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MULTIELEMENT CONODONT FAUNAS FROM THE PROPOSED MID-CARBONIFEROUS BOUNDARY STRATOTYPE LOCALITY AT STONEHEAD BECK, COWLING, NORTH YORKSHIRE, ENGLAND[1]

W. John VARKER[2]

(1 figure and 4 plates)

ABSTRACT. A multielement conodont taxonomy has been applied to rich faunas obtained by re-sampling the two most productive horizons at Stonehead Beck and described in Riley *et al.* 1987 and Varker *et al.* 1990. The 7635 elements obtained from sample MPA 26024 are dominated by multielement species *Gnathodus bilineatus, G. postbilineatus, Lochriea commutata, L. nodosa* and *L. mononodosa* but also include less well represented *Kladognathus complectens, K. tenuis* and *Idioprioniodus healdi.* More than 60 fused conodont clusters were also retrieved from this sample, each being considered to represent the remains of a single apparatus. Unlike the fauna of sample MPA 26024, which was from a calcareous concretion, that from sample MPA 26038 shows very strong non-platform under-representation due to selective loss of the fragile elements resulting from fracturing during diagenetic compaction of the sediment. This fauna consisted almost entirely of platforms of declinognathodids and associated forms. A multielement range chart has been compiled by applying multielement taxonomy to the range charts already published in Riley *et al.* (op. cit.) and Varker *et al.* (op.cit).

KEY-WORDS: Conodont, multielement, Mid-Carboniferous, boundary, stratotype, Stonehead, England.

RESUME. Faunes de conodontes à multiéléments dans le stratotype proposé pour la limite mi-Carbonifère à Stonehead Beck, Cowling, nord Yorkshire, Angleterre. Une taxonomie de conodontes à multiéléments a été appliquée à des faunes riches obtenues par le rééchantillonnage des deux horizons les plus productifs à Stonehead Beck et décrite dans Riley *et al.* 1987 et Varker *et al.,* 1990. Les 7635 éléments obtenus de l'échantillon MPA 26024 sont dominés par les espèces à multiéléments *Gnathodus bilineatus, G. postbilineatus, Lochriea commutata, L. nodosa* et *L. mononodosa* mais comprennent également les espèces moins bien représentées *Kladognathus complectens, K. tenuis* et *Idioprioniodus healdi.* Plus de 60 assemblages de conodontes fusionnés ont été également isolés de cet échantillon, chacun étant considéré comme représentant les restes d'un seul appareil. Au contraire de la faune de l'échantillon MPA 26024, qui a été isolée d'une concrétion calcaire, celle de l'échantillon MPA 26038, montre une sous-représentation très importante des conodontes autres que ceux en plateforme, due à une perte sélective des éléments fragiles résultant d'une fracturation pendant la compaction diagénétique du sédiment. Cette faune consistait presque entièrement en plateformes de declinognathodids et de formes associées. Un tableau de distribution stratigraphique de multiéléments a été compilé en appliquant la taxonomie à multiéléments au tableau de distribution stratigraphique déjà publié par Riley *et al.* (op. cit.).

MOTS-CLE: Conodontes, multiéléments, Carbonifère moyen, limite, stratotype, Stonehead, Angleterre.

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[1] *Manuscript received and accepted September 1993.*

[2] *Department of Earth Sciences, The University, Leeds LS 2 9 JT, England.*

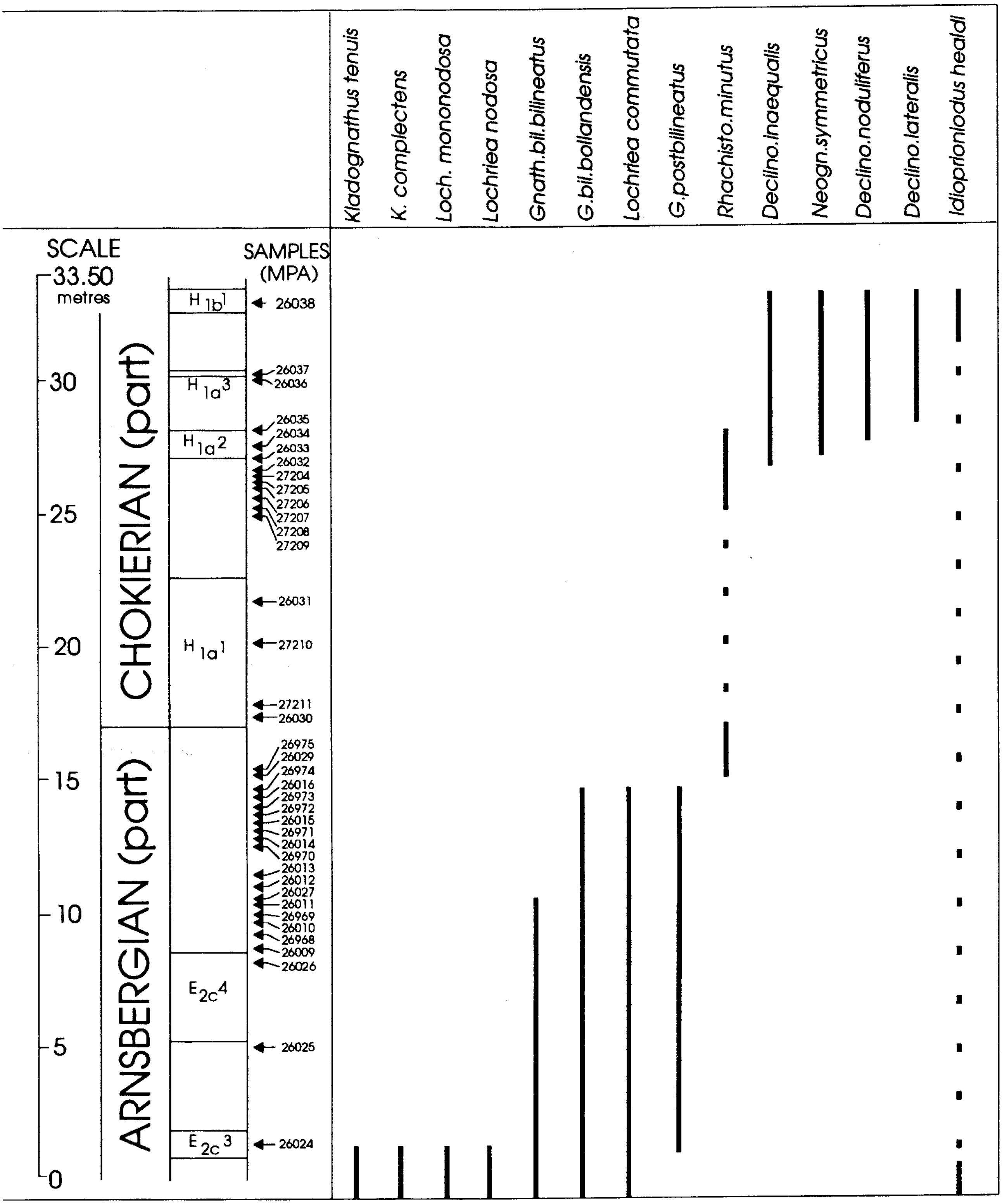

Fig. 1.- A multielement conodont range chart for Stonehead Beck. This chart has been compiled by applying a multielement conodont taxonomy to the single-element range charts already published in Riley *et al.* 1987 and Varker *et al.* 1990 and it therefore includes all multielement species occurring at this locality.

1. INTRODUCTION

Stonehead Beck, North Yorkshire, England, is one of several of localities which have been proposed as the stratotype for the new Mid-Carboniferous Boundary (the others are in China, the Ukraine, Uzbekistan and the U.S.A.), which is defined and recognised by the entrance of the conodont *Declinognathodus noduliferus* (Lane and Manger, 1985). The Stonehead Beck conodont faunas have already been described by Riley *et al.*(1987) and Varker *et al.*(1990). These authors adopted a discrete or single element conodont taxonomy because a high proportion of the samples from the middle part of the sequence were either barren or had unacceptably low conodont concentrations (see Riley *et al.* op.cit., p.164) and there was also clear evidence that the faunas recovered did not completely represent the original apparatuses. In common with many conodont faunas, ranging in age from Ordovician to Triassic, platform elements were strongly over-represented (or to be more correct, since it appears to have been the ramiform elements which have been selectively removed rather than platforms which have been added, it was the non-platform elements which were strongly under-represented). Indirect support for this stance has been provided by Merrill *et al.* (1990,p.405) who concluded that whilst being less important than the Pa elements for specific determinations, the S complex of elements is nevertheless useful for multielement generic determinations and may also be an aid in determining which genera are confamilial.

