi* STAUFFER and *Polygnathus dobrogensis* MIRAUTA are distinguished by their lack of transverse ridge development posteriorly.

Morphological variability. Within the group, morphological variability is great and the above divisions may be somewhat artificial in being based on the extremes of this variability. Also involved is an assessment of the relative significance of the various characters for taxonomic differentiation, always difficult and unavoidably biased toward the material under study. Furthermore, the subdivision here proposed involves form species only. While it is acknowledged that a multielement taxonomy may eventually modify these divisions, it is thought that, particularly from a stratigraphical point of view, they are of value in providing some distinctions within what may be an essentially intergrading complex.

The morphological variation involves the following characters: relative length of the tongue vs. platform; degree of downward and inward deflection of the tongue, particularly as manifest in the course of the outer border; flatness of the platform and obversely the persistence of an outer platform trough and flange development; the ornament and profile outline of the platform margins; degree of constriction of the tongue; degree of taper and oral, lateral and terminal outline of the tongue; development of transverse ridges on tongue; size and height of blade denticles; persistence of carina and position of its termination; relative size of pit and degree of anterior furrowing aborally. The thickness and general robustness of the units if also variable, though this provides one of the most constant features within the recognised subspecies.

In a study of morphological variability it is useful to consider a "central morphotype". *Po. l. linguiformis* γ morphotype is the most suitable such form and the variability considered with respect to this has many parallels with that described by Dreesen & Orchard (1974) for Po. semicostatus; these authors recognised seven trends, in addition to the central type - morphotype 1. Following their enumeration thus:-

Trend 2 involves the irregular splitting of the transverse ridges of the tongue (e.g. pl.19, fig.4; pl.22, figs. 1.5). The course of the ridges may be straight, curved or chevron-shaped.

Trend 3 involves the constriction of the tongue at the posterior end of the platform. This may be exaggerated by lateral flare of the platform (e.g. pl.22, fig.7). It is one of the principal characters of Po. mucronatus (e.g. pl. 23, fig. 5); at the other extreme we have Po.l.cooperi.

Trend 4 involves the fusion of marginal nodes with those of the carina to form irregular transverse ridges (e.g. pl.18, figs. 13,17).

Trend 5 involves the upturning and thickening of an anterior platform margin into a pseudocarinal crest. True rostral development is occasionally developed. The inner platform of Po.l.linguiformis commonly shows this trend, and it is evident on either or both sides in Po. serratus. Po. transversus bears true rostral ridges.

Trend 6 - A pathological disturbance is as probably responsible for those forms in which the carina deviates from its normal course and ends at or near the platform margin, though Po.l.linguiformis α morphotype is characterised by a carina which terminates very near to the inner margin. All members of the Po. linguiformis group have a carina which lies nearer to the inner side.

Trend 7 involves the asymmetrical thickening, widening and flattening of the platform margins. (e.g. pl.19, fig.4; pl.22, fig.8). Lateral thickening of the platform margins is a trend associated with the robust nature of the ornament in Po. mucronatus. The platform of Po.l.cooperi and Po.l.nova forma 1 is flattened without being thickened, whereas that of Po.l. nova forma 2 is both flattened and thickened.

Trend 8 involves the development of an incipient carina on the tongue. Dreesen and Dusar (1974) separate those specimens with a true carina development as a new species (Po.sp.a). In Po.l cooperi, Po. mucronatus and Po. serratus, a carina may be variably developed. (e.g. pl.23, figs. 3,5,6; pl.24, fig.6). A weak incipient carina is sometimes present on the anterior part of the tongue in Po.l.linguiformis (e.g. pl.21, fig.7,8,10), but within the revised concept of this subspecies, no specimen has been observed with a true carina development though such is not excluded.

Another trend in "Po. linguiformis" appears in the literature, i.e. a tendency for the platform to be anteriorly restricted with respect to the laterally flared posterior platform (e.g. Ziegler 1956, pl.7, figs. 11,12; Bryant 1921, pl.11, figs.7,8). Such a platform outline also characterises Po. parawebbi and Po.l.cooperi (see also pl.18, fig.16).

Within the group the proposed division is based on the form of the platform, as distinct from the tongue, and the nature of the passage of the one into the other. The oral configuration of the tongue is not here considered of primary importance, though its relative length is probably significant.

Juvenile specimens of "Po. linguiformis" are fewer in number than adult representatives in the Plymouth faunas. Although they exhibit some variation, all have some features in common. Early growth stages (e.g. pl.18, figs. 3,4,7,8) are characterised by a very small or absent tongue development and consequently a carina which persists to the posterior end. The inner platform is very reduced, and the pit is relatively large and situated near the anterior platform margins.

Klapper and Phillip (1971) and Chatterton (1974) have described the multielement Polygnathus linguiformis. This involves the type 1 apparatus of Klapper and Philip (see Foreword). One will notice that the compound elements illustrated by Chatterton (1974, pl.2, figs. 15-21) are somewhat more "bar like" than those figured by Klapper and Philip (1971, fig.2, p.432).

Polygnathus linguiformis cooperi KLAPPER

* 1971 *Polygnathus linguiformis cooperi* subsp.nov. KLAPPER, p.64 pl.1, figs. 17-22; pl.2, fig.21. (includes synonomy).

Diagnosis: Forms of *Polygnathus linguiformis* in which a flange-like outer margin is not developed. The platform is consequently relatively flattened. The outer margin of the platform meets that of the tongue in a curve. The tongue bears a variable development of transverse ridges.

Remarks: This diagnosis, essentially unchanged from Klapper's original would seem to embrace Po.l.linguiformis α morphotype BULTYNCK since this form is also characterised by a smoothly curved outer border and a platform lacking the flange development of the outer margin. These features may relate the morphotype to *Po.l.cooperi* rather than to *Po.l.linguiformis*, which it would thus be tending toward. Similarly the specimen figured by Klapper (1971, pl.3, figs. 13-14) as *Po.l.linguiformis* γ morphotype ("unusual specimen with a round outer margin") may also be related and one notes that the outer platform margin of this specimen is equally, if not more, flattened than the holotype of *Po.l.cooperi* (Klapper 1971, pl.1, fig.17).

Po.l.linguiformis α morphotype has a limited range within the Belgian Couvinian (rare in Co$_{1c}$; Co$_{2bI-II}$) - i.e. within the *corniger* Zone. It is also recorded from the New York succession by Klapper who found it above his first polygnathid fauna which was characterised, in part, by *Po.l.cooperi*. This latter fauna is considered to be equivalent to the upper part of the *corniger* Zone (see zonation review), so the α morphotype would appear to range above this latter zone in New York; both are, however, low Eifelian/Couvinian species.

Some specimens from Plymouth - from the *varcus* Zone - are also characterised by an evenly curved outer border and relatively flattened platform. These have a greater tongue development however and in any case clearly have a different stratigraphical meaning (see *Po.l.*nova forma 1).

The relatively flattened platform and the evenly curved outer border distinguish *Po.l.cooperi* from most other members of the group. *Po.l.transversus* has a similar platform outline but bears rostral ridges.

Polygnathus linguiformis linguiformis HINDE 1879

Plates 18-22 *partim*

Diagnosis: A subspecies of *Polygnathus linguiformis* with a trough-shaped outer platform resulting from a strongly upturned flange-like margin. The inner platform is relatively flattened at mid length, just anterior of the strongly downward and inward deflected tongue, the outer margin of which is usually clearly differentiated from that of the platform. The carina terminates at, or near the first transverse ridge of the tongue.

Remarks: The above diagnosis gives the subspecies a more precise meaning than hitherto. Of the three morphotypes recognised by Bultynck, the Couvinian forms α and β deviate slightly and are considered as atypical. It may be that they should be given subspecific status and/or related to other members of the *Polygnathus linguiformis* group (see also Remarks under *Po. linguiformis*). If they were, the γ morphotype would be the only representative of *Po.l.linguiformis* and the latter concept could be considered as equal to the former, as it was originally. To take the conjecture further, if *Po.l.cooperi* were to be given specific status, *Po. linguiformis* would be reserved for the *Po.l.linguiformis*. Hinde's original *Po. linguiformis* does appear to correspond to the γ morphotype of Bultynck. The value of such a revision can only be assessed after the study of further material however. For the moment, *Po.l.linguiformis* is retained to embrace Bultynck's morphotypes, only one of which, the γ, is represented in the Plymouth faunas.

The β morphotype BULTYNCK 1970 (p.126, pl.10, figs. 3,6-8) is characterised by a short, broad and somewhat flattened platform, relatively low in the inner anterior part, and a laterally expanded outer platform margin abruptly turned posteriorly toward a short tongue. It has a very limited stratigraphical range in the Belgian Couvinian, being found found only in the interval Co2bII. See under *Po.l.cooperi* for details of the α morphotype.

Po. mucronatus differs in the more symmetrical development of the outer and inner platform margins, in the usually strongly constricted tongue and the occasional persistence of a carina to the posterior tip. *Po. transversus* differs in its flattened platform and in the presence of rostral ridges. *Po.l. cooperi* also differs in the former respect, in the short tongue development and, in common with *Po.l.* nova forma 1, in the evenly curved outer platform margin. *Po.l.* forma 2 has a flatter, more robust platform and tongue and coarse marginal ornamont.

γ morphotype BULTYNCK

Plate 18, figs.1,2,4-6, 9,10,13; Pl.19, figs. 3,7-12; Pl.20, fig.6;
Pl. 21, figs. 1-11; Pl.22, figs.1-6

* 1879 *Polygnathus linguiformis* n.sp. - HINDE, p.367, pl.17, fig.15.
p 1921 *Polygnathus linguiformis* HINDE - BRYANT, p.25, pl.11, figs.1,3,4,6.
1934 *Polygnathus linguiformis* HINDE - HUDDLE, p.95-6, pl.8, figs. 4,5.
1938 *Polygnathus sanduskiensis* n.sp. - STAUFFER, p.438, pl.53,figs.27,36,37.
1940 *Polygnathus sanduskiensis* STAUFFER - STAUFFER, p.430,pl.60,figs.82,89.
. 1956 *Polygnathus linguiformis* HINDE - HASS, pl.4, figs.16,17.
. 1957 *Polygnathus linguiformis* HINDE - BISCHOFF & ZIEGLER, p.92-3, pl.1, figs.1-3,5-9,12-3; pl.16, figs.34, 35; pl.17, figs.1-4.

. 1957 *Polygnathus linguiformis* HINDE - RHODES & DINELY, p.365-6, pl.37, figs. 17-19, 21.
. 1959 *Polygnathus linguiformis* HINDE - HASS, Pl. 50, fig. 11.
. 1960 *Polygnathus linguiformis* HINDE - SPASOV, p. 71, pl.1, figs. 17,18.
1962 *Polygnathus linguiformis* HINDE - REICHSTEIN, pl. figs. 17,18.
. 1962 *Polygnathus linguiformis* HINDE - BARTENSTEIN & BISCHOFF, p.47, pl.3, figs. 18, ? 19, 20.
. 1963 *Polygnathus linguiformis* HINDE - SCHRIEL & STOPPEL, p.87, pl.3, fig.11 (only).
1964 *Polygnathus linguiformis* HINDE - ORR, pl.16,18, pl.4, fig.8.
. 1965 *Polygnathus linguiformis* HINDE - BULTYNCK, p.B68-9, pl.fig.3.
. 1965 *Polygnathus linguiformis* HINDE - ZIEGLER, (a)pl.1,figs. 7,10 (only).
. 1967 *Polygnathus linguiformis* HINDE - CLARK & ETHINGTON, p.62-3, pl.7, fig.10.
. 1967 *Polygnathus linguiformis* HINDE - WIRTH, p.229, pl.22, figs. 3,4.
. 1969 *Polygnathus linguiformis linguiformis* HINDE - PEDDER, JACKSON & ELLENOR, pl.16, fig.16.

. 1969 *Polygnathus linguiformis linguiformis* HINDE - KLAPPER, pl.6, figs.31-34.
. 1970 *Polygnathus linguiformis linguiformis* HINDE γ morphotype nov.
- BULTYNCK, p.126-7, pl.11, figs.1-3,6; pl.12, figs. 2,3,5.
. 1971 *Polygnathus linguiformis linguiformis* HINDE - SCHUMACHER(a), pl.10,fig.11.
. 1971 *Polygnathus linguiformis* HINDE γ morphotype BULTYNCK- KLAPPER,
p.64, pl.2, figs. 18,19,22-27, 30-40; pl.3, fig.15.
. 1971 *Polygnathus linguiformis* HINDE - UYENO & NORRIS, pl.3,fig.10 (only).
. 1971 *Polygnathus linguiformis linguiformis* HINDE - ADRICHEM BOAGAERT,
p. 184, pl.2, fig.44 (only).
. 1971 *Polygnathus linguiformis linguiformis* HINDE- ORR, p.51,pl.5,fig.3.
1974 *Polygnathus linguiformis linguiformis* HINDE - CHATTERTON, p.1472-3,
pl. 1, figs. 20 - 24.

Description: This morphotype is characterised by the flange-like development of the outer platform margin which is regularly upturned so as to produce a trough extending the full length of the platform. In contrast, the inner platform, which is somewhat shorter, is sharply upturned in the anterior half so as to produce a deep adcarinal groove, but flattens out completely posteriorly. Typically, the outer platform margin is straight but may be slightly undulose and/or finely serrate, the ornament, if present, consisting of numerous fine perpendicular ridges which disappear rapidly toward the carina. The inner platform bears a high, usually serrate, ridge anteriorly which tends to lie subparallel to the fixed blade or converges towards it in a fashion suggestive of a rostrum. The flattening of the posterior portion of the inner platform is accompanied by a lateral expansion, occasionally extreme, which produces a convex border. The oral surface of this portion of the platform commonly bears nodes randomly distributed and occasionally fused into irregular ridges.

The flat tongue varies between a third and a half of the total platform and tongue length, and is clearly differentiated from the platform by a downward and inward deflection. The degree of deflection is variable, as is the length, terminal sharpness and regularlity of the taper. In oblique side view, the outer border of the unit is angular at the platform/ tongue junction and this point is often marked by a postero-lateral expansion of the platform immediately anterior of the tongue. This point marks a change in the oral ornament. Transverse ridges appear in the central part of the platform in which the carina is only incipiently developed, if at all.

The course of the inner platform margin changes immediately posterior of the flattened nodose part and thereafter transverse ridges cross the entire width of the tongue. The ridges may be straight, sinuous or chevron shaped and may be continuous or irregular and broken. A true carina is never developed.

A free blade is a little over a quarter of the total unit length and bears up to nine laterally compressed, pointed denticles fused to near their tips. The posterior three, immediately anterior of the platform margins, are typically higher and much larger than the others which diminish in height and size to the anterior end, thus producing, in profile, a regular upward convexity. Traced on to the platform, the denticles decrease in size, height and discreteness posteriorward, extending into the posterior part of the platform (s.s.) as a row of low, fused nodes which always lie nearer to the inner margin, and which terminate at the anterior end of the tongue.

The aboral surface of the morphotype is characterised by a small triangular pit situated at mid-platform length. Posteriorly a sharp keel extends to the posterior tip of the unit, while anteriorly a narrow furrow extends on to the underside of the blade.

Remarks: Thus described, the morphotype has a more precise meaning than previously but nevertheless it remains the most commonly figured form of Polygnathus linguiformis in the literature, as the synonomy list demonstrates (only those forms clearly belonging here are included). The concept still embraces a wide range of morphological variability as is demonstrated in the description and plate figures.

Within the Plymouth material it has also been observed that pseudorostral development in the inner anterior platform, lateral expansion of the posterior inner platform and nodose ornament of this latter part, is more commonly found in high Givetian forms. On the other hand, short transverse ridges may be encountered on the posterior inner platform in low Givetian (and earlier) forms which may also have a sharper, more abrupt tongue deflection on the outer side. It is not known whether these observations are applicable elsewhere.

Polygnathus linguiformis forma nova 1

Plate 23, figs. 6,7

aff. 1965 Polygnathus linguiformis linguiformis HINDE - WITTEKINDT, p. 635-6, pl.2, fig.11.

aff. 1971 Polygnathus linguiformis linguiformis HINDE γ morphotype BULTYNCK - KLAPPER, p. 64, pl.3, figs. 13-14 (only).

Description: Forms in which the platform margins are regularly curved and relatively flattened. Platform ornament consists of strong transverse ridges which extend almost to the carina from which they are separated by shallow adcarinal grooves. The ridges continue on to the tongue which is about equal in length to the platform from which it is not well differentiated. An incipient carina is developed in one specimen.

Remarks: Several specimens from Richmond Walk belong to this new form. They lie close to *Po.l. linguiformis* α morphotype from which they differ in so much as the carina of the latter terminates very near to the inner platform margin. *Po. linguiformis cooperi* differs in having a smaller tongue development and a laterally expanded outer platform margin (similar to the *Po. costatus* group and *Po. parawebbi*) In other respects this form resembles the above two, but it clearly has a different stratigraphical meaning. The specimen illustrated by Klapper has a very short tongue and a much flattened platform (see also Remarks under *Po.l. cooperi*), but one wishes to make the comparison here.

Occurrence: Sample 28, Richmond Walk. *Varcus* Zone association. Wittekindt illustrates a comparable specimen from what may be a comparable level, certainly Givetian at least (Benner Quarry, Bicken - unspecified level). Klapper's specimen is from the Early Middle Devonian.

Polygnathus linguiformis nova forma 2

Pl. 20, figs. 1-5; aff.Pl.18, figs.11,12,17,19

1956 Polygnathus linguiformis HINDE - ZIEGLER, p.103-4, pl.7, figs. 15-18(only).

. 1957 Polygnathus linguiformis HINDE - BISCHOFF & ZIEGLER, p.92-3, pl.1,fig.4; pl.16, figs. 32,33; pl.17, figs. 5,6 (only).

. 1962 Polygnathus linguiformis HINDE - BARTENSTEIN & BISCHOFF, p.47, pl.3, fig. 20 (only).

. 1965 Polygnathus linguiformis linguiformis HINDE - WITTEKINDT, p.635-6, pl.2, figs. 10,12 (non-fig. 11 = Po.l.forma nova 1).

1965 Polygnathus linguiformis HINDE - ZIEGLER (a), pl.1, figs. 8,9.

aff.1969 Polygnathus linguiformis HINDE forma nova - PEDDER, JACKSON & ELLENOR, p.259,266 , pl.16, fig. 17.

aff.1970 Polygnathus linguiformis linguiformis HINDE γ morphotype nov. BULTYNCK, p. 126-7, pl.12, fig. 1 (only).

