LLANDOVERY CONODONTS FROM THE WELSH BORDERLAND

BY

RICHARD JOHN ALDRIDGE

University of Nottingham, England

Pp. 125–231; 9 *Plates*, 13 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 22 No. 2
LONDON : 1972

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22 *No.* 2 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 31 *December,* 1972 *Price* £4.45

LLANDOVERY CONODONTS FROM THE WELSH BORDERLAND

By R. J. ALDRIDGE

CONTENTS

ABSTRACT

Conodont extraction techniques were applied to rock samples from Llandovery and early Wenlock strata of Wales and the Welsh Borderland. The samples yielded 11,750 identifiable specimens, referred to 36 genera and 108 species and subspecies. The species *Amorphognathus tenuis, Diadelognathus nicolli, Icriodella deflecta, Icriodella inconstans, Icriodella malvernensis, Ozarkodina alisonae, Spathognathodus abruptus* and *Spathognathodus gulletensis* are new.

The genera *Icriodella* and *Spathognathodus* are particularly valuable in local stratigraphy. The faunas are divided into four conodont assemblage zones, spanning an interval from the Idwian to the early Wenlock. These zones are compared with those recognized in Europe and North America.

The existence of two faunal provinces in the *Icriodina irregularis* Assemblage Zone, recognized in North America by Pollock, Rexroad & Nicoll (1970), is substantiated by the British faunas. The probable existence of three provinces in Telychian (C_5) times is also recognized. The local distribution of simple cones is significantly related to sea-depth, abundances being greatest in deeper water.

It is concluded that conodonts are of considerable value in Llandovery stratigraphy. Further research should establish phylogenetic lineages and enable precise definition of zones. Precise international correlations will only be achieved when the full effects of faunal provincialism and facies control are appreciated.

I. INTRODUCTION

THE distribution of outcrops of Llandovery strata in Wales and the Welsh Borderland is shown in Text-fig. 1. The Llandovery Series of the type area around Llandovery, Carmarthenshire, was mapped by O. T. Jones, who in 1925 published a detailed account of the southern part. Jones proposed a division of the Llandovery Series into three units, referred to as A (Lower Llandovery), B (Middle Llandovery) and C (Upper Llandovery). He further recognized lithological subdivisions of each unit, designated A_1 to A_4 for the Lower, B_1 to B_3 for the Middle and C_1 to C_6 for the Upper Llandovery. Cocks, Toghill & Ziegler (1970) defined four stage names, consistent with contemporary stratigraphic nomenclature, within the Llandovery Series. The stage names Rhuddanian, Idwian, Fronian and Telychian were proposed as alternatives or substitutes for the letters and numbers used by Jones. The relationship between the two schemes is illustrated in Text-fig. 2.

A succession of graptolite assemblage zones was established in the British Lower Palaeozoic graptolitic sequences by Lapworth (1879–80) and Elles & Wood (1901–18). This scheme, with some subsequent modification, has become accepted as a standard for international correlation. Eleven graptolite zones span the Llandovery (Text-fig. 2), the base being taken at the base of the *Glyptograptus persculptus* Zone and the top at the base of the *Cyrtograptus centrifugus* Zone. Direct reference of the almost exclusively shelly sequence at Llandovery to these zones has only been achieved at three horizons, where Jones (1925 : 360, 370; 1949 : 52) recorded diagnostic graptolites (Text-fig. 2). The association of C_5 brachiopods with *greistoniensis* Zone graptolites in the Welsh Borderland was recorded by Cocks and Walton (1968 : 226) and by R. K. Jones *et al.* (1969), thus providing an additional, indirect tie between the type succession and the graptolitic sequences.

Brachiopods are currently used for the correlation of outcrops of the shelly facies. Evolutionary lineages for the genera *Eocoelia* and *Stricklandia*/*Costistricklandia* were tabulated by Ziegler, Cocks & McKerrow (1968 : text-fig. 2) and are reproduced in Text-fig. 3. In addition, brachiopods have proved to be valuable indicators of sea-depth, particularly in the Fronian and Telychian. Five animal communities, each

named after a prominent brachiopod genus, have been recognized in collections dominated by brachiopods (Ziegler 1965; Cocks 1967; Ziegler, Cocks & Bambach 1968). These are, in order of increasing depth, the *Lingula* community, the *Eocoelia* community, the *Pentamerus* community, the *Stricklandia* community and the *Clorinda* community. *Eocoelia* may be replaced by a homeomorph rhynchonellid possibly referable to the genus *Rostricellula* (Cocks & Rickards 1969 : 220, 222). In C_5 and C_6, *Pentamerus* is replaced by *Pentameroides* and *Stricklandia* by *Costistricklandia*.

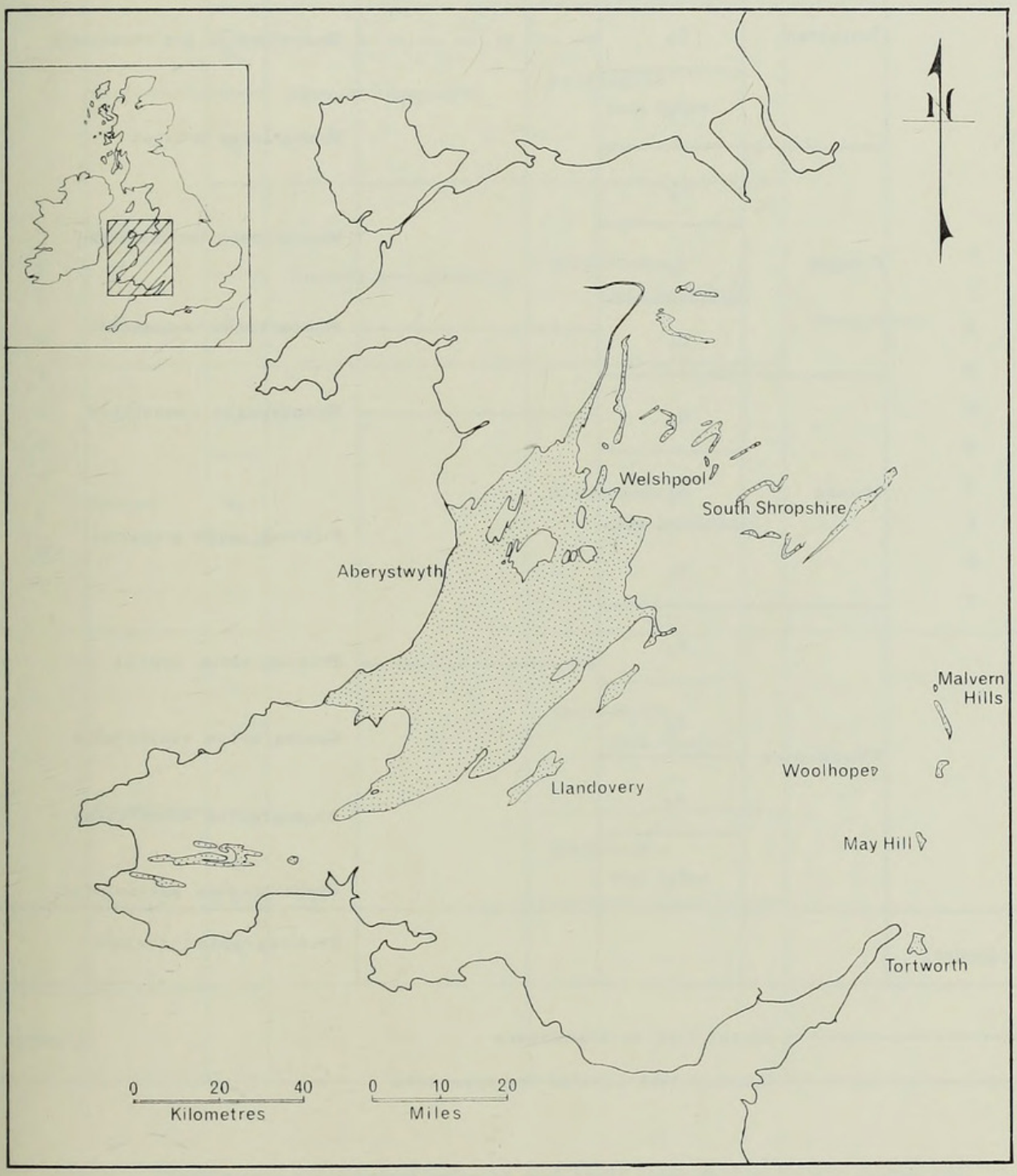


FIG. 1. Outcrop pattern of the Llandovery Series in Wales and the Welsh Borderland.

SERIES	STAGE	DIVISION		GRAPTOLITE ZONES
WENLOCK				Cyrtograptus centrifugus
LLANDOVERY	Telychian	C_6		Monoclimacis crenulata
		C_5	← - - - - - →	Monoclimacis greistoniensis
		C_4		Monograptus crispus
	Fronian	C_3		Monograptus turriculatus
		C_2		
		C_1	← →	Monograptus sedgwickii
	Idwian	B_3	← →	Monograptus convolutus
		B_2		Pristiograptus gregarius
		B_1		
	Rhuddanian	A_4	← →	Pristiograptus cyphus
		A_3		Cystograptus vesiculosus
		A_2		Akidograptus acuminatus
		A_1		Glyptograptus persculptus
ASHGILL				Dicellograptus anceps

← → Direct ties at Llandovery

← - - - - - → Indirect ties outside the type area

FIG. 2. Llandovery Stages (Cocks, Toghill & Ziegler 1970), Lithological Divisions (Jones 1925) and Graptolite Zones.

<table>
<tr><td colspan="2">WENLOCK</td><td></td><td></td><td></td><td></td></tr>
<tr><td rowspan="11">LLANDOVERY</td><td rowspan="3">Telychian</td><td>C6</td><td>Eocoelia sulcata</td><td>Costistricklandia lirata typica</td><td rowspan="2">Pentameroides</td></tr>
<tr><td>C5</td><td>Eocoelia curtisi</td><td>Costistricklandia lirata alpha</td></tr>
<tr><td>C4</td><td rowspan="2">Eocoelia intermedia</td><td rowspan="2">Stricklandia lens ultima</td><td rowspan="6">Pentamerus</td></tr>
<tr><td rowspan="3">Fronian</td><td>C3</td></tr>
<tr><td>C2</td><td rowspan="2">Eocoelia hemisphaerica</td><td rowspan="2">Stricklandia lens progressa</td></tr>
<tr><td>C1</td></tr>
<tr><td rowspan="3">Idwian</td><td>B3</td><td rowspan="8"></td><td rowspan="3">Stricklandia lens intermedia</td></tr>
<tr><td>B2</td></tr>
<tr><td>B1</td></tr>
<tr><td rowspan="4">Rhuddanian</td><td>A4</td><td rowspan="2">Stricklandia lens typica</td><td rowspan="4"></td></tr>
<tr><td>A3</td></tr>
<tr><td>A2</td><td>Stricklandia lens prima</td></tr>
<tr><td>A1</td><td></td></tr>
<tr><td colspan="2">ASHGILL</td><td></td></tr>
</table>

FIG. 3. Llandovery brachiopod lineages and their relationship to the stages and lithological divisions defined in the type area (after Ziegler, Cocks & McKerrow 1968).

The value of conodonts as an additional tool for stratigraphic correlation, both locally and internationally, is examined in this paper. The stratigraphic distribution of conodonts in the Llandovery and early Wenlock of Wales and the Welsh Borderland has been investigated by means of samples collected from a number of well-documented localities. The British faunas are compared with those described from the European continent by Walliser (1964) and from North America by Rexroad (1967), Nicoll & Rexroad (1968) and Pollock, Rexroad & Nicoll (1970). The effects of faunal provincialism on geographic distribution are examined in the light of existing evidence. Comparisons are made between the distribution of conodonts and brachiopods in the shelly facies of the Llandovery in an attempt to recognize some of the effects of facies control on local geographic distribution.

II. PREVIOUS RESEARCH ON LOWER SILURIAN CONODONTS

The first systematic description of a lower Silurian conodont fauna was published by Branson & Branson (1947), who described seventeen species from the Brassfield Formation of Kentucky. They considered the species *Icriodina irregularis* to have the most stratigraphic value, as it was readily identifiable, stratigraphically restricted and abundant.

The next major contribution was made by Walliser (1957, 1962, 1964), who published detailed accounts of Silurian and lower Devonian conodonts from Europe. Walliser (1964) proposed a provisional division of the Silurian into eleven conodont zones, three of which (Bereich I, the *celloni*-Zone and the *amorphognathoides*-Zone) are represented in Llandovery strata. The type section for these zones is within a condensed sequence exposed at Cellon in the Carnic Alps of Austria (Walliser 1964 : pl. 1). The conodont fauna of Bereich I displays similarities to upper Ordovician faunas, with the genera *Ambalodus* and *Amorphognathus* present throughout. The upper part of Bereich I is characterized by specimens referred by Walliser to *Icriodina irregularis*. The *celloni*-Zone is characterized by abundant specimens of *Neospathognathodus celloni* and *Ozarkodina adiutricis*; the *amorphognathoides*-Zone is characterized by *Pterospathodus amorphognathoides* and *Ozarkodina gaertneri*.

After the publication of Walliser's work Llandovery conodont faunas were reported from many parts of the world. Manzoni (1965) recognized Bereich I and the *amorphognathoides*-Zone in the central and eastern Carnic Alps and Schönlaub (1969) recorded Llandovery conodonts from the Hohe Trieb region of the Carnic Alps. Spasov (1966) recorded *N. celloni*, *P. amorphognathoides* and other lower Silurian species in the Balkan peninsula and Spasov and Filipović (1966) recognized the *amorphognathoides*-Zone in Bosnia. Stein (1964 : fig. 17; 1965 : fig. 5) recorded conodonts in the Llandovery of the Frankenwald, Bavaria. Drygant & Tsegelnyuk (1968) found *amorphognathoides*-Zone conodonts in association with *Monoclimacis* cf. *crenulata* in the Retevsky horizon of the Silurian of Podolia. The *celloni*-Zone and the *amorphognathoides*-Zone were recognized in several sections in the northern greywacke belt of the Kitzbuhl Alps, Tyrol, Austria by Mostler (1966, 1967, 1968) and Al-Hasani & Mostler (1969).

Fragmentary Llandovery conodonts have been recorded from Thailand in black

shales containing *Monograptus cyphus* (Igo & Koike 1966 : 15). Igo & Koike (1967, 1968) also recorded a lower Silurian conodont fauna containing *N. celloni* and *P. amorphognathoides* within the Setul Limestone sequence of the Langkawi Islands, Malaya.

In North America, Rexroad (1964) reported the occurrence of *Icriodina* in the lower Silurian of Kentucky and noted the presence of two younger conodont zones. Rexroad recognized the close resemblance between North American and European lower Silurian conodont faunas and pointed out their potential use in international correlation. In 1965 Rexroad & Rickard published the results of their attempt to recognize Walliser's Silurian zones in the Niagara Gorge section of North America. Several zones, including the *amorphognathoides*-Zone, were identified. The *celloni*-Zone was not recognized in the Gorge, but *N. celloni, O. adiutricis* and other characteristic species were recovered from the Reynales Limestone in New York. Rexroad & Rickard (1965 : 1218, text-fig. 1) suggested that the boundary between the *celloni*-Zone and the *amorphognathoides*-Zone coincided with the boundary between the Llandovery and the Wenlock.

Rexroad (1967) next described the conodont fauna of the Brassfield Formation in the Cincinnati Arch region of Kentucky and Ohio. The dominant important species was *Icriodina irregularis,* with *Icriodina stenolophata* and *Spathognathodus oldhamensis* also being characteristic. Rexroad referred the fauna to the upper part of Walliser's Bereich I. This correlation was based largely on the presence of *Icriodina,* although Rexroad (1967 : 34) considered that specimens referred to this genus by Walliser were in fact fragments of *Icriodella* (at that time regarded by Rexroad to be a junior synonym of *Scyphiodus*). The position of the boundary between Bereich I and the *celloni*-Zone was to some extent clarified by Rexroad's report in this paper (1967 : 13) of the recovery by Bergström of high Bereich I or low *celloni*-Zone conodonts in association with graptolites referable to the *Monograptus sedgwickii* Zone.

Nicoll & Rexroad (1968) extended the limits of the Brassfield Formation to include the Lee Creek Member at the top, and described the conodont faunas of this new member and of the overlying Salamonie Dolomite in Indiana and Kentucky. The overlap of *N. celloni* at the lower end of its range with *I. irregularis* and at the upper end with *P. amorphognathoides* was regarded by Nicoll & Rexroad as an indication that slight redefinition of Walliser's zonal scheme was necessary. They therefore proposed the erection of three assemblage zones, the *Icriodina irregularis* Assemblage Zone, the *Neospathognathodus celloni* Assemblage Zone and the *Pterospathodus amorphognathoides—Spathognathodus ranuliformis* Assemblage Zone. The critical point of Nicoll & Rexroad's zonal scheme was their definition of the *Neospathognathodus celloni* Assemblage Zone by the total range of the genus *Neospathognathodus.* Walliser (1964 : table 1) showed that *Neospathognathodus pennatus,* which occurs as a complementary form to *P. amorphognathoides,* ranged throughout the *amorphognathoides*-Zone in Europe. As pointed out by Schönlaub (*in* Jaeger & Schönlaub 1970), this necessitates the conclusion that the whole of the *celloni*- and *amorphognathoides*-Zones of Europe are equivalent to the *Neospathognathodus celloni* Assemblage Zone of North America. This clearly is not what Nicoll

& Rexroad believed nor what they intended in their definition, as they stated (1968 : 7) that their *N. celloni* Zone included the larger part, if not all, of Walliser's *celloni*-Zone and the lower part of his *amorphognathoides*-Zone. It follows that the boundary between the *N. celloni* Zone and the *P. amorphognathoides—S. ranuliformis* Zone of North America is, at present, unsatisfactorily defined. Craig (1969) applied both the European and North American zonal schemes to the sequence of lower Silurian conodont faunas he investigated from the Batesville district of Arkansas.

Conodonts from the *Icriodina irregularis* Assemblage Zone and from older Silurian strata of northern Michigan and Ontario were described by Pollock, Rexroad & Nicoll (1970). The fauna of the *I. irregularis* zone differed appreciably from that of time-equivalent strata in the Cincinnati Arch area and the authors considered that this was due to faunal provincialism. In particular, *Icriodina* itself was absent and was replaced by *Icriodella* as the dominant platform element. Pollock *et al.* proposed the erection of the *Panderodus simplex* Assemblage Zone for those faunas below the *I. irregularis* zone and above characteristic Ordovician faunas.

There are few records of Llandovery conodonts from Britain. Whittard (1927 : 743) noted their presence in the Pentamerus Beds of Harper's Dingle, Shropshire, and Squirrel & Tucker (1960 : 178) listed conodont genera from the upper Haugh Wood Formation of the Woolhope Inlier, Herefordshire. Brooks & Druce (1965) described forty specimens, referable to nine species, from a limestone conglomerate at the base of the Wych Formation at Gullet Quarry in the Malvern Hills. On the basis of six specimens of a spathognathodid, which they identified as *Spathognathodus* cf. *celloni*, they referred the fauna to the *celloni*-Zone. The conodonts from an upper Llandovery limestone exposed at Hollybush Quarry in the Malvern Hills were listed by Jones, Brooks, Bassett, Austin & Aldridge (1969), who also re-examined the Wych Formation in Gullet Quarry. The Hollybush Quarry fauna included specimens of *Neospathognathodus celloni*, but these were not considered to be conspecific with the specimens described by Brooks & Druce. Species characteristic of both the *celloni*-Zone and the *amorphognathoides*-Zone were abundant in the Hollybush and in the Gullet collections.

III. TECHNIQUES

Techniques of conodont extraction have become well-established and the most efficient method of large-scale recovery has proved to be the disintegration of calcareous rocks by dilute acetic, monochloracetic or formic acid. This method has an additional advantage in the commonly high quality of preservation of conodonts in limestones. Calcareous rocks were, therefore, collected preferentially in the field. The shale and turbidite sequences of west-central Wales lack calcareous strata, but thin limestone horizons are comparatively common in the shelf successions of the Welsh Borderland and adjacent parts of Wales. Calcareous rocks are rare in the type area around Llandovery. The hard mudstones and arenites of the Llandovery area resisted all attempts at disintegration, and the rare calcareous horizons did not yield conodonts. The stratigraphic distribution of Llandovery conodonts was, therefore, examined in the Welsh Borderland by

means of collections from several separate localities. This approach necessitated concentration on major exposures, for which adequate stratigraphic information was already available.

The standard laboratory techniques of digestion in 10% acetic acid and separation of the residues in bromoform were employed to recover conodonts from calcareous rock samples. Selected specimens were coated with ammonium chloride or magnesium oxide prior to photography. Photographs were taken using a Leitz Dialux polarizing microscope and a Leica M3 35 mm camera loaded with Kodak Panatomic X film.

IV. DETAILS OF SAMPLING LOCALITIES

Each of O. T. Jones' subdivisions of the Llandovery Series, with the exception of the uppermost (C_6), was sampled at a well-documented locality within the type area. No identifiable conodonts were recovered from any of the samples, nor from samples collected at the Sawdde Gorge, Llandeilo (SN/715260) and the Craig-wen Quarry, Meifod (SJ/099091) in Wales; Middletown (SJ/301128), Buttington Brick Works (SJ/265100), the Norbury to Linley Lane (SO/359928), the Onny River section (SO/426853) and Gilberries Brook (SO/512926) in Shropshire. Conodonts recovered from the Rhuddanian Powis Castle Formation of the Gwern-y-Brain section (SJ/219128), near Welshpool, Montgomeryshire, were most probably derived from locally exposed Upper Ordovician strata.

Samples that yielded conodonts were collected from several localities, viz.:

a. Llansantffraid ym Mechain, Montgomeryshire

Conodonts, including the species *Icriodella discreta* and *Icriodina irregularis* were recovered from limestone bands exposed in a trackside quarry 200 m north-west of Gelli Farm (SJ/236193) (Text-fig. 4). The age of these beds in terms of the type succession has not been established, but Whittington (1938 : 440) equated them with the V_{2b} subdivision defined at Meifod, Montgomeryshire by King (1928). Ziegler, Cocks and McKerrow (1968 : 768) gave a range from late Rhuddanian possibly into the Fronian for the V_2 Formation. The Gelli Farm Quarry sequence, therefore, is probably of Idwian age.

b. The Hope Valley, Shropshire

The outcrop pattern of the Llandovery Series in South Shropshire is shown in Text-fig. 5. Two Llandovery formations, the Venusbank Formation and the Minsterley Formation, were defined in the Hope Valley area of the outcrop bordering the Shelve by Ziegler, Cocks & McKerrow (1968 : 742). The type section for both formations is in Hope Brook.

The Venusbank Formation is exposed in Hope Quarry (SJ/355021), where 10 m of thickly-bedded sandstones, becoming flaggy towards the top, are displayed. The basal calcareous sandstone is not exposed in the quarry face, but was collected from a small roadside exposure in front of the quarry. This sample (H.Q.1) and sample H.Q.3, from low in the section, yielded abundant conodonts, including *Icriodella deflecta*, *Icriodina irregularis*, *Spathognathodus abruptus*, *S. hassi* and *S. oldhamensis*.

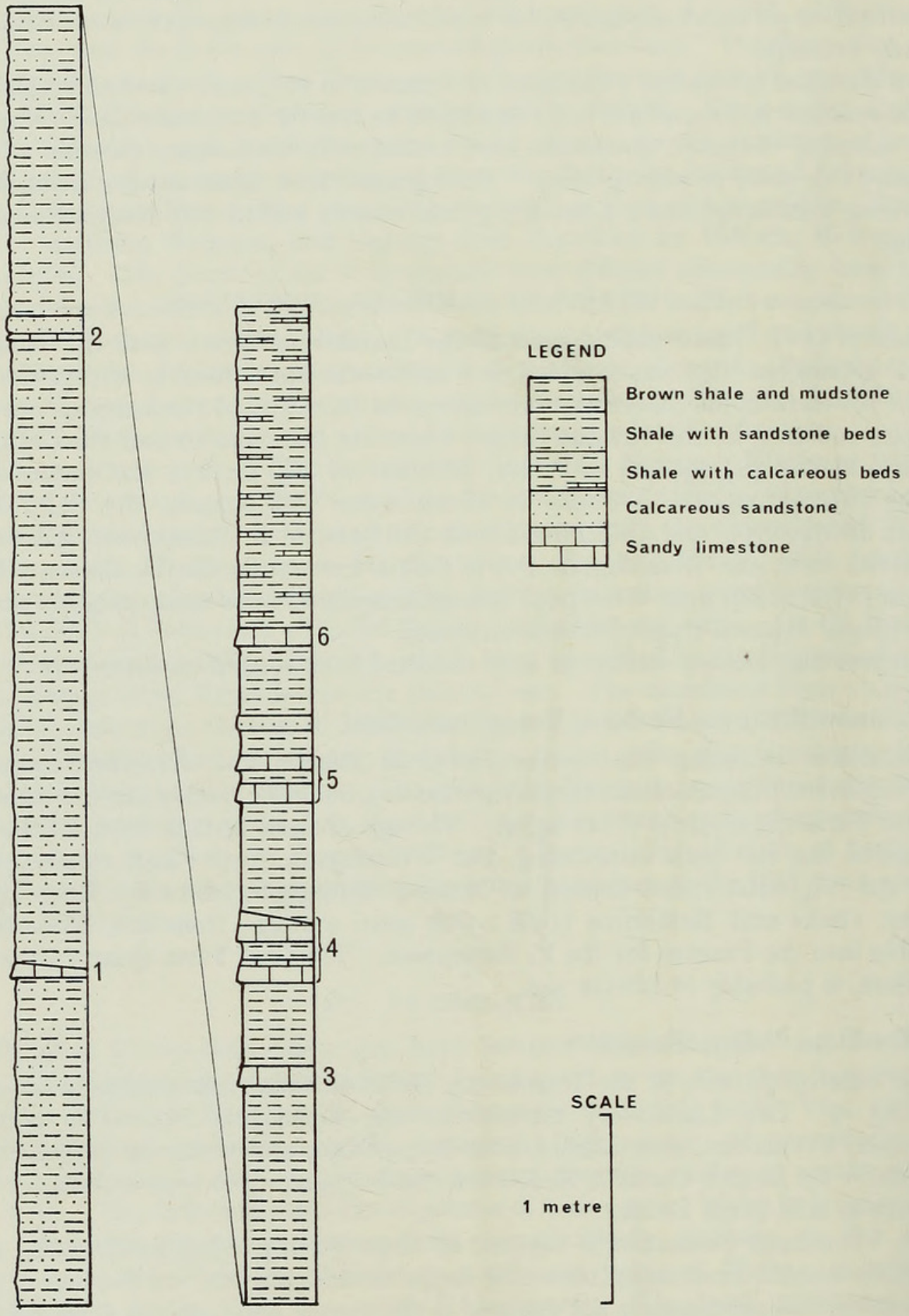


FIG. 4. Section at Gelli Farm Quarry, Llansantffraid ym Mechain. The base and top of the formation are not exposed. The horizons of samples Gelli Farm 1–6 are indicated.

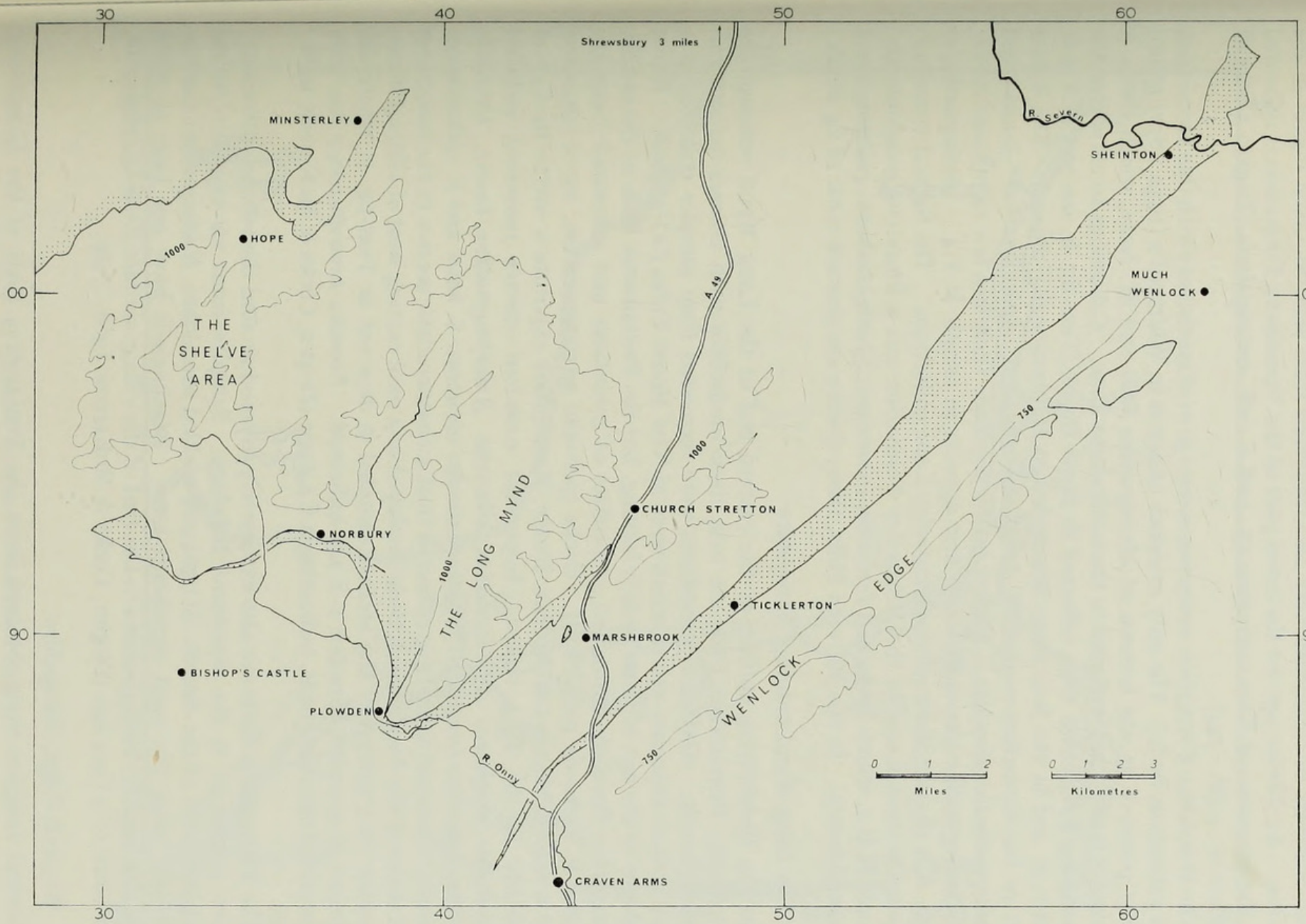


FIG. 5. Outcrops of the Llandovery Series in South Shropshire. After Whittard (1928, 1932) with minor modifications.

Small numbers of conodonts were also recovered from samples taken higher in the section. An Idwian age for the lower part of the Venusbank Formation is indicated by the presence of *Climacograptus* sp. and *C.* aff. *rectangularis* (Ziegler, Cocks & McKerrow, 1968 : 744).

The Minsterley Formation comprises some 130 m of mudstones with thin arenaceous and calcareous beds. The only evidence of age is in Whittard's (1932 : 877) record of the presence at one horizon of *Monograptus halli* and *M. becki*, which Cocks & Rickards (1969 : 225) referred to the *turriculatus* Zone. Calcareous levels within the Minsterley Formation were collected in Hope Brook (Text-fig. 6, samples H.V.3–6, H.B.1, 2) and in the lane from Minsterley to Habberley (SJ/380049). The lowest part of the formation contained *Ambalodus anapetus*, *Aphelognathus siluricus* and *Spathognathodus abruptus*. Higher in the sequence there are few significant forms, but *Hadrognathus staurognathoides* first appears in sample H.V.4. *Spathognathodus* n. sp. A is characteristic of the Minsterley Lane collections. The highest conodont-bearing horizon found in the Minsterley Formation was a limestone conglomerate, sample H.B.2, which contained *Icriodella inconstans*, *Spathognathodus gulletensis* and *S. ranuliformis*. In the Malvern Hills, these species are characteristic of C_5 strata.

c. The Long Mynd outcrop, Shropshire

In the Marshbrook outlier, at the eastern end of the Long Mynd outcrop, the Llandovery Pentamerus Beds are soft, dark mudstones with arenaceous and calcareous bands. Abundant conodonts were recovered from samples collected at a small stream exposure 250 m south-west of New House Farm (SO/434898). Direct evidence of the age of these beds is lacking, but the Pentamerus Beds of the nearby Hamperley Borehole contained graptolites of *convolutus* and *sedgwickii* Zone age (Cocks & Rickards 1969 : 217). Cocks (personal communication, 1970) suggested that a reasonable age for the New House, Marshbrook exposure is within B_1–C_1 and probably in the B_{2-3} region. Important conodont species recovered included *Ambalodus anapetus*, *Aphelognathus siluricus*, *Amorphognathus tenuis*, *Icriodella deflecta*, *Icriodina irregularis*, *Spathognathodus abruptus*, *S. hassi* and *S. oldhamensis*. A similar conodont fauna was collected from a characteristic section in the limestones and shales of the Pentamerus Beds displayed in a road cutting west of Hillend Farm, Plowden (SO/396877). The section sampled is depicted in Text-fig. 7, where the horizons of samples Plowden 1–8 are indicated. *Eocoelia hemisphaerica* has been recovered from these beds, indicating a C_{1-2} age (Ziegler, Cocks & McKerrow 1968 : 746).

The Pentamerus Beds are also extensively exposed around the village of Norbury, where sandstone is the dominant lithology. Samples from an exposure in the roadside south of the church (SO/364928) yielded conodonts, *Hadrognathus staurognathoides* being the most significant form. Brachiopods have not been recorded from this locality, but exposures to the west of the village contain *Eocoelia intermedia*, indicative of a C_{3-4} age (Ziegler, Cocks & McKerrow 1968 : 746).

d. Wenlock Edge, Shropshire

Several samples were obtained from the Pentamerus Beds of the Llandovery

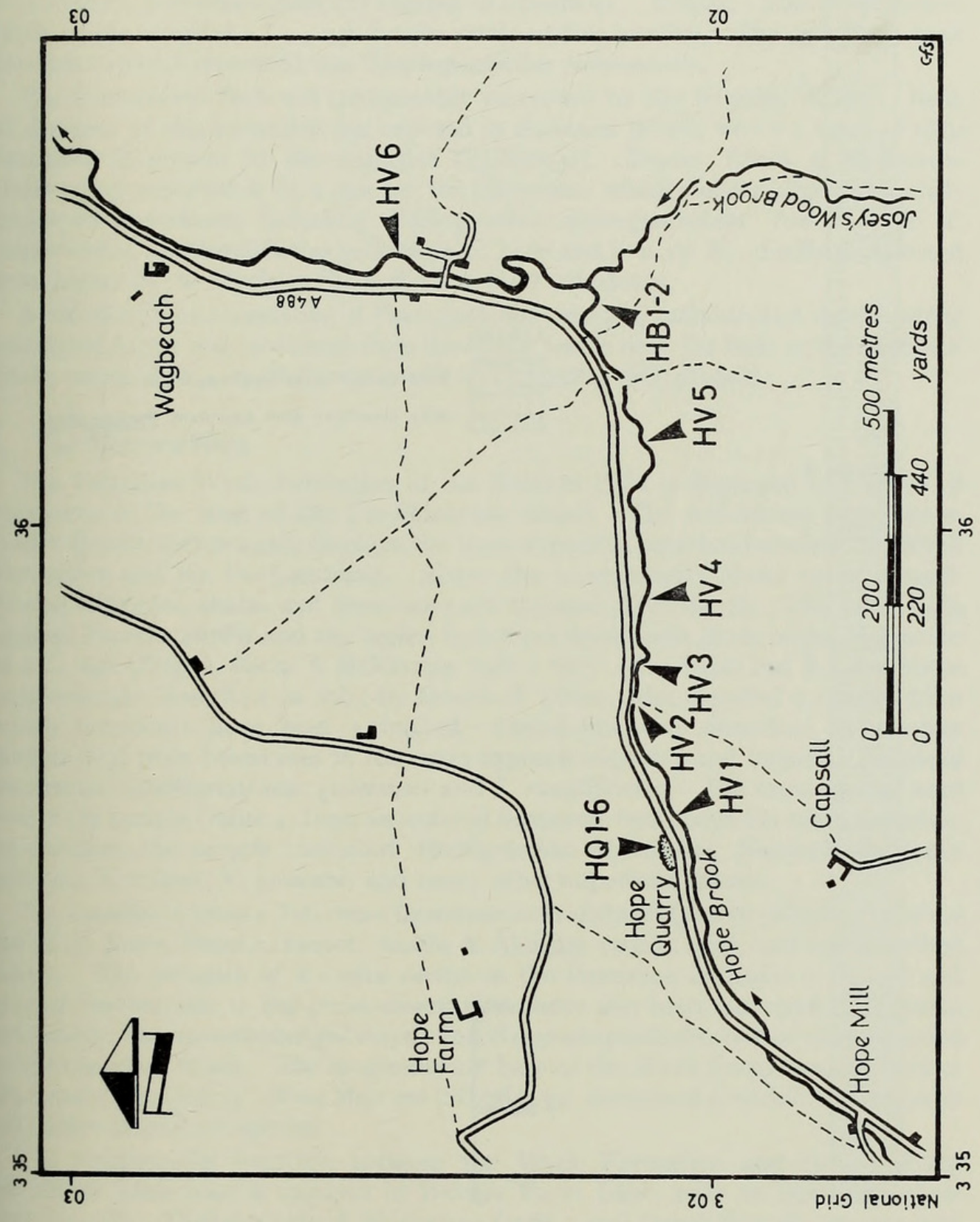


FIG. 6. Sample localities in the Hope Valley.

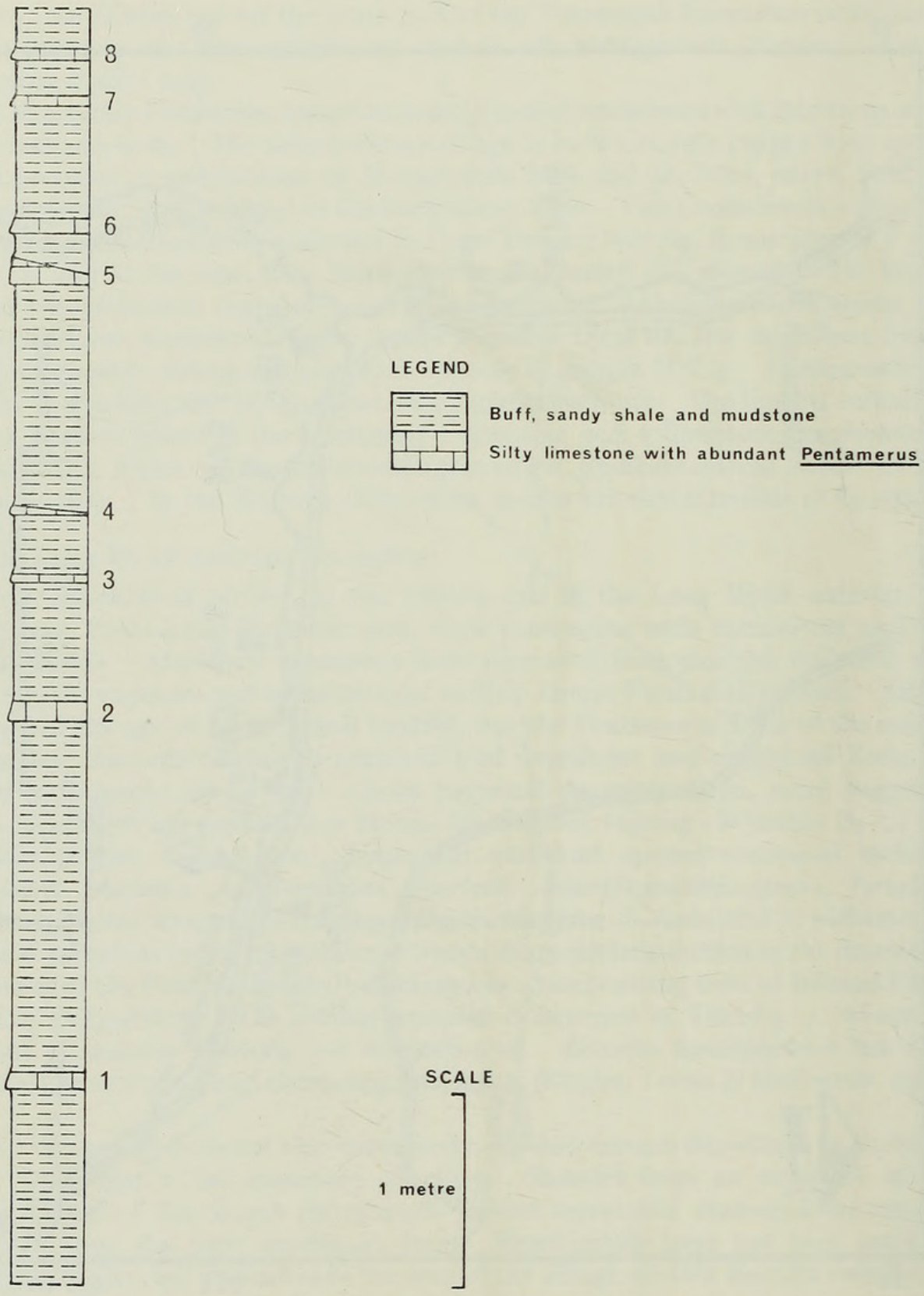


FIG. 7. Section in the Pentamerus Beds at Hillend Farm, Plowden. The base and top of the formation are not exposed. The horizons of samples Plowden 1–8 are indicated.

outcrop lying parallel to Wenlock Edge, but only one, from Ticklerton Brook (SO/482909), yielded a significant number of conodonts. Ziegler, Cocks & McKerrow (1968 : 748) recorded a C_{1-2} age for the strata at this locality. The only important conodont species recovered was *Spathognathodus oldhamensis*.