Non-platform element under-representation is a common phenomenon which has been noted by a number of authors. Higgins and Bouckaert (1968, p.16) considered post-depositional breakage resulting from compaction of sediment to be the main factor in controlling conodont abundance in the Namurian and drew attention to a marked contrast between faunas from hard calcareous concretions (traditionally called bullions in the Namurian of the UK) and those of shales and mudstones. Merrill and Powell (1980) suggested that the progressive reduction in the proportion of ramiforms up the geological column is the single-most compelling argument for a biological cause. However they also pointed out that the relationship between rock-type and platform over-representation is so strong that in some circumstances the environmental implications of the rock type were probably the only factors involved (op.cit.p.1061).

In the case of the Stonehead Beck faunas a strong relationship does exist between non-platform under-representation and lithology, and a comparison between the conodont fauna recovered from mudstone and that from a calcareous concretion contained within the same mudstone suggests that differential compaction is the critical factor, rather than any environmental factors *per se*. The Stonehead Beck sequence consists predominantly of shales and mudstones (Riley *et al.* op.cit p.161) and fracturing of the more fragile conodont elements would have occurred during the burial compaction of this muddy sediment. According to Meade (1966), freshly deposited mud consists of about 80% water and 20% solid grains, and where compaction reduces pore space toward zero, the mud interval is reduced toward one fifth of its original thickness. The extent to which this compaction process takes place is clearly related to depth of burial, since it is predominantly a pressure-controlled mechanical process, accompanied by fluid expulsion. There is consequently a considerable potential for damage to conodont elements which accumulated in muddy sediment, even where burial depths have not been great and where compaction has been no more than the often quoted figure of 50% (e.g. Twenhofel, 1950, p.279).

2. SAMPLES AND LABORATORY TECHNIQUES

Diagenetic fracturing of the Stonehead Beck conodonts was enhanced during laboratory processing, which for the majority of the samples had been prolonged and arduous, and involved frequent handling of samples and residues. All of the samples described in Riley *et al.* (op.cit.) and Varker *et al.* (op.cit.) were argillaceous, most of them were non-calcareous and many of them were ferruginous, and as a result total disintegration of the rock was difficult; in some cases impossible. Most of the samples also gave rise to a very large residue (up to two litres in volume), necessitating further processing (electro-magnetic separation plus in some cases heavy liquid separation) to concentrate the conodont elements, thus providing further opportunities for breakage to occur. It may be significant that the two samples which gave the highest yield of conodonts in Riley *et al.*(op.cit) were samples which disintegrated readily and totally.

The present work describes two large conodont faunas resulting from the re-sampling of the two most productive horizons of Riley *et al.* (op.cit.), which happened to be the lowest and highest samples recorded in the Stonehead Beck sequence.

2.1. SAMPLE MPA 26024

This sample was taken from the E_2c^3 *Nuculoceras nuculum* band, 15.6 metres below the Arnsbergian/Chokierian boundary and 25 metres below the position of the proposed Mid-Carboniferous Boundary. The conodont concentration was recorded in Riley *et al.* (op.cit.p.164) as 170 specimens per kilogram. The new sample MPA 26024 consisted of part of a large calcareous concretion (Riley et al. op.cit p.161) approximately 30 cms by 25 cms in cross section, which projected from the outcrop. It was of unknown length, although it is known to have exceeded 40 cms. The concretion consisted of fine-grained, dark, compact, argillaceous, ferruginous limestone, with a high organic content and an orange limonitic skin about one centimetre in thickness. The eight kilogram sample was split into eight approximately equal portions for processing. Digestion in 5% formic acid produced a vigorous initial reaction which rapidly subsided as a black insoluble surface film built up on each rock fragment, necessitating daily acid changes. At each washing the insoluble residue was removed with the absolute minimum of sieving, and retained. After total breakdown the bulk residue, which amounted to approximately one litre in volume, was washed and sieved with the greatest possible care, thus ensuring the minimum of damage to the conodonts. Most of the very soft, black residue passed through the sieve, leaving approximately 25 mls of highly concentrated residue for hand-picking. A total of 7635 conodonts was recovered, including well-preserved specimens of even the most fragile elements. The most distinctive and potentially the most useful feature of this fauna was however the presence of more than sixty fused conodont clusters.

Since this sample had been taken from a calcareous concretion, it would have suffered little compaction and it therefore contrasted strongly with the earlier (Riley *et al.*) mudstone sample from the same horizon. There had been far less selective loss of elements from the concretion sample during laboratory processing; the recovery rate had increased more than five-fold, giving an unexpectedly high concentration of conodonts of 954 per kgm.; there was a significant increase in the number of taxa recorded; and the proportion of the fauna which was specifically identifiable had increased. In Riley *et al.* (op.cit.) 48% of the total number of elements retrieved from sample MPA 26024 were specifically identifiable but the figure has increased to 61% in the current study. It therefore appears that much of the damage and subsequent loss of fragmental specimens from the Riley *et al.* (op.cit.) and Varker *et al.*(op.cit.) faunas resulted from fracturing caused by sediment compaction. Consideration of the apparatuses indicates that the fauna from the concretion is probably as close to the original assemblage of elements as could be reasonably expected.

2.2. SAMPLE MPA 26038

The second fauna was from sample MPA 26038, which was the most productive horizon recorded by Riley *et al.* (op.cit.) at 300 specimens per kilogram. This sample was taken from the H_1b^1, *Homoceras beyrichianum* band, 16 metres above the Arnsbergian/Chokierian boundary and 6.6 metres above the horizon of the proposed Mid-Carboniferous Boundary. It consisted of 4 kgms of non-calcareous, soft, dark, friable shale, with a limonitic stain. Total and rapid breakdown was achieved using the paraffin (Kerosine) method (Varker 1987). Since there is no volume reduction during this process, an equivalent volume of very fine-grained sludge was carefully sluiced through the sieves. The 800 mls of «conodont residue» were then dried and concentrated electro-magnetically, giving a «non-magnetic» conodont fraction of about 50mls. Hand picking of this residue produced 2639 conodonts, representing a concentration for the sample of 660 per kgm.

When compared with the concretion sample it is clear that sample MPA 26038 released a smaller number of taxa, and perhaps more significantly, a disproportionate occurrence of morphological types, i.e. non-Pa elements were grossly under-represented. This suggests that once again damaged fragmental specimens had been lost, in spite of the fact that during laboratory processing both of these samples were treated with the same extreme level of care. Consequently, even though the recovery rate from new sample MPA 26038 had more than doubled, when compared with the earlier sample from the same horizon (Riley *et al.*, op.cit.), there was no increase in the proportion of elements which was specifically identifiable (67%). Since the old and the new samples MPA 26038 were from precisely the same horizon and were of identical lithology, the increase in recovery rate in the new sample must reflect the inordinate amount of care taken to avoid damage during laboratory processing, suggesting that standard laboratory processing techniques play a significant role in modifying retrieved faunas.