Description: Forms of Po. linguiformis characterised by an ornament of coarse transverse ridges which extend to near the carina, and which produce a distinctly serrate outer platform margin. The inner platform also bears a coarser ornament. The tongue is turned strongly downward and in mature forms is thick, broad and equal in length to the platform. The transverse ridges of the tongue is not generally marked by a distinct change in the curvature of the outer border but rather by a change in the marginal ornament. Aborally, the pit is relatively large amd the keel widely furrowed anteriorly.

Remarks: A few small specimens from Plymouth (p.18, figs. 11,12,17) are thought to be juvenile forms of this morphotype, which is not a late growth stage of other forms. Included together are specimens from several different stratigraphical levels. It may be that further subdivision will be possible.

In the thickened platform margins and robust tongue, some forms (pl.20, figs. 3,5) approach Po.l. forma nova illustrated by Pedder et al. from the late Givetian. Specimens which are most readily comparable with the Plymouth material from the varcus Zone (pl.20, figs. 1,2,4,7) are those illustrated by Bischoff & Ziegler, Wittekindt, Ziegler and Bartenstein and Bischoff - which mostly come from a comparable level. A single specimen illustrated by Bischoff & Ziegler (fig. 4) comes from the U. Eifelian Gunteröder Lst. but is quite similar. Bultynck illustrated a Couvinian form which is transitional in a sense from his γ morphotype.

Apart from the stronger ornament, this form differs from *Po.l.linguiformis* the nearest member of the group, in the thick tongue with its regular transverse ribs which tend to "curve around" it, the sometimes thickened platform margins, the greater regularlity of the outer platform margin and, in the Plymouth specimens, in the size of the basal cavity and degree of anterior furrowing. (Compare pl. 20, figs. 1 and 6). In this latter respect, they are nearer to *Po. mucronatus* and *Po.serratus* , which differ in the stronger marginal ornament and posterior constrictions of the tongue.

Occurrence: Samples 20, Gasworks Quarry; 32, Mutton Cove.

Polygnathus mucronatus WITTEKINDT

Plate 23, figs. 1,3,4,5

p. 1957 *Polygnathus linguiformis* HINDE - BISCHOFF & ZIEGLER, p.100 pl.17, fig.8; pl.19, fig. 18 (only);(?pl.16, figs.30-31, juv.).
* 1965 *Polygnathus linguifomis mucronata* n.subsp. - WITTEKINDT, p. 636, pl.2, figs. 13,15.
. 1967 *Polygnathus linguiformis mucronata* WITTEKINDT - ADRICHEM BOOGAERT, p.184, pl. 3, fig. 2.
aff. 1967 *Polygnathus linguiformis* ssp.-WIRTH,p.229,pl.21,fig.26;pl.22,figs.1,2.
. 1969 *Polygnathus linguiformis mucronata* .. WITTEKINDT - POLSLER, p. 424, pl.3, figs. 1 - 3.
non 1971 *Polygnathus linguiformis mucronatus* s.l. WITTEKINDT - UYENO & NORRIS, pl. 3, figs. 4a - b (= *Polygnathus parawebbi*).
non 1972 *Polygnathus linguiformis mucronatus* WITTEKINDT- MCGREGOR & UYENO, pl. 5, figs. 22,23.

Description(revised): A rather robust linguiform polygnathid with coarse marginal platform ribs separated from the carina by narrow adcarinal grooves. The tongue is strongly constricted and reduced to a variable degree. A carina may be developed posteriorly.

Description: The platform is thick and marginally upturned. The sides are steep and strongly serrate. Coarse ridges extend perpendicular to near the carina from which they are separated by narrow adcarinal grooves. The latter do not deepen greatly anteriorly but are rather fairly constantly developed throughout. The outer platform is both wider and longer than the inner platform but both sides are otherwise similar in development. The outer platform margin, traced from the anterior end, is more or less straight initially but is strongly deflected inwards at a point taken to be the beginning of the tongue. The inner margin is more regular, but the constriction of the tongue is usually evident.

The tongue is between one third and one half the total (platform and tongue) length and tends to be very narrow, pointed and rather thick with an oval cross section. The tongue development is rather variable: in forms with more strongly reduced tongues, the latter has subparallel sides, while in others the taper is stronger. Typically, the tongue lacks continuous transverse ridges but bears a carina. However, other forms, here included, bear regular transverse ridges development and intermediate types with both a reduced carina and interrupted ridges are represented.

The free blade is about equal in length to the tongue and bears 6 - 9 sharp, oval (in cross section) denticles, which are longest and highest at the mid length of the blade. Traced posteriorly, the fixed blade continues as a low fused carina which may extend to the posterior tip with little change. Alternatively, the carina may be represented posteriorly by a row of discrete nodes, which may or may not extend onto the tongue, or, in an incipient form, as a narrow longitudinal ridge. By virtue of the greater development of the outer platform, the carina tends to lie nearer to the inner margin.

Aborally, a thick lipped, slightly asymmetrical pit is situated a little anterior of the platform (minus tongue) mid -length. A sharp keel extends posteriorly, whilst anteriorly, a relatively wide furrow with (in common with the pit) somewhat raised edges, can be traced onto the underside of the blade.

Remarks: Wittekindt's subspecies is herein raised to specific level for reasons mentioned previously. The concept of <u>Po. mucronatus</u> is also broadened to include forms both with and without a carina, and conversely without and with continuous transverse ridge development posteriorly. This deviates somewhat from Wittekindt's concept of the form but brings together specimens, from the same population, which are clearly related in their general robust nature, platform ornament and in their cross section. These characters, perhaps surprisingly, are the most constant features of the units whereas the carina development and general outline is not. (see also remarks under Polygnathus linguiformis).

Occurrence: Sample 36, Mount Wise; cf. Sample 28, Richmond Walk. This subspecies has a limited range in the uppermost Givetian. Wittekindt recorded it from the varcus and transversus Zones, and the other examples are from comparable levels in Europe. According to Ziegler (1971, Chart 2), the (unspecified) "subspecies" is indicative of the upper part of the varcus Zone.

In Spain: Probe 112, 115, Quinto Peal (Wirth)
Sample CAL4, Gildar-Montó area, Cantabrian Mts. (Adrichem Boogaerd)
In Austria: Probe 5/104A, E/124A, Findenig, Carnic Alps (Polsler)
In Germany: Meggener Lagerkalk, Rhenish Schiefergebirge (Bischoff & Ziegler)

Polygnathus serratus n. sp.

Pl. 23, fig.2; Pl.24, figs.6,7

Diagnosis: Polygnathid with general linguiformid shape but differing from other forms in possessing coarse tuberculate marginal ornamentation separated from the carina by adcarinal grooves which deepen anteriorly. There is no trough development. A posterior carina may be developed.

Description: Unit is typically elongate and narrow with a clear distinction between an anterior, somewhat flat, platform and a posterior downward and inward deflected tongue. The platform is narrowest at the anterior end where it's margins are strongly denticulate, relatively steep and separated from the fixed blade by deep adcarinal grooves. Posteriorly, the platform margins flatten out and the outer platform in particular is much broader reaching its maximum development a little anterior of the abrupt deflection which marks the beginning of the tongue. The ornament of the outer platform is marked by elongate nodes or tubercles tending to ridges which lie a little in from the margins and are separated from the carina by shallow adcarinal grooves in the posterior part of the platform. The same is true, though to a lesser extent, for the inner platform.

The tongue is between a quarter and a third of the complete (platform and tongue) length. This is narrow and tapers progressively to a point. The ornament varies from somewhat irregular transverse ridges with no carina extension beyond the platform (pl. 24, fig.7), through a form (pl.23, fig. 2) with transverse ridge development punctuated by an incipient carina, to a form (pl.24, fig. 6) in which the carina continues uninterrupted as a row of fairly discrete nodes and in which there is no cross-ridge development, but rather irregular marginal nodes (if at all).

The blade(only preserved in one specimen) is deepest anteriorly and bears seven sharp denticles of approximately uniform size and height (except for the anteriormost) fused to near their tips. They decrease slightly in height as the blade is traced in a posterior direction onto the platform, but drop abruptly to be continued as a carina one third the distance along the platform.

Aborally, these forms have a diamond shaped pit which is situated in the anterior half of the platform at a point below the change in height of the fixed blade. Posteriorly a sharp keel continues to the posterior end of the unit, while anteriorly a groove extends from the pit onto the underside of the blade.

Remarks: In common with Po. mucronatus included together here are forms with very different oral configurations of the tongue. However, the three figured specimens have almost identical outlines and platform ornament and are clearly related.

Po. serratus lies closest to Po. mucronatus from which it is distinguished by the form of the posterior platform. The margins of the latter are upturned and sculptured into coarse ridges, whereas the posterior platform of the former is relatively flat beneath the tubercles and nodes which lie in from the margins and rise above them.

Occurrence: Sample 36, Mount Wise.

Polygnathus transversus WITTEKINDT
aff. Plate 24, fig. 5

* 1965 Polygnathus linguiformis transversus - WITTEKINDT, p.636-7, pl.2, figs. 16-18.

. 1969 Polygnathus linguiformis transversus - POLSLER, p.424, pl.2, figs.9-11.

Diagnosis: A linguiform polygnathid differing from all others in the development of one or more diagonal rows of nodes in the anterior part of the platform.

Description: The unit is flat, evenly arched and slightly turned inward posteriorly. A tongue is not clearly differentiated since the outer border tends to be evenly curved. The anterior platform bears one or more diagonal rows of partially fused nodes rising above the surrounding platform and equal in height to the fixed blade with which it/they make an angle of about 30°; deep adcarinal notches separate these. The rest of the platform carries an ornament of coarse ridges and elongate, partly fused nodes lying roughly perpendicular to the carina from which they are separated by shallow and narrow adcarinal grooves. The posterior part of the unit typically bears uninterrupted transverse ridges, but a carina may be variably developed.

The free blade is typically short and bears sharp, mostly fused denticles of equal height. Traced onto the platform, they become relatively lower and increasingly fused. Posterior of the rostral development, their continuation is marked by a row of fairly discrete, rounded nodes. This carina typically persists to the first transverse ridge of the posterior part of the unit, but may extend beyond.

The aboral surface of this form bears a small pit with weakly raised edges situated anterior of the midline of the (whole) platform. A keel is developed to the sharp posterior tip, and anteriorly a narrow furrow extends to beneath the blade.

Remarks: Po. transversus is herein given specific status (see Po. linguiformis). The single specimen from Mount Wise differs from the holotype in three respects: the development of a posterior carina, the longer free blade, and in the thicker lipped pit and furrow. Furthermore only one row of nodes is present on the anterior platform. Wittekindt's figured specimens have one on each side of the carina, whilst Polsler illustrated a form with a total of three, so this is a variable character, though, by definition, the most diagnostic. Polsler's specimens (from the Austrian Carnic Alps) also appear to have a longer carina development than the types, and by analogy with Po. mucronatus and Po. serratus (as herein described), the presence of a posterior carina may perhaps be considered as a variable character. The aboral configuration is not unlike other members of the Po. linguiformis group from Plymouth. The relative length of the blade is less easy to incorporate into the concept of the species, hence the aff. designation.

The aboral character of the Plymouth specimens is very similar to that of Po. tuberculatus with which a relationship probably exists (see Remarks under the latter). In fact the specimens of Po. tuberculatus (= Po. bryanti) figured by Wittekindt are not dissimilar from this form particularly in the carina development. Although Po. tuberculatus also has diagonal ridges anteriorly, the character of the platform and ornament is much more robust, and since the Plymouth specimen is more readily related to "Po. linguiformis" than the "typical" specimens of Po. tuberculatus (compare Pl. 24, figs. 4,5,6), it is included here.

Occurrence: Sample 36, Mount Wise.

Po. transversus was recorded by Wittekindt from the uppermost Givetian, where it was restricted to the zone named after it. The specimens of Polsler (2 specimens from his samples 5/104A (?) and E/124, Finlenig) and the Plymouth form come from comparable levels. It is not recorded from North America.

Polygnathus latus WITTEKINDT

Plate 9, figs. 2,3

* 1965 Polygnathus lata n.sp. - WITTEKINDT, p.635, pl.2, figs.6,8,9.

Diagnosis: The platform is about one and one half times long as broad. In lateral view the unit is strongly arched; the posterior part is turned inward slightly. The outer margin is strongly convex, the inner margin is convex in the anterior half but straight posteriorly. The platform is broadest anterior of the midpoint.

The oral surface of the platform is covered with strong, closely spaced, transverse ribs which are separated from the carina by narrow, shallow adcarinal grooves. The anterior platform margins are curved downwards and meet the blade, (?) further to the anterior in the inner side.

The free blade is very short and increases in height anteriorly. It bears denticles, oval in cross section, fused except for their small pointed tips. Traced onto the platform, there is a slight inward deflection of the carina at a point,posterior of which it is represented by more discrete, rounded nodes, which extend to the posterior end of the platform. Aborally, a small pit is located about midway between platform midlength and the anterior end. It is rounded and has raised margins with extend anteriorly on either side of a furrow; a keel runs posteriorward.

Remarks: Only two specimens have been found and although both are incomplete they are placed here because of their distinct nature and close similarity to Wittekindt's types. Since both lack the blades and posterior platforms the description of these characters are based on the figured types. The two specimens appear to represent a juvenile and adult growth stage, but are otherwise very similar.
Occurrence: Sample NP2, Neal Point (2 specimens). This appears to be a very rare form. Wittekindt found only 10 specimens, his holotype coming from the Benner quarry, Bicken. No other record appears in the literature, though Bultynck recorded one specimen of Polygnathus cf. Po. latus from the Menil section in Belgium (in Bouckaert & Street 1974, E. p.15, sample 57).

Wittekindt (1965, tbl. 1, p.626) recorded Po. latus from, and restricted to, his eiflia Zone = Lower obliquimarginatus Zone. Bultynck's specimen comes from a comparable level.

Polygnathus aff. Po. latus WITTEKINDT
Plate 9, fig. 1

Remarks: A single broken, but complete specimen has been retrieved which is quite unique in several respects. In particular, the platform bears an ornament of irregularly sinuous, discontinuous and bifurcating, transverse ribs which in some cases extend to, and join the nodes of, the carina. At the posterior end of the platform, the ridges deteriorate into irregularly connected nodes. In profile, the thin blade is triangular in shape due to the strong posteriorward inclination of the indistinct denticles, these being almost entirely fused. Furthermore, the anterior platform development is strongly asymmetrical.

In the general shape and strongly arched nature of the platform, the relative length and height of the free blade, the carina and adcarinal groove development (in part), and in the aboral configuration, the specimen is considered to lie close to Po. latus.

Occurrence: One specimen from sample 20, Gasworks Quarry, Cattedown, Plymouth.

Polygnathus n.sp.aff.Polygnathus porcillus STAUFFER
Plate 9, fig. 6

aff. 1940 Polygnathus porcillus n.sp. - STAUFFER, p.430, pl.60, figs. 86-8.
. 1970 Polygnathus linguiformis linguiformis HINDE - BULTYNCK, p.125-7, pl.10, figs. 1,2,5.

Diagnosis: This form is characterised by an inward turned posterior tip and an asymmetrically developed platform, the outer side of which is larger and extends further posteriorly and anteriorly. The platform margins bear a nodose ornament separated from the carina by adcarinal grooves. The anterior end of the platform lies perpendicular to the blade which is between a third and a half the total unit length. A relatively large basal cavity is situated near the anterior end of the platform.

Remarks: This form differs from Po. angustipennatus s.l. in the asymmetry of the platform and in the posterior deflection. It is excluded from Po. linguiformis because of the clear carina extension and lack of a tongue development, the nature of the anterior platform margins, the general form of the blade and the relatively large basal cavity. (compare with pl.18, same magnification).

The (sub) triangular shape of the platform and the posterior extension of the carina in particular are considered to relate it to Po. angustipennatus s.l.

Bultynck (1970, fig.16, p.122) considered Po. angustipennatus to have evolved from Po. linguiformis during the mid Couvinian (Co_{2h}). He figures specimens of Po. l. linguiformis (pl.10, figs. 1,5) which lack a tongue development and he doesn't exclude the possibility of them being the first stage in such a development. The author has seen numerous examples from the Zwischenschicten Limestone of Blauer Bruch, Germany (kockelianus Zone). The author considers that these forms represent a distinct stage in the phylogeny of Polygnathus and deserve specific status.

Stauffer 1940 described Polygnathus porcillus n.sp. from the clay above the Cedar Valley Limestone of Austin, Minnesota. The blade of his types are missing, but the form of the platform is very similar. An examination of these may reveal that this is the same form.

Occurrence: Sample 39, Richmond Walk (South). The form would appear to be mid to late Eifelian in age. Stauffer's fauna was derived and mixed.

The Polygnathus robusticostatus Group

Klapper (1971) recognised this group to include the intergrading series of Polygnathus robusticostatus, Po. angusticostatus, Po. angustipennatus, and Po. intermedius.

The group embraces units with a relatively straight axis and a variable but symmetrical, platform development. This is large and broad in Po. robusticostatus while at the other extreme, it is only incipiently developed in Po. intermedius. The carina terminates at the posterior end of the platform in Po. robusticostatus but extends backward of this point in other forms. Platform ornament is generally coarse and separated from the carina by adcarinal grooves. The free blade is usually between a third and a half unit length, and the pit is located between the midpoint and the anterior end of the platform.

The author is in agreement with Klapper in considering that some of these forms would fall into synonomy in a broader concept of intraspecific variation. The difficulty in confidently assigning illustrated forms from the literature into one particular category makes one question the value of retaining all these form species. The author has considered the feasibility of a three fold division of the group which may be more readily maintained.

Polygnathus robusticostatus - forms with large platform developments and a carina which terminates at the end of the platform.

Polygnathus angustipennatus sensu lato-to embrace all those forms with a relatively small, but distinct platform development and a carina which clearly extends posterior of the platform.

Polygnathus intermedius - to include those specimens having only an incipient platform development.

Before such a scheme is adopted, the author feels it is very important to assess the ontogenetic development within this group. This has not been possible with the material herein studied, but illustrated specimens would seem to indicate that the ontogeny of an individual probably involves at least two of the recognised form species. The multielement association of these forms may also involve more than the single morphotype.