The Pentamerus Beds are conformably succeeded by the Hughley Shales. Beds at the base of this formation are exposed in Sheinton Brook, where a band of silty limestone is present in the sequence (SJ/612031). Ziegler, Cocks & McKerrow (1968 : 749) reported a C_{3-4} age for the limestone, which yielded abundant, well-preserved conodonts, including *Hadrognathus staurognathoides*, *Icriodella* cf. *I. malvernensis*, *Spathognathodus gulletensis*, *S. hassi* and *S.* n. sp. B. Samples collected from higher in the Hughley Shale did not yield conodonts.

A conodont fauna consisting of *Pterospathodus amorphognathoides* and characteristic associated forms was recovered from limestone bands near the base of the Wenlock Shale, exposed in a small stream south of Ticklerton (SO/481901).

e. The Malvern Hills

The Telychian Wych Formation of the Malvern Hills is displayed in a series of exposures to the west of the Pre-Cambrian massif. The well-known exposure in Gullet Quarry (SO/761318) displays the unconformable junction between the Wych Formation and the Pre-Cambrian. Above the unconformity about 30 m of sandstones, siltstones, shales and limestones are exposed (Text-fig. 8). The lower beds yielded *Eocoelia curtisi* and the higher beds *Costistricklandia lirata alpha*, indicative of a C_5 age (Ziegler, Cocks & McKerrow 1968 : 757). The basal bed is a limestone conglomerate, described in 1965 by Brooks & Druce, who supplied a sample from which conodonts have been extracted. Conodonts were abundant in samples (Gullet 1–3) from limestones in the main exposed sequence and included *Icriodella inconstans*, *Spathognathodus gulletensis* and *S. ranuliformis*. The same species were present in sample Gullet 4, from an isolated limestone lens above the main sequence. In addition, this sample contained *Apsidognathus tuberculatus*, *Neospathognathodus bullatus*, *N. celloni*, *N. pennatus* and many other important species.

The conodonts from a Telychian limestone in Hollybush Quarry (SO/760371) were listed by Jones, Brooks, Basset, Austin & Aldridge (1969 : 465), and are described herein. The presence of *Eocoelia curtisi* in the limestone indicates a C_5 age and graptolites referable to the *greistoniensis* Zone have also been recovered. *Icriodella inconstans*, *Spathognathodus gulletensis* and *Neospathognathodus celloni* were included in the conodont fauna. The conglomeratic base of the Wych Formation exposed at 'Sycamore tree Quarry', West Malvern (SO/765459), contained *Icriodella malvernensis* and other important species.

The conformable junction between the Wych Formation and the overlying Woolhope Limestone is exposed in Birches Farm Lane, near an open air school (SO/760468). Ziegler, Cocks & McKerrow (1968 : 757) found that the greater part of the Wych Formation is of C_6 age, and the beds of this exposure are presumably of high C_6 age. The conodont fauna recovered from a limestone band 1·5 m below the junction (sample Cowleigh Park 1) consisted of *Pterospathodus amorphognathoides*

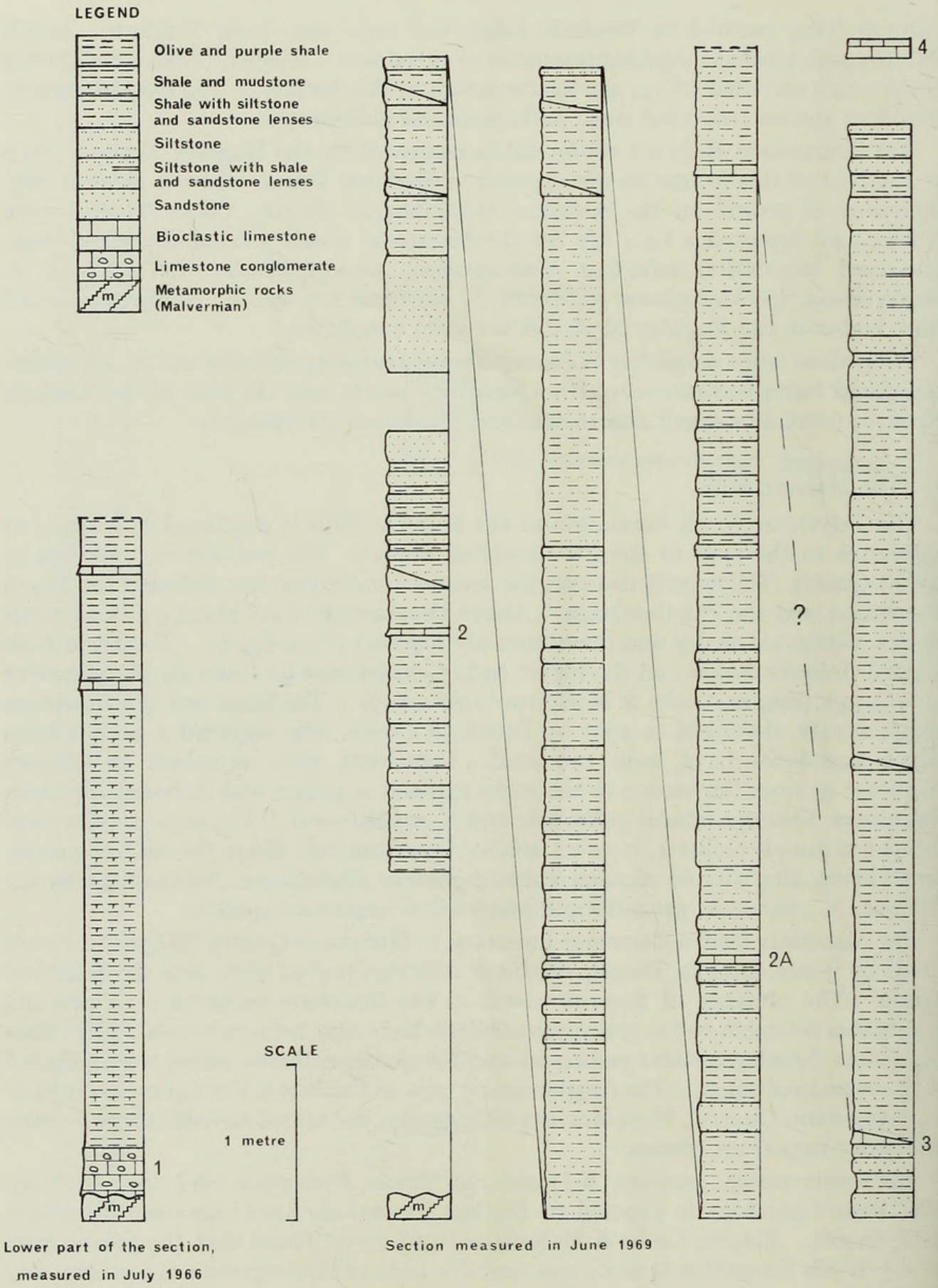


FIG. 8. Section in the Wych Formation at Gullet Quarry, Malvern Hills. The base of the formation is unconformable on the Malvernian. The upper part of the section is obscured by rubble and the top of the formation is not exposed. The horizons of samples Gullet 1–4 are indicated.

and characteristic associated forms. Samples from the Woolhope Limestone at this locality did not yield useful conodonts.

f. Woolhope, Herefordshire

A conodont fauna recovered from limestones at the top of the upper Haugh Wood Formation (sample Haugh Wood 3) at the track junction in Haugh Wood (SO/589358) included *Pterospathodus amorphognathoides* and *Ozarkodina gaertneri*. A C_6 age for this horizon is indicated by the presence of *Costistricklandia lirata typica* (Ziegler, Cocks & McKerrow 1968 : 757). The Woolhope Limestone south of Woolhope village (SO/612353) yielded abundant simple cones.

g. Tortworth, Gloucestershire

Collections made by the author from the Telychian strata of the Tortworth inlier did not yield a significant number of conodonts, but conodonts have been recovered from the Damery Formation near Damery Bridge (ST/706943) by Miss M. Roberts, who kindly made her collection available for description. *Icriodella inconstans* and *Spathognathodus gulletensis* were among the species present. Ziegler, Cocks & McKerrow (1968 : 761) recorded *Eocoelia curtisi* and *Costistricklandia lirata alpha* from the Damery Formation, indicative of C_5 age.

In addition, rock specimens collected by Dr A. M. Ziegler from localities listed in Ziegler, Cocks & McKerrow (1968) were kindly supplied by Dr W. S. McKerrow. Specimens M-G-C, from the C_5 Yartleton Beds of May Hill, and T-R-A, from the Damery Beds of Tortworth, yielded a small number of conodonts.

V. THE CONODONT FAUNAS

a. General Review

Of the 101 rock samples collected from Llandovery and early Wenlock strata of Wales and the Welsh Borderland, 58 yielded identifiable conodonts. A total of 11,750 specimens are referred to 36 genera and 108 species and subspecies. 34 of the genera and 94 of the species and subspecies are named. The species *Amorphognathus tenuis, Diadelognathus nicolli, Icriodella deflecta, Icriodella inconstans, Icriodella malvernensis, Ozarkodina alisonae, Spathognathodus abruptus* and *Spathognathodus gulletensis* are new. The collections are dominated by the genus *Panderodus*, to which about half the specimens are referred. *Panderodus unicostatus* is by far the most abundant species and is represented by 3,750 specimens.

b. Stratigraphic Distribution

No idnigenous conodonts were recovered from strata of Rhuddanian age. The distribution of conodonts recovered from strata of Idwian, Fronian, Telychian and early Wenlock age is summarised in Tables 1–4. The genera of most stratigraphic value are the platforms and *Spathognathodus*. Some species of the bar and blade genera are also useful, but the simple cones appear to be of very limited stratigraphic value.

TABLE I

Conodont Stratigraphic Ranges: I

SPECIES \ SAMPLE NO.	LLANDOVERY																			lower Wenlock	
	B_{1-3}			C_{1-2}					C_{3-4}		C_5						C_6				
	Gelli Farm 1–6	New House, Marshbrook	H. Q. 1, H. Q. 3	Plowden 1–8	Ticklerton Brook	H. V. 3	Minsterley Lane	H. V. 4	Norbury 1–3	Sheinton 2	H. B. 2	Gullet 1–3	Gullet 4	Hollybush (MB 68/16)	West Malvern 1, 2	Damery Beds	Cowleigh Park 1	Haugh Wood 3	Woolhope 1	Ticklerton 1–3
Acodus curvatus					21	4	6	35		2		4	10							2
A. unicostatus	6		1		35	6	26	83	3	5	2	2	9	1			2			4
Ambalodus anapetus		100		19		13														
A. galerus													44							
Ambalodus spp.	2	2		2	4			1												
Amorphognathus tenuis		47		13																
Aphelognathus siluricus		7		19		4														
Apsidognathus tuberculatus													60							
Astrognathus tetractis													16							
Astropentagnathus irregularis														1						
Aulacognathus kuehni												14		3						
Carniodus carinthiacus																	73	7		25
C. carnicus																	13			2
C. carnulus													2				81	1		48
C. carnus													2	1			68	2		26
Carniodus spp.		15		3																
Diadelognathus nicolli																				11
D. primus									1											
Distacodus obliquicostatus							1													
Distomodus? egregius				10						15		5	4	1	1		6			4
D? extrorsus		3	6	4					5		5	4		7	1			1		
D. kentuckyensis	2	6	10	27		2	1	3	10	13	9	14	7	6		1	2	2		7
D. triangularis tenuirameus					3								10							
D. triangularis triangularis		17		6								4	17				27			17
Distomodus n. sp.										3										
Distomodus? spp.			1	5						2		2	2			1				
Drepanodus aduncus										1				1			12	1		2
D. suberectus		7	8		2	5						3	14	1	1					
Drepanodus spp.	1		2	1	8			1					4							2
Exochognathus brassfieldensis	4	2	6	14	1	2		2	2	4	1		14	1	4					1
E. brevialatus		23	4	3		1	1					1								13

TABLE II

Conodont Stratigraphic Ranges: II

SPECIES \ SAMPLE NO.	LLANDOVERY																		lower Wenlock	
	B_{1-3}			C_{1-2}					C_{3-4}		C_5						C_6			
	Gelli Farm 1–6	New House, Marshbrook	H. Q. 1, H. Q. 3	Plowden 1–8	Ticklerton Brook	H. V. 3	Minsterley Lane	H. V. 4	Norbury 1–3	Sheinton 2	H. B. 2	Gullet 1–3	Gullet 4	Hollybush (MB 68/16)	West Malvern 1, 2	Damery Beds	Cowleigh Park 1	Haugh Wood 3	Woolhope 1	Ticklerton 1–3
Exochognathus caudatus		3		6						13	2	7	12	2	2		7			8
E. detortus			3	3						8		4		1			10	1		6
E. keislognathoides		6	10	1		1	1													
E. latialatus																	25	3		
Exochognathus n. sp.				1																
Exochognathus spp.	3	13	5	14		1	1	1	4	3	6	3	1	2	2	1	1	1		5
Gothodus? n. sp.		3					1													
Hadrognathus staurognathoides								1	3	16	2	26	1	3	3	1	5	4		5
Hibbardella? prima				2																
H? trichonodelloides										5			2				2			
Hibbardella n. sp.										3										
Hindeodella equidentata				13	6	6		20	1	1		4	8	3	2		2			4
Hindeodella spp.		2	3	15		1	2	21			2	2	4	1				1	2	2
Icriodella deflecta		13	38	2																
I. discreta	15																			
I. inconstans											6	186	121	13	3	27				
I. malvernensis															63					
I. cf. I. malvernensis										2										
Icriodina irregularis	1	1	2	8																
Icriodina sp.								1												
Ligonodina kentuckyensis		1	6	10	5	11	1	6	1	15	5	1	1							11
L. petila										1			3							6
L. salopia		3				1				1		2					2			7
L. silurica				4			2		1	11		13	3	1						
L? variabilis				4		1		4	1	23		21		1						12
Ligonodina spp.		3	4	9	1	4	1	1	4		6	5	7		5					17
Lonchodina detorta				1		1		17	1	6	1									
L. fluegeli								17		4										
L. greilingi	1		4	5	7	2		7		5		4	1				2			3
L. walliseri		1	4	9	1	11	1	1	3	11	4	4	4		2	1	2			25
Lonchodina sp. A			1	1				2				1								

TABLE III

Conodont Stratigraphic Ranges: III

SPECIES \ SAMPLE NO.	LLANDOVERY																		lower Wenlock	
	B_{1-3}			C_{1-2}					C_{3-4}				C_5					C_6		
	Gelli Farm 1-6	New House, Marshbrook	H. Q. 1, H. Q. 3	Plowden 1-8	Tickterton Brook	H. V. 3	Minsterley Lane	H. V. 4	Norbury 1-3	Sheinton 2	H. B. 2	Gullet 1-3	Gullet 4	Hollybush (MB 68/16)	West Malvern 1, 2	Damery Beds	Cowleigh Park 1	Haugh Wood 3	Woolhope 1	Tickterton 1-3
Lonchodina sp. B				4	1	3	1			3			2							
Lonchodina sp. C										1										23
Lonchodina spp.				2				4				1								1
Neoprioniodus costatus costatus														1			34	4		37
N. costatus paucidentatus			2	1								2	21							
N. excavatus	1	3	3	5	1	1		5	3	4	1	3	13	1			1	1		14
N. latidentatus						5		3		2							2			1
N. multiformis		3		13	3	12	1	14		1		1	1	1	1					22
N. planus				4	6	4	1	28		16		3	3	1	1					
N. subcarnus												1	5	2			41			19
Neoprioniodus spp.	1			8		3		1	2			1	3							1
Neospathognathodus bullatus													1							
N. celloni												1	161	14						
N. pennatus													45	2			2			4
Neospathognathodus? sp.			1																	
Ozarkodina adiutricis													3	6						
O. alisonae												24		3	5	2				
O. cf. O. edithae		1	4	21	1	1	4			3				1						
O. gaertneri													104	2			35	5		74
O. hanoverensis													1		1					
O. media		7	1	19	15	3		15	6	8	3	13	9	1			5	1		2
O. typica	1	3	1	6		2	4	3				1								1
Ozarkodina spp.		6	1	10	6	1		1			1	1	2	1						
Paltodus costulatus					3		1			3		1	2				30	3		24
P. deboli	2				12	3	6	39			1									
P. dyscritus	1		2	1	21	4	10	42			3	4	9	1						3
P. migratus	1				13	3	5	27					4							
Panderodus cf. P. gracilis			1	12	24	10	3	19	3		3	7	102							
P. serratus		13	27	79	7	30		59	3	4	1				2			13		
P. simplex	41	19	59	212	152	28	24	53	27	64	7	75	352	27	20	1	89	20	24	156
P. cf. P. staufferi		2	4	8	20	10		35	8	7	4	7	188				15			21

Table IV

Conodont Stratigraphic Ranges: IV

SPECIES \ SAMPLE NO.	LLANDOVERY																		lower Wenlock	
	B_{1-3}			C_{1-2}					C_{3-4}		C_5						C_6			
	Gelli Farm 1–6	New House, Marshbrook	H. Q. 1, H. Q. 3	Plowden 1–8	Ticklerton Brook	H. V. 3	Minsterley Lane	H. V. 4	Norbury 1–3	Sheinton 2	H. B. 2	Gullet 1–3	Gullet 4	Hollybush (MB 68/16)	West Malvern 1, 2	Damery Beds	Cowleigh Park 1	Haugh Wood 3	Woolhope 1	Ticklerton 1–3
Panderodus unicostatus	78	19	129	416	275	51	27	107	30	181	11	179	1304	51	29	7	292	40	91	361
Panderodus sp. A		1		11	7	2		4	2	6			41				23	3		16
Plectospathodus extensus				1				25		2	1	1	5				6			
P. flexuosus					4	1	2					1	1							
P. irregularis				2		2			1											
Plectospathodus spp.				1									1							
Pt. amorphognathoides																	88	9		77
Pygodus? lyra													20							
Sagittodontus edentatus	5	5	12	2			2			2	9	1		1	4		1			
Spathognathodus abruptus		3	7	16		2														
S. cf. S. abruptus							1													
S. gulletensis										1	1	258	29	8	18	7				
S. hassi		5	1	26		1				1										
S. inclinatus				15		7	1	20	21	7	4	8	23		3	1		1		
S. oldhamensis		10	8	15	18															
S. polinclinatus												1		12						
S. ranuliformis											3	16	18		3	1		1		4
Spathognathodus n. sp. A							14													
Spathognathodus n. sp. B										5					1					
Spathognathodus spp.		1	2	7		1			3	2				1						
Synprioniodina bicurvata		1					2			2		1	3	1						
S. silurica				1	1						1	4	9	1	1					
Trichonodella asymmetrica				1	1					2	1	2	2							
T. excavata			1	5	1	5		4		2	2	1	17	2			4			5
T? expansa			2	3		3	2			6		7	5	2	1	1				4
T. inconstans		1	7	9	3	4	6	6	2	11	3	2	4	1	2		1			35
T. symmetrica		3	1	1	1		1	9	3		1	21	6	4					1	
Trichonodella spp.		7	3	10	4	6		1	10		4	3	12	1	1					11
gen. et sp. indet. A									1											
gen. et sp. indet. B										1										

Of the platform genera, *Icriodella*, which ranges from the Idwian to the Telychian (C_5), is of particular stratigraphic importance. The stratigraphic distribution and possible phylogenetic relationships of the four species recognized are illustrated in Text-fig. 9. The oldest fauna recovered, probably of early Idwian age, contains *Icriodella discreta*, which is succeeded by *Icriodella deflecta* in the late Idwian. Icriodellids are rare in the C_{1-4} interval of the Welsh Borderland; two broken specimens from the early Fronian are probably referable to *I. deflecta* and two specimens from a horizon of C_{3-4} age are identified as *I.* cf. *I. malvernensis*. The latter appear to be transitional forms in the development of *I. malvernensis* from *I. deflecta*. The genus *Icriodella* is abundant in strata of C_5 age, where it is represented by two species, *I. inconstans* and *I. malvernensis*. *Icriodella inconstans* is the more abundant and widespread, being present in all faunas of C_5 age, whereas *I. malvernensis* is currently known only from the West Malvern locality. No icriodellids have been recovered from strata of younger than C_5 age.

The genus *Icriodina* is morphologically similar to *Icriodella* and the two are possibly phylogenetically related. *Icriodina irregularis* is an important constituent of faunas from the midwestern area of the United States (Rexroad 1967), but is rare in the British collections. A few specimens have been recovered from Idwian and early Fronian strata. A single specimen of *Icriodina* from a younger horizon (Minsterley Lane) is similar in many characteristics to the North American species *I. stenolophata*. These occurrences are depicted in Text-fig. 9.

The genus *Amorphognathus* is represented by a single species, *A. tenuis*, which has been recovered only from strata of late Idwian and early Fronian (C_{1-2}) age. Al-Hasani & Mostler (1969 : text-fig. 12) illustrated an apparent lineage between *Amorphognathus* and *Astropentagnathus*, the latter of which Mostler (1967) considered to be the ancestor of *Apsidognathus* and *Aulacognathus*. A single specimen of *Astropentagnathus irregularis* and several specimens of *Aulacognathus kuehni* and *Apsidognathus tuberculatus* have been recovered from C_5 strata in the Malvern Hills. These occurrences, however, can only be regarded as local and no stratigraphic importance can at present be attached to them. This is also true of the occurrences in C_5 strata of *Astrognathus tetractis*, *Pygodus*? *lyra* and *Ambalodus galerus*. Another possible descendent of *Amorphognathus* is *Hadrognathus staurognathoides*, which is present in small numbers in most samples of C_{3-4} age and younger.

The genus *Neospathognathodus* is important in both the European and North American zonal schemes, but its occurrence may be anomalous in Britain, where it is almost entirely restricted to strata of C_5 age. The species *N. celloni* and *N. pennatus* are common and a single specimen of *N. bullatus* has been recovered. A few specimens of *N. pennatus* occur in C_6 and the early Wenlock. The monospecific genus *Pterospathodus*, which is descended from *Neospathognathodus*, is also stratigraphically important in Europe and North America. In the Welsh Borderland, *Pterospathodus amorphognathoides* is abundant in strata of C_6 and early Wenlock age.

The genus *Spathognathodus* is represented by several species, whose distribution and possible relationships are illustrated in Text-fig. 10. Three species, *S. abruptus*, *S. hassi* and *S. oldhamensis*, are present in the Idwian and range into the Fronian. Morphological similarities between *S. hassi* and *S. oldhamensis* suggest that they

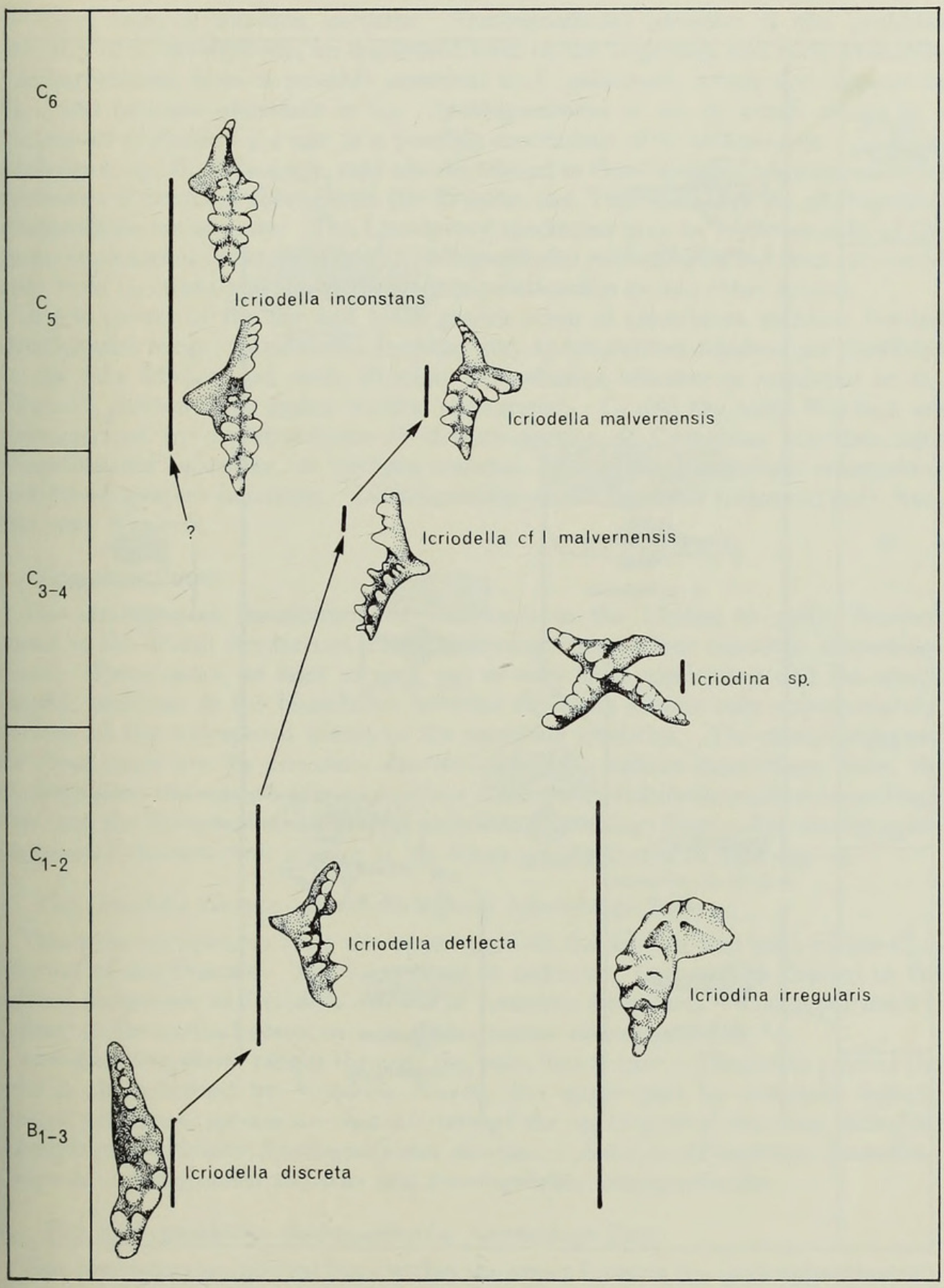


FIG. 9. The genera *Icriodella* and *Icriodina*. Heavy vertical lines indicate approximate stratigraphic ranges. Arrows indicate suggested phylogenetic relationships.

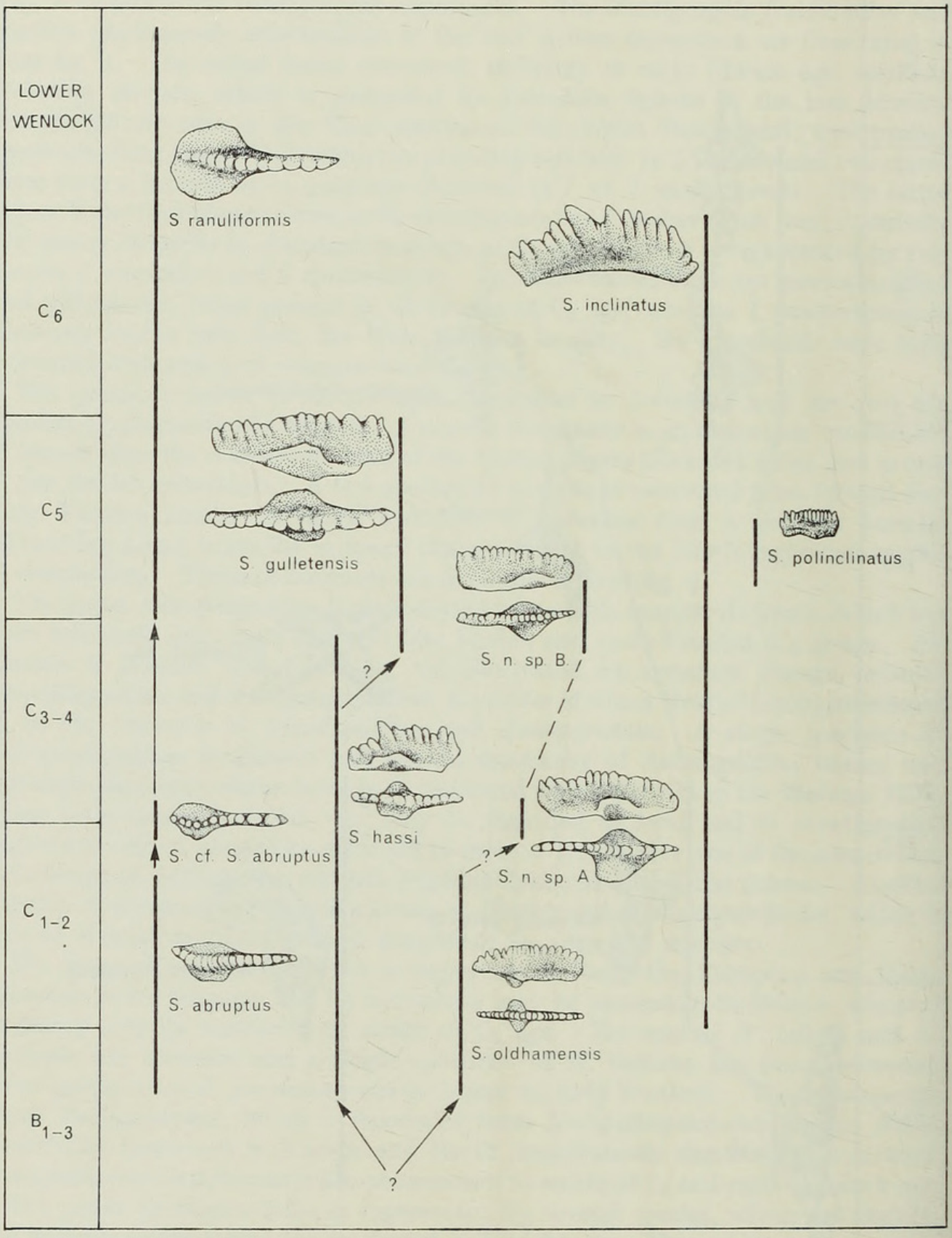


FIG. 10. The genus *Spathognathodus*. Heavy vertical lines indicate approximate stratigraphic ranges. Arrows indicate suggested phylogenetic relationships.

diverged from a common ancestor. *Spathognathodus abruptus* is the probable ancestor of *S. ranuliformis*, an important form in the Telychian and early Wenlock. *Spathognathodus hassi* is possibly ancestral to *S. gulletensis*, which first appears in C_{3-4} and becomes abundant in C_5. *Spathognathodus* n. sp. A, which occurs in a horizon of probable C_{2-4} age, is a possible descendent of *S. oldhamensis*. *Spathognathodus* n. sp. B, of C_{3-5} age, may also be related to these species. *Spathognathodus inclinatus* is common throughout the Fronian and Telychian, but its phylogenetic relationships are obscure. The Llandovery specimens may be homeomorphs of the forms from higher in the Silurian. *Spathognathodus polinclinatus* has been recovered only from C_5 strata and shows no obvious relationship to any other species.

A few species of the bar and blade genera occur in abundance within a limited stratigraphic range. *Ambalodus anapetus* and *Aphelognathus siluricus* are restricted to the late Idwian and early Fronian. *Ozarkodina alisonae* is restricted to C_5, where *O. gaertneri* also makes its first appearance. C_6 and the early Wenlock are characterized by an abundance of diverse species of *Carniodus*, together with *Neoprioniodus subcarnus*, *N. costatus costatus*, *Distomodus triangularis triangularis* and *Exochognathus latialatus*. *Diadelognathus nicolli* has been recovered only from the early Wenlock.

c. Conodont Zones

The stratigraphic distribution of conodonts in the Idwian to early Wenlock strata of the Welsh Borderland allows the recognition of four conodont assemblage zones. These zones, at least in part, are of only local application and the stratigraphic positions of the boundaries between them are known only approximately, because of the widespread nature of the sampling localities. The names proposed for these zones are the *Icriodella discreta—Icriodella deflecta* Assemblage Zone, the *Hadrognathus staurognathoides* Assemblage Zone, the *Icriodella inconstans* Assemblage Zone and the *Pterospathodus amorphognathoides* Assemblage Zone. The stratigraphic ranges and characteristic species of the zones are illustrated in Text-fig. 11.

i. The *Icriodella discreta—Icriodella deflecta* Assemblage Zone

This zone occupies at least the upper part of the Idwian and part of the C_{1-2} interval of the Fronian. The lower limit is unknown, but may be defined at the earliest occurrence of *Icriodella discreta* or *Icriodina irregularis*. The upper limit is defined at the earliest occurrence of *Hadrognathus staurognathoides*.

Icriodina irregularis ranges through the zone, but is rare. The lower part of the zone is characterized by *Icriodella discreta*, the upper part by *Icriodella deflecta*. Several additional species are characteristic of the upper part of the zone, including *Amorphognathus tenuis*, *Spathognathodus abruptus*, *S. hassi*, *S. oldhamensis*, *Ambalodus anapetus*, *Aphelognathus siluricus* and *Exochognathus keislognathoides*.

ii. The *Hadrognathodus staurognathoides* Assemblage Zone

This zone spans an interval from within the upper Fronian (C_{2-3}) to approximately the top of the C_4 division of the Telychian. Graptolites referred to the *turriculatus* Zone have been identified from a horizon within the zone (Cocks & Rickards 1969 :

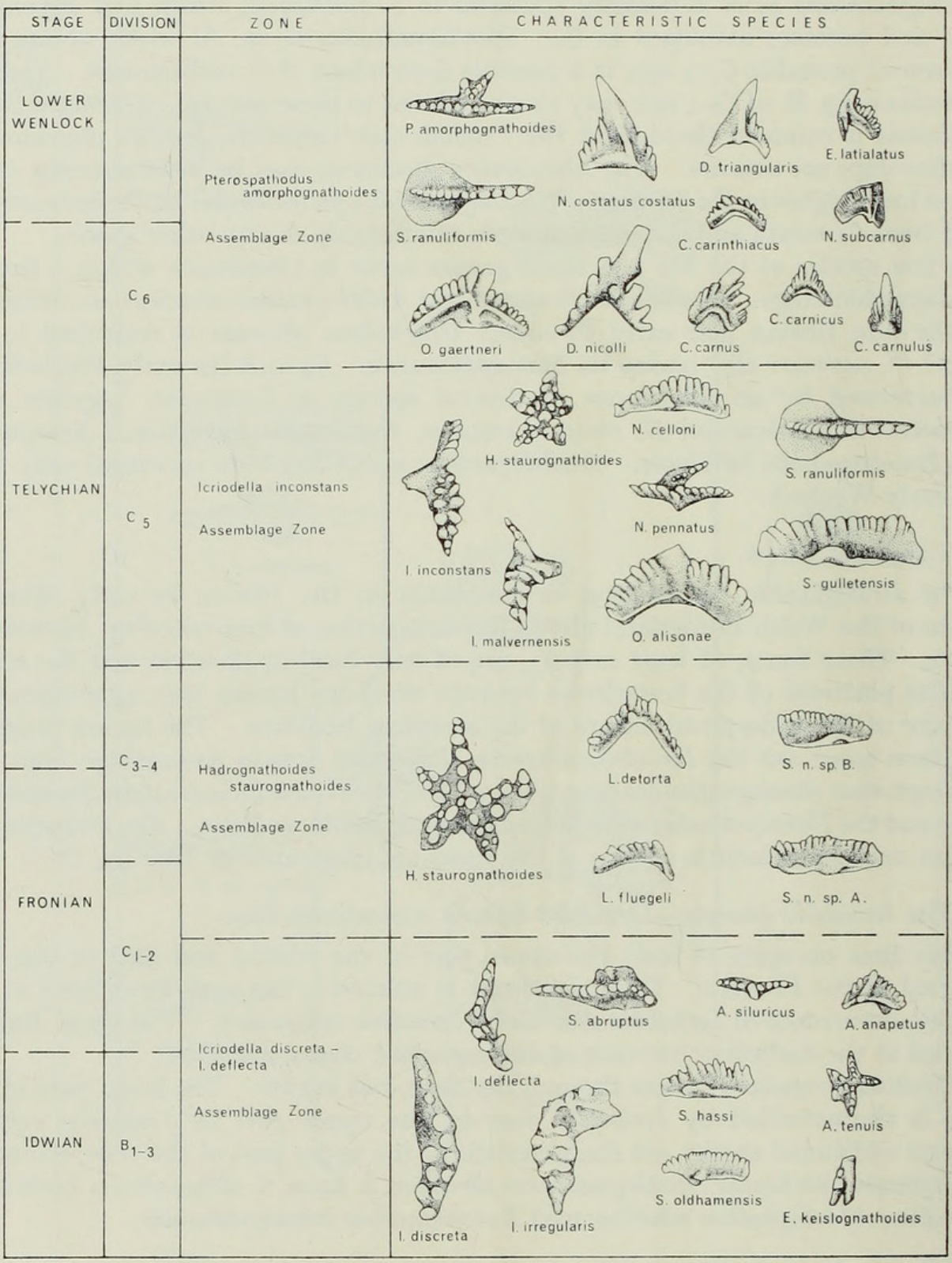


FIG. 11. Llandovery conodont zones of the Welsh Borderland.

225). The lower limit is defined by the earliest appearance of *Hadrognathus staurognathoides* and the upper limit by the earliest occurrence of *Icriodella inconstans* or *Icriodella malvernensis*. *Hadrognathus staurognathoides* itself ranges far above the upper limit of the zone.

Distinctive forms are few, but *Lonchodina detorta* and *Lonchodina fluegeli* are common. *Spathognathodus* n. sp. A, *Spathognathodus* n. sp. B and forms that appear to be transitional from *Spathognathodus abruptus* to *S. ranuliformis* also occur. It is possible that further collecting may enable better definition of the zone in terms of *Icriodella* or *Spathognathodus*.

iii. The *Icriodella inconstans* Assemblage Zone

This zone is approximately equivalent to the C_5 subdivision of the Telychian. A tie between part of this zone and a horizon in the *greistoniensis* graptolite zone was established by Jones, Brooks, Basset, Austin & Aldridge (1969). The lower limit of the zone is defined at the earliest occurrence of *Icriodella inconstans* or *Icriodella malvernensis*. The upper limit is defined by the earliest occurrence of *Pterospathodus amorphognathoides* in association with other characteristic species of the succeeding zone.

Characteristic species include *Icriodella inconstans, I. malvernensis, Spathognathodus gulletensis, Ozarkodina alisonae, Neospathognathodus celloni* and *N. pennatus*. *Spathognathodus ranuliformis* and *Ozarkodina gaertneri* make their first appearances in this zone.

iv. The *Pterospathodus amorphognathoides* Assemblage Zone

This zone is present in at least the upper part of the C_6 subdivision of the Telychian, and extends into the early Wenlock. The lower limit is marked by the earliest occurrence of *Pterospathodus amorphognathoides*. The occurrence of *P. amorphognathoides* in older strata in North America and the European continent was, however, recorded by Nicoll & Rexroad (1968 : 6). In view of this, it is probably advisable to define the lower limit of the *Pterospathodus amorphognathoides* Assemblage Zone at the earliest occurrence of *P. amorphognathoides* in association with other species characteristic of the zone. The upper limit of the zone is unknown and cannot at present be defined.

Species characteristic of this zone are *Pterospathodus amorphognathoides, Spathognathodus ranuliformis, Ozarkodina gaertneri, Carniodus carinthiacus, C. carnicus, C. carnulus, C. carnus, Distomodus triangularis triangularis, Diadelognathus nicolli, Exochognathus latialatus, Neoprioniodus subcarnus* and *N. costatus costatus*.

d. Correlation with Europe and North America

The approximate relationships between the zones recognized in the Welsh Borderland and those erected in Europe by Walliser (1964) and in North America by Nicoll & Rexroad (1968) are tabulated in Text-fig. 12. The local stratigraphic ranges of several species are affected by faunal province or facies control, and this is a complicating factor in correlation. In the present state of knowledge there is sufficient evidence for several broad intercontinental correlations to be suggested.

<table>
<tr><th>CARNIC ALPS
Walliser (1964)</th><th>INDIANA AND KENTUCKY
Nicoll & Rexroad (1968)</th><th>WALES AND THE WELSH BORDERLAND</th></tr>
<tr><td rowspan="2">amorphognathoides-Zone</td><td>Pterospathodus amorphognathoides - Spathognathodus ranuliformis Assemblage Zone</td><td>Pterospathodus amorphognathoides Assemblage Zone</td></tr>
<tr><td rowspan="3">Neospathognathodus celloni Assemblage Zone</td><td rowspan="2">Icriodella inconstans Assemblage Zone</td></tr>
<tr><td rowspan="2">celloni-Zone</td></tr>
<tr><td>Hadrognathus staurognathoides Assemblage Zone</td></tr>
<tr><td>Bereich 1 (upper part)</td><td>Icriodina irregularis Assemblage Zone</td><td>Icriodella discreta - Icriodella deflecta Assemblage Zone</td></tr>
</table>

FIG. 12. Approximate relationships between the European, American and British Llandovery conodont zones.

The *Icriodella discreta—Icriodella deflecta* Assemblage Zone is approximately equivalent to the *Icriodina irregularis* Assemblage Zone of North America. The upper limits of the zones are defined differently, due to the apparently locally restricted ranges of *Neospathognathodus* and *Ozarkodina adiutricis* in Britain. On a broad scale the two zones may be regarded as equivalent. Due to faunal provincialism, *Icriodina* is replaced by *Icriodella discreta* and *Icriodella deflecta* in the lower Silurian of northern Michigan and Ontario (Pollock, Rexroad & Nicoll 1970). The ornamentation of the fragments of *Icriodella* illustrated by Walliser (as *Icriodina irregularis*) is similar to that displayed by *I. deflecta* and *I. discreta* and the upper part of Walliser's Bereich I interval in the Carnic Alps possibly correlates with the *Icriodella discreta—Icriodella deflecta* Assemblage Zone of Britain.

