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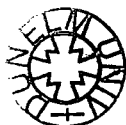
**THE ASBIAN TO ARNSBERGIAN
CONODONTS AND
SEQUENCE STRATIGRAPHY
OF THE
NORTHUMBERLAND TROUGH**

A thesis submitted in fulfilment of the requirements
for the degree of Master of Science,
University of Durham

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March 2001

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Abstract

Yoredale sequences are excellent exemplars of the sequence stratigraphy model; the spacial and temporal variation of these complex shallow marine/fluviodeltaic/coastal plain cycles, exhibit all the internal facies architecture that would be expected of a shelf succession. The detailed analysis of Yoredale successions has led to the designation of 15 sequences during the Namurian, which have true chronostratigraphic value.

The stacking pattern of Yoredale sequences shows that deposition during the Asbian-Arnsbergian was influenced by three orders of eustatic sea-level change (high, medium and low frequency), which produced three orders of sequence stratigraphic unit (sequences, sequence sets and mega-sequences). Though all three orders of eustatic sea-level change had an influence on deposition, it was the interference of the cycles that produced the major sequence stratigraphic events.

Almost two hundred conodont samples, containing 1039 identifiable elements, representing eleven species, have been used in this study. The multielement species described in the systematic palaeontology and the extensive synonymy lists are a useful addition to British mid-Carboniferous conodont taxonomy.

Five biozones have been erected based upon the first appearance of conodont species. The three Brigantian biozones can each be confidently related to a significant rise in sea level caused by the constructive interference of all three frequencies of sea-level cycle. Whatsmore, each successive biozone is related to a deeper water species which corresponds to the long-term rise in the low-frequency sea-level cycle during this period.

The palaeoecology of the Great Limestone was studied using constrained seriation. This proved a clear shallowing-upward trend and was used to define four biofacies. A comparison between biofacies distribution and sequence stratigraphy proved an intimate relation between sea-level change and the resulting distribution of nekto-benthonic biofacies.

Acknowledgements

First and foremost I wish to acknowledge and thank my main supervisor Howard Armstrong for his help, support, patience and most importantly a judicious use of carrot and stick, in bringing me after four and a half years to the completion of this thesis. Almost 10 years after first introducing me to *Gnathodus et al.*, Howard has been instrumental in this modest contribution to science. Secondly I must thank Maurice Tucker, who gave great support during the early phase of this study and offered essential aid when I was completing the thesis; I must also apologise profusely for not maintaining communications whilst I changed jobs twice and concentrated on the little chaps to the detriment of sequence stratigraphy.

As this research has been carried out over many years, largely isolated from my supervisors, there are many, many geologists who I must thank who have listened patiently and offered advice; this generous support has been invaluable. In particular I would like to thank the staff at the British Geological Survey and the Yorkshire Geological Society. The members of the Pander Society also need special mention for being so inviting and friendly to a relative outsider.

I would like to thank Brian Turner and Mark Purnell for their very helpful examination of this thesis; in many respects it is regrettable that we did not have the opportunity for a viva, but your written comments were very stimulating and will be considered fully as I prepare to write up papers based on this thesis.

Finally, I must thank those close to me over the past few years who have made my research possible. For the first couple of years, Mum, Dad and Katie helped get me started, shouldered the burden of looking after me and kept me going whilst I 'got into the literature' and picked conodont samples into the wee early hours after long days at work. In later years, Sonia has shown characteristic patience with me and this project and was a rock during the last six months writing up.

To all of you above and the many other people who have helped - many, many thanks.

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1. INTRODUCTION

1.1 Regional setting

Topography

This study covers a large area of northeast England, including most of Northumberland and parts of Tyne and Wear, Cumbria, County Durham and southern Scotland (Fig 1.1). The region varies from high open moorland of sheep grazing and forestry plantations, to a broad coastal plain of mixed farming. Much of the region is sparsely populated, however the conurbation of Tyneside and, to a lesser extent, the urban centres of Morpeth, Hexham and Carlisle, support vast areas of rural northern England.

Geology

The geology varies from Lower Palaeozoic to Mesozoic sediments (Fig 1.2). The Ordovician and Silurian basement outcrops in the Southern Uplands and Lake District, as well as in the Cross Fell and Teesdale inliers. The Carboniferous basin fill dominates the area. The thick Dinantian deposits drape the basement uplands and underlie most of the region. The thinner Namurian deposits are restricted to the higher parts of the Northern Pennines and underlie the Vale of Eden. The Westphalian deposits underlie the Durham and Newcastle coalfields in the eastern part of the area and also outcrop as a series of small outliers to the west of Hexham. Post-Carboniferous Permian and Triassic deposits are found in the Vale of Eden and in the south east of the area draping the Carboniferous.

Structural geology

The region is traversed by a number of major faults (Fig. 1.3). During the Carboniferous, these structures delineated the upstanding blocks, from the



granite and the associated buoyant effect was partly responsible for their upstanding nature during the Dinantian (see section 1.2.2 below).

Throughout the Carboniferous, the Northumberland Trough and Solway Basin were connected and deposition was very similar in both basins. However there was a consistent minor raised feature to the north of the Pennine Fault, in the area of the Bewcastle Anticline, that is used to delineate the two basins, in effect minor sub-basins. This study concentrates on the conodont faunas and sequence stratigraphy of the Northumberland Trough, but it is likely that many of the conclusions apply equally to the Solway Basin.

The Northumberland Trough was a half-graben, bounded to the south by the Stublick-Ninety Fathom fault system (Fig 1.4). The Carboniferous basin fill, particularly the Dinantian sediments, thin to the north over the Cheviot Block. There were a number of intrabasinal faults which influenced the thickness of sediment and sometimes the surface drainage pattern, again largely during the Dinantian. During the Silesian, sediment thickness was fairly constant throughout the region, over the basins and blocks.

Stratigraphy

The lithostratigraphy of the different basin and block areas varies due to local facies of deposition (Fig 1.5). This is particularly clear during the early to mid-Dinantian, when the blocks were either exposed or close to sea level and the basins were isolated from each other. By the late Dinantian, deposition across the region was broadly similar, which is reflected by the consistency of lithostratigraphic nomenclature.

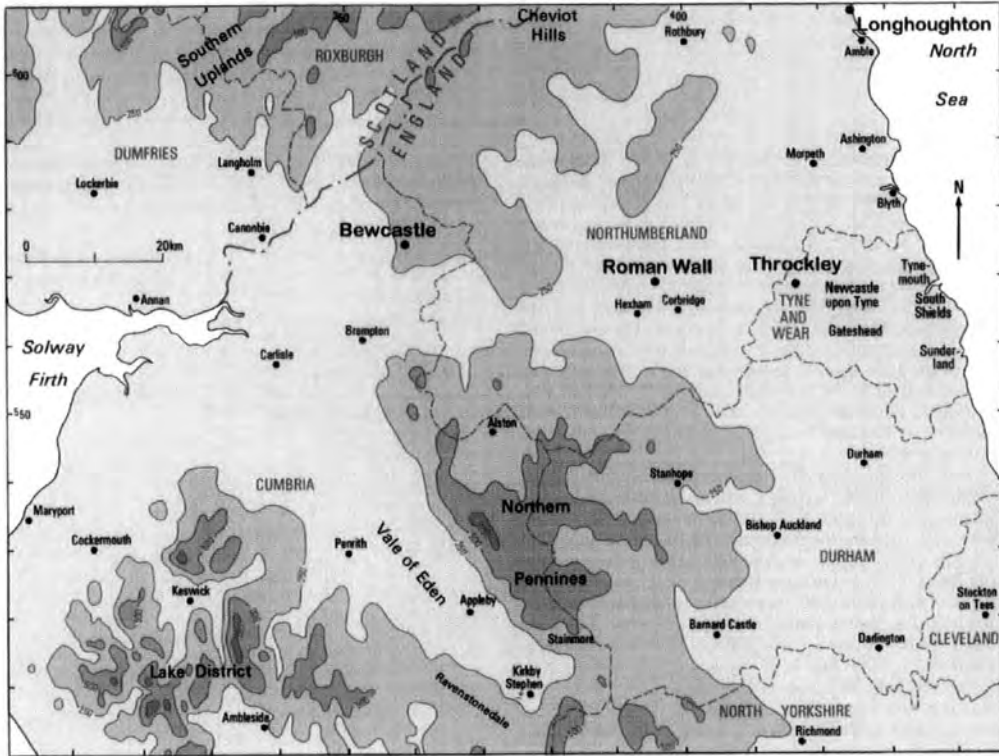


Fig. 1.1 Topographic map of the region showing the four study areas: Bewcastle, Roman Wall, Throckley, Longhoughton (from Chadwick *et al.*, 1995, Fig. 1).

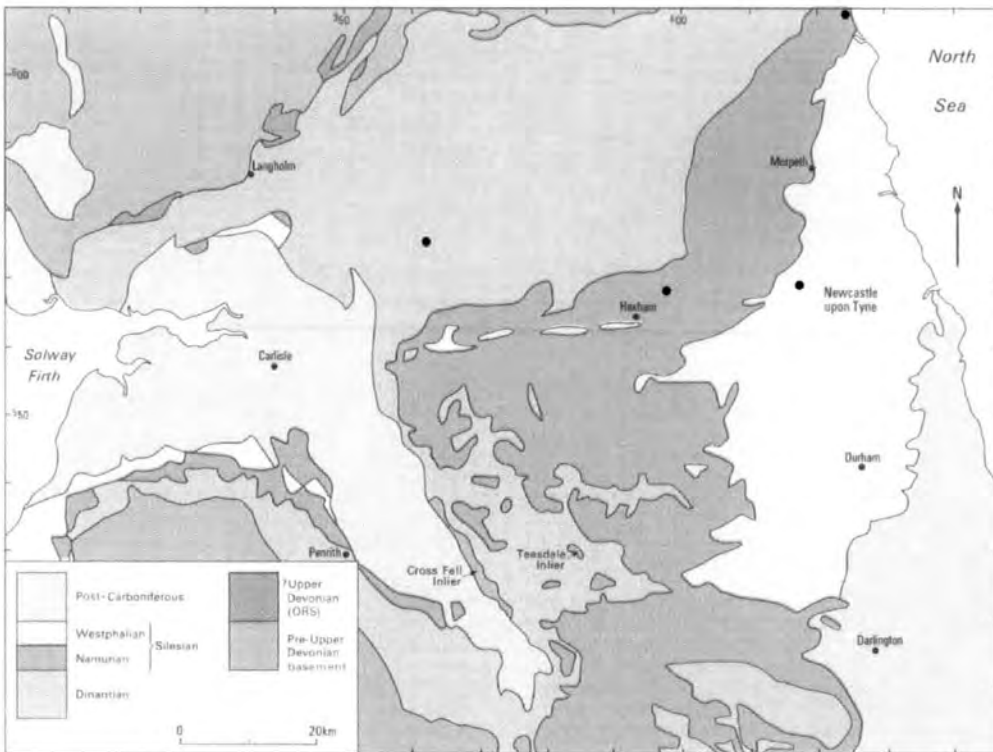


Fig. 1.2 Geological map of the region (from Chadwick *et al.*, 1995, Fig. 2).

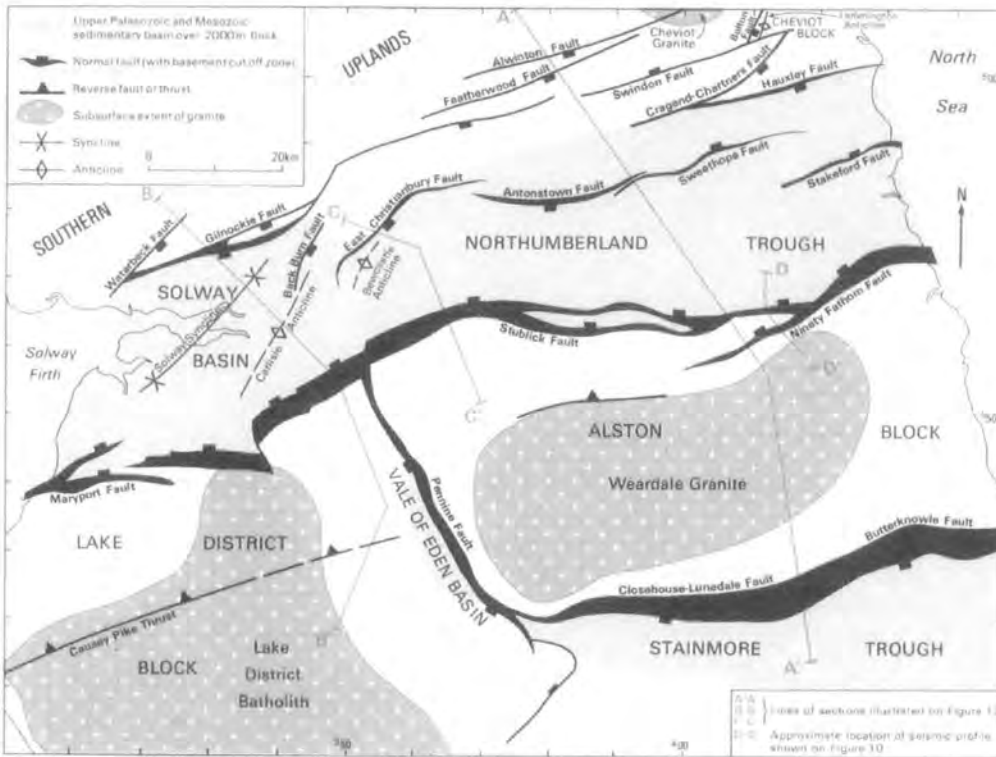


Fig. 1.3 Structural geology of the region: basins and blocks identified (from Chadwick *et al.*, 1995, Fig. 3).

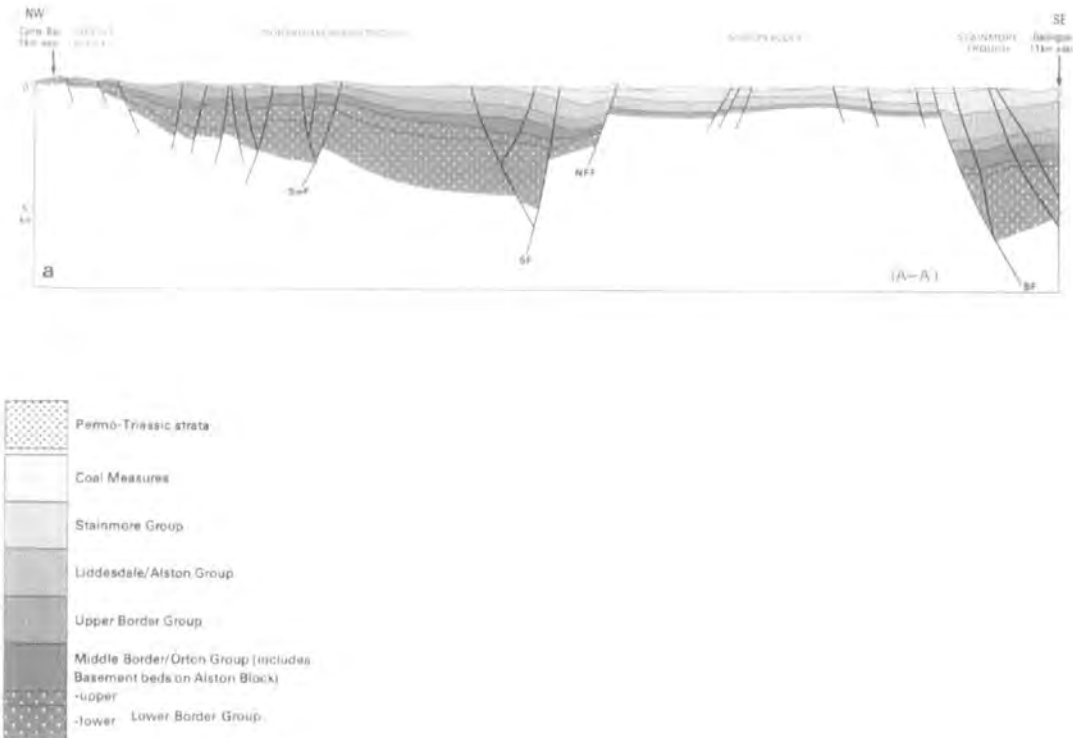


Fig. 1.4 Cross sections through the region (from Chadwick *et al.*, 1995, Fig. 12).

1.2 Basin History

1.2.1 Tectonic and basement controls

The Carboniferous basins of northern England were formed in an extensional regime related to back-arc extension (Fig. 1.6). This was associated with the collision of Gondwanaland and Laurasia and the closure of the Proto-Tethys Ocean (Leeder, 1987, 1988).

The main controls on the formation of the Northumberland Trough were pre-existing structures and basement lithology. The most significant of these controls was the Iapetus Suture Zone, which formed during the collision of Laurentia and Avalonia and the closure of the Iapetus Ocean (Hall *et al.*, 1984; Freeman *et al.*, 1988; Chadwick & Holliday, 1991; Soper *et al.*, 1992). It is thought that the Stublick-Ninety Fathom fault system, which forms the southern margin of the Northumberland Trough, formed by extensional reactivation of this deep crustal shear zone (Fig. 1.7). Many other east to east-north-east trending faults with smaller throws than the Stublick-Ninety Fathom fault system may also be related to deep crustal fractures.

The Alston and Southern upland blocks contain large basement granite intrusions. These acted as structural highs which resisted subsidence throughout much of the synextensional phase of sedimentation, but were buried during later regional subsidence (Leeder, 1982).

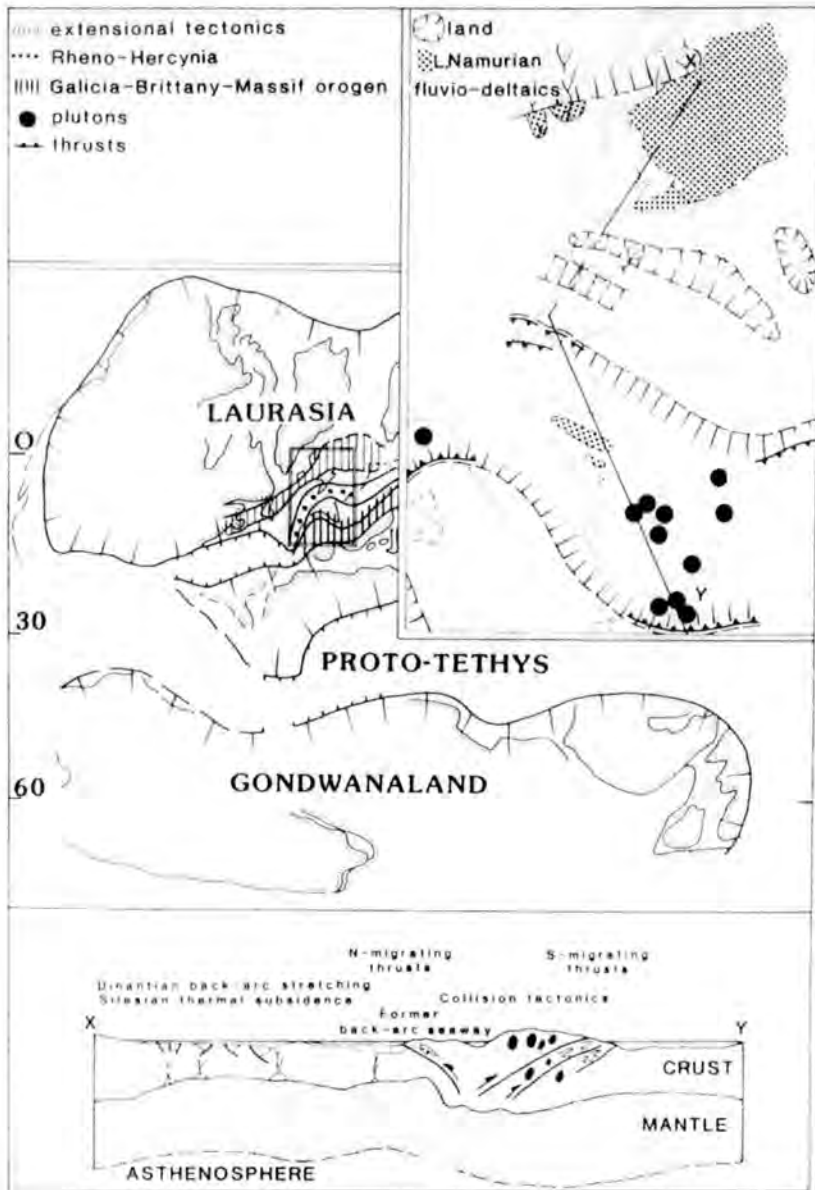


Fig. 1.6 Palaeogeographic reconstruction showing plate tectonic environment and arrangement of continents during the Carboniferous; inset map shows a detail from the Namurian; section shows relationship of collision tectonics and back-arc extension (from Leeder, 1987, Fig. 6)

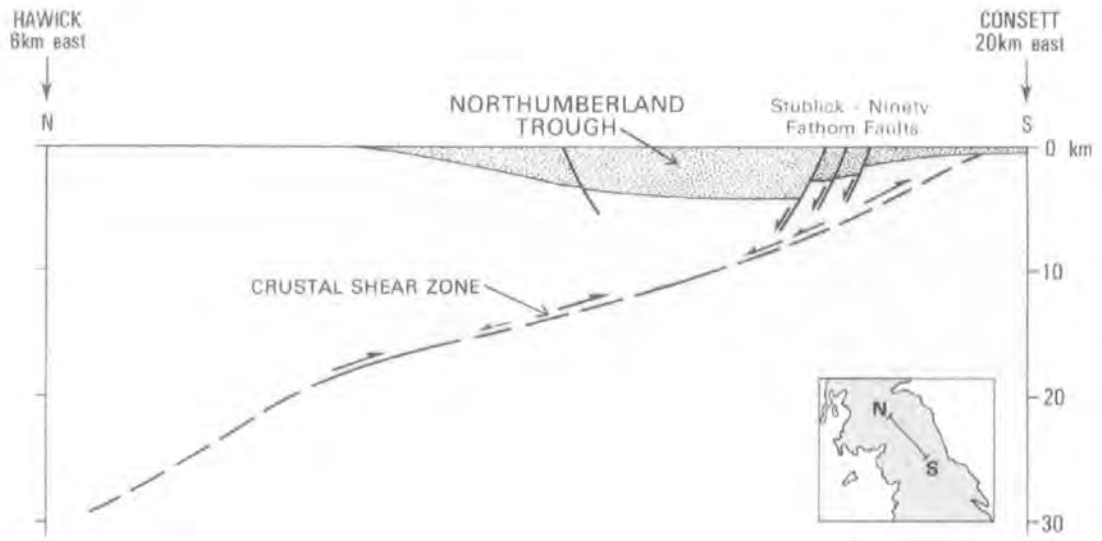


Fig. 1.7 Relationship between the Northumberland Trough and the inferred Iapetus Suture Zone (from Chadwick *et al.*, 1995, Fig. 8).

1.2.2 Rift phase of basin evolution

Studies of the subsidence history of the Northumberland Trough have shown that fault controlled early to mid Dinantian subsidence was much more rapid than the subsequent late Dinantian to Westphalian regional subsidence, the rate of which declined approximately exponentially with time (Leeder & McMahon, 1988; Kimbell *et al.*, 1989). This type of subsidence history where a rapid extensional or 'rift' phase is followed by a more gradual post extensional or 'sag' phase, is common to many sedimentary basins and has been attributed to the process of uniform lithospheric extension (McKenzie, 1978).

In the Northumberland Trough most of the synsedimentary normal faulting (rift phase) occurred during the Courceyan to Holkerian. Thermal subsidence was the dominant mechanism from the Asbian to Westphalian times (sag phase), however minor normal faulting did continue (Chadwick *et al.*, 1995).

The synextensional phase in the Northumberland Trough has been interpreted as a continuous uniform period of subsidence, resulting from basin margin faulting, the rate at which gradually reduced with time (Kimbell *et al.*, 1989). This is probably an over simplification and extension is thought to have been pulsed. Fraser & Gawthorpe (1990) considered that all basins in Northern England had similar trends, whereas Chadwick *et al.* (1995), thought the magnitude and timing of extensional movement varied between basins.

Upper Old Red Sandstone

Red siltstones, sandstones and conglomerates, up to 200m thick, outcrop on the southern flank of the Southern Uplands Block. The lack of faunal control causes ambiguity over the base and top, though a late Devonian to early Dinantian range is thought likely. These siliciclastic sediments are thought to represent a fluvial interior drainage system flowing to the north east in a hot, semi-arid climate (Leeder, 1973).

Lower Border Group

The Lower Border Group was deposited during the main rift phase of basin development, from the Courceyan to the Chadian. It attains a thickness of up to 4000m next to the Stublick-Ninety Fathom fault system, however this varies considerably due to intrabasinal syndepositional normal faulting (Chadwick *et al.*, 1995).

Little is known about the lower (Courceyan) part of the Lower Border Group, due to lack of outcrop. The upper part of the group is well exposed and has received considerable attention (Leeder, 1974, 1975a, 1975b; Leeder *et al.*, 1989). Mudstone, siltstone, sandstone, limestone and dolomite are all exposed and sabkha anhydrite is seen in the seismic profiles. The overall picture is of cycles of fluvio-deltaic deposition from the north east followed by marine transgression with carbonate and evaporite formation; local sediment accumulated at the margins of the basin.

Middle Border and Fell Sandstone Groups

These two laterally equivalent units formed during the Arundian to Holkerian. The rate of fault controlled subsidence decreased during this period, with little fault related variation in the thickness of the units. The period also represents the beginning of thermal subsidence, which is marked by the gradual thickening of these units toward the basin centre. The change from rift to sag subsidence mechanisms, resulted in the first onlapping deposition onto the blocks, with up to 200m being deposited (Chadwick *et al.*, 1995).

This was a period of marked lateral facies variation. The Fell Sandstone Group, in the north and east of the basin, is a coarse arenaceous unit representing a braided river system flowing from the north east (Hodgson, 1978; Turner *et al.*, 1997). In the south and west, the Middle Border Group represents fluvio-deltaic and shallow marine deposition of mudstones, siltstones, fine sandstones and limestones of a hot semi arid climate (Leeder *et al.*, 1989).

1.2.3 Sag phase of basin evolution

During the early Asbian, extensional fault movement greatly decreased and regional subsidence truly dominated the basin development. Sedimentation quickly encroached onto the blocks. By late Asbian - early Brigantian, there were no barriers to sedimentation and relatively uniform conditions prevailed over the entire area. The variation in sediment thickness from this time onwards, is a function of the compaction of underlying unconsolidated sediments. For some time therefore, the units are more condensed on the blocks (Chadwick *et al.*, 1995).

Upper Border Group

These early Asbian sediments are mainly restricted to the basins. Less than 800m of sediment was deposited in the Northumberland Trough, with thin deposits on the margins. The variable sequence of siliciclastics, limestones and coals are thought to represent coastal plain, fluvio-deltaic and shallow marine environments. Cyclicality, also common in the superseding groups, formed from marine incursions from the south west, followed by fluvio-deltaic progradation from the north east (Frost & Holliday, 1980; Leeder *et al.*, 1989).

Liddesdale Group

The late Asbian and Brigantian was a period dominated by regional subsidence. The earliest sediments were restricted to the Northumberland Trough, as with the Upper Border Group, where the group is over 800m thick. During the latest Asbian however, there was a major marine transgression which covered the Alston Block (Chadwick *et al.*, 1995).

The Liddesdale Group is the early part of the so called Yoredale sedimentation (Phillips, 1836). This period is most notable for the development pure, thick, laterally persistent limestone horizons, with an abundant open marine fauna. These are best developed in the south west and become thinner and more siliciclastic rich towards the north east. The remainder of the typical Yoredale sedimentation is made up of a prograding fluvio-deltaic sequence of distal mudstones grading into proximal sandstones. The top of the sequence is marked by a palaeosol and coal.

These limestone to coal packages are found in rhythmic cycles (traditionally termed cyclothems). The limestone represents a marine transgression and the succeeding sequence represents the prograding fluvio-deltaic system and establishment of the coastal plain (see Leeder & Strudwick, 1987 and Reynolds, 1992 for a recent discussion of Yoredale sequences). These Yoredale facies continue for some time into the Namurian, but are best developed in the Brigantian.

Stainmore Group

The Stainmore Group (Burgess & Holliday, 1979) represents the whole of the Namurian, when over 800m of sediment were deposited, most of it during the Pendleian and Arnsbergian. The period was dominated by regional subsidence and compaction of previous sediments, with only minor movement on the faults (Chadwick *et al.*, 1995). The entire group is poorly understood; this is due to very poor exposure, a lack of borehole data and an inadequate biostratigraphic framework.

The Stainmore Group can be divided into two parts: the 'Upper Limestone Group' and 'Millstone Grit' of previous classifications (Hull, 1968). The lower has numerous limestone horizons and represents a Yoredale facies, though the cycles become thinner and more terrestrially dominated up the succession (Farmer & Jones, 1969; Elliott, 1976a). Thick channel sandstones are seen towards the top of many cycles, some of which may have cut out much of the underlying strata (Elliott, 1976b; Hodge & Dunham, 1991). The upper division is characterised by widespread coarse sandstone units. These are thought to represent braided river deposits, that flowed from the north east (Leeder *et al.*, 1989). Though they lie on minor erosion surfaces, there is little evidence of great down-cutting and removal of lower sediments. Contrary to early opinion, these sheet sands are now thought to be of limited lateral extent and are only of local correlative value (Brian Young pers. comms.). Marine horizons in this upper division are rare and contain restricted faunas of limited biostratigraphic value.

Coal Measures

These are exposed in the Northumberland and Durham coalfields where they attain a maximum thickness of 830m, with small outliers north of the Stublick Fault. They were laid down under relatively uniform regional subsidence, which resulted in similar facies throughout the region (Chadwick *et al.*, 1995). Repeated cycles of mudstone, siltstone, sandstone, and coal representing coastal and delta plain environments extended over the basins and blocks alike. Thin marine shales representing marine incursions are found sporadically (Fielding, 1984).

1.2.4 Basin Inversion

By the late Carboniferous, the Variscan Orogeny had culminated in significant deformation in northern France, Belgium, southern England, south Wales and southern Ireland. Northern England was subjected to minor compressional deformation, which terminated basin evolution, resulted in local reactivation of pre-existing weaknesses and caused varying degrees of basin inversion. This occurred sometime after the deposition of the preserved Westphalian strata and before the deposition of late Permian strata which lies unconformably on the Carboniferous (Chadwick *et al.*, 1995). Precise dating of this compression is difficult, but may have started as early as the Bolsovian (Glover *et al.*, 1993).

1.3 Aims

Aim 1 - To review and update mid-Carboniferous multielement conodont taxonomy

The systematic palaeontology of the conodont faunas underpins this study. Almost all the published record of conodont taxonomy from the Asbian to Arnsbergian of Britain has been based on single element, form taxonomic concepts (see summary of Varker & Sevastopulo, 1985; Higgins, 1985). The previous research has also been dominantly focused towards biostratigraphic results (e.g. Higgins, 1975; Metcalfe, 1981).

This study aims to review international work on the multielement species of the late Viséan to early Namurian and to clearly establish a British multielement taxonomy at this horizon based on the faunas from the Northumberland Trough as a benchmark for further work. It is hoped that this work will form the basis of a published monograph.

Aim 2 - To test the biostratigraphic potential of the conodont faunas

The British conodont biostratigraphy of the Asbian - Arnsbergian has a healthy research record (Rhodes *et al.*, 1969; Higgins, 1975; Metcalfe, 1981; Varker & Sevastopulo, 1985; Higgins, 1985; Dean, 1987; Armstrong & Purnell, 1987). The established biozonal scheme is largely based on form taxonomy (as discussed above) and is based on deep-water faunas from the Dinantian Craven Basin (Varker & Sevastopulo, 1985) and Silesian Pennine Basin (Higgins, 1975; 1985)

This study aims to build upon the work of Armstrong & Purnell (1987), by testing the established scheme using modern biologically based multielement taxonomy and the shallow water faunas of the Northumberland Trough.

Aim 3 - To compare palaeoecological models for mid-Carboniferous conodont faunas

A number of palaeoecological models exist for the mid-Carboniferous (e.g. Austin, 1976; von Bitter, 1976; Higgins, 1981; Austin & Davies, 1984; Rexroad & Horowitz, 1990; Davies *et al.*, 1993; Krumhardt *et al.*, 1996). The aim of this study is to compare these previous schemes to the Northumberland faunas and to set up a palaeoecological model for shelf faunas of the Asbian - Arnsbergian.

Aim 4 - To critically compare the Exxon sequence stratigraphic model against spacial and temporal variation within 'Yoredale' type sequences

The sequence stratigraphic model originally proposed by Vail *et al.* (1977) has revolutionised the way that sedimentary packages are interpreted. The aim of this study is to compare this model with the Yoredale sequences of the Liddesdale and Stainmore Groups, which for many years have been considered to result from glacio-eustatic sea level change.

Aim 5 - To produce a sea-level curve for the Asbian - Arnsbergian of the Northumberland Trough

A number of authors have produced a sequence stratigraphic scheme for correlation in the Carboniferous basins of Northern England (e.g. Fraser & Gawthorpe, 1990). These schemes have concentrated on the Dinantian rift phase of basin evolution throughout all the basins of Northern England; as a result, the major control is extensional tectonic activity.

This study aims to concentrate on glacio-eustatic induced sea level change to elucidate events of global significance and therefore of global correlative value.

Aim 6 - Ultimately, to consider the influence of sea level change as a fundamental control on the conodont faunas

The basic premise of sequence stratigraphy, as a modern stratigraphic discipline, is that change in sea level is the fundamental influence that controls lithostratigraphic and biostratigraphic variation. In this study, it is hoped that by comparing the conodont biostratigraphy and palaeoecology with the sequence stratigraphy, we may gain some impression as to the importance of sea level change as a control during Asbian - Arnsbergian times in the Northumberland Trough.

2. SEQUENCE STRATIGRAPHY

2.1 Introduction

Sequence stratigraphy is now firmly established as a key interpretative and predictive tool. Since the Exxon model was first proposed (Vail *et al.*, 1977), much work has been published exploring many detailed facets of the theory. As a result the model has evolved, but still the most commonly cited references for the definitive principles is the seminal collection of papers edited by Wilgus *et al.* (1988) (in particular, van Wagoner *et al.*, 1988; Posamentier *et al.*, 1988; Posamentier & Vail, 1988) and the later work on high resolution sequence stratigraphy (van Wagoner *et al.*, 1990). Unless stated otherwise, it is this concept of sequence stratigraphy that will be used in this study.

Key definitions

The term sequence will be used throughout following the original definition - "a relatively conformable succession of genetically related strata bounded at its top and base by unconformities and their correlative conformities" (Vail *et al.*, 1977).

The term cyclothem is used in this study in the traditional way to define the strata from the base of one limestone unit up to the base of the succeeding limestone unit, taking its name from the lower limestone unit. It will be seen that this is not a valid definition in modern sequence stratigraphic terms, i.e. a sequence does not correspond with a cyclothem.

2.2 Sedimentology of Yoredale Cyclothems

The finest area to study Yoredale cyclothems within the Northumberland Trough, is found near the village of Longhoughton, to the east of Alnwick, Northumberland (Fig 2.1, 2.2). This coastal section from the hamlet of Howick in the north (NU258178), to the hamlet of Boulmer in the south (NU266143) exposes almost the entire succession of the Stainmore Group. This unique section has therefore attracted considerable academic attention (Carruthers *et al.*, 1930; Westoll *et al.*, 1954; Farmer & Jones, 1969; Farmer *et al.*, 1970; Elliot, 1976a; Tucker, 1977, 1995; Reynolds, 1992; Turner & Spinner, 1992).

2.2.1 *The Howick Limestone Cyclothem*

The best exposed of the Stainmore Group Yoredale cyclothems is that with the Howick Limestone (*sensu* Farmer *et al.*, 1970) at its base. Four sections through this cyclothem at different localities show considerable variation, allowing a good two-dimensional picture to be constructed (Fig 2.3).

The Howick Limestone is a dark grey to black bioclastic lime mudstone-wackestone and has a fauna typical of the local Yoredale limestones: productid and spiriferid brachiopods, crinoid ossicles and fenestellid bryozoans. It outcrops as a continuous bed or as a series of large (1.5-2m) septarian nodules up to 30cm thick. Above and below the limestone bed is a thin marine mudstone with a similar benthic fauna to the limestone itself. The limestone and associated mudstones are considered to represent deposition in an open-marine environment with a mud dominated substrate, during a period when there was little siliciclastic input into the basin.

In all the sections, the limestone is overlain by mudstone containing small siderite nodules (1-4cm). With the exception of the central Howick Bathing House section, in the other sections this mudstone grades upwards into a fine sandstone. At Howick Bay, this takes the form of interbedded mudstone and sandstone becoming gradually more sand dominated. At Howick Haven, the mudstone becomes lenticular bedded (containing small sand ripples), then grades upwards into flaser

bedded sandstone (dominated by sand ripples with thin mud streaks) and ultimately into fine planar cross-bedded sandstone. At Howick Burn Mouth, the mudstone grades into fine sandstone as at Howick Bay, however the unit is only thin (1.3m) with another mudstone bed overlying the fine sandstone.

In the two northern sections, this first coarsening-upward unit is quickly cut out by a medium to coarse-grained, trough cross-bedded sandstone unit. The three-dimensional architecture of this sandstone is very clearly that of a channel that is aligned west to east and pinches out to the north and south (channel width 850m; depth 12-15m). This multistorey sandbody with a restricted and definable channel form, made up of large trough cross-sets (with a unimodal west to east palaeocurrent), of coarse sandstone (with no mud/silt fraction), is interpreted as a braided river deposit.

In the southerly section at Howick Burn Mouth, there is no evidence of this channel sandstone. Instead, there is a very well exposed succession of coarsening-upward units, varying in thickness from 2-5m (Fig. 2.4); each unit has a mudstone at the base and grades upwards into fine-medium grained sandstone. The lower units are less terrestrially influenced, with a limestone at the base of the first and a non-marine bivalve fauna at the base of the second. The upper units tend to have a rootlet bed at the top and these become thicker in each succeeding unit; the penultimate unit is capped by a carbonaceous horizon and the final unit is overlain by a coal. Elliott (1974a, 1976a) interpreted these coarsening-upward units as the result of deposition in a deltaic environment, dominantly within interdistributary bays.

It is quite clear from this description that deposition within Yoredale cyclothem was very complex, with considerable lateral variation taking place within relatively short distances. The poor outcrop of most of the Liddesdale and Stainmore Groups therefore creates two major problems: it makes detailed lithostratigraphic correlation very difficult indeed, in fact totally reliant on thin limestones which are assumed to be regional in extent; it also makes it impossible to produce anything but the most rudimentary three-dimensional palaeoenvironmental reconstructions.

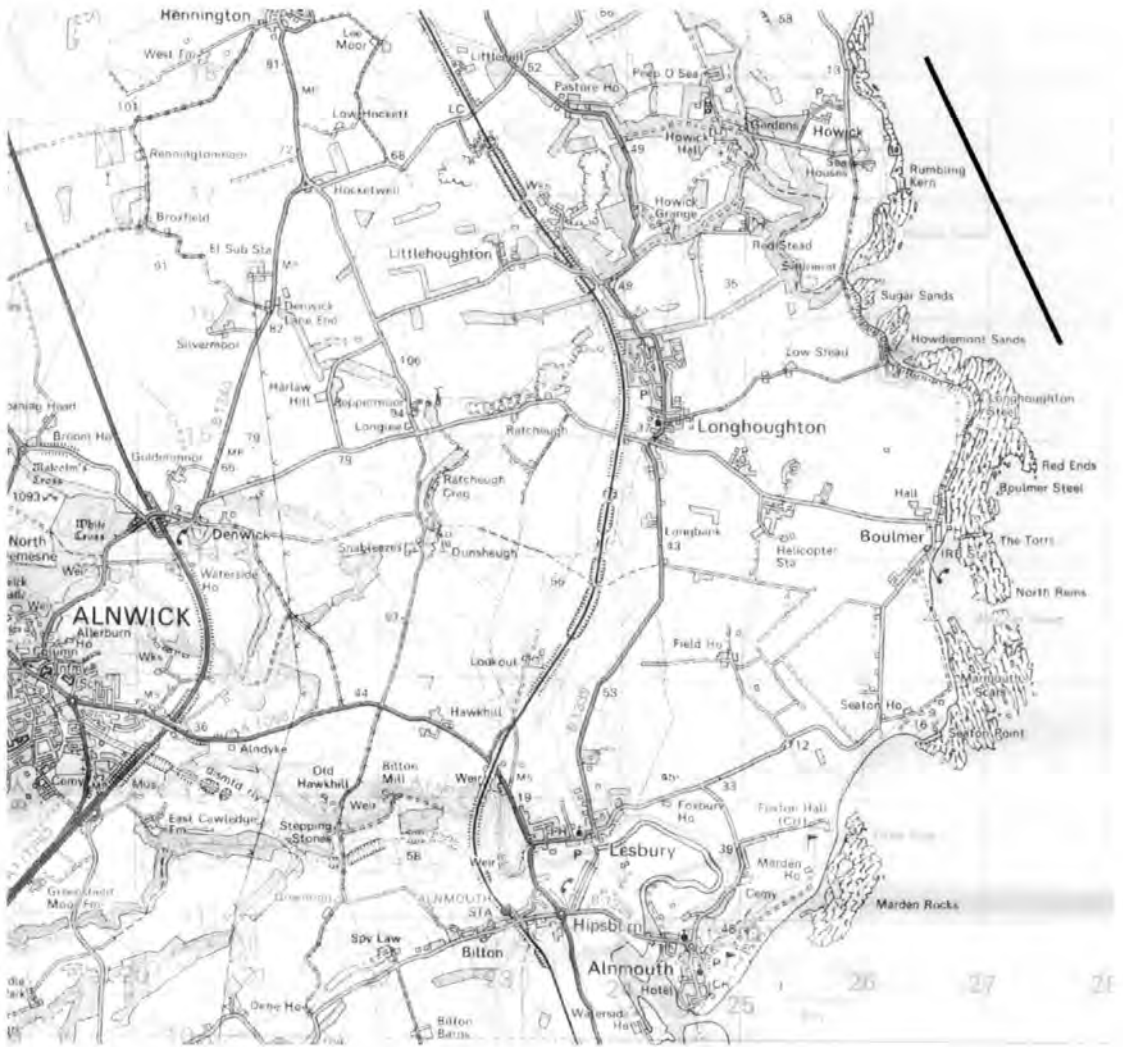


Fig. 2.1 Scan of Ordnance Survey Landranger Sheet 81, (Alnwick, Morpeth & surrounding area), with 1km grid squares shown and national grid reference eastings and northings marked; black line marks the Longhoughton section.

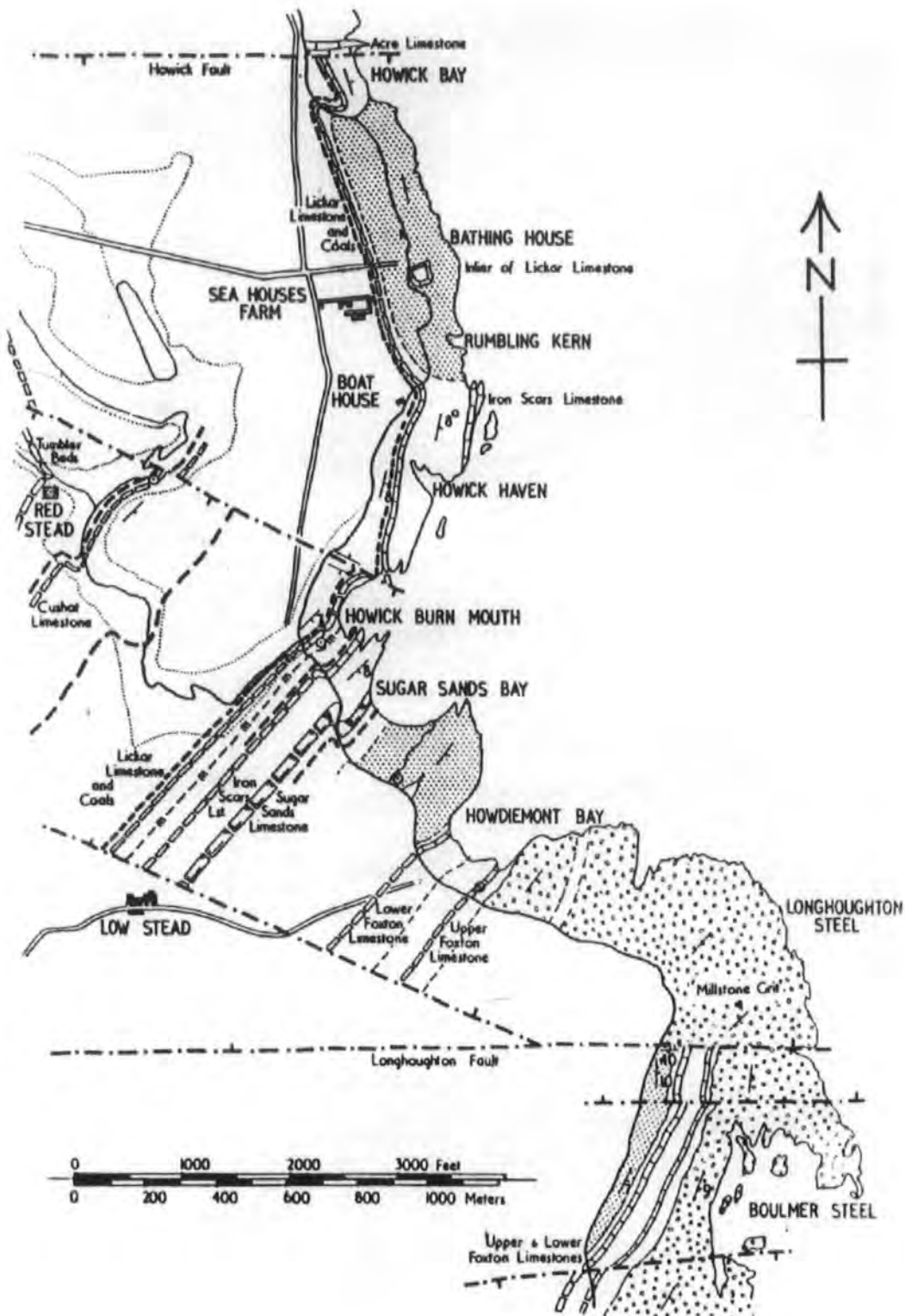


Fig. 2.2 Map of the coastal section at Longhoughton (from Farmer & Jones, 1969, Fig. 1).

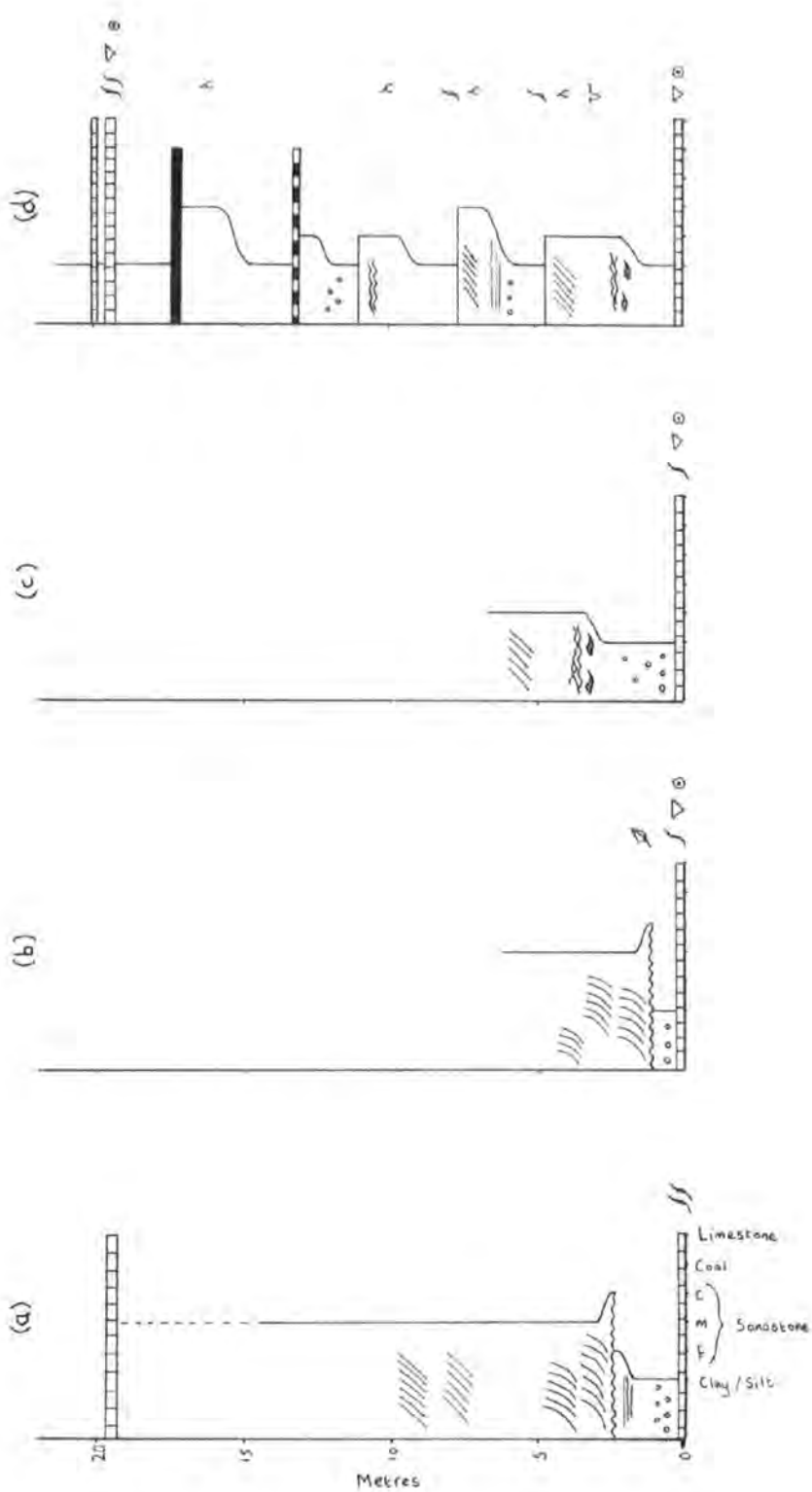


Fig. 2.3 Cross section through the Howick Limestone Cyclothem: a) Howick Bay (NU259179); b) Howick Bathing House (NU263174); c) Howick Haven (NU262169); d) Howick Burn Mouth - see Fig 2.4 for details (NU258163).

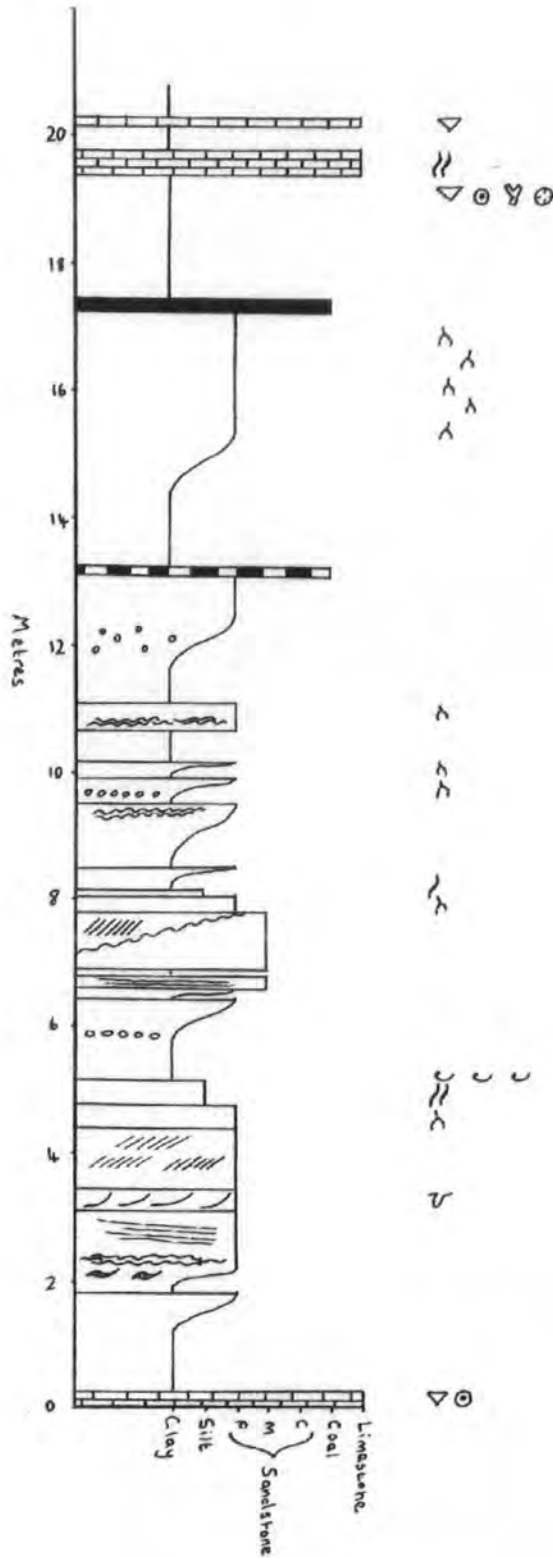


Fig. 2.4 Graphic log of the Howick Limestone Cyclothem at Howick Burn Mouth (NU258163).

2.2.2 *The Longhoughton succession*

Almost the entire Stainmore Group can be seen along the valley of Howick Burn and along the coast: from the Great Limestone (NU252168) to the Longhoughton Grits that form the foreshore for 3km to the south of Howdiemont Bay (NU263157). The sections that are not exposed were cored in a study by Farmer & Jones (1969).

The Great Limestone is poorly exposed in the stream beneath Red Stead and Howick Hall (Carruthers *et al.*, 1930). Above this, the cyclothem is dominated by a coarse-grained, cross-bedded sandstone. This outcrops in an old quarry beneath Red Stead Farm (NU253167) and the thickness and lithology resemble the major channel on the coast beneath Howick Bathing House. Above this 20m thick sandstone unit, the remainder of the cyclothem consists of 8m of alternating sandstone and mudstone units (Fig. 2.5).