Polygnathus angustipennatus BISCHOFF & ZIEGLER *sensu lato*
Plate 9, figs. 8,10,cf. 4

* 1957 *Polygnathus angustipennata* n.sp. - BISCHOFF & ZIEGLER, p.85, pl.2, fig.16; pl.3, figs. 1-3.

. 1962 *Polygnathus angustipennatus* BISCHOFF & ZIEGLER - BARTENSTEIN & BISCHOFF, p.47, pl.3, figs. 22-4.

1965 *Polygnathus angustipennata* BISCHOFF & ZIEGLER - BULTYNCK, p. B67, pl. fig.5.

. 1965 *Polygnathus* n.sp.A - SCHRIEL & STOPPEL, p.88, pl.3, figs. 5a-d.

. 1965 *Polygnathus angustipennata* BISCHOFF & ZIEGLER - WITTEKINDT, p. 631-2, pl.1, fig. 14.

1965 *Polygnathus angusticostatus* n.sp. - WITTEKINDT, p.631,pl.1, fig.15 (only).

1966 *Polygnathus angustipennata* BISCHOFF & ZIEGLER - BULTYNCK, p.B198-9, pl.1, figs. 1-6.

. 1966 *Polygnathus angustipennata* BISCHOFF & ZIEGLER - PHILIP, p. 157, pl.1, figs. 15,16.

1966 *Polygnathus* sp.nov.A - PHILIP, p.158, pl.1, figs.1-2 (only).

1969 *Polygnathus angustipennatus* BISCHOFF & ZIEGLER - SKALA, p.260, pl.1,fig.9.

1969 *Polygnathus angustipennatus* BISCHOFF & ZIEGLER - PEDDER, PHILIP & JACKSON, pl.15, figs. 10,12.
1970 *Polygnathus angustipennata* BISCHOFF & ZIEGLER - BULTYNCK, p.124, pl.17, figs. 3-6, 9,10; pl.18, fig.1,non-pl.17,figs.7-9=Po.intermedius.
1971 *Polygnathus angustipennatus* BISCHOFF & ZIEGLER - SCHONLAUB,pl.4,figs.7,8.
1971 *Polygnathus angustipennatus* BISCHOFF & ZIEGLER - UYENO & NORRIS, pl.3, fig. 2.
1971 *Polygnathus* n.sp.A SCHRIEL & STOPPEL - UYENO & NORRIS, pl.3, figs.3a-c.
1971 *Polygnathus* sp.A - SCHUMACHER (a), p. 62, pl. 10, figs. 5,6.
1971 *Polygnathus angustipennatus* BISCHOFF & ZIEGLER - KLAPPER,p.65,pl.3,fig.27.
1972 *Polygnathus angusticostatus* WITTEKINDT - BOOGAARD, p.6, pl.1, fig. b.
1972 *Polygnathus angusticostatus* WITTEKINDT - ORR, p.47, pl.4, figs. 12-17.

Description: Specimens of *Polygnathus angustipennatus* are characterised by a relatively small platform beyond which a carina clearly extends posteriorly. The platform bears marginal nodes which tend to become transversely elongate in specimens with larger platforms. Platform margins may be biconvex but are commonly more or less straight and parallel before turning fairly sharply to meet the carina at a point between two and five denticles in front of the posterior end of the unit.

The platform margins are weakly to (more commonly) strongly upturned so as to produce deep adcarinal grooves, and an often strongly denticulate profile. The platform is centred on a point posterior of the unit midlength. The denticulation clearly changes at a point above the anterior end of the platform. Posterior of this point, the carina denticles are larger than those of the free blade to the anterior. The denticles of the blade tend to become higher anteriorly to a maximum height at the third or fourth denticle before the anterior end, though such a blade development is not always evident. The free blade is usually about half the total unit length.

Aborally, a pit, relatively larger in smaller specimens, is located at the anterior end of the platform or a little posterior of that point.

Remarks: This above description embraces some specimens previously assigned to *Polygnathus angusticostatus*. The latter and *Polygnathus angustipennatus* have often been confused in the literature because of the inadequate criterion for their separation. Admittedly gradational, the two forms have only been reliably separated on the basis of the relative length of the free blade. This is here considered inadequate because of the dependence of this character on the extremely variable platform development, and the otherwise identical form and variation demonstrated by the specimens previously separated on that basis. The relative length of the free blade is also variable in *Po. robusticostatus* which is separated on the basis of the larger, more strongly ornamented platform and the absence of a posterior carina extension. Furthermore, in *Po. robusticostatus*, the change in the size of the "blade" denticles often comes at a point posterior of the front of the platform, rather than at the front. (see Remarks under *Po. robusticostatus* gp.)

The high anterior blade denticles have been cited by some authors (e.g. Klapper 1971, p.65) as a distinguishing character of *Po. angustipennatus*. Bischoff & Ziegler's types are thought to be extreme in this respect since not all specimens have such a blade development and some specimens previously assigned to *Po. angusticostatus* (e.g. Orr 1972, pl.4, figs. 12-14) also have such a blade.

Only three specimens of *Po. angustipennatus s.l.*. have been found in the Plymouth Limestone. None are well preserved and each is unique in some respect, but all conform with the above description.

The specimen illustrated on Plate 9, fig. 8 is very similar to that from the Timor Limestone figured by Pedder *et al*. (1969, pl.15, fig.10) and, to a lesser extent, to that from the Detroit River formation figured by Orr (1972, pl.4, figs. 15-17).

Occurrence: Sample 10 (cf.),Cattedown Quarry; Samples D15,D16,Drakes Island. The form is considered to date from the late Eifelian : *bidentatus* and *Kockelianus* Zones (Wittekindt 1965 , p.627).

Polygnathus tuberculatus HINDE

Plate 24, figs. 1-4

* 1879 Polygnathus tuberculatus n.sp. - HINDE, p.366, pl.17, figs. 9,10.
. 1921 Polygnathus tuberculatus HINDE - BRYANT, p.25-6, pl.12, figs. 7-9.
. 1928 Polygnathus tuberculatus HINDE - HOLMES, p.18,pl.7, fig.18 (cop. HINDE 1879).
p. 1933. Polygnathus tuberculata HINDE - BRANSON & MEHL, p. 148, pl.11, fig. 2 (non fig.9 - Ancyrodella rotundiloba) (p.cop. HINDE 1879).
. 1934 Polygnathus bryanti n.sp. - HUDDLE, p.97-8, pl.8, figs. 9-10.
? 1956 Polygnathus sp.A - HASS, p.18-19, pl.4, fig. 19.
1965 Polygnathus bryanti HUDDLE - WITTEKINDT, p.632-3, pl.1, fig. 22-25.

Diagnosis: Polygnathid with a massive, broad, strongly tuberculate platform. Anteriorly, deep adcarinal grooves separate the blade from high, subparallel ridges.

Description: Platform tends to be irregularly subelliptical in outline, being broadest at midlength. Near the posterior end, the platform is pinched so as to produce an incurved tongue-like projection. Anteriorly, the platform margins taper progressively to meet the blade at equal points on the inner and outer sides. In plan view, the axis is gently curved anteriorly and strongly incurved in the posterior half of the platform. In side view, the thick unit is quite strongly arched, the plane of the platform changing abruptly at midlength.

The blade, which is deepest at the anterior end, is equal to between one third and one half of the overall unit length. There are about eight stout blade denticles, fused to near their pointed tips and decreasing in height progressively posteriorward. The latter continues as a mostly fused carina to the middle of the platform, at which point it is represented by discrete nodes equal in height to the adjacent ornament. Posterior of this point the carina may be represented by a row of tubercles which, however, may be obscure and discontinuous in large specimens.

The oral surface of the platform is ornamented by nodes and tubercles which coalesce to form ridges,these tending to converge toward the centre. In the anterior part of the platform the oral ridges (one or two on both sides) lie subparallel to the blade and are separated from each other by deep grooves, particularly adcarinally.

Aborally, a small, thick lipped, diamond shaped pit is situated half way between platform mid-length and the anterior platform margin. Posterior of the pit, a keel is developed but in large specimens, as in the carina development, this may be indistinct at the posterior end. Anteriorly, the keel is strongly grooved, a wide furrow extending forward under the blade.

Remarks: The deep adcarinal "notches" in the anterior part of the platform may be responsible for what Hinde originally described as "a partially detached lobe on either side of the central line". This is not to be confused with Ancyrodella. Hinde figured two specimens, one in oral view and the other in aboral view (1879, pl.17, figs.9 and 10 respectively), and he noted that "the surface of the reverse side is smooth". Subsequently, Branson & Mehl (1933, pl.11, fig.9) figured the "un-numbered co-type" of Hinde, which is not clearly the same specimen; their specimen has two well developed secondary keels and is clearly an Ancyrodella. However Bryant (1921) was in "no doubt" that Hinde's fig.10 was the reverse side of "Polygnathus rotundilobus"(= Ancyrodella rotundiloba), though it is difficult to understand why Hinde failed to note the presence of keels.

Polygnathus bryanti HUDDLE was erected on the minor distinction of the lateral deflection of the "anterior" (read posterior) portion of the plate and carina; in other respects this is identical.

The specimens described and figured by Hinde, Branson & Mehl, and Huddle were all large and closely comparable with the illustrated Plymouth specimens. These are characterised by a carina which does not extend to the posterior tip but rather is developed only in the anterior two thirds of the platform. No young growth stages of this form had been figured in the earlier works and thus some doubt surrounds the designation by Wittekindt of his figured specimens to this taxon. Wittekindt's specimens all bear a carina extending the full length of the platform and separated from the coarse tuberculate ornament by adcarinal grooves. The latter deepen anteriorly and separate tuberculate ridges from the blade, as in the holotype; the units also conform to the type species in other respects. Thus it seems reasonable to suppose that the posterior carina development was lost in the later growth stages and that Wittekindt's specimens (though the magnification is not given) are the only earlier stages hitherto figured. A single, smaller and poorly preserved specimen from Plymouth supports this.

The relationship of Polygnathus tuberculatus with Polygnathus linguiformis group has been indicated by Wittekindt (1965, p.633). The juvenile forms of the two are similar and it is suggested that the latter gave rise to Po. tuberculatus possibly by way of forms such as Po. serratus. A comparison of the aboral configurations supports this conjecture.

Some specimens of Polygnathus ordinatus (Bischoff & Ziegler 1957, pl.18, figs. 25, 26, 28) have comparable platform shape, robustness and strong anterior adcarinal grooves and ridges. They apparently differ only in the nature of the ornament which is predominantly nodose, the nodes tending to be aligned antero-posteriorly. Bryant's type of Po. ordinatus (1921, pl.10 figs. 10,11) is very much slimmer and more elongate.

Occurrence: Sample 36, Mount Wise, Plymouth.

Polygnathus tuberculatus has been recorded previously only from the Genundewah Limestone of New York (Hinde, Bryant), the Lower Albany Shale of Indiana (Huddle) and in Germany, from the upper part of Wittekindt's transversus Zone (Syring and Benner Quarries). It thus has a limited range about the Middle/Upper Devonian boundary.

The Polygnathus varcus Group

Klapper, Philip & Jackson (1970) presented a revision of the Polygnathus varcus group based on the study of the type material of Stauffer (1940) and comparative material from N. America, Germany and Australia. As noted by these authors (p.651), much of literature in which "Po. varcus" has been identified includes illustrations of an inadequate nature for confident inclusion in synonomy lists.

Definition: Polygnathids with narrow parallel-sided platforms with deep adcarinal grooves extending the full length. The platform which may be smooth or may bear low nodes, generally terminates a little anterior of the carina. In lateral view the blade is long and subquadrate.

Discussion: Within the group, species have been differentiated by the relative size of the platform, platform ornament, position of the basal cavity, and the nature of the anterior terminations of the platform. Klapper et al.

have used these criteria to distinguish four forms. Polygnathus varcus STAUFFER and Po. rhenanus KLAPPER, PHILIP & JACKSON are characterised by smooth, unornamented platforms whereas Po. xylus STAUFFER and particularly Po. timorensis KLAPPER, PHILIP & JACKSON have platforms bearing marginal nodes.

The Plymouth material includes many forms which apparently belong in the varcus group, including over 250 simple polygnathids from a locality at Mount Wise (plates 11-16, partim). A major difficulty arising in the study of this fauna, is the lack of a complete blade in many of the specimens. Hence distinctions based on the relative platform/blade length are not always possible to make. However, discrete free blades are common in the fauna and these, together with a comparison of platforms of specimens with and without attached blades (the blades of some illustrated forms became detached prior to photography) support the validity of the distinctions made below.

The majority of specimens from Mount Wise have a platform which bears marginal ornament. Strictly, this would exclude assignment to either Po. varcus or Po. rhenanus, though it must be stressed that, in the studied material, development of platform ornament appears to be in part ontogenetic since few juveniles bear distinct nodes. Furthermore, specimens assigned to these two form-species, including the types, tend to be rather small, whereas the Mount Wise forms are on the whole, relatively large and robust; there is the possibility of ecological adaptation . This withstanding, adherence to the scheme of Klapper et al. provides Po. timorensis as the most suited concept to describe the majority of the polygnathids. Po. xylus is characterised by steep anterior trough margins, unlike most of the forms.

The basal cavity is always at the anterior end of the platform. Variation in its position from the junction of the platform and blade to one at a point just posterior of this, also appears to be ontogenetic. No studied juvenile has a pit in the latter position, and larger specimens demonstrate its progressive (apparent) migration posteriorly. Klapper et al. seem to have recognised this in regard to Po. xylus, but for no other. In the adult specimens, apparent variation in this character arises from the variation in relative positions of the anterior platform margins and in the degree of lateral flare of the cavity lip (as well as in the orientation of the illustrated specimens).

Platform symmetry, specifically that of the anterior trough margins (see Klapper et al. 1970, p.652) is a highly variable character in the studied material. Po. varcus and Po. rhenanus are distinguished by the opposition of the inner and outer margins in the former, and the greater lateral and anterior extent of the outer margin of the latter. Po. xylus has steep, usually opposed margins. These three polygnathids also have opposed geniculation points. Po. timorensis in contrast to the three above forms, is a relatively broad concept in these respects since, by definition, it embraces all variations in these characters, though the holotype (Klapper et al. 1970, pl.1, figs. 7-10) has opposed anterior platform margins and longitudinally staggered geniculation points.

In Po. varcus and Po. rhenanus, the free blade is about two thirds the total unit length, in Po. xylus and Po. timorensis it is about a half the total length. In many of the ornamented Plymouth specimens, the blade is nearer the former in this respect. There is some evidence that the relative length of the blade also varies during ontogency (see remarks under Po. timorensis Po. xylus).

The Plymouth material would appear to warrant the separation of an additional form species within the varcus group,but suggests a redefinition of other forms is necessary. The original intention of Klapper and others' revision was to facilitate a more refined definition of the varcus Zone. Though the distinctions here proposed are based principally on the fauna from a single locality, the study has necessarily involved an appraisal of the variability within a single population and thus, these distinctions are thought to have some substance and this may be reflected in such a refinement.

Thus, Po. timorensis is redefined so as to only involve forms with asymmetrically developed posterior platforms, but otherwise it remains essentially the same. Po. biconvexus n.sp. is introduced to accommodate forms with strong platform ornament but with symmetrically developed posterior platforms and a relatively longer blade. Po. rhenanus is maintained for small smooth forms with asymmetrical anterior platforms but the possibility of later growth stages being outside the present diagnosis is considered to be a real one. Forms herein called Po. aff. Po. rhenanus may be such expressions.

Similarly, Po. varcus is based on relatively small specimens. Large ornamented forms from Plymouth in association with small ones which correspond to Klapper et al.'s diagnosis suggest that the concept should be broadened, at least to include subdued platform ornament in later growth stages.

As presently defined, Po. rhenanus and Po. varcus differ only in the relative symmetry of the anterior trough margin development. Insomuch as Po. timorensis, and Po. biconvexus, involve variation from a symmetrical to an asymmetrical anterior platform development, one is forced to question the validity of the distinction based on this character. The occurrences of Po. rhenanus and Po. varcus (see Klapper et al. 1970, p.655, 658) are not the same, though both occur 0-0.12 m. below the lower of two Terebratula pumilio beds at Syring Quarry near Odershausen, Germany, and, if the concepts are broadened as discussed, at Mount Wise, Plymouth. In this latter fauna, some forms are apparently transitional.

Polygnathus biconvexus n.sp.

Plate 14, figs. 1-3,5,7,8,10; Pl.15,figs.5,6;Pl.16,figs.6,8

Diagnosis: A long, slim polygnathid with a biconvex posterior platform, and a more or less straight carina. Anterior trough margins are usually asymmetrically developed and the geniculation points are generally not opposite. The platform margins bear a distinctly nodose ornament. The free blade is about two thirds the total unit length. The basal cavity is situated at the anterior end of the platform.

Remarks: This form is characterised by the presence of coarse marginal nodes which tend to become elongated into ridges lying perpendicular to the carina. The platform margins are consequently relatively thickened.

The anterior trough development varies from near symmetrical (e.g. pl.4, fig. 1) to strongly asymmetrical (e.g. pl.4, fig. 10) and the geniculation points may be opposite (e.g.pl.4, fig.10) or not (e.g. pl.4,fig.8).

The posterior platform margins are straight and parallel initially and then evenly curved and tapered to the pointed posterior tip. Occasionally the platform margins at the posterior tip are flattened and smooth (e.g. pl.15, figs. 5,6).

The blade may be composed of upright or inclined denticles demonstrating the usual variability of the varcus group. The carina may terminate in front of the posterior end of the platform (pl.14, fig. 8) but usually extends beyond it.

Polygnathus biconvexus differs from Po. varcus and Po. rhenanus in the presence of strong platform ornament and often in the form of the anterior platform. Po. timorensis differs in the asymmetry of the posterior platform and the relative length of the blade. Po. xylus is also distinguished by the latter character and by the form of the anterior platform margins.

Forms designated Po. aff. Po. biconvex are characterised by a rounded posterior platform tip and a carina which terminates anterior of that "point". The specimen illustrated on pl.11, fig. 7 shows a tendency toward this type of platform.

Occurrence: Sample 36, Mount Wise.