Formations referred to the *Icriodina irregularis* Assemblage Zone of North America or the upper part of Bereich I in Europe are considered to be of similar age to the Idwian and early Fronian strata of Britain. These formations include the Brassfield Formation of midwestern America (Branson & Branson 1947, Rexroad 1967), exclusive of the Lee Creek Member at the top (Nicoll & Rexroad 1968). The conodont faunas of the Manitoulin Dolomite and Cabot Head Shale of northern Michigan and Ontario (Pollock, Rexroad & Nicoll 1970) are similar in age and faunal province to the British faunas. The Neahga Shale of the Niagara Gorge section also contains abundant icriodellids (Rexroad & Rickard 1965 : 1220) and was placed in the *Icriodina irregularis* Assemblage Zone by Pollock *et al.* (1970). *Icriodella* is present in all but the lower part of the 'Untere Schichten' of the Cellon section in the Carnic Alps (Walliser 1964).

The *Hadrognathus staurognathoides* Assemblage Zone is an interval poor in stratigraphically useful conodonts, occurring above the distinctive fauna of the *Icriodella discreta—Icriodella deflecta* Assemblage Zone and below the *Icriodella inconstans* Assemblage Zone, in which *Neospathognathodus* first appears. In Europe there is no recorded gap between *Icriodella* and *Neospathognathodus*, and in North America the ranges of *Icriodina* and *Neospathognathodus* overlap (Nicoll & Rexroad 1968 : 6; Craig 1969 : 1626). *Hadrognathus staurognathoides* and *Lonchodina fluegeli* first appear at the base of the *celloni*-Zone in Europe (Walliser 1964 : table 2) and it is very possible that the *H. staurognathoides* Assemblage Zone is equivalent to the lower part of the *celloni*-Zone and that *Neospathognathodus celloni* and *Ozarkodina adiutricis* are absent because of facies control or faunal provincialism. Rexroad (*in* Craig 1969 : 1625) has suggested that the *celloni*-Zone in Europe may be bounded by unconformities, and if this is the case the *Hadrognathus staurognathoides* Assemblage Zone could occupy an interval that is not represented in the Carnic Alps. The fact that the *celloni*-Zone occupies less than three metres of strata in the Cellon section indicates that the sequence may be considerably condensed. The Lee Creek Member of the Brassfield Limestone of North America is only one metre thick, but contains the entire stratigraphic range of the *Neospathognathodus celloni* Assemblage Zone of Nicoll & Rexroad (1968). It is possible that the *Hadrognathus staurognathoides* Assemblage Zone of the Welsh Borderland is represented by such a small thickness of strata elsewhere that it has not been differentiated.

Many diagnostic species of the *Icriodella inconstans* Assemblage Zone have

not been recorded outside Britain and cannot, as yet, be applied to international correlation. The zone contains elements of both the *celloni*-Zone and the *amorphognathoides*-Zone of Europe, *Neospathognathodus celloni*, for example, being associated with *Ozarkodina gaertneri* and *Spathognathodus ranuliformis*. Nicoll & Rexroad (1968 : 6) recorded a similar overlap of Walliser's guide species, but in North America it is *Pterospathodus amorphognathoides* that is associated with species of *Neospathognathodus*. The suggestion by Rexroad (*in* Craig 1969 : 1625) that there may be an unconformity between Walliser's zones is a possible explanation of the mutually exclusive ranges of zonal species in the Carnic Alps. The *Icriodella inconstans* Assemblage Zone is probably equivalent to the upper part of Walliser's *celloni*-Zone and may include the lower part of his *amorphognathoides*-Zone. There is correlation with at least the upper part of the *Neospathognathodus celloni* Assemblage Zone of North America. At least the upper part of the Lee Creek Member of the Brassfield Limestone, therefore, appears to be of C_5 age. Unconformities in the Niagara Gorge section (Rexroad & Rickard 1965 : 1219) and in northern Arkansas (Craig 1969 : 1624) at least partially encompass this interval. Beds of C_5 age are probably present within the 'Trilobiten und Aulacopleura Schichten' of the Carnic Alps, either side of the boundary between Walliser's *celloni*- and *amorphognathoides*-Zones.

The *Pterospathodus amorphognathoides* Assemblage Zone of the Welsh Borderland is of particular importance, as it traverses the Llandovery/Wenlock boundary. It is approximately equivalent to the *Pterospathodus amorphognathoides—Spathognathodus ranuliformis* Assemblage Zone of North America and to the *amorphognathoides*-Zone of Europe. North American strata containing conodonts indicative of the level include the lower part of the Osgood Member of the Salomonie Dolomite of Indiana and Kentucky (Nicoll & Rexroad 1968 : 3), the upper part of the Cason Shale and the lower part of the St. Clair Limestone of northern Arkansas (Craig 1969 : fig. 1) and the Rockway Dolomite Member of the Irondequoit Limestone in the Niagara Gorge (Rexroad & Rickard 1965 : fig. 1). The Llandovery/Wenlock boundary at the latter locality may be within the Rockway Dolomite or it may be within the interval represented by the unconformity at the base of the dolomite. The Llandovery/Wenlock boundary in the Cellon section of the Carnic Alps can be placed within that part of the 'Trilobiten-und-Aulacopleura Schichten' that is referred to the *amorphognathoides*-Zone. The *amorphognathoides*-Zone at this locality occupies less than two metres of strata.

e. Faunal Provincialism

The restriction of some lower Silurian conodont species to faunal provinces was first reported by Nicoll & Rexroad (1968 : 6), who noted that *Icriodina*, which was common in the Cincinnati Arch area, appeared to be absent from the Silurian sections of the Niagara Gorge and Europe, where it was replaced by *Icriodella*. They also noted that several species that were common in North America were not recorded by Walliser from the Carnic Alps.

Faunal provincialism in the *Icriodina irregularis* Assemblage Zone of North America was discussed by Pollock, Rexroad & Nicoll (1970), who recognized different

provinces in the Cincinnati Arch area of midwestern America and in the northern Michigan and Ontario area. As well as the replacement of *Icriodina* by *Icriodella* in the northern area, several differences were noted at the species level. In particular, *Aphelognathus siluricus* and *Ambalodus anapetus* were present only in the northern area. *Spathognathodus* was more abundant in the north, where it was represented by a greater variety of species. In all, 22 species were recorded only from the northern area and 12 occurred only in the midwestern area.

Faunas of similar age from the Welsh Borderland show a much closer similarity to those of the northern area than to those of the midwestern area. *Icriodella discreta* and *I. deflecta* are the dominant platform elements and *Icriodina irregularis* is rare. *Aphelognathus siluricus* is present and *Ambalodus anapetus* is abundant. The genus *Spathognathodus* is represented by three common species, *S. hassi*, *S. oldhamensis* and *S. abruptus*. *S. hassi* and *S. oldhamensis* occur in both North American provinces. *S. abruptus* may be a geographic variant of *S. manitoulinensis*, which is present only in the northern province of America. Of the other species recorded only in the northern area by Pollock *et al.* (1970 : table 1), *Ligonodina silurica*, *Neoprioniodus planus*, *Plectospathodus flexuosus*, *Synprioniodina silurica* and *Trichonodella symmetrica* are present, but rare, in the British faunas. Of the species recorded only in the midwestern area, *Icriodina irregularis*, *Exochognathus* (*Rhynchognathodus*?) n. sp., *Distomodus*? *extrorsus* and *Plectospathodus irregularis* are present, but rare, in the British faunas. *Icriodina* and *Icriodella* have not previously been definitely recorded in association. On this evidence, the British faunas show a link with the northern province of North America, but there is some admixing of forms characteristic of the southern area. The species *Sagittodontus robustus*, *Spathognathodus comptus* and *S. elibatus* which are common in the northern province of America, are absent from the Welsh Borderland collections. *Amorphognathus tenuis*, which is an important constituent of the British faunas, has not been recorded in North America.

The upper part of Bereich I in Europe is characterized by *Icriodella*, in association with *Amorphognathus* and *Ambalodus triangularis* (Walliserj1964). Walliser recorded only eight species in this interval and, although simple cones were not included, this is very few in comparison with the number present in time-equivalent strata in Britain and North America. Whether this low diversity is due to faunal provincialism, local facies control, post-mortem sorting or some other factor cannot at present be determined.

No significant differences were recorded by Pollock *et al.* (1970 : 745) in the *Neospathognathodus celloni* and *Pterospathodus amorphognathoides*—*Spathognathodus ranuliformis* Assemblage Zones of the northern and midwestern areas. There are, however, several notable differences between the faunas from this interval in the United States and in the Carnic Alps. The European species *Ambalodus galerus*, *Astrognathus tetractis* and *Pygodus*? *lyra* have not been recorded in North America. *Astropentagnathus irregularis* and *Spathognathodus tyrolensis*, described from Austria by Mostler (1967), are also absent from known American faunas. Species described from North America that have not been recorded from the European continent include all the known species of *Diadelognathus*, together with *Distomodus kentucky-*

ensis, Exochognathus brassfieldensis, Icriodina stenolophata, Neospathognathodus bullatus, N. ceratoides, N. latus, Ozarkodina hanoverensis, Sagittodontus edentatus, Spathognathodus polinclinatus and *Trichonodella? expansa.* Several of these species are very abundant in North America and faunal provincialism may explain their absence from the European collections.

In Britain, there is some intermixing of European and American forms, in association with several new forms whose known occurrence is at present restricted to the Welsh Borderland. *Diadelognathus* occurs sporadically and *Distomodus kentuckyensis, Exochognathus brassfieldensis, Sagittodontus edentatus* and *Trichonodella? expansa* are common, indicating a similarity to the American faunas. With these, in strata of C_5 age, is associated a great variety of species, including *Ambalodus galerus, Apsidognathus tuberculatus, Astrognathus tetractis, Astropentagnathus irregularis, Aulacognathus kuehni, Neospathognathodus bullatus, Pygodus? lyra* and *Spathognathodus polinclinatus.* This association indicates a considerable intermixing of North American and European provincial forms. This intermixing may be taking place within a third province, characterized by *Icriodella inconstans, I. malvernensis, Spathognathodus gulletensis* and *Ozarkodina alisonae.* It thus appears possible to recognize three provinces in upper *N. celloni* Zone times, a North American province a European province and a British province. The British province contains several species of restricted geographic occurrence, but is also characterized by an intermixing of important species that are mutually excluded from the other two provinces. The extent and nature of the Llandovery faunal provinces are unknown and they may be due to some physical barrier to migration, to climatic control, to sea-depth control or to some other factor.

Of particular interest in the Welsh Borderland is the occurrence of *Spathognathodus ranuliformis* in association with *Neospathognathodus celloni* in strata of C_5 age. Walliser (1964 : table 2) recorded the earliest occurrence of *S. ranuliformis* in the Carnic Alps at a level above the base of the *amorphognathoides*-Zone. Similarly, Nicoll & Rexroad (1968 : 8) noted that *S. ranuliformis* was generally found higher in the *P. amorphognathoides—S. ranuliformis* Assemblage Zone than any other of the characteristic species. It is possible that *S. ranuliformis* represents a species which first appeared in the British province and migrated at a later date into the North American and European provinces. Other forms characteristic of the British province in C_5 times may have become extinct before such migration became possible.

f. Facies Control

A full appreciation of facies control requires a comparative study of a large number of collections from widespread localities where detailed information concerning facies is available. Such a wide synthesis is outside the scope of this study, but some effects of facies control on local distribution can be appreciated. The animal communities defined by Ziegler, Cocks & Bambach (1968) provide useful information about the depth of the sea in which Llandovery sediments accumulated. These communities have been recognized at many localities in Wales and the Welsh Borderland by Ziegler, Cocks & McKerrow (1968). Several of the samples

collected during the present investigation are from these localities and the animal communities are known. Comparisons can, therefore, be made between faunas of similar age that occur in sediments deposited in different sea-depths.

Of the collections referred to the *Icriodella discreta—Icriodella deflecta* Assemblage Zone, three are from localities where the animal community is known. The Pentamerus Beds of New House, Marshbrook, contain a mixed *Lingula/Rostricellula*? community, while those of Plowden contain a *Pentamerus* community (Ziegler, Cocks & McKerrow 1968 : 746). The Venusbank Formation at Hope Quarry contains a *Stricklandia* community (Ziegler *et al.* 1968 : 743). There are several minor differences in the faunas, all of which could be accounted for by the restrictions of sampling. A major trend, however, is apparent in the species *Amorphognathus tenuis* and *Ambalodus anapetus*, which are abundant in the shallow water fauna of New House, Marshbrook. These two species are present, but in much smaller numbers, in the deeper water fauna of Plowden and they are totally absent from the collections from Hope Quarry. It is possible that *Amorphognathus tenuis* and *Ambalodus anapetus* are restricted to a shallow water facies, although other factors, such as post-mortem sorting, could account for their distribution. Simple cones are much more abundant in the collections from deeper water sediments than in those from shallow water. In the New House, Marshbrook collection 16% of the specimens are simple cones, in the Plowden collections the figure is 63% and in the Hope Quarry fauna, 66%.

The *Icriodella inconstans* Assemblage Zone is the only other interval within which several collections of known animal community have been examined. The variety of species at this level is so great that it is difficult to differentiate any definite trends from the variation due to sampling restrictions. In addition to this, several samples are from a high-energy environment and post-mortem sorting has obviously affected conodont distribution. However, some general observations may be made. The zonal species, *Icriodella inconstans*, appears to be independent of sea-depth, occurring in samples from *Costistricklandia*, *Pentameroides* and *Eocoelia* communities as well as in samples in which the brachiopod fauna is a mixture of soft bottom and rocky bottom forms. The unique occurrence of *Icriodella malvernensis* at the West Malvern locality may be due to facies or ecological control, although this does not appear to be related to sea depth. As in the *Icriodella discreta—I. deflecta* Assemblage Zone, the simple cones are much more abundant in the deeper water collections. For example, in Gullet Quarry a progressive increase in depth up the section is indicated by the animal communities. The percentages of simple cones at the sampling horizons are as follows: Gullet 1 18%, Gullet 2 13%, Gullet 2A 70%, Gullet 3 66%, Gullet 4 70%. In the shallow water conglomerates of West Malvern the percentage is 28% and in the *Eocoelia* community at Hollybush Quarry simple cones comprise 40% of the fauna. This evidence suggests a direct or indirect relationship between increasing sea depth and abundance of simple cones in the Llandovery of the Welsh Borderland.

g. Homeomorphy

Homeomorphy in Silurian conodonts was comprehensively discussed by Walliser

(1964 : 20–22) and only a few observations need be stated here. Convergent homeomorphy is apparent in the outline and arrangement of the processes of *Aulacognathus kuehni* (Pl. 2, fig. 6) and the holotype of *Kockelella patula* (Walliser 1964 : pl. 15, fig. 16). The two Llandovery species *Aphelognathus siluricus* (Pl. 3, fig. 13) and *Neospathognathodus celloni* (Pl. 3, figs 9–12) are also closely similar.

It is important that the frequent occurrence of homeomorphy is borne in mind when isolated conodont faunas are under examination. In particular, failure to recognize those forms which periodically split off from a common antecedent and morphologically similar forms that are separated by a morphologically distinct intermediate form could lead to incorrect stratigraphic interpretation. In view of this, some genera and species from this study whose stratigraphic range is not known to be continuous with similar forms of older or younger age must be regarded as possible homeomorph forms. Pollock, Rexroad & Nicoll (1970 : 754) suggested that, as a continuous lineage has not been recognized, the lower Silurian specimens referred to *Icriodella* may be homeomorphs of those from the Ordovician. Other Llandovery conodonts that are possibly homeomorphs of Ordovician forms include *Panderodus* cf. *P. gracilis*, *Panderodus* cf. *P. staufferi* and the genera *Pygodus*? and *Gothodus*?. Forms that may be homeomorphs of younger Silurian species include those referred to *Ozarkodina* cf. *O. edithae*, *Ozarkodina typica* and *Spathognathodus inclinatus*.

VI. SYSTEMATIC PALAEONTOLOGY

In the erection of new species care has been taken to distinguish between the two procedures of naming and definition. A single specimen of a sampled population has been selected as a named holotype and, as stressed by Simpson (1961 : 30), that name belongs to the species in which the type specimen is placed. The holotype is in no way considered to be morphologically 'typical' of the species to which it belongs. Study of the variation of statistically significant populations from varied ecological and geographical localities is necessary to satisfactorily define a species, and in this respect it is considered misleading to designate selected 'paratypes', which cannot adequately represent a whole population (see Simpson 1961 : 47 for detailed argument).

In consideration of subspecies, only those that are geographically or successionally isolated are valid in evolutionary theory. Where previous authors have defined, within a single species, subspecies that occur at the same locality and horizon, the subspecific status is considered invalid (see Sylvester-Bradley 1956 : 3). In such cases, the taxa are either combined as a single species or given separate specific status.

The morphological terminology and orientation employed in the systematic descriptions of this section are illustrated in Text-fig. 13. The occurrences of species are given for the Welsh Borderland within the stratigraphic range Idwian to early Wenlock, although many species are known to have a stratigraphic range that extends beyond these limits.

The repository of the figured specimens (pre-fixed X.) is the British Museum (Natural History). The remainder of the collections are deposited at the Department of Geology, University of Southampton.

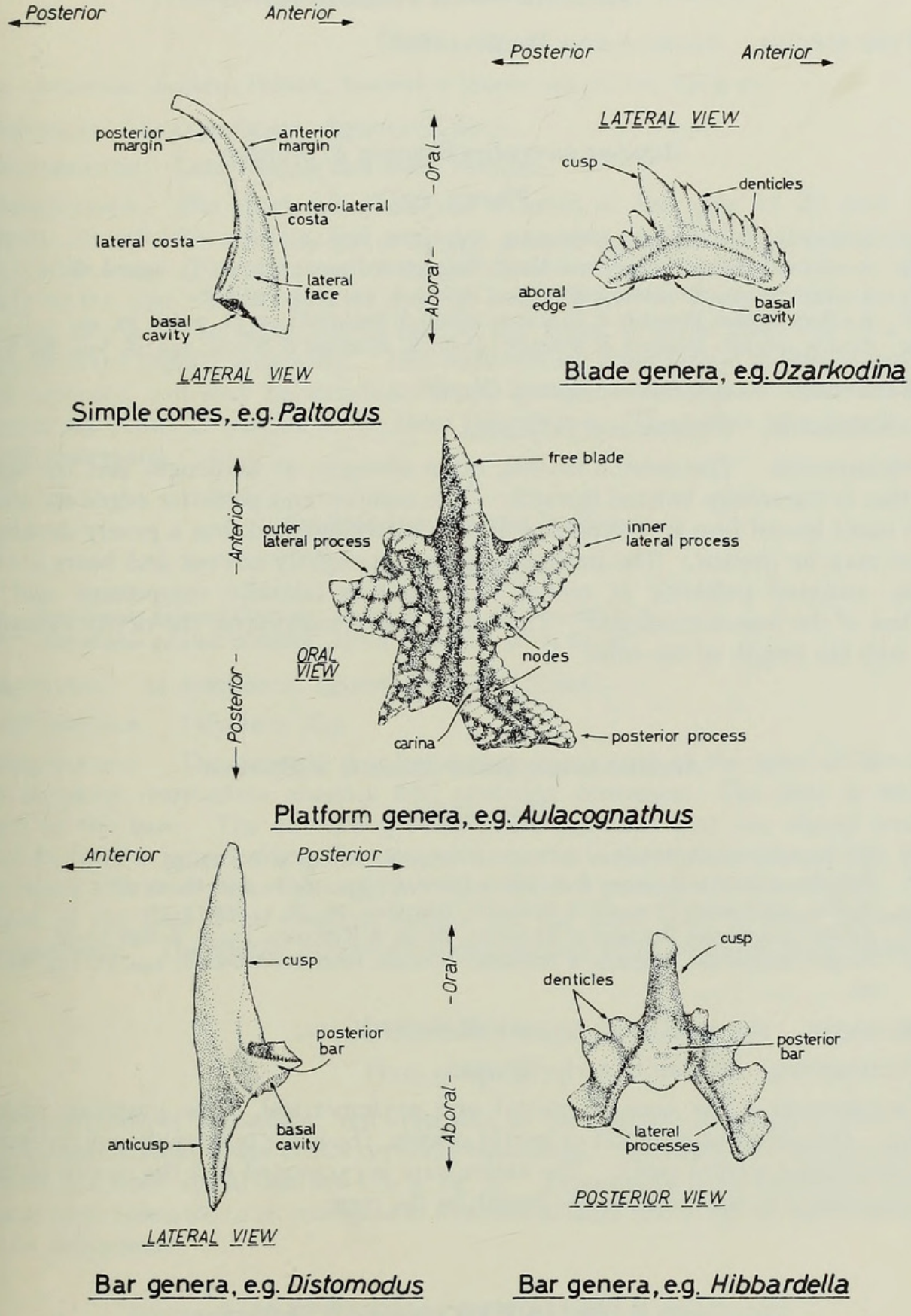


FIG. 13. Morphological terminology and orientation.

Genus *ACODUS* Pander, 1856

TYPE SPECIES. *Acodus erectus* Pander, 1856.

Acodus curvatus Branson & Branson

Plate 9, fig. 1

1947 *Acodus curvatus* Branson & Branson: 554, pl. 81, fig. 20.
1964 *Acodus* cf. *mutatus* (Branson & Mehl) Serpagli & Greco: 196, pl. 34, figs 2a, b.
1967 *Acodus curvatus* Branson & Branson; Rexroad: 25, pl. 4, figs 9–12.
1968 *Acodus curvatus* Branson & Branson; Nicoll & Rexroad: 23, pl. 7, figs 19, 20.
1970 *Acodus curvatus* Branson & Branson; Pollock, Rexroad & Nicoll: 749, pl. 114, fig. 35.

MATERIAL. 86 specimens: figured (X.708).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cone is curved, often strongly, at midlength and the apical portion is commonly twisted inwards. The anterior and posterior edges are sharp. The outer lateral face is convex and usually unornamented, but a poorly developed costa may be present. The inner lateral face is slightly convex and bears a small costa, situated posterior of centre. The unit is laterally compressed and the outline of the base is lenticular. The entire base is excavated, the cavity extending for half the length of the cone.

Acodus unicostatus Branson & Branson

Plate 9, figs 2, 3

1947 *Acodus unicostatus* Branson & Branson: 554, pl. 82, figs 9, 10, 41, 43.
1947 *Paltodus acostatus* Branson & Branson (*partim*): 554, pl. 82, figs 23, 24 only.
1967 *Acodus unicostatus* Branson & Branson; Rexroad: 26, pl. 4, figs 13–16.
1968 *Acodus unicostatus* Branson & Branson; Nicoll & Rexroad: 23, pl. 7, figs 34–36.
1970 *Acodus unicostatus* Branson & Branson; Pollock, Rexroad & Nicoll: 749, pl. 114, figs 36, 37.

MATERIAL. 185 specimens: figured (X.709), (X.710).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cone is curved and asymmetrical. The posterior edge is sharp. One lateral face is flat or gently convex, the other is strongly convex with a well-developed medial costa. The entire base is excavated and the cavity extends for one-third to two-thirds of the length of the cone.

Genus *AMBALODUS* Branson & Mehl, 1933

TYPE SPECIES. *Ambalodus triangularis* Branson & Mehl, 1933.

Ambalodus anapetus Pollock, Rexroad & Nicoll

Plate 3, fig. 4

1970 *Ambalodus anapetus* Pollock, Rexroad & Nicoll: 749, pl. 112, figs 9–15.

MATERIAL. 132 specimens: figured (X.619).

OCCURRENCE. Late Idwian and early Fronian.

DESCRIPTION. The short, stout cusp is situated at the apex of the unit and supports denticulate anterior and posterior processes, which flare downwards to give a wide base. The processes bear small denticles that may be discrete or fused nearly to the tips. Either process may be longer than the other, or they may be of equal length. The outer lateral face of the apical denticle gives rise to a low ridge, directed slightly anteriorly. This rudimentary outer lateral process is usually unornamented, but may be serrated. Some specimens also bear a small serrated ridge on the posterior portion of the inner lateral face. The entire aboral surface is deeply excavated.

Ambalodus galerus Walliser

Plate 3, figs 6, 8

1964 *Ambalodus galerus* Walliser: 27, pl. 6, fig. 1; pl. 12, figs 1–7.
1968 *Ambalodus galerus* Walliser; Igo & Koike: 7, pl. 2, fig. 23.

MATERIAL. 44 specimens: figured (X.622), (X.623).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The strongly developed cusp is situated at the apex of the unit and supports denticulate anterior and posterior processes. The unit is widely flared at the base. The anterior process bears denticles that are almost totally fused to form a jagged ridge; the posterior process is shorter, lower and less well-developed. In oral view, the angle between the two processes is about 170°. The outline of the base is an irregular ellipse and the basal edge of some specimens is tuberculate. The deeply excavated aboral surface often contains basal material.

Ambalodus spp.

Plate 3, figs 5, 7

11 specimens of *Ambalodus*, not referable to the species described above, have been recovered from strata of Idwian and Fronian age. Included here is a pyramidal form with a stout apical denticle (Pl. 3, fig. 5). 4 specimens from Ticklerton Brook appear to be referable to *A. triangularis* Branson & Mehl (Pl. 3, fig. 7), but these may not be indigenous.

Genus *AMORPHOGNATHUS* Branson & Mehl, 1933

TYPE SPECIES. *Amorphognathus ordovicica* Branson & Mehl, 1933.

Amorphognathus tenuis sp. nov.

Plate 2, figs 3, 4

Derivation of name. Latin, thin.

Diagnosis. *Amorphognathus* Branson & Mehl in which the anterior and posterior processes together form a slightly curved blade, which supports a bifurcating inner lateral process and a blade-like outer lateral process.

Holotype. Specimen (X.572).

Material. *ca.* 60 specimens: figured (X.572), (X.573).

Type locality and horizon. Pentamerus Beds, Plowden, Shropshire. Sample Plowden 3.

Occurrence. Late Idwian and early Fronian.

Description. The slightly curved antero-posterior blade bears up to 15 laterally compressed denticles and may be a little expanded in the posterior half. A denticle near the midlength of the blade is slightly higher than its neighbours, forming a small cusp. The bifurcating inner lateral process is situated at, or just posterior to, midlength of the unit. The anterior branch of the process is the longer, bearing three to five sharp denticles and forming an angle of about 50° with the blade. The posterior branch of the process forms a similar angle with the blade and bears two or three denticles. The outer lateral process is situated at, or just anterior to, midlength of the unit and is never directly opposite the inner lateral process. It consists of a single, somewhat posteriorly bent branch, which is approximately perpendicular to the blade and bears up to six denticles. The denticle row of the outer lateral process may be connected to the cusp by a low costa. A wide basal cavity is excavated beneath the blade and the processes.

Remarks. In most descriptions of species of *Amorphognathus* mention has been made of the delicate nature of the specimens and the consequent rarity of complete, well-preserved examples. This is also true of the present material, and the presence of a large number of fragments probably representing parts of *A. tenuis* sp. nov. makes the estimation of true abundance impossible. The totals given herein are based only on the more complete specimens.

Bergström (1964 : 13–14) discussed the apparent dimorphism shown by species of *Amorphognathus* with special reference to *A. ordovicicus* Branson & Mehl. The latter species includes forms with an anterior blade that is continued as a platform-like posterior process ('blade' type) and forms in which both the anterior and posterior processes are expanded into a platform ('non-blade' type). The present specimens show no marked dimorphism, both processes being bladelike in all cases, although in a few examples the posterior process is slightly expanded.

Genus *APHELOGNATHUS* Branson, Mehl & Branson, 1951

Type species. *Aphelognathus grandis* Branson, Mehl & Branson, 1951.

Aphelognathus siluricus Pollock, Rexroad & Nicoll

Plate 3, fig. 3

1970 *Aphelognathus siluricus* Pollock, Rexroad & Nicoll: 749, pl. 114, figs 1–4.

MATERIAL. 30 specimens: figured (X.618).

OCCURRENCE. Late Idwian and early Fronian.

DESCRIPTION. The slightly bowed blade bears a row of 11 to 14 small denticles of subequal size. In lateral view, the denticle row forms an arc. The lateral faces diverge towards the base and flare out near the midpoint on each side to form slightly offset lateral processes, which are short and unornamented. The entire aboral surface is deeply excavated.

REMARKS. The morphology of this species is similar to that of the combined anterior and posterior processes of *Amorphognathus tenuis* The lateral processes of *A. siluricus*, however, project only a short distance laterally and are unornamented. There is a possibility of confusion between broken specimens of the two species.

A morphological resemblance also exists to *Neospathognathodus celloni*, which is also a blade form with offset, unornamented lateral processes. The wide, deep basal cavity of *A. siluricus* serves to distinguish the two species.

Genus ***APSIDOGNATHUS*** Walliser, 1964

TYPE SPECIES. *Apsidognathus tuberculatus* Walliser, 1964.

Apsidognathus tuberculatus Walliser

Plate 2, figs 7, 9

1964 *Apsidognathus tuberculatus* Walliser: 29, pl. 5, fig. 1; pl. 12, figs 16–22; pl. 13, figs 1–5.
1968 *Apsidognathus tuberculatus* Walliser; Nicoll & Rexroad: 24, pl. 3, fig. 8.

MATERIAL. 61 specimens: figured (X.593), (X.594).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The short free blade continues as a prominent curved carina more or less medially over the arched platform. Two rows of nodes diverge from the carina on each side, but do not form well-marked lateral processes. The oral surface between the rows of nodes is generally ornamented by tubercles, arranged concentrically and parallel to the irregular margin of the platform. In mature specimens the coarse development of these tubercles may mask the pattern of the lateral nodose rows. The aboral surface is deeply excavated and commonly contains basal material.

Genus ***ASTROGNATHUS*** Walliser, 1964

TYPE SPECIES. *Astrognathus tetractis* Walliser, 1964.

DIAGNOSIS. The unit consists of a basally excavated blade, bearing a lateral

process on each side. The two lateral processes are situated directly opposite one another and each forms an angle of approximately 90° with the blade.

REMARKS. Walliser (1964 : 30) erected the genus *Astrognathus* for four specimens, and in diagnosis stated that these conodonts comprised four processes of equal length. Specimens from this study possess lateral processes that do not arise from the mid-point of the blade and the four processes are, therefore, of unequal length. These specimens indicate a greater range of variation for the genus. In view of this, the diagnosis has been emended and the revised version is given above.

Astrognathus tetractis Walliser

Plate 3, fig. 1

1964 *Astrognathus tetractis* Walliser: 30, pl. 5, fig. 4; pl. 14, figs 1, 2.

MATERIAL. 16 specimens: figured (X.608).

OCCURRENCE. Telychian (C_5).

DIAGNOSIS. The genus is at present monospecific and the emended diagnosis for the genus also applies to this species.

DESCRIPTION. A slightly arched blade, bearing fused denticles of equal size, supports a lateral process on each side. The two processes are perpendicular to the blade and are situated opposite each other. The processes bear fused denticles of equal size and together form an arch, which is steeper than that of the blade. In most specimens the processes arise from a point up to two-thirds along the length of the blade and can be clearly distinguished. The basal cavity, which is enlarged beneath the junction of the processes, continues only under the blade.

REMARKS. These specimens differ from those described by Walliser (1964) in that the blade and the lateral processes can be clearly distinguished in oral view. Aborally, the blade of all specimens can be distinguished by the extension of the basal cavity along it. The present specimens resemble the formerly described specimens of *A. tetractis* in all other characteristics and are considered conspecific with them.

Genus ***ASTROPENTAGNATHUS*** Mostler, 1967

TYPE SPECIES. *Astropentagnathus irregularis* Mostler, 1967.

Astropentagnathus irregularis Mostler

Plate 2, fig. 5

1967 *Astropentagnathus irregularis* Mostler: 298–300, pl. 1, figs 1–11.

MATERIAL. 1 specimen: figured (X.596).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The blade occupies half the length of the unit and bears in excess

of eight tall, erect denticles, subcircular in cross-section. The blade continues over the curved, platform-like posterior process as a row of nine low nodes. The posterior tip is sharp. On the inner side is a pointed, unornamented lateral process, directed anteriorly at an angle of 50° with the blade. A low, wide trough joins the blade and the process at the anterior end. On the outer side a bifurcating lateral process is situated opposite the inner lateral process, but is broken on this specimen. The process comprises two lobes, each ornamented by a row of nodes and expanded to form a platform. The entire aboral surface of the unit is deeply excavated.

Remarks. The arrangement of the processes in *Astropentagnathus* is reminiscent of the genus *Amorphognathus*. Mostler (1967 : 299, 300) discussed the relationship between these two genera and stressed the fact that in *Astropentagnathus* the lateral processes are situated opposite one another, whereas in *Amorphognathus* the processes are offset.

Genus ***AULACOGNATHUS*** Mostler, 1967

Type species. *Aulacognathus kuehni* Mostler, 1967.

Aulacognathus kuehni Mostler

Plate 2, fig. 6

?1965 *Apsidognathus tuberculata* Walliser; Brooks & Druce: 375, pl. 12, figs. 1, 9, 10.
1967 *Aulacognathus kuehni* Mostler: 301, pl. 1, figs 12–15, 21, 24, 25.

Material. 17 specimens: figured (X.595).

Occurrence. Telychian (C_5).

Description. The short free blade continues over the platform as a prominent nodose carina, becoming less pronounced towards the posterior end where it is deflected inwards at an angle of up to 50°. The inner side of the platform is characterized by a straight lateral process, directed anteriorly and bearing a prominent row of nodes, which forms an angle of approximately 45° with the carina. This process is ornamented by low nodes on the posterior side, but between the ridge and the carina on the anterior side is a deep, unornamented portion. The outer side of the platform is characterized by a tri-lobed process, which is separated from the carina by a trough which deepens anteriorly and posteriorly. The anteriorly and posteriorly directed lobes of the outer lateral process bear prominent rows of nodes, which are joined to form a ridge, curved convex to the carina. The central lobe is ornamented by tubercles. The expanded, inwardly deflected posterior process is also tuberculate. The aboral surface is deeply excavated and commonly contains basal material.

Remarks. These specimens resemble in most characteristics those illustrated by Mostler (1967), but show a more marked inward deflection and expansion of the posterior end of the carina.

A morphological similarity to *Apsidognathus* is apparent in the tuberculate

ornamentation of the oral surface. The broken specimens illustrated by Brooks & Druce (1965) as *Apsidognathus tuberculata* are probably referable to *Aulacognathus kuehni*.

Genus ***CARNIODUS*** Walliser, 1964

TYPE SPECIES. *Carniodus carnulus* Walliser, 1964.

Carniodus carinthiacus Walliser

Plate 5, figs 8–10

1964 ?*Carniodus carinthiacus* Walliser: 31, pl. 6, fig. 8; pl. 27, figs 20–26; text-fig. 4n.
1966 *Carniodus carinthiacus* Walliser; Spasov & Filipović: 38, pl. 1, fig. 3.
1966 *Carniodus carinthiacus* Walliser; Spasov: pl. 1, fig. 3.
1968 *Carniodus carinthiacus* Walliser; Nicoll & Rexroad: 24, pl. 5, figs 1, 2.
1969 ?*Carniodus carinthiacus* Walliser; Schönlaub: pl. 1, fig. 12.
1969 *Carniodus? carinthiacus* Walliser; Drygant: 54, pl. 1, fig. 5.

MATERIAL. 105 specimens: figured, S.2.64, S.2.65, (X.610).

OCCURRENCE. Telychian (C_6) and early Wenlock.

DESCRIPTION. The arched and bowed blade is thickened laterally to form a prominent marginal lip below the denticle row. The cusp is usually small and may be difficult to differentiate from the other high, central denticles of the blade. The denticles on both the anterior and posterior parts of the blade are strongly posteriorly inclined, laterally compressed and fused nearly to the tip. Each part of the blade bears up to nine denticles. The anterior part of the blade is commonly longer than the posterior. The basal groove is widest beneath the cusp and may contain basal material.

REMARKS. The specimens from this study show a greater range of variation than displayed by those illustrated by Walliser (1964). Forms with a long posterior extension of the blade, similar to those described by Nicoll & Rexroad (1968 : 25), are present. In some specimens the cusp is comparatively well developed and a closer similarity to other species of the genus is achieved.

A single specimen from the early Wenlock (Ticklerton 3) bears a small, posteriorly inclined aberrant branch, supporting two small denticles. The branch is situated on the outer side of the unit, beneath the denticle immediately posterior to the cusp.

Carniodus carnicus Walliser

Plate 5, fig. 11

1964 *Carniodus carnicus* Walliser: 32, pl. 6, fig. 11; pl. 28, figs 8–11.
1966 *Carniodus carnicus* Walliser; Spasov & Filipović: 38, pl. 1, fig. 16.
1968 *Carniodus carnicus* Walliser; Nicoll & Rexroad: 25, pl. 5, fig. 3.
1969 *Carniodus carnulus* Walliser; Schönlaub: pl. 1, fig. 5.

MATERIAL. 15 specimens: figured (X.611).

OCCURRENCE. Telychian (C_6) and early Wenlock.

DESCRIPTION. The unit is almost symmetrical and consists of a large, laterally compressed cusp, which is flanked on each side by three to six small, laterally compressed denticles. The size of the denticles and the height of the blade decrease away from the cusp, resulting in a marked tapering of the unit. The basal cavity is slightly flared beneath the cusp and continues as a groove to the ends of the blade.

Carniodus carnulus Walliser

Plate 5, figs 12–14

1964 *Carniodus carnulus* Walliser: 32, pl. 6, fig. 10; pl. 10, figs 20, 21; pl. 27, figs 27–38; pl. 28, fig. 1; text-fig. 4 a–f.
1966 *Carniodus carnulus* Walliser; Spasov & Filipović: 39, pl. 1, fig. 15.
1968 *Carniodus carnulus* Walliser; Nicoll & Rexroad: 25, pl. 5, figs 4, 5.

MATERIAL. 132 specimens: figured (X.612), (X.613), (X.614).

OCCURRENCE. Telychian (C_5) to early Wenlock.

DESCRIPTION. The unit is slightly arched and more or less symmetrical with a tall, erect, central cusp. The anterior and posterior limbs of the blade are short and bear from two to six small, closely packed denticles, which decrease in size away from the cusp. The cusp and the denticles are laterally compressed. Beneath the denticle row the blade is commonly somewhat laterally expanded, whence it narrows towards the base. The basal cavity is slightly expanded below the cusp and extends as a shallow groove to the tips of the blade.

Aberrant forms bearing a denticulate lateral branch are common (Pl. 5, fig. 14). The branch usually arises from the posterior edge of the cusp, but may be situated on the anterior portion of the blade. A single aberrant specimen from the early Wenlock displays branches on both sides of the unit.

Carniodus carnus Walliser

Plate 5, figs 15, 16

1964 *Carniodus carnus* Walliser: 34, pl. 5, fig. 3; pl. 10, fig. 13; pl. 28, figs 2–7; text-fig. 4 y–z.
1966 *Carniodus carnus* Walliser; Spasov & Filipović: 40, pl. 1, figs 12, 13.
1968 *Carniodus carnus* Walliser; Nicoll & Rexroad: 26, pl. 5, figs 6–8.

MATERIAL. 99 specimens: figured, (X.615), S.2.72.

OCCURRENCE. Telychian (C_5) to early Wenlock.

DESCRIPTION. The unit is asymmetrical with a tall cusp that may be erect or slightly curved posteriorly. The posterior limb of the blade is straight and bears from three to eleven short, closely packed denticles. A single, somewhat larger denticle may be present near the midlength of the limb. The anterior limb of the blade is directed downwards, bowed inwards and bears three to six small denticles. The denticle nearest the cusp is often considerably taller than the rest. The basal

cavity is widest under the cusp and continues as a groove beneath the limbs of the blade, widening on the posterior limb beneath the single large denticle, when present.

Remarks. The wide variation, remarked upon by Walliser (1964), in the angle between the limbs of the blade, the curve of the anterior limb and the dentition is apparent in this material.

The presence of a larger denticle on the posterior limb of some specimens was interpreted by Walliser (1964 : 17) as a fusion of the conodont of the species *Carniodus carnus* with one of the species *C. carnulus*, indicating association of the two forms in a single natural species. This type of fusion with *C. carnulus* is also displayed by some specimens of *Exochognathus latialatus* and *Neoprioniodus subcarnus*.

Carniodus spp.

Plate 5, figs 18, 19

Eighteen specimens referable to the genus *Carniodus* were recovered from Idwian and Fronian strata. Many specimens are too poorly preserved for specific identification, but a few resemble those illustrated by Walliser (1964 : pl. 4, fig. 12; pl. 29, figs 1–4) as *Carniodus* sp. In 11 of the specimens the anterior limb of the blade is directed downwards and bowed inwards, and these are referred to *Carniodus* cf. *C. carnus* Walliser (Pl. 5, fig. 18). A single specimen is referred to *Carniodus* cf. *C. eocarnicus* Walliser (Pl. 5, fig. 19).

Genus ***DIADELOGNATHUS*** Nicoll & Rexroad, 1968

Type species. *Diadelognathus excertus* Nicoll & Rexroad, 1968.

Diadelognathus nicolli sp. nov.

Plate 8, figs 2, 3

1968 *Diadeolognathus* n. sp. A. Nicoll & Rexroad: 30, pl. 6, figs 9, 10.

Derivation of name. After R. S. Nicoll, one of the authors who originally described this species.

Diagnosis. *Diadelognathus* Nicoll & Rexroad with a well-developed anterior process and an almost equally well-developed outer lateral process.

Holotype. Specimen (X.583).

Material. 11 specimens: figured (X.583), (X.584).

Type locality and horizon. Wenlock Shales, Ticklerton, Shropshire. Sample Ticklerton 1.

Occurrence. Early Wenlock.

Description. The posteriorly inclined cusp is expanded posteriorly at the base.

The transverse section of the cusp is a laterally compressed ellipse. The inner anterior margin of the cusp gives rise to a straight anterior process, which supports three to seven widely-spaced denticles. The denticles are elliptical in transverse section, inclined posteriorly and they decrease in size anteriorly. The anterior process narrows towards the tip. The outer lateral process arises from the outer anterior margin of the cusp and is directed perpendicularly outwards. The straight process bears two to four discrete, posteriorly curved denticles, subcircular in cross section. The aboral surface of the cusp is excavated by a very shallow cavity which continues as grooves under the processes.