3. CONODONT FAUNAS FROM SAMPLE MPA 26024

3.1. DISCRETE ELEMENT MORPHOSPECIES

Reference to Fig. 5 of Riley *et al.* (op.cit.p.164) indicates that the fauna of sample MPA 26024 included 15 identifiable discrete element taxa; actual numbers of specimens were not provided. A faunal list is now presented for that fauna, complete with numbers of specimens:-

Gnathodus bilineatus bilineatus (Roundy 1926)	17
Gnathodus bilineatus bollandensis Higgins & Bouckaert 1968	56
gnathodid fragments	12
Hibbardella pennata Higgins 1961	1
Hindeodella germana Holmes 1928	13
Hindeodella ibergensis Bischoff 1957	12
Hindeodella incurva Higgins 1975	5
Hindeodella uncata (Hass 1953)	9
hindeodellid fragments	168
Ligonodina roundyi Hass 1953	2
Neoprioniodus singularis (Hass 1953)	31
Ozarkodina delicatula (Stauffer & Plummer 1932)	6
Paragnathodus commutatus (Branson & Mehl 1941)	3
Paragnathodus mononodosus (Rhodes, Austin & Druce 1969)	1
Paragnathodus nodosus (Bischoff 1957)	20
Subbryantodus stipans Rexroad 1957	2
Synprioniodina microdentata Ellison 1941	7
indeterminate fragments	17
Total	382

Examination of the 7635 discrete specimens of the present study, from the same horizon, has resulted in the following discrete element faunal list:-

Geniculatus claviger (Roundy 1926)	1
Gnathodus bilineatus bilineatus (Roundy 1926)	97
G. bilineatus bollandensis Higgins & Bouckaert 1968	1179
G. postblineatus Nigmagdanov and Nemirovskaya 1992	20
Gnathodus bilineatus var.	66
gnathodid blades	277
Hibbardella acuta Murray & Chronic 1965	80
Hibbardella pennata Higgins 1961	59
Hindeodella germana Holmes 1928	462
Hindeodella ibergensis Bischoff 1957	345
Hindeodella incurva Higgins 1975	43
Hindeodella simplex (Higgins & Bouckaert 1968)	277
Hindeodella sinuosa Higgins 1975	148
Hindeodella uncata (Hass 1953)	147
hindeodellid fragments	2302
Kladognathus sp.	9
Ligonodina levis Branson and Mehl 1941	2
Ligonodina typa (Gunnell 1933)	18
Lonchodina bischoffi Higgins & Bouckaert 1968	20
Lonchodina furnishi Rexroad 1958	2
lonchodinid fragments	35
Magnilaterella complectens (Clarke 1960)	1
Metalonchodina bidentata (Gunnell 1931)	3
Neoprioniodus peracutus (Hinde 1900)	63
Neoprioniodus singularis (Hass 1953)	539
Ozarkodina delicatula (Stauffer & Plummer 1932)	243
ozarkodinid fragments	102
Paragnathodus commutatus (Branson & Mehl 1941)	313
Paragnathodus mononodosus (Rhodes, Austin & Druce 1969)	62
Paragnathodus nodosus (Bischoff 1957)	271
Roundya barnettana Hass 1953	17
Subbryantodus stipans Rexroad 1957	12
Subbryantodus subaequalis Higgins 1961	192
Synprioniodina microdentata Ellison 1941	137
indeterminate fragments	91
Total	7635

3.2. MULTIELEMENT SPECIES

3.2.1. Multielement analysis of discrete elements

The discrete element fauna listed above represents the remains of just over one thousand conodont apparatuses belonging to a small number of multielement species. The 1362 specimens of discrete element species *Gnathodus bilineatus* can be taken to represent the Pa elements of 681 apparatuses of multielement species *Gnathodus bilineatus* and since the structure of this apparatus is well known, following the work of Norby (1976) and others, it is a simple matter to calculate the numbers of the other elements belonging to this species which should also be present within this fauna. All of the non-Pa elements are present although not in their expected proportions. The Pb element *Ozarkodina delicatula* for example occurs at only 18% of its predicted concentration, whilst the M element *Synprioniodina microdentata* is present at only 10% of its required number, the Sa element *Hibbardella acuta* at 6%, the Sb element *Hindeodella simplex* at 20%, the Sc element *Hindeodella ibergensis* at 8% and the Sd element *Hindeodella uncata* at 11% of predicted concentrations. Note however that the short-fall in ramiform elements is to some extent compensated by the large number of fragmental ramiforms which remained unidentified specifically.

Nigmagdanov and Nemirovskaya 1992 have recently described an evolutionary series linking *Gnathodus bilineatus* to *Declinognathodus noduliferus* through intermediate forms which have been named *G. postbilineatus* and *D. praenoduliferus*. It is clear that this evolutionary change had already started at Stonehead Beck and that some of the forms already figured by Riley *et al.* 1987 and Varker *et al.* 1990 as *G. bilineatus bollandensis* with restricted platforms are in fact *G. postbilineatus*. Since the structure of *G. bilineatus* and its descendants seems to have been stable except for the evolving Pa elements, it seems a reasonable assumption that the structure of *G. postbilineatus* was the same as that outlined above. See section 6 (conclusions) for further discussion.

Also present in this fauna are the three multielement species *Lochriea commutata* (Branson and Mehl, 1941), *L. mononodosa* (Rhodes, Austin and Druce, 1969) and *L. nodosa* (Bischoff, 1957). These apparatuses each share the same elemental structure, except for their Pa elements, so the latter may be totalled, to represent 323 individuals. This being so, the Pb element *Ozarkodina (Subbryantodus) subaequalis* occurs at 30% of its predicted concentration, the M element *Neoprioniodus singularis* at 83%, the Sa element

Hibbardella pennata at 18% and the Sc element *Hindeodella germana* at 23% of predicted concentrations. Norby (1976) considered that *O. recta* Rexroad and *Subbryantodus subaequalis* Higgins were both Sb elements of *Lochriea*, and since *Subbryantodus stipans* Rexroad may well be synonymous with *Ozarkodina recta* Rexroad, *S. stipans* should perhaps be included in this *Lochriea* count. The small number of additional specimens involved in including *S.stipans* has only a marginal effect upon the percentage occurrence of the Sb elements. Consideration of the conodont clusters (see below) suggests that discrete element species *Hindeodella incurva* Higgins, 1975 and H. *sinuosa* Higgins, 1975 should also be included in the group of ramiforms within the *Lochriea* apparatus, perhaps occupying the Sb position. Their inclusion would of course have the effect of doubling the percentage occurrence of *Hindeodella germana*, the figures for which were calculated on the basis of four pairs in the apparatus rather than two.

Multi-element species of *Gnathodus* and *Lochriea* therefore dominate this fauna; they represent over 90% of the elements recovered and all of the required elements have been recorded in large numbers. However, even in an exceptionally well-preserved and well-represented fauna such as this there has been some selective removal of the more fragile elements. It is therefore puzzling that the M element *Neoprioniodus singularis* is so well represented compared with other apparently equally fragile morphospecies and it may be that this element was vicariously shared, in a manner not yet recognised, with one of the other multielement species represented in this collection.

The remaining apparatuses are fewer in number and are less completely represented. The structure of multielement species *Idioprioniodus healdi* (Roundy, 1926) was suggested by Norby (1976) to consist of Pb element *Metalonchodina bidentata*, M element *Neoprioniodus conjunctus*, Sa element *Roundya barnettana*, Sb elements *Lonchodina furnishi*, *L. bischoffi* or *L. paraclaviger* (3 morphotypes), and Sc element *Ligonodina typa*. Although the M element has not been recovered from Stonehead Beck, it would appear that two of the three morphotypes are present. The single doubtful specimen of *Geniculatus claviger* probably also belongs to *I. healdi* since Norby (op.cit.), included this discrete element in the Sb position; it is probably an ecological variant of no specific importance. The remaining elements in this fauna may be referred to the multielement species *Kladognathus tenuis* (Branson and Mehl, 1941) or *K. complectens* (Clarke, 1960), neither of which is fully represented.

3.2.2. Evidence provided by Fused Conodont Clusters

Sixty-four fused conodont clusters were recovered from sample MPA 26024 in addition to the discrete elements. Whilst it is well known that clusters vary in significance and their origin may be open to interpretation, it is also clear that in some instances they can be of great value in the multielement interpretation of conodont faunas.

The first fused clusters to be described were in the form of fused pectiniform pairs from the Silurian of Indiana (Rexroad and Nicoll, 1964). Since then clusters have been recorded from all of the conodont-bearing systems and from many parts of the world (Aldridge 1987 lists Lange 1968, Austin and Rhodes 1969, Pollock 1969, Behnken 1975, Landing 1977, Ramovs 1978, Nowlan 1979, Repetski 1980 and Nicoll 1982,1985). Fused clusters nevertheless remain relatively rare.