Polygnathus rhenanus KLAPPER, PHILIP & JACKSON

Plate 9, figs. 18,19

. 1970 Polygnathus varcus STAUFFER - PEDDER, JACKSON & ELLENOR,pl.16,fig.4(only).
* 1970 Polygnathus rhenanus n.sp. - KLAPPER, PHILIP & JACKSON, figs.654-5, pl.2, figs. 13-15, 19-22.

Diagnosis: 'A form with a short, asymmetrical platform which is smooth except for the carina and a node which may be present at the opposed geniculation points. The blade is about two thirds the total unit length. In all growth stages the basal cavity is at the junction of the free blade and the anterior end of the platform.

Remarks: The specimens confidently placed here are small and probably juvenile. These strongly resemble the specimen illustrated by Pedder et al. (1970,pl.16, fig. 4) as well as the holotype figured by Klapper et al. (1970, pl.2, figs.19-22) which are also relatively small specimens. All are characterised by a rather short platform which in lateral view appears to grow out from the sides (as indeed it does) in such a way as to leave a deep posterior keel, the oral compliment of which, i.e. the carina, extends beyond the platform posteriorly. The posterior platform is symmetrically developed but may vary a little in shape, as may the form of the blade (discussed by Klapper et al. 1970, p.658). The unornamented platform and the position of the basal cavity have been considered as diagnostic features of this form.

In Po. timorensis and Po. biconvexus the basal cavity is typically situated posterior of the blade/platform junction but in small specimens it is always at the junction, and thus the apparent posterior migration is ontogenetic. Klapper et al. make a point of noting that the position of the basal cavity in large specimens of Po. rhenanus is also at the junction.

Unfortunately, the Plymouth fauna which includes the typical Po.rhenanus has yielded few larger growth stages for study. From Mt. Wise, some relatively large specimens come close to Po. rhenanus (pl.11, fig.4; pl.12,fig.2), but these are in a fauna dominated by ornamented forms and completely lacking small specimens comparable with the "typical" Po. rhenanus. Some specimens occur in this fauna which conform in all respects other than in their ornamented platforms. (e.g. pl.11, fig. 3). Whether or not large specimens of Po. rhenanus bear a platform ornament (especially when viewed by a stereoscan) is a question which is left open for the time being. It may be that Po. rhenanus is essentially a "small specimen concept". Until this is established or refuted those specimens which do deviate in the ways discussed are placed under Po. aff. Po. rhenanus.

Occurrence: Sample 25, Richmond Walk; BF3 near Botus Fleming. See Klapper et al. 1970, p. 655 for other occurrences.

Polygnathus aff. Po. rhenanus
Plate 11, figs.1,3-5,10; Pl.12, figs.1,2,9;
pl.16, figs. 9

. 1971 Polygnathus varcus STAUFFER - ORR, p.53, pl.5, figs. 4-8.

Remarks: Included here are those forms with an asymmetrical anterior trough development and blades about two thirds the total unit length. They differ from Po. rhenanus in three ways: the geniculation points are not always opposite, in larger specimens the basal cavity lies a little behind the anterior platform margin, and the posterior platform margins may bear a nodose ornament.

The relative position of the geniculation points varies a great deal in Po. timorensis and also in Po. biconvexus. There is also some indication that they do in Po. rhenanus and Po. varcus (q.v.) as well (see Klapper et al. 1970, pl. 2, fig. 22, 14, 3) though Klapper and others (p. 654, 657) state that they are opposite.

The specimen illustrated by Orr is very similar to some of the Plymouth material and also illustrates the difficulty of applying Klapper et al. scheme.

Occurrence: Samples BF2, BF3, Lane section, near Botus Fleming; 28, Richmond Walk; 36, Mount Wise.

Polygnathus timorensis KLAPPER, PHILIP & JACKSON

Plate 12, figs. 7,11; Pl .13, figs. 1-11; Pl.14, figs.4,6; Pl .15, figs.1-4,7,8

? 1965 Polygnathus xyla STAUFFER - WITTEKINDT, p.642, pl.3, fig.18 (only).
1970 Polygnathus timorensis sp.nov.- KLAPPER, PHILIP & JACKSON, p.655-6, pl.1, figs. 1-3, 7-10, text fig. 2 (see synonomy).

Diagnosis (revised): A long, slim polygnathid with an asymmetrically developed platform. The outer margin is weakly to strongly convex outward, as is the carina, whereas the inner margin is straight or only weakly curved. Platform margins usually bear a nodose ornament. Anterior trough margins and geniculation points are variable in development and in their relative position. The blade is between a half to three fifths total unit length.

Remarks: The amended diagnosis excludes forms with symmetrically developed posterior platforms previously embraced by the rather broad concept of Polygnathus timorensis sensu Klapper et al. Included are forms with relatively short and broad platforms and longer blades which were not embraced by the original diagnosis. Two morphotypes seem to be represented, both having characters which distinguish them from other members of the varcus group, i.e. an asymmetrically developed posterior platform, ± a sinuous carina.

In contrast to some other members of the varcus group, Po. timorensis embraces extreme variability in the development of the anterior platform (compare pl.13, fig.10 and pl.14, fig. 6).

Very small specimens of Po. timorensis (pl.12, figs. 7,11) are thought to have rather flat platforms and incompletely developed carinae, yet display a tendency to asymmetry in the posterior platform outline. (Note also the position of the basal cavity).

Large forms (e.g. pl.13, fig.10) and ones which correspond closely to the holotype (Klapper et al. 1970, pl.1, figs. 7-10), have a relatively long and narrow platform. The anterior margins are commonly opposite on either side of the blade, though the outer margin may lay further anteriorward. In such forms, the outer trough margin may be strongly flared laterally and, in side view, long and gently dipping. The inner trough margin is generally relatively short and steep, but may be equally developed. The geniculation points are generally not opposite (Klapper et al. 1970, p.655), but this too is a variable character. Posterior of this point, the inner margin tends to be straighter than the outer which is typically convex outward in the middle portion of the platform, in part due to the greater constriction of the outer platform at the geniculation point. The posterior third of the platform is tapered, more strongly on the outer side, and terminates in a pointed posterior tip which is commonly twisted laterally.

The oral surface of the platform posterior of the geniculation points bears marginal nodes separated from the central carina by deep and narrow adcarinal grooves which extend to near the posterior tip and are deepest at the anterior end where the margins are highest and steepest.

The free blade is about one half of the total unit length and bears numerous denticles which are of a variable nature. In some specimens the denticles are of equal size whilst others have smaller denticles irregularly intercalated; the anteriormost denticles are generally smaller. A common tendency of the blade denticles is for them to be longitudinally inclined in either direction. Traced onto the platform, the fixed blade continues as a low mostly fused carina which may deteriorate into rounded nodes posteriorly. The course of the carina may be straight, but is more commonly curved or sinuous, reflecting the irregular platform margins. The carina persists to a point a little in front or a little behind the posterior end of the platform.

Aborally, the basal cavity lies at the anterior end of the platform or a little behind that point. A keel runs posteriorly, and anteriorly there may be a slight furrowing of the underside of the blade.

Forms which are generally smaller overall have relatively shorter platforms and blades about three fifths the total unit length (e.g. pl.13, figs. 1-9, 11). The geniculation points in these forms are often opposed and the anterior trough margins are typically asymetrically developed, but again the variation is sometimes pronounced. The posterior platform is characteristically asymmetrical with both the outer margin and the carina being convex outward. This development is considered to relate these forms to the larger, aforementioned specimens in which these characters are not so pronounced. Hence it is suggested that the ontogeny of Po. timorensis involves longitudinal growth of the platform in later growth stages to produce the relatively longer, slimmer forms.

Specimens referred to Po. aff. Po. timorensis (pl.16, figs. 2-4) have asymmetrical posterior platforms and carinae which pass posteriorward into irregular ridges and nodes covering the full width of the platform. One specimen (pl.16, fig.2) is unique in having an adcarinal node and a high carina. Such forms as these must be viewed with the suspicion their rarity warrants, but it is tempting to speculate on the reasons for such extreme oral ornament. One will only note here that the fauna from which they come include such highly ornamented forms as Po. tuberculatus. Insomuch as the evolution of conodonts appears to have involved the lateral spread of the units in order to accommodate more oral ornament (Lindstrom 1964, p.15) these forms may, perhaps, be considered as advanced.

Occurrence: Sample 36, Mount Wise; NP15, Neal Point, near Landulph (small morphotype only).

Polygnathus varcus STAUFFER

Plate 12, figs. 3,4, aff.6

* 1940 Polygnathus varcus n.sp. - STAUFFER, p.430, pl.60, figs. 49,55. (fig. 53 - Polygnathus sp.indet., free blade broken).

1970 Polygnathus varcus STAUFFER - KLAPPER, PHILIP & JACKSON, p. 657-8, pl.2, figs. 1-3, 23-25. (See synonomy).

non1972 Polygnathus varcus STAUFFER - ORR, p.53, pl.5, figs. 4-8, (= Polygnathus aff. Po. rhenanus).

Diagnosis (revised): A slim polygnathid with a symmetrical platform one third the total unit length. Anterior trough margins are equally developed and the geniculation points are generally opposite. In small specimens the basal cavity is at the junction of the free blade and the platform, in larger specimens it may lie posterior of that point.

Remarks: Klapper et al. (1970, p.658) have stated that the short symmetrical platform and the characteristic position of the basal cavity (at the blade/platform junction) remain constant throughout growth. The "large specimen" they illustrate (1970, pl.2, figs. 23-25) is still relatively small compared with their Po. timorensis. A small specimen from Mount Wise (pl.12, fig. 4) conforms exactly to Klapper and others' diagnosis. Large associated specimens (pl.12, fig.3) differ in having subdued marginal ornament, and basal cavities a little posterior of the junction; the geniculation points are not necessarily exactly opposite. It is thought unreasonable to separate these forms, hence the revised diagnosis.

Some other forms (e.g. pl.12, fig.6) are very similar but have a slightly asymmetrical anterior platform development, one which is not, however, as strongly so as in Po. rhenanus. Such forms could, perhaps, be considered as transitional. It is not excluded that there is complete morphological gradation between Po. varcus and Po. rhenanus. (See remarks under Po. varcus group).

Occurrence: Sample 36, Mount Wise.

Polygnathus xylus STAUFFER

Plate 9, figs.9,11,12; Pl.10, fig.13; Pl.11,fig.8

* 1940 *Polygnathus xylus* n.sp. - STAUFFER, p.430-31, pl.60, fig.54,66,72-4
(non fig. 42,50,65,67,69,78,79 = *Polygnathus* sp. indet).
non 1962 *Polygnathus xyla* STAUFFER - BARTENSTEIN & BISCHOFF, p.48-9, pl.4, figs.8,9.
non 1965 *Polygnathus xyla* STAUFFER - BULTYNCK, pl. figs. 4a-b.
1966 *Polygnathus xylus* STAUFFER - BULTYNCK, p. B199-200, pl.2, figs. 1,2.
(non fig.3 = *Polygnathus pseudofoliatus*).
? 1965 *Polygnathus varca* STAUFFER - ZIEGLER(a), pl.1, fig.6 (side view only).
1970 *Polygnathus xylus* STAUFFER - KLAPPER, PHILIP & JACKSON, p.659,60,62,64,66;
pl.1, figs. 4-6, 11; pl.2, figs.4,5,7-12,16-18. (includes synonomy).
1970 *Polygnathus xyla* STAUFFER - BULTYNCK, p.131, pl.15, figs. 2,8
(non fig. 5 = *Polygnathus pseudofoliatus*).
? 1971 *Polygnathus xyla* STAUFFER - SCHONLAUB, pl.4, fig.11 (side view only).
1971 *Polygnathus xylus* STAUFFER - UYENO & NORRIS, pl.3, figs. 8a - c.
1974 *Polygnathus xylus* STAUFFER - UYENO, pl.4, figs. 6,8.

Diagnosis: A slim polygnathid with a smooth or (subdued) nodose platform margins. The platform is about one half the unit length and has steep anterior trough margins and opposed geniculation points. The basal cavity is situated at the anterior end of the platform in small specimens, and posterior of this point in larger specimens.

Remarks: The diagnosis is after Klapper *et al.* (1970), who also discussed the forms they placed in synonomy and the author agrees with most of their conclusions. As noted by Klapper *et al.* *Po. xylus* is distinguished from *Po. varcus* and *Po. rhenanus* by the relatively longer platform and the steeper anterior trough margins. Both characters also differ in *Po. biconvex* and the latter character differs in *Po. timorensis*. Uyeno 1974 (p.41) has noted that some juvenile specimens exhibit a blade slightly less than two thirds the length of the unit, i.e. relatively longer than is typical.

Polygnathus strongi STAUFFER is not considered to be synonomous. This differs in the strong anterior constriction of the platform, the posterior biconvexity of the flare, and the flatter, nodose posterior platform.

Juvenile specimens of Po. xylus and Po. pseudofoliatus differ in that the latter lacks deep adcarinal grooves posteriorly and the outer platform is also slightly more expanded laterally. Klapper et al. (1970, p.666) note that small specimens of Po. pseudofoliatus may possess a blade that increases noticeably in height toward the anterior end and one infers that in this respect they differ from Po. xylus. Elsewhere (p.653) these authors cite the posteriorly decreasing height of the blade denticles as a distinguishing character of Po. xylus (in comparison with Po. decorosus) The blade of Po. xylus would thus seem to be intermediate. Po. decorosus also differs in its sagittate platform outline and distinct marginal nodes.

The specimens figured by Downs and Youngquist (1950) as Po. decorosus (pl. 87, fig.3,4), Po. xylus (pl.87, figs. 15,16), Po. decorosus (figs.23-26) and Po. stainbrooki (pl.87, figs. 19,20) appear to show a continuous transition from, respectively, a parallel sided platform, through slightly sagittate and strongly sagittate platform outline to the extreme in which the carina is also sinuous.

All the specimens studies are from the M. Devonian, and most are small. They share steep anterior trough margins, deep adcarinal grooves, a narrow, parallel-sided platform, and a basal cavity situated at the junction of the platform and blade. Platform margins are smooth (pl.9, fig.11) or bear subdued nodes (pl.9, fig.12). The single large specimen (pl.11, fig.8) illustrated also shows the above characters, but in addition has the strongly denticulate anterior platform margins, which characterise many forms from the Plymouth Limestone (e.g. see pl.11, and also Po. pseudofoliatus), and a blade which is clearly higher anteriorly. This latter specimen is similar to the one illustrated by Klapper et al. (1970, pl.2, figs. 10-12) from the Timor Limestone, Australia, and also to that figured by Ziegler 1965a and included by Klapper et al. in synonomy with Po. timorensis.

Occurrence: Samples 20, Gasworks Quarry, Cattedown; 28, Richmond Walk; 32, Mutton Cove; cf. 44 (3), Teat's Hill Quarry, Coxside; cf. BF3, Botus Fleming; cf. NP15, Neal Point.

Polygnathus aff. Polygnathus xylus

Plate 9, fig.13; Plate 10, fig.16

Remarks: These forms differ from Po. xylus in the asymmetrical development of the platform. The anterior trough margins are steep but strongly staggered and similarly the geniculation points are not opposite. The blade is not regularly developed as in Po. xylus but, where preserved, is similar to that sometimes demonstrated by Po. varcus and Po. rhenanus, i.e. an alternation of large and small denticles (e.g. pl.10, fig.16).

The specimens included here are all small and have a basal cavity situated at the platform/blade junction. Forms such as these may be the precursor of the later Givetian Po. varcus s.l. and may well have provided many of the records of "Po. varcus" from low Givetian levels.

Occurrence: Samples CR3, Cattewater Road; PS4, Princerock Quarry.

Form genus:	Spathognathodus BRANSON & MEHL 1934
Type species:	Spathodus primus BRANSON & MEHL 1933

In multielement terms, Spathognathodus has been described as belonging to a type 1 apparatus of sensu Klapper & Philip 1971. A spathognathodontan is the P element in the multielement genera Ozarkodina and Pandorinellina, which differ in their A_3 elements.

Spathognathodus bidentatus BISCHOFF & ZIEGLER

Plate 7, figs. 5,9,cf.8

* 1957 Spathognathodus bidentatus n.sp. - BISCHOFF & ZIEGLER, p.114-5, pl.6, figs. 8-10,12,13 (nonfig.11 = Po. intermedius).

. 1962 Spathognathodus bidentatus BISCHOFF & ZIEGLER - BARTENSTEIN & BISCHOFF, p.47-8, pl.3, figs. 25-7.

. 1965 Spathognathodus bidentatus BISCHOFF & ZIEGLER - WITTEKINDT, p. 642, pl.3, figs. 16, 20 - 22.

. 1966 Spathognathodus bidentatus bidentatus BISCHOFF & ZIEGLER - BULTYNCK p. B201, pl.2, figs. 11, 12.

. 1966 Spathognathodus bidentatus BISCHOFF & ZIEGLER - PHILIP, p.159,pl.2,fig.1-3.

. 1969 Spathognathodus bidentatus BISCHOFF & ZIEGLER - POLSLER, pl.2, figs.1-2.

- . 1969 . *Spathognathodus bidentatus bidentatus* BISCHOFF & ZIEGLER - PEDDER, JACKSON & ELLENOR, pl.15, figs. 3,6,7.
- . 1970 *Spathognathodus bidentatus* - BULTYNCK, p.133, pl.18, figs. 7,8.
- . 1971 *Spathognathodus bidentatus* BISCHOFF & ZIEGLER - SCHONLAUB, pl.4, fig.9.
- . 1972 *Spathognathodus bidentatus* BISCHOFF & ZIEGLER -BOOGAARD , p.7, fig.5.
- . 1972 *Spathognathodus bidentatus* BISCHOFF & ZIEGLER - ORR, p.57, pl.4, fig.11.

Diagnosis: Spathognathodid with a symmetrical, elongate basal cavity developed in and extending under, the posterior half of the unit. In oral view this is triangular, being broadest at unit midlength and tapering posteriorly. The oral margin is characterised by small, fused denticles in the anterior half and longer, more discrete denticles posteriorly. In the latter direction, the oral edge slopes downwards.

Occurrence: Sample 44 (3), Teat's Hill Quarry, Coxside; 19 (1), Gasworks Quarry Cattedown; PS4 (cf.), Princerock Quarry. The form is rare in the Plymouth Limestone. In Germany, Ziegler 1971 (Chart 2, p.253) records *S. bidentatus* from the base of the mid Eifelian *bidentatus* Zone throughout the remainder of the L.M. Devonian and sporadically in the Lower *obliquimarginatus* Zone. In Belgium the form appears in Co_{2d} (equivalent to the upper part of the *kockelianus* Zone) and ranges through the low Givetian. In Australia, Pedder *et al.* 1969 recorded it almost into their *varcus* Zone (but see Devonian Conodont Zonations).