The Cushat Limestone outcrops on the south side of Howick Burn, approximately 125m upstream of the confluence with the small tributary beneath Red Stead Farm (NU255168). A 25cm lower bed of limestone is separated by 1m of mudstone from a 30cm upper bed of limestone. The macrofauna is similar to that of the Howick Limestone noted above, however a bradyodont fish tooth is recorded by Farmer & Jones (1969). The upper limestone is an exceptional rock that has been totally leached of all carbonate, leaving a weakly cemented orange, ochrous, spongy residue with almost no density. The remainder of the 80m Cushat Limestone Cyclothem (Fig. 2.6, 2.7) is made up of six coarsening-upward units that do not outcrop. From the log of a borehole given by Farmer & Jones (1969), it resembles the cyclic succession of the Howick Limestone Cyclothem described above from Howick Burn Mouth. It is assumed that these coarsening-upward units were also deposited in an deltaic environment.

The Howick Limestone Cyclothem at Howick Burn Mouth, described above, is encountered up-section of the Cushat Limestone in Howick Burn (Fig. 2.4). The overlying Iron Scars Limestone is exposed on the coast to the south (Fig. 2.7). It begins with a distinctive orange weathering limestone (thus the name Iron Scars). This hard compact limestone (40cm thick) is overlain by mudstone (30cm) and then

another thinner limestone bed (15cm). Both beds of limestone are laterally continuous across the foreshore and are not nodular like the Howick Limestone. Both beds of limestone are only sparsely fossiliferous, however the mudstone below the lower bed has a fauna similar to the Howick Limestone with the notable addition of solitary zaphrentid corals. The overlying siliciclastic sediments are covered by sand on the foreshore, however Farmer and Jones (1969) recorded two coarsening-upward units (Fig. 2.7).

The Sugar Sands Limestone Cyclothem (Fig. 2.8) begins with a thick, dark, compact limestone that is divided into a number of layers with thin, wavy mudstone partings, possibly the result of pressure dissolution, rather than a depositional feature. The fauna is dominated by brachiopods and large gigantoproductids can be seen on the bedding-plane surfaces. The overlying mudstone dominated lower part of the cyclothem has been eroded away and forms the pretty sandy inlet of Sugar Sands Bay. The upper part of the cyclothem is exposed on the next headland to the south and is made up of coarse-grained, trough cross-bedded sandstone, very similar to the channel fill sandstone from the Howick Limestone Cyclothem. It is important to note that Farmer & Jones (1969) showed that there is a mudstone unit in the middle of the coarse cross-bedded sandstone (see later sequence stratigraphic interpretation of this succession; section 2.3.5)

The Lower Foxtan Limestone and Upper Foxtan Limestone Cyclothems (Fig. 2.9) are mudstone dominated and have been eroded to form Howdiemont Bay. A borehole of this interval (Farmer & Jones, 1969) showed two mudstone-dominated, coarsening-upward units in the Lower Foxtan Limestone Cyclothem and a single coarsening-upward unit in the Upper Foxtan Limestone Cyclothem.

Eroding down into the siliciclastic sediments of the Upper Foxtan Limestone Cyclothem is another coarse-grained channel sandstone. This thick unit dominates the coastal outcrop from Longhoughton Steel (NU270155) for 5 km to the south. Previous authors have considered these 'Longhoughton Grits' to be a single coarse sandstone unit broadly similar to some of the coarse Namurian grits from the Pennine Basin and they have been mapped as a lithological unit termed the 'Millstone Grit' throughout the Northumberland Trough (e.g. Carruthers *et al.*, 1930;

Johnson, 1995). Since the definition of the Stainmore Group, these sandstone units at the top of the group have been considered to be individual channels or extensive sheets similar to those found in lower levels of the group, but more densely arranged (e.g. Mills & Holliday, 1998). Leeder (1989) considered these sandstone units to be thick multi-storey sheet sands of fluvial braid-plain origin.

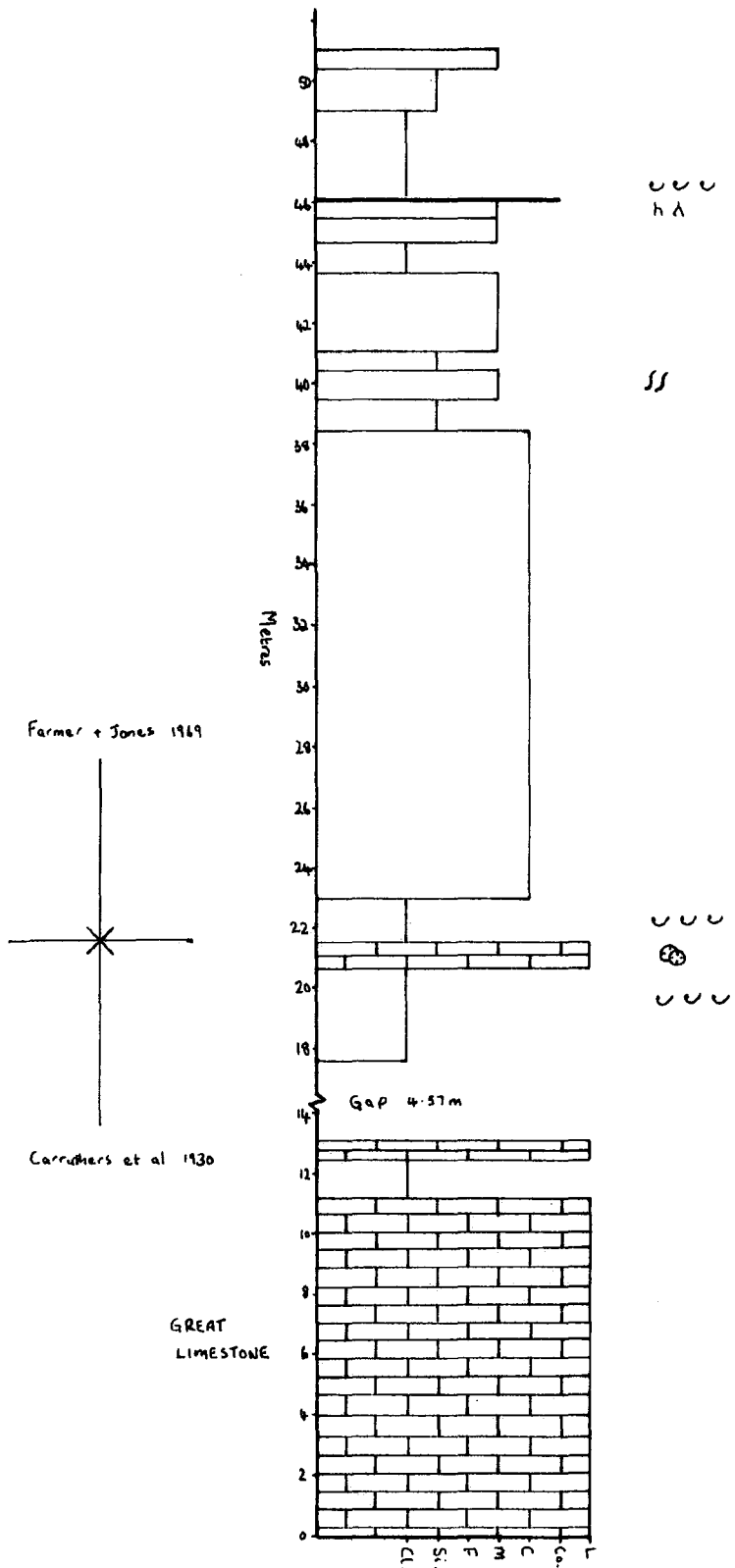


Fig. 2.5 Graphic log of the Great Limestone Cyclothem (lithologies as Fig. 2.4): lower part based on Carruthers *et al.* (1930) from stream sections beneath Red Stead (NU252168) and beneath the bridge east of Howick Grange (NU251173); upper part based on personal field work and Farmer & Jones (1969) downstream of Red Stead.

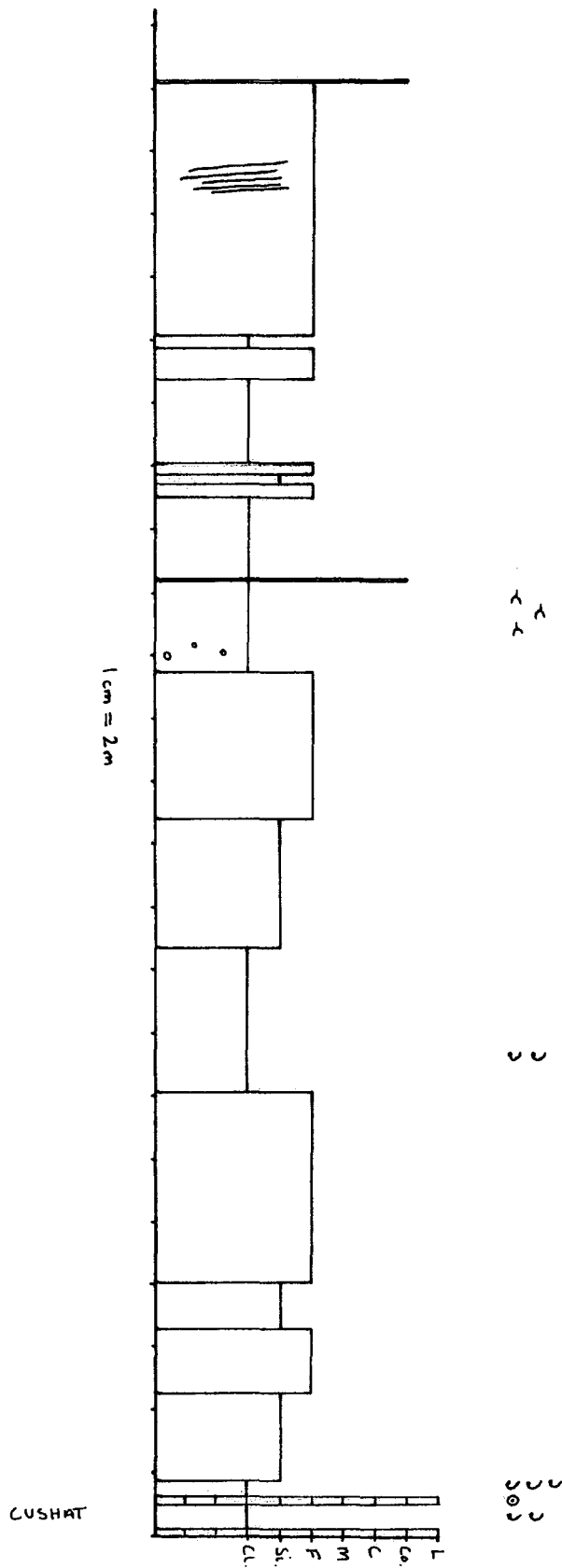


Fig. 2.6 Graphic log of the lower part of the Cushtat Limestone Cyclothem in Howick Burn (NU254168) based on Farmer & Jones (1969).

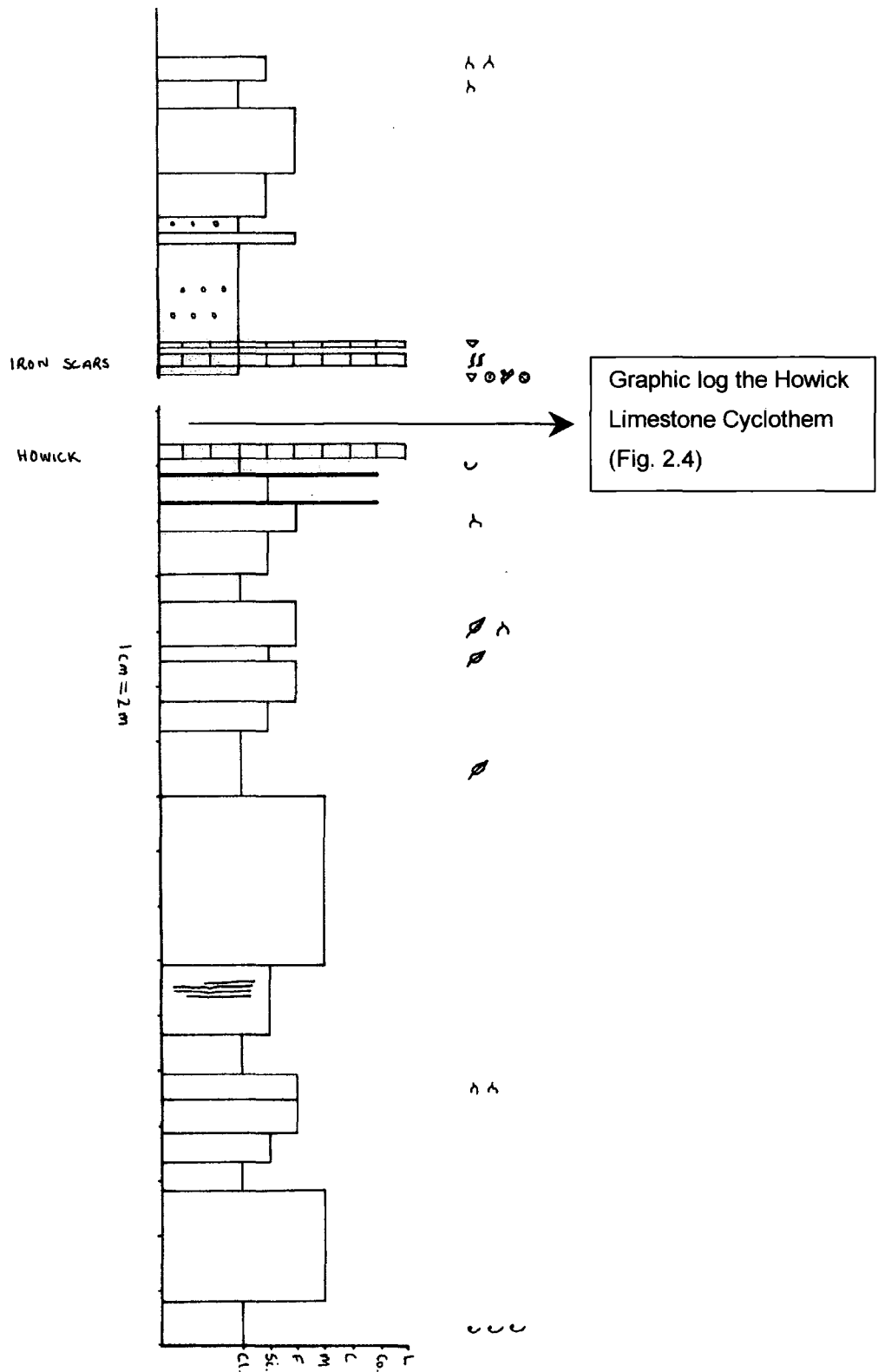


Fig. 2.7 Graphic log of the upper part of the Cusht Limestone Cyclothem in Howick Burn (NU254168) and the Iron Scars Cyclothem on the coast south of Howick Burn Mouth (NU260162) based on personal fieldwork and Farmer & Jones (1969).

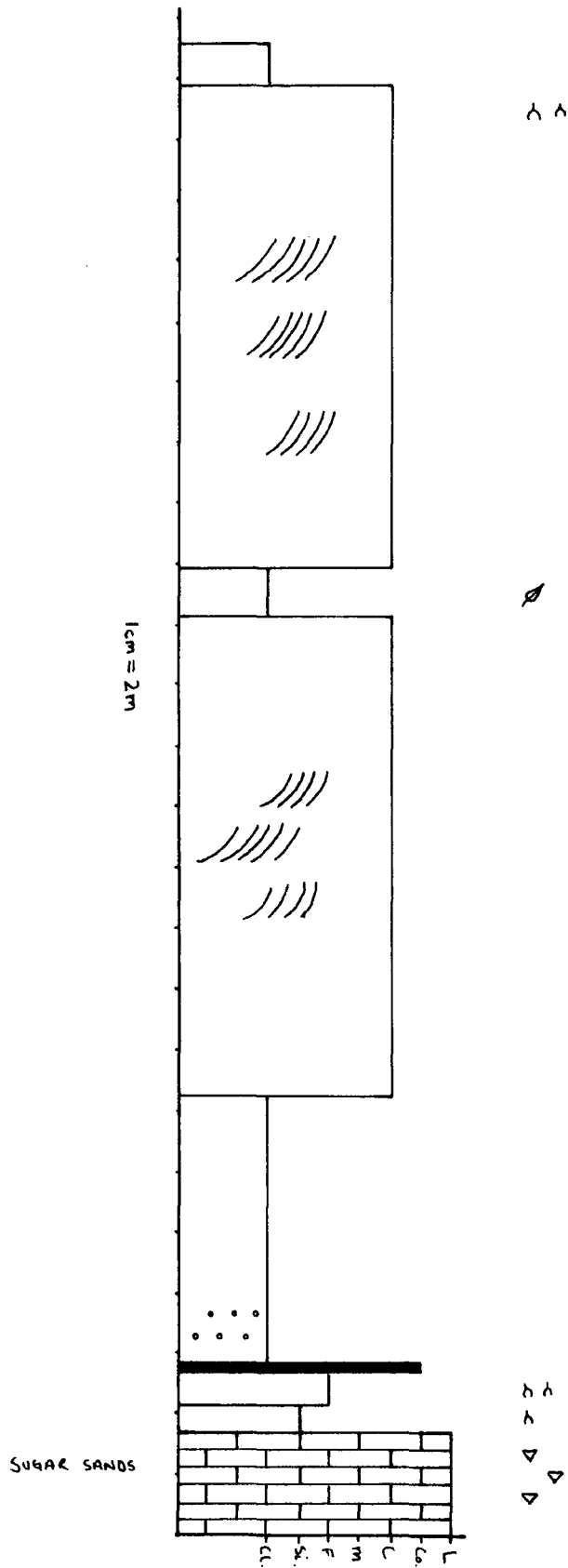


Fig. 2.8 Graphic log of the Sugar Sands Limestone Cyclothem north of Sugar Sands Bay (NU260161) based on personal fieldwork and Farmer & Jones (1969).

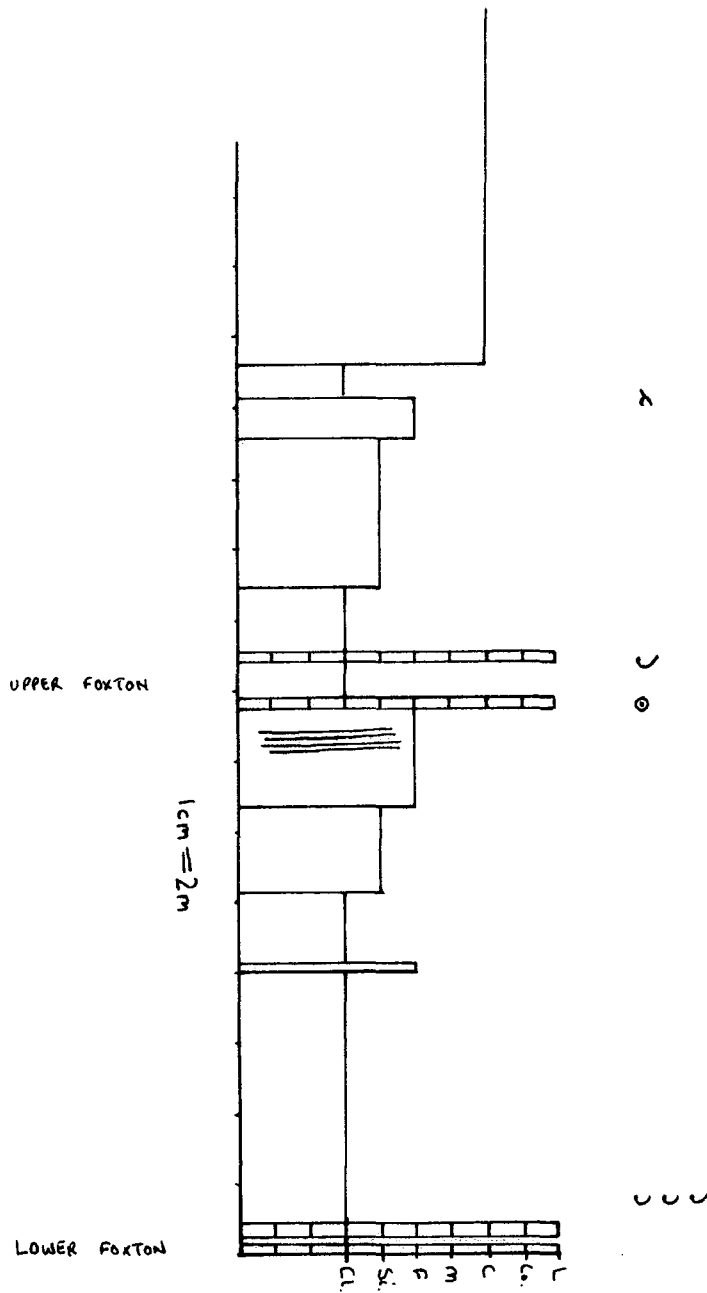


Fig. 2.9 Graphic log of the Lower and Upper Foxton Limestone Cyclothem at Howdiemont Bay (NU263157) based on Farmer & Jones (1969).

2.3 High Resolution Sequence Stratigraphy

Sequence stratigraphy is an ideal tool for interpreting Yoredale successions, as true sequences, their constituent systems tracts and key bounding surfaces can be clearly defined. Each Yoredale sequence broadly equates to a cyclothem, however there are distinct differences between these units and these have significant chronostratigraphic implications.

Yoredale sequences fall within the concept of high resolution sequence stratigraphy (*sensu van Wagoner et al., 1990*). This is because they are defined using outcrop and borehole evidence and the internal architecture and relationships between Yoredale sequences is beyond the resolution of seismic profiling.

2.3.1 Evidence for the lowstand systems tract

Sequence boundary

This key stratal surface forms when sea level falls below the shelf-margin break, exposing the shelf. This forms an unconformity over the shelf and a correlative conformity beyond the shelf-margin break. The actual unconformity on the exposed shelf can be defined by the terrestrial processes that take place (Fig. 2.10).

Incised-valley

During the early lowstand systems tract, after the initial fall of relative sea-level, the fall in base-level and resultant re-adjustment of the graded river profile, caused strong fluvial erosion which created incised-valleys across the shelf (Schumm, 1993). If this lowstand of relative sea-level was short lived, this would have produced a number of discrete incised-valleys separated by large areas of interfluvial. If however the period of lowstand was prolonged, then the incised-valleys would have migrated laterally forming large areas of erosion with smaller interfluvials. Ultimately, if these lowstand conditions had continued, the entire shelf would have become denuded to the level of the new graded river profile, eroding through the sediments of the previous sequence and leaving no interfluvial.

Incised-Valley Fills

During the late lowstand systems tract, once relative sea level begins to rise, deposition occurred within the incised-valleys on the shelf and aggradation began within the fluvial system. Large braided rivers built up in the incised-valleys, with deposition being dominated by the coarse fraction of the bedload, with all mud and fine sand being transported into the basin. Thus the incised-valley fill is a coarse sandstone with trough cross bedding. The form of a sequence boundary at the base of an incised-valley fill is illustrated in figure 10a.

Interfluvial palaeosols

The lateral equivalent of the incised-valley and the later sediment fill is an area of exposed shelf that underwent terrestrial, pedogenic processes (Aitken & Flint, 1996; Davies & Elliott, 1996). The interfluvial palaeosols developed during the lowstand represent a prolonged period of exposure and pedogenesis; the result is a thick layer of pale, quartz-rich, fine-grained, massive sandstone dense with rootlets, *Stigmaria* roots and other organic traces. The best example is that at the top of the Howick Limestone Sequence which is 2m thick. The form of a sequence boundary above an interfluvial palaeosol is illustrated in figure 10b.

The underlying sediment that underwent pedogenesis was usually of the highstand systems tract. Palaeosols are not uncommon within the highstand systems tract itself; they are the result of temporary exposure of a crevasse splay sand-sheet or an old distributary after avulsion has taken the channel in another direction. These palaeosols are therefore the result of short lived pedogenesis prior to inundation of the area or another flood deposit and less mature than those formed on an interfluvial during lowstand systems tract conditions.

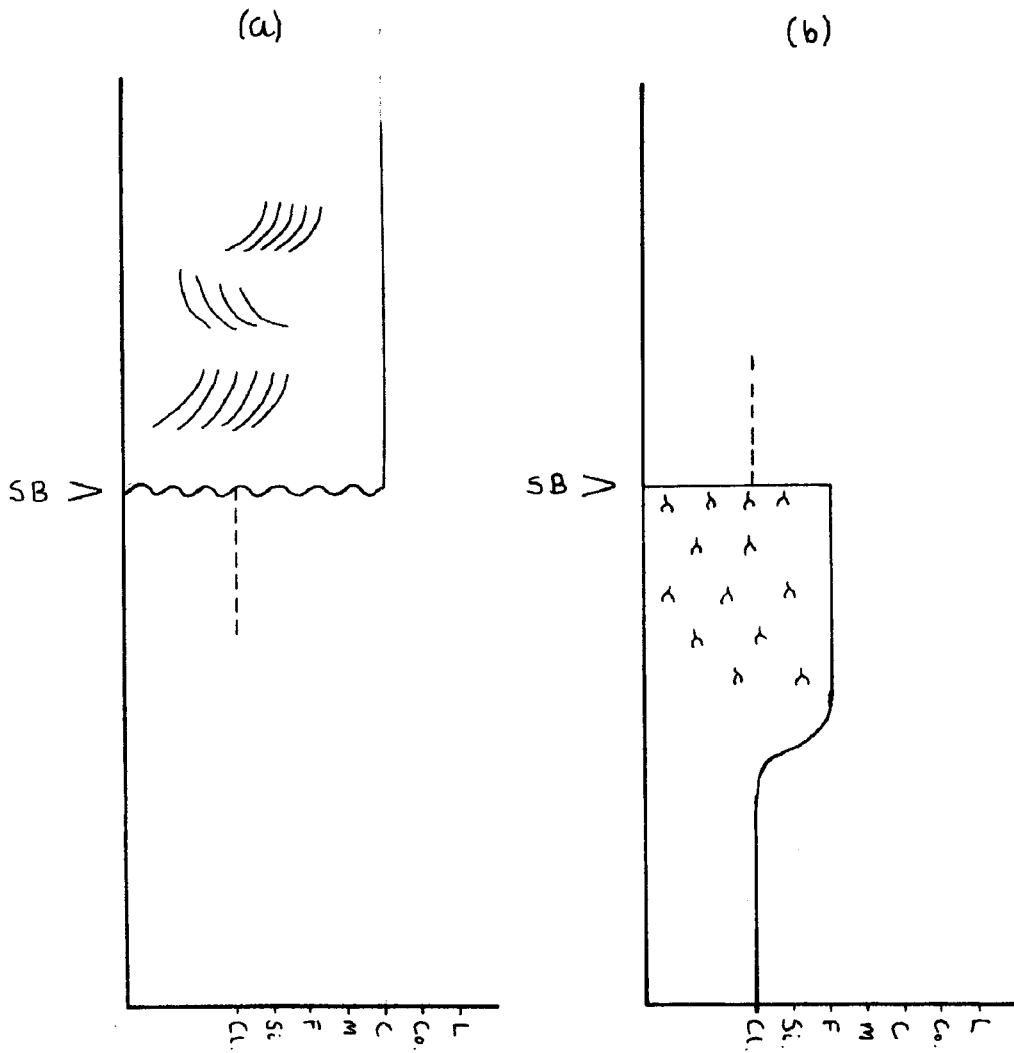


Fig. 2.10 Hypothetical graphic log for the position of the sequence boundary within a Yoredale sequence: a) below an incised-valley fill; b) above an interfluvial palaeosol.

2.3.2 Evidence for the transgressive systems tract

Initial flooding surface

This key stratal bounding surface occurs when sea-level rises above the shelf-margin break. Also called the transgressive surface, this starts to affect sedimentation right across the shelf, regardless of whether this covers previous interfluves or incised-valley fills (Figs. 2.11 c & d).

Regionally extensive coals and stacked palaeosol complex

Considerable work has taken place applying sequence stratigraphy to the deposition of coal in the British Carboniferous (e.g. Flint *et al.* 1995; Hampson, 1995; Read, 1995). This has emphasised the timing of coal formation, which is usually during the early transgressive systems tract. As relative sea-level and the graded stream profile slowly rise, and aggradation dominates the shelf area, raised mires form on interfluves between fluvial belts transporting sediment into the basin. These coal horizons may therefore be laterally extensive over much of the shelf. They are likely to be the thickest coal horizons and may have chronostratigraphic correlative value. Other minor coals are present, but are usually only of local occurrence related to vegetation of small temporary features, such as an active distributary system where sediments filled local accommodation space and caused exposure. The form of an initial flooding surface below a coal is illustrated in figure 2.11a.)

A stacked palaeosol complex may also form during this early transgressive systems tract when aggradation occurs close to a channel so that repeated crevasse splay sheet sands undergo pedogenesis before being covered by another flood. No examples of this facies architecture are found in the Longhoughton succession, but clear examples are seen in the Throckley borehole (see below) and elsewhere in the Namurian (Hampson, 1997). This association has also been highlighted by the above authors whilst discussing the use of sequence stratigraphy in understanding coal deposition.

Transgressive lag sandstones and bone beds

During transgression, the previous underlying sediments can become reworked by shallow-marine shoreface processes, possibly removing the underlying raised bog/coal described above; this can produce a significant, diagnostic horizon. The thin bed (~10cm) of sandstone beneath the Sugar Sandstones Limestone at Longhoughton was formed by this process. It has a clearly erosive base, with an uneven, wavy surface; critically it contains fish remains pointing to its marine origins and isolated bone fragments (Maurice Tucker pers. comm.) from a reworked terrestrial fauna. The underlying palaeosol has also had its coal removed and has been partially eroded. The form of an initial flooding surface below a coal is illustrated in figure 2.11b.

Limestones

During the late transgressive systems tract, true marine flooding of the shelf occurs as the rate of relative sea-level rise increases, drowning all terrestrial systems. Initially, distal prodelta muds influence deposition and a marine mudstone with a benthic fauna is formed; an excellent example of this is the marine mudstone underlying the Iron Scars Limestone.

As the relative sea level continues to rise, the fluvio-deltaic system is forced farther away into its hinterland to the northeast and siliciclastic sediment input into the basin ceases. This results in the build up of micrite-rich bioclastic limestones. It is these horizons that characterise the transgressive systems tract and have regional chronostratigraphic correlative value. The form of the late transgressive systems tract is illustrated in figure 2.11 a & b.

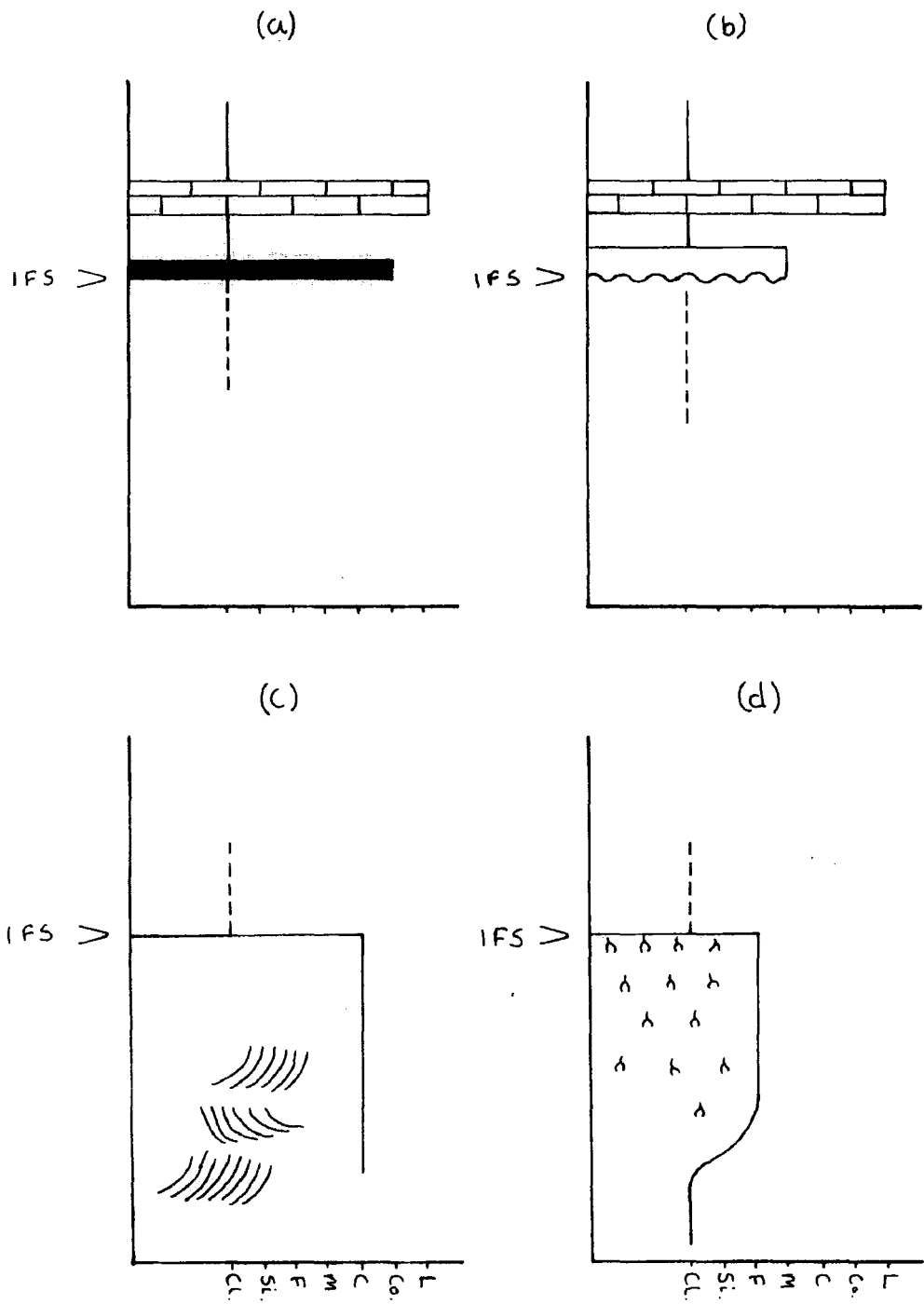


Fig 2.11 Hypothetical graphic log for the position of the initial flooding surface within a Yoredale sequence: a) below a coal; b) below a transgressive lag sandstone; c) above an incised-valley fill; d) above an interfluvial palaeosol (note this is the same as Fig 10b).

2.3.3 Evidence for the highstand systems tract

Maximum flooding surface

This marks the time when relative sea level was at its highest, water depth was at its greatest and the shoreline was at its most landward limit. It is typically marked by a condensed unit on the outer shelf and in the basin with the minimum rate of input of terrestrial siliciclastic sediment. In the Northumberland Trough, a number of surfaces could be designated the maximum flooding surface:

- Arbitrary mid-point of a limestone, marking the mid-point of open-marine deposition (Fig. 2.12a).
- A point two-thirds of the way up a limestone, marking the peak conodont element density which may equate with maximum water depth (Fig. 2.12b). Varker (1968) highlighted this conodont element peak whilst working on Yoredale sequences to the south of the Alston Block (Fig. 2.13).
- A surface some distance above the limestone which marks an anoxic horizon contemporaneous with maximum flooding (Fig. 2.12c). This surface would be associated with a pelagic fauna and lack of any benthos and may be marked by the products of anoxic processes (e.g. the band of siderite nodules seen above the limestone in the Howick Limestone Sequence).
- Commonly Yoredale limestones are made up of two beds separated by mudstone (e.g. Cushat, Iron Scars, Lower Foxton and Upper Foxton at Longhoughton). Heckel (1990) describing North American Pennsylvanian cyclothems marked the intervening black mudstone as the point of maximum flooding (Fig. 2.14). This marks a time of maximum flooding before and after which, lower sea levels and oxygenated bottom waters produce an abundant benthic fauna (Fig. 2.12d).
- The top of the limestone, marking an end of carbonate production before the overlying distal prodelta muds prograded from the north east (Figs. 2.12e & f).

There is clearly an unresolved debate on where to mark the maximum flooding surface in Yoredale sequences and it is beyond the scope of this study to discuss this topic in detail. In this study, the top of the limestone (Fig. 2.12e & f) will be used as the maximum flooding surface. This surface is very clear at outcrop and in borehole records, and it does not vary if there are one, two or more limestone beds. It is also

a clear, unambiguous horizon which will become very useful for work carried out in a later part of this study (Section 2.4).

Fluvio-deltaic deposition

Highstand systems tract deposition is dominated by prograding fluvio-deltaic systems. Initially this deposition tends towards aggradation, under high rates of relative sea level rise, but as this rate decreases, deposition becomes more and more progradational. This pushes fine prodelta mud out over the distal shelf covering the transgressive systems tract limestone. As the delta progrades into the basin, siltstone and then sandstone is deposited, and as accommodation space is filled and water depth decreases, shoreface processes start to act on the delta-front sediments producing winnowing and the formation of ripples, flaser bedding, lenticular bedding, cross-lamination and herringbone cross-bedding; all of which are seen towards the top of coarsening-upward units at Longhoughton.

As the delta-front progrades basinward over the underlying prodelta sediments, most of the area becomes influenced by interdistributary bay processes and sedimentation. This is dominated by low-energy mudstone and siltstone deposition, interrupted by sheet sandstones laid down during flood events that caused crevasse splay deposition beyond the distributary channel levees. The delta-top sediments also contain distributary channels; these formed during peak floods, by the avulsion of an old choked river into a newly eroded channel, which in turn slowly choked due the amount of sediment it carried. The result is an erosive based channel filled with low-angle, lateral accretion beds deposited on the point bar of the inside of a distributary meander. No distributary channels are seen on the logs in the present study, however one is visible below the Howick Limestone in Howick Bay (Elliot, 1976a; Tucker, 1995) and a full description of such a facies can be found in the work of Elliott (1976b) from the Great Limestone Sequence of the Alston Block. Throughout the delta-top environment, total filling of the accommodation space and cessation of fluvially dominated sedimentation results in the establishment of vegetation, pedogenesis of the underlying sediment and local development of peat. All these sediments resulting from all the above environments can be seen in the Longhoughton succession (Section 2.2).

Deltaic deposition tends to be cyclic in nature even without eustatic influence. Distributary avulsion moves an entire set of depositional environments laterally, allowing the old mouth-bar area to subside and interdistributary-bay sediments to take over again. This autocyclic deposition leads to repeated coarsening-upward units and this is typical of the highstand systems tract in the Northumberland Trough. The sedimentary package above the Howick Limestone at Howick Burn Mouth is a typical example. Broadly, this is a section of five coarsening-upward units, probably controlled by distributary avulsion; even within these units, there are more minor units caused by smaller-scale events such as individual floods and crevasse-splay deposits. This section does not even correlate with a log made just 500m to the north (NU263169), described by Farmer & Jones (1969, Fig. 6b), and as such units can not be considered to be laterally continuous. It is therefore assumed that all coarsening-upward units within the highstand systems tract prograding delta succession were deposited as a result of autocyclic processes, and were not eustatically controlled (see discussion in Leeder & Strudwick, 1987).

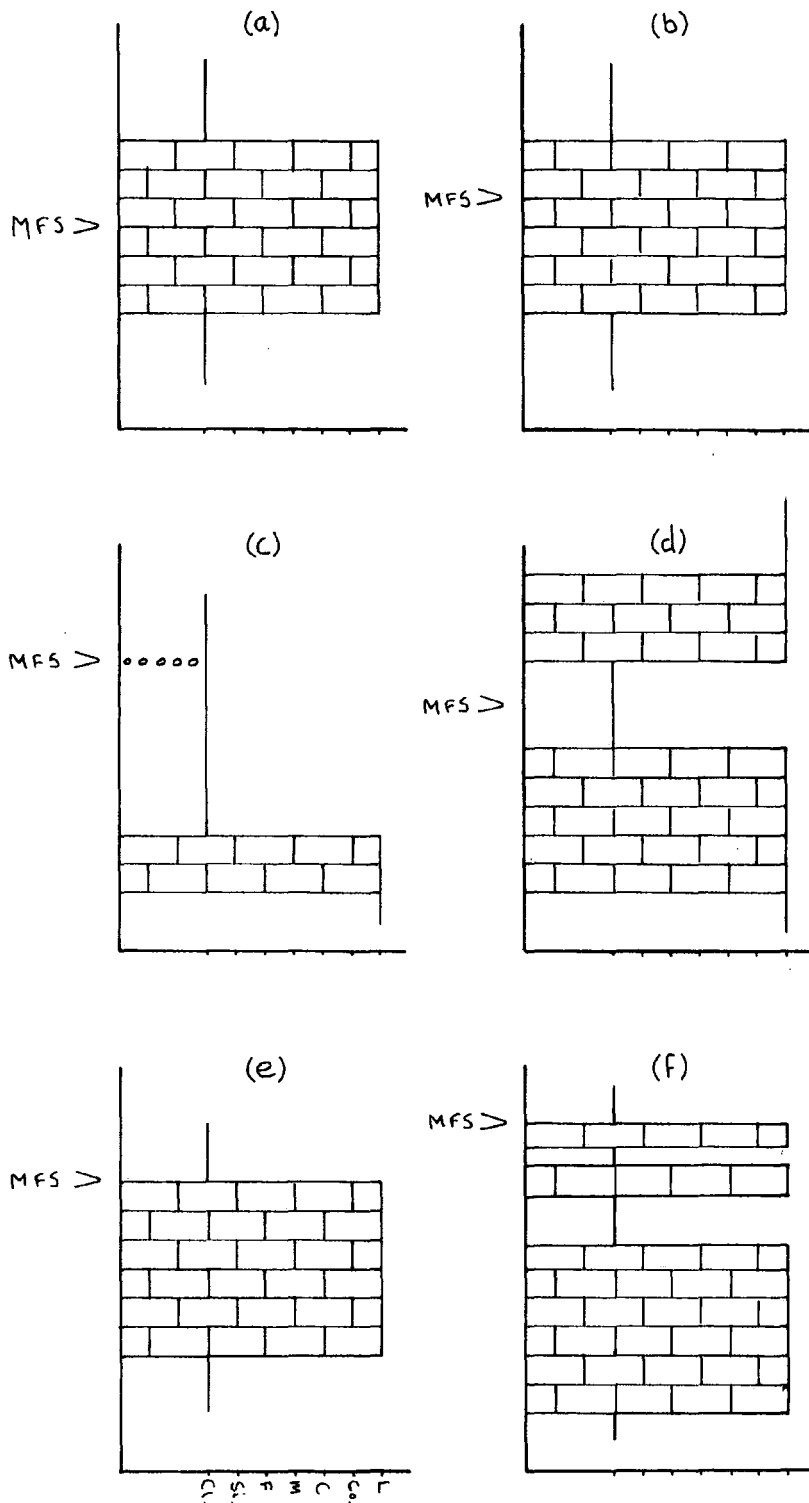


Fig 2.12 Hypothetical graphic log for the position of the maximum flooding surfaces within a Yoredale sequence; a) centre of a limestone; b) two-thirds the thickness of a limestone; c) an anoxic surface above a limestone; d) the mudstone between two beds of limestone; e) the top of a limestone; f) the top of the upper bed of a limestone.

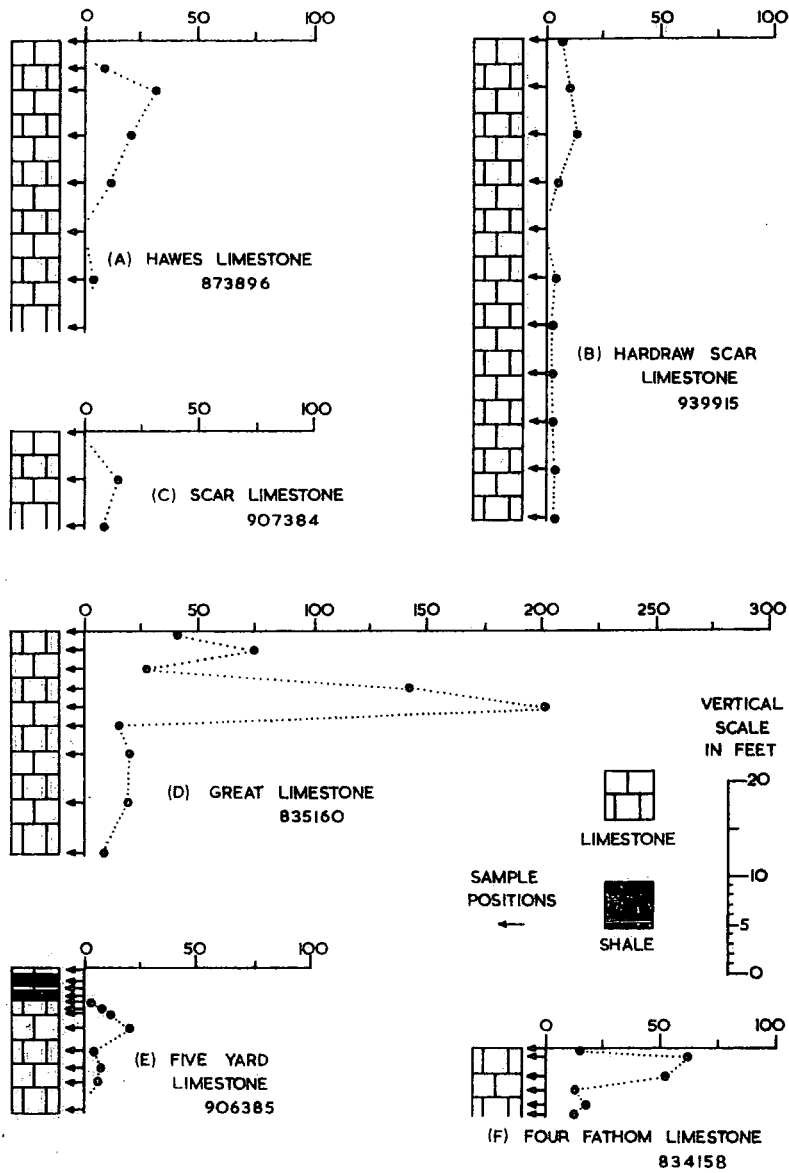


FIG. 1.—Distribution of conodonts through individual limestones in terms of number of conodonts per kilogram of rock. The locality of each of the samples is given by the six-figure grid reference.

Fig. 2.13 Conodont distribution in Yoredale limestones to the south of the Alston Block (from Varker, 1968).

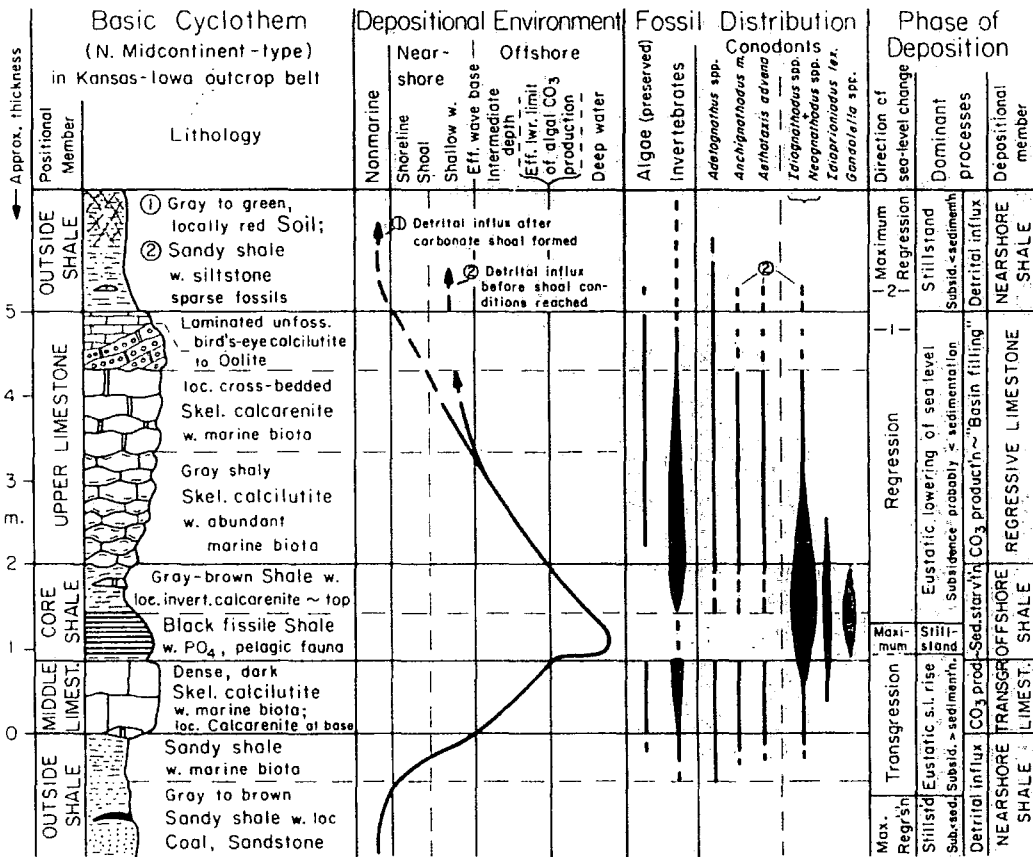


Fig. 2.14 "Basal Midcontinent (Kansas) cyclothem ... representing one sufficiently slow and extensive inundation and withdrawal of the sea to produce both transgressive and regressive limestones and intervening black phosphatic shale" (from Heckel, 1990).

2.3.4 Sequence stratigraphy of the Longhoughton succession

The Howick Limestone Cyclothem

The sedimentology of the Howick Limestone Cyclothem has already been described (Section 2.2.1, Figs. 2.3, 2.4). It is now possible to apply the concepts developed on systems tracts and key surfaces in Yoredale sequences (Sections 2.3.2-2.3.4) to explore lithological (Fig. 2.15) and chronostratigraphic implications (Fig. 2.16).

The Howick Limestone was deposited during the late transgressive systems tract as open-marine conditions were established across the flooded shelf. The upper surface of this limestone is taken to be the maximum flooding surface. The succeeding highstand systems tract consisted of a number of phases of deltaic deposition, largely in an interdistributary bay setting.

During the early lowstand systems tract of the next sequence, an incised-valley was cut through sediments of the previous highstand. During the late lowstand, this was filled by an aggrading, braided fluvial system to form the incised-valley fill. During the early and late lowstand, a palaeosol developed on the interfluvium, where pedogenesis altered the underlying highstand sediments (Howick Burn Mouth section, NU259163).

During the early transgressive systems tract, aggradation occurred across the alluvial plain forming a raised mire which resulted in a 20cm thick coal (originally up to 2m of peat), as a result of the slow rise of relative sea level above the initial flooding surface. This was followed by deposition of the Iron Scars Limestone in open-marine conditions during the late transgressive systems tract.

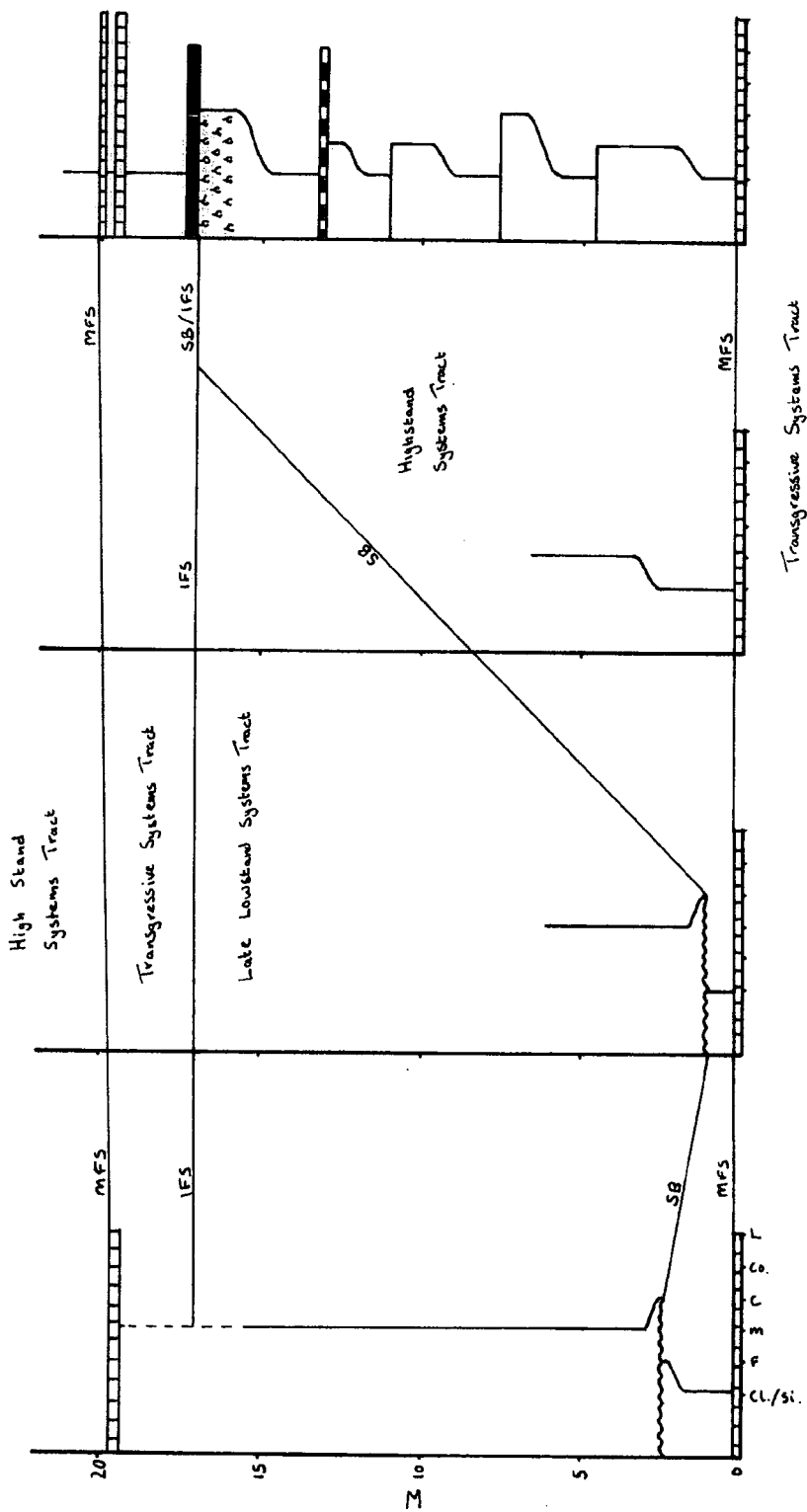


Fig. 2.15 Litho-sequence stratigraphic interpretation of the Howick Limestone Cyclothem at Longhoughton, Northumberland (see Figs. 2.3, 2.4X for details of sedimentology).