Austin and Rhodes (1969), described a single fused cluster from the carbonate sequence of the Avon Gorge (S.W.England), consisting of four apatognathids and one *Spathognathodus scitulus,* which they interpreted as the remains of a single conodont-bearing animal. Nicoll and Rexroad (1987) re-examined over 700 Silurian clusters from northern Indiana, and their conclusion was that these clusters also represented the preserved skeletal remains of conodont animals. Higgins (1975, p.24) on the other hand described two types of cluster from the *Gastrioceras listeri* Marine Band (Westphalian) from the south and central Pennines (northern England), which he considered to be coprolitic in origin. One type consisted of up to 40 individual specimens grouped together in a brown groundmass, whilst the second consisted in each case of only two fused specimens.

It appears therefore that fused conodont clusters may have a dual origin. Those representing the remains of single conodont animals must clearly contain elements of type and number which are consistent with a single apparatus. Those which are coprolitic in origin often appear to have a phosphatic cement (Higgins, op.cit.;Aldridge 1987, p.21) as well as displaying a characteristic elemental disorganization, with morphotypes present in numbers not consistent with any known multielement species. They may also include conodont elements from different multielement species, if the predator did not confine itself to a single species of prey.

The Stonehead Beck clusters are well preserved and include elements with prominently projecting processes, e.g. the morphospecies *Hindeodella uncata* (Pl. 1: 7). The cementing medium in each case is a fine-grained, dark brown material which in the residue resembles iron oxide. However, X-ray (energy dispersive) analysis of this material indicates that it primarily consists of calcium phosphate but with significant amounts of clay mineral and albite. In spite of the presence of a predominantly calcium phosphate cement, the combination of morphotypes strongly suggests that each Stonehead Beck cluster represents the remains of a single apparatus. The elemental arrangement within the clusters is also significant. Parallel alignment of similar elements is common, whilst the most complete cluster (Pl. 1: 7) retains a crude bi-lateral symmetry, suggesting oblique compression of the apparatus in the direction of its plane of symmetry which resulted in some foreshortening.

The individual elements of the cluster in Pl. 1: 7 are in several respects arranged in the manner defined by Schmidt (1934) and outlined by Aldridge (1987,p.19). All elements are longitudinally aligned with respect to a central, vertical plane of symmetry; the ramiform elements are at one end and the platform(s) at the other; and the distal ends of the ramiform elements point in the same direction as the platform ends of the Pa element(s). However the denticulated surfaces of the ramiform elements are directed inwards rather than outwards. In this latter respect the cluster has more in common with the reconstruction by Rhodes (1952). In addition there has clearly been some disturbance of the original arrangement of the Sd (*Hindeodella uncata*) elements, since that on the left (as seen in Pl. 1: 7) has its anterior process directed upwards, whilst that on the right has its aboral surface upwards and its anterior process directed inwards towards the centre. Perhaps it was the unusual shape of these particular elements, with their prominent, laterally projecting anterior processes, which influenced their rotation during the presumed gentle compression of the apparatus. This cluster may be fairly complete; one of the Pa elements is definitely absent whilst the phosphatic matrix may be obscuring one of the Pb elements and one of the M elements.

Twenty-three of the remaining clusters also clearly belong to multielement species *Gnathodus bilineatus,* although only nine of them include a Pa element. A further thirteen clusters contain the M element *Neoprioniodus singularis* and/or the Sc element *Hindeodella germana*, and must belong to the multielement genus *Lochriea*, even though in this case no Pa elements are attached. The *G. bilineatus* clusters indicated that an absence of Pa elements is apparently quite normal, since their position within the apparatus seems to have rendered them the most likely elements to become detached from the cluster, even though they may be the most robust elements of the apparatus. Perhaps they did not overlap the other elements longitudinally. A number of the *Lochriea* clusters also include the discrete element species *H. sinuosa* (see Pl. 1: 6). To include this species or a combination of this species and *H. incurva* within the *Lochriea* apparatus would be consistent with the earlier consideration of the single element fauna, since these single element ramiforms remained unallocated to a known apparatus. The remaining twenty-seven clusters cannot be taxonomically assigned because they consist primarily of ramiform elements heavily obscured by cementing medium.

4. CONODONT FAUNAS FROM SAMPLE MPA 26038

4.1. DISCRETE ELEMENT MORPHOSPECIES

Reference to Fig.5 of Riley *et al.* (op.cit. p.164) indicates that sample MPA 26038 contained only six specifically identifiable morphospecies. A complete faunal list is now provided for that sample, complete with numbers of specimens:-

possible *Adetognathus gigantus*? fragment	1
Declinognathodus inaequalis (Higgins 1975)	222
Declinognathodus lateralis (Higgins & Bouckaert 1968)	62
Declinognathodus noduliferus (Ellison & Graves 1941)	178
declinognathodid blade fragments	93
declinognathodid platform fragments	122
hindeodellid fragments	16
Lonchodina sp.	2
Neognathodus symmetricus (Lane 1967)	8
Roundya barnettana Hass 1953	1
Subbryantodus fragments	6
Synprioniodina microdentata Ellison 1941	1
indet. fragments	2
Total	714

The following faunal list was obtained from the re-sampling study of sample MPA 26038

Declinognathodus inaequalis (Higgins 1975)	854
Declinognathodus lateralis (Higgins and Bouckaert 1968)	396
Declinognathodus noduliferus (Ellison and Graves 1941)	499
declinognathodid blade fragments	559
declinognathodid platform fragments	180
Geniculatus claviger (Roundy 1926)	8
hindeodellid fragments	78
Lonchodina bischoffi Higgins and Bouckaert 1968	11
Lonchodina furnishi Rexroad 1958	2
Lonchodina fragments	14
Metalonchodina bidentata (Gunnell 1931)	3
Neognathodus symmetricus (Lane 1967)	12
Roundya barnettana Hass 1953	2
Subbryantodus fragments	20
Synprioniodina microdentata Ellison 1941	1
Total	2639

4.2. MULTIELEMENT SPECIES

The above list indicates a gross under-representation of non-Pa elements typical of the situation which occurs in mudstones and shales. Specimens belonging to discrete element genus *Declinognathodus* must represent the Pa elements of almost one thousand apparatuses, the precise structure of which is not fully known. Non-Pa elements are very poorly represented.

Non-Pa elements which at the base of the Stonehead Beck sequence are associated with the *Gnathodus bilineatus* apparatus, extend up the top of the sequence, beyond the upper limit of discrete element *G. bilineatus*. Higgins and Bouckaert (1968) and Higgins (1975) also described Namurian faunas which included *Ozarkodina delicatula*, *Hindeodella ibergensis* etc. at horizons above the limit of *Gnathodus bilineatus* but which contained *Declinognathodus* spp.. It is therefore considered likely that the apparatus of *Declinognathodus* is very similar to, if not the same as that of *Gnathodus bilineatus*, except for the rapidly evolving Pa elements. The following elements recovered from Stonehead Beck sample MPA 26038 would therefore have belonged to the *Declinognathodus noduliferus* s.l. apparatus:- Pa element *Declinognathodus noduliferus* or *D. inaequalis*, M element *Synprioniodina microdentata* (only a single specimen recovered), whilst the Sb and Sc elements are represented by the small number of hindeodellid fragments.

The remaining elements in this sample clearly include components of the multielement species *Idioprioniodus healdi*, plus *Neognathodus symmetricus*. The latter must represent the Pa element of multielement species *N. symmetricus*, which may have shared many elements with the *Declinognathodus* group and therefore may be represented more fully than is apparent.

5. SYSTEMATIC PALAEONTOLOGY

The synonymies provided in this section are not a complete record of all references to each element for each species. None of the multielement species described is new, and in general their structure is well established. Many of the discrete elements are themselves long-established and common morphospecies, with long and complex synonymies in their own right, and since many of them are also vicariously shared complete synonymies would be unnecessarily long. This work therefore follows the recent trend in presenting only selected references, from which details of synonymy and/or descriptions of the individual elements may be determined.

Genus *DECLINOGNATHODUS* Dunn, 1966
Type Species *Cavusgnathus noduliferus* Ellison and Graves, 1941

Declinognathodus noduliferus (Ellison and Graves, 1941)

Declingnathodus inaequalis (Higgins, 1975)

Pa Elements : plate 4, figs. 1-3.