Spathognathodus bipennatus BISCHOFF & ZIEGLER *s.l.*

- * 1957 *Spathognathodus bipennatus* n.sp. - BISCHOFF & ZIEGLER, p.115-6,pl.21,fig.31.
- 1957 *Spathognathodus* cf. *bipennatus* n.sp. BISCHOFF & ZIEGLER, p. 116, pl.6, figs. 7a - b.
- . 1965 *Spathognathodus bipennatus* BISCHOFF & ZIEGLER - ZIEGLER(a), pl.1,fig.11.
- . 1966 *Spathognathodus* sp.cf. *bipennatus* BISCHOFF & ZIEGLER - PHILIP, p. 159, pl.3, fig. 12.
- 1966 *Spathognathodus* cf. *bipennatus* BISCHOFF & ZIEGLER - BULTYNCK, p. B202-4, pl.1, fig.13; pl.2, figs. 4-8.
- . 1967 *Spathognathodus bipennatus* BISCHOFF & ZIEGLER - ADRICHEM BOOGAERD, p. 186, pl.3, fig.21.

. 1969 Spathognathodus bipennatus BISCHOFF & ZIEGLER - PEDDER, JACKSON & ELLENOR, pl.16, figs. 8,10.

1970 Spathognathodus cf. bipennatus BISCHOFF & ZIEGLER - BULTYNCK, p. 134, pl.18, fig.9; pl.19, figs. 1-5.

Diagnosis : Spathognathodid with a broad, flat basal cavity strongly expanded laterally so as to project far beyond both sides of the unit. The oral surface of the posterior two thirds of the unit is broad and bears marginal rows of nodes. The anterior blade is high and fused.

Remarks: This distinctive form-species demonstrates variation in the oral configuration of the platform. Bischoff & Ziegler's types (from the Givetian) are characterised by a central furrow or trough separating the marginal nodes. A single Eifelian specimen described by these authors (S. cf. bipennatus) lacked such a trough. Philip (1966, p.159) described S. sp.cf. bipennatus from the Moore Creek,Limestone of New South Wales which he considered intermediate insomuch as the oral ornament was composed rather of transverse ridges which faded medially. Similarly, Bultynck (1966, 1970) described Couvinian representatives which had a limited trough development restricted to the middle part of the unit. The latter author favoured a confer designation because he felt that it might be possible to distinguish between Couvinian and Givetian forms. A single (Givetian) specimen from Plymouth (subsequently lost) differs from all the aforementioned forms insomuch that the platform is icriodid-like. There are three distinct rows of nodes. The median row clearly represents the posterior extension of the blade, and is composed of six laterally elongate nodes followed posteriorly by four discrete nodes. Each lateral row consists of three low nodes, followed posteriorly by five - six short ridges and finally two marginal nodes. The posteriormost quarter of the platform is smooth and somewhat undulatory in profile.

There may well be grounds for stratigraphically meaningful morphotype distinction but the lack of material and the variation of the aforementioned illustrated specimens suggest that, for the moment, these are best kept together under a broad concept of the form species.

Material: Sample NP 15, north of Neal Point on the Tamar, S.W. Cornwall.

Spathognathodus brevis BISCHOFF & ZIEGLER

Plate 7, figs. 1-4, 6,7; cf. 14

* 1957 *Spathognathodus brevis* n.sp. - BISCHOFF & ZIEGLER, p.116-7, pl.19, figs. 24, 27-9.

. 1957 *Spathognathodus* ? sp. RHODES & DINELY, p.367, pl.37, fig.11.

. 1962 *Spathognathodus brevis* BISCHOFF & ZIEGLER - BARTENSTEIN & BISCHOFF, p. 50, pl.4, figs. 23-6.

. 1965 *Spathognathodus brevis* BISCHOFF & ZIEGLER - WITTEKINDT, p. 643, pl.3, figs. 23-4.

. 1968 *Spathognathodus brevis* BISCHOFF & ZIEGLER - SCHULZE, p.222,pl.20,fig.29

. 1969 *Spathognathodus brevis* BISCHOFF & ZIEGLER - PEDDER, JACKSON & ELLENOR, p.15, figs. 4,5.

. 1969 *Spathognathodus brevis* BISCHOFF & ZIEGLER - POLSLER, pl.2, figs.3,4.

1970 *Spathognathodus brevis* BISCHOFF & ZIEGLER - SEDDON(a), p.748,pl.16, figs. 11, 12.

. 1971 *Spathognathodus brevis* BISCHOFF & ZIEGLER - UYENO & NORRIS, pl.13, figs. 5 a-b.

Diagnosis: A short spathognathodid with a subquadrate basal cavity situated at the posterior extremity of the unit. The posteriormost denticle is largest and posteriorly inclined.

Description: The blade is short and more or less rectangular in profile, being about half as high (measured to the denticle tip) as long. There are usually between nine and twelve denticles most of which tend to be of a similar size though smaller intercalated denticles may be developed.
The posteriormost denticle is subcircular in cross-section and tends to be larger than the others and to be inclined in a posterior direction.
The denticles of the blade anterior of the basal cavity are oval in cross section, upright at midlength and tending to be inclined anteriorward in that direction. The denticles are fused to within one quarter of the total unit height.

The basal cavity is subquadrate in outline, is distinctly flared laterally, and extends slightly beyond the back of the blade; it is twice as wide as long. The axis of this basal cup tends to be set at an angle to the blade axis in such a way that it extends further backward on the outer side.

The posterior edge is straight, the lateral edges rounded, and the anterior edges straight, the latter meet the blade in a curve at a point one to three denticles in from the end. A furrow extends along the aboral side of the unit in front of the basal cavity.

Remarks: This is an unusual but distinctive spathognathodid. Variation involves the number of denticles (e.g. see Bischoff & Ziegler 1957, pl.19, fig.24) and the inclination and size of the posteriormost cusp. The specimen figured by Seddon (1970, pl.16, figs. 11-12) has an unusually large cusp. Uyeno (1974, p. 42, pl.7, figs. 11-13; pl.8, figs. 4,9) described Spathognathodus cf. S. brevis from the Waterways Fromation of Alberta. This differs from typical representatives of the form - species in the development of a small denticle posterior of the largest one; thus the cavity may be in front of the posterior end. Herein possibly lies the basis of meaningful morphotype differentiation. The specimen referred to as S. aff. S. brevis (pl.7, fig.14) is not well preserved but all the denticles other than the largest appear to be inclined anteriorly; the latter is, atypically, large and upright. This single specimen comes from supposed high Eifelian strata. It may be possible in the future to differentiate stratigraphically useful morphotypes, though at the moment the form is herein considered to have a greater stratigraphical range than hitherto thought.

S. triangularis BENDER is a Triassic homeomorph which differs in the aboral profile.

Occurrence: Samples 25, Richmond Walk; 36, Mount Wise; 32, Mutton Cove; 50, Coxside; CR3 (aff.)., Cattewater Road, Princerock; BF3, near Botus Fleming.

Both Wittekindt (1965, taf.1, p.627) and Ziegler (1970, chart 2) considered Spathognathodus brevis to range from the base of the varcus Zone. Pedder et al. (1969, p.263, 265) record it from the Timor Limestone in association with Po. pseudofoliatus, S. bipennatus and Po. eiflius, an association here considered to be older than the varcus Zone, i.e. more suitably placed in their kockelianus - robusticostatus assemblage zone (Pedder et al. fig.2, p.245; sect.6, unit 10; section 5, unit no.9). S. brevis ranges up to the Middle Po. asymmetricus Zone (Bischoff & Ziegler 1957, taf. 4).

Spathognathodus planus BISCHOFF & ZIEGLER

Plate 8, figs. 1,2,4, aff.7

* 1957 Spathognathodus planus n.sp. - BISCHOFF & ZIEGLER, p.117, pl.19, figs.34,35.

. 1965 Spathognathodus planus BISCHOFF & ZIEGLER - WITTEKINDT, p.643-4,pl.3,fig.30.

. 1969 Spathognathodus planus BISCHOFF & ZIEGLER - PEDDER, JACKSON & ELLENOR, pl.16, figs. 5,7.

. 1971 Spathognathodus planus BISCHOFF & ZIEGLER - ORR, p.57, pl.4, fig.23.

Diagnosis: Spathognathodid which is gently arched in profile and bears closely spaced, inclined denticles, small in the posterior half and larger anteriorly.

Remarks: The Plymouth material is identical to the German types. The form differs from S. obliquus WITTEKINDT only in bearing more numerous and closer spaced denticles. One specimen has small intercalated denticles in the anterior part of the unit (S. aff. S. planus). The variability of this form needs further study.

Occurrence: Samples 36, Mount Wise; BF3, Botus Fleming. In Germany, S. planus is first recorded within the lower obliquimarginatus Zone and thereafter it persists throughout the Givetian.

PART III

FACIES AND ENVIRONMENTS

Introduction

On the subject of Devonian carbonate complexes and their facial analyses there have been a multitude of investigations. Many deal with the broad distinctions between 'non-reefal carbonate buildups' and 'true reefal, rigid-skeletal frameworks' and the macro-and micro-facial divisions within them. Such works have relied heavily upon differences in faunal association and the relationship of form to environment, particularly with respect to stromatoporoids and corals. The distribution of reef building organisms is not central to this study, but wherever possible, observations have been made on the gross morphology and general disposition of the organisms, especially in relation to other aspects of the sediments, and particularly to the conodont faunas. Much work remains to be done on the large group of calcified organisms which contribute to the limestone mass, particularly the denroid tabulates, stromatoporoids, bryozoans and algae, between which the distinctions are often obscure.

As far as the conodont distributions are concerned, a biofacial approach is relatively new, but the distributional anomalies, which clearly exist, are considered to reflect primary environmental preferences. These are examined and discussed, in relation to inferences from other fossil and sedimentary distributions, though much work remains to be done in relating these.

In so much as the work of the palaeoenvironmentalists are relevant, their classifications are reviewed and discussed in relation to Plymouth situation, and possible comparisons therein. In particular, the work of Krebs (1968a,b,1969,1971) in Germany, and Lecompte (1961, 1968) and Tsien (1968, 1971) on the Belgium reefs are considered.

The Carbonate environment

Krebs and Mountjoy (1972, p.295) discussed the disparity in the nomenclature of carbonate bodies and made a primary distinction between the carbonate platform and the carbonate buildup. The carbonate complex of Krebs (1967, p. 4819) involved both the bank or Schwelm facies and the reef complex and appears to be equivalent to both the carbonate platform (or foundation platform) and the carbonate buildup of Canadian authors. The open (non-rigid) skeletal communities of Jamieson (1969, p. 1308) can be considered as corresponding to the former, though his rigid skeletal-frame accretions appears to be a somewhat narrower concept than the carbonate buildup (see also Cook *et al.* 1972, footnote 7, p.440). Martin (1972) has noted the need for a uniformity of expression, and introduced four new terms.

Krebs (1968a, p.297-8) distinguished three types of "*Massenkalk*" in the late Middle and early Upper Devonian of the eastern Rhenish Schiefergebirge of Germany, namely the Bank type (*Schwelm* facies), Reef type (*Dorp* facies) and Cap type (*Iberg* facies).

The *Schwelm* facies is an association of stromatoporoids and corals not possessing the ecological potential to build a rigid, wave resistant structure. The *Dorp* facies ("true-reefs"- Krebs 1971, p. 46) is distinguished by the growth of organisms forming "biogenic structures" that rise gradually over their surroundings resulting in a differentiation of the morphologically rising structure into fore-reef, reef-core, and back-reef areas. The *Iberg* facies, which is developed in response to slow subsidence, usually consists of "gray sparry calcite-cemented brachiopod crinoid limestones" often interfingering with the surrounding "flinz" facies (=stagnant, anaerobic shales); there is no back-reef time equivalent.

It appears that both in Germany and in Western Canada the *Schwelm* or bank facies is the initial development on top of which the *Dorp*, or reef facies may, or may not, develop. The Iberg facies is of local significance only. "The facies terms do not describe time - stratigraphic intervals, but apply to rock stratigraphic units. Each facies may develop in different stratigraphic levels ..." (Krebs 1971, p.46).

In his study of Belgian carbonate bodies, Tsien (1971, p. 121) has adopted a terminology as follows:-

> An organic reef - a massive limestone body which is built directly by organisms.
>
> A bioherm - an isolated, convex arched organic reef completely surrounded by shaly sediments.

A biostrome - a tabulate or layered organic-reef; in later stage of this reef development, the growth of mounds on the barrier reef edge at the shelf margin may separate an open marine development and a restricted marine environment. Bank or reef-bank - all wave resistant limestone bodies which result from the activities or organisms, from wave transportation and from sedimentation.

Reef-complex - the ensemble of reef limestones and their related sedimentary rocks.

It appears that the organic reef sensu Tsien is comparable with the very restricted use of 'reef' by some authors, and is incorporated within the Dorp facies of Krebs. The bank of Schwelm is probably equivalent to the reef bank sensu Tsien and though the biostrome is similar in some respects, it does appear to have a narrower meaning. Again, the differentiation of the latter into relatively open and restricted environments by the growth of "mounds" would seem to have a parallel in the Dorp facies of Krebs.

The 'Reef-complex' of Tsien appears to be equivalent to the 'carbonate complex' of Krebs.

The Belgian workers have also used a scheme based on bathymetry which is worthy of note. Lecompte (e.g. 1961, 1968, 1970) established and used to great effect the scheme, i.e. Zone profonde, Zone quiscente, Zone sous-turbulent, Zone subturbulent, and Zone turbulent, in order of descreasing depth, each of which is characterised by particular facies (in the original sense of the word - see Erben 1964, p.61). indicative of shelf or basinal environments. Thus a gradual buildup of a reef bank with decreasing depth and increasing turbulence is characterised by particular sediments and by associations of particular organisms in the same way as the transition from Schwelm to Dorp facies and subsequent subfacial differentiation has been recognised in Germany. An advantage of the bathymetric expression of tectonic evolution lies in the more direct appreciation of both the vertical and lateral facies variations. In the same way the tendency of the Belgian students is to talk in terms of transgressive and regressive phases, of relatively stable phases and of transitional phases, each characterised by events which may include 'reefal' developments.

"The precise rhythm of the Hercynian movement which controlled the different facies is much better marked by the organisms than by the sediments" (Tsien 1971, p. 135-6).

The distribution of organisms across various reef-complexes has been demonstrated in many publications (e.g. Krebs 1971, fig. 7, p. 47; Krebs and Mountjoy 1972, fig. 7-8, p. 305). There is much debate over the significance of some forms, the environmental tolerance and the value which can be attached to the absence or presence of others. The question of whether of not stromatoporoid accumulations formed wave resistant, rigid frameworks, is yet to be answered, but this is outside the scope of the present study.

Jamieson (1969, p. 1327-1337) has reviewed the various interpretations applied to the Devonian 'reef' - faunas, whilst Tsien (1971, p. 136-145) presented his views on the whole spectrum of contributing organisms.

"The Devonian carbonate complexes and shelf carbonates of Middle Europe reflect the palaeogeographic differentiation of the Variscan Geosyncline" (Krebs 1971, p. 51). Krebs distinguished five types of carbonate complexes (A, B_1, B_2, B_3, C) in Central Europe, these being variously developed on the external shelf on the Brabant Massif, within the Rhenish Trough on local (volcanic) highs, and on the internal shelf of the south. Krebs and Mountjoy (1972, p. 297) also distinguished five types (1-5) of carbonate bodies, seemingly comparable to A, B_1, B_2 and C plus one more.

Type A (=1) are isolated carbonate complexes involving bank and reef developments built on submarine volcanic rises within a basin or geosyncline.

Type B_1 (=2) are isolated carbonate complexes (bank and reef) at the shelf or platform margin.

Type B_2 (=3) are isolated reefs on banks within the external shelf or platform.

Type $\underline{B}_3$ are biohermal reefs, (see above). These are developed only on the southern flank of the Dinant Syncline in Belgium (stages F_{2d}, F_{2h}, F_{2j}).

Type C (= 5) are extensive banks forming on shelves or platforms and sometimes interfering with littoral deposits.

Type 4 of Krebs and Mountjoy are buildups fringing a landmass.

Within the German reef complexes, Krebs has also distinguished many microfacies. Here is not the place to examine each, but suffice it to say that he outlined eleven facies types in the back reef limestones of the eastern Rhenish Schiefergebirge (1968b), five of which he judged to be intertidal and others subtidal. Krebs (1969) distinguished seven types of fore reef limestones, and in the Meggen Reef environments he (1972) was able to divide the complex into eleven microfacies, each characterised by specific bio- and litho- characters.

Regional and structural context

The deposition of the Plymouth Limestones took place in the Amorican Province of the Variscan geosynclinal belt which extended eastwards embracing the areas of North-west France, Belgium, and the German Rhineland. Further eastward lay the Polish embayment, and southward there was a sea connection to the Barrandian basin, and to Spain and North Africa. Similarly, there was clearly a sea link with North America, and this was probably trans-Arctic rather than trans-Atlantic (House 1968, p. 1067). All these connections are established by distinct faunal relations, and it is to be expected that conditions which led to magna-facial differentiation, are comparable throughout.

The European tract, the Cornubian-Rhenish Geosyncline, lay to the south of the Old Red Sandstone Continent, the approximate shoreline of which is well delineated. Parallel to this lie the longitudinal structural units of the Variscan Orogeny, which are thus superimposed on the broad longitudinal divisions of the geosyncline resulting from the southward deeping. To the south, a landmass has been inferred in Germany from the clastic nature of the sediments (the Franco-Alemannian Island), while in Belgium the

Rocroi and Stavelots Massifs are thought to have been smaller islands within the geosyncline.