REMARKS. Nicoll & Rexroad (1968 : 27–28) described a phylogenetic sequence from *Diadelognathus primus*. through *D. excertus* to *D. nicolli*. Insufficient material has been recovered from the Welsh Borderland for this sequence to be recognized, but those specimens of *D. nicolli* with less well-developed lateral processes indicate a transition towards *D. excertus*. *D. excertus* itself has not, as yet, been recognized in Britain.

Diadelognathus primus Nicoll & Rexroad

Plate 8, fig. 1

1968 *Diadelognathus primus* Nicoll & Rexroad: 29, pl. 6, figs 7, 8.

MATERIAL. 1 specimen: figured (X.729).

OCCURRENCE. C_{3-4}.

DESCRIPTION. The stout cusp is strongly curved posteriorly and is subcircular in transverse section. The base of the cusp is expanded and gives rise to two short processes, one directed outwards and the other directed inwards and anteriorly. Each process bears two very small denticles, those nearer the cusp being the larger. The entire aboral surface is occupied by a shallow cavity.

Genus ***DISTACODUS*** Hinde, 1879

TYPE SPECIES. *Machairodus incurvus* Pander, 1856.

Distacodus obliquicostatus Branson & Mehl

Plate 9, fig. 4

1933 *Distacodus obliquicostatus* Branson & Mehl: 41, pl. 3, fig. 2.
1964 *Acontiodus procerus* (Ethington) Serpagli & Greco: 198, pl. 37, figs 5, 6.
1968 *Distacodus obliquicostatus* Branson & Mehl; Nicoll & Rexroad: 31, pl. 7, figs 1–4.

MATERIAL. 1 specimen: figured (X.711).

OCCURRENCE. Fronian.

DESCRIPTION. The apical portion of this specimen is missing, so the degree of

curvature of the cone cannot be determined. The basal part of the unit is strongly laterally compressed and triangular in shape. The anterior and posterior edges are sharp. Each lateral face bears a medial costa that does not extend to the base. The entire base is excavated and the cavity is deep.

Genus ***DISTOMODUS*** Branson & Branson, 1947

TYPE SPECIES. *Distomodus kentuckyensis* Branson & Branson, 1947.

Distomodus? egregius (Walliser)

Plate 6, figs 3, 4, 9

1964 *Ligondina egregia* Walliser: 40, pl. 6, fig. 5; pl. 32, figs 3, 4.
1968 *Distomodus? egregia* (Walliser) Nicoll & Rexroad: 33, pl. 5, figs 26–28.

MATERIAL. 46 specimens: figured (X.641), (X.642), (X.643).

OCCURRENCE. Fronian to early Wenlock.

DESCRIPTION. The long, stout cusp is curved posteriorly and in transverse section is biconvex, the outer side usually being more strongly convex than the inner. The inner anterior margin of the cusp bears a costa, which extends downwards to form a denticulate anticusp. The straight posterior bar is inclined downwards and bears several laterally compressed denticles, which are sometimes partially fused. A rounded or sharp lip, directed downwards and slightly posteriorly, is present at the base of the cusp on the outer side. In a very few specimens the lip bears a ridge, which continues onto the posterior edge of the cusp. A conical cavity beneath the cusp continues as a groove under the posterior bar and usually contains basal material.

Distomodus? extrorsus (Rexroad)

Plate 6, fig. 2

1964 *Neoprioniodus?* cf. *brevirameus* Walliser: pl. 29, fig. 11.
1967 *Ligondina? extrorsa* Rexroad: 36, pl. 2, figs 9, 10, 15–17.
1968 *Distomodus? extrorsus* (Rexroad) Nicoll & Rexroad: 34, pl. 5, fig. 23.

MATERIAL. 36 specimens: figured (X.640).

OCCURRENCE. Idwian to Telychian.

DESCRIPTION. The long, stout cusp is curved posteriorly. The anterior and posterior edges are sharp, the outer lateral face is convex and the inner lateral face is flat or gently convex. The inner anterior margin is extended downwards into a short anticusp that may not be denticulate. The posterior bar is short and may only be a slight extension of the posterior margin of the cusp. The small denticles of the posterior bar are subcircular in transverse section. The cusp is excavated by a conical cavity, which extends beneath the posterior bar.

REMARKS. Nicoll & Rexroad (1968 : 34) noted that *D.? extrorsus* evolved into *D.? egregius* by the development of a lip-like projection on the outer side and an increase in the denticulation of the anticusp. This lineage is also apparent in the Welsh Borderland, where *D.? extrorsus* first appears in older strata than *D.? egregius*.

Distomodus kentuckyensis Branson & Branson

Plate 6, figs 5–8, 11

1947 *Distomodus kentuckyensis* Branson & Branson: 553, pl. 81, figs 21–23, 27, 29–33, 36–41.
1967 *Distomodus kentuckyensis* Branson & Branson; Rexroad: 28, pl. 2, figs 11–14.
1968 *Distomodus kentuckyensis* Branson & Branson; Nicoll & Rexroad: 34, pl. 5, figs 24, 25.
1970 *Distomodus kentuckyensis* Branson & Branson; Pollock, Rexroad & Nicoll: 750, pl. 112, figs 7, 8.

MATERIAL. 125 specimens: figured (X.644), (X.645), (X.646), (X.647), (X.648).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The very large cusp is curved slightly posteriorly and inwards. The transverse section of the cusp is biconvex, the convexity of the inner face increasing markedly near the base. The anterior and posterior edges of the cusp are sharp. The anterior edge is extended downwards to form an anticusp, which in a few specimens bears fused denticles. The posterior bar, when present, is usually short and bears laterally compressed denticles that are commonly fused. The base of the cusp is deeply excavated and the cavity continues as a groove under the posterior bar.

REMARKS. The range of variation of this species is very wide, especially in the development and dentition of the posterior bar and the anticusp. A few specimens have discrete denticles on the posterior bar. A single, poorly preserved specimen possesses a long posterior bar that bears nine closely packed denticles.

Distomodus triangularis tenuirameus (Walliser)

Plate 6, fig. 13.

1964 *Neoprioniodus triangularis tenuirameus* Walliser: 53, pl. 4, fig. 15; pl. 28, figs 21–24; text-fig. 6 a–c.
1968 *Neoprioniodus triangularis tenuirameus* Walliser; Igo & Koike: 13, pl. 3, figs 18, 19.
1970 *Distomodus* cf. *Neoprioniodus triangularis tenuirameus* Walliser; Pollock, Rexroad & Nicoll: 751, pl. 112, fig. 1.

MATERIAL. 14 specimens: figured (X.650).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cusp is stout with sharp anterior and posterior edges. The inner lateral face is more strongly convex than the outer and may bear a blunt medial costa. The anterior margin may be very slightly extended to form a rudi-

mentary anticusp. A short posterior bar bearing one or two poorly developed denticles may or may not be present. The moderately deep basal cavity occupies the entire aboral surface.

REMARKS. Walliser (1964) separated his subspecies of *N. triangularis* by morphological differences and by differences in stratigraphic range. In the Welsh Borderland, however, the ranges of the two subspecies overlap. The distinction between the two subspecies may not be valid, but they are not, at present, considered synonymous, as clear evidence of morphological transition has not been found.

Distomodus triangularis triangularis (Walliser)

Plate 6, fig. 12.

1964 *Neoprioniodus triangularis triangularis* Walliser: 52, pl. 6, fig. 13; pl. 28, figs 25–30; text-fig. 6 d–f.
1966 *Neoprioniodus triangularis triangularis* Walliser; Spasov & Filipović: 43, pl. 2, fig. 4.
1968 *Neoprioniodus triangularis* Walliser; Nicoll & Rexroad: 42, pl. 5, fig. 17.
1970 *Distomodus triangularis triangularis* (Walliser) Pollock, Rexroad & Nicoll: 750, pl. 112, figs 2–6.

MATERIAL. 90 specimens: figured (X.651).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cusp is stout, with sharp anterior and posterior edges. The outer side of the cusp is gently convex, the inner side bears a sharp ridge, which is extended laterally as a deep costa near the base. The antero-lateral and postero-lateral faces are concave. The anterior margin is extended downwards to form an anticusp, which is not denticulate. The posterior bar is directed downwards and bears from two to eight small, sharp denticles. The aboral surface is moderately deeply excavated beneath the cusp and is grooved beneath the anticusp and the posterior bar.

Distomodus sp. nov.

Plate 6, fig. 10

MATERIAL. 3 specimens: figured, S.3.30.

OCCURRENCE. C_{3-4}.

DESCRIPTION. The cusp is tall, laterally compressed and slightly curved posteriorly. The anterior and posterior edges of the cusp are sharp, the lateral faces gently convex. The inner lateral face increases in convexity towards the base, where it flares inwardly and a little posteriorly. The anterior margin is extended downwards to form an anticusp, which bears three or four small, laterally compressed, partially fused denticles. The base of the cusp is excavated by a fairly shallow conical cavity, which terminates at a point near the anterior margin. The cavity continues as a narrow groove below the anticusp, and may be filled with basal material.

Remarks. This species differs from other species of *Distomodus* in the possession of a denticulate anticusp combined with the absence of a posterior bar. There are too few specimens to warrant the erection of a specific name.

Genus ***DREPANODUS*** Pander, 1856

Type species. *Drepanodus arcuatus* Pander, 1856.

Drepanodus aduncus Nicoll & Rexroad

Plate 9, fig. 17

1968 *Drepanodus aduncus* Nicoll & Rexroad: 35, pl. 7, figs 11–15.

Material. 17 specimens: figured (X.715).

Occurrence. Telychian and early Wenlock.

Description. The small cone is bent markedly inwards along its length. The anterior and posterior edges are sharp. The anterior margin is laterally compressed near the base and is extended to form a small, flat anticusp, which is inwardly flexed. Both lateral faces are convex, the unit flaring towards the base. The basal cavity is circular under the posterior portion of the unit and continues as a groove to the anterior tip. The cavity extends for less than half the length of the cone.

Drepanodus suberectus (Branson & Mehl)

Plate 9, fig. 16

1933 *Oistodus suberectus* Branson & Mehl: 111, pl. 9, fig. 7.
1935 *Oistodus suberectus* Branson & Mehl; Stauffer: 147, pl. 12, figs 14, 19, 28, 31, 35.
1951 *Oistodus suberectus* Branson & Mehl; Branson, Mehl & Branson: 8, pl. 2, figs 1–4.
1953 *Oistodus suberectus* Branson & Mehl; Rhodes: 229, pl. 21, figs 93, 94.
1954 *Drepanodus suberectus* (Branson & Mehl) Lindström: 568, pl. 2, figs 21, 22.
1955 *Drepanodus suberectus* (Branson & Mehl); Sannemann: 27, pl. 1, fig. 22, pl. 2, fig. 1.
1957 *Oistodus suberectus* Branson & Mehl; Glenister: 726, pl. 86, figs 12, 14.
1959 *Drepanodus suberectus* (Branson & Mehl); Ethington: 276, pl. 39, fig. 17.
1959 *Drepanodus suberectus* (Branson & Mehl); Stone & Furnish: 222, pl. 31, fig. 7.
1959 *Drepanodus suberectus* (Branson & Mehl); Sweet *et al.*: 1049, pl. 130, fig. 4.
1960 *Drepanodus suberectus* (Branson & Mehl); Pulse & Sweet: 253, pl. 35, figs 2, 7.
1960 *Drepanodus suberectus* (Branson & Mehl); Carlson: pl. 2, fig. 10.
1961 *Drepanodus suberectus* (Branson & Mehl); Bergström: 41, pl. 5, fig. 7, text-figs 3K, 4B.
1961 *Drepanodus suberectus* (Branson & Mehl); Wolska: 349, pl. 1, figs 8a, b.
1962 *Drepanodus suberectus* (Branson & Mehl); Sweet & Bergström: 1226, pl. 169, fig. 8.
1964 *Drepanodus suberectus* (Branson & Mehl); Ethington & Clark: 689, pl. 113, fig. 18.
1965 *Drepanodus suberectus* (Branson & Mehl); Barnett: 70, pl. 1, fig. 29; pl. 2, fig. 22.
1965 *Drepanodus suberectus* (Branson & Mehl); Merrill: 376, pl. 1, fig. 8.
1966 *Drepanodus suberectus* (Branson & Mehl); Winder: pl. 9, fig. 6.
1966 *Drepanodus suberectus* (Branson & Mehl); Oberg: 137, pl. 16, fig. 1.
1966 *Drepanodus suberectus* (Branson & Mehl); Webers (*partim*): 29, pl. 6, fig. 9 only.

1966 *Drepanodus suberectus* (Branson & Mehl); Hamar: 58 pl. 1 figs 8, 9.
1966 *Drepanodus suberectus* (Branson & Mehl); Schopf: 54 pl. 5 fig. 25.
1966 *Drepanodus suberectus* (Branson & Mehl); Bergström & Sweet: 330 pl. 35 figs 22, 23.
1966 *Drepanodus suberectus* (Branson & Mehl); Fahraeus: 23, pl. 2, fig. 10, text-fig. 20.
1967 *Drepanodus suberectus* (Branson & Mehl); Rexroad: 30, pl. 2, fig. 4.
1970 *Drepanodus suberectus* (Branson & Mehl); Pollock, Rexroad & Nicoll: 751, pl. 114, fig. 21.

MATERIAL. 41 specimens: figured (X.714).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The symmetrical cone is slightly inclined or curved posteriorly and is somewhat laterally compressed. The anterior and posterior edges are sharp, the lateral faces are convex. The base is flared in all directions to produce a subcircular or oval outline. A shallow, conical cavity is excavated on the aboral surface.

Drepanodus spp.

Plate 9, figs 14, 15

Eighteen specimens representing various species of *Drepanodus* are present in the collections. Some of the specimens may be indigenous, others are probably not. In particular, eight specimens from the Pentamerus Beds of Ticklerton Brook are associated with other species that appear to be derived from Ordovician strata. Since the number of specimens is small and their stratigraphic value negligible, they have not been compared closely with described species of *Drepanodus*, but some of the forms recovered are illustrated.

Genus ***EXOCHOGNATHUS*** Pollock, Rexroad & Nicoll, 1970

TYPE SPECIES. *Trichonodella brassfieldensis* Branson & Branson, 1947.

Exochognathus brassfieldensis (Branson & Branson)

Plate 7, fig. 4

1947 *Trichonodella brassfiedensis* Branson & Branson (*partim*): 551, pl. 81, fig. 12 only; pl. 82, fig. 47 only.
1967 *Trichonodella brassfieldensis* Branson & Branson; Rexroad: 56, pl. 3, figs 27, 28.
1968 *Trichonodella brassfieldensis* Branson & Branson; Nicoll & Rexroad: 62, pl. 5, figs 13, 14.
1970 *Exochognathus brassfieldensis* (Branson & Branson) Pollock, Rexroad & Nicoll: 753, pl. 112, fig. 24.

MATERIAL. 59 specimens; figured (X.665).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The asymmetrical unit consists of a stout cusp, two lateral processes and a posterior bar. The posteriorly curved cusp bears three prominent costae, which merge downwards with the processes. The outer lateral process, which is shorter and is directed more sharply downwards than the inner lateral process, bears three or four compressed denticles, which may be completely fused.

In a few specimens the outer lateral process is not denticulate. The inner lateral process points downwards and inwards, and bears up to six discrete or fused denticles. The posterior bar is short and may not be denticulate, although up to five denticles are usually present. The cavity is deep beneath the cusp and extends almost to the tips of the processes.

Exochognathus brevialatus (Walliser)

Plate 7, figs 8, 9

1964 *Roundya brevialata* Walliser: 69, pl. 4, fig. 16; pl. 31, figs 8–10.
1964 *Roundya truncialata* Walliser: 72, pl. 4, fig. 7; pl. 31, figs 3–6.
1970 *Exochognathus brevialatus* (Walliser) Pollock, Rexroad & Nicoll: 753, pl. 112, figs 29, 30.

MATERIAL. 46 specimens: figured (X.668), (X.669).

OCCURRENCE. Idwian to early Wenlock. Most abundant in the Idwian.

DESCRIPTION. The curved cusp supports two lateral processes and a posterior bar, all of which are directed downwards. Three costae extend along the cusp in line with the processes. The lateral processes together form a steep, symmetrical or slightly asymmetrical arch, and display considerable variation in length and denticulation. The denticulate posterior bar is inclined downwards and is sometimes directed slightly laterally, causing asymmetry of the unit. The cavity is small under the cusp and extends for a short distance beneath the processes.

REMARKS. The species *Roundya truncialata* of Walliser (1964) included forms with long lateral processes, bearing several denticles. Walliser considered that *R. brevialata* evolved from *R. truncialata* by a decrease in the length and dentition of the lateral processes. Pollock, Rexroad & Nicoll (1970 : 753) recorded numerous specimens intermediate between the two extremes and considered they were conspecific. In the Welsh Borderland collections, specimens of the '*truncialata*-type' are common in the Idwian and can be readily distinguished from those of the '*brevialata*-type' that occur in small numbers in younger strata. It is possible that two chronological subspecies could be defined, but there is inadequate material for an attempt to be made here.

Exochognathus caudatus (Walliser)

Plate 7, fig. 13

1964 *Roundya caudata* Walliser: 70, pl. 5, fig. 9; pl. 31, figs 18, 19.
1967 *Roundya caudata* Walliser; Rexroad: 58, pl. 3, figs 29, 30.
1970 *Exochognathus caudatus* (Walliser) Pollock, Rexroad & Nicoll: 753, pl. 112, figs 31–33.

MATERIAL. 62 specimens: figured (X.674).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The slightly twisted, curved cusp bears three costae that give rise to two lateral processes and a posterior bar. The lateral processes point

sharply downwards and together form an arch, which is more or less symmetrical Both lateral process bear discrete denticles. The posterior bar is inclined downwards and is commonly very long, bearing discrete, laterally compressed denticles. The cusp is deeply excavated and the cavity continues as a groove beneath the processes.

Remarks. There is a close relationship between *E. caudatus* and *E. detortus*, the latter possessing a more strongly twisted cusp and more strongly asymmetrical lateral processes. Both species are probably descended from *E. brassfieldensis*. Specimens showing morphological transition between the three species occur frequently in the collections.

Exochognathus detortus (Walliser)

Plate 7, figs 7, 12

1964 *Roundya detorta* Walliser: 70, pl. 5, fig. 8; pl. 31, figs 15–17.
1968 *Roundya detorta* Walliser; Nicoll & Rexroad: 58, pl. 6, figs 16–18.

Material. 36 specimens: figured (X.672), (X.673).

Occurrence. Idwian to early Wenlock.

Description. The cusp is curved posteriorly and strongly twisted. Three costae on the cusp give rise to two lateral processes and a posterior bar. The lateral processes bear discrete denticles and together form an asymmetrical arch. The posterior bar is commonly directed horizontally and is of similar length to the lateral processes. The laterally compressed denticles of the posterior bar may be discrete or fused. The cusp is deeply excavated and the cavity extends as a groove beneath the processes.

Exochognathus keislognathoides Pollock, Rexroad & Nicoll

Plate 7, fig. 5

1967 *Keislognathus*? n. sp. Rexroad: 59, pl. 3, figs 20, 21.
1970 *Exochognathus keislognathoides* Pollock, Rexroad & Nicoll: 753, pl. 112, figs 25–28.

Material. 19 specimens: figured (X.666).

Occurrence. Idwian and Fronian.

Description. The curved cusp is approximately triangular in transverse section and bears a costa at each edge. The inner antero-lateral process is a long, slender, non-denticulate anticusp, bearing a continuation of the inner anterior costa of the cusp. The outer lateral process is inclined outwards and downwards, and bears discrete denticles. The posterior bar is inclined slightly downwards and also bears discrete denticles. The cavity is deep beneath the cusp and continues as a deep groove beneath the processes.

Exochognathus latialatus (Walliser)

Plate 7, figs 10, 11

1964 *Roundya latialata* Walliser: 71, pl. 6, fig. 15; pl. 31, figs 11–14.

MATERIAL. 28 specimens: figured (X.670), (X.671).

OCCURRENCE. Telychian (C_6).

DESCRIPTION. The curved cusp is almost square in transverse section and supports two lateral processes and a posterior bar. The lateral processes are deep, more or less symmetrical and bear several closely-packed denticles. The long posterior bar is directed slightly downwards and bears several small, appressed denticles. A larger denticle may be present near the midlength of the bar. The cavity is deep beneath the cusp and continues as a groove under the processes, widening beneath the larger denticle on the posterior bar.

REMARKS. Some specimens show the probable fusion of *E. latialatus* and *Carniodus carnulus*. A similar development is noted in some specimens of *Carniodus carnus* and *Neoprioniodus subcarnus*.

Exochognathus sp. nov.

Plate 7, fig. 6

1967 *Rhynchognathodus*? n. sp. Rexroad: 60, pl. 3, fig. 23.

MATERIAL. 1 specimen: figured (X.667).

OCCURRENCE. Fronian.

DESCRIPTION. Near the apex of the unit the cusp is posteriorly curved. The anterior face is gently convex, with sharp lateral edges. The posterior edge is sharp. One lateral face is broader than the other. The cusp flares towards the base and the lateral edges on the proximal portion bear small, sharp denticles, fused nearly to their apices. The posterior margin of the proximal portion is broken on the only specimen available for study. The entire base of the unit is deeply excavated.

REMARKS. This specimen appears to belong to the same species as those described by Rexroad (1967) as *Rhynchognathodus*? n. sp. Pollock, Rexroad & Nicoll (1970 : 752) include this species in their list of those referable to the genus *Exochognathus*. It is considered inadvisable to erect a specific name for the species herein on the basis of a single specimen.

Rexroad (1967) described the denticulate margins of his specimens as extending slightly beyond the lamellae of the flared base as lateral processes. This feature is not apparent on the specimen described above.

Genus ***GOTHODUS*** Lindström, 1954

TYPE SPECIES. *Gothodus costulatus* Lindström, 1954.

Gothodus? sp. nov.

Plate 6, fig. 1

MATERIAL. 4 specimens: figured (X.649).

OCCURRENCE. Idwian and Fronian.

DESCRIPTION. The slender cusp is sharply recurved at about midlength. One lateral face of the cusp is flat or very gently convex, the other is strongly convex and bears a poorly developed costa, which may only be apparent towards the base. The anterior and posterior edges of the cusp are sharp. The cusp supports three processes, one lateral, one anterior and one posterior. The anterior process is a short undenticulated anticusp, in direct continuation with the anterior margin of the cusp. The posterior margin of the cusp gives rise to the posterior process, which is short, directed downwards and bears one or two discrete, rounded denticles. The lateral process is a short downward continuation of the lateral costa and bears one or two small denticles. The basal cavity is deep and conical, terminating in a point near the anterior edge, close to the point of recurvature of the cusp.

REMARKS. Lindström (1954 : 569) defined *Gothodus* as follows: 'The genus *Gothodus* realizes the combination three processes or definite costae, two of which are undenticulated. The third costa runs into the denticulated oral margin.' The specimens described above depart from this definition in that only one process is undenticulated. The generic assignment of the species is therefore questioned. This species also differs from the previously described species of *Gothodus*, *G. costulatus* Lindström (1954 : 569, pl. 5, figs 23–25) and *G. communis* Ethington & Clark (1964 : 690, pl. 114, figs 6, 14), in possessing only a short, poorly denticulate posterior process. The arrangement of the processes and the characteristics of the basal cavity of the present specimens are morphologically consistent with an assignment to *Gothodus*.

Too few specimens have been recovered to warrant the erection of a specific name.

Genus ***HADROGNATHUS*** Walliser, 1964

TYPE SPECIES. *Hadrognathus staurognathoides* Walliser, 1964.

Hadrognathus staurognathoides Walliser

Plate 2, figs 8, 10, 11

1964 *Hadrognathus staurognathoides* Walliser: 35, pl. 5, fig. 2; pl. 13, figs 6–15.
1965 *Hadrognathus staurognathoides* Walliser; Brooks & Druce: 376, pl. 12, figs 5, 6.
1968 *Hadrognathus staurognathoides* Walliser; Nicoll & Rexroad: 36, pl. 3, figs 12–14.

MATERIAL. 70 specimens: figured (X.590), (X.591), (X.592).

OCCURRENCE. Fronian to early Wenlock.

DESCRIPTION. The unit consists of an anterior process, a posterior process, an

inner lateral process and a bifurcating outer lateral process. All the processes are expanded to give a platform. The anterior process is often longer than the others and commonly bears a central row of well-developed, tall denticles, which are discrete at the anterior end. The posterior process is curved inwardly. The ornamentation of the oral surface of the posterior and lateral processes varies from feebly nodose to extremely irregular. The less nodose forms possess a low central ridge along each process. The outline of each process may be lanceolate or expanded and lobate. In some specimens the anterior process is of similar length and morphology to the others and may be difficult to distinguish. The entire aboral surface is deeply excavated and is often filled with basal material.

REMARKS. The wide range of variation of this species is apparent in this material. A single juvenile specimen is similar to that illustrated by Walliser (1964 : pl. 13, fig. 6) and is morphologically close to representatives of the genus *Amorphognathus*. A phylogenetic link between *Amorphognathus* and *Hadrognathus* is possible.

Genus ***HIBBARDELLA*** Ulrich & Bassler, 1926

TYPE SPECIES. *Prioniodus angulatus* Hinde, 1879.

REMARKS. The type specimens of *Hibbardella* were restudied by Huddle (1968 : 12–15), who concluded that *Roundya* Hass was a junior synonym of *Hibbardella* Bassler. The diagnosis given by Huddle for *Hibbardella* was as follows: 'Conodonts consisting of a denticulate posterior bar, terminal cusp, and symmetrical anterior arch. Bars thick and round. Denticles discrete and rounded.' Those Llandovery species that have been referred to *Roundya*, but show a degree of asymmetry, were transferred to *Exochognathus* by Pollock, Rexroad & Nicoll (1970 : 751–753). Llandovery species that show no phylogenetic relationship to *Exochognathus* and possess a symmetrical anterior arch are herein included in *Hibbardella*.

Hibbardella? prima (Walliser)

Plate 6, fig. 16

1964 ?*Roundya prima* Walliser: 71, pl. 4, fig. 6; pl. 31, figs 1, 2.

MATERIAL. 2 specimens: figured (X.703).

OCCURRENCE. Fronian (C_{1-2}).

DESCRIPTION. The cusp is posteriorly curved and bears three ridges, one on each antero-lateral margin and the third on the posterior face. The anterior face of the cusp is gently convex. The two antero-lateral ridges expand laterally near the base to form small, serrated processes. The ridge on the posterior face is extended into a denticulate posterior bar. The entire aboral surface is deeply excavated.

REMARKS. The arrangement of the processes and the symmetry of the unit are consistent with a generic assignment to *Hibbardella*. The poor development and denticulation of the processes, however, render this assignment questionable.

Hibbardella? trichonodelloides (Walliser)

Plate 6, figs 17, 18

1964 *?Roundya trichonodelloides* Walliser: 72, pl. 6, fig. 2; pl. 31, figs 22–25.

MATERIAL. 9 specimens: figured (X.704), (X.705).

OCCURRENCE. Telychian.

DESCRIPTION. The lateral processes are directed laterally and anteriorly and bear flat, closely-packed denticles. The cusp is curved posteriorly and is extended into a posterior bar at the base. The posterior bar may or may not bear a few irregular denticles. The basal cavity is deepest beneath the junction of the processes. The cavity extends as a narrow groove under the lateral processes and as a wide groove beneath the posterior bar.

REMARKS. There is a close relationship with *Trichonodella excavata*, the two species being linked by intermediate forms. Only those specimens with a clearly developed posterior bar are included in *H.? trichonodelloides*.

Hibbardella sp. nov.

Plate 6, figs 14, 15

MATERIAL. 3 specimens: figured (X.706), (X.707).

OCCURRENCE. C_{3-4}.

DESCRIPTION. The stout, posteriorly curved cusp is subcircular in transverse section. The anterior margin of the cusp gives rise to two lateral processes, directed laterally and downwards and together forming an almost symmetrical arch. Each lateral process bears three or four discrete denticles, which are subcircular in transverse section. The posterior bar is straight and bears discrete, posteriorly inclined denticles, the one nearest the cusp being the smallest. The aboral surface of the processes is occupied by a wide, shallow groove, which deepens slightly to form a shallow cavity beneath the cusp.

REMARKS. Too few specimens have been recovered to enable comment on the range of variation or the relationships of this species.

Genus ***HINDEODELLA*** Ulrich & Bassler, 1926

TYPE SPECIES. *Hindeodella subtilis* Ulrich & Bassler, 1926.

Hindeodella equidentata Rhodes

Plate 8, fig. 19

1953 *Hindeodella equidentata* Rhodes: 303, pl. 23, figs 248, 252–254.
1957 *Hindeodella equidentata* Rhodes; Walliser: 34, pl. 2, fig. 33.
1960 *Hindeodella equidentata* Rhodes; Ziegler: 182, pl. 15, fig. 10.
1960 *Hindeodella* cf. *H. equidentata* Rhodes; Walliser: 30, pl. 8, fig. 15.

1962 *Hindeodella equidentata* Rhodes; Ethington & Furnish: 1267, pl. 173, fig. 2.
1962 *Hindeodella equidentata* Rhodes; Spasov & Veselinović, 238 pl. 2, figs 10, 11.
1964 *Hindeodella equidentata* Rhodes; Walliser: 36, pl. 8, fig. 3; pl. 32, fig. 11.
1965 *Hindeodella equidentata* Rhodes; Philip: 102, pl. 8, fig. 11.
1966 *Hindeodella equidentata* Rhodes; Spasov & Filipović: 41, pl. 2, fig. 12.
1966 *Hindeodella equidentata* Rhodes; Philip: 445, pl. 3, fig. 1.
1969 *Hindeodella excavata* (Branson and Mehl) Jeppson (*partim*): 18, text-figs 1J, 3D.

MATERIAL 70 specimens: figured (X.695).

OCCURRENCE. Fronian to early Wenlock.

DESCRIPTION. The slender cusp is slightly posteriorly inclined. The anterior and posterior edges of the cusp are sharp. The posterior bar is long, deep, straight or a little curved, and bears several discrete, posteriorly inclined denticles. The denticle height decreases away from the cusp. The anterior bar is bent sharply inwards and bears five or more slender denticles. A basal groove underlies the entire unit and is slightly widened beneath the cusp.

Genus ***ICRIODELLA*** Rhodes, 1953

TYPE SPECIES. *Icriodella superba* Rhodes, 1953.

REMARKS. In recent publications the genus *Icriodella* has been orientated with the blade posterior and the platform anterior (Bergström & Sweet 1966; Schopf 1966; Pollock, Rexroad & Nicoll 1970). Pollock *et al.* (1970 : 754) pointed out that this orientation was necessitated by the slight inclination of the denticles of the blade away from the platform.

Icriodella deflecta sp. nov.
Plate 1, figs 4–7

1970 *Icriodella* n. sp. Pollock, Rexroad and Nicoll: 755, pl. 111, figs 20, 21.

DERIVATION OF NAME. With reference to the deflection of the platform inwards from the line of the blade.

DIAGNOSIS. *Icriodella* Rhodes with a blade and platform of approximately equal length. The platform is deflected out of line with the blade by about 45°.

HOLOTYPE. Specimen (X.561).

MATERIAL. 53 specimens: figured (X.561), S.1.2, (X.562), S.1.4.

TYPE LOCALITY AND HORIZON. The Venusbank Formation of Hope Quarry, sample H.Q.3.

OCCURRENCE. Late Idwian and early Fronian.

DESCRIPTION. The platform is narrow and bears two rows of nodes that are usually offset. The two rows may merge into a single row towards the anterior tip. The blade is of similar length to the platform and typically bears seven denticles

fused nearly to the tips. The anterior denticle forms a small cusp, but is only slightly larger than the remainder. The platform is deflected by about 45° from the line of the blade. A strong lateral flange is present on the outer side of the unit at the junction of the blade and the platform. A ridge runs from the sharp tip of the flange to the cusp, and in mature forms may bear small denticles. A small, unornamented lateral flange is also present on the inner side, somewhat posterior of midlength. The entire aboral surface is excavated, the cavity being deepest beneath the centre of the unit.

REMARKS. *Icriodella deflecta* sp. nov. differs from *I. discreta*, from which it is probably descended, in the sharp angular deflection between the blade and platform, and in the greater number of denticles on the blade. It differs from the younger species, *I. inconstans* and *I. malvernensis*, in that the nodes of the platform are not laterally elongated.

Icriodella discreta Pollock, Rexroad & Nicoll

Plate 1, figs 1–3

1970 *Icriodella discreta* Pollock, Rexroad & Nicoll: 754, pl. 111, figs 27–30.

MATERIAL. 15 specimens: figured (X.585), (X.586), (X.587).

OCCURRENCE. Strata of probable early Idwian age.

DESCRIPTION. The platform bears two rows of nodes that are commonly laterally paired. The blade may be of similar length to the platform or a little shorter. The blade bears about four fused denticles, of which the anterior is conspicuously the largest and forms a prominent cusp. The platform is deflected by a few degrees from the line of the blade. An outer lateral flange is present at the junction of the blade and platform, and an inner lateral flange is situated posterior of the centre of the unit. The aboral surface is entirely excavated, the cavity being deepest beneath the cusp.

REMARKS. *Icriodella discreta* shows morphological similarities to the Ordovician species *I. superba* Rhodes, but a phylogenetic link has not, as yet, been demonstrated.

Icriodella inconstans sp. nov.

Plate 1, figs 13–17

DERIVATION OF NAME. Latin, variable.

DIAGNOSIS. *Icriodella* Rhodes with a straight platform bearing two parallel rows of nodes, which are laterally elongated, especially in the central portion. A well-developed cusp is situated at the anterior end of the blade and is flanked by a strong, unornamented lateral flange on the outer side and a poorly-developed flange on the inner side.

HOLOTYPE. Specimen (X.563).

MATERIAL. 356 specimens: figured (X.563), (X.564), S.1.9, (X.565), (X.566).

TYPE LOCALITY AND HORIZON. The Wych Formation of Gullet Quarry, sample Gullet 2.

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The unit is narrow and elongated and consists of a posterior blade and an anterior platform. The tall, laterally compressed blade is straight or slightly curved and is shorter than the platform. The blade consists of five to eight fused denticles, the anterior being considerably larger than the remainder and forming a prominent cusp. The platform is straight and may be in direct continuation with the blade or deflected by an angle of up to 20°. In many specimens the blade and platform diverge from a common point, in others there is considerable lateral offset. The platform is low, lanceolate in oral view and bears two parallel rows of nodes, which are laterally elongated, particularly in the central portion. On the outer side of the unit a well-developed, pointed flange is situated immediately anterior to the cusp. The posterior edge of the flange bears a ridge which extends upwards onto the antero-lateral margin of the cusp. The anterior portion of the outer lateral flange is wide and unornamented. A less prominent lateral flange is situated below the cusp on the inner side of the unit. The entire aboral surface is excavated, the cavity being deepest beneath the area immediately anterior of the cusp. The cavity may contain basal material.

REMARKS. This species differs from older species of *Icriodella* in the ornamentation of the platform and in the length and height of the blade. The small angle between the blade and platform also serves to distinguish *I. inconstans* sp. nov. from *I. deflecta* sp. nov. The straight platform and the absence of ornamentation on the outer lateral flange distinguishes the species from *I. malvernensis* sp. nov.

Icriodella malvernensis sp. nov.

Plate 1, figs 9–12

DERIVATION OF NAME. After the Malvern Hills.

DIAGNOSIS. *Icriodella* Rhodes with a blade and platform that are curved in opposing directions to give a sigmoidal shape in oral view. The outer lateral flange is very well developed and bears from one to three laterally elongated ridges.

HOLOTYPE. Specimen (X.567).

MATERIAL. 63 specimens: figured (X.567), (X.568), (X.569), (X.570).

TYPE LOCALITY AND HORIZON. 'Sycamore Tree Quarry', West Malvern, sample West Malvern 1.

OCCURRENCE. Telychian (probably C_5).

DESCRIPTION. The unit consists of a posterior blade and an anterior platform, which are curved in opposing directions to give a sigmoidal shape in oral view. The tall blade comprises five to eight laterally compressed, fused denticles, the anterior being the largest and forming a cusp. The platform bears two parallel

rows of nodes, which are laterally elongated, especially somewhat posterior of the central portion. The angle between the line of the blade and the platform is between 20° and 40°. There may or may not be lateral offset between the blade and platform. The outer lateral flange is very strongly developed and at the posterior edge bears a ridge, which continues onto the antero-lateral margin of the cusp. The anterior portion of the flange is ornamented by one to three tall, laterally elongated ridges, which diverge from a point anterior to the cusp. A poorly developed, unornamented inner lateral flange is developed below the cusp on the inner side of the unit. The entire aboral surface is deeply excavated.

REMARKS. The relationship between this species and *I. inconstans* sp. nov. is clearly apparent in the form of the blade and in the form and ornamentation of the platform. *I. malvernensis* is easily distinguished, however, by the curvature of the blade and platform and by the ornamentation of the outer lateral flange.

Specimens of *Icriodella malvernensis* appear to have been paired asymmetrically in the conodont-bearing organism. The asymmetry is apparent in the ornamentation of the outer lateral flange. Mature specimens of left forms display two or three well-developed ridges on the flange (Pl. 1, figs 9, 10, 12), whereas right forms possess one, or occasionally two, less well-developed nodose ridges (Pl. 1, fig. 11).

Two specimens from strata of C_{3-4} age are identified as *Icriodella* cf. *I. malvernensis* (Pl. 1, fig. 8). These appear to be transitional from *I. deflecta* sp. nov. to *I. malvernensis* sp. nov. and indicate a phylogenetic relationship between the two species. These intermediate forms show slight sigmoidal curvature, but the nodes on the platform are not laterally elongated. The outer lateral flange is ornamented by a single node.

Genus ***ICRIODINA*** Branson & Branson, 1947

TYPE SPECIES. *Icriodina irregularis* Branson & Branson, 1947.

REMARKS. Representatives of the genus *Icriodina* are fragile and the original description (Branson & Branson 1947 : 550–551) was based on incomplete specimens. Rexroad (1967 : 32–33) recognized that complete specimens bear four processes and are cruciform in shape. No complete specimens were recovered in this study, but some examples have up to three of the processes intact.

Icriodina irregularis Branson & Branson

Plate 2, fig. 1

1947 *Icriodina irregularis* Branson & Branson: 551, pl. 81, figs 3–11, 18, 19.
1967 *Icriodina irregularis* Branson & Branson; Rexroad: 33, pl. 2, figs 18–21.
1968 *Icriodina irregularis* Branson & Branson; Nicoll & Rexroad: 37, pl. 3, figs 10, 11.

MATERIAL. *ca.* 12 specimens: figured (X.588).

OCCURRENCE Idwian and early Fronian.

DESCRIPTION. The complete unit consists of four processes, situated approxi-

mately at right angles to one another to give a cruciform shape. In none of the specimens are all the processes intact. The anterior and posterior processes are commonly longer than the lateral processes. The oral surface is ornamented by irregular nodes, which often coalesce to form low ridges. In oral view, the outline of the individual processes is commonly lanceolate, but in some examples the tips are expanded and broad rather than pointed. The entire aboral surface is deeply excavated and may contain basal material.

REMARKS. *Icriodina* appears to be closely related to *Icriodella*, and representatives of the two genera occur in association in the Welsh Borderland. The platform portion of mature specimens of *Icriodella* may show a similar lanceolate shape and nodose ornamentation to that of the processes of *Icriodina irregularis*, and broken specimens are sometimes difficult to differentiate. As remarked by Rexroad (1967 : 34) the broken specimens figured by Walliser (1964 : pl. 4, fig. 3; pl. 11, figs 10, 11) as *I. irregularis* are probably referable to *Icriodella*.

Estimation of the abundance of *I. irregularis* is complicated by the frequent occurrence of fragments for which positive identification is impossible. The figures given herein are based mainly upon specimens which display two or more ornamented processes and the true abundance of the species is probably a little greater.

Icriodina sp.

Plate 2, fig. 2

MATERIAL. 1 specimen: figured (X.589).

OCCURRENCE. Late Fronian or early Telychian.

DESCRIPTION. The slightly damaged specimen consists of four processes of similar length, arranged approximately at right angles. Denticulation is preserved on only three of the processes, each of which bears a single row of erect denticles. On two opposing processes, the denticles are fused nearly to the tip, the longer process bearing eight denticles and the shorter five. The third denticulate process bears six free, slightly appressed denticles. Each process flares downwards from the base of the denticles. The aboral surface is very deeply excavated and the walls of the processes are consequently thin.

REMARKS. This specimen is similar in many respects to *Icriodina stenolophata* Rexroad (1967 : 34–35, pl. 2, figs 22–24), which, however, shows distinct lateral processes that are 'no more than one-half the length of the longitudinal processes'. The possession of four processes of similar length causes this specimen to fall outside the known variation range of *I. stenolophata*.

Genus ***LIGONODINA*** Ulrich & Bassler, 1926

TYPE SPECIES. *Ligonodina pectinata* Ulrich & Bassler, 1926.

Ligonodina kentuckyensis Branson & Branson

Plate 8, figs 15, 16

1947 *Ligonodina kentuckyensis* Branson & Branson: 555, pl. 82, figs 28, 35.
1967 *Ligonodina kentuckyensis* Branson & Branson; Rexroad: 35, pl. 2, fig. 5.
1970 *Ligonodina kentuckyensis* Branson & Branson; Pollock, Rexroad & Nicoll: 755, pl. 114. figs 9, 10.

MATERIAL. 76 specimens: figured (X.696), (X.697).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The posteriorly curved cusp is subcircular to elliptical in transverse section. The inner lateral process is directed downwards and somewhat anteriorly, bearing four or five denticles. The posterior bar is straight or slightly curved and bears about six posteriorly inclined denticles. The two denticles nearest the cusp are commonly much smaller than the others. The basal cavity is widest beneath the cusp and is extended as a groove below the posterior bar.

REMARKS. In addition to specimens that are readily referable to *L. kentuckyensis*, there are several that show transition towards *L. salopia* and *L. silurica*. Ethington & Furnish (1962 : 1272) placed *L. silurica*, *L. kentuckyensis* and *L. salopia* in synonymy, but there appear to be valid morphological differences as well as differences in stratigraphic distribution. Several specimens that belong to this group of species are, however, difficult to refer with certainty to any single species, the situation being complicated by the fragmentary nature of much of the material.