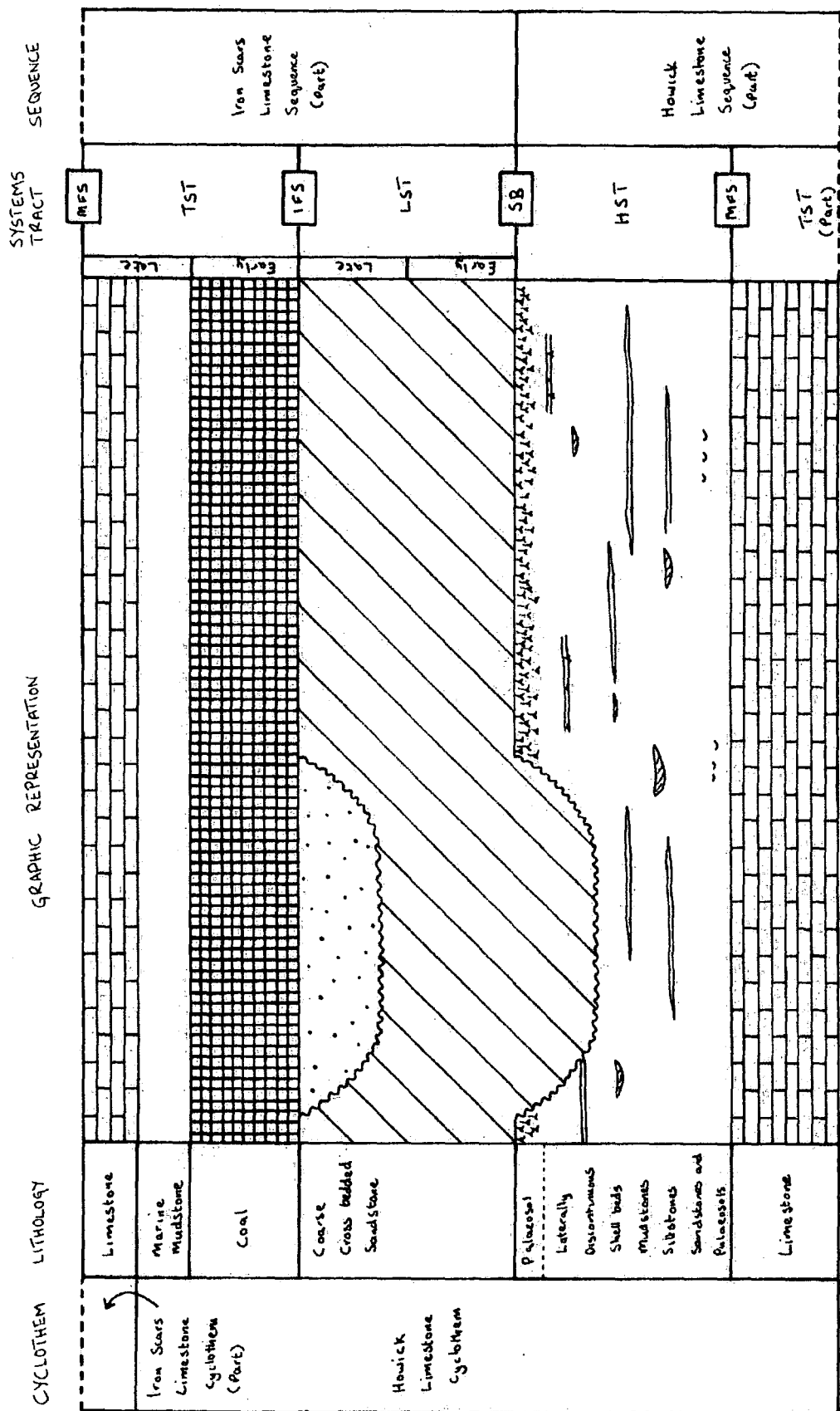


Fig. 2.16 Chrono-sequence stratigraphic interpretation of the Howick Limestone Cyclothem (compare with Fig. 2.15).

The Longhoughton succession

The Howick Limestone Cyclothem described above establishes the spatial relationship between lithofacies and systems tracts. The Longhoughton succession (Section 2.2.2, Figs. 2.5-2.9) provides an excellent opportunity to study the temporal variation.

The sequence stratigraphic interpretation is dominated by sediments deposited during the highstand systems tract, with thin transgressive systems tract coals, marine mudstones and limestones and local major incised-valley fills of the lowstand systems tract (Fig. 2.26). Overall this is similar to the situation in the Howick Limestone Cyclothem. To enable eventual regional correlation, each sequence has been numbered (Fig. 2.26), but where relevant it will take its name from the limestone horizon it contains.

Particular topics of note within the succession are:

- The base of sequence 0 (Great Limestone Sequence) is not seen within the area, so the first key surface is the maximum flooding surface at the top of the Tumbler Beds.
- The relationship of a shell bed lying above a coal at the base of sequence 2, is considered to represent the true base of a transgressive systems tract. This study re-affirms the proposal of Farmer & Jones (1969) that this shell bed is equivalent to the Crag (Oakwood) Limestone farther the south. (Only a shell bed above a coal is considered to represent transgression, whereas coals and shells beds on their own, are a normal feature of highstand systems tract deposition (Elliott, 1976b).)
- It is apparent that the sequences, and to some extent the limestones themselves, become thinner above sequence 0 (Great Limestone Sequence), before the deposition of another relatively thick sequence and limestone (Sugar Sands Sequence), though the succeeding sequence thicknesses are complicated by subaerial erosion and the removal of sediment.
- The upper part of the succession is dominated by incised-valley fills and thus the erosion of considerable underlying highstand systems tract sediments. Sequence 7 is considered to have eroded so deeply that it has

cut down beneath the level of the maximum flooding surface and has removed the limestone of sequence 6 completely.

A comparison between traditional cyclothems and modern sequences

It is now quite clear that the traditional cyclothem and modern sequence are fundamentally different (Fig. 2.16).

A sequence is related to sea-level change and has true chronostratigraphic significance.

A cyclothem is a loose lithostratigraphic definition with almost no chronostratigraphic significance:

- It is wholly dependant on the development of limestones. Where these are not developed (e.g. at the base of sequence 2) or have been removed by overlying incised-valley fills (e.g. where the incised-valley beneath sequence 7 has eroded most of the transgressive systems tract and the limestone from sequence 6) the system falls apart.
- It pays no attention to the internal architecture of sediments and facies, therefore missing a number of potentially useful stratigraphic markers (e.g. the typical arrangement of sediments around an initial flooding surface (Fig. 11) or the importance of sequence boundaries and incised-valley fills).
- Each cyclothem is bounded by the base of a limestone unit. If this surface is the same as the initial flooding surface, then it has sequence stratigraphic, relative sea-level change and chronostratigraphic significance. However, there is commonly a coal or marine mudstone present beneath the limestone, in which case the base of the limestone has no significance, as it marks a period 'sometime' during transgression.

2.3.5 A sequence stratigraphic depositional model

The spacial and temporal variation within the Longhoughton succession has been described in traditional terms (Section 2.2) and it has then been explored (Sections 2.2.2-2.3.4) and interpreted (Section 2.3.5) in modern sequence stratigraphic terms. It is now possible to distil the essential factors that characterise the influence of relative sea-level change, to produce a model:

Early lowstand systems tract

- Fluvial rejuvenation caused incised-valleys on the exposed shelf
- Interfluvial palaeosols formed between incised-valleys

Late lowstand systems tract

- Aggradation within the fluvial system resulted in coarse cross-bedded incised-valley fills
- Palaeosols continued to develop on interfluvies

Early transgressive systems tract

- Raised mires developed across the coastal plain

Late transgressive systems tract

- Clear open-marine conditions established across the shelf resulting in limestone deposition

Highstand systems tract

- Prograding delta sediment deposited across the shelf, made up of autocyclic coarsening-upward units resulting from normal avulsion and distributary switching.

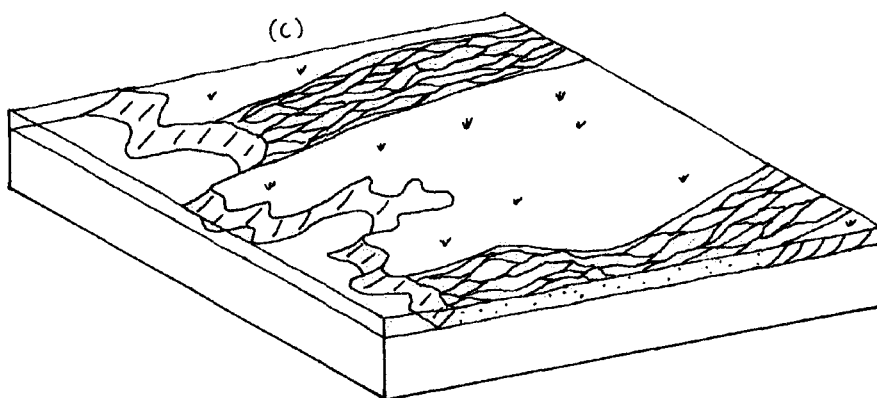
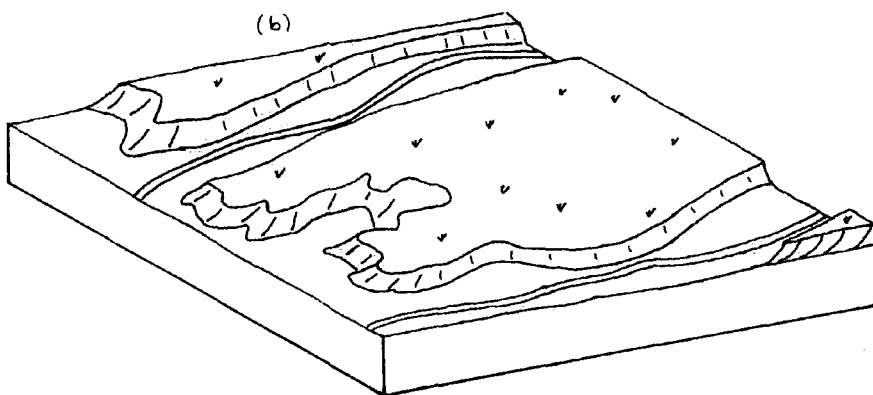
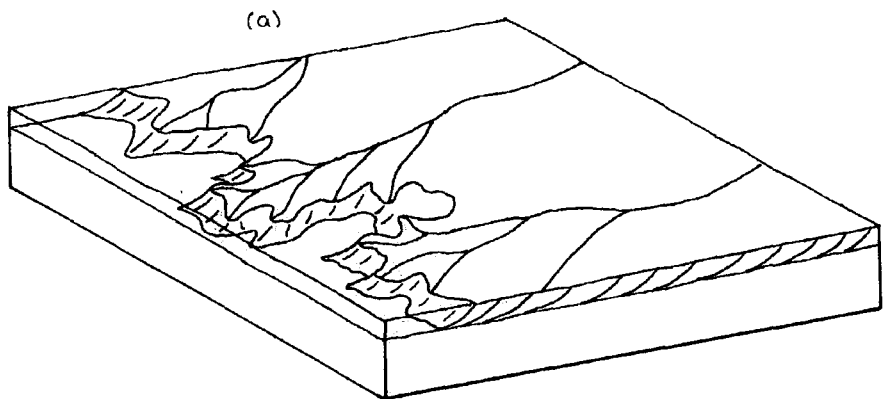
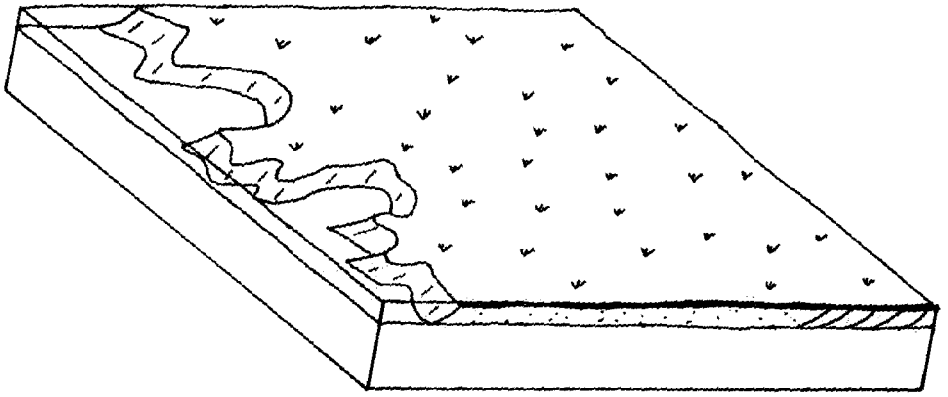
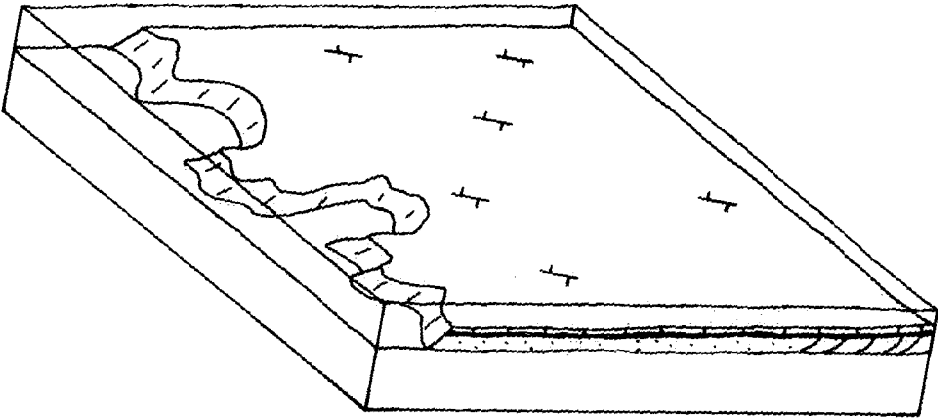


Fig 2.17 Block diagrams showing the proposed sequence stratigraphic model for the deposition of Yoredale sequences: (a) Highstand Systems Tract; (b) Early Lowstand Systems Tract; (c) Late lowstand Systems Tract.

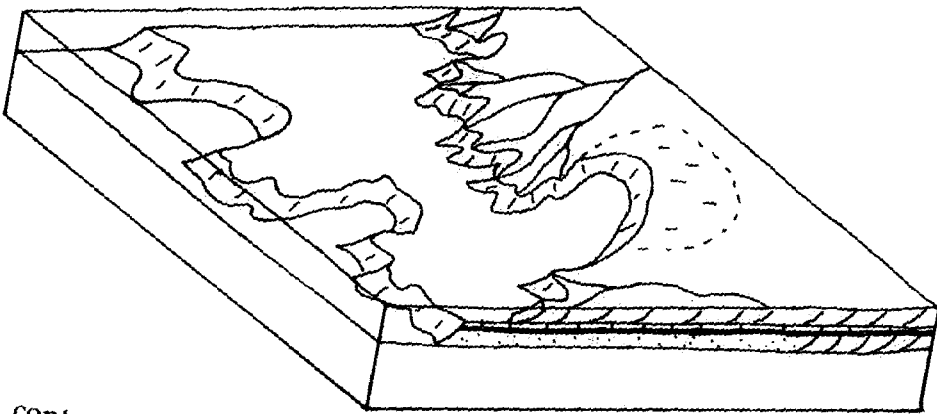
(d)



(e)



(f)



2.17 cont. : (d) Early Transgressive Systems Tract; (e) Late Transgressive Systems Tract; (f) Highstand Systems Tract.

2.3.6 Chrono-sequence stratigraphy for the Namurian

Throckley borehole

The model for the deposition of Yoredale sequences described above can be applied regionally to produce a chrono-sequence stratigraphy. The succession from the Throckley borehole will be used as the type section (Fig 2.26), as it is the best Namurian succession in the entire Northumberland Trough (Richardson, 1965, 1966; Mills & Holliday, 1998).

Sequences will be numbered rather than named, as it is essential to erect a neutral naming terminology, to de-emphasise the importance of limestone beds (see Table 2.1 for comparison of the sequences with the named limestone units they contain). This also helps to avoid compounding the confusion over the naming of limestone horizons in the southern Northumberland Trough; recent publications can not even agree on the names of limestone units within the Throckley borehole (Mills & Holliday, 1998; Chadwick *et al.*, 1995; Johnson *et al.*, 1995).

The first sequence (S0) is dominated by a thick limestone bed (the Great Limestone); above this are four sequences that become thinner, progressively more arenaceous, contain more and thicker palaeosols and thinner limestones (S1-4). Sequence 5 contains another thick limestone, above which the sequence thickness and the thickness of the limestone beds become much thinner. Towards the top, a number of thick, medium-coarse grained sandstones and stacked palaeosols dominate the succession.

There are a number of similarities with the Longhoughton succession:

- Both successions are dominated by sediments of the highstand systems tract.
- The sequence and limestone thickness generally decrease from sequences 0-4 and then again above sequence 5.
- The top of both successions is dominated by major incised-valley fill sandbodies.

There are also a number of differences with the Longhoughton succession:

- The Throckley borehole succession is more argillaceous highlighting its more basinal position and the Longhoughton succession is more arenaceous highlighting its position at the northern hinge region of the basin.
- The Longhoughton succession was seen to contain more incised-valley fill deposits at lower stratigraphic levels, again highlighting its more proximal position.

The upper part of the Throckley borehole gives evidence from the mid-late Namurian right up to the base of the Westphalian, a period not covered by the Longhoughton succession. The Throckley sequences 13, 14 and 15 are quite distinct from those previously described. They each begin with a thick incised-valley fill of the late lowstand systems tract proving a significant amount of relative sea level fall at the start of each sequence. These are followed by terrestrially dominated transgressive systems tract sediments, commonly stacked palaeosols deposited in an aggradational regime. The lower two sequences are lacking any highstand sediments due to erosion by the overlying sequence. The final sequence however, contains marine sediments associated with the maximum flooding surface which is overlain by highstand sediments. It is these late transgression/maximum flooding marine sediments in the uppermost sequence (sequence 15), that contain the fauna considered to mark the base of the Westphalian.

The incised-valley fills from the early Namurian are generally thought to be laterally discontinuous. Careful study of the many boreholes in the Newcastle area however (Mills & Holliday, 1998), shows that the incised-valley fills from the upper part of the Namurian succession from the Throckley borehole can be traced laterally for many tens of kilometres. This suggests that the erosion during the early lowstand systems tract lasted for a long period, was very extensive and removed all intervening interfluvial palaeosols (see Section 2.3.1). This depositional regime was significantly different from that in the early Namurian.

Sequence number	Limestone name
12	Whitehouse
11	Un-named
10	Un-named
9	Styford
8	Grindstone
7	Upper Felltop
6	Pike Hill
5	Lower Felltop
4	Belsay Dene
3	Aydon Shell Bed
2	Crag
1	Little
0	Great

Table 2.1 Sequence numbers and the transgressive systems tract limestone unit that characterises each sequence. (Limestone names are those used by Mills & Hull (1998) in their description of the Throckley borehole.)

Comparison with the established chronostratigraphy

It is now possible to relate the Yoredale sequences with the standard chronostratigraphy (Fig. 2.18). The base of the Pendleian stage and Stainmore Group is considered to be at the base of the Great Limestone (Johnson *et al.*, 1962). This equates with the sequence boundary at the base of Sequence 0, which is synonymous with the initial flooding surface just below the base of the Great Limestone; marked by an early transgressive systems tract coal in the Throckley borehole. (Note: it is not unreasonable to assume that in certain areas of the Northumberland Trough there may be an incised-valley fill below the Great Limestone, in which case the sequence boundary at the base of Sequence 0 would be considerably beneath the base of the Great Limestone.)

The base of the Arnsbergian is a much more difficult horizon to define and correlate. Biostratigraphic information is sparse and there are considerable problems with lateral correlation (see the summaries of Hull, 1968; Ramsbottom *et al.* 1978; Johnson *et al.*, 1995; Chadwick *et al.*, 1995). Recent work on the Longhoughton succession (Turner & Spinner, 1992) gives the most accurate published biostratigraphic control. The sediments from immediately below the Iron Scars Limestone up to the base of the Sugars Sands Limestone are ascribed to the early - mid Arnsbergian (E_{2a}-E_{2b}). It is therefore considered that the base of the Arnsbergian be placed at the base of the Iron Scars Limestone.

The upper part of the succession at Longhoughton, (S4-11), comes from a zone which has been ascribed to the late Arnsbergian - Chokierian (E_{2c}-H₁), but it is not possible to accurately place the top of the Arnsbergian.

The higher part of the succession recorded in the Throckley borehole allows the mid-late Namurian to be considered. The Chokierian - Alportian interval is very poorly represented in the Northumberland Trough (Hull, 1968; Ramsbottom *et al.*, 1978; Johnson *et al.*, 1995). It has even been suggested that the Alportian is completely missing in Northern England, north of the Craven Fault system (Ramsbottom, 1977b). It is here considered that no significant sedimentation occurred during this period and no sequence can be related to this period. (It is possible that a lowstand systems tract, interfluvial palaeosol formed during this

period and contains a Chokierian - Alportian palynological fauna.) It is here proposed that this interval represented a long-term period of low relative sea-level; it is further proposed that this correlates with the unconformity beneath sequence 12.

The upper three sequences found in the Northumberland Trough (S13-15) are very different from those of the underlying Yoredale sequences. They are made up of sediments of the lowstand and transgressive systems tract (major incised-valley fills overlain by stacked palaeosols) with no evidence of sediments of the highstand systems tract that dominate the underlying sequences. It is here proposed that each of these sequences represents one of the three upper stages of the Namurian. These relate to the major transgressive-regressive sequences proposed by Ramsbottom (1977b), on which the official chronostratigraphic stages were based (Ramsbottom *et al.*, 1978). In other words, these sequences are of a greater period than the other Yoredale sequences, that is they represent a longer time period. There was very little accommodation space available, therefore each sequence is actually only thin, though it represents a significant period of time.

This maximum flooding surface of sequence 15 is marked by a marine band which is considered to be the base of the Westphalian (Mills & Holliday, 1998); the underlying sediments can therefore be positively identified as Yeadonian and the incised-valley fill is therefore equivalent with the extensively studied Rough Rock of the Pennine Basin (Shackleton, 1962; Bristow, 1988; Maynard, 1992; Hampson, 1995; Hampson *et al.*, 1996).

Chronostrat.	Lithostrat.	Sequence	Thickness (m)
Westphalian A (part)	Coal Measures		
Yeadonian	Stainmore Group	S 15	26+
? Marsdenian		S 14	11
? Kinderscoutian		S 13	25
Alportian		S 4-12	200
Chokierian			
Amsbergian			
Pendleian			

Fig. 2.18 Relationship between the established chronostratigraphy / lithostratigraphy and the Yoredale sequences described in this study.

Comparison with the Namurian succession outside the basin

The lithology and palaeontology of the mid-Carboniferous of the Northumberland Trough differs significantly from the stratotype areas in the Pennine Basin. In particular the marine bands that are the basis of the stage boundaries contain a diagnostic ammonoid fauna which is difficult to correlate with the more shallow-marine faunas of the Northumberland Trough. A number of correlations have been proposed (Ramsbottom 1977a, 1977b, Ramsbottom *et al.*, 1978, Johnson *et al.*, 1995), but none are based on clear biostratigraphic evidence and none take sequence stratigraphy into account. As a result of the sequence stratigraphy work carried out during this study, the following correlation is proposed (Table 3.2).

Realistically, the greatest confidence can be placed in the Pendleian correlation, where both the Northumberland Trough and Pennine Basin successions have four clear transgressive events. Here, we can correlate these horizons as 'real' chronostratigraphic markers. It seems likely that the basal Arnsbergian is also reasonably well correlated, however the further up the successions, the greater the doubt about actual true correlation, without more accurate and abundant biostratigraphic markers in sequences 8-14 in the Northumberland Trough.

Namurian Stage	Northumberland			Pennine Basin	
	Seq.	Lmst name: Howick	Lmst name: Throckley	Index	Zone ammonoid
Yeadonian	15	-	-	-	-
? Marsdenian	14	-	-	-	-
? Kinderscoutian	13	-	-	-	-
Arnsbergian	12	-	Whitehouse	E2c2	N. nuculum
	11	-	-	E2c1	N. stellarum
	10	-	-	E2b3	Ct. nititoides
	9	-	Styford	E2b2	Ct. nitidus
	8	-	Grindstone	E2b1	Ct. edalensis
	7	Upper Foxton	Upper Felltop	E2a3	E. yatsae
	6	Lower Foxton	Pike Hill	E2a2a	C. gressinghamense
	5	Sugar Sands	Lower Felltop	E2a2	E. ferrimontanum
	4	Iron Scars	Belsay Dene	E2a1	C. cowlingense
Pendleian	3	Howick	Aydon Shell Bed	E1c1	C. malhamense
	2	Un-named	Crag	E1b2	T. pseudobilinguis
	1	Cushat	Little	E1b1	C. brandoni
	0	Great	Great	E1a1	C. leion

Table 2.2 Comparison of the Northumberland Trough sequences proposed in this study and their diagnostic limestones, and the established marine bands of the Pennine Basin (marine band index and ammonoid data from Riley *et al.*, 1995).

2.4 Low Resolution Sequence Stratigraphy

2.4.1 Introduction

Low resolution sequence stratigraphy (Posamentier & Weimer, 1993), is a title that has been given to sequence stratigraphic work based on seismic profiles and borehole wireline logs, which look at broad cycles, typically third-order sequences. This is in contrast to high resolution sequence stratigraphy (van Wagoner *et al.*, 1990), which uses outcrop and borehole core data to work in more detail on higher-order cycles. In the context of this study, low resolution sequence stratigraphy refers to the more broad scale cycles than the Yoredale sequences discussed earlier (Section 2.3).

This study has already diagnosed two orders of relative sea-level fluctuations in the Northumberland Trough:

- The tectonically-controlled, low-order (second-order?), major transgressive -regressive facies cycle of the regional basin development is summarised in section 1.2 of this study and has been described by many authors (e.g. Johnson, 1984; Leeder & McMahon, 1988; Leeder *et al.*, 1989; Chadwick *et al.*, 1995)
- The high-order (fifth-order?), Yoredale sequences are described in section 2.3.

It is therefore important to elucidate the background, intermediate relative sea-level change, to understand fully the nature of relative sea-level change on sedimentation and the influence on the conodont faunas of the Northumberland Trough.

The method that will be used to study intermediate relative sea-level change is a type of graph developed by Fischer (1964) to explain variations in the thickness of the peritidal Triassic "Lofer cyclothems" of the Calcareous Alps. This type of graph has been termed a 'Fischer plot' and has been utilised to study cycles in almost every sedimentary environment of deposition, including alluvial systems (Brian

Turner, pers. comm.). A full description and discussion of Fischer plots can be found in Sadler *et al.* (1993) and references to papers contained therein.

In this study, Fischer plots are deemed particularly apt because of the type of cycle being studied. Typical Yoredale sequences represent regular infilling of available accommodation space by transgressive and then highstand systems tract sediments, with open-marine rocks at the base and exposed terrestrial rocks at the top. Thus, though the sediments have undergone compaction, the thickness of sediment can be directly related to accommodation space.

This simple situation is complicated by incised-valley fills of the lowstand systems tract, which represent erosion into the highstand systems tract sediments of the underlying sequence. However, as can be seen in the Howick Limestone 'Cyclothem' (Figs. 3, 15), the thickness of the incised-valley fill is the same as that of the sediments that were eroded from the highstand systems tract. To overcome this problem, the base of the transgressive systems tract has been used in this study to define the base of each sequence; thus where an incised-valley fill is present, it has no effect on the sequence thickness and the Fischer plot produced.

During this section, the different orders of relative-sea level cycle that were influencing the deposition of Yoredale sediments will be explored. To avoid confusion, a system of naming will be introduced at this point (Table 2.3). The three orders of relative sea-level cycle will be referred to be their frequency, low, medium and high. This is separate from the sequence stratigraphic units that are produced, mega sequences, sequence sets and sequences respectively. Following the discussion of the results, the order of sea-level cycle and sequence will be explored more fully.

Sea-level cycle	Sequence stratigraphic unit	Symbol	Numbering
Low frequency	Mega sequence	MS	A, B, C
Medium frequency	Sequence set	SS	I, II, III
High frequency	Sequence	S	1, 2, 3

Table 2.3 Relationship between the frequency of sea-level cycle and the sequence stratigraphic unit deposited (incl. naming and numbering system).

2.4.2 The Stainmore Group (Namurian)

The detailed information from the Longhoughton succession (Sections 2.2, 2.3.5) and from the Throckley borehole (Section 2.3.7), allow a precise interpretation of the Namurian part of the Yoredale succession; the data available for the Viséan is more robust (Section 2.4.3). This has been integrated with the previous sequence stratigraphic interpretation (Section 2.3). Fischer plots for both successions have been produced (Longhoughton, Fig. 2.19; Throckley, Fig. 2.20), using the total sequence thickness (Figs. 2.19a, 2.20a) and the thickness of the basal limestones in each sequence (Figs. 2.19b, 2.20b).

Reviewing the plots produced from total sequence thickness, it is clear that both successions show similar trends:

- an initial rise in relative sea level to a peak at the end of sequence 2
- a fall in relative sea level until sequence 4 (Longhoughton) and sequence 6 (Throckley)
- a slight rise again, before falling away finally at the top of both successions

The plots produced from limestone thickness also show a similar trend, but emphasise two broad cycles more clearly. This is dominated by two thick limestones in each succession, sequence 0 and sequence 5, which indicate strong sea level rise, whilst the remaining thinner limestones indicate a series of smaller sea level rises during an overall regressive period of the third-order sea level curve.

Two higher-order sequence stratigraphic units, which will be termed sequence sets (Table 2.3), are clearly apparent from this data. The first sequence set, begins with a short period of transgression (S0-1), followed by a longer period of regression (S2-4). The second sequence set is similar, with a short transgression (S5-6) followed by a longer regression (S7-10). This 'bundling' of sequences is a common phenomena, which has been termed composite eustacy (Goldhammer *et al.*, 1990; Tucker, 1999). It is thought to form when different orders of sea-level change interfere: when the interference is constructive, particularly thick sequences are deposited; when interference is destructive, thin sequences or unconformities form.

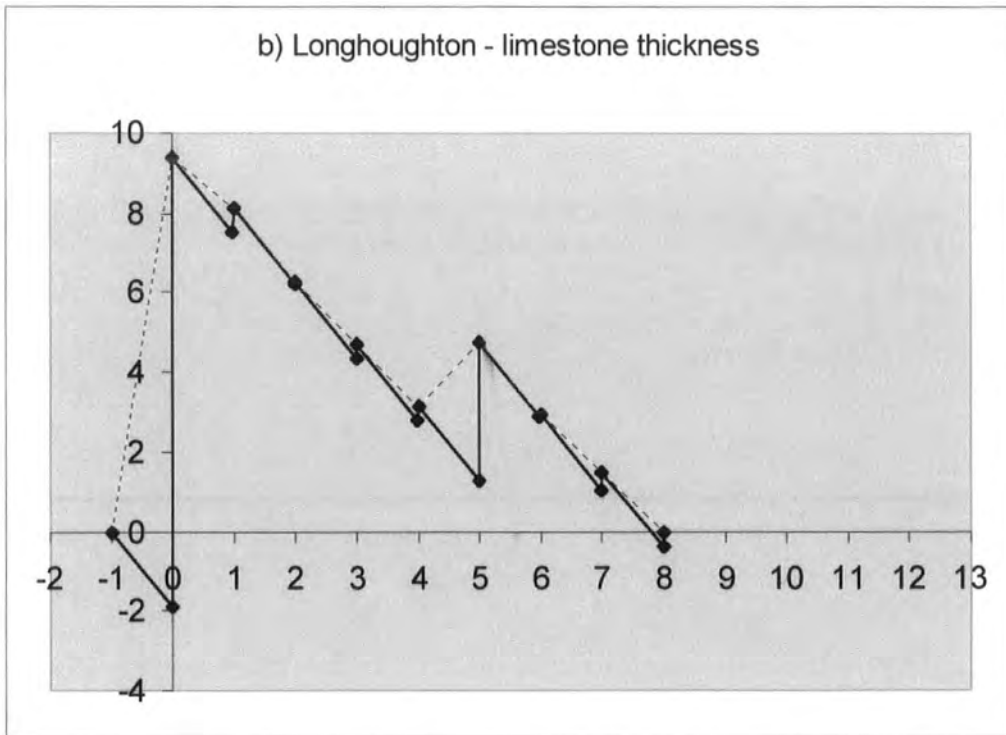
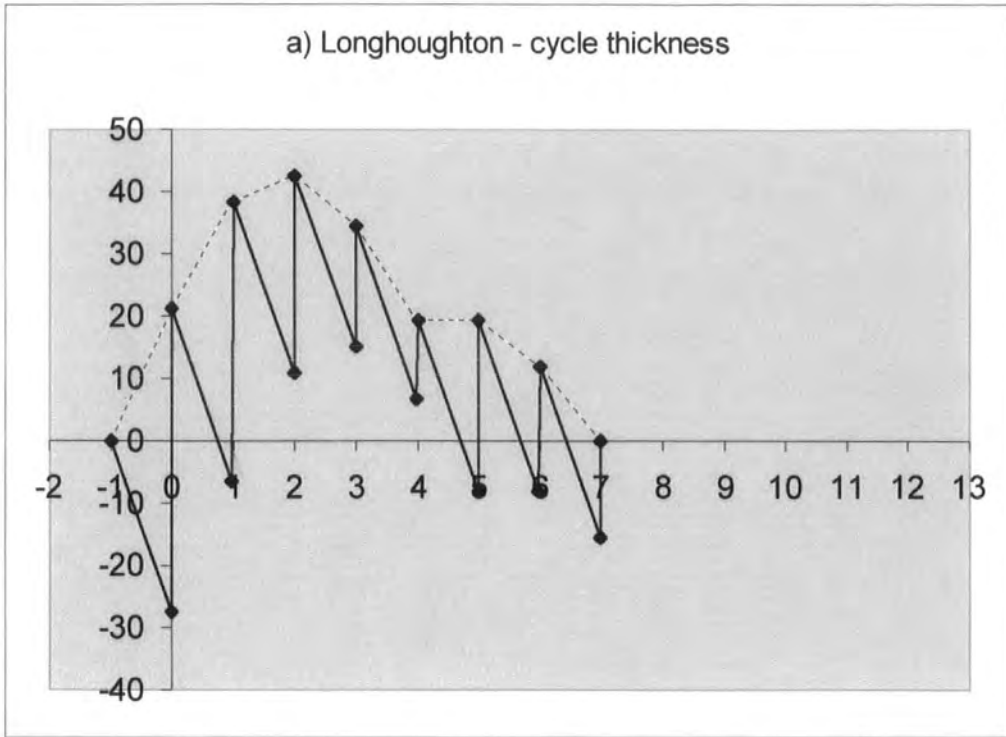


Fig 2.19 Longhoughton succession Fischer plots: a) sequence thickness; b) limestone thickness; horizontal axis shows the sequence number (0 = Great Limestone), vertical axis shows the cumulative departure from mean sequence thickness in metres of the sequence (plot a) or limestone (plot b).

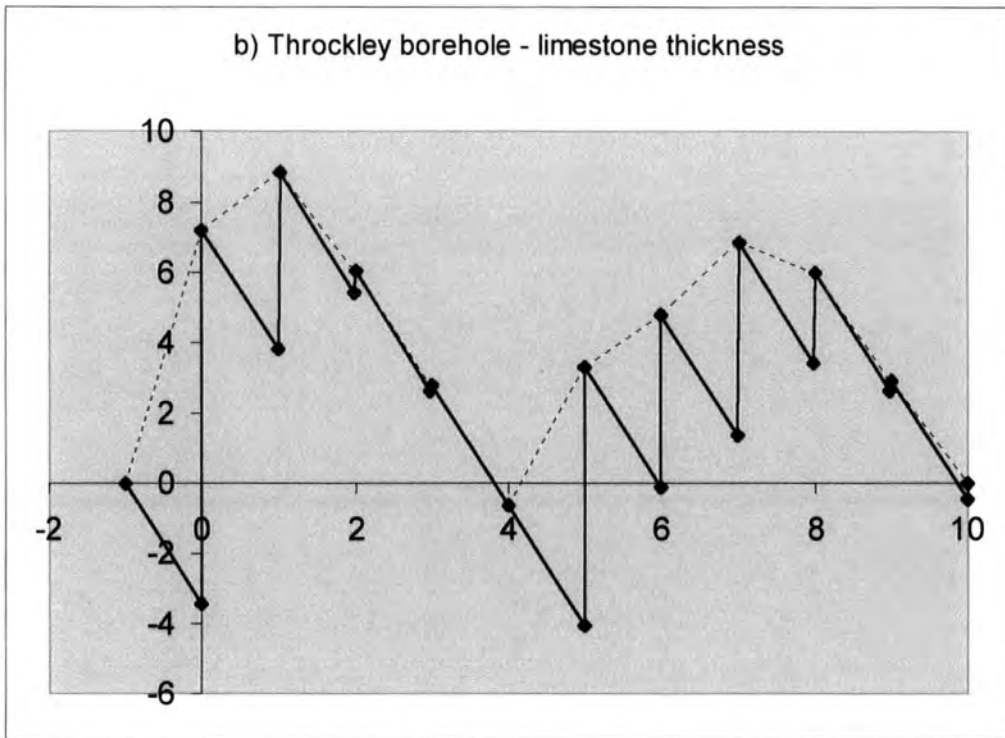
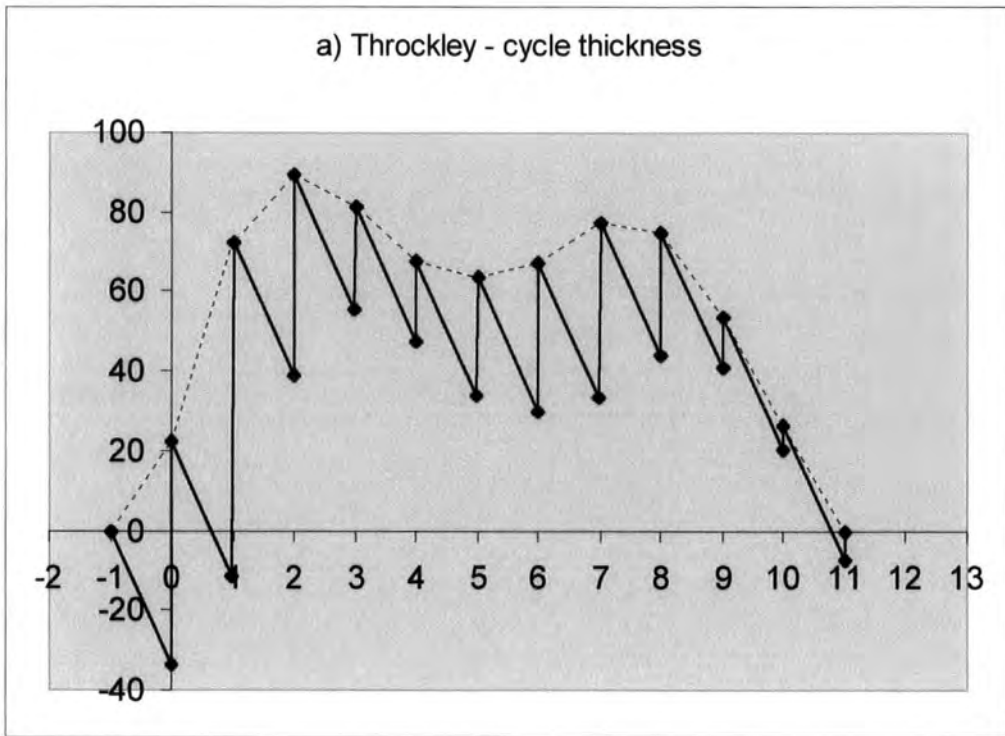


Fig 2.20 Throckley borehole Fischer plots: a) sequence thickness; b) limestone thickness (data taken directly from British Geological Survey core log); horizontal axis shows the sequence number (0 = Great Limestone), vertical axis shows the cumulative departure from mean sequence thickness in metres of the sequence (plot a) or limestone (plot b).

2.4.3 The Lower and Upper Liddesdale Group (Late Viséan)

Fischer plots have been produced for three late Viséan successions: the Longhorsley borehole (Fig. 2.21); the Harton borehole (Fig. 2.22); the Rookhope borehole (Fig. 2.23). The basic data on these three boreholes is of a much poorer quality than the data available for the Stainmore Group successions (i.e. the data used for Figs. 2.19, 2.20). As a consequence, the results can not be calibrated. In each borehole, only the Great Limestone Sequence (Sequence 0) can be confidently correlated. Each sequence in each borehole is measured relative to this fixed point; therefore numbered sequences in different boreholes do not necessarily correlate. It is the overall form of the plots that is important, rather than the precise sequence number at which an event takes place.

Three orders of sequence stratigraphic unit can be seen on the Fischer plots (see Table 2.3 for details): sequences; sequence sets; mega-sequences. The sequence sets and mega-sequences are described below, however it ought to be noted that the interference between high, medium and low frequency sea-level cycles cause these three sequence stratigraphic units to be inter-related.

Sequence sets

Following the trend seen in the sequences of the Stainmore Group, a series of sequence sets, each deposited during a medium-frequency sea-level cycle, can be defined. As with the Namurian Fischer plots (Section 2.4.2), these commonly take the form of a single thick sequence followed by a number of thin sequences (usually 3-6 thin sequences).

The Longhorsley borehole shows the longest and most detailed succession (Fig. 2.21). There was a short rise of relative sea level at the base of the Lower Liddesdale Group, marked by a series of thick sequences (SS-I). (It should be noted that this rise may have been the end of a considerable longer rise that is not shown by the Longhorsley borehole.) This was followed by a long fall of relative sea-level well into the middle part of the Upper Liddesdale Group; this was marked by a series of regular thin sequences, interrupted by two thicker sequences (base of SS-II, SS-III).

It ought to be noted that SS-II contains 11 sequences, around twice the normal number; it seems likely that an initial thick sequence in the centre of SS-II has not been noted. This may be due to it being subdivided into two or more thin sequences by a marine horizon that did not have sequence stratigraphic significance, or the expected sequence may have been subdued by the strong falling relative sea-level form of the low-frequency sea-level cycle.

There was a particularly thick sequence in the middle of the Upper Liddesdale Group, which marked the start of a long period of relative sea-level rise (base of SS-IV). This is considered to result from the constructive interference of all three frequencies of sea-level cycle causing a particularly large rise in sea-level.

Constructive interference between the low-frequency and medium-frequency sea-level cycles has caused a number of thick sequences to form in series (SS-V). The final, particularly thick sequence (S0), which forms the base of the following sequence set (SS-VI), is significant in that it contains the important marker horizon, the Great Limestone. The final two sequence sets (SS-VI, SS-VII) correspond with the two sequence sets described from the Longhoughton succession and the Throckley borehole (Section 2.4.2).

The Fischer plot of the Harton borehole (Fig. 2.22) is very similar to that of the Longhorsley borehole described above. The main difference is that it starts slightly later in the Lower Liddesdale Group and also that the thick sequence at the start of SS-IV is only poorly defined. In all other respects the Fischer plots from both boreholes are very similar. In particular, the thick sequence in the middle of the Upper Liddesdale Group (base of SS-V) is clearly defined and the Great Limestone sequence comes at the steepest point of the curve.

The Fischer plot of the Rookhope borehole and surrounding area (Fig. 2.23) shows a similar overall profile. However the sequence sets are difficult, almost impossible, to define, largely due to the lack of thick sequences. This more subdued signature might be expected from the more stable area of the Alston Block.

Mega sequences

The overall form of all three Fischer plots is very similar (Figs. 21, 22, 23); a long fall of sea level from the middle of the Lower Liddesdale Group to the middle of the Upper Liddesdale Group, followed by a rise into the middle Stainmore Group. This is thought to reflect the low-frequency sea-level cycle, with a period that is equivalent to more than a chronostratigraphic stage. The sequence stratigraphic unit produced has been termed a mega-sequence (Table 2.3); two mega-sequences can be diagnosed from the Liddesdale Group data, with a sequence boundary separating them. The first mega sequence (MS-A) is represented by highstand systems tract conditions in the early Lower Liddesdale Group, marked by relatively high sea-levels on all three Fischer plots (Figs. 21, 22, 23). A sequence boundary is at the beginning of a long period of thin sequences that occurred during the middle Lower Liddesdale Group (base of SS-II); this is thought to be a type 2 sequence boundary, as no significant unconformity has ever been recorded at this stratigraphic position. The second mega sequence (MS-B) is represented by lowstand systems tract conditions during the mid Lower Liddesdale Group to the mid Upper Liddesdale Group (S-II, SS-III) which ended with an initial flooding surface (base of SS-IV). This was followed by transgressive systems tract conditions until the maximum flooding surface at the base of the Stainmore Group (base of SS-VI). The later part of the second mega-sequence (MS-B) is represented by highstand systems tract conditions into the middle Stainmore Group.

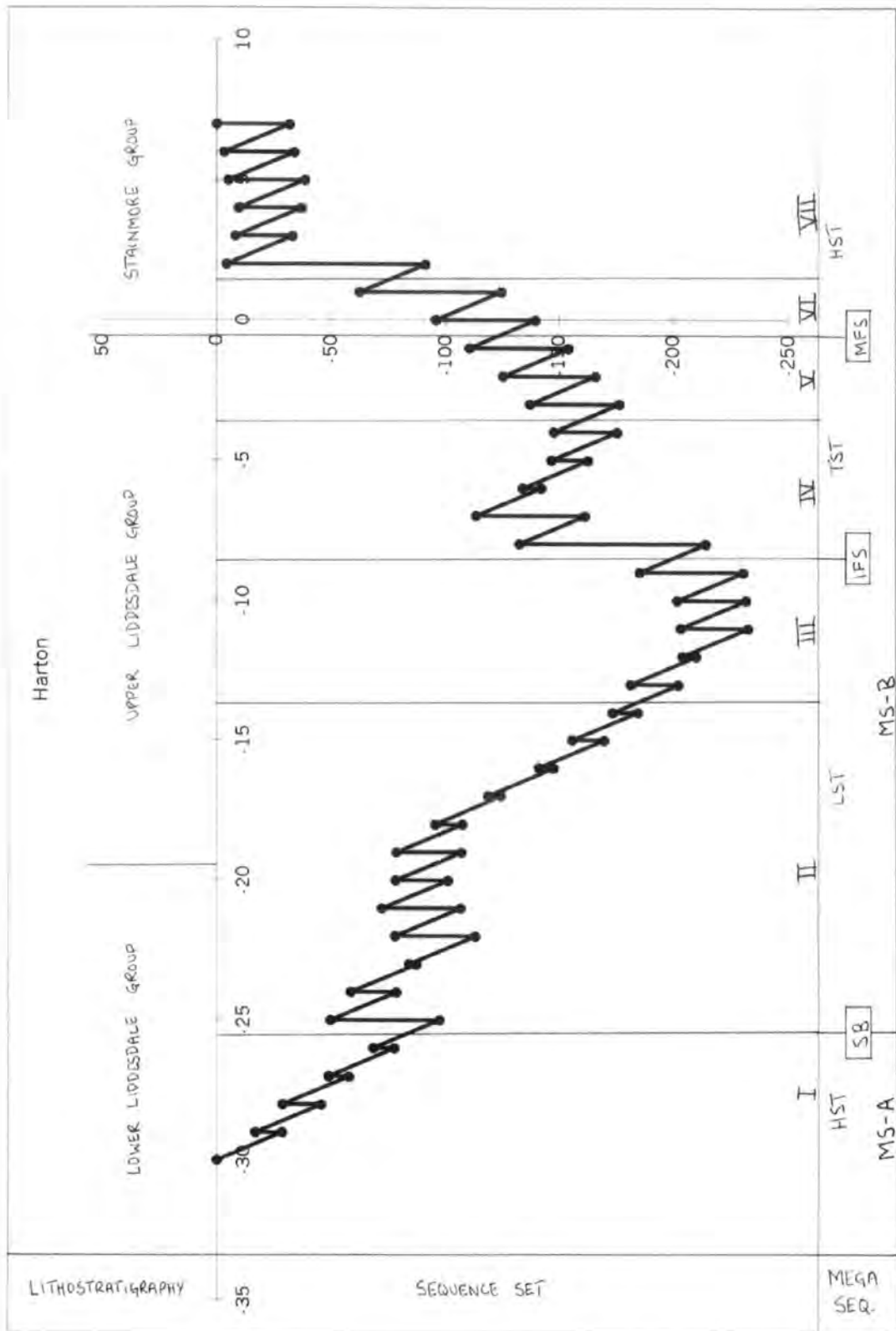


Fig 2.22 Fischer plot of the Harton borehole (Ridd *et al.*, 1970); horizontal axis shows the sequence number (0 = Great Limestone), vertical axis shows the cumulative departure from mean sequence thickness in metres.

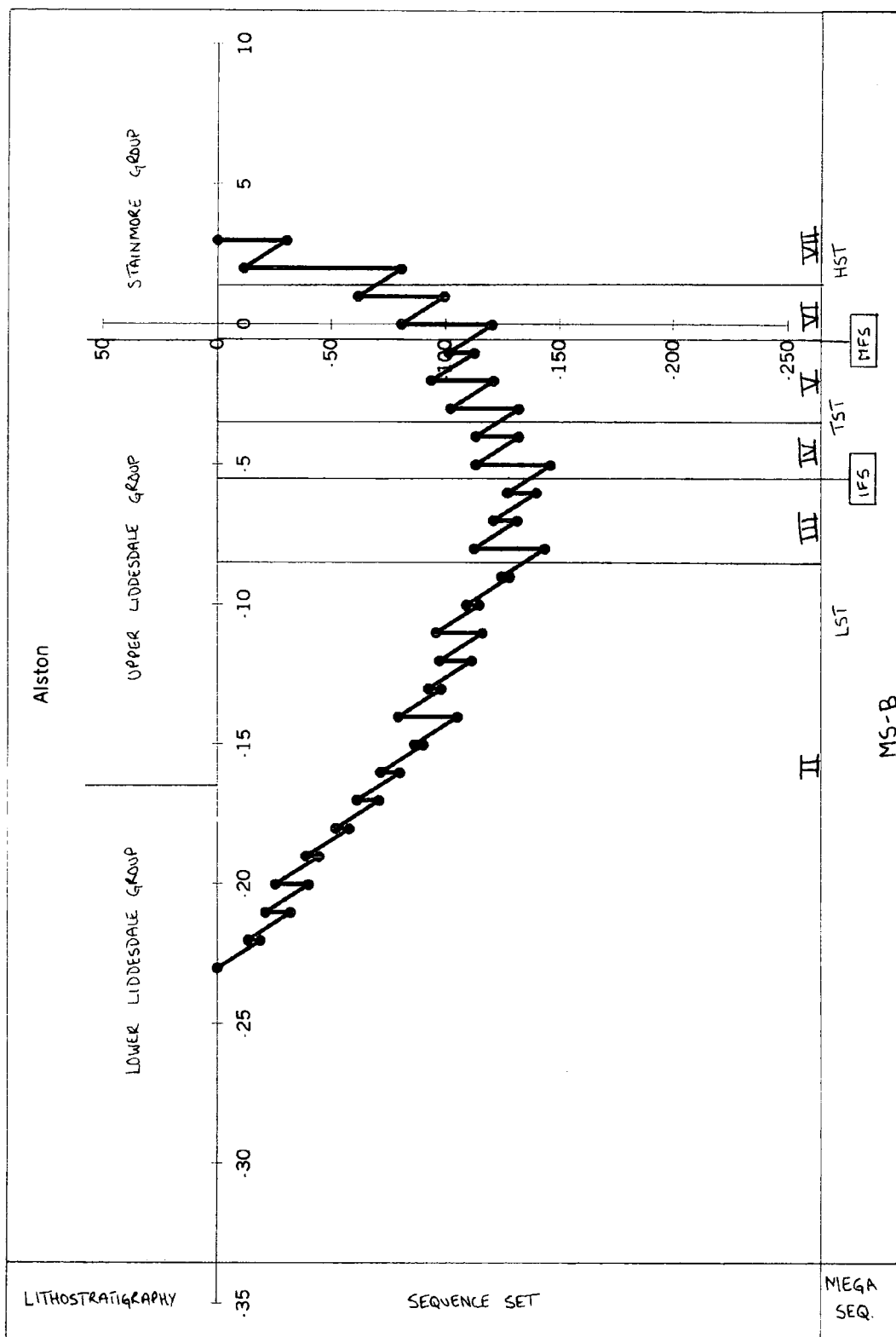


Fig 2.23 Fischer plot of the central Alston Block based on the Rookhope borehole (Johnson & Nudds, 1996) and outcrop data for the surrounding area (Dunham, 1990); horizontal axis shows the sequence number (0 = Great Limestone), vertical axis shows the cumulative departure from mean sequence thickness in metres.

2.4.4 Chrono-sequence stratigraphy for the Yoredales

The overall relative sea-level curve (Fig. 2.24) is a summary of all the results described to this point, including information on the late Namurian based on evidence from the higher part of the Throckley borehole (Section 2.3). It covers the interval from the mid-Asbian through to the base of the Westphalian, but the highest degree of confidence can be ascribed to the Asbian to Arnsbergian period, in particular the lowest Namurian.