Cavusgnathus nodulifera Ellison and Graves, 1941, p.4-5, pl.3, figs.4,6
Gnathodus nodulifera (Ellison and Graves) Koike, 1967, p.297-298, pl.3, fig.10.
Idiognathoides noduliferus noduliferus (Ellison and Graves) Higgins,1975, p.54, pl.14, figs.15,16.
Idiognathoides noduliferus inaequalis (Ellison and Graves) Higgins, 1975, p.53, pl.12, figs.1-7,14, pl.14, figs.11-13, pl.15, figs.10,14.
Declinognathodus noduliferus (Ellison and Graves) Grayson, 1984, p. 47, pl.3, fig. 20.

Declinognathodus lateralis (Higgins and Bouckaert, 1968)

Pa Element : plate 3, fig. 5.

Streptognathodus lateralis Higgins and Bouckaert 1968, pp 45,46, pl.5, figs.1-4, 7.
Declinognathodus lateralis (Higgins and Bouckaert) Dunn 1970, p.330, pl.62, figs. 5-7.

Genus *GNATHODUS* Pander 1856
Type species *Polygnathus bilineatus* Roundy 1926, ICZN decision (Tubbs 1986)

Gnathodus bilineatus bilineatus (Roundy 1926)

Gnathodus bilineatus bollandensis
(Higgins and Bouckaert 1968)

Gnathodus postbilineatus
Nigmagdanov and Nemirovskaya 1992

The structure of the *G. bilineatus* apparatus has been well-established and stable since the work particularly of Norby (1976). The distinction between the two sub-species is based entirely upon the Pa elements; all other elements are shared. To this may be added the recently erected species *G. postbilineatus* as a direct descendant of *G. bilineatus bollandensis*. See plate one, figs. 1, 2, 3, 4 and 7, and plate two, figs. 1, 2, 3 and 6 for illustrations of fused clusters of *G. bilineatus.*

Pa Elements : plate 3, figs. 1 - 4.

Polygnathus bilineatus Roundy 1926, p.13, pl.3, figs 10a-c.

Gnathodus bilineatus (Roundy) Hass 1953, p.78, pl.14, figs.25-29.
Gnathodus bilineatus bilineatus (Roundy) Higgins and Bouckaert 1968, p.29, pl.3, fig.9.
Gnathodus bilineatus (Roundy) *bollandensis* Higgins and Bouckaert 1968, p.29, pl.2, figs.10,13; pl.3, figs.4-8, 10.
Gnathodus bilineatus (Roundy), Norby 1976, p.102, pl.4, fig.1; pls.5-8; pl.10. fig.5; text-fig.20.
Gnathodus postbilineatus Nigmagdanov and Nemirovskaya 1992, p.262, pl.1, figs.7-12, pl.2, figs.1-5.

Pb Elements : plate 3, figs. 6 and 9,

Ozarkodina delicatula (Stauffer and Plummer) Ellison 1941, p.120, pl.20, figs 40-42, 47.

M Elements : plate 3, figs. 7 and 10.

Synprioniodina microdentata Ellison 1941, p.119, pl.20, Figs.43,44,45?,46?.

Sa Element : plate 3, fig. 8.

Hibbardella fragilis Higgins 1961, p.213-4, pl.12, fig.4.
Hibbardella acuta Murray and Chronic 1965, p.598, pl.73, figs.3-5.
Sb Elements : plate 3, fig. 14.

Angulodus walrathi (Hibbard) Higgins 1961, pl.10, fig.16.
Angulodus simplex Higgins and Bouckaert 1968, p.28, pl.1, fig.7.
Hindeodella simplex (Higgins and Bouckaert) Higgins 1975, p.42, pl.5, figs.10,12,13.

Sc Elements : plate 3, figs, 11 and 12.

Hindeodella ibergensis Bischoff 1957, p.28, pl.6, fig.33.

Sd Elements : plate 3, figs. 13 and 15.

Hindeodella uncata (Hass) Austin and Husri 1974, pl.15, fig.13.

Genus *IDIOPRIONIODUS* Gunnell 1933
Type Species *Idioprioniodus typus* Gunnell 1933 by original designation

This long-ranging genus was first described from the Pennsylvanian of North America (e.g. Rhodes 1952, Merrill and Merrill 1974) but is now known to range from the Mississippian into the Pennsylvanian. Merrill and Merrill (1974) considered *I. conjunctus* (=*I. healdi*) to occur in pre-Missourian rocks, being replaced upwards by *I. typus*, which had lost its metalonchodinan element. The apparatus structure used here follows that proposed by Norby (1976, p. 127).

Idioprioniodus healdi (Roundy 1926)

Pb Elements

Prioniodus bidentatus Gunnell 1931, p.247, pl.29, fig.6.
Metalonchodina bidentata (Gunnell), Rhodes, Austin and Druce 1969, p.154, pl.24, figs.8-11.
Idioprioniodus paraclaviger (Rexroad), Nicoll and Rexroad 1975, aff. *bidentata* element, p.25, pl.3, figs.12-14.

Sa Element : plate 2, fig. 9.

Prioniodus subacodus Gunnell 1931, p.246, pl.29, fig.5.
Hibbardella subacoda (Gunnell) Ellison 1941, p.118, pl.20, figs.22,26.
Roundya barnettana Hass 1953, p.89, pl.16, figs.8,9.
Idioprioniodus paraclaviger (Rexroad), Nicoll and Rexroad 1975, aff.*subacoda* element p.23, pl.3, fig.15.

Sb α Elements : plate 2, fig. 5.

Prioniodus healdi Roundy 1926, p.10, pl.4, figs.5a,5b.
Ligonodina lexingtonensis (Gunnell), Ellison 1941, p.115, pl.20, figs.13-15.
Geniculatus claviger Hass 1953,p.77, pl.15, fig.17.
Lonchodina furnishi Rexroad 1958, p.22, pl.4, figs.11-13.

Sb β Elements : plate 2, fig. 7.

Prioniodus clarki Gunnell 1931, p.247, pl.29, fig.8.
Lonchodina clarki (Gunnell) Ellison 1941, p.116, pl.20, Figs.21,27,30,31.
Lonchodina paraclarki Hass 1953, p.83, pl.16, figs.15,16.
Lonchodina cf.*projecta* Ulrich and Bassler, Higgins 1961, pl.XI, fig.10.
Lonchodina bischoffi Higgins and Bouckaert 1968, p.43.

Sc Elements : plate 2, fig. 4.

Idioprioniodus typus Gunnell 1933, p.265, pl.31, fig.47.
Ligonodina typa (Gunnell) Ellison 1941, p.114, pl.20, figs. 8-11.
Ligonodina roundyi Hass 1953, p.82, pl.15, figs.5-9.
Geniculatus claviger Hass 1953, p.77,pl.15, figs.10-16,18,19.
Idioprioniodus paraclaviger (Rexroad) Nicoll and Rexroad 1975, *typus* element, p.23, pl.3, figs.4-7.

Genus *KLADOGNATHUS* Rexroad 1958
Type Species *Cladognathus prima* Rexroad 1957, by original designation

Kladognathus complectens (Clarke), Mapes and Rexroad 1986

Mapes and Rexroad(1986) suggested the structure for this apparatus, with additions by Rexroad and Horowitz (1990, p.507). Only the Sb element, alpha morphotype, as envisaged by Rexroad and Horowitz (op.cit.), plus one of the shared elements, has been recovered from the Stonehead Beck locality.

Sb α Element : plate 2, fig. 8.

?*Ligonodina complectens* Clarke 1960, p.9, pl.1, figs. 14,15.
Magnilaterella complectens (Clarke), Rhodes, Austin and Druce 1969, p.145, pl.23, figs.14-17.

Kladognathus tenuis (Branson and Mehl), Rexroad 1981

The apparatus structure suggested by Rexroad and Horowitz (1990, p.505) is accepted as consistent with what occurs at the Stonehead Beck locality.

Sc β Element

Ligonodina levis Branson and Mehl 1941, p.185, pl.6, fig.10.
Ligonodina obunca Rexroad 1957, p.32, pl.1, figs.22,23.

According to Rexroad and Horowitz (1990, p.507) these two species of *Kladognathus* share the following M element:

M Element

Prioniodus peracutus Hinde 1900, p.343, pl.10, fig.22.
Neoprioniodus peracutus (Hinde) Clarke 1960, p.14, pl.2, fig.6.