Ligonodina petila Nicoll & Rexroad

Plate 8, fig. 11

1968 *Ligonodina petila* Nicoll & Rexroad: 38, pl. 5, figs 20–22.

MATERIAL. 10 specimens: figured (X.702).

OCCURRENCE. Late Fronian or early Telychian to early Wenlock.

DESCRIPTION. The cusp is curved slightly posteriorly and is subcircular to elliptical in transverse section. The inner lateral process is directed downwards and posteriorly, bearing four discrete denticles. The short posterior bar is straight and slender, supporting three or four widely spaced denticles, which are inclined a little posteriorly. The basal cavity is small and is not laterally expanded beneath the cusp.

Ligonodina salopia Rhodes

Plate 8, fig. 17

1953 *Ligonodina salopia* Rhodes: 307, pl. 23, figs 245, 257, 260.

MATERIAL. 19 specimens: figured (X.698).

OCCURRENCE: Idwian to early Wenlock.

DESCRIPTION. The cusp is stout and posteriorly curved. The transverse section

of the cusp is subcircular to elliptical. The antero-lateral process is directed downwards, inwards and more or less anteriorly, and is not in direct continuation with the cusp. Five or six posteriorly inclined denticles are situated on the process. The posterior bar is straight and deep and bears discrete, posteriorly inclined denticles. The basal cavity is widest and deepest beneath the cusp and continues as a shallow groove beneath the processes.

Remarks. The specimens figured by Rhodes (1953) possess antero-lateral processes that are clearly isolated from the cusp. Only specimens that exhibit this feature have been included in *L. salopia* of this study. The specimens figured by Walliser (1964 : pl. 32, figs 5, 10) as *L. salopia* do not show this feature and Rexroad (1967 : 35) considered that they probably belonged in *L. kentuckyensis*. Specimens from this study which are morphologically similar to those of Walliser have been included in *L. kentuckyensis*.

Ligonodina silurica Branson & Mehl

Plate 8, figs 10, 13

1933 *Ligonodina silurica* Branson & Mehl: 48 pl. 3 figs 18–20.
1957 *Ligonodina ingens* Walliser: 37 pl. 2, fig. 20.
1957 *Ligonodina silurica* Branson & Mehl; Walliser: 38, pl. 2, fig. 10.
1964 *Ligonodina silurica* Branson & Mehl; Walliser: 42, pl. 8, fig. 13; pl. 2, fig. 10.
1969 *Ligonodina silurica* Branson & Mehl; Philip: 291, pl. 18, figs 18, 19, 23, 25.
1970 *Ligondina* cf. *L. silurica* Branson & Mehl; Pollock, Rexroad & Nicoll: 755, pl. 114, figs 7, 8.

Material. 36 specimens: figured (X.699), (X.700).

Occurrence. Fronian to early Wenlock.

Description. The stout, posteriorly curved cusp is subcircular in transverse section. The inner lateral process is essentially a downward extension of the inner anterior margin of the cusp and bears five to seven discrete, closely spaced denticles. The posterior bar is commonly curved in lateral view and bears closely packed denticles. The cavity is deepest and widest beneath the cusp and extends as a wide, shallow groove beneath the processes.

Remarks. The diagnostic feature of this species, as noted by Walliser (1964 : 42), is that a true antero-lateral branch does not exist, but the denticles are on the inner side of a long, downward continuation of the cusp.

Ligonodina? variabilis Nicoll & Rexroad

Plate 8, fig. 14

1964 *Hindeodella* n. sp. Walliser: 36, pl. 7, fig. 16; pl. 32, figs 25, 28, 30.
1968 *Ligonodina? variabilis* Nicoll & Rexroad: 39, pl. 4, figs 12–14.
1970 *Ligonodina? variabilis* Nicoll & Rexroad; Pollock, Rexroad & Nicoll: 755, pl. 114, figs 11, 12.

Material. 67 specimens: figured (X.701).

Occurrence. Fronian to early Wenlock.

DESCRIPTION. The cusp is posteriorly curved, often a little twisted, and is laterally compressed with sharp anterior and posterior margins. The antero-lateral process is bent inwards and, to a varying degree, downwards. The denticles of the process are two to five in number and are compressed in the plane of the process. The posterior bar is laterally compressed, straight or curved, and bears a large number of closely-packed, posteriorly inclined denticles. The small basal cavity is situated beneath the cusp and extends as a rapidly tapering groove beneath each process.

REMARKS. This species is very variable and includes forms that approach *Hindeodella* and *Ligonodina* in morphology. The generic assignment is, therefore, questioned.

Genus ***LONCHODINA*** Ulrich & Bassler, 1926

TYPE SPECIES. *Lonchodina typicalis* Ulrich & Bassler, 1926.

Lonchodina detorta Walliser

Plate 8, fig. 6

1957 *Lonchodina* n. sp. (a) Walliser: 39, pl. 3, figs 29, 30.
1964 *Lonchodina detorta* Walliser: 43, pl. 9, fig. 20; pl. 30, figs 34–37.
1969 *Ligonodina elegans* Walliser; Jeppsson (*partim*): 21, text-fig. 4D.

MATERIAL. 27 specimens: figured (X.686).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The straight cusp is laterally compressed and inclined posteriorly. The anterior branch is bowed and bears laterally compressed denticles that may be discrete or partially fused. A little to the posterior of the cusp, the posterior branch is abruptly bent and flexed. The denticles of the posterior branch are discrete. The two branches are of approximately equal length. The shallow basal cavity is flared beneath the cusp and continues as a groove under the anterior branch.

Lonchodina fluegeli Walliser

Plate 8, fig. 7

1964 *Lonchodina fluegeli* Walliser: 44, pl. 6, fig. 4; pl. 32, figs 22–24.
1966 *Lonchodina fluegeli* Walliser; Spasov & Filipović: 42, pl. 2, fig. 10.

MATERIAL. 21 specimens: figured (X.687).

OCCURRENCE. Late Fronian and early Telychian.

DESCRIPTION. The cusp is straight, laterally compressed and inclined posteriorly. The anterior branch is straight and bears closely packed, laterally compressed

denticles. The posterior branch is slightly bent downwards and inwards and is strongly twisted, so that at the posterior tip the denticles lie in a plane almost at right angles to the plane of the anterior branch. The denticles of the posterior branch are flat and closely packed. A narrow, shallow basal groove that extends beneath both branches is widened only very slightly below the cusp.

Remarks. All the specimens exhibit strongly twisted posterior branches and the less bent variety noted by Walliser (1964) is not recorded.

Lonchodina greilingi Walliser

Plate 8, fig. 4

1957 *Lonchodina greilingi* Walliser: 38, pl. 3, figs 20–26.
1960 *Lonchodina greilingi* Walliser; Walliser: 31, pl. 8, figs 17, 18.
1960 *Lonchodina greilingi* Walliser; Ziegler: 188, pl. 14, figs 15, 16, 18, 20.
1962 *Lonchodina greilingi* Walliser; Ethington & Furnish: 1274, pl. 173, fig. 10.
1964 *Lonchodina greilingi* Walliser; Walliser: 44, pl. 8, fig. 7; pl. 30, figs 7–9.
1965 *Lonchodina greilingi* Walliser; Philip: 104, pl. 9, fig. 22.
1966 *Lonchodina greilingi* Walliser; Barnett *et al.*: pl. 58, fig. 8.
1969 *Lonchodina greilingi* Walliser; Philip: 292, pl. 17, figs 17, 18, 21; text-fig. 1e.

Material. 41 specimens: figured (X.688).

Occurrence. Idwian to early Wenlock.

Description. The cusp is tall, slender, inwardly inclined and circular in transverse section. Each branch bears four to six widely spaced denticles and is slightly twisted near the cusp. Together the branches form an asymmetrical arch. The base of the cusp is moderately deeply excavated and the cavity flares inwardly. The aboral surface of each branch is grooved.

Remarks. Some specimens are readily identifiable as *L. greilingi*, but several specimens that display transition towards other forms are present and the limits of the species are indistinct. As noted by Walliser (1964 : 44), there are transitional forms towards *Trichonodella inconstans*, *Synprioniodina silurica* and representatives of the genus *Plectospathodus*.

Lonchodina walliseri Ziegler

Plate 8, fig. 5

1957 *Lonchodina* n. sp. (b) Walliser: 40, pl. 3, figs 27, 28.
1960 *Lonchodina walliseri* Ziegler: 188, pl. 14, figs 2, 6, 7.
1964 *Lonchodina walliseri* Ziegler; Walliser: 44, pl. 8, fig. 17; pl. 30, figs 26–33.
1965 *Lonchodina walliseri* Ziegler; Philip: 104, pl. 8, fig. 35.
1967 *Lonchodina walliseri* Ziegler; Rexroad: 37, pl. 3, fig. 6.
1968 *Lonchodina walliseri* Ziegler; Nicoll & Rexroad: 40, pl. 4, figs 8, 9.
1969 *Lonchodina walliseri* Ziegler; Philip: 292, pl. 17, fig. 19.

Material. 85 specimens: figured (X.689).

Occurrence. Idwian to early Wenlock.

DESCRIPTION. The cusp is stout and subcircular in transverse section. The anterior and posterior branches are of similar length and bear discrete denticles, which are slightly laterally compressed. The aboral surface of the unit is flat, widest beneath the cusp and tapers sharply anteriorly and less sharply posteriorly. The basal cavity is in the form of a shallow pit beneath the cusp.

REMARKS. A single aberrant specimen bears an additional branch, closely similar in position and morphology to that of the specimen illustrated by Walliser (1964 : pl. 10, fig. 16). The short branch, which diverges from the anterior branch and is directed anteriorly and inwardly, bears two or three fused denticles. The aboral surface of the branch is narrow and is not excavated.

Lonchodina sp. A

Plate 8, fig. 9

MATERIAL. 5 specimens: figured (X.690).

OCCURRENCE. Idwian to Telychian.

DESCRIPTION. This species resembles *Lonchodina walliseri* in general morphology, but lacks a cusp. The denticles are more closely packed than is typical for *L. walliseri*.

Lonchodina sp. B

Plate 8, fig. 8

1967 *Lonchodina*? sp. Rexroad: 38, pl. 3, fig. 5.

MATERIAL. 15 specimens: figured (X.691).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. There is no cusp. The blade is sigmoidal and bears about 10 discrete denticles. The denticles at the anterior end are laterally compressed, those of the posterior are subcircular in section. The aboral surface is widest near the midlength of the unit and tapers more sharply anteriorly than posteriorly. A small pit is excavated in the aboral surface, slightly anterior to the midpoint.

REMARKS. This species is similar to *Lonchodina* sp. C, but is less bowed and bears fewer denticles. *Lonchodina* sp. B is from earlier strata than *Lonchodina* sp. C, to which it is probably ancestral.

Lonchodina sp. C

Plate 8, fig. 12

MATERIAL. 24 specimens: figured (X.692).

OCCURRENCE. C_{3-4} to early Wenlock.

DESCRIPTION. None of the denticles is so well-developed as to be distinguishable as a cusp. The branches are bowed in opposing directions and the posterior section

of the unit is bent downwards. The denticles are closely packed and inclined posteriorly, those of the posterior branch being larger than those of the anterior. The aboral surface is flattened below the posterior branch and slightly grooved below the anterior branch. A small pit is situated anterior to the midpoint of the unit.

Remarks. In several respects this species resembles the lower Devonian species *Lonchodina cristagalli* Ziegler (1960 : pl. 14, fig. 1). Since there are slight morphological differences and there is a wide separation in known stratigraphic occurrence, the specimens from this study are not placed in *L. cristagalli*.

Genus ***NEOPRIONIODUS*** Rhodes & Müller, 1956

Type species. *Prioniodus conjunctus* Gunnel, 1931.

Neoprioniodus costatus costatus Walliser

Plate 5, fig. 22

1964 *Neoprioniodus costatus costatus* Walliser: 48, pl. 6, fig. 14; pl. 28, figs 36–41; text-fig. 6 l–n.
1966 *Neoprioniodus costatus costatus* Walliser; Spasov: pl. 1, fig. 5.
1966 *Neoprioniodus costatus costatus* Walliser; Spasov & Filipović: 42, pl. 1, figs 10, 11.
1968 *Neoprioniodus costatus* Walliser; Nicoll & Rexroad: 40, pl. 5, figs 15, 16.

Material. 79 specimens: figured (X.654).

Occurrence. Telychian (C_6) and early Wenlock.

Description. The cusp is inclined posteriorly and has sharp anterior and posterior edges. The outer lateral face of the cusp is flat, the inner lateral face is convex and bears a ridge, which is extended into a distinct rib near the base. The posterior bar is laterally thickened immediately beneath the denticle row, which consists of three to eight laterally compressed denticles, fused nearly to their apices. The anterior margin of the cusp is extended downwards as an anticusp, which commonly bears one to five partially fused denticles. In a few specimens the anticusp is not denticulate. The basal cavity is widest and deepest beneath the cusp and extends as a groove beneath the processes. Basal material is often present.

Remarks. As noted by Walliser (1964), representatives from lower stratigraphic levels have a strongly denticulate anticusp, while those from higher levels possess a poorly denticulate or non-denticulate anticusp. A few aberrant specimens occur in which the anticusp is split to form two adjacent branches.

Neoprioniodus costatus paucidentatus Walliser

Plate 5, figs 20, 21

1964 *Neoprioniodus costatus paucidentatus* Walliser: 48, pl. 4, fig. 23; pl. 28, figs 31–35; text-fig 6 i–k.

Material. 27 specimens: figured (X.652), (X.653).

Occurrence. Idwian to Telychian (C_5).

DESCRIPTION. The stout cusp is inclined posteriorly and has sharp anterior and posterior edges. The outer lateral face of the cusp is flat or gently convex, the inner lateral face is convex and bears a low ridge. The anterior margin of the cusp is extended downwards to form an anticusp, which in most specimens is poorly denticulate or non-denticulate. The posterior bar is short and bears three to six fused, laterally compressed denticles. The basal cavity is deepest and widest beneath the cusp and continues as a groove under the processes.

REMARKS. As noted by Walliser (1964), there is a reduction in the denticulation of the anticusp and in the elevation of the inner lateral ridge with time. This development is similar to that shown by the younger subspecies, *N. costatus costatus*.

Neoprioniodus excavatus (Branson & Mehl)

Plate 5, fig. 25

1933 *Prioniodus excavatus* Branson & Mehl: 45, pl. 3, figs 7, 8.
1957 *Prioniodina excavata* (Branson & Mehl); Walliser: 46, pl. 2, figs 18, 19.
1958 *Prioniodina excavata* (Branson & Mehl); Bischoff & Sannemann: 103, pl. 15, figs 7, 10, 13.
1962 *Prioniodina bicurvata* (Branson & Mehl); Ethington & Furnish: 1283, pl. 173, fig. 17.
1964 *Neoprioniodus excavatus* (Branson & Mehl); Walliser: 49, pl. 8, fig. 4; pl. 29, fig. 26; text-fig. 5c.
1965 *Neoprioniodus excavatus* (Branson & Mehl); Spasov: 28, pl. 1, fig. 10.
1965 *Neoprioniodus excavatus* (Branson & Mehl); Philip: 105, pl. 9, figs 16, 17.
1969 *Hindeodella excavata* (Branson & Mehl); Jeppsson (*partim*): 18, text-figs 1I, 3C.

MATERIAL. 60 specimens: figured (X.655).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The stout, inwardly inclined cusp is slightly compressed laterally and has rounded anterior and posterior margins. The posterior bar is long and strongly downcurved. The aboral surface of the bar is broad. The rounded denticles of the posterior bar may be closely packed or discrete. The anterior bar is very short and is directed slightly outwards, commonly bearing only a single denticle, although two or three may be present. In inner lateral view, the aboral edge is smoothly curved below the junction between the cusp and anterior bar. The cavity is wide and moderately deep beneath the cusp.

Neoprioniodus latidentatus Walliser

Plate 5, fig. 24

1957 *Prioniodina excavata* (Branson & Mehl) Walliser (*partim*): 46, pl. 2, fig. 17 only.
1964 *Neoprioniodus latidentatus* Walliser: 50, pl. 8, fig. 15; pl. 29, figs 34, 35; text-fig. 5b.

MATERIAL. 13 specimens: figured (X.656).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION The cusp is erect or inwardly bent and has sharp anterior and posterior edges. The posterior bar is straight and inclined slightly downwards, bearing widely-spaced denticles, which are subcircular in transverse section. The

aboral edge rises steeply from the base of the anterior edge of the cusp, producing a sharp, acutely angled outline. The basal cavity is deep beneath the cusp and continues as a wide groove to the tip of the posterior bar.

Neoprioniodus multiformis Walliser

Plate 5, fig. 26

1957 *Prioniodina excavata* (Branson & Mehl) Walliser (*partim*): 46, pl. 2, fig. 16 only.
1964 *Neoprioniodus multiformis* Walliser: 50, pl. 8, fig. 10; pl. 29, figs 14, 16–25; text-fig 5a.

MATERIAL. 74 specimens: figured (X.657).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The stout, erect cusp is commonly slightly twisted and has sharp anterior and posterior edges. The posterior bar is long and slightly curved downwards, bearing discrete, closely spaced denticles. An anterior bar may or may not be developed. When developed, the bar is directed somewhat outwardly and bears one to three closely spaced denticles. The cavity is wide and deep beneath the cusp and continues as a wide groove beneath the posterior bar.

REMARKS. Less variation is shown by these specimens than by those from younger strata described by Walliser (1964).

Neoprioniodus planus Walliser

Plate 5, fig. 23

1964 *Neoprioniodus planus* Walliser: 51, pl. 4, fig. 10; pl. 6, fig. 3; pl. 29, figs 12, 13, 15.
1968 *Neoprioniodus planus* Walliser; Igo & Koike: 12, pl. 1, figs 15, 18; pl. 3, fig. 21.
1968 *Neoprioniodus planus* Walliser; Nicoll & Rexroad: 41, pl. 5, figs 11, 12.
1970 *Neoprioniodus planus* Walliser; Pollock, Rexroad & Nicoll: 756, pl. 114, figs 13, 14.

MATERIAL. 68 specimens: figured (X.658).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cusp is very tall and inclined posteriorly, with a sharp, non-denticulate anterior edge. The unit is considerably laterally compressed. The bent posterior bar bears eight to ten discrete or closely packed denticles, which are inclined posteriorly. The shallow basal cavity is widest below the posterior edge of the cusp and continues along the posterior bar, terminating short of the tip.

Neoprioniodus subcarnus Walliser

Plate 5, fig. 17

1964 *Neoprioniodus subcarnus* Walliser: 51, pl. 5, fig. 7; pl. 28, figs 12–18.
1966 *Neoprioniodus subcarnus* Walliser; Spasov & Filipović: 42, pl. 1, figs 8, 9.
1967 *Neoprioniodus subcarnulus* Walliser; Rexroad: pl. 3, fig. 14.
1968 *Neoprioniodus subcarnus* Walliser; Nicoll & Rexroad: 41, pl. 5, fig. 10.
1969 *Neoprioniodus subcarnus* Walliser; Drygant: 53, pl. 1, figs 12–14.

MATERIAL. 68 specimens: figured (X.659).

OCCURRENCE. Telychian (C_5) to early Wenlock.

DESCRIPTION. The cusp is tall, slender and laterally compressed, the inner side being less strongly convex than the outer. The posterior margin is sharp to rounded, the anterior margin is sharp and is extended strongly downwards to form an anticusp. The outer anterior portion of the cusp bears a small ridge towards the base, often extended aborally to form a small free rib. The posterior bar is inclined downwards and bears 10 to 20 laterally compressed denticles. The denticle adjacent to the cusp is comparatively long and in some specimens a large, well-developed denticle is present at, or slightly posterior to, the midpoint of the bar. A shallow basal cavity, occasionally containing basal material, is excavated beneath the cusp, continuing as a groove under the posterior bar.

REMARKS. Walliser (1964 : 51) suggested that the larger denticle developed in the posterior bar of some specimens indicated fusion of a conodont of the species *N. subcarnus* with one of the species *Carniodus carnulus*. A similar development is noted in *Carniodus carnus* and *Exochognathus latialatus*.

Neoprioniodus subcarnus shows morphological similarities to *Carniodus carnus*, which possesses a denticulate anterior process in place of the anticusp. Transitional forms between the two species have not been found.

Genus ***NEOSPATHOGNATHODUS*** Nicoll & Rexroad, 1968

TYPE SPECIES. *Neospathognathodus bullatus* Nicoll & Rexroad, 1968.

Neospathognathodus bullatus Nicoll & Rexroad

Plate 3, fig. 15

1968 *Neospathognathodus bullatus* Nicoll & Rexroad: 44, pl. 1, figs 5–7.

MATERIAL. 1 specimen: figured (X.604).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. A free blade, consisting of denticles fused nearly to their apices, comprises half the length of the conodont and continues over the platform as a carina, which bends inwards at the posterior end. On the outer side a single nodose lateral process, directed outwards and anteriorly, forms an angle of about 40° with the carina, from which it is separated by a trough. On the inner side a similar nodose process forms an angle of about 20° with the carina and is directed anteriorly. An irregularly nodose, posterior outer lateral process projects from the posterior tip of the carina. Aborally, the lateral processes and the area beneath the carina at their junction are excavated, but basal material masks the depth of the cavity. A groove is excavated beneath the free blade, but the aboral surface of the posterior process shows only a small, shallow excavation.

Neospathognathodus celloni (Walliser)

Plate 3, figs 9–12

1964 *Spathognathodus celloni* Walliser: 73, pl. 4, fig. 13; pl. 14, figs 3–16; text-fig. 1b; text-fig. 7 b–f.
1968 *Spathognathodus celloni* Walliser; Igo & Koike: 18, pl. 2, figs 1–4.
1968 *Neospathognathodus celloni* (Walliser) Nicoll & Rexroad: 45, pl. 2, figs 1–4.

MATERIAL. 176 specimens: figured (X.597), (X.598), (X.599), (X.600).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The straight blade bears erect or slightly posteriorly inclined denticles, commonly fused nearly to their apices. Two offset lateral processes are situated at, or slightly posterior to, midlength. The processes are poorly developed and usually unornamented. The lateral process nearer the posterior tip is often the more extensively flared. The processes are excavated aborally and the cavity extends as a shallow groove to the tips of the blade.

REMARKS. A few specimens, with rudimentary nodes on one lateral process, are transitional to *N. pennatus*.

Neospathognathodus pennatus (Walliser)

Plate 3, figs 13, 16

1964 *Spathognathodus* sp., ex aff. *Sp. celloni* Walliser: 74, pl. 14, figs 17, 18; text-fig. 7a.
1964 *Spathognathodus pennatus angulatus* Walliser (*partim*): 79, pl. 14, fig. 19 only; text-fig. 1c.
1964 *Spathognathodus pennatus pennatus* Walliser: 79, pl. 14, figs 23–26; pl. 15, fig. 1; text-fig. 1d.
1964 *Spathognathodus pennatus procerus* Walliser: 80, pl. 15, figs 2–8; text-fig. 1c.
1966 *Spathognathodus pennatus procerus* Walliser; Spasov & Filipović: 50, pl. 1, fig. 6.
1968 *Spathognathodus pennatus procerus* Walliser; Igo & Koike: 18, pl. 2, figs 8–11.
1968 *Neospathognathodus pennatus* (Walliser) Nicoll & Rexroad: 47, pl. 2, fig. 5.
1969 *Spathognathodus pennatus procerus* Walliser; Schönlaub: pl. 1, fig. 13.
1969 *Spathognathodus pennatus procerus* Walliser; Drygant: 50, pl. 1, figs 2, 3.

MATERIAL. 53 specimens: figured (X.601), (X.602).

OCCURRENCE. Telychian (C_5) to early Wenlock.

DESCRIPTION. The blade is straight or somewhat sigmoidal in oral view and bears erect denticles, fused nearly to their apices. In some specimens the blade is expanded and the denticles nodose. Two offset lateral processes are situated at, or posterior to, midlength of the unit. The process nearer the anterior of the unit is usually unornamented, the other bears a row of denticles that is directed outwardly and anteriorly, making an angle of 45°–70° with the blade. The aboral surface of the blade and processes is deeply excavated.

REMARKS. The close relationship to *Pterospathodus amorphognathoides*, pointed out by Walliser (1964 : 80), is evident. Nicoll & Rexroad (1968 : 48) considered *N. pennatus* to be intermediate between *N. celloni* and *N. bullatus*.

Neospathognathodus? sp.

Plate 3, fig. 14

MATERIAL. 1 specimen: figured (X.603).

OCCURRENCE. Idwian.

DESCRIPTION. The specimen is slightly broken, but consists of a straight blade supporting two lateral processes, situated almost opposite each other. The broken blade bears eight denticles, one of which is noticeably, though not greatly, larger than the others. The lateral processes arise below the main denticle and are directed almost perpendicularly away from the blade. One process is unornamented, the other bears three discrete, sharp denticles that are strongly inclined parallel to the blade. The entire aboral surface is excavated, the cavity being deepest under the main denticle.

REMARKS. The morphology of this specimen is consistent with an assignment to *Neospathognathodus*, but the anomalous stratigraphic occurrence renders such an assignment questionable. This specimen is from strata of high Idwian age, whereas *Neospathognathodus* otherwise makes its first appearance in the Welsh Borderland in strata of Telychian (C_5) age. Of the younger species of *Neospathognathodus* the specimen most resembles *N. pennatus*.

Genus ***OZARKODINA*** Branson & Mehl, 1933

TYPE SPECIES. *Ozarkodina typica* Branson & Mehl, 1933.

Ozarkodina adiutricis Walliser

Plate 5, figs 2, 3

1964 *Ozarkodina adiutricis* Walliser: 54, pl. 4, fig. 14; pl. 27, figs 1–10; text-fig. 1a; text-fig. 7h, i, k–m.
1968 *Ozarkodina adiutricis* Walliser; Nicoll & Rexroad: 48, pl. 2, figs 6–8.
1969 *Ozarkodina adiutricis* Walliser; Schönlaub: pl. 1, fig. 18.

MATERIAL. 9 specimens: figured, S.3.12, (X.631).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The tall cusp is inclined posteriorly and is situated somewhat posterior of midlength. The anterior part of the blade is much higher than the posterior and bears four to six denticles, which are fused nearly to their apices. The posterior part of the blade bears two to four low denticles. The entire aboral surface is excavated, the cavity being deepest beneath the cusp. The cavity is commonly extended laterally beneath the cusp on one side and is enclosed by a flaring lip.

Ozarkodina alisonae sp. nov.

Plate 5, figs 4, 6

DERIVATION OF NAME. After my wife, Alison.

DIAGNOSIS. *Ozarkodina* Branson and Mehl with a cusp that is much taller and broader than the other denticles of the blade. The blade is arched and bowed, and possesses anterior and posterior portions of approximately equal length and height. The denticles are of uniform size and fused nearly to their apices. The basal cavity is situated beneath the cusp and is flanked by lips that flare laterally and aborally.

HOLOTYPE. Specimen (X.581).

MATERIAL. 34 specimens: figured (X.581), (X.582).

TYPE LOCALITY AND HORIZON. The Wych Formation of Gullet Quarry, sample Gullet 2.

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The unit is strongly bowed and arched. In lateral view, the anterior and posterior parts of the blade form an angle of 100°–160°. The cusp is situated at midlength of the unit and is tall, sharply pointed and slightly inclined posteriorly. The anterior and posterior edges of the cusp are sharp and the lateral faces flat or gently convex. The anterior part of the blade bears four to nine laterally compressed denticles, which are fused nearly to their apices and decrease only a little in height anteriorly. The denticles nearest the cusp are more or less erect, those at the anterior end are directed a little anteriorly. The posterior part of the blade bears five to nine laterally compressed and almost completely fused denticles, which are more slender than those of the anterior. The denticles are inclined posteriorly and are of subequal height. A rounded basal cavity is situated beneath the cusp and is flanked by lips that flare laterally and aborally. The cavity is extended as a groove beneath the blade.

REMARKS. This species is easily distinguished from other Llandovery species of *Ozarkodina* by the strong arching and bowing of the unit and by the prominently flared lips of the basal cavity. There is a fairly close similarity to younger specimens of *O. typica*, which possess a larger number of more slender denticles and do not display flared lips to the basal cavity. There is also a morphological resemblance to *O. jaegeri* Walliser (1964 : 57, pl. 25, figs 11–18), but there is no evidence of a phylogenetic link.

It is possible that the specimens referred by Igo & Koike (1968 : 8, pl. 2, fig. 7) to *Bryantodus* sp. belong here.

Ozarkodina cf. ***O. edithae*** Walliser

Plate 4, fig. 17

cf. 1964 *Ozarkodina edithae* Walliser: 55, pl. 26, figs 12–18.
1970 *Ozarkodina* cf. *O. edithae* Walliser; Pollock, Rexroad & Nicoll: 756, pl. 113, figs 1–4.

MATERIAL. 37 specimens: figured (X.632).

OCCURRENCE. Idwian to Telychian (C_5).

DESCRIPTION. The blade is flat with an aboral margin that is straight or very feebly arched. The anterior part of the blade bears fused denticles, increasing

in height regularly towards the cusp. The tips of the denticles and of the cusp form a straight line. The posterior part of the blade is lower and the denticles are partially or almost completely fused. The denticles decrease in height posteriorly. The basal cavity is small and only slightly flared beneath the cusp.

REMARKS. Pollock, Rexroad & Nicoll (1970 : 756) noted that their specimens had a less angular oral outline than those illustrated by Walliser (1964). This is also true of the specimens from this study. As there are slight morphological differences, and because the stratigraphic ranges have not been shown to be continuous, the Llandovery specimens are not, at present, placed with certainty in *O. edithae.*

Ozarkodina gaertneri Walliser

Plate 5, figs 5, 7

1964 *Ozarkodina gaertneri* Walliser: 57, pl. 6, fig. 6; pl. 27, figs 12–19; text-fig. 1g.
1966 *Ozarkodina gaertneri* Walliser; Spasov & Filipović: 44, pl. 1, figs 1, 2.
1968 *Ozarkodina gaertneri* Walliser; Igo & Koike: 14, pl. 1, figs 5–9.
1968 *Ozarkodina gaertneri* Walliser; Nicoll & Rexroad: 49, pl. 2, figs 12–14.
1969 *Ozarkodina gaertneri* Walliser; Schönlaub: pl. 1, fig. 15.

MATERIAL. 220 specimens: figured (X.633), (X.634).

OCCURRENCE. Telychian (C_5) to early Wenlock.

DESCRIPTION. The unit is arched and slightly bowed. The strong cusp is situated near midlength and is inclined posteriorly. The transverse section of the cusp is lenticular. The denticles of the blade are laterally compressed and partially fused. Those to the posterior of the cusp are lower than those to the anterior. The blade is laterally thickened below the denticle row to form a narrow platform. On one side the aboral edge of the blade is projected downwards beneath the cusp to form a prominent lip. The aboral surface of the blade is grooved and the cavity is enlarged beneath the cusp.

REMARKS. Transition from *O. adiutricis* is shown by specimens from strata of C_5 age, which display less thickening and possess a less well-developed aboral lip than those from younger levels.

Ozarkodina hanoverensis Nicoll & Rexroad

Plate 5, fig. 1

1968 *Ozarkodina hanoverensis* Nicoll & Rexroad: 50, pl. 2, fig. 9

MATERIAL. 2 specimens: figured (X.635).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The unit is slightly arched and bowed. The cusp is broad, slightly posteriorly inclined and situated near midlength. The anterior part of the blade bears five denticles that are closely packed, but not fused. The posterior part

bears seven closely packed denticles. The cavity is small beneath the cusp and is slightly flared on the inner side. Grooves extend a short distance anteriorly and posteriorly from the cavity.

Ozakodina media Walliser

Plate 4, fig. 21

1953 *Ozarkodina* sp. Rhodes: pl. 23, fig. 244.
1957 *Ozarkodina media* Walliser: 40, pl. 1, figs 21–25.
1958 *Ozarkodina media* Walliser; Bischoff & Sannemann: 99, pl. 14, figs 15, 16, 18, 19, 21.
1962 *Ozarkodina media* Walliser; Ethington & Furnish: 1278, pl. 173, fig. 9.
1962 *Ozarkodina media* Walliser; Spasov & Veselinović: 240, pl. 1, figs 6, 8, 14.
1964 *Ozarkodina media* Walliser; Walliser: 58, pl. 8, fig. 5; pl. 26, figs 19–34.
1965 *Ozarkodina media* Walliser; Philip: 106, pl. 9, figs 1, 3.
1966 *Ozarkodina media* Walliser; Barnett *et al.*: pl. 58, fig. 21.
1966 *Ozarkodina media* Walliser: Spasov & Filipović: 44, pl. 2, fig. 7.
1966 *Ozarkodina media* Walliser; Spasov: pl. 1, fig. 2.
1966 *Ozarkodina media* Walliser; Philip: 447, pl. 1, figs 29, 32, 33.
1968 *Ozarkodina media* Walliser; Igo & Koike: 15, pl. 3, fig. 5.
1969 *Hindeodella excavata* (Branson & Mehl) Jeppsson (*partim*): 18, text-figs 1H, 3B.

MATERIAL. 112 specimens: figured (X.636).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cusp is tall, laterally compressed and curved posteriorly. The anterior and posterior parts of the blade are of approximately equal length, but the anterior is deeper. The denticles are laterally compressed and closely packed, those of the anterior being a little larger than those of the posterior. The arch of the blade, in lateral view, is between 120° and 180°. The basal cavity is wide and flared beneath the cusp and extends as a groove to the tips of the blade.

REMARKS. The recognition of *O. media* in this study extends the known stratigraphic range of the species downwards to the upper part of the Idwian. Walliser (1964) described and illustrated the wide variation shown by specimens from the *patula*-Zone (Wenlock) to the lower Devonian. Much less variation is apparent in the older specimens from the present study.

Ozarkodina typica Branson & Mehl

Plate 4, figs 18–20

1933 *Ozarkodina typica* Branson & Mehl: 51, pl. 3, figs 43–45.
1953 *Ozarkodina typica* Branson & Mehl; Rhodes: 320, pl. 23, figs 251, 261, 262.
1964 *Ozarkodina typica typica* Branson & Mehl; Walliser: 61, pl. 9, fig. 21; pl. 25, figs 20, 21; pl. 26, figs 1, 2.
1967 *Ozarkodina typica* Branson & Mehl; Rexroad: 39, pl. 2, figs 7, 8.
1970 *Ozarkodina typica* Branson & Mehl; Pollock, Rexroad & Nicoll: 757, pl. 113, figs 16–18.

MATERIAL. 22 specimens: figured (X.637), (X.638), (X.639).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The unit is arched and slightly bowed. The cusp is tall and posteriorly inclined, with sharp anterior and posterior edges. The anterior part of the blade bears eight to eleven slender, laterally compressed, posteriorly inclined denticles, fused nearly to their apices. The posterior part is commonly shorter and bears six to ten partially fused denticles, which may be lower than those of the anterior. The aboral surface is grooved from tip to tip, the cavity deepening and widening beneath the cusp, where it is flanked by slightly laterally flared lips.

REMARKS. As noted by Pollock *et al.* (1970 : 757), lower Silurian representatives of this species are shorter than those from younger strata. In other respects, however, these specimens are comparable with those illustrated by Branson and Mehl (1933), although the possibility of homeomorphy cannot be disregarded.

Genus ***PALTODUS*** Pander, 1856

TYPE SPECIES. *Paltodus subaequalis* Pander, 1856.

Paltodus costulatus Rexroad

Plate 9, fig. 21

1967 *Paltodus costulatus* Rexroad: 40, pl. 4, figs 26–29.
1968 *Paltodus costulatus* Rexroad; Nicoll & Rexroad: 51, pl. 7, figs 16–18.
1970 *Paltodus costulatus* Rexroad; Pollock, Rexroad & Nicoll: 757, pl. 114, figs 29, 30.

MATERIAL. 68 specimens: figured (X.728).

OCCURRENCE. Fronian to early Wenlock.

DESCRIPTION. The small cone is slightly curved and bowed. The anterior and posterior edges are sharp. The posterior portion of each lateral face bears a poorly developed costa. The base is entirely excavated and the cavity terminates at a point at about one-third of the length of the cone.

Paltodus debolti Rexroad

Plate 9, fig. 18

1947 *Paltodus unicostatus* Branson & Mehl; Branson & Branson (*partim*): 554, pl. 82, figs 20–22 only.
1967 *Paltodus debolti* Rexroad: 41, pl. 4, figs 22–25.
1968 *Paltodus debolti* Rexroad; Nicoll & Rexroad: 52, pl. 7, fig. 26.
1970 *Paltodus debolti* Rexroad; Pollock, Rexroad & Nicoll: 758, pl. 114, figs 32, 33.

MATERIAL. 63 specimens: figured (X.725).

OCCURRENCE. C_{3-4} to early Wenlock.

DESCRIPTION. The cone is curved and asymmetrical. The convex antero-lateral face is bounded by prominent costae at its anterior and posterior margins. A less well-developed costa is situated in the centre of the face. On the inner side a

flat lateral face is bordered by the anterior costa and a second posterior costa. The base is entirely excavated, the cavity extending for about half the length of the cone.

Paltodus dyscritus Rexroad

Plate 9, fig. 19

1947 *Paltodus unicostatus* Branson & Mehl; Branson & Branson (*partim*): 554, pl. 82, figs 6?, 17–19 only.
1967 *Paltodus dyscritus* Rexroad: 42, pl. 4, figs 30–34.
1968 *Paltodus dyscritus* Rexroad; Nicoll & Rexroad: 52, pl. 7, figs 31–33.
1970 *Paltodus dyscritus* Rexroad; Pollock, Rexroad & Nicoll: 758, pl. 114, fig. 31.

MATERIAL. 102 specimens: figured (X.726).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The curved cone is nearly symmetrical. The anterior face is gently convex, almost flat, and is flanked on each side by a prominent antero-lateral costa. The lateral faces are flat to gently concave, and become broad towards the base. The posterior margin bears two or three costae. The base is entirely excavated, the cavity extending for half the length of the cone.

Paltodus migratus Rexroad

Plate 9, fig. 20

1967 *Paltodus migratus* Rexroad: 44, pl. 4, figs 17–21.
1968 *Paltodus migratus* Rexroad; Nicoll & Rexroad: 52, pl. 7, fig. 27.
1970 *Paltodus migratus* Rexroad; Pollock, Rexroad & Nicoll: 758, pl. 114, fig. 34.

MATERIAL. 53 specimens: figured (X.727).

OCCURRENCE. Idwian to Telychian (C_5).

DESCRIPTION. The cone is curved, laterally compressed and only slightly asymmetrical. The anterior and posterior edges are costate. Each lateral face bears two prominent costae, one central and one posterior of centre. These costae may bifurcate and there may be additional poorly-developed costae. The entire base is excavated and the cavity extends for about half the length of the cone.

Genus ***PANDERODUS*** Ethington, 1959

TYPE SPECIES. *Paltodus unicostatus* Branson & Mehl, 1933.

Panderodus cf. ***P. gracilis*** (Branson & Mehl)

Plate 9, figs 12, 13

cf. 1933 *Paltodus gracilis* Branson & Mehl: 108, pl. 8, figs 20, 21.

MATERIAL. 187 specimens: figured (X.722), (X.723).

OCCURRENCE. Idwian to Telychian (C_5).

DESCRIPTION. The cone is curved posteriorly and has a broadly rounded anterior margin and a sharp posterior edge. The posterior portion of the cone is laterally compressed and is separated from the anterior portion by a sharp offset on each lateral face, originating at, or near, the base. The basal cavity is conical and extends for half the length of the cone.

REMARKS. Most of the specimens from this study show less antero-posterior extension near the base than displayed by the specimens of *P. gracilis* illustrated by Branson & Mehl (1933). There is a closer resemblance to those illustrated by Glenister (1957 : pl. 85, figs 2–5).

Panderodus gracilis has not previously been recorded from strata of younger than upper Ordovician age. The oldest specimens from this study are of Idwian age and there is, at present, no evidence of continuity of stratigraphic range. As it is possible that the Llandovery specimens are homeomorphic with those from the Ordovician, they are not positively included in *P. gracilis*.

Panderodus serratus Rexroad

Plate 9, fig. 7

1967 *Panderodus unicostatus serratus* Rexroad: 47, pl. 4, figs 3, 4.

MATERIAL. 240 specimens: figured specimen (X.718).

OCCURRENCE. Idwian to Telychian.

DESCRIPTION. The cone is curved and asymmetrical. The anterior margin is rounded, the posterior edge is sharp and ornamented by a row of germ denticles for about two-thirds of its length. The lateral costa on one face is more strongly developed than on the other. In lateral view, the unit is broad and flat near the base, becoming more slender towards the apex. The basal cavity is deep and conical.

REMARKS. Rexroad (1967) remarked that this form differed only in the possession of a denticulate posterior margin from *P. unicostatus* (Branson & Mehl) and consequently named it as a subspecies of that species. The specimens recovered in the present study are similar to those illustrated by Rexroad and resemble only the broader, flatter specimens of *P. unicostatus*, which represent one extreme of the variation range of that species. Rexroad recorded only a few specimens from a very limited stratigraphic horizon, but in Britain the species is common throughout the Idwian to Telychian, where it occurs in association with *P. unicostatus*.

It is probable that *P. denticulatus* Schwab from the upper Silurian Aymestry Limestone (Schwab 1969 : 521–525, text-figs 1, 2) belongs here, but in view of the gap in stratigraphic ranges it is not at present included in synonymy.

Panderodus simplex (Branson & Mehl)

Plate 9, figs 8, 9

1933 *Paltodus simplex* Branson & Mehl: 42, pl. 3, fig. 4.
1947 *Paltodus acostatus* Branson & Branson (*partim*): 554, pl. 82, figs 1–5 only.