In sequence stratigraphy terms, the base of the Lower Liddesdale Group marks a period of highstand in the low-frequency sea-level cycle (end of MS-A), prior to a mega-sequence boundary in the middle Asbian (base of SS-II). The following sequences deposited during the mid-late Lower Liddesdale Group, show a marked basinward shift of facies with minor marine and strong terrestrially dominated sedimentation; also notable is the absence of any significant unconformity during this interval. This implies that this mega-sequence boundary is a type II (van Wagoner *et al.*, 1988); unlike the mega-sequence boundary at the end of the Arnsbergian (see below). A type II mega-sequence boundary is thought to have formed, because the rate of subsidence during this period was relatively higher than during the Namurian, as it was at the end of the fault controlled rift-phase of subsidence. Therefore, the rate of subsidence was greater than the rate of sea-level fall, due to the low-frequency sea-level cycle, causing progradation and regression, but not subaerial exposure.

The mega-sequence 'B' initial flooding surface took place in the mid-Brigantian (at the start of SS-IV), followed by transgression and the deposition of successively thicker limestones (sequences in SS-IV & SS-V). Maximum flooding occurred at the Brigantian - Pendleian boundary (base of SS-VI), at the time that the thickest limestone was deposited (the Great Limestone). The early Namurian can be seen to be a period of highstand deposition, with little new accommodation being formed, with successively thinner limestones.

Taking the ideas developed earlier (Section 2.3.7) the Chokierian-Alportian (which is not actually imaged on these Fischer plots) was a time of significant sea-level fall in the low-frequency sea-level cycle, with subaerial exposure and unconformities forming on the shelf, seen as a type I mega-sequence boundary. This is thought to have formed as the rate of subsidence was relatively lower during the Namurian than in the late Viséan due to the lack of rift induced syn-extensional faulting and the dominance of lower rates of thermal subsidence. Therefore the rate of sea-level fall due to the low-frequency sea-level cycle was greater than the rate of subsidence. In fact there would have been occasion during this long-term fall in sea-level when the rate of sea-level rise due to the medium and high frequency sea-level cycle and the rate of subsidence together (i.e. all contributing the relative sea-level rise) did not outweigh the rate of sea-level fall due to the low-frequency sea-level cycle.

During the late Namurian, three sequences were deposited (S13-15), during a period of sea-level rise in the low-frequency sea-level cycle. These sequences are thought to be related to the times of constructive interference between the low, medium and high-frequency sea-level cycles, which produced relative sea-level rise. The intervening unconformities and erosion on the shelf result from the destructive interference of the sea-level cycles, dominated by the falling rate of sea-level of the medium frequency sea-level cycle. Therefore each sequence also represents a full sequence set (SS-8, SS-9, SS-10), where the only accommodation space that was created, resulted in the deposition of the initial thick sequence.

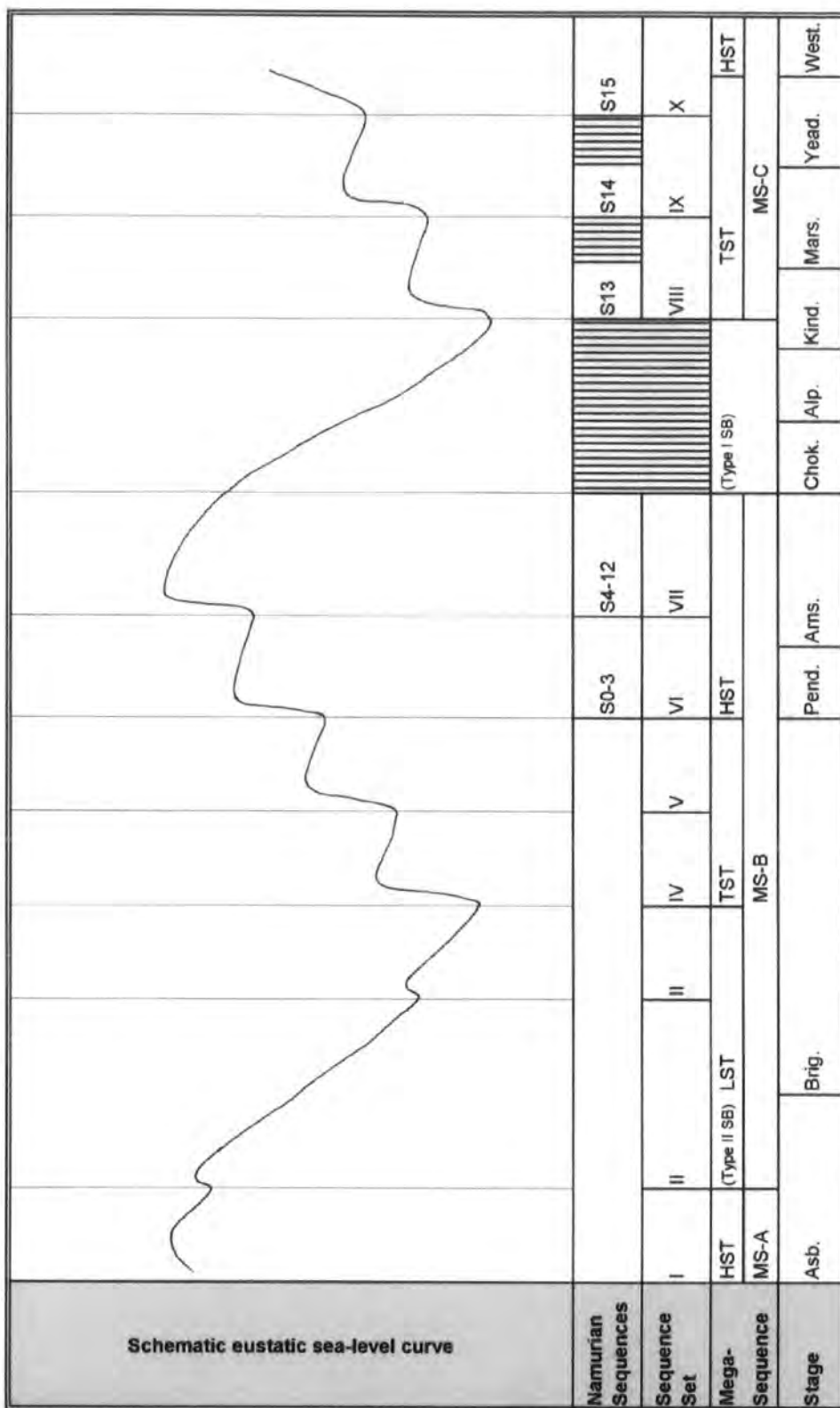


Fig. 2.24 Schematic eustatic sea-level curve showing low and medium frequency cycles, produced from all previously described data, focusing upon the sea-level changes that influenced sedimentation.

Stage	Sequences	Sequence sets	Mega-sequences
Yeadonian	15	X	C
? Marsdenian	14	IX	
? Kinderscoutian	13	VIII	
Alportian			Type I U/C
Chokierian			
Arnsbergian	12	VII	B
	11		
	10		
	9		
	8		
	7		
	6		
	5		
Pendleian	4	VI	
	3		
	2		
	1		
Brigantian	0	V	
	2 sequences		
	4 sequences		
	6 sequences		
Asbian (part)	11 sequences	IV	
	6 sequences	III	
		II	
		I	A

Table 2.4 Summary of the sequence stratigraphic units designated in this study (number of sequences in the Brigantian and Asbian sequence sets was arbitrarily taken from the Longhorsley Borehole).

Comparison with the Namurian succession outside the basin

Previous studies of the sequence stratigraphy of the Carboniferous of northern and central England have focused upon the local-regional tectonic controls (Ebdon *et al.*, 1990; Fraser & Gawthorpe, 1990; Fraser *et al.* 1990). The sequences that have been proposed are controlled by extension and inversion tectonics (Fig. 2.25), rather than eustatic sea-level change.

The EC5 sequence (late Asbian - early Brigantian), as defined in the area south of the Craven Fault System, formed within an extensional regime (various forms of outcrop (Craven Basin) and seismic (mainly Widmerpool Gulf) evidence are given by Ebdon *et al.*, 1990; Fraser & Gawthorpe, 1990). This is clearly contrary to the evidence from the Northumberland Trough which shows a regression taking place during this period. Though fault-induced influence of sedimentation can not be ruled out in Northumberland, as the relatively high sea levels south of the Craven Fault System is a result of extension, then the trend in Northumberland is likely to be reflecting the actual eustatic sea level during this period.

The EC6 sequence (early - mid Brigantian) marks a short period of inversion which resulted in a regressive phase of deposition, marked by the deposition of relatively coarse deposits south of the Craven Fault System. This seems to relate unequivocally with the very low relative sea level seen in the Northumberland Trough during this period, at the end of a long phase of relative sea level fall (SS-III).

The LC1a sequence (late Brigantian - late Pendleian) was the first sequence within the post rift megasequence and marks the beginning of thermal subsidence south of the Craven Fault System. This correlates with the rise in relative sea level also seen in the Northumberland Trough from the mid - late Brigantian (SS-IV to SS-VI).

The LC1b sequence (late Pendleian - Alportian) continued to be dominated by thermal subsidence, but began with the influence of minor fault reactivation forming the pre-Grassington Grit unconformity (Arthurton *et al.* 1988). This fault activity does not seem to have affected sedimentation in the Northumberland

Trough: there are no notable results of increased water depths in the Throckley borehole succession and no notable unconformities in the relatively shallow Longhoughton succession. In fact the regression trend to thinner limestones and sequence thickness from the mid Pendleian to early-mid Arnsbergian shows no significant event occurring during the late Pendleian at all.

The LC1c sequence (Kinderscoutian - late Westphalian A) is proposed as another period of thermal subsidence started by a phase of extensional fault re-activation south of the Craven Fault System. This period in the Northumberland Trough is represented by a relatively thin succession dominated by coarse sandbodies, interpreted in this study as three sequences, perhaps equating with the three late Namurian Stages; this shows a more detailed picture than seems to be present in the south, however there is little evidence for the notable fault reactivation during the Kinderscoutian that is seen south of the Craven Fault System.

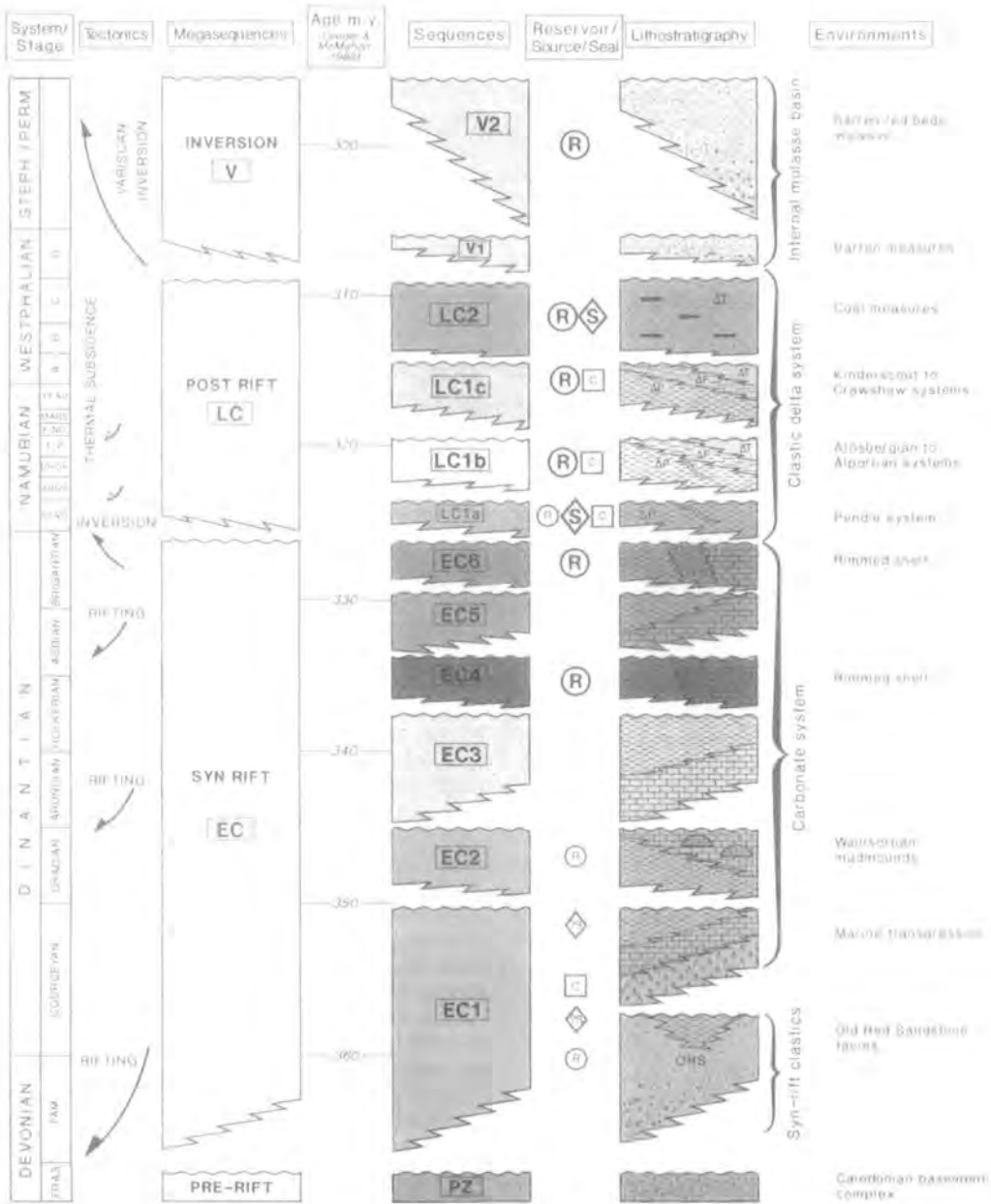


Fig. 2.25 Summary stratigraphy of the Variscan plate cycle in the East Midlands; ΔT =delta top, ΔF =delta front, ΔP =pro delta (from Fraser & Gawthorpe, 1990, but essentially the same as that proposed in Ebdon *et al.*, 1990 and also Fraser *et al.*, 1990).

2.5 Conclusions

Sequence stratigraphy is a powerful interpretative technique for understanding the deposition of Yoredale facies.

Yoredale sequences fit the Exxon model exceptionally well. Deposition took place in a shelf environment and the spacial and lateral variation includes examples of all the systems tracts and key surfaces. The majority of the sediments represent highstand systems tract fluvio-deltaic facies, with subordinate transgressive systems tract coals and marine mudstones and limestones. Lowstand systems tract incised-valley fills are present in the succession, either as laterally restricted channels or extensive sandsheets.

A model for the deposition of Yoredale sequences has been produced, which relates all the sedimentary facies with a period on an idealised sea-level curve. This creates a framework in which the spacial and temporal variation can be understood. The model has been used to define 15 sequences in the Namurian succession of the Northumberland Trough.

Three different orders of sea-level cycle (high, medium and low-frequency), influenced the formation of three orders of sequence stratigraphic units (sequences, sequence sets and mega-sequences). However the most significant sequence stratigraphic events took place during interference between the three frequencies of sea-level change: constructive interference increased accommodation space resulting in thick sequences; destructive interference decreased accommodation space causing thin sequences or an unconformity.

3. CONODONTS

3.1 Introduction

Almost two hundred conodont samples, containing 1039 identifiable elements, representing eleven species, have been used in this study (Appendix I). The samples come from across the Northumberland Trough (Fig. 1.1, Appendix II). The earliest material comes from the eastern part of the region around Bewcastle, from the Lower and Upper Liddesdale Groups. The youngest material comes from the Stainmore Group around Hadrian's Wall and from the Throckley borehole. Material from the northern part of the area, referred to generally as Longhoughton, includes individual locations covering much of the Asbian - Arnsbergian succession.

The actual conodont samples used during this study come from a variety of places (Appendix III). Much of the material was already in the micropalaeontology collections of the University of Durham, which include the collections from the University of Newcastle. The Throckley borehole samples were loaned from the British Geological Survey. Recent re-mapping of the Morpeth area by the British Geological Survey was the source of the Mootlaw Quarry samples; these were collected by BGS staff, but processed as part of this study. Additional samples were collected and processed as part of this study from the succession on the foreshore at Longhoughton.

Armstrong and Purnell (1993) dealt in some detail with colour alteration index of conodont elements in the Northumberland Trough, therefore no further mention is made of CAI in this study.

3.2 Biostratigraphy

3.2.1 *Conodont biozonation*

Biostratigraphic utility

A range of conodont species are present in marine units from the Asbian-Arnsbergian of the Northumberland Trough (Appendix I). Overlapping ranges of strata have been studied in three areas: Bewcastle - Asbian to Brigantian (Fig. 3.1); Longhoughton - Brigantian to Arnsbergian (Fig. 3.2); Throckley borehole - Pendleian to Arnsbergian (Fig. 3.3). Based upon the presence/absence, the biostratigraphic utility of each species will be studied in turn:

Adetognathus unicornis

This species was only found in a single sample, which was from the late Arnsbergian of the Throckley borehole. This species has only ever been found in two other samples from the whole of Britain, both of which were considered to be of Arnsbergian age: the Mirk Fell Beds of the Askrigg Block (Varker & Austin, 1974); the Coral Limestone of Arran (Dean, 1987). The Mirk Fell sample is thought to be older (see discussion on chronostratigraphy below) and the sample from Arran is poorly constrained, so it can not be proved categorically that these samples were coeval.

Cavusgnathus naviculus

This species appears in the mid-late Brigantian in the Bewcastle and Longhoughton successions. Its first appearance may represent a biostratigraphic event, however it is rather sporadic and therefore its absence in earlier faunas may be due to statistical rarity.

Gnathodus girtyi

This is one of the first species that appear in the Northumberland Trough samples from the early Brigantian of Bewcastle. It is also one of the most common and is found throughout the overlying faunas including the

youngest sample from both the Longhoughton succession and Throckley borehole.

Gnathodus bilineatus

This species is not seen in the Bewcastle area, however it is seen in the earliest of the samples from the Throckley borehole and in one of the youngest samples from the Longhoughton succession. The variation in the presence of *G. bilineatus* is thought to be directly related to water depth (see below).

Two subspecies of *G. bilineatus* have been proposed in the past: *G. bilineatus bilineatus* (Roundy); *G. bilineatus bollandensis* Higgins & Bouckaert. The later subspecies is used to define the base of a biozone in the standard British Upper Carboniferous conodont biostratigraphy based upon its appearance at the base of the Arnsbergian (Higgins, 1975; 1985). In the Northumberland Trough the generally weaker, more poorly formed *G. bilineatus bollandensis* type P₁ element dominates all faunas of this species; the more robust, fully formed *G. bilineatus bilineatus* type P₁ element has only rare, sporadic appearances. Therefore, not only are the two subspecies not considered valid in this study (see discussion in systematic palaeontology), but the end member morphotypes offer no useful biostratigraphic utility.

Idioprioniodus healdi

Though not common, this species is found throughout the faunas of all three locations, from the very oldest to the very youngest, and is therefore of no biostratigraphic use.

Kladognathus complectens

This is one of the most common species in the Northumberland Trough faunas, largely due to ease with which it can be identified from diagnostic, robust M elements. As with *Idioprioniodus healdi*, it is found in the earliest and latest of the samples and is therefore of no use for biostratigraphic correlation.

Lochriea commutata

One of the most wide-ranging and common of the species in this study. Unfortunately however it is found in one the earliest and one of the latest samples and is of little biostratigraphic use.

Lochriea mononodosa

This species makes a notable arrival in the late Viséan of the Bewcastle and Longhoughton/Beadnell succession and is found sporadically in the Throckley borehole.

Lochriea nodosa

This species is the least common of the genus *Lochriea*, being found in only four samples from the Throckley borehole and Longhoughton. However these do not correlate and therefore the species is of little biostratigraphic use.

Mestognathus beckmanni

This very rare and sporadic species is found in one sample from each location, but has no biostratigraphic use.

Syncladognathus scitulus

This species is found in one of the earliest samples and is found throughout the successions at Bewcastle, Longhoughton and Throckley.

Group	Limestone	Sample No.	I. Healdi	K. complectens	G. girtyi	L. commutata	S. scitulus	C. naviculus	M. beckmanni	L. monodosa
Upper Liddesdale	u. Harelawhill	N551	X	X		X				
	"	N572a						X		
	"	N572b	X							
	m. Harelawhill	N552	X	X	X	X				X
	l. Harelawhill	N553	X	X		X				
	"	N554	X	X		X	X		X	
	m. Gastropod	N555	X	X		X				
		N556	X			X	X			
		N557	X	X						
	u. Tombstone	N550a								
	"	N550b								
	m. Tombstone	N558	X	X		X	X	X		
	"	N565								
	"	N559								
	l. Tombstone	N560				X	X			
	"	N561								
	m. Bridge	N564a	X			X				
	"	N564b								
u. Penton	N562a									
"	N562b									
"	N563a	X	X	X	X					
"	N563b		X							
Lower Liddesdale	Denton Mill	N1207								
	Un-named	N1201	X	X						
Upper Border	Gavelock	N530								
	Leahill	N531								
	Spy Hole	N527								
		N528								
	Appletree	N533								
	Millerhill	N526								

Fig. 3.1 Conodont species ranges from the Lower and Upper Liddesdale Groups of Bewcastle.

Group	Limestone	Sample No.	M. beckmanni	K. complectens	G. girlyi	S. scitulus	L. mononodosa	L. commutata	I. healdi	C. naviculus	G. bilineatus	L. nodosa	
Stainmore	u. Foxton	D775	X	X	X								
	I. Foxton	D776	X	X					X				
	Sugar Sands	D764	X								X		
		D763	X	X							X		
		D762	X	X	X			X			X		X
		D761	X	X	X			X			X	X	
		N55	X	X	X					X			
		D765											
	Iron Scars	D767	X		X						X		
		D766											
		N56a	X		X						X		
	N56b												
	Howick	D777											
	Cushat	D768	X								X		
	Great	D769	X										
Upper Liddesdale	Sandbanks	N50a	X	X	X						X		
		N50b											
		N51a	X		X				X	X			
		N51b											
		N53a	X										
		N53b											
		N276	X										
		N278											
		N280	X	X	X								
		N281	X	X	X								
		N282	X										
		N283	X		X						X		
		N284			X						X		
		N285			X						X		
		N286											
	N287												
	N288				X								
	N376												
	N377	X	X	X									
	N373		X										
	N375	X											
	N379				X								
	Acre	N913											
		N914a			X	X							
		N914b			X								
		N915			X					X			
		N916a			X								
		N916b	X	X	X								
		N917a											
		N917b	X	X	X								
N918a				X									
N918b													
N918c		X	X	X	X	X							
N919		X	X	X									
N920		X	X										
N921		X	X										
N923													
N925			X										
N926													
Eelwell	N358	X	X										
U. Border	Dun	N1128	X	X									

Fig. 3.2 Conodont species ranges from the Upper Liddesdale Group and Stainmore Group of Longhoughton and Beadnell.

Group	Limestone	Sample No.	G. girtyi	G. bilineatus	K. complectens	L. commutata	S. scitulus	L. mononodosa	C. naviculus	L. nodosa	I. healdi	M. beckmanni	A. unicomis	
Stainmore	Un-named (C10)	BGS 587	X	X	X			X	X	X	X		X	
		BGS 588		X	X									
	Grindstone	BGS 605												
		BGS 589		X	X		X							
		BGS 634		X										
		BGS 635		X	X	X	X					X		
		BGS 606		X		X								
		BGS 590			X									
	Upper Felltop	BGS 591	X		X									
		BGS 592												
		BGS 613											X	
		BGS 636												
		BGS 593	X		X	X						X		
		BGS 594	X			X								
		BGS 614												
	Pike Hill	BGS 595												
		BGS 596				X								
	Lower Felltop	BGS 597	X	X	X									
		BGS 632	X		X									
		BGS 607	X		X	X	X		X		X			
		BGS 608		X	X	X								
		BGS 609												
	Aydon Shell Bed	BGS 641												
		BGS 598												
	Crag	BGS 642			X									
		BGS 643			X									
		BGS 644												
	Little	BGS 645												
		BGS 646												
		BGS 599			X									
		BGS 633	X											
	Great	BGS 610			X									
		BGS 600	X	X	X									
		BGS 601		X	X	X	X	X	X	X				
		BGS 602					X							
		BGS 603	X		X		X	X		X				
BGS 604		X	X	X	X									
BGS 637		X	X	X		X	X	X						
BGS 638				X		X	X							
BGS 639			X	X	X		X							
BGS 640					X									
BGS 611		X	X	X	X	X								
BGS 612														

Fig. 3.3 Conodont species ranges from the Stainmore Group of the Throckley borehole.

Conodont biozonation

Based upon the species ranges (Figs. 3.1-3.3), it is possible to erect a conodont biozonation for the Asbian - Arnsbergian of the Northumberland Trough (Fig. 3.4).

Kladognathus complectens First Appearance Biozone

Defined on the first appearance of *K. complectens* in the un-named limestone below the Denton Mill Limestone (Lower Liddesdale Group). Prior to this, the Lower Liddesdale Group samples were barren, so this biozone also marks the beginning of a phase of marine influence that could support conodont animals. The upper limit of this biozone is marked by the first appearance of *G. girtyi* and *S. scitulus* in the Penton Limestone. *I. healdi* also appears at this horizon in Bewcastle, but not at Longhoughton, and only sporadically in the overlying samples.

Gnathodus girtyi - *Synchlydogathus scitulus* Concurrent Range Biozone

The base of this biozone is defined by the first appearance of *G. girtyi* and *S. scitulus* in the early part of the Upper Liddesdale Group of Bewcastle. The upper limit is defined by the base of the next biozone. *L. commutata* is also a characteristic species of the biozone, however it occurs more sporadically than the eponymous zonal species.

Lochriea mononodosa First Appearance Biozone

Defined on the first appearance of *L. mononodosa* towards the top of the Upper Liddesdale Group. Using traditional lithostratigraphic correlations (e.g. Day, 1970; Johnson *et al.*, 1995; Chadwick *et al.*, 1995) the Under Limestone of Bewcastle is considered to be equivalent to the Sandbanks Limestone, and this results in the first appearance of *L. mononodosa* slightly earlier in the Bewcastle area (in the Harelawhill Limestone), than at Longhoughton (in the Acre Limestone). This suggests a lithostratigraphical miscorrelation at this level. The most obvious solution, is that the Under and Catsbit Limestones in Bewcastle, are together the equivalent of the Great Limestone further east; thus the Buccleugh and Sandbanks Limestone would correlate, and the Harelawhill and Acre Limestone would correlate. Therefore the first appearance of *L. mononodosa* is in the second limestone beneath the Great Limestone and Under/Catsbit Limestone.

G. bilineatus First Appearance Biozone

The base of this biozone is marked by the first appearance of *G. bilineatus* in the Great Limestone. The top of the biozone is marked by the base of the overlying biozone.

Adetognathus unicornis First Appearance Biozone

The presence of *A. unicornis* marks a significant change in the conodont faunas in the highest sample from the Stainmore Group of the Throckley borehole and is used to define the base of this biozone. The upper limit of this biozone is not seen in this study.

Lithostrat.	Succession			Biozone
	Bewcastle	Longhoughton	Throckley	
Stainmore Group			Un-named	<i>A. unicornis</i>
		Upper Foxton Lower Foxton Sugar Sands Iron Scars Howick Cushat Great	Styford Grindstone Upper Felltop Pike Hill Lower Felltop Belsay Dene Aydon Shell Bed Crag Little Great	<i>G. bilineatus</i>
Upper Liddesdale Group	Buccleugh Harelawhill	Sandbanks Acre		<i>L. mononodosa</i>
	Gastropod Tombstone Bridge Penton	Eelwell		<i>G. girtyi</i> - <i>S. scitulus</i>
	Un-named Un-named Low Tipalt Un-named Un-named Denton Mill Un-named			<i>K. complectens</i>
Lower Liddesdale Group		Dun		
Upper Border Group	Naworth Naworth Bryozoan			Barren
	Gavelock Leahill Spy Hole Appletree Millerhill			

Fig. 3.4 Comparison between the lithostratigraphy (based on Johnson *et al.*, 1995), the limestones in the three successions sampled for conodonts and the resulting conodont biozonal scheme.

3.2.2 Correlation with other conodont biozonations

The Asbian - Arnsbergian interval (Fig. 3.5), bridges the divide between the classic biostratigraphic Dinantian studies of Metcalfe (1981) and Varker & Sevastopulo (1985) and the Silesian studies of Higgins (1975, 1985); the only significant additional conodont biozonation is that proposed by Armstrong & Purnell (1987) on the Dinantian succession of the Northumberland Trough. The biostratigraphic scheme of Armstrong & Purnell (1987) is broadly similar to that proposed here (the same Bewcastle samples were the basis of both Asbian - Brigantian studies).

The established British conodont biostratigraphy is based on form taxonomy, which was largely based on ozarkodinid P₁ element morphology and with biostratigraphic use in mind, rather than biological reality. During the Asbian - Arnsbergian interval, emphasis has been placed on phylogenetic changes in the *Gnathodus* lineage. In this study, these are not considered to be true biologically valid subspecies. In addition, the subspecies of *Gnathodus* in the Northumberland Trough have a more random stratigraphic distribution than in the Pennine Basin. Therefore the established biozonation schemes give greater subdivision, particularly during the early Namurian, than is possible in the present study.

The biozonal scheme of Metcalfe (1981) and Varker & Sevastopulo (1985) can be correlated with that proposed for the Northumberland Trough. *L. commutata* is found much earlier in the Pennine Basin, from the mid-Arundian, rather than from the mid-Brigantian of the Northumberland Trough. The time that the first late Asbian faunas are found in Northumberland corresponds approximately with the appearance of *G. bilineatus* in the Craven Basin (Metcalfe, 1981). This may indicate a regional/global eustatic rise in sea level bringing deeper water faunas into the Craven Basin and allowing shallow water faunas into the more restricted Northumberland Trough. The appearance of *L. mononodosa* is a biostratigraphic event which appears to be synchronous across the north of England, during the Asbian - Arnsbergian interval and may be related to a late Brigantian rise in relative sea level recognised in this study (Section 2.4).

The base of the *G. bilineatus* biozone coincides with the base of the Pendleian stage. The appearance of *G. bilineatus* in the Pennine Basin has also been used to mark the base of a biozone, but this much lower in the succession during the Asbian (Varker & Sevastopulo, 1985). The late arrival of this typical deep water species in the Northumberland Trough, is interesting and will be discussed later in this chapter (Section 3.4.1).

The consistent Namurian conodont fauna prevents the erection of biozones in the Northumberland Trough and therefore prohibits correlation with the Pennine Basin (Higgins, 1975; 1985). In fact, it is possible from data in this study to highlight the 'local' nature of the biozones proposed by Higgins in the Pennine Basin. Shallow water forms such as *C. naviculus* and *G. bilineatus bollandensis*, were used by Higgins (*op. cit.*) to define the base of a biozone comparable with the base of the Arnsbergian; in the Northumberland succession they are both found much stratigraphically lower than in the Pennine Basin, in the mid Brigantian and basal Pendleian respectively.

The major Mississippian - Pennsylvanian conodont evolutionary event is not recorded in the samples from this study. The late Arnsbergian samples from the Throckley borehole must have been stratigraphically very close to this event, however none of the diagnostic species were present (Riley *et al.*, 1987; Varker *et al.*, 1990; Varker, 1994).

Chronostrat	Higgins 1975	Metcalf 1981	Varker & Sevastopulo 1985	Higgins 1985	Armstrong & Purnell 1987	This study	Chronostrat
Chokerian				D. noduliferous			Chokerian
Amsbergian	G. bilineatus bollandensis - C. naviculus			G. bilineatus bollandensis		A. unicornis	Amsbergian
Pendleian	Kladognathus - G. girtyi simplex			Kladognathus - G. girtyi simplex		G. bilineatus	Pendleian
Brigantian	G. girtyi collinsoni	L. nodososa	G. girtyi collinsoni L. mononodosa	G. girtyi collinsoni	L. mononodosa	L. mononodosa	Brigantian
		G. bilineatus	G. bilineatus		G. girtyi - G. bilineatus	G. girtyi-S. scitulus	
Asbian					?	K. complectens	Asbian
Holkerian		L. commutata	L. commutata		Barren	Barren	Holkerian

Fig. 3.5 Comparison of British Asbian - Arnsbergian conodont biozonation.

3.2.3 Influence of sequence stratigraphy on biostratigraphy

Sea level change had a profound influence on the appearance of different conodont species and thus, the resultant biozones (Fig. 3.6). Taking this into account, the first appearance biozones are simply the result of local migrations and this clearly limits their biostratigraphic utility outside the Northumberland Trough. In this section, an attempt is made to correlate the biostratigraphy and sequence stratigraphy.

K. complectens biozone

The first appearance of *K. complectens*, during the mid-Asbian of the Lower Liddesdale Group, is tentatively correlated with a particularly thick mid-Asbian sequence (base of SS-II). This thick sequence is clearly recorded in the Longhorsley and Harton boreholes (Figs. 2.21, 2.22), and implies a significant rise in relative sea-level.

G. girtyi - *S. scitulus* biozone

This biozone almost certainly coincides with one of the most important sequence stratigraphic events during this interval of time in the Northumberland Trough. This mega-sequence initial flooding surface (base of SS-IV), is marked by one of the thickest sequences in the entire Asbian-Arnsbergian succession.

L. mononodosa biozone

This biozone coincides with a particularly thick sequence (SS-V), in the Upper Liddesdale Group just below the Great Limestone. It is part of a trend of increasing sea-level and marks a flooding event that brings a new species into the basin. It is most notable that this biozone is also registered in the Pennine Basin and we can therefore postulate that this sea level rise was at least regional in its effect.

G. bilineatus biozone

The base of this biozone also marks a major sequence stratigraphic event, as it coincides with the thickest limestone in the basin which is considered to have formed at a mega-sequence maximum flooding surface (base of SS-VI). The fact that *G. bilineatus* is a typical deep water species and its first appearance coincides with a

mega-sequence maximum flooding event, proves beyond doubt the inter-relation of sea level change and biostratigraphy.

A. unicornis biozone

It is impossible to point directly to a sequence stratigraphic event correlating with the appearance of *A. unicornis* and as this species is only found in one sample, no significance can be attributed to its presence.

The fact that there are no mid-late Namurian marine faunas is also considered to be a result of sequence stratigraphy. The Chokierian - Alportian is represented by a Type I mega-sequence boundary (i.e. an unconformity) and the Kinderscoutian - Yeadonian was a period of non-marine deposition related to lowstand and early transgressive systems tract sedimentation.

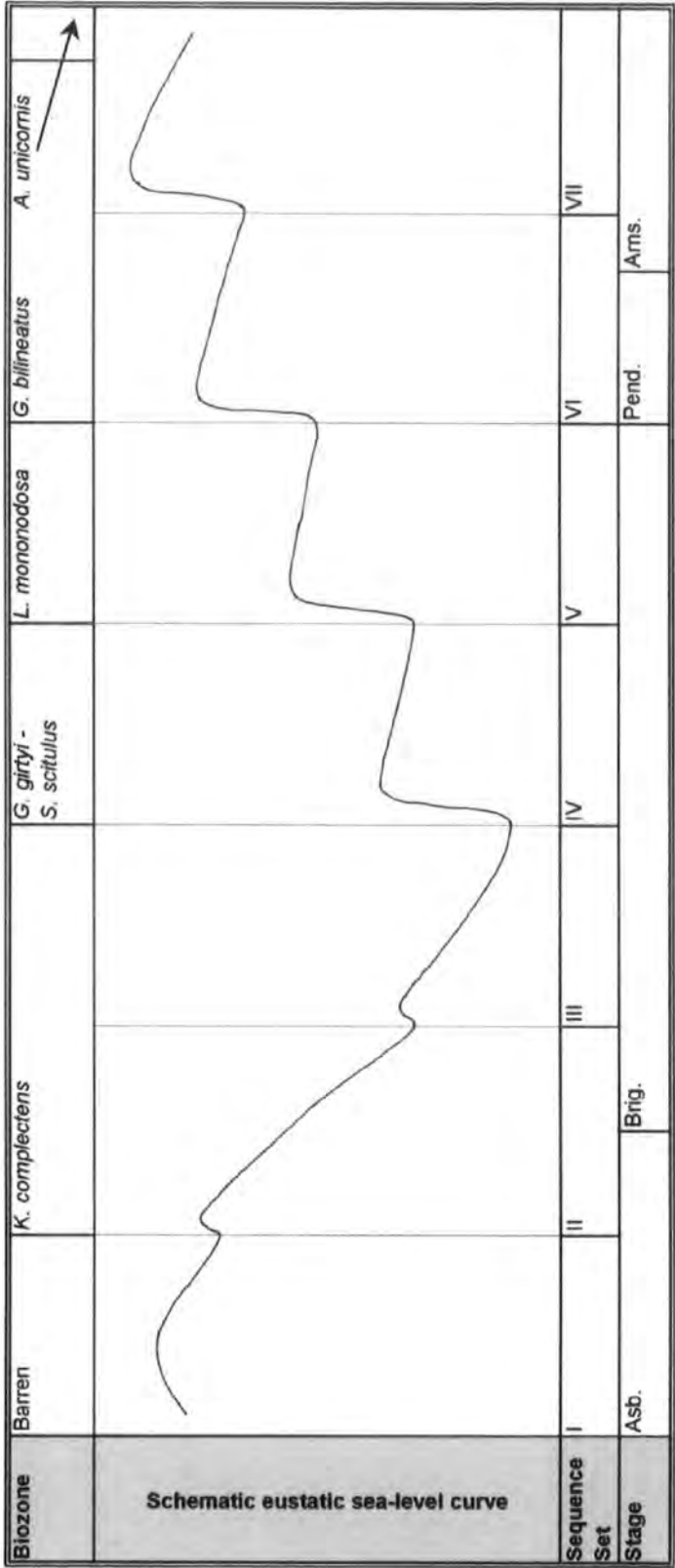


Fig. 3.6 Sequence stratigraphy of the Asbian - Arnsbergian with the biozones superimposed.

3.3 Palaeoecology

3.3.1 Context

Introduction

The spacial distribution of conodonts is thought to have been controlled by an inter-related series of physical (water depth, hydraulic energy, circulation, temperature), chemical (pH, salinity) and biological (nutrient availability, competition, susceptibility to predation) factors (e.g. Merrill & von Bitter, 1976; Sandberg, 1976; Davies *et al.* 1984).

Established palaeoecological models

Two end-member models have been proposed. The depth stratification model is based on the premise that the all conodonts was pelagic (Seddon, 1970; Seddon & Sweet, 1971; Druce, 1973) and predicts sediments deposited in shallow water would contain limited taxa that lived in the upper part of the water column, whilst sediments from the deeper parts of the shelf and basin contain more taxa relating to faunas adapted to gradually deeper water depths (Fig. 3.7a).

The lateral segregation model (Barnes *et al.*, 1973; Barnes & Fåhræus, 1975) considered that conodonts were pelagic and benthonic or nekto-benthonic, and onshore-offshore differences in conodont faunas were due to facies changes down the shelf (Fig. 3.7b).

Both these models have greatly influences the interpretation of conodont biofacies studies which have been largely model driven. For example Druce (1973) applied directly the depth stratification model to Upper Palaeozoic and Triassic conodonts using previously published data (Fig. 3.7a). Later studies have favoured the lateral segregation model (Fig. 3.7b). This distinguishes between shallow shelf (*Cavusgnathus* dominated faunas) and outer shelf environments (dominated by *Gnathodus* species).

The Asbian-Arnsbergian succession in Northumberland extends from nearshore (Longhoughton) to outer shelf settings (Bewcastle & Throckley). In common with other biofacies studies for this interval (Varker, 1967; 1968; Aldridge *et al.*, 1968; Austin, 1973; Druce, 1973; Austin, 1976; von Bitter, 1976; Higgins, 1981; Austin & Davies, 1984; Rexroad & Horowitz, 1984; Davis & Webster, 1985; Rexroad & Merrill, 1985; Armstrong & Purnell, 1987; Rexroad & Horowitz, 1990; Morrow & Webster, 1991; 1992; Davies *et al.*, 1993; Krumhardt *et al.*, 1996 - see Fig. 3.8), conodont faunas from the inner to mid shelf are dominated by *Cavusgnathus*. *Gnathodids* (including *Lochriea*) range across the shelf into restricted near-shore settings. This apparent difference from published studies plus the apparent ecological controls have stimulated an analysis of the spacial and temporal changes in conodont biofacies distribution in Northumberland with particular emphasis on effects of relative sea-level change on conodont biofacies at a local and regional scale.

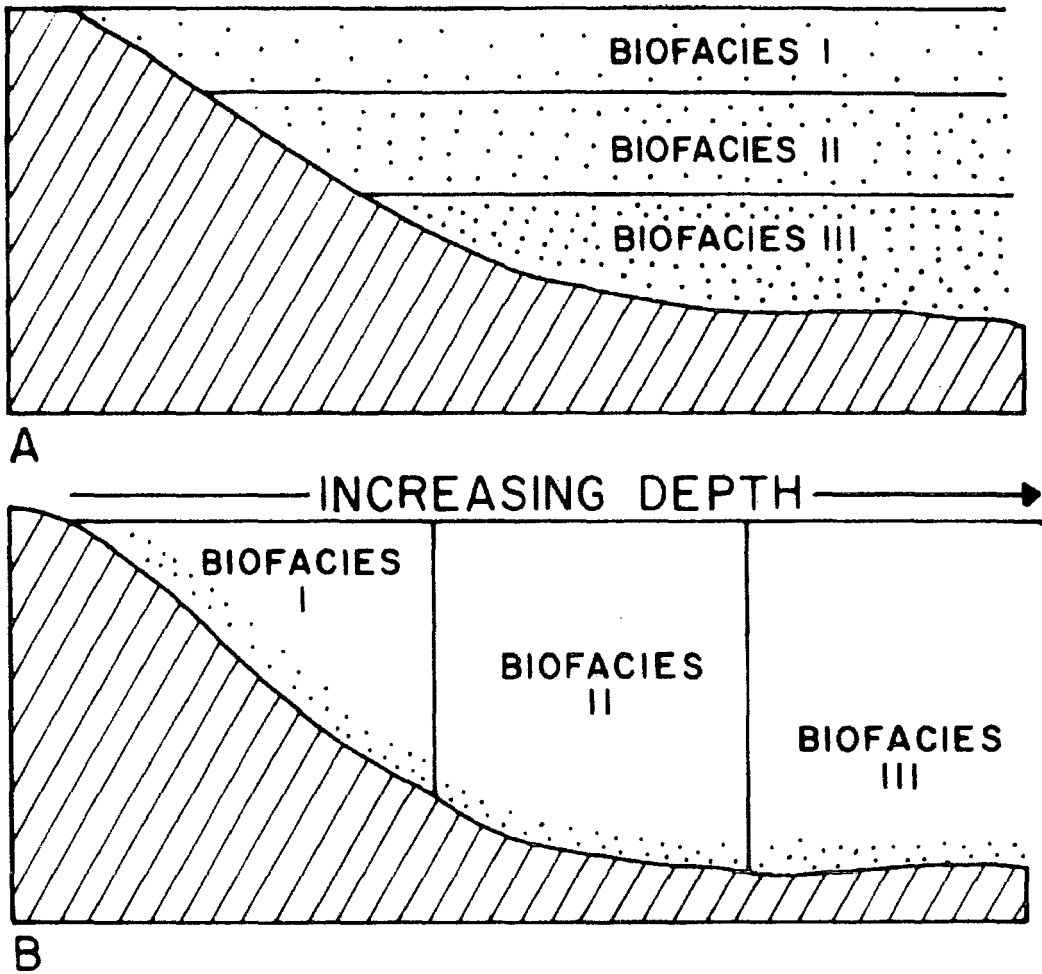
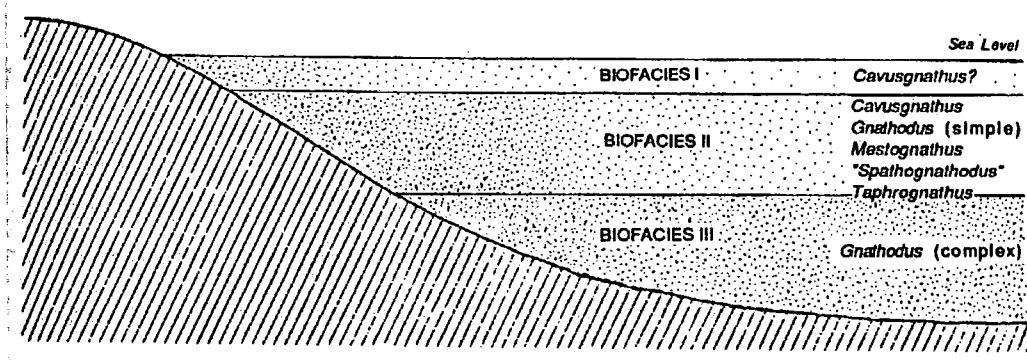
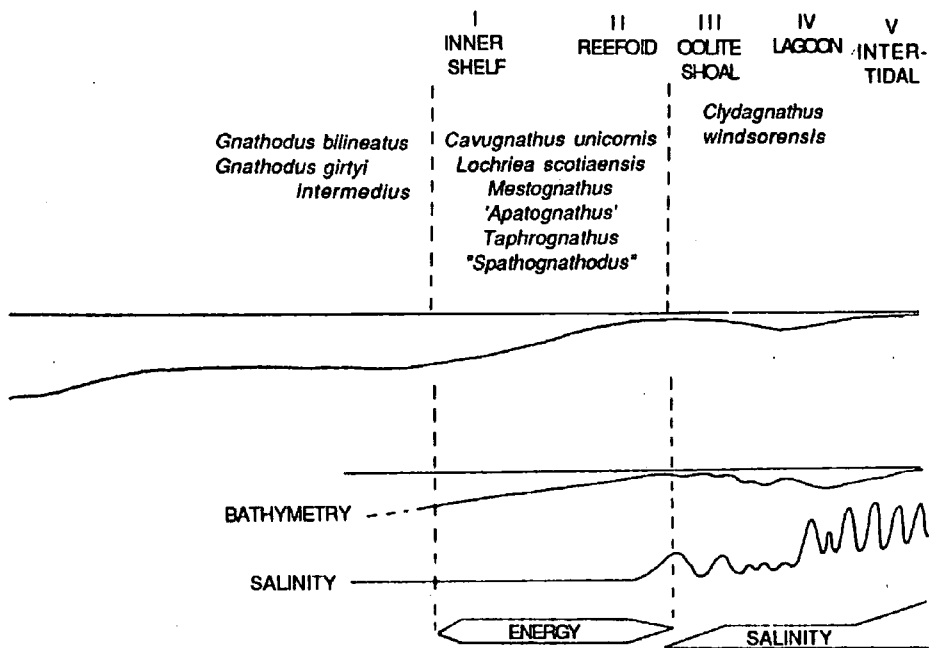


Fig. 3.7 The two main end-member models of conodont distribution:
a) bathymetric model (after Seddon, 1970; Seddon & Sweet, 1971; Druce, 1973);
b) lateral segregation model (after Barnes *et al.*, 1973; Barnes & Fåhraeus, 1975).



(a)

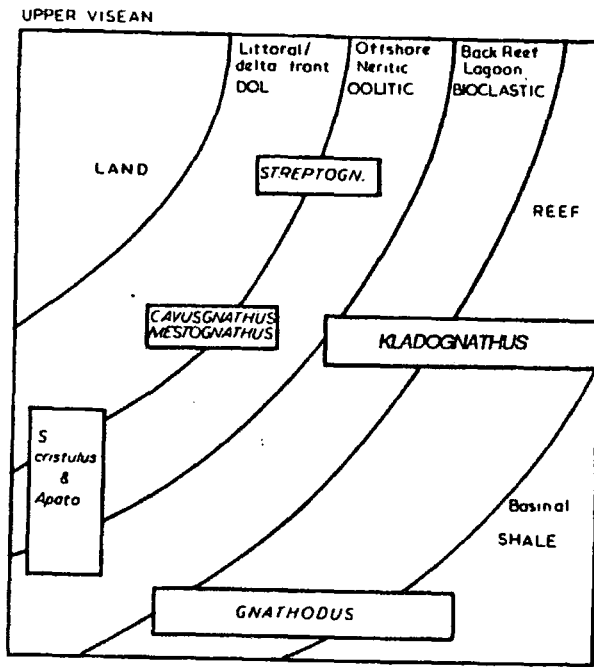


(b)

Fig. 3.8 Different models of Asbian - Arnsbergian conodont palaeoecology:

a) Druce (1973)

b) von Bitter (1976)



(c)

series	stages	environ-ment	SHALLOW WATER				DEEP WATER	
			HYPER-SALINE (dolomites)	BACK-REEF (cokite mudstones)	LAGOONAL (black, fine limestones)	INNER SHELF (bioclastic limestone)	BASIN (shales)	PELAGIC PLATFORM (red, nodular lssts)
NAMURIAN	CHOKIERIAN						<i>Meognathodus</i> <i>DECLINOGNATHODUS</i> <i>Adetognathus</i> <i>Rhachistognathus</i>	
	ARNSBERGIAN	E _{2c}					<i>Rhachistognathus</i> <i>Adetognathus</i>	
		E _{2a,b}					<i>Adetognathus</i>	
PENDLEIAN								
VISEAN	BRIGANTIAN		<i>Pcommutatus</i>	<i>Pcommutatus</i> <i>NESTOGNATHUS</i> <i>G homopunctatus</i>	<i>Pcommutatus</i> <i>Mestognathus</i> <i>G homopunctatus</i>	<i>Pcommutatus</i> <i>Mestognathus</i> <i>G homopunctatus</i>	<i>Pcommutatus</i> <i>Mestognathus</i> <i>G homopunctatus</i>	<i>Pcommutatus</i> <i>Mestognathus</i> <i>G homopunctatus</i>
			<i>CAVUSGNATHUS</i> <i>G girtyi</i> <i>APATOGNATHUS</i>	<i>CAVUSGNATHUS</i> <i>G girtyi</i> <i>APATOGNATHUS</i>	<i>CAVUSGNATHUS</i> <i>P NODOSUS</i> <i>G BILINEATUS</i> <i>G GIRTYI</i> <i>APATOGNATHUS</i>	<i>CAVUSGNATHUS</i> <i>P NODOSUS</i> <i>G BILINEATUS</i> <i>G GIRTYI</i>	<i>P NODOSUS</i> <i>G BILINEATUS</i> <i>G GIRTYI</i>	<i>P NODOSUS</i> <i>G BILINEATUS</i>

(d)

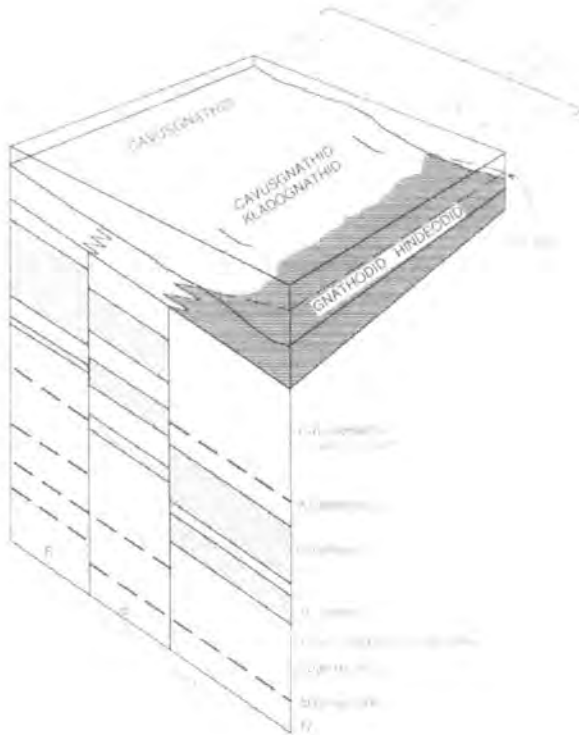
Fig. 3.8 Different models of Asbian - Arnsbergian conodont palaeoecology:

c) Austin (1976)

d) Higgins (1981)

BASINAL FAUNAS	SHELF FAUNAS	STAGES
<i>Paragnathodus nodosus</i>		BRIGANTIAN
<i>Gnathodus bilineatus</i>		ASBIAN
<i>G. pseudosemiglaber</i>	<i>Cavusgnathus</i> - <i>Apatognathus</i>	HOLKERIAN
<i>G. commutatus</i>	<i>Taphrognathus</i>	ARUNDIAN
<i>G. homopunctatus</i>	<i>Cloghergnathus</i>	CHADIAN
	<i>Mestognathus beckmanni</i>	
<i>S. anchoralis</i>	<i>S. anchoralis</i>	COURCEYAN
<i>Gnathodus delicatus</i>	<i>Polygnathus mehli</i> - <i>D. bouckaerti</i>	
	<i>Polygnathus communis carina</i>	
Lower <i>S. crenulata</i> ?	<i>Pseudopolygnathus multistriatus</i>	
<i>S. tobata</i> ?	<i>Bispathodus</i> - <i>Pseudopolygnathus</i>	
<i>S. duplicata</i> ?	<i>Siphonodella</i> - <i>P. inornatus</i>	
<i>S. sandbergi</i> ?	<i>Polygnathus spicatus</i>	
<i>Siphonodella sulcata</i>	<i>P. variabilis</i> - <i>B. plumulus</i>	

(e)



(f)

Fig. 3.8 Different models of Asbian - Arnsbergian conodont palaeoecology:

e) Austin & Davies (1984)

f) Krumhardt *et al.* (1996)



3.3.2 *Local temporal changes in biofacies*

The Great Limestone at Mootlaw Quarry (NZ020760), 10km north of Corbridge, was sampled intensively to provide evidence for palaeoecological variation within a single limestone unit (Fig. 3.9). Both limestone and mudstone interbeds were sampled.

Diversity and abundance

The varied diversity of the samples is clearly related to the lithology: mudstones consistently contain a low diversity fauna (0-2 species); limestones (Fig. 3.10) conversely contain a more diverse fauna (1-7 species).

Varker (1968) highlighted a peak of conodont abundance in the upper part of each limestone, commonly at approximately two-thirds the thickness of the unit (Fig. 2.13). He concluded that this pattern resulted from an increased rate of deposition in the lower part of the limestone, diluting the conodont element abundance. Working on similar Yoredale facies, Dean (1987) lent some support to Varker's conclusions, however intense sampling of the Gayle Limestone on the Askrigg Block by Davies *et al.* (1994), failed to find results consistent with those found by Varker (*op. cit.*). Indeed in the Gayle Limestone, conodont abundances were highest at the very top of the limestone.