Genus *LOCHRIEA* Scott 1942
Type Species *Spathognathodus commutatus* Branson and Mehl 1941

The *Lochriea* apparatus was first described by Scott from his work on bedding-plane assemblages. The structure of the apparatus was however established by Norby (1976), with statistical confirmation being provided by Horowitz and Rexroad (1982, p.966), who were able to partially reconstruct the genus. The three species outlined here share the same non-Pa elements. See plate one, figs 5 and 6 for fused conodont clusters representing this group of species.

Lochriea commutata (Branson and Mehl 1941)

Pa Elements : plate 4, fig. 6.

Spathognathodus commutatus Branson and Mehl 1941, p.98, pl.19, figs.1-4.
Lochriea montanaensis Scott 1941, p.298, figs.1-7; pl.38. figs.1-4,6,7,10,12; pl.39, figs.1,4,7,9; pl.40,figs.2-5,9,10,12,13,15,18,19.
Gnathodus commutatus (Branson and Mehl) Rhodes, Austin and Druce 1969, p.95, pl.19, figs.9a-12d.
Paragnathodus commutatus Branson and Mehl) Higgins 1975, p.70, pl.7, figs.7-9,11,13,16,20,21.
Lochriea commutata (Branson and Mehl) Varker and Sevastopulo 1985, p.200, pl.5.5, figs.11,12.

Lochriea mononodosa (Rhodes, Austin and Druce 1969)

Pa Elements : plate 4, figs. 4, 5, 9.

Gnathodus mononodosus Rhodes, Austin and Druce 1969, p.103, pl.19, figs.13a-15d.
Paragnathodus mononodosus (Rhodes, Austin and Druce) Higgins 1975, p.71, pl.7, fig.14.
Lochriea mononodosa (Rhodes, Austin and Druce) Varker and Sevastopulo 1985, p.200, pl.5.5, figs.13,16-18,20.

Lochriea nodosa (Bischoff 1957)

Pa Elements : plate 4, figs. 8, 10.

Gnathodus commutatus (Branson and Mehl) *nodosus* Bischoff 1957, p.23, pl.4, figs.12,13.
Gnathodus nodosus (Bischoff) Rhodes, Austin and Druce 1969, p.104, pl.19, figs.16a-20c.
Paragnathodus nodosus (Bischoff) Higgins 1975, p.72, pl.7, figs.12,15,17-19,22,23.

Non-Pa elements for these three species are as follows:

Pb Elements : plate 4, figs. 11, 12.

Subbryantodus stipans Rexroad 1957, p.39, pl.4, fig.1.
Subbryantodus subaequalis Higgins 1961, p.218, pl.12, fig.15.

M Elements : plate 4, figs. 13, 14.

Prioniodus singularis Hass 1953, p.88, pl.16, fig.4.
Neoprioniodus singularis (Hass) Stanley 1958, p.471, pl.66, figs.2,3.

Sa Element : plate 4, fig. 7.

Hibbardella pennata Higgins 1961, p.213, pl.12, figs.5,6.

Sb Elements : plate 4, figs 16, 18.

Hindeodella sinuosa Higgins 1975, p.43, pl.6, figs.1-3,5.

Sc Elements : plate 4, figs. 15, 17.

Hindeodella germana Holmes 1928, p.25, pl.9, fig.9.

6. CONCLUSIONS

By applying multielement taxonomy to the discrete element conodont range-chart figured in Varker *et al.* (1990, p.223) a true pattern of conodont distribution can be determined for the Stonehead Beck sequence (fig 1). Nine multielement taxa occur in the E_2c^3 ammonoid horizon at the base of the succession and of these *Lochriea nodosa*, *L. mononodosa*, *Kladognathus complectens* and *K. tenuis* have not been recorded higher in the succession. *G. bilineatus bilineatus* ranges up to 6.4 metres below the Arnsbergian/Chokierian boundary, whilst *G. bilineatus bollandensis* and *G. postbilineatus* disappear at a point 2.1 metres below the Arnsbergian/Chokierian boundary, at the same point that sees the demise of *Lochriea commutata.*

Above this point, and prior to the appearance of the *Declinognathodus* fauna, there is in interval with a very sparse and restricted conodont fauna not included in this re-sampling study. This distinctive fauna consists of Pa elements belonging to the discrete element species *Rhachistognathus minutus* (Higgins and Bouckaert) and non-Pa elements *Ozarkodina delicatula* and hindeodellids. Non-platform under-representation was extreme throughout this interval; in some samples there were no non-platform elements recovered. There is therefore little evidence at Stonehead Beck for the structure of the *Rhachistognathus* apparatus. Whatever its structure however, *R. minutus* extends discontinuously from sample MPA 26029, 1.5 metres below the Arnsbergian/Chokierian boundary as far as the top of the H_1a^2 marine horizon, 10.9 metres above the base of the Chokierian.

D. inaequalis first appears in sample MPA 26032 at 0.4 metres below the H_1a^2 horizon, 9.4 metres above the Arnsbergian/ Chokierian boundary (see fig. 1), and in so-doing marks the position of the Mid-Carboniferous Boundary at Stonehead Beck.

The middle part of the Stonehead Beck sequence is therefore important to the understanding of mid-

Carboniferous conodont biostratigraphy. The presence of the near-shore lagoonal alga *Botryococcus* in some of the palynological preparations, combined with a paucity of macrofauna and generally low conodont concentrations, were taken by Varker *et al.*(op.cit.p.230) to indicate a change in depositional regime in the middle part of the succession. This may be the reason why *Gnathodus bilineatus* disappears from the Pennine Basin earlier than it did from Belgium, where it ranges through into the Chokierian. *Gnathodus* is generally accepted to have been relatively intolerant of environmental changes (Rexroad and Horowitz 1990, p.496), so perhaps it simply migrated away from the Pennine Basin when conditions deteriorated.

The origin of *Declinognathodus noduliferus* s.l. has been discussed by several authors and whilst there has been doubt over the precise ancestor of *D. noduliferus*, most workers agree that this species evolved from a species of *Gnathodus.* Dunn (1970,p.331) considered it to have evolved from *Gnathodus girtyi simplex* Dunn, although this was without knowledge of the multielement apparatus. Grayson and Merrill (1987) expressed the view that *Gnathodus bilineatus* was its most likely ancestor. As far as the Stonehead Beck faunas are concerned, *G.bilineatus* is obviously the more attractive ancestor, since it is a major component of faunas from the base of the sequence up to a point just below the Arnsbergian/Chokierian boundary. In addition, *Gnathodus bilineatus bollandensis* was evolving rapidly through the Arnsbergian, giving rise in late Arnsbergian times to forms in which the outer lateral platform had become greatly reduced in size, approximately triangular in shape, and with a highly modified and reduced ornamentation (see Riley *et al.*1987, plate 2, figs.5-8,12; and Varker *et al.*1990, pl.1, figs.2-12). Following the work of Nigmagdanov and Nemirovskaya these forms must be recognised as *G. postbilineatus.* It is clear that the sequence of events which led ultimately to *Declinognathodus noduliferus* had already begun at Stonehead Beck before adverse environmental conditions resulted in the sparse faunas of the middle part of the sequence. By the time conditions had ameliorated for this group of conodonts *D. noduliferus* had already evolved. At Stonehead Beck there is therefore an 11.5 m interval between the highest recorded specimens of *Gnathodus bilineatus* and *G. postbilineatus* in sample MPA 26974 and the incoming of the declinognathodids in sample MPA 26032.

All of the non-Pa elements of the *G. bilineatus* apparatus are known to continue in the Pennine Basin (see Higgins 1975) up through the Namurian, beyond the point where the eponymous element disappears, and on into the Westphalian. Consequently the only necessary modification to the apparatus would involve the Pa elements. Since the non-Pa elements also continue upwards beyond even the range of *Declinognathodus noduliferus* it appears that this was an actively evolving line which gave rise to still later forms in the upper part of the Namurian and Westphalian.