1953 *Paltodus acostatus* Branson & Branson; Rhodes: 296, pl. 21, figs 111, 112; pl. 22, figs 163, 164; pl. 23, figs 212, 213.
1957 *Paltodus? acostatus* Branson & Branson; Glenister: 727, pl. 85, fig. 7.
1960 *Paltodus* cf. *P. acostatus* Branson & Branson; Walliser: 31, pl. 7, fig. 10.
1961 *Paltodus acostatus* Branson & Branson: Bergström: 48, pl. 1, figs 13, 14.
1964 *Panderodus acostatus* (Branson & Branson); Serpagli & Greco: 204, pl. 36, figs 4a, 4b.
1966 *Panderodus simplex* (Branson & Mehl); Clark & Ethington: 682, pl. 82, figs 10, 14.
1967 *Panderodus simplex* (Branson & Mehl); Rexroad: 45, pl. 4, figs 7, 8.
1968 *Panderodus simplex* (Branson & Mehl); Nicoll & Rexroad: 54, pl. 7, fig. 28.
1969 *Panderodus simplex* (Branson & Mehl); Philip: 294, pl. 17, figs. 2, 3, 5, 12, text-fig. 1c.
1970 *Panderodus simplex* (Branson & Mehl); Pollock, Rexroad & Nicoll: 758, pl. 114, figs 23–25.

MATERIAL. 1,465 specimens: figured (X.719), (X.720).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cone is moderately curved and strongly laterally compressed. The anterior and posterior edges are sharp and the transverse section of the cone is lenticular. The basal cavity extends for about two-thirds of the length of the cone, terminating at a point close to the anterior margin.

Panderodus cf. ***P. staufferi*** (Branson, Mehl & Branson)

Plate 9, fig. 10

cf. 1951 *Paltodus staufferi* Branson, Mehl & Branson: 7, pl. 1, figs 23–27

MATERIAL. 332 specimens: figured (X.721).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cone is curved posteriorly and has sharp anterior and posterior edges. The anterior edge is commonly keeled from a point just above the base to the point of maximum recurvature, at about midlength of the cone. Each lateral face bears a costa, which is variable in position and development, but in no case extends to the base. The basal cavity is deep and conical, extending for about half the length of the cone.

REMARKS. These specimens are less antero-posteriorly extended at the base than those illustrated by Branson, Mehl & Branson (1951). *P. staufferi* has previously been recorded only from the upper Ordovician and it is possible that the Llandovery specimens represent homeomorphs of the Ordovician forms.

Panderodus unicostatus (Branson & Mehl)

Plate 9, figs 5, 6

1933 *Paltodus unicostatus* Branson & Mehl: 42, pl. 3, fig. 3.
1947 *Paltodus unicostatus* Branson & Mehl; Branson & Branson (*partim*): 554, pl. 82, figs 11–16 only.
1953 *Paltodus unicostatus* Branson & Mehl; Rhodes: 298, pl. 21, figs 84–88; pl. 22 figs 155, 156; pl. 23 figs 214–216.
1955 *Paltodus* cf. *P. unicostatus* Branson & Mehl; Rhodes: 127 pl. 10 figs 1, 3.

1957 *Paltodus*? *unicostatus* Branson & Mehl; Glenister: 729 pl. 85, fig. 1.
1957 *Paltodus unicostatus* Branson & Mehl; Walliser: 43, pl. 2, fig. 1.
1959 *Panderodus unicostatus* (Branson & Mehl); Sweet *et al.*: 1057, pl. 131, fig. 3.
1961 *Panderodus unicostatus* (Branson & Mehl); Wolska: 353, pl. 4, figs 3a, b.
1962 *Panderodus unicostatus* (Branson & Mehl); Kockel & Stoppel: 161, pl. 1, fig. 2.
1962 *Panderodus unicostatus* (Branson & Mehl); Sweet & Bergström: 1234, text-fig. 1d.
1964 *Panderodus unicostatus* (Branson & Mehl); Serpagli & Greco: 206, pl. 36, fig. 7; pl. 37, figs 1a, b.
1964 *Panderodus* cf. *unicostatus* (Branson & Mehl); Hamar: 272, pl. 1, figs 28, 29.
1965 *Panderodus unicostatus* (Branson & Mehl); Merrill: 390, pl. 2, fig. 8.
1965 *Panderodus unicostatus* (Branson & Mehl); Brooks & Druce: 376, pl. 12, fig. 8.
1966 *Panderodus unicostatus* (Branson & Mehl); Hamar: 67, pl. 1, fig. 6.
1966 *Panderodus unicostatus* (Branson & Mehl); Winder: pl. 9, fig. 7.
1966 *Panderodus unicostatus* (Branson & Mehl); Clark & Ethington: 683, pl. 82, figs 17, 19.
1966 *Panderodus unicostatus* (Branson & Mehl); Philip: 447, pl. 1, figs 10–12, 19.
1967 *Panderodus unicostatus unicostatus* (Branson & Mehl); Rexroad: 46, pl. 4, figs 1, 2.
1968 *Panderodus unicostatus unicostatus* (Branson & Mehl); Nicoll & Rexroad: 54, pl. 7, figs 29, 30.
1969 *Panderodus unicostatus* (Branson & Mehl); Philip: 295, pl. 17, figs 1, 4, 13, 14, text-fig. 1d.
1970 *Panderodus unicostatus unicostatus* (Branson & Mehl); Pollock, Rexroad & Nicoll: 758, pl. 114, figs 26–28.

MATERIAL. 3,750 specimens: figured (X.716), (X.717).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The asymmetric cone is curved, with a rounded anterior margin and a sharp posterior edge. The lateral costa on one face is more strongly developed than on the other. There is a variation from slender to robust forms. The basal cavity extends for about two-thirds of the length of the cone.

Panderodus sp. A

Plate 9, fig. 11

MATERIAL. 117 specimens: figured (X.724).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The stout cone is strongly recurved posteriorly at about half its length. The anterior margin is broadly rounded, the posterior margin sharply rounded. The base is only a little extended antero-posteriorly. The posterior portion is laterally compressed and is separated from the anterior portion by a sharp offset on each lateral face. The deep basal cavity terminates at the point of maximum recurvature.

REMARKS. The relationships of these specimens are difficult to determine. Rexroad (1967 : pl. 4, figs 5, 6) illustrated two specimens similar to those described above and assigned them to *Panderodus* cf. *P. unicostatus*. It is possible that these do represent an extreme variant of *P. unicostatus*, but there do not appear to be any intermediate forms in the Welsh Borderland material. Morphologically

similar conodonts from the upper Ordovician were referred to *P. robustus* by Branson, Mehl & Branson (1951 : 8, pl. 1, figs 28–33).

Genus ***PLECTOSPATHODUS*** Branson & Mehl, 1933

TYPE SPECIES. *Plectospathodus flexuosus* Branson & Mehl, 1933.

REMARKS. The orientation of the genus *Plectospathodus* has been the subject of some discussion by previous authors. Branson & Mehl (1933) did not define the orientation of their specimens, but compared the genus to *Ozarkodina*, in which the limbs are anterior and posterior. Rhodes (1953) considered that the processes were lateral, a view endorsed in 1957 by Walliser, who pointed out that with this orientation the cusp is recurved posteriorly. In 1964, however, Walliser described several species of *Plectospathodus* orientated such that the limbs were anterior and posterior. Rexroad (1967) pointed out the close relationship between *Plectospathodus* and *Trichonodella* and applied the same orientation, with the processes lateral, to each genus. Transitions between species of *Plectospathodus* and *Trichonodella* are apparent and the orientation applied by Rexroad is followed here.

Plectospathodus extensus Rhodes

Plate 7, figs 21, 22

1953 *Plectospathodus extensus* Rhodes: 323, pl. 23, figs 236–240
1957 *Plectospathodus extensus* Rhodes; Walliser: 43, pl. 3, figs 1, 2.
1958 *Plectospathodus extensus* Rhodes; Bischoff & Sannemann: 101, pl. 15, figs 11, 14, 15.
1960 *Plectospathodus extensus* Rhodes; Walliser: 32, pl. 8, fig. 20.
1962 *Plectospathodus extensus* Rhodes; Ethington & Furnish: 1281, pl. 173, fig. 6.
1962 *Plectospathodus extensus* Rhodes; Spasov & Veselinović: 241, pl. 2, fig. 4.
1964 *Plectospathodus extensus* Rhodes; Walliser: 64, pl. 8, fig. 1; pl. 30, figs 13, 14.
1965 *Plectospathodus extensus* Rhodes; Philip: 110, pl. 9, figs 9, 10.
1966 *Plectospathodus extensus* Rhodes; Barnett *et al.*: pl. 58, fig. 13.
1966 *Plectospathodus extensus* Rhodes; Spasov & Filipović: 47, pl. 2, figs 13, 17.
1968 *Plectospathodus extensus* Rhodes; Igo & Koike: 15, pl. 3, fig. 12.
1969 *Hindeodella excavata* (Branson & Mehl) Jeppsson (*partim*): 18, text-figs 1K, 3E.

MATERIAL. 41 specimens: figured (X.675), (X.676).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cusp is slender, sharp, posteriorly curved and circular in transverse section. The lateral processes may be straight or curved and are bowed posteriorly. One lateral process bears discrete denticles of subequal size, the other discrete denticles of unequal size, the largest being developed at the tip. The aboral margin of the cusp is extended posteriorly to form a prominent lip. The cavity is broadest and deepest beneath the cusp and extends as a shallow groove on the aboral surfaces of the lateral processes.

REMARKS. The recovery of *P. extensus* from the Llandovery of the Welsh Borderland extends the known stratigraphic range of the species down to the Fronian.

Plectospathodus flexuosus Branson & Mehl

Plate 7, fig. 24

1933 *Plectospathodus flexuosus* Branson & Mehl: 47, pl. 3, figs 31, 32.
1953 *Plectospathodus elegans* Rhodes: 323, pl. 23, figs 255, 263, 264.
1964 *Plectospathodus flexuosus* Branson & Mehl; Walliser: 65, pl. 9, fig. 10; pl. 30, figs 15, 16.
1969 *Hindeodella confluens* Branson & Mehl; Jeppsson (*partim*): 15, text-figs 1E, 2E, $2E_2$.
1970 *Plectospathodus flexuosus* Branson & Mehl; Pollock, Rexroad & Nicoll: 758, pl. 113, figs 19, 20.

MATERIAL. 9 specimens: figured (X.677).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The erect cusp is elliptical in transverse section, with the lateral diameter greatest. The lateral processes are thin, deep and of unequal length. The shorter process bears flat denticles, fused nearly to their apices and of unequal size, the largest being situated near midlength. The longer process is flexed posteriorly and bears short, flat denticles, fused nearly to their apices. The aboral surface is excavated only beneath the cusp, where a shallow, scarcely flared pit is present.

Plectospathodus irregularis (Branson & Branson)

Plate 7, fig. 23

1947 *Prioniodina irregularis* Branson & Branson: 555, pl. 82, figs 30, 31.
1967 *Plectospathodus irregularis* (Branson & Branson); Rexroad: 48, pl. 3, fig. 15.

MATERIAL. 5 specimens: figured (X.678).

OCCURRENCE. Fronian.

DESCRIPTION. The cusp is tall, posteriorly curved and subcircular in transverse section. The lateral processes are of unequal length, the shorter bearing two or three denticles of subequal size. The longer process is flexed a little posteriorly and bears five shorter, discrete denticles. The aboral surface of each process is grooved and the cavity widens and deepens beneath the cusp.

REMARKS. These specimens differ from those described by Branson & Branson (1947) in possessing a greater number of denticles on the longer lateral process and, in one example, an additional denticle on the shorter process. In all other features the specimens are comparable.

Genus *PTEROSPATHODUS* Walliser, 1964

TYPE SPECIES. *Pterospathodus amorphognathoides* Walliser, 1964.

Pterospathodus amorphognathoides Walliser

Plate 3, figs 17–19

1964 *Pterospathodus amorphognathoides* Walliser: 67, pl. 6, fig. 7; pl. 15, figs 9–15; text-fig. 1f.

1964 *Spathognathodus pennatus angulatus* Walliser (*partim*): 79, pl. 14, figs 21, 22 only.
1966 *Pterospathodus amorphognathoides* Walliser; Spasov & Filipović: 48, pl. 1, figs 4, 5.
1966 *Pterospathodus amorphognathoides* Walliser; Spasov: pl. 1, fig. 1.
1968 *Pterospathodus amorphognathoides* Walliser; Igo & Koike: 16, pl. 2, figs 12, 13.
1968 *Pterospathodus amorphognathoides* Walliser; Nicoll & Rexroad: 56, pl. 3, figs 1–7.
1969 *Pterospathodus amorphognathoides* Walliser; Schönlaub: pl. 1, fig. 8.
1969 *Pterospathodus amorphognathoides* Walliser; Drygant: 49, pl. 1, fig. 6.

MATERIAL. 174 specimens: figured (X.605), (X.606), (X.607).

OCCURRENCE. Telychian (C_6) and early Wenlock.

DESCRIPTION. The unit consists of a nearly straight blade with a bifurcating inner lateral process situated at, or slightly anterior to, midlength. A small outer lateral process may be situated directly opposite, or somewhat anterior to, the inner lateral process. The blade is commonly laterally thickened in mature specimens to form a narrow platform, bearing up to 40 closely packed, rounded denticles, which are often higher and sharper at the anterior end. The denticles are rounded in cross-section, but in large specimens become compressed and are extended laterally, particularly near the junction of the blade with the inner lateral process. In specimens showing marked platform development the denticle row may be bordered by a narrow trough on each side. The blade may be bent outwards at the posterior end. The inner lateral process consists of two branches, the longer of which is directed inwards and anteriorly and bears up to 10 low denticles. The shorter, posteriorly directed branch bears one to five low denticles. The branches diverge from the blade at angles that vary from 25° to 70°, but may be separated from it by a low ridge, which is itself perpendicular to the blade. In specimens where the blade is thickened to form a platform, the branches of the inner lateral process are similarly thickened. The small outer lateral process may be in the form of a trough-like lateral extension of the thickened blade. In other specimens it is low and unornamented, but in large examples it may support a small number of denticles. A wide, deep basal groove, commonly containing basal material, underlies the blade and the lateral processes.

REMARKS. Mature specimens show a large range of variation and marked differences are apparent between forms from the late Llandovery and those from the early Wenlock. In the Telychian (C_6), all but the smallest specimens display thickening of the blade into a platform and mature specimens possess a large number of denticles (Pl. 3, figs 18, 20). In the material from the Wenlock Shale the adults are morphologically closer to the juveniles and develop a smaller number of denticles. There is no thickening of the blade, which is usually separated from the inner lateral process by a low ridge (Pl. 3, fig. 19). If this sequence is observed elsewhere, it may be possible to define two chronological subspecies of *P. amorphognathoides*.

Genus ***PYGODUS*** Lamont & Lindström, 1957

TYPE SPECIES. *Pygodus anserinus* Lamont & Lindström, 1957.

REMARKS. There has been some controversy about the identification of the specimens described by Lamont & Lindström (1957) as conodonts. The genus

Pygodus was rejected from the Conodontophorida in the *Treatise on Invertebrate Paleontology* (Hass 1962 : W65) and included in the Paraconodontida (1962 : W248). Sweet & Bergström (1962 : 1250), however, stated that representatives of *Pygodus* grew similarly to all other conodonts and Lindström (1964 : 20, fig. 5C : 26, fig. 7E) showed that *Pygodus* had the structure of a true conodont. Rhodes & Müller (1966 : 4) still voiced doubts about the genus and suggested that further histological investigation was necessary before it could be assigned with certainty to the Conodontophorida.

Pygodus? lyra Walliser

Plate 3, fig. 2

1964 *Pygodus lyra* Walliser: 68, pl. 5, fig. 5; pl. 12, figs 8–14.

MATERIAL. 19 specimens: figured (X.609).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. Two corrugated ridges diverge from the short free blade to form a lyre shape. In some specimens the blade bisects the angle between the two ridges and bilateral symmetry is approached, but in others the blade is not central and is continuous with one of the ridges. A low, but prominent carina, dipping posteriorly, is present between the two ridges, from which it is separated by an unornamented trough on each side. This carina continues beyond the posterior limit of the rest of the unit forming a sharp posterior tip. The entire aboral surface is deeply excavated.

REMARKS. These specimens differ in several respects from those described by Walliser (1964), which do not possess a marked central carina and display an indented posterior termination. Walliser mentioned that some of his larger specimens possessed a central ridge, but in the present material specimens of all sizes display this feature. The side ridges exhibited by some of Walliser's specimens (e.g. Walliser 1964 : pl. 12, fig. 12) are absent. Despite these differences, these specimens appear to be conspecific with Walliser's, and may represent geographical or successional variants.

No phylogenetic link has been demonstrated between Ordovician and Llandovery specimens referred to *Pygodus*, and it is possible that the two groups are homeomorphic.

Genus ***SAGITTODONTUS*** Rhodes, 1953

TYPE SPECIES. *Sagittodontus robustus* Rhodes, 1953.

Sagittodontus edentatus (Branson & Branson)

Plate 7, figs 1–3

1947 *Trichonodella? edentata* Branson & Branson: 552, pl. 81, fig. 28; pl. 82, figs 40, 44, 48.
1947 *Trichonodella brassfieldensis* Branson & Branson (*partim*): 551 pl. 82, fig. 49 only.

1947 *Trichonodella carinata* Branson & Branson (*partim*): 552, pl. 82, figs 27, 34 only.
1967 *Trichonodella? edentata* Branson & Branson; Rexroad: 55, pl. 3, figs 31–34.
1968 *Trichonodella? edentata* Branson & Branson; Nicoll & Rexroad: 63, pl. 4, figs 16–18.
1970 *Sagittodontus edentatus* (Branson & Branson) Pollock, Rexroad & Nicoll: 759, pl. 112, figs 21–23.

MATERIAL. 45 specimens: figured (X.662), (X.663), (X.664).

OCCURRENCE. Idwian to Telychian.

DESCRIPTION. The stout cusp is erect or slightly posteriorly curved, with sharp posterior and lateral edges. The transverse section of the cusp is triangular with the outer lateral face broader than the inner lateral face. The base of the cusp is expanded and gives rise to three processes, two lateral and one posterior, continuous with the sharp edges of the cusp. The inner lateral process is directed aborally as an anticusp-like extension of the cusp and does not usually support denticles. The outer lateral process is directed aborally and outwards and commonly bears short denticles, fused nearly to their apices. The posterior bar is directed a little downwards, and commonly bears low, fused denticles, although these may be absent. The cusp is deeply excavated and the cavity extends as deep grooves beneath the processes.

REMARKS. As suggested by Pollock, Rexroad & Nicoll (1970 : 752), *S. edentatus* appears to be a transitional form in the evolution of *Exochognathus* from *Sagittodontus*. Poorly denticulate specimens resemble *S. robustus* Rhodes (1953 : 311, pl. 21, figs 141, 142) and those with well-developed denticulation of the processes are close to *E. brassfieldensis*.

Genus ***SPATHOGNATHODUS*** Branson & Mehl, 1941

TYPE SPECIES. *Spathodus primus* Branson & Mehl, 1933.

Spathognathodus abruptus sp. nov.

Plate 4, figs 6, 7

DERIVATION OF NAME. Latin, steep, with reference to the sudden decrease in the height of the denticles near the posterior tip of the blade.

DIAGNOSIS. *Spathognathodus* Branson & Mehl with a blade that is deflected inwards in the posterior quarter of its length. A small number of denticles at the posterior end of the blade are considerably shorter than the remainder. The flared basal cavity extends to the posterior tip of the unit.

HOLOTYPE. Specimen (X.574).

MATERIAL. 29 specimens: figured (X.574), (X.575).

TYPE LOCALITY AND HORIZON. Venusbank Formation of Hope Quarry, sample H.Q.3.

OCCURRENCE. Idwian and Fronian.

DESCRIPTION. Along the greater part of its length the blade consists of a row of 11 to 13 denticles, of subequal size and laterally compressed. The posterior denticle of this row is commonly slightly larger than the others and the three or four denticles anterior to it are compressed antero-posteriorly. Beyond the main denticle, the posterior part of the blade is deflected inwards by up to 30° and supports three or four considerably smaller denticles. The basal cavity is flanked by widely flaring lips from the posterior tip to almost the midlength of the unit, and continues as a groove to the anterior tip. The cavity is deepest and most widely flared beneath the point of deflection of the blade. The flaring is stronger on the outer side of the unit and the oral surface may be wrinkled into low ridges on the outer anterior portion.

REMARKS. There are close similarities to *Spathognathodus manitoulinensis* Pollock, Rexroad & Nicoll (1970 : 761–762, pl. 111, figs 17–19), which also displays a deflected blade and abrupt lowering of the denticles over a flared basal cavity. In *S. manitoulinensis*, however, the deflection is typically about 60°, and a greater number of denticles are present on the posterior part of the blade, which extends beyond the limit of the flared cavity. The flaring of the cavity is almost totally restricted to the outer side, where the outline approaches semicircular. The similarities between the two species suggest a relationship, and the differences may be due to facies control, geographical isolation or successional isolation.

A single specimen (X.576) of Fronian age is identified as *Spathognathodus* cf. *S. abruptus* (Pl. 4, fig. 8). The posterior end of the blade is characterized by two low denticles, which curve only slightly away from the line of the rest of the blade. The lips of the cavity, although broken, appear to be more symmetrically flared than is typical for *S. abruptus*. It is possible that this specimen is a transitional form in the evolution of *S. ranuliformis* from *S. abruptus*.

Spathognathodus gulletensis sp. nov.

Plate 4, figs 9–12

1965 *Spathognathodus* cf. *celloni* Walliser; Brooks & Druce: 377, pl. 12, figs 2, 3.

DERIVATION OF NAME. After Gullet Quarry in the Malvern Hills, where this species is particularly abundant.

DIAGNOSIS. *Spathognathodus* Branson & Mehl with fused denticles that are lower in the posterior one-third of the unit. The basal cavity is situated at, or slightly posterior to, midlength and has asymmetrically flared lips, which in outline are either rounded or posteriorly extended into an arrow shape.

HOLOTYPE. Specimen (X.577).

MATERIAL. 323 specimens: figured (X.577), (X.578), S.1.37, (X.580).

TYPE LOCALITY AND HORIZON. The Wych Formation of Gullet Quarry, sample Gullet 2.

OCCURRENCE. A single specimen from C_{3-4}, abundant in C_5 (Telychian).

DESCRIPTION. The blade is straight and bears a row of laterally compressed,

sharp denticles, fused nearly to their apices. The denticles vary in number from 13 to 18, but most specimens possess 15 or 16. The posterior four to seven denticles are lower than the remainder, which are of subequal height. There is often a single, slightly larger denticle immediately anterior to the low posterior denticles. One or two denticles at the anterior end of the blade may be somewhat broader than the others. The basal cavity is situated at, or slightly posterior to, midlength of the unit and has flared lips. The outline of the cavity is asymmetrical and may be subcircular or somewhat extended posteriorly to give an arrow shape. The cavity continues as a groove under the blade to the anterior and posterior tips.

REMARKS. There is a general morphological resemblance to *S. hassi*, from which *S. gulletensis* appears to have evolved by a decrease in the size of the apical denticle and an alteration in the outline of the basal cavity. There is also some similarity to *Spathognathodus primus* (Branson & Mehl), which differs in possessing very tall anterior denticles.

Spathognathodus hassi Pollock, Rexroad & Nicoll

Plate 4, figs 2, 3

1967 *Spathognathodus* cf. *S. oldhamensis* Rexroad: pl. 3, fig. 3.
1970 *Spathognathodus hassi* Pollock, Rexroad & Nicoll: 760, pl. 111, figs 8–12.

MATERIAL. 35 specimens: figured (X.624), (X.625).

OCCURRENCE. Idwian and Fronian.

DESCRIPTION. The blade is straight or slightly bowed and bears a row of tall, laterally compressed denticles, fused nearly to their apices. The blade is commonly a little thickened below the denticle row. The denticle above the basal cavity, a little posterior of centre, is larger than the others. The denticles to the posterior of the apical denticle are shorter than those to the anterior. The basal cavity is flanked by widely flared lips, which are rounded and a little asymmetrical in outline.

REMARKS. A single specimen of Fronian age has a poorly developed apical denticle and a somewhat elongated cavity, and appears to be transitional towards *S. gulletensis* sp. nov. The relationship of *S. hassi* to *S. oldhamensis* is discussed under that species.

Spathognathodus inclinatus (Rhodes)

Plate 4, figs 15, 16

1953 *Prioniodella inclinata* Rhodes: 324, pl. 23, figs 233–235.
1957 *Spathognathodus inclinatus* (Rhodes) Walliser: 47, pl. 1, figs 16–20.
1960 *Spathognathodus* n. sp. Walliser: 35, pl. 8, fig. 7.
1964 *Spathognathodus inclinatus inclinatus* (Rhodes) Walliser: 76, pl. 8, fig. 6; pl. 19, figs 6–21.
1966 *Spathognathodus inclinatus* (Rhodes) Barnett *et al.*: pl. 58, fig. 23.
1966 *Spathognathodus inclinatus inclinatus* (Rhodes) Philip: 450, pl. 1, figs 30, 31, 34, 35, 37–39.
1969 *Hindeodella excavata* (Branson & Mehl) Jeppson (*partim*): 18, text-figs 1G, 3A.

MATERIAL. 111 specimens: figured (X.627), (X.628).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The blade is straight or arched and is commonly laterally thickened below the denticle row. The denticles are closely packed, often partially fused, and inclined posteriorly. The denticles in the central portion of the blade are a little larger than those at the ends, and some specimens possess a single denticle that is markedly larger than the others. Beneath the largest denticle the basal cavity is expanded laterally and is flanked by flared lips. The cavity continues as a groove on the aboral surface of the blade to the anterior and posterior tips.

REMARKS. Some specimens, which possess an apical denticle and show less thickening of the blade than is typical, resemble *Ozarkodina* n. sp. A and *Ozarkodina* n. sp. B of Pollock, Rexroad & Nicoll (1970 : 757, pl. 113, figs 5–11). The phylogenetic relationships of this group of species are obscure, and it is possible that the Llandovery specimens may be homeomorphs of the *Spathognathodus inclinatus* group from younger Silurian strata.

Spathognathodus oldhamensis Rexroad

Plate 4, fig. 1

1967 *Spathognathodus oldhamensis* Rexroad: 49, pl. 3, figs 1, 2.
1970 *Spathognathodus oldhamensis* Rexroad; Pollock, Rexroad & Nicoll: 762, pl. 111, figs 13–16.

MATERIAL. 51 specimens: figured (X.626).

OCCURRENCE. Idwian and Fronian.

DESCRIPTION. The blade is straight or slightly bowed and bears a row of laterally compressed denticles. The denticles at the anterior end are inclined slightly anteriorly and fused nearly to their apices. The denticles immediately posterior of centre are completely fused and are commonly succeeded posteriorly by a very small denticle. The denticles at the posterior end are inclined a little posteriorly and are partially to almost completely fused. The shallow basal cavity is situated somewhat posterior of centre and has very widely flared lips. The outline of the asymmetrical cavity is a laterally elongated ellipse.

REMARKS. As remarked by Pollock, Rexroad & Nicoll (1970 : 761), there is a close relationship to *S. hassi*, which differs in possessing an apical denticle and in the more uniform spacing of the denticles. The two species have similar stratigraphic ranges and probably evolved from a common ancestor.

Spathognathodus polinclinatus Nicoll & Rexroad

Plate 4, fig. 13

1968 *Spathognathodus polinclinatus* Nicoll & Rexroad: 60, pl. 2, figs 19, 20.

MATERIAL. 13 specimens: figured, S.3.8.

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The blade is straight and bears a row of erect, laterally compressed denticles. The denticles are of subequal size and are fused nearly to their apices. Beneath the posterior half of the blade is a shallow basal cavity, flanked by very narrow lips. The cavity continues as a groove under the anterior half of the blade.

Spathognathodus ranuliformis Walliser

Plate 4, fig. 14

1964 *Spathognathodus ranuliformis* Walliser: 82, pl. 6, fig. 9; pl. 22, figs 5–7.
1968 *Spathognathodus ranuliformis* Walliser; Nicoll & Rexroad: 60, pl. 2, figs 10, 11.
1969 *Spathognathodus ranuliformis* Walliser; Drygant: 50, pl. 1, fig. 4.

MATERIAL. 46 specimens: figured (X.630).

OCCURRENCE. Telychian to early Wenlock.

DESCRIPTION. The blade is almost straight, but curves slightly inwards at the posterior end. The denticles are erect and fused nearly to their tips. The posterior end of the blade commonly comprises a single larger denticle, succeeded posteriorly by one or two smaller denticles. The cavity is flanked by extensively flared lips at the posterior end and continues as a groove to the anterior tip of the blade. The flared cavity is subcircular in outline and extends beyond the posterior limit of the blade.

REMARKS. Two specimens from C_{3-4} are identified as *Spathognathodus* cf. *S. ranuliformis*. The cavity of these specimens is less flared than is typical and the blade extends to the posterior tip of the unit. These specimens appear to be transitional from *S. abruptus*.

Spathognathodus sp. A nov.

Plate 4, fig. 4

MATERIAL. 14 specimens: figured, S.3.9.

OCCURRENCE. Fronian/Telychian.

DESCRIPTION. The straight blade bears 15 to 18 denticles of subequal height. The denticles in the central portion are completely fused, those at each end partially fused. The basal cavity is situated posterior of midlength and is enclosed by asymmetrical, widely-flared lips, which have a rounded to somewhat arrow-shaped outline. The cavity extends as a narrow groove to the tips of the blade.

REMARKS. The denticulation is similar to that of *S. oldhamensis*, from which this species may be descended. The outline of the basal cavity is similar to that of *S. gulletensis*.

Spathognathodus sp. B nov.

Plate 4, fig. 5

MATERIAL. 6 specimens: figured (X.629).

OCCURRENCE. Fronian/Telychian.

DESCRIPTION. The straight blade bears 13 to 16 denticles that decrease in height posteriorly. The denticles are fused nearly to their sharp apices, and a few to the posterior of midlength may be more completely fused. Alternatively, a few much broader denticles may be present in this position. The flaring of the basal cavity begins slightly anterior of midlength and extends nearly to the posterior tip. The outline of the almost symmetrical cavity is an antero-posteriorly elongated ellipse. The cavity extends as a groove to the tips of the blade.

REMARKS. The relationships to other species of *Spathognathodus* are obscure. The denticulation is somewhat similar to that of *S. oldhamensis* and *S.* sp. nov. A, and this species possibly evolved from that lineage. There is a morphological resemblance to some of the specimens of *S. inclinatus inflatus*, illustrated by Walliser (1964 : pl. 19, fig. 24).

Genus ***SYNPRIONIODINA*** Ulrich & Bassler, 1926

TYPE SPECIES. *Synprioniodina alternata* Ulrich & Bassler, 1926.

Synprioniodina bicurvata (Branson & Mehl)

Plate 5, fig. 28

1933 *Prioniodus bicurvatus* Branson & Mehl: 44, pl. 3, figs 9–12.
1956 *Prioniodina tropa* (Stauffer) Ziegler: 104, pl. 6, fig. 29; pl. 7, fig. 29.
1958 *Prioniodina bicurvata* (Branson & Mehl) Bischoff & Sannemann: 102, pl. 15, figs 6, 12.
1960 *Prioniodina bicurvata pronoides* Walliser: 33, pl. 8, figs 8–10.
1960 *Prioniodina bicurvata pronoides* Walliser; Ziegler: 193, pl. 15, figs 8, 9.
?1964 *Prioniodina bicurvata* (Branson & Mehl); Serpagli & Greco: 207, pl. 37, fig. 11.
1964 *Neoprioniodus bicurvatus* (Branson & Mehl) Walliser: 46, pl. 29, figs 27–30, 31–33?; text-fig. 5d.
1965 *Neoprioniodus bicurvatus* (Branson & Mehl); Philip: 105, pl. 9, figs 13, 18, 20.
1966 *Neoprioniodus bicurvatus* (Branson & Mehl); Barnett *et al.*: pl. 58, fig. 22.
1966 *Neoprioniodus bicurvatus* (Branson & Mehl); Philip: 446, pl. 3, figs 12–16.
1969 *Hindeodella confluens* Branson & Mehl; Jeppsson (*partim*): 15, text-figs 1C, 2C.
1969 *Neoprioniodus bicurvatus* (Branson & Mehl); Philip: 292, pl. 17, fig. 15.
1970 *Synprioniodina bicurvata* (Branson & Mehl) Pollock, Rexroad & Nicoll: 762, pl. 114, figs 16, 17.

MATERIAL. 10 specimens: figured (X.661).

OCCURRENCE. Idwian to Telychian.

DESCRIPTION. The cusp is straight, with sharp anterior and posterior edges. The posterior bar is curved strongly downwards and may be bowed inwards. The denticles of the posterior bar are of subequal size and may be discrete or closely packed.

The anterior bar forms a sharply pointed downward extension of the cusp, is very short and may or may not bear a few small, fused denticles. The basal cavity is slightly flared beneath the cusp, but narrows rapidly below the posterior bar.

Synprioniodina silurica Walliser

Plate 5, fig. 27

1964 *Synprioniodina silurica* Walliser: 88, pl. 6, fig. 12; pl. 8, fig. 18; pl. 29, figs 38–41; pl. 30, figs 1–4, 6.
1968 *Synprioniodina silurica* Walliser; Nicoll & Rexroad: 61, pl. 4, fig. 10.
1970 *Synprioniodina silurica* Walliser; Pollock, Rexroad & Nicoll: 762, pl. 114, fig. 15.

MATERIAL. 18 specimens: figured (X.660).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cusp is stout and straight, with sharp anterior and posterior edges. The posterior bar is deep, strongly downcurved and bears several discrete denticles. The anterior bar is usually very much shorter and bears only two or three denticles. The cavity is widened and flared beneath the cusp and is slightly extended posteriorly.

REMARKS. Most of these specimens are broken, and the range of variation cannot be determined. The sharp anterior and posterior margins of the cusp indicate a closer similarity to the specimens described from Europe by Walliser (1964) than to those described from North America by Nicoll & Rexroad (1968).

Genus ***TRICHONODELLA*** Branson & Mehl, 1948

TYPE SPECIES. *Trichognathus prima* Branson & Mehl, 1933.

Trichonodella asymmetrica Nicoll & Rexroad

Plate 7, fig. 17

1968 *Trichonodella asymmetrica* Nicoll & Rexroad: 62, pl. 4, fig. 7.

MATERIAL. 9 specimens: figured (X.680).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cusp is inclined posteriorly and twisted. The transverse section of the cusp is subtriangular. The denticulate lateral processes are deep and one is considerably longer than the other. The shorter process bears about four comparatively tall, discrete denticles. The longer process bears about six shorter, discrete denticles. The basal cavity is shallow beneath the cusp and is slightly extended posteriorly.

Trichonodella excavata (Branson & Mehl)

Plate 7, fig. 20

1933 *Trichognathus excavata* Branson & Mehl: 51, pl. 3, figs 35, 36.
1953 *Trichonodella aborflexa* Rhodes: 312, pl. 23, figs 231, 241, 242.
1957 *Trichonodella excavata* (Branson & Mehl) Walliser: 48, pl. 3, figs 3, 4, 6–8.
1958 *Trichonodella excavata* (Branson & Mehl); Bischoff & Sannemann: 109, pl. 15, figs 16, 18.
1962 *Trichonodella excavata* (Branson & Mehl); Ethington & Furnish: 1287, pl. 173, fig. 8.
1964 *Trichonodella excavata* (Branson & Mehl); Walliser: 89, pl. 8, fig. 2; pl. 31, figs 26, 27.
1966 *Trichonodella excavata* (Branson & Mehl); Barnett *et al.*: pl. 58, fig. 14.
1968 *Trichonodella excavata* (Branson & Mehl); Nicoll & Rexroad: 63, pl. 4, fig. 2.
1969 *Hindeodella excavata* (Branson & Mehl); Jeppsson (*partim*): 18, text-figs 1L, 3F.

MATERIAL. 49 specimens: figured (X.685).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cusp is tall, slender and posteriorly inclined. The lateral processes bear closely packed denticles and diverge at an angle of 120°–160°, together forming a symmetrical arch. The basal cavity beneath the cusp is shallow, but is considerably expanded posteriorly, forming a wide groove which extends upwards for about a quarter of the length of the cusp. The cavity continues as a shallow groove on the aboral surface of the processes.

REMARKS. A few specimens show a degree of asymmetry and flexing of the processes, indicative of transition towards *Plectospathodus extensus*.

Trichonodella? expansa Nicoll & Rexroad

Plate 7, fig. 14

1968 *Trichonodella? expansa* Nicoll & Rexroad: 64, pl. 4, figs 19–22.

MATERIAL. 36 specimens: figured (X.679).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The tall, stout cusp is posteriorly inclined and a little twisted. The transverse section of the cusp varies from square to triangular. The base is expanded and gives rise to three or four variably developed processes, which are also expanded to give a platform. The two lateral processes and the posterior process are usually well-developed and denticulate. The posterior process is commonly the longest. A poorly developed anterior process may be present. A shallow cavity, usually containing basal material, is excavated on the aboral surface.

REMARKS. Specimens from older strata display a less expanded base and a squarer cusp than those from younger strata. There appears to be a gradual increase in the expansion of the base with time.

The generic position of this species is very questionable. Nicoll & Rexroad (1968) suggested that it evolved from *Sagittodontus edentatus*, but such a phylogenetic relationship is not apparent in this material, There is no evidence for any relation-

ship with representatives of the genus *Trichonodella*, but the name assigned by Nicoll & Rexroad is retained until the generic position has been satisfactorily resolved.

Trichonodella inconstans Walliser

Plate 7, fig. 16

1957 *Trichonodella inconstans* Walliser: 50, pl. 3, figs 10–17.
1958 *Trichonodella inconstans* Walliser; Bischoff & Sannemann: 109, pl. 15, figs 20, 21.
1960 *Trichonodella inconstans* Walliser; Ziegler: 197, pl. 14, figs 14, 17.
1962 *Trichonodella inconstans* Walliser; Ethington & Furnish: 1287, pl. 173, fig. 7.
1964 *Trichonodella inconstans* Walliser; Walliser: 90, pl. 8, fig. 8; pl. 30, figs 10–12.
1965 *Trichonodella inconstans* Walliser; Philip (*partim*): 112, pl. 9, fig. 15 only.
1965 *Trichonodella* aff. *T. inconstans* Walliser; Brooks & Druce: 378, pl. 12, fig. 4.
1966 *Trichonodella inconstans* Walliser; Philip: 451, pl. 3, fig. 23; pl. 4, figs 21, 23, 27, 30.
1967 *Trichonodella* cf. *T. inconstans* Walliser; Rexroad: 54, pl. 3, fig. 19.
1968 *Trichonodella inconstans* Walliser; Nicoll & Rexroad: 64, pl. 4, fig. 1.
1969 *Trichonodella inconstans* Walliser; Philip: 295, pl. 18, figs 9, 12, 14, 15.
1970 *Trichonodella inconstans* Walliser; Pollock, Rexroad & Nicoll: 762, pl. 113, figs 26, 27.

MATERIAL. 99 specimens: figured (X.684).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The posteriorly inclined cusp is circular in transverse section. The lateral processes are more or less symmetrical and bear widely spaced denticles. The basal cavity is wide and deep beneath the cusp and continues as a groove under the processes.

REMARKS. The wide range of variation remarked upon by previous authors is apparent in this material. Many specimens are included that are transitional to *Lonchodina greilingi* and it is possible that Pollock, Rexroad & Nicoll (1970 : 763) were correct in considering that these two species should be grouped together.

Trichonodella symmetrica (Branson & Mehl)

Plate 7, figs 15, 18, 19

1933 *Trichognathus symmetrica* Branson & Mehl: 50, pl. 3, figs 33, 34.
1953 *Trichonodella symmetrica* (Branson & Mehl); Rhodes (*partim*): 315, pl. 23, fig. 246 only.
1964 *Trichonodella symmetrica* (Branson & Mehl); Walliser: 90, pl. 9, fig. 11; pl. 31, figs 28–30.
1965 *Trichonodella symmetrica* (Branson & Mehl); Philip: 112, pl. 9, figs 19, 21.
1968 *Trichonodella symmetrica* (Branson & Mehl); Igo & Koike: 19, pl. 3, figs 10, 11.
1969 *Hindeodella confluens* Branson & Mehl; Jeppsson (*partim*): 15, text-figs 1F, 2F.
1969 *Trichonodella symmetrica* (Branson & Mehl); Philip: 295, pl. 18, fig. 24.
1970 *Trichonodella symmetrica* (Branson & Mehl); Pollock, Rexroad & Nicoll: 763, pl. 113, figs 22–24.

MATERIAL. 53 specimens: figured (X.681), (X.682), (X 683).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The erect cusp is triangular to subtriangular in transverse section. The posterior edge of the cusp is sharp, the anterior face is flat or gently convex. The lateral processes are symmetrical and bear closely packed denticles. A shallow cavity is excavated beneath the cusp, but is not conspicuously extended posteriorly or laterally.

gen. et sp. indet. A

Plate 8, fig. 18

MATERIAL. 1 specimen: figured (X.693).

OCCURRENCE. C_{3-4}.

DESCRIPTION. The unit consists of a long bar, which does not appear to be broken at either end. In lateral view, the aboral edge of the bar is gently projected aborally near one end to form a slight lip. The bar bears 17 discrete denticles of unequal size, without a distinguishable cusp. The denticles are somewhat laterally compressed and are elliptical in transverse section. The aboral surface of the bar is grooved along its entire length, the groove being widest and deepest in the area of the aborally projecting lip.

gen. et sp. indet. B

Plate 5, fig. 29

MATERIAL. 1 specimen: figured (X.694).

OCCURRENCE. C_{3-4}.

DESCRIPTION. The unit consists of a straight, denticulate bar and a short, denticulate lateral process. The main bar bears a large denticle at one end, which may be taken as the cusp. The cusp is laterally compressed with sharp anterior and posterior edges and a sharp tip. Anterior to the cusp are seven sharp, laterally compressed denticles. The two denticles at the anterior end of the bar are short and almost totally fused. The remaining five denticles are nearly as tall as the cusp and fused only near their bases. The lateral process arises adjacent to the denticle immediately anterior to the cusp and points laterally and slightly anteriorly, making an angle of about 75° with the blade. The process bears two short, partially fused denticles that are compressed in the plane of the process. The entire aboral surface is excavated by a shallow groove, which is filled with basal material.