Purnell (1989) tested the wider utility of the distribution pattern documented by Varker (1968) on the Bogside Limestone (Chadian, Lower Border Group). Bed by bed sampling revealed a very different abundance pattern in which peak conodont element abundance occurred towards the base of the limestone (Fig. 3.11). Purnell (*op. cit.*) concluded that Varker's model (*op. cit.*) did not fit the Bogside Limestone abundance and that a simple interplay between conodont animal abundance and sedimentation rate alone can not adequately explain the pattern found. Closer scrutiny shows that the Gayle Limestone contains a thin mudstone horizon with very low conodont abundances. The minor upper and lower limestone units contain an increasing conodont abundance with a peak at two-thirds to three-quarters the thickness of each minor unit, fitting the pattern proposed by Varker. The Bogside Member has the opposite trend with a peak in the lower quarter of

each minor limestone unit, above which the conodont abundance decreases. Could these differences reflect systematic changes of sea level?

Conodont element abundance in the Mootlaw Quarry samples from the Great Limestone, broadly increases towards the top of the limestone (Fig. 3.10). This supports the work of Varker (1968) and contradicts Davies *et al.* (1994).

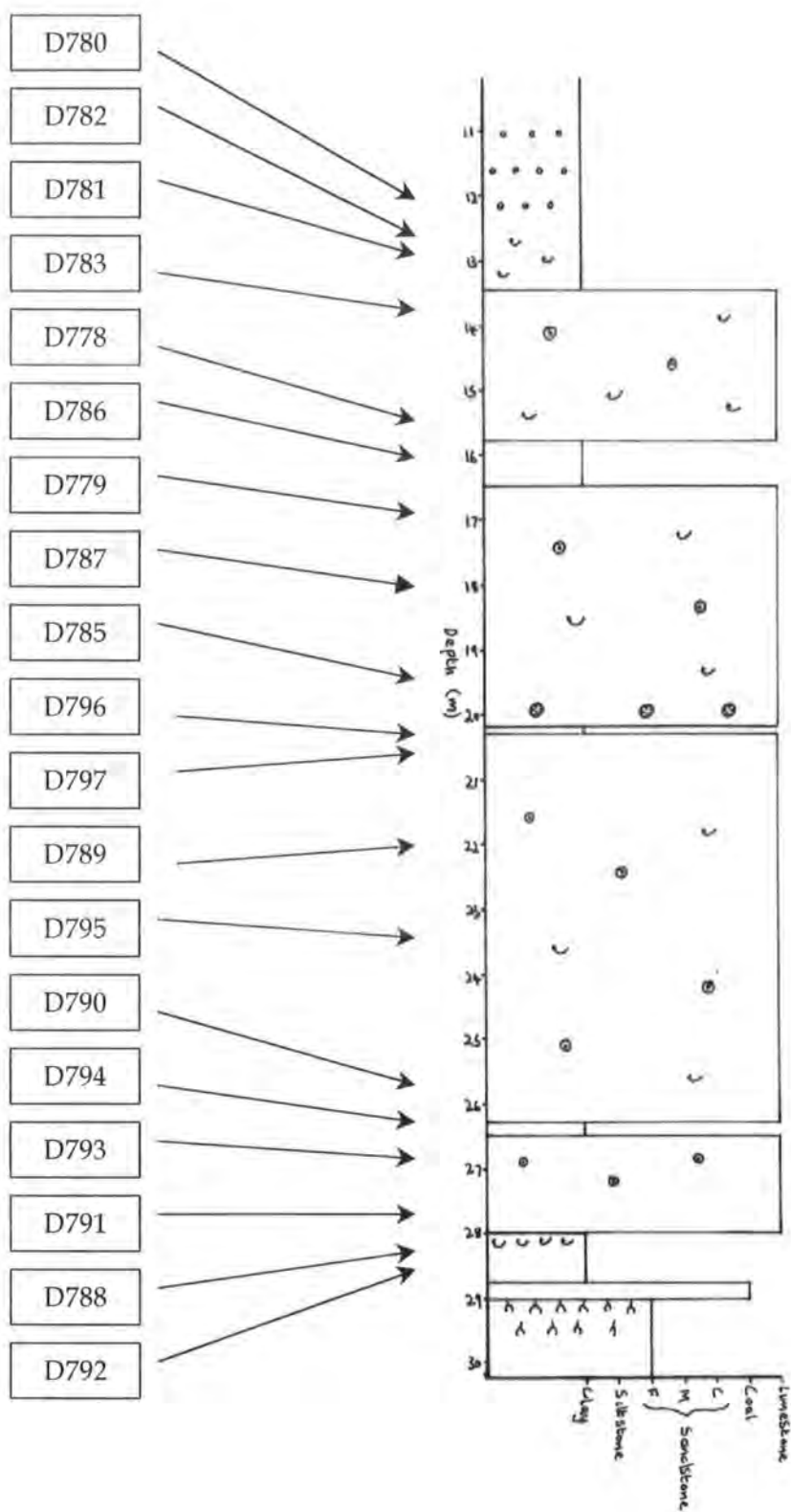


Fig. 3.9 Graphic log of the Great Limestone at Mootlaw Quarry (NZ020760); taken from a written description by Mark Dean, British Geological Survey, Murchison House, Edinburgh.

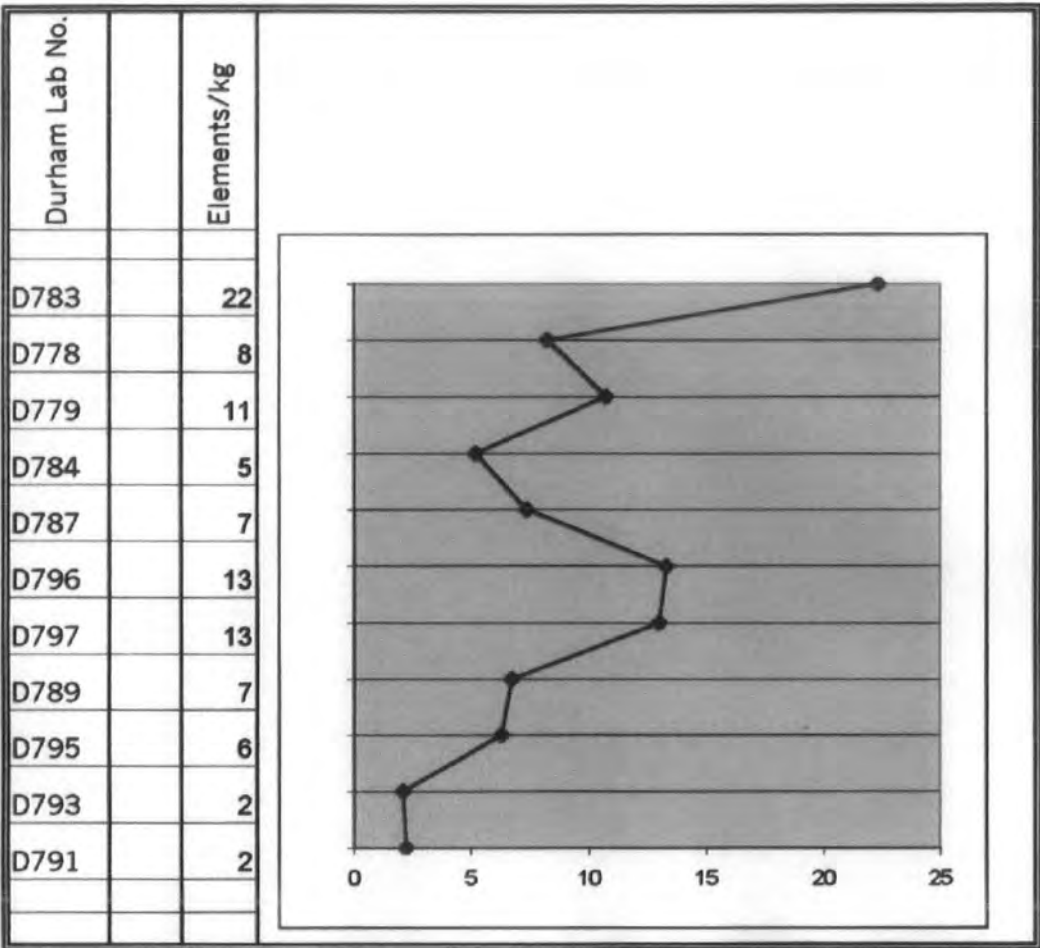


Fig. 3.10 Abundance of conodont elements through the Great Limestone (limestone samples only, i.e mudstone samples not shown) at Mootlaw Quarry (NZ020760).

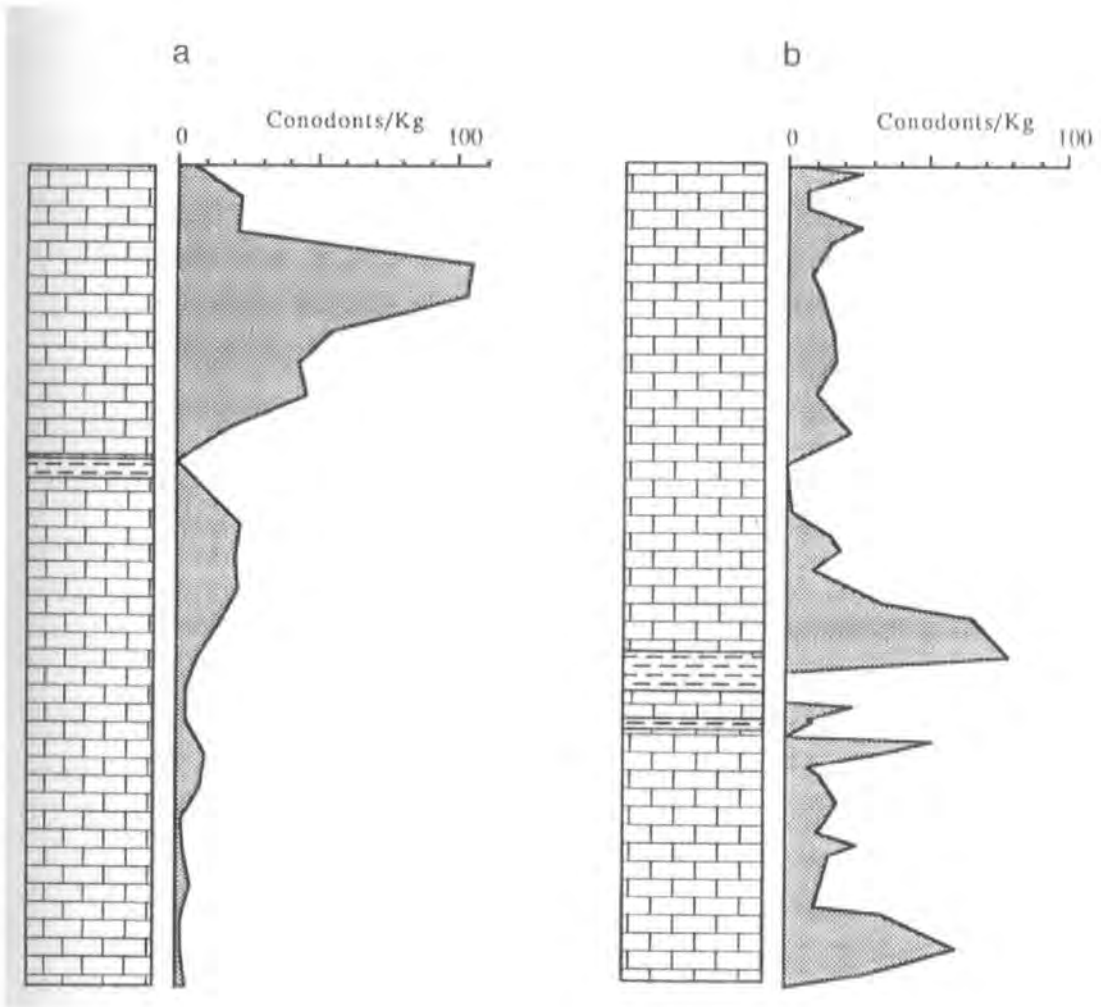


Fig. 3.11 Comparison of conodont abundance between a Yoredale limestone and a Lower Border Group Limestone (from Purnell, 1989): a) The Gayle Limestone Member (SD872893; data from Varker, 1968); b) The Bogside Limestone Member, Ashy Clough (NY56497700; data from Purnell, 1989).

Gradient Analysis

The most interesting palaeoecological results relate to the systematic variation of conodont species from the bottom to top of the Great Limestone (Fig. 3.12). A constrained seriation of the presence / absence of species was carried out on the 20 samples (technique described in Appendix IV). There are two trends of species presence: firstly those that have a more restricted range; secondly those that occur throughout the limestone. It is this first group which have been organised in descending order of their mean rank.

The constrained seriation, coupled to an extensive and well established published literature on mid-Carboniferous conodont palaeoecology, can be used to show changing ecology through the Great Limestone. The palaeoecological signature of each species differs and by relating these results with the established models, a detailed breakdown can be produced.

Gnathodus bilineatus

This species of *Gnathodus* is restricted to the lowest parts of the Great Limestone at Mootlaw Quarry; though only present in two samples, both of these are distinct in their depth within the section and this species clearly has the highest mean rank emphasising its position towards the base of the Great Limestone. Due to the well established association of this species with deep water biofacies (e.g. Higgins, 1981), *Gnathodus bilineatus* is marking an extreme end-member position, suggesting that the base of the Great Limestone was deposited in a deep water, outer shelf environment.

Lochriea commutata / *Lochriea mononodosa* / *Lochriea nodosa*

All three species of *Lochriea* have a very similar range, within the mid-upper limestone. The three species are ordered in their traditional accepted phylogenetic order (i.e. in order of increasing ornamentation), which may indicate a subtle but systematic variation in palaeoecological range (perhaps ecophenotypes), suggestive of different ecological niches. Traditionally the genus *Lochriea* is included with the deep water biofacies association that includes *Gnathodus* (e.g. Higgins, 1981; Austin & Davies, 1984). The gradient

analysis suggests that there is a difference, even if it is subtle, between these two genera.

Idioproniodus healdi

The range of this species is similar to that of the species of *Lochriea*; relatively central in the section, but slightly higher. The genus *Idioproniodus* has previously been associated with rocks that are dark coloured, organic-rich, formed under conditions of quiet water and relatively low pH (Merrill, 1973; Merrill & von Bitter, 1976; 1984; Rexroad, 1993). *I. healdi* in the Mootlaw section is related to the upper sample of the two limestone beds. This was a time when carbonate production was diminishing prior to deposition of mudstone; though not directly related to the conditions described above, this perhaps points to a period during the deposition of the Great Limestone which is most similar. The absence of *I. healdi* from the mudstone layers may well just be a problem of low yields due to poor disaggregation of these samples or very low abundances of all conodont species during this period.

Syncladognathus scitulus

This species is one of the most frequently present and has a broad range of over half the samples in the Mootlaw section. This suggests a broad range of environmental tolerance and places this species in a rather unique position: it is distinctly longer ranging than most of the species, but not comparable with *K. complectens* and *G. girtyi*. Traditionally this genus, known by the form taxonomic name '*Apatognathus*', is characteristic of shallow water faunas (e.g. Varker, 1967; Austin, 1976; Higgins, 1981).

Cavusgnathus naviculus

C. naviculus is the species in the Mootlaw section at the top of the limestone. It is also the classic diagnostic genus for shallow water faunas and defines the opposite biofacies to *G. bilineatus* (e.g. Austin, 1976; Higgins, 1981; Krumhardt *et al.*, 1996). This suggests that the top of the Great Limestone was deposited in a shallow water, inner shelf environment.

Kladognathus complectens / *Gnathodus girtyi*

Both of these species occur throughout the limestone. *K. complectens* is generally found in a broad range of environments (Krumhardt *et al.*, 1996). *G. girtyi* is traditionally associated with deep water biofacies (e.g. Austin, 1976; von Bitter, 1976; Higgins, 1981; Krumhardt *et al.*, 1996). The evidence from the Great Limestone at Mootlaw suggests that the tolerance of both species to varying water depths was greater than that of other species. This leads to the conclusion that *K. complectens* and *G. girtyi* were pelagic and not restricted to specific nekto-benthonic environments.

It is also worthy of note, that based upon this data it would appear that *G. bilineatus* and *G. girtyi* are truly separate species which inhabited very distinct palaeoecological niches.

Sample No.	Mudstone / Limestone	K. ccomplectens	G. girtyi	G. bilineatus	L. commutata	L. mononodosa	L. nodosa	I. Healdi	S. scitulus	C. naviculus	Rank
D780	M									■	1
D782	M		■								2
D781	M		■								3
D783	L								■		4
D778	L	■	■						■	■	5
D786	M										6
D779	L	■	■					■	■		7
D784	L		■				■		■		8
D787	L		■			■					9
D785	M	■									10
D796	L	■	■	■	■	■		■	■		11
D797	L		■				■	■			12
D789	L				■			■			13
D795	L	■				■					14
D790	M										15
D794	M	■	■								16
D793	L		■								17
D791	L	■		■							18
D788	M										19
D792	M										20
Mean rank		12.3	8.7	14.5	12.0	11.5	10.0	9.0	8.7	3.0	

Fig. 3.12 Constrained seriation of presence (black) / absence (white) of species in the Great Limestone at Mootlaw Quarry (NZ020760).

Biofacies model

From the above discussion of the gradient analysis, it is possible to propose an informal, qualitative biofacies model for the Asbian - Arnsbergian Yoredale limestones of the Northumberland Trough (Fig. 3.13).

***G. girtyi* - *K. complectens* Biofacies.** Both of these species are considered to be pelagic, being found throughout the Mootlaw Quarry section, in samples which contain typical deep and shallow water faunas.

***C. naviculus* Biofacies.** The genus *Cavusgnathus* is commonly considered to be diagnostic of shallow water environments (e.g. Krumhardt *et al.*, 1996) and this seems to be the case from the gradient analysis evidence where it is found in end-member samples, at the opposite extreme from *G. bilineatus*, a typical deep water species.

***Lochriea* - *I. healdi* Biofacies.** *L. commutata*, *L. mononodosa*, *L. nodosa* and *I. healdi* all seem to have inhabited an intermediate palaeoecological niche. There is overlap with the more inshore and offshore nekto-benthonic biofacies, but the constrained seriation of the Great Limestone faunas from Mootlaw Quarry clearly suggests a distinct intermediate biofacies which lacks the end member species diagnostic of the bordering biofacies.

***G. bilineatus* Biofacies.** This species of *Gnathodus* in particular, has long been associated with deep water (e.g. Davies *et al.*, 1994). In the gradient analysis described above, *G. bilineatus* has a very distinct position at the base of the limestone unit and with a higher mean rank than any other species.

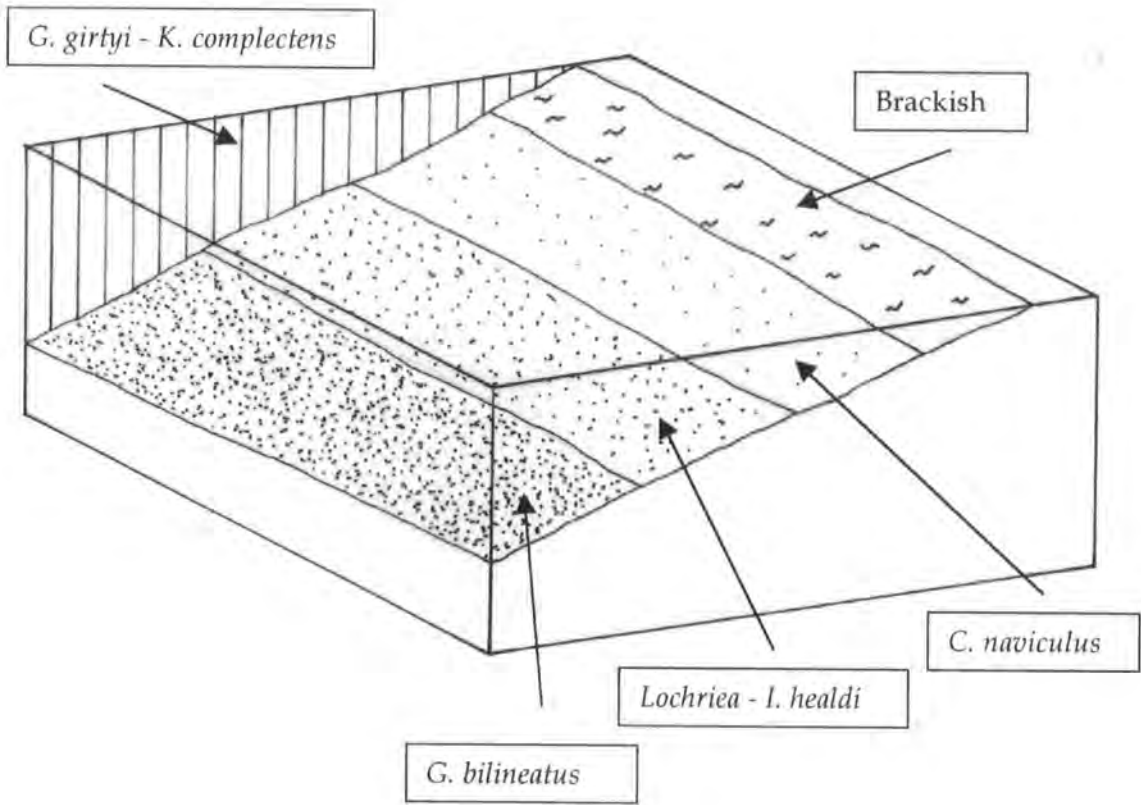


Fig. 3.13 Biofacies model for the Asbian - Arnsbergian Yoredale limestones of the Northumberland Trough.

3.3.3 Regional biofacies

The Northumberland Trough was essentially a half-graben: Dinantian subsidence was controlled by extensional faulting, whilst thermal subsidence and differential compaction were the dominant mechanisms during the Silesian (Section 1.2). During the Asbian - Arnsbergian, topographic variation across this area would have been relatively subdued in relation to preceding times (Fig. 3.14a). However, the southern part of the basin (around Throckley) would still have been deeper than the northern part (around Longhoughton), due to differential subsidence and continued irregular extensional fault movement. During periods of relatively high sea level, the Northumberland Trough would have been an area of shallow shelf, whilst during periods of relative low sea level, then the area would have been exposed low-lying alluvial/coastal plain. The actual deep basin throughout this period was off to the west, beyond Bewcastle, in what is termed the Solway Basin (Fig. 1.3).

It is now possible to apply the biofacies model developed above, to the Asbian - Arnsbergian succession of the Northumberland Trough. The *G. girtyi* - *K. complectens* are found with *C. naviculus* (the typical shallow water indicator) and *G. bilineatus* (typical of deep water) and are therefore considered to be pelagic; the following regional biofacies concentrate on benthonic-nektobenthonic faunas. The definition of each biofacies period is given in Table 3.1.

Late Brigantian (Fig. 3.14b). During the transgressive systems tract limestones in this period (Table 3.1), the faunas represent the *C. naviculus* biofacies, with P₁ elements of the diagnostic conodont found in Bewcastle and Longhoughton faunas. This is thought to indicate shallow water depths across the entire shelf area.

Early Pendleian (Fig. 3.14c). The presence of *G. bilineatus* in the Throckley borehole samples of this age indicates that during marine incursions, water depths were considerably deeper, at least in the southern part of the area during this period. Only the pelagic fauna is represented at Longhoughton, which may indicate very shallow water brackish conditions; alternatively, the diagnostic conodont elements of the *C. naviculus* or *Lochriea* - *I. healdi* biofacies may not have been found due to the

poor sampling density at this horizon (single sample taken from the Great Limestone and only one species was present).

Late Pendleian (Fig. 3.14d). The Longhoughton faunas during this period were diagnostic of *C. naviculus* biofacies, indicating shallow water. However the Throckley borehole samples, only contain pelagic faunas; the lack of benthonic - nektobenthonic faunas suggests that bottom waters were inhospitable, possibly anoxic.

Early Arnsbergian (Fig. 3.14e). *G. bilineatus* biofacies dominated samples from Throckley and Longhoughton during this period (the presence of *C. naviculus* in the Longhoughton faunas is thought to have resulted from downslope movement). This represents the period of maximum water depths across the entire shelf, seen during this study.

Late Arnsbergian (Fig. 3.14f). *Lochriea - I. healdi* biofacies dominated samples from the Longhoughton area whilst *G. bilineatus* biofacies dominated the Throckley area. This indicates intermediate water depths, slightly higher than those during the late Brigantian and late Pendleian, but not as high as those during the early Pendleian and early Arnsbergian.

Period	Location			Cycle No.	Fig. 3.14
	Bewcastle	Throckley	Longhoughton		
Late Brigantian	L. Harelawhill - U. Harelawhill		Sandbanks - Acre		b
Early Pendleian		Great	Great	0	c
Late Pendleian		Little - Belsay Dene	Cushat - Iron Scars	1-3	d
Early Arnsbergian		Lower Felltop	Sugar Sands	4	e
Late Arnsbergian		Pike Hill - Whitehouse	L. Foxton - U. Foxton	5-12	f

Table 3.1 Definition of palaeoecological biofacies periods (Section 3.3.3); the location details give the lower and upper limestone unit in each period; the cycle number refers to those defined in sequence stratigraphy chapter (Sections 2.3, 2.4); the final column gives the particular biofacies figure for each period (Fig. 3.14).

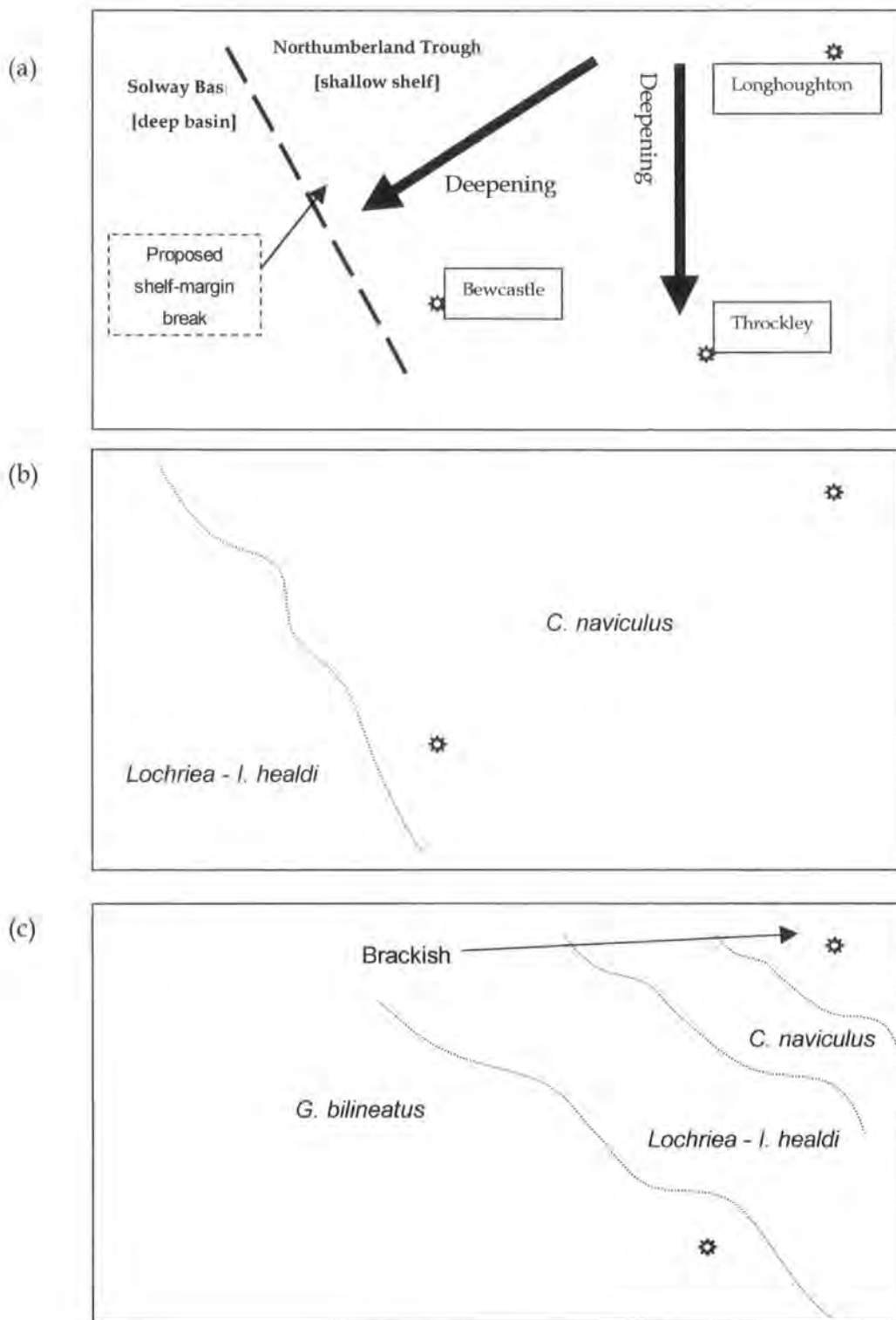


Fig. 3.14 Biofacies maps for key periods during the Asbian - Arnsbergian

(a) Template of the following figures.

(b) Late Brigantian

(c) Early Pendleian

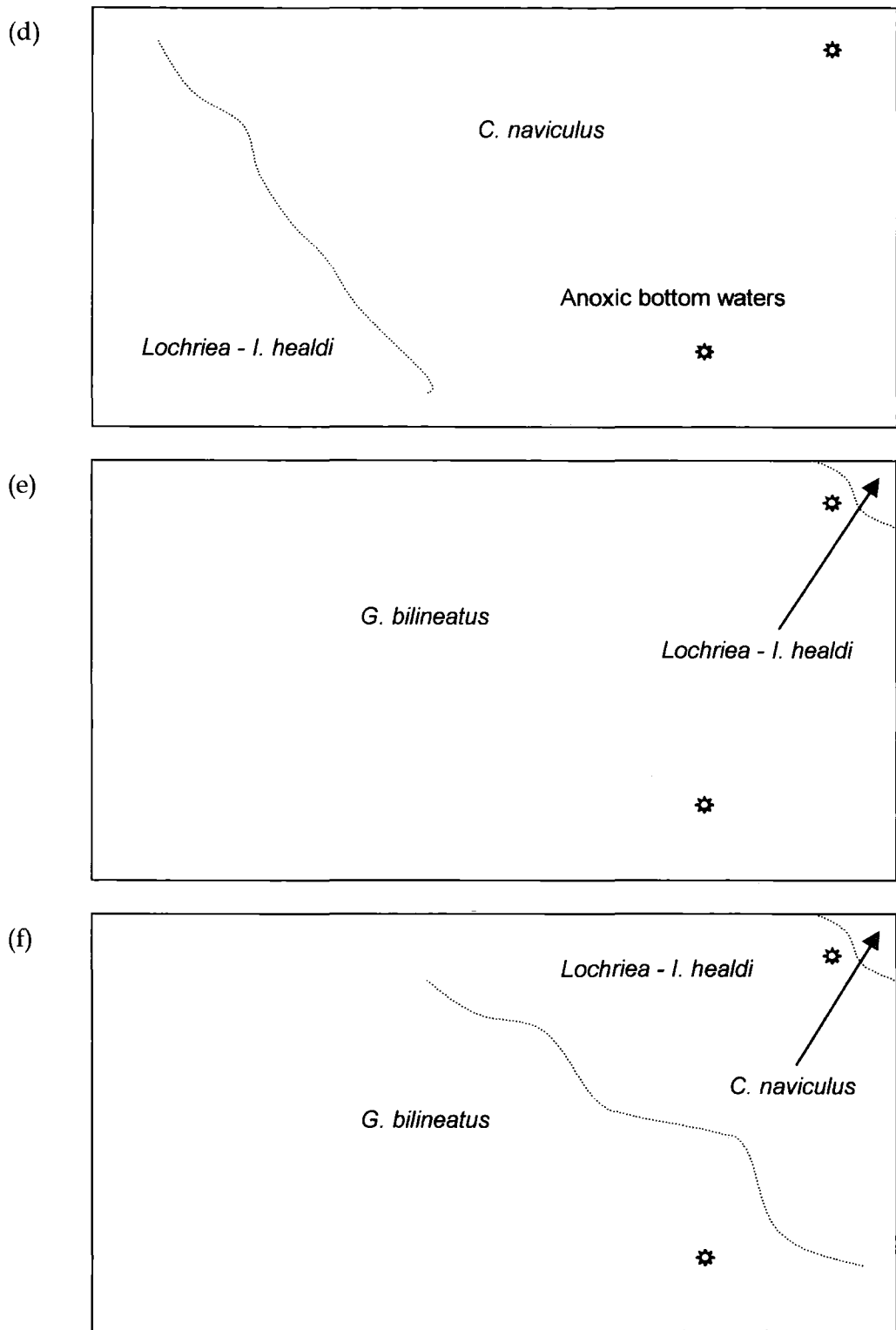


Fig. 3.14 cont.

- (d) Mid-late Pendleian
- (e) Early Arnsbergian
- (f) Mid-late Arnsbergian

3.3.4 Influence of sequence stratigraphy on palaeoecology

The change of biofacies through time (Table 3.1, Fig. 3.14) can be directly related to the sequence stratigraphy proposed for the Asbian -Arnsbergian of the Northumberland Trough.

Late Brigantian (late SS-V). *C. naviculus* biofacies across the entire shelf area, indicative of shallow water depths, correlates well with the sequence stratigraphic interpretation for this interval. This was a period soon after the mega-sequence initial flooding event (base of SS-IV); even when relative sea-level was at its highest water depths would still have been relatively shallow.

Early Pendleian (early SS-VI). The *G. bilineatus* biofacies encroached upon the deeper parts of the basin during what is interpreted as the mega-sequence maximum flooding event, bringing deep water faunas into the Northumberland Trough for the first time. However sea level rise was not great enough to influence the Longhoughton area, where *C. naviculus* biofacies prevailed during this period.

Late Pendleian (mid-late SS-VI). The entire shelf area of the Northumberland Trough returned to *C. naviculus* biofacies during the later part of sequence set VI. This period is represented by a series of relatively thin sequences, interpreted as relatively shallow water depths.

Early Arnsbergian (early SS-VII). This period marks the maximum encroachment of the *G. bilineatus* biofacies, indicating the period of greatest water depth across the entire shelf. This coincides with the period of mega-sequence highstand, as well as the transgression at the base of sequence set VII.

Late Arnsbergian (mid-late SS-VII). The mega-sequence highstand conditions prevailed during the regressive later part of sequence set VII, with *G. bilineatus* biofacies in the area of Throckley and *Lochriea-I. healdi* biofacies in the Longhoughton area. However sea levels were considerably higher than during the

regression in the later part of the previous sequence set (SS-VI), when *C. naviculus* biofacies prevailed across the entire area.

In summary, the biofacies mimic the sequence stratigraphy very well. The thick initial sequence in each sequence set (related to transgression) coincides with relatively deep-water biofacies, whereas the series of thin sequences in the later part of each sequence set (related to regression) coincides with relatively shallow water faunas - as would be expected. Furthermore, comparable periods within sequence set VI and VII, showed relatively deeper water environments during highstand conditions (SS-VII), than during maximum flooding (SS-VI).

The possible contradiction, is between the sedimentology and conodont biofacies evidence. The Great Limestone, the thickest and most dominant marine unit in the Asbian - Arnsbergian succession, is considered in this study to correlate with the mega-sequence maximum flooding event and a transgression at the base of a sequence set (SS-VI). By inference, this is assumed to mark a time of maximum relative water depths. The conodont biofacies evidence however, seems to indicate maximum marine conditions at the base of the following sequence set (SS-VII), during mega-sequence highstand conditions.

3.4 Conclusions

Asbian - Arnsbergian conodont faunas are closely linked to the sequence stratigraphy of the Northumberland Trough. This relationship is due to a combination of three different frequencies of eustatic sea-level change. High-frequency sea-level cycles produced the individual sequences, most importantly the transgressive systems tract limestones which contain a marine fauna. Medium-frequency sea-level cycles produced sequence sets, in particular the initial transgressive sequences, that controlled the first appearance of important conodont species. Low-frequency sea-level cycles controlled the mega-sequence scale events that influenced the range of the conodont fauna present at any particular time.

Conodont biozone boundaries can be clearly linked to eustatic sea-level change. The biozonal boundaries are related to the initial transgression at the base of sequence sets; the diagnostic species is related to water depth which is controlled by the low-frequency sea-level cycle.

Conodont biofacies also correlate well with the sequence stratigraphy. The periods dominated by the deepest water biofacies, correspond to the transgression at the base of each sequence set, whilst the periods of relatively shallow water biofacies correspond to the regressive mid-late period of each sequence set. Overall the pattern is also one of increasing water depth above the mega-sequence initial flooding surface.

A strong link has been established between sea level change, sequence stratigraphy and conodont faunas. The inter-relationship between biozones and biofacies has long been known, this study proposes that the fundamental control on both of these is sea -level change.

4. SYSTEMATIC PALAEOLOGY

In the following section, the family-group classification follows Sweet (1988) and the suprafamilial classification follows Aldridge & Smith (1993). The genus *Synclidognathus* has been assigned to the Ozarkodinid family Anchignathodontidae (see remarks under that genus).

Element notation and descriptive terminology follows Purnell *et al.* (2000) (Figs. 4.1, 4.2).

Complete synonymy lists have been given for each species, as previously published lists are incomplete or are based on form taxonomy. All synonymy lists are annotated according to Matthews (1973).

The Ph.D. theses of Norby (1976) is integral to understanding Carboniferous multielement taxonomy and is referred to in the present work, though Ph.D. theses are not recognised as valid references for taxonomic purposes.

The processing techniques used to recover conodont elements are described in Appendix V.

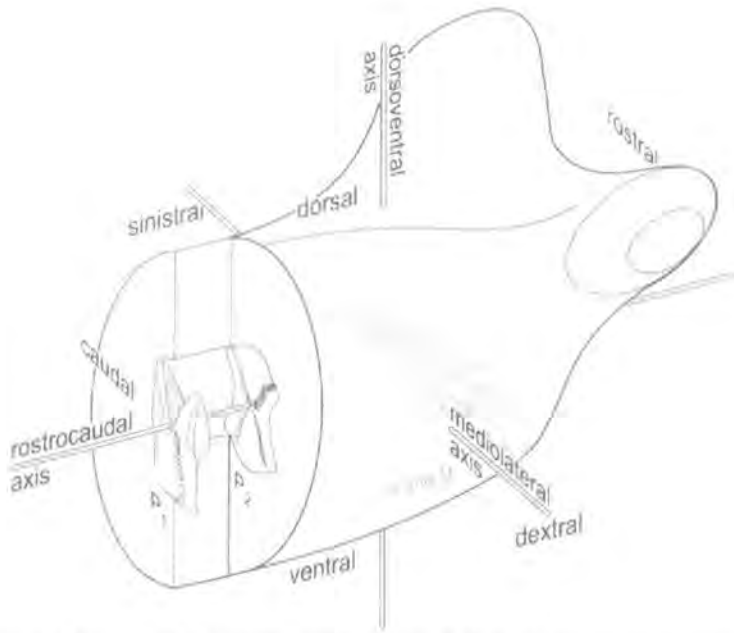


FIGURE 7. Biological orientation in conodonts; the new terminology as applied to the head and apparatus of an ozarkodimid conodont.

Fig. 4.1 Biological orientation of elements (from Purnell *et al.*, 2000, fig. 1).

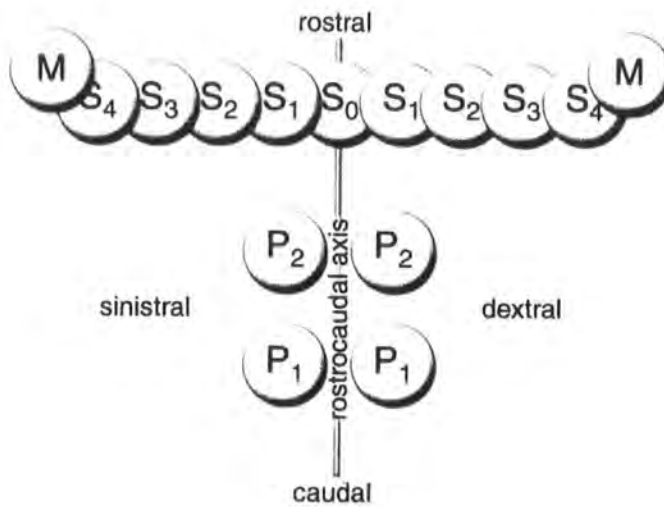


Fig. 4.2 Element notation and relative positions (from Purnell *et al.*, 2000, fig. 3).

Phylum CHORDATA Bateson, 1886

Class CONODONTA Eichenberg, 1930

Sensu Clark, in Robinson 1981

Order OZARKODINA Dzik, 1976

Family ANCHIGNATHODONTIDAE Clark, 1972

Genus *Syncladognathus* Rexroad & Varker, 1992

- non 1934? *Apatognathus* Branson & Mehl, p. 201
1967 *Apatognathus?* Varker, p. 129
1985 "*Apatognathus*" Varker & Sevastopulo, p. 196
1992 *Syncladognathus* Rexroad & Varker, p. 166

Type species. *Polygnathus scitulus* Hinde 1900.

Emended diagnosis. (After Rexroad and Varker 1992, p. 166.) Septimembrate apparatus comprising carminiscaphate P₁, angulate P₂, digyrate M, alate S₀, alate to bipennate S₁, bipennate S₂, and bipennate S₃₋₄ elements. The M and S elements are all of the unusual mid Carboniferous form previously referred to the genus "*Apatognathus*" (*sensu* Varker 1967).

Remarks. The multielement concept of *Syncladognathus* is based upon the work of Rexroad and Varker (1992), following the earlier suggestions of Austin and Rhodes (1969) and Nicoll (1980, p. 137).

It is thought that the genus *Syncladognathus* is only represented by a single species, here termed *Syncladognathus scitulus* (the P₁ element has page priority over the other elements described by Hinde (1900)). This is based on the belief that the 'geminus' and 'cuspidatus' S elements of Rexroad and Varker (1992) and indeed of Varker (1967), are in fact synonymous. Following on from this, there is no significant

difference in the ranges of the 'geminus' and 'libratus' elements used by Rexroad and Varker (1992) to diagnose their two species of *Synclydogmathus*. In fact in the Northumberland faunas, it is the 'geminus' morphotype that has the longer and later range, though this is considered to be a result of low abundances and therefore not to have any taxonomic interest.

Synclydogmathus has not been assigned to a family previously, however it is considered that the genus is most closely related to *Hindeodus* and has therefore been included in the *Anchignathodontidae* (see Sweet 1988, p. 115, fig. 5.54 under *Hindeodus scitulus*).

***Synclydogmathus scitulus* (Hinde, 1900)**

Pl. 1 Figs. 1-7.

- 1900 *Prioniodus geminus* Hinde, p. 344, pl. 10, fig. 25 [S₃₋₄ element].
- ? 1900 *Prioniodus porcatus* Hinde, p. 344, pl. 10, fig. 26 [?S₃₋₄ element].
- * 1900 *Polygnathus scitulus* Hinde, p. 343, pl. 9, figs. 9, 11 [P₁ element].
- 1928 *Prioniodina? gemina* (Hinde). Holmes, p. 19, pl. 5, fig. 10. (One of Hinde's specimens refigured (1900, pl. 10, fig. 25)). [S₃₋₄ element]
- 1960 *Apatognathus geminus* (Hinde). Clarke, p. 4, pl. 1, figs. 1, 2 [S₃₋₄ element].
- 1960 *Apatognathus porcatus* (Hinde). Clarke, p. 5, pl. 1, figs. 3, 4 [?S₃₋₄ element].
- 1960 *Spathognathus minutus?* (Ellison). Clarke, p. 20, pl.3, figs. 9, 14, 15 [P₁ element].
- 1960 *Spathognathus scitulus* (Hinde). Clarke, p. 21, pl.3, figs. 12, 13 [P₁ element].
- 1963 *Apatognathus porcatus* (Hinde). Rexroad & Collinson, p. 8, pl. 1, figs. 7-9 [M element]; figs. 10, 11 [S₃₋₄ element].
- 1963 *Apatognathus gemina* (Hinde). Rexroad & Collinson, p. 7, pl. 1, fig. 12-17 [S₂ element].
- 1963 *Ozarkodina laevipostica* Rexroad & Collinson, p. 19, pl. 1, figs. 1-6 [P₂ element].
- 1963 *Spathognathus scitulus* (Hinde). Rexroad & Collinson, p. 20, pl. 2, figs. 14, 19, 29-31 [P₁ element].
- 1967 *Apatognathus? porcata* (Hinde). Globensky, p. 438, pl. 56, fig. 12 [S₃₋₄ element]; fig. 24 [S₀ element].

- 1967 *Apatognathus? gemina* (Hinde). Globensky, p. 438, pl. 56, figs. 3, 4, 5 [S₂ element].
- 1967 *Ozarkodina laevipostica* Rexroad & Collinson. Globensky, p. 446, pl. 56, figs. 1, 2 [P₂ element].
- 1967 *Spathognathus scitulus* (Hinde). Globensky, p. 447, pl. 56, figs. 7, 17, 21 [P₁ element].
- 1967 *Apatognathus? chauliodus* Varker, p. 129, pl. 17, figs. 1-3, 5 [S₁ element].
- 1967 *Apatognathus? cuspidatus* Varker, p. 131, pl. 17, figs. 4, 6-8, 10 [S₃₋₄ element].
- 1967 *Apatognathus gemina* (Hinde). Varker, p. 133, pl. 17, figs. 9, ?12, ?13 [S₃₋₄ element].
- 1967 *Apatognathus? librata* Varker, p. 134, pl. 18, figs. 3, 6, 8, 9, 12, 13 [S₀ element].
- 1967 *Apatognathus? scalena* Varker, p. 136, pl. 18, figs. 1, 2, 4, 5 [S₂ element].
- 1967 *Apatognathus petila* Varker, p. 135, pl. 17, fig. 11, pl. 18, figs. 7, 10, 11 [M element].
- 1968 *Spathognathus scitulus* (Hinde). Aldridge, Austin & Husri, p. 256, table 1, not figured [P₁ element].
- 1969 *Ozarkodina* sp. cf. *O. laevipostica* Rexroad & Collinson. Thompson & Goebel, p. 40, pl. 3, figs. 21, 24 [P₂ element].
- 1969 *Apatognathus geminus* (Hinde). Rhodes *et al.*, p. 71, pl. 20, figs. 3, 4, 6, 7 [S₃₋₄ element].
- 1969 *Apatognathus chauliodus* Varker. Rhodes *et al.*, p. 71, pl. 20, figs. 1, 2 [S₁ element].
- 1969 *Apatognathus* cf. *libratus* Varker. Rhodes *et al.*, p. 75, pl. 20, fig. 8 [S₀ element].
- 1969 *Apatognathus petilus* Varker. Rhodes *et al.*, p. 72, pl. 20, figs. 12-14, 17 [M element].
- 1969 *Apatognathus porcatus* (Hinde). Rhodes *et al.*, p. 73, pl. 31, fig. 27 [S₃₋₄ element].
- 1969 *Apatognathus scalena* Varker. Rhodes *et al.*, p. 74, pl. 20, figs. 9-11 [S₂ element].
- 1969 *Apatognathus* sp. nov. A. Rhodes *et al.*, p. 76, pl. 31, fig. 22 [S₂ element].
- 1969 *Prioniodina laevipostica* (Rexroad & Collinson). Rhodes *et al.*, p. 195, pl. 28, figs. 11-12 [P₂ element].

- 1969 *Spathognathus scitlus* (Hinde). Rhodes *et al.*, p. 232, pl. 8, figs 9-11 [P₁ element].
- 1969 *Apatognathus? porcata* (Hinde). Thompson & Goebel, p. 21, pl. 2, fig. 1; pl. 4, fig. ?23 [S₃₋₄ element].
- 1969 *Spathognathus scitulus* (Hinde). Thompson & Goebel, p. 43, pl. 4, figs. 26, 27 [P₁ element].
- 1974 *Apatognathus chauliodus* Varker. Austin & Husri, pl. 10, figs. 3?, 13 [S₁ element].
- 1974 *Apatognathus cuspidatus* Varker. Austin & Husri, pl. 10, figs. 4, 8, 15 [S₃₋₄ element].
- 1974 *Apatognathus geminus* (Hinde). Austin & Husri, pl. 10, figs. 10, 17 [S₃₋₄ element].
- 1974 *Apatognathus libratus* Varker. Austin & Husri, pl. 10, fig. 6 [M element].
- 1974 *Apatognathus minutus* Austin & Husri, pl. 10, figs. 1, 2, 5, 9 [P₂ element].
- 1974 *Apatognathus petilus* Varker. Austin & Husri, pl. 10, fig. 7 [M element].
- 1974 *Apatognathus scalenus* Varker. Austin & Husri, pl. 10, fig. 12 [S₂ element].
- ? 1974 *Apatognathus* sp. nov. A. Austin & Husri, p. 51, pl. 12, figs. 10, 14.
- 1974 *Spathognathus dentiscitulus* Austin & Husri, p. 56, pl. 8, figs. 4, 5 [P₁ element].
- 1974 *Spathognathus scitlus* (Hinde). Austin & Husri, pl. 7, fig. 10; pl. 8, fig. 6 [P₁ element].
- 1975 *Prioniodina laevipostica* (Rexroad & Collinson). Austin & Mitchell, p. 45, table 2 [P₂ element].
- 1975 *Spathognathus scitlus* (Hinde). Austin & Mitchell, p. 53, pl. 2, fig. 26 [P₁ element].
- ? 1980a *Apatognathus scalenus* Varker. Metcalfe, p. 300, pl. 37, fig. 2 [S₁ element].
- 1980a *Spathognathus scitlus* (Hinde). Metcalfe, pl. 38, fig. 7 [P₁ element].
- ? 1981 *Apatognathus chauliodus* Varker. Metcalfe, pl. 13, fig. 11 [S₁ element].
- 1981 *Apatognathus cuspidatus* Varker. Metcalfe, pl. 13, figs. 8, 9 [S₃₋₄ element].
- ? 1981 *Apatognathus libratus* Varker. Metcalfe, pl. 13, figs. 1, 2 [S₀ element].
- ? 1981 *Apatognathus petilus* Varker. Metcalfe, pl. 13, figs. 4, 5, 6, 7 [M element].

- 1981 *Apatognathus scalenus* Varker. Metcalfe, pl. 13, fig. 3 [S₂ element].
- 1981 *Prioniodina laevispostica* (Rexroad & Collinson). Metcalfe, pl. 19, fig. 1 [P₂ element].
- 1981 *Spathognathus scitlus* (Hinde). Metcalfe, pl. 8, fig. 4 [P₁ element].
- 1982 *Apatognathus libratus* Varker. Higgins & Varker, p. 157, pl. 19, fig. 12 [S₀ element].
- 1982 *Spathognathus scitlus* (Hinde). Higgins & Varker, p. 164, pl. 19, fig. 14 [P₁ element].
- 1984 *Apatognathus cuspidatus* Varker. Austin & Davies, pl. 3, fig. 19 [S₃₋₄ element].
- 1984 *Apatognathus petilus* Varker. Austin & Davies, pl. 3, fig. 20 [M element].
- 1984 *Spathognathus scitlus* (Hinde). Austin & Davies, pl. 1, fig. 15 [P₁ element].
- 1985 '*Apatognathus*' *cuspidatus* Varker. Varker & Sevastopulo, p. 196, pl. 5.4, figs. 1, 2 [S₃₋₄ element].
- 1985 '*Apatognathus*' *libratus* Varker. Varker & Sevastopulo, p. 198, pl. 5.4, figs. 8-11 [S₀ element].
- 1985 '*Apatognathus*' *petilus* Varker. Varker & Sevastopulo, p. 198, pl. 5.4, figs. 3-5 [M element].
- 1985 '*Apatognathus*' *scalenus* Varker. Varker & Sevastopulo, p. 198, pl. 5.4, figs. 6, 7 [S₂ element].
- 1991 '*Apatognathus*' *cuspidatus* Varker. Stone, p. 48, pl. 5, fig. 14 [S₃₋₄ element].
- 1991 '*Apatognathus*' *libratus* Varker. Stone, p. 48, pl. 5, fig. 15 [S₀ element].
- 1991 '*Apatognathus*' *petilus* Varker. Stone, p. 49, pl. 5, fig. 16 [M element].
- 1991 *Hindeodus?* *scitulus* Hinde. Stone, p. 13, pl. 1, fig. 4 [P₁ element]; fig. 3 [?P₂ element]; fig. 6 [?S₀ element]; fig. 7 [M element].
- p 1991 *Vogelgnathus* cf. *campbelli* (Rexroad). Stone, p. 38, pl. 4, fig. 10 [P₂ element].
- 1992 "*Apatognathus*" *cuspidatus* Varker. Purnell, p. 41, pl. 8, fig. 8 [P₁ element]; fig. 9 [P₂ element]; figs. 4, 5 [S₀ element]; fig. 6 [S₃₋₄ element]; fig. 7 [?M element].
- 1992 *Synclydoghnathus geminus* (Hinde). Rexroad & Varker, p. 168, pl. 3, figs. 1-3 [P₁ element]; figs. 4, 5 [P₂ element]; figs. 7, 11-14 [S₀ elements]; fig. 10 [S₁ elements]; figs. 8, 9 [S₂ elements]; fig. 6 [S₃₋₄ elements].

- 1993 *Syncladognathus geminus* (Hinde). Dumoulin & Harris, fig 8, D [Pa element]; E [S₀ element]; F [?S₂ element].
- ? 1993 *Syncladognathus geminus* (Hinde). Dumoulin, Harris & Schmidt, fig 9, U [?S₂ element].
- 1994 *Syncladognathus* elements. Davies, Austin & Moore, pl. 2, fig 10, [P₁ element]; fig. 15 [P₂ element]; fig. 21 [M element]; fig. 22 [S₁ element]; fig. 23 [S₀ element]; fig. 24 [S₃₋₄ element]; fig. 25 [S₂ element].
- 1997 *Syncladognathus libratus* (Varker). Dzik, p. 130, fig. 42, A [P₁ element]; fig. 42, B, E, ?G [S₃₋₄ element]; fig. 42, C [S₀ element]; fig. 42, D [M element] (*non*. fig. F).