In Germany, Erben (1965,p.55) recognised three belts trending (as the coastline) roughly north-eastwards. The northwestern belt was marginal to the O.R.S. continent and was characterised by great subsidence and accummulation of a thick clastic sequence. Within this belt, the geosynclinal floor was "broadly corrugated" into a few longitudinal ridges which were sometimes emergent (e.g. Siegen ridge). A central belt was characterised by numerous small submarine ridges on which carbonate deposition took place while in between argillaceous sediments accumulated in the basins; subsidence was slow. A southeastern trough was of a uniform nature and within it an intermediate thickness of shales and carbonates with occasional sandstone intercalations accumulated. This tripartite division of the Rhenish Geosyncline was effectively unaltered during the Lower and early Middle Devonian, but during the Upper Devonian the widespread transgression changed the picture somewhat. The distribution of the Rhenish and Bohemian (Hercynian) magna-facies, the essential difference between which is in the sediment type, itself related to the distance from shore (sandy and nearshore; muddy, calcareous and offshore, respectively), was transposed onto the above troughs in such a way that the Rhenish magnafacies was at first widespread and progressively retreated northwards as the amount of clastic material from the Old Red Sandstone continent decreased. A mixed facies was developed in places. This northward transgression is well documented and can be similarly recognised in Belgium and in South-west England (see Erben 1965, fig.2, p. 58 for the German situation).

Within the Belgium Devonian, Tsien (1971, p. 121) has noted the existence of a number of transversal axes of subsidence with alternating "bulges" on which 'reef' formations are better developed. These cross the longitudinal divisions of the Dinant and Namur Basins etc. (see Tsien 1974,p.8).

In South-west England the longitudinal structural units trend east-west. A northern region of North Devon and West Somerset is comparable with the northern belt in Germany insomuch as it is characterised by a thick clastic, near shore sequence. The Culm sediments mask the Central Devon region and consequently there is no information on the nature of the Devonian rocks here.

In Cornubia there has been speculation about the existence of a southern landmass. The Gramscatho greywackes of southern Cornwall are thought to derive from a geanticimal cordillera rising in the south (Simpson 1951, p. 61) and Braithwaite (1967, p. 318) posed the question of whether such an area is now represented by the Lizard, Eddystone, and Start Point metamorphics. Marshall (1962, p. 19-20), from a study of small structures, considered the Start Schists and the Lower Devonian Dartmouth Slates to the north, to be part of the same orogenic cycle, and thus ".....for the schists to pre-date the slates, one must conclude that no major structural break exists between the Silurian and Devonian in South Devon". The base of the Devonian is not seen in South west England, though Sadler (1973, p.542) reports the Gedinnian _Icriodus_ _woschmidti postwoschmidti_ Fauna from a limestone lense within the Roseland Volcanics of of South Cornwall.

Hendriks (1959, p.254) regarded the Staddon Grits as having formed on a ridge or geanticlinal schwell. Hendriks(1951 p.256, 292) considered the grits to be a flysch deposit and linked them to the Gramscatho flysch. Hendriks (1959) distinguished two regions in South West England: the over ridden and the over-riding, the former being divided into a number of geantridinal ridges of which the Staddon ridge was one. It seems that the Cornubian trough may also have been divided by secondary longitudinal ridges. Dineley 1968 (p.11) has described a second phase in the "Tectonic timetable" of Cornubia characterised by the differentiation of the geosynclinal area into deeps and shoals in response to varying degrees of downwarp. As in Germany, submarine vulcanism, sometimes strong, is associated with these mobiles belts and must have contributed to the shallowing in some areas. The intra-Devonian movements of the geosynclinal floor were epeirogenic and resulted in localised non-deposition or occasionally in erosion (Erben 1965, p. 56), as well as widespread volcanism.

Local context

In South Devon, the Dartmouth Slates, which are comparable with the non-marine Old Red Sandstone, are the oldest Devonian rocks known and appear to represent a relatively uniform continental phase preceding the marine sedimentation of the over-lying Meadfoot Beds. South of Plymouth, the latter, dominantly argillaceous beds, pass northwards into the Staddon Grits. These are, in the main, sandstones with subordinate shales and include conglomerate bands apparently lying on erosion surfaces (Dineley 1961, p.12). Hendriks (1951, p. 281) considered the slates to the south of the Grits in Bigbury Bay and those to the north in Jennycliff Bay were of an identical age, a proposition subsequently supported by the structural work of Fyson (1962, p. 209-10). Hendriks (1951, p. 289) was in no doubt that the Jennycliff / Staddon junction marked the base of the latter, reiterating the view of the nineteenth century geologists. These horizons have yielded Spirifer cultrijugatus, indicative of a Lower Couvinian or Upper Emsian age (German usage) (Dineley 1961, p.13), whereas the surrounding slates (in the north, everything south of the "? Great Thrust" of Batten Bay) were considered by Hendriks (1951, p. 281, 290) to be Siegenian or Emsian. Thus Hendriks conceived the Staddon Synclinorium and later she (1966) incorporated this in expounding her belief that there were four unlike facies of Middle Devonian age in South Devon and Cornwall, the Staddon Grits and the Plymouth Limestone being coeval. Dineley (1961, p.12, fig. 4) thought there was a "strong possibility" that the Grits and the shales of the Meadfoot Beds, were in part lateral equivalents.

Latterly, the Staddon Grits have been considered as no older than Emsian (Goldring et al. 1968, p. 9), the northern margin being the top. Though the author is not aware of any palaeontological evidence supporting this, it does seem likely particularly in view of the conodont evidence from the northern slate belt which indicates a high Emsian age in Rum Bay and clearly places the Durness Point argillaceous limestones in the low Eifelian. Hence there is northward younging hereabouts, but the structure is so complex that no interpretation can be ruled out.

In terms of magnafacies, Erben (1964, p. 104) considered the Staddon Grits, and, to a certain degree, the Meadfoot Group to be of Rhenish aspect, whereas the grey slates with some horizons rich in crinoid ossicles were transitional to the Hercynian magnafacies, the advance of which resulted in the 'infrafacial' differentiation of the region. Thus in Cornwall, the Trevone deepwater argillates (Gauss and House 1972) correspond to the Badeholz infrafacies while the shallow water limestones of South Devon are of the Koneprusy infrafacies type (see Erben 1964, tbl. 2, p. 103).

Within the mid-Devonian geosyncline the areas of carbonate deposition are centred on Plymouth and around Torbay (Newton Abbot - Torquay - Brixham) as well as small isolated developments at Brixton, Yealmpton, Modbury and Ugborough. It may well be that these carbonates arose in response to a variety of factors which were not necessarily the same in all these centres. Krebs (1971) has discussed the distribution of various carbonate complexes in Central Europe and indicated some such differences (see carbonate environments). The palaeoenvironmental situation of the carbonates has been variously interupted. Edmonds <u>et al.</u> (1969, fig.8, p.22) pictured the thick limestones as occupying a position on the edge of the shelf bordering the Old Red Sandstone Continent though elsewhere (fig. 11, p.28 and p. 29-30) they envisage areas of local shallowing, in parts associated with volcanoes, within the "deep sea". Scrutton (1971, fig. 4, p.7 and oral communication 1974) in his study of the Torbay environments, recognises a restricted environment to the north (Newton Abbot area) behind the massive stromatoporoid banks and bioclastic limestones southward and seaward (Torbay area). In contrast, Braithwaite (1967, p. 318) favoured a southerly provenance, one of low relief, including relatively high metamorphic grade terrain, and at no great distance. The latter author considered the Devon carbonates as a whole, yet it is apparent that it is not possible to make generalisations about provenance. The Torbay complex would appear to have developed on the south of an area of shallowing whereas available evidence suggests that within the Plymouth carbonate complex, a restricted environment was developed in the west and south (-west) (see on). A picture emerges of local highs, or geanticlines of authors.

The Plymouth situation

The transition from shale into limestone is seen only in one area of Plymouth, that is to the north east, in Princerock and Saltram (see fig.18) where there is a small thickness of shale immediately to the south of the presumed fault zone which brings down Upper Devonian variegated purple and green slates to the north. The southern margin of the limestone is in faulted and plicated contact with slates and volcanics south of Mount Batten while on the Cremyl (Cornish) coast a major break is inferred from the probable upward facing nature and Upper Devonian age of the limestones there. To the east, the limestone appears to die out into shales, in part calcareous, and volcanics, mainly tuffs. Westward, the termination of the limestone is quite abrupt in the vicinity of the Tamar where volcanics are widespread and where the Wearde Grit is also developed; beyond, the Middle and Upper Devonian are developed in pelagic facies.

"(The Limestone) rests on clayslate, alternating with it, at the place of junction, in a remarkably distinct manner, tables of limestone, of a few inches in thickness, and many feet in length, appearing in considerable numbers, as may be seen at the western landing place of the Flying Bridge" (Hennah 1824, p.9).

. . . .

Thus the transition from the dominantly argillaceous rocks are seen on the margin of the limestones in northern Princerock (SX 499543) and Laira (SX 500543) west of the Plym (fig. 9) and east of the Plym near the entrance to Saltram Quarry (SX504543 ; fig. 8) and northwards in that quarry. To the west, what appear to be the transition beds at the northern end of Richmond Walk (SX 461544) are younger (fig. 13).

The (large-eyed) Laira trilobites (the first trilobite locality in the area) are found some five metres below the earliest coral-stromatoporoid limestones, in an association of small horn corals, frilly brachiopods, fenestellid bryozoans, ostracods and occasional small tabulates - the '<u>Rubenriffe</u>' biotope ('<u>Beet-reef</u>') of German authors. According to C. Burton (1971, written communication), the trilobite fauna contains elements of both Rhenish (phacopids) and Bohemian (otarionid) aspect and probably lived in conditions of turbid, rather muddy water of about fifty metres depth (dysphotic Zone). Burton has tentatively dated the trilobites as Middle-Upper Emsian or possibly Lower Eifelian. This development may thus be equivalent in age to the Staddon Grits in part in which case one envisages a gradual deepening northwards from the latter. During the Lower Eifelian, a facies represented by pyritic, lenticular argillaceous limestones and shales with a fauna of smooth ostracods, dacryoconarids (<u>Nowakia</u>) microgastropods, fenestellid bryozoans, micro-bryozoans, crinoid ossicles, and conodonts, is developed at Dunstone Point (SX 489526) and at the southern end of Richmond Walk (SX 459540); the latter, which is brought up by a fault, may be a little younger. The conodonts are almost exclusively icriodids. The faunal association is typically Bohemian (see Erben 1965, taf. 1, p.56) and in some respects resembles the flinz-facies of German authors which characteristically develops in rather restricted environments with poor water circulation, though one which is still open insomuch as normal marine, pelagic organisms dominate. However, since tne bryozoans and crinoids represent benthonic elements of the fauna, the bottom conditions were not stagnant and were probably quite shallow, though in no way turbulent. These argillaceous sediments and the contained fauna has elements of both the "Zone profounde" and the "Zone quiescente" of Lecompte's (1968, pl.lV, p.26) basinal bathymetric scheme. At Durness Point at least four metres of these carbonates represent the first limestone development of any consequence in the area. This facies has not been found in the 'sublimestone' transition beds of Princerock but it may be that the 'Beet-reef' developed there is at a comparable stratigraphical level. If this were the case, the area was developing in the lowest Middle Devonian on at least two different facial lines. Above the Laira trilobite-bearing slates and beneath the limestone (which is thought to be Middle-Upper Eifelian in age) there may exist a structural break or perhaps a sedimentary hiatus; alternatively, the shale sequence may be very condensed, but there is no evidence for this either. It does, perhaps, seem more probable that the trilobite fauna is older than the Lower Eifelian in which case equivalence to the Staddon Grits seems probable. This being the case, the transitional (Rhenish→ Bohemian) dark slates of Jennycliff Bay, to the south of Durness Point, would either be contemporaneous, in which case there would be some justification for the idea of local "schwelles"; or, an unknown thickness of shale is not (presently) represented beneath the Laira limestones. In the latter case, there would also be some grounds for suggesting local shallowing.

Northwards along the Mount Batten coast from Dunstone Point, the section continues, with much faulting and plication, in dark shales, volcanics and subordinate limestone beds and lenses, often crinoidal. The brown and pale green volcanics are often tuffs, sometimes vesicular, but include much sheared and highly altered material, the original nature of which is obliterated. Zaphrentoid corals occur occasionally in the slates (see Smith 1951). South east of Mount Wise (SX 458539) dark shales with volcanic horizons are also known to the south of Richmond Walk. It may be that these continue higher in the succession than in the east (see later). The volcanic horizons mark the latest phase in the activity which is well documented through the Lower Devonian of the area. The volcanic belt strikes east-west. It has been traced by Ussher (1912) bordering the main limestone outcrop to the east at Hooelake, Plymstock and beyond. To the west, thick green tuffs are met with on Drake's Island (SX 467528; fig. 16) and in

Cornwall along the Empacombe coast and in Southdown Quarry (SX 435528). Bordering the Hamoaze, there are many varied volcanics at Torpoint, Devonport and Barne Barton (Ussher draws a northern limit to the volcanics at about the line of the present toll bridge) while in the immediate vicinity the Wearde Grit is developed (at the Lynher-Hamoaze confluence). There is no evidence forthcoming for the age of these western volcanics, but on Drake's Island, a limestone raft within the tuffs appears to date from the mid to late Eifelian, so, allowing a little time for consolidation (probably rapid, cf. Braithwaite 1967, p. 299) and subsequent incorporation, this puts a lower limit on the age of these tuffs. Northward, tuffs are recorded sporadically in the logs of ditches and boreholes compiled in the last century (e.g. Ussher 1907, p. 59-61) from north of The Hoe and eastwards there is also tuffaceous material near the base of , and mixed with, the limestone in Princerock. The latter - dark, thin-bedded and argillaceous - are considered to be Upper Eifelian in age and thus the age of the tuffs, both here, on Drake's Island and on the Mount Batten coast, are thought to date from the Middle-Upper Eifelian.

It has been suggested by several authors that volcanism played an important role in the formation, and maintenance, of shallow 'shoals' on which the carbonates accumulated. The volcanism was probably also responsible for the periodic destruction of organisms by poisons effusions, the blanketing effect of the pyroclastic material and because of the associated crustal movements. In Germany, type A carbonate complex of Krebs 1971 is characterised by an underlying volcanic phase which is also responsible for giving relief to these isolated rises within the basin. Braithewaite (1967, p. 315) suggested that "local highs on the sea floor resulting from movements associated with volcanic activity may have acted as centres of deposition". Richter (1965) considered that during much of the Middle and Upper Devonian, volcanic activity interupted the normal accumulation of sediments, and that only at times of reduced activity could the biogenic limestones accumulate. Richter's observations were made in the Torquay area, as were those of Holwill (1966) who thought that the tuff originated from subaerial explosions or forceful submarine activity which blew ash into the air to be subsequently deposited over a wide area. The 'schalsteins' (diabasic tuffs) probably grade into, and interdigitate with limestone locally but these relationships cannot be established in

Plymouth due to later tectonism. However, it is clear that immediately preceding and associated with the establishment of a carbonate environment in south-west Devon, there was a period of widespread volcanism. This was presumably related to the mobility of the geosynclinal floor which itself may have contributed to the change in bathymetry which heralded the limestone deposition. The (present day) distribution of the volcanics suggests a centre of activity in the south; similarly the relatively reduced thickness to the north indicates this was more removed from the source. Elsewhere in Devon, volcanism of this age is known south of Newton Abbot (Middleton 1960), though the extensive Ashrington Group is thought to be later (low in Upper Devonian).

The Upper Eifelian is represented in Princerock by dark, thin-bedded or slaty, argillaceous limestones. There is, especially in the lower horizons, quite a lot of interbedded shale and, though Braithewaite (1967, p. 295) though this might be a result of pressure solution of limestone margins, the environment was certainly quite muddy.
Upward, the beds became increasingly more calcareous and the fauna more prolific. Solitary Rugosa are the major faunal element but small stramotoporoids and branching tabulates are common and the former is found encrusting solitary corals in some places. Pools of crinoidal debris are common throughout but some horizons contain quite large, articulated columnals. Small brachiopods and sponge spicules are occasionally found in the shales and amongst the microfauna vertebrate phosphatic debris, occasional bryozoans, ostracods and dacryoconarids accompany a conodont fauna dominated by the simple cone group, principally Belodella. This conodont usually comprises about 50% of the fauna (see figs. 9, 19) but maybe as much as 80%. Polygnathus linguiformis, simple polygnathids, icriodids and spathognathids are minor but important constituents, which appear to vary in relative numbers from place to place, but overall are represented about equally. The environment represented here seems to be one of low-medium energy, perhaps the under-turbulent Zone of the Belgians.

The lower limestones of Coxside (SX 485541) are an equivalent development in which one can see great numbers of Rugosa, especially cystifers, as well as the colonial 'Cyathophyllum' and tabulates (e.g. Heliolites) set in a muddy matrix. A little higher in the succession small stemmed fasciculate corals are common at one horizon. The cystifers are large and generally have a straight, cylindrical form while stromatoporoids from these levels are small and dome-like. These sediments and fauna also suggest a low energy, under turbulent conditions. The Eifelian has not been proven elsewhere but in the eastern outcrop, the limestones of Saltram Quarry (SX 504543; fig. 8) and in the inverted area of Hooelake, lateral equivalents are probably represented by dark, argillaceous, rather barren limestones. In Saltram Quarry, the fauna is limited to a little crinoidal debris and rare tabulates while at the base of the succession at Hooelake, Amphipora is often the only fossil. Evidently, these western and southwestern areas were somewhat restricted environments. The latter horizons are seen again at Mount Batten and probably extend through the Lower Givetian at least. The environment, it appears, may have been a back reef or sub lagoonal one and it is notable that no conodonts have been found in strata older than Lower Frasnian west of the River Plym or south of the Cattewater (within the main limestone outcrop).

In the Lower Givetian, facial differentiation becomes clearer. In the east and southeast, argillaceous Amphipora micrites with occasional solitary Rugosa, tabulates and stromatoporoids with invaginated flanks dominate. In Hooelake Quarry, the limestones become thicker bedded and there are occasional horizons rich in solitary rugosa. In Pomphlett Quarry (SX 504543) and in Saltram Quarry (SX 511545) Braithewaite (1966, p. 187; 1967, p. 298) has noted the occurrence of muddy intraclasts which are cited as indicating erosion of consolidated carbonate mud synchronous with normal limestone deposition.