VII. CONCLUSIONS

Samples collected from Llandovery and early Wenlock strata of the Welsh Borderland yielded well-preserved and diversified conodont faunas. The collecting techniques employed in this investigation were largely those of reconnaissance and only well-documented, major exposures were visited in the separate areas. There is strong evidence that conodont faunal assemblages changed considerably through

the period studied, and four assemblage zones can be broadly recognized in the Welsh Borderland. The potential value of conodonts in refined stratigraphic correlation of the Llandovery has, therefore, been established and it is now necessary to undertake detailed sampling in each area where valuable conodont faunas are known to occur. When completed, this should enable clear definition of zonal boundaries. In addition, it is probable that phylogenetic lineages for important genera such as *Spathognathodus* and *Icriodella* will be established by studies of successional populations, and these will form an important tool for local and intercontinental correlation. Before detailed correlations can be achieved, it will be necessary to add to the knowledge of the effects of facies control and faunal provincialism on the distribution of Llandovery conodonts.

VIII. ACKNOWLEDGMENTS

This research was undertaken during the period of tenure of a Research Studentship grant awarded by the Nature Environment Research Council.

The investigation was suggested by Dr R. L. Austin of the University of Southampton. The help, advice and encouragement given by Dr Austin throughout the study is acknowledged with gratitude. Professor F. Hodson of the University of Southampton also provided advice and encouragement and made available the facilities of his department.

Fieldwork was facilitated by the guidance and assistance at various times of Dr P. R. Ashton of British Petroleum, Sunbury, Middlesex, Dr M. G. Bassett of the National Museum of Wales, Cardiff, Mr T. Clayton of the University of Southampton, Dr L. R. M. Cocks of the British Museum (Natural History), Dr R. A. Davis of the University of Cincinnati and Professor F. H. T. Rhodes of The University of Michigan. Dr M. Brooks of University College, Swansea greatly assisted by providing rock samples from Gullet Quarry and, with Mr R. K. Jones and Dr M. G. Bassett, from Hollybush Quarry. Dr M. Brooks and Miss M. Roberts provided for description a conodont collection from the Damery Formation of Tortworth. Dr W. S. McKerrow of the University of Oxford kindly made available the rock specimens collected in the Welsh Borderland by Dr A. M. Ziegler. Valuable information on Llandovery palaeontology and stratigraphy was provided by many workers, including Professor C. H. Holland of Trinity College, Dublin, Miss J. Vinnicombe of Kingston College of Technology and Dr V. G. Walmsley of University College, Swansea.

Advance information about undescribed lower Silurian conodont faunas from North America was kindly provided by Dr R. S. Nicoll, University of Iowa, Dr C. A. Pollock, Pan American Petroleum Company, Calgary and Dr C. B. Rexroad, Indiana Geological Survey. Dr Rexroad, in particular, gave a considerable amount of information and also supplied topotype specimens for comparison. Information about European conodont faunas was supplied by Dr H. Mostler of the University of Innsbruck, Dr H. P. Schönlaub of the University of Graz and Professor O. H. Walliser of the University of Göttingen.

The patient work of Frau J. Sprotte in the translation into English of German literature is gratefully acknowledged. Sincere thanks are due to Mrs P. Lawrence,

who gave invaluable assistance and advice in the photography of specimens. Mrs A. Dunkley, who prepared the charts of Llandovery conodont zones and phylogenies, and Mr C. Stuart are thanked for assistance in the preparation of text-figures.

IX. REFERENCES

Al-Hasani, N. & Mostler, H. 1969. Zur Geologie der Spiessnägel südlich Kirchberg (Nördliche Grauwackenzone, Tirol). *Veröff. Univ. Innsbruck, Alpenkdl. Stud.*, **5** : 1–26.

Barnett, S. G. 1965. Conodonts from the Jacksonburg limestone (Middle Ordovician) of northwestern New Jersey and eastern Pennsylvania. *Micropaleontology*, New York, **11** : 59–80, pls. 1–2.

Barnett, S. G., Kohut, J. J., Rust, C. C. & Sweet, W. C. 1966. Conodonts from Nowshera Reef Limestones (Uppermost Silurian or Lowermost Devonian), West Pakistan. *J. Paleont.*, Tulsa, **40** : 435–438, pl. 58.

Bergström, S. M. 1961. Conodonts from the Ludibundus limestone (Middle Ordovician) of the Tvaren area (South-east Sweden). *Ark. Min.*, Stockholm, **3** : 1–64, pls. 1–5.

—— 1964. Remarks on some Ordovician conodont faunas from Wales. *Acta Univ. lund.*, **128,** Section II, No. 3 : 1–67.

Bergström, S. M. & Sweet, W. C. 1966. Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky and its lateral equivalents in Ohio and Indiana. *Bull. Amer. Paleont.*, Ithaca, **50,** no. 299 : 271–441, pls. 28–35.

Bischoff, G. & Sannemann, D. 1958. Unterdevonische Conodonten aus dem Frankenwald. *Notizbl. hess. Landesamt. Bodenforsch.*, Wiesbaden, **86** : 87–110, pls. 12–15.

Branson, E. B. & Branson, C. C. 1947. Lower Silurian conodonts from Kentucky. *J. Paleont.*, Tulsa, **21** : 549–556, pls. 81–82.

Branson, E. B. & Mehl, M. G. 1933. Conodonts from the Bainbridge (Silurian) of Missouri. *Univ. Mo. Stud.*, Columbia, **8** : 39–52, pl. 3.

—— —— 1933*a*. Conodonts from the Plattin (Middle Ordovician) of Missouri. *Univ. Mo. Stud.*, Columbia, **8** : 101–119, pls. 8–10.

—— —— 1933*b*. Conodonts from the Maquoketa-Thebes (Upper Ordovician) of Missouri. *Univ. Mo. Stud.*, Columbia, **8** : 121–131, pl. 10.

Branson, E. B., Mehl, M. G. & Branson, C. C. 1951. Richmond conodonts of Kentucky and Indiana. *J. Paleont.*, Tulsa, **25** : 1–17, pls. 1–4.

Brooks, M. & Druce, E. C. 1965. A Llandovery Conglomeratic Limestone in Gullet Quarry, Malvern Hills, and its Conodont Fauna. *Geol. Mag.*, London, **102** : 370–382, pl. 12.

Carlson, C. C. 1960. Stratigraphy of the Winnipeg and Deadwood Formations in North Dakota. *Bull. N. Dak. geol. Surv.*, Grand Forks, **35** : 1–149, pls. 1–2.

Clark, D. L. & Ethington, R. L. 1966. Conodonts and Biostratigraphy of the Lower and Middle Devonian of Nevada and Utah. *J. Paleont.*, Tulsa, **40** : 659–689, pls. 82–84.

Cocks, L. R. M. 1967. Depth patterns in Silurian Marine Communities. *Marine Geol.*, Amsterdam, **5** : 379–382.

Cocks, L. R. M. & Rickards, R. B. 1969. Five boreholes in Shropshire and the relationships of shelly and graptolitic facies in the lower Silurian. *Quart. J. geol. Soc. Lond.*, **124** (for 1968) : 213–238.

Cocks, L. R. M., Toghill, P. & Ziegler, A. M. 1970. Stage names within the Llandovery Series. *Geol. Mag.*, Cambridge, **107** : 79–87.

Cocks, L. R. M. & Walton, G. 1968. A large temporary exposure in the Lower Silurian of Shropshire. *Geol. Mag.*, London, **105** : 390–397.

Craig, W. W. 1969. Lithic and conodont succession of Silurian strata, Batesville District, Arkansas. *Bull. geol. Soc. Amer.*, New York, **80** : 1621–1628.

Drygant, D. M. 1969. Conodonts from the Restevsky, Kytaigorodsky and Mukshinsky Horizons (Silurian of Podolia). *Paleont. Sborn.*, Bratislava, **6** : 49–56, pl. 1.

DRYGANT, D. M. & TSEGELNYUK, P. D. 1968. Pro vik Restevskogo ta Kitaygorodskogo gorizontiv siluru Podillya. *Akad. Nauk Ukr. RSR, Dopov.*, Kiev, Ser. B, No. 12 : 1066–1069.

ELLES, G. L. & WOOD, E. M. R. 1901–18. A monograph of British graptolites. *Palaeontogr. Soc.* (*Monogr.*), London, 1–539, pls. 1–52.

ETHINGTON, R. L. 1959. Conodonts of the Ordovician Galena Formation. *J. Paleont.*, Tulsa, **33** : 257–292, pls. 39–41.

ETHINGTON, R. L. & CLARK, D. L. 1964. Conodonts from the El Paso Formation (Ordovician of Texas and Arizona). *J. Paleont.*, Tulsa, **38** : 685–704, pls. 113–115.

ETHINGTON, R. L. & FURNISH, W. M. 1962. Silurian and Devonian conodonts from Spanish Sahara. *J. Paleont.*, Tulsa, **36** : 1253–1290, pls. 172–173.

FAHRAEUS, L. E. 1966. Lower Viruan (Middle Ordovician) Conodonts from the Gullhogen quarry, Southern Central Sweden. *Sverig. geol. Unders.*, Stockholm, Ser. C, no. **610** : 1–33, pls. 2–4.

GLENISTER, A. T. 1957. The conodonts of the Ordovician Maquoketa Formation in Iowa. *J. Paleont.*, Tulsa, **31** : 715–736, pls. 85–88.

HAMAR, G. 1964. The Middle Ordovician of the Oslo region, Norway. 17. Conodonts from the lower Middle Ordovician of Ringerike. *Norsk. geol. Tidsskr.*, Oslo, **44** : 243–292, pls. 1–6.

—— 1966. The Middle Ordovician of the Oslo region, Norway. 22. Preliminary report on conodonts from the Oslo-Asker and Ringerike Districts. *Norsk. geol. Tidsskr.*, Oslo, **46** : 27–83, pls. 1–7.

HASS, W. H. 1962. Conodonts. *In* Moore, R. C., *Treatise on Invertebrate Paleontology, Part, W. Miscellanea*, Univ. Kansas Press. Lawrence W.3–W.69.

HUDDLE, J. W. 1968. Redescription of Upper Devonian Conodont Genera and Species proposed by Ulrich and Bassler in 1926. *Prof. Pap. U.S. geol. Surv.*, Washington, **578** : 1–55, pls. 1–17.

IGO, H. & KOIKE, T. 1966. Recent Progress of Conodont Research in Asia. *Mem. Mejiro Gakuen Wom. Jun. Coll.*, Tokyo, **3** : 9–17.

—— —— 1967. Ordovician and Silurian Conodonts from the Langkawi Islands, Malaya, Part 1. *Geol. Palaeont. S.E. Asia*, Univ. Tokyo Press, Tokyo. **3** : 1–29, pls. 1–3.

—— —— 1968. Ordovician and Silurian Conodonts from the Langkawi Islands, Malaya, Part 2. *Geol. Palaeont. S.E. Asia*, Tokyo, **4** : 1–21, pls. 1–3.

JAEGER, H. & SCHÖNLAUB, H. P. 1970. Ein Beitrag zum Verhältnis Conodonten-Parachronologie/Graptolithen-Orthochronologie im älteren Silur. *Öst. Akad. Wissen.*, **5** : 1–6.

JEPPSSON, L. 1969. Notes on some Upper Silurian multielement conodonts. *Geol. Fören. Stockh. Förh.*, **91** : 12–24, figs 1–4.

JONES, O. T. 1925. Geology of the Llandovery District. Part 1: the southern area. *Quart. J. geol. Soc. Lond.*, **81** : 344–388, pl. 21.

—— 1949. Geology of the Llandovery District. Part 2: the northern area. *Quart. J. geol. Soc. Lond.*, **105** : 43–64, pl. 3.

JONES, R. K., BROOKS, M., BASSETT, M. G., AUSTIN, R. L. & ALDRIDGE, R. J. 1969. An Upper Llandovery limestone overlying Hollybush Sandstone (Cambrian) in Hollybush Quarry, Malvern Hills. *Geol. Mag.*, London, **106** : 457–469.

KING, W. B. R. 1928. The geology of the district around Meifod, Montgomeryshire. *Quart. J. geol. Soc. Lond.*, **84** : 671–702, pl. 52.

KOCKEL, F. & STOPPEL, D. 1962. Nuevos Hallazgos de Conodontos y Algunos Cortes en el Paleozoico de Malaga (sur de España). *Notas Inst. geol. Esp.*, Madrid, **68** : 133–170, pls. 1–2.

LAMONT, A. & LINDSTRÖM, M. 1957. Arenigian and Llandeilian cherts identified in Southern Uplands of Scotland by means of conodonts. *Trans. Edinb. geol. Soc.*, **17** : 60–70, pl. 5.

LAPWORTH, C. 1879–1880. On the geological distribution of the Rhabdophora. *Ann. Mag. nat. Hist.*, London, Ser. 5 : vols. **3** : 245–57, **4** : 333–41, 423–31; **5** : 45–62, 273–85, 358–69; **6** : 16–29, 185–207.

LINDSTRÖM, M. 1954. Conodonts from the lowermost Ordovician strata of south-central Sweden. *Geol. Fören. Stockh. Förh.*, **76** : 517–601, pls. 1–7.

—— 1964. *Conodonts*. Elsevier, Amsterdam. 196 pp.

MANZONI, M. 1965. Faune a Conodonti del Siluriana e Devoniano Delle Alpi Carniche. *G. Geol.*, Bologna, **33** : 179–203.

MERRILL, G. K. 1965. Conodonts from the Burnam Limestone of Central Texas. *Tex. J. Sci.*, San Marcos, **17** : 345–403, pls. 1–4.

MOSTLER, H. 1966. Zur Einstufung der 'Kieselschiefer' von der Lachtal-Grundalm (Fieberbrunn, Tirol). *Verh. geol. Bundesanst. Wien*, **1/2** : 157–169.

—— 1967. Conodonten aus dem tieferen Silur der Kitzbühler Alpen (Tirol). *Ann. In. naturh. Mus. Wien*, **71** : 295–303, pl. 1.

—— 1968. Das Silur im Westabschnitt der Nördlichen Grauwackenzone (Tirol und Salzburg). *Mitt. geol. Ges. Wien*, **18** : 89–150.

NICOLL, R. S. & REXROAD, C. B. 1968. Stratigraphy and Conodont Paleontology of the Salamonie Dolomite and Lee Creek Member of the Brassfield Limestone (Silurian) in South-eastern Indiana and Adjacent Kentucky. *Bull. Indiana geol. Surv.*, Bloomington, **40** : 1–73, pls. 1–7.

OBERG, R. 1966. Winnipeg conodonts from Manitoba. *J. Paleont.*, Tulsa, **40** : 130–147, pls. 15–16.

PHILIP, G. M. 1965. Lower Devonian conodonts from the Tyers area, Gippsland, Victoria. *Proc. roy. Soc. Vict.*, Melbourne **79** : 95–118 pls. 8–10.

—— 1966. Lower Devonian conodonts from the Buchan Group, eastern Victoria. *Micropaleontology*, New York, **12** : 441–460, pls. 1–4.

—— 1969. Silurian conodonts from the Dirk Hartog Formation, Western Australia. *Proc. roy. Soc. Vict.*, Melbourne, **82** : 287–298, pls. 17–18.

POLLOCK, C. A., REXROAD, C. B. & NICOLL, R. S. 1970. Lower Silurian conodonts from Northern Michigan and Ontario. *J. Paleont.*, Tulsa, **44** : 743–764, pls. 111–114.

PULSE, R. R. & SWEET, W. C. 1960. The American Upper Ordovician Standard. III. Conodonts from the Fairview and McMillan Formations of Ohio, Kentucky and Indiana. *J. Paleont.*, Tulsa, **34** : 237–264, pls. 35–37.

REXROAD, C. B. 1964. Silurian conodonts from central Kentucky and their relation to European zones (Abstract). *Bull. Amer. Ass. Petrol. Geol.*, Tulsa, **48** : 543.

—— 1967. Stratigraphy and Conodont Paleontology of the Brassfield (Silurian) in the Cincinnati Arch Area. *Bull. Indiana geol. Surv.*, Bloomington, **36** : 1–64, pls. 1–4.

REXROAD, C. B. & RICKARD, L. V. 1965. Zonal Conodonts from the Silurian Strata of the Niagara Gorge. *J. Paleont.*, Tulsa, **39** : 1217–1220.

RHODES, F. H. T. 1953. Some British Lower Palaeozoic conodont faunas. *Phil. Trans.* (Ser. B), London, **237** : 261–334, pls. 20–23.

—— 1955. The conodont fauna of the Keisley Limestone. *Quart. J. geol. Soc. Lond.*, **111** : 117–142, pls. 7–10.

RHODES, F. H. T. & MÜLLER, K. J. 1966. Comments on Conodonts. *Paleont. Contr. Univ. Kans.*, Topeka, Paper 9 : 2–5.

SANNEMANN, D. 1955. Ordovicium und Oberdevon der Bayerischen Fazies des Frankenwaldes nach Conodonten-funden. *Neues Jb. Geol. Paläont.*, Stuttgart, **102** : 1–36, pls. 1–3.

SCHÖNLAUB, H. P. 1969. Das Paläozoikum zwischen Bischofalm und Hohem Trieb (Zentrale Karnische Alpen). *Jb. geol. Bundesanst., Wien*, **112** : 265–320, pls. 1–2.

SCHOPF T. J. M. 1966. Conodonts of the Trenton Group (Ordovician) in New York, Southern Ontario and Quebec. *Bull. N. Y. St. Mus.*, Albany **405** : 1–105 pls. 1–6.

SCHWAB K. W. 1969. *Panderodus denticulatus* a new conodont species from the Aymestry Limestone (Upper Silurian) of England. *J. Paleont.*, Tulsa **43** : 521–525.

SERPAGLI E. & GRECO A. 1964. Osservazioni preliminari su alcuni Conodonti ordoviciani e siluriani delle Alpi Carniche italiane. *Boll. Soc. Paleont. ital.*, Roma, **3** : 192–211, pls. 34–37.

SIMPSON, G. G. 1961. *Principles of Animal Taxonomy*. 247 pp. New York.

Spasov, H. 1964. Beitrag zur Stratigraphie des Silurs und Devons im Kraiste. *Rev. bulg. geol. Soc.*, Sofia **25** : 267–283, pls. 1–2.

—— 1965. Paleozoic and Triassic Conodont Fauna from West Macedonia. *Bull. Inst. geol. Macedon.*, Skopje, **12** : 23–32, pl. 1.

—— 1966. Significance of the Conodont Fauna for the Stratigraphy of the Palaeozoic. *Bull. Inst. Geol. 'Strasimir Dimitrov'*, Sofia, **15** : 89–97, pl. 1.

Spasov, H. & Filipović I. 1966. Konodontska Fauna Starijeg i Mladeg Paleozoica Ji. i Sz Bosne. *Geol. Glasn.*, Sarajevo, **11** : 33–53, pls. 1–3.

Spasov, H. & Veselinović, M. 1962. Conodont Fauna from the Upper Ludlovian Limestones on Suva Planina (Eastern Serbia, Yugoslavia). *Zav. Geol. Geof. istrazivanja*, **20** : 233–244, pls. 1–2.

Squirrell, H. C. & Tucker, E. V. 1960. The geology of the Woolhope inlier (Herefordshire). *Quart. J. geol. Soc. Lond.*, **116** : 139–185, pl. 15.

Stauffer, C. R. 1935. Conodonts of the Glenwood Beds. *Bull. geol. Soc. Amer.*, New York, **46** : 125–168, pls. 9–12.

Stein, V. 1964. A section through the Llandovery of N.E. Bavaria, Germany. *Geol. Mag.*, London, **101** : 322–328.

—— 1965. Stratigraphische und paläontologische Untersuchungen im Silur des Frankenwaldes. *Neues Jb. Geol. Paläont.*, Stuttgart, **121** : 111–200.

Stone, G. L. & Furnish, W. M. 1959. Bighorn conodonts from Wyoming. *J. Paleont.*, Tulsa, **33** : 211–228 pls. 31–32.

Sweet, W. C. & Bergström, S. M. 1962. Conodonts from the Pratt Ferry Formation (Middle Ordovician) of Alabama. *J. Paleont.*, Tulsa, **36** : 1214–1252, pls. 168–171.

Sweet, W. C., Turco, C. A., Warner, E. Jr. & Wilkie, L. C. 1959. The American Upper Ordovician standard. I. Eden conodonts from the Cincinnati region of Ohio and Kentucky. *J. Paleont.*, Tulsa, **33** : 1029–1068, pls. 130–133.

Sylvester-Bradley, P. C. 1956. The New Palaeontology. *In* Sylvester-Bradley [Ed.] *The Species Concept in Palaeontology*, Systematics Association, London : 1–8.

Walliser, O. H. 1957. Conodonten aus dem oberen Gotlandium Deutschlands und der Karnischen Alpen. *Notizbl. hess. Landesamt., Bodenforsch.*, Wiesbaden **85** : 28–52, pls. 1–3.

—— 1960. Scolecodonts, Conodonts and Vertebrates. *In* Boucot, A. J. *et al.* A Late Silurian fauna from the Sutherland River Formation, Devon Island, Canadian Arctic Archipelago. *Bull. geol. Surv. Can.*, Ottawa, **65** : 21–39, pls. 5–8.

—— 1962. Conodontenchronologie des Silurs (Gotlandiums) und des tieferen Devons mit besonderer berücksichtigung der Formationsgrenze. In Erben, H.K. [Ed.] *Symposiums-Band der 2 internat. Arbeitstatung uber die Silur/Devon-Grenze und die Stratigraphie von Silur und Devon, Bonn Bruxelles*, 1960 Schweizerbartsche Verlag, Stuttgert : 281–287.

—— 1964. Conodonten des Silurs. *Abh. hess. Landesamt. Bodenforsch.*, Wiesbaden, **41** : 1–106, pls. 1–32.

Webers, G. 1966. The Middle and Upper Ordovician Conodont Faunas of Minnesota. *Bull. Minn. geol. Surv.*, Minneapolis, SP-4 : 1–123, pls. 1–15.

Whittard, W. F. 1927. The stratigraphy of the Valentian rocks of Shropshire: the Main Outcrop. *Quart. J. geol. Soc. Lond.*, **83** : 737–759, pls. 56–57.

—— 1932. The stratigraphy of the Valentian rocks of Shropshire. The Longmynd-Shelve and Breidden outcrops. *Quart. J. geol. Soc. Lond.*, **88** : 859–902, pls. 58–62.

Whittington, H. B. 1938. The geology of the district around Llansantffraid ym Mechain, Montgomeryshire. *Quart. J. geol. Soc. Lond.*, **94** : 423–457, pls. 38–39.

Winder, C. G. 1966. Conodonts from the Upper Coburg Formation (Late Middle Ordovician) at Colbourne, Ontario. *J. Paleont.*, Tulsa, **40** : 46–63, pls. 9–10.

Wolska, Z. 1961. Konodonty z Ordowickich glasow narzutowych Polski. *Acta palaeont. polon.*, Warsawa, **6** : 339–365, pls. 1–6.

Ziegler, A. M. 1965. Silurian marine communities and their environmental significance. *Nature, Lond.*, **207** : 270–272.

ZIEGLER, A. M., COCKS, L. R. M. & BAMBACH, R. K. 1968. The composition and structure of Lower Silurian marine communities. *Lethaia*, Oslo, **1** : 1–27.

ZIEGLER, A. M., COCKS, L. R. M. & MCKERROW, W. S. 1968. The Llandovery transgression of the Welsh Borderland. *Palaeontology*, London, **11** : 736–782.

ZIEGLER, W. 1956. Unterdevonische Conodonten, insbesondere aus dem Schönauer und dem Zorgensis-Kalk. *Notizbl. hess. Landesamt. Bodenforsch.*, Wiesbaden **84** : 93–106, pls. 6–7.

—— 1960. Conodonten aus dem Rheinischen Unterdevon (Gedinnium) des Remscheider Sattels (Rheinisches Schiefergebirge). *Paläont. Z.*, Berlin, **34** : 169–201, pls. 13–15.

X. APPENDIX

a. List of sample localities

District	*Sample No.*	*Grid Ref.*	*District*	*Sample No.*	*Grid Ref.*
Llandovery	LL 1a	SN/729308		Minsterley Lane	SJ/380049
	LL 2a, b	SN/753309	Long Mynd	Hillend Farm	SO/394876
	LL 3a	SN/744289		Plowden B1	SO/391873
	LL 4a	SN/747289		Plowden 1–8	SO/396877
	LL 5a–c	SN/757324		Norbury 1–3	SO/364928
	LL 6a	SN/753319		Norbury A1, A2	SO/359928
	LL 7a	SN/757312		New House, Marshbrook	SO/434898
	LL 8a	SN/758311		Onny River	SO/426853
	LL 9a, b	SN/759311	Wenlock Edge	Ticklerton Brook	SO/482909
	LL 10a	SN/761309		Ticklerton 1–3	SO/481901
	LL 11a	SN/759309		Gilberries	SO/512936
	LL 12a	SN/775328		Sheinton 1	SJ/610032
	LL 13a	SN/762325		Sheinton 2	SJ/612031
	LL 14a	SN/775326		Domas	SJ/594006
	LL 15a	SN/775325		Dingle	SJ/633070
	LL 16a	SN/775324	Malvern Hills	Gullet 1–4	SO/761381
	LL 17a	SN/775323		MB 68/16, 16a–c (Hollybush)	SO/760371
Llandeilo	Sawdde Gorge	SN/715260		West Malvern 1, 2	SO/765459
Montgomery-shire	Graig-wen Quarry	SJ/099091		Cowleigh Park 1, 2	SO/760468
	Gelli Farm 1–6	SJ/236193	Woolhope	Haugh Wood 2–4	SO/589358
	Welshpool 1–3	SJ/219128		Woolhope 1	SO/612353
Breidden Hills	Middletown	SJ/301128	Tortworth	Tortworth 1–3	ST/706943
	Buttington 1–3	SJ/265100		Tortworth 4	ST/688957
Hope Valley	H.Q.1–6	SJ/355021		Damery Beds	ST/706934
	H.V.1	SJ/355021			
	H.V.2	SJ/357022			
	H.V.3	SJ/358022			
	H.V.4	SJ/360022			
	H.V.5	SJ/361022			
	H.V.6	SJ/364025			
	H.B.1, 2	SJ/364022			

b. Sample weights and conodont abundances

Samples that did not respond to chemical treatment are not included.

Sample No.	*Weight (kg)*	*Conodonts*	*Conodonts/kg*
LL 4a	1·50	0	0
LL 8a	1·75	0	0
LL 10a	1·00	0	0
LL 17a	3·25	0	0
Sawdde Gorge	2·50	0	0
Graig-wen Quarry	1·25	0	0
Gelli Farm 1	1·50	0	0
Gelli Farm 2	1·25	83	66
Gelli Farm 3	3·50	72	20
Gelli Farm 4	2·00	8	4
Gelli Farm 5	2·25	2	1
Gelli Farm 6	1·75	1	1
Welshpool 1	1·50	27	18
Welshpool 2	1·00	0	0
Welshpool 3	1·25	0	0
Middletown	1·00	0	0
H.Q.1	14·00	108	8
H.Q.2	1·00	0	0
H.Q.3	14·00	291	21
H.Q.4	2·00	0	0
H.Q.5	1·00	4	4
H.Q.6	1·25	32	26
H.V.1	1·50	0	0
H.V.2	1·50	2	1
H.V.3	2·00	285	142
H.V.4	5·00	748	150
H.V.5	2·00	15	7
H.V.6	1·00	0	0
H.B.1	1·00	4	4
H.B.2	5·00	116	23
Minsterley Lane	3·50	163	46
Plowden B1	2·50	13	5
Plowden 1	25·00	424	17
Plowden 2	13·50	215	16
Plowden 3	17·00	245	14
Plowden 4	7·00	43	6
Plowden 5	11·00	28	3
Plowden 6	9·50	88	9
Plowden 7	9·50	65	7
Plowden 8	9·50	63	7
Norbury 1	1·00	70	70
Norbury 2	1·25	6	5
Norbury 3	3·50	89	25
Norbury A1	2·50	4	2
Norbury A2	1·00	0	0
New House, Marshbrook	3·00	391	130
Onny River	1·00	0	0
Ticklerton Brook	1·25	692	550
Ticklerton 1	5·00	544	109
Ticklerton 2	2·00	116	58
Ticklerton 3	4·50	531	118
Gilberries	1·00	1	1
Sheinton 1	1·25	0	0
Sheinton 2	6·00	519	87
Domas	1·75	0	0
Dingle Grit	1·50	18	12
Dingle Conglom.	2·50	13	5
Gullet 1	9·00	50	6
Gullet 2	8·50	645	76
Gullet 2A	2·25	175	78
Gullet 3	6·00	78	13
Gullet 4	5·00	2913	583
MB 68/16a	2·00	29	14
MB 68/16b	2·00	137	68
MB 68/16c	2·00	3	2
MB 68/16	2·00	30	15
West Malvern 1	6·00	146	24
West Malvern 2	2·00	35	17
Cowleigh Park 1	3·00	1011	337
Cowleigh Park 2	2·25	27	12
Haugh Wood 2	2·25	0	0
Haugh Wood 3	6·00	125	21
Haugh Wood 4	1·50	0	0
Woolhope 1	3·00	118	39
Tortworth 1	2·00	0	0
Tortworth 2	1·25	0	0
Tortworth 3	1·00	0	0
Tortworth 4	5·25	11	2
Damery Beds	—	52	—
T-R-A	—	9	—
M-G-C	—	8	—

c. Register of figured specimens

Slide No.	*Conodont*	*Sample No.*
X.561	*Icriodella deflecta* sp. nov. holotype	H.Q.3
S.1.2	*Icriodella deflecta* sp. nov.	H.Q.1
X.562	*Icriodella deflecta* sp. nov.	H.Q.3
S.1.4	*Icriodella deflecta* sp. nov.	H.Q.3
X.563	*Icriodella inconstans* sp. nov. holotype	Gullet 2
X.564	*Icriodella inconstans* sp. nov.	Gullet 2
S.1.9	*Icriodella inconstans* sp. nov.	Gullet 2
X.565	*Icriodella inconstans* sp. nov.	Gullet 4
X.566	*Icriodella inconstans* sp. nov.	Gullet 4
X.567	*Icriodella malvernensis* sp. nov. holotype	West Malvern 1
X.568	*Icriodella malvernensis* sp. nov.	West Malvern 1
X.569	*Icriodella malvernensis* sp. nov.	West Malvern 1
X.570	*Icriodella malvernensis* sp. nov.	West Malvern 1
X.571	*Icriodella* cf. *I. malvernensis* sp. nov.	Sheinton 2
X.572	*Amorphognathus tenuis* sp. nov. holotype	Plowden 3
X.573	*Amorphognathus tenuis* sp. nov.	New House, Marshbrook
X.574	*Spathognathodus abruptus* sp. nov. holotype	H.Q.3
X.575	*Spathognathodus abruptus* sp. nov.	Plowden 7
X.576	*Spathognathodus* cf. *S. abruptus* sp. nov.	Minsterley Lane
X.577	*Spathognathodus gulletensis* sp. nov. holotype	Gullet 2
X.578	*Spathognathodus gulletensis* sp. nov.	Gullet 2
S.1.37	*Spathognathodus gulletensis* sp. nov.	Gullet 2
X.580	*Spathognathodus gulletensis* sp. nov.	West Malvern 1
X.581	*Ozarkodina alisonae* sp. nov. holotype	Gullet 2
X.582	*Ozarkodina alisonae* sp. nov.	Gullet 2
X.583	*Diadelognathus nicolli* sp. nov. holotype	Ticklerton 1
X.584	*Diadelognathus nicolli* sp. nov.	Ticklerton 1
X.585	*Icriodella discreta*	Gelli Farm 3
X.586	*Icriodella discreta*	Gelli Farm 3
X.587	*Icriodella discreta*	Gelli Farm 3
X.588	*Icriodina irregularis*	H.Q.3
X.589	*Icriodina* sp.	H.V.4
X.590	*Hadrognathus staurognathoides*	Sheinton 2
X.591	*Hadrognathus staurognathoides*	Sheinton 2
X.592	*Hadrognathus staurognathoides*	Ticklerton 1
X.593	*Apsidognathus tuberculatus*	Gullet 4
X.594	*Apsidognathus tuberculatus*	Gullet 4
X.595	*Aulacognathus kuehni*	Gullet 1
X.596	*Astropentagnathus irregularis*	MB 68/16b
X.597	*Neospathognathodus celloni*	Gullet 4
X.598	*Neospathognathodus celloni*	Gullet 4
X.599	*Neospathognathodus celloni*	MB 68/16b
X.600	*Neospathognathodus celloni*	MB 68/16b
X.601	*Neospathognathodus pennatus*	Gullet 4
X.602	*Neospathognathodus pennatus*	Cowleigh Park 1
X.603	*Neospathognathodus*? sp.	H.Q.3
X.604	*Neospathognathodus bullatus*	Gullet 4
X.605	*Pterospathodus amorphognathoides*	Cowleigh Park 1
X.606	*Pterospathodus amorphognathoides*	Cowleigh Park 1
X.607	*Pterospathodus amorphognathoides*	Ticklerton 2
X.608	*Astrognathus tetractis*	Gullet 4

Slide No.	*Conodont*	*Sample No.*
X.609	*Pygodus? lyra*	Gullet 4
S.2.64	*Carniodus carinthiacus*	Cowleigh Park 1
S.2.65	*Carniodus carinthiacus*	Cowleigh Park 1
X.610	*Carniodus carinthiacus*	Cowleigh Park 1
X.611	*Carniodus carnicus*	Cowleigh Park 1
X.612	*Carniodus carnulus*	Cowleigh Park 1
X.613	*Carniodus carnulus*	Cowleigh Park 1
X.614	*Carniodus carnulus* aberrant form	Cowleigh Park 1
X.615	*Carniodus carnus*	Cowleigh Park 1
S.2.72	*Carniodus carnus*	Cowleigh Park 1
X.616	*Carniodus* cf. *C. carnus*	New House, Marshbrook
X.617	*Carniodus* cf. *C. eocarnicus*	New House, Marshbrook
X.618	*Aphelognathus siluricus*	Plowden 2
X.619	*Ambalodus anapetus*	New House, Marshbrook
X.620	*Ambalodus* sp.	New House, Marshbrook
X.621	*Ambalodus triangularis*	Ticklerton Brook
X.622	*Ambalodus galerus*	Gullet 4
X.623	*Ambalodus galerus*	Gullet 4
X.624	*Spathognathodus hassi*	Plowden 1
X.625	*Spathognathodus hassi*	New House, Marshbrook
X.626	*Spathognathodus oldhamensis*	H.Q.1
X.627	*Spathognathodus inclinatus*	Sheinton 2
X.628	*Spathognathodus inclinatus*	Gullet 2
S.3.8	*Spathognathodus polinclinatus*	MB 68/16b
S.3.9	*Spathognathodus* sp. nov. A	Minsterley Lane
X.629	*Spathognathodus* sp. nov. B	Sheinton 2
X.630	*Spathognathodus ranuliformis*	Ticklerton 2
S.3.12	*Ozarkodina adiutricis*	MB 68/16b
X.631	*Ozarkodina adiutricis*	MB 68/16b
X.632	*Ozarkodina* cf. *O. edithae*	MB 68/16b
X.633	*Ozarkodina gaertneri*	Ticklerton 1
X.634	*Ozarkodina gaertneri*	Cowleigh Park 1
X.635	*Ozarkodina hanoverensis*	West Malvern 1
X.636	*Ozarkodina media*	Ticklerton Brook
X.637	*Ozarkodina typica*	H.V.4
X.638	*Ozarkodina typica*	Minsterley Lane
X.639	*Ozarkodina typica*	New House, Marshbrook
X.640	*Distomodus? extrorsus*	H.Q.3
X.641	*Distomodus? egregius*	H.Q.3
X.642	*Distomodus? egregius*	Sheinton 2
X.643	*Distomodus? egregius*	Ticklerton 1
S.3.30	*Distomodus* sp. nov.	Sheinton 2
X.644	*Distomodus kentuckyensis*	H.Q.3
X.645	*Distomodus kentuckyensis*	H.Q.3
X.646	*Distomodus kentuckyensis*	Plowden 1
X.647	*Distomodus kentuckyensis*	Sheinton 2
X.648	*Distomodus kentuckyensis*	Sheinton 2
X.649	*Gothodus?* sp. nov.	New House, Marshbrook
X.650	*Distomodus triangularis tenuirameus*	Gullet 4
X.651	*Distomodus triangularis triangularis*	Cowleigh Park 1
X.652	*Neoprioniodus costatus paucidentatus*	H.Q.3
X.653	*Neoprioniodus costatus paucidentatus*	Gullet 4

Slide No.	*Conodont*	*Sample No.*
X.654	*Neoprioniodus costatus costatus*	Ticklerton 1
X.655	*Neoprioniodus excavatus*	Ticklerton 3
X.656	*Neoprioniodus latidentatus*	Sheinton 2
X.657	*Neoprioniodus multiformis*	H.V.3
X.658	*Neoprioniodus planus*	Sheinton 2
X.659	*Neoprioniodus subcarnus*	Cowleigh Park 1
X.660	*Synprioniodina silurica*	Gullet 2
X.661	*Synprioniodina bicurvata*	Sheinton 2
X.662	*Sagittodontus edentatus*	Gelli Farm 3
X.663	*Sagittodontus edentatus*	H.Q.3
X.664	*Sagittodontus edentatus*	West Malvern 1
X.665	*Exochognathus brassfieldensis*	H.V.4
X.666	*Exochognathus keislognathoides*	H.Q.3
X.667	*Exochognathus* sp. nov.	Plowden 2
X.668	*Exochognathus brevialatus*	New House, Marshbrook
X.669	*Exochognathus brevialatus*	Ticklerton 2
X.670	*Exochognathus latialatus*	Cowleigh Park 1
X.671	*Exochognathus latialatus*	Cowleigh Park 1
X.672	*Exochognathus detortus*	Sheinton 2
X.673	*Exochognathus detortus*	Cowleigh Park 1
X.674	*Exochognathus caudatus*	Cowleigh Park 1
X.675	*Plectospathodus extensus*	Cowleigh Park 1
X.676	*Plectospathodus extensus*	H.V.4
X.677	*Plectospathodus flexuosus*	Gullet 2
X.678	*Plectospathodus irregularis*	H.V.3
X.679	*Trichonodella? expansa*	Sheinton 2
X.680	*Trichonodella asymmetrica*	Sheinton 2
X.681	*Trichonodella symmetrica*	H.B.2
X.682	*Trichonodella symmetrica*	H.V.4
X.683	*Trichonodella symmetrica*	Gullet 2
X.684	*Trichonodella inconstans*	Sheinton 2
X.685	*Trichonodella excavata*	Ticklerton 3
X.686	*Lonchodina detorta*	H.V.4
X.687	*Lonchodina fluegeli*	H.V.4
X.688	*Lonchodina greilingi*	Gullet 2
X.689	*Lonchodina walliseri*	H.Q.3
X.690	*Lonchodina* sp. A	H.Q.1
X.691	*Lonchodina* sp. B	Plowden 2
X.692	*Lonchodina* sp. C	Ticklerton 3
X.693	gen. et sp. indet. A	Norbury 3
X.694	gen. et sp. indet. B	Sheinton 2
X.695	*Hindeodella equidentata*	Gullet 4
X.696	*Ligonodina kentuckyensis*	H.V.3
X.697	*Ligondina kentuckyensis*	Sheinton 2
X.698	*Ligonodina salopia*	Ticklerton 1
X.699	*Ligonodina silurica*	Sheinton 2
X.700	*Ligondina silurica*	Sheinton 2
X.701	*Ligonodina? variabilis*	Gullet 2
X.702	*Ligonodina petila*	Ticklerton 1
X 703	*Hibbardella? prima*	Plowden 3
X.704	*Hibbardella? trichonodelloides*	Gullet 4
X.705	*Hibbardella? trichonodelloides*	Cowleigh Park 1

Slide No.	*Conodont*	*Sample No.*
X.706	*Hibbardella* sp. nov.	Sheinton 2
X.707	*Hibbardella* sp. nov.	Sheinton 2
X.729	*Diadelognathus primus*	Norbury 1
X.708	*Acodus curvatus*	H.V.4
X.709	*Acodus unicostatus*	H.V.4
X.710	*Acodus unicostatus*	Gullet 2
X.711	*Distacodus obliquicostatus*	Minsterley Lane
X.712	*Drepanodus* sp.	Gelli Farm 3
X.713	*Drepanodus* sp.	Ticklerton Brook
X.714	*Drepanodus suberectus*	H.Q.3
X.715	*Drepanodus aduncus*	Cowleigh Park 1
X.716	*Panderodus unicostatus*	Sheinton 2
X.717	*Panderodus unicostatus*	Cowleigh Park 1
X.718	*Panderodus serratus*	H.Q.3
X.719	*Panderodus simplex*	H.Q.3
X.720	*Panderodus simplex*	Gullet 2
X.721	*Panderodus* cf. *P. staufferi*	H.B.1
X.722	*Panderodus* cf. *P. gracilis*	H.V.4
X.723	*Panderodus* cf. *P. gracilis*	Gullet 2
X.724	*Panderodus* sp. A	Cowleigh Park 1
X.725	*Paltodus debolti*	H.V.4
X.726	*Paltodus dyscritus*	H.V.4
X.727	*Paltodus migratus*	H.V.4
X.728	*Paltodus costulatus*	Cowleigh Park 1

Dr R. J. Aldridge,
Department of Geology,
University of Nottingham,
Nottingham,
England.

PLATE 1

All figures are ×35

FIGS 1–3. ***Icriodella discreta*** Pollock, Rexroad & Nicoll

1. Oral view of specimen (X.585). 2. Oral view of specimen (X.586). 3. Outer lateral view of specimen (X.587).

FIGS 4–7. ***Icriodella deflecta*** sp. nov.

4. Oral and aboral views of specimen S.1.4. 5. Oral view of specimen S.1.2. 6. Oral and outer lateral views of holotype (X.561). 7. Oral view of specimen (X.562).