Holotype. British Geological Survey, Edinburgh PS 871; Hinde, 1900, p. 344, pl. 10, fig. 25. From the Lower Limestone Group, of Penniel Water, Douglas, Scotland, UK.

Emended diagnosis. (After Rexroad and Varker 1992, p. 168.) A species of *Syncladognathus* with a carminiscaphate P₁ element with an asymmetrical basal cavity, projecting strongly on the rostral side, and restricted to the mid-portion of the element. The angulate P₂ element is very strongly arched and has a large basal cavity; the digyrate M element has a characteristic ventral process with elongated, fused denticles next to the cusp; the alate S₀ element has a series of uniform denticles pointing perpendicular to the processes; the alate to bipennate S₁ element has one enlarged denticle part way down both processes; the bipennate S₂ element has 1-3 enlarged denticles part way along the caudal process; the bipennate S₃ and S₄ element is simply ornamented with small regular denticles.

Description. *P₁ element* See Clarke (1960, p. 21) and Rhodes *et al.* (1969, p. 232); *P₂ element* See Rexroad & Collinson (1963, p. 19) and Rhodes *et al.* (1969, p. 195); *M element* See Varker (1967, p. 135); *S₀ element* See Varker (1967, p. 134); *S₁ element* See Varker (1967, p. 129); *S₂ element* See Varker (1967, p.136); *S₃₋₄ element* See Hinde (1900, p. 344) and Varker (1967, p. 131).

Remarks. The greatest difficulty with this species, is the assignment of element morphologies to positions within the apparatus, as no bedding plane assemblages have been found. The P₁ and P₂ elements are very similar to those of the genus *Hindeodus* (e.g. Wardlaw 1985, pl. 3, figs. 1-6; Krumhardt *et al.* 1996, pl. 1, figs. 1, 2.) and are typical of *Ozarkodinids*. The remainder of the apparatus is made up of distinctive elements of the form taxonomic genus "*Apatognathus*" (*sensu* Varker 1967)

and the assignment of these elements to specific positions is difficult. The rationale behind the assignment of "*Apatognathid*" elements in this study is defined below.

The M element is unique in many respects: it is the only digyrate element; the apical zone consists of strong, elongate, fused denticles; the denticles are circular to oval in section, rather than flattened in the S elements; the adaxial process lacks the rectangular basal section common to the S elements. This element also closely resembles the M element of *Hindeodus* (e.g. Mapes & Rexroad 1986, pl. 1, fig. 15; Krumbhart *et al.* 1996, pl. 1, fig. 3).

The alate S₀ element is consistently symmetrical (e.g.). It is also distinct from the other S elements in the high angle of divergence of the two processes, around 45-50°, whereas the S₁ to S₄ elements have processes that diverge at between 20-35° (angles from Varker 1967).

The S₁ element figured from this study (pl. 1, fig. 5) is almost symmetrical, however this element morphotype is usually more asymmetrical and obviously bipennate (e.g. Varker 1967, pl. 17, figs. 1-3, 5; Rexroad & Varker 1992, fig. 3.10). The strong symmetry of this element suggests a medial position close to the rostrocaudal axis of the animal.

The S₂ element is similar to the S₁, however it is clearly bipennate and only possesses enlarged denticles part way along the caudal process.

The S₃₋₄ element is the most conservative of the "*Apatognathid*" elements and has most in common with normal *Ozarkodinid* S₃ and S₄ elements - very similar except for an extended adaxial process. The numerical abundance of this element in the present study (see below) seems to suggest that a morphologically similar element filled both the S₃ and the S₄ positions within the apparatus.

Material studied. P₁ element 44; P₂ element 17; M element 29; S₀ element 5; S₁₋₂ element 3; S₃ element 15; S₄ element 45.

Family CAVUSGNATHIDAE Austin & Rhodes *in* Robinson,
1981

Genus ADETOGNATHUS Lane, 1967

1967 *Adetognathus* Lane, p. 930.

Type species. *Cavusgnathus latus* Gunnell 1933 by subsequent designation of Lane (1967 p. 930).

Diagnosis. See Lane 1967, p. 930.

Remarks. No multielement diagnosis for this genus yet exists. It has long been supposed that *A. unicornis* and *C. unicornis* shared their non-P₁ elements (Horowitz & Rexroad, 1982, p. 962; Rexroad & Merrill, 1985, p. 44), however bedding plane assemblages indicate that these elements are quite different between these species (Mark Purnell pers. comms., see Purnell & Donoghue, 1998, text-fig. 15). The material from the present study only contains P₁ elements and therefore adds nothing to the elucidation of the multielement taxonomy of this genus.

Adetognathus unicornis (Rexroad & Burton, 1961)

Pl. 1 Fig. 9.

- * 1961 *Streptognathodus unicornis* Rexroad & Burton, p. 1157, pl. 138, figs. 1-9.
- 1967 *Adetognathus unicornis* (Rexroad & Burton). Lane, p. 930, pl. 119, figs. 16-21.
- 1974 *Adetognathus unicornis* (Rexroad & Burton). Lane & Straka, p. 66, fig. 33:16-18.
- 1974 *Adetognathus unicornis* (Rexroad & Burton). Varker & Austin, pl. 6, figs. 1?, 2?, 16-18.
- 1980 *Adetognathus unicornis* (Rexroad & Burton). Tynan, p. 1299, pl. 2, fig. 14.
- 1980 *Adetognathus* n.sp. Tynan, p. 1299, pl. 2, figs. 15-17.

- 1985 *Adetognathus unicornis* (Rexroad & Burton). Grayson *et al.*, p. 162, pl. 1, fig. 11; pl. 2, fig. 10.
- 1986 *Adetognathus unicornis* (Rexroad & Burton). Mapes & Rexroad, p. 117, pl. 1, figs. 1-6.
- 1992 *Adetognathus unicornis* (Rexroad & Burton). Morrow & Webster, pl. 1, figs. 10, 11.
- 1992 *Adetognathus unicornis* (Rexroad & Burton). Nemirovskya, Poletaev & Vdovenko, pl. 3, fig. 19.
- 1992 *Adetognathus unicornis* (Rexroad & Burton). Weibel & Norby, p. 43-4, pl. 1, figs. 1-16.

Holotype. Illinois State Geological Survey, 15P39; Rexroad & Burton, 1961, p. 1157, pl. 138, figs. 1a, 1b. From the Kinkaid Formation, Chesterian, Mississippian, of Johnson County, Illinois, U.S.A. (section in gully west of road up bluff from Cedar Grove Church).

Diagnosis. See Lane (1967, p. 930).

Description. *P*₁ element See Rexroad & Burton (1961, p. 1157)

Remarks. Apparent transitional specimens between *A. uniconis* and *C. unicornis* *P*₁ elements have been proposed (e.g. Rexroad & Burton, 1961, p. 1157, pl. 138, figs. 7, 8; Varker & Austin, 1974, pl. 6, figs. 3-5). However the material in the present study very closely resembles the original description and the figures of the holotype (the long median blade with a conspicuously large posterior denticle can in no way be confused with any specimens of *Cavusgnathus*) and therefore *A. uniconis* is here considered a distinct taxon. The specimens illustrated by Rexroad & Burton are *A. uniconis* and those of Varker & Austin appear to be *Cavusgnathus unicornis* *P*₁ elements.

All the *A. uniconis* *P*₁ elements found during this study came from a single sample. This was taken from the shallowest marine horizon sampled for conodonts in the Throckley borehole, somewhere in the early to mid Arnsbergian (*E*₂) Stage. The other records of this species in Britain have been found at a very similar horizon. Varker & Austin (1974) reported an early Arnsbergian (*E*₂) fauna from the Askrigg Block, just to the south of the Northumberland Trough and Dean (1987) had a single example of a *P*₁ element from the early Arnsbergian of Arran, Scotland.

Material studied. *P*₁ element 5.

Genus CAVUSGNATHUS Harris & Hollingworth, 1933

1933 *Cavusgnathus* Harris & Hollingsworth, p. 200.

1942 *Lewistownella* Scott, p. 299.

1975 *Windsorgnathus* Austin & Mitchell, p. 53.

Type species. *Cavusgnathus alta* Harris & Hollingsworth 1933 by original designation.

Diagnosis. See Purnell, 1992, p. 7.

Remarks. All the *Cavusgnathid* material in the present study has been assigned to *Cavusgnathus naviculus*. It is thought that *C. naviculus* is a late Viséan-early Namurian chrono-species developed from Viséan ancestral stock, probably *C. unicornis*, however it is beyond the scope of the present research to consider the relationships within this genus in detail.

Cavusgnathus naviculus (Hinde, 1900)

Pl. 2 Figs. 1-4.

- p 1900 *Ctenognathus obliquus* Pander. Hinde, p. 344, pl. 10, fig. 28 (only) [S₄ element].
- 1900 *Polygnathus dubius* Hinde, p. 341, pl. 9, fig. 1 [P₂ element].
- * 1900 *Polygnathus navicula* Hinde, p. 342, pl. 9, fig. 5 [P₁ element].
- p 1900 *Prioniodus angulatus* Hinde, p. 343, pl. 10, fig. 18 (only) [S₀ element].
- ? 1941a *Hindeodella* sp. Branson & Mehl, p. 170, pl. 5, fig. 1 [S₄ element].
- ? 1941a *Ozarkodina mutabilis* Branson & Mehl, p. 177, pl. 5, fig. 16 [P₂ element].
- 1941a *Prioniodus varians* Branson & Mehl, p. 174, pl. 5, figs. 7, 8 [M element].
- 1953 *Hindeodella ensis* Hass, p. 81, pl. 16, figs. 19-21 [S₄ element].
- 1957 *Neoprioniodus varians* (Branson & Mehl). Rexroad, p. 35, pl. 2, fig. 10 [M element].
- 1957 *Ozarkodina compressa* Rexroad, p. 36, pl. 2, figs. 1, 2 [P₂ element].
- 1958 *Hibbardella ortha* Rexroad, p. 18, pl. 2, figs 9-12 [S₀ element].
- 1960 *Cavusgnathus inflexa* Clarke, p. 23, pl. 3, figs. 17, 19 [P₁ element].

- 1960 *Hibbardella ortha* Rexroad. Clarke, p. 6, pl. 1, fig. 7 [S₀ element].
- ? 1960 *Hindeodella tenuis* Clarke, p. 8, pl. 1, figs. 10, 11 (?) [S₄ element].
- 1960 *Neoprioniodus brevis* Clarke, p. 13, pl. 2, fig. 7 [P₂ element].
- 1960 *Ozarkodina hindei* Clarke, p. 18, pl. 3, figs. 1, 6 [P₂ element].
- 1960 *Cavusgnathus navicula* (Hinde). Clarke, p. 23, pl. 4, fig. 1-3 [P₁ element].
- 1961 *Cavusgnathus unicornis* Youngquist & Miller. Higgins, pl. 10, fig. 3 [P₁ element].
- p 1967 *Ozarkodina compressa* Rexroad. Globensky, p. 446, pl. 56, figs. 22 only [P₂ element].
- 1969 *Cavusgnathus naviculus* (Hinde). Rhodes *et al.*, p. 81, pl. 13, fig. 12; pl. 14, figs. 1, 4-6 [P₁ element].
- 1969 *Hibbardella (Hibbardella) ortha* Rexroad. Rhodes *et al.*, p. 113, pl. 25, fig. 22 [S₀ element].
- 1969 *Hindeodella tenuis* Clarke. Rhodes *et al.*, p. 126, pl. 28, fig. 27 [S₄ element].
- 1969 *Neoprioniodus varians* (Branson & Mehl). Rhodes *et al.*, p. 165, pl. 21, fig. 18 [M element].
- ? 1969 *Ozarkodina compressa* Rexroad. Rhodes *et al.*, p. 169, pl. 27, fig. 23 [P₂ element].
- 1969 *Ozarkodina hindei* Clarke. Rhodes *et al.*, p. 171, pl. 27, figs. 16, 17, 22 [P₂ element].
- 1974 *Cavusgnathus naviculus* (Hinde). Austin & Husri, pl. 1, figs. 6, 7 [P₁ element].
- 1974 *Hibbardella (Hibbardella) ortha* Rexroad. Austin & Husri, pl. 13, figs. 6, 7 [S₀ element].
- 1974 *Neoprioniodus varians* (Branson & Mehl). Austin & Husri, pl. 12, figs. 21, 22 [M element].
- ? 1974 *Ozarkodina compressa* Rexroad. Austin & Husri, pl. 12, figs. 6, 25 [P₂ element].
- ? 1974 *Cavusgnathus naviculus* (Hinde). Varker & Austin, pl. 6, fig. 7 [P₁ element].
- 1975 *Cavusgnathus naviculus* (Hinde). Higgins, p. 26, pl. 8, figs. 3-5, 12, 13 [P₁ element].
- 1981 *Cavusgnathus naviculus* (Hinde). Metcalfe, pl. 1, figs. 1, 2 [P₁ element].
- ? 1981 *Cavusgnathus unicornis* Youngquist & Miller. Metcalfe, pl. 1, figs. 3, 4 [P₁ element].
- ? 1981 *Hibbardella ortha* Rexroad. Metcalfe, pl. 14, fig. 3 [S₀ element].

- ? 1981 *Neoprioniodus varians* (Branson & Mehl). Metcalfe, pl. 18, fig. 6 [M element].
- p 1981 *Cavusgnathus* spp. Rexroad, pl. 1, figs. 1-3 (only) [S₄ element], pl. 1, fig. 9 (only) [S₀ element].
- 1985 *Cavusgnathus naviculus* (Hinde). Higgins, p. 218, pl. 6.1, fig. 3 [P₁ element].
- 1987 *Cavusgnathus* c.f. *naviculus* (Hinde). Armstrong & Purnell, pl. 1, figs. 8, 9 [P₁ element].

Holotype. British Geological Survey, Edinburgh PS 871; Hinde, 1900, p. 342, pl. 9, fig. 5. From the Lower Limestone Group, of Penniel Water, Douglas, Scotland, UK.

Diagnosis. See Clarke 1960, p. 24.

Description. *P*₁ element See Rhodes *et al.* (1969, p. 81); *P*₂ element See Rexroad (1957, p. 36) and Rhodes *et al.* (1969, p. 171); *M* element See Rhodes *et al.* (1969, p. 165); *S*₀ element See Rexroad (1958, p. 18); *S*₄ element See Hass (1953, p. 81) and Clarke (1960, p. 8).

Remarks. Purnell (1992) working on *C. hudsoni* from the Tournaisian and *C. unicornis* from the early Viséan of the Northumberland Trough developed a scheme for describing different blade types (fig 4.3). All the *C. naviculus* from the present study have α blade types, however Purnell's Arundian *C. unicornis* exhibited all three forms, α type, β type and γ type blades. Perhaps the diagnostic difference between *C. unicornis* and *C. naviculus*, which appear to be chrono-species, is the uniform blade type; this will take further study to confirm.

Material studied. P₁ element 32; P₂ element 2; M element 2; S₀ element 1; S₄ element 2.

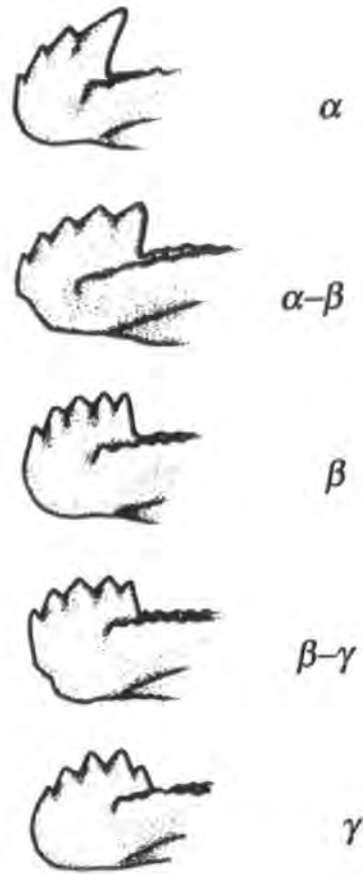


Fig. 4.3 Blade form in *Cavusgnathus* - blade type indicated by Greek letter.
(from Purnell 1992, text-fig. 5; based on Rexroad, 1981).

Family GNATHODONTIDAE Sweet, 1988

Genus GNATHODUS Pander, 1856

- 1856 *Gnathodus* Pander, p. 33
1939 *Dryphenotus* Cooper, p. 386.
1957 *Westphalicus* Moore & Sylvester-Bradley, p. 21.

Type species. *Polygnathus bilineatus* Roundy 1926, by subsequent designation (I.C.Z.N. opinion 1415, Tubbs, 1986).

Diagnosis. See Purnell, 1992, p. 30.

Remarks. There appears to have been marked conservatism in the rostral domain of the *Gnathodus* apparatus. With the available collections it is difficult to assign the non-P₁ elements unless samples are monospecific. All non-P₁ elements are therefore assigned *a priori* to *G. girtyi*, as this is by far the most common species in the present study.

Gnathodus girtyi Hass, 1953

Pl. 2 Figs. 5-12.

- * 1953 *Gnathodus girtyi* Hass, p. 80, pl. 14, figs. 22-24 [P₁ element].
1953 *Subbryantodus roundyi* Hass, p. 89, pl. 14, figs. 3-6 [P₂ element].
1956 *Gnathodus girtyi* Hass. Elias, p. 118, pl. 3, figs. 30, 31 [[P₁ element].
1957 *Gnathodus girtyi* Hass. Bischoff, p. 24, pl. 4, figs. 16-23 [P₁ element].
1957 *Angulodus walrathi* (Hibbard). Bischoff, p. 17, pl. 5, figs. 44, 45 [S₂ element].
1957 *Hindeodella brevis* Branson & Mehl. Bischoff, p. 26, pl. 6, fig. 24 [S₁ element].
1957 *Hindeodella ibergensis* Bischoff, p. 28, pl. 6, figs. 33, 37, 39 [S₄ element].
1957 *Ozarkodina roundyi* (Hass). Bischoff, p. 40, pl. 1, figs. 29-32 [P₂ element].
?1957 *Ozarkodina delicatula* (Stauffer & Plummer). Bischoff, p. 39, pl. 1, figs. 25-28 [P₂ element].
1960 *Gnathodus clavatus* Clarke, p. 25, pl. 4, figs. 4-8, ?9 [P₁ element].

- 1960 *Ozarkodina* spp. Clarke, p. 18, pl. 3, figs. 2, 3 [P₂ element].
- 1960 *Subbryantodus planidorsalis* Clarke, p. 22, pl. 3, fig. 18 [P₂ element].
- 1961 *Angulodus walrathi* (Hibbard). Higgins, pl. 10, fig. 16 [S₂ element].
- 1961 *Gnathodus girtyi* Hass. Higgins, pl. 10, fig. 4 [P₁ element].
- 1961 *Hibbardella fragilis* Higgins, p. 213, pl. 12, fig. 4, text-fig. 2 [S₀ element].
- 1961 *Hindeodella brevis* Branson & Mehl. Higgins, pl. 10, fig. 14 [S₁ element].
- 1961 *Hindeodella ibergensis* Bischoff. Higgins, pl. 10, fig. 15 [S₄ element].
- 1961 *Ozarkodina delicatula* Ellison (sic). Higgins, p. 220, pl. 12, fig. 13 [P₂ element].
- 1961 *Synprioniodina forsenta* Stauffer. Higgins, pl. 12, fig. 8 [M element].
- 1962 *Gnathodus girtyi* Hass. Higgins, pl. 3, fig. 31 [P₁ element].
- 1962 *Hindeodella ibergensis* Bischoff. Higgins, pl. 1, fig. 11 [S₄ element].
- 1965 *Gnathodus girtyi simplex* Dunn, p. 1148, pl. 140, figs. 2, 3, 12 [P₁ element].
- 1965 *Ozarkodina roundyi* (Hass). Dunn, p. 1149, pl. 140, figs. 19, 20 [P₂ element].
- 1967 *Gnathodus girtyi intermedius* Globensky, p. 440, pl. 58, figs. 11, 15-20 [P₁ element].
- 1967 *Ozarkodina delicatula* (Stauffer & Plummer). Globensky, p. 446, pl. 56, fig. 19 [P₂ element].
- 1969 *Euprioniodina caverna* (Collinson & Druce). Rhodes *et al.*, p. 90, pl. 22, fig. 11 [M element].
- 1969 *Euprioniodina microdenta* (Ellison). Rhodes *et al.*, p. 91, pl. 22, fig. 16 [M element].
- 1969 *Gnathodus girtyi collinsoni* Rhodes *et al.*, p. 99, pl. 16, figs. 5-8 [P₁ element].
- 1969 *Gnathodus girtyi girtyi* Hass. Rhodes *et al.*, p. 98, pl. 17, figs. 9-12 [P₁ element].
- 1969 *Gnathodus girtyi simplex* Dunn. Rhodes *et al.*, p. 100, pl. 16, figs. 1-4 [P₁ element].
- 1969 *Gnathodus girtyi soniae* Rhodes *et al.*, p. 101, pl. 17, figs. 5-8 [P₁ element].
- 1969 *Gnathodus girtyi turritus* Rhodes *et al.*, p. 102, pl. 31, fig. 23 [P₁ element].
- 1969 *Gnathodus girtyi* subsp. nov. A. Rhodes *et al.*, p. 102, pl. 17, figs. 1-3 [P₁ element].

- 1969 *Hibbardella (Hibbardella) acuta* Murray & Chronic. Rhodes *et al.*, p. 112, pl. 25, figs. 19, 20 [S₀ element].
- 1969 *Hindeodella cooperi* (Elias). Rhodes *et al.*, p. 120, pl. 31, figs. 18, 19 [Sc₁ element].
- 1969 *Hindeodella croka* Collinson & Druce (*nom. nud.*). Rhodes *et al.*, p. 121, pl. 28, figs. 15-17 [S₁ element].
- 1969 *Hindeodella hibbardi* Collinson & Druce (*nom. nud.*). Rhodes *et al.*, p. 122, pl. 28, figs. 18-20 [S₂ element].
- 1969 *Hindeodella ibergensis* Bischoff. Rhodes *et al.*, p. 123, pl. 28, figs. 22-24, 30, 31 [S₄ element].
- 1969 *Ozarkodina delicatula* (Stauffer & Plummer). Rhodes *et al.*, p. 170, pl. 27, figs. 15, 19 [P₂ element].
- 1969 *Ozarkodina cf. delicatula* (Stauffer & Plummer). Rhodes *et al.*, p. 177, pl. 27, figs. 14 [P₂ element].
- 1969 *Gnathodus girtyi simplex* Dunn. Webster, p. 32, pl. 5, fig. 10 [P₁ element].
- 1969 *Ozarkodina roundyi* (Hass). Webster, p. 43, pl. 7, fig. 8 [P₂ element].
- ? 1969 *Synprioniodina microdenta* Ellison. Webster, p. 50, pl. 8, fig. 15 [M element].
- 1970a *Gnathodus girtyi simplex* Dunn. Dunn, p. 331, pl. 62, fig. 17; text-fig. 9B [P₁ element].
- 1970a *Ozarkodina delicatula* (Stauffer & Plummer). Dunn, p. 337, pl. 62, fig. 31 [P₂ element].
- 1970a *Synprioniodina denticamura* Rexroad & Liebe. Dunn, p. 340, pl. 62, figs. 33, 34 [M element].
- 1970 *Gnathodus girtyi* Hass. Reynolds, p. 10, pl. 1, figs. 4, 10-13 [P₁ element].
- 1973 *Gnathodus girtyi* Hass. Austin & Aldridge, pl. 1, figs. 4-6; pl. 2, figs. 2, 13-15 [P₁ element].
- 1974 *Euprioniodina microdenta* (Ellison). Austin & Husri, pl. 13, figs. 19, 20 [M element].
- 1974 *Gnathodus girtyi girtyi* Hass. Austin & Husri, pl. 3, figs. 9-11 [P₁ element].
- 1974 *Gnathodus girtyi meischneri* Austin & Husri, p. 53, pl. 3, figs. 1-3, 6; pl. 9, fig. 9 [P₁ element].
- 1974 *Gnathodus girtyi soniae* Rhodes *et al.*. Austin & Husri, pl. 3, figs. 12, 14 [P₁ element].

- 1974 *Hibbardella (Hibbardella) acuta* Murray & Chronic. Austin & Husri, pl. 13, figs. 10, 12 [S₀ element].
- 1974 *Hindeodella hibbaridi* Collinson & Druce. Austin & Husri, pl. 15, figs. 9, 10 [S₂ element].
- 1974 *Hindeodella ibergensis* Bischoff. Austin & Husri, pl. 12, fig. 26; pl. 15, fig. 18 [S₄ element].
- 1974 *Hindeodella uncata* (Hass). Austin & Husri, pl. 15, fig. 13 [S₁ element].
- 1974 *Ozarkodina delicatula* (Stauffer & Plummer). Austin & Husri, pl. 12, fig. 5 [P₂ element].
- 1974 *Gnathodus girtyi* Hass. Matthews & Thomas, pl. 51, figs. 16, 17, 28-31 [P₁ element].
- 1975 *Gnathodus girtyi collinsoni* Rhodes *et al.*. Higgins, p. 30, pl. 10, figs. 1, 2 [P₁ element].
- 1975 *Gnathodus girtyi girtyi* Hass. Higgins, p. 31, pl. 10, figs. 5, 6 [P₁ element].
- 1975 *Gnathodus girtyi intermedius* Globensky. Higgins, p. 31, pl. 9, figs. 1-5, 8, 9 [P₁ element].
- 1975 *Gnathodus girtyi rhodesi* Higgins, p. 32, pl. 10, figs. 3, 4 [P₁ element].
- 1975 *Gnathodus girtyi simplex* Dunn. Higgins, p. 33, pl. 9, figs. 6, 7, 11 [P₁ element].
- 1975 *Gnathodus girtyi soniae* Rhodes *et al.*. Higgins, p. 33, pl. 9, figs. 10 [P₁ element].
- 1975 *Hibbardella acuta* Murray & Chronic. Higgins, p. 34, pl. 1, figs. 7, 9; pl. 6, fig. 13 [S₀ element].
- 1975 *Hindeodella ibergensis* Bischoff. Higgins, p. 38, pl. 4, figs. 10, 11, 14, 15; pl. 6, fig. 13; text-fig. 8 [S₄ element].
- 1975 *Hindeodella uncata* (Hass). Higgins, p. 44, pl. 4, figs. 1-3 [S₁ element].
- 1975 *Hindeodella simplex* (Higgins & Bouckaert). Higgins, p. 42, pl. 5, figs. 10, 12, 13 [S₂ element].
- 1975 *Ozarkodina delicatula* (Stauffer & Plummer). Higgins, p. 69, pl. 5, figs. 9, 11, 16; pl. 6, figs. 15, 16 (pars) [P₂ element].
- 1975 *Ozarkodina cf. delicatula* (Stauffer & Plummer). Higgins, p. 69, pl. 5, fig. 2 [P₂ element].
- 1975 *Synprioniodina microdenta* Ellison. Higgins, p. 75, pl. 3, figs. 10, 15, 16 [M element].
- 1980a *Gnathodus girtyi simplex* Dunn. Metcalfe, p. 304, pl. 38, fig. 1 [P₁ element].

- 1980a *Gnathodus girtyi rhodesi* Higgins. Metcalfe, p. 304, pl. 38, fig. 6 [P₁ element].
- 1980 *Gnathodus girtyi collinsoni* Rhodes *et al.*. Tynan, p. 1301, pl. 1, figs. 10, 11 [P₁ element].
- 1980 *Gnathodus girtyi girtyi* Hass. Tynan, p. 1302, pl. 1, figs. 9, 16-18 [P₁ element].
- 1980 *Gnathodus girtyi intermedius* Globensky. Tynan, p. 1302, pl. 1, figs. 8, 12, 13 [P₁ element].
- ? 1980 *Gnathodus girtyi simplex* Dunn. Tynan, p. 1303, pl. 1, figs. 5-7 [P₁ element].
- 1981 *Gnathodus girtyi* Hass. Metcalfe, p. 23, 25, pl. 4, figs. 2, 4, 5, 7 [P₁ element].
- 1981 *Hibbardella acuta* Murray & Chronic. Metcalfe, pl. 14, fig. 6 [S₀ element].
- 1981 *Hindeodella ibergensis* Bischoff. Metcalfe, pl. 15, figs. 5, 6 [S₄ element].
- 1981 *Hindeodella simplex* (Higgins & Bouckaert). Metcalfe, pl. 15, figs. 1, 7(?) [S₂ element].
- 1981 *Hindeodella uncata* (Hass). Metcalfe, pl. 15, fig. 2 [S₁ element].
- 1981 *Synprioniodina microdenta* Ellison. Metcalfe, pl. 19, figs. 8, 9 [M element].
- 1981 *Ozarkodina delicatula* (Stauffer & Plummer). Metcalfe, pl. 19, figs. 3, 4 [P₂ element].
- 1982 *Gnathodus girtyi girtyi* Hass. Higgins & Wagner-Gentis, p. 334, pl. 34, fig. 9 [P₁ element].
- 1984 *Gnathodus girtyi* Hass. Austin & Davies, pl. 2, fig. 17; pl. 3, figs. 23, 28, 32 [P₁ element].
- 1984 *Ozarkodina delicatula* (Stauffer & Plummer). Austin & Davies, pl. 3, fig. 24 [P₂ element].
- 1985 *Gnathodus* sp. cf. *G. girtyi* subspp. Grayson *et al.*, p. 166, pl. 1, figs. 4, 23; pl. 2, figs. 1, 12, 18 [P₁ element].
- 1985 *Gnathodus girtyi girtyi* Hass. Higgins, p. 220, pl. 6.2, fig. 2 [P₁ element].
- 1985 *Gnathodus girtyi rhodesi* Higgins. Higgins, p. 220, pl. 6.2, fig. 1 [P₁ element].
- 1985 *Gnathodus girtyi collinsoni* Rhodes *et al.*. Varker & Sevastopulo, p. 202, pl. 5.6, fig. 3, 4 [P₁ element].
- 1985 *Gnathodus girtyi girtyi* Hass. Varker & Sevastopulo, p. 202, pl. 5.6, fig. 1, 2 [P₁ element].

- 1985 *Gnathodus girtyi girtyi* Hass. Wardlaw, pl. 1, fig. 12 [P₁ element].
- 1985 *Gnathodus girtyi rhodesi* Higgins. Wardlaw, pl. 1, fig. 11 [P₁ element].
- 1987 *Gnathodus girtyi* Hass. Armstrong & Purnell, pl. 2, figs. 12 [P₁ element]; 13 [M element].
- ?1987 *Gnathodus girtyi girtyi* Hass. Wang, Lane & Manger, p. 128, pl. 7, figs. 9, 10 [P₁ element].
- 1991 *Gnathodus girtyi collinsoni* Rhodes *et al.*. Higgins *et al.*, pl. 3, fig. 2 [P₁ element].
- 1991 *Gnathodus girtyi girtyi* Hass. Higgins *et al.*, pl. 3, figs. 3-5 [P₁ element].
- 1991 *Gnathodus girtyi simplex* Dunn. Higgins *et al.*, pl. 3, figs. 6, 12 [P₁ element].
- 1991 *Gnathodus girtyi girtyi* Hass. Morrow & Webster, pl. 3, fig. 9 [P₁ element].
- 1991 *Gnathodus girtyi simplex* Dunn. Morrow & Webster, pl. 3, fig. 8 [P₁ element].
- 1992 *Gnathodus girtyi girtyi* Hass. Morrow & Webster, pl. 1, fig. 3 [P₁ element].
- 1992 *Gnathodus girtyi simplex* Dunn. Morrow & Webster, pl. 1, fig. 4 [P₁ element].
- 1994 *Gnathodus girtyi* Hass. Davies, Austin & Moore, pl. 2, fig. 1 [P₁ element].
- 1996 *Gnathodus girtyi girtyi* Hass. Krumhardt *et al.*, p. 40, pl. 2, figs. 20-22 [P₁ element].
- 1996 *Gnathodus girtyi simplex* Dunn. Krumhardt *et al.*, p. 41, pl. 2, figs. 25-27 [P₁ element].
- 1997 *Gnathodus girtyi* Hass. Dzik, p. 130, fig. 43 A-C [P₁ element]; D-F [P₂ element]; M, N [M element]; G [S₀ element]; H₁, H₂ [S₁ element]; I, J [S₂ element]; K [S₄ element].

Holotype. United States National Museum, USNM 115097; Hass, 1953, p. 80, pl. 14, figs 22-24. From Barnett Formation, Mississippian, at C-15, about 2000 feet N. 88° W. of southwest bank of Llano River at White's Crossing, Mason County, Texas, U.S.A.

Diagnosis. See Hass, 1952, p. 80.

Description. *P*₁ element See Higgins (1975, p. 29); *P*₂ element See Hass (1953, p. 89); *M* element See Rhodes *et al.* (1969, p. 91) and Higgins (1975, p. 75); *S*₀ element See

Higgins (1961, p. 213); *S*₁ element See Rhodes *et al.* (1969, p. 121) ; *S*₂ element See Rhodes *et al.* (1969, p. 122); *S*₃ element See Rhodes *et al.* (1969, p. 120); *S*₄ element See Rhodes *et al.* (1969, p. 123).

Remarks. Many authors have divided *Gnathodus girtyi* into a number of subspecies due to the broad range of variation in morphological characteristics. The motivation for this subdivision has been to improve the biostratigraphical utility of this species. This study confirms the conclusions of many previous authors, in that the intraspecific morphological features of the P₁ elements suggest that there is a complete continuum between end-members. It is particularly noteworthy that Higgins (1975, p. 29), who proposed a standard method of subspeciation to avoid a situation in which "... its stratigraphical usefulness would be impaired", actually pointed out that *Gnathodus girtyi* was made up of "...a large number of continuously varying specimens...". Therefore there seems no distinct phenotypic characteristics on which to define subspecies and it seems appropriate to consider all the varieties as part of a single taxon. It has also been noted by Metcalfe (1981, p. 23-5) that "the ranges of the various subspecies appear to be anomolous from area to area" and therefore do not even live up to their biostratigraphical potential. This suggests that the 'subspecies' are in fact ecophenotypes.

G. girtyi soniae morphotypes were absent from the Northumberland samples of the present study, however this form does fall within my concept of the species so references have been included in the above synonymy list.

Material studied. P₁ element 257; P₂ element 6; M element 8; S₀ element 0; S₁ element 0; S₂ element 0; S₃ element 1; S₄ element 1.

Gnathodus bilineatus (Roundy, 1926)

Pl. 3 Figs. 1-3.

- 1900 *Polygnathus (Gnathodus) Mosquensis* Pander. (sic) Hinde, p. 342, pl. 9, figs. 2-4 [P₁ element].
- * 1926 *Polygnathus bilineatus* Roundy, p. 13, pl. 3, fig. 10 [P₁ element].
- 1926 *Polygnathus texanus* Roundy, p. 14, pl. 3, fig. 13 [P₁ element].
- 1941a *Gnathodus pustulosus* Branson & Mehl, p. 172, pl. 5, figs. 32-39 [P₁ element].

- 1949 *Gnathodus liratus* Youngquist & Miller, p. 619, pl. 101, figs. 15-17 [P₁ element].
- 1953 *Gnathodus bilineatus* (Roundy). Hass, p. 78, pl. 14, figs. 25-29 [P₁ element].
- 1956 *Gnathodus bilineatus* (Roundy). Elias, p. 118, pl. 3, figs. 23-29 [P₁ element].
- 1956 *Gnathodus cf. bilineatus* (Roundy). Elias, p. 118, Pl. 3, fig. 40 [P₁ element].
- 1956 *Gnathodus multilineatus* Elias, p. 119, pl. 3, 49-53 [P₁ element].
- 1956 *Gnathodus pustulosus* Branson & Mehl. Elias, p. 115, pl. 3, figs. 1-8 [P₁ element].
- 1956 *Gnathodus streptognathoides* Elias, p. 119, pl. 3, figs. 54-57 [P₁ element].
- 1957 *Gnathodus bilineatus bilineatus* (Roundy). Bischoff, p. 21, pl. 3, figs. 11, 15-20; pl. 4, fig. 1 [P₁ element].
- 1957 *Gnathodus bilineatus bilineatus* (Roundy). Ziegler in Flügel & Ziegler, p. 38, pl. 3, figs. 1, 2, 3?, 7? [P₁ element].
- 1957 *Hindeodella ibergensis* Bischoff. Ziegler in Flügel & Ziegler, p. 42, pl. 5, figs. 14, 21 [S₄ element].
- 1957 *Hindeodella germana* Bischoff. Ziegler in Flügel & Ziegler, p. 41, pl. 5, figs. 16 [S₃ element].
- 1957 *Ozarkodina delicatula* (Stauffer & Plummer). Ziegler in Flügel & Ziegler, p. 45, pl. 5, fig. 2 [P₂ element].
- 1957 *Ozarkodina roundyi* (Hass). Ziegler in Flügel & Ziegler, p. 45, pl. 5, figs. 1, 5, 8, 9 [P₂ element].
- 1957 *Gnathodus modocensis* Rexroad, p. 30, pl. 1, figs. 15-17 [P₁ element].
- 1957 *Ozarkodina roundyi* (Hass). Rexroad, p. 37, pl. 2, fig. 7 [P₂ element].
- 1958 *Hindeodella redunca* Stanley, p. 466, pl. 63, figs. 1-4 [S₄ element].
- 1958 *Gnathodus bilineatus* (Roundy). Stanley, p. 464, pl. 68, fig. 7 [P₁ element].
- 1958 *Ozarkodina pachyamba* Stanley, p. 473, pl. 68, figs. 1, 2? [P₂ element].
- 1958 *Gnathodus modocensis* Rexroad. Rexroad, p. 17, pl. 1, figs. 1, 2 [P₁ element].
- 1960 *Gnathodus smithi* Clarke, p. 26, pl. 4, figs. 13, 14; pl. 5, figs. 9, 10 [P₁ element].
- 1961 *Gnathodus bilineatus* (Roundy). Higgins, pl. 10, fig. 5 [P₁ element].
- 1962 *Gnathodus bilineatus* (Roundy). Higgins, pl. 2, figs. 25; pl. 3, fig. 32 [P₁ element].

- 1964 *Gnathodus bilineatus modocensis* Rexroad. Rexroad & Furnish, p. 670, pl. 111, figs. 4, 5 [P₁ element].
- 1965 *Gnathodus bilineatus* (Roundy). Dunn, p. 1148, pl. 140, figs. 7-9 [P₁ element].
- 1966 *Gnathodus (Harltonodus) bilineatus* (Roundy). Elias, p. 11, pl. 1, figs. 3-12 [P₁ element].
- 1966 *Gnathodus (Harltonodus) bilineatus smithi* Clarke. Elias, p. 12, pl. 1, figs. 13, 14 [P₁ element].
- 1966 *Gnathodus (Harltonodus) bransoni* Elias, p. 12, pl. 1, figs. 15-20 [P₁ element].
- 1966 *Gnathodus (Harltonodus) delicatus hassi* Elias, p. 15, pl. 1, fig. 21 [P₁ element].
- 1966 *Gnathodus (Harltonodus?) liratus* (Youngquist & Miller). Elias, p. 15, pl. 1, figs. 22-24 [P₁ element].
- 1966 *Gnathodus (Harltonodus) minutus* Elias. Elias, p.16, pl. 1, figs. 25-28 [P₁ element].
- 1966 *Gnathodus (Harltonodus) multilineatus* Elias. Elias, p. 17, pl. 1, figs. 29-31 [P₁ element].
- 1966 *Gnathodus (Harltonodus) cf. G. (H.) multilineatus* Elias. Elias, pl. 1, fig. 32 [P₁ element].
- 1967 *Gnathodus bilineatus* (Roundy). Globensky, p. 440, pl. 58, figs. 9, 13 [P₁ element].
- 1967 *Gnathodus bilineatus bilineatus* (Roundy). Wirth, p. 205, pl. 19, figs. 6-9 [P₁ element].
- 1968 *Angulodus simplex* Higgins & Bouckaert, p. 28, pl. 1, fig. 7 [S₂ element].
- 1968 *Gnathodus bilineatus bilineatus* (Roundy). Higgins & Bouckaert, p. 29, pl. 3, fig. 9 [P₁ element].
- 1968 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert, p. 29, pl. 2, figs. 10, 13; pl. 3, figs. 4-8, 10 [P₁ element].
- 1968 *Hibbardella acuta* Murray & Chronic. Higgins & Bouckaert, p. 36, pl. 1, fig. 9 [S₀ element].
- 1968 *Hindeodella ibergensis* Bischoff. Higgins & Bouckaert, p. 37, pl. 1, fig. 1-3 [S₄ element].
- 1968 *Hindeodella uncata* (Hass). Higgins & Bouckaert, p. 37, pl. 1, fig. 5 [S₁ element].
- 1968 *Synprioniodina microdenta* Ellison. Higgins & Bouckaert, p. 47, pl. 1, fig. 6 [M element].

- 1969 *Gnathodus bilineatus* (Roundy). Rhodes *et al.*, p. 94, pl. 18, figs. 14-17 [P₁ element].
- 1969 *Gnathodus bilineatus* (Roundy). Webster, p. 30, pl. 5, figs. 11, 12 [P₁ element].
- 1970a *Gnathodus bilineatus* (Roundy). Dunn, p. 330, pl. 62, figs. 13, 14 [P₁ element].
- 1970 *Gnathodus bilineatus* (Roundy). Marks & Wensink, p. 258, pl. 2, figs. 3-11 [P₁ element].
- 1970 *Ozarkodina roundyi* (Hass). Marks & Wensink, p. 267, pl. 1, fig. 11 [P₂ element].
- 1970 *Gnathodus bilineatus* (Roundy). Reynolds, p. 10, pl. 1, fig. 6 [P₁ element].
- 1970 *Gnathodus delicatus* Branson & Mehl. Reynolds, p. 10, pl. 1, figs. 1-3, 5 [P₁ element].
- 1971 *Gnathodus bilineatus* (Roundy). Rhodes & Austin, pl. 2, fig. 1 [P₁ element].
- 1973 *Gnathodus bilineatus* (Roundy). Austin & Aldridge, pl. 1, fig. 1; pl. 2, fig. 1, 7, 11 [P₁ element].
- 1974 *Gnathodus bilineatus bilineatus* (Roundy). Austin, Conil, Groessens & Pirlet, pl. 1, figs. 4, 5, 15, 19, 22-25 [P₁ element].
- 1974 *Gnathodus bilineatus* (Roundy). Austin & Husri, pl. 3, figs. 4, 5, 7, 8, 13 [P₁ element].
- 1974 *Gnathodus bilineatus* (Roundy). Matthews & Thomas, pl. 50, fig. 19; pl. 51, figs. 12-15, 21-24 [P₁ element].
- 1974 *Gnathodus delicatus*. Matthews & Thomas, pl. 50, fig. 21 [P₁ element].
- 1974 *Gnathodus sp.*. Matthews & Thomas, pl. 50, figs. 20, 22 [P₁ element].
- 1974 *Gnathodus cf. bilineatus* (Roundy). Varker & Austin, pl. 6, fig. 15 [P₁ element].
- 1975 *Gnathodus bilineatus bilineatus* (Roundy). Higgins, p. 28, pl. 11, figs. 1-4, 6, 7 [P₁ element].
- 1975 *Gnathodus bilineatus bollandensis* Higgins & Boukaert. Higgins, p. p. 29, pl. 11, figs. 8-13 [Pa element].
- 1976 *Gnathodus bilineatus* (Roundy). Norby, p. 102, pl. 4, fig. 1, pl. 8, figs. 1-10, pl. 10, fig. 5 [bedding plane assemblages]; pl. 5, figs. 1-16 [P₁ element]; pl. 6, figs. 6-8 [P₂ element]; pl. 6, figs. 1-5 [M element]; pl. 7, figs. 12, 13 [S₀ element]; pl. 7, figs. 6, 8, 9, 11 [S₁ element]; pl. 7, figs. 1, 7 [S₂ element]; pl. 7, figs. [S₃ element]; pl. 7, figs. [S₄ element].

- 1979 *Gnathodus bilineatus bilineatus* (Roundy). Aisenverg *et al.*, pl. 6, figs. 11, 12 [P₁ element].
- 1979 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert. Aisenverg *et al.*, pl. 6, figs. 13, 14 [P₁ element].
- 1979 *Gnathodus bilineatus* Roundy. Einor *et al.*, pl. 14, fig. 1 [P₁ element]
- 1980a *Gnathodus bilineatus* (Roundy). Metcalfe, p. 302, pl. 38, figs. 5, 8, 9 [P₁ element].
- 1981 *Gnathodus bilineatus* (Roundy). Metcalfe, pl. 3, figs. 2-4 [P₁ element].
- 1984 *Gnathodus bilineatus bilineatus* (Roundy). Austin & Davies, pl. 3, fig. 36 [P₁ element].
- 1985 *Gnathodus bilineatus* (Roundy). Grayson *et al.*, p. 165, pl. 1, figs. 7, 14, 17, 19, 20; pl. 2, fig. 7 [P₁ element].
- 1985 *Gnathodus bilineatus bilineatus* (Roundy). Higgins, pl. 6.1, figs. 1, 2 [P₁ element].
- 1985 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert. Higgins, pl. 6.1, figs. 4, 5 [P₁ element].
- 1985 *Gnathodus bilineatus* (Roundy). Varker & Sevastopulo, p. 199, pl. 5.4, figs. 19, 20 [P₁ element].
- 1985 *Gnathodus bilineatus* (Roundy). Wardlaw, pl. 1, fig. 10 [P₁ element].
- 1986 *Gnathodus bilineatus* (Roundy). Mapes & Rexroad, p. 117, pl. 2, figs. 29-37 [P₁ element]. [Multi-element 22-37.]
- 1987 *Gnathodus bilineatus* (Roundy). Armstrong & Purnell, pl. 2, fig. 11 [P₁ element].
- 1987 *Gnathodus bilineatus* (Roundy). Riley *et al.*, pl. 2, figs. 2, 4 [P₁ element].
- 1987 *Gnathodus bilineatus bilineatus* (Roundy). Wang, Lane & Manger, p. 128, pl. 1, fig. 6 [P₁ element].
- 1987 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert. Wang, Lane & Manger, p. 128, pl. 1, fig. 7-10 [P₁ element].
- 1989 *Gnathodus bilineatus bilineatus* (Roundy). Wang & Higgins, p. 277, pl. 6, figs. 7-11 [P₁ element].
- 1989 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert. Wang & Higgins, p. 278, pl. 12, figs. 8-11 [P₁ element].
- 1990 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert. Nemirovskaya *et al.*, pl. 3, figs. 1, 5, 8, 10-12, 14, 16, 17 [P₁ element].
- 1990a *Gnathodus bilineatus* (Roundy). Ramovs, p. 91, pl. 4, figs. 2, 4, 5, 8, 9, 12 [P₁ element].
- 1990b *Gnathodus bilineatus* (Roundy). Ramovs, p. 109, pl. 1, figs. 1-3, 11 [P₁ element].

- 1990 *Gnathodus bilineatus modocensis* Rexroad. Rexroad & Horowitz, p. 501, pl. 2, figs. 26, 27, 33-42 [P₁ element]; pl. 2, fig. 32 [P₂ element]; pl. 2, fig. 31 [M element]; pl. 2, fig. 30? [S₁ element]; pl. 2, fig. 28, 29 [S₄ element].
- 1990 *Gnathodus bilineatus bilineatus* (Roundy). Varker *et al.*, pl. 1, fig. 1 [P₁ element].
- 1990 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert. Varker *et al.*, pl. 1, fig. 2-12 [P₁ element].
- 1991 *Gnathodus bilineatus bilineatus* (Roundy). Higgins *et al.*, pl. 3, fig. 19 [P₁ element].
- 1991 *Gnathodus bilineatus* (Roundy). Morrow & Webster, pl. 3, fig. 10 [P₁ element].
- 1992 *Gnathodus bilineatus* (Roundy). Dumoulin & Harris, fig. 8A [P₁ element].
- 1994 *Gnathodus bilneatus bilineatus* (Roundy). Davies *et al.*, pl. 2, fig2 [P₁ element].
- 1994 *Gnathodus bilineatus* (Roundy). Kolar-Jurkovsek & Jurkovsek, p. 432, pl. 2, figs. 1-8 [P₁ element].
- 1994 *Gnathodus bilineatus bilineatus* (Roundy). Varker, p. 308, pl. 3, fig. 3 [P₁ element].
- 1994 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert. Varker, p. 308, pl. 2, figs. 3, 6 [cluster]; pl. 3, figs. 1, 2, 4 [P₁ element].
- 1994 *Gnathodus bilineatus* (Roundy). Varker, p. 308, pl. 1, figs. 1-4, 7, pl. 2, figs. 1, 2, [cluster]; pl. 3, figs. 6, 9 [P₂ element]; pl. 3, figs. 7, 10 [M element]; pl. 3, fig. 8 [S₀ element]; pl. 3, figs. 13, 15 [S₁ element]; pl. 3, fig. 14 [S₂ element]; pl. 3 figs. 11, 12 [S₄ element].
- 1996 *Gnathodus bilineatus bilineatus* (Roundy). Krumhardt *et al.*, p. 39, pl. 2, figs. 18, 19, pl. 5, fig. 23 [P₁ element].
- 1997 *Gnathodus bilineatus* (Roundy). Dzik, p. 13, fig. 43, O-R [P₁ element].
- 1998 *Gnathodus bilineatus* (Roundy). Belka & Lehmann, pl. 1, figs. 1-5 [P₁ element]; figs. 9, 10 [P₂ element]; 6 [M element]; 8 [S₃ element]; 7 [S₄ element].

Holotype. United States National Museum, USNM 115101 (=USGS Carb. cat. 4021a); Roundy, 1926, p. 13, pl. 3, figs 10a-c. From the lower part of the Barnett Shale, Mississippian; locality 2609, south side of road to Bend post office, about 6 miles from San Saba, San Saba County, Texas, U.S.A.

Diagnosis. See Bischoff, 1957, p. 21 (under *Gnathodus bilineatus bilineatus*).

Description. *P*₁ element See Hass (1953, p. 79) and Rhodes *et al.* (1969, p. 95).

Remarks. The *P*₁ elements of *G. bilineatus* found in the Northumberland fauna were generally weak (pl. 4, figs. 2, 3): the caudal parapet was commonly made up of a single row of nodes, rather than broad lateral ridges and the rostral platform was usually sub-rounded, weakly ornamented with irregular small nodes and stopped abruptly well short of the dorsal end. A single complete element (pl. 4, fig. 1) and five fragments were found that were of a more strong and robust nature.

Higgins (e.g. 1968, 1975) and other authors have described the two *P*₁ morphotypes as subspecies: the robust variety as *G. bilineatus bilineatus*; the weaker variety as *G. bilineatus bollandensis*. The biological validity of this division has not been discussed previously, however in the Pennine Basin to the south, the arrival of *G. bilineatus bollandensis* is a useful biostratigraphic marker and is the zone fossil defining the base of the *G. bilineatus bollandensis* - *Cavusgnathus naviculus*, which Higgin's considers to be synonymous with the Arnsbergian (*E*₂) Stage. In the present study, the *G. bilineatus bollandensis* morphotypes were found from the base of the underlying Pendelian (*E*₁) Stage, which directly contradicts the work of Higgins.

What now seems likely, is that the two morphotypes of *G. bilineatus* are in fact ecophenotypes. In the Pennine Basin to the south, which represented a more deep-water open-marine setting than the Northumberland Trough, *G. bilineatus bilineatus* is found from the late Asbian to the end of the Arnsbergian. Towards the end of this period, as marine conditions became more shallow, *G. bilineatus bollandensis* appears in the Pennine Basin. In the Northumberland Trough, marine conditions were more shallow and restricted and the *G. bilineatus bollandensis* morphotype is seen significantly earlier, from at least the base of the Pendleian (Throckley boehole: Great Limestone samples) and is the dominant form throughout the basin.

Material studied. *P*₁ element 44.

Family MESTOGNATHIDAE Austin & Rhodes *in* Robinson,
1981

Genus MESTOGNATHUS Bischoff, 1957

1957 *Mestognathus* Bischoff, p. 37.

Type species. *Mestognathus beckmanni* Bischoff 1957 by original designation.

Diagnosis. See von Bitter *et al.* 1986, p. 32.

Remarks. von Bitter *et al.* (1986, p. 12) considered that this taxon lacked ramiform elements. More recent work on the Dinantian of the Northumberland Trough (Armstrong & Purnell 1987, Purnell 1992) has included non-P₁ elements, however a full reconstruction and a multielement diagnosis has yet to be published.

Mestognathus beckmanni Bischoff, 1957

Pl. 1 Fig. 8.

- * 1957 *Mestognathus beckmanni* Bischoff, p. 37, pl. 2, figs. 4-6, 8, 9 [P₁ element].
- 1969 *Mestognathus beckmanni* Bischoff. Rhodes *et al.*, p. 150, pl. 15, fig. 7 [P₁ element].
- 1969 *Mestognathus neddensis* Rhodes *et al.*, p. 153, pl. 13, figs. 2, 3 [P₁ element].
- 1970 *Mestognathus beckmanni* Bischoff. Reynolds, p. 14, pl. 2, Fig. 1 [P₁ element].
- 1973 *Mestognathus beckmanni* Bischoff. Austin & Aldridge, pl. 2, fig. 12 [P₁ element].
- 1974 *Mestognathus beckmanni* Bischoff. Austin & Husri, pl. 5, fig. 8 [P₁ element].
- 1974 *Mestognathus beckmanni* Bischoff. Matthews & Thomas, pl. 50, figs. 27, 28 [P₁ element].
- 1980b *Mestognathus beckmanni* Bischoff. Metcalfe, pl. 13, fig. 11 [P₁ element].