In marked contrast to the common occurrence of *Gnathodus bilineatus* in the Stonehead Beck sequence, *Gnathodus girtyi simplex* has not been recorded from any of the thirty eight sampled horizons, which were represented by a total of approximately 170 Kgms of sampled rock and in excess of 15,000 recovered conodont specimens. However this need not be significant, since if *Declinognathodus noduliferus* was indeed an immigrant, as suggested earlier, the absence of *G. girtyi simplex* would not necessarily preclude this species from being the ancestral form.

Idioprioniodus healdi was only found in the two re-sampled horizons, from the base and from the top of the sequence, so this species must have ranged throughout the Stonehead Beck time interval. Its absence from the 36 intervening samples could simply reflect the generally lower conodont concentrations; alternatively it could indicate that this species was also a migrant, being present only when there were what it perceived to be optimum conditions. The observation by Rexroad and Horowitz (1990, p.496) that this species is very sporadic in its distribution in Mississippian rocks probably lends support to the latter explanation.

7. DEPOSITORY OF SPECIMENS

All specimens figured in this work have been placed under the care of the curator at the headquarters of the British Geological Survey, Keyworth, Nottingham NG12 5GG, England.

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PLATE 1

1. Detail from *Gnathodus bilineatus* fused cluster (sub-species not determined) showing parallel alignment of almost identical Sc elements X 120. Specimen MPK 9774, Sample MPA 26024.

2. *Gnathodus bilineatus* (sub-species not determined) fused cluster showing Sa element and the blade of a Pa element. X 70. Specimen MPK 9775, Sample MPA 26024.

3. *Gnathodus bilineatus* (sub-species not determined) fused cluster showing bundle of S elements, including Sc and Sd, plus the Sa element. X50 Specimen MPK 9776, Sample MPA 26024.

4. *Gnathodus bilineatus* (sub-species not determined) fused cluster showing predominantly S elements plus one Pb element. X 50 Specimen MPK 9777, Sample MPA 26024.

5. *Lochriea* sp. fused cluster (species not determined) showing one M element and several S elements, which appear to be Sc elements. X 60 Specimen MPK 9778, Sample MPA 26024.

6. *Lochriea* sp. fused cluster (species not determined), showing an M element associated with single element species *Hindeodella incurva* Higgins 1975 and *H. sinuosa* Higgins 1975, which appear to have replaced at least some of the *H. germana* Sc elements at this horizon. X 60 Specimen MPK 9779, Sample 26024.

7. *Gnathodus bilineatus* fused cluster (sub-species not determined) showing a crude bilateral symmetry. Note that the anterior processes of the Sc elements are directed outwards and the denticulated surfaces inwards. Both Sd elements are visible (the anterior process of the left specimen is directed upwards at the anterior end of the Pa blade). The anterior central element is probably the Sa element, whilst posterior to that can be seen the anterior end of the right M element. A probable Pb element is visible to the lower right of the specimen. X 60 Specimen MPK 9780, Sample MPA 26024.

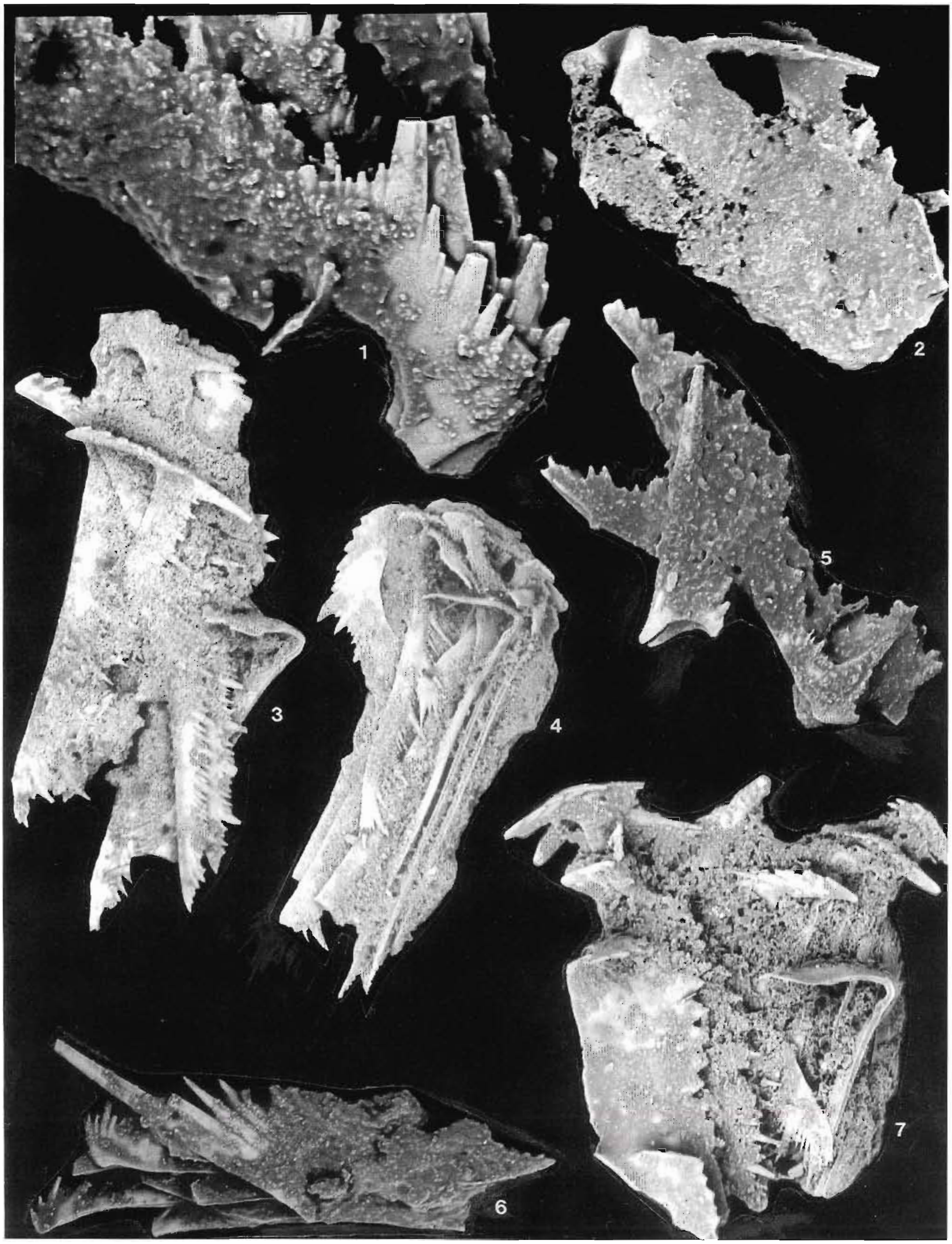
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PLATE 2

1. *Gnathodus bilineatus* fused cluster (sub-species not determined) showing the bundle of S elements, including Sb and Sc elements. Part on a single Pb element may be seen projecting from the right side of the specimen. X 60 Specimen MPK 9781, Sample MPA 26024.
2. *Gnathodus bilineatus* fused cluster. Since the outer platform of the Pa element is obscured the sub-species cannot be determined with certainty but it is probably *G. bilineatus bollandensis* (Higgins and Bouckaert 1968). Broken S elements are fused to the outer platform of the Pa element. X 60 Specimen MPK 9782, Sample MPA 26024.
3. *Gnathodus bilineatus bollandensis* Pa element with attached Sd element. X 60 Specimen MPK 9783, Sample MPA 26024
4. *Idioprioniodus healdi* (Roundy 1926) Sc element. X 50 Specimen MPK 9784, Sample MPA 26024.
5. *Idioprioniodus healdi* (Roundy 1926) Sb element. X 50 Specimen MPK 9785, Sample MPA 26024.
6. *Gnathodus bilineatus bollandensis* (Higgins and Bouckaert 1968) fused cluster showing a complete Pa element fused to a bundle of S elements of which Sc elements are clearly visible. X 60 Specimen MPK 9786, Sample MPA 26024.
7. *Idioprioniodus healdi* (Roundy 1926) Sb element. X 70 Specimen MPK 9787, Sample MPA 26024.
8. *Kladognathus complectens* (Clarke) Mapes and Rexroad 1986 Sb element. X 83 Specimen MPK 9789, Sample MPA 26024.
9. *Idiopriondiodus healdi* (Roundy 1926) Sa element. X 70 Specimen MPK 9788, Sample MPA 26024.