Westwards, the Princerock succession continues southwards through Cattedown in often richly fossiliferous, thin to thick bedded and finally massive, limestones. The lower horizons in the Cattedown (SX 494539; fig.10) and Esso (SX 493539; fig.10) Quarries contain local concentrations of broken and disarticulated shelly material and fine crinoidal debris. Such horizons alternate rapidly with relatively unfossiliferous muddy micrite beds at the base of which the occasional coral or stromatoporoid appears to be colonising the preceding surface of bioclastic debris. Such alternation is evident through much of the Cattedown section, and suggests a rapidly fluctuating environment. The sediments in the northern belts are dominantly pelsparites and calcilutites (Braithewaite 1966, p. 185). Individual beds of detrital limestones locally show 'wedging' and two-way grading: "Traceable over several metres, the lack of orientated fossils and absence of internal depositional features suggests the bed (s) was deposited as a unit" (Braithewaite 1967, p. 297). The macrofauna often consists of broken (but not abraded) corals around which up to three generations of stromatoproid and tabulates (Alveolites commonly) have encrusted, also suggesting rapid, albeit subtle, changes in the environment. In so much as these generations of 'encrusters' must have been in continual competition, each dominating or declining in response to slight changes in the environment, it is nevertheless clear that as a whole they shared similar tolerances and all appear to have been prolofic. Tsien 1974 (p. 23) considers the encrusting morphology is an adaptation to increased salinity and decreased water circulation. Besides the encrusting stromatoporoids, massive forms are common. These include bulbous forms, the point of attachment to the substrate still evident, small spherical 'tennis balls' which likely arise from dislodgement of the former, and large, expansive low 'mushrooms'. That these, and associated Thamnopora 'rasens', colonised a substrate of bioclastic debris is evident, but the degree of cohesion of that substrate is open to question. Often, though not always, the contact is a bedding plane and Braithewaite (1967, p. 294-6) has discussed the meaning and significance of these, but concludes only that they are indicative of some change in the conditions of supply or transport. They must certainly represent a real break in the continuity of the organic pile, but there is no evidence for an intervening period of erosion or emergence.

In at least two localities, (SX 495537; SX 493537) stromatoproids are very important and appear to have developed to the exclusion of all else. These 'bloc-riffes' of massive stromatoporoids come nearer to a true reef development than any other known in Plymouth and they have seemingly resisted the forces of transport that have affected much of the surrounding, locally prolific, organisms, though it must be stressed that the sources of derivation were probably very close. The situation envisaged is one of periodic turbulence which had the effect of dislodging organisms, sometimes breaking them, and gently rolling them over (hence even encrustation by other organisms). Influx of muddier sediments brought finer bioclastic material from elsewhere (not necessarily very far) and subsequently this provided a substrate for further colonisation; the larger stromatoporoids were able to survive such influxes by virtue of their greater size and by vertical, as opposed to lateral, growth.

From the dark, thin-bedded, often bituminous, limestones of northern Cattedown, conodont faunas are still dominated by Belodella but Polygnathus linguiformis is locally abundant. Icriodids, spathognathodids and simple polygnathids are also represented. Southwards, in the direction of younging, the beds become thicker, less argillaceous and more fossiliferous and it is these horizons in which stromatoporoids locally dominate; no conodonts have been found but they are considered to be mid-Givetian.

To the west of Coxside, the limestone above proven Eifelian strata also becomes progressively less argillaceous but residues continue to be pyritic. The limestones are thin bedded to massive, coarse biosparites. The fauna includes articulated crinoid stems, lamellar Alveolites and stromatoporoids, and solitary corals. Hennah (1824, p. 34) records "a most perfect specimen of Encrinite" from hereabouts. The size and form of the macrofauna suggest an underturbulent condition. Conodonts are not common but within the faunas retrieved, Icriodus is the dominant element with Belodella and Polygnathus linguiformis of secondary importance. On Drakes Island very similar conodont faunas have been yielded by the rather dolomitised but probably identical limestones in the western part of the island.

Further westwards, no evidence for the lower Givetian is forthcoming within the main limestone mass but across the Tamar to the north, the turbidite-like limestones of Neal Point (SX436613; fig.16) are considered to date in part from this time (Matthews 1962, and herein). These are thin-bedded, argillaceous and pyritic limestones interbedded with shales in which criconarids are found. Poorly preserved and fragmented tabulates occur in some of the limestones whilst others have produced a conodont fauna the composition of which is not unlike that of the limestone in northern Cattedown.

Limestone deposition appears to have reached its maximum during the upper Givetian. Proven strata of this age comes from Coxside, Richmond Walk, Mount Wise and also from Botus Fleming, across the Tamar. Comparable strata are inferred at Western King, southern Cattedown, in the Plymstock area, at Hooelake and at Mountbatten. The whole of the Hooe foreshore is also thought to be of Upper Givetian age, as are the northern beds of Cremyl.

The southern limestones of Cattedown (e.g. Fisons Quarry, SX 495536; fig.11) are thick bedded to massive, very pure, biomicrites. The fauna, often prolific, is similar to the lower beds with massive stromatoporoids (expansive, dome like) alternating with coarse bioclastic horizons containing coral, stromatoporoids and crinoid debris; less common are muddy horizons with isolated solitary Rugosa. Thamnoporoids are locally abundant and form rasens. Southward, Amphipora becomes more important and this fills some beds in the southernmost outcrop (SX 495535). No conodonts have been found.

Across the Cattewater, similar beds are found at Mount Batten though here, and at Hooelake, the limestones are thinner bedded and more argillaceous. Eastwards, in Bedford (SX 504538; fig.8) and Pomphlett Mill (SX509538; fig. 8)Quarries, equivalent strata is also dark and argillaceous. In the latter, there are local concentrations of abraded corals having the appearance of current sorted accumulations.

Towards the west, the highest beds of Coxside, in Dead Man's Bay (SX 486538), are richly fossiliferous biosparites which give way to thin bedded, pink crinoidal limestones. Masses of stromatoporoids and Alveolites suggest a turbulent, agitated environment while Braithewaite (1967, p. 298) noted muddy intraclasts from hereabouts too. The conodonts include Belodella, Icriodus, Polygnathus linguiformis, Spathognathodus and simple polygnathids, the latter being the most common in these not over-abundant faunas. Along the Hoe foreshore, massive white weathered limestone, very similar to that of southern Cattedown, is found. The eastern outcrop is richly fossiliferous and bioclastic material is negligible whereas to the northwest in the higher horizons this is common.

The lowest beds of Richmond Walk (SX 461545; fig.13)are thin, irregularly bedded dark, argillaceous and pyritic limestones. Faunally, these are characterised by Heliolites (or Callopora) and stromatoporoids in intimate association, if not in situ, certainly not far removed from their growth positions. Both have a lamellar form, though smaller ovoid Heliolites (in two dimensions) are found within associated bioclastic beds. The latter contains much fine crinoidal debris and solitary Rugosa which increase in size upward through individual beds, finally giving way to 'spreads' which appear to colonise the surface of the debris. These black bitumous limestones have yielded a conodont fauna in which Belodella is dominant, and Polygnathus linguiformis, Spathognathodus and the simple polygnathids are equally represented; the complete absence of Icriodus from the fauna and from all faunas of a Givetian age in the whole of this western area, is considered to be of undoubted significance. The macrofauna and sediments suggests an argillaceous sub-turbulent environment. Southwards and upwards the limestone becomes less argillaceous, thicker bedded and more dominantly bioclastic in nature. Some horizons (best seen on the long east wall) contain large, massive, hemispherical stromatoporoids, unbroken but obviously transported; one envisages them having 'floated in' to their present position. The irregular form of some suggests the turbulent zone of the Belgians, and it is thought that they originated in clear, agitated water and that they were subsequently transported into the quieter, muddier, environment represented here. The debris-rich 'packstones' are probably the product of an even more turbulent environment; some fragments are coated with stromatoporoids. Braithewaite (1967, p. 295) noted the wedge shape of some of these beds and the fact that they lack internal lamination. Braithewaite (p. 297) furthermore suggests a series from in situ organisms through stromatoporoid breccias to these detrital beds of Richmond Walk in which the mud content is considerably diminished. He felt that the deposition was not primarily the result of normal current activity, but he did not envisage flood sheets. The greater breakage and degree of sorting, the low mud content and the wedge-bedding indicate a large distance of transport, and swift depositional currents (Braithewaite 1967, p. 302).

The brachiopod bearing horizons at the Dock Yard (no longer exposed), Mutton Cove (SX 453540) and Mount Wise (SX 455541; fig. 13) are thought to represent local shell beds similar to those of Lummaton and Wolborough, and whilst those localities have produced a more varied macrofauna, the richness of the conodont fauna from Mount Wise is much more abundant and varied. Belodella, the Polygnathus linguiformis group and the simple polygnathids are about equally represented, but over half the fauna consists of bars and blades; Icriodus is totally absent in a studied fauna of about one and half thousand elements. Solitary corals, fenestellid bryozoans, rare bivalves and gastropods and articulated crinoid ossicles are also found at Mount Wise which is considered to be a small lenticular, bank-like accumulation within a relatively quiet environment. A comparable shelly fauna mentioned in the literature is in Stonehouse (=St. Georges Hall), east of Richmond Walk, but the locality no longer exists for study.

In Western King, at Devils Point (SX 459533), the Upper Givetian is characterised by a very different facies. These limestones are very rich in solitary and colonial Rugosa, tabulates and stromatoporoids which often fill the rock completely. The limestone is quite muddy and crinoid ossicles are scattered throughout. Alveolites occur as lamellar forms which sometimes appear to have been rolled into spherical forms, so presumably the environment was somewhat agitated though not as turbulent nor as shallow as the contemporaneous Cattedown limestones. Except for a few fragmentry undiagnostic forms, no conodonts have been found. Comparable levels are seen across the Hamoaze in northern Cremyl.

Across the Tamar and into the basinal facies, the argillaceous, pyritic limestones of Botus Fleming (SX 409612) have yielded conodonts of high Givetian age. This refutes Ussher's belief that these were of Upper Devonian age (1907, p. 74). They contain an abundant fauna of stick bryozoans, smooth ostracods, Nowakia and microgastropods, while small rugosa and crinoid ossicles would appear to suggest derivation from a near reef source. The conodont fauna is dominated by Belodella and while most of the other common elements are present, Icriodus is not. Some of the Neal Point limestones may be correlative too.

The lowest horizons of Upper Devonian age are found in West Hoe (SX 474538) and though the preservation of the conodonts is poor and reworking cannot be ruled out, their position at the top of the massive limestones of the Hoe suggests that this facies spanned the Middle-Upper Devonian boundary in this immediate area. To the west at Eastern King Point (SX466535) and in Western King (SX461533) particularly, the proven Upper Devonian horizons are lithologically and faunally different from those immediately below. The latter (to the north) are thicker and pale grey with a fauna of solitary corals and stromatoporoids, while those above contain Rugosa, lamellar stromatoporoids and Alveolites and beds of pink crinoidal limestone. The latter are thinner, more argillaceous and are inter-bedded, with red shale.

Conodonts from below the 'boundary' are few and undiagnostic, whereas from the pink crinoidal matrix above, a rich fauna includes typical Frasnian forms. Icriodus, Ancyrodella and the wide plated polygnathids are well represented, simple polygnathids less so, and Belodella only sporadically; higher in the succession Palmatolepis is also represented. Some beds are rich in Rugosa whereas others contain much debris in a red argillaceous matrix. The lamellar stromatoporoids are often very long and they must be in situ or only slightly transported. The environment envisaged is a relatively deep one, deeper than most represented in the Plymouth Limestone, in which the organisms were subjected to little turbulence though periodically debris was introduced from a higher energy source: a seaward slope, or a 'fore-reef' situation. This facies persists for approximately 20 metres, but towards Western King Point the beds become less argillaceous, thicker bedded to massive and take on a more 'reefal' aspect. The highest beds here are not dated by conodonts but are thought to be high in the Lower Frasnian.

Comparable horizons can be traced on the Cornish coast - the Barn Pool Limestones (SX 456532), but here diagnostic conodonts are scarce and Icriodus and particularly the simple polygnathids are dominant. Nothognathella is found to be an important constituent of some samples here. The Durnford Street (SX 464536) cutting is in Frasnian Limestones too and a fauna from the top of the section confirms the persistence of carbonate deposition into the Middle Frasnian. These limestones are, noteably, pink and red. The southern limestones of Richmond Walk were thought by Taylor (1950, p. 153-4) to be Frasnian but conodonts from here are worn, fragmented and of Middle Devonian aspect, and though these may be reworked, no coral evidence exists for Taylor's assertion. These limestones are pure micrites, highly recrystallised but with scattered tabulates still discernible. In some respects they resemble the lower beds of Eastern King, those below proven Upper Devonian strata.

In Cattedown, it is not known whether the Amphipora - micrites persist into the Upper Devonian. The same applies to the northern beds of Turnchapel and Hooelake sequences which are very fine grained, pure and sparsely fossiliferous.

In Radford Quarry (SX 505532) however, firm evidence for the Upper Devonian comes from both ends of the inverted section. The lowest beds equate with those of Western King. These are dark, reddish-grey, argillaceous and thin-thick bedded limestones with no visible macrofauna, except for the occasional crinoid ossicle. In common with the Western King equivalents, they are interbedded (albeit irregularly) with red shale. The conodont fauna is dominated by _Icriodus_ with the simple polygnathids of secondary importance. The presence of _Ancyrodella_ and _Polygnathus asymmetricus_ may be fortuitous (? swept into this restricted environment by strong currents) but enables the correlation to be made. Northwards in the quarry, the limestones thicken and becomes less argillaceous while the conodont faunas are invariably poorly preserved simple polygnathids. The northernmost beds have yielded _Palmatolepis_ and _Ancyrognathus_, again poorly preserved and questionably reworked. A few Famennian forms are incorporated in the fauna, but unfortunately they are rare.

A similar _Palmatolepis_ fauna comes from an isolated (? tectonically) limestone outcrop, in Hooelake Quarry (SX 496531; fig.6) lying below red shales, in part calcareous. Here, the red shales have not yielded a conodont fauna and the same applies to the green shales overlying the limestone in Langshill Quarry(SX 499532; fig. 6), the one locality where the contact is clearly seen. Unfortunately the limestone in the latter quarry has also failed to produce any conodonts, so the age of this transition remains unknown. The evidence from elsewhere is always from the red beds which permeate much of the limestone, and date from a time when the limestone was probably being subjected to widespread solution and subsidence.

The Fison Quarry conglomerate (SX 493538) was first described by Braithewaite (1967, p. 313) who was unable to present an explanation for this unique deposit. The grey, apparently unfossiliferous, limestone clasts are well rounded and set in a red argillaceous matrix which has yielded from several points on the north face of that (disused) quarry a sometimes prolific conodont fauna of Middle Frasnian age. This includes, in order of abundance, _Icriodus_, _Palmatolepis_, simple polygnathids, _Belodella_ and the _Ancyro_ group; the bars and blades tend to be small and fragile. This deposit is much younger than the containing limestones, thought to be of mid Givetian age, and it is worthy of note that the clasts are, in contrast to the former, non-fossiliferous which suggests that they too are spatially and/or temporally distinct. Braithewaite noted the essentially local nature of this deposit and the association of possible slump structures. It is herein suggested that this deposit represents a crevasse infill within the older limestones. It is suggested that synsedimentary tectonics may have resulted in the initial fracturing of the old 'reef core' and that the limestone boulders possibly originating from the same episode and having been meanwhile rounded by erosion were subsequently incorporated within the mud matrix during a further phase of crustal movement at which time the whole melange may have slumped down.

A younger stratigraphic leak within the Plymouth Limestone has been described and discussed previously (Orchard 1975). These are the discordant red shale 'dykes', breccias and infills of solution hollows seen in Western King and also in Durnford Street. They date from near the Frasnian/Famennian boundary and are considered to represent firstly the results of widespread solution of the dead reef followed by early Famennian subsidence, the whole being finally modified by later tectonics. Just when limestone deposition ceased and the reef destruction commenced is not known exactly since a long period of erosion and solution is indicated by the mixed conodont faunas of the youngest limestones. The red calcareous shales would seem to signal the onset of subsidence in much of the limestone outcrop, but then we have the anomalous situation of green shales directly overlying the limestone in Langshill Quarry, with no apparent sign of disconformity. The details are still in need of clarification, but it does seem that during the Lower Famennian, and probably throughout the Frasnian, parts of the Plymouth area constitued a shallow marine area which may have been emergent during the later part of this interval.

Evidence from the Torpoint area, west of the Tamar (Gooday 1975 - see fig. 3) and areas north of the limestone (House 1963) indicate the establishment of the deepwater 'ostracod slate' facies during the Frasnian. This contrast is probably exaggerated by tectonics but the evidence for a Plymouth Schwelle is strong. Unfortunately condensed successions like that of the Chudleigh Schwelle are not known, though the presence of the Wearde-Efford Grits within the Upper Devonian Slate belt may be easier to explain in the light of the suggested local highs at this time.

Environmental synopsis

In terms of European models, the Plymouth Limestone can be considered as a carbonate-complex (sensu Krebs) or reef-complex sensu Tsien. A bank or reef-bank seems an appropriate description of the earliest limestone development; in the German nomenclature, the Schwelm facies is recognised during the mid-late Eifelian and early Givetian. Later Givetian limestones are biostromal (sensu Tsien) and, although the development of true reef subfacies within a Dorp facies is not established, the author considers there to have been differentiation of the carbonate environment into relatively open and restricted situations. That this was caused by the growth of 'biogenic structures' comparable to a 'true reef' is not certain, though such structures are relatively minor in the well known complexes, comprising only a narrow Zone. In Germany, within the reef phase of the Massenkalk, Krebs (1968) estimates the back-reef areas to be about 80% of the total.

Maximum 'reef' development was during the late Givetian/early Frasnian at which time the limestone deposition had its maximum spread, apparently appearing in the west for the first time (Richmond Walk area). At this time, the centre of deposition is thought to have been in the Hoe-Cattedown area which could perhaps be considered as the 'reef-core'. These latter were, nevertheless, restricted in the sense of being back-reef. To the east and south-east, the rather barren, argillaceous limestones are judged to represent a semi-restricted contemporaneous situation, perhaps a sublagoonal one. In this case, one is forced to conjecture the presence of a barrier in that direction. No limestones are known further to the south or east which could have been the counterpart of an atoll-like development 'containing' these restricted environments. If such was not developed, then an area of shallowing with a fringe-reef development might explain the distributions. Hence one must look in the direction of Staddon for such an area.

Westwards, the area of Richmond Walk and Mount Wise represent a deeper water, further seaward environment which, in part, may have received much of the bioclastic material from the surf-zone of the 'barrier-edge' perhaps. Scanty information from the southwestern outcrops suggests shallower areas in that direction too, but this is near the hinge zone of the Tamar where subsequent tectonism has confused the picture.