- 1981 *Mestognathus beckmanni* Bischoff. Metcalfe, pl. 8, figs. 1, 2 [P₁ element].
- 1982 *Mestognathus beckmanni* Bischoff. Higgins & Wagner-Gentis, pl. 34, figs. 16, 17 [P₁ element].
- 1983 *Mestognathus beckmanni* Bischoff. Belka, p. 76, pl. 1, figs. 3, 4; pl. 2, figs. 3, 4(?), 5 [P₁ element].
- 1985 *Mestognathus beckmanni* Bischoff. Varker & Sevastopulo, pl. 5.5, figs. 1, 3, 5 [P₁ element].
- ?1985 *Mestognathus beckmanni* Bischoff. Belka, pl. 10, figs. 4, 7 [P₁ element].
- 1986 *Mestognathus beckmanni* Bischoff. von Bitter *et al.*, p. 35, pl. 1, figs. 1-8, 23; pl. 2, figs. 1-5, 9; pl. 3, figs. 1-5, 9; pl. 4, figs. 1-5, 9; pl. 12, figs. 1-6; pl. 13, figs. 1-9; pl. 14, figs. 1-12; pl. 15, figs. 1-12; pl. 16, figs. 1-12; pl. 17, figs. 1-13; pl. 19, figs. 1-5; pl. 20, figs. 3, 6, 10, 12; pl. 23, figs. 1-3; pl. 25, figs. 7-9; pl. 26, fig. 4; pl. 27, figs. 3, 4, 7 [P₁ element].
- 1987 *Mestognathus beckmanni* Bischoff. Armstrong & Purnell, pl. 3, figs. 4, 6 [P₁ element]; pl. 3, fig. 5 [P₂ element]; pl. 3, fig. 7 [M element].
- 1991 *Mestognathus beckmanni* Bischoff. Stone, p. 32, pl. 1, figs. 10, 11 [P₁ element].
- 1992 *Mestognathus beckmanni* Bischoff. Purnell, p. 31, pl. 5, figs. 8a, 8b [P₁ element]; pl. 5, fig. 9 [P₂ element].

Holotype. Phillips University, Marburg, Germany (PUM Bi 1957/35); Bischoff, 1957, p. 37, pl. 2, fig. 4. From the Lower *Goniatites* Stufe, cuIII, found in a small quarry 1km north of Lethmathe immediately north of the Waldcafé, on the road between Lethmathe and Schwerte, Topographic Sheet Hohenlimburg.

Diagnosis. See von Bitter *et al.* (1986, p. 36, 37).

Description. *P₁ element* See von Bitter *et al.* (1986, p. 36).

Remarks. *M. beckmanni* P₁ elements were rare, but well spread in this study of the Northumberland faunas. Specimens were found from Bewcastle, Throckley and Howick, and were found in rocks of Brigantian, Pendleian and Arnsbergian age. Unfortunately however, the very low abundance and broad stratigraphic and spacial distribution means that this species is of little biostratigraphic or palaeoecological utility.

It is worthy of note that in the Pennine Basin at the same stratigraphic horizon, Higgins (1975) found no *M. beckmanni*. He did however find reasonable numbers of a species with a denticulated parapet, *M. bipluti* Higgins, that were not found during this study.

Material studied. P₁ elements 4.

Family Spathognathodontidae Hass, 1959

Genus *Lochriea* Scott, 1942

1942 *Lochriea* Scott, p.298

1970 *Paragnathodus* Meischner, p. 1173 (*nom. nud.*).

1975 *Paragnathodus* Higgins, p. 50.

Type species. *Lochriea montanaensis* Scott, 1942, by original designation (but a subjective junior synonym of *Spathognathodus commutatus* Branson & Mehl, 1941c).

Diagnosis. See Norby (1976, p. 140, text-fig. 21).

Remarks. The multielement concept of *Lochriea* was developed using bedding plane assemblages (Scott, 1942; Norby, 1976; Purnell & Donoghue, 1997) and statistical techniques (Horowitz & Rexroad, 1982). Purnell & Donoghue (1998, p. 65-6) showed that *Lochriea* is a typical ozarkodinid conodont, the main difference in the apparatus architecture being the more posterior and ventral location of the M elements.

Difficulties of designating non-Pa elements at species level has meant that where two species of *Lochriea* occur in a single sample these elements have been assigned *a priori* to *L. commutata*.

Lochriea commutata (Branson & Mehl, 1941c)

Pl. 3 Figs. 4-8.

- ? 1931 *Prioniodus alatoideus* Cooper, p. 232, pl. 28, fig. 1 [M element].
- 1941a *Spathognathodus commutatus* Branson & Mehl, p.172, pl. 5, figs. 19-22 [P₁ element].
- 1941a *Hindeodella* sp. Branson & Mehl, p. 170, pl. 5, fig. 9 (only) [S₂₋₄ element].
- * 1941c *Spathognathodus commutatus* Branson & Mehl, p.98, pl. 19, figs. 1-4 [P₁ element].
- 1941 *Spathognathodus commutatus* Branson & Mehl. Ellison & Graves, pl. 2, figs. 4?, 6 [P₁ element].
- p 1942 *Lochriea bigsnowyensis* Scott, p. 299, pl. 40, figs. 4, 5 [P₂ element]; pl. 40, fig. 3 [M element] only.
- 1942 *Lochriea montanaensis* Scott, p. 298, text-fig. 1; pl. 37, figs. 1-7; pl. 38, figs. 1-4, 6, 7, 10, 12 [clusters]; pl. 40, figs. 13, 15, 19 [P₁ elements]; pl. 40, figs. 9, 10 [P₂ element]; pl. 39, fig. 9, pl. 40, fig. 12 [M elements]; pl. 39, fig. 1?, 4, 7; pl. 40, fig. 2?, 18 [S₄ element].
- 1942 Unassigned element, Scott, pl. 40, fig. 16 [S₀ element].
- 1949 *Spathognathodus pellaensis* Youngquist & Miller, p. 622, pl. 101, fig. 6 [P₁ element].
- 1953 *Gnathodus inornatus* Hass, p. 80, pl. 14, figs. 9-11 [P₁ element].
- 1953 *Prioniodus singularis* Hass, pl. 16, fig. 4 [M element].
- 1953 *Subryantodus roundyi* Hass, p. 89, pl. 14, figs. 3-6 [P₂ element].
- ? 1956 *Hindeodella mehli* Elias, p. 108, pl. 1, figs. 22-24 [S₄ element].
- ? 1956 *Prioniodus singularis* Hass. Elias, pl. 2, fig. 15 [M element].
- 1956 *Spathognathodus commutatus* Branson & Mehl. Elias, p.119, pl. 3, figs. 19-22 [P₁ element].
- 1957 *Gnathodus commutatus commutatus* (Branson & Mehl). Bischoff, p. 23, pl. 4, figs. 2-6, 15 [P₁ element].
- 1957 *Prioniodina alatoidea* (Cooper). Bischoff, p. 45, pl. 5, figs. 33, 34, 36 [M element].
- 1957 *Ozarkodina recta* Rexroad, p. 36, pl. 2, figs. 5, 6 [P₂ element].
- 1957 *Spathognathodus* cf. *S. commutatus* Branson & Mehl. Rexroad, p. 38, pl. 3, figs. 23, 24 [P₁ element].
- 1957 *Gnathodus commutatus commutatus* (Branson & Mehl). Zeigler in Flügel & Zeigler, p. 39, pl. 3, fig. 21 [P₁ element].

- 1958 *Hindeodella montanaensis* (Scott). Stanley, p. 465, pl. 64, figs. 1-4, 5 [S₂₋₄ element].
- 1958 *Gnathodus inornatus* Hass. Stanley, p. 465, pl. 68, figs. 5, 6 [P₁ element].
- 1958 *Neoprioniodus singularis* (Hass). Stanley, p. 471, pl. 66, figs 2, 3 [M element].
- 1958 *Neoprioniodus* sp. A. Stanley, p. 472, pl. 66, figs. 4, 5 [M element].
- 1958 *Ozarkodina deflecta* Stanley, p. 472, pl. 65, figs. 4, 5 [P₂ element].
- 1958 *Prioniodina montanaensis* (Scott). Stanley, p. 474, pl. 64, fig. 5, pl. 65, fig. 1 [P₂ element].
- 1958 *Prioniodina* sp. A. Stanley, p. 474, pl. 65, fig. 3 [P₂ element].
- 1958 *Prioniodina* sp. B. Stanley, p. 474, pl. 65, fig. 7 [P₂ element].
- 1958 *Prioniodina* sp. C. Stanley, p. 475, pl. 65, fig. 2 [P₂ element].
- 1958 *Hindeodella* spp. Rexroad, p. 19, pl. 2, figs. 1, 4? only [S₀ element].
- 1958 *Spathognathodus* cf. *S. commutatus* Branson & Mehl. Rexroad, p. 26, pl. 6, fig. 8 [P₁ element].
- 1960 *Spathognathodus commutatus* Branson & Mehl. Clarke, p. 19, pl. 3, figs. 4, 5 [P₁ element].
- 1961 *Gnathodus commutatus* (Branson & Mehl) var. *commutatus* Bischoff. Higgins, p. 212, pl. 10, fig. 6, text-fig. 1a [P₁ element].
- 1961 *Hibbardella pennata* Higgins, p. 213, pl. 12, figs. 5, 6 [S₀ element].
- 1961 *Hindeodella germana* Holmes, Higgins, pl. 10, figs. 12, 13 [S₄ element].
- 1961 *Neoprioniodus singularis* (Hass). Higgins, pl.11, fig. 5 [M element].
- 1961 *Subbryantodus subaequalis* Higgins, p. 218, pl. 12, fig. 15, text-fig. 6 (1a&b only) [P₂ element].
- 1961 *Gnathodus commutatus* (Branson & Mehl). Rexroad & Burton, p. 1153, pl. 139, figs. 1-3 [P₁ element].
- 1961 *Neoprioniodus singularis* (Hass). Rexroad & Burton, p. 1155, pl. 140, figs. 13, 14, 18 [M element].
- 1962 *Gnathodus commutatus commutatus* (Branson & Mehl). Higgins, pl. 2, fig. 22 [P₁ element].
- 1962 *Neoprioniodus singularis* (Hass). Higgins, pl. 1, fig. 8 [M element].
- 1964 *Gnathodus commutatus pellaensis* (Youngquist & Miler). Rexroad & Furnish, p.671, pl. 111, fig. 3 [P₁ element].
- 1964 *Neoprioniodus singularis* (Hass). Rexroad & Furnish, p. 674, pl. 111, fig. 32 [M element].

- 1964 *Ozarkodina recta* Rexroad. Rexroad & Furnish, p. 674, pl. 111, fig. 8 [P₂ element].
- 1968 *Gnathodus commutatus* (Branson & Mehl). Higgins & Bouckaert, p. 30, pl. 2, fig. 5 [P₁ element].
- 1968 *Hibbardella pennata* Higgins. Higgins & Bouckaert, p. 36, pl. 1, fig. 10 [S₀ element].
- 1968 *Hindeodella germana* Holmes, Higgins & Bouckaert, p. 36, pl. 1, fig. 12 [S₂₋₄ element].
- 1968 *Neoprioniodus singularis* (Hass). Higgins & Bouckaert, p. 45, pl. 1, fig. 8 [M element].
- 1968 *Subbryantodus subaequalis* Higgins. Higgins & Bouckaert, pl. 3, fig. 1, 2 [P₂ element].
- 1969 *Gnathodus commutatus* (Branson & Mehl). Rhodes *et al.*, p.95, pl. 19, figs. 9-12 [P₁ element].
- 1969 *Hibbardella (Hibbardella) parva* Rhodes *et al.*, p. 114, pl. 25, figs. 21a, b [S₀ element].
- 1969 *Hindeodella montanaensis* (Scott). Rhodes, *et al.*, p. 123, pl. 28, figs. 21, 26 [S₄ element].
- 1969 *Neoprioniodus montanaensis* (Scott). Rhodes *et al.*, p. 160, pl. 22, figs. 5-8 [M element].
- 1969 *Prioniodina subaequalis* Higgins. Rhodes *et al.*, p. 198, pl. 28, figs. 1-4 [P₂ element].
- 1969 *Gnathodus commutatus* (Branson & Mehl). Thompson & Goebel, p. 23, pl. 4, figs. 4, 6, 7 [P₁ element].
- 1969 *Gnathodus commutatus* (Branson & Mehl). Webster, p. 31, pl. 5, fig. 13 [P₁ element].
- 1969 *Neoprioniodus singularis* (Hass). Webster, p. 40, pl. 7, fig. 14 [M element].
- 1970a *Gnathodus commutatus commutatus* (Branson & Mehl). Dunn, p. 331, pl. 62, figs. 11, 12 [P₁ element].
- 1970a *Neoprioniodus singularis* (Hass). Dunn, p. 337, pl. 64, figs. 32, 33 [M element].
- 1970a *Ozarkodina* cf. *O. recta* Rexroad. Dunn, p. 338, pl. 62, figs. 25, 26 [P₂ element].
- 1970 *Gnathodus commutatus commutatus* (Branson & Mehl). Marks & Wensink, p. 258, pl. 3, figs. 1 [P₁ element].
- 1970 *Neoprioniodus montanaensis* (Scott). Marks & Wensink, p. 266, pl. 1, figs. 9, 10 [M element].

- 1970 *Ozarkodina subaequalis* (Higgins). Marks & Wensink, p. 267, p. 1, figs. 12, 13 [P₂ element].
- 1970 *Gnathodus commutatus commutatus* (Branson & Mehl). Reynolds, p. 7, pl. 1, figs. 7, 9 [P₁ element].
- 1970 *Hibbardella pennata* Higgins. Reynolds, p. 10, pl. 2, figs. 8, 9 [S₀ element].
- 1970 *Hindeodella germana* Holmes. Reynolds, p. 11, pl. 4, fig. 2 [S₄ element].
- 1970 *Neoprioniodus singularis* (Hass). Reynolds, p. 15, pl. 3, fig. 12 [M element].
- 1970 *Ozarkodina roundyi* (Hass). Reynolds, p. 15, pl. 2, fig. 11 [P₂ element].
- 1970 *Ozarkodina plana* (Huddle). Reynolds, p. 15, pl. 2, fig. 12 [P₂ element].
- 1970 *Ozarkodina sp. nov.?* Reynolds, pl. 2, fig. 15 [P₂ element].
- 1971 *Gnathodus commutatus* (Branson & Mehl). Rhodes & Austin, pl. 2, fig. 6 [P₁ element].
- 1972 *Gnathodus commutatus* (Branson & Mehl). Thompson, p.33, pl. 1, figs. 6, 7 [P₁ element].
- 1972 *Neoprioniodus singularis* (Hass). Thompson, p. 37, pl. 1, figs. 21, 22 [M element].
- 1973 *Gnathodus commuatatus* (Branson & Mehl). Austin & Aldridge, pl. 1, fig. 3, pl. 2, fig. 10? [P₁ element].
- 1973 *Neoprioniodus montanaensis* (Scott). Austin & Aldridge, pl. 1, fig. 10 [M element].
- 1973 *Neoprioniodus singularis* (Hass). Austin & Aldridge, pl. 2, fig. 4 [M element].
- ? 1973 *Gnathodus commutatus palaensis* (Younquist & Miller). Merrill, p. 310, pl. 3, figs. 58, 59 [P₁ element].
- ? 1974 *Gnathodus commutatus* (Branson & Mehl). Varker & Austin, pl. 6, fig. 21 [P₁ element].
- 1974 *Gnathodus commutatus commutatus* (Branson & Mehl). Austin & Husri, pl. 3, figs. 1-3, 12 [P₁ element].
- 1974 *Hibbardella (Hibbardella) parva* Rhodes *et al.*. Austin & Husri, pl. 13, figs. 1, 2 [S₀ element].
- 1974 *Hindeodella montanaensis* (Scott). Austin & Husri, pl. 15, fig. 16 [S₄ element].
- 1974 *Neoprioniodus montanaensis* (Scott). Austin & Husri, pl. 12, figs. 11, 16, 18 [M element].
- 1974 *Prioniodina subaequalis* (Higgins). Austin & Husri, pl. 12, figs. 1-3, 9 [P₂ element].

- 1974 *Gnathodus commutatus commutatus* (Branson & Mehl). Mathews & Thomas, pl. 51, figs. 10, 11 [P₁ element].
- 1975 *Paragnathodus commutatus* (Branson & Mehl). Higgins, p. 70, pl. 7, figs. 7-9, 11, 13, 16, 20, 21 [P₁ element].
- p 1975 *Hibbardella pennata* Higgins. Higgins, p. 36, pl. 1, fig 6 (only) [S₀ element].
- 1975 *Hindeodella germana* Holmes. Higgins, p. 38, pl. 5, fig. 6 [S₄ element].
- 1975 *Neoprioniodus singularis* (Hass). Higgins, p. 68, pl. 3, fig. 11 [M element].
- 1975 *Subbryantodus subaequalis* Higgins. Higgins, p. 74, pl. 5, fig. 17 [P₂ element].
- 1976 *Lochriea commutatus* (Branson & Mehl). Norby, p. 143, pl. 13, figs. 1a, 2a, 3a, pl. 14, figs. 1, 3-9 [bedding plane assemblages]; pl. 11, figs. 1-10, 12-14, 16 [P₁ element]; pl. 11, fig. 11, pl. 12, figs. 9-13 [P₂ element]; pl. 12, figs. 4, 7, 8, 14 [M element]; pl. 11, figs. 15, 17, 18 [S₀ element]; pl. 12, fig. 5 [S₁ element]; pl. 12, figs. 1-3, 6 [S₄ element].
- 1979 *Gnathodus commutatus* (Branson & Mehl). Aisenverg *et al.*, pl. 6, figs. 3, 4 [P₁ element].
- 1979 *Gnathodus commutatatus commutatus* Bischoff. Einor *et al.*, pl. 14, fig. 2 [P₁ element].
- 1980a *Gnathodus commutatus* (Branson & Mehl). Metcalfe, p. 304, pl. 38, figs. 3, 4 [P₁ element].
- 1980a *Hibbardella pennata* Higgins. Metcalfe, p. 305, pl. 37, fig. 11 [S₀ element].
- 1980a *Hindeodella mehli* Elias. Metcalfe, p. 305, pl. 37, fig. 8 [S₄ element].
- 1980a *Neoprioniodus singularis* (Hass). Metcalfe, p. 307, pl. 37, fig. 15 [M element].
- 1980a *Subbryantodus subaequalis* Higgins. Metcalfe, p.309, pl. 37, fig. 20 [P₂ element].
- 1980b *Gnathodus commutatus* (Branson & Mehl). Metcalfe, pl. 13, fig. 10 [P₁ element].
- 1981 *Gnathodus commutatus* (Branson & Mehl). Metcalfe, p. 21, pl. 7, figs. 6, 7 [P₁ element].
- 1981 *Hibbardella pennata* Higgins. Metcalfe, pl. 14, figs. 1, 4 [S₀ element].
- 1981 *Hindeodella mehli* Elias. Metcalfe, pl. 15, fig. 3 [S₄ element].
- 1981 *Neoprioniodus singularis* (Hass). Metcalfe, pl. 18, figs. 1-3 [M element].

- 1981 *Subbryantodus subaequalis* Higgins. Metcalfe, pl. 19, fig. 7 [P₂ element].
- 1982 *Paragnathodus commutatus* (Branson & Mehl). Belka, pl. 1, fig. 11 [P₁ element].
- 1984 *Neoprioniodus singularis* (Hass). Austin & Davies, pl. 3, fig. 27 [M element].
- 1984 *Paragnathodus commutatus* (Branson & Mehl). Austin & Davies, pl. 3, figs. 26, 31 [P₁ element].
- 1984 *Paragnathodus* cf. *P. commutatus* (Branson & Mehl). Austin & Davies, pl. 3, fig. 17 [P₁ element].
- ? 1985 *Paragnathodus commutatus* (Branson & Mehl). Belka, pl. 11, fig. 7?, 8? [P₁ element].
- 1985 *Paragnathodus cracoviensis* Belka, p. 40, pl. 11, figs. 5, 6 [P₁ element].
- 1985 *Lochriea commutata* (Branson & Mehl). Higgins, pl. 6.1, fig. 10. [P₁ element].
- 1985 *Lochriea commutata* (Branson & Mehl). Varker & Sevastopulo, p. 200, pl. 5.5, figs. 11, 12 [P₁ element].
- 1985 *Neoprioniodus singularis* (Hass). Varker & Sevastopulo, pl. 5.6, fig. 13 [M element].
- 1985 *Paragnathodus commutatus* (Branson & Mehl). Wardlaw, pl. 1, fig. 13 [P₁ element].
- 1986 *Lochriea commutatus* (Branson & Mehl). Mapes & Rexroad, pl. 1, figs. 19, 20 [P₁ element]; pl. 1, figs. 22, 23 [M element]; pl. 1, fig. 21? [S₀ element].
- 1987 *Lochriea commutata* (Branson & Mehl). Armstrong & Purnell, pl. 3, fig. 1 [P₁ element].
- 1987 *Hibbardella pennata* Higgins. Riley *et al.*, pl. 2, fig. 15 [S₀ element].
- 1987 *Hindeodella germana* Holmes. Riley *et al.*, pl. 2, figs. 16, 17 [S₄ element].
- 1987 *Neoprioniodus singularis* (Hass). Riley *et al.*, pl. 2, fig. 25 [M element].
- 1987 *Paragnathodus commutatus* (Branson & Mehl). Riley *et al.*, pl. 2, figs. 1, 3 [P₁ element].
- 1990 *Lochriea commutata* (Branson & Mehl). Rexroad & Horowitz, p. 508, pl. 2, figs. 18-23 [P₁ element]; pl. 2, figs. 10-12 [P₂ element]; pl. 2, figs. 13-17 [M element]; pl. 2, fig. 25 [S₀ element]; pl. 2, fig. 24 [S₄ element].
- 1990 *Paragnathodus commutatus* (Branson & Mehl). Nemirovskaya *et al.* pl. 3, fig. 4 [P₁ element].

- 1990 *Neoprioniodus singularis* (Hass). Nemirovskya et al., pl. 3, figs. 7, 15 [M element].
- 1990 *Paragnathodus commutatus* (Branson & Mehl). Varker et al., pl. 1, figs. 13-15 [P₁ element].
- 1990 *Neoprioniodus singularis* (Hass). Varker et al., pl. 1, figs. 18, 19 [M element].
- p 1991 *Lochriea commutata* (Branson & Mehl). Stone, p. 34, pl. 4, figs. 6, 9 [P₁ element]; pl. 4, fig. 14 (only) [P₂ element]; pl. 4, fig. 13 [M element]; pl. 4, fig. 12 [S₄ element].
- 1992 *Lochriea commutata* (Branson & Mehl). Weibel & Norby, pl. 2, fig. 36 [P₁ element]; pl. 2, figs. 35? [M element].
- 1994 *Lochriea commutata* (Branson & Mehl). Kolar-Jurkovsek & Jurkovsek, p. 432, pl. 1, figs. 3, 4 [P₁ element].
- 1994 *Lochriea commutata* (Branson & Mehl). Varker, p. 310, pl. 4, fig. 6 [P₁ element].
- 1994 *Lochriea* sp. Varker, p. 310, pl. 1 figs. 5, 6 [clusters]; pl. 4, figs. 11, 12 [P₂ element]; pl. 4, fig. 13, 14 [M element]; pl. 4, fig. 7 [S₀ element]; pl. 4, figs. 15, 17 [S₄ element].
- 1994 *Lochriea commutata* (Branson & Mehl). von Bitter & Norby, fig. 2, 1-5, fig. 3, 1-6, fig. 4. 1-12, fig. 5, 1-12, fig. 6, 1-16, fig. 7, 1-20 [P₁ element].
- 1995 *Lochriea commutata* (Branson & Mehl). Skompski et al., pl. 1, fig. 10; pl. 4, figs. 1-3 [P₁ element].
- 1996 *Lochriea commutata* (Branson & Mehl). Krumhardt et al., p. 46, pl. 3, fig. 26 [P₁ element]; pl. 3, fig. 27 [M element].
- 1997 *Lochriea commutata* (Branson & Mehl). Dzik, p. 130, fig. 41, E [P₁ element]; F [P₂ element]; N [M element]; I [S₀ element]; L [S₄ element].
- 1998 *Lochriea commutata* (Branson & Mehl). Belka, pl. 3, figs. 5, 6 [P₁ element]; figs. 7, 8 [M element].

Holotype. University of Missouri, C552-2; Branson & Mehl, 1941c, p.98, pl. 19, figs. 1-4 (four syntypes designated). From the Pitkin Limestone, of Afton, Craig County, Oklahoma, U.S.A. (See von Bitter & Norby 1994, p.869, Locality 4, for details).

Emended diagnosis. A species of *Lochriea* in which the P₁ element lacks surface ornamentation on the platform.

Description. *P*₁ element See Branson & Mehl (1941c, p. 98) and Rhodes *et al.* (1969, p.95); *P*₂ element See Rhodes *et al.* (1969, p. 198); *M* element See Rhodes *et al.* (1969, p. 160); *S*₀ element See Higgins (1961, p. 213); *S*₁ element See Norby (1976, p. 156); *S*₄ element See Rhodes *et al.* (1969, p. 123).

Remarks. Considerable morphological variation is seen within the *P*₁ element: the platform may be robust and circular (e.g. Skompski *et al.* 1995, pl. 4, figs. 2, 3) or sub-diamond shape (e.g. Skompski *et al.* 1995, pl. 4, fig. 1), or more rarely it may be a much reduced form (e.g. Austin & Aldridge 1973, pl. 1, fig. 3; Matthews and Thomas 1974, pl. 51, figs 10, 11); the platform may be between one third (e.g. Higgins 1961, pl. 10, fig. 6) and almost two thirds (e.g. Riley *et al.* 1987, pl. 2, fig. 1) of the length of the element; the element may be straight (e.g. Skompski *et al.* 1995, pl. 4, fig. 1) to curved (e.g. Skompski *et al.* 1995, pl. 4, fig. 2); the rostral and caudal sides of the platform may meet at the dorsal end of the element (e.g. Wardlaw 1983, pl. 1, fig. 13) or the carina may extend well beyond the dorsal margin (e.g. Metcalfe 1981, pl. 7, fig. 6); in side view, the profile may be rectangular, with the oral and aboral surfaces almost parallel (e.g. Rhodes *et al.* 1969, pl. 19, fig. 10a), the oral surface reducing towards the dorsal end (e.g. Rhodes *et al.* 1969, pl. 19, fig. 9a).

Branson & Mehl (1941c) figured four syntypes and gave a description including most of the variation above. This paper also noted the tendency for the nodes to become thickened towards the dorsal end. Lateral thickening of nodes is consistent if somewhat rare in the published record of this species (e.g. Rexroad 1957, pl. 3, fig. 24; Metcalfe 1980, pl. 13, fig. 10; Rexroad & Horowitz 1990, pl 2, fig. 20). Belka (1985, p. 40, pl. 11, figs. 5, 6) actually designated elements with considerable thickening as a new species, *L. cracoviensis*. von Biter and Norby (1994) looked at ontogenetic variation in the *L. commutata* *P*₁ element and concluded that lateral thickening of the dorsal nodes was a normal result of growth in some animals, therefore Belka's *L. cracoviensis* is included here in this species.

The material in the present study showed an ontogenetic series. The small transparent juvenile forms had reduced platforms which took up approximately half the length of the element. The more robust adult forms had circular to sub-circular platforms and long free blades, two thirds the length of the element. The elements were all conservative and conformed to the description of Branson and Mehl (1941c). None of the more extreme, rare variations were seen (e.g. the lateral thickening of the dorsal nodes described above).

The largest variation in the P₂ element, is in the spacing of the denticles, particularly on the ventral process. These may be largely fused together (e.g. Stone 1990, pl. 4, fig. 14; Rexroad & Horowitz 1990, pl. 2, figs. 10-12) or with large individual denticles (e.g. Metcalfe 1981, pl. 19, fig. 7; Dzik 1997, fig. 41F). The material in the present study showed examples of both extremes; the figured element (plate 4, fig. 6) has isolated denticles, however there are also examples of elements with denticles that are more tightly fused.

In this study, the M element was the most abundant of the genus *Lochriea*. The variation within the morphology of this element was within the range of that seen in previous studies: relative length of cusp, anticusp and lateral process and the flexure of the cusp and lateral process in relation to the aboral cavity.

There was only a single S₀ element found during this study; it was very fragile and already broken, and so it was not figured. This element was very similar to that figured by Higgins (1975, pl. 1, fig. 6).

The bipennate element with a short, upturned lateral process that has been commonly found in prior studies of faunas containing *Lochriea* (previously termed "Sc"), is here designated the S₄ element. The S₄ element has been found to be morphologically very conservative in previous studies. This has been borne out during the present study, where all elements were found to be almost identical, except in size and robustness.

Material studied. P₁ element 49; P₂ element 12; M element 72; S₀ element 1; S₄ element 26.

Lochriea mononodosa (Rhodes *et al.*, 1969)

Pl. 3 Figs. 9-14.

- p 1961 *Gnathodus commutatus* (Branson & Mehl) var. *nodosus* Bischoff.
Higgins, p.213, pl. 10, fig. 7 (only) [P₁ element].
- * 1969 *Gnathodus mononodosa* Rhodes *et al.*, p.103, pl. 19, figs. 13-15 [P₁ element].
- p 1974 *Gnathodus commutatus nodosus* Bischoff. Austin & Husri, pl. 3, figs. 6, 7, 8 (only) [P₁ element].

- 1975 *Paragnathodus mononodosus* (Rhodes *et al.*). Higgins, p. 71, pl. 7, fig. 14 [P₁ element].
- 1979 *Gnathodus mononodosus* Rhodes *et al.*. Aisenverg *et al.*, pl. 6, figs. 5, 6 [P₁ element].
- p 1981 *Gnathodus nodosus* Bischoff. Metcalfe, pl. 7, figs. 3 (only) [P₁ element].
- 1982 *Paragnathodus mononodosa* (Rhodes *et al.*). Belka, pl. 1, fig. 10 [P₁ element].
- 1985 *Lochriea mononodosa* (Rhodes *et al.*). Varker & Sevastopulo, pl. 5.5, figs. 13, 16-18, 20 [P₁ element].
- 1985 *Lochriea mononodosa* (Rhodes *et al.*). Higgins, pl. 6.1, figs. 7, 8, 11, 12 [P₁ element].
- 1987 *Lochriea mononodosa* (Rhodes *et al.*). Armstrong & Purnell, pl. 3, fig. 2 [P₁ element].
- 1987 *Paragnathodus mononodosus* (Rhodes *et al.*). Riley *et al.*, pl. 2, fig. 9 [P₁ element].
- 1990 *Paragnathodus mononodosa* (Rhodes *et al.*). Nemirovskaya *et al.*, pl. 3, fig. 2 [P₁ element].
- 1994 *Lochriea mononodosa* (Rhodes *et al.*). Varker p. 310, pl. 4, figs. 4, 5, 9 [P₁ element].
- 1995 *Lochriea monocostata* (Pazukhin & Nemirovskaya). Skompski *et al.*, pl. 1, fig. 6 [P₁ element].
- 1995 *Lochriea mononodosa* (Rhodes *et al.*). Skompski *et al.*, pl. 1, figs. 1, 2; pl. 3, fig. 8; pl. 4, figs. 5, 14 [P₁ element].
- p 1997 *Lochriea mononodosa* (Rhodes *et al.*). Dzik, p. 130, fig. 41, A, C, D [P₁ element]; G, H [P₂ element]; M [M element]; J [S₀ element]; K [S₄ element].

Holotype. British Museum (Natural History) X124; Rhodes *et al.*, 1969, pl. 19, figs. 14a-d. From the D₃ (late Brigantian-early Pendleian) at Mellte Bridge, Craig-y-Dinas, Glamorgan, Wales, UK (NGR. SN911079) (see Rhodes *et al.* p. 23 for further details).

Emended diagnosis. A species of *Lochriea* in which the P₁ element has ornamentation developed on the caudal side of the platform.

Description. *P₁ element.* The straight to slightly curved blade is a half to two thirds the length of the element and the oral surface contains a single line of denticles from the ventral to the dorsal end of the element. The rostrocaudal profile is rectangular,

with a slight reduction in the oral surface towards the dorsal end. The bold platform is sub-circular to sub-diamond shaped and contains ornamentation on the caudal side, typically a single large node.

Remarks. Higgins (1961, p. 213), Austin & Husri (1974) and Metcalfe (1981) all included forms of *Lochriea* P₁ elements with ornamentation restricted to the caudal side of the platform within their concept of "nodosus" (each using a different generic classification), which differs from the present study.

Previously, the P₁ element of *L. mononodosa* has consistently been described with a single large node on the caudal platform. This type of element is the most common in the Northumberland fauna, however a number of other variants have also been seen. A form with two small nodes (pl. 3, figs. 9, 10), another with three small nodes (pl. 3, figs. 11, 12) and another with a long ridge, made up of three fused nodes (pl. 3, figs. 13, 14). Though unusual, these are all considered to be morphological variants of *L. mononodosa*, possibly resulting from ecophenotypic variation in a restricted shallow water shelf environment.

L. monocostata Pazukhin & Nemirovskaya includes forms in which platform nodes are replaced by one or two ridges. Skompski *et al.* (1995, p. 181) concluded that this form probably constituted part of a morphological series with *L. mononodosa*, and as such may only represent a variety of this species. This agrees with the concept of the species from this study, as one in which considerably more variation exists than has been previously discussed.

Material studied. P₁ element 30.

Lochriea nodosa (Bischoff, 1957)

Pl. 4 Figs. 1-5.

- *1957 *Gnathodus commutatus nodosus* Bischoff, p. 23, pl. 4, figs. 12, 13 [P₁ element].
- 1957 *Gnathodus commutatus nodosus* Bischoff. Zeigler in Flugel & Zeigler, p. 40, pl. 3, fig. 4 [P₁ element].
- 1960 *Gnathodus cruciformis* Clarke, p. 25, pl. 4, figs. 10-12 [P₁ element].
- p 1961 *Gnathodus commutatus* (Branson & Mehl) var. *nodosus* Bischoff. Higgins, p.213, pl. 10, fig. 8 (only) [P₁ element].

- 1962 *Gnathodus nodosus* Bischoff. Higgins, pl. 2, fig. 19 [P₁ element].
- 1969 *Gnathodus nodosus* Bischoff. Rhodes *et al.*, p. 104, pl. 19, figs. 16-20 [P₁ element].
- 1970 *Gnathodus commutatus nodosus* Zeigler. Marks & Wensink, p. 260, pl. 3, fig. 3, 4? [P₁ element].
- p 1974 *Gnathodus commutatus nodosus* Bischoff. Austin & Husri, pl. 3, figs. 4, 5 (only) [P₁ element].
- 1974 *Gnathodus commutatus nodosus* (Bischoff). Mathews & Thomas, pl. 51, fig. 5 [P₁ element].
- 1975 *Paragnathodus nodosus* (Bischoff). Higgins, p. 72, pl. 7, figs. 12, 15, 17-19, 22, 23 [P₁ element].
- 1979 *Gnathodus nodosus* Bischoff. Aisenverg *et al.*, pl. 6, fig. 7 [P₁ element].
- 1979 *Gnathodus commutatus nodosus* Bischoff. Einor *et al.*, pl. 14, fig. 3 [P₁ element].
- p 1981 *Gnathodus nodosus* Bischoff. Metcalfe, pl. 7, figs. 1, 2, 4, 5 (only) [P₁ element]. [non pl. 7, fig. 3 = *L. monodosa*.]
- 1982 *Paragnathodus nodosa* (Bischoff). Belka, pl. 1, figs. 8, 9 [P₁ element].
- 1985 *Paranathodus nodosus* (Bischoff). Higgins, p. 222, pl. 6.1, fig. 9 [P₁ element]. [Plate caption printed with pl. 6.3.]
- 1987 *Paragnathodus nodosus* (Bischoff). Riley *et al.*, pl. 2, figs. 10, 11, 13, 14 [P₁ element].
- 1990 *Paragnathodus nodosus* (Bischoff). Nemirovskaya *et al.*, pl. 4, figs. 3, 9 [P₁ element].
- 1994 *Lochriea nodosa* (Bischoff). Kolar-Jurkovsek & Jurkovsek, p. 433, pl. 1, figs. 5-8 [P₁ element].
- 1994 *Lochriea nodosa* (Bischoff). Varker, pl. 4, figs. 8, 10 [P₁ element].
- 1995 *Lochriea nodosa* (Bischoff). Skompski *et al.*, pl. 1, figs. 3?, 4; pl. 2, fig. 4; pl. 3, figs. 1, 3, 6, 7, 9; pl. 4, fig. 4 [P₁ element].
- 1995 *Lochriea multinodosa* (Wirth). Skompski *et al.*, pl. 2, figs. 9, 11, 12 [Pa element].
- 1995 *Lochriea senckenbergia* (Nemirovskaya, Perret & Meschner). Skompski *et al.*, pl. 2, figs. 1-3, 5, 6; pl. 3, fig. 13; pl. 4, figs. 8, 10-12 [Pa element].
- 1995 *Lochriea ziegleri* (Nemirovskaya, Perret & Meischner). Skompski *et al.*, pl. 1, figs. 5, 7-9, 11, 12.; pl. 2, figs. 7, 10; pl. 3, figs. 2, 4, 5, 11, 14; pl. 4, figs. 6, 7, 9, 13, 15 [P₁ element].
- p 1997 *Lochriea mononodosa* (Rhodes *et al.*). Dzik, p. 130, fig. 41, B [P₁ element].

Holotype. Bi 1957/104; Bischoff, 1957, pl. 4, fig. 13. From the Rhenar Kalk (cuIIIy₁), at Stbr. am NW - Ausgang von Rhena, Bl. Goddelsheim, Germany.

Emended diagnosis. A species of *Lochriea* in which the P₁ element has ornamentation developed on both platforms.

Description. *P₁ element.* The element is sub-rectangular in rostrocaudal profile, with the denticulated oral surface dipping slightly towards the dorsal end. The straight to slightly curved blade is a half to two thirds the length of the element. The bold platform is sub-circular to sub-diamond shaped and contains ornamentation on the caudal and rostral side, typically a single large node.

Remarks. Higgins (1961), Austin & Husri (1974) and Metcalfe (1981) included specimens of *Lochriea* P₁ elements with a node just on the caudal side of the platform, as well as those with ornamentation on both side of the platform, in their concept of "*nodusus*" (using various generic pre-fixes), which differs from the diagnosis in this study.

The emended concept of *Lochriea nodosa* is broad and includes a diverse range of platform ornamentation: a single, bold node; a smooth ridge; an ornamented ridge; a broad, high area of nodes; any of the previous ornamentations fused onto the carina. The types of ornamentation on each platform is rarely the same and thus the total number of end member variations is large. With larger collections and more detailed study, it may be possible to define distinct subspecies or even species within this plexus. The work of Skompski *et al.* (1995), which seems to be led by biostratigraphic concerns and pay little regard to multielement taxonomy, therefore seems to be somewhat less rigorous than is needed to discuss five variants of *L. nodosa* as separate species. Admittedly, these species were actually proposed by different authors, but this summary work emphasises the weak, undefendable basis for such definitions. All these variations have been seen within the current study, except perhaps the absolute end member of *L. multinodosa*. However very nodose forms of *L. zeigleri*, which are almost equivalent, have been seen.

Material studied. P₁ element 13.

Order PRIONIODINIDA Sweet, 1988

Family PRIONIODINIDAE Bassler, 1925

Genus IDIOPRIONIODUS Gunnell, 1933

- 1926 *Prioniodus* Roundy, p. 10, pl. 4, fig. 5.
1933 *Idioproniodus* Gunnell, p. 265, pl. 32, figs. 36, 37.
1952 *Duboisella* Rhodes, p. 895, pl. 128, figs. 1-6; text-fig. 3.

Type species. *Idioproniodus typus* Gunnell, 1933.

Diagnosis. See Norby 1976, p. 123.

Remarks. See Stone (1991, p. 39) for a review of *Idioproniodus*. Element notation is based on bedding plane assemblages (Purnell and von Bitter, 1996), as updated by Purnell *et al.* (2000, p. 117).

Idioproniodus healdi (Roundy, 1926)

Pl. 4 Figs. 6-8.

- ?p 1900 *Polygnathus (Centrodus) convexus* Pander. Hinde, p. 342, pl. 9, fig. 8 (only) [S_1 element].
- ? p 1900 *Prioniodus peracutus* Hinde, p. 343, pl. 10, fig. 23 [$?S_1$ element].
- * 1926 *Prioniodus healdi* Roundy, p. 10, pl. 4, fig. 5 [S_2 element].
- ? 1926 *Prioniodus* sp. A. Roundy, p. 11, pl. 4, fig. 9 [S_{3-4} element].
- ? 1926 *Prioniodus* sp. C. Roundy, p. 11, pl. 4, fig. 11 [S_{3-4} element].
- ? 1926 *Prioniodus* sp. D. Roundy, p. 11, pl. 4, fig. 12, 13 [P_1 element].
- 1931 *Prioniodus bidentata* Gunnell, p. 247, pl. 29, fig. 6 [S_1 element].
- ? 1931 *Prioniodus clarki* Gunnell, p. 247, pl. 29, fig. 8 [P_2 element].
- ? 1931 *Prioniodus conjunctus* Gunnell, p. 247, pl. 29, fig. 7 [M element].
- ? 1931 *Prioniodus lexingtonensis* Gunnell, p. 246, pl. 29, fig. 4 [Sb2 element].
- 1931 *Prioniodus missouriensis* Gunnell, p. 247, pl. 29, fig. 9 [S_0 element].
- 1931 *Prioniodus subacodus* Gunnell, p. 246, pl. 29, fig. 5 [S_0 element].
- ? 1931 *Prioniodus tridentatus* Gunnell, p. 246, pl. 29, fig. 3 [S_2 element].

- ? 1931 *Prioniodus tridentatus* Gunnell, p. 246, pl. 29, fig. 3 [S₂ element].
- 1933 *Idioproniodus striatus* Gunnell, p. 265, pl. 32, figs. 36, 37 [S₀ element].
- ? 1933 *Idioproniodus typus* Gunnell, p. 265, pl. 31, fig. 47 [S₃₋₄ element].
- 1933 *Prioniodus dactylodus* Gunnell, p. 265, pl. 31, fig. 1 [S₁ element].
- ? 1933 *Prioniodus? galesburgensis* Gunnell, p. 267, pl. 31, fig. 12 [S₃₋₄ element].
- 1941c *Metalonchodina bidentata* (Gunnell). Branson & Mehl, p. 106, pl. 19, fig. 34 [S₁ element].
- ? 1941c *Metalonchodina* sp. A, Branson & Mehl, pl. 19, fig. 33 [S₁ element].
- 1941 *Hibbardella subacoda* (Gunnell). Ellison, p. 118, pl. 20, figs. 22, 26 [S₀ element].
- 1941 *Ligonodina lexingtonensis* (Gunnell). Ellison, p. 115, pl. 20, figs. 13-15 [S₂ element].
- 1941 *Ligonodina type* (Gunnell). Ellison, p. 114, pl. 20, figs. 8-11 [S₃₋₄ element].
- 1941 *Lonchodina clarki* (Gunnell). Ellison, p. 116, pl. 20, figs. 21, 27, 30, 31 [Pb element].
- 1941 *Lonchodina? ponderosa* Ellison, p. 116, pl. 20, figs. 37-39 [Pa element].
- 1941 *Metalonchodina bidentata* (Gunnell). Ellison, p. 116, pl. 20, figs. 35, 36 [S₁ element].
- 1941 *Ligonodina lexingtonensis* (Gunnell). Ellison & Graves, p. , pl. 1, figs. 23, 24 [S₂ element].
- 1941 *Metalonchodina* sp. Ellison & Graves, pl. 1, fig. 20 [S₁ element].
- 1941 *Trichognathus subacoda* (Gunnell). Ellison & Graves, p. 3, pl. 1, fig. 19 [S₀ element].
- 1952 *Duboisella typica* Rhodes, p. 895, pl. 128, figs. 1-6 [clusters]; text-fig. 3.
- 1953 *Ligonodina roundyi* Hass, p. 82, pl. 15, figs. 5-9 [S₃₋₄ element].
- ? 1953 *Lonchodina paraclarki* Hass, p. 83, pl. 16, figs. 15, 16 [P₂ element].
- 1953 *Metalonchodina* sp. A, Hass, p. 85, pl. 16, 17, 18 [S₁ element].
- 1953 *Prioniodus inclinatus* Hass, p. 87, pl. 16, figs. 10, 11, 12?-14? [M element].
- 1953 *Roundya barnettana* Hass, p. 89, pl. 16, figs. 8, 9 [S₀ element].
- 1956 *Roundya barnettana* Hass. Elias, p. 121, pl. 4, figs. 22, 23 [S₀ element].
- 1957 *Metalonchodina bidentata* (Gunnell). Bischoff, p. 37, pl. 5, figs. 13, 15, 46 [S₁ element].
- 1957 *Prioniodina* sp. a. Bischoff, p 49, pl 5, fig. 32 [M element].
- 1957 *Roundya barnettana* Hass. Bischoff, p. 52, pl. 5, figs. 19, 20 [S₀ element].

- ? 1957 *Roundya delicata* (Mehl & Thomas). Bischoff, p. 53, pl. 5, figs. 22, 23 [S₀ element].
- 1958 *Lonchodina furnishi* Rexroad, p. 22, pl. 4, figs. 11-13 [S₂ element].
- 1958 *Lonchodina paraclaviger* Rexroad, p. 22, pl. 4, figs. 7-10 [P₁ element].
- 1958 *Roundya costata* Rexroad, p. 26, pl. 2, figs. 5-8 [S₀ element].
- 1960 *Metalonchodina conflecta* Clarke, p. 17, pl. 2, fig. 14 [S₁ element].
- ? 1960 *Roundya* sp. Clarke, p. 15, pl. 2, fig. 5 [S₀ element].
- 1961 *Lonchodina* cf. *projecta* Ulrich & Bassler. Higgins, pl. 11, fig. 10 [P₂ element].
- 1961 *Metalonchodina bidentata* (Gunnell). Higgins, p. 12, fig. 9 [S₁ element].
- 1961 *Neoprioniodus inclinatus* (Hass). Higgins, pl. 11, fig. 3 [M element].
- 1961 *Roundya subacoda* (Gunnell). Higgins, pl. 11, fig. 13 [S₀ element].
- 1962 *Metalonchodina bidentata* (Gunnell). Higgins, pl. 1, fig. 3 [S₁ element].
- 1962 *Neoprioniodus conjunctus* (Gunnell). Higgins, p. 10, pl. 1, fig. 2 [M element].
- 1962 *Roundya subacoda* (Gunnell). Higgins, p. 11, pl. 1 fig. 1 [S₀ element].
- 1968 *Lonchodina bischoffi* Higgins & Bouckaert, p. 43, illustrated in Higgins 1961, pl. 11, fig. 10 [P₂ element].
- 1969 *Hibbardella (Roundya) barnettana* Hass. Rhodes *et al.*, p. 116, pl. 25, figs. 2-5 [S₀ element].
- 1969 *Hibbardella (Roundya)* sp. Rhodes *et al.*, p. 116, pl. 25, fig. 1 [S₀ element].
- 1969 *Ligonodina roundyi* Hass. Rhodes *et al.*, p. 137, pl. 26, figs. 13, 14, 16 [S₃₋₄ element].
- 1969 *Lonchodina furnishi* Rexroad. Rhodes *et al.*, p. 141, pl. 24, figs. 20-23 [S₂ element].
- ? 1969 *Lonchodina obtunda* Collinson & Druce (*nom. nud.*). Rhodes *et al.*, p. 142, pl. 24, fig. 7 [S₂ element].
- 1969 *Lonchodina paraclarki* Hass. Rhodes *et al.*, p. 143, pl. 24, fig. 16 [P₂ element].
- 1969 *Lonchodina paraclaviger* Rexroad. Rhodes *et al.*, p. 143, pl. 24, figs. 15, 18 [P₁ element].
- ? 1969 *Lonchodina transitans* Collinson & Druce (*nom. nud.*). Rhodes *et al.*, p. 144, pl. 31, fig. 14 [P₂ element].
- 1969 *Metalonchodina bidentata* (Gunnell). Rhodes *et al.*, p. 154, pl. 24, figs. 8-11 [S₁ element].
- 1969 *Neoprioniodus conjunctus* (Gunnell). Rhodes *et al.*, p. 159, pl. 21, figs. 16, 17, 20 [M element].

- p 1969 *Neoprioniodus? inclinatus* (Hass). Thompson & Goebel, p. 39, pl. 3, fig. 13 (*non. fig 16*) [M element].
- 1969 *Roundya* sp. Webster, p. 43, pl. 8, figs. 7, 8 [S₀ element].
- 1970a *Hibbardella* sp. Dunn, p. 332, pl. 64, fig. 29 [S₀ element].
- 1970 *Roundya subacoda* (Gunnell). Reynolds, pl. 5, fig. 3 [S₀ element].
- 1972 *Ligonodina lexingtonensis* (Gunnell). von Bitter, p. 76, pl. 12, fig. 2 [S₂ element].
- 1972 *Lonchodina? ponderosa* Ellison. von Bitter, p. 79, pl. 12, fig. 5 [P₁ element].
- 1972 *Neoprioniodus conjunctus* (Gunnell). von Bitter, p. 69, pl. 12, fig. 4 [P₂ element]; pl. 9, fig. 6 [M element]; pl. 16, fig. 2 [S₀ element]; pl. 12, fig. 3 [S₃₋₄ element].
- 1973 *Idioprioniodus lexingtonensis* (Gunnell). Baesemann, p. 703, pl. 3, figs. 4, 5 [P₁ element]; fig. 2 [P₂ element]; fig. 7 [M element]; fig. 9 [S₀ element]; figs. 3, 8 [S₂ element]; fig. 1 [S₃₋₄ element].
- 1973 *Lonchodina furnishi* Rexroad. Austin & Aldridge, pl. 1, fig. 9 [S₂ element].
- 1974 *Hibbardella (Roundya) barnettana* Hass. Austin & Husri, pl. 13, figs. 17, 18 [S₀ element].
- 1974 *Ligonodina roundyi* Hass. Austin & Husri, pl. 14, figs. 5, 8, 11 [S₃₋₄ element].
- ? 1974 *Ligonodina* sp. Austin & Husri, pl. 14, fig. 12 [S₃₋₄ element].
- 1974 *Lonchodina furnishi* Rexroad. Austin & Husri, pl. 11, figs. 2, 16, 18 [S₂ element].
- ? 1974 *Lonchodina paraclarki* Hass. Austin & Husri, pl. 11, fig. 17 [P₂ element].
- 1974 *Lonchodina paraclaviger* Rexroad. Austin & Husri, pl. 11, figs. 10, 15 [P₁ element].
- ? 1974 *Lonchodina transitans* Collinson & Druce (*nom. nud.*). Austin & Husri, pl. 11, fig. 3; pl. 14, fig. 6 [P₂ element].
- 1974 *Metalonchodina bidentata* (Gunnell). Austin & Husri, pl. 11, figs. 1, 6, 7, 11-13 [S₁ element].
- 1974 *Ligonodina typha* (Gunnell). Varker & Austin, pl. 6, fig. 13 [S₃₋₄ element].
- 1974 *Metalonchodina bidentata* (Gunnell). Varker & Austin, pl. 6, fig. 9 [S₁ element].
- 1975 *Ligonodina roundyi* Hass. Higgins, p. 58, pl. 3, fig. 14 [S₃₋₄ element].

- 1975 *Lonchodina bischoffi* Higgins & Bouckaert. Higgins, p. 59, pl. 2, figs. 1-4, 8 [P₂ element].
- 1975 *Lonchodina furnishi* Rexroad. Higgins, p. 60, pl. 2, fig. 6 [S₂ element].
- 1975 *Lonchodina paraclaviger* Rexroad. Higgins, p. 60, pl. 2, fig. 9 [P₁ element].
- 1975 *Metalonchodina bidentata* (Gunnell). Higgins, p. 63, pl. 1, fig. 13 [S₁ element].
- 1975 *Metalonchodina multidentata* Higgins, p. 63, pl. 1, figs. 14-16 [S₁ element].
- 1975 *Neoprioniodus conjunctus* (Gunnell). Higgins, p. 66, pl. 3, fig. 7 [M element].
- 1975 *Roundya barnettana* Hass. Higgins, p. 72, pl. 1, figs. 1-3, 12 [S₀ element].
- 1975 *Idioprioniodus paraclaviger* (Rexroad). Nicoll & Rexroad, p. 20, pl. 3, figs. 16, 17 [P₁ element]; figs. 8-11 [P₂ element]; figs. 1-3 [M element]; fig. 15 [S₀ element]; figs. 12-14 [S₁ element]; figs. 4-7 [S₃₋₄ element].
- 1976 *Idioprioniodus healdi* (Roundy). Norby, p. 124, pl. 10, figs. 1, 2, 4; pl. 14, fig. 2; pl. 19, figs. 2, 3 [cluster]; pl. 9, figs. 3, 8 [P₁ element]; pl. 9, fig. 11 [P₂ element]; pl. 9, fig. 7, 9 [M element]; pl. 9, fig. 16, 17 [S₀ element]; pl. 9, figs. 6, 12, 13 [S₁ element]; pl. 9, fig. 2, 5, 10 [S₂ element]; pl. 9 figs. 1, 14 [S₃₋₄ element].
- 1981 *Idioprioniodus* sp. aff. *I. healdi* (Roundy). Rexroad, p. 11, pl. 2, fig. 8 [M element]; fig. 6 [?S₂ element]; fig. 7 [?S₃₋₄ element].
- 1981 *Lonchodina bischoffi* Higgins & Bouckaert. Metcalfe, pl. 16, fig. 2 [P₂ element].
- 1981 *Lonchodina furnishi* Rexroad. Metcalfe, pl. 16, figs. 1, 8 [S₂ element].
- ? 1981 *Lonchodina transitans* Collinson & Druce (*nom. nud.*). Metcalfe, p. 31, pl. 16, fig. 3 [P₂ element].
- 1981 *Metalonchodina bidentata* (Gunnell). Metcalfe, pl. 17, fig. 1 [S₁ element].
- 1981 *Neoprioniodus conjunctus* (Gunnell). Metcalfe, pl. 18, figs. 7, 9 [M element].
- 1981 *Neoprioniodus discretus* Metcalfe, p. 37, pl. 18, fig. 8 [M element].
- 1981 *Roundya barnettana* Hass. Metcalfe, pl. 16, fig. 4 [S₀ element].
- 1982 *Idioprioniodus conjunctus* (Gunnell). Higgins & Wagner-Gentis, p. 332, pl. 34, fig. 29 [P₁ element]; fig. 21 [M element]; fig. 18 [S₀ element]; fig. 27 [S₁ element]; fig. 28 [S₃₋₄ element].