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PLATE 3

1. *Gnathodus bilineatus bollandensis* (Higgins and Bouckaert 1968) Pa element. X 50 Specimen MPK 9790, Sample MPA 26024.
2. *Gnathodus bilineatus bollandensis* (Higgins and Bouckaert 1968) Pa element. X 72 Specimen MPK 9791, Sample MPA 26024.
3. *Gnathodus bilineatus bilineatus* (Roundy 1926) Pa element. X 55 Specimen MPK 9792, Sample MPA 26024.
4. *Gnathodus bilineatus bollandensis* (Higgins and Bouckaert 1968) Pa element. X 55 Specimen MPK 9793, Sample MPA 26024.
5. *Declinognathodus lateralis* (Higgins and Bouckaert 1968) Pa element. X 85 Specimen MPK 9794, Sample MPA 26028.
6. *Gnathodus bilineatus* subsp. Pb element. X 70 Specimen MPK 9795, Sample MPA 26024.
7. *Gnathodus bilineatus* subsp. M element. X 70 Specimen MPK 9796, Sample MPA 26024.
8. *Gnathodus bilineatus* subsp. Sa element. X 65 Specimen MPK 9797, Sample MPA 26024.
9. *Gnathodus bilineatus* subsp. Pb element. X 70 Specimen MPK 9798, Sample MPA 26024.
10. *Gnathodus bilineatus* subsp. M element. X 70 Specimen MPK 9799, Sample MPA 26024.
11. *Gnathodus bilineatus* subsp. Sc element. X 45 Specimen MPK 9800, Sample MPA 26024.
12. *Gnathodus bilineatus* subsp. Sc element. X 45 Specimen MPK 9801, Sample MPA 26024.
13. *Gnathodus bilineatus* subsp. Sd element. X 45 Specimen MPK 9802, Sample MPA 26024.
14. *Gnathodus bilineatus* subsp. Sb element. X 40 Specimen MPK 9803, Sample MPA 26024.
15. *Gnathodus bilineatus* subsp. Sd element. X 45 Specimen MPK 9804, Sample MPA 26024.


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PLATE 4

1. *Declinognathodus inaequalis* (Higgins 1975) Pa element. X 90 Specimen MPK 9805, Sample MPA 26038.

2. *Declinognathodus inaequalis* (Higgins 1975) Pa element. X 95 Specimen MPK 9806, Sample MPA 26038.

3. *Declinognathodus noduliferus* (Ellison and Graves 1941) Pa element. X 95 Specimen MPK 9807, Sample MPA 26038.

4. *Lochriea mononodosa* (Rhodes, Austin and Druce 1969) Pa element. X 80 Specimen MPK 9808, Sample 26024.

5. *Lochriea mononodosa* (Rhodes, Austin and Druce 1969) Pa element. X 80 Specimen MPK 9809, Sample MPA 26024.

6. *Lochriea commutata* (Branson and Mehl 1941) Pa element. X 80 Fig. 7. *Lochriea* sp. Sa element. X 80 Specimen MPK 9811, Sample MPA 26024.

7. *Lochriea* sp. Sa element. X 80 Specimen MPK 9811, Sample MPA 26024.

8. *Lochriea nodosa* (Bischoff 1957) Pa element. X 80 Specimen MPK 9812, Sample MPA 26024.

9. *Lochriea mononodosa* (Rhodes, Austin and Druce 1969) Pa element. X 80 Specimen MPK 9813, Sample MPA 26024.

10. *Lochriea nodosa* (Bischoff 1957) Pa element. X 80 Specimen MPK 9814, Sample MPA 26024.

11. *Lochriea* sp. Pb element. X 80 Specimen MPK 9815, Sample MPA 26024.

12. *Lochriea* sp. Pb element. X 80 Specimen MPK 9816, Sample MPA 26024.

13. *Lochriea* sp. M element. X 80 Specimen MPK 9817, Sample MPA 26024.

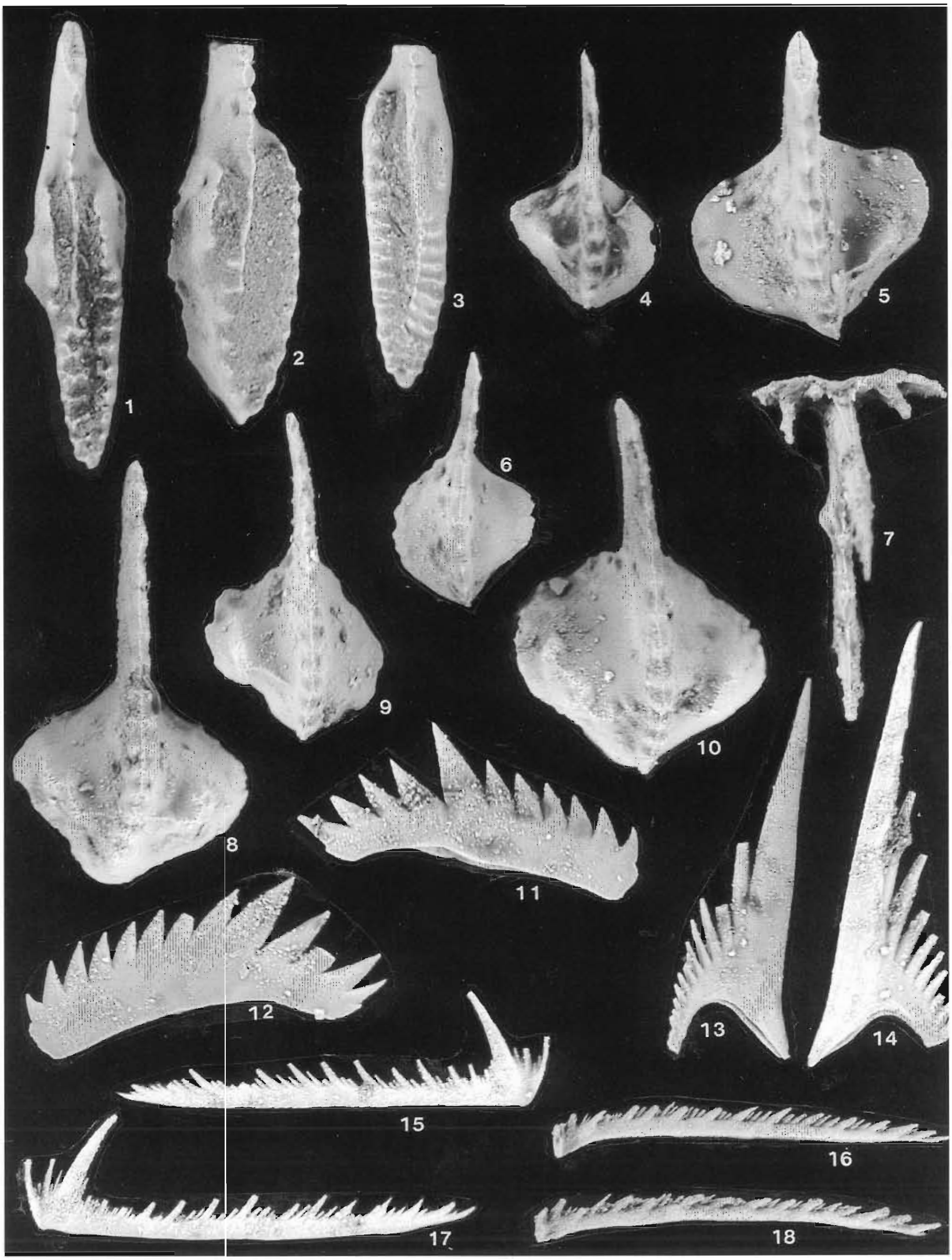
14. *Lochriea* sp. M element. X 80 Specimen MPK 9818, Sample MPA 26024.

15. *Lochriea* sp. Sc element. X 45 Specimen MPK 9819, Sample MPA 26024.

16. *Lochriea* sp. probable Sb element. X 45 Specimen MPK 9820, Sample MPA 26024.

17. *Lochriea* sp. Sc element. X 45 Specimen MPK 9821, Sample MPA 26024.

18. *Lochriea* sp. probable Sb element. X 45 Specimen MPK 9822, Sample MPA 26024.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