A sudden subsidence in Lower asymmetricus Zone times is most marked in Western King where the facies is a relatively deep one. That this event was felt throughout the area is witnessed by the lowest horizons of Radford Quarry, though here the environment was still relatively restricted. Renewed 'reef' growth is indicated by the higher limestones in both areas which have yielded mid Frasnian faunas. The western area seems to have been the more unstable and fluctuated somewhat as the shale beds and (?) megabreccia horizons testify. The 'reef-core' at this time is thought to have been undergoing erosion and collapse. A late Frasnian and early Famennian record from the western and eastern outcrops suggests a prolonged phase of reef destruction and solution in these areas.

In Germany, 'dead reefs' are known to have remained exposed until mid Lower Carboniferous time (e.g. Krebs 1967, p. 304) before being totally incorporated into the sedimentation area. Others have a reduced Upper Devonian sequence (e.g. Attendorn). Similar reefs have been described from Canada (Pollock and Fuller 1972). It is not known when the Plymouth area was thus incorporated; that parts of it remained above the level of sedimentation for some time after the latest suggested subsidence cannot be ruled out. Certainly a source for the reworked Upper Devonian conodonts in nearby Carboniferous sediments has been demanded (Matthews 1966). The German examples are of the B_1 type of carbonate complex of Krebs. In many respects, the Plymouth Limestone is comparable with this type which are isolated developments at the shelf or platform margin. One will infer from the situation envisaged that a position on the edge of the northern shelf is excluded. The suggestion of a southern landmass, and thus a southern shelf are difficult to prove or disprove, and must be entertained as a possibility.

Prior to, and during the early stage of, the development of the Plymouth Limestone, volcanism was widespread and this quite likely contributed to the establishment of a bathymetrically suitable situation for reef growth. The type A complex of Krebs is built on submarine volcanic rises within the basin or geosyncline. The amount of volcanism associated with the establishment of limestone deposition in Plymouth is not considered to be indicative of a volcanic rise. The rise is rather judged to be primary in the sense of it being an area of shallowing of the sea floor.

The idea of a longitudinal corrugation of the geosynclinal floor seems to be a reasonable explanation, certainly a Schwelle with its maximum relief south of the present limestone outcrop would explain the disposition of facies as presently understood. The possibility of a Staddon Schwelle during Emsian time provides at least a geographical model for comparison. In Germany, the boundary between dead reefs with slow subsidence and more mobile basins is often located at synsedimentary faults (Krebs 1971, p. 55); such may have been the case in the Tamar area.

Conodont distributions and biofacies

Introduction

The study of conodont palaeoecology is currently gaining momentum (e.g. Rhodes 1973) as the distribution of conodont faunas are accounted for in terms of environmental controls or preferences. Similarly, within a particular species, biometric analysis promises to be of value: for example, Barnett (1971) identified eight characters of the Silurian Spathognathodus remschiedensis and found that some reacted plastically to a lagoonal environment.

The distributional anomalies of conodonts has been accounted for in different ways. During the lower Palaeozoic, and specifically, during the Ordovician, Bergstrom (1973, p. 49) has considered that the distribution of conodont faunas "may well provide one of the most striking illustrations of faunal provinvialism known anywhere in the geological record". Bergstrom favours a climatic control to explain this. Within the Upper Palaeozoic, Druce (1972) has recognised a number of conodont biofacies which he relates to depth and, to a lesser extent, distance from land. Such a bathymetric zonation is supported to a degree by known distributions and also more recently by the work of Chamberlain and Clark (1973). These authors found there to be a close correlation between the Carboniferous trace fossil communities and the conodont faunas in the Oquirrh Formation of Utah.

Within the Devonian, the relationship between conodont distributions and facies has often been overlooked, mainly because of the success and world-wide applicability of the zonal schemes. Ziegler (1960) demonstrated the identical nature of the palmatolepid faunas in both the Rhenish and Bohemian-Hercynian Provinces, the other faunal elements of which are almost wholly dissimilar and mutually exclusive. Anomalies clearly do exist, however, and these have proven to be particularly evident in the Devonian reef environments.

Previous work

Because of the widespread occurrence of the Upper Devonian Palmatolepis, several authors originally supposed that sedimentary facies control of conodont faunas was minimal (e.g. Klapper and Furnish 1962, p. 2074;

Mound 1968, p. 455). Winder (1966, p. 1291) suggested that conodonts were near bottom dwellers and lived in shallow shelf seas because of their numerically inverse relationship with radiolarians. He explained their apparent independence from lithology by suggesting that necktonic predators passed the conodont elements as excreta. These suppositions and hypotheses break down in the light of the distributional anomalies which clearly exist.

Krebs (1959, p. 378) was the first to note the common occurrence of the simple cone Belodella in near reef limestones. Similarly, Müller (1962, p. W87-9) noted the rarity of conodonts in bioherms and biostromes composed largely of corals, stromatoporoids, sponges and calcareous algae and suggested that the abundance of Icriodus and "Belodus" (=Belodella) in near reef situations may be accounted for by the adaptation of these forms to a benthonic, or near benthonic mode of life. Muller and Clark (1967, p. 904) thought that both Icriodus and Polygnathus linguiformis may have lived in a more shallow water environment than that represented by the faunal associations of the Squaw Bay limestone.

Seddon (1969) recognised two disparate but contemporaneous conodont sequences in the Devonian reef environments of the Canning Basin of Australia. He found the European standard, or Palmatolepis sequence, was applicable in the fore-reef and inter-reef areas whereas the back-reef environment was characterised by an Icriodus sequence for which he constructed a parallel zonation. To explain this distribution, Seddon introduced the concept of a biological filter, through which Icriodus could pass but through which Palmatolepis could not.

Seddon and Sweet (1971) proposed a vertical stratification of the conodont communities and drew a parallel with the distribution of the modern chaetognaths in which such a stratification is most pronounced. These authors recognised a bathymetrically shallower community of Icriodus, Polygnathus and the Spathognathodus stock and a deeper community of Palmatolepis and Ancyrodella.

Druce (1972) recognised three biofacies, bathymetrically stratified but incorporating a 'distance from land' factor. Thus he considered an upper 'simple cone' community and an intermediate biofacies characterised by simple icriodids, polygnathids and spathognathodids; both of these faunas increased in density landward. A third community included complex polygnathids, Palmatolepis and the Acyro group which were of fairly constant abundance throughout the biofacies. Druce (1972,p.209) noted that the presence and exclusiveness of the Belodella biofacies may have been caused by different factors (for example protection from predators) to those which caused the other biofacies, but he favoured a similar cause which he considered, however, was unknown. Druce also noted that the biofacies were often manifest in the lack of specimens rather than their complete exclusion, the biologic filter not always operating at the same intensity.

Plymouth distributions: discussion

In figures 5-16 (see appendix) the ratios of the conodont elements in each fauna has been depicted in relation to the sampled section and the related fauna (see fig. 4 for key). Similarly, figs. 18-21 illustrate how the faunas relate in space and time. The following is an individual assessment of the main conodont groups in relation to proposed biofacies and finally, the overall environmental picture.

Simple cones

Most of the forms here included are assignable to Belodella. Coelocerodontus and Panderodus also occur, almost always in association with Belodella. Acodina is only a very occasional component of the Plymouth faunas and, in contrast to the above forms, is never found without Icriodus. There are insufficient grounds for relating Icriodus and Acodina in a multi-element association as far as the studied material is concerned, but the two may well belong in the same biofacies.

As mentioned previously, Belodella has commonly been associated with a near-reef situation. Seddon (1969, p. 735) related Belodella and Acodina, and noted that they were rare in the Palmatolepis faunas and common in the Icriodus (backreef) faunas, though always subordinate. Druce (1972, p.206) included the simple cones in his ubiquitous group during the earlier part of their history but included them in his patchy distribution group during the final period before their extinction. It is worth noting that during the Ordovician, forms such as Belodus and Panderodus constituted a somewhat limited community in the North American Midcontinent (northern subprovince). Druce (1972, fig. 1, tbl. 2) considered the shallowest of his biofacies (I) as being represented by Panderodus, Belodella and Acodina in, respectively, the Lower Devonian, mid Devonian, and Frasnian and Famennian. Thus, simple cones may presumably be found in environments from which all other forms are excluded.

In the Plymouth faunas, samples from the Middle Devonian limestones all contain a high percentage of simple cones. Belodella (mainly) commonly comprises 50% of the total fauna, rarely less than 25% and sometimes 90% or more. Besides the Icriodus dominated faunas (see below), the simple cones are rarely subordinate to the other groups, and where the percentage is low (e.g. Richmond Walk area) it is due to a large number of bar and blade elements. Although all faunas are treated identically and so provide a constant model for comparison, it must be remembered that in terms of conodont assemblages the numerical ratios would be very different. Thus bars and blades are, perhaps, more likely associated with Polygnathus and Spathognathodus but not with Icriodus or Belodella. Similarly, it is possible, though admittedly far from certain, that all but the simple cones were most likely paired in assemblages, and consequently, in terms of conodont animals, there would be half as many as the individual element count. In contrast, Belodella is thought to belong in a multi-element association consisting of six pairs of this form (Lange 1968), and hence a twelve fold division gives the number of conodont animals. Suddenly, the simple cone group ceases to be the dominant group, certainly in the proportions indicated by the numbers of single elements. The lack of Plymouth faunas containing only Belodella rather suggests that Biofacies I sensu Druce does not exist. If it did, it is surprising that no such faunas have been found since much of the Plymouth Limestone is barren (in terms of conodonts) and presumably in bathymetric terms, such a fauna should exist within a vertical sequence from biofacies II sensu Druce and the barren, coralline limestones. No such fauna has been found in Plymouth.

Acodina is not common in the Plymouth faunas. Suffice it to say that when present, it is accompanied by Icriodus, though the opposite is certainly not true.

Icriodus and Polygnathus

Simple polygnathids, icriodids, Spathognathodus and Pelekysgnathus represent the intermediate biofacies of Druce 1972. Icriodus has often been cited as a facies restricted form in the Devonian. Clearly, it has not always been so as the zonal parallelism of Icriodus woschmidti and Monograptus uniformis at the base of the Devonian demonstrates. As Druce (1972,p. 206) has indicated, Icriodus seems to have passed from a ubiquitous to a patchy distribution during the Late Devonian. During the Silurian, Walliser (1971,p. 201) noted that Icriodus was more typical of shallow, turbulent waters. Similarly, Bultynck (1970,p. 143) noted the dominance of Icriodus high in the first Belgian biostromal development, above the muddy (polygnathid-bearing) base. The same observation has been made in the section at Teat's Hill Quarry, Coxside (see fig. 11), though the faunas are rather sparse higher in the section.

Muller and Clark (1967, p. 904) have noted that Icriodus is the prevailing and commonly the only conodont in faunas of early to early Late Devonian age. In Plymouth, the oldest faunas studied (from Durness Point and Richmond Walk - fig. 18) which date from the low Eifelian, are dominated by Icriodus, as are those (?) low Givetian associations of Coxside and Drakes Island (fig. 16). The low Eifelian environment is interpreted as a shallow but fully open, marine situation whereas the younger faunas come from within the reefal complex. Both share a similar lithology, i.e. dark, argillaceous and pyritic limestones. However, the same lithology characterises the northern lowest horizons of Richmond Walk and therein not a single specimen of Icriodus has been found in an otherwise highly variable association. The same is true for all the Givetian limestones in this western area incorporating the exposures of Richmond Walk, Mount Wise and Mutton Cove. The total conodont fauna, involving some 2000 individual elements, includes only a single fragment of Icriodus. The simple cone group, Po. linguiformis gp., and simple polygnathids are here equally represented. Elsewhere, in the somewhat restricted facies represented by the Cattedown and Princerock sections, Icriodus has a sporadic occurrence and where present is almost invariably subordinate both to the dominant simple cone group and to Polygnathus.

Low in the Upper Devonian, the argillaceous, thin-bedded limestones of Western King represent a deeper facies and are characterised by fauna of large plated polygnathids, occasional palmatolepids and Acyrodella. These faunas also include Icriodus in comparable or greater proportions than simple Polygnathus. The same is true for the coeval faunas of Radford Quarry. Higher horizons in both these sections and in the coeval Cremyl section are pure, massive limestones in which simple polygnathids are dominant, often to the complete exclusion of Icriodus. So we have faunas dominated by Icriodus, ones totally devoid of Icriodus, a Middle Devonian succession which involves Icriodus and simple polygnathids in an inverse relationship, and Upper Devonian successions which apparently involve these two form-genera in a similar, but opposite relationship.

A fauna composed entirely of Icriodus would seem at odds with the biofacies distribution as envisaged by Druce, since one would expect to find other elements of the biofacies II fauna as well as simple cones. The hydrodynamic properties and resiliance of these elements must have been very different under the influence of post-mortem current sorting and winnowing. Thus a depletion of the fragile Belodella and a concentration of the robust icriodids might be expected. Of course, there is also the time factor: Icriodus is the major constituent of low Devonian conodont faunas, while Belodella is less common in Upper Devonian faunas. The absence of Icriodus from Givetian faunas of the western limestone outcrops (see figs. 19-20) is more difficult to explain. There seems to be no constant relationship between lithology and the occurrence of Icriodus and, additionally, since some form species have world-wide distribution, this argues against a benthonic habitat. If Icriodus did require a rather specialised set of environmental conditions, then they have not been recognised in the rock nor in the inferred environmental situation. Whether the preferred habitat was a function of depth, turbulence, temperature or some other variable, or of a combination of these, is not known. Certainly all these factors must have been important and insomuch as all are to a varying degree dependent on bathymetry it is appealing to consider the distributions in terms of the latter. Thus Icriodus would appear to indicate a somewhat deeper situation than the simple polygnathids. This works for most of the faunal successions studied, though in the case of the Coxside succession, and other Icriodus dominated faunas in which Polygnathus as well as Belodella is absent one is forced to conclude that post-mortem effects were responsible; this is easier to envisage with regard to these sparse faunas than the relatively abundant ones of the western region.

Seddon (1969) found that Icriodus was dominant in the back reef environment, though they were in no way restricted to this environment. He found that Polygnathus was present also, so there is no contradiction here. It may be that Icriodus preferred a near-reef environment whereas the shallow realm of Polygnathus was much more widespread.

Druce (personal communication 1974) has suggested that particular icriodiforms are related to certain environments. The ratio of length to breadth and the denticle cross-section (round or oval, tending to transverse ridge development) are the most environmentally revealing characters according to Druce. He suggests that relatively short, broad icriodids with transversely elongate nodes characterise somewhat restricted facies, whereas long, narrow forms with discrete rounded nodes are more typical of open marine environments. Such a scheme does not hold up completely in the Plymouth material (for example, ontogeny seems to include such variation) but there would appear to be some substance in the approach. Certainly, icriodid faunas tend to demonstrate a great degree of variation and plasticity of form, as is evident in published studies, which is why it has always proved very difficult to select constant characters for form-specific distinctions.

The Polygnathus linguiformis group appears to have a somewhat specialised environment too. In terms of bathymetry it seems to have shared a similar biofacies to simple Polygnathus, but like Icriodus it may have preferred a near reef situation.

Spathognathodus is not a common component of the Plymouth faunas but appears always with the simple polygnathids.

Pelekysgnathus is rare in Plymouth and no comment on its distribution is here feasible.

Ancyrodella and Palmatolepis

During the Middle Devonian, Druce (1972, p. 161-2) considered complex *Polygnathus* as the representative of the deeper areas. Therein, presumably, would be included the wide-plated forms which occur occasionally during this interval: e.g. *Polygnathus latus*. This latter form has been found in the deeper limestones of Neal Point, but it is very rare.

Within the Upper Devonian, the biofacies is represented by the *Ancyro* group and *Palmatolepis* according to Druce. To these could be added the broad plated *Po*. *asymmetricus* group.

The *Ancyro* group do, however, appear in faunas devoid of *Palmatolepis* and the complex polygnathids. The most notable case of this is in the Belgian lower Upper Devonian and to a lesser extent in North America and Australia, where the *Ancyro* group provide zonal indices in the absence of *Palmatolepis* and its forebears. In Plymouth, within the Western King section, *Ancyrodella* and *Polygnathus asymmetricus* make a simultaneous appearance (closer spaced collecting may reveal the contrary) but elsewhere these forms are too rare to provide relative information on environmental preferences. *Palmatolepis* is found in the higher limestones but large, coarsely ornamented forms of *Palmatolepis transitans* and *Pa*. *punctata*, for example, are not found. Rather, small unsculptured specimens are represented. The absence of typical *hermanni-cristatus* faunas and particularly *Schmidtognathus* itself is considered significant. Large ornamented *Palmatolepis* only appear in significant numbers in the muddy red limestones of the younger Frasnian and Famennian.

The distribution of these 'biofacies III' forms are thus thought to be divisible into bathymetrically shallow *Ancyrodella* biofacies and a deeper biofacies characterised by *Palmatolepis* and the *Polygnathus asymmetricus* group. *Palmatolepis* may be represented by large ornamented forms in the more open marine stations and by small smooth forms in the near reef environment; it is not clear, however, whether such a distribution of *Palmatolepis* is applicable elsewhere.

Summary

In regard to the distribution of conodonts in the studied carbonate complex, the following observations have been made:

Biofacies I *sensu* Druce has not been recognised as such; rather, in the Middle Devonian, as an association of simple cones plus simple polygnathids, including *Po. linguiformis* (group) is considered to represent the most shallow fauna; *Spathognathodus* is associated. During the Frasnian, the biofacies is probably represented by the same association, though *Po. linguiformis* soon disappeared and the simple cones were much reduced. The other elements appear to have been more diverse and proportionately more significant, though there may have been some shifting of the biofacial boundaries.

Biofacies II can perhaps be considered as the realm of *Icriodus* throughout the Middle Devonian and during the early Late Devonian.

During the Middle Devonian, complex *Polygnathus* may be the biofacies III representatives, though data is lacking. During the late Devonian *Acyrodella* may be considered as occupying a deeper zone than *Icriodus*, though conceivably it may be the more basinward equivalent of the latter. The same may be true for the *Polygnathus asymmetricus* group, which appears to have constituted a biofacies III fauna along with *Palmatolepis*. Small (?juvenile) representatives of the latter genus are more frequently encountered in the near-reef environment.

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