- 1984 *Roundya barnettana* Hass. Austin & Davies, pl. 3, fig. 5 [S₀ element].
- 1987 *Roundya barnettana* (Hass). Riley *et al.*, pl. 2, fig. 24 [S₀ element].
- 1991 *Idioproniodus cf. healdi* (Roundy). Stone, p. 40, pl. 5, fig. 5 [P₁ element]; fig. 1 [M element]; figs. 7, 8 [S₃₋₄ element].
- 1994 *Idioproniodus healdi* (Roundy). Varker, p. 309, pl. 2, fig. 5 [P₁ element]; fig. 9 [S₀ element]; fig. 4 [S₃₋₄ element].
- 1996 *Idioproniodus cf. I. healdi* (Roundy)? Krumhardt *et al.*, p. 45, pl. 5, fig. 13 [S₁ element].
- p 1997 *Idioproniodus* sp. Dzik, p. 129, figs. 39B, 39C [P₁ element]; fig. 39F [P₂ element]; fig. 39H [M element]; figs. 39E, 39I [S₁ element]; figs. 39G, 39J [S₃₋₄ element] (*non*. fig. 39A [*Lochriea* P₂ element]; fig. 39D [*Kladognathus* S₀ element]).

Holotype. Specimen number not known; Roundy, 1926, p. 10, pl. 4, figs. 5a, 5b. From the Upper part of the Barnett shale, Mississippian, of San Saba County, Texas, U.S.A. (4.9 miles east and 0.9 miles south from the courthouse at San Saba).

Diagnosis. See Norby 1976, p. 124.

Description. *P₁ element* See Rexroad (1958, p. 22); *P₂ element* See Hass (1953, p. 83); *M element* See Rhodes *et al.* (1969, p. 159); *S₀ element* See Hass (1953, p. 89); *S₁ element* See Rhodes *et al.* (1969, p. 154); *S₂ element* See Rexroad (1958, p. 22); *S₃₋₄ element* See Rhodes *et al.* (1969, p. 137).

Remarks. *Idioproniodus healdi* is historically the most unstable of the species in this study. The assignment of elements to locations within the apparatus has been in constant flux since early attempts by authors such as von Bitter (1972), Baeseman (1973) and Norby (1976). This is largely due to a lack of bedding plane assemblages and a clearly defined Bauplan for the prioniodinids as a whole. Purnell & von Bitter (1996) concluded that the three-dimensional architecture of the prioniodinids was similar to the ozarkodinids and assigned *Idioproniodus* elements to eight locations, then termed Pa, Pb, M, Sa, Sb₁, Sb₂, Sc₁, Sc₂.

In the present study, *I. healdi* elements have been found sporadically from the earliest to the latest samples and in all locations. Unfortunately however, they were only recovered in very low numbers and can not add further information to the debate on apparatus architecture.

Material studied. *P₁ element* 8; *P₂ element* 0; *M element* 0; *S₀ element* 1; *S₁ element* 0; *S₂ element* 0; *S₃₋₄ element* 9.

Genus KLADOGNATHUS Rexroad, 1958

- 1847 *non Cladognathus* Burmeister, p. 364.
1957 *Cladognathus* Rexroad, p. 28.
1958 *Kladognathus* Rexroad, p. 19; Rexroad, 1981, p. 11.
1958 *Lambdagnathus* Rexroad, p. 19.
1961 *Cladognathus* Rexroad & Collinson, p. 6.
1963 *Magnilaterella* Rexroad & Collinson, p. 11-14.

Type species. *Cladognathus prima* Rexroad 1957, by original designation.

Diagnosis. See Purnell 1993, p. 878.

Remarks. The multielement concept of *Kladognathus* is based on statistical studies (Horowitz and Rexroad 1982), recurrent associations of isolated elements (Mapes & Rexroad 1986; Rexroad & Horowitz 1990) and bedding plane assemblages (Purnell 1993).

The largest variation is found within the P elements of this genus; from bipennate elements, with a short lateral process containing a single denticle or a long lateral process with several denticles, to distinctive tertiopedate elements. It is here proposed that these elements ought to be used to diagnose species, rather than the traditionally used conservative S elements.

The element notation of Purnell *et al.* (2000) is adopted here following their discussion of the prioniodinids and the evidence of the homology with the ozarkodinid Bauplan given by Purnell (1993).

Kladognathus complectens (Clarke, 1960)

Pl. 4 Figs. 9-14.

- ? p 1900 *Prioniodus peracutus* Hinde, p. 343, pl. 10, fig. 22 [?M element].
1941a *Ligonodina tenuis* Branson & Mehl, p. 170, pl. 5, figs. 13, 14 [S₁₋₂ element].
1941a *Ligonodina* sp. Branson & Mehl, p. 171, pl. 5, fig. 11 [P₂ element].
1941a *Lonchodina* sp. Branson & Mehl, p. 171, pl. 5, figs. 10, 12 [P₂ element].

- 1941a *Prioniodus scitulus* Branson & Mehl, p. 173, pl. 5, figs. 5, 6 [M element].
- 1941b *Ligonodina levis* Branson & Mehl, p. 185, pl. 6, figs. 10 [S₃₋₄ element].
- p 1949 *Ligonodina* sp. Youngquist & Miller, p. 620, pl. 101, figs. 11 (only) [S₁₋₂ element].
- 1949 *Lonchodina?* spp. Youngquist & Miller, p. 620, pl. 101, figs. 7, 8 [P₂ element].
- 1953 *Prioniodus ligo* Hass, p. 87, pl. 16, figs. 1-3 [M element].
- 1956 *Lonchodina* sp. A Elias, p. 122, pl. 5, fig. 1 [P₁ element].
- 1956 *Metalonchodina* sp. B Elias, p. 124, pl. 5, fig. 2 [P₁ element].
- 1956 *Metalonchodina?* sp. Elias, p. 124, pl. 5, fig. 3 [P₁ element].
- ? 1957 *Hibbardella* n. sp. Rexroad, p. 31, pl. 1, fig. 19 [S₀ element].
- 1957 *Ligonodina hamata* Rexroad, p. 32, pl. 1, fig. 24, 25 [S₁₋₂ element].
- 1957 *Ligonodina obunca* Rexroad, p. 32, pl. 1, fig. 22, 23 [S₃₋₄ element].
- 1957 *Neoprioniodus erectus* Rexroad, p. 34, pl. 2, figs. 23, 25 [M element].
- 1957 *Neoprioniodus scitulus* (Branson & Mehl). Rexroad, p. 35, pl. 2, figs. 22, 26 [M element].
- 1957 Genus indeterminate Rexroad, p. 42, pl. 4, figs. 19-22 [P₁ element].
- 1958 *Hibbardella milleri* Rexroad, p. 18, pl. 2, figs. 13, 14(?), 15, 16(?) [S₀ element].
- 1958 *Ligonodina obunca* Rexroad. Rexroad, p. 21, pl. 3, fig. 7, 8 [S₃₋₄ element].
- 1958 *Neoprioniodus scitulus* (Branson & Mehl). Rexroad, p. 23, pl. 5, figs. 10-14 [M element].
- 1958 Genus indeterminate Rexroad, p. 26, pl. 5, figs. 1, 2 [P₁ element].
- * 1960 *Ligonodina complectens* Clarke, p. 9, pl. 1, figs. 14, 15 [P₂ element].
- ? 1960 *Ligonodina craigi* Clarke, p. 10, pl. 2, figs. 1, 2 [S₁₋₂ element].
- 1960 *Ligonodina tulensis* (Pander). Clarke, p. 11, pl. 2, fig. 4 [S₁₋₂ element].
- ? 1960 *Ligonodina ultima* Clarke, p. 12, pl. 2, figs. 9, 11 [S₃₋₄ element].
- 1960 *Neoprioniodus peracutus* (Hinde). Clarke, p. 14, pl. 2, fig. 6 [M element].
- 1960 Genus Novum? Clarke, p. 15, pl. 2, fig. 8, 10, 12, 13; pl. 3, fig. 16 (incl. Gen. et sp. nov, p. 16) [P₁ element].
- 1961 *Neoprioniodus scitulus* (Hinde). Higgins, p. 14, pl. 11, fig. 1 [M element].
- 1961 *Ligonodina levis* Branson & Mehl. Rexroad & Burton, p. 1154, pl. 141, figs. 7, 8 [S₃₋₄ element].

- 1961 *Ligonodina* n. sp.? Rexroad. Rexroad & Burton, p. 1154, pl. 141, figs. 2-4 [S₁₋₂ element].
- 1961 *Neoprioniodus scitulus* (Branson & Mehl). Rexroad & Burton, p. 1155, pl. 140, figs. 15-17 [M element].
- 1963 *Magnilaterella robusta* Rexroad & Collinson, p. 14, pl. 2, figs. 4, 5, 9, text-figs. 3, 4 [P₁ element].
- 1963 *Magnilaterella* spp. Rexroad & Collinson, p. 17, pl. 2, figs. 1, 3, 10 [P₁ element]; 6 [P₂ element].
- 1963 New genus and new species Rexroad & Collinson, p. 21, pl. 2, figs. 2, 7, 8, text-fig. 5 [P₁ element].
- 1963 *Neoprioniodus tulensis* (Pander). Rexroad & Collinson, p. 18, pl. 2, figs. 17, 22, 23 [M element].
- 1964 *Magnilaterella robusta* Rexroad & Collinson. Rexroad & Furnish, p. 673, pl. 111, figs. 27-31 [P₁ element].
- 1964 *Neoprioniodus peracutus* (Hinde). Rexroad & Furnish, p. 674, pl. 111, fig. 25 [M element].
- 1964 *Neoprioniodus scitulus* (Branson & Mehl). Rexroad & Furnish, p. 674, pl. 111, figs. 36, 37 [M element].
- 1965 *Neoprioniodus scitulus* (Branson & Mehl). Rexroad & Nicoll, p. 23, pl. 2, figs. 21, 22 [M element].
- ? 1967 *Ligonodina levis* Branson & Mehl. Globensky, p. 442, pl. 56, fig. 16 [S₃₋₄ element].
- 1967 *Neoprioniodus peracutus* (Hinde). Globensky, p. 433 pl. 55, figs. 18, 25 [M element].
- 1967 *Neoprioniodus scitulus* (Branson & Mehl). Globensky, p. 443, pl. 55, figs. 22, 26 [M element].
- ? 1967 *Neoprioniodus* sp. Globensky, p. 445, pl. 55, fig. 21 [M element].
- 1969 *Kladognathus clarensis* Collinson and Druce. Rhodes *et al.*, p. 131, pl. 23, figs. 1, 2 [P₂ element].
- 1969 *Hibbardella (Hibbardella) milleri* Rexroad. Rhodes *et al.*, p. 113, pl. 25, figs. 23-25 [S₀ element].
- 1969 *Ligonodina levis* Branson & Mehl. Rhodes *et al.*, p. 134, pl. 26, fig. 15 [S₁₋₂ element]; pl. 26, figs. 17-19 [S₃₋₄ element].
- 1969 *Ligonodina magnilaterina* Rhodes *et al.*, p. 135, pl. 26, figs. 8-11 [?S₁₋₂ element].
- 1969 *Ligonodina tenuis* Branson & Mehl. Rhodes *et al.*, p. 138, pl. 31, figs. 4, 16 [S₁₋₂ element].

- ? 1969 *Magnilaterella clarkei* Rhodes *et al.*, p. 146, pl. 23, figs. 11-13 [P₁ element].
- 1969 *Magnilaterella complectens* (Clarke). Rhodes *et al.*, p. 145, pl. 23, figs. 14-17 [P₂ element].
- 1969 *Magnilaterella contraria* Rhodes *et al.*, p. 147, pl. 23, figs. 8, 18? [P₁ element].
- ? 1969 *Magnilaterella robusta* Rexroad & Collinson. Rhodes *et al.*, p. 148, pl. 31, figs. 25, 26 [P₁ element].
- 1969 *Magnilaterella?* sp. Rhodes *et al.*, p. 149, pl. 23, fig. 7 [P₁ element].
- 1969 *Neoprioniodus scitulus* (Branson & Mehl). Rhodes *et al.*, p. 162, pl. 22, figs. 9, 10, 12 [M element].
- 1973 *Ligonodina levis* Branson & Mehl. Austin & Aldridge, pl. , fig. 14 [S₃₋₄ element].
- ? 1973 *Neoprioniodus scitulus* (Branson & Mehl). Austin & Aldridge, pl. 2, fig. 3 [M element].
- 1974 *Magnilaterella clarki* Rhodes Austin & Druce. Austin & Husri, pl. 15, fig. 3 [P₁ element].
- 1974 *Magnilaterella robusta* Rexroad & Collinson. Austin & Husri, pl. 15, fig. 7 [P₁ element].
- 1974 *Neoprioniodus scitulus* (Branson & Mehl). Austin & Husri, pl. 12, figs. 12, 13, 17 [M element].
- 1974 *Ligonodina levis* Branson & Mehl. Varker & Austin, pl. 6, fig. 12 [S₃₋₄ element].
- 1974 *Magnilaterella complectens* (Clarke). Varker & Austin, pl. 6, fig. 14 [P₂ element].
- 1975 *Ligonodina levis* Branson & Mehl. Higgins, p. 57 [S₃₋₄ element].
- 1975 *Ligonodina tenuis* Branson & Mehl. Higgins, p. 59 [S₁₋₂ element].
- 1975 *Magnilaterella complectens* (Clarke). Higgins, p. 61, pl. 1, figs. 10, 11 [P₂ element].
- 1975 *Neoprioniodus peracutus* (Hinde). Higgins, p. 67, pl. 3, figs. 1-4, 6 [M element].
- p 1975 *Ligonodina levis* Branson & Mehl. Nicoll & Rexroad, pl. 6, fig. 14 (only) [S₃₋₄ element].
- 1975 *Magnilaterella* spp. Nicoll & Rexroad, pl. 6, figs. 10-13, 16 [P₁ element].
- 1976 *Hibbardella milleri* Rexroad. Norby, p. 184, pl. 20, figs. 16-20 [S₀ element].

- 1976 *Magnilaterella robusta* Rexroad & Collinson, p. 192, pl. 20, figs. 1, 2 6 [P₁ element].
- 1976 *Neoprioniodus peracutus* (Hinde). Norby, p. 193, pl. 20, figs. 3-5, 10-13 [M element].
- 1981 *Ligonodina fragilis* Hass. Metcalfe, pl. 15, figs. 9a-c [P₁ element].
- ? 1981 *Ligonodina levis* Branson & Mehl. Metcalfe, pl. 15, fig. 10 [S₃₋₄ element]:
- 1981 *Neoprioniodus scitulus* (Branson & Mehl). Metcalfe, pl. 18, fig. 4 [M element].
- 1981 *Neoprioniodus peracutus* (Hinde). Metcalfe, pl. 18, fig. 10 [M element].
- 1981 *Kladognathus tenuis* (Branson & Mehl). Rexroad, p. 13, pl. 2, figs. 19, 20, 24-26 [S₁₋₂ element]; fig. 21 [S₃₋₄ element].
- 1981 *Kladognathus* sp. Rexroad, p. 13, pl. 2, figs. 16, 17, 18 [S_{b2} element].
- 1981 *Kladognathus* spp. Rexroad, pl. 2, pl. 2, figs. 27-29 [P₁ element]; figs. 30-32 [M element]; pl. 2, figs. 22, 23 [S₀ element].
- ?p 1985 *Kladognathus* spp. Rexroad & Merrill, pl. 1, figs. 16, 36 (only) [P₁ element]; pl. 1, fig. 21 [M element]; pl. 1, figs. 11, 20, 22?, 31? [S₁₋₂ element].
- p 1986 *Kladognathus* n. sp. Mapes & Rexroad, p. 117, pl. 2, figs. 8?, 15 [P₂ element]; figs. 1, 3 [M element]; figs. 2, 4, 14 [S₀ element]; figs. 10-13 [S₁₋₂ element].
- p 1990 ?*Kladognathus complectens* (Clarke). Rexroad & Horowitz, p. 506, pl. 3, figs. 1-4 [P₁ element]; figs. 6, 7 [P₂ element]; fig. 5 [S₀ element].
- 1990 *Kladognathus tenuis* (Branson & Mehl). Rexroad & Horowitz, p. 505, pl. 3, fig. 25-27 [S_{b2} element]; figs. 28-30 [M element]; figs. 21-24 [S₀ element]; figs. 16-18 [S₁₋₂ element]; figs. 19, 20 [S₃₋₄ element].
- 1992 *Kladognathus tenuis* (Branson & Mehl). Purnell, p. 39, pl. 8, figs. 2a, 2b [S₀ element]; fig. 12 [P₁ element].

Holotype. British Geological Survey PS882; Clarke, 1960, pl. 1, figs. 14, 15. From the Lower Limestone, of Law, Dalry, Scotland.

Diagnosis. See Rexroad (1981, 13).

Description. *P₁ element* See Rhodes *et al.* (1969, p. 147 and p. 148); *P₂ element* See Rhodes *et al.*, (1969, p. 145); *M element* See Rhodes *et al.* (1969, p. 161 and p. 162); *S₀ element* See Rhodes *et al.* (1969, p. 113); *S₁₋₂ element* See Branson & Mehl (1941a, p.

170) and Rexroad (1957, p. 32, under *L. hamata*); S_{3-4} element See Rexroad (1957, p. 32, under *L. obunca*) and Rhodes *et al.* (1969, p. 134).

Remarks. The P_1 and P_2 elements are broadly considered to be similar, except for the length of the lateral process and number of denticles on its surface. The P_2 element has a short lateral process with a single large denticle, commonly found as isolated fragments and only once has it been figured as a complete element (Rexroad & Collinson, 1963, pl. 2, fig. 6). The P_1 element is known from examples of the lateral process which are common and from complete elements which are more rare, but have been figured regularly in the published record (e.g. Rexroad & Collinson, 1963; Rhodes *et al.* 1969; Rexroad & Horowitz, 1990)

Though not seen in the present study, teriopodate elements have been assigned to *Kladognathus* in the past. These elements, commonly assigned to the form taxonomic genus "*Lambdagnathus*", have been found in Britain (e.g. Higgins 1961, Rhodes *et al.* 1969), but are more common in North American faunas (e.g. Rexroad, 1958; Rexroad & Horowitz, 1990). Where present, it is thought that these elements filled one of the P locations in the conodont apparatus; in such faunas, the *Kladognathus* species ought to take the name of this element.

Material studied. P_1 element 20; P_2 element 23; M element 112; S_0 element 15; S_{1-2} element 18; S_{3-4} element 55.

5. CONCLUSIONS

Aim 1 - To review and update mid-Carboniferous multielement conodont taxonomy

The Asbian - Arnsbergian faunas of the Northumberland Trough generally have a low abundance. As a result, few non-P₁ elements have been found, therefore reconstructing multielement species has been inhibited. However, the systematic palaeontology chapter of this research is a useful work in updating British mid-Carboniferous conodont taxonomy. The synonymy lists contain clear assigned lists stating the opinion of the author as to element positions in the modern apparatus reconstructions which will be useful to future research.

Aim 2 - To test the biostratigraphic potential of the conodont faunas

Conodont faunas have proved to be useful in defining biostratigraphic boundaries. Five biozones have been defined from the mid-Asbian to late Arnsbergian. The greatest degree of biostratigraphic control is achieved during the Brigantian where three zonal boundaries can be defined.

Aim 3 - To compare palaeoecological models for mid-Carboniferous conodont faunas

The shelf faunas of the Northumberland Trough occupy clear palaeoecological niches. Four biofacies have been defined including three nektobenthonic associations related to different water depths and a pelagic association. The established biofacies for mid-Carboniferous conodonts compare favourably with those set up for the Northumberland Trough.

Aim 4 - To critically compare the Exxon sequence stratigraphic model against spacial and temporal variation within 'Yoredale' type sequences

Careful scrutiny has shown that Yoredale sequences fit the Exxon model for shelf facies excellently; the complex spacial and temporal variation within Yoredale sequences of the Northumberland Trough shows all systems tracts and key surfaces.

Aim 5 - To produce a sea-level curve for the Asbian - Arnsbergian of the Northumberland Trough

Three orders of eustatic sea-level change have influenced the deposition of Yoredale strata in the Northumberland Trough. High-frequency sea-level cycles induced the deposition of individual Yoredale sequences. Medium-frequency sea-level cycles induced the deposition of sequence sets, consisting of an initial thick sequence followed by three to six thin sequences. Low-frequency sea-level cycles influenced the long-term deposition of mega-sequences. The interference of these three frequencies of sea-level cycle affected deposition: where this was constructive, particularly thick sequences were deposited; conversely, when this was destructive, thin sequences were deposited.

Aim 6 - Ultimately, to consider the influence of sea level change as a fundamental control

It has been shown that sea-level change had a huge influence on conodont species distribution. Water depth was the fundamental control on the majority of species in this study. Therefore, sea-level change influenced the onshore - offshore distribution of the nektobenthonic fauna. Whatsmore the change in biofacies through time can be closely linked to sequence stratigraphic events. It is therefore not surprising that the first appearance of conodont species was also controlled by sea-level change. Furthermore each of the biozones can also be directly related to sequence stratigraphic events.

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Plate 1

(x80 unless otherwise stated)

Figs. 1-7 *Syncladognathus scitulus* (Hinde, 1900)

Fig. 1. Rostral view of P₁ element; sample D787.

Fig. 2. Rostral view of P₂ element; sample D789.

Fig. 3. Adaxial view of M element; sample D796.

Fig. 4. Caudal view of S₀ element; sample BGS/Mil(c)602.

Fig. 5. Adaxial view of S_{1,2} element; sample N280.

Fig. 6. Adaxial view of S₃ element; sample BGS/Mil(c)611.

Fig. 7. Adaxial view of S₄ element; sample BGS/Mil(c)601, (x60).

Fig. 8 *Mestognathus beckmanni* Bischoff, 1957

Fig. 8. Apical view of P₁ element; sample N547, (x60).

Fig. 9 *Adetognathus unicornis* (Rexroad & Burton, 1961)

Fig. 9. Apical view of P₁ element; sample BGS/Mil(c)587, (x60).

Plate 2

(x60 unless otherwise stated)

Figs. 1-4 *Cavusgnathus naviculus* (Hinde, 1900)

Fig. 1. Apical view of P₁ element; sample D762.

Fig. 2. Rostral view of P₂ element; sample N284.

Fig. 3. Adaxial view of M element; sample D764.

Fig. 4. Adaxial view of S₄ element; sample D767.

Figs. 5-12 *Gnathodus girtyi* Hass, 1953

Fig. 5. Apical view of P₁ element; sample N281.

Fig. 6. Apical view of P₁ element; sample D762.

Fig. 7. Apical view of P₁ element; sample D776.

Fig. 8. Apical view of P₁ element; sample BGS/Mil(c)600.

Fig. 9. Rostral view of P₂ element; sample D796.

Fig. 10. Adaxial view of M element; sample N916, (x80).

Fig. 11. Adaxial view of S₃ element; sample N916, (x80)

Fig. 12. Adaxial view of S₄ element; sample D762, (x80)

Plate 3

(x80 unless otherwise stated)

Figs. 1-3 *Gnathodus bilineatus* (Roundy, 1926)

Fig. 1. Apical view of P₁ element; sample BGS/Mil(c)606.

Fig. 2. Apical view of P₁ element; sample BGS/Mil(c)606.

Fig. 3. Apical view of P₁ element; sample BGS/Mil(c)606, (x60).

Figs. 4-8 *Lochriea commutata* (Branson & Mehl, 1941c)

Fig. 4. Apical view of P₁ element; sample D762.

Fig. 5. Apical view of P₁ element; sample D762.

Fig. 6. Rostral view of P₂ element; sample N918.

Fig. 7. Adaxial view of M element; sample D764.

Fig. 8. Adaxial view of S₄ element; sample N918.

Figs. 9-14 *Lochriea mononodosa* (Rhodes *et al.*, 1969)

Fig. 9. Apical view of P₁ element; sample BGS/Mil(c)637.

Fig. 10. As above, close up of ornamentation on rostral platform, (x160).

Fig. 11. Apical view of P₁ element; sample BGS/Mil(c)603.

Fig. 12. As above, close up of ornamentation on rostral platform, (x160).

Fig. 13. Apical view of P₁ element; sample D787.

Fig. 14. As above, close up of ornamentation on rostral platform, (x160).

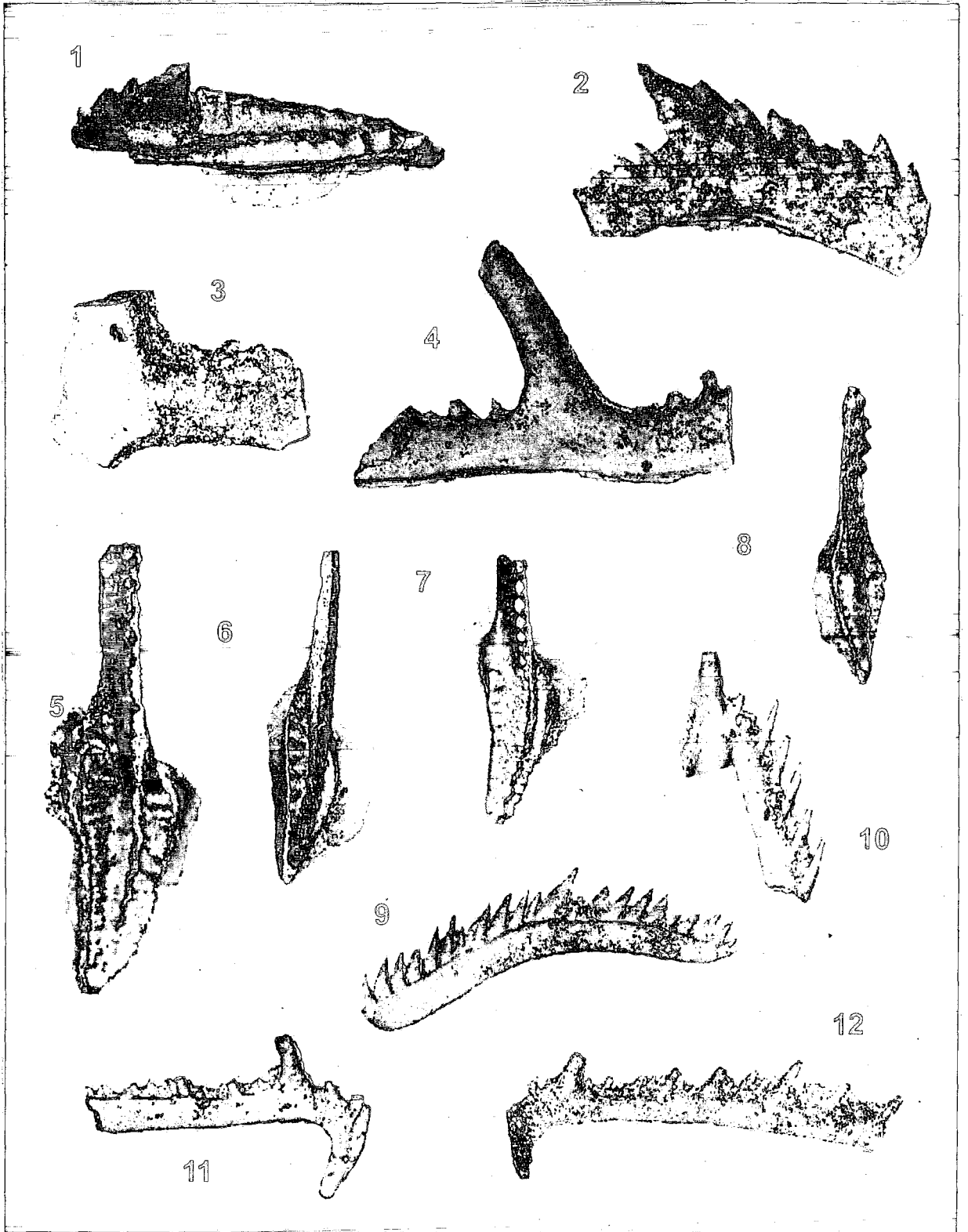


Plate 4

(x60 unless otherwise stated)

Figs. 1-5 *Lochriea nodosa* (Bischoff, 1957)

Fig. 1. Apical view of P₁ element; sample D784.

Fig. 2. Apical view of P₁ element; sample D797, (x80).

Fig. 3. Apical view of P₁ element; sample D797, (x80).

Fig. 4. Apical view of P₁ element; sample BGS/Mil(c)587.

Fig. 5. Apical view of P₁ element; sample BGS/Mil(c)601.

Figs. 6-8 *Idioproniodus healdi* (Roundy, 1926)

Fig. 6. Rostral view of P₁ element; sample N915.

Fig. 7. Caudal view of S₀ element; sample N1037, (x80).

Fig. 8. Adaxial view of S₄ element; sample BGS/Mil(c)607.

Figs. 9-14 *Kladognathus complectens* (Clarke, 1960)

Fig. 9. Rostral view of P₁ element; sample D789.

Fig. 10. Rostral view of P₂ element; sample D797.

Fig. 11. Adaxial view of M element; sample N914.

Fig. 12. Caudal view of S₀ element; sample D775, (x80).

Fig. 13. Adaxial view of S₃₋₄ element; sample D791, (x80).

Fig. 14. Adaxial view of S₁₋₂ element; sample D784, (x80).

Plate 3

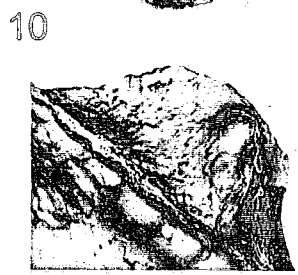
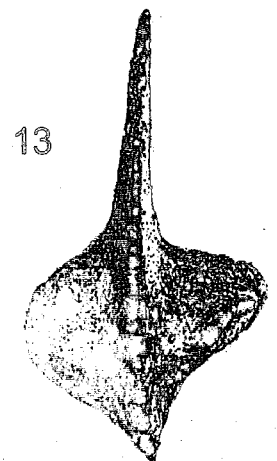
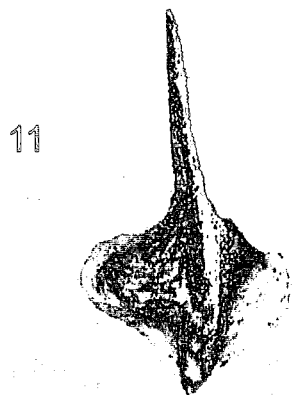
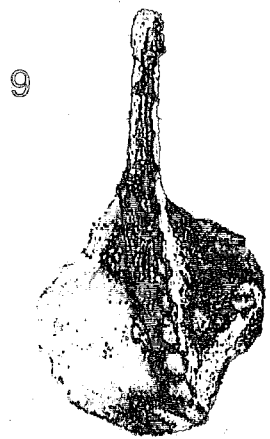
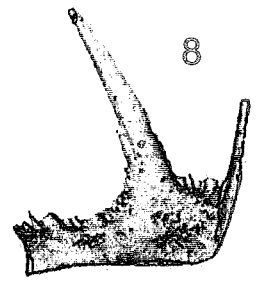
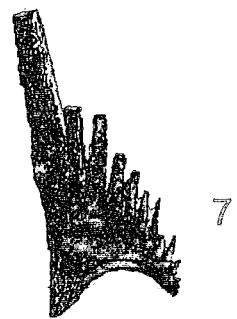
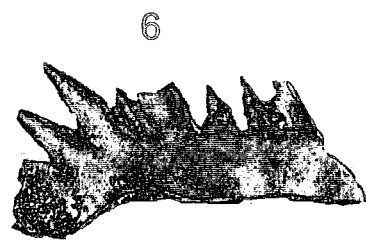
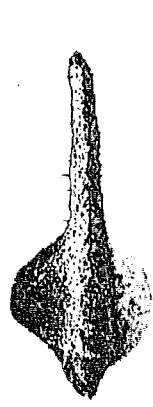
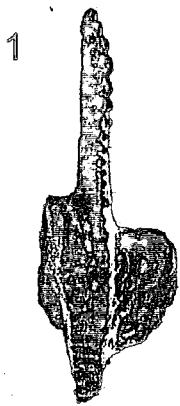
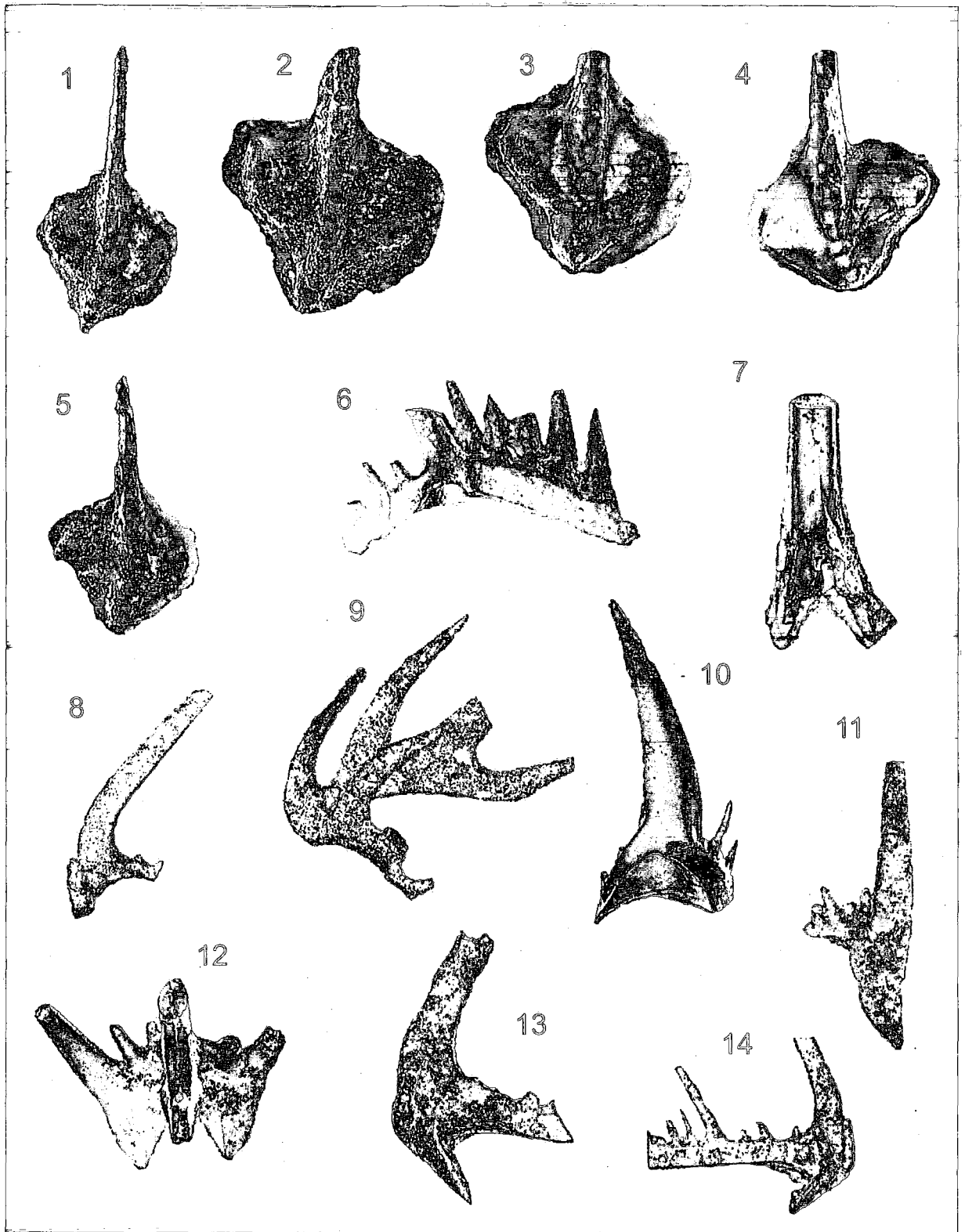


Plate 4



Appendix II

Localities

These can be divided into three main areas:

Locality	Description	NGR	Ref.
1. Longhoughton			
Longhoughton (Howick)	Foreshore section	NU258178 - NU266143	Tucker, 1995
Beadnell	Foreshore section, on south side of Beadnell Bay	NS225227	Armstrong & Strens, 1987; Armstrong & Purnell, 1987
2. Hadrian's Wall			
Throckley borehole	BGS Record No. NZ16NW28	NZ14556761	Richardson, 1965; 66; Mills & Holliday, 1998
Mootlaw	Large active limestone quarry	NZ0276	
Allendale		NY800650	Dunham, 1990
Frosterly	Main Quarry, Teesdale		Dunham, 1990
Haltwistle Burn	Stream section	NY710658	Jones, 1995; Johnson, 1997
Corbridge	Disused quarry	NY995656	
3. Bewcastle			
River Irthing	Stream section	NY686750	Day, 1970
Tippalt Burn	Stream section	NY6868	Day, 1970
Liddel Water	Stream section	NY4377	Day, 1970

Appendix III

Conodont collections

Sample Numbers	Repository	Collected by	Processed by
N50-N1209	Dept. of Geological Sciences University of Durham	Howard Armstrong	Howard Armstrong
D16-D25	Dept. of Geological Sciences University of Durham	Howard Armstrong	Howard Armstrong
D761-D777	Dept. of Geological Sciences University of Durham	Alistair Bowden	Alistair Bowden
D778-D797	Dept. of Geological Sciences University of Durham	Mark Dean	Alistair Bowden
BGS Mil(c)	British Geological Survey	-	Reynolds

Appendix IV

Constrained seriation technique (after Purnell, 1989)

In constrained seriation, the order of the rows of the matrix are fixed while the columns are "shuffled" to concentrate presences along the matrix diagonal axis. Alternatively, the column order can be fixed and the rows re-arranged. Brower and Burroughs (1982) discuss constrained seriation in more detail.

		Columns				
		1	2	3	4	5
Rows	1					
	2					
	3					
	4					
	5					
	6					
	7					
	8					
	9					
		2.6	5.6	3.6	1.5	8

Constrained seriation of hypothetical data set. Row orders have been fixed: columns have been re-ordered according to their means, thereby concentrating presences along the matrix diagonal.

		Columns				
		4	1	3	2	5
Rows	1					
	2					
	3					
	4					
	5					
	6					
	7					
	8					
	9					
		1.5	2.6	3.6	5.6	8

1. Calculate column means (sum of row positions of presence / no. of presences in column)

2. Re-order columns according to means

Constrained seriation has only rarely been applied in a palaeoecological context. Samples of species can be arranged along a known gradient represented by the fixed axis of the matrix; used in this way the technique represents a form of direct gradient analysis. In the present study, the fixed axis is the rows represent the relative vertical position of samples in the Great Limestone.

Appendix V

Processing procedure

Initially samples were crushed to approximately 2-3cm pieces. A 1500-2000g sample was then covered by 10% warm acetic acid in a 10l plastic bucket. Digestion was allowed to continue for 1 week. After this time the spent acid was poured off through a sieve stack comprising a 1mm and a 60 μ m sieve and the fine fraction collected and dried. The coarse fraction was returned to the bucket and fresh warm acetic acid was added. This was continued for 4 weeks, after which time the undigested rock was dried and weighed to enable calculation of digested mass.

All dried fine residues were subjected to heavy liquid density separation using bromoform (tribromomethane; S.G. 2.89). Heavy residues were then run slowly through a magnetic separator, conodont elements were collected as non-magnetic particles. The magnetic fraction was run through a second time to ensure that it contained no conodonts.

Conodont elements were then picked using standard grid-tray and wet paint brush methods.

Stone (1987) gives a useful overview to typical processing techniques.



Plate 1

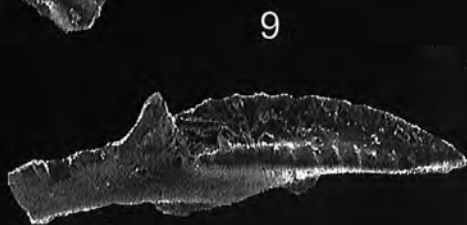
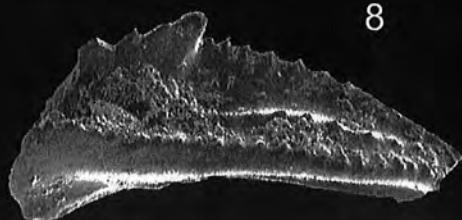
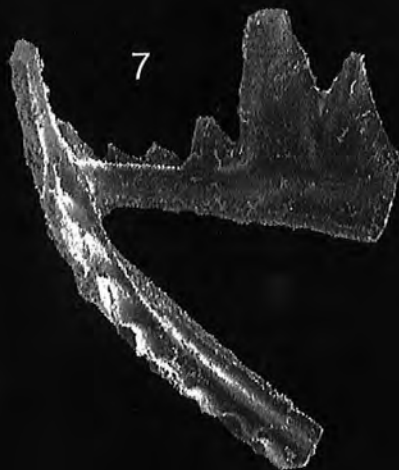
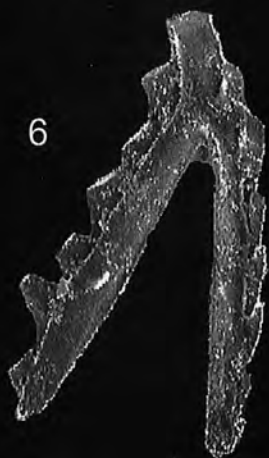
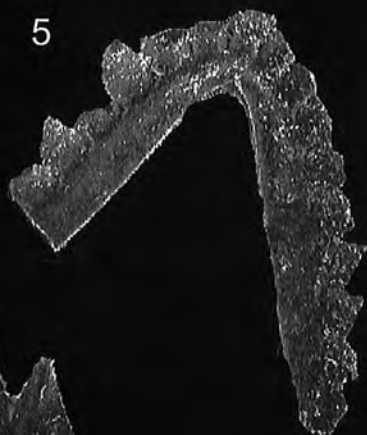
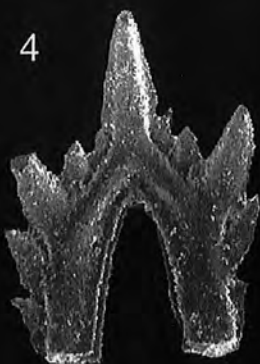
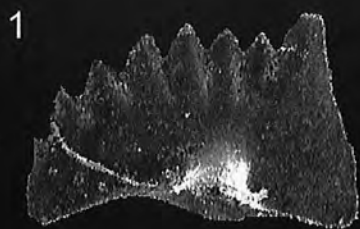


Plate 2

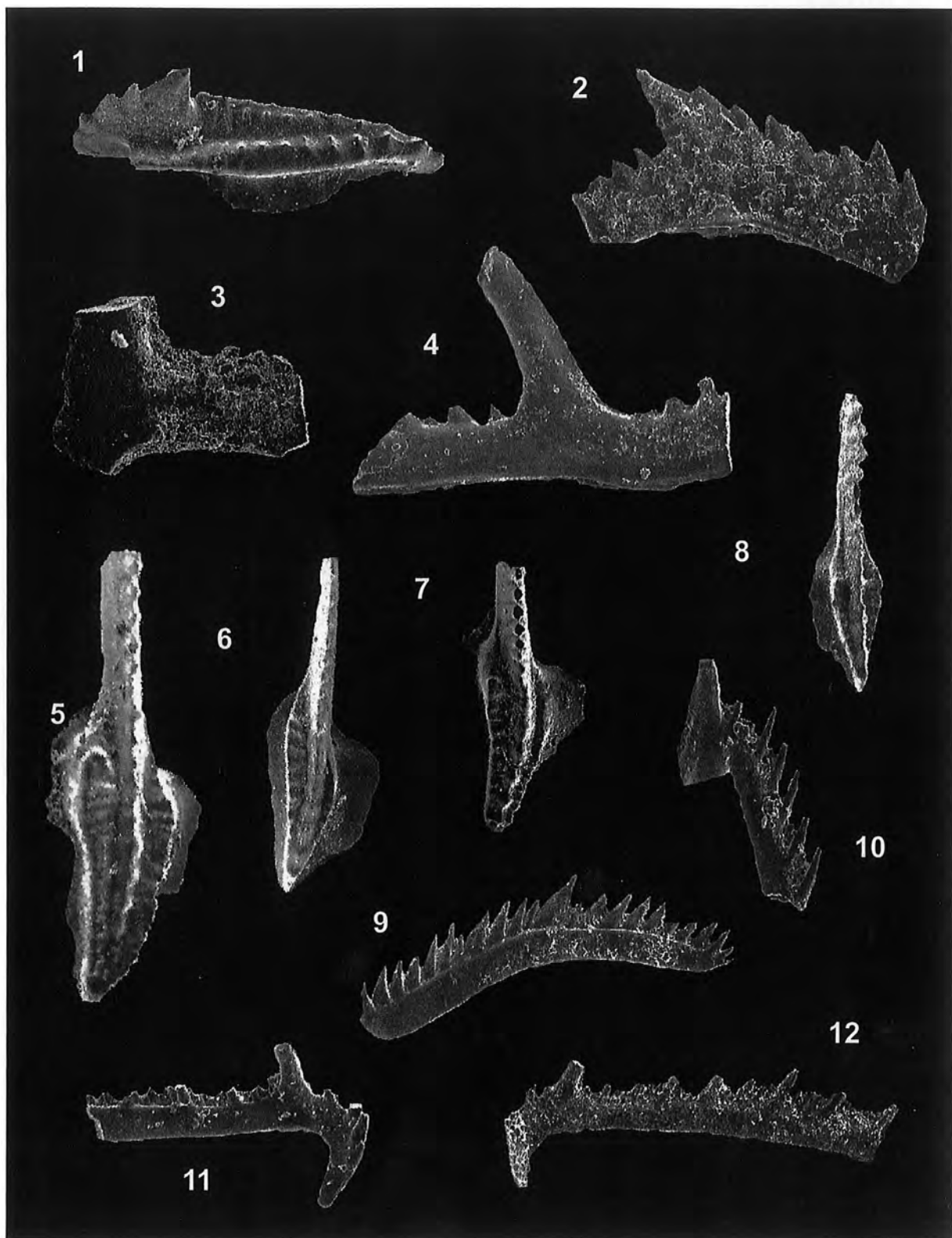


Plate 3

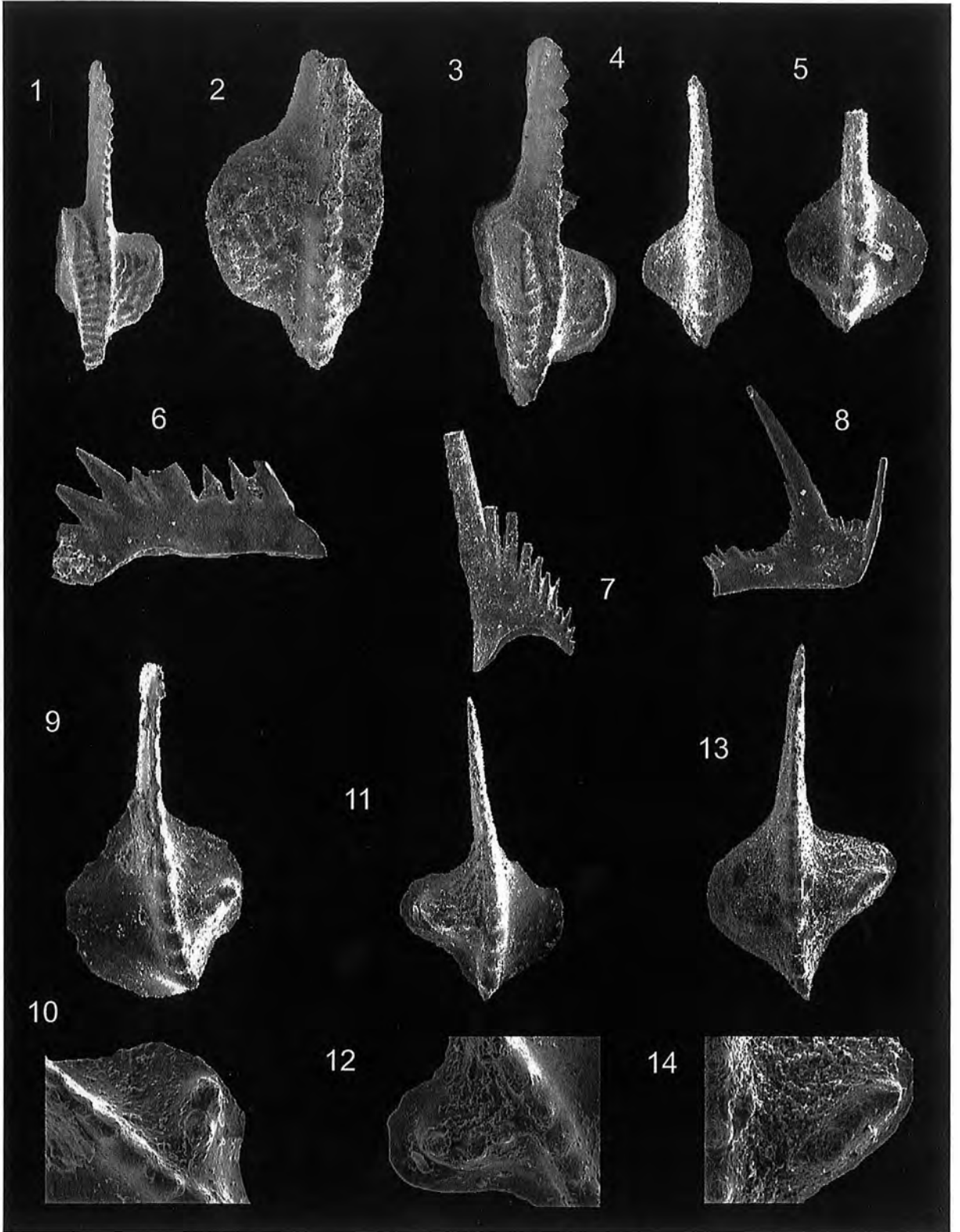


Plate 4

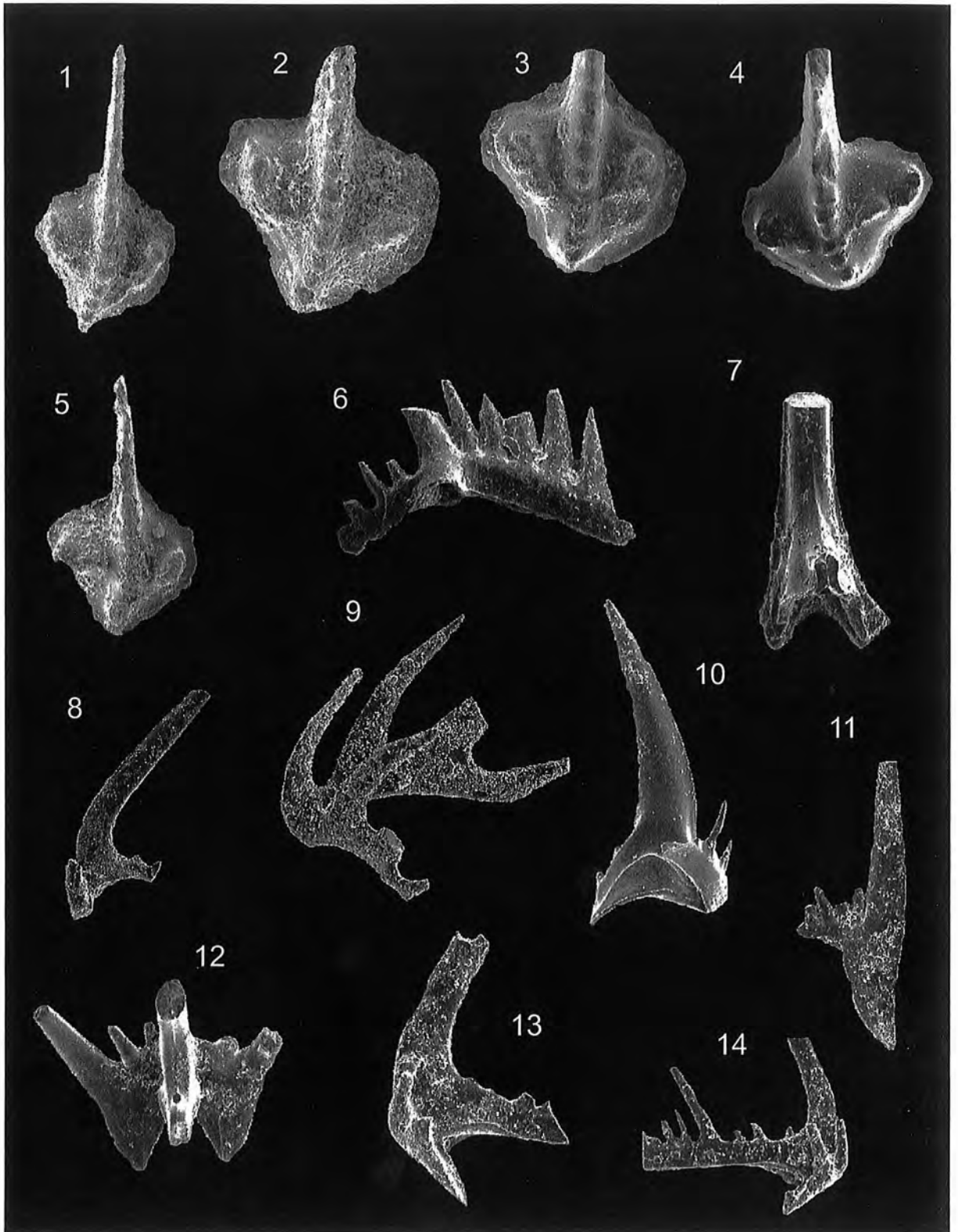


Fig. 2.26 Graphic log and sequence stratigraphic interpretation of the Throckley borehole and Longhoughton succession.