FIG. 8. ***Icriodella*** cf. ***I. malvernensis*** sp. nov.

Oral view of specimen (X.571).

FIGS 9–12. ***Icriodella malvernensis*** sp. nov.

9. Oral and outer views of specimen (X.569). 10. Aboral and oral views of holotype (X.567). 11. Oral view of specimen (X.570). 12. Oral view of specimen (X.568).

FIGS 13–17. ***Icriodella inconstans*** sp. nov.

13. Oral view of specimen (X.564). 14. Oral view of specimen S.1.9. 15. Oral, aboral and outer lateral views of holotype (X.563). 16. Oral view of specimen (X.566). 17. Oral view of specimen (X.565).

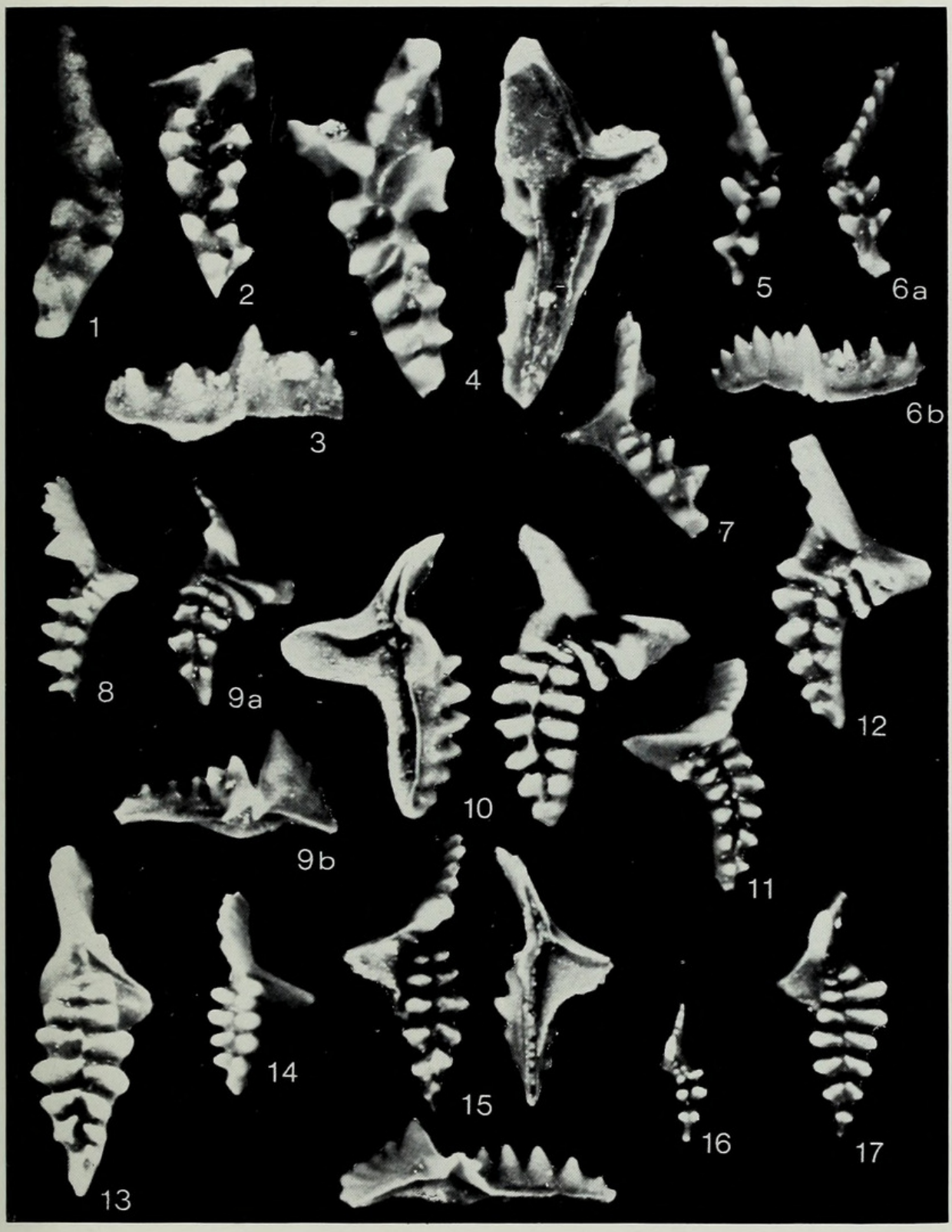

1
2
3
4
5
6a
6b
7
8
9a
9b
10
11
12
13
14
15
16
17

PLATE 2

All figures are ×35

FIG. 1. ***Icriodina irregularis*** Branson & Branson
Aboral and oral views of specimen (X.588).

FIG. 2. ***Icriodina*** sp.
Aboral and oral views of specimen (X.589).

FIGS 3–4. ***Amorphognathus tenuis*** sp. nov.
3. Aboral and oral views of holotype (X.572). 4. Oral view of specimen (X.573).

FIG. 5. ***Astropentagnathus irregularis*** Mostler
Oral view of specimen (X.596).

FIG. 6. ***Aulacognathus kuehni*** Mostler
Oral view of specimen (X.595).

FIGS 7, 9. ***Apsidognathus tuberculatus*** Walliser
7. Aboral and oral views of specimen (X.593). 9. Oral view of specimen (X.594).

FIGS 8, 10, 11. ***Hadrognathus staurognathoides*** Walliser
8. Oral view of specimen (X.591). 10. Oral and aboral views of specimen (X.592).
11. Oral view of specimen (X.590).


1
2
3
4
5
6
7
8
9
10
11

PLATE 3

All figures are ×35

FIG. 1. ***Astrognathus tetractis*** Walliser
Oral and aboral views of specimen (X.608).

FIG. 2. ***Pygodus? lyra*** Walliser
Oral and aboral views of specimen (X.609).

FIG. 3. ***Aphelognathus siluricus*** Pollock, Rexroad & Nicoll
Lateral and oral views of specimen (X.618).

FIG. 4. ***Ambalodus anapetus*** Pollock, Rexroad & Nicoll
Lateral and oral views of specimen (X.619).

FIG. 5. ***Ambalodus*** sp.
Lateral and oral views of specimen (X.620).

FIGS 6, 8. ***Ambalodus galerus*** Walliser
6. Lateral view of specimen (X.622). 8. Lateral and oral views of specimen (X.623).

FIG. 7. ***Ambalodus triangularis*** Branson & Mehl
Lateral and oral views of specimen (X.621).

FIGS 9–12. ***Neospathognathodus celloni*** (Walliser)
9. Lateral view of specimen (X.597). 10. Lateral view of specimen (X.598). 11. Lateral view of specimen (X.599). 12. Oral view of specimen (X.600).

FIGS 13, 16. ***Neospathognathodus pennatus*** (Walliser)
13. Oral and lateral views of specimen (X.601). 16. Oral view of specimen (X.602).

FIG. 14. ***Neospathognathodus?*** sp.
Oral and lateral views of specimen (X.603).

FIG. 15. ***Neospathognathodus bullatus*** Nicoll & Rexroad
Oral view of specimen (X.604).

FIGS 17–19. ***Pterospathodus amorphognathoides*** Walliser
17. Oral view of specimen (X.606). 18. Oral view of specimen (X.607). 19. Oral, lateral and aboral views of specimen (X.605).

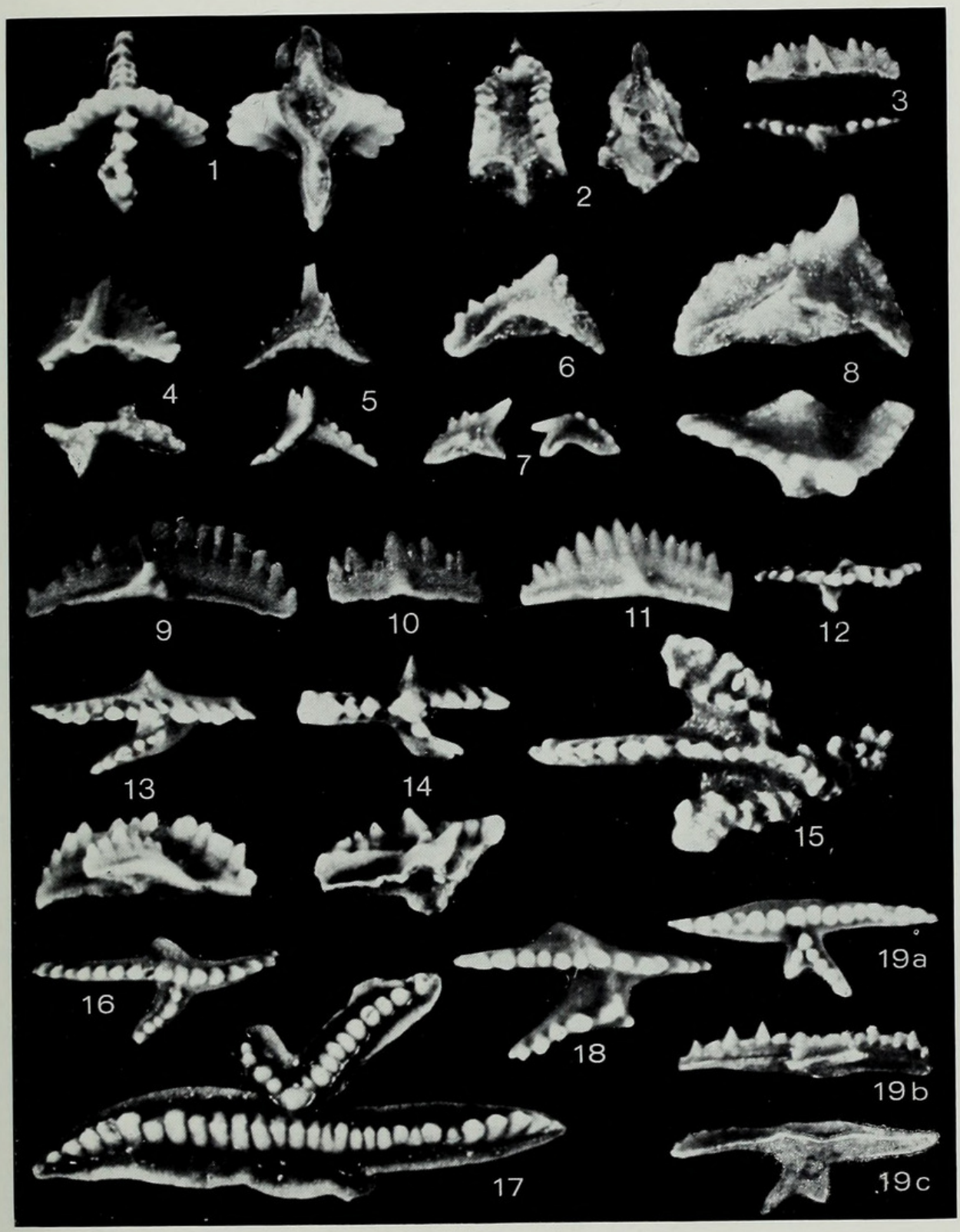

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19a
19b
19c

PLATE 4

All figures are ×35

FIG. 1. ***Spathognathodus oldhamensis*** Rexroad

Lateral and oral views of specimen (X.626).

FIGS 2, 3. ***Spathognathodus hassi*** Pollock, Rexroad & Nicoll

2. Lateral and oral views of specimen (X.624). 3. Lateral and oral views of specimen (X.625).

FIG. 4. ***Spathognathodus*** sp. nov. A

Lateral and oral views of specimen S.3.9.

FIG. 5. ***Spathognathus*** sp. nov. B

Lateral and oral views of specimen (X.629).

FIGS 6, 7. ***Spathognathodus abruptus*** sp. nov.

6. Outer lateral and oral views of holotype (X.574). 7. Outer lateral and oral views of specimen (X.575).

FIG. 8. ***Spathognathodus*** cf. ***S. abruptus*** sp. nov.

Oral view of specimen (X.576).

FIGS 9–12. ***Spathognathodus gulletensis*** sp. nov.

9. Lateral and oral views of holotype (X.577). 10. Lateral view of specimen (X.578). 11. Oral view of specimen S.1.37. 12. Lateral view of specimen (X.580).

FIG. 13. ***Spathognathodus polinclinatus*** Nicoll & Rexroad

Lateral view of specimen S.3.8.

FIG. 14. ***Spathognathodus ranuliformis*** Walliser

Lateral and oral views of specimen (X.630).

FIGS 15, 16. ***Spathognathodus inclinatus*** (Rhodes)

15. Lateral view of specimen (X.628). 16. Lateral view of specimen (X.627).

FIG. 17. ***Ozarkodina*** cf. ***O. edithae*** Walliser

Lateral view of specimen (X.632).

FIGS 18–20. ***Ozarkodina typica*** Branson & Mehl

18. Lateral view of specimen (X.637). 19. Lateral view of specimen (X.638). 20. Lateral view of specimen (X.639).

FIG. 21. ***Ozarkodina media*** Walliser

Lateral view of specimen (X.636).

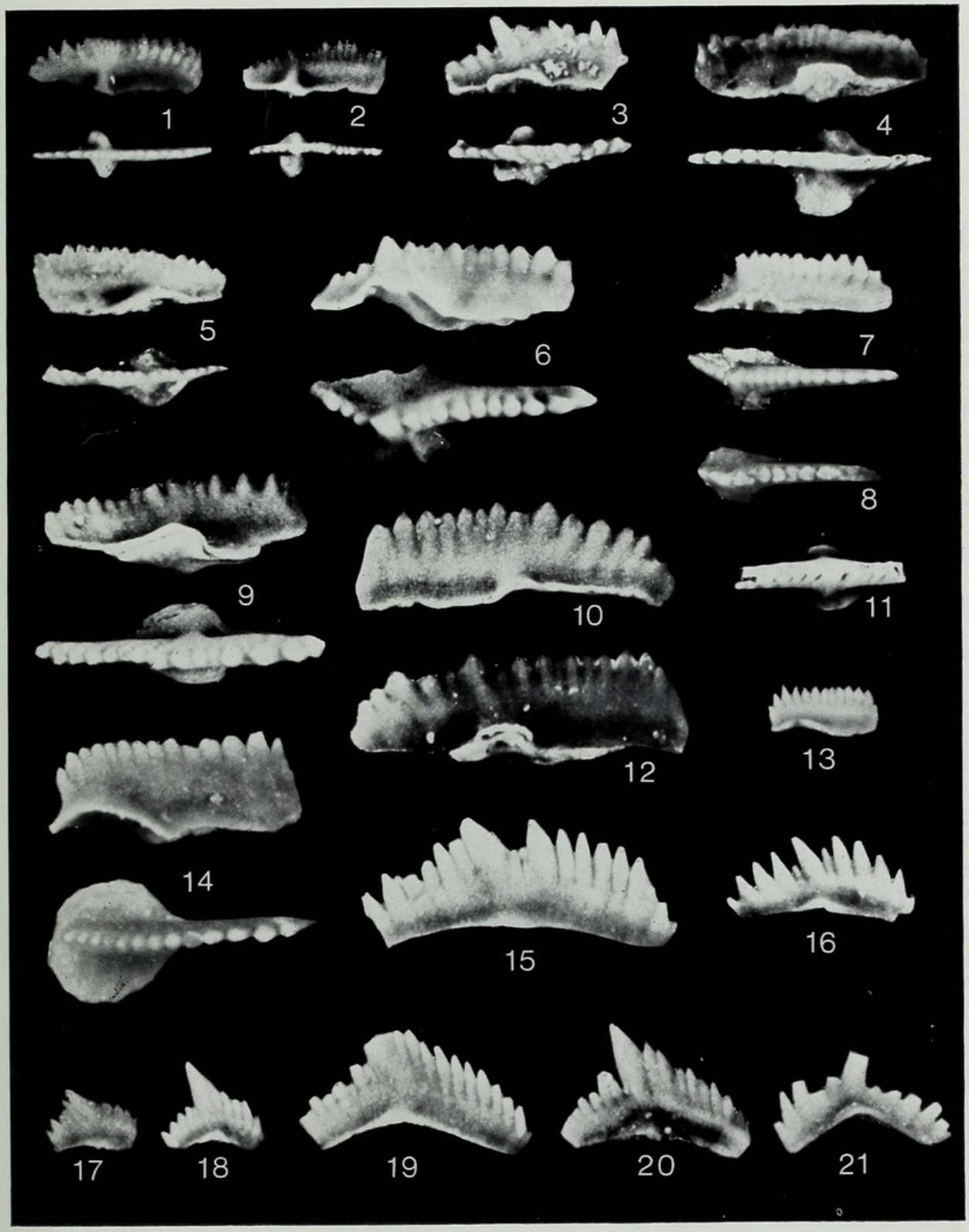

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

PLATE 5

All figures are ×35

FIG. 1. ***Ozarkodina hanoverensis*** Nicoll & Rexroad
Lateral view of specimen (X.635).

FIGS 2, 3. ***Ozarkodina adiutricis*** Walliser
2. Lateral view of specimen S.3.12. 3. Lateral view of specimen (X.631).

FIGS 4, 6. ***Ozarkodina alisonae*** sp. nov.
4. Lateral views of holotype (X.581). 6. Lateral view of specimen (X.582).

FIGS 5, 7. ***Ozarkodina gaertneri*** Walliser
5. Lateral views of specimen (X.634). 7. Lateral view of specimen (X.633).

FIGS 8–10. ***Carniodus carinthiacus*** Walliser
8. Lateral view of specimen S.2.64. 9. Lateral view of specimen S.2.65. 10. Lateral view of specimen (X.610).

FIG. 11. ***Carniodus carnicus*** Walliser
Lateral view of specimen (X.611).

FIGS 12–14. ***Carniodus carnulus*** Walliser
12. Lateral view of specimen (X.612). 13. Lateral view of specimen (X.613). 14. Lateral view of aberrant specimen (X.614).

FIGS 15, 16. ***Carniodus carnus*** Walliser
15. Lateral view of specimen (X.615). 16. Lateral view of specimen S.2.72.

FIG. 17. ***Neoprioniodus subcarnus*** Walliser
Lateral view of specimen (X.659).

FIG. 18. ***Carniodus*** cf. ***C. carnus*** Walliser
Lateral view of specimen (X.616).

FIG. 19. ***Carniodus*** cf. ***C. eocarnicus*** Walliser
Lateral view of specimen (X.617).

FIGS 20, 21. ***Neoprioniodus costatus paucidentatus*** Walliser
20. Inner lateral view of specimen (X.652). 21. Inner lateral view of specimen (X.653).

FIGS 22. ***Neoprioniodus costatus costatus*** Walliser
Inner lateral view of specimen (X.654).

FIG. 23. ***Neoprioniodus planus*** Walliser
Inner lateral view of specimen (X.658).

FIG. 24. ***Neoprioniodus latidentatus*** Walliser
Inner lateral view of specimen (X.656).

FIG. 25. ***Neoprioniodus excavatus*** (Branson & Mehl)
Inner lateral view of specimen (X.655).

FIG. 26. ***Neoprioniodus multiformis*** Walliser
Inner lateral view of specimen (X.657).

FIG. 27. ***Synprioniodina silurica*** Walliser
Inner lateral view of specimen (X.660).

FIG. 28. ***Synprioniodina bicurvata*** (Branson & Mehl)
Inner lateral view of specimen (X.661).

FIG. 29. gen. et sp. indet. B
Oral and lateral views of specimen (X.694).

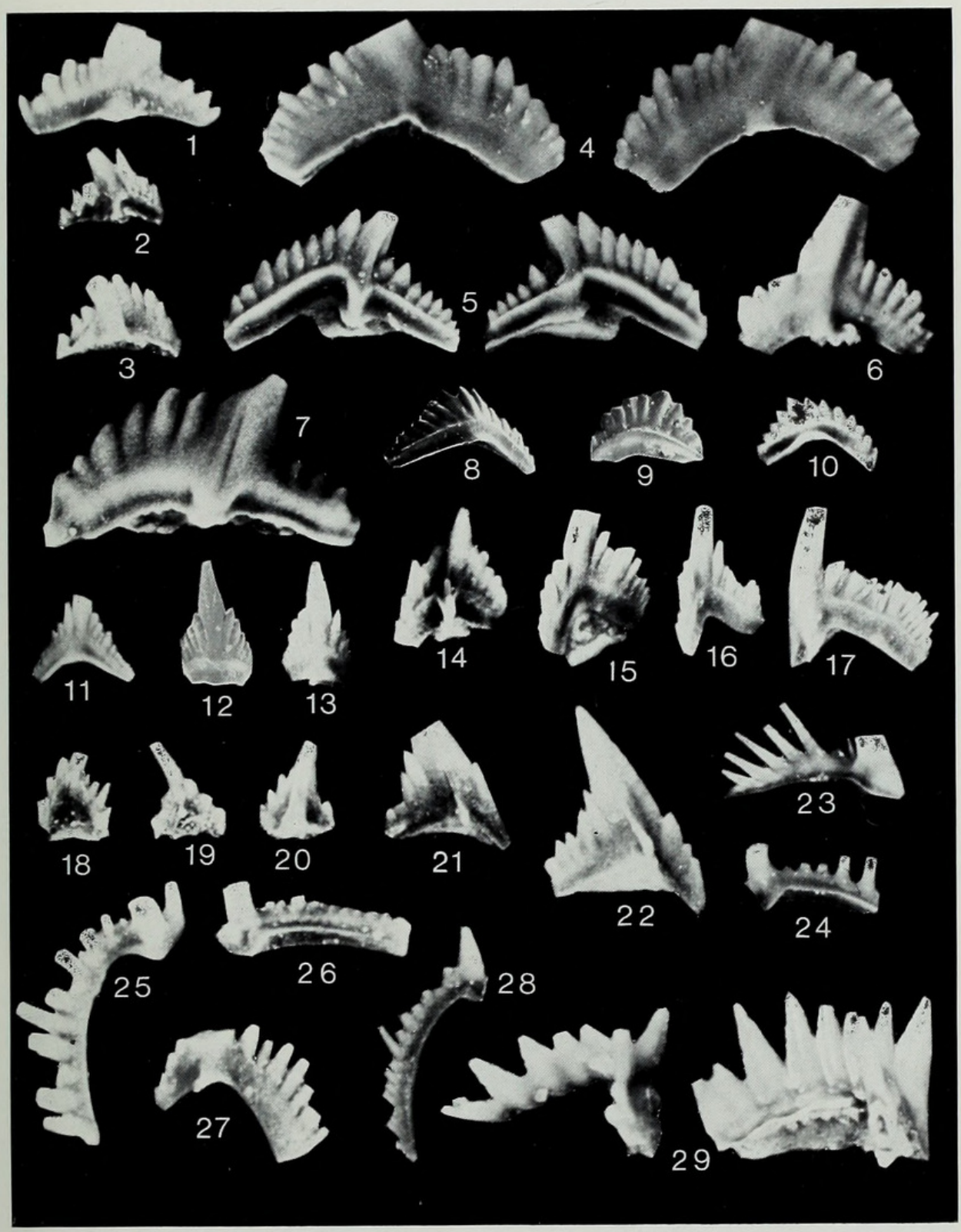

1
4
2
5
3
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
28
27
29

PLATE 6

All figures are ×35

FIG. 1. ***Gothodus?*** sp. nov.

Lateral views of specimen (X.649).

FIG. 2. ***Distomodus? extrorsus*** (Rexroad)

Inner lateral and outer lateral views of specimen (X.640)

FIGS 3, 4, 9. ***Distomodus? egregius*** (Walliser)

3. Outer lateral view of specimen (X.641). 4. Outer lateral and inner lateral views of specimen (X.643). 9. Outer lateral and inner lateral views of specimen (X.642).

FIGS 5–8, 11. ***Distomodus kentuckyensis*** Branson & Branson

5. Inner lateral view of specimen (X.645). 6. Inner lateral view of specimen (X.646). 7. Inner lateral view of specimen (X.647). 8. Inner lateral view of specimen (X.644). 11. Inner lateral view of specimen (X.648).

FIG. 10. ***Distomodus*** sp. nov.

Inner lateral and outer lateral views of specimen S.3.30.

FIG. 12. ***Distomodus triangularis triangularis*** (Walliser)

Inner lateral view of specimen (X.651).

FIG. 13. ***Distomodus triangularis tenuirameus*** (Walliser)

Inner lateral view of specimen (X.650).

FIGS 14, 15. ***Hibbardella*** sp. nov.

14. Oral and lateral views of specimens (X.706). 15. Posterior view of specimen (X.707).

FIG. 16. ***Hibbardella? prima*** (Walliser)

Posterior view of specimen (X.703).

FIGS 17, 18. ***Hibbardella? trichonodelloides*** (Walliser)

17. Aboral and oral views of specimen (X.704). 18. Lateral view of specimen (X.705).

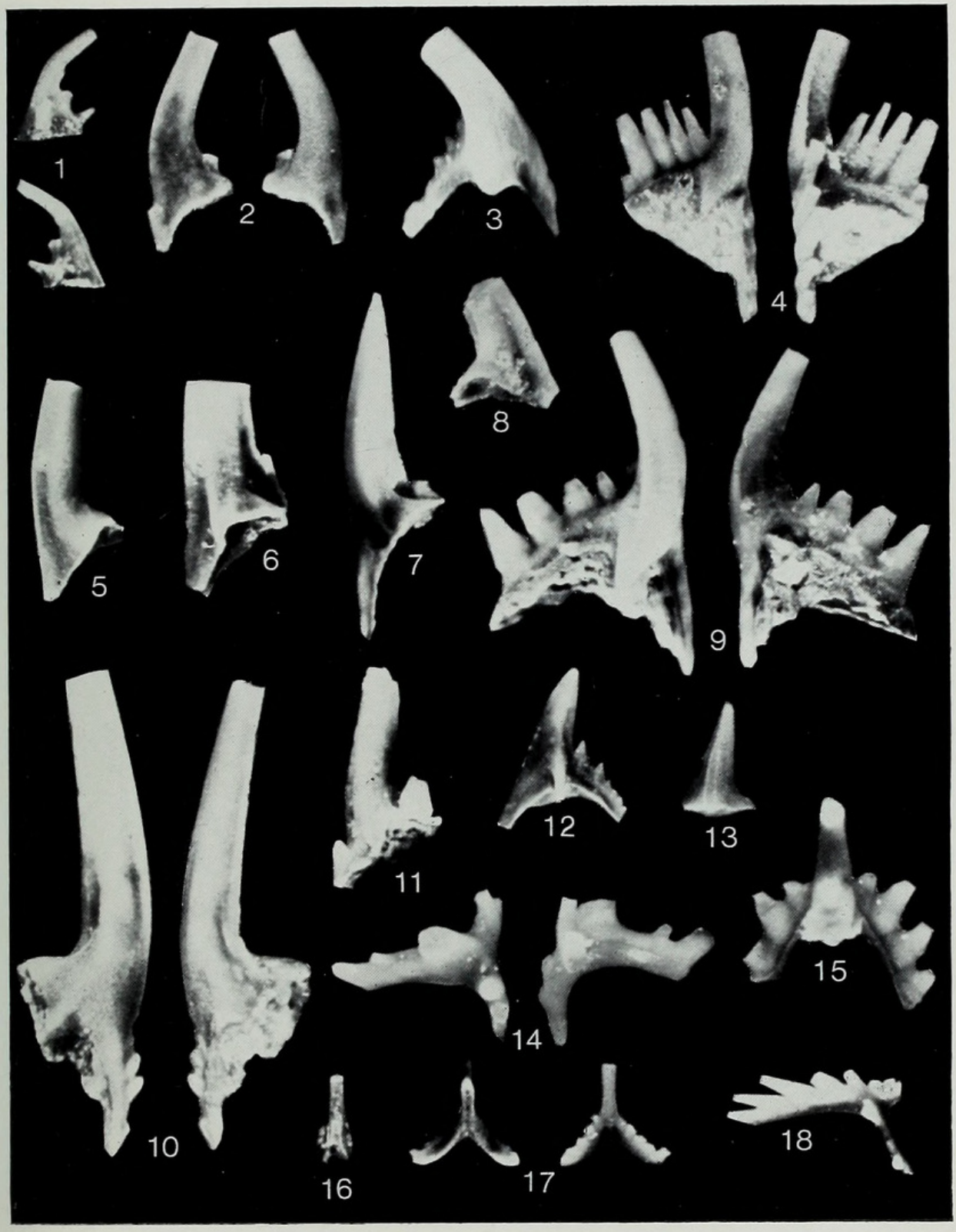

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

PLATE 7

All figures are ×35

FIGS 1–3. ***Sagittodontus edentatus*** (Branson & Branson)

1. Posterior and inner lateral views of specimen (X.662). 2. Posterior view of specimen (X.663). 3. Posterior view of specimen (X.664).

FIG. 4. ***Exochognathus brassfieldensis*** (Branson & Branson)

Posterior view of specimen (X.665).

FIG. 5. ***Exochognathus keislognathoides*** Pollock, Rexroad & Nicoll

Posterior view of specimen (X.666).

FIG. 6. ***Exochognathus*** sp. nov.

Posterior view of specimen (X.667).

FIGS 7, 12. ***Exochognathus detortus*** (Walliser)

7. Lateral and posterior views of specimen (X.673). 12. Posterior and lateral views of specimen (X.672).

FIGS 8, 9. ***Exochognathus brevialatus*** (Walliser)

8. Posterior view of specimen (X.669). 9. Posterior view of specimen (X.668).

FIGS 10, 11. ***Exochognathus latialatus*** (Walliser)

10. Posterior view of specimen (X.670). 11. Lateral view of specimen (X.671).

FIG. 13. ***Exochognathus caudatus*** (Walliser)

Lateral view of specimen (X.674).

FIG. 14. ***Trichonodella? expansa*** Nicoll & Rexroad

Lateral, oral and posterior views of specimen (X.679).

FIGS 15, 18, 19. ***Trichonodella symmetrica*** (Branson & Mehl)

15. Posterior view of specimen (X.681). 18. Posterior view of specimen (X.682). 19. Posterior view of specimen (X.683).

FIG. 16. ***Trichonodella inconstans*** Walliser

Posterior view of specimen (X.684).

FIG. 17. ***Trichonodella asymmetrica*** Nicoll & Rexroad

Posterior view of specimen (X.680).

FIG. 20. ***Trichonodella excavata*** (Branson & Mehl)

Posterior view of specimen (X.685).

FIGS 21, 22. ***Plectospathodus extensus*** Rhodes

21. Posterior view of specimen (X.675). 22. Posterior view of specimen (X.676).

FIG. 23. ***Plectospathodus irregularis*** (Branson & Branson)

Posterior view of specimen (X.678).

FIG. 24. ***Plectospathodus flexuosus*** Branson & Mehl

Posterior view of specimen (X.677).


1
2
3
4
5
6
7
8
9
10
11
12
13
14a
14b
14c
15
16
17
18
19
20
21
22
23
24

PLATE 8

All figures are ×35

FIG. 1. ***Diadelognathus primus*** Nicoll & Rexroad
Oral and aboral views of specimen (X.729).

FIGS 2, 3. ***Diadelognathus nicolli*** sp. nov.
2. Lateral view of specimen (X.584). 3. Aboral and oral views of holotype (X.583).

FIG. 4. ***Lonchodina greilingi*** Walliser
Lateral view of specimen (X.688).

FIG. 5. ***Lonchodina walliseri*** Ziegler
Lateral view of specimen (X.689).

FIG. 6. ***Lonchodina detorta*** Walliser
Oral and lateral views of specimen (X.686).

FIG. 7. ***Lonchodina fluegeli*** Walliser
Oral and aboral views of specimen (X.687).

FIG. 8. ***Lonchodina*** sp B
Lateral view of specimen (X.691).

FIG. 9. ***Lonchodina*** sp. A
Aboral view of specimen (X.690).

FIGS 10, 13. ***Ligonodina silurica*** Branson & Mehl
10. Inner lateral view of specimen (X.699). 13. Inner lateral view of specimen (X.700).

FIG. 11. ***Ligonodina petila*** Nicoll & Rexroad
Inner lateral view of specimen (X.702).

FIG. 12. ***Lonchodina*** sp. C
Lateral view of specimen (X.692).

FIG. 14. ***Ligonodina? variabilis*** Nicoll & Rexroad
Inner lateral view of specimen (X 701)

FIGS 15, 16. ***Ligonodina kentuckyensis*** Branson & Branson
15 Inner lateral view of specimen (X.696). 16. Inner lateral view of specimen (X.697).

FIG. 17. ***Ligonodina salopia*** Rhodes
Inner lateral view of specimen (X.698).

FIG. 18. gen. et sp. indet. A
Lateral view of specimen (X.693).

FIG. 19. ***Hindeodella equidentata*** Rhodes
Inner lateral view of specimen (X.695).

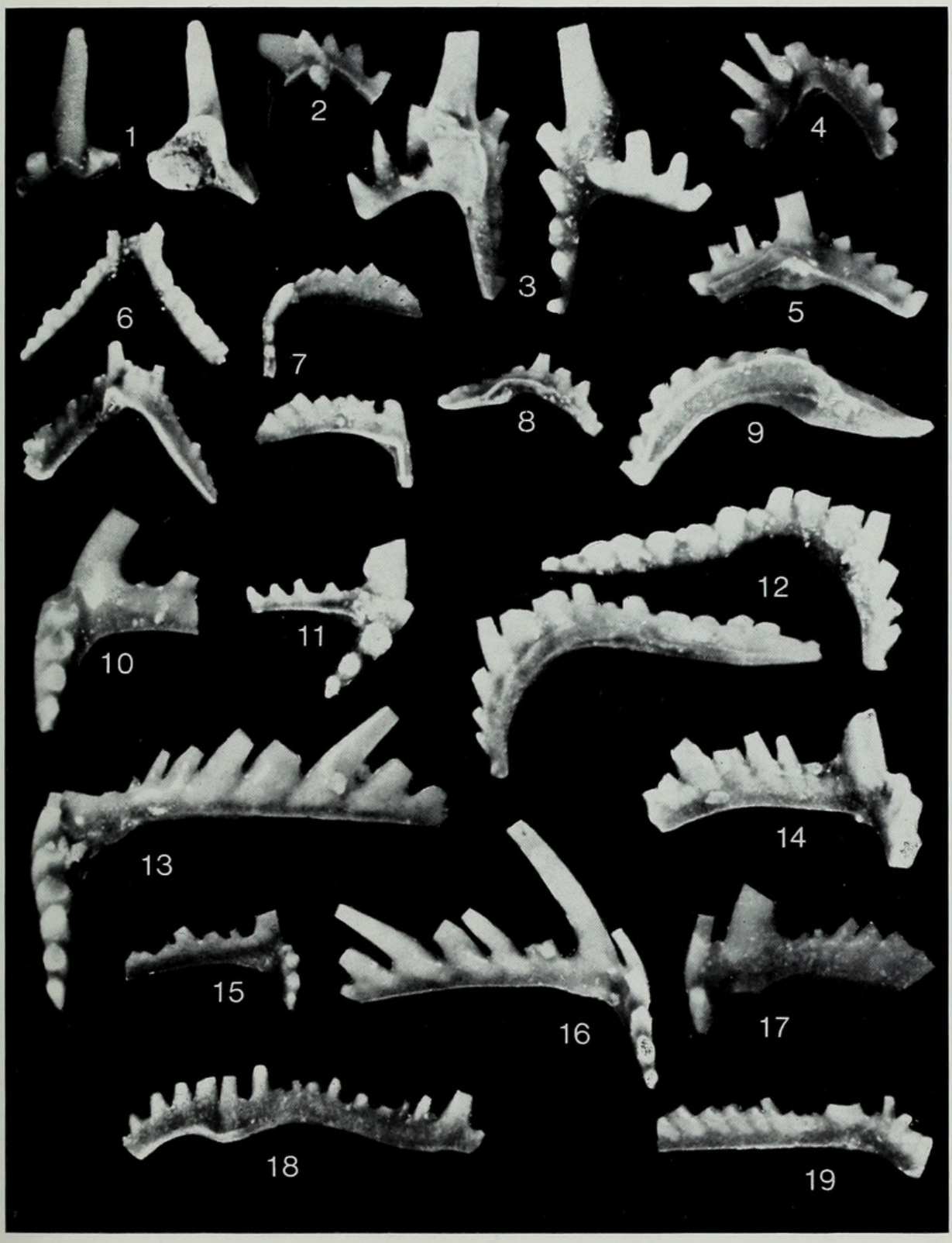

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19

PLATE 9

All figures are ×35

FIG. 1. ***Acodus curvatus*** Branson & Branson
Inner lateral and outer lateral views of specimen (X.708).

FIGS 2, 3. ***Acodus unicostatus*** Branson & Branson
2. Inner lateral and outer lateral views of specimen (X.709). 3. Outer lateral view of specimen (X.710).

FIG. 4. ***Distacodus obliquicostatus*** Branson & Mehl
Lateral views of specimen (X.711).

FIGS 5, 6. ***Panderodus unicostatus*** (Branson & Mehl)
5. Lateral view of specimen (X.716). 6. Lateral views of specimen (X.717).

FIG. 7. ***Panderodus serratus*** Rexroad
Lateral view of specimen (X.718).

FIGS 8, 9. ***Panderodus simplex*** (Branson & Mehl)
8. Lateral views of specimen (X.719). 9. Lateral view of specimen (X.720).

FIG. 10. ***Panderodus*** cf. ***P. staufferi*** (Branson, Mehl & Branson)
Lateral views of specimen (X.721).

FIG. 11. ***Panderodus*** sp. A
Lateral views of specimen (X.724).

FIGS 12, 13. ***Panderodus*** cf. ***P. gracilis*** (Branson & Mehl)
12. Lateral views of specimen (X.722). 13. Lateral view of specimen (X.723).

FIG. 14. ***Drepanodus*** sp.
Lateral view of specimen (X.712).

FIG. 15. ***Drepanodus*** sp.
Lateral view of specimen (X.713).

FIG. 16. ***Drepanodus suberectus*** (Branson & Mehl)
Lateral view of specimen (X.714).

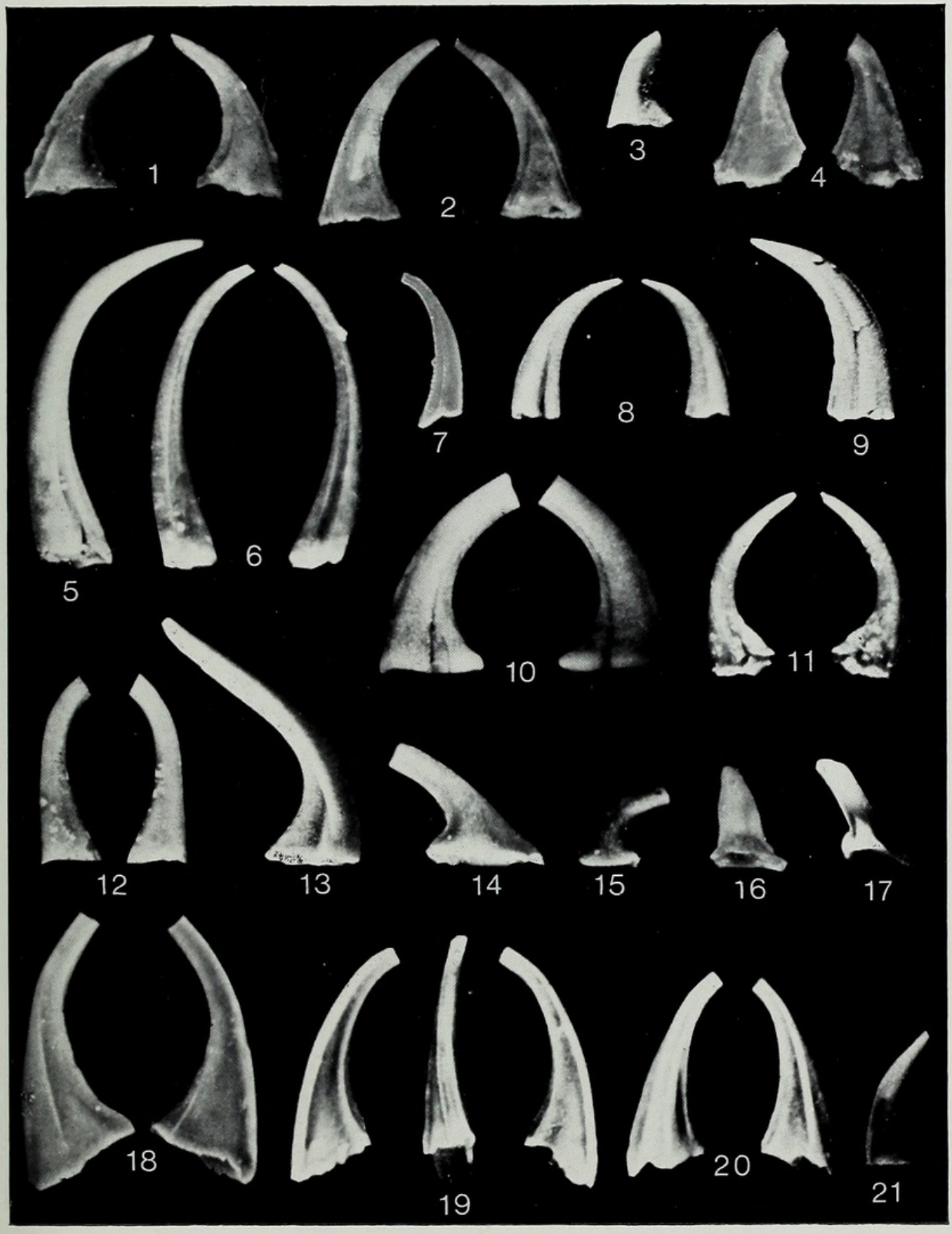
FIG. 17. ***Drepanodus aduncus*** Nicoll & Rexroad
Lateral view of specimen (X.715).

FIG. 18. ***Paltodus debolti*** Rexroad
Outer lateral and inner lateral views of specimen (X.725).

FIG. 19. ***Paltodus dyscritus*** Rexroad
Lateral, posterior and lateral views of specimen (X.726).

FIG. 20. ***Paltodus migratus*** Rexroad
Lateral views of specimen (X.727).

FIG. 21. ***Paltodus costulatus*** Rexroad
Lateral view of specimen (X.728).


